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The Ecology of Shallow Lakes

– Trophic Interactions in the Pelagial

Doctor's dissertation (DSc)
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Erik Jeppesen
Department of Lake and Estuarine Ecology

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Abstract: The thesis includes 25 selected original scientific publications and a summary, and in June 1998 it was approved by The Faculty of Natural Sciences at the University of Copenhagen for defence for the doctor's degree in Natural Sciences (DSc). The thesis describes how biological structure and interactions in the pelagial change across both nutrients and depth gradients in freshwater as well as in brackish lakes. Particular importance is given to the role that fish and submerged macrophytes play in determining the structure and function of shallow lakes. Other points of discussion include factors responsible for resilience when nutrient loading changes and the potential of utilising biomanipulation as a restoration tool. The research strategy combines cross-analysis of data from a vast number of lakes with whole-lake experiments as well as mechanistic enclosure studies and palaeoecological sediment analyses.

Keywords: Lakes, shallow, freshwater, saline, brachish, trophic structure, trophic interactions, fish, plankton, nutrients, mass balances, recovery, lake restoration, biomanipulation, alternative states.

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P.O. box 314
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Preface

The present doctor's dissertation is an English summary of 25 selected papers. It was submitted in June 1997 to the University of Copenhagen to be evaluated for the scientific doctor's degree.

The work on which this dissertation is based was initiated at the Environmental Agency's Freshwater Laboratory. Subsequent to the founding in 1988 of the National Environmental Research Institute (NERI), the activities were transferred to NERI's Department of Freshwater Ecology, now the Department of Lake and Estuarine Ecology. I wish to thank my employers and the various heads of departments (Carsten Hunding, Torben Moth Iversen and Kurt Nielsen) for giving me optimum working conditions. I am deeply indebted to the former and present Lake Group academics (Martin Søndergaard, Torben L. Lauridsen, Jens Peder Jensen, Erik Mortensen, Esben Agerbo, Mogens Erlandsen, Peter Kristensen, Anne-Mette Hansen and Ole Sortkjær) and technicians (Lone Nørgaard, Lissa Skov Hansen, Birte Lausten, Jane Stougaard-Pedersen, Karina Jensen, John Glargaard and Lisbet Sortkjær) for their enthusiastic co-operation and for many pleasant hours spent in their company. In particular I wish to thank Martin Søndergaard for our many years of close collaboration both scientifically and in our efforts to keep the group intact in times with markedly increasing demands for external financing of activities. The highly efficient and highly qualified efforts of the Lake Group technicians have been extremely valuable. It has also been a great joy to feel their interest in and understanding for the huge accumulation of samples in the basement!! This has warmed my heart in hard times. Also I wish to thank our secretaries Anne Mette Poulsen and Pia Sørensen for quick and efficient translation of my hieroglyphs to text and turning my Dinglish into acceptable English, and thanks to Kathe Møgelvang, Juana Jacobsen and Henrik Flagstad Rasmussen for many years of assistance with graphic presentations and with the present dissertation.

Moreover, I wish to thank my international colleagues in team "The Shallow Lakers" for inspiring, fruitful co-operation and lots of fun. Among these special thanks are due to Brian Moss, Marten Scheffer, Marie-Louise Meijer, Harry Hosper, Geoff Phillips, Martin Perrow, Stuart Mitchell, Ellen van Donk, Eddy Lammens and Bjørn Faafeng. Together we have shown that the subject of "shallow lakes" has come to stay. I am particularly indebted to Brian Moss and Geoff Phillips for having shown me "the way" at an early stage and to Marten Scheffer for his lucid presentations of complex problems. Over the years I have also been greatly inspired by the Wisconsin group headed by Steven R. Carpenter and James F. Kitchell.

I have had valuable and fruitful co-operation with a wide range of people employed at Danish research institutions and the Danish county environmental departments. In particular, I wish to thank Torben M. Iversen, who introduced me to science – even though he rejected my original (and superb) proposal for a M.Sc.-thesis - and afterwards helped me in my early career and later on as my boss; Kaj Sand-Jensen for many valuable discussions; Morten Søndergaard for efficient scientific co-operation about Strategic Environmental Research Programme (SERP) projects and SERP-management, and N. John Anderson, Bent Odgaard, Peter Rasmussen as well as "small" and "big" K(C)laus (Klaus Brodersen and Claus Lindegaard) for many pleasant hours and active joint efforts on the mudbanks. Thanks to Søren Berg and Lene Jacobsen for sharing many wet nights "in" the field enclosures. I also wish to thank the county environmental employees. Some of the data presented in this dissertation are the result of a close dialogue or active co-operation with county technicians, co-operation which has been of great inspiration to me (and to them as well, hopefully!). In some of the papers, county monitoring data have been used, and I wish to express my gratitude for the opportunity to do so.

Thanks to Martin Søndergaard, Bo Riemann, Bent Odgaard, Kurt Nielsen, Peter Kofoed Bjørnsen, Bent Lauge Madsen and Torben L. Lauridsen for their critical review of the dissertation, and I am grateful to N. John Anderson, Gary Larson and Stuart Mitchell for their editorial comments on the English version.

Also some thoughts to my now deceased parents Anna and Aksel Jeppesen for giving me a good start in life and to my sister Inge and brother Bjarne and their respective families. My brother and sister's interest has been legendary – not least in whether their tax money has indirectly financed my travels to far away parts of the world, or if the money has been derived from other sources.

I am particularly grateful to Kirsten Christoffersen for her valuable scientific co-operation, critical comments over the years and on the dissertation and for her loving care as well as her – usually – patient listening to my many enthusiastic outbursts about life in shallow lakes. Her cat Rille's legendary interest in the dissertation's sections on fish, or perhaps rather in the keyboard of my lap-top computer, has resulted in many lost files amounting to approximately one man year. Also a wee thought to Kirsten's closest family.

Finally, I wish to thank Carlsbergfondet for awarding financial support to the dissertation. In the past, our investigations have received valuable support from among others the Danish Natural Scientific Research Council, the Strategic Environmental Research Program, the Commission for Scientific Investigations in Greenland, Åge V. Jensen's Foundation, the National Agency of Environmental Protection and the National Forest and Nature Agency.

1 Papers included in the dissertation

The dissertation comprises the papers listed below and references are made to the numbers listed.

1 Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H.J. Jensen, J.P. Müller, O. Sortkjær, J.P. Jensen, K. Christoffersen, S. Bosselmann & E. Dall (1990): Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. – Hydrobiologia 200/201: 205-218.

2 Jeppesen, E., J.P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik (1990): Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. – Hydrobiologia 200/201: 219-227.

3 Jeppesen, E., M. Søndergaard, O. Sortkjær, E. Mortensen & P. Kristensen (1990): Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. - Hydrobiologia 191: 139-148.

4 Jeppesen, E., P. Kristensen, J.P. Jensen, M. Søndergaard, E. Mortensen & T. Lauridsen (1991): Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. – Mem. Ist. Ital. Idrobiol. 48: 127-148.

5 Jeppesen, E., O. Sortkjær, M. Søndergaard & M. Erlandsen (1992): Impact of a trophic cascade on heterotrophic bacterioplankton production in two shallow fish-manipulated lakes. – Arch. Hydrobiol. Ergebn. Limnol. 37: 219-231.

6 Jeppesen, E., M. Søndergaard, E. Kanstrup, B. Petersen, R.B. Henriksen, M. Hammershøj, E. Mortensen, J.P. Jensen & A. Have (1994): Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? – Hydrobiologia 275/276: 15-30.

7 Jeppesen, E., E. Agerbo Madsen, J. P. Jensen & N. J. Anderson (1996): Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibration data set from shallow lakes. – Freshw. Biol. 36: 115-127.

8 Jeppesen, E., J.P. Jensen, M. Søndergaard & O. Sortkjær (1996): Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a long-term study in shallow hypertrophic Lake Søbygård. – J. Plank. Res. 18: 1605-1625.

9 Jeppesen, E., M. Erlandsen & M. Søndergaard (1997): Can simple empirical equations describe the seasonal dynamics of bacterioplankton in lakes: an eight year study in shallow hypertrophic and biologically highly dynamic Lake Søbygård, Denmark. – Microb. Ecol. 34: 11-26.

10 Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, L.J. Pedersen & L. Jensen (1997): Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. – Hydrobiologia 342/343: 151-164.

11 Jeppesen, E., T. Lauridsen, S.F. Mitchell & C. Burns (1997): Do planktivorous fish structure the zooplankton communities in New Zealand lakes? – N. Z. J. Mar. Freshwat. Res. 31: 163-173.

12 Jeppesen, E., M. Søndergaard, J.P. Jensen, E. Kanstrup & B. Petersen (1998): Macrophytes and turbidity in brackish lakes with special emphasis on the role of top-down control. In: E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen (Eds.), The structuring role of submerged macrophytes in lakes. Ecological Studies. Springer Verlag, 131: 369-380.

13 Jeppesen, E., T.L. Lauridsen, T. Kairesalo & M. Perrow (1998): Impact of submerged macrophytes on fish-zooplankton interactions in lakes. In: E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard & K. Christoffersen (Eds.), The structuring role of submerged macrophytes in lakes. Ecological Studies. Springer Verlag. 131: 91-114.

14 Jeppesen, E., Ma. Søndergaard, Mo. Søndergaard, K. Christoffersen, K. Jürgens, J. Theil-Nielsen & L. Schlüter (submitted): Cascading trophic interactions in the littoral zone of a shallow lake.

15 Jeppesen, E., J. P. Jensen, J. Windolf, T. Lauridsen, M. Søndergaard, K. Sandby & P. Hald Møller (1998): Changes in nitrogen retention in shallow eutrophic lakes following a decline in density of cyprinids. – Arch. Hydrobiol. 142: 129-152.

16 Jeppesen, E., M. Søndergaard, J.P. Jensen, E. Mortensen & T. Jørgensen (1998): Cascading trophic interactions from fish to bacteria and nutrientsafter reduced sewage loading: a 18 year study of a shallow hypertrophic lake. – Ecosystems 1: 250-267.

17 Jeppesen, E., M. Søndergaard, B. Kronvang, J.P Jensen, L.M. Svendsen & T. Lauridsen (1998): Lake and catchment management in Denmark. In: D. Harper, A. Ferguson, B. Brierley & G. Phillips (Eds.), Ecological basis for lake and reservoir management. – Hydrobiologia.

18 Jensen, J.P., E. Jeppesen, P. Kristensen, P.B. Christensen & M. Søndergaard (1992): Nitrogen loss and denitrification as studied in relation to reductions in nitrogen loading in a shallow, hypertrophic lake (Lake Søbygård, Denmark). – Int. Revue gesamt. Hydrobiol. 77: 29-42.

19 Jensen, J.P., E. Jeppesen, K. Olrik & P. Kristensen (1994): Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. – Can. J. Fish. Aquat. Sci. 51: 1692-1699.

20 Lauridsen, T., L.J. Pedersen, E. Jeppesen & M. Søndergaard (1996): The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. – J. Plank. Res. 18: 2283-2294.

21 Meijer, M-L., E. Jeppesen, E. Van Donk., B. Moss, M. Scheffer, E. Lammens, E. Van Nes, J.A. Berkum, G. J. de Jong, B.A. Faafeng & J.P. Jensen (1994): Long-term responses to fish-stock reduction in small shallow lakes: Interpretation of five year results of four biomanipulation cases in the Netherlands and Denmark. – Hydrobiologia 275/276: 457-466.

22 Scheffer, M., S.H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen (1993): Alternative equilibria in shallow lakes. – Trends Ecol. Evol. 8: 275-279.

23 Schriver, P., J. Bøgestrand, E. Jeppesen & M. Søndergaard (1995): Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. – Freshw. Biol. 33: 255-270.

24 Søndergaard, M., E. Jeppesen & S. Berg (1997): Pike (*Esox Lucius* L.) stocking as a biomanipulation tool. 2. Effects on lower trophic levels in Lake Lyng (Denmark). – Hydrobiologia 342/343: 319-325.

25 Aaser, H.F., E. Jeppesen & M. Søndergaard (1995: Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake. – Mar. Ecol. Prog. Ser. 127: 47-56.

2 Introduction, research strategy and main theme

2.1 Background

Danish lakes are generally highly eutrophic and turbid, the latter primarily due to extensive growth of phytoplankton. In 65% of the lakes, Secchi depth is less than 1 m during summer and in 90% less than 2 m (*Kristenten et al. 1990*). Investigations made at the turn of the century and during the first half of this century, as well as palaeoecological studies, suggest that most Danish lakes were in a clearwater state 50 to 200 years ago (section 5). Submerged macrophytes were abundant in shallow lakes, and from the experience gained from contemporary clearwater lakes it must be assumed that they had a rich flora and fauna including high densities of waterfowl such as mute swan (*Cygnus olor*), coot (*Fulica atra*) and various species of diving ducks (Fig. 1). Since then the lakes have become more eutrophic due to high nutrient loading mainly derived from sewage and leakage from arable soils, and this has been further intensified by the introduction of phosphate-rich detergents and fertilizers.

The increased nutrient loading has resulted in a number of changes in lake trophic structure (Figs 1-3) and significant alterations have occurred at the top of the food-web. Earlier, predatory perch (*Perca fluviatilis*) and pike (*Esox lucius*) were the dominant fish species. Synchronous with eutrophication, a shift occurred to dominance by cyprinids, especially roach (*Rutilus rutilus*) and bream (*Abramis brama*) (Fig. 3). Simultaneously, the biomass of planktivorous fish increased (Fig. 2). Roach and bream are planktivorous, and the higher biomass resulted in increased predation pressure on zooplankton and thereby reduced grazing pressure on phytoplankton. The biomass ratio of zooplankton to phytoplankton decreased from 0.5-0.8 in mesotrophic lakes to less than 0.2 when phosphorus concentrations were above 0.10-0.20 mg $\mathrm{P\,l^{-1}}$ (Fig. 2). The latter figure is so low that zooplankton cannot control phytoplankton whose turnover time in eutrophic lakes may be 0.5-2 days (*Reynolds 1984*). With decreasing grazing pressure and increased nutrient supply, the biomass of phytoplankton increased, resulting in reduced Secchi depth, which in turn impoverished the growth conditions for submerged macrophytes. The plants either disappeared or died back and the food sources for plant-eating birds and diving ducks consequently disappeared. In summary, high external loading of phosphorus has resulted in lakes characterized by large biomasses of roach and bream, high abundance of phytoplankton, few or no submerged macrophytes, greatly reduced densities of plant-eating birds and diving ducks and, instead, dominance by fish-eating bird species such as great crested grebe (*Podiceps cristatus*) (Figs 1-3).

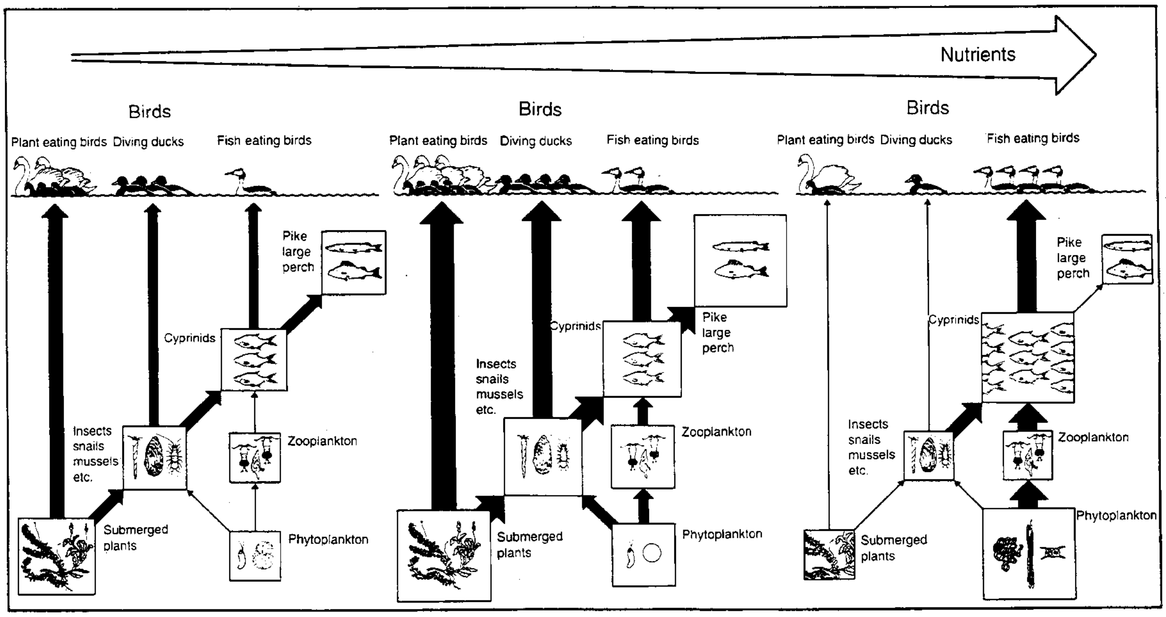

Fig. 1. Scheme illustrating how biological structure and the impact of various processes change with increasing nutrient supply (from left to right). Today, the majority of Danish lakes are found to the right of the scale, whereas they last century typically were found to the left. Partly from Andersson et al. (1990).

Recently, serious efforts have been made to reduce the nutrient loading of Danish lakes. During the past 20 years there has been a marked reduction in nutrient loading from point sources, both due to introduction of phosphorus stripping and, in some instances, nitrogen removal at the sewage treatment plants, or because sewage has been diverted. In addition, efforts are now being made to improve the nutrient retention capacity of lake catchments, e.g. by establishment of cultivation-free buffer strips along watercourses, re-establishment of wetlands, new stream management practices and remeandering of previously channelized streams. These measures, with sewage treatment being of prime importance, have led to a significant reduction in phosphorus concentrations of stream input to lakes (17). This has, however, only rarely resulted in an immediate improvement of the trophic status of the lakes. In some cases this has been attributed to reduction of the external nutrient loading being insufficient. Significant changes in the biological community and Secchi depth cannot be expected to occur until phosphorus concentrations in the lakes have been reduced to levels below 0.1-0.2 mg P l^{-1} (Fig. 2).

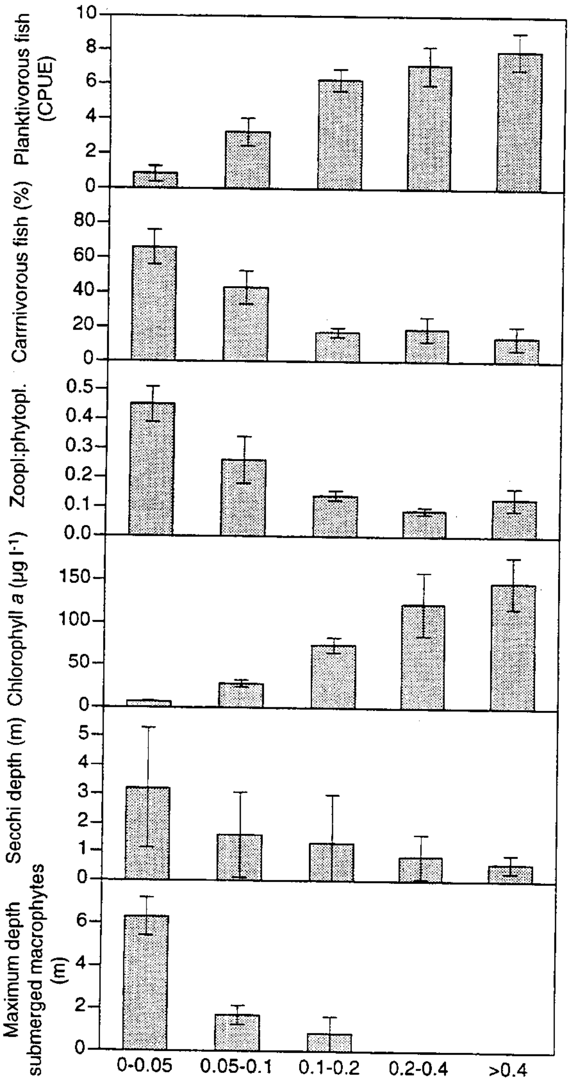

Fig. 2. August biomass of planktivorous fish (CPUE, catch in survey gillnets, 14 different mesh sizes ranging between 6.25-75 mm) *v* summer mean lake water concentrations of total phosphorus (n=65). Also shown are the percentage of carnivorous fish, summer mean (1 May - 1 October) of zooplankton:phytoplankton biomass ratio, epilimnion chlorophyll *a* concentration, Secchi depth and the maximum depth limit of submerged macrophytes *v* total phosphorus. Mean ± SD of five total phosphorus groups is shown. The impact of changes in total phosphorus on biological structure and physico-chemical variables is particularly high at low phosphorus concentrations, while only small changes occur when total phosphorus is higher than 0.1-0.2 mg P l^{-1} (from 17).

But even when external loading has been reduced to sufficiently low levels, resilience towards improvement has often been observed (see section 3). About 10-30 years may pass before the phosphorus concentration in the lakes reach equilibrium with those of inflows (4, 17). To accelerate the recovery process, lake restoration projects have been undertaken in several places in Denmark. Physico-chemical methods have been used, with examples being sediment removal as in Lake Brabrand near Århus (*Århus Kommune & Århus Amtskommune 1996*) or oxidation of the hypolimnion with either pure oxygen as in Lake Hald at Viborg (*Rasmussen 1995*) or with nitrate as in Lake Lyng at Silkeborg (*M. Søndergaard & E. Jeppesen, unpubl.*). Biological methods, such as removal of cyprinids, stocking of predatory fish, and protection and planting of submerged macrophytes, have also been used (section 4).

2.2 Main theme and research strategy

The typical Danish lake is shallow. Half of the approximately 500 lakes registered in the NERI lake database have a mean depth of less than 2 m, and only 3% have a mean depth of more than 10 m (*Kristensen et al. 1990*). Despite this fact, Danish lake research has primarily focused on deep lakes. Until the mid-1980s, the most intensive long-term ecological studies were undertaken in the deep Lake Esrom (e.g. *Jónasson 1972, 1977*), Furesøen (*Berg et al. 1958*) and Mossø (*Riemann & Mathiesen 1977*). International lake research has also mainly concentrated on deep lakes. Shallow lakes differ from deep lakes in several important respects. Deep lakes are often thermally stratified during the summer. This stratification results in poor exchange of nutrients and oxygen between the photic zone and the lake bottom in summer compared with shallow lakes that are typically homothermal. Moreover, shallowness implies higher sedimentation and higher nutrient release from the sediment and, if light conditions allow, higher primary production at the sediment surface. The sediment of shallow lakes is, therefore, more important to nutrient turnover and trophic dynamics than in deep lakes – the benthic-pelagic coupling is stronger. Other factors are important as well. Vertical migration of prey may be a less efficient anti-predator defense mechanism in the pelagial of shallow lakes than in deep lakes. Moreover, in shallow lakes a larger part of the lake area and volume may be colonized by submerged macrophytes that have proved to be of wide-ranging regulatory importance for lake ecosystems. It is therefore obvious that the ecological knowledge obtained by studying deep lakes can only be partly transferred to shallow lakes.

In 1984, when I was encouraged to start a lake group at the Freshwater Laboratory in Silkeborg (now the National Environmental Research Institute, NERI), it was only natural that the interest focused on shallow lakes. Apart from being the most common Danish lake type, shallow lakes have been most strongly exposed to eutrophication. Resilience against improvement was therefore expected to be particularly pronounced in these lakes. We have directed our research at the recovery phase following nutrient loading reduction and at the possibilities of accelerating lake restoration by means of biomanipulation. A multi-faceted research strategy has been used (Fig. 4). We have conducted cross-analyses of data from a large number of lakes and long-term studies of lakes that are in the recovery phase following a reduction in external nutrient loading. Furthermore, we have undertaken full-scale field experiments and enclosure experiments, and some of these experiments have been supplemented by laboratory investigations. More recently we have added a palaeoecological dimension to our research.

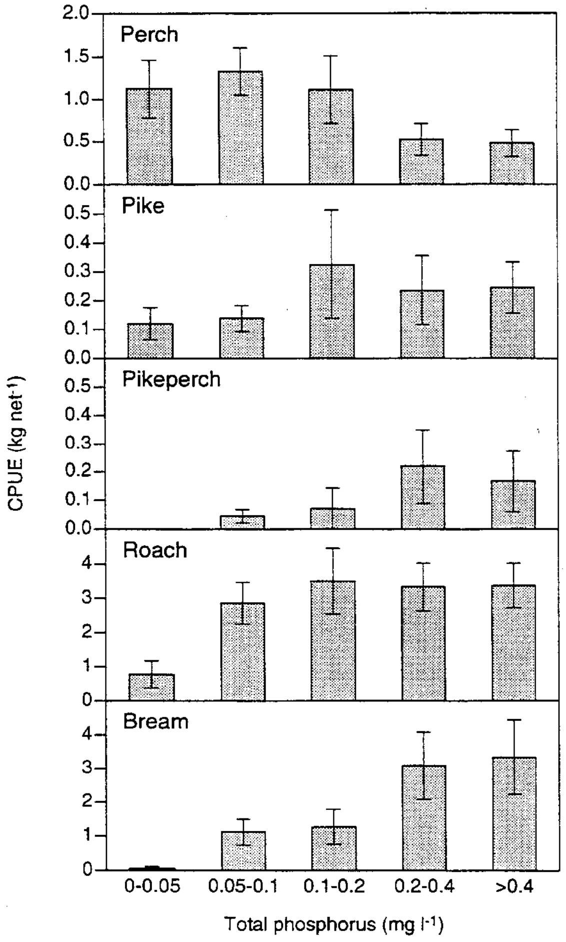

Fig. 3. Biomass (CPUE, catch in multiple mesh size gillnets ±SD, cf. Fig. 2) of various quantitatively important fish species in Danish lakes *v* summer mean total phosphorus (*E. Jeppesen, unpubl.*).

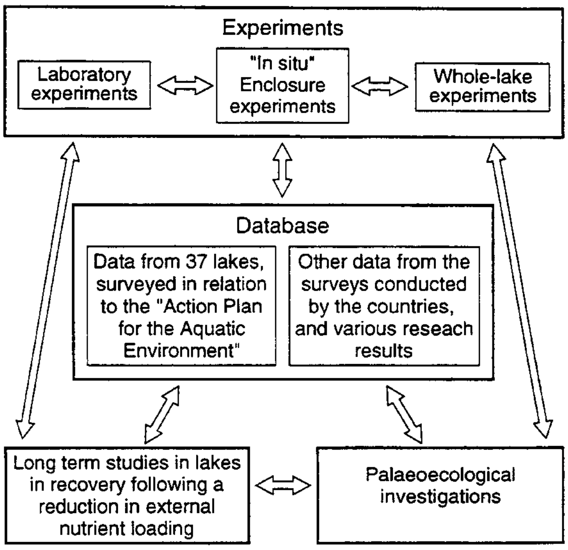

Fig. 4. Scheme illustrating the research strategy of the NERI Lake Group. Work is undertaken interactively at various levels and the interaction between research and county monitoring is close.

The subject of this dissertation is the ecology of shallow lakes. The main emphasis is placed on trophic dynamics in the pelagial, and I intend to illustrate how the knowledge gained may be used for purposes of lake restoration. The main part of the dissertation concerns freshwater lakes, but in the concluding chapter I discuss the trophic structure and interactions of brackish lakes, which differ substantially from freshwater lakes. Chapter 3 describes trophic interactions in the pelagic food web. The main focus is on the role of fish and fish fry and how their importance changes along a nutrient gradient and during the season. Moreover, differences between deep and shallow lakes are discussed. Chapter 4 deals with the changes of shallow lake ecosystems with increasing and decreasing nutrient loading, including resilience factors. Moreover, the occurrence and reasons for alternative stable states at intermediate nutrient levels are discussed. Finally, I evaluate the feasibility of using biomanipulation to improve the environmental state following a reduction of external nutrient loading. Chapter 5 focuses on describing past developments in the biological community and environmental state using analyses of animal and plant remains in the lake sediment. In addition, examples of reconstruction of the abundance of planktivorous fish are given. Chapter 6 deals with brackish lakes. Finally, a summary is given in Chapter 7, and future research needs within the subject area are identified.

3 Predatory control vs. resource control

In recent years the food-web structure and interactions in the pelagial of lakes have been subject to intense debate. With a few exceptions (e.g. *Hrbaček* et al. 1961; Brooks & Dodson 1965; Brooks 1969) the prevailing view a decade or two ago was that food-webs are primarily regulated from "the bottom", i.e. via the available resources. By way of example, phytoplankton are regulated by nutrients and light, zooplankton by phytoplankton. This is called resource control or "bottom up" control (sensu *McQueen et al. 1986*). This view also constituted the basis of the comprehensive world-wide IBP-investigations undertaken from 1965-1975, which aimed at determining primary production and energy flow through food-webs in, for example, limnetic systems (*Golterman 1990*). Since then it has become evident that food-webs may be strongly regulated "from the top" (called predatory control or "top-down control"), i.e. that the zooplankton are regulated by fish, phytoplankton by zooplankton, etc. (*Carpenter et al. 1985; Gulati et al. 1990; Carpenter & Kitchell 1993; Mortensen et al. 1994*). However, opinions vary on the relative importance of resource control and predatory control along a nutrient gradient.

On the basis of Fretwell's (1977) and Oksanen et al.'s (1981) studies of terrestrial environments, Persson et al. (1988) claimed that herbivory on phytoplankton depends on the number of food-web links, and that the zooplankton grazing pressure is high in lakes with an even number of links (e.g. lakes with only zooplankton and phytoplankton or lakes with predatory fish, planktivorous fish, zooplankton and phytoplankton), and low in lakes with an odd number of links. Predatory control will therefore be strongest in food-webs with an even number of links (2, 4, etc.) and resource control highest in food-webs with an odd number of links. Persson et al. (1988) furthermore suggested that with increasing nutrient supply a gradual increase in the number of food-web links occurs from one link in the ultra-oligotrophic lakes (phytoplankton) to two (+ zooplankton), three (+ planktivorous fish) and finally in mesotrophic lakes four links (+ predatory fish). In eutrophic lakes, the food-web will be reduced to three links as predatory fish are of no significance. To this may be added a two-linked system in the hypertrophic lakes in which the importance of planktivorous fish decreases due to frequent fish kills (Fig. 5) (see section 4.3).

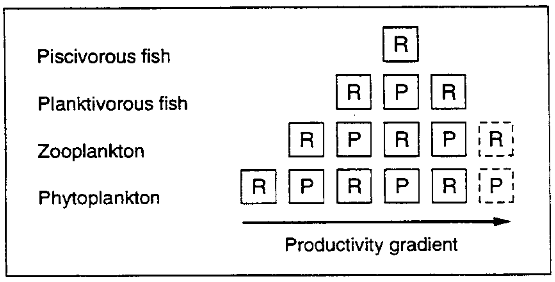

Fig. 5. Scheme illustrating the development in number of food-web links in the pelagial along a nutrient gradient. R = resource control, P = predatory/grazing control. The two-linked chain at the highest nutrient level has been added by the author, otherwise after Persson et al. (1988).

There are several illustrative examples supporting the hypothesis by Persson et al. (1988) (*Persson et al. 1992; Wurtsbaugh 1992; Hansson 1992*). There are, however, also many exceptions from both lakes and streams (*Leibold 1990; Flecker & Townsend; McIntosh & Townsend 1994; Mazumder 1994; Brett & Goldman 1996*). Among the reasons for the deviations are behavioural changes of prey, aiming at reducing the predation risk (*McIntosh & Townsend 1994*), and changes in the composition of primary producers towards grazing-tolerant/grazing-resistant forms at high grazer density. Moreover, at each food-web level there will often be species having variable sensitivity towards potential predators. In addition, some species occur at more than one trophic level or show ontogenetic shifts in food preference. In nature, simple food-webs are therefore rare.

Based on statistical analyses of experimental data, McQueen et al. (1986, 1989) suggested that resource control is highest at the bottom of the food-web (e.g. between nutrients and phytoplankton) and decreases upwards through the web and, conversely, that predatory control is strongest at the top of the web and decreases downwards (Fig. 6). They furthermore claimed that predatory control is high in oligotrophic lakes and low in eutrophic lakes, particularly because the latter lake type is dominated by cyanobacteria that are difficult to handle for the zooplankton. In contrast, Sarnelle (1992) argued that changes in the biomass of planktivorous fish have greatest impact on the phytoplankton (via the zooplankton) in eutrophic lakes.

Elser & Goldman (1990) and Carney & Elser (1990) argued that zooplankton grazing pressure on phytoplankton is:

- low in oligotrophic lakes due to low nutrient availability. In addition, the zooplankton are dominated by copepods that are less efficient grazers than are large-sized cladocerans.

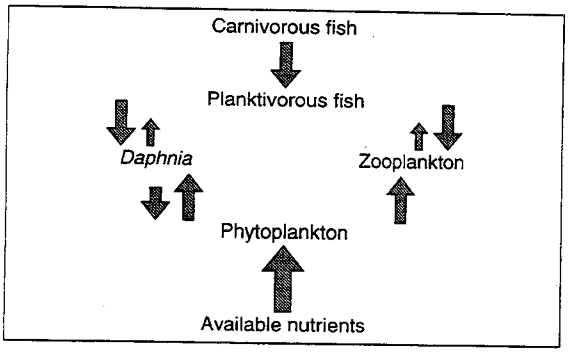

Fig. 6. Scheme illustrating changes in the impact of resource and predatory control through the food-web. The length of the arrows indicates the strength of the regression relationship between food-web levels (the slope) and the width the percentage of the variation explained (r^2). The figure shows that phytoplankton are especially regulated by nutrients and are only significantly influenced by zooplankton in the presence of *Daphnia*. The growth capacity of zooplankton is influenced by phytoplankton, but the actual biomass is affected by planktivorous fish predation. Finally, planktivorous fish may be markedly influenced by carnivorous fish (modified from *McQueen et al. 1986*).

- high in mesotrophic lakes in which the zooplankton are dominated by the efficient grazer, *Daphnia*.

- low in eutrophic lakes in which the phytoplankton are dominated by grazing-resistant species, such as cyanobacteria.

Recent investigations emphasize the importance of including nutrient recirculation when evaluating the strength of predatory and resource control (*McNaugton 1988; DeAngelis 1992; Sterner & Hessen 1994; Hessen 1997*). The carbon(C):nitrogen(N):phosphorus(P) ratios vary significantly both within species at a given food-web level and among species at the various levels, and this may have indirect cascading effects on trophic interactions. An increase in predation pressure on zooplankton will, for instance, diminish the cladoceran:copepod ratio since fish tend to prey selectively on cladocerans. This will reduce the N:P ratio of the matter excreted by zooplankton, because the copepod N:P ratio is higher than that for cladocerans, and the potential risk of dominance by cyanobacteria will consequently be greater (*Sterner et al. 1992; Hessen 1997*).

In several of the chapters below I return to these hypotheses when discussing our results.

3.1 Predation pressure on zooplankton along a phosphorus gradient

The increasing biomass of planktivorous fish CPUE observed in several Danish lakes at increasing phosphorus concentrations (Figs 2 and 3) indicate that the predatory control of zooplankton is strongest in eutrophic lakes. This is, however, not necessarily true. In oligotrophic lakes population growth of zooplankton is generally lower than in eutrophic lakes due to lower food concentrations (*Lampert & Muck 1985*). In oligotrophic lakes, it may therefore be more difficult for zooplankton to compensate for fish predation despite lower fish densities. Furthermore, Secchi depth is generally higher, making the zooplankton more visible to visually hunting, planktivorous fish. Finally, predatory fish may be lacking in these lakes, if, for instance, the fish stock consists exclusively of dwarf char (*Salvelinus alpinus*) (*Hofer & Medgyesy 1997*), or they may be only weakly represented in other char- and in trout-dominated lakes (tendencies towards a three-linked web, see *Persson et al. 1988*). It may therefore be hypothesized that the predation pressure on the large-sized zooplankton is unimodally linked with nutrient levels, i.e. that the predation pressure is:

- high in oligotrophic lakes due to low growth of prey zooplankton, clear water and a lack of or a weakly developed community of predatory fish.

- low in mesotrophic lakes in which there is more food available to the zooplankton, and in which a relatively high number of predatory fish may control the planktivorous fish, and macrophytes may offer refuges.

- low in slightly eutrophic and consequently turbid lakes. The turbidity may offer the zooplankton a refuge against visually hunting predators, and there is still a significant predation pressure by predatory fish on planktivorous fish.

- high in hypertrophic lakes in which the fish community is totally dominated by the highly abundant planktivorous fish.

To further elucidate these hypotheses we made a cross-analysis of data from a large number of Norwegian and Danish lakes. This data set is remarkable for its coverage of a large nutrient gradient. In the analysis we focused on *Daphnia*, which is particularly sensitive to fish predation due to its large size (*Brooks & Dodson 1965*). We found that *Daphnia* as a percentage of total cladoceran biomass was highest at 0.05-0.10 mg P l^{-1} (mean = 70%) and decreased markedly to low values (<7%) at the highest and lowest phosphorus concentrations (Fig. 7). This corresponds well with the hypothesis. It has earlier been argued that absence of *Daphnia* in oligotrophic lakes can be ascribed to the competitive advantage of calanoid copepods at low food concentrations (*McNaught 1975*), but later studies by Lampert & Muck (1985) and Schulze et al. (1995) have not been able to confirm this. In both studies the threshold concentration for positive growth was on a par with the one found in ultraoligotrophic lakes (*Schulze et al. 1995*). In oligotrophic, fishless mountain lakes and in the Arctic it is in fact often *Daphnia* species (*D. pulex* or *D. pulicaria*) and not calanoid copepods that dominate the filter-feeding zooplankton (*Røen 1977; Anderson*

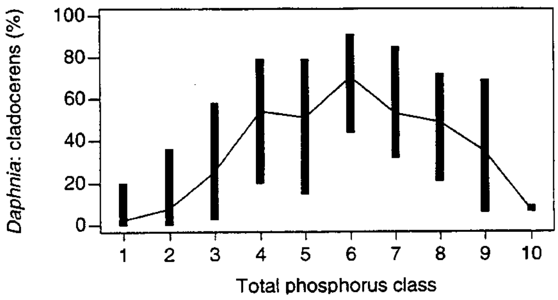

Fig. 7. Box-plot diagram showing the *Daphnia* proportion of total cladoceran biomass during summer in 300 Norwegian and Danish lakes with different lake water total phosphorus contents. Median as well as 25 and 75% percentiles are shown. Class (mg P l^{-1}) 1: 0-0.003; 2 = 0.003-0.006; 3 = 0.006 - 0.0125: 4 = 0.0125 - 0.025; 5 = 0.025 - 0.050; 6 = 0.050 - 0.1; 7 = 0.1 - 0.2; 8 = 0.2 - 0.4; 9 = 0.4 - 0.8; 10 ≥ 0.8. The *Daphnia* proportion is largest at 0.05 - 0.1 mg P l^{-1} (*E. Jeppesen, B. Faafeng, J.P. Jensen & D. Hessen, unpubl.*).

1980; Gliwicz 1985; Paul et al. 1996). The observation that zooplankton in oligotrophic lakes seem particularly sensitive to fish predation is supported by the fact that introduction of potentially planktivorous trout leads to a marked reduction or total elimination of *Daphnia* spp. in such lakes (*Anderson 1980; Paul et al. 1996*).

Investigations in New Zealand

To further elucidate the role of fish in oligo-mesotrophic lakes, we undertook investigations in a number of shallow lakes in the southern part of New Zealand together with colleagues at the University of Otago. The prevailing view was that fish do not markedly influence the abundance or composition of zooplankton in New Zealand lakes (*Chapman et al. 1975, 1985; Burns & Xu 1990; Burns 1992*). This view is based on the fact that only few obligate planktivorous fish species are found in the lakes (*Chapman et al. 1985*). Likewise, there are few species and low densities of invertebrate predators in the pelagial (*Chapman et al. 1985; Burns 1992*) and, finally, several studies point at food limitation as a main regulating factor (*Burns 1979, 1992; Chapman et al. 1985*).

Based on experience from Danish lakes we have, however, argued for a high predation risk in New Zealand lakes (11). First, fish fry of the frequently abundant, but mainly benthic, endemic species, common bully (*Gobiomorphus cotidianus*) and upland bully (*Philypnodon breviceps*) are planktivorous during the early larval stage (*Staples 1975*). Moreover, both common and upland bully may have several cohorts during summer, and according to our experience (6) this will lead to a continuously high fry predation pressure on the zooplankton. Second, species of trout (*Salmo trutta, Oncorhynchus mykiss*) are dominant top-predators in several of the lakes. Apart from preying on other fish these species also prey on invertebrates such as snails, crayfish and insects in New Zealand lakes (*D. Scott, unpubl. results*), and they are probably then relatively weak predators on fish compared with, for instance, perch and pike. To this must be added that trout also prey on large-sized zooplankton (e.g. *Swift 1970; Lynott et al. 1995; Sægrov et al. 1996*). Third, the zooplankton community is completely dominated by small species and, fourth, the biomass relationship between zooplankton and phytoplankton is low in most New Zealand lakes compared with northern European lakes (*Malthus & Mitchell 1990*).

To further evaluate our hypothesis we made a comparative analysis of data from limnological investigations in selected New Zealand and Danish lakes (11). We found that the zooplankton community in New Zealand lakes seems to be highly regulated by fish predation, perhaps even more than is the case in Danish lakes with comparable nutrient concentrations. Enclosure experiments conducted in the eutrophic Tomahawk Lagoon provided further evidence. Larvae of common bully almost completely eliminated *Daphnia carinata* (the most common *Daphnia* species) at a density of 8-16 0+ and 1^{+} fish m^{-2}. In comparison, the density of planktivorous fish may reach maximum values of 114-208 m^{-2} in New Zealand lakes (*Staples 1975; Rowe & Chisnall 1997*). Furthermore, we undertook studies in 25 shallow lakes with varying nutrient levels (from 0.002-0.17 mg P l^{-1}) and fish densities (*Jeppesen et al. submitted*). The results showed that *D. carinata* was the dominant cladoceran in fishless lakes, even at low phosphorus concentrations; medium-sized cladocerans, such as *Ceriodaphnia*, dominated in oligotrophic and mesotrophic lakes with even low densities of fish, while medium-sized and small-sized species dominated in eutrophic lakes with high fish densities.

These results support our hypothesis that fish predation plays a major regulating role for the zooplankton communities of New Zealand lakes. The results, moreover, support the view that the predation pressure on large-sized species is high in oligotrophic lakes with fish.

Effects on phytoplankton

Our results indicate that the predatory control of large-sized zooplankton is high in oligotrophic and eutrophic lakes and lower in mesotrophic lakes. The question is if this difference in predation control of zooplankton affects the next link in the food-web. The Danish-Norwegian data set shows that the summer zooplankton:phytoplankton biomass ratio is relatively constant and high (~0.5) in the phosphorus interval 0.003-0.050 mg P l^{-1} and declines with increased phosphorus concentrations (*E. Jeppesen, B. Faafeng, J.P. Jensen & D. Hessen, unpubl.*), suggesting that the presumed high predatory control of zooplankton is channeled downwards the food-web in eutrophic lakes, but not in oligotrophic lakes. A shift to dominance by small-sized zooplankton species may not, therefore, have the same effect in oligotrophic lakes as in eutrophic lakes, perhaps because the phytoplankton in oligotrophic lakes is more strongly resource-controlled and therefore unable to take advantage of the presumed weaker grazing control by zooplankton. Even though one has to be careful when drawing conclusions from empirical relations and biomass ratios, the results indicate that the cascading effects (sensu *Carpenter & Kitchell 1985*) on phytoplankton of changes in the abundance of planktivorous fish are most significant in eutrophic lakes. This supports the hypothesis advanced by Sarnelle (1992), but contradicts those of McQueen et al. (1986) and Elser & Goldman (1990).

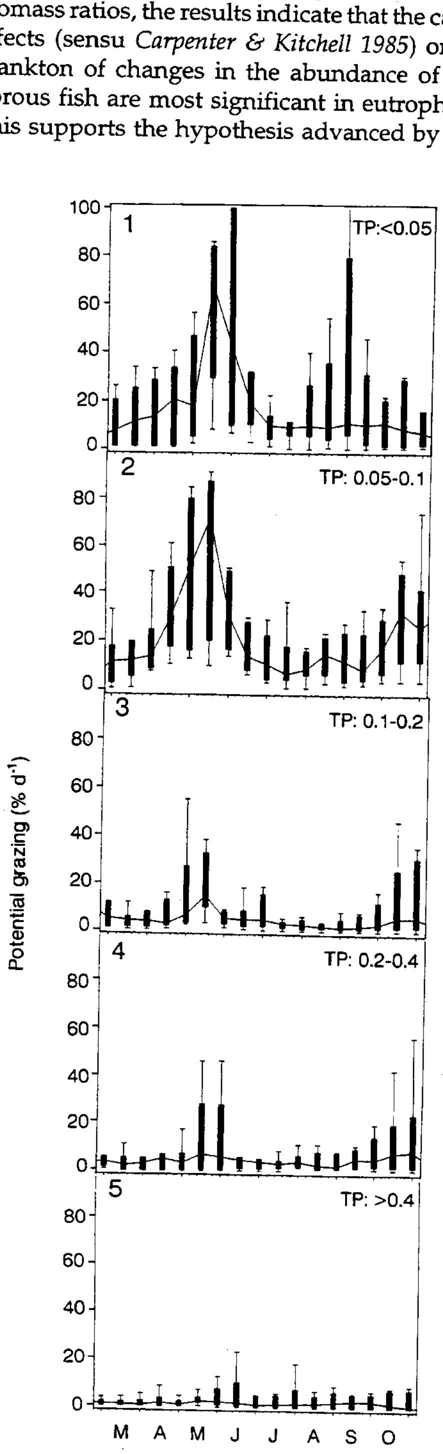

Fig. 8. Seasonal variation in the zooplankton potential grazing pressure on phytoplankton (% of the phytoplankton biomass ingested per day) *v* summer mean concentrations of total phosphorus (mg l^{-1}). Median, the 25-75% and the 10-90% quantiles are shown. Each phosphorus category includes 6-10 lakes. The potential grazing pressure is calculated assuming that cladocerans and copepods ingest phytoplankton corresponding to 100% and 50%, respectively, of their biomass per day (from 10).

3.2 Seasonal variations in predatory control

The cross-analysis of lake data described in the previous section was based on mean summer data. There may, however, be significant seasonal variations in the grazing pressure on phytoplankton (*Sommer et al. 1986*). Based on analyses of data from Danish lakes we found that the seasonal pattern in the grazing pressure on phytoplankton changed markedly with changing phosphorus concentrations (10; Fig. 8). In mesotrophic lakes, the potential grazing pressure on phytoplankton is high in early summer, low in mid-summer, and in some lakes high again in late summer. However, at increasing phosphorus concentrations the spring and autumn peaks become smaller, and they almost disappeared in lakes with very high phosphorus concentrations and high density of planktivorous fish (11). Simultaneously, the duration of the summer minimum was prolonged. Earlier, it has been claimed that the marked mid-summer decline in zooplankton grazing pressure, which has been observed in many lakes, can be ascribed to blooms of cyanobacteria, as these are often difficult to handle for the zooplankton. Furthermore, cyanobacteria may be toxic, and their nutritive value to many zooplankton species is comparatively low (see e.g. review by *Bernardi & Guissani 1990*). We did find, however, a decrease in grazing pressure in lakes dominated by edible phytoplankton species such as green algae and we observed that the pattern was repeated from year to year in lakes that are alternately dominated by cyanobacteria and green algae (*Windolf et al. 1993*). Dominance by cyanobacteria does not, therefore, appear to be the most important factor for the low summer grazing pressure on phytoplankton, which contradicts the hypotheses advanced by McQueen et al. (1986) and Elser & Goldman (1990).

The role of fish fry – an example from Lake Lyng
A number of recent investigations indicate that fish fry may prey heavily on zooplankton during summer (e.g. *Mills & Forney 1983; Cryer et al. 1986; Crowder et al. 1987; Mills et al. 1987; Luecke et al. 1990*). In Danish lakes fish fry are abundant in the pelagial at the time when the grazing pressure on phytoplankton declines, suggesting that fry predation is a likely explanation of the declining zooplankton grazing pressure. Predation by fish fry may also explain our observations that the duration of the period with low grazing pressure diminished with decreasing phosphorus concentrations. Mesotrophic Danish lakes have a higher percentage of predatory fish than eutrophic lakes (Figs 2 and 3). In mesotrophic lakes, the predators may, therefore, decimate the fry, within a short time period, resulting in reduced predation pressure on zooplankton and con-

sequently faster re-establishment of a high grazing pressure on phytoplankton in the autumn than in eutrophic lakes. (Fig. 8).

To elucidate the impact of fish fry we conducted full-scale experiment in eutrophic Lake Lyng (24; *Berg et al. 1997*). Varying densities of pike fry (0-3,600 ha^{-1}) were stocked in early summer for six years with the aim of creating a differential predation pressure on planktivorous fish fry. We succeeded in achieving a considerable gradient in the density of planktivorous fry between years (17-172 fish net^{-1}), without causing any major changes in the abundance of older fish (*Berg et al. 1997*). Simultaneously, marked changes took place in the density of zooplankton and phytoplankton, phosphorus concentrations and Secchi depths, suggesting major cascading effects (Fig. 9). With increasing density of fish fry the concentrations of chlorophyll *a* and total phosphorus as well as rotifer abundance increased significantly, whereas Secchi depth and the proportion of *Daphnia* spp. in total cladoceran abundance decreased markedly (24). These results support the hypothesis that fish fry significantly regulate zooplankton and phytoplankton. The effects of variations in fish fry recruitment in Lake Søbygård provide further evidence in support of this hypothesis (8, 16, see section 4.3).

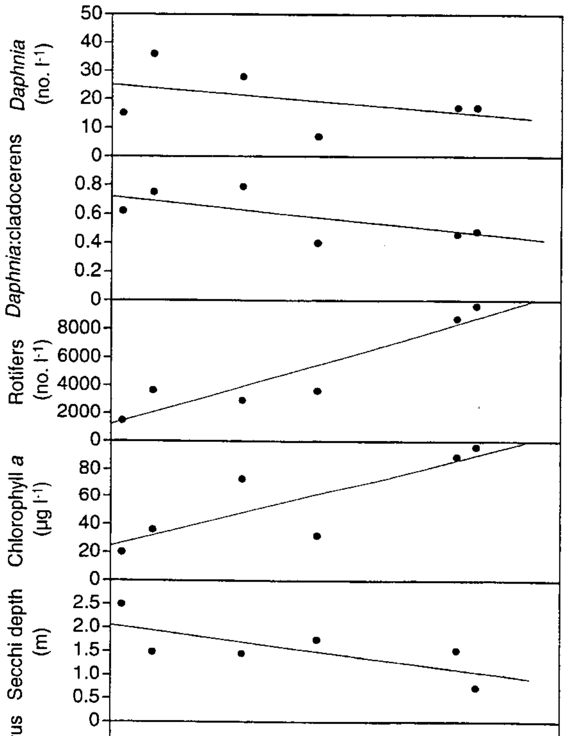

Fig. 9. Abundance of *Daphnia* and their share of total cladoceran abundance, rotifer abundance, chlorophyll *a*, Secchi depth and summer mean lake water total phosphorus *v* number of planktivorous fish (<10 cm) in Lake Lyng during 6 years when 0$^+$ pike (*Esox lucius*) were stocked in varying densities (0-3,600 indiv. ha^{-1}). CPUE = catch in multiple mesh size gill nets, cf. Fig. 2 (from 24).

Fish fry seem to have a significant influence on the summer grazing capacity of zooplankton in mesotrophic and eutrophic lakes, whereas, in the short term, they seem to be less important in hypertrophic lakes, as the biomass of >0$^+$ fish is sufficiently high to control zooplankton throughout the year (Fig. 8). In these lakes, cladocerans are dominated by small-sized forms such as *Bosmina longirostris* throughout the year (11). Food limitation cannot explain the low zooplankton grazing pressure as the phytoplankton in these lakes is typically dominated by edible green algae.

3.3 Shallow vs. deep lakes

The empirical data discussed so far (Fig. 2) were derived from both shallow and deep lakes. However, significant differences in the trophic structure and interactions between deep, stratified lakes and shallow, fully mixed lakes seem to occur (10).

Higher predatory control in shallow lakes

Cross-analyses of data from a large number of lakes indicate that the biomass and production of fish per unit of area at a given nutrient level do not depend on lake depth (*Hanson & Leggett 1982; Downing et al. 1990*). The biomass of fish per unit of volume is, therefore, considerably higher in shallow than in deep lakes, and it is therefore likely that the fish predation pressure on zooplankton increases with decreasing mean depth (10). In addition, the ability of zooplankton to escape predators in shallow lakes (without submerged macrophytes) is presumably lower. Zooplankton avoid predation by undertaking vertical diel migration (e.g. *Lampert 1993*). They hide near the bottom during the day, and at night, when they are less exposed to the risk of predation from visually hunting fish, they migrate to surface water in search for food (*Ringelberg 1991; Lampert 1993*). It is obvious that the lower water depth makes vertical migration a less efficient anti-predator protection measure in shallow lakes.

Better possibilities for exploiting alternative food sources such as benthic invertebrates are also indicative of a potentially higher predation pressure on zooplankton in shallow lakes (10). Apart from in highly wind-exposed lakes, the biomass and production of benthic invertebrates are generally higher in shallow lakes (*Hanson & Peters 1984; Lindegaard 1994*), perhaps because the organic matter settled from the water column is considerably less decomposed than in deep lakes due to the shorter settling distance. Low oxygen concentrations in the hypolimnion of stratified lakes may also contribute to the lower production of benthic invertebrates (*Wiederholm 1975; Jónasson 1972*). Since zooplankton biomass per unit of area is lower in shallow lakes, the zooplankton:zoobenthos biomass ratio decreases substantially with decreasing mean depth (22 times higher in a lake with a mean depth of 10 m than in one with 1 m; Fig. 10). Most planktivorous fish are facultatively planktivorous, also feeding on benthic invertebrates. Hence, the higher production of benthic invertebrates in shallow lakes makes it possible for the fish to maintain a higher biomass than if zooplankton were the only food source. Since fish may shift from benthic to pelagic feeding, their potential for controlling zooplankton is greater in shallow than in deep lakes.

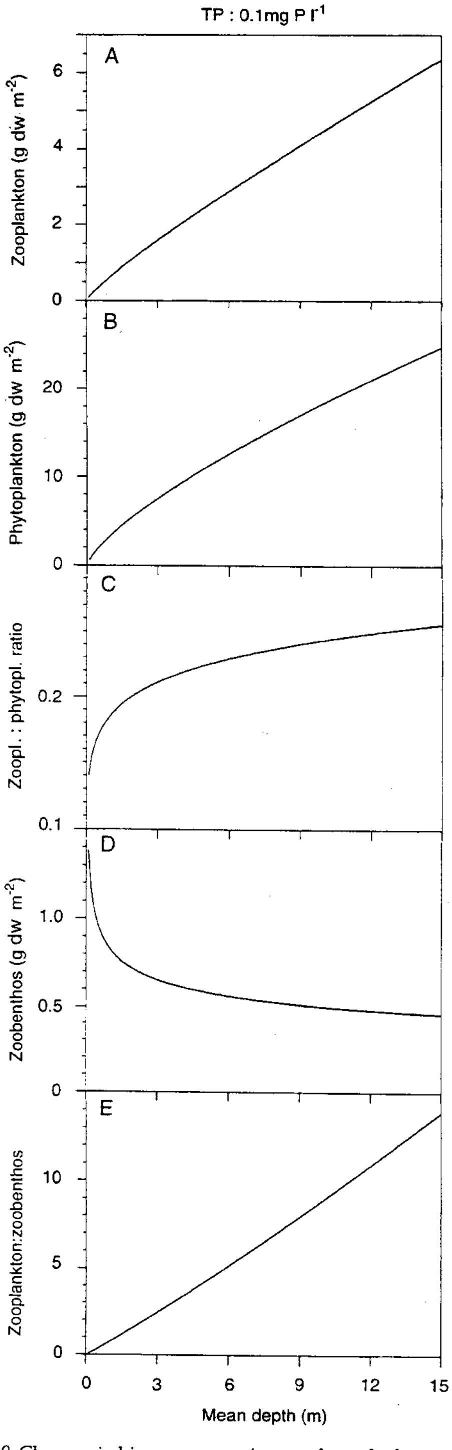

Fig. 10. Changes in biomass per unit area of zooplankton and phytoplankton, zooplankton:phytoplankton biomass ratio, zoobenthos biomass and the zooplankton:zoobenthos biomass ratio along a depth gradient in lakes with an epilimnion summer mean total phosphorus concentration of 0.1 mg P l⁻¹. The curves in A and B are based on the equations from Danish lakes, while that in D is based on an equation from Hanson & Peters (1984) (from 10).

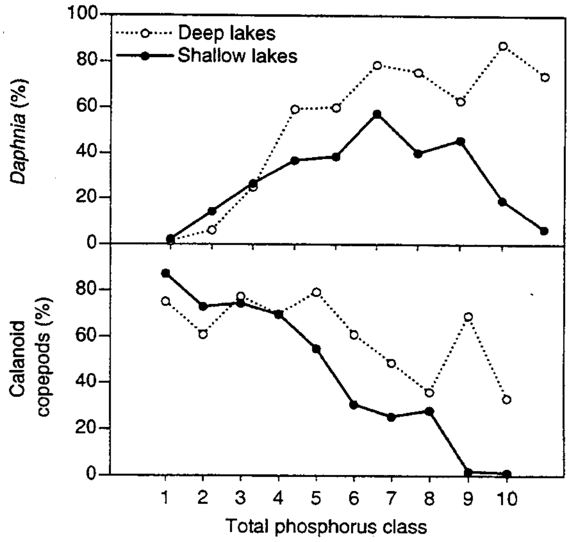

Fig. 11. Summer mean values of *Daphnia* as a percentage of total cladoceran biomass and percentage calanoid copepods of total copepod biomass in deep (>5 m) and shallow (≤5 m) Norwegian and Danish lakes *v* summer mean lake water total phosphorus concentrations (class division as in Fig. 7). When total phosphorus is higher than 0.0125 mg P l⁻¹, the percentage of *Daphnia* and calanoid copepods is highest in deep lakes (*E. Jeppesen, B. Faafeng, J.P. Jensen & D. Hessen, unpubl.*).

The view that the predation pressure by fish on zooplankton is highest in shallow lakes is supported by the data from Danish and Norwegian lakes (*E. Jeppesen, B. Faafeng, J.P. Jensen & D. Hessen, unpubl.*, Fig. 11). Above a phosphorus concentration range of 0.012-0.025 mg TP l⁻¹, *Daphnia* as a percentage of cladoceran biomass and calanoid copepods as a percentage of total copepod biomass were greater in deep than in shallow lakes (Fig. 11). Calanoid copepods are generally more exposed to fish predation than are cyclopoid species (*Winfield 1986*), and the proportion of calanoid copepods may therefore also provide information on fish predation pressure (11). A higher predation pressure on zooplankton suggests lower zooplankton grazing pressure on phytoplankton, which is supported by the decreasing biomass ratio between zooplankton and phytoplankton with decreasing mean depth (Fig. 10).

Higher nutrient availability in shallow lakes

Several factors therefore suggest a more important regulating role of fish in shallow lakes than deep lakes. The argument for the importance of predatory control is further strengthened by the fact that resource control generally appears to be weaker than in deep lakes. In lakes with similar mean annual phosphorus concentrations we found higher total phosphorus concentrations in the photic zone during summer than in deep lakes, which is most likely due to the more direct contact between nutrients released from the sediment and phytoplankton (10). In deep, stratified lakes, nutrients settled from epilimnion or released from the sediment remain in the hypolimnion until the thermocline erodes in autumn, while in shallow homothermal lakes nutrients return to the photic zone with only a minor delay. Furthermore, near-sediment water temperature is higher in unstratified lakes, which stimulates turnover and release of nutrients from the sediments under aerobic conditions (*Kamp Nielsen 1974; Jensen & Andersen 1992*). Finally, the higher predation on benthic invertebrates and increased detritivory in shallow lakes may result in increased nutrient release from the lake sediment to the water, thereby weakening resource control of phytoplankton (*Peréz-Fuentetaja et al. 1996; Persson 1997*). It is characteristic that the difference in summer phosphorus concentrations between shallow and deep lakes increases with increasing mean annual phosphorus concentrations (Fig. 12). The same is true for chlorophyll *a*, except when phosphorus concentrations are below 0.1 mg P l^{-1}, that is lakes with extensive submerged macrophyte coverage (cf. Section 4).

Differences in phytoplankton dominance

The more efficient benthic-pelagic coupling in shallow lakes may also be important for the differences in the response of the phytoplankton community to increased nutrient loading. The data from Danish and Norwegian lakes (*J.P. Jensen, B. Faafeng & E. Jeppesen, unpubl.*, and 19) revealed that the biomass of cyanobacteria in eutrophic lakes in temperate latitudes tends to be proportionally lower in the shallow ones. Chlorophyceae (green algae) are frequently dominant in hypertrophic, shallow lakes as opposed to deep lakes in which cyanobacteria remain dominant. The reasons for these differences are poorly understood. Large cyanobacteria are characterized by their excellent nutrient storage capacity, low settling rates, and relatively low growth rates, while green algae

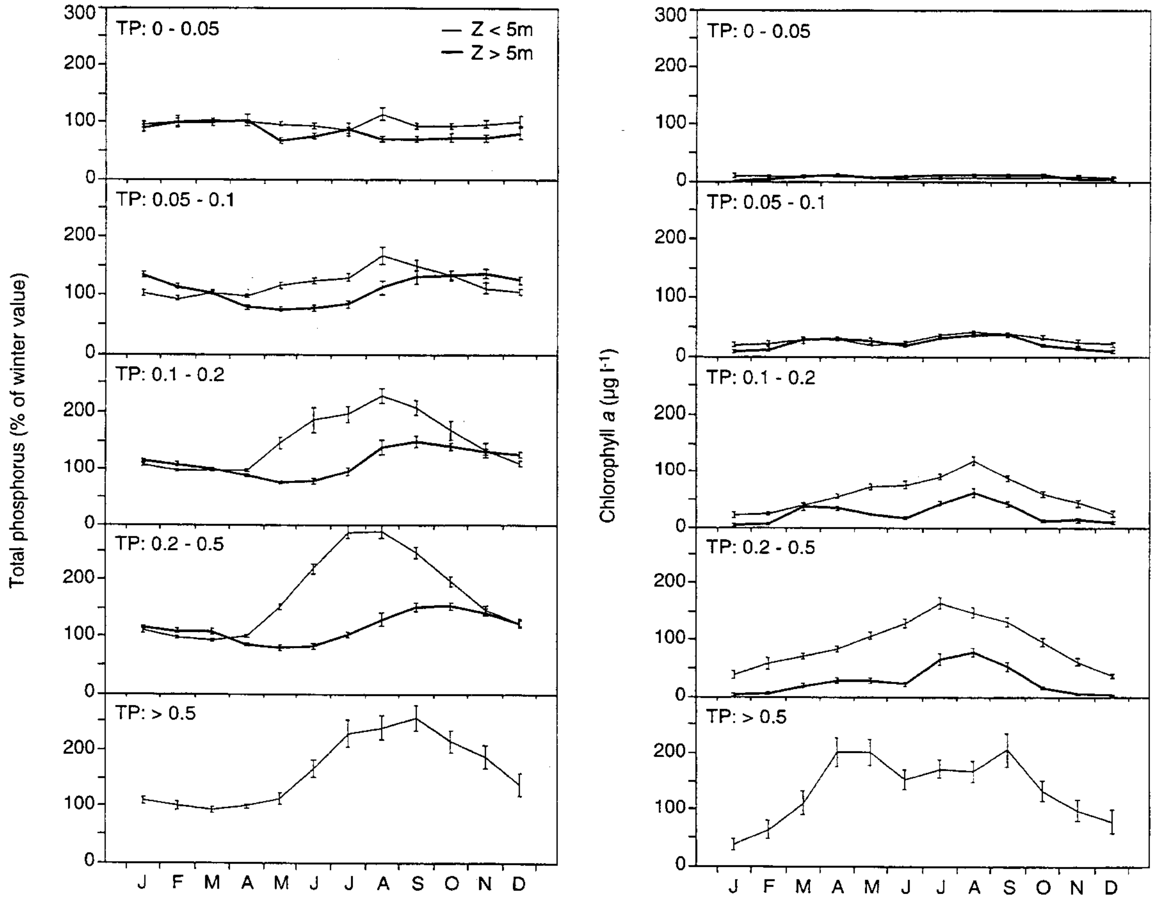

Fig. 12. Left: Seasonal variation in epilimnion total phosphorus concentration expressed in per cent of the Jan. – April mean in Danish lakes in different categories of mean annual total phosphorus (TP, mg l^{-1}). The data set is divided into lakes with a mean depth <5 m (n = 191) and >5 m (n = 42). Right: The corresponding values for chlorophyll *a*. Note that the difference in summer TP between shallow and deep lakes increases with increasing TP concentrations and that summer chlorophyll *a* in shallow lakes does not increase in the two lowest phosphorus categories despite increasing phosphorus concentrations. These are the phosphorus concentrations at which submerged macrophytes are most widely distributed in shallow lakes (from 10 and *E. Jeppesen & J.P. Jensen, unpubl.*).

such as *Scenedesmus* and *Chlorella*, grow fast at high nutrient levels, but suffer high losses by sedimentation (*Reynolds 1984*). These differences may contribute to the greater importance of green algae in shallow, fully mixed lakes, in which nutrient release is high during summer and nutrients lost by sedimentation are returned to the photic zone (1, 19), while algae that can minimize nutrient loss from the photic zone are favoured in deep, stratified lakes. In addition, wind-induced resuspension of sediment (*Kristensen et al. 1992*) and fluctuations in temperature on diurnal and day-to-day scales (3) are of great importance in shallow lakes. This may lead to nutrients being released in pulses from the sediment to the water (19). Laboratory experiments have shown these conditions to favour green algae (*Sommer 1985*).

It has been claimed that due to high pH (pH >9.5), eutrophic lakes will be dominated by cyanobacteria because they have a low half-saturation constant for CO_2 uptake and consequently a competitive advantage at low CO_2 concentrations (*Shapiro 1990*). However, we found (19) that green algae in Danish lakes were dominant at the highest pH, which in some instances became as high as 11 (1). According to Shapiro, cyanobacteria should be dominant at this pH level. Subsequent studies have confirmed our observations (*Beklioglu & Moss 1995*). The reasons for these differences remain to be fully elucidated, but are perhaps related to the continuous release of CO_2 from the sediment in shallow lakes, implying constant CO_2 supersaturation or absorption of CO_2 when phytoplankton circulate near the sediment.

It has also been claimed that nitrogen-fixing cyanobacteria are favoured by low total nitrogen:total phosphorus ratios (*Smith 1983*). We found, however, that non-heterocystous cyanobacteria and green algae dominated at the lowest nitrogen:phosphorus ratios (Fig. 13), whereas heterocystous species were more often dominant in early summer when nitrate was still found (19). Our analyses suggest that it is differences in phosphorus affinity that determine the outcome of the competition among the two cyanobacteria types in shallow Danish lakes, implying that heterocystous species occur at lower phosphorus concentrations than non-heterocystous species.

I conclude that several factors suggest a higher predatory control and a weaker resource control in shallow lakes than deeper lakes with similar nutrient levels, and that the more intense benthic-pelagic coupling in shallow lakes influences both the abundance and composition of phytoplankton. As will be described in section 4, extensive coverage of submerged macrophytes in shallow lakes may affect the relative contributions of resource and predator control significantly.

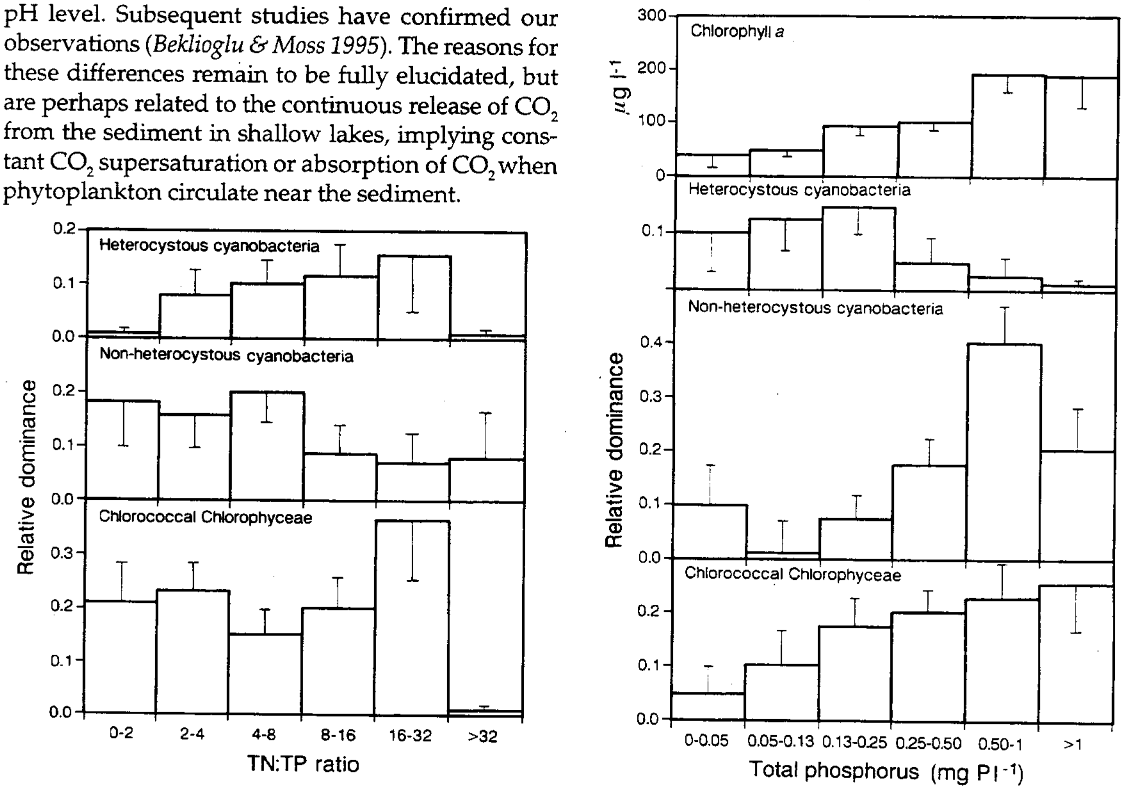

Fig. 13. The contribution of summer samples with dominance of cyanobacteria (±heterocysts) and chlorophytes in relation to nitrogen:phosphorus (TN:TP) by weight and total phosphorus concentrations. Note that cyanobacteria without heterocysts do not dominate at particularly low TN:TP ratios, but at the lower phosphorus levels. Additionally, green algal dominance is most significant at the highest phosphorus concentrations (from 19).

4 Alternative equilibria in shallow lakes

The relationship between the trophic structure and phosphorus described in Fig. 2 and Section 3 may give the impression that changes in trophic structure occur gradually concurrently with changes in nutrient loading. This is also the classic view (*Phillips et al. 1978*) according to which changes along a nutrient gradient in shallow lakes primarily reflect changes in the competition among primary producers. Increased nutrient supply stimulates the growth of phytoplankton and epiphytes which in turn degrades the benthic light climate and hence the abundance of submerged macrophytes. Consequently, more nutrients become available which further stimulates the growth of phytoplankton. A self-perpetuating process has been initiated, and continuing supply of nutrients will lead to a gradual disappearance of submerged macrophytes and a phytoplankton-dominated community.

However, studies undertaken in collaboration with, in particular Dutch and British colleagues, have radically changed the view of causal relations (2, 4; *Moss 1989, 1990; Scheffer 1989, 1990* – summary in 20). Our hypothesis is that oligotrophic shallow lakes tend to be clear (excepting dystrophic lakes) and extensively covered by submerged macrophytes, if not prevented by physical/climatic conditions. If the lakes are not ultraoligotrophic, predatory fish are often sufficiently abundant to control the planktivorous fish stock. When more nutrients are added, lake trophic structure does not respond immediately. The productivity in the food-web increases, but a series of feedback mechanisms prevents substantial changes in trophic structure (Fig. 1). Predatory fish create a high predation pressure on planktivorous fish, enabling zooplankton to control phytoplankton and snails to control epiphytes on plant surfaces (*Brönmark & Weisner 1992*). If the nutrient supply increases further, a threshold will eventually be reached at which the system breaks down and an abrupt change occurs to a turbid state with high phytoplankton biomass, few or no submerged macrophytes and total dominance

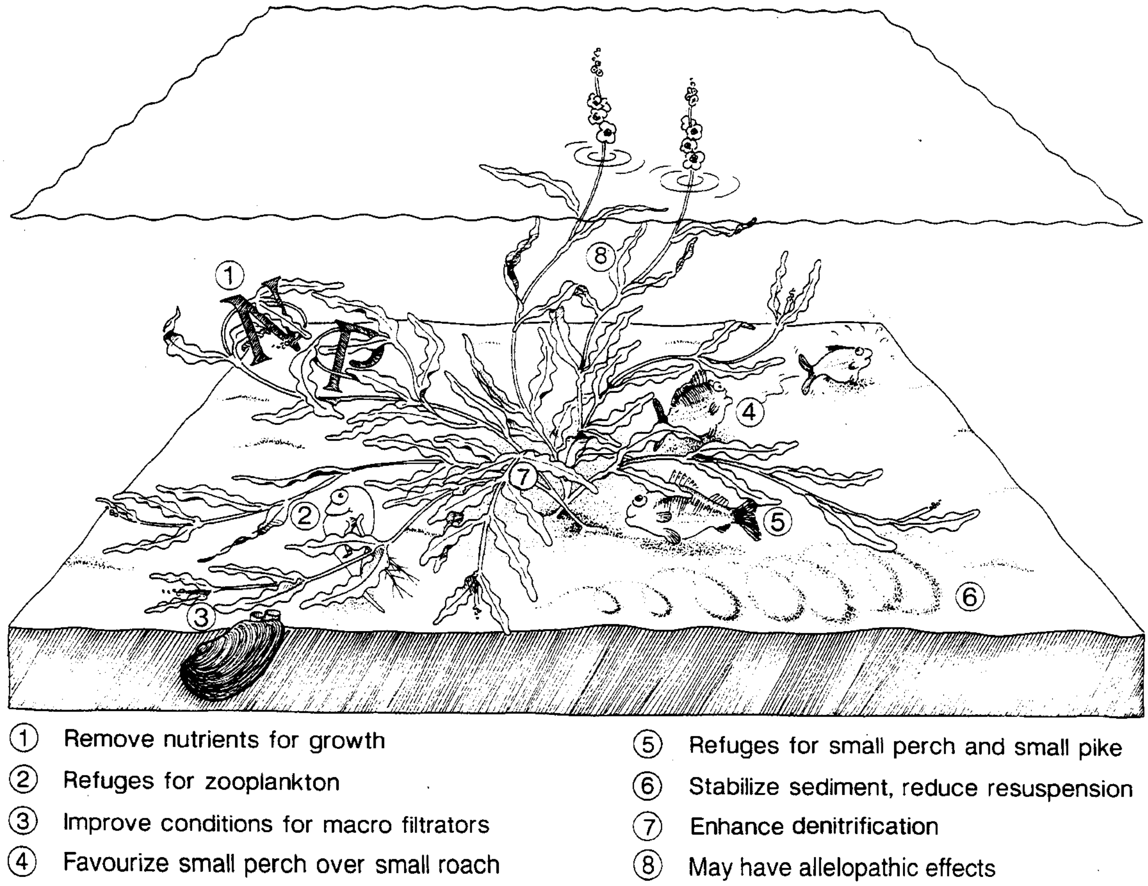

Fig. 14. Via various mechanisms submerged macrophytes may stabilize the clearwater state in lakes (modified from *Jeppesen et al. 1989*).

of the fish community by planktivorous fish. This state has a number of new feedback mechanisms impeding a shift back to the clearwater state. When the nutrient supply is reduced, planktivorous fish and, in some instances, the grazing pressure on submerged macrophytes by grazing waterfowl, may create a resilience towards a shift to the clearwater state. Provided that there are no major perturbations in the system either due to artificial interventions (e.g. biomanipulation) or natural events (e.g. fish kill during ice cover), the shift will occur at a lower nutrient level than that which initially led to the turbid state (Fig. 15).

Our hypothesis is supported by both empirical observations (20, 2, 4, 10, 13, 14; *Blindow et al. 1993; Moss et al. 1996*), full-scale and enclosure investigations (1, 14, 15, 18 19, 21) and theoretical models (*Scheffer 1989, 1990; Scheffer & Jeppesen 1997*). The theoretical possibility that ecosystems may have more than one equilibrium is not new (*Noy-Meir 1975; May 1977; Uhlmann 1980*), but so far only few empirical data support it (*Scheffer* 1997).

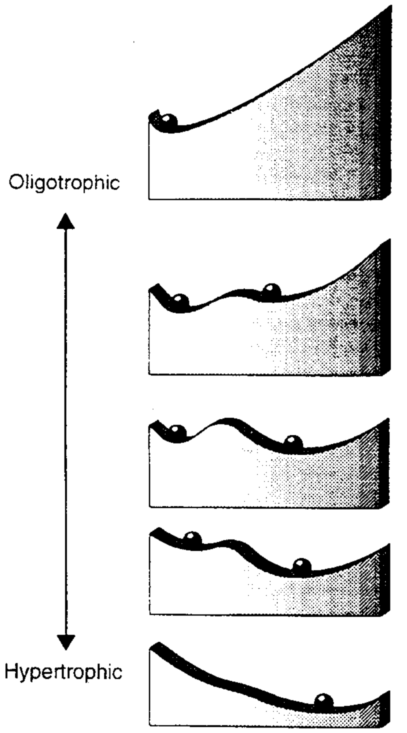

Fig. 15. Illustration of the response of shallow lakes to changes in nutrient supply. At low nutrient supply the lakes are clear. With increasing nutrient loading two alternative states occur, but major ecosystem changes are needed to shift the lake to the turbid state. With continuously rising nutrient levels the lakes may more easily shift to the turbid state and it gets more difficult to bring them back to the clearwater state. Finally, there is only one stable state - the turbid one. A switch back following a nutrient loading reduction shows similar resilience (from 22 and *Scheffer 1990*).

4.1 The stabilizing role of submerged macrophytes

As mentioned above, submerged macrophytes are of great importance for maintaining originally oligotrophic-mesotrophic lakes in the clearwater state after a moderate increase in nutrient supply. One of the reasons is that macrophyte biomass increases, resulting in increased nutrient fixation in macrophytes and epiphytes (*Sand-Jensen & Borum 1991*). During summer, part of the added nutrients is therefore not available to the phytoplankton. Moreover, submerged macrophytes may indirectly reduce available nutrients. They reduce sediment resuspension (*James & Barko 1990; Dieter 1990; Hamilton & Mitchell 1996*), which often increases nutrient release to the water (*Søndergaard et al. 1992*). The larger surface area contributed by the plants may promote denitrification in the opiphyte layer on the surfaces and thereby increase nitrogen loss from the lake (*Weisner et al. 1994*). Low oxygen concentrations within the macrophyte beds, particularly at night (*Frodge et al. 1990*), are supposed to have similar effects. Finally, submerged macrophytes may locally diminish phytoplankton by shading them (*Wetzel 1983; Pokorny et al. 1984*).

Indirect effects

The effect of plants on nutrients and light does not, however, fully explain why submerged macrophytes promote clearwater conditions. An analysis of data from 210 Danish freshwater lakes has shown that lakes with a plant coverage above 30% are more transparent than lakes with the same phosphorus concentrations, but without macrophytes or with low macrophyte coverage (2, 4; Fig. 16). This is also true for lakes having macrophyte beds along the shore and open water in the centre, implying that the effect must reach beyond the plant-covered area. The same pattern was found in Florida lakes (*Canfield et al. 1984*). Recent investigations from Norway (*Faafeng & Mjelde 1997*) and the Netherlands (*Scheffer 1997*) also suggest that lakes with high abundance of submerged macrophytes are more transparent than was to be expected from the phosphorus level. A number of indirect effects have been offered as an explanation. Submerged macrophytes promote sedimentation (*Van den Berg et al. 1997*) and reduce, as mentioned, resuspension (*James & Barko 1990; Dieter 1990*), and this may lead to more transparent water in shallow lakes in which wind-induced resuspension otherwise may be quite significant. Lake Arresø in Denmark serves as an example of this effect. In this lake, measurements and modelling indicate that, as a consequence of resuspension alone, Secchi depth is below 1 m for half of the time (*Kristensen et al. 1992*).

Resuspension may also be reduced via the effect of macrophytes on the fish stock. Benthivorous fish such as bream (*Abramis brama*) may stir up sediment when searching for food, which may substantially increase the concentrations of suspended sediment and nutrients (*Lammens 1986; Meijer et al. 1990; Breukelaar et al. 1994*). Bream is favoured in eutrophic lakes without macrophytes, and generally are of little importance in macrophyte-rich lakes (*Meijer et al. 1995*). Resuspension may also be reduced as improved light conditions mediated by the reduced sediment mixing by fish may result in increased growth of filamentous and microbenthic algae (*Delgado et al. 1991*). The observation that submerged macrophytes affect suspended solids is supported by results from New Zealand lakes where Hamilton & Mitchell (1996) found that besides being affected by wind exposure, suspended solids were negatively related to submerged macrophyte coverage.

It has been claimed that the quiescent water within macrophyte beds may enhance phytoplankton sedimentation and hence reduce phytoplankton biomass (*Meijer & Hosper 1997*). This is not, however, consistent with our observations: when the grazing pressure by filter-feeders was low, phytoplankton biomass in the macrophyte beds was high in eutrophic freshwater and brackish lakes even at very high macrophyte coverage (6, 14, 21). This is probably due to the fact that phytoplankton with low specific sedimentation rates, such as cyanobacteria and flagellates, become dominant in the water among plants (23).

Chemical cues from submerged macrophytes inhibiting phytoplankton growth have been suggested to promote clearwater conditions in macrophyte-rich lakes (called allelopathy). Laboratory experiments by Wium Andersen (1982) demonstrated that sulphuric compounds extracted from characeans have a negative impact on the photosynthesis of phytoplankton cultures in concentrations of only a few μmol l^{-1}. The role of allelopathy in nature, however, remains to be elucidated (*Sand-Jensen & Borum 1991*).

Submerged macrophytes may also influence the abundance of a number of phytoplankton filterers. Large mussels such as *Anodonta* and *Unio* may appear abundantly within the vegetation and Ogilvie & Mitchell (1995) have shown that uniods may yield a high grazing pressure on phytoplankton in shallow lakes. Within the macrophyte beds also small, filter-feeding crustaceans such as *Sida, Simocephalus* and *Eurycercus* are found, and calculations indicate that they may considerably suppress phytoplankton biomass within the macrophyte beds (*Stansfield et al. 1997*). Further studies are, however, needed to fully evaluate whether their effect reaches beyond the macrophyte-covered areas.

Effects on fish and zooplankton

Macrophytes may influence zooplankton both indirectly and directly. First, macrophytes may favour predatory fish such as perch and pike at the expense of planktivorous fish such as roach and bream. Pike are associated with vegetation (*Grimm & Backx 1990*), and perch have a competitive advantage over roach within the vegetation as they are more efficient predators in a structured environment and are better at exploiting plant-associated invertebrates (*Persson et al. 1988*). Conversely, roach is a better forager in the pelagial (*Persson 1991*). In lakes covered by submerged macrophytes, perch stand a better chance of growing large enough to become predatory. Higher abundance of predatory fish means lower abundance of roach and bream, reduced predation pressure on zooplankton and hence lower phytoplankton biomass.

Second, submerged macrophytes may act as a refuge for zooplankton. Timms & Moss (1984) concluded that large-sized zooplankton congregate within the vegetation during day, but migrate into the pelagic zone at night. They argued that zooplankton used the macrophytes as a daytime refuge against predation by visually hunting predators. Consequently, submerged macrophytes may indirectly influence water transparency as increased zooplankton survival will enhance the grazing pressure on phytoplankton both within the vegetation during the day and in the pelagic zone at night.

Diel investigations undertaken in a number of Danish, Northern American and New Zealand lakes confirm the hypothesis of Timms & Moss. Horizontal migration between macrophytes and the pelagial is often significant (10, 14, 20; *Lauridsen & Buenk 1996; Lauridsen et al. 1997*). The migration intensity seems to be greatest in lakes with high densities of plank-

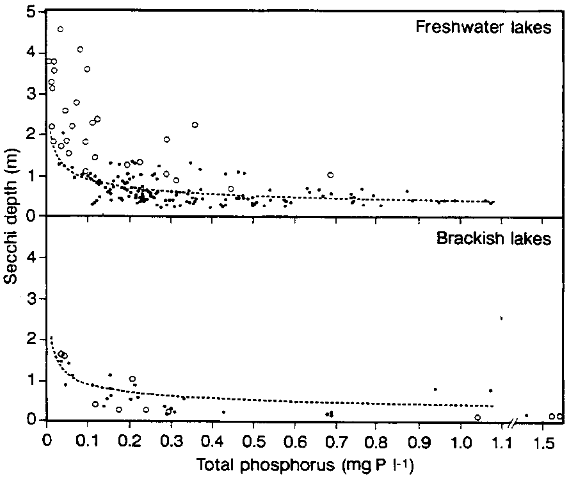

Fig. 16. Summer mean Secchi depth in relation to summer mean lake water total phosphorus for a number of shallow, Danish freshwater and brackish lakes. o: lakes with more than 30% submerged macrophyte coverage, •: lakes with little coverage (<30%) or an unknown submerged macrophyte coverage. Each point represents one lake and is a time-weighted average of all data collected between 1 May and 1 October. The broken line is an exponential curve developed by Kristensen et al. (1991) on data from freshwater lakes with low submerged macrophyte coverage. At a given phosphorus concentration, freshwater lakes with high submerged macrophyte coverage are more clear than lakes without macrophytes. The same does not apply to brackish lakes (from 6).

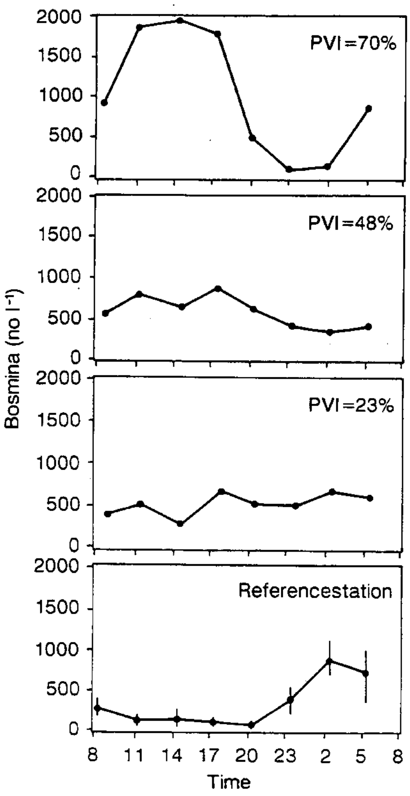

Fig. 17. Diel variation in the density of *Bosmina* spp. (mainly *B. longirostris*) in exclosures with various submerged macrophyte densities and at a reference station (without macrophytes) in Lake Stigsholm. Average density and diel amplitude (high during day and low during night) are highest at high macrophyte densities. At the reference station, in contrast, the highest density of *Bosmina* occurred at night (from 10).

tivorous fish (*Watt & Young 1994; Lauridsen et al. 1998*). The capacity of zooplankton to detect the predation risk may be related to their ability to react to chemical cues released by fish. It is interesting that zooplankton cluster in the vegetation even though several zooplankton species may be repelled by submerged macrophytes (*Hasler & Jones 1949; Pennak 1966*). In this case too, chemical cues seem to be involved (*Lauridsen & Lodge 1996*). If viewed separately, it would seem likely that zooplankton seek to avoid macrophyte beds in which the concentration of potential food items may be low and the densities of various predatory invertebrates high. Consequently, macrophyte-covered areas are hardly attractive habitats to pelagic zooplankton (13). In lakes with high fish densities, the cues from fish seem, however, to be more intense than those of submerged macrophytes, and zooplankton consequently move into the vegetation. At the population level, this would be an adaptive behaviour, if lower growth conditioned by the lower food concentrations within the vegetation is more than compensated for less predation than in the pelagic zone.

Experiments in Lake Stigsholm demonstrated that diel migration of large-sized zooplankton between macrophytes and the pelagial was particularly high from small macrophyte beds (20). This may be related to the tendency of zooplankton to aggregate near the edge of the macrophyte beds (*Lauridsen & Buenk 1996*). In addition, diel migration was observed to be highest from dense beds (10; Fig. 17). In the Lake Stigsholm experiments, there were only few fish in dense beds, which may explain why the refuge possibilities for zooplankton seemed better here than in more open areas (13).

The possibility of zooplankton finding refuge within macrophyte beds depends highly on the habitat choice of fish, because fish fry may also use the vegetation as a daytime refuge against predatory fish (*Savino & Stein 1982; Werner et al. 1983; Carpenter & Lodge 1986*). As mentioned above, fish often prefer the less dense areas (*Engels 1988; Phillips et al. 1996; Stansfield et al., 1997*), which may be related to reduced food-search efficiency at the high structural complexity represented by high macrophyte density (*Crowder & Cooper 1979; Savino & Stein 1982; Anderson 1984; Diehl 1988*). There are, however, exceptions to this rule (*Winfield 1986*). The consequences of the presence of fish for the zooplankton are not yet fully clarified and depend on whether the fish actually feed within the vegetation or not (*Perrow et al., unpubl. ms*). Young perch, for instance, forage at dusk and dawn when they have left the littoral zone (*Gliwicz & Jachner 1992*). Also, the abundance of alternative food sources and competition among the various age groups and species of fish may influence feeding behaviour (*Persson & Greenberg 1990; Persson 1993*) and the predation risk for the zooplankton.

If predatory fish are abundant in the vegetation, the situation becomes even more complex. On the one hand, the predation pressure on zooplankton may decline if the activity level of planktivorous fish decreases in the presence of predatory fish (*Bean & Winfield 1995; Jacobsen et al. 1997*) or if the fish turn to alternative food sources when the size of their foraging field diminishes (*Persson 1993*). On the other hand, the presence of predatory fish within the macrophytes may force the planktivorous fish into the most dense vegetation (*Savino & Stein 1982; Werner et al. 1983; Persson & Eklöv 1995*) and consequently further reduce the refuge possibilities for the zooplankton (*E. Jeppesen & M. Søndergaard, unpubl.*).

Experiments in Lake Stigsholm

We have worked intensively to clarify how submerged macrophytes influence fish-zooplankton interactions in lakes, particularly in Lake Stigsholm (10, 13, 14, 23). The cascading effects on phytoplankton and the microbial community were investigated (14, 23; *Jürgens & Jeppesen 1998; Søndergaard et al. 1998; Søndergaard & Moss 1998*). Firstly, we conducted experiments in 100 m^2 enclosures at varying densities

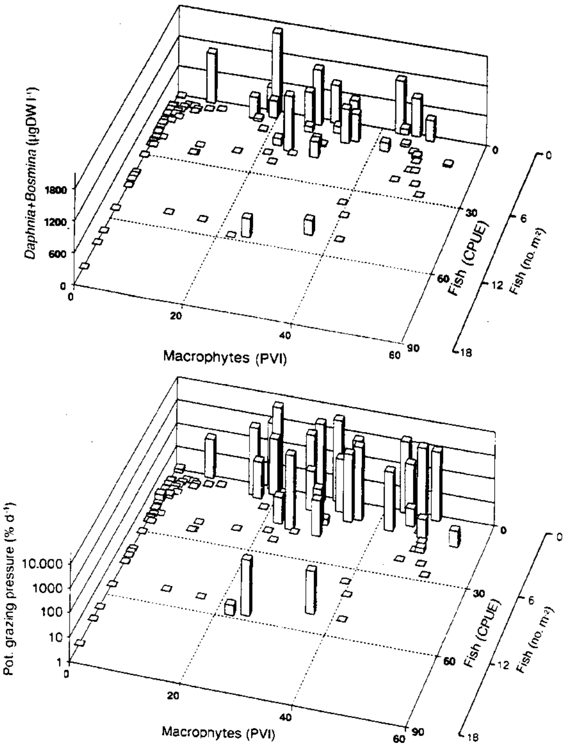

Fig. 18. Biomass of dominant cladocerans (*Bosmina* + *Daphnia*, upper panel) in the pelagic and their potential grazing pressure on phytoplankton *v* the number of 0^+ and 1^+ roach (*Rutilus rutilus*) and three-spined stickleback (*Gasterosteus aculeatus*) and plant density (% of water volume with plants, PVI) in enclosures in Lake Stigsholm. At low fish densities the abundance of *Daphnia* + *Bosmina* and phytoplankton grazing pressure remain high provided that PVI >15-20%. At fish densities of 2-4 m^{-2} there is a steep decline in both density and grazing pressure (from 23).

of plants and abundances of fish (0^+ and 1^+stickleback (*Gasterosteus aculeatus*) and roach) (23). We found high zooplankton densities and high zooplankton:-phytoplankton ratios when the plant volume infested (PVI) was above 10-15% and fish density lower than 2 individuals m^{-2} (Fig. 18). When 2-4 fish m^{-2} were added, a shift to small-sized cladocerans and cyclopoid copepods took place, and the zooplankton:-phytoplankton ratio decreased markedly. When the density was above approximately 4 fish m^{-2} no essential differences between the effect at low and high macrophyte densities were found. Cyclopoid copepods and rotifers dominated, and the zooplankton:phytoplankton ratio was low. These experiments suggest relatively abrupt changes in refuge effect when the specific thresholds in macrophyte and fish densities are reached. Reduced effect of macrophyte refuge with increasing fish density has also been observed by Beklioglu & Moss (1996). Persson & Eklöv (1995) and Kairesalo et al. (1997) found marked effects on zooplankton at 0^+ perch densities of 2-3 individuals m^{-2} in relatively dense vegetation (13).

The significant changes in the abundance and composition of zooplankton observed with changes in the density of submerged macrophytes and planktivorous fish in the Lake Stigsholm experiments had significant cascading effects on phytoplankton (Fig. 19). In the absence of fish when zooplankton grazing was high, phytoplankton biomass was low and was dominated by *Cryptomonas* and *Chlamydomonas*, despite these two genera being particularly palatable to zooplankton (23, *Søndergaard & Moss 1998*). These phytoplankton genera probably dominated because their high growth rates allowed them to partly escape grazing (23). At high fish density and low grazing pressure on phytoplankton, the biomass was high and cyanobacteria and dinoflagellates dominated.

Cascading effects on phytoplankton, ciliates, flagellates and bacteria

To obtain more detailed information on the biological interactions within macrophytes we conducted a number of experiments in Lake Stigsholm using 20 m^2 enclosures with varying densities of submerged macrophytes. We made direct measurements of zooplankton grazing and also analysed for effects on protozoans and free-living bacteria. In dense vegetation (plant volume infested, PVI=50%) large-sized zooplankton, such as *Daphnia galeata/hyalina* and *Ceriodaphnia* sp., and cyclopoid copepods, including several large-sized species such as *Macrocyclops albidus* and *Megacyclops viridis*, dominated whereas small species (rotifers, small cyclopoid copepods) dominated at low plant densities (PVI=24%) and in macrophyte-free enclosures (Fig. 20). Total biomass of zooplankton was 88-fold higher in enclosures with high PVI than in macrophyte-free enclosures (Fig. 21). This difference was also reflected in zooplankton grazing. The clearance rates of both phytoplankton and bacteria by large-sized zooplankton (>140 µm) were exceedingly high at high PVI (200-300% of the water volume d^{-1}) and only 2-5% d^{-1} at low PVI and in macrophyte-free enclosures (Fig. 20). Accordingly, chlorophyll *a* was substantially lower at high PVI. In contrast, the abundance of ciliates, heterotrophic flagellates and bacterioplankton were 4, 74, 4 and 3 times higher in macrophyte-free enclosures, respectively (Figs 20 and 21).

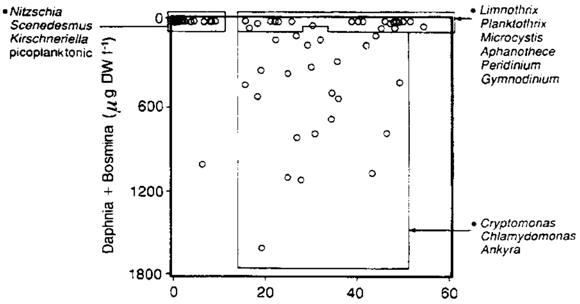

Fig. 19. General scheme of the changes in phytoplankton community along with changes in macrophyte density and biomass of planktonic cladocerans (*Daphnia* and *Bosmina*) in experiments in Lake Stigsholm (see Fig. 18) (from 23).

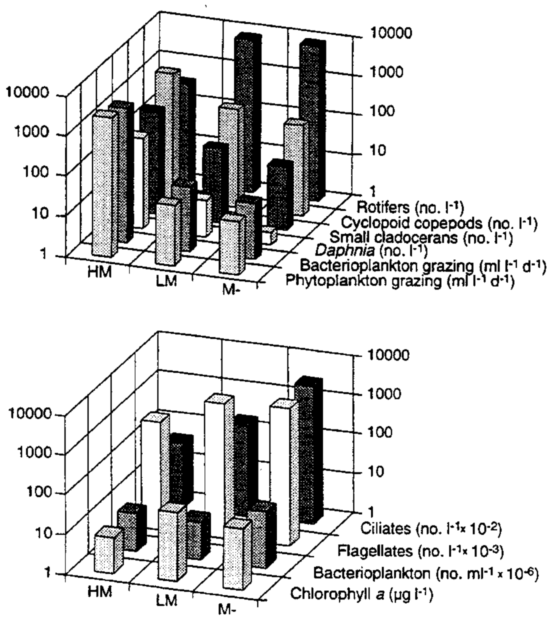

Fig. 20. Abundance of various zooplankton taxons, protozoans and bacterioplankton, chlorophyll *a* and the zooplankton filtration rate on phytoplankton and bacterioplankton in Lake Stigsholm with contrasting densities of submerged macrophytes (HM: plant volume infested (PVI) = 50%, LM: PVI = 24%, M-: no submerged macrophytes). Note the logarithmic scale. We found significant differences between trophic structure and dynamics in enclosures with low and high PVI, but only minor differences between those with low PVI and macrophyte-free enclosures (from 13).

The key role of zooplankton in the observed structural differences was evidenced by concurrent experiments involving removal of large-sized zooplankton from half of a set of samples from high PVI and macrophyte-free enclosures (*Jürgens & Jeppesen 1998*). In the high PVI enclosures, zooplankton removal resulted in a 3-9-fold increase in the abundance of free-living bacterioplankton and heterotrophic nanoflagellates during the first 24 h as well as a pronounced increase in chlorophyll *a*, ciliate and picoplankton abundance during the subsequent four days. Only negligible changes were observed in corresponding experiments using water from the macrophyte-free enclosures (*Jürgens & Jeppesen 1998*).

The results from eutrophic Lake Stigsholm have shown that zooplankton use submerged macrophytes as a refuge if fish density is low. Enhanced survival of zooplankton may lead to both clear water within the vegetation and increased herbivory on phytoplankton in the pelagial. The experiments also demonstrated, however, that the refuge effect of zooplankton declines abruptly when the fish density within the vegetation exceeds a certain threshold (2-4 fish m^{-2} in our experiments), and the phytoplankton biomass within the vegetation then approach the level found in the pelagial. The latter suggests that plant-associated filtrators (such as *Sida*) are also influenced by fish, which is consistent with the findings of Whiteside (1988).

A hypothesis for the refuge effect

As described above, the interactions between submerged macrophytes, predatory and planktivorous fish and the cascading effects on zooplankton are highly complex. We have discussed how the use of submerged macrophytes as a refuge for zooplankton during sum-

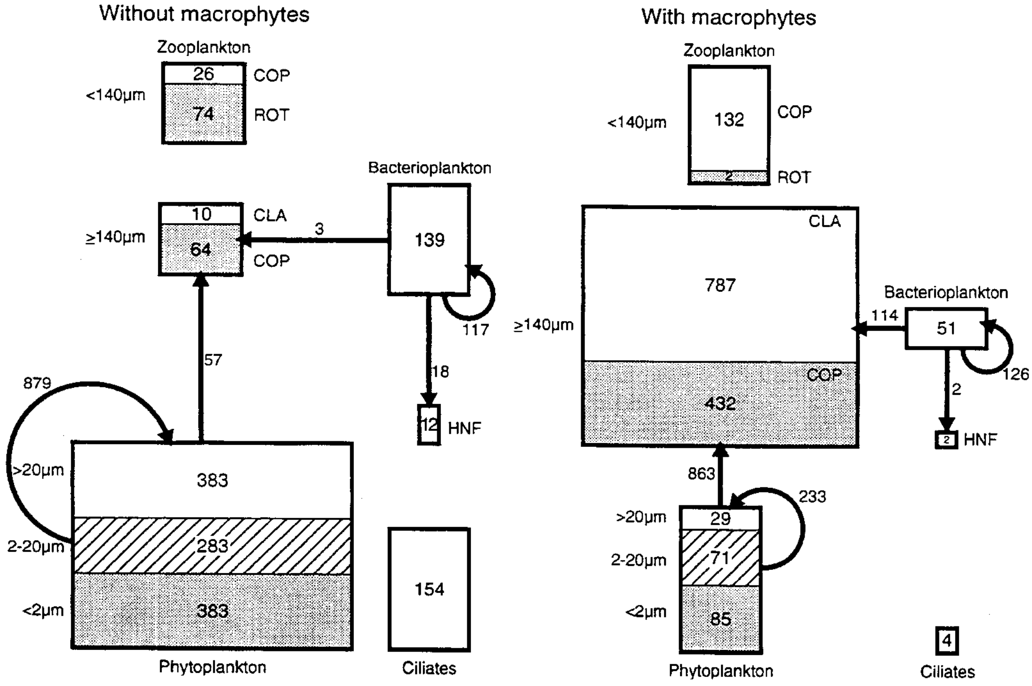

Fig. 21 Carbon (µg l^{-1} or µg l^{-1} d^{-1}) weightbudget in Lake Stigsholm enclosures with, respectively, no and high density of submerged macrophytes. COP = copepodes, ROT = rotifers, CLA = cladocerans, HNF = heterotrophic nanoflagellates. See also Fig. 20 (from 14).

mer will change along a nutrient gradient (13; Fig. 22). We suggest that the refuge effect in summer is:

- relatively low in the most eutrophic lakes with few or no submerged macrophytes, where the refuge is restricted to floating-leaved plants and reeds. Stem density is low compared with areas covered by submerged macrophytes, and the refuge effect is thus low.
- relatively high in eutrophic lakes with submerged macrophytes, as the vegetation is often dense and tall. The fish stock is dominated by planktivorous species, which in the absence of predatory fish do not need to seek refuge within the vegetation.
- relatively low in mesotrophic lakes, because macrophyte density is often lower, and predatory fish are more abundant. Planktivorous fish will consequently seek refuge within the macrophyte beds, thereby increasing the predation pressure on the refuging zooplankton.
- relatively low in oligotrophic lakes due to low plant height.

Predation on epiphyte grazers

Apart from preying on zooplankton, fish may also impose a significant predation pressure on plant-associated invertebrates, including snails (see reviews of *Jones et al. 1998; Brönmark & Vermaat 1998*). The result is reduced grazing pressure on the epiphyte cover on plant surfaces, which may, in turn, enhance epiphyte growth (*Brönmark & Vermaat 1998*) and thereby cause deterioration in the light climate for submerged macrophytes. It has been suggested that such an increase in epiphyte coverage, mediated by predation on epiphyte grazers, may play a key role in the reduced abundance of submerged macrophytes at increased nutrient supply (*Brönmark & Weisner 1992*).

Conclusions and perspectives concerning lake restoration

In conclusion, it appears that submerged macrophytes – via a number of direct and indirect effects on nutrient levels and phytoplankton – may counteract the effect of increased nutrient supply. The results shown in Fig. 2 and Fig. 16 indicate that in most lakes there is a threshold of approximately 0.1-0.15 mg P l^{-1}, above which submerged macrophytes may no longer contribute to maintaining the clearwater state. This shift is probably caused by a combination of a high nutrient level and a high density of planktivorous and snail-eating fish. The lake will therefore shift to a turbid state with few or no submerged macrophytes.

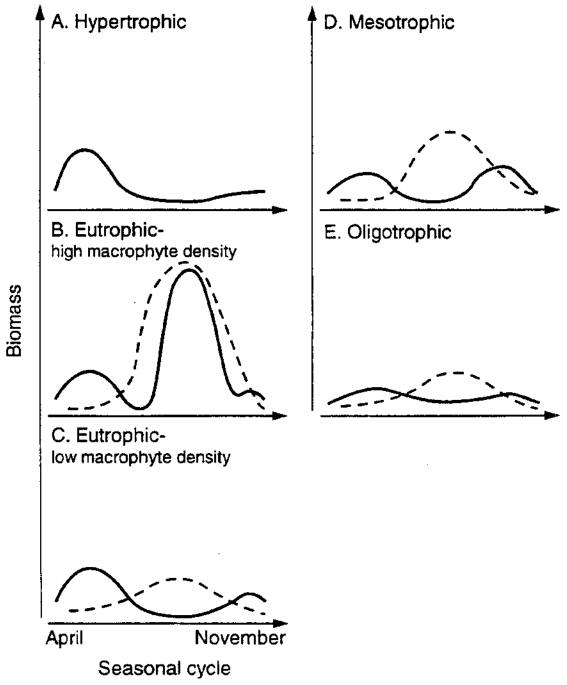

Fig. 22. Conceptual model showing how the biomass of plant-associated microcrustaceans and zooplankton (solid line) in the littoral zone is expected to change with varying nutrient levels. The broken line represents the average biomass of submerged macrophytes in plant-covered areas (from 13).

Despite the relatively poor knowledge of interactions between the littoral and the pelagic zone, the results obtained for eutrophic lakes can today be applied in lake management. Consequently, it has been suggested to use macrophyte beds protected against bird grazing as a lake restoration tool (4; *Moss 1990* – see section 4.2). Our own results (10, 13, 14, 20, 23) suggest that in eutrophic lakes, the most significant refuge effect and the highest migration from macrophyte beds to open water may be obtained if the macrophyte beds are dense and the periphery of the plant beds is large (many small beds or oblong strips). Using this knowledge as a starting point a number of investigations are presently being undertaken by NERI and the Danish counties.

4.2 Resilience in the response to a nutrient loading reduction

As described in the introduction to this section, resilience in the response to reduced nutrient loading has frequently been observed (4, 16; *Marsden 1989; Sas, 1989; Cullen & Forsberg 1988; Van der Molen & Boers 1994; Welch & Cooke 1995*). Resilience may be determined by both chemical and biological factors and interactions among these. Chemical resilience is typically related to phosphorus (Fig. 23). Lake water phosphorus concentrations may remain high for a long time due to phosphorus release from the sediment pool accumulated during the time when loading was high (e.g. *Sas 1989; Søndergaard et al. 1993*). The duration of the resilience depends especially on the magnitude and duration of the former loading, hydraulic retention time, iron input (4; *Søndergaard et al. 1993, 1996*) and trophic structure (4).

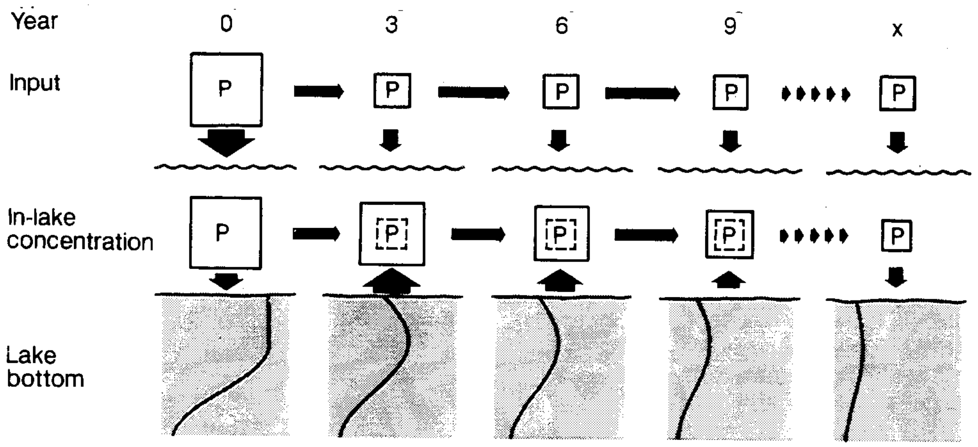

Fig. 23. Scheme illustrating chemical resilience following an external nutrient loading reduction. The lake remains turbid for a prolonged period due to release of phosphate from the sediment pool which was accumulated when phosphorus loading was high. Release may take place as far down as 20 cm depth (from *Jeppesen et al. 1991*).

The biological community may also show resilience after a nutrient loading reduction, which may primarily be ascribed to fish (*Shapiro & Wright 1978; Benndorf 1990)* and occasionally to bird grazing on submerged macrophytes (*Lauridsen et al. 1993; Søndergaard et al 1996, 1997; Van Donk et al. 1994*) (Fig. 24). It seems logical therefore to conclude that an intervention in the trophic structure may accelerate the improvement of lakes showing biological resilience (Fig. 25). Shapiro et al. (1975) were those who first suggested fish manipulation as a restoration tool in eutrophic lakes. Later, fish manipulation has been used to reduce the transitional period after a loading reduction (2, 4, 17; *Benndorf 1987, 1990; Moss 1990; Hosper & Jagtman 1990*). The causes of fish-induced resilience are various. Following a loading reduction, eutrophic lakes will initially be dominated by planktivorous and benthivorous fish. By predating zooplankton, and by stirring up sediment these fish may maintain a high algal biomass and high concentration of suspended solids and thereby keep the lake in a turbid state. Low turbidity prevents an increase in the abundance of visually hunting predatory fish such as perch and also prevents colonization by submerged macrophytes. The purpose of fish manipulation is to establish clearwater conditions and improve the colonization potential of submerged macrophytes and hence the conditions for predatory fish. This may, in turn, lead to a shift to the clearwater state.

If the light climate improves, rapid colonization of submerged macrophytes may occur (21), although several examples of a delayed response have been observed. This resilience may be caused by grazing by coot and swans of the sparse shoots appearing in the early phase of colonization (21; *Lauridsen et al. 1993; Søndergaard et al. 1996*). Enclosures protecting the macrophyte shoots against birds grazing have, therefore, been suggested as a restoration tool (*Moss 1990*) and in several instances they have led to a marked increase in plant biomass (*Lauridsen et al. 1993; Søndergaard et al. 1996; Lauridsen et al. unpubl.*). Whether bird grazing may delay colonization of submerged macrophytes is still debated however (*Mitchell & Perrow 1998*). Also a reduced seed bank following many years without submerged macrophytes may presumably cause a delay in the re-establishment of submerged macrophytes even though light conditions have improved.

In the following sections I will provide examples of resilience and the effects of manipulation using data from long-term, intensive studies on Lake Søbygård

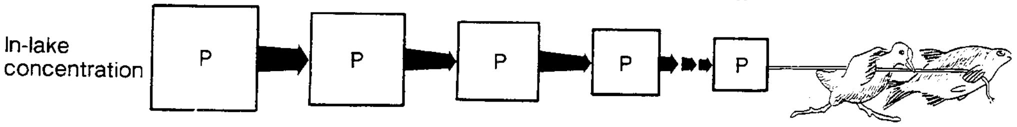

Fig. 24. Scheme illustrating biological resilience. Planktivorous and benthivorous fish (roach and bream) may maintain the turbid state for years by stirring up sediment and excreting sediment-derived nutrients. Moreover, they ingest zooplankton, resulting in low grazer control of phytoplankton. This leads to high turbidity and prevents re-establishment of submerged macrophytes and carnivorous fish. Plant-eating birds may also delay the process by grazing the tender shoots of submerged macrophytes in the re-establishment phase (from *Jeppesen et al. 1991*).

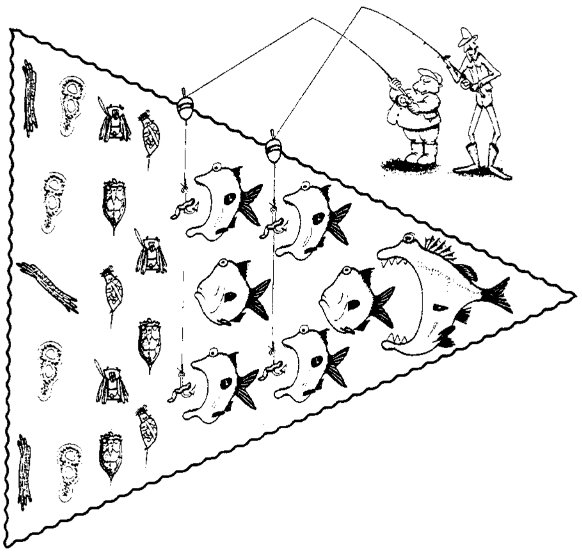

Fig. 25. Fish stock interventions (biomanipulation) may speed up lake environmental recovery. Biomanipulation is for thin and thick as well as high and low (from *Jeppesen et al. 1989b*).

and Lake Væng. The examples presented will be supplemented with a cross-analysis and evaluation of a number of other biomanipulation studies.

4.3 Lake Søbygård – an example of chemically induced resilience and the role of fish

Lake Søbygård is an example of chemical resilience. The lake is highly eutrophic – primarily as a result of heavy sewage loading over several decades. Oxygen depletion and fishkills occurred frequently in the 1970s. To improve the environmental state, biological treatment was implemented at the Hammel sewage treatment plant in 1976 and phosphorus stripping was introduced in 1982. Nitrogen supply was reduced in 1987 after the closing of a major slaughterhouse. Despite these changes, the lake is still hypertrophic, which may be primarily ascribed to high phosphorus release from the sediment (*Søndergaard et al. 1993*). The phosphorus release fluctuated significantly from 1983-1994 (Fig. 26), which, in particular, can be attributed to variations in trophic structure (16). During the first years following the reduction in external phosphorus loading, phosphorus release was derived mainly from the upper sediment layers, whereas today it is derived from a depth of 20-30 cm (*Søndergaard et al. 1993; Søndergaard et al., unpubl.*). Despite a retention time of only 15-25 days, net retention of phosphorus has been negative during the 13 years following the marked reduction in phosphorus loading. Another decade can be expected to pass before the lake will reach a new equilibrium adapted to the present external loading (16, *Søndergaard et al. 1993; Jensen et al. 1994b*).

A similar resilience has not been found for nitrogen (Fig. 26). Mass balances of nitrogen for Lake Søbygård have shown no changes in net retention since 1987 when the nitrogen input was reduced by approximately 30% (15, 18). This difference between nitrogen and phosphorus can be ascribed to the fact that nitrate may be lost by denitrification.

Despite the relatively modest changes at the nutrient level, marked changes have occurred in the concentration of chlorophyll *a* and hence Secchi depth, which can primarily be attributed to changes in the fish predation pressure. Frequent fish kills in the 1970s may explain the high summer Secchi depth (*Århus Amtskommune 1979*). In the absence of fish, the densities of large-sized *Daphnia* species (*D. magna*, *D. pulex*) were so high that they managed to keep chlorophyll *a* low during the summer (*Holm & Tuxen-Pedersen 1975*). After the establishment of biological wastewater treatment, an increase was recorded in the abundance of fish (especially roach and rudd, *Scardinius erythrophtalmus*), which resulted in increased predation pressure on zooplankton and hence a marked increase in phytoplankton biomass. Chlorophyll *a* therefore increased from a summer mean of 50 µg l^{-1} in 1978 to 840 µg l^{-1} in 1984 (Fig. 27). The increase continued in the years following the reduction in external phosphorus loading. After 1985, chlorophyll *a* decreased to a minimum in 1988. Thereafter it fluctuated widely, until an increase was observed in 1994 and 1995 (16). Again, the interannual variations in planktivorous fish abundance and in zooplankton predation pressure seem to be the main reasons for the fluctuations (8, 16).

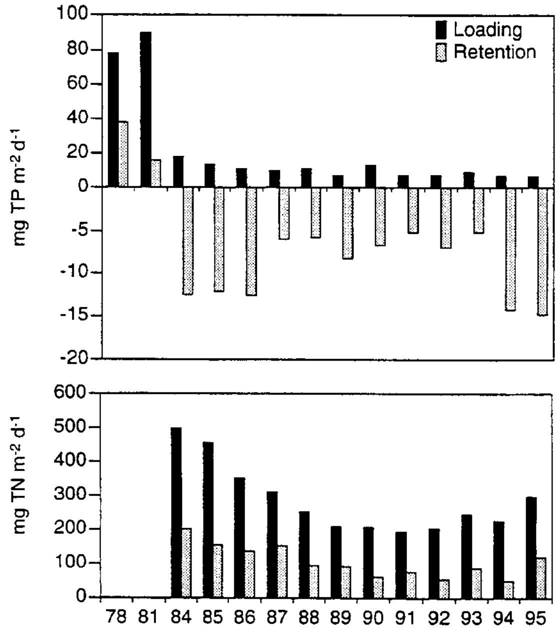

Fig. 26. Annual loading and net retention of total phosphorus and total nitrogen in Lake Søbygård 1978-1995. Phosphorus loading was markedly reduced in 1982 when phosphorus stripping was established at the Hammel wastewater treatment plant. Sewage derived nitrogen loading was reduced when the Hammel slaughterhouse was closed in the summer of 1987. The figure among other things shows that the lake – 13 years after the initiation of phosphorus stripping – still releases more phosphorus than it receives (from 16).

Effects of high pH

High pH also affected the zooplankton community. Analyses of seasonal zooplankton variations from 1984-87 suggested that *Daphnia longispina* was negatively influenced by pH>10.2 (3). Subsequent enclosure experiments in the lake, with pH maintained at three different levels (pH 9, 10 and 10.6), showed that the abundance of *D. longispina*, *B. longirostris* and *Chydorus sphaericus* was significantly negatively related to pH (*Hansen et al. 1991*). In support, Vijverberg et al. (1996) found reduced survival of juvenile and adult stages of *D. galeata* at pH>10.5 and of eggs and newly hatched individuals at pH>10. In the Lake Søbygård experiments *D. magna* was not influenced by pH, however (*Hansen et al. 1991*). This species only occured at low fish densities at which pH does not reach critically high values due to efficient zooplankton grazing. It is therefore likely that the particularly low densities of *D. longispina* and *B. longirostris* in 1984 and 1985 can be ascribed to high pH, as mean summer pH was 10.2-10.3 and reached a maximum value of 11 (16). High pH, however, also has a negative impact on fish recruitment and fry survival (*Timmermann 1987; Mortensen et al., in prep.*). Reduced fry densities mean lower predation pressure on zooplankton and hence lower phytoplankton biomass. As a result of reduced phytoplankton biomass, pH decreases, improving the recruitment potential of fish, which results in reduced zooplankton biomass and consequently higher phytoplankton biomass and higher pH.

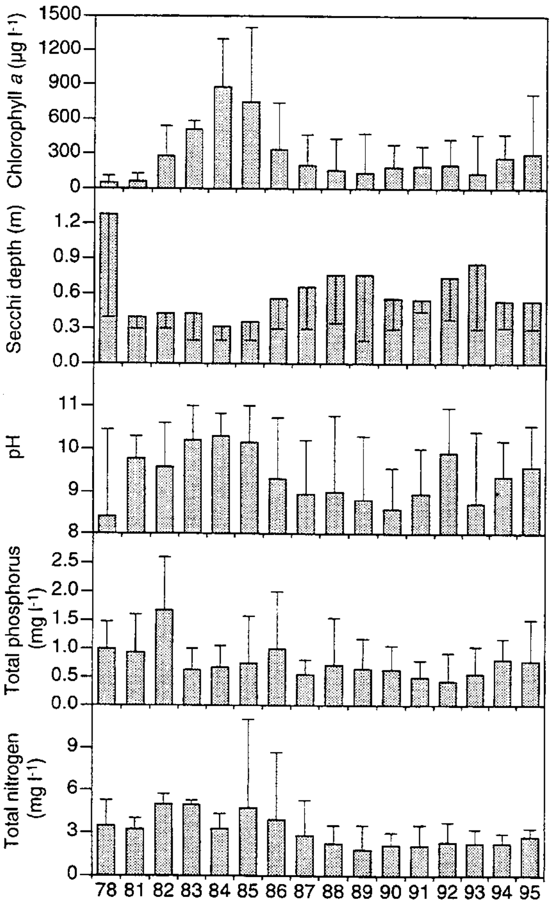

Fig. 27. Summer mean of chlorophyll *a*, Secchi depth, pH, total phosphorus and total nitrogen in Lake Søbygård 1978-1995. Maximum values are also recorded. Chlorophyll *a* rose significantly in the years immediately after the phosphorus loading reduction in 1982, and pH reached extreme values. Since then chlorophyll *a* decreased – primarily due to an increased zooplankton grazing phytoplankton (from 16).

Zooplankton grazing and its effects

The significant annual variations in zooplankton biomass and relative contribution of different taxa had a marked impact on zooplankton grazing on phytoplankton and bacterioplankton (Figs 28 and 29). From *in situ* measurements of zooplankton filtration rates at various compositions of zooplankton, regression relationships were established allowing calculation of zooplankton grazing on phytoplankton and bacterioplankton from biomass data of the different taxa (8). According to these calculations annual zooplankton grazing on phytoplankton and bacterioplankton was <5% of production in 1984-85 when zooplankton biomass was low and dominated by cyclopoid copepods, small cladocerans and rotifers. If *Bosmina* and rotifers dominated (1990-91), bacterioplankton grazing was also low in years with high zooplankton biomass. Conversely, grazing was high on both phytoplankton and bacterioplankton in years with dominance and high densities of *Daphnia longispina*. The highest calculated grazing rates were observed in 1988, when they comprised 39% and 75% of phytoplankton and bacterioplankton production, respectively (Figs 28 and 29). For both phytoplankton and bacterioplankton grazing, as a percentage of both biomass and production, was negatively related to CPUE of planktivorous fish caught in gill nets in open water and by electrofishing in the littoral zone. The most pronounced changes were recorded for grazing on bacterioplankton (8), and this lends support to the hypothesis that fish play a major regulatory role in lakes.

With changes in zooplankton grazing pressure both the size structure, biomass and absolute and volume-specific production of phytoplankton changed and so did that part of phytoplankton production which was channeled through bacterioplankton (8, 16). When the zooplankton were dominated by small-sized species and grazing pressure was low, the phytoplankton were also dominated by small species such as *Chlorella* and *Scenedesmus*, and biomass was high with maximum values of 1400-1500 µg chlorophyll *a* l^{-1} (16). The finding that small-sized species dominated at high phytoplankton biomass is in direct contrast to the hypotheses advanced by Agustí & Kalff (1989), Duartes et al. (1990) and Agustí (1991). They suggested that the mean size of phytoplankton generally increases with increasing phytoplankton biomass. We agree that small species have a competitive advantage at low nutrient levels, where a high chlorophyll *a* content and large surface per volume

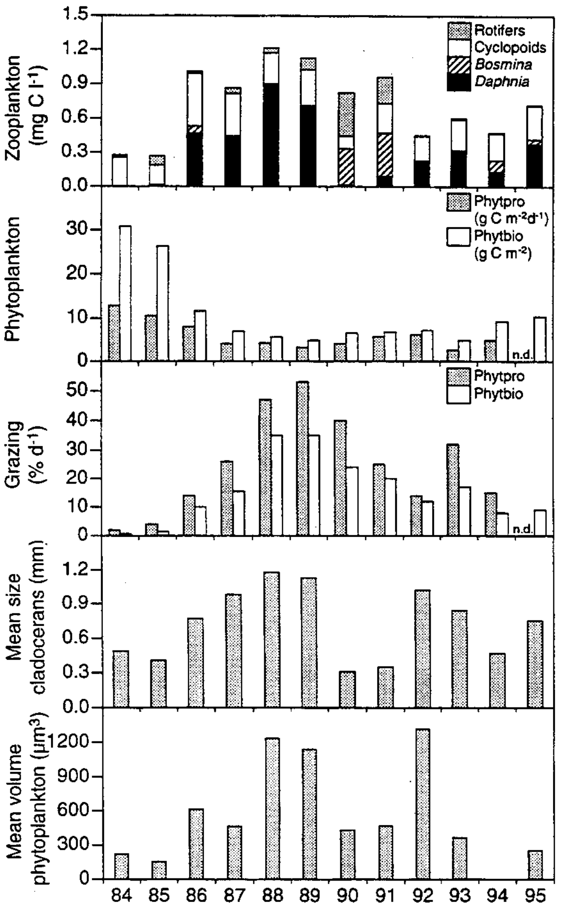

Fig. 28. Summer mean biomass of various zooplankton taxons, phytoplankton production and biomass, zooplankton grazing on phytoplankton in % of phytoplankton production and biomass and mean size of cladocerans and mean volume of phytoplankton in Lake Søbygård 1984-1995. Grazing was particularly high in 1988 and 1989, when zooplankton biomass was high and dominated by *Daphnia*. Average phytoplankton volume reflects changes in zooplankton size rather than in phytoplankton grazing pressure (from 16).

unit ensure maximum nutrient uptake and specific production (*Hein et al. 1995; Enriquez et al. 1996*). We believe, however, that small phytoplankton species are also favoured at very high nutrient levels as the light climate is so poor that a maximization of the light intake becomes an important regulating factor, implying that phytoplankton with a high specific chlorophyll *a* content (= small algae, *Enriquez et al. 1996*) should have a competitive advantage in such environments. That small species are dominant at extreme phytoplankton biomass is confirmed by data from other lakes dominated by green algae having a high biomass and by data from eutrophic brackish lakes that are often dominated by *Aphanothece* spp. (*E. Jeppesen & J.P. Jensen, unpubl. data*).

With increased grazing pressure and especially increasing size of zooplankton, phytoplankton cell volume increased in Lake Søbygård (Fig. 28). During summer phytoplankton were dominated by large forms such as *Pediastrum* spp. or grazing-resistant forms such as *Oocystis* spp. (16). Concurrently, there was a decrease in phytoplankton biomass and production. The decrease in production could partly be ascribed to a reduction in phytoplankton specific production conditioned by the increased cell size and hence the reduced chlorophyll *a* content per cell (16). This corresponds with "the trophic cascade hypothesis" suggested by Carpenter et al. (1985). According to this hypothesis, a reduction in the fish predation pressure on zooplankton will lead to an increase in zooplankton size. The result will be an increase in phytoplankton size and hence a decline in phytoplankton production, as the specific growth rate decreases with increasing phytoplankton size. They have, however, found little support for this part of the hypothesis (*Carpenter & Kitchell 1993*), but it seems to apply to green algal-dominated hypertrophic lakes.

Factors regulating pelagic bacterioplankton

The ratio of bacterioplankton to annual phytoplankton production was highest (5-6%) in years when the filter-feeding zooplankton were dominated by *Bosmina* and rotifers, and lower (2-4%) in years when *Daphnia* dominated (Fig. 29). Consequently, the contribution of bacterioplankton to the turnover of organic matter showed a slight increase with increasing predation pressure by fish. Generally, however, the

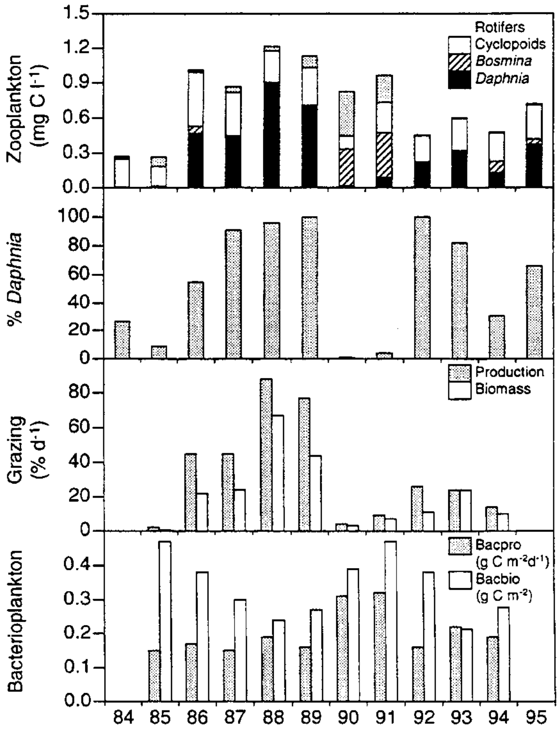

Fig. 29. Summer mean biomass of various zooplankton taxons, the contribution of *Daphnia* as a percentage of total total cladoceran biomass, zooplankton grazing on bacterioplankton as a percentage of bacterioplankton production and biomass, and bacterioplankton production and biomass in Lake Søbygård 1984-1995. Grazing pressure on bacterioplankton was particularly high when *Daphnia* were abundant and dominated the zooplankton (from 16).

bacterioplankton:phytoplankton production ratio was low compared with other investigations from less eutrophic lakes. For example, Cole et al. (1988) found a mean of 17% in their cross-analyses of data from a number of freshwater and marine environments. The low ratio recorded in our investigation may be ascribed to the extremely high sedimentation rate of phytoplankton due to low lake depth as well as the dominance of phytoplankton with high specific sedimentation rates (5, 8). The turnover, therefore, takes place in the sediment rather than in the pelagial (8).

During the investigation the abundance and production of bacterioplankton were measured 358 days in Lake Søbygård (5, 9). As significant changes in trophic structure have occurred, the data set is particularly suitable for empirical analyses. Cross-analyses of data from a large number of lakes have earlier shown that bacterioplankton production is positively related to chlorophyll *a* (e.g. *White et al. 1991*) and phytoplankton production (e.g. *Cole et al. 1988*) and that it increased with temperature (*White et al. 1991; Ducklow & Shiah 1993*). Multiple regression analyses of data from Lake Søbygård revealed that besides chlorophyll *a*/primary production and temperature, the abundance of bacterioplankton and the combined biomass of *Bosmina*, rotifers and cyclopoid copepods contributed significantly and positively to bacterioplankton production. Bacterioplankton abundance was positively related to the same variables, with the exception of temperature. *Daphnia* biomass contributed negatively to the relationship. One has to be cautious when inferring causal mechanisms from regression models, but the high measurement frequency and the fact that only few zooplankton species dominated or exhibited marked fluctuations throughout the period make it more probable that the regression models provide an accurate picture of the impact of zooplankton. The results suggest that the presence of cyclopoid copepods, *Bosmina* and rotifers stimulates bacterioplankton production, whereas *Daphnia* via a negative impact on bacterioplankton abundance, reduce production. These results are also consistent with the grazing experiments showing that only *Daphnia* grazing on bacterioplankton was significant (8). Several past investigations have also shown that *Daphnia* may have a negative influence on bacterioplankton (*Riemann 1985; Christoffersen et al. 1993; Jürgens 1994*), while studies of oligotrophic systems often show a negligible effect (*Pace & Funke 1991; Brett et al. 1994*). The positive effect of *Bosmina* and cyclopoid copepods may be attributed to low grazing on bacterioplankton combined with zooplankton secretion of substrate for bacterioplankton via phytoplankton grazing (5, 9).

Apart from the variables above, pH>10.2 contributed negatively to bacterioplankton production and specific growth rates in the multiple regression on data from Lake Søbygård, but not to total bacterioplankton abundance (9). The negative effect of high pH was supported by laboratory experiments (9). Our results therefore suggest that part of the residual variation in the previously described empirical relations may be ascribed to zooplankton and, if conditions are extreme, to high pH (9).

A long way to go

The Lake Søbygård investigations provide an illustrative example of resilience following nutrient loading reduction, and new information on biological interactions at extreme nutrient levels. They have also provided a more general understanding of overall trophic dynamics in shallow lakes. There is now some indication that the environmental state of Lake Søbygård is improving (16). Perch CPUE has increased, although only moderately, and diatoms and cryptophytes have increased at the expense of green algae. Yet, another decade can be expected to pass before the lake reaches equilibrium with the present external loading (17, *Søndergaard et al. 1993*).

4.4 Lake Væng – an example of biological resilience and the effect of fish manipulation

Lake Væng is shallow (mean depth 1.2 m) and has a surface area of 16 ha. Until 1981 the lake was heavily loaded with domestic sewage. During the subsequent five years following loading reduction, however, no changes were recorded in trophic structure and environmental state. Secchi depth was still low (Fig. 30A), the phytoplankton were dominated by cyanobacteria and the fish community was characterized by high abundance of roach and bream (Fig. 30B). Mass balance calculations showed future phosphorus equilibrium of 0.05 mg TP l^{-1}, at which level – according to the data shown in Fig. 2 – the lake would be clear with high abundance of submerged macrophytes and predatory fish. We postulated that

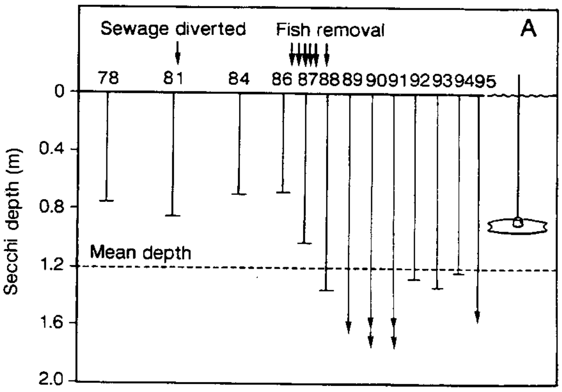

Fig. 30A. Trend in summer mean Secchi depth in Lake Væng following the cessation of sewage discharge in 1981 and fish manipulation in 1986-88 involving removal of 50% of the planktivorous fish biomass. Arrows indicate that Secchi depth reached the bottom at some of the sampling dates; the mean values were therefore higher. Secchi depth increased markedly following fish manipulation (from 17).

fish manipulation could accelerate the transition towards the clearwater state. In co-operation with Vejle County we removed approximately 50% of the roach and bream biomass between autumn 1986 and spring 1988.

The intervention had a significant effect on pelagic trophic structure and water quality (1, 4, 18; Fig. 30B; *Søndergaard et al. 1990; Jeppesen et al. 1997*). *Daphnia* increased 10-fold from 1986 to 1987 and their average size increased markedly. As a result, phytoplankton biomass and production decreased considerably, and transparency to the bottom prevailed throughout the summer. The predatory fish proportion of total fish biomass (catch per net using multiple mesh-sized gill nets) increased and has remained high since, and predatory control of planktivorous fish seems to have increased. Moreover, the nitrogen level – and during most years also the phosphorus level – decreased implying that the fish manipulation has had a cascading effect down to the nutrient level.

Initially, the submerged macrophytes responded slowly to the improved light climate (1, 4; *Søndergaard et al. 1990*) and a number of experiments with shoots of curly pondweed (*Potamogeton crispus*) placed at different locations around the lake suggested that bird grazing might also be of importance for the observed resilience (*Lauridsen et al. 1993*). This observation was also supported by the fact that the subsequent colonization began in the areas where bird grazing was lowest (deep water and exposed shoreline) (*Lauridsen et al. 1994*). The impact of bird grazing as a potentially controlling factor for plant coverage and abundance in lakes with low plant biomass has since been confirmed by experiments in Lake Stigsholm (*Søndergaard et al. 1996*) and Lake Engelsholm (Vejle County, unpubl.; Lauridsen et al. unpubl.).

In 1988, large areas of Lake Væng were colonized by *Elodea canadensis* and since then coverage has fluctuated widely (4; *Søndergaard et al. 1997*). In 1992, plants almost disappeared from the lake. Despite this drastic reduction, only a short-term shift to the turbid state took place. The temporary nature of this change may be ascribed to the fact that the predatory:prey fish ratio remained high, allowing the zooplankton to maintain a high grazing pressure on phytoplankton.

With the shift from the turbid state with few submerged macrophytes to the clearwater state a marked increase in the number of waterfowl, especially plant-eating species such as coot and mute swan, occurred. Since then the numbers of coot and mute swan have fluctuated widely from year to year following the changes in plant coverage (*Søndergaard et al. 1997*).

Lake Væng illustrates, therefore, that a single intervention (here removal of planktivorous fish) following an external nutrient loading reduction may lead to a marked and long-lasting shift from a turbid to a clearwater state. Whether the lake remains in the clearwater state or whether it will alternate between the two alternative equilibrium states, as is the case

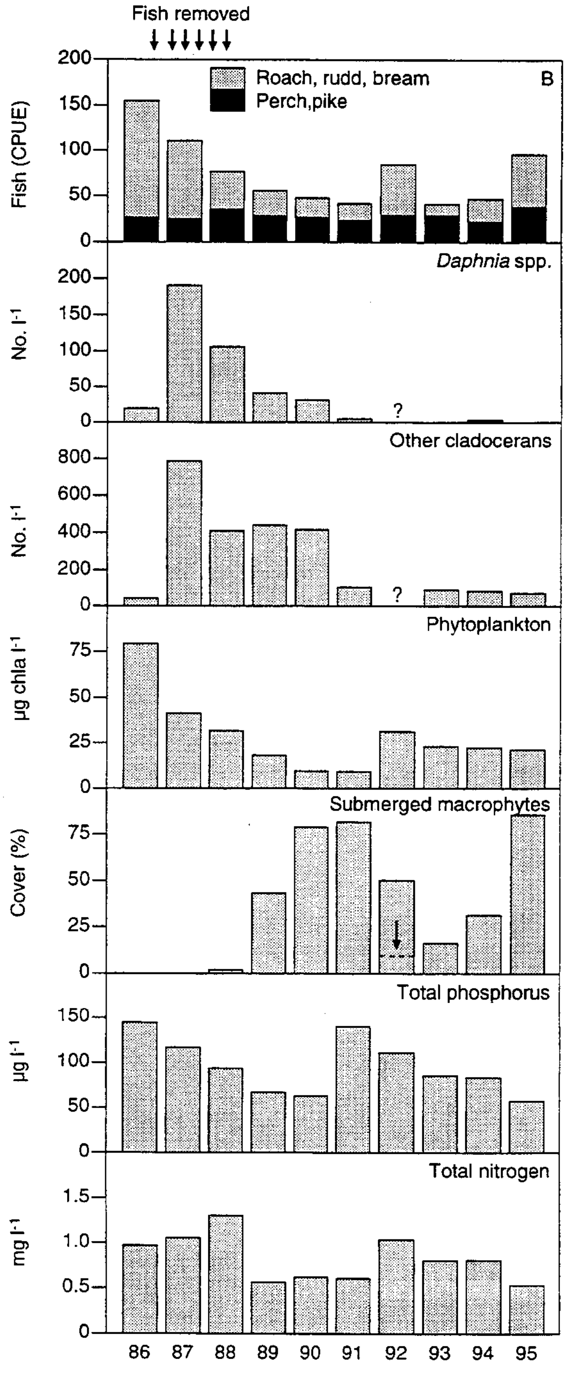

Fig. 30B. Trend in fish biomass (CPUE, catch in multiple mesh size gill nets, kg net^{-1}, cf. Fig. 2) of the dominant fish species in Lake Væng following fish manipulation. Also shown are summer mean abundance of *Daphnia* and other cladocerans, chlorophyll *a*, lake water total phosphorus and total nitrogen concentrations and maximum submerged macrophyte coverage. The arrows indicate that in 1992 there was a significant decrease in biomass during summer. Biomanipulation has led to considerable changes in trophic structure and nutrient levels (from 17).

at e.g. Lake Stigsholm (*Søndergaard et al. 1997*) and Lake Krankesjön in Southern Sweden (*Blindow et al. 1993*), remains to be elucidated. Recently, more small-sized fish have been caught in the annual survey fishing (Mortensen et al., unpubl.), which may explain the observed reduction in the number of large-sized zooplankton species (e.g. *Daphnia* spp.) (Fig. 30B) and plant-associated crustaceans (unpubl. data). Only time can tell whether it will lead to a long-lasting shift to the turbid state.

4.5 Cross-analysis of biomanipulation experiments

An essential question in lake management today is whether fish manipulation will promote a long-term shift to the clearwater state. In the 1980s – the "pioneer phase" of biomanipulation – a "trial-and-error" attitude prevailed. You learned exclusively by experimentation. Primarily on the basis of experiments undertaken in two German lakes and analyses of the results from various others European experiments, Benndorf (1990) did, however, claim that the chances of obtaining a long-lasting success were greatest if the phosphorus loading was below 0.6 g TP m^{-2} $year^{-1}$.

Danish experiments

Based on the findings presented in Fig. 2, we proposed the hypothesis that shallow lake fish manipulation is most efficient if the phosphorus level in the future equilibrium state is below 0.08-0.15 mg l^{-1}, corresponding to a phosphorus loading of 0.5-2 g TP m^{-2} $year^{-1}$ depending on the lake water retention time (2,4). Only below this limit a permanent establishment of submerged macrophytes can be expected and the abundance of predatory fish become so high that they may exert a considerable predation pressure on the planktivorous fish. If phosphorus concentrations are higher only temporary effects may be expected. The lake will probably sooner or later revert to the turbid state, unless a permanent management programme is implemented. An exception would, however, be lakes with low nitrogen loading (for instance lakes with small catchments); they may shift to a more permanent clearwater state at higher phosphorus levels.

Comparisons of the results from the first three Danish experiments with biomanipulation seemed to confirm our hypothesis (1). Lake Væng with calculated equilibrium of 0.05 mg TP l^{-1} shifted to the clearwater state and this has now lasted for 10 years. Frederiksborg Castle Lake has a phosphorus level of 0.30-0.70 mg TP l^{-1}, which is above the calculated threshold level of 0.08-0.15 mg TP l^{-1}. Here, 80% of the planktivorous fish biomass was removed, and 1.5 g m^{-2} wet weight predatory perch were stocked (*Riemann et al. 1990*). The intervention was far more comprehensive than in Lake Væng in which only 50% of the planktivorous fish biomass was removed and no predatory fish were stocked. However, in agreement with our hypothesis, there was only a short-lived (1-2 years) and slight increase in zooplankton biomass and a minor decrease in chlorophyll *a*, after which the lake returned to its earlier condition (1; *Riemann et al. 1990* – and later data in *Christoffersen 1994*). In the two highly eutrophic lakes, Lake Søbygård (see section 4.3), relatively small fish stock changes led to major but not stable changes of state and similar results were obtained in Lake Lyng (see section 3.2).

Dutch-Danish analysis

We have since made a comparative analysis of data from three biomanipulated Dutch lakes and Danish Lake Væng (21). The four lakes cover an initial phosphorus concentration range – prior to manipulation – of 0.15-1 mg TP l^{-1}. After the fish manipulation experiments, all four lakes shifted to a clearwater state with extensive coverage of submerged macrophytes. Only in the lake with the lowest phosphorus level (Lake Væng) the proportion of predatory fish increased markedly in the years following the intervention (21; *Meijer et al. 1995*), so only in Lake Væng was the predation pressure on planktivorous fish by predatory fish of any significance. After three years the biomass of planktivorous fish increased in the two lakes with the highest phosphorus concentrations, and this may be the first indication of a reversion to the turbid state. These results seem to support our general hypothesis. It is, however, surprising that highly eutrophic Lake Zwemlust remained clear for five years (*Gulati 1996; Van Donk 1997*). The explanation may be that all fish were removed (the lake was completely drained), and only rudd and pike were stocked after refilling. The lake consequently lacks typical zooplanktivores such as roach and bream.

When to use biomanipulation?

We are now doing a cross-analysis of data from 20 Danish fish manipulation experiments and the results seem to support our original prediction (2, 4) of when to expect significant, permanent effects from fish manipulation in shallow lakes, although there may be a need to reduce the suggested threshold level from 0.08-0.15 mg TP l^{-1} to 0.05-0.10 mg TP l^{-1} (10). The new results moreover suggest that the chances of success are greatest near the upper phosphorus limit, if 80-90% of the planktivorous fish biomass are removed, and if the intervention for a number of years is followed by stocking of pike fry to control the planktivorous fish fry. If not, the favourable growth conditions for planktivorous fish fry resulting from the fish removal could cause the system to revert to the turbid state. Moreover, experiments in Dutch Lake Wolderwijd indicate that near the upper phosphorus limit, high coverage of submerged macrophytes seems necessary if the clearwater state is to be maintained (*Meijer & Hosper 1997*). The analysis also confirms that long-term effects of fish manipulation may be obtained at higher phosphorus concentrations in lakes with low nitrogen input.

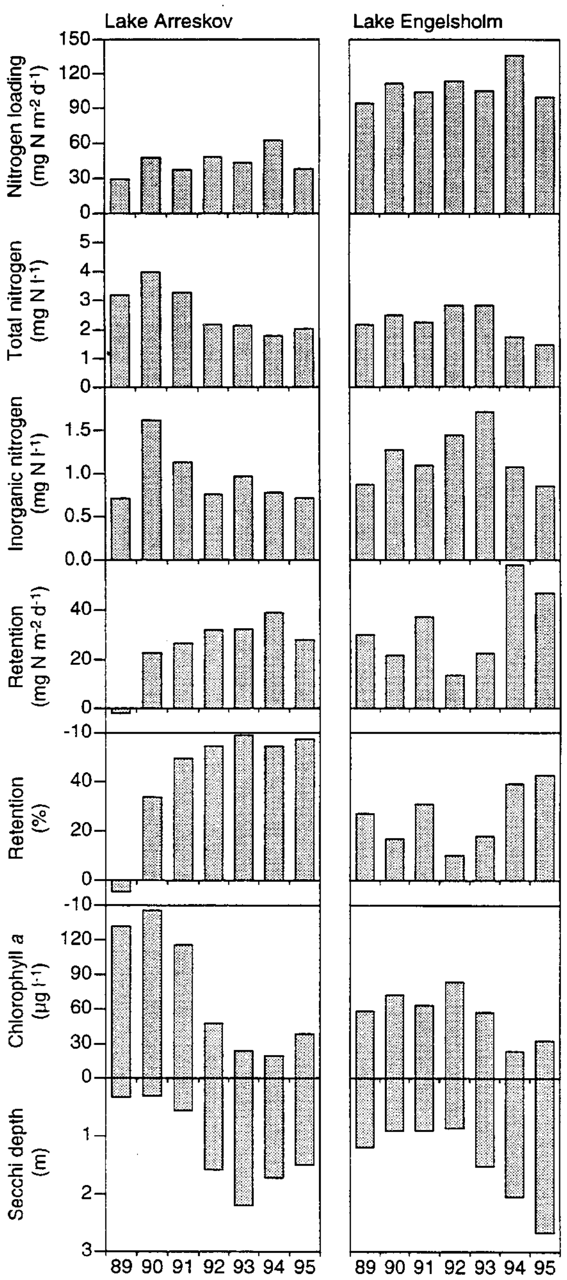

Fig. 31. Mean external loading, retention and retention percentage of total nitrogen, mean concentrations of lake water total and inorganic nitrogen, chlorophyll *a* and Secchi depth in Lake Arreskov and Lake Engelsholm during a period in which drastic fish community changes took place. In Lake Arreskov, a large proportion of the planktivorous fish died in summer-autumn 1991, and in Lake Engelsholm roach (*Rutilus rutilus*) and bream (*Abramis brama*) were removed in 1992-94. The nitrogen retention percentage increased in both lakes after the switch to the clearwater state (from 15).

4.6 Effects of fish manipulation on nutrient levels and nutrient retention

In several of the biomanipulation experiments undertaken so far a shift to the clearwater state has also resulted in a decreasing phosphorus level (e.g. *Shapiro & Wright 1984; Reintertsen & Olsen 1984*). The analysis of the three Danish experiments showed a decrease in total phosphorus in Lake Væng, but no changes in the more eutrophic Frederiksborg Castle Lake and Lake Søbygård (1). A longer time series on Lake Søbygård seems, however, to indicate that the phosphorus level is lower in years with lower abundance of planktivorous fish and a higher grazing pressure on phytoplankton. Moreover, the experiment undertaken in Lake Lyng showed a marked phosphorus reduction in years with lower predation pressure from fish, and consequently lower chlorophyll *a* (Fig. 9). The analysis of data from the 20 fish manipulation experiments indicates a decrease in phosphorus concentrations in all the lakes that have changed to the clearwater state (*E. Jeppesen, M. Søndergaard & J.P. Jensen, unpubl.*).

There are only few investigations of the impact on nitrogen. We have made an analysis based on data from the three Dutch lakes and Lake Væng (21). In all four lakes fish manipulation led to a marked reduction in total nitrogen, especially following the re-establishment of submerged macrophytes. To elucidate more clearly the effects of fish manipulation on nitrogen we have subsequently conducted mass balance studies of three biomanipulated lakes (15). In all three lakes, manipulation resulted in increased nitrogen retention, even in lakes in which submerged macrophytes had not yet re-established or only appeared randomly (Fig. 31). It was generally believed (21) that the reduction in nitrogen levels was caused by colonization of submerged macrophytes as they remove nitrogen for growth and may stimulate denitrification (*Granéli & Solander 1988; Weisner et al. 1994*), but this cannot be the entire explanation. We have discussed possible reasons for the reduction in nitrogen and phosphorus concentrations and the increased retention percentages in biomanipulated lakes with few or no submerged macrophytes (15; Jeppesen et al. in prep.). We conclude that various factors may be involved:

- The reduction of particulate nitrogen and phosphorus due to the decrease in phytoplankton biomass results in reduced nitrogen transport from the lake with this in turn leading to increased retention.
- The reduction of the phytoplankton biomass means that more inorganic nitrogen is available for denitrification, leading to increased degassing of nitrogen.
- Reduced fish predation results in higher abundance of benthic invertebrates (*Andersson et al. 1978; Giles 1992*), which may stimulate the denitrification based on nitrate from the water phase as well as the denitrification based on nitrate arising from sediment nitrification.
- Reduced biomass of benthivorous fish results in reduced phosphorus and nitrogen release from

the sediment because the sediment food intake and hence the nutrient release to the water by excretion are lower.

- Improved light climate at the sediment surface results in an increased production of benthic algae which may, in turn, stimulate the coupled nitrification-denitrification and reduce nitrogen release from the sediment (*Jansson 1989; Risgaard-Petersen et al. 1994; Van Luijn et al. 1995*),

- Higher abundance of benthic invertebrates, higher sediment algal production and reduced phytoplankton sedimentation result in an increased redox potential, which may diminish the sediment phosphorus release (*Mortimer 1941, 1942*). The latter is supported by the fact that also the iron retention percentage has increased in the fish-manipulated lakes (*Jensen et al., in prep.*). The influence of benthic invertebrates is, however, not unambigously clear as some experiments have shown an increasing and others a decreasing phosphorus release rate with increasing density of benthic invertebrates (*Andersson et al. 1988*).

Finally, fish manipulation typically leads to a reduced biomass of cyanobacteria, which may theoretically result in a decrease in nitrogen fixation and hence total nitrogen. We did not, however, find convincing evidence that nitrogen fixation was significant in our lakes (15).

Experiments are needed to provide better knowledge of the causal reasons for changes in nitrogen and phosphorus retention. Notwithstanding the causes, however, the results show that the effects of fish manipulation may cascade down the food-web and eventually reach the nutrient level. They also show that restoration of lakes using fish manipulation may lead to increased lake retention and loss of nitrogen and usually of phosphorus as well, thereby reducing the nutrient loading on downstream lakes. Hence, lake restoration will not only improve the environmental state of lakes, but will also reduce eutrophication of downstream aquatic ecosystems (10, 15, 18).

5 The historical development in nutrient levels and trophic structure

For the majority of Danish lakes information about the environmental state of most Danish lakes is only available for the last 10-20 years. By including analyses of plant and animal remains preserved in lake sediments (palaeoecological investigations) we may obtain information on the past development in biological community structure, environmental state and indirectly on lake catchment use (e.g. *Anderson & Battarbee 1994*).

Palaeoecological investigations may also be an important tool in the evaluation of trophic dynamics and their relationship to physico-chemical factors (7; *Anderson 1993; Anderson & Battarbee 1994*). They may provide valuable information on the mechanisms behind changes in lake ecosystems caused by, for instance, changes in the fish community and behind the existence of alternative stable states. This reflect the fact that the duration of existing monitoring series and field and enclosure experiments conducted so far is so short that as a rule they only allow evaluation of the immediate effects of naturally or artificially induced ecosystem changes. The maximum longevity of several of the dominant fish species is, for example, so high that a shift in fry recruitment may affect the ecosystem for several decades. In the evaluation of long-term effects, palaeoecological investigations have proved to be unique.

Palaeoecological methods have been used in lake research for many years, but have until recently mainly been qualitative. New quantitative methods have been developed which have turned palaeoecological investigations into a convincing tool in the study of trophic interactions in lakes. Relationships (transfer functions) are established between lake variables and relevant biological remains in lake surface sediments from many lakes with contrasting levels of the lake variables to be inferred. The transfer functions may then be used to reconstruct the past development of various lake variables from the composition of remains found in the different layers of the lake sediment. Statistical methods include Canonical Correspondence Analyses (CCA) (*ter Braak 1987*) and weighted averaging partial least square regression, with and without built-in ecological tolerance limits for each zooplankton taxa (*Birks et al 1990; ter Braak & Juggins 1993*). Application of the latter method to diatoms has enabled reconstruction of changes in, for example, lake pH and phosphorus (*Stevenson et al. 1991; Andersson & Odgaard, 1994; Bennion et al. 1996*).

Reconstructing the abundance of planktivorous fish

We have established functions for quantifying historical changes in planktivorous fish abundance (7). It may be possible to quantify remains of fish in lake sediments such as scales and bones, but preliminary analyses showed, however, that this would require analyses of a huge quantity of sediment (*B. Odgaard, unpubl. results*). Instead we chose to use the zooplankton record as former investigations had shown that zooplankton remains were valuable qualitative indicators of past changes in fish predation pressure (*Kerfoot 1974; Kitchell & Kitchell 1980; Leavitt et al. 1989*).

Using data from 30 Danish lakes we succeeded in developing a transfer function between the abundance of planktivorous fish (CPUE, overnight test-fishing between 15 August and 15 September with gillnets having 14 different mesh sizes), and the relative proportion of *Daphnia, Leptodora, Bosmina coregoni, Bosmina longirostris* and rotifer remains (Fig. 32). The five zooplankton groups were selected because they dominate at contrasting fish densities due to differences in their sensitivity to fish predation (*Brooks & Dodson 1965*). As empirical relations exist

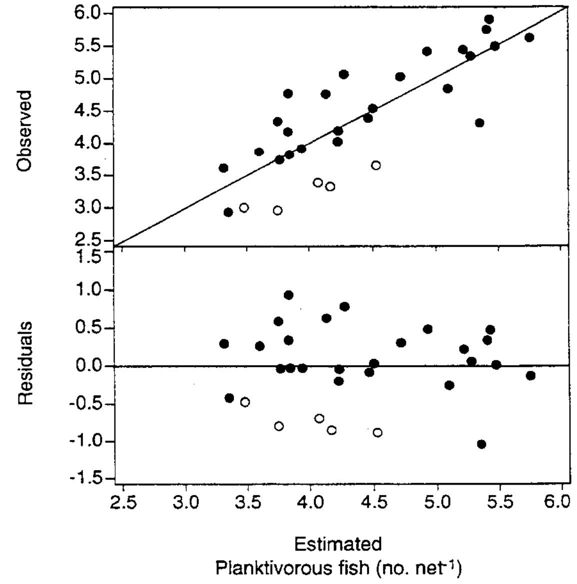

Fig. 32. Observed density of planktivorous fish (CPUE, catch in multiple mesh size gillnets cf. Fig.2) *v* corresponding values calculated from the proportion of the remains of five zooplankton taxons in the upper 1 cm of the lake sediment (both are $\log_e$-transformed). Also residuals are shown. ○ = lakes with high abundance of submerged macrophytes (coverage >10%), • other lakes (from 7).

between contemporary CPUE and a number of other lake variables such as the relationship between predatory fish and planktivorous fish, the maximum depth distribution of submerged macrophytes, the zooplankton:phytoplankton biomass ratio and water clarity (7, Fig. 33), it may be possible to obtain information about these variables and thereby to describe historical changes in the environmental state of the lakes.

Fish community changes in three Danish lakes

The relationship between zooplankton remains in the sediment and fish has been used to describe the development in the abundance of planktivorous fish in three Danish lakes during the past 200-300 years (Fig. 34; *Jeppesen et al., unpubl.*). In Lake Søbygård, calculated CPUE was high in the upper 1 cm of the sediment. It declined steeply at approximately 10 cm depth, coinciding with the period when fish kill was recorded (cf. section 4.3). A new peak was observed at approximately 30 cm depth (about 50 years ago), after which CPUE decreased sharply to relatively low values at depths >65 cm. In Lake Lading, calculated CPUE was also very high in the surface sediment and decreased as in Lake Søbygård sharply at 50-60 cm depth to a stable, lower value over the subsequent 50 cm. On the basis of the relationships shown in Fig. 33 it is to be presumed that the two lakes have shifted from a state with low abundance of planktivorous fish and high abundance of predatory fish to almost exclusive dominance by planktivorous fish.

By comparing the estimated changes in planktivorous fish with sediment macrophyte remains (*B. Odgaard and P. Rasmussen, unpubl.*) we found that calculated CPUE of planktivorous fish increased prior to the period when the plants disappeared from the lake (*Jeppesen et al., unpubl.*). This seems to support the hypothesis of Brönmark & Weisner (1992) that increasing fish density via predation on zooplankton and plant-associated invertebrates, including snails, may contribute to the decreasing abundance of submerged macrophytes; i.e. in the absence of grazing phytoplankton and epiphytes growth on plant surfaces may increase which may, in turn, lead to deterioration in the light climate to the detriment of the plants.

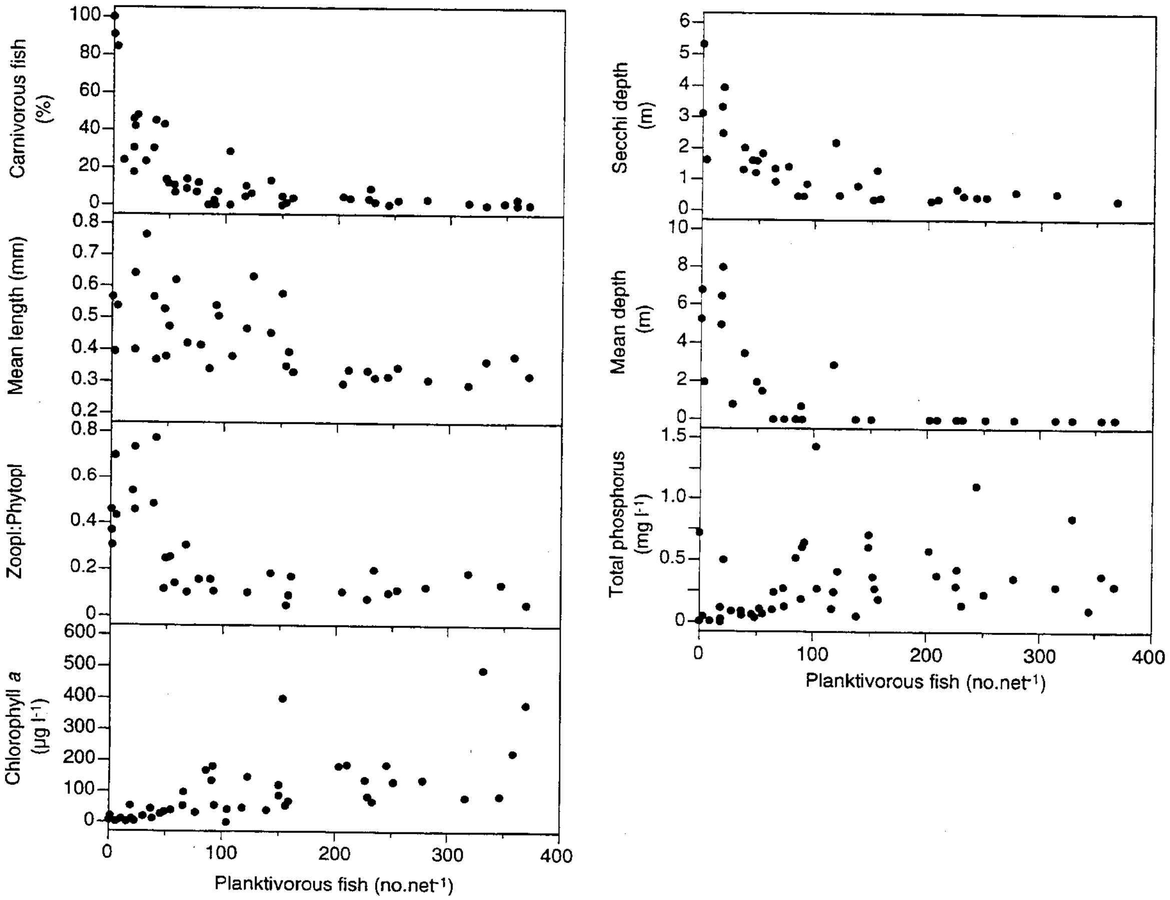

Fig. 33. Percentage carnivorous fish in multiple mesh size gillnet catch, mean size of cladocerans, zooplankton:phytoplankton biomass ratio, epilimnion chlorophyll *a* concentration, Secchi depth, maximum depth of submerged macrophyte and total phosphorus concentration *v* planktivorous fish (CPUE in multiple mesh size gillnets, cf. Fig. 2) in a number of Danish lakes. The depth limit of submerged macrophyte was measured in July-August at biomass maximum. All other data are summer means (1 May – 1 October). Zooplankton and phytoplankton summer means were calculated before estimating the ratio. With increasing CPUE of planktivorous fish marked changes occurred in lake trophic structure (From 7).

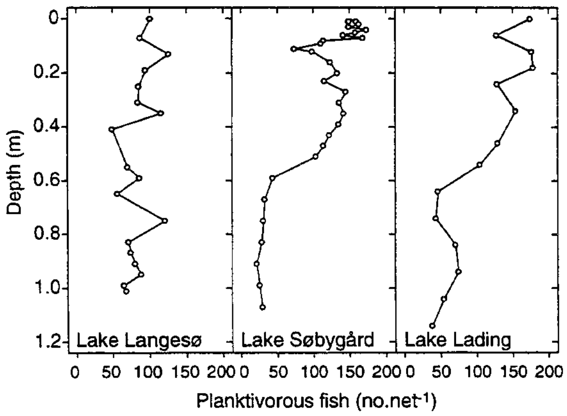

Fig. 34. Reconstruction of the historical development of the number of planktivorous fish (CPUE, catch in multiple mesh size gillnets, cf. Fig. 2) in Langesø, Lake Søbygård, and Lake Lading. 0 is the sediment surface (*E. Jeppesen, J.P. Jensen & E. Agerbo, unpubl.*).

In Langesø, calculated CPUE showed only a weak declining trend from the surface of one meter depth in the sediment. In correspondence with this, the fish community in 1927 was similar to the present one, i.e. dominated by bream, roach and small perch (*Otterstrøm 1927*). Our results suggest that this situation prevailed even further back in time, probably as a consequence of early eutrophication of the lake by nutrient-rich wastewater and manure derived from managing the Estate of Langesø (*County of Funen 1994*).

Other transfer functions

Recently, we have developed transfer functions relating remains of cladocerans and rotifers to coverage and plant-filled volume of submerged macrophytes and lake water total phosphorus (*Jeppesen et al., unpubl.* and Fig. 35). Transfer functions for Danish lakes have been established between total phosphorus and diatoms (*Anderson 1993; Anderson & Odgaard 1994*), and a function relating total phosphorus to chironomid remains is currently being developed (*K. Brodersen, unpubl.*). By comparing such functions we expect soon to arrive at a better description of the past lake nutrient levels and trophic structure. The results have, however, already demonstrated the future potential for using palaeoecology to elucidate long-term biological interactions in lakes.

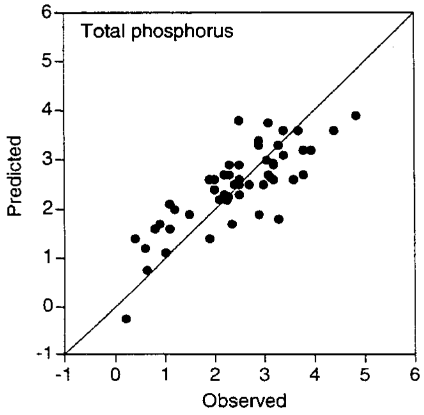

Fig. 35. Observed summer mean of the concentration of lake water total phosphorus compared with values calculated from the composition of zooplankton remains in the upper 1 cm of the sediment (both $\log_e$-transformed) (*E. Jeppesen, J.P. Jensen & E. Agerbo, unpubl.*).

6 Brackish lakes

In Denmark, there are a large number of both naturally and artificially made brackish lakes of which some are large (e.g. Saltbækvig, Vejlerne and Lake Ferring). Species diversity is often low. The lakes are dominated by organisms that tolerate intermediate and varying salinities (e.g. the mysid *Neomysis integer* and the copepod *Eurytemora affinis*). Early in this century various autecological investigations were undertaken in Danish brackish waters (e.g. *Johansen et al. 1933-36; Muus 1967*), but only few studies have been made at ecosystem level. Some facts may, however, be obtained from studies in other countries (e.g. *Leah et al. 1978; Irvine et al 1990; Moss 1994*). Our studies on trophic dynamics in Danish brackish lakes (6, 12, 25) have provided surprising results.

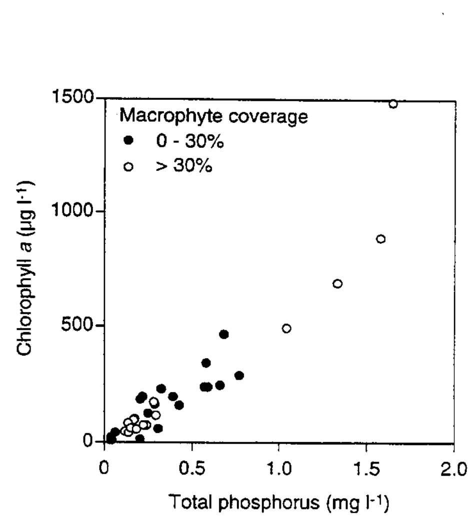

Fig. 36. Summer mean of chlorophyll *a v* total phosphorus in some Danish brackish lakes with a submerged macrophyte coverage of 0-30% or >30%. There is no tendency towards a reduction in chlorophyll *a* at a given phosphorus level in macrophyte-rich lakes as is the case in freshwater lakes (from 12).

Stronger predator control in brackish lakes?

A characteristic feature of Danish eutrophic brackish lakes is that high density of submerged macrophytes does not result in high transparency as in freshwater lakes (6, Fig. 16 and 36). In Vejlerne, for instance, Secchi depth is 20-30 cm despite high density of submerged macrophytes. Consequently, presence of submerged macrophytes does not lead to increased zooplankton grazing on phytoplankton as is the case in freshwater lakes. There are several possible reasons for this result. Cross-analyses of data from a number of Danish eutrophic brackish lakes indicate that the predation pressure on zooplankton is higher than in comparable freshwater lakes and that it is not diminished in the presence of submerged macrophytes (6, 12). This interpretation is based on several observations. As in freshwater lakes (Fig. 2) the abundance of planktivorous fish increases with increasing phosphorus levels (Fig. 37), but in brackish lakes a shift to stickleback dominance is often observed at high phosphorus concentrations. Sticklebacks have 2-3 generations in brackish lakes per year. Fish fry, which yield a particularly high predation pressure on zooplankton (see section 3.2), may therefore be abundant throughout the summer and in the autumn as well. In contrast, the dominant planktivorous fish in freshwater lakes, such as roach and bream, spawn only once a year, and for this reason alone it is highly probable that the predation pressure on zooplankton is higher in eutrophic brackish lakes (12).

Also important is that large-sized pelagic invertebrates are highly abundant in very eutrophic brackish lakes while they are almost absent in freshwater lakes (12, Fig. 37). In Danish freshwater lakes, the pelagic invertebrate predators present are mainly the cladoceran *Leptodora kindtii*, and the phantom midge fly *Chaoborus*, whereas the mysid, *Neomysis integer*, is dominant in brackish lakes. In freshwater lakes, the density of large invertebrates increases with increasing phosphorus levels up to approximately 0.1-0.2

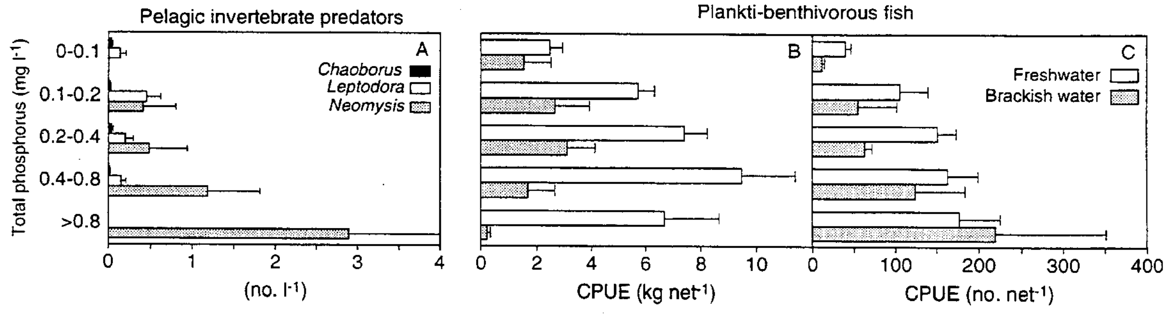

Fig. 37. Summer mean of the abundance of some pelagic invertebrate predators in Danish freshwater and brackish lakes (A), CPUE of planktivorous fish as biomass (B) and abundance (C) in July-August *v* the summer mean total phosphorus concentration (from 12).

mg TP l^{-1}. At higher concentrations, the abundance decreases, and they almost disappear at the highest nutrient levels, despite favourable food conditions including many small rotifers and juvenile stages of cyclopoid copepods. This indicates that increased fish predation is the main reason for the decrease, which is supported by the fact that abundance increases when the fish density decreases, e.g. by biomanipulation (e.g. *Berg et al. 1994*). In brackish lakes, no corresponding decrease occurs. In contrast, mysid density increases markedly at high nutrient levels and they may reach average densities as high as 13 specimens l^{-1}. This increase coincides with fish community changes from large species which prey on *Neomysis integer* to complete dominance by sticklebacks that only prey on the smallest *Neomysis integer* and not on egg-carrying specimens (*Søndergaard & Jeppesen, submitted*).

In eutrophic brackish lakes the density of both sticklebacks and *Neomysis integer* is often high and both prey on the dominant zooplankton *Eurytemora affinis*. Enclosure experiments in Lake Ferring (25) suggest that *Neomysis integer* had a negative impact on the nauplii of *Eurytemora affinis*, whereas three-spined sticklebacks, as has been observed in other studies (e.g. *Worgan & FitzGerald 1981; Pont et al. 1991*), preyed on copepodites and adults. This implies that *Eurytemora affinis* can experience a particularly high predation pressure in such lakes. This conclusion is supported by the observation that the zooplankton:-phytoplankton biomass ratio in eutrophic brackish lakes is 3-5-fold lower than in freshwater lakes (6) and therefore the grazing pressure on phytoplankton is most likely also substantially lower (Fig. 38).

Example from Lake Ørslevkloster

In freshwater lakes, submerged macrophytes appear to provide a refuge for zooplankton against predation from fish and mysids. This seems, however, not to be the case in brackish lakes, because the potential predators are abundant in the macrophyte beds of the littoral zone (12). In Lake Ørslevkloster, we found that the annual average concentration of mysids was 120-fold higher in the littoral than in the pelagial (12) (Fig. 39), and within the littoral zone 80% higher within the vegetation than in areas from which vegetation had been cleared (*Petersen 1994*). The gillnet catches of three-spined sticklebacks were 10-25-fold higher in the littoral than in the pelagial during the major part of summer (12). No daytime aggregation of zooplankton within the vegetation was observed (*Petersen 1994*) as in freshwater lakes with high fish predation pressure (*Lauridsen et al. 1998*).

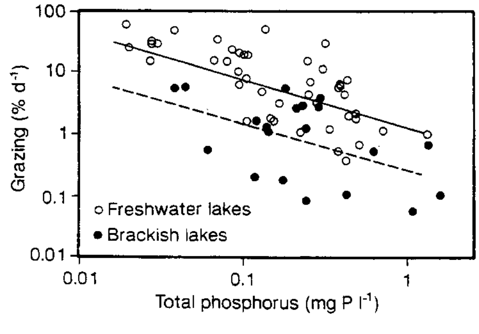

Fig. 38. Calculated zooplankton grazing pressure on phytoplankton *v* summer mean concentrations of total phosphorus in freshwater lakes and brackish lakes (>0.5 ‰). The zooplankton grazing pressure is about 5 times greater in eutrophic freshwater lakes than in corresponding brackish lakes (from 6).

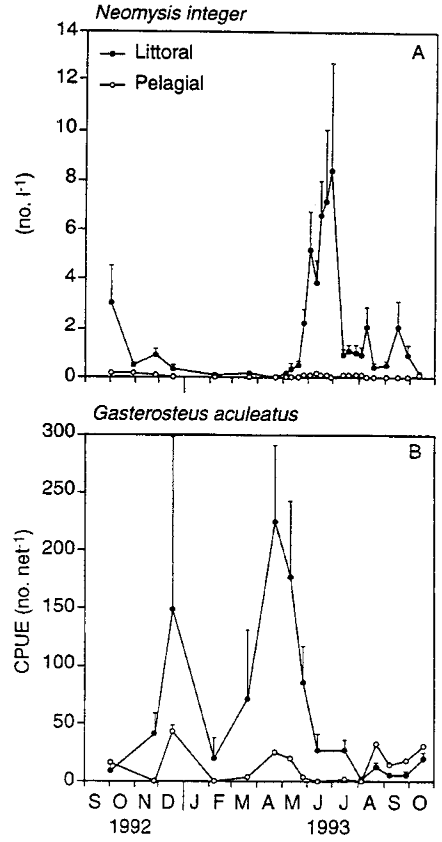

Fig. 39. Seasonal variations in the abundance (±SE) of *Neomysis integer* (A) and catch per net of three-spined sticklebacks (*Gasterosteus aculeatus*) in multiple mesh size gillnets (B) in the littoral zone and the pelagial of Lake Ørslevkloster in 1992-1993. Both species prefer the littoral zone during most of the year (from 12).

Differences in zooplankton composition may contribute to the observed differences in the relationship between submerged macrophytes and zooplankton grazing pressure on phytoplankton in freshwater and brackish lakes (6). In Danish brackish lakes, the zooplankton are typically dominated by calanoid copepods, such as *Eurytemora affinis* and *Acartia* spp., and by rotifers, whereas cladocerans play a larger role in freshwater lakes. Cladocerans, especially *Daphnia* may potentially grow faster and exploit a broader food spectrum than calanoid copepods (e.g. *Rothaupt 1997*), which makes them more efficient grazers in systems with reduced predation pressure by fish. However, *Daphnia* typically disappear at salinities of 2-4 ‰. *Daphnia magna* may tolerate higher salinities (*Jürgens & Stolpe 1995*), but since it typically appears in totally or almost fishless lakes it is rarely observed in brackish lakes. Absence of *Daphnia* and low densities of other cladocerans may, therefore, be presumed to reduce the grazing pressure on phytoplankton (6).

If the above interpretations are correct, we would expect that eutrophic brackish lakes with extensive coverage of submerged macrophytes that shifts to a freshwater state are likely to become clear. Such a shift has been observed in Lake Ørslevkloster (12) (Fig. 40A,B). Together with the County of Viborg, we studied the lake from 1993-1995, and monitoring data were available from 1986 (*Viborg County 1988*). During the observation period significant changes in salinity occurred without simultaneous changes in external nutrient supply (*Viborg County 1995*). In 1986 and 1995, the lake was almost freshwater (< 1 ‰) and in 1993-1994 it became more brackish (1-3 ‰). During the brackish period, the zooplankton were dominated by *Eurytemora affinis* and rotifers. During summer and autumn the chlorophyll *a* level was high and Secchi depth low (Fig. 40B). In the freshwater state, in contrast, the zooplankton were dominated by *Daphnia galeata*, and the lake was clear. *Neomysis integer* was highly abundant in 1993, but disappeared in 1994 and was not observed in 1995 (12; *Petersen 1994* and *E. Jeppesen & M. Søndergaard, unpubl.*). Unfortunately, no fish data were collected in 1995 and it can, therefore, not be completely excluded that the higher zooplankton biomass and higher transparency of 1995 were the result of a sudden decrease in planktivorous fish density.

It is interesting that Canadian saline lakes show a different pattern from brackish Danish lakes (*Evans et al. 1996*). Here, phytoplankton biomass is lower than in corresponding freshwater lakes, which may be explained by low density of planktivorous fish and lower accessibility of the phosphorus to phytoplankton (*Evans et al. 1996*).

Great need for more knowledge

We have only begun to understand the trophic structure and dynamics of brackish lakes and they still offers many challenges. From a management perspective, more knowledge of brackish lakes is desirable because the significant differences in trophic structure and dynamics of freshwater and brackish lakes mean that the biological restoration methods employed in freshwater lakes (fish manipulation, protection or implantation of submerged macrophytes) cannot be directly applied to brackish lakes.

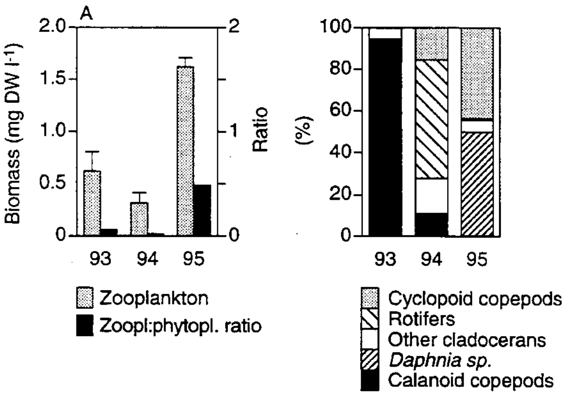

Fig. 40A. Zooplankton biomass and zooplankton:phytoplankton biomass ratio (left panel) and percentage of biomass accounted for by the various zooplankton groups in Lake Ørslevkloster in 1993, 1994, 1995. No quantitative data are available for 1986, but high density of *Daphnia hyalina* was observed in littoral fauna samples (*Viborg County 1988*), indicating that the lake was then in a cladoceran state (from 12).

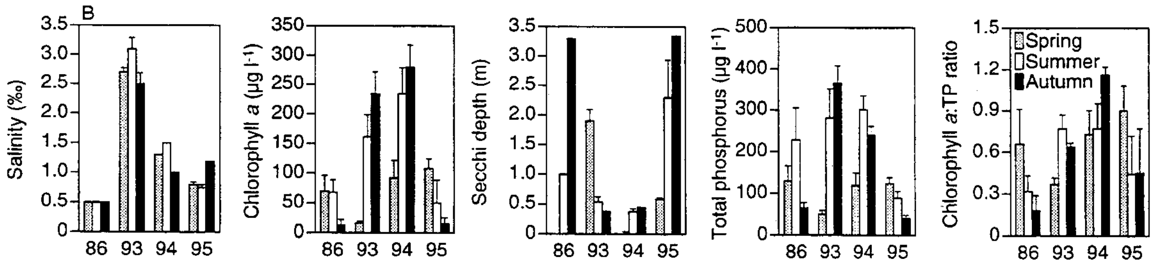

Fig. 40B. Seasonal variations in the mean value (±SE) of chlorophyll *a*, Secchi depth and total phosphorus and chlorophyll *a*:total phosphorus ratio in Lake Ørslevkloster during four years differing widely in salinity. The year is divided into 3 periods: 1 January – 1 May, 1 May – 1 October and 1. October – 1. Jan. From 1 May – 1 Jan. Chlorophyll *a* was lower and Secchi depth considerably higher in years with high salinity (from 12).

7 Summary and future research needs

7.1 Summary

On the basis of the dissertation and the papers on which it is based a number of conclusions can be drawn. These are:

The majority of Danish lakes are shallow with a mean depth of typically 1-3 m. Fifty-200 years ago most lakes were clear with many submerged macrophytes. They had considerable stocks of predatory fish and rich sub-surface flora and fauna as well as many plant-eating birds and diving ducks. Due to increased nutrient supply most lakes have since shifted to a turbid state with phytoplankton blooms. Cyprinids such as roach and bream came to dominate fish communities, and the abundance and diversity of waterfowl rapidly decreased. Nutrient loading to many of the lakes during the past 20 years has been significantly reduced, especially as a consequence of wastewater treatment, but most lakes have shown little improvement. This resilience may be caused by slow release of accumulated phosphorus in the lake sediment. The duration of the transitional period depends on conditions such as the former scale of loading and its duration, water renewal time, iron supply and biological conditions. The transitional period may be long even in lakes with short hydraulic loading. For example, the sediment of Lake Søbygård (which has a hydraulic retention time of only a few weeks) still releases more phosphorus than it receives 13 years after an external loading reduction. It has been estimated that another decade will pass before the lake will reach equilibrium with the present external loading. The resistance to environmental improvement may also be biologically conditioned.

Both resource control (by for instance, nutrients and light) and predator control (for instance by fish) seem to influence lake trophic structure and dynamics. The predation pressure of fish on zooplankton appears to be high in oligotrophic and eutrophic lakes and lower in mesotrophic lakes. The cascading effects on phytoplankton are seemingly small in oligotrophic lakes, but significant in eutrophic lakes. Fish fry may exert a significant predation pressure on zooplankton during summer, which may have a marked cascading impact on the zooplankton grazing pressure on phytoplankton. The impact of fish fry in Danish lakes seems to be most pronounced in mesotrophic to slightly eutrophic lakes (0.02-0.05 mg P l^{-1}), whereas in hypertrophic lakes the biomass of older planktivorous fish will often be so high that they may exert a relatively constant predation pressure on the zooplankton throughout the year.

These results suggest that the relative importance of predatory control is higher in the pelagic zone of shallow lakes than in deep lakes, because fish play a more significant regulatory role and resource control is less pronounced. The first suggestion is supported by the fact that the abundance of fish per unit of volume is markedly higher in shallow lakes, the biomass of *Daphnia* and calanoid copepods relative to the total number of cladocerans and copepods is considerably lower, and the zooplankton:phytoplankton biomass ratio increases with increasing mean depth. The reduced resource control may be explained by more direct contact between sediment and the photic zone of shallow lakes which are fully-mixed. To this should be added higher sedimentation and resuspension which together with higher temperatures in the surface sediment increase the sediment nutrient release.

In moderately eutrophic shallow lakes (typically 0.05-0.15 mg P l^{-1}) two alternative stable states may occur: the clearwater state with extensive coverage of submerged macrophytes and the turbid one with high abundance of phytoplankton. Both states have a number of built-in buffer mechanisms preserving the state, implying that major (natural or artificial) changes are needed if a shift between states is to occur. Submerged macrophytes and predatory fish play important roles in the maintenance of the clearwater state, whereas cyprinids and plant-eating birds help to maintain the turbid state.

Submerged macrophytes may significantly influence trophic structure and dynamics including the relative importance of predatory and resource control. Freshwater lakes with extensive submerged vegetation are consequently much more transparent than lakes having similar nutrient levels, but no plants. The explanations are various. One may be that the plants act as a daytime refuge for zooplankton against fish predation, resulting in increased grazing pressure on phytoplankton within the vegetation and also in the pelagial to which the zooplankton migrate at night. The refuge effect is strongly influenced by plant density and the density of planktivorous fish within the vegetation, and it seems to change abruptly when given fish and plant density thresholds are reached. If the refuge effect is high, very significant cascading effects may be observed in the food chain of eutrophic lakes, and these may result in a low phytoplankton biomass, reduced abundance of microorganisms and clear water within the vegetation.

Given certain premises, biomanipulation may accelerate a shift to the clearwater state following an external loading reduction. Biomanipulation may include removal of cyprinids, stocking of predatory fish and protection of macrophytes against bird grazing, possibly combined with macrophyte planting. Experiments and cross-analyses of data from a large number of lakes indicate that biomanipulation in shallow lakes may lead to a long-term shift to a clearwater state provided that the nutrient supply has been reduced to a level so low that the future phosphorus equilibrium is below 0.05-0.10 mg P l^{-1}. If nitrogen loading is low, the effect may be obtained at higher phosphorus concentrations.

Biomanipulation is accompanied by a significant reduction in both lake water phosphorus and nitrogen contents and increased net retention during summer. This effect can be ascribed to reduced transport of particulate matter (phytoplankton) from the lake, reduced sediment release due to increased growth of benthic algae, reduced oxygen consumption as a consequence of lower sedimentation and consequently improved redox conditions and stimulation of denitrification. Biomanipulation and diminished nutrient supply may therefore increase the net retention of nitrogen and phosphorus and hence reduce the transport of these nutrients to downstream aquatic ecosystems.

Palaeoecological methods are an important tool that may be used to describe the historical development of lake ecosystems and to elucidate trophic dynamics in a longer time perspective than experiments and monitoring series allow. Recently, new quantitative techniques have revolutionized palaeoecology. We have developed transfer functions allowing quantitative reconstruction of the abundance of planktivorous fish, total phosphorus and submerged macrophyte coverage in lakes from remains of crustaceans and rotifers found in the lake sediment. Marked changes have been found in the abundance of planktivorous fish during the period immediately prior to the disappearance of submerged macrophytes from two lakes. This indicates that predation on snails and zooplankton may have been a contributory factor in the disappearance of macrophytes as it has led to improved growth conditions for epiphytes and phytoplankton and consequently a deteriorating light climate for submerged macrophytes.

The trophic structure and dynamics of brackish lakes deviate substantially from those of shallow freshwater lakes. Predatory control seems to be considerably higher in eutrophic brackish lakes, which may be ascribed to the coexistence of the dominant fish (stickleback) and mysids (*Neomysis*). Extensive submerged vegetation does not lead to clear water as in freshwater lakes, which may be ascribed to the higher predation pressure on zooplankton, lack of *Daphnia*, and the high abundance of zooplankton predators within the vegetation. The results are supported by data from the macrophyte-rich Lake Ørslevkloster, where a shift from a freshwater to a brackish state and back resulted in a shift from clear to turbid water and to clear water again.

7.2 Future research needs

Both from scientific and management perspectives, there is a great need for intensifying research on the mechanisms behind alternative equilibria in shallow lakes and the possibilities of using biomanipulation to encourage a shift from the turbid to the clearwater state. In particular, there is a great need for improving our understanding of the interactions between the littoral and the pelagic zones. Also our knowledge of the role played by fish fry in shallow lakes is poor. Regulating factors for appearance, habitat choice and the effect of fry on the ecosystem need to be further elucidated.

Furthermore, we need more knowledge of benthic-pelagic couplings, including interactions between biological communities and nutrient interchange. Biomanipulation experiments have shown that biological structural shifts may markedly change the concentration and retention of nutrients. We know, however, far too little about the mechanisms involved, and about how the pattern will change along a nutrient gradient. Today we are therefore not able to predict the effects of natural or imposed structural shifts on nutrient retention and consequently we cannot predict future lake water nutrient concentrations.

In the future we may expect a major increase in the number of Danish lakes in which fish manipulation will be used as a restoration tool since most lakes have shown resisitance to improvement following nutrient loading reductions. There is, therefore, a great need for further development of biomanipulation methods so that interventions may be undertaken in the most appropriate manner. Particularly, we need information about:

- long-term effects of manipulation at fish community and ecosystem level based on experiments, palaeoecology and the development of dynamic mathematical models,
- effects of predatory fish stocking – especially pike, perch and pike-perch,
- effects of combined interventions, i.e. removal and stocking to render the efforts more efficient and to reduce costs.

More knowledge is also needed about the effects of fish manipulation related to commercial and recreational fishing. In Denmark, for instance, some lakes (e.g. Lake Esrom and Slåensø), and a number of put-and-take waters have been, or are presently being stocked with large numbers of trout. Knowledge of the impact of such stocking on the lake ecosystem is poor, which is unfortunate when environmental authorities are required to evaluate applications for stocking on a scientifically sound basis.

New quantitative techniques for reconstructing a number of historical biological and physico-chemical variables (transfer functions) have already contributed significantly to our understanding of trophic interactions and to the analysis of past developments in trophic structure related to human-related activities. There is no doubt that palaeoecological transfer functions will be important for both ecosystem research and lake management. As an extensive monitoring tool, transfer functions must be regarded as being highly relevant – today a single sample from the surface sediment may give a seasonally integrated picture of the total phosphorus concentration, pH, the abundance of planktivorous fish and at least a rough estimate of submerged macrophyte coverage. The time resolution will, however, depend on the mixing of the lake sediment. New transfer functions and relations must be developed combining signals from several groups of organisms (e.g. phosphorus relations to diatoms, zooplankton and chironomids). Moreover, we need to test the reliability of past reconstructions, i.e. whether the signal from the surface sediment can be transferred to deeper-lying sediments. Comparative analysis of the sediment and water phases from lakes for which long time series of data exist may prove highly useful in this context.

In addition, we need to initiate intensive studies of brackish and freshwater lakes and studies under extreme environmental conditions (cold/warm climates). Investigations in extreme environments will not only produce relevant specific information about these lake types, but also information that may be used to interpret results from, for instance, temperate freshwater lakes. Arctic lakes will be paticularly useful because they are species-poor and have simple foodwebs. These characteristics make it easier to identify regulating mechanisms, including the relative importance of predatory and resource control.

Ecological studies of shallow lakes have a relatively short past, but an exciting future.

8 References

Agustí, S. (1991): Light environment within dense algal populations: cell size influences on shelf-shading. J. Plank. Res. 13: 863-871.

Agustí, S. & Kalff, J. (1989): The influence of growth conditions on the size dependence of maximal algal density and biomass. Limnol. Oceanogr. 34: 1104-1108.

Anderson, N.J. (1993): Natural vs. anthropogenic changes in lakes. The role of the sediment record. Trends Ecol. Evol. 8: 356-361.

Anderson, N.J. & Battarbee, R.W. (1994): Aquatic community persistence and variability: a palaeolimnological perspective. *In:* Giller, P.S., Hildrew, A.G. & Raffeli, D., eds. Aquatic Ecology: Scale, Pattern and Process. Blackwell Scientific Publications, Oxford, pp. 233-259.

Anderson, N.J. & Odgaard, B. (1994): Recent palaeolimnology of three shallow Danish lakes. Hydrobiologia 275/276: 411-422.

Anderson, N.J., Rippey, B. & Gibson, C.E. (1993): A comparison of sedimentary and diatom-inferred phosphorus profiles: implications for defining predisturbance nutrient conditions. Hydrobiologia 254: 357-366.

Anderson, O. (1984): Optimal foraging by largemouth bass in structured environments. Ecology 65: 851-861.

Anderson, R.S. (1980): Relationship between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. *In:* Kerfoot, W.C., ed. Evolution and ecology of zooplankton communities. University Press of New England, Hanover, N.H., pp. 635-641.

Andersson, G., Granéli, W. & Stenson, J. (1988): The influence of animals on phosphorus cycling in lake ecosystems. Hydrobiologia 170: 267-284.

Andersson, G., Berggren, H., Cronberg, G & Gelin (1978): Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9-15.

Andersson, G., Blindow, I., Hargeby, A. & Johansson, S. (1990): Det våras för Krankesjön. – Anser 29: 53-62.

Bean, C.W. & Winfield, J. (1995): Habitat use and activity patterns of roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erythorphtalmus* (L.)), perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the laboratory: the role of predation threat. Ecol. Freshwat. Fish 4: 37-46.

Beklioglu, M. & Moss, B. (1995): The impact of pH on interactions among phytoplankton algae, zooplankton and perch (*Perca fluviatilis*) in a shallow, fertile lake. Freshw. Biol. 33:497-509.

Beklioglu, M. & Moss, B. (1996): Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants with the structure of phytoplankton and zooplankton communities. Freshw. Biol. 36: 315-325.

Benndorf, J. (1987): Food web manipulation without nutrient control: A useful strategy in lake restoration? Schweiz. Z. Hydrol. 49: 237-248.

Benndorf, J. (1990): Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe. Hydrobiologia 200/201: 187-203.

Bennion, H., Juggins, S. & Anderson, N.J. (1996): Predicting epilimnetic phosphorus concentrations using an improved diatom-based transfer function and its application to lake eutrophication management. Environ. Sci. & Technol. 30: 2004-2007.

Berg, K. et al. (1958): Furesøundersøgelser 1950-54. Limnologiske studier over Furesø's kulturpåvirkning. (Investigation on Fure Lake 1950-54, Limnological studies on cultural influences). Folia Limnol. Scand. 10: 1-189.

Berg, S., Jeppesen, E., Søndergaard, M. & Mortensen, E. (1994): Environmental effects of introducing whitefish *Coregenus lavaretus* (L.) in Lake Ring. Hydrobiologia 275/276: 71-79.

Berg, S., Jeppesen, E. & Søndergaard, M. (1997): Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng (Denmark). Hydrobiologia 342/343: 311-318.

Bernardi, R. de & Guisanni, G. (1990): Are blue-green algae suitable food for zooplankton? An overview. Hydrobiologia 200/201: 29-41.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. & ter Braak, C.J.F. (1990): Diatoms and pH reconstruction. Land 327: 263-278.

Blindow, I., Andersson, G., Hargeby, A. & Johansson, S: (1993): Long-term pattern of alternative stable states in two shallow eutrophic lakes. Freshw. Biol. 30: 159-167.

Brett, M.T. & Goldman, C.R. (1996): Consumer versus resource control in freshwater pelagic food webs. Science 275: 384-386.

Brett, M.T., Wiackowski, K., Lubner, F.S., Mueller-Solger, A., Elser, J.J. & Goldman, C.R. (1994): Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle Lake, California. Ecology 75: 2243-2254.

Breukelaar, A.W., Lammens, E.H.R.R., Klein Breteler, J.P.G. & Tatrai, L. (1994): Effects of benthivorous bream (*Abramis brama* L.) and carp (*Cyprinus caprio* L.) on sediment resuspension and concentration of nutrients and chlorophyll *a*. Freshwat. Biol. 32: 113-121.

Brooks, J.L. (1969): Eutrophication and changes in the composition of zooplankton. *In:* Eutrophication, causes, consequences, correctives. Proceedings of a symposium held at the University of Wisconsin, Madison, June 11-15, 1967. National Academy of Sciences, Washington DC, pp. 236-255.

Brooks, J.L. & Dodson, S.I. (1965): Predation, body size and composition of plankton. Science 150: 28-35.

Brönmark, C. & Weisner, S. (1992): Indirect effects of fish community structure on submerged vegetation in shallow eutrophic lakes: an alternative mechanism. Hydrobiologia 243/244: 293-301.

Brönmark, C. & Vermaat, J. (1998): Complex fish-snail-epiphyte interactions and their effects on submerged freshwater macrophytes. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 47-69.

Burns, C.W. (1979): Population dynamics and production of *Boeckella dilatata* (Copepoda:Calanoida) in Lake Hayes, New Zealand. Arch. Hydrobiol. 54: 409-465.

Burns, C. W. (1992): Population dynamics of crustacean zooplankton in a mesotrophic lake, with emphasis on *Boeckella hamata* BREHM (Copepoda:Calanoida). Int. Rev. ges. Hydrobiol. 77: 553-577.

Burns, C. W. & Xu, Z. (1990): Utilization of colonial cyanobacteria and algae by freshwater calanoids: Survivorship and reproduction of adult *Boeckella* spp. Arch. Hydrobiol. 117: 257-270.

Canfield, D.E., Shireman, J.V., Colle, D.E., Haller, W.T., Watkins, C.E & Maceina, M.J. (1984): Prediction of chlorophyll *a* concentrations in Florida lakes: Importance of aquatic macrophytes. Can. J. Fish. Aquat. Sci. 44: 497-501.

Carney, J.J. & Elser, J.J. (1990): The strength of zooplankton-phytoplankton coupling in relation to trophic state. *In:* Tilzer, M.M., ed. Ecology of Large Lakes. Springer. New York, pp. 616-631.

Carpenter, S.R. & Lodge, D.M. (1986): Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26: 341-370.

Carpenter, S.R. & Kitchell, J.F., eds. (1993): The trophic cascade in lakes. Cambridge: Cambridge University Press.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985): Cascading trophic interactions and lake productivity. BioScience 35: 634-639.

Chapman, M. A., Green, J. D. & Jolly, V. H. (1975): Zooplankton. *In:* Jolly, V.H., Brown, J.M.A., eds. New Zealand lakes. Auckland, Auckland University Press, pp. 209-230.

Chapman, M.A., Green, J. D. & Jolly, V.H. (1985): Relationships between zooplankton abundance and trophic state of seven New Zealand lakes. Hydrobiologia *123*: 119-136.

Christoffersen, K. (1991): Biomanipulation som sørestaureringsværktøj - del 2. Frederiksborg Slotssø. Rapport til Miljøstyrelsen, 23 p.

Christoffersen, K., Riemann, B., Klysner, A. & Søndergaard, M. (1993): Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. Limnol. Oceanogr. 38: 561-573.

Cole, J.J., Findlay, S. & Pace, M.L. (1988): Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar. Ecol. Prog. Ser. 43: 1-10.

Crowder, L.B. & Cooper, W.E. (1979): Structural complexity and fish-prey interactions in ponds: A point of view. *In:* Johnson, D.L. & Stein, R.A., eds. Response of fish to habitat structure in standing water. North Central Division. Amer. Fish. Soc. Spec. Pub. 6: 1-10.

Crowder, L.B., McDonald, M.E. & Rice, J.A. (1987): Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. Can. J. Fish. Aquat. Sci. 44: 141-147.

Cryer, M., Pierson, G. & Townsend, C.R. (1986): Reciprocal interactions between roach *Rutilus rutilus*, and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31: 1022-1038.

Cullen, P. & Forsberg, C. (1988): Experience with reducing point sources of phosphorus to lakes. Hydrobiologia 170: 321-336.

DeAngelis, D:L. (1992): Dynamics of nutrient cycling and food webs. Chapman and Hall, New York, 270 pp.*Århus Kommune & Århus Amtskommune (1996):* Restaureringen af Brabrand sø - resultater og fremtid. Pjece fra Århus Kommunes Naturforvaltning. 12 p.

Delgado, M., de Jonge, V.N. & Peletier, H. (1991): Experiments on resuspension of natural microphytobenthos populations. Mar. Biol. 108: 321-328.

Diehl, S. (1988): Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. Oikos 53: 207-214.

Dieter, C.D. (1990): The importance of emergent vegetation in reducing sediment resuspension in wetlands. J. Freshwat. Ecol. 5: 467-473.

Downing, J.A., Plante, C. & Lalonde, S. (1990): Fish production correlated with primary productivity and the morphoedaphic index. Can. J. Fish. Aquat. Sci. 47: 1929-1936.

Duartes, C.E., Agustí, S. & Canfield, D.E. (1990): Size plasticity of freshwater phytoplankton: implications for community structure. Limnol. Oceanogr. 35: 1846-1851.

Ducklow, H.W. & Shiah, F.K. (1993): Bacterial production in estuaries. *In:* Ford, T.E., ed. Aquatic microbiology. Blackwell Scientific Publications, Boston, pp. 261-287.

Elser, J.J. & Goldman, C.R. (1990): Zooplankton effects on phytoplankton in lakes of contrasting trophic status. Limnol. Oceanogr. 36: 64-90.

Engels, S. (1988): The role and interactions of submersed macrophytes in a shallow Wisconsin lake. J. Freshwat. Ecol. 4: 329-340.

Enriquez, S., Duarte, C.M., Sand-Jensen & Nielsen, S.L. (1996): Broad-scale comparison of photosynthetic rates across phototrophic organisms. Oecologia 108: 197-206.

Evans, M.S., Arts, M.T. & Robarts, R.D. (1996): Algal productivity, algal biomass, and zooplankton biomass in a phosphorus-rich saline lake: deviations from regression model predictions. Can. J. Fish. Aquat. Sci. 53: 1048-1060.

Faafeng, B. & Mjelde, M. (1998): Clear and turbid water in shallow Norwegian lakes related to submerged vegetation. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 361-368.

Flecker, A.S. & Townsend, C.R. (1994): Community-wide consequences of trout introduction in New Zealand streams. Ecol. Appl. 4: 798-807.

Fretwell, S.D. (1977): The regulation of plant communities by food chains exploiting them. Perspectives in Biology and Medicine 20: 169-185.

Frodge, J.D., Thomas, G.L. & Pauley, G.B.(1990): Effects of canopy formation by floating and submerged macrophytes on the water quality of two shallow pacific north-west lakes. Aquat. Bot. 38: 231-248.

Fyns Amtskommune (1994): Langesø 1993. Vandmiljøplan overvågningsrapport. 109 p. (In Danish)

Giles, N., Street, M., Wright, R., Phillips, V & Traill-Stevenson, A.J. (1989): Food for wildfowl increases after fish removal. Game Conservancy Annual Review 20: 137-140.

Gliwicz, Z.M. (1985): Predation or food limitation: an ultimate reason for extinction of planktonic cladoceran species. Arch. Hydrobiol. Beih. Ergb. Limnol. 21: 419-430.

Gliwicz, Z.M. & Jachner, A. (1992): Diel migration of juvenile fish: a ghost of predation past or present. Arch. Hydrobiol. 124: 385-410.

Granéli, W. & Solander, D. (1988): Influence of aquatic macrophytes on phosphorus cycling in lakes. Hydrobiologia 170: 245-266.

Grimm, M.P. & Backx, J. (1990): The restoration of shallow eutrophic lakes and the role of northern pike, aquatic vegetation and nutrient concentration. Hydrobiologia 200/201: 557-566.

Gulati, R.D. (1996): Food-chain manipulation as a tool in lake management of small lakes in the Netherlands: the Lake Zwemlust example. *In:* Bernardi, R. De & Giussani, eds. Biomanipulation in lakes and reservoirs management. Guidelines of Lake Management 7: 147-161.

Gulati, R.D., Lammens, E.H.H.R., Meijer, M.-L. & van Donk, E. (1990): Biomanipulation, tool for water management. Hydrobiologia 200-201: 1-628.

Hamilton, D.P. & Mitchell, S.F. (1996): An empirical model for sediment resuspension in shallow lakes. Hydrobiologia 317: 209-220.

Hansen, A-M., Christensen, J.V. & Sortkjær, O. (1991): Effect of high pH on zooplankton and nutrients in fish-free enclosures. Arch. Hydrobiol. 123: 143-164.

Hansson, L.-A. (1992): Effects of competitive interactions on the biomass development of planktonic and periphytic algae in lakes. Limnol. Oceanogr. 73: 241-247.

Hanson, J.M. & Leggett, W.C. (1982): Empirical prediction of fish biomass and weight. Can. J. Fish. Aquat. Sci. 39: 257-263.

Hanson, J.M. & Peters, R.H. (1984): Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. Can. J. Fish. Aquat. Sci. 41: 439-445.

Hasler, A.D. & Jones, E. (1949): Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30: 359-364.

Hein, M., Pedersen, M.F. & Sand-Jensen, K. (1995): Size-dependent nitrogen uptake in micro- and macroalgae. Mar. Ecol. Prog. Ser. 118: 247-253.

Hessen, D.O. (1997): Stoichiometry in food webs - Lotka revisited. Oikos 79: 195-200.

Hofer, R. & Medgyesy, N. (1997): Growth, reproduction and feeding of dwarf char, *Salvelinus alpinus*, from an Alpine high mountain lake. Arch. Hydrobiol. 138: 509-524.

Holm, T. & Tuxen-Pedersen, F. (1975): Gudenåen 1984. Geologisk Institut, Århus Universitet. 108 pp.

Hosper, S.H. & Jagtman, E. (1990): Biomanipulation additional to nutrient control for restoration of shallow lakes in the Netherlands. Hydrobiologia 200/201: 523-534.

Hrbaček , J., Dvorakova, V., Korinek, V. & Prochazkova, L. (1961): Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Internat. Verein. Limnol. 14: 192-195.

Irvine, K., Bales, M.T:, Moss, B., Stansfield, J.H. & Snook, D. (1990): Trophic relations in Hickling Broad - a shallow and brackish eutrophic lake. Verh. Internat. Verein. Limnol. 24: 576-579.

Jacobsen, L., Perrow, M.R., Landkildehus, F., Hjørne, M., Lauridsen, T.L. & Berg, S. (1997): Interactions between piscivores, zooplanktivores and zooplankton in submerged macrophytes: preliminary observations from enclosure and pond experiments. Hydrobiologia 342/343: 197-205.

James, W.F. & Barko, J.W. (1990): Macrophyte influences on the zonation of sediment accretion and composition in a north-temperate reservoir. Arch. Hydrobiol. 120: 129-142.

Jansson, M. (1989): Role of benthic algae in transport of nitrogen from sediment to lake water in a shallow clearwater lake. Arch. Hydrobiol. 89: 101-109.

Jensen, H.S. & Andersen, F.Ø. (1992): Importance of temperature, nitrate and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. Limnol. Oceanogr. 37: 577-589.

Jeppesen, E., Jensen, J.P. & Kristensen, P. (1991): Fosfor i lavvandede søer. Vand & Miljø 3: 122-126. (In Danish)

Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. (1998): The structuring role of submerged macrophytes in lakes. Ecological Studies. Springer Verlag Vol. 131, 423 pp.

Jeppesen, E., Jensen, J.P., Kristensen, P., Søndergaard, M., Mortensen, E., Sortkjær, O. & Hansen, A-M. (1989): Bundplanters betydning for miljøkvaliteten i søer. Vand & Miljø 8: 345-349. (In Danish).

Jeppesen, E., Lauridsen, T.L., Mitchell, S.F., Christoffersen, K. & Burns, C. (1998): Trophic structure in the pelagial of 25 shallow New Zealand lakes: Changes along a nutrient and fish gradient (submitted).

Johansen, A.C., Blegvad, H. & Spärck, R. (1933-1936): Ringkøbing Fjords Naturhistorie i brakvandsperioden 1915-1931. Høst. (In Danish)

Jónasson, P.M. (1972): Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. Oikos Suppl. 14: 1-148.

Jónasson, P.M. (1977): Lake Esrom research 1967-1977. *In:* Hunding, C., ed. Danish Limnology Reviews and Perspectives. Fol. Limnol. Scand. 17: 49-54.

Jones, J.I., Moss, B. & Young, J.O. (1998): Periphyton-non-molluscan invertebrates-fish interactions in lakes. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 69-90.

Jürgens, K. (1994): The impact of *Daphnia* on microbial food webs - a review. Mar. Microb. Food Web 8: 295-324.

Jürgens, K. & Stolpe, G. (1995): Seasonal dynamics of crustacean zooplankton, heterotrophic nanoflagellates and bacteria in a shallow, eutrophic lake. Freshwat. Biol. 33: 27-38.

Jürgens, K. & E. Jeppesen, E. (1998): Cascading effects on microbial food web structure in a dense macrophyte canopy. 1997. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 262-273.

Kairesalo, T., Tátrai, I. & Luokkanen, E. (1997): Impacts of waterweed (*Elodea canadensis* Michx) on plankton-fish interactions in lake littoral. Verh. Internat. Verein. Limnol. 25: 000-000.

Kamp Nielsen, L. (1974): Mud-water exchange of phosphate and other ions in undisturbed sediment cores and factors affecting the exchange rates. Arch. Hydrobiol. 73: 218-237.

Kerfoot, W.C. (1974): Net accumulation rates and the history of cladoceran communities. Ecology 55: 51-61.

Kitchell, J.A. & Kitchell, J.F. (1980): Size-selective predation, light transmission and oxygen stratification: evidence from recent sediments of manipulated lakes. Limnol. Oceanogr. 25: 389-403.

Kristensen, P., Jensen, J.P. & Jeppesen, E. (1990): Simple empirical lake models. *In:* Miljøstyrelsen, ed. Nitrogen and phosphorus in fresh and marine waters. C-abstract: 125-145.

Kristensen, P., Søndergaard, M. & Jeppesen, E. (1992): Resuspension in a shallow eutrophic lake. Hydrobiologia 228: 101-109.

Lammens, E.H.R.R. (1986): Interactions between fishes and the structure of fish communities in Dutch shallow, eutrophic lakes. PhD thesis, Agricultural University Wageningen, the Netherlands.

Lampert, W. (1993): Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39: 79-88.

Lampert, W. & Muck, P. (1985): Multiple aspects of food limitation in zooplankton communities: the *Daphnia - Eudiaptomus* example. Arch. Hydrobiol. Beih. 21: 311-322.

Lauridsen, T.L., Jeppesen, E. & Andersen, F.Ø. (1993): Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: Impact of sediment composition and waterfowl grazing. Aquat. Bot. 46: 1-15.

Lauridsen, T.L., E. Jeppesen & M. Søndergaard (1994): Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish-manipulation. Hydrobiologia 275/276: 33-42.

Lauridsen, T.L. & Buenk, I. (1996): Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. Arch. Hydrobiol. 137: 161-176.

Lauridsen, T. L. & Lodge, D.M. (1996): Avoidance by *Daphnia magna* of fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. Limnol. Oceanogr. 41: 794-798.

Lauridsen, T.L., Jeppesen, E., Søndergaard, M. & Lodge, D. *(1998):* Horizontal migration of zooplankton: Predator-mediated use of macrophyte habitat. 1997. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 233-239.

Leah, R.T., Moss, B. & Forrest, D.E. (1978): Experiments with large enclosures in a fertile, shallow brackish lake. Hickling Broad, United Kingdom. Int. Revue. Gesamt. Hydrobiol. 63: 291-310.

Leavitt, P., Carpenter, S.R. & Kitchell, J.F. (1989): Whole-lake experiments: The annual record of fossil pigments and zooplankton. Limnol. Oceanogr. 34: 700-717.

Leibold, M.A. (1990): Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. Am. Nat. 134: 922-949.

Lindegaard, C. (1994): The role of zoobenthos in energy flow in two shallow lakes. Hydrobiologia 275/276: 313-322.

Luecke, C., Vanni, M.J., Magnuson, J.J., Kitchell, J.F. & Jacobson, P.J. (1990): Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the clearwater phase. Limnol. Oceanogr. 35: 1718-1733.

Lynott, S.T., Bryan, S.D. & Hill, T.D. (1995): Monthly and size-related changes in the diet of rainbow trout in Lake Oahe, South Dakota. J. Freshwat. Ecol. 10: 399-407.

Malthus, T. J. & Mitchell, S. F. (1990): On the occurrence, causes and potential consequences of low zooplankton to phytoplankton ratios in New Zealand lakes. Freshw. Biol. 22: 383-394.

Marsden, S. (1989): Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshw. Biol. 21: 139-162.

May, R.M. (1977): Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269: 471-477.

Mazumder, A. (1994): Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. Ecology 75: 1141-1149.

McIntosh, A.R. & Townsend, C.R. (1994): Inter-population variation in mayfly antipredator tactics: differential effects. Ecology 75: 2078-2090.

McNaught, D.C. (1975): A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. Int. Ver. Theor. Angew. Limnol. Verh. 19: 724-731.

McQueen, D.J., Post, J.R. & Mills, E.L. (1986): Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43: 1571-1581.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J. & Lean, D.R.S. (1989): Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monographs 59: 289-310.

Meijer, M.-L. & Hosper, H. (1997): Effects of biomanipulation in the large and shallow lake Wolderwijd, the Netherlands. Hydrobiologia. 392/343: 335-349

Meijer, M.L., de Haan, W., Breukelaar, A.W. & Buiteveld, H. (1990): Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia 200/201: 303-316.

Meijer, M.-L., Lammens, E.H.R.R., Raat, A.J.P., Klein Breteler & Grimm, M.P. (1995): Development of fish communities in lakes after biomanipulation. Netherlands Journal of Aquatic Ecology 29: 91-101.

Mills, E.L. & Forney, J.L. (1983): Impact on *Daphnia pulex* of predation by yellow perch in Oneida Lake, New York. Trans. am. Fish. Soc. 112: 154-161.

Mills, E.L., Forney, J.L. & Wagner, K.J. (1987): Fish predation and its cascading effect on the Oneida Lake food chain. *In:* Kerfoot, W.C. & Sih, A., eds. Predation: Direct and indirect effects on aquatic communities. University Press of New England, Hanover, New Hampshire, pp. 118-131.

Mitchell, S.F. & Perrow, M.R. (1998): Interactions between grazing birds and macrophytes. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 175-196.

Mortensen, E., Jeppesen, E., Søndergaard, M. &, Kamp Nielsen, L., eds. (1994): Nutrient dynamics and biological structure in shallow freshwater and brackish lakes. Kluwer Academic Publishers, reprinted from Hydrobiologia 275/276, 507 p.

Mortensen, E., Søndergaard, Ma., Jeppesen, E:, Timmermann, M., Jensen, H.J. & Müller, J.P. Fish community structure and changes in abundance of species in shallow hypertrophic Lake Søbygård (In prep.)

Mortimer, C.H. (1941): The exchange of dissolved substances between mud and water in lakes. I. J. Ecol. 29: 280-329.

Mortimer, C.H. (1942): The exchange of dissolved substances between mud and water in lakes. II. J. Ecol. 30: 147-201.

Moss, B. (1989): Water pollution and the management of ecosystems: a case study of science and scientist. *In:* Grubb, P.J. & Whittaker, R.H., eds. Toward a More Exact Ecology. Thirtieth Symposium of the British Ecological Society. Blackwell Scientific, Oxford: 401-422.

Moss, B. (1990): Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201: 367-378.

Moss, B. (1994): Brackish and freshwater lakes - different systems or variations on the same theme? Hydrobiologia 275/276: 1-14.

Moss, B., Stansfield, J., Irvine, K., Perrow, M. & Phillips, G. (1996): Progressive restoration of a shallow lake - a twelve-year experiment in isolation, sediment removal and biomanipulation. J. Appl. Ecol. 33: 71-86.

Muus, B.J. (1967): The fauna of Danish estuaries and lagoons. Medd. Danmarks Fiskeri- og Havundersøgelser. Ny Serie, bd. 5, nr. 1.

Noy-Meir, I. (1975): Stability of grazing systems – an application of predator prey graphs. J. Ecol. 63: 459-482.

Ogilvie, S.H. & Mitchell, S.F. (1995): A model of mussel filtration in a shallow New Zealand lake, with reference to eutrophication control. Arch. Hydrobiol. 133: 471-482.

Oksanen, L.D., Fretwell, S.D., Arruda, J. & Niemela, P. (1981): Exploitation ecosystems in gradients of primary productivity. Am. Nat. 118: 240-261.

Otterstrøm, C.V. (1927): Notat om Langesø, 12.-15. oktober 1927. Danmarks Fiskeri- og Havundersøgelser, 14 p. (In Danish)

Pace, M.L. & Funke, E. (1991): Regulation of planktonic microbial communities by nutrients and herbivores. Ecology 72: 904-914.

Paul, A.J., Leavitt, P.R., Schindler, D.W. & Hardie, A.K. (1996): Direct and indirect effects of predation by a calanoid copepod (subgenus: *Hesperodiaptomus*) and of nutrients in a fishless alpine lake. Can. J. Fish. Aquat. Sci. 52: 2628-2638.

Pennak, R.W. (1966): Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. Trans. Am. Microsc. Soc. 85: 329-349.

Pérez-Fuentetaja, A., McQueen, D.J. & Demers, E. (1996): Stability of oligotrophic and eutrophic planktonic communities after disturbance by fish. Oikos 75: 98-110.

Perrow, M.R., Stansfield, J.H., Jowitt, A.J.D.& Tench, L.D. (unpubl. ms): Macrophytes as a refuge for grazing zooplankton from fish predation.

Persson, A. (1997): Effects of fish predation and excretion on the configuration of aquatic food webs. Oikos 79: 137-146.

Persson, L. (1991): Behavioral response to predators reverses the outcome of competition between prey species. Behav. Ecol. Sociobiol. 28: 101-105.

Persson, L. (1993): Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. Oikos 68: 12-22.

Persson, L. & Greenberg, L.A. (1990): Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca fluviatilis.* Oikos 59: 97-106.

Persson, L. & Eklöv, P. (1995): Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76: 763-784.

Persson, L., Anderson, G., Hamrin, S.F. & Johansson, L. (1988): Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. *In:* Carpenter, S.R., ed. Complex interactions in lake communities. Springer Verlag, New York, pp. 45-65.

Persson, L. Diehl, S., Johansson, L. Andersson, G. & Hamrin, S.F. (1992): Trophic interactions in temperate lake ecosystems: a test of food chain theory. Am. Nat. 140: 59-84.

Petersen, B. (1994): Den økologiskse rolle for *Neomysis integer* i en lavvandet, eutrof brakvandssø. MSc-thesis, the National Environmental Research Institute and Biological Institute, Dept. of Zoology, Århus University, 63 p. (In Danish)

Phillips, G., Eminson, D.F. & Moss, B. (1978): A mechanism to account for macrophyte decline in progressively eutrophicated fresh waters. Aquat. Bot. 4: 103-126.

Phillips, G.L., Perrow, M.R. & Stansfield, J. (1996): Manipulating the fish-zooplankton interaction in shallow lakes: a tool for restoration. *In:* Greenstreet, S.P.R. & Tasker, M.L., eds. Aquatic predators and their prey. Oxford: Blackwell Scientific Publications, pp. 174-183.

Pokorny, J., Kvet, J.P., Ondok, J.P., Toul, Z. & Ostry, I. (1984): Production-ecological analysis of a plant community dominated by *Elodea canadensis*. Aquat. Bot. 19: 263-292.

Pont, D., Crivelli, A.J. & Guillot, F. (1991): The impact of three-spined sticklebacks on the zooplankton of a previously fish-free pool. Freshwat. Biol. 26: 149-163.

Rasmussen, K. (1995): Hald Sø blev reddet. Hedeselskabets tidsskrift. Vækst nr. 1 1995. (In Danish)

Reinertsen, H. & Olsen, Y. (1984): Effects of fish elimination on the phytoplankton community of a eutrophic lake. Verh. int. Verein. Limnol. 22: 649-658.

Reynolds, C.S. (1984): The ecology of freshwater phytoplankton. Cambridge University Press. Cambridge, 384 p.

Riemann, B. (1985): Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. Appl. Environ. Microbiol. 50: 187-193.

Riemann, B. & Mathiesen, H. (1977): Danish research into phytoplankton primary production. *In:* Hunding, C., ed. Danish Limnology Reviews and Perspectives. Fol. Limnol. Scand. 17: 49-54.

Riemann, B., Christoffersen, K., Jensen, H.J., Müller, J.P., Lindegaard, C. & Bosselmann, S. (1990): Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. Hydrobiologia 200/201: 241-250.

Ringelberg, J. (1991): Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). J. Plankton. Res. 13: 17-25.

Risgaard-Petersen, N.; Rysgaard, S., Nielsen, L.P. & Revsbech, N.P. (1994): Diurnal variation of denitrification in sediments colonized by benthic microphytes. Limnol. Oceanogr. 39: 573-579.

Rothaupt, K. O. (1997): Grazing and nutrient influences of *Daphnia* and *Eudiaptomus* on phytoplankton in laboratory microcosms. J. Plank. Res. 19: 125-139.

Rowe, D.K. & Chisnall, B.L. (1997): Size-related differences in diel feeding activity, prey selection and nocturnal migration strategy of the planktonic larvae of *Gobiomorphus cotidianus* in Lake Rotoiti (NI), New Zealand. Hydrobiologia (In press)

Røen, U. (1977): Revision of freshwater entomostracan fauna in the Thule Area, Angmassalik Area and Southwest Greenland. Fol. Limnol. Scand. 17: 107-110.

Sand-Jensen, K. & Borum, J. (1991): Interactions among phytoplankton, periphyton and macrophytes in temperate freshwaters and estuarines. Aquat. Bot. 41: 137-175.

Sarnelle, O. (1992): Nutrient enrichment and grazer effects of phytoplankton in lakes. Ecology 73: 551-560.

Sas, H. (ed.) (1989): Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation. Acad. Ver. Richardz Gmbh., 497 p.

Savino, J. & Stein, R.A. (1982): Predator-prey interaction between Largemouth Bass and Bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111: 255-266.

Scheffer, M. (1989): Alternative stable states in eutrophic shallow freshwater systems: a minimal model. Hydrobiol. Bull. 23: 73-85.

Scheffer, M. (1990): Multiplicity of stable states in freshwater systems. Hydrobiologia 200/201: 475-486.

Scheffer, M. (1998): Community dynamics of shallow lakes. Population and community biology series. London: Chapman & Hall. 22, 357 p.

Scheffer, M. & Jeppesen, E. (1998): Alternative stable states in shallow lakes. *In:* Jeppesen, E., Søndergaard, Ma, Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 397-407.

Schulze, P.C., Zagarese, E. & Williamson, C.E. (1995): Competition between crustacean zooplankton in continuous cultures. Limnol. Oceanogr. 40: 33-45.

Shapiro, J. (1990): Biomanipulation: the next phase - making it stable. Hydrobiologia 200/201: 13-27.

Shapiro, J., Lamarra, V. & Lynch, M. (1975): Biomanipulation: an ecosystem approach to lake restoration. *In:* Brezonik, P.L. & Fox, J.L., eds. Proc. Symp. on Water Quality Management Through Biological Control. University of Florida: 85-96.

Shapiro, J. & Wright, D.I. (1984): Lake restoration by biomanipulation. Round Lake, Minnesota - the first two years. Freshwat. Biol. 14: 371-383.

Smith, V.H. (1983): Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. Can. J. Fish. Aquat. Sci. 43: 1101-1112.

Sommer, U. (1985): Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. Limnol. Oceanogr. 30: 335-346.

Sommer, U., Gliwicz, Z.M., Lampert, W. & Duncan, A. (1986): The Plankton Ecology Group model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106: 433-472.

Stansfield, J.H., Perrow, M.R., Tench, L.D., Jowitt, A.J.D. & Taylor, A.A.L. (1997): Submerged macrophytes as refuges for grazing *Cladocera* against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. Hydrobiologia 342/343: 229-240.

Staples, D.J. (1975): Production biology of the upland bully *Philypnodon breviceps* Stokell in a small New Zealand lake II. Population dynamics. J. Fish. Biol. 7: 25-45.

Sterner, R.W. & Hessen, D.O. (1994): Algal nutrient limitation and the nutrition of aquatic herbivors. Annu. Rev. Ecol. Syst. 25: 1-29.

Sterner, R.W., Elser, J.J. & Hessen, D.O. (1992): Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry 17: 49-67.

Stevenson, A.C. et al. (1991): The Surface Waters Acidification Project Palaeolimnology Programme: Modern Diatom/Lake-water Chemistry Dataset. Ensis Ltd, London.

Swift, M.C. (1970): A qualitative and quantitative study of trout food in Castle Lake, California. California Fish and Game 56: 109-210.

Sægrov, H., Hobæk, A. & LÀbé-Lund, J.H. (1996): Vulnerability of melanic *Daphnia* to brown trout predation. J. Plank. Res. 18: 2113-1228.

Søndergaard, M. & Moss, B. (1998): Impact of submerged macrophytes on phytoplankton in shallow freshwater lakes *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 115-132.

Søndergaard, M., Kristensen, P. & Jeppesen, E. (1992): Phosphorus release from resuspended sediment in the shallow and wind exposed Lake Arresø, Denmark. Hydrobiologia 228: 91-99.

Søndergaard, M., Kristensen, P. & Jeppesen, E. (1993): Eight years of internal phosphorus loading and changes in the sediment phosphorus profile of Lake Søbygård, Denmark. Hydrobiologia 253: 345-356.

Søndergaard, M., Jeppesen, E. & Berg, S. (1997): Pike (*Esox lucius*) stocking as a biomanipulation tool, 2. effects on lower trophic levels in Lake Lyng, Denmark. Hydrobiologia 342/343: 319-325.

Søndergaard, M., Olufsen, L., Lauridsen, T., Jeppesen, E. & Vindbæk Madsen, T. (1996): The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. Aquat. Bot. 53: 73-84.

Søndergaard, M., Jeppesen, E., Mortensen, E., Dall, E., Kristensen, P. & Sortkjær, O. (1990): Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: A combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200/201: 229-240.

Søndergaard, Mo., Theil-Nielsen, J., Christoffersen, K., Schlüter, L., Jeppesen, E. & Søndergaard, Ma. (1998): Bacteria and carbon turnover in a dense macrophyte canopy. *In:* Jeppesen, E., Søndergaard, Ma, Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 250-261.

ter Braak, C.J.F. (1987): Unimodal models to relate species to environment. PhD thesis, University of Wageningen, the Netherlands.

ter Braak, C.J.F. & Juggins, S. (1993): Weighted averaging partial least squares regression (WAPLS): An improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269/270: 485-502.

Timmermann, M. (1987): Manglende reproduktion af skalle (*Rutilus rutilus* (L.)) og rudskalle (*Scardinius erythrophthalmus* (L.)) og skalle- (*R. rutilus* (L.)), brasen- (*Abramis brama* (L.)) og aborre- (*Perca fluviatilis* (L.)) yngelens densitet og vækst i Væng Sø. MSc-thesis, Miljøstyrelsens Ferskvands Laboratorium og Ferskvandsbiologisk Laboratorium, Københavns Universitet. (In Danish)

Timms, R.M &, Moss, B. (1984): Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceanogr. 29: 472-486.

Uhlmann, D. (1980): Stability and multiple steady states of hypertrophic ecosystems. *In:* Barica, J.M. & Mur, L. eds. Hypertrophic Ecosystems, pp. 235-247.

Van den Berg, M.S., Coops, H., Meijer, M.-L., Scheffer, M. & Simons, J. (1998): Clear water associated with a dense *Chara* vegetation in the shallow and turbid lake Veluwemeer, The Netherlands. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 339-352.

Van der Molen, D.T. & Boers, P.C.M. (1994): Influence of internal loading on phosphorus concentration in shallow lakes before and after reduction of external loading. Hydrobiologia 275/276: 479-492.

Van Donk, E. (1998): Switches between clear and turbid water states in a biomanipulated lake (1986-1996): the role of herbivory on macrophytes. *In:* Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christoffersen, K., eds. The structuring role of submerged macrophytes in lakes. Ecological Studies. New York: Springer Verlag 131: 290-297.

Van Donk, E., De Deckere, E., Klein Breteler, J.G.P. & Meulemans, J. (1994): Herbivory by waterfowl and fish on macrophytes in a biomanipulated lake: Effects on long-term recovery. Verh. int. Ver. Limnol. 25: 2139-2143.

Van Luijn, F.; Van der Molen, D.T.; Luttmer, W.J. & Boers, P.C.M. (1995): Influence of benthic diatoms on the nutrient release from sediments of shallow lakes recovering from eutrophication. Wat. Sci. Tech. 32: 89-97.

Viborg Amtskommune (1988): Miljøtilstanden i Ørslevkloster Sø 1986-1987. Viborg, Denmark. (In Danish)

Viborg Amtskommune (1995): Ørslevkloster Sø 1994. Belastning, fysisk-kemiske forhold, vegetation samt fiskebestand. Viborg, Denmark. (In Danish).

Vijverberg, J., Kalf, D.F. & Boersma, M. (1996): Decrease in *Daphnia* egg viability at elevated pH. Limnol. Oceanogr. 41: 789-794.

Watt, P. & Young, S. (1994): Effect of predator chemical cues on *Daphnia* behaviour in both horizontal and vertical planes. Anim. Behav. 48: 861-869.

Weisner, S., Eriksson, G., Granéli, W. & Leonardson, L. (1994): Influence of macrophytes on nitrate removal in wetlands. Ambio 23: 363-366.

Welch, E.B. & Cooke, G.D. (1995): Internal phosphorus loading in shallow lakes: importance and control. Lake and Reserv. Manage. 11: 273-281.

Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983): An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Wetzel. R.G. (1983): Limnology. Saunders College Publishing, New York, 767 p.

White, P.A., Jacob, K., Rasmussen, J.B. & Gasol, J.M. (1991): The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microb. Ecol. 21: 99-118.

Whiteside, M.C. (1988): 0^+ fish as major factors affecting abundance patterns of littoral zooplankton. Verh. Internat. Verein. Limnol. 23: 1710-1714.

Wiederholm, T. (1976): Chironomids as indicators of water quality in Swedish lakes. Naturvådsverkets Limnologiska Undersökninger Information 10: 197-214.

Windolf, J., Jeppesen, E., Søndergaard, M., Jensen, J.P. & Sortkjær, L. (1993): Vandmiljøplanens Overvågningsprogram 1992. Ferske vandområder – Søer. Faglig rapport fra DMU, nr. 90. 129 p. (In Danish)

Winfield, I.J. (1986): The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophalmus*, and perch, *Perca fluviatilis*. J. Fish. Biol. 29: 37-48.

Wium-Andersen, S., Anthoni, U., Christophersen, C. & Houen, G. (1982): Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (Charales). Oikos 39: 187-190.

Worgan, J.P. & FitzGerald, G.J. (1981): Diel activity and diet of three sympatric sticklebacks in tidal salt marsh pools. Can. J. Zool. 59: 2375-2379.

Wurtsbaugh, W.A. (1992): Food-web modification by an invertebrate predator in the Great Lake (USA). Oecologia 89: 168-175.

Århus Amtskommune (1979): Søbygård Sø 1978. (In Danish)

*Århus Kommune & Århus Amtskommune (1996):*Restaureringen af Brabrand sø – resultater og fremtid. Pjece fra Århus Kommunes Naturforvaltning. 12 p. (In Danish)

Appendix

Papers included in the dissertation

Hydrobiologia **200/201**: 205–218, 1990.
R. D. Gulati, E. H. R. R. Lammens, M.-L. Meijer & E. van Donk (eds), Biomanipulation – Tool for Water Management.

Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies

E. Jeppesen,[1] M. Søndergaard,[1] E. Mortensen,[1] P. Kristensen,[1] B. Riemann,[2] H. J. Jensen,[3] J. P. Müller,[3] O. Sortkjær,[1] J. P. Jensen,[1] K. Christoffersen,[4] S. Bosselmann[5] & E. Dall[6]
[1] *National Environmental Research Institute, 52, Lysbrogade, DK-8600 Silkeborg, Denmark;*
[2] *International Agency for 14C Determination Water Quality Institute, 15, Agern Allé, DK-2970 Hørsholm, Denmark;* [3] *Fish Ecology Laboratory, 31 A, Classensgade, DK-2100 Copenhagen, Denmark;*
[4] *Freshwater Biological Laboratory, University of Copenhagen, 51, Helsingørsgade, DK-3400 Hillerød, Denmark;* [5] *Environmental Biology Laboratory, 5, Baunebjergvej, DK-3050 Humlebaek, Denmark;*
[6] *County of Vejle, Dept. Technique and Environment, 12, Damhaven, DK-7100 Vejle, Denmark*

Key words: lake restoration, biomanipulation, trophic cascade, shallow, eutrophic, lakes, cross-analysis

Abstract

The use of fish manipulation as a tool for lake restoration in eutrophic lakes has been investigated since 1986 in three shallow, eutrophic Danish lakes. The lakes differ with respect to nutrient loading and nutrient levels (130–1000 μg P l^{-1}, 1–6 mg N l^{-1}). A 50% removal of planktivorous fish in the less eutrophic cyanobacteria-diatom dominated Lake Væng caused marked changes in lower trophic levels, phosphorus concentration and transparency. Only minor changes occurred after a 78% removal of planktivorous fish in eutrophic cyanobacteria dominated Frederiksborg Castle Lake. In the hypertrophic, green algae dominated Lake Søbygård a low recruitment of all fish species and a 16% removal of fish biomass created substantial changes in trophic structure, but no decrease in phosphorus concentration. The different response pattern is interpreted as (1) a difference in density and persistence of bloomforming cyanobacteria caused by between-lake variations in nutrient levels and probably also mixing- and flushing rates, (2) a difference in specific loss rates through sedimentation of the algal community prevaling after the fish manipulation, (3) a decreased impact of planktivorous fish with increasing mean depth and (4) a lake specific difference in ability to create a self-increasing reduction in the phosphorus level in the lake water. This in turn seems related to the phosphorus loading.

Introduction

Since the early work of Hrbácek *et al.* (1961) and Hrbácek (1962) several papers have demonstrated that changes in biomass and age structure of planktivorous fish stock can markedly affect trophic structure and lake water quality (e.g. Stenson *et al.*, 1978; Andersson *et al.*, 1978; Shapiro, 1980; Lynch & Shapiro, 1981; Andersson & Cronberg, 1984; Cryer *et al.*, 1986). These studies have stimulated the use of fish manipulation as a restoration tool, either as measures *per se* or in combination with reduced external nutrient loading. However, few whole-lake experiments have been made (seen Benndorf, 1987; Van Donk *et al.*, 1989; Meijer *et al.*, 1989), and these have mainly dealt with short-term effects of very substantial reductions in fish density. Few studies (Henriksson *et al.*, 1980; Benndorf *et al.*, 1988; Reinartsen *et al.*, in press) have continued sufficiently long to test the long-term stability of changes in the fish stock structure.

Currently, some of the key questions concerning fish manipulation as a restoration tool, i.e. the questions of long-term stability and threshold levels for permanent improvements, therefore, can mainly be addressed to theoretical analysis (Benndorf & Rechnagel, 1982; Kasprzak *et al.*, 1988; Persson *et al.*, 1988; Scheffer, 1989 and 1990) or by empirical approaches (McQueen *et al.*, 1986).

This first part of the paper deals with short term effects of fish manipulation in shallow eutrophic lakes doing a cross-analysis of whole-lake experiments in three Danish lakes. In the second part (Jeppesen *et al.*, 1990) we discuss the question of thresholds for a long-term stability by including data from 300 shallow Danish lakes.

Study areas

The three case-studies were carried out in Frederiksborg Castle Lake (21 ha) situated in Hillerød on Zealand, Lake Væng (15 ha) near Brædstrup, and Lake Søbygård (40 ha) near Hammel, both in Jutland. Lake Væng and Lake Søbygård are completely mixed, shallow (mean depth about 1 m) and have high flushing rates (15–25 days), while Frederiksborg Castle Lake is stratified in summer, deeper (mean depth 3.1 m) and has a long hydraulic retention time (4–18 years) (Table 1).

Table 1. Morphometric data of the study lakes.

Lake		Surface area ($10^4\,m^2$)	Catchment area ($10^4\,m^2$)	Maximum depth (m)	Mean depth (m)	Hydraulic retention time (y)	Stratified in summer
Lake Væng	(LV)	15	900	2	1.2	0.04–0.05	no
Frederiksborg Castle Lake	(FCL)	21	660	8	3.1	4–18	yes
Lake Søbygård	(LS)	40	1160	2	1.0	0.04–0.06	no

Table 2. External phosphorus and nitrogen loadings and mean summer concentration (1st May to 1st Oct.) of total phosphorus and total nitrogen.

Lake		Loading		Concentration	
		$g\,P\,m^{-2}\,y^{-1}$	$g\,N\,m^{-2}\,y^{-1}$	$\mu g\,P\,l^{-1}$	$mg\,N\,l^{-1}$
Lake Væng	(LV)				
before 1981:		4	78		
after 1981:		1.5	71	130	1
Frederiksborg Castle Lake	(FCL)	?	?	300–700	2–4
Lake Søbygård	(LS)				
before 1982:		27–33	130–210	550–1000	4–6
after 1982:		4–7			

Lake Væng and Frederiksborg Castle Lake are eutrophic, while Lake Søbygård is hypertrophic (Table 2). The nutrient loadings to Lake Væng and Lake Søbygård were reduced in the early eighties. In Lake Væng the nitrogen loading and in particular the phosphorus loading were reduced in 1981 by sewage diversion (Table 2). Because of high internal loading only minor improvements in water quality were recorded during the following five years prior to the biomanipulation experiment (Søndergaard *et al.*, 1990). In Lake Søbygård phosphorus loading was reduced in 1982 by chemical treatment at the sewage plant (Table 2). No data for the nutrient loading of Frederiksborg Castle Lake are available. For further details see Table 1 and Table 2, Søndergaard *et al.* (1990), Jeppesen *et al.* (1989a,b and 1990a in press), and Riemann *et al.* (1990).

Materials and methods

Most of the methods used have been described elsewhere (Søndergaard *et al.*, 1990a,b; Riemann *et al.*, 1990; Jeppesen *et al.*, 1990a,b). Therefore, only additional methods used in the present analysis are described.

The fish stock was estimated by the mark-recapture method prior to the manipulation, except from young-of-the-year, which was estimated by setting buoyant nets several days in mid August. Planktivorous fish were removed by fishing with different fish gears including beach seine, electrofishing and gill, fyke and pound nets. The dry weight was assumed to be 25% of the wet weight (from Penczak, 1985).

Zooplankton biomass in Lake Væng and Lake Søbygård was estimated from length-weight equations (rotifers: Dumont *et al.*, 1975; cladocerans: Bottrell *et al.*, 1976). When possible 50 individuals of each *Daphnia* species and 20 individuals of all other filter-feeders, which contributed significantly to the total biomass at the specific sampling date, were selected randomly and measured using a digitalized micrometer connected to the microscope. The biomass of filter feeding crustaceans in Frederiksborg Castle Lake was found by direct measurements (Cahn-microbalance) of pre-dried (105 °C) subsamples of each species, divided into various size-groups.

The phytoplankton volume in Lake Væng and Lake Søbygård was estimated by fitting the species or subspecies at each sampling date to simple geometrical figures. The biovolume in Frederiksborg Castle Lake was estimated from the size-fractioned chlorophyll-*a* concentrations ($> 50\,\mu$m, $< 50\,\mu$m) using a conversion factor between chlorophyll-*a* and biovolume (0.13 ± 0.02 (S.E.) mg DW (μg chlorophyll-a^{-1})) obtained from Lake Væng data from 1986, when cyanobacteria dominated. The dry weight of phytoplankton in all three lakes was calculated using a conversion factor between the carbon content and biovolume of 0.22 μg C m^{-3} (Reynolds, 1984), and between carbon and dry weight of 2.2 g DW g C^{-1} (Winberg, 1971). The conversion factor was validated successfully on Lake Søbygård data using the particulate COD-concentration, which during most of the summer represent the content of phytoplankton. Using the O_2/dry weight factor of Winberg (1971) the mean dry weight in summer (May to Oct.), based on particulated COD, could be estimated for 1984–1987 to 51, 47, 25, and 16 mg DW l^{-1}, respectively, while the conversion factor used in the analysis gave 52, 46, 28, and 14, respectively.

Results

Fish stock and fish manipulation

Bream (*Abramis brama*), roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) dominated the planktivorous fish stock in the three lakes both in terms of biomass and numbers, while pike (*Esox lucius*), large perch (*Perca fluviatilis*) and in Frederiksborg Castle Lake also zander (*Stizostedion lucioperca*) were the most abundant piscivorous. Planktivorous fish biomass was reduced by 50% in Lake Væng to 15 g WW m^{-2}, and in Frederiksborg Castle Lake by 78% to 8 g WW m^{-2} in 1986 and 1987. Furthermore, 1.5 g WW m^{-2} of piscivorous

Table 3. Artificial biomass removal of planktivorous and increase in biomass of piscivorous fish in the study lakes.

	Lake Væng (LV)	Frederiksborg Castle Lake (FCL)	Lake Søbygård (LS)
Removal of planktivorous fish biomass (g WW m^{-2})	1986–1987	1986	1988
Roach	8	14	
Bream	8	9	10
Rudd	<0.1	<0.1	
Crucian carp	<0.1	4	
Total	16	27.5	10
Reduction %	50	78	17
Stocking of piscivorous fish biomass (g WW m^{-2})	1986–1987	1986	1988
Perch	0	1.5	0
Increase %	0	15	0

perch was stocked in Frederiksborg Castle Lake (Table 3).

In Lake Søbygård no recruitment of bream, roach or rudd took place during 1983–1986. This was probably due to high pH values reaching about 10.5–11.0 in the spawning period. The age group composition of the planktivorous fish stock in 1986, therefore, was composed of 6–8 years old bream, 4–11 years old roach and 4–8 years old rudd. In 1987 and 1988, some recruitment took place, but the survival was low. In 1986–1988 2%, 1% and 14%, respectively, of the calculated biomass in 1986 (63 g WW m^{-2}), were removed by experimental and commercial fishing.

Changes in the lower trophic levels

The three lakes responded differently to changes in the fish stock (Fig. 1). Hence, pronounced changes occurred in the lower trophic levels in the less eutrophic Lake Væng and in the hypertrophic Lake Søbygård. Only minor changes were observed in eutrophic Frederiksborg Castle Lake (Fig. 1 and Figs. 2–4).

Lake Væng

Immediately after the fish manipulation the biomass of filter feeding zooplankton increased from a mean summer level of 0.4 mg DW l^{-1} in 1986 to 2.7 and 1.3 mg DW l^{-1} in 1987 and 1988, respectively (Fig. 1). Zooplankton composition shifted from rotifers to dominance of larger cladocerans (*Daphnia* and *Bosmina* spp.). Simultaneously, the biomass of large algal species (greatest axial length or diameter (GALD) $> 50\ \mu m$) decreased from 5.9 mg DW l^{-1} in 1986 to 3.0 in 1987 and 0.8 mg DW l^{-1} in 1988. Small species (GALD $< 50\ \mu m$) decreased from 4.2 mg DW l^{-1} in 1986 to 2.5 in 1987 and 2.3 mg DW l^{-1} in 1988. The biomass ratio of large filter feeding zooplankton to phytoplankton increased from 0.03 in 1986 to 0.50 in 1987 and 0.45 in 1988.

The dominating cyanobacteria (mainly *Anabaena flos-aquae*) and small diatoms (mainly *Stephanodiscus hantzschii*) almost disappeared after fish manipulation, whereas cryptophytes and periodically larger species such as *Asterionella formosa* and *Closterium* sp. appeared in higher densities.

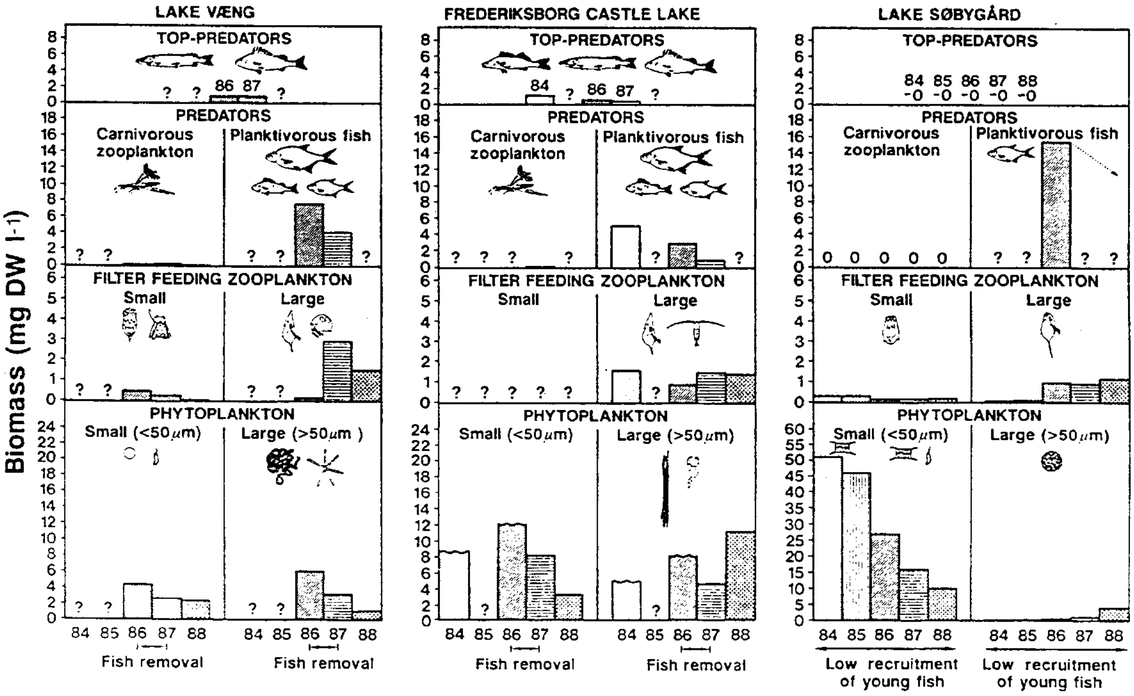

Fig. 1. The biomass of different biological components in the three lakes before and after fish manipulation. The wave forms at the top of the phytoplankton columns in Frederiksborg Castle Lake in 1984 and 1986 indicate that no data on the size of phytoplankton are available those two years, but the ratio of small to large algae in 1987 has been used as a conversion factor. The ratio in Frederiksborg Castle Lake in 1988 is also uncertain because of lack of data on the size distribution in May–June that year. Note the different phytoplankton scale.

Chlorophyll-*a* concentrations decreased and transparency increased during the major part of summer following the fish removal (Figs. 2 and 3). Median values of chlorophyll-*a* were 81, 36 and 24 $\mu g\ l^{-1}$ in 1986, 1987 and 1988, respectively. Median transparency was 56 and 57 cm in 1984–1986 and 98 cm to 140 cm in 1987–1988.

The concentration of total phosphorus decreased from 157–178 μg P l^{-1} in the pre-biomanipulation period (1978, 1986) to 125 μg P l^{-1} in 1987 and 81 μg P l^{-1} in 1988 (Fig. 4). Further details are presented by Søndergaard *et al.* (1990).

Frederiksborg Castle Lake

Comparatively minor changes were observed in Frederiksborg Castle Lake after the reduction of planktivorous fish (Fig. 1, Figs. 2–4).

The large zooplankton filter feeders were dominated by *Daphnia cucullata* and *Eudiaptomus graciloides*. No changes occurred in the mean summer biomass of filter feeding zooplankton (0.8 and 1.4 mg DW l^{-1} before, and 1.2 and 1.3 mg DW l^{-1} after fish manipulation).

No changes occurred in the mean phytoplankton biomass in surface water (12–20 mg DW l^{-1} before, 12–13 mg DW l^{-1} after fish manipulation). However, median chlorophyll-*a* values decreased from 80–152 $\mu g\ l^{-1}$ to 62–69 $\mu g\ l^{-1}$ (Fig. 2) suggesting that the periods with low chlorophyll content might have been prolonged (Fig. 2). The relative proportion of large algae (GALD > 50 μm) seems to have increased from about 40% in the first year after the fish manipulation to 80% in the second year (only few data were, however, available for 1988). Blooms of cyanobacteria occurred between June and October, dominated by *Microcystis* in 1986. In 1988, *Microcystis* was replaced by *Aphanizomenon*

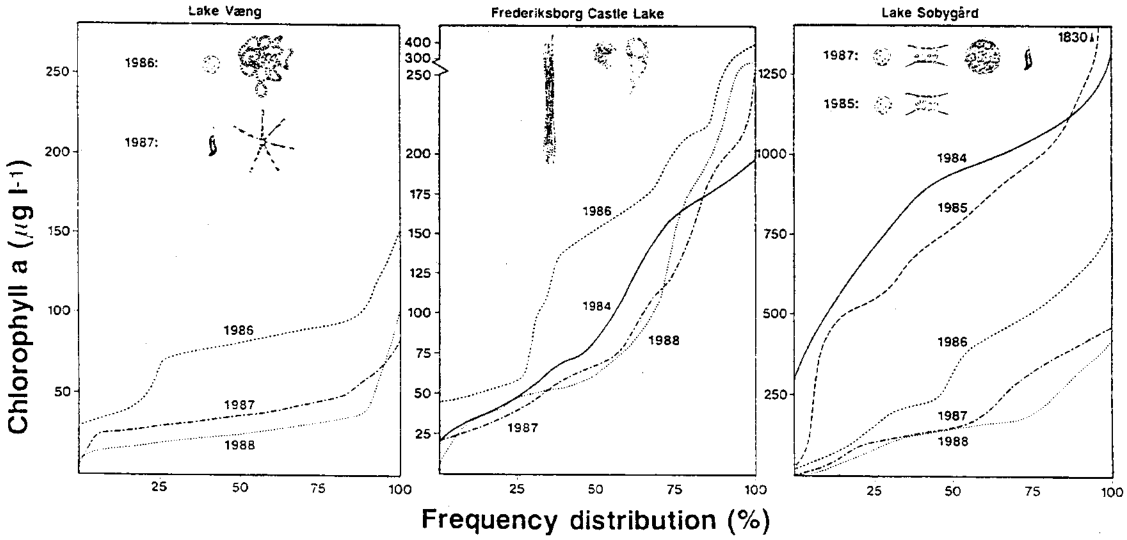

Fig. 2. Frequency distribution of chlorophyll-*a* (1st May to 1st Oct.) in Lake Væng, Frederiksborg Castle Lake and Lake Søbygård in the years before and after reduction of the planktivorous fish stock. Note the different chlorophyll-*a* scales.

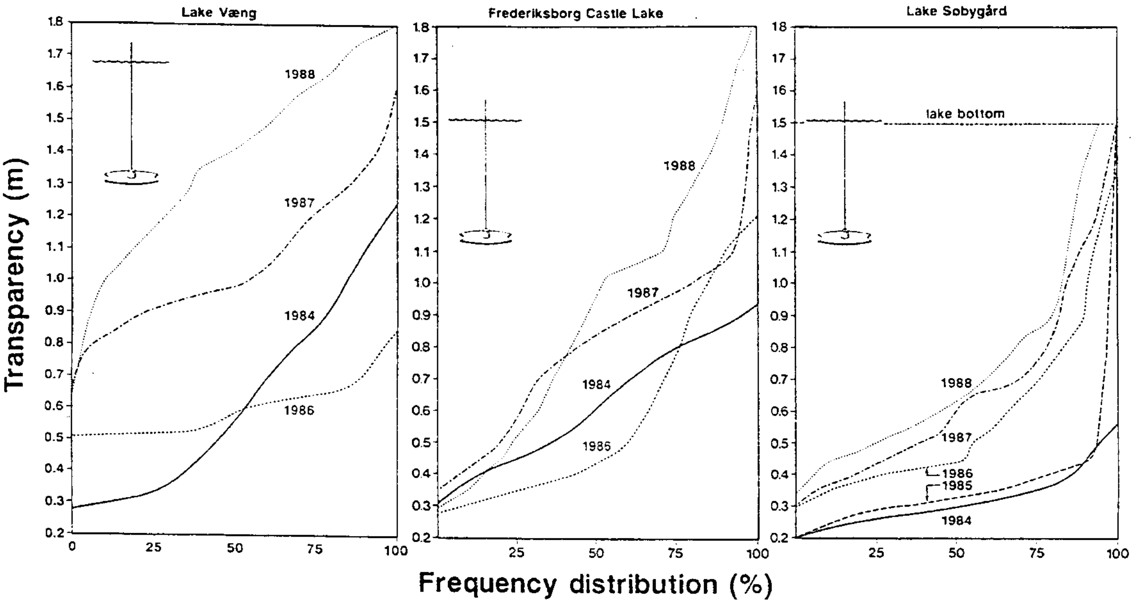

Fig. 3. Frequency distribution of Secchi-depth (1st May to 1st Oct.) in Lake Væng, Frederiksborg Castle Lake and Lake Søbygård in the years before and after reduction of the planktivorous fish stock.

in late summer. The biomass ratio of large filter feeding zooplankton to phytoplankton ranged from 0.07–0.11 before the fish manipulation to 0.09–0.10 after the fish manipulation.

Median values of lake transparency increased from 44–60 cm in 1984–1986 to 84–95 cm in 1987–1988.

Further details are presented by Riemann *et al.* (1990).

Lake Søbygård

Mean summer biomass of filter feeding zooplankton increased from 0.02 mg DW l^{-1} in 1984–1985 to 0.8–1.2 mg DW l^{-1} in 1986–1988 (Fig. 1). Species composition changed from rotifer dominance in 1984 and 1985 to cladoceran dominance (*B. longirostris* and *D. longispina*) in 1986–1988. Mean phytoplankton biomass decreased steadily from 52 mg DW l^{-1} in 1984 to 14 mg DW l^{-1} in 1988. Qualitatively, the phytoplankton community changed from a monoculture of *Scenedesmus* spp. to a more diverse community of *Scenedesmus, Chlorella, Stephanodiscus* and periodically also cryptophytes.

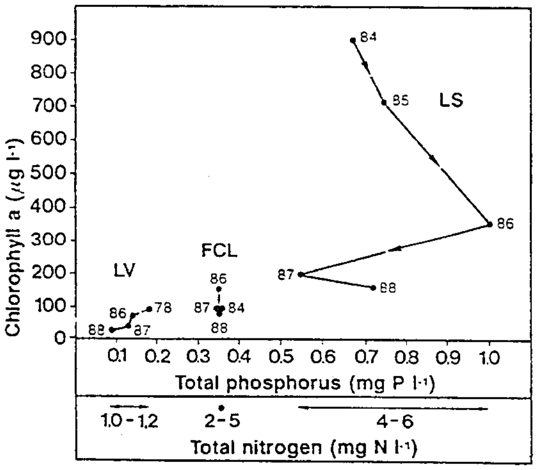

Fig. 4. Mean chlorophyll-*a* concentration in the surface water in relation to mean lake water concentration of total phosphorus (1st May to 1st Oct.) and total nitrogen in Lake Væng (LV), Frederiksborg Castle Lake (FCL) and Lake Søbygård (LS) in the years before and after reduction of the planktivorous fish stock.

During periods of high zooplankton grazing in 1986–1988 the less edible or the less digestible algae *Pediastrum*, *Oocystis* and *Coelastrum* were important contributors to the phytoplankton biomass. The increase of large algae could, however, in no way balance the decrease of small algae (Fig. 1). The ratio of zooplankton to phytoplankton biomass was 0.003 in 1984–1985 and 0.10 in 1988.

Summer chlorophyll-*a* decreased, while transparency increased progressively from 1985 to 1988 (Figs. 2 and 3). The median concentration of chlorophyll-*a* decreased from 940 μg l^{-1} in 1984 to 140 μg l^{-1} in 1987–1988, but the improvements were even more pronounced in the upper quartiles indicating that not only the level but also the duration of the periods with relative low chlorophyll-*a* levels increased (Fig. 2). The median transparency was 30–32 cm in 1984–85 and 60–63 cm in 1987–88 (Fig. 3).

The concentration of total phosphorus varied between years. Except for the cold summer of 1987 there was a tendency towards increasing mean phosphorus levels in connection with the changes of the trophic structure (Fig. 4). Further details are presented by Jeppesen *et al* (1989a, b, and 1990a), Søndergaard *et al.* (1990b).

Discussion

Impact of planktivorous fish

Prior to fish manipulation the density of planktivorous fish was sufficiently high in all three lakes to affect composition and density of the zooplankton, though the predation pressure seemed different. Hence, in the two shallow and completely mixed lakes (Lake Væng, Lake Søbygård) with a high biomass of planktivorous fish per unit of volume (8–15 mg DW l^{-1}) (Fig. 1) the large filter feeding cladocerans were almost absent during summer, in spite of high densities of small and edible algae (*Stephanodiscus hantzschii*) in Lake Væng, and *Scenedesmus* spp. in Lake Søbygård. Instead rotifers dominated, although they occurred in low densities in Lake Søbygård, probably because of high pH (summer mean 10.3–10.6, maximum 11.2) (Jeppesen *et al.*, 1990a). Moreover, carnivorous *Leptodora* occurred in low densities (Lake Væng) or were not recorded at all (Lake Søbygård). These results are in agreement with the top-down control and size-efficiency hypothesis (McQueen *et al.*, 1986, and Dodson, 1974, respectively) and indicate a high predation pressure from planktivorous fish.

The biomasses of large filter feeding zooplankton per unit of volume were, however, 5–10 times higher in Frederiksborg Castle Lake in the pre-manipulation period than in Lake Væng and Lake Søbygård though the biomass of planktivorous fish per unit of surface area was equally high in Frederiksborg Castle Lake and in Lake Væng (Table 3). Because the biomass of edible algae was much above the threshold level of food limitation for cladocerans (~ 0.2 mg C l^{-1}, Lampert *et al.*, 1986) both in Lake Væng and in Lake Søbygård the different density of cladocerans can only be explained by differences in predation pressure (in Lake Søbygård also high pH (Jeppesen *et al.*, 1990a)) most likely related to the 2- to 3-fold and 3- to 6-fold higher density of planktivorous fish per unit of volume in Lake Væng and Lake Søbygård, respectively.

The impact of planktivorous fish seems to increase with decreasing mean depth. This is indicated by the higher density of planktivorous fish per unit of volume in Lake Væng and Lake Søbygård compared with the deeper Frederiksborg Castle Lake, and by the higher ratio of planktivorous fish to larger filter feeding zooplankton biomass in the two shallow lakes (40 in Lake Væng, 750 in Lake Søbygård and only 4 in Frederiksborg Castle Lake) (Fig. 1).

Several factors may be involved: (1) The production of prey zooplankton per unit of volume is potentially higher in shallow lakes due to the higher primary production per unit of volume and the fact that the residence volume for zooplankton (low water column) is more restricted. Therefore, if planktivorous fish are only feeding on cladocerans when the concentration is above a certain threshold level (Townsend *et al.*, 1986), and if the shift to other food sources occurs at almost the same concentrations in deep as well as in shallow lakes, the areal density of cladocerans in the shallow lake may be reduced to levels far below the densities in the deeper lakes. (2) The higher gross and net loss of phytoplankton by sedimentation in shallow lakes (Kristensen & Jensen, 1987) in comparison with deeper lakes, and the consequently higher quality of food in the upper sediment layer improve the conditions for potentially zooplanktivorous fish such as roach and especially bream to sustain high densities by using sediment including benthic organisms as an alternative food source. Therefore, we suggest that the potential predation pressure on cladocerans is continuously high in eutrophic, shallow lakes with low densities of piscivorous fish. (3) The ability of cladocerans to avoid predation by vertical migration probably increases with increasing depth (Harris, 1986), and even when they escape to the sediment surface in shallow lakes they may be strongly exposed to predation from planktivorous fish (Winfield & Townsend, 1988). (4) Finally, the higher temperature in shallow lakes may favour planktivorous fish, because young roach is favoured in the competition with young perch at high temperatures (Lessmark, 1983).

In summary we suggest that due to a potentially higher predation pressure from fish the possibilities for the cladocerans to regulate edible phytoplankton species is relatively lower in eutrophic, shallow lakes than in deeper lakes as long as the density of planktivorous fish is high. In contrast, the potential grazing pressure of cladocerans is expected to be higher in shallow lakes than in deeper lakes when the planktivorous fish density is low, because cladocerans in shallow lakes may utilize detritical food sources and thereby maintain sufficient high densities to control successive phytoplankton blooms (Harris, 1986, and unpubl. results from Lake Søbygård). This also implies that accidental fish kill or removal of planktivorous fish may have a stronger impact on the algal biomass in shallow lakes than in deeper lakes.

Traditionally, critical levels of planktivorous fish, above which daphnia populations may severely be depressed, are most often determined per unit of area. Critical levels have ranged from 20–30 kg ha^{-1} (Mills *et al.*, 1987), 30–50 kg ha^{-1} (McQueen & Post, 1988), 45 kg ha^{-1} (Walker, 1989), > 150 kg ha^{-1} (Søndergaard *et al.*, 1990), >600 kg ha^{-1} (this paper) to 900 kg ha^{-1} (Gliwicz & Prejs, 1977). Different size composition of the fish stock and thus variations in the predation on zooplankton per unit of fish biomass may partly explain the large variation in the critical density. However, our results also suggest that the critical density should more likely be expressed per unit of volume, because the critical density is not independent of, but in fact seems very sensitive to lake depth. Depth differences may thus also explain part of the large variations in the published critical densities.

Impact of cyanobacteria

The remarkable different response following the induced changes in the fish structure cannot be explained by variations in the efficiency of the fish manipulations. Hence, though the composition and age structure of planktivorous fish were almost identical in Lake Væng and in Frederiksborg Castle Lake before biomanipulation, the top-down response to a 50% reduction of the biomass in Lake Væng was much more pronounced than in the more substantial fish manipulation in Frederiksborg Castle Lake (Fig. 1). It cannot be referred directly to the eutrophication level either, because the most eutrophic Lake Søbygård showed a significant top-down response to comparatively minor changes in biomass of planktivorous fish. Instead, as discussed in the following, we suggest that the different response is mainly due to differences in phytoplankton composition and persistence of cyanobacteria related to differences in nutrient levels and perhaps also mixing conditions and flushing rates.

The low response in Frederiksborg Castle Lake compared to that in Lake Søbygård may be related to the phytoplankton composition. Hence, whereas the small green algae occurring in Lake Søbygård are nutritious and easily ingested (Infante, 1973; Geller, 1975; Horn, 1981), the cyanobacteria species occurring in Frederiksborg Castle Lake have been shown to affect growth and mortality of large filter feeders: (1) by producing toxics and noxious chemicals (Arnold, 1971; Lampert, 1981), (2) by being poorly assimilated (Arnold, 1971), (3) by inhibiting feeding on co-occurring nutritious food (Gliwicz, 1975; Fulton & Pearl, 1987). Nevertheless, a marked top-down response and an almost complete disappearance of cyanobacteria was observed in the cyanobacteria dominated Lake Væng. It has been shown in several studies that the interference of cyanobacteria on cladocerans increases with increasing proportions and densities of filamentous or colonial cyanobacteria (Lampert, 1981; Richman & Dodson, 1983; Fulton & Pearl, 1987; Burns *et al.*, 1989; Davidowicz *et al.*, 1988; De Bernardi & Giussani, 1990; Gliwicz, 1990). Hence, in laboratory experiments Davidowicz *et al.* (1988) showed that clutch size of *Daphnia magna* was severely depressed when the chlorophyll-*a* level of cyanobacteria was above approx. 60 $\mu g\ l^{-1}$ and reached zero above 150 $\mu g\ l^{-1}$, in the latter case followed by disappearance of daphnids a few days later. Although based on laboratory experiments, where the cladocerans in contrast to the lake situation cannot escape from high densities, these results give evidence of a higher grazing resistance of cyanobacteria in Frederiksborg Castle Lake. Hence, the chlorophyll-*a* in Lake Væng prior to fish manipulation never exceeded 150 $\mu g\ l^{-1}$ although the cladoceran density was low (Figs. 1 and 2) and below 100 $\mu g\ l^{-1}$ during 88% of days in summer, while chlorophyll-*a* in Frederiksborg Castle Lake exceeded 150 $\mu g\ l^{-1}$ during 30–52%, 100 $\mu g\ l^{-1}$ during 44–69% of the days in summer, and reached maximum levels of 250–400 $\mu g\ l^{-1}$ in late summer (Fig. 2).

However, the nutrient level may also have been a determining factor. This is supported by data from 200 Danish lakes with mean depths less than 3 m showing that at total phosphorus (Fig. 1, Jeppesen *et al.*, 1990b) and total nitrogen concentrations (unpubl. data), similar to those in the surface waters of Frederiksborg Castle Lake, cyanobacteria are most often dominant during summer. In contrast, the two nutrients in Lake Væng were at lower concentrations, where cyanobacteria dominate less frequently, and where a minor reduction in the nutrient concentration may create large changes in the phytoplankton community.

The difference in competition capacity of cyanobacteria in Frederiksborg Castle Lake and Lake Væng may, however, also be influenced by lake morphometry and hydraulic retention time. Hence, Lake Væng is completely mixed during summer, while Frederiksborg Castle Lake is stratified with oxygen depletion occurring in the hypolimnion, which may increase the competitive capacity of bloom-forming cyanobacteria such as *Microcystis* (George & Heaney, 1978; Reynolds & Walsby, 1975). Furthermore, the Lake Væng has an extremely short retention time in comparison with Frederiksborg Castle Lake (Table 1). This affects the phytoplankton community in two ways. First, it implies a high Si/P-ratio during summer in Lake Væng (approx. 100) due to the high loading of silicate-rich water favouring the diatoms (Tilman *et al.*, 1986). From the latter work a competitive exclusion of cyanobacteria by diatoms at the Si/P-ratio in Lake Væng seems possible. Second, it implies that the competitive capacity of slow-growing cyanobacteria probably was affected negatively by both the high flushing rate (Reynolds, 1984) and the consequently higher impact of CO_2-rich waters and lower pH (Shapiro, 1980; Benndorf *et al.*, 1988).

Besides the effects of nutrient levels, the persistence of cyanobacteria is also suggested to be sensitive to the extent of fish removal. Thus, a total removal of the fish stock almost eliminated the former dominating cyanobacteria in a number of small lakes (Van Donk *et al.*, 1989; Faafeng & Brabrand, submitted; Reinertsen *et al.*, in press) with nutrient levels, where cyanobacteria is expected to be favoured (Fig. 1, Jeppesen *et al.*, 1990b). Elimination of cyanobacteria was also found in fish free experimental enclosures in Frederiksborg Castle Lake (Riemann & Søndergaard, 1986) and in pleasant Pond (Lynch & Shapiro, 1981), while in contrast, cyanobacteria were still dominant in the two lakes where the enclosure experiments were carried out after an extensive reduction. Hence, even in lakes where the competitive capacity of cyanobacteria is supposed to be high, cyanobacteria may be excluded on a short-term scale, when all fish are eliminated. In such lakes drastic changes in the fish stock may, however, create large instabilities (Benndorf *et al.*, 1988) accompanied by negative side effects, e.g. high ammonia concentration, low oxygen concentration, high densities of trematodes causing human skin irritation (Van Donk *et al.*, 1989). Furthermore, the fish manipulation probably needs to be repeated frequently to avoid re-appearance of cyanobacteria.

Fish elimination may, however, also stimulate cyanobacteria in some lakes. Thus *Aphanizomenon flos-aquae* often occurs in small lakes and ponds at high densities of large daphnids, where *Aphanizomenon* by forming flakes partly avoids being grazed (Hrbácek, 1964; Lynch, 1980; Fott *et al.*, 1980; Shapiro, 1980). In that case both the chlorophyll-*a* content and transparency may be high. A transition to an *Aphanizomenon-Daphnia magna* community and high transparency occurred in Lake Søbygård in the seventies in connection with major fish kill (Jeppesen *et al.*, in prep.), and a shift from dominance of *Microcystis* to mainly *Aphanizomenon* (partly as flakes) has been found in Frederiksborg Castle Lake in connection with the fish manipulation (Riemann *et al.*, 1990; Simonsen & Stensgaard, unpubl. results). This may also explain the higher transparency in Frederiksborg Castle Lake in 1987–1988.

Impact on size distribution of phytoplankton

The size distribution of phytoplankton responded differently following fish manipulations (Fig. 1c). According to theoretical investigations (Briand & McCauley, 1978) and experimental work (e.g. McCauley & Briand, 1979; Lynch & Shapiro, 1981) the biomass of large algae (Fig. 1), and less edible or fast growing algae, increased in Lake Søbygård following the increase in grazing pressure from large filter feeders. Despite the high nutrient level in Lake Søbygård the increase in biomass of large algae was, however, much less than the decrease in small algae. This is in contradiction to what has been found in some cyanobacteria lakes (Benndorf, 1987), which may be interpreted by differences in sensitivity to loss through sedimentation being high for green algae and most often low for cyanobacteria (Reynolds, 1984). Results from sedimentation trap experiments in green algae dominated Lake Søbygård (Kristensen & Jensen, 1987, and unpubl. results) have shown that the specific loss through sedimentation in periods with maximum phytoplankton biomass was high, ranging from 0.2 d^{-1} in 1985, when the small *Scenedesmus* dominated, to 0.6–0.8 d^{-1} in 1988, when the larger *Pediastrum* dominated. The specific loss rate of phytoplankton during 1988 was so high, compared with the maximum recorded growth rates of large green algae (1–1.3 d^{-1}, Reynolds, 1984), that it is likely that the biomass was heavily influenced by sedimentation. This is further supported by the fact that the mean ratio of filter feeding zooplankton to phytoplankton biomass in 1988 was still low (~ 0.1) in spite of the marker reduction in phytoplankton biomass (Fig. 1). By shifting the size of the phytoplankton towards larger algae species, large filter feeders may, therefore, also indirectly amplify the relative loss rate of phytoplankton in lakes dominated by species with a high specific sinking rate.

In shallow, green algae dominated lakes the indirect effect, i.e. shift in size of phytoplankton, may in some cases thus be even higher than the direct effect, i.e. loss by grazing. Correspondingly, the marked decrease of both small and large algae in Lake Væng may be explained by a combination of high grazing rate and a related shift in species composition from large cyanobacteria less sensitive to sedimentation to diatoms and green algae. Variations in the sensitivity to loss by sedimentation of the algae dominating at different nutrient regimes, flushing rates, and lake morphometry, therefore, may also affect the outcome of fish manipulation.

Impact on phosphorus

The phosphorus concentration in the three lakes was altered differently by changes in the fish stock. In Lake Søbygård the phosphorus concentration in the lake water in summer has not decreased (Fig. 4) despite ongoing exhaustion of exchangeable phosphorus from the surface sediment after the significant decrease of the external phosphorus loading in Lake Søbygård in 1982 (Table 2).

Excluding the cold summer of 1987 there has instead been a tendency to an increase in connection with the changes in the age composition of the fish stock. This is explained by changes in the balance between gross phosphorus sedimentation and gross phosphorus release from the sediment (Kristensen & Jensen, 1987; Søndergaard *et al.*, 1990). The decrease in phytoplankton biomass resulted in a decrease in gross sedimentation of particulate phosphorus. A lower percentage of the phosphorus, released from the sediment, was thus returned to the sediment. Hence, ortho-phosphate accumulated in the lake water and thus compensated for the reduction in gross phosphorus release from the sediment.

Unfortunately, no data exists on changes in the concentration of total phosphorus in the lake water in Frederiksborg Castle Lake, but marked increases in mean summer concentration of orthophosphate after the fish manipulations (1986: 113; 1987: 248, and 1988: 447 $\mu g\ P\ l^{-1}$; Riemann *et al.*, 1990) indicate that the net internal loading has not decreased. In contrast, the net internal loading in the least eutrophic Lake Væng has decreased significantly after fish removal, reducing the phosphorus concentration to half of the pre-biomanipulation value. As discussed by Søndergaard *et al.* (1990), this decrease is probably due to improved redox conditions in the sediment and an increased production of benthic algae, rather than due to a decrease in the pool of exchangeable phosphorus in the sediment.

On basis of several case studies Benndorf (1987) concluded that the loading probably have to be reduced to 0.5–1.0 $g\ P\ m^{-2}\ y^{-1}$ for lakes with a mean depth below 7 m, before a fish manipulation can lead to an self-increasing reduction in the phosphorus level. Our results support this conclusion.

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References

Andersson, G. & G. Cronberg, 1984. Aphanizomenon flos-aquae and Daphnia. An interesting plankton association in hypertrophic waters. In S. Bosheim & M. Nicholls (eds.), Interaksjoner mellom trofiske nivåer i ferskvann. Norks Limnologförening, Blindern, Oslo, Norway: 63–76.

Andersson, G., H. Berggren, G. Cronberg & C. Gelin, 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

Arnold, D. E., 1971. Ingestion, assimilation, survival, and reproduction by Daphnia pulex fed seven species of blue-green algae. Limnol. Oceanogr. 16: 906–920.

Benndorf, J., 1987. Food web manipulation without nutrient control: a useful strategy in lake restoration? Schweiz. Z. Hydrol. 49: 237–248.

Benndorf, J. & F. Recknagel, 1982. Problems of application of the ecological model SALMO to lakes and reservoirs. Ecol. Model 17: 129–145.

Benndorf, J., H. Schulz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, U. Hornig, R. Kruspe & S. Reichel, 1988. Food-web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. Limnologica 19: 97–110.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, & T. Weglenska, 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

Briand, F. & E. McCauley, 1978. Cybernetic mechanisms in lake plankton systems: how to control undesirable algae. Nature 273: 228–230.

Burns, C. W., D. S. Forsyth, J. F. Naney, M. R. Jones, W. Lampert & R. D. Pridmore, 1989. Co-existence and exclusion of zooplankton by Anabaena minutissima var. attenuata in lake Rolongaio New Zealand. Arch. Hydrobiol. Beih. Ergebn. Limnol. 32: 63–82.

Cryer, M., G. Peirson & C. R. Townsend, 1986. Reciprocal interactions between roach (*Rutilus rutilus* L.) and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31, 5: 1022–1038.

De Bernardi, R. & G. Giussani, 1990. Are blue-green algae a suitable food for zooplankton? An overview. Hydrobiologia 200/201: 29–41.

De Bernardi, R. & G. Giussani, 1990. Are blue-green algae a suitable food for zooplankton? An overview. Hydrobiologia 200/201: 29–41.

Dodson, S. I., 1974. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. Ecology 55: 605–613.

Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from plankton, periphyton and benthos of continental waters. Oecologia (Berl.) 19: 75–97.

Faafeng, B. A. & Å. Braband, submitted. Biomanipulation of a small urban lake – removal of fish exclude bluegreen blooms. Verh. Int. Ver. Limnol. 1990.

Fott, J., L. Pechar & M. Prazakova, 1980. Fish as a factor controlling water quality in ponds. In J. Barica & L. R. Mur (eds.), Hypertrophic ecosystems. Developments in Hydrobiology 2: 255–261.

Fulton, R. S. & H. W. Pearl, 1987. Toxic and inhibitory effects of the blue-green algae Microcystis aeruginosa on herbivorous zooplankton. J. Plankton Res. 9,5: 837–855.

Geller, W., 1975. Die Nährungsausnahme von Daphnia pulex in Abhängigkeit von der Futterkonzentration, der Temperatur, der Körpergrösse und dem Hungerzustand der Tiere. Arch. Hydrobiol/Suppl. 48: 47–107.

George, D. G. & S. I. Heaney, 1978. Factors influencing the spatial distribution of phytoplankton in a small productive lake. J. Ecol. 66: 133–155.

Gliwicz, M. Z., 1975. Effect of zooplankton grazing on photosynthetic activity and composition of phytoplankton. Int. Ver. Theor. Angew. Limnol. Verh. 19: 1490–1497.

Gliwicz, M. Z., 1990. Why do cladocerans fail to control algal blooms? Hydrobiologia (this volume).

Gliwicz, M. Z. & A. Prejs, 1977. Can planktivorous fish keep in check planktonic crustacean populations? A test of the size-efficiency hypothesis in typical Polish lakes. Ekol. Polska 25: 567–591.

Harris, G. P., 1986. Phytoplankton Ecology. Chapman and Hall, London.

Henrikson, L., H. G. Nymann, H. G. Oscarson & J. A. E. Stenson, 1980. Trophic changes without changes in external nutrient load. Hydrobiologia 68: 257–263.

Horn, W., 1981. Phytoplankton losses due to zooplankton grazing in a drinking water reservoir. Int. Revue ges. Hydrobiol. 69: 781–817.

Hrbácek, J., 1962. Species composition and the amount of zooplankton in relation to fish stock. Rozpravy Csekolovenske Akademie Ved. 72, 10: 114 pp.

Hrbácek, J., 1964. Contribution to the ecology of water-bloom-forming blue-green algae Aphanizomenon flos-aquae and Microcystis aeruginosa. Verh. int. Ver. Limnol. 15: 837–846.

Hrbácek, J., M. Dvorakova, V. Korinek & L. Procházková, 1961. Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Int. Ver. Limnol. 14: 192–195.

Infante, A., 1973. Untersuchungen über die Ausnutzbarkeit verschiedener Algen durch das Zooplankton. Arch. Hydrobiol/Suppl. 42, 3/4: 340–405.

Jeppesen, E., E. Mortensen, O. Sortkjær, P. Kristensen, J. Bidstrup, M. Timmerman, J. P. Jensen, A.-M. Hansen, M. Søndergaard, J. P. Müller, H. J. Jensen, B. Riemann, C. Lindegaard, S. Bosselmann, K. Christoffersen, E. Dall & J. M. Andersen, 1989a. Restoration of lakes by changing the fish structure. Results from ongoing investigations. Part 2: Case-studies from Frederiksborg Castle Lake, Lake Væng and Lake Søbygård [Restaurering af søer ved indgreb i fiskebestanden. Status for igangværende undersøgelser. Del 2: Undersøgelser i Frederiksborg Slotssø, Væng Sø og Søbygård Sø]. Danmarks Miljøundersøgelser, Silkeborg, Denmark, 114 pp. (in Danish).

Jeppesen, E., M. Søndergaard, H. J. Jensen & J. P. Müller, 1989b. Restoration of lakes by changing the fish structure. Results from ongoing investigations. Part 1: Main report [Restaurering af søer ved indgreb i fiskebestanden. Status for igangværende undersøgelser. Del 1: Hovedrapport]. Danmarks Miljøundersøgelser, Silkeborg, Denmark, 73 pp. (in Danish).

Jeppesen, E., M. Søndergaard, O. Sortkjær, E. Mortensen & P. Kristensen, 1990a. Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. Hydrobiologia 191: 149–164.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik, 1990b. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia 200/201: 219–227.

Kasprzak, P., J. Benndorf, R. Koschel & F. Rechnagel, 1988. Applicability of the food-web manipulation in the restoration programme of a hypertrophic stratified lake: model studies for Lake Haussee (Feldberg, GDR). Limnologica 19: 87–95.

Kristensen, P. & P. Jensen, 1987. Sedimentation and resuspension in Lake Søbygård [Sedimentation og resuspension i Søbygård Sø]. M. sc. thesis. Freshwater Laboratory, Silkeborg, & Botanical Institute, University of Aarhus, Denmark, 176 pp. (in Danish).

Lampert, W., 1981. Inhibitory and toxic effects of blue-green algae on Daphnia. Int. Revue ges. Hydrobiol. 66: 285–298.

Lampert, W., W. Fleckner, H. Rai & B. E. Taylor, 1986. Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. Limnol. Oceanogr. 31, 3: 478–490.

Lessmark, O., 1983. Influence of abiotic and biotic factors on the structure of perch and roach populations in thirteen Swedish lakes, with special reference to interspecific competition. Part of Ph.D. thesis, University of Lund, Sweden, 1983: 135–170.

Lynch, M., 1980. Aphanizomenon blooms: alternate control and cultivation by Daphnia pulex. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3. Univ. Press New England, Hanover: 299–304.

Lynch, M. & J. Shapiro, 1981. Predation, enrichment and phytoplankton community structure. Limnol. Oceanogr. 26: 86–102.

McCauley, E. & F. Briand, 1979. Zooplankton grazing and phytoplankton species richness, field tests of the predation hypothesis. Limnol. Oceanogr. 24: 243–252.

McQueen, D. J. & J. R. Post, 1988. Cascading trophic interactions: uncoupling at the zooplankton-phytoplankton link. Hydrobiologia 159: 277–296.

McQueen, D. J., J. R. Post & E. L. Mills, 1986. Tropic relationships in freshwater pelagic ecosystems. Can. J. Fish. aquat. Sci. 43: 1571–1581.

Meijer, M. L., A. J. P. Raat & R. W. Doef, 1989. Restoration by biomanipulation of the Dutch shallow, eutrophic Lake Bleiswijkse Zoom: first results. Hydrobiol. Bull. 23: 49–57.

Mills, E. L., J. L. Fornes & K. S. Wagner, 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In W. C. Kerfoot & A. Sik (eds.), Predation: direct and indirect impacts on aquatic communities. United Press of New England: 118–131.

Penczak, T., 1985. Phosphorus, nitrogen, and carbon cycling by fish populations in two small lowland rives in Poland. Hydrobiologia 120: 159–165.

Persson, L., G. Andersson, S. F. Hamrin, L. Johansson, 1988. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. In S. R. Carpenter (ed.), Complex interactions in lake communities. Springer Verlag: 45–65.

Reinertsen, H., A. Jensen, J. I. Koksvik, A. Langeland & Y. Olsen, in press. Effects of fish removal on the limnetic ecosystem of a eutrophic lake. Can. J. Fish. aquat. Sci., 1989.

Reynolds, C. S., 1984. The ecology of freshwater phytoplankton. Cambridge University Press, 384 pp.

Reynolds, C. S. & A. E. Walsby, 1975. Water blooms. Biol. Rev. 50: 437–481.

Richman, S. & S. I. Dodson, 1983. The effect of food quality on feeding and respiration by Daphnia and Diaptomus. Limnol. Oceanogr. 28: 948–956.

Riemann, B. & M. Søndergaard, 1986. Regulation of bacteria secondary production in two eutrophic lakes and in experimental enclosures. J. Plankton Res. 8: 519–536.

Riemann, B., K. Christoffersen, H. J. Jensen, J. P. Müller, C. Lindegaard & S. Bosselmann, 1990. Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. Hydrobiologia 200/201: 241–250.

Scheffer, M., 1989. Alternative stable states in eutrophic shallow freshwater systems: a minimal model. Hydrobiol. Bull. 23: 73–89.

Schefer, M., 1990. Multiplicity of stable states in fresh water systems. Hydrobiologia 200/201: 475–486.

Shapiro, J., 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes. In J. Barica & L. R. Mur (eds.), Hypertrophic ecosystems. Development in Hydrobiology 2: 105–116.

Stenson, J. A. E., T. Bohlin, L. Henrikson, B. I. Nilsson, H. G. Nyman, H. G. Oscarson & P. Larsson, 1978. Effects of fish removal from a small lake. Verh. int. Ver. Limnol. 20: 794–801.

Søndergaard, M., E. Jeppesen, P. Kristensen & O. Sortkjær, 1990a. Interactions between sediment and water in a shallow and hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. Hydrobiologia 191: 139–148.

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen & O. Sortkjær, 1990b. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200/201: 229–240.

Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham & F. A. Johnson, 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. 106: 473–485.

Townsend, C. R., I. J. Winfield, G. Peirson & M. Cryer, 1986. The response of young roach Rutilus rutilus to seasonal changes in abundance of microcrustacean prey: a field demonstration of switching. Oikos 46: 372–378.

Van Donk, E., R. D. Gulati & M. P. Grimm, 1989. Food web manipulation in Lake Zwemlust: positive and negative effects during the first two years. Hydrobiol. Bull. 23: 19–34.

Walker, P. A., 1989. The feasibility of lake restoration through biomanipulation, a literature study. DBW/RIZA (No. 89.033), Aquasense (NO. 89012), Amsterdam/Lelystad, 60 pp.

Winberg, G. G. (ed.), 1971. Symbols, units and conversion factors in studies of freshwater productivity. IBP London, 23 pp.

Winfield, I. J. & C. R. Townsend, 1988. Factors affecting prey selection by young bream Abramis brama and roach Rutilus rutilus: insights provided by parallel studies in laboratory and field. Environ. Biol. Fishes 21: 279–292.

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Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions

E. Jeppesen, J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik[1]
National Environmental Research Institute, Division of Freshwater Ecology, 52 Lysbrogade, DK-8600 Silkeborg, Denmark; [1]*Environmental Biology Laboratory, 5 Baunebjergvej, DK-3050 Humlebæk, Denmark*

Key words: biomanipulation, shallow, eutrophic, lakes, threshold levels, long-term stability, submerged macrophytes, fish, phytoplankton, empirical relationships

Abstract

In order to evaluate short-term and long-term effects of fish manipulation in shallow, eutrophic lakes, empirical studies on relationships between lake water concentration of total phosphorus (P) and the occurrence of phytoplankton, submerged macrophytes and fish in Danish lakes are combined with results from three whole-lake fish manipulation experiments. After removal of less than 80 per cent of the planktivorous fish stock a short-term trophic cascade was obtained in the nutrient regimes, where large cyanobacteria were not strongly dominant and persistent. In shallow Danish lakes cyanobacteria were the most often dominating phytoplankton class in the P-range between 200 and 1 000 μg P l^{-1}. Long-term effects are suggested to be closely related to the ability of the lake to establish a permanent and wide distribution of submerged macrophytes and to create self-perpetuating increases in the ratio of piscivorous to planktivorous fish. The maximum depth at which submerged macrophytes occurred, decreased exponentially with increasing P concentration. Submerged macrophytes were absent in lakes > 10 ha and with P levels above 250–300 μg P l^{-1}, but still abundant in some lakes < 3 ha at 650 μg P l^{-1}. Lakes with high cover of submerged macrophytes showed higher transparencies than lakes with low cover above *ca.* 50 μg P l^{-1}. These results support the alternative stable state hypothesis (clear or turbid water stages). Planktivorous fish > 10 cm numerically contributed more than 80 per cent of the total planktivorous and piscivorous fish (> 10 cm) in the pelagical of lakes with concentrations above 100 μg P l^{-1}. Below this threshold level the proportion of planktivores decreased markedly to *ca.* 50 per cent at 22 μg P l^{-1}. The extent of the shift in depth colonization of submerged macrophytes and fish stock composition in the three whole-lake fish manipulations follows closely the predictions from the relationships derived from the empirical study. We conclude that a long-term effect of a reduction in the density of planktivorous fish can be expected only when the external phosphorus loading is reduced to below 0.5–2.0 g m^{-2} y^{-1}. This loading is equivalent to an in-lake summer concentration below 80–150 μg P l^{-1}. Furthermore, fish manipulation as a restoration tool seems most efficient in shallow lakes.

Introduction

Jeppesen *et al.* (1990) suggested that the short-term response of biomanipulation in terms of a trophic cascade (*in sensu* Carpenter *et al.*, 1985) and improved Secchi depth in shallow, eutrophic temperate lakes depends largely on the ability to combat large cyanobacteria, irrespective of the nutrient levels in the lake water. The long-term stability of the shift is, however, more speculative basically because only a few biomanipulated lakes have so far been monitored sufficiently long to, confirm long-term stability (Benndorf *et al.*, 1988; Benndorf, 1990). Submerged macrophytes are important in regulating the biological structure in shallow, eutrophic lakes (Moss, 1980; Timms & Moss, 1984); besides they may be one of the key factors determining threshold levels for a long-term effect of fish manipulation in shallow, eutrophic lakes (Grimm, 1989; Scheffer, 1989).

As a second key factor we identify the ability of the lake to achieve a permanent shift in the fish-stock composition, namely increased importance of piscivores as compared with planktivorous fish. Lessmark (1983) and Persson *et al.* (1988) found a decreasing ratio of piscivores to planktivores with increased eutrophication as regards levels of P and chlorophyll *a*. Apart from nutrients the ratio of piscivorous fish to planktivorous fish is also interconnected to the wax and wane of submerged macrophytes, being generally higher when submerged macrophytes are abundant (Grimm, 1989). Once established, the planktivorous fish both directly and indirectly may accelerate eutrophication and thereby further impair the conditions for piscivorous fish (Persson, 1987). The results of Persson indicate that the ability to permanently shift the fish stock composition decreases with increasing eutrophication.

To find the nutrient threshold levels necessary to obtain a long-term effect of fish manipulation *per se* in shallow lakes, we established empirical relationships of the P concentration with: 1) macrophyte depth distribution; 2) dominating phytoplankton groups, and 3) fish composition. We also provide evidence of the alternative stable state theory (clear/turbid water stage) as defined for shallow lakes by Scheffer (1989; 1990). Nutrient threshold levels for the shifts between the two stages are discussed.

Materials and methods

A data base that includes limnological variables from 300 Danish lakes with mean depth <5 m was used in the empirical analysis. The data were mainly collected by Danish local water authorities and by the National Environmental Research Institute. The median-, minimum-, and maximum-values of some relevant variables of the lakes are: surface area, 22, 0.1, 4 100 ha; retention time, 38, 1, 7 500 days; total phosphorus (P) in the surface water, 316, 10, 5 900 μg P l^{-1}; and Secchi depth, 0.55, 0.15, 5.0 m.

Maximum depth at which submerged macrophytes occurred was measured using modified rakes in some cases and with detailed analysis along vertical transects on the lake shore in other cases. In the most advanced quantitative studies divers and videos were used. Submerged macrophytes included the isoetids, characeans, elodeids and the moss, *Fontinalis antipyretica*. Mean lake pH in summer was higher than 6.

The number of fish species and their relative abundance were estimated using standardized test-fishing with survey gillnets of multiple mesh sizes. For the Danish and Swedish lakes the actual numbers and settings of gillnets are given by Mortensen *et al.* (in press) and Lessmark (1983).

Phytoplankton abundance for 200 shallow Danish lakes (mean depth <3 m) was classified into five categories: absent, low numbers, moderate, high, and dominant (Olrik, 1981). In a few cases ($<15\%$) only four categories were used, i.e. absent, present, moderate/high and dominant. Only data classified in the uppermost class, 'dominant' was used in this study. More than 70% of the samples were analyzed by one person (K. Olrik), which reduces heterogeneity in the classification related to methodological errors. We use the term 'large cyanobacteria' because the picoplanktonic cyanobacteria were not included in this analysis.

The total phosphorus concentration (P) in the surface water at mid-lake station was measured as orthophosphate, using the method of Murphy & Riley (1972) after persulphate digestion (Koroleff, 1970). Regarding the relationships to fish and macrophytes the P-values used are means for May to September, and for July to September regarding the relationships of P to phytoplankton. Mean values are based on 3–40 samples. Model parameters were estimated by non-linear regressions using NLIN in SAS and the Marquardt algorithm (SAS Institute, 1985).

Whole-lake experiments

The fish stock composition in Lake Væng and Lake Søbygård was estimated from test-fishing with survey gillnets as described above. The depth distribution of submerged macrophytes in Lake Væng was measured at biomass maximum on 15 transects running from the centre of the lake to different sites of the shore. The macrophyte presence was measured at 9–13 stations along each transect using a modified rake and a hydroscope. In Lake Søbygård a hydroscope was used frequently during summer. For other methods and lake descriptions, see Jeppesen *et al.* (1990), Søndergaard *et al.* (1990) and Riemann *et al.* (1990).

Results

Phytoplankton

From July to September large cyanobacteria contributed < 30% of the 'dominant' samples in the two lower P-ranges as well as in the highest P-range. In the P-range between 250–500, 500–750 and 750–1 000 μg P l^{-1} large cyanobacteria were classified as dominant in 50, 88 and 51% of the 'dominant' samples, respectively. Green algae contributed < 20% of the 'dominant' samples below 750 μg P l^{-1}, 25% in the range 750–1 000 μg P l^{-1}, and 70% above 1 000 μg P l^{-1}. Diatoms and chrysophytes (not shown) made up the majority of the remaining 'dominant' samples (Fig. 1).

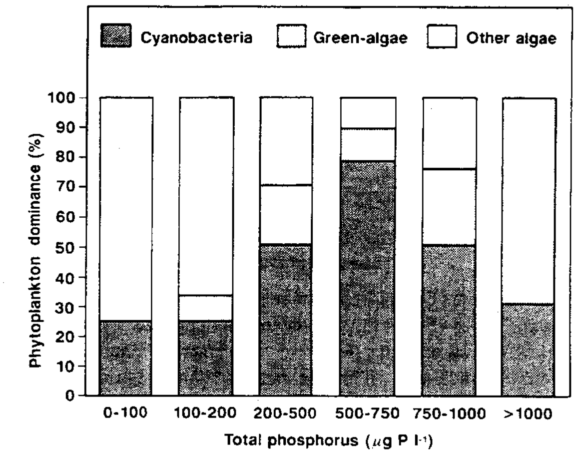

Fig. 1. The relative composition of the numbers of dominating species and genera among some phytoplankton classes in relation to mean levels of total-P (July-Sept.) in 200 shallow Danish lakes. Only phytoplankton classified as 'dominant' are included.

Submerged macrohytes

Submerged macrophyte cover decreased with increasing P concentration and increasing depth (Fig. 2) in 37 shallow lakes > 10 ha, with a mean depth < 5 m and with summer mean N/P-ratios (weight basis) above 6. The maximum depth at which submerged macrophytes occurred was < 1 m, when mean P concentration during summer exceeded ca. 150 μg P l^{-1}. Except one lake with frequent fish kill and consequently high transparency, submerged macrophytes were

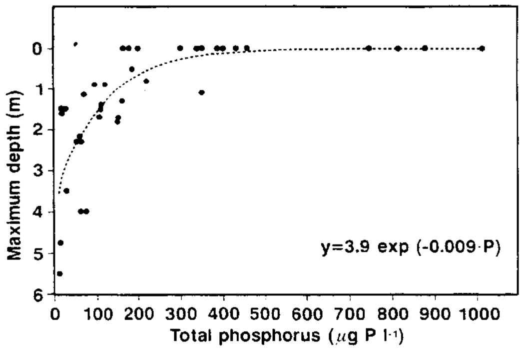

Fig. 2. Maximum depth colonization of submerged macrophytes in relation to mean concentration of total-P in lake water in summer (May-Sept.) for shallow lakes with a surface area > 10 ha and mean depth < 5 m. The fitted exponential curve and the equation are also shown.

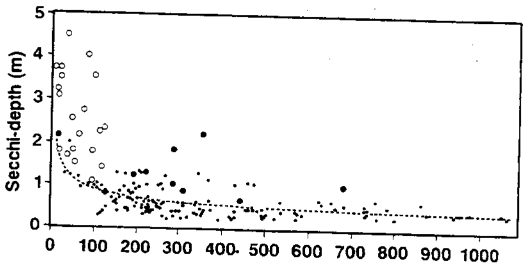

Fig. 3. Mean Secchi-depth in relation to mean lake water total-P (May–Sept.) for shallow (mean depth <3 m) Danish lakes. ○ = lakes with a high cover of submerged macrophytes and a surface area >3 ha; ● = lakes with a high cover of submerged macrophytes and a surface area <3 ha; and • = lakes with only minor or unknown cover of submerged macrophytes. The exponential curve and equation developed by Krisensen *et al.* (1988) are shown.

totally absent above 250 μg P l^{-1}. The data were fitted as follows:

$$\text{Maximum depth (m)} = 3.9 \pm 0.5\ \text{S.E.}\ e^{-0.009 \pm 0.002\ (\text{S.E.})\ P\ (\mu g\ P\ l^{-1})}\ (r^2 = 0.80). \quad (1)$$

The relationship between Secchi depth and P level in the lake water in lakes with a low cover of submerged macrophytes or without submerged macrophytes closely followed the relationship known from the works of Kristensen *et al.* (1988) on shallow Danish lakes (Fig. 3). Lakes with submerged macrophyte cover $>30\%$ and with P exceeding *ca.* 50 μg l^{-1} deviated markedly from the overall pattern, however, showing transparencies higher than expected. Small lakes (<3 ha) could apparently sustain a high macrophyte cover and often also a related high transparency at higher phosphorus concentrations than large lakes (Fig. 3).

Fish stock

In 30 lakes >10 ha the ratio in numbers of planktivorous fish to plantivorous plus piscivorous fish (>10 cm) increased with increasing P concentration up to a threshold level of *ca.* 100 μg P l^{-1} (Fig. 4). At higher phosphorus levels, *viz.* to 1000 μg P l^{-1}, the ratio was relatively constant, and the fish stock was almost exclusively dominated by planktivores. The data were fitted to a Monod equation; the half-saturation coefficient was 22 ± 4 (S.E.) μg P l^{-1}, and the saturation coefficient was 100 ± 3 (S.E.)% ($r^2 = 0.98$).

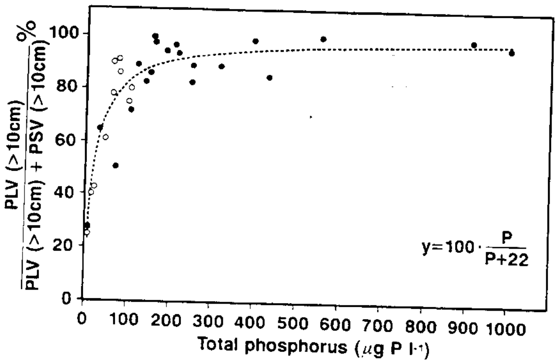

Fig. 4. Ratio (per cent) of planktivorous fish (PLV) (roach, rudd and bream) to planktivorous fish plus piscivorous fish (PSV) (perch, pike and zander), all larger than 10 cm *versus* mean total-P in lake water (May–Sept.). The estimation of the fish density and relative composition are based upon gillnet catches (nets with 14 mesh sizes ranging from 6.5 to 75 mm). ○ = lakes in south Sweden (Lessmark, 1983) where piscivores include only perch and planktivores only roach; and ● = Danish lakes. The fitted Monod-curve and the equation are shown.

Whole-lake experiments

The major results of the three whole-lake fish manipulations are described by Jeppesen *et al.* (1990), Søndergaard *et al.* (1990) and Rieman *et al.* (1990). In this paper we only compare the response of fish stocks and submerged macrophytes with the empirical relationships developed (Figs. 2, 4 and 5).

Fish: In the hypertrophic lake Søbygård no changes occurred in the proportion of planktivores >10 cm to piscivores >10 cm fish after a 15% reduction in the biomass of roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) in 1988–89 (Fig. 5A) and a low recruitment of young planktivores since 1983–89 (Jeppesen *et al.*,

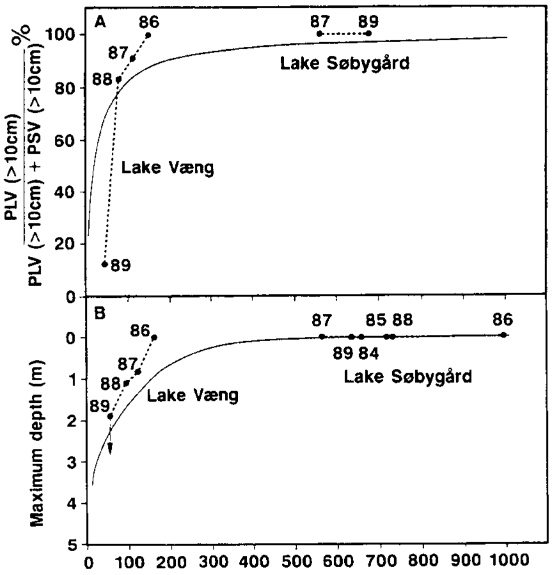

Fig. 5. A. Ratio (per cent) of planktivorous fish (PLV) to planktivorous fish plus piscivorous fish (PSV) all larger than 10 cm before, during and after fish manipulation of Lake Væng and Lake Søbygård *versus* mean total-P in the lake water (May–Sept.). The empirical model (Fig. 4) is shown by the unbroken curve. B. Maximum depth colonization of submerged macrophytes before, during and after fish manipulation of Lake Væng and Lake Søbyård *versus* mean total-P in the lake water (May–Sept.). The empirical model (Fig. 2) is shown by the unbroken curve. The arrow indicates that the maximum depth of macrophytes reached maximum depth of the lake (1.8 m).

1990). Marked changes in the density of young perch < 10 cm (*Perca fluviatilis*) or pike < 10 cm (*Esox lucius*) have neither occurred (unpubl. results). Only minor changes have occurred in the proportion of planktivores > 10 cm to piscivores > 10 cm in eutrophic (P ~ 350 μg P l^{-1}) Frederiksborg Castle Lake (Riemann *et al.*, 1990). On the contrary, major changes have occurred in the fish stock in the less eutrophic Lake Væng. The ratio in terms of numbers of planktivores > 10 cm to total planktivores > 10 cm and piscivores > 10 cm decreased during the experimental period from December 1986 to July 1988 (99% in 1986, 88% in 1987, and 81% in 1988). The most dramatic decrease was found in 1989 in spite of no fish manipulation that year (Fig. 5A). The ratio decreased to 14% which suggests a marked self-perpetuating effect of the fish removal on fish stock composition. The marked response in Lake Væng in comparison with that in the two other lakes agrees well with the threshold hypothesis derived from the developed empirical equation (Figs. 4 and 5A).

Submerged macrophytes: No submerged macrophytes have appeared in shallow (mean depth ~ 1 m) Lake Søbygård (Fig. 5B) despite an increase in median Secchi depth in summer from 0.3 m in 1984–85 to 0.6 m in 1987–88 (Jeppesen *et al.*, 1990). No quantitative data of depth distribution of submerged macrophytes are available from Frederiksborg Castle Lake. Submerged macrophytes appeared in Lake Væng in 1987 following the initiation of the fish manipulation (Søndergaard *et al.*, 1990). The maximum depth at which submerged macrophytes occurred increased from 0 m in 1986 to *ca.* 1 m in 1987–88, while they colonized the deepest part of the lake (1.8 m) in 1989 (Fig. 5B; Lauridsen, unpubl.). The marked response in Lake Væng in comparison with that in Lake Søbygård agrees well with the predictions from the developed empirical equation (Figs. 2 and 5B).

Discussion

Phytoplankton

Abundance and persistence of large cyanobacteria seem to be one of the major factors determining the short-term response of a fish manipulation in shallow, eutrophic lakes (Jeppesen *et al.*, 1990). Our results suggest that the dominance of large cyanobacteria is strong in the shallow Danish lakes with total P concentrations between 500 and 750 μg P l^{-1}, but it becomes weak at P concentrations above or below this range (Fig. 1). The results partly confirm the observations of Olrik (1978) from 15 Danish lakes and of Sas (1989). Sas found a stepwise shift to dominance by large cyanobacteria above *ca.* 200 μg P l^{-1} in a number of European shallow lakes and a second threshold, about *ca.* 800 μg P l^{-1}, where a shift to green algae occurred in some of the lakes studied. Sas argued that the second shift to dominance by green algae most likely reflects the short retention time in these lakes, which, does not favour the slow growing large cyanobacteria. On the contrary, Olrik (1981) and Jensen *et al.* (1990) observed that green algae dominate in hypertrophic, shallow lakes with retention times as high as 1–2 y. In lakes with high retention times, however, green algae dominated only when the lakes were strongly exposed to wind-induced turbulence which facilitates resuspension of both sediment and increased nutrient concentration in the water column. Thus, the results of Olrik (1981) and of Jensen *et al.*, (1990) suggest that high loadings of nutrients, whether derived from external or internal sources (e.g. sediment release, fish excretion, resuspension), are more important controlling factors for green algae dominance in hypertrophic lakes than is retention time. Besides, high turbulence and high ratio of euphotic to mixing depth are important factors for dominance of green algae (Olrik, 1981; Reynolds, 1984).

Nevertheless, differences in the driving factors mentioned cannot explain why, e.g., most of the Dutch shallow, hypertrophic lakes of size and depth similar to those of the Danish lakes tend to be blue-green *Oscillatoria* lakes (Sas, 1989; Berger, 1989), while green algae often dominate in Danish lakes (Olrik, 1981; Fig. 1). The relatively higher winter and spring temperatures may favour *Oscillatoria* because they can maintain high winter and spring densities, facilitating their competitive ability over other algae during spring and summer.

Sas (1989) also reported that in deep lakes the lower threshold level for large cyanobacteria dominance was in a much lower P-range, 10–50 μg P l^{-1}, than in shallow lakes, and that no upper threshold for cyanobacteria was found in the deep lakes. Although the number of lakes in his study was limited, data of Sas as well as, our results indicate that below 200 μg P l^{-1} the competitive capacity of large cyanobacteria decreases with decreasing mean depth, and consequently the ability to combat large cyanobacteria blooms temporarily by fish manipulation increases with decreasing mean depth. Furthermore, since no upper P-threshold of shift from cyanobacteria to green algae was found in the deep lakes as opposed to most shallow Danish lakes (Fig. 1), we suggest that the ability to create major short-term changes in the trophic structure by fish manipulation in the more hypertrophic lakes is most likely to increase with decreasing mean depth at least at the meteorological conditions prevailing in Denmark.

Submerged macrophytes

The depth at which submerged macrophytes occurred decreased exponentially with increasing nutrient level in lakes > 10 ha (Figs. 2 and 5B). It seems to support the widely accepted view that increasing nutrient loading in the long-term gradually increases the dominance of phytoplankton at the expense of submerged macrophytes (Phillips *et al.*, 1978). However, Scheffer (1989; 1990) and Irvine *et al.* (1989) alternatively suggested a stepwise rather than a gradual shift from macrophyte to phytoplankton dominance. They proposed the following sequence: level 1) at low nutrient concentrations submerged macrophytes are abundant; level 2) at higher concentrations two alternative stable states can exist: dominance of macrophytes and clear water, or dominance of phytoplankton and turbid water; and level 3) at even higher nutrient levels phytoplankton dominance is the only stable state.

This hypothesis is supported by 1) the large scattering in the relationship between depth distribution of submerged macrophytes and P concentrations (Fig. 2), 2) especially the high and the low transparency in lakes with a high and a low cover of submerged macrophytes (Fig. 3). In shallow Danish lakes > 3 ha the shift from level 1) to level 2) occurred at *ca.* 50 μg P l^{-1}, and from level 2) to level 3) at *ca.* 125 μg P l^{-1}.

In relatively small lakes (< 3 ha), however, alternative stable states were still observed when the P concentration was as high as 650 μg l^{-1}

(Fig. 3). These threshold levels must be carefully interpreted because number of data is limited. The difference in threshold levels between small and large lakes may be caused by difference in the strength of some of the buffering mechanisms maintaining the macrophyte stages. Four main points that emerge are: 1) the higher shoreline development and thus often shallow areas may improve colonization conditions and above-surface growth of submerged macrophytes in which case phytoplankton may more easily be outcompeted; 2) the high ratio of shoreline to surface area in the small lake may favour piscivorous fish such as pike (Grimm, 1989) which will then control planktivorous fish. This will indirectly improve the chances of zooplankton to escape predation and exert increased grazing pressure on phytoplankton; 3) the macrophytes in small lakes are better protected against wind-stress and wind-induced resuspension and reduction in transparency; and 4) winter fish-kill due to oxygen depletion may occur more frequently in small lakes, which are often shallow and have long retention time. Subsequently in summer, the reduced predation by fish may lead to a higher zooplankton density, and thus higher grazing and improved transparency (Shapiro *et al.*, 1982).

The difference in response between small (< 3 ha) and large lakes (> 10 ha) may also have implications on the outcome of biomanipulation in shallow lakes. Hence, we may expect that the nutrient threshold levels for a long-term effect of a fish manipulation *per se* decreasing with decrease ratio of shoreline length to surface area and increasing lake size (see also Hosper & Jagtman, 1990).

Fish

The marked decrease in the relative abundance of piscivorous fish, with increasing eutrophication, to less than 20%, at P levels above *ca.* 100 μg P l^{-1}, suggests that the ability to bring about long-term changes in the ratio of piscivorous fish to planktivorous fish decreases with increasing eutrophication. This is also supported by the fact that the predation pressure on zooplankton increases with eutrophication in shallow, temperate lakes, not only because of the shifts to a higher density of planktivorous fish but also because of a shift in age composition of the planktivores towards younger fish (Lessmark, 1983; Persson *et al.*, 1988). This shift implies a higher impact on zooplankton because small planktivorous fish often predate more selectively on zooplankton than large planktivorous fish (Cryer *et al.*, 1986). Furthermore, in eutrophic lakes the competitive and reproductive capacity of planktivorous fish is high (Persson, 1987).

Our view-point is also supported by a number of whole-lake experiments which showed marked differences in the response pattern below and above the suggested threshold of *ca.* 100 μg P l^{-1}.

Hence, in lakes with P levels $>$ *ca.* 100 μg P l^{-1} the removal of planktivorous fish was either 1) not compensated by an increase in the proportion of piscivores (Fig. 5A); or 2) planktivorous fish re-appeared due to recruitment or immigration from river systems (e.g. Andersson *et al.*, 1985; Faafeng & Braband, in press); or 3) they are now increasing in numbers (e.g. Riemann *et al.*, 1990; Meijer *et al.*, 1990; Jeppesen *et al.*, 1990). Alternatively the planktivorous fish could only be depressed by continuous fishing and/or stocking of piscivorous fish (Benndorf *et al.*, 1988). Furthermore, in these lakes fish manipulation has not resulted in decreased P levels (Fig. 5A; Benndorf, 1987; Jeppesen *et al.*, 1990), which could have stimulated a shift in the fish stock composition (Figs. 4 and 5A). On the contrary, in eutrophic lakes with P levels between 50–100 μg P l^{-1} or approaching this regime after reduction of external loading some of the whole-lake manipulations have resulted in marked and probably long-lasting shifts (in scales of decades) in the fish stock towards a more piscivorous stage (Reinertsen *et al.*, 1990; Søndergaard *et al.*, 1990; Fig. 5A), and a self-perpetuating decrease in the P level and fish stock composition has been found as well (Fig. 5A; Søndergaard *et al.*, 1990). Nevertheless, fish manipulation in Lake Sövdeborgsjöen (57–73 μg P l^{-1}) failed in terms of both long-term changes in fish stock composition, nutrient levels and dominance of cyanobacteria (Andersson *et al.*, 1985). Hence, more experiences within the latter P-range seem desirable.

Concluding discussion

The relationships between P concentration and the proportion of piscivores in the fish stock, the cover of submerged macrophytes, and the phytoplankton composition as well as results from the Danish whole-lake experiments indicate that the threshold level for long-term effects of fish manipulation in shallow, temperate lakes > 10 ha (not severely limited by nitrogen) is *ca.* 100 μg P l^{-1} (80–150 μg P l^{-1}). According to the loading-response models obtained for shallow Danish lakes, P concentrations of 80–150 μg P l^{-1} corresponds to P loading of 0.5 to 2.0 g P m^{-2} y^{-1}, depending on lake morphometry and flushing rate (Kristensen *et al.*, 1988). Loading rates between 1 and 2 g P m^{-2} y^{-1} are only within the threshold regime in lakes with a high flushing rate (Kristensen *et al.*, 1988). The threshold regime agrees with the suggested by Benndorf (1987). In small lakes (< 3 ha) the threshold level may be higher because of more favourable conditions for submerged macrophytes and piscivorous fish.

Fish removal may cause temporary changes in trophic structure in lakes with higher P loadings and higher nutrient levels than the threshold levels. The shifts are expected to be most pronounced in shallow, green algal lakes and less pronounced in lakes with heavy blooms of large cyanobacteria in summer. In such lakes changes in trophic structure may only persist in the long term, if fish-stock manipulations are frequently repeated.

Fish manipulation as a restoration tool is likely to be more efficient in shallow lakes than in deeper lakes because 1) the impact of planktivorous fish on lower trophic levels at comparable nutrient levels is suggested to be larger in shallow lakes than in the deeper lakes (Jeppesen *et al.*, 1990); 2) submerged macrophytes and microbenthic algae can colonize larger parts of the lake bottom, thereby amplifying the lake recovery (Søndergaard *et al.*, 1990); and 3) the competition capacity of large cyanobacteria is generally weaker at least in fully mixed and shallow Danish lakes than in deep or stratefied lakes, as long as the P concentrations are below 200 μg l^{-1} or above 1000 μg l^{-1}.

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References

Andersson, G., S. Hamrin, O. Lessmark & L. Persson, 1985. Fish composition and fish manipulation in eutrophic lake ecosystems – final report. [Fisksamhällan och fiskemanipulering i eutrofa sjöekosystem – slutrapport]. Institute of Limnology, University of Lund, ISSN 0348-0798, 24 pp. (in Swedish).

Benndorf, J., 1987. Food web manipulation without nutrient control: a useful strategy in lake restoration? Schweiz. z. Hydrol. 49: 237–248.

Benndorf, J., H. Schulz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, U. Hornig, R. Kruspe & S. Reichel, 1988. Food-web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. Limnologica 19: 97–110.

Benndorf, J., 1990. Conditions for effective biomanipulation: conclusions derived from whole-lake experiments in Europe. Hydrobiologia 200/201: 187–203.

Berger, C., 1989. In situ primary production, biomass and light regime in the Wolderwijd, the most stable Oscillatoria agardhii lake in The Netherlands. Hydrobiologia 185: 233–244.

Carpenter, S. R., J. K. Kitchell & J. R. Hodgeson, 1985.

Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

Cryer, M., G. Peirson & C. R. Townsend, 1986. Reciprocal interactions between roach (Rutilus rutilus L.) and zooplankton in a small lake: prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31,5: 1022–1038.

Faafeng, B. A. & Å. Braband, in press. Biomanipulation of a small urban lake – removal of fish exclude bluegreen blooms. Verh. int. Ver. Limnol.

Grimm, M. P., 1989. Northern pike (Esox lucius) and aquatic vegetation, tools in the management of fisheries and water quality. Hydrobiol. Bull. 23: 59–65.

Hosper, S. H. & E. Jagtman, 1990. Biomanipulation additional to nutrient control for restoration of shallow lakes in the Netherlands. Hydrobiologia 200/201: 523–534.

Irvine, K., B. Moss & H. Balls, 1989. The loss of submerged plants with eutrophication II. Relationships between fish and zooplankton in a set of experimental ponds, and conclusions. Freshwat. Biol. 22: 89–107.

Jensen, J. P., E. Jeppesen, P. Kristensen & S. N. Nielsen, 1990. Biologiske strukturmodeller for lavvandede søer. Status fase 1 og 2 [Modelling biological structure in shallow lakes. Status phase 1 and 2]. National Environmental Research Institute, Division of Freshwater Ecology, Silkeborg (in Danish).

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H. J. Jensen, J. P. Müller, O. Sortkjær, J. P. Jensen, K. Christoffersen, S. Bosselmann & E. Dall, 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 1: cross-analysis of three Danish case-studies. Hydrobiologia 200/201: 205–218.

Koroleff, F., 1970. Determination of total phosphorus in natural water by means of the persulphate oxidation. An Interlab. report No. 3, Cons. Int. pour l'Explor de la Mer.

Kristensen, P., J. P. Jensen & E. Jeppesen, 1988. Reevaluation of simple lake models. NPO-project No. 4.5. Midterm status 1988 [Revurdering af simple sømodeller. NPO-projekt 4.5. Midtvejsrapport pr. 25 juli 1988]. Freshwater Laboratory, Silkeborg, Denmark: 15 pp. and 6 supplements (in Danish).

Lessmark, O., 1983. Influence of abiotic and biotic factors on the structure of perch and roach populations in thirteen Swedish lakes, with special reference to interspecific competition. Part of Ph.D. thesis, University of Lund, Sweden: 135–172.

Meijer, M.-L., M. W. de Haan, A. Breukelaar & H. Buiteveld, 1990. Is reduction of benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia 200/201: 303–315.

Mortensen, E., H. J. Jensen & J. P. Müller, in press. Guidelines for standardized testfishing in lakes and a description of fish gears and methods [Retningsliner for standardiseret forsøgsfiskeri i søer og en beskrivelse af fiskeredskader og -metoder]. National Environmental Research Institute (in Danish).

Moss, B., 1980. Ecology of fresh waters. Blackwell Scientific Publications London, 332 pp.

Murphy, J. & J. R. Riley, 1972. A modified single solution method for the determination of phosphate in natural waters. Analyt. chim. Acta 27: 21–26.

Olrik, M., 1978. Cyanophyceae and environmental factors in 15 Danish Lakes. Verh. int. Ver. Limnol. 20: 690–695.

Olrik, M., 1981. Succession of phytoplankton in response to environmental factors in Lake Arresø, North Zealand, Denmark. Schweiz. Z. Hydrol. 43,1: 6–19.

Persson, L., 1987. Effects of habitat and season on competitive interactions between roach (Rutilus rutilus) and perch (Percha fluviatilis). Oecologia 73: 170–177.

Persson, L., G. Andersson, S. F. Hamrin & L. Johansson, 1988. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. In S. R. Carpenter (ed.), Complex interactions in lake communities. Springer Verlag: 45–65.

Phillips, G. L., D. Eminson & B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated waters. Aquat. Bot. 4: 103–126.

Reinertsen, H., A. Jensen, J. I. Koksvik, A. Langeland & Y. Olsen, 1990. Effects of fish removal on the limnetic ecosystem of a eutrophic lake. Can J. Fish. aquat. Sci. 47: 166–173.

Reynolds, C. S., 1984. The ecology of freshwater phytoplankton. Cambridge University Press, 384 pp.

Riemann, B., K. Christoffersen, H. J. Jensen, J. P. Müller, C. L. Lindegaard & S. Bosselmann, 1990. Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. Hydrobiologia 200/201: 241–250.

SAS Institute Inc., 1985. SAS user's guide: statistics. Version 5 edition. Cary, NC: SAS Institute Inc., 956 pp.

Sas H. (ed.), 1989. Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation. Acad. Ver. Richarz GmbH, 497 pp.

Scheffer, M., 1989. Alternative stable states in eutrophic freshwater ecosystems. A minimal model. Hydrobiol. Bull. 23: 73–83.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200/201: 475–486.

Shapiro, J., B. Forsberg, V. Lamarra, G. Lindemark, M. Lynch, E. Smeltzer & G. Zoto, 1982. Experiments and experiences in biomanipulation: studies of biological ways to reduce algal abundance and eliminate blue-greens. Environmental Protection Agency (EPA), 251 pp.

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen & O. Sortkjær, 1990. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200/201: 229–240.

Timms, R. M. & B. Moss, 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish in a shallow wetland ecosystem. Limnol. Oceanogr. 29: 472–486.

Hydrobiologia **191**: 149–164, 1990.
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Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study of phytoplankton collapses in Lake Søbygård, Denmark

Erik Jeppesen, Martin Søndergaard, Ole Sortkjær, Erik Mortensen & Peter Kristensen
National Environmental Research Institute, Lysbrogade 52, DK-8600 Silkeborg, Denmark

Key words: phytoplankton collapses, hypertrophic lake, high pH, phytoplankton, zooplankton, fish

Abstract

Since 1983 severe phytoplankton collapses have occurred 1-4 times every summer in the shallow and hypertrophic Lake Søbygård, which is recovering after a ten-fold decrease of the external phosphorus loading in 1982. In July 1985, for example, chlorophyll *a* changed from 650 $\mu g\ l^{-1}$ to about 12 $\mu g\ l^{-1}$ within 3-5 days. Simultaneously, oxygen concentration dropped from 20-25 mg $O_2\ l^{-1}$ to less than 1 mg $O_2\ l^{-1}$, and pH decreased from 10.7 to 8.9. Less than 10 days later the phytoplankton biomass had fully recovered. During all phytoplankton collapses the density of filter-feeding zooplankton increased markedly, and a clear-water period followed. Due to marked changes in age structure of the fish stock, different zooplankton species were responsible for the density increase in different years, and consequently different collapse patterns and frequencies were observed.

The sudden increase in density of filter-feeding zooplankton from a generally low summer level to extremely high levels during algae collapses, which occurred three times from July 1984 to June 1986, could neither be explained by changes in regulation from below (food) nor from above (predation). The density increase was found after a period with high N/P ratios in phytoplankton or nitrate depletion in the lake. During that period phytoplankton biomass, primary production and thus pH decreased, the latter from 10.8-11.0 to 10.5. We hypothesize that direct or indirect effects of high pH are important in controlling the filter-feeding zooplankton in this hypertrophic lake. Secondarily, this situation affects the trophic interactions in the lake water and the net internal loading of nutrients. Consequently, not only a high content of planktivorous fish but also a high pH may promote uncoupling of the grazing food-web in highly eutrophic shallow lakes, and thereby enhance eutrophication.

A tentative model is presented for the occurrence of collapses, and their pattern in hypertrophic lakes with various fish densities.

Introduction

Marked shifts in species composition of phytoplankton and zooplankton occur every summer in most lakes due to changes of environmental variables or interactions within the biological community. Hypertrophic lakes are characterized by dominance of a few species and a significant lack of feed-back mechanisms. Therefore, a marked shift in the populations of a species commonly results in great oscillations in the whole lake-water ecosystem, ranging from periods with dominance of autotrophic organisms and low transparency to periods with mainly heterotrophs and clear-water conditions (Uhlmann, 1971; Barica, 1975; Fott *et al.*, 1980; Benndorf *et al.*, 1984; Jeppesen *et al.*, in press).

In most oligotrophic and mesotrophic lakes, species richness is higher and the food web more complex. Consequently, a collapse of a population of one species due to unfavourable conditions is, at least during summer, often compensated by an increase in abundance of one or more species belonging to the same trophic level (e.g. Stewart & Wetzel, 1986).

Nevertheless, the biologically buffered oligotrophic or mesotrophic lake periodically also suffers from lack of timing between autotrophy and heterotrophy, which results in similar but less pronounced changes in the ecosystem. The clear-water period in early summer in many lakes (Lampert *et al.*, 1986; Stewart & Wetzel, 1986; Sommer *et al.*, 1986) is an example of lack of timing.

The simplicity of the ecological network and the generally higher process rates in the hypertrophic lake make such lakes more suitable for studies of interactions within the biological community and of inter-relationships between the biological community and its chemical and physical environment. The hypertrophic lake is thus a full-scale laboratory experiment in the field, from which knowledge can be obtained in order to interpret results, including those more biologically complex lake systems.

We have studied the hypertrophic and highly oscillating shallow Lake Søbygård for 10 years, but most intensively after a reduction of its loading of organic matter and phosphorus. Here we analyse both the causes of phytoplankton collapses, which occur 1-4 times every summer, and the consequences of the collapses for the dynamics of other trophic levels.

The lake has been followed intensively since 1984. The most comprehensive sampling programme which included continuous measurements of oxygen and pH was, however, run during the single collapse in 1985. This event is described in detail, while the collapses in 1984, 1986 and 1987 are discussed more briefly.

In a related paper (Søndergaard *et al.*, 1989) we discuss the impact of these shifts on the chemical environment and the internal loading.

Study-area

The calcareous Lake Søbygård is situated in central Jutland, Denmark (9° 48′ 35″ E, 56° 15′ 20″ N) (Fig. 1). It is 0.38 km^2 in area and shallow, with a mean depth of 1.0 m and maximum of 1.9 m. The hydraulic retention time is short, on average 15-20 days on a yearly basis and 21–30 days in summer. The lake is surrounded by decidous and coniferous forest, except to the west where it is exposed to prevailing wind. Emergent and floating-leaved macrophytes are only sparsely developed, and submerged vegetation is totally missing.

In the 1960's and 1970's the lake received large amounts of only mechanically treated sewage water from the sewage plant in the town of Hammel. In 1976 a biological treatment plant was established.

Marked changes in phosphorus loading have occurred during the last ten years. Until 1982, when the sewage plant was extended with a chemical step to remove phosphorus, the phosphorus loading of the lake was extremely high (28-33 g P m^{-2} yr^{-2}); since then it has been reduced to a much lower but still relatively high level of 4-7 g P m^{-2} yr^{-1}.

Corresponding to the changes in loading, the concentration of phosphorus in the main inlet has changed from 1-4 mg P l^{-1} before 1982 to 0.15-0.25 mg P l^{-1} since 1983. This decrease was, however, not reflected in an equivalent lower phosphorus concentration in the lake because of high phosphorus release from the sediment.

A brief description of the lake and loading history is given in Jeppesen *et al.* (1985) and Søndergaard *et al.* (1987), and a more comprehensive description by Jeppesen *et al.* (in press).

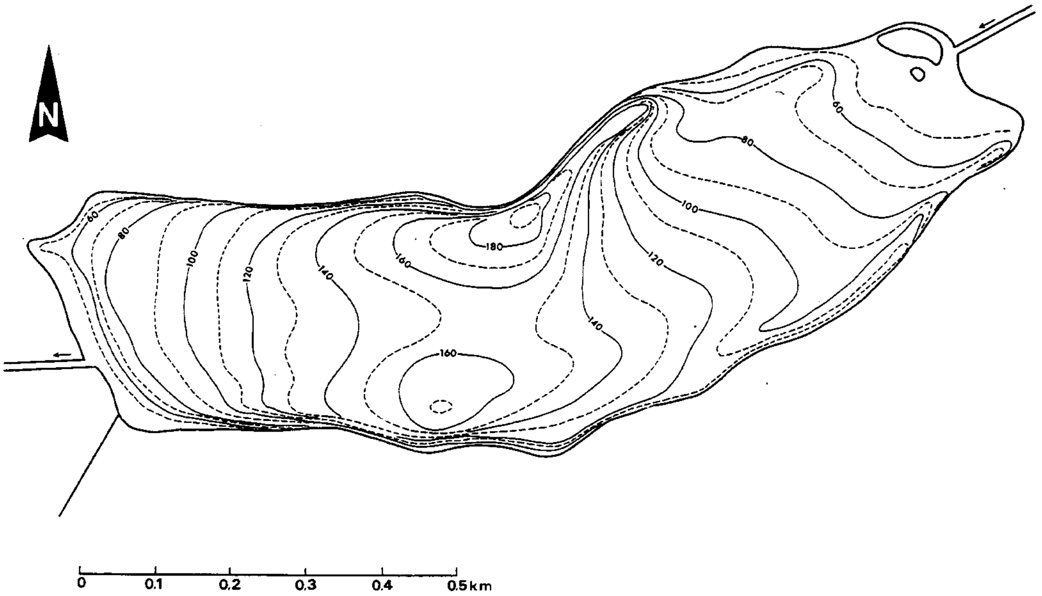

Fig. 1. Map of Lake Søbygård, with depth-contours in cm.

Methods

Phytoplankton:

Samples of 3.3 l were taken with a Patalas sampler from depths of 0.5 m and 1.2 m, then pooled, whereafter a 100-ml subsample was fixed with 1 ml lugol. Phytoplankton was quantified by counting a fixed water volume in an inverted microscope. Usually at least 100 individuals of each of the 2-3 dominating species were counted, and fewer of the other species. The maximum statistical error of the total number of algae was generally within 20-30% (S.E.).

Phytoplankton biomass expressed as biovolume was estimated by fitting the species or subspecies at each sampling date to simple geometrical figures.

Zooplankton:

Samples of 3.3 l were taken with a Patalas sampler from depths of 0.5 m and 1.5 m, then pooled, whereafter 6.6 l were filtered through a mesh net with a pore size of 50 μm (1984) or 20 μm (1985-87), and finally fixed with 1 ml lugol solution and in 100 ml tap water. Triplicate samples were collected randomly in the pelagial at each sampling date.

During most periods with peak densities of zooplankton, 2-3 samples have been counted; otherwise only a single sample was counted. Various counting procedures have been used. Usually the samples were pre-filtered on a 140 μm net, and all animals retained on the filter were counted. In periods with high densities, however, animals were enumerated on subsamples.

Zooplankton < 140 μm was counted in an inverted microscope. After filtration on a 20 μm net, the animals retained were transferred into fifteen 2.9-ml chambers and either counted totally or partly using counting strips, at 40-100 fold magnification, depending on the size of the zooplankton. In periods with a high content of resuspended matter, it was necessary to dilute the samples 5-10 fold before counting, and zooplankton was then enumerated on sub-samples. Between 2 and 100% of each sample was counted on each sampling date.

Rotifer and cladoceran biomass were estimated from length measurements by use of published length-weight equations (rotifers: Dumont *et al.*, 1975; cladocerans: Bottrell *et al.*, 1976).

Length measurements were made on each sampling date on at least 20 rotifers and 20-50 cladocerans of these species which then contributed significantly to the total zooplankton biomass.

Biomass of cyclopoid nauplii was set to 0.2 μg d.w. indiv.$^{-1}$ according to Culver *et al.* (1985).

For estimation of zooplankton grazing rate on algae, the *in vitro* principle of Bjørnsen *et al.* (1986) was used. Water samples were filtered on a 20 μm mesh net to remove grazing animals. ^{14}C-marked bicarbonate (NaH $^{14}CO_3$, 20 μCi per ampoule) was added to a subsample to a final concentration of 20-30 μCi per liter, and before the experiment incubated in light either in the laboratory for 18 hours at *in situ* temperature (until October 1985), or *in situ* for 2-3 hours (from October 1985). Prior to the grazing experiments the labelled phytoplankton was refiltered through a 20 μm mesh net.

The experiments were run on mid-lake composite samples (60-70 l) from depths of 0.5 and 1.5 m. Some 200 ml of ^{14}C-labelled phytoplankton were added to six 800-ml subsamples. Triplicate samples were incubated *in situ* for 20-60 min, depending on the temperature, while the remaining triplicate samples were used as blanks. Incubations were stopped by filtering the water from the experimental bottles through a 140 μm and then a 20 μm mesh net (diameter 25 mm). Zooplankters remained on the net were washed eight times in lake water by rapid back-filtration. The nets were drained on filter paper, transferred to glass vials, and assayed on a LKB-WALLAC 1210 liquid scintillation counter after dissolution in a 10 ml Ready-solv Hp/b (Beckmann) liquid for at least 24 h. Quenching was determined by the external standard-channels-ratio-method.

The ^{14}C-activity of phytoplankton before and after incubation was measured on 10-ml aliquots of the samples; filtered *in situ* on cellulose nitrate filters (0.45 μm), and in the laboratory transferred to glass vials and assayed as described above. Mean ^{14}C-activity during the incubation was used as the tracer activity.

Chemical variables:

Oxygen was measured either manually at each sampling date by use of the modified Winkler-technique (Limnologisk Metodik, 1977), or over periods automatically every 0.5 h by use of oxygen probes (pHOX system). The pH was either measured manually at each sampling date or over periods automatically (Great Lakes Instruments) every 0.5 h. The probes were calibrated automatically once a day by pumping air-bubbled, oxygen-saturated and borax-buffered water (pH = 9.18) through the probe chambers. The probe signals were recorded on microchips. For more details, see Jeppesen *et al.* (1985) and Sortkjær & Jeppesen (1987). For other chemical variables, see Søndergaard *et al.* (1989).

Results

1985

The collapse in 1985 occurred in two steps (Figs. 2, 3). First, the algae biomass (largely *Scenedesmus* spp.) (Fig. 2) decreased during a period of 20 days, from 1200 μg chl.-*a* l^{-1} to a lower but still high level of 650 μg l^{-1} (Fig. 5). Then, a fast decline to 12 μg l^{-1} occurred within 3-5 days (Figs. 3, 5), followed by a rapid recovery after 3-4 days later. The second step of the collapse was accompanied by marked changes in the oxygen concentration from a highly supersaturated level of 20-25 mg O_2 l^{-1} to 1 mg O_2 l^{-1} within 7 days, after which a fast recovery was observed simultaneously with the reappearance of phytoplankton. The pH was reduced from 10.7 to 8.9 before it slowly increased again.

There was a tendency to a less pronounced change in the maximum photosynthetic capacity, P_{max}, than in chl.-*a* (Fig. 5). P_{max} thus altered from 1.45 to 1.25 (mg C l^{-1} h^{-1}) from 11 to 18 July, while chl.-*a* in the same period changed from 650 μg l^{-1} to 350 μg l^{-1}.

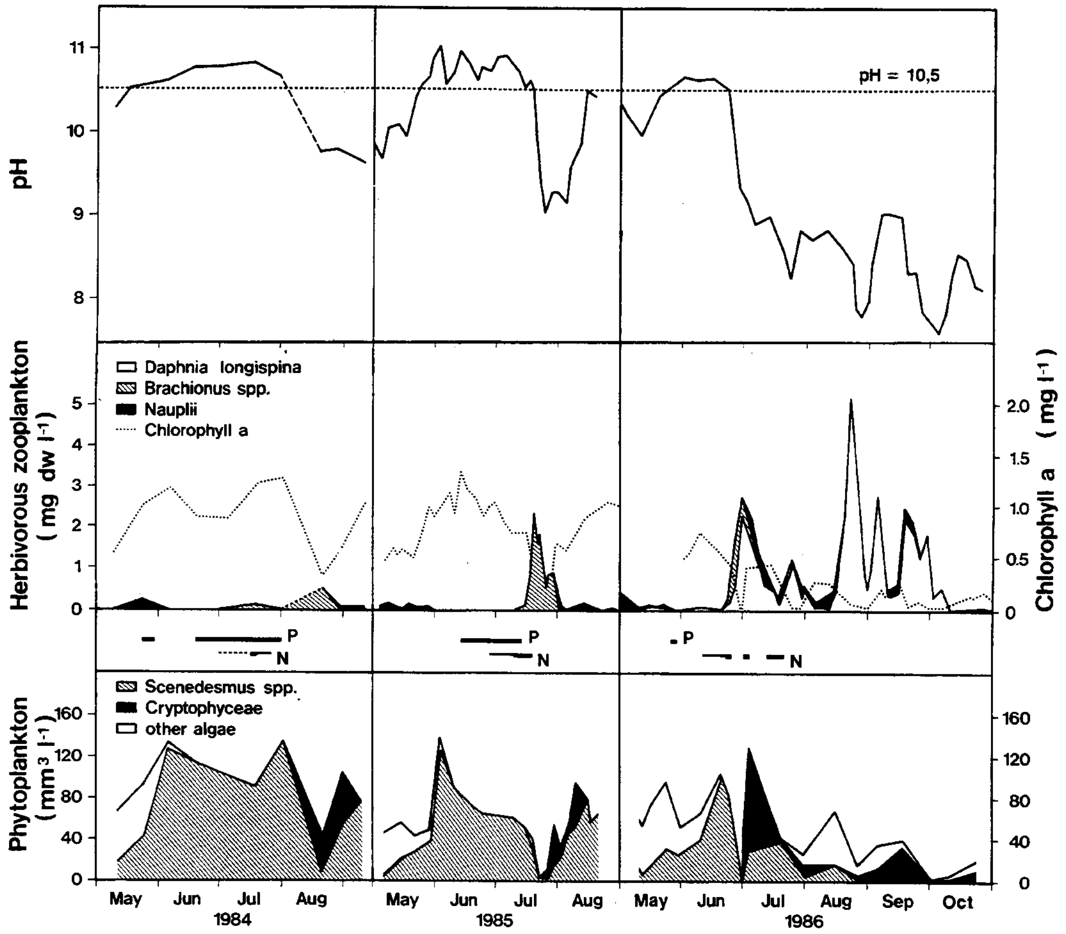

Fig. 2. Seasonal and year-to-year variation in pH, biomass of herbivorous zooplankton, and biovolume of various groups of phytoplankton. In between the latter two further incidences are shown; periods with low nitrogen input from the inlet (closed thin bars), and nitrate depletion ($<2\ \mu g\ N\ l^{-1}$) in the lake (closed thick bars), and periods with orthophosphate concentration in the lake below $10\ \mu g\ P\ l^{-1}$.

During the first step in the collapse, pH was reduced from a mid-morning level of 10.7-10.8 to 10.5. Herbivorous zooplankton density was extremely low prior to the collapse, and remained low during its first step (Figs. 2 and 5).

In spite of the high level of total phosphorus and total nitrogen, the concentration of inorganic phosphorus was low ($<20\ \mu g\ P\ l^{-1}$), and nitrate was fully depleted ($<2\ \mu g\ N\ l^{-1}$) towards the end of the first step in the collapse (Fig. 2 and Søndergaard *et al.*, 1989).

The nitrogen content in the particulate organic matter (mainly phytoplankton) ranged from 6.7 to 8.6% of organic d.w. from May to the clear-water period in July, and showed no trends during that period (Fig. 4). However, the N/P-ratio in the particulate organic matter showed considerable variations, from 6.2 in May to peak values of 10 and later 9.6 during the first step in the collapse (Fig. 4). In between those peaks the N/P-ratio declined to 8, concurrently with a tendency to a temporary increase in chl.-*a*.

The rapid decline in phytoplankton biomass in the second phase of the collapse followed the

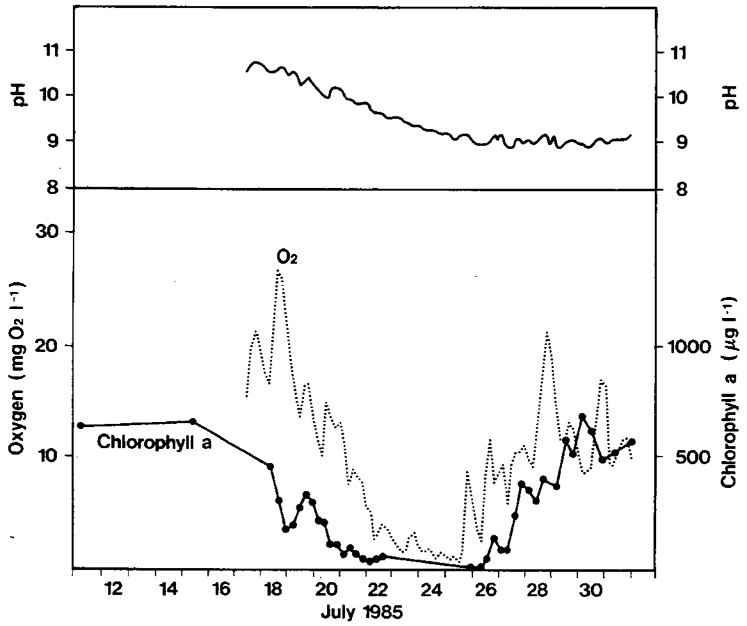

Fig. 3. Diel variations in pH and concentrations of oxygen and chlorophyll *a* during the phytoplankton collapse in 1985.

nitrate depletion (Fig. 2), and was accompanied by an abrupt increase in numbers of the rotifers *Brachionus calyciflorus* and *Brachionus urceolaris*, which reached a maximum density of 17 000 indiv. l^{-1} or 2.8 mg d.w. l^{-1} within 10 days after the initiation of growth (Figs. 2, 5). Concurrently, the zooplankton clearance rate on phytoplankton increased from near-zero values of 23 ml l^{-1} h^{-1} (Table 1).

The rotifer peak was followed by a rapid decrease in density and formation of mictic resting eggs (Fig. 5). Simultaneously, due to growth of especially *Cryptomonas spp.* and *Scenedesmus spp.* (Fig. 2), the phytoplankton biomass increased to 750 µg chl.-*a* l^{-1} within 14 days.

1984

In 1984 the sampling was run only bi-weekly. A collapse in phytoplankton was observed in August, accompanied by a temporary increase in the density of *Brachionus calyciflorus* (Fig. 2). Sampling was made towards the end of the col-

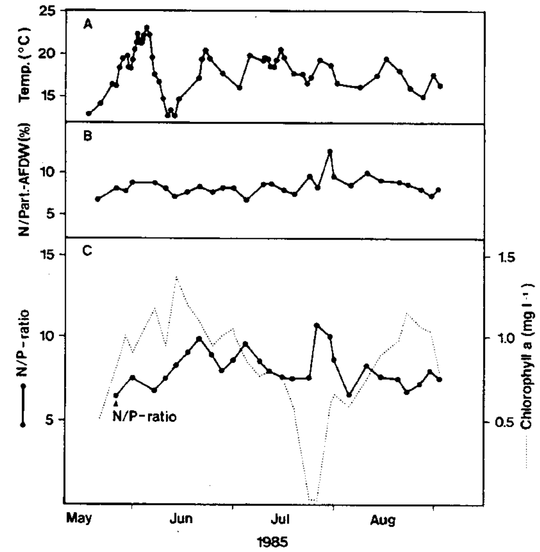

Fig. 4. Changes in A) temperature, nitrogen content in organic mater (AFDW) (mainly algae), B) N/P ratio in organic matter (AFDW), and C) chlorophyll *a* concentration in lake water during summer 1985.

Table 1. Mid-morning level of estimated zooplankton clearance rates of phytoplankton in Lake Søbygård (ml l^{-1} h^{-1}).

Date	Zooplankton size groups			
	> 140 μm	20–140 μm	total (> 20 μm)	
18 June 85	0	0	0	before collapse
19 July 85	0.7	10.3	10.9	during collapse
23 July 85	2.7	20.0	22.7	during collapse
8 Aug. 85	0	1.0	1.0	after collapse
24 June 86	0.2	0.2	0.2	before collapse
21 Aug. 86	0	21.7	21.7	during collapse
29 Aug. 86	13.7	5.9	19.6	during collapse

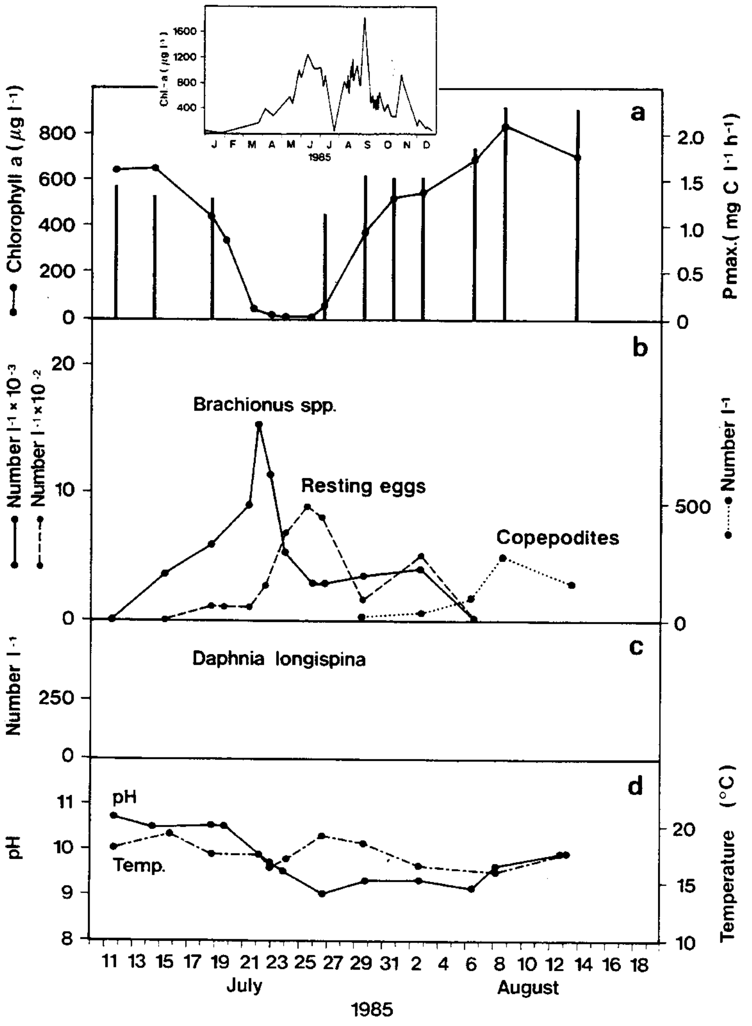

Fig. 5. Changes in selected variables during the collapse in 1985: a) chlorophyll *a* (full line) and maximum photosynthetic capacity, P_{max} (full bars). Small figure: Seasonal variation in chlorophyll *a* concentration. b) numbers of *Brachionus urceolaris* and *Brachionus calyciflorus* (full line), numbers of resting eggs (broken line), and numbers of copepodites (mainly of *Cyclops vicinus*) (dotted line). c) numbers of *Daphnia longispina* above 1 indiv. l^{-1}. d) mid-morning level of pH and temperature.

lapse, at which the rotifer population was in the decreasing phase as indicated by high numbers of resting eggs. The rotifer density had probably been much higher earlier in the collapse.

This year cryptophytes and *Scenedesmus spp.* also dominated phytoplankton communities in post-collapse period of re-growth. A small decrease in phytoplankton biomass and a peak of *Brachionus urceolaris* were also observed in July (Fig. 2), but the *Scenedesmus* community recovered simultaneously with an increase in the nitrate input to the lake, and consequently an increase in the nitrate concentration in the lake (Fig. 2).

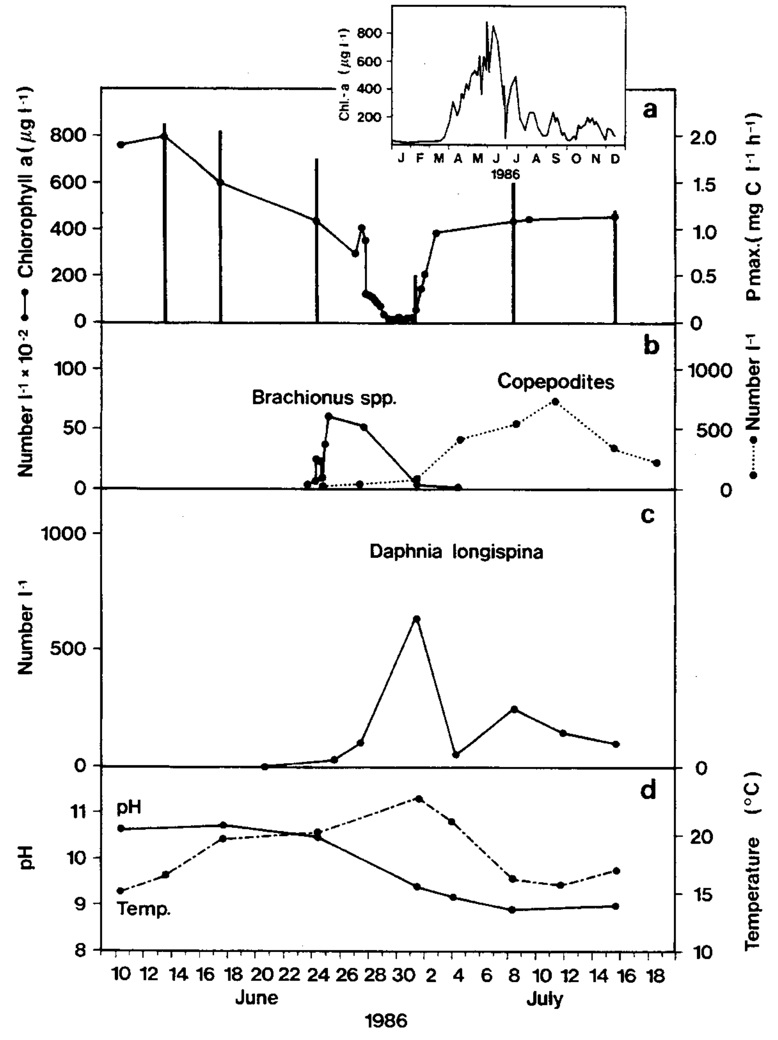

Fig. 6. Changes in selected variables during the first collapse in 1986: a) chlorophyll *a* (full line) and maximum photosynthetic capacity, P_{max} (full bars). Small figure: Seasonal variation in chlorophyll *a* concentration. b) numbers of *Brachionus urceolaris* and *Brachionus calyciflorus* (full line), and numbers of copepodites (mainly of *Cyclops vicinus*) (dotted lines). c) numbers of *Daphnia longispina*. d) mid-morning level of pH and temperature.

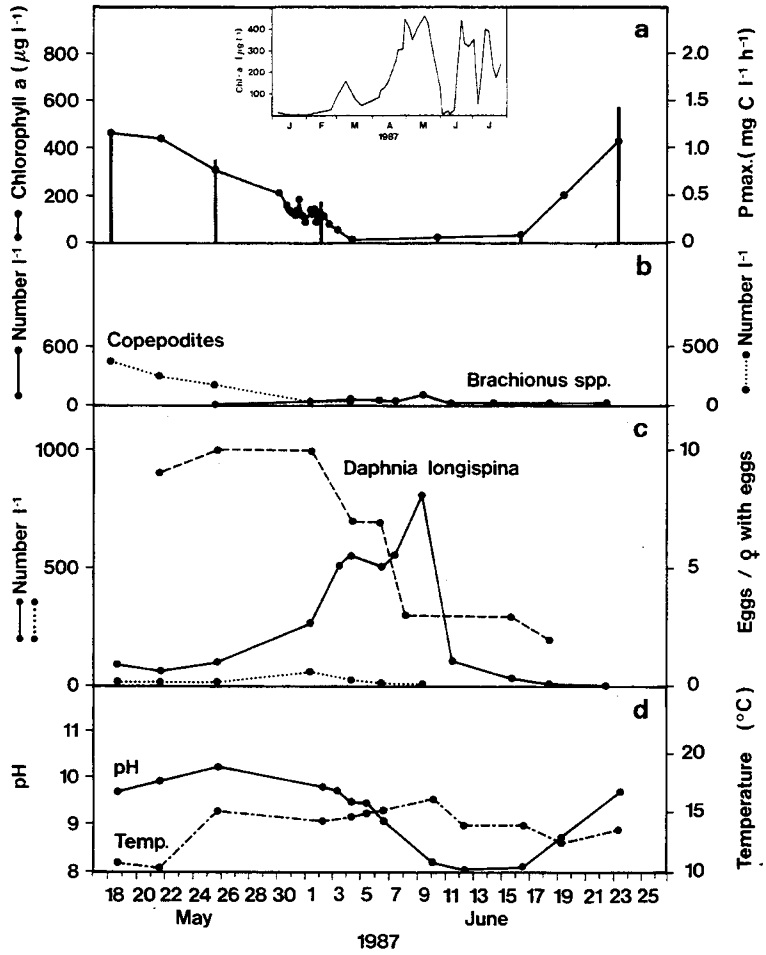

Fig. 7. Changes in selected variables during the first collapse in 1987: a) Chlorophyll *a* (full line) and maximum photosynthetic capacity, P_{max} (full bars). Small figure: Seasonal variation in chlorophyll *a* concentration. b) numbers of *Brachionus urceolaris* and *Brachionus calyciflorus* and numbers of copepodites (mainly of *Cyclops vicinus*). c) numbers of *Daphnia longispina* (full line), numbers of eggs per female with eggs (broken line), and numbers (left Y-axis) of female with eggs (dotted line) of *D. longispina*. d) mid-morning level of pH and temperature.

1986

In 1986 four events of phytoplankton collapses were observed. The first collapse occurred three weeks earlier than in 1985, but followed a remarkable similar pattern (Figs. 2, 6). It involved initial decline in chl.-*a* accompanied by a tendency to an increase in the P_{max}/chl.-*a* ratio, a decline in pH from 10.6-10.7 to less than 10.5, and nitrate depletion (<2 µg N l^{-1}). Then a steep decrease followed in connection with an increase in the density of rotifers (mainly *Brachionus calyciflorus*), but in 1986 additionally succeeded by a marked increase in the abundance of *Daphnia longispina* and a simultaneously reduction in rotifers (Fig. 6). Probably due to the relatively high water temperature (Fig. 6) and high irradiance (not shown), a fast recovery of phytoplankton (mainly cryptophyceae) was then observed (Fig. 2). In 1986 the chl.-*a* level after the collapse only reached half of the pre-collapse level before a new decline occurred, simultaneously with a rapid increase in the density of *B. calyciflorus* and especially *D. longispina* (Fig. 2). Additionally, two further collapses were observed in 1986 in connection with new peaks of *D. longispina* (Fig. 2).

1987

Up to July there was one major collapse in 1987 (May) which occurred four weeks earlier than the first one in 1986, and seven weeks earlier than that in 1985. The 1987-collapse followed a somewhat different pattern than the collapses in the two preceding years (Fig. 7). Due to unusual climatic conditions in early summer, with only half of the mean irradiance for the period and low water temperature (Fig. 7), chl.-*a* level, P_{max}, and consequently pH were lower prior to the collapse than in the preceding years (Figs. 5–7).

Hence, chl.-*a* was then 450 $\mu g\ l^{-1}$ in 1987, but 800-1200 $\mu g\ l^{-1}$ in 1985-86, and pH 9.8-10.2 in 1987 compared to 10.7-10.8 in the two previous years. The nutrient level was also different prior to the collapse. Neither phosphate nor nitrate were depleted, and these nutrients, therefore, cannot have been responsible for the phytoplankton collapse in this year. However, the collapse occurred simultaneously with an increase in the density of *Daphnia longispina* from near-zero numbers to 800 indiv. l^{-1} (Figs. 2, 7), and a temperature increase from 10 °C to 14-15 °C (Fig. 7).

During the collapse, the number of egg-bearing females and the percentage of females with eggs were reduced markedly (Fig. 7), and simultaneously the number of eggs per female with egg decreased from 9-10 to 2-3 (Fig. 7). Subsequently, a steep decline in the density of *D. longispina* was observed.

In accordance with the lower water temperature and the expected lower re-growth rate of phytoplankton in 1987 compared to 1985 and 1986 (Figs. 5, 6), the clear-water period lasted longer than in the preceding years, being 13 days in 1987 compared to 3-5 days in 1985-86.

Discussion

In spite of large differences from year to year and within years, the collapses in phytoplankton generally seem to follow a common pattern. Hence, when the pre-collapse level of chl.-*a* and pH were above 700-800 $\mu g\ l^{-1}$ and 10.5, respectively (July 1985, May 1986) the collapses in phytoplankton seem to occur in two steps, otherwise in one step (June-Sept. 1986, and May-July 1987) (Fig. 2).

First step in the collapse:

The first step in the two-step collapses may be due to one or more of the following factors: reduced primary production, increased grazing by zooplankton, infections by viral pathogens, bacteria or fungi, increased sedimentation rate, or exhaustion of nutrients.

The first hypothesis can probably be rejected, since the maximum potential production per unit phytoplankton volume or chl.-*a* generally showed tendency to increase during the first step in all events with a two-step collapse (Figs. 2, 5, 6). This might be due to the improved light conditions as transparency increased. The production per m^2 was consequently altered less than phytoplankton biomass during that period. The primary production was, nevertheless, either not transformed to growth, or the phytoplankton produced was eliminated due to an increase in one or another of the loss factors.

Zooplankton grazing is responsible for short-lasting clear-water periods in many lakes (e.g. Sommer *et al.*, 1986). However due to the low density of herbivorous zooplankton grazing on phytoplankton was insignificant during the first step of the collapse in 1985 and the first collapse in 1986 (Table 1 and Fig. 2).

Infections by various pathogens can affect sedimentation velocity of phytoplankton (e.g. Jewson *et al.*, 1981). During the first step in collapses mentioned, no evidence of infection of the dominating phytoplankton group, *Scenedesmus* was found. Neither encysted zoospores, sporangia nor hyphae were observed, and we did not find any increase in the numbers of dead cells during that period.

Nevertheless, by means of sediment traps and by mass balance calculations, Kristensen & Jensen (1987) did find a steady increase in the specific loss rate by sedimentation in Lake Søbygård 1985. This rose from about 2-3% d^{-1} in the exponential growth phase of *Scenedesmus* (May), to 14-17% d^{-1} in the stationary phase (June), with a further increase to 25% d^{-1} towards the end of the first step in the collapse. Large differences in the specific loss rate by sedimentation between phytoplankton in the exponential growth phase and in nutrient-limited stationary phase have been observed, both in laboratory investigations (e.g. Titman & Kilham, 1976) in lakes or *in situ* enclosures (e.g. Jassby & Goldmann, 1974; Reynolds & Wiseman, 1982). Thus Titman & Kilham (1976) found a 3.3-fold higher specific loss rate by sedimentation in the nutrient-limited stationary phase than in the exponential growth phase in laboratory experiments with *Scenedesmus quadricauda*, which is an abundant *Scenedesmus* species in Lake Søbygård. The observed increase in specific loss rates by sedimentation might, therefore, indicate nutrient limitation. This is supported by the fact that orthophosphate concentration was low, and nitrate was depleted towards the end of the first step in the collapse in 1985 (Fig. 2). Although the nitrogen content in particulate organic matter (mainly phytoplankton) showed only minor changes from May to the clear-water period in 1985, marked changes in the N/P-ratio and consequently in the P-content occurred during this period. Maximum N/P-ratios were obtained after a period of relatively low water temperature (Fig. 4), when the net phosphorus release from the sediment was relatively low (Søndergaard *et al.*, 1989). Since the release of phosphate from the sediment was an important contribution to the overall phosphate pool, which can be used for phytoplankton growth in summer (Søndergaard *et al.*, 1989), a reduced sediment release might explain the observed increase in the N/P-ratio in the phytoplankton. Since N/P-ratios near or above 10 may indicate phosphorus limitation for *Scenedesmus* (Kunikane *et al.*, 1984), lack of phosphorus might have been a regulating factor for the decline in phytoplankton biomass in 1985. Conversely, the first two collapses in 1986 occurred when nitrate was depleted ($<2\ \mu g\ N\ l^{-1}$) but orthophosphate was above 25 $\mu g\ P\ l^{-1}$. Nitrate was also depleted during the end of the first step in the collapse in 1985 (Fig. 2 and Søndergaard *et al.*, 1989). Therefore, we suggest that the first step in the two-step collapses was due to exhaustion of nutrient, probably either phosphate or nitrate, or both.

Second step and single-step collapses:

The second and fastest step in the collapses in 1984 to June 1986 and the single step collapse since June 1986 occurred simultaneously with a marked increase in numbers of filter-feeding zooplankton, which changed from very low values to extremely high peak densities (Fig. 2). Accordingly, high grazing rates were obtained (Table 1).

The relative importance of the different filter-feeders during the collapse changed from year to year. The rotifers *Brachionus spp.* dominated totally in 1984 and 1985, whereas a peak of *Daphnia longispina* succeeded the rotifer maximum during the first collapse in 1986, after which the importance of the rotifers steadily declined. This structural shift from small rotifers to larger crustaceans may be explained by changes in the age-structure of the fish population, which is totally dominated by roach (*Rutilus rutilus*) and rudd (*Scardinius erythropthalmus*). Probably due to direct or indirect effects of high pH (e.g. ammonia), all planktivorous fish species did not spawn in 1984–86 (Timmermann, 1987). Consequently their younger year-classes, which are believed to have a more severe impact on structure and density of zooplankton in shallow eutrophic lakes than older age-classes (Cryer *et al.*, 1986), have gradually become less abundant since 1984. Concurrently, as expected, the predation pressure on the larger zooplankton has been reduced portionally, and we observed the well-described shift towards larger zooplankton (e.g. Hrbáček, 1962).

The increase in abundance of *D. longispina* in summer from 1984 until 1986 could, however, also have been self-strengthened by an increase in the production of resting eggs in autumn, according to a successive increase in numbers of mictic reproducing females. Conversely, some years earlier in summer 1983, both *D. longispina* and *Daphnia magna* were in a short time able to develop high densities from sediment isolated within '*in situ*' enclosures without fish (Andreasen *et al.*, 1984). The population growth, therefore, seems not to be seriously limited by the quantity of resting eggs in Lake Søbygård.

pH-effect:

Although changes in fish stock and perhaps to a minor extent a delay in recolonization might explain the year-to-year changes in the zooplankton structure during the collapses, it still remains striking that filter-feeding zooplankton in summer was abundant only during the phytoplankton collapses in 1984 and 1985 (Fig. 2). This was despite the absence of predaceous zooplankton (mainly *Cyclops vicinus*) from the pelagial during a long period in mid-summer. Insufficient amounts of food or poor food-quality could be a possible explanation for the absence of the filter-feeders. However, several authors have shown that various species of *Scenedesmus* are suitable as food for different species of *Daphnia*, including *D. longispina* (e.g. Infante, 1973; Geller, 1975; Horn, 1981; Muck & Lampert, 1984; Bloem & Vijverberg, 1984). Additionally, Lyche (1984) found that one of the two most abundant species of *Scenedesmus* in Lake Søbygård, *S. quadricauda*, is ingested and also assimilated with a high efficiency by *D. longispina*. Furthermore, Gilbert & Starkweather (1978) have shown that *Brachionus calyciflorus* is able to feed on the other abundant *Scenedesmus* species in Lake Søbygård, *S. acuminatus*, although it seems to select for smaller particles by use of various rejection mechanisms (Starkweather, 1978).

Therefore, neither food-quality nor insufficient amounts of food (see Fig. 2) can explain the delayed initiation of growth of *D. longispina* in 1986 compared to 1987, and the only short-term occurrence of *Brachionus* spp. in 1984-85.

However, high pH has been shown to influence survival and reproduction of zooplankton. Bogatova (1962), Walter (1969) and Ivanova (1969) all found an upper pH limit of 10.5-11.5 for survival of cladocerans, and from experiments in fish ponds O'Brien & deNoyelles (1972) suggested that high pH (above 10.6) was responsible for a temporary disappearance of *Ceriodaphnia reticulata* from the ponds. Additionally, Hessen & Nielssen (1985) found reduced egg production at high pH values, and also concluded that a change in pH from 9.5 to 10.5 was the main reason for the disappearance of cladocerans (among others *D. longispina*) and most rotifers in fishless enclosures in Lake Gjersjøen. Mitchell & Joubert (1986) obtained highest capacity of population increase and highest longevity of *B. calyciflorus* between pH 8.5 and 9.5, and lowest values of both parameters between 10 and 10.5 in a series of batch experiments run at pH intervals of 7.5 to 10.5. *B. calyciflorus* thus prefers moderately high pH, but is severely affected when pH is above 10.

Therefore, it seems reasonable to suggest that direct or indirect effects of high pH are responsible for low density of filter-feeders in Lake Søbygård prior to the collapses in 1984 and 1985, and to the first collapse in 1986. This hypothesis is further supported by the fact that *D. longispina* in 1987, when the spring pH was relatively low (below 10.2), was abundant already in late May compared to the beginning of July in 1986. In 1987 the first peak in *D. longispina* of 800 indice 1^{-1} occurred 15 days after a marked increase in water temperature from 10 to 14-15 °C. Hence, temperature seems to be a more important regulating factor in this year.

In summary, high pH thus may suppress reproduction and survival of filter-feeding zooplankton, and consequently their abundance in hypertrophic lakes. High pH may, therefore, affect the grazing food-web in a similar way as high numbers of planktivorous fish. Hence, in the short-term, high pH may increase the effect of the fish on the trophic structure in the lake, leading to an enhanced eutrophication in terms of increased chl.-*a* and decreased Secchi transparency. Conversely, on a long time scale (more than, say, two years), high pH may result in a temporary reduction of the predation pressure on filter-feeders owing to the negative effect of high pH on fish spawning. This leads to a high density of filter-feeding zooplankton and high grazing pressure on phytoplankton. Consequently, phytoplankton biomass and production are reduced, and pH then lowered, which again positively and in a self-amplifying manner affects the reproduction and survival of the filter-feeders. Concurrently, the chl.-*a* level decreases, and Secchi transparency increases.

Zooplankton dynamics during and after the collapse:

During the second step of the two-step collapses, in which pH dropped to below 10.5, and during the single-step collapses, the filter-feeding zooplankton showed a somewhat similar response pattern in 1984-87. First, an almost exponential increase in the population was observed. Second, when the phytoplankton biomass was almost exhausted, the numbers of cladoceran females with eggs as well as the numbers of eggs per female declined (1986 and 1987), and rotifers formed mictic resting eggs (1984 and 1985). Third, due to the low egg production in the cladocerans and the formation of only resting eggs by the rotifers, the population decreased abruptly. The second and the third statements indicate food-limitation, at least for the cladocerans. This initially affects the egg production, when the available food concentration reaches a lower threshold level of about 0.2 mg C l^{-1} (Lampert & Schober, 1978), and concurrently a decrease in the population density follows.

A similar pattern was observed by Lampert *et al.* (1986) during clear-water conditions in the Schönsee.

The formation of mictic eggs in *B. calyciflorus* has been shown to be induced by crowding (Gilbert & Starkweather, 1978), but it is also possibly an adaptive reaction to low food concentrations.

The rotifers reacted differently in 1986, as no mictic eggs were produced. The decline in population occurred simultaneously with a density increase of both *D. longispina* and copepodites of mainly *Cyclops vicinus* (Fig. 6). The rotifer decline might, therefore,be due to a competitive exclusion by the cladocerans, as shown by e.g. Gilbert & Starkweather (1978); or to predation by the copepodites and adult cyclopoids, which has been shown to have positive electivity for the genus *Brachionus* (Brandl & Fernando, 1978); or both factors could be involved. The total disappearance of rotifers in early August 1985 (Fig. 5) and in late August 1984 (Fig. 2), in spite of re-development of phytoplankton and the still only moderately high pH, could also be due to the increased density of copepodites and adult cyclopoids.

Hence, while high pH is suggested to be the major controlling factor for the pre-collapse densities of filter-feeding zooplankton in 1985 to June 1986, food and possibly also predation by carnivorous zooplankton were important regulators during and immediately after the collapses mentioned.

The post-collapse response pattern in the lake varied from year to year. In 1984 and 1985, when rotifers were the most abundant filter-feeders during the collapse, phytoplankton biomass and pH reached to the pre-collapse level shortly after the collapse, and the regulating role of pH was suggestively re-obtained. However, in 1986 and 1987, when *D. longispina* was more important, phytoplankton biomass and pH did not reach the pre-collapse level before a new collapse was encountered in connection with new peaks in zooplankton density (Fig. 2). The role of pH as a strong regulator of the abundance of filter-feeders was thus restricted to the period before the first collapse in 1986, and due to unusual weather conditions pH was less important in 1987 even in the pre-collapse period.

Clear-water periods and collapse pattern:

Clear-water periods occur in many eutrophic lakes, although the duration and the frequency vary considerably (Barica, 1975; Lampert & Schober, 1978; Fott *et al.*, 1980; Lampert *et al.*, 1986; Sommer *et al.*, 1986). In shallow hypertrophic lakes the composition of the fish stock, including density and age composition of planktivorous fish, seems to play the major role for the pattern and length of the clear-water phase. In fish-free conditions, either due to winter kill under ice, summer kill, or intensive fish harvesting, a high spring peak in phytoplankton is often followed by a long-lasting clear-water period (Barica, 1975; Fott *et al.*, 1980; Lynch, 1980; Andersson & Cronberg, 1984).

The clear-water period is sustained by large cladocerans (as *D. magna* and *D. pulex*) which frequently occur in high densities, and is often accompanied by dominance of the cyanobacterium, *Aphanizomenon flos-aquae* (Lynch, 1980; Andersson & Cronberg, 1984; Benndorf *et al.*, 1984). This pattern has also been found in Lake Søbygård in the seventies (Holm & Tuxen-Petersen, 1975; Andersen *et al.*, 1979; Jeppesen *et al.*, 1985) in connection with fish kill in summer.

Conversely, when the fish stock recovers, and the hypertrophic lakes explodes with young year-classes of planktivorous fish, or alternatively when the lake is manually stocked with high densities of planktivorous fish, the phytoplankton community often changes to small chlorococcal greens (Fott *et al.*, 1980; Benndorf *et al.*, 1984; Jeppesen *et al.*, in press). In that case no or only a few short-term collapses, and consequently clear-water periods, may occur (Fig. 2). This is due to the fact that growth and survival of filter-feeding zooplankton, and then grazing on phytoplankton, is suppressed by both predation by planktivorous fish and by direct or indirect effects of elevated pH, the latter due to a more-or-less unlimited growth of phytoplankton. The collapses occur only when pH is reduced below about 10.5, e.g. due to a low nutrient or cloudy weather mediated reduction in primary production. High-pH tolerant rotifers (e.g. *Brachionus calyciflorus*, *Brachionus urceolaris*) dominate the zooplankton community during the collapse.

However, when predation pressure of planktivorous fish on zooplankton is moderate, here due to lack of fish spawning for more than two years, phytoplankton is often dominated by cryptomonads (Fott *et al.*, 1980; Shapiro & Wright, 1984; Reinartsen & Olsen, 1984) which can compensate for grazing by high growth rates (Fott *et al.*, 1980), or large chlorococcal greens or gelatinous algae (Benndorf *et al.*, 1984; Jeppesen *et al.*, in press). In that case several collapses and short-lasting clear-water periods may occur during the summer in the hypertrophic lake, primarily due to grazing by intermediate-sized cladocerans (e.g. *D. longispina*). The oscillations may be due to alternations in 1) food conditions for zooplankton (e.g. below or above a threshold for egg production), 2) predation pressures by predatory zooplankton and fish (e.g. lack of timing in growth of prey and predator), 3) pH, or 4) climatic conditions.

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References

Andersen, J. M., J. Jensen, Aa. Kristensen & K. Kristensen, 1979. Undersøgelse af forureningstilstanden i Søbygård sø 1978. Report from Århus County: 29 pp (in Danish).

Andersson, G. & G. Cronberg, 1984. *Aphanizomenon flos-aqua* and *Daphnia*. An interesting plankton association in hypertrophic waters. In Bosheim & Nicholls (eds.), Interaksjoner mellom trofiske nivåer i ferskvann. Norsk Limnologförening, Blindern, Oslo, Norway: 63–76.

Andreasen, K., M. Søndergaard & H. H. Schierup, 1984. En karakteristik afforureningstilstanden i Søbygård sø – samt en undersøgelse af forskellige restaureringsmetoders anvendelighed til en begrænsning af den interne belasting. Publ. No. 7 from The Botanical Institute, University of Århus, Denmark: 164 pp (in Danish).

Barica, J., 1975. Collapses of algal blooms in prarie pothole lakes: their mechanism and ecological impact. Verh. int. Ver. Limnol. 19: 606–615.

Benndorf, J., H. Kneschke, K. Kossatz & E. Penz, 1984. Manipulation of the pelagical food web by stocking with predaceous fishes. Int. Revue ges. Hydrobiol. 69: 407–428.

Bjørnsen, P. K., J. B. Larsen, O. Geertz-Hansen & M. Olsen, 1986. A field technique for the determination of zooplankton grazing on natural bacterioplankton. Freshwat. Biol. 16: 245–253.

Bloem, J. & J. Vijverberg, 1984. Some observations on diet and food selection of *Daphnia hyalina* (Cladocera) in an eutrophic lake. Hydrobiol. Bull. Amsterdam18: 39–45.

Bogatova, I. B., 1962. Lethal ranges of oxygen content, temperature and pH for some representatives of the family Chydoridae. Zool. Zh. 41: 58–62 (in Russian).

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

Brandl, Z. & C. H. Fernando, 1978. Prey selection by the cyclopoid copepods *Mesocyclops edax* and *Cyclops vicinus*. Verh. int. Ver. Limnol. 20: 2505–2510.

Cryer, M., G. Peirson & C. R. Townsend, 1986. Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31: 1022–1038.

Culver, D. A., M. M. Bourcherle, D. J. Bean & J. W. Fletcher, 1985. Biomass of freshwater Crustacean zooplankton from length-weight regressions. Ca. J. Fish. aquat. Sci. 42: 1380–1390.

Dumont, H. J., I. Van De Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from plankton, periphyton and benthos of continental waters. Oecologia (Berl.) 19: 75–97.

Fott, J., L. Pechar & M. Prazaková, 1980. Fish as a factor controlling water quality in ponds. In J. Barica & L. R. Mur (eds.): Hypertrophic ecosystems. Developments in Hydrobiology 2: 255–261.

Geller, W., 1975. Die Nährungsaufnahme von *Daphnia pulex* in Abhängigkeit von der Futterkonzentration, der Temperatur, der Körpergrösse und dem Hungerzustand der Tiere. Arch. Hydrobiol/Suppl. 48: 47–107.

Gilbert, J. L. & P. L. Starkweather, 1978. Feeding in the rotifer *Brachionus calyciflorus* III. Direct observations on the effect of food type, food density, change in food type and starvation on the incidence of pseudotrochal screening. Verh. int. Ver. Limnol. 20: 2382–2388.

Hessen, D. O. & J. P. Nielssen, 1985. Factors controlling rotifer abundancies in a Norwegian eutrophic lake: an experimental study. Ann. Limnol. 21: 97–105.

Holm, T. F. & F. Tuxen-Petersen, 1975. Gudenåen 1974. Rep. from Lab. Physical Geography, Geological Institute, University of Århus, Denmark: 108 pp (in Danish).

Horn, W., 1981. Phytoplankton losses due to zooplankton grazing in a drinking water reservoir. Int. Revue ges. Hydrobiol. 69: 781–817.

Hrbáček, J., 1962. Species composition and the amount of zooplankton in relation to fish stock. Rozpravy Československe Akademie Ved. 72,10: 114 pp.

Infante, A., 1973. Untersuchungen über die Ausnutzarkeit verschiedener Algen durch das Zooplankton. Arch. Hydrobiol./Suppl. 42: 340–405.

Ivanova, M. B., 1969. The influence of active water reaction on filtering rate of Cladocera. Pol. Arch. Hydrobiol. 16: 115–124.

Jassby, A. D. & C. R. Goldmann, 1974. Loss rates from a lake phytoplankton community. Limnol. Oceanogr. 19: 618–624.

Jeppesen, E., O. Sortkjær, Aa. Rebsdorf, M. Søndergaard, P. Jensen, P. Kristensen, K. Andreasen, H. H. Schierup & J. M. Andersen, 1985. Recovery of a shallow lake. Reprint from a poster session ('Phosphorus in freshwater ecosystems', Uppsala, Sweden, 1985). Publ. No. 33 from the Freshwater Laboratory, National Agency of Environmental Protection: 10 pp.

Jeppesen, E., M. Søndergaard, E. Mortensen, J. P. Jensen, P. Kristensen, B. Riemann, H. J. Jensen, J. P. Müller, O. Sortkjær, K. Christoffersen, S. Bosselmann & E. Dall (in press). Fish Manipulation as a lake restoration tool in shallow, eutrophic lakes: analysis of three case-studies and data from 300 Danish lakes. Proc. Int. Conf. 'Biomanipulation, Tool for Watermanagement', Developments in Hydrobiology.

Jewson, D. H., B. H. Rippey & W. K. Gilmore, 1981. Loss rates from sedimentation, parasitism and grazing during the growth, nutrient limitation, and dormancy of diatom crop. Limnol. Oceanogr. 26: 1045–1056.

Kristensen, P. & P Jensen, 1987. Sedimentation og resuspension i Søbygård sø. M. sc. thesis. Publ. No. 64 from the Freshwater Laboratory, The National Agency of Environmental Protection, Silkeborg, Denmark, in cooperation with Botanical Institute, University of Århus, Denmark: 176 pp (in Danish).

Kunikane, S., M. Kaneko & R. Maehare, 1984. Growth and nutrient uptake of green algae *Scenedesmus dimorphus* under a wide range of nitrogen/phosphorus ratios. 1. Experimental study. Wat. Res. 18: 1299–1311.

Lampert, W. & U. Schober, 1978. Das regelmässige Auftreten von Frühjahrs-Algenmaximum und 'Klarwasserstadium' im Bodensee als Folge klimatischen Bedingungen und Wechselwirkungen zwischen Phyto- und Zooplankton. Arch. Hydrobiol. 82: 364–386.

Lampert, W., W. Fleckner, H. Rai & B. E. Taylor, 1986. Phytoplankton control by grazing zooplankton: a study on the spring clearwater phase. Limnol. Oceanogr. 31: 478–490.

Limnologisk Metodik, 1977. Freshwater Laboratory, University of Copenhagen and Akademisk Forlag: 163 pp (in Danish).

Lyche, A., 1984. Experimentelle studier av beitbarhet og assimilerbarhed av 6 planktonalger for *Daphnia longispina*. In S. Bosheim and Nicholls (eds.), Interaksjoner mellom trofiske nivåer i ferskvann. Norsk Limnologförening, Blindern, Oslo, Norway: 49–62 (in Norwidish).

Lynch, M., 1980. *Aphanizomenon* blooms: Alternate control and cultivation by *Daphnia pulex*. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3: 299–304. Univ. Press New England, Hanover.

Mitchell, S. A. & J. H. B. Joubert, 1986. Effect of elevated pH on the survival and reproduction of *Brachionus calyciflorus*. Aquaculture 55: 215–220.

Muck, P. & W. Lampert, 1984. An experimental study on the importance of food conditions for the relative abundance of calanoid copepods and cladocerans. 1. Comparative feeding studies with *Eudiaptomus gracilis* and *Daphnia longispina*. Arch. Hydrobiol. Suppl. 66: 157–169.

O'Brien, W. J. & F. deNoyelles, 1972. Photosynthetically elevated pH as a factor in zooplankton mortality in nutrient enriched ponds. Ecology 53: 605–614.

Reinertsen, H. & Y. Olsen, 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. Verh. int. Ver. Limnol. 22: 649–657.

Reynolds, C. S. & S. W. Wiseman, 1982. Sinking losses of phytoplankton in closed limnetic systems. J. Plankton Res. 5: 203–234.

Shapiro, J. & D. I. Wright, 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwat. Biol. 14: 371–383.

Sommer, U., Z. M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of plankton in freshwater. Arch. Hydrobiol. 106: 433–471.

Sortkjær, O. & E. Jeppesen, 1987. Hyppige feltmålinger øger forståelsen af lavvandede søers udvikling. In Annual Report 1986 from the Freshwater Laboratory, The National Agency of Environmental Protection: 21–28 (in Danish).

Starkweather, P. L., 1978. Behavioral determinants of diet quantity and diet quality in *Brachionus calyciflorus*. In Special symposium. Amer. Soc. of Limnol. Oceanogr.: 151–157.

Stewart, J. & R. G. Wetzel, 1986. Cryptophytes and other microflagellates as couplers in planktonic community dynamics. Arch. Hydrobiol. 106: 1–19.

Søndergaard, M., E. Jeppesen & O. Sortkjær, 1987. Lake Søbygård: a shallow lake in recovery after a reduction in phosphorus loading. GeoJournal 14: 381–384.

Søndergaard, M., E. Jeppesen, P. Kristensen & O. Sortkjær, 1990. Interactions between sediment and water in a shallow and hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. Hydrobiologia 191: 139–148.

Timmermann, M., 1987. Manglende reproduktion af skalle (*Rutilus rutilus*) (L.)) og rudskalle (*Scardinius erythrophthalmus* (L.)) og skalle- (*R. rutilus* (L.)), brasen- (*Abramis brama* (L.)) of aborre- (*Perca fluviatilis L.*) yngelens densitet og vækst i Væng Sø. Publ. No. 85 from the Freshwater Laboratory, The Agency of Environmental Protection, Silkeborg, Denmark: 81 pp (in Danish).

Titman, D. & P. Kilham, 1976. Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. Limnol. Oceanogr. 21: 409–417.

Uhlmann, D., 1971. Influence of dilution, sinking and grazing rate on phytoplankton populations of hyperfertilized ponds and micro-ecosystems. Mitt. int. Ver. Limnol. 19: 100–124.

Walter, B., 1969. Interrelations of Cladocera and algae. Ph.D. thesis. Westfield Coll., Univ. London.

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RECOVERY RESILIENCE FOLLOWING A REDUCTION IN EXTERNAL PHOSPHORUS LOADING OF SHALLOW, EUTROPHIC DANISH LAKES: DURATION, REGULATING FACTORS AND METHODS FOR OVERCOMING RESILIENCE

Erik JEPPESEN, Peter KRISTENSEN, Jens Peder JENSEN,
Martin SØNDERGAARD, Erik MORTENSEN and Torben LAURIDSEN

National Environmental Research Institute, Department of Freshwater Ecology
25 Vejlsøvey, DK 8600 Silkeborg, Denmark

ABSTRACT

The present paper give a brief characterization of Danish lakes, including the level and sources of external nutrient loadings. In addition, plans to reduce loading of the lakes are described and 27 case-studies of lakes recovery following phosphorus (P) loading reduction are analysed. Finally, additional methods to reduce the recovery period are discussed. Danish lakes are mainly shallow, fast-flushed and eutrophic, with nutrients from sewage and runoff from agricultural land being the main sources of eutrophication. In the case-studies of lake recovery the P loading reduction ranged from 34 to 94%, although was usually above 70%. In most cases a new steady state concerning P was not reached within 4-16 years following loading reduction and there seems to be no difference in the extent of the delay in lakes with a low or high hydraulic retention time (tw). In lakes with a high tw, the recovery occurred faster than expected from simple dilution of the P-pool in the water whereas lakes with a low tw (<0.5 y), the delay, expressed in terms of tw, was more than 10-300 times longer than expected from the simple dilution theory. The relatively slow response in lakes with a low tw may be attributed to a higher P-pool in the sediment reflecting a higher P-loading. In addition, the slow process of diffusion from the deeper layers of the sediment and the seasonal fluctuation in tw, with low flushing rates during summer, when the internal loading is high, may have contributed to the relative long delay period in lakes with a low annual mean tw. Biological resilience was mainly attributable to homeostasis in the fish community and its impact at other trophic levels and to the poor conditions for macrophyte recolonization resulting from enhanced turbidity, enhanced sediment resuspension and grazing by herbivorous birds, in particular coot. Analysis of data from 300 lakes and from 3 whole-lake fish manipulation experiments suggests that a marked reduction in recovery time of lakes larger than 10 ha that are not severely nitrogen limited can only be obtained by fish manipulation or by forming refuges for submerged macrophytes if

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the P level is reduced to below 80-150 μg total P l^{-1}. Sediment dredging or iron treatment are potential alternatives in cases where the exchangeable phosphorus pool is so high that the lake P concentration would not be expected to fall to the P threshold for biomanipulation within an acceptable period of time. However, iron treatment is risky and must therefore be used with caution.

Key words: lakes recovery, resilience, homeostasis, internal loading, biological structure, fish, macrophytes, restoration, biomanipulation.

1. INTRODUCTION

Attempts to improve environmental quality of eutrophic lakes by reducing the external nutrient loading are often hindered by resilience: in-lake nutrient concentration either fails to decrease, or decrease very slowly (e.g. Sas 1989; Marsden 1989). In some cases the delay in reduction of in-lake nutrient concentration could simply be attributable to dilution (Ahlgreen 1980). In other cases the lakes were truely resilient and high in-lake phosphorus concentration was maintained by phosphorus release from the sediment, i.e. internal loading (e.g. Sas 1989; Marsden 1989) In shallow eutrophic lakes internal nitrogen loading seems not to play any major role (Jensen *et al.* 1991 b). Biological structure of eutrophic lakes is also resilient, mainly because of homeostasis in the fish community due to their longevity, and the potentially high impact of the fish community on the biological structure (for review see Benndorf 1987, 1990 and Shapiro 1990). In order to reduce the recovery time of eutrophic lakes following reduction of external nutrient loading a number of physical, chemical and biological methods have been used such as dredging, chemical treatment of the sediment and manipulation of the fish stock (for review see EPA 1988).

In the present paper we review the recent Danish experience with the effects of reducing external nutrient loading on shallow eutrophic lakes and describe efforts to reduce the delay in recovery by using additional measures.

2. RESULTS AND DISCUSSION

2.1. Eutrophication level of Danish lakes

The characteristics of Danish lakes are illustrated by figure 1, which shows the frequency distribution and median value for relevant physical, chemical and biological data on 220-450 lakes. In general they are small (20 ha), shallow (mean depth 1.8 m), fast-flushed (hydraulic retention time 0.3 y) and highly eutrophic (total phosphorus 0.14 mg P l^{-1}). Consequently, the chlorophyll level is high (0.051 mg l^{-1}) and the transparency low (Secchi-depth 0.9 m) (Fig. 1). Earlier studies and paleolimnological analysis have revealed that in the last century shallow Danish lakes were characterized by dense submerged macrophytes and clear water (Baagø & Kølpin Ravn 1896; Arresøgruppen 1989; CowiConsult 1989). The present high level of eutrophication is mainly due to the high impact of nutrients: the mean and median values for external P loading were 13.1 and 2.5 g P m^{-2} y^{-1} (n=131), respectively, with the corresponding values for external N-loading being 142 and 52 g N m^{-2} y^{-1} (n=69) (Tab. 1).

A detailed analysis of the different nutrient sources of 35 representative lakes in 1989 revealed that on average, point sources i.e. sewage plants, sewage overflow channel and rain water basins accounted for 27% of the P loading and 8% of the N loading, whereas non-point sources accounted for 67% and 75%, respectively. Based upon the estimated loading coefficient from areas with a low human impact (Kristensen *et al.* 1990), it can be calculated that the impact from agricultural areas, including scattered villages, accounts for 44 and 46%, respectively, of the P and N loading attributable to non-point sources (Fig. 2).

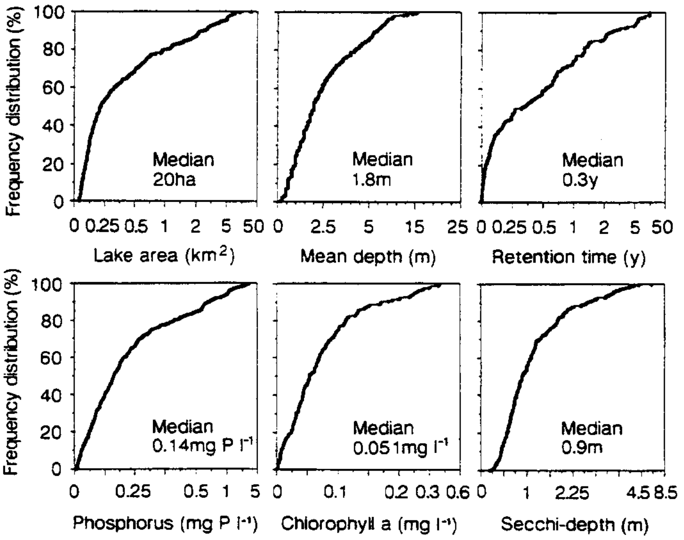

Fig. 1. Frequency distribution of lake area, mean depth, hydraulic retention time, P-concentration in lake water, algal biomass and Secchi-depth in 220-450 Danish lakes larger than 5 ha.

Tab. 1. Annual mean, median, minimum and maximum loading inlet concentration and in-lake concentration of total nitrogen (N) and total phosphorus (P) of a number (n) of Danish lakes; s.e. = standard error.

	n	mean	s.e.	min.	median	max.
P-loading (g P m^{-2} y^{-1})	131	13.1	2.5	0.06	2.5	217
P-inlet (μg P l^{-1})	131	415	39	34	260	2396
P-lake (μg P $^{l-1}$)	131	301	35	16	162	3130
N-loading (g m^{-2} y^{-1})	69	142	35	0.3	52	8400
N-inlet (mg N l^{-1})	69	5.6	0.8	0.6	5.0	15
N-lake (mg N l^{-1})	69	2.8	0.2	0.5	2.5	9

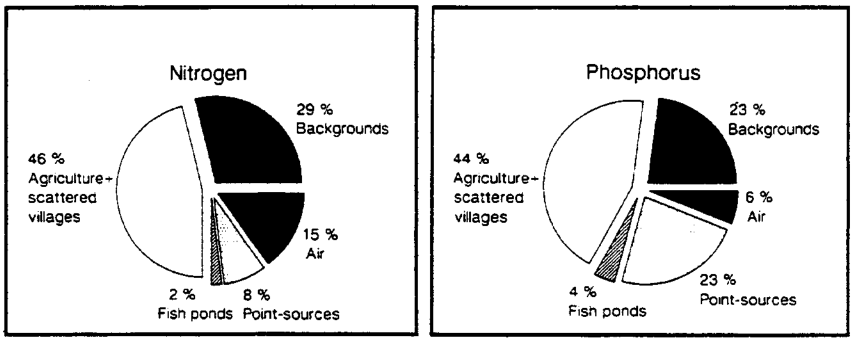

Fig. 2. The relative composition of the different sources to the extent of phosphorus and nitrogen loading of 35 Danish lakes, which have been selected to be representative for Danish lakes in general.

2.2. Action plans for reduction of nutrient loading

In order to combact eutrophication in Danish lakes two action plans have been formulated: the "Action Plan for Aquatic Environment" and the "Recipient Quality Plan". The former is a general plan initiated in 1987, which aims for reduction of loading from land-based sources of 50% for nitrogen and 80% for phosphorus. In contrast, the "Recipient Quality Plan" is a differentiated plan where loading reduction in each catchement is adapted according to the specific objectives for that catchment and the sensitivity of its environment. In shallow Danish lakes a shift from turbid to clear water (*sensu* Scheffer 1989, 1990) demands not only a reduction in the P-loading from point sources, but also a marked reduction in input from soil leaching and from scattered villages.

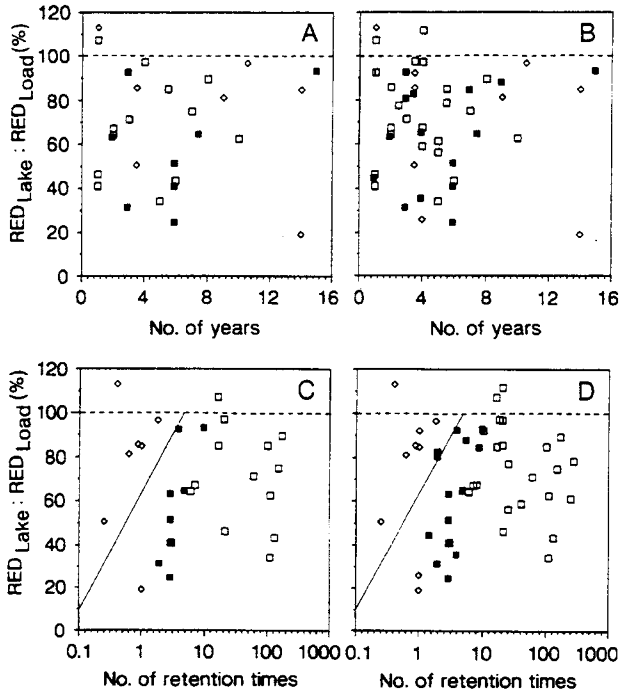

Fig. 3. The ratio of the percentage reduction in lake P-concentration and P-loading and the number of years (A, B) after the loading reduction and versus hydraulic retention time (tw) (C, D), respectively. A and C are from Danish lakes; B and D are as A and C but supplemented with data from Cullen and Forsberg (1988). □ tw ≤ 0.5 y, ■ tw > 0.5 y, tw ≤ 2.5 y, ◇ tw > 2.5 y. The full line in C and D shows the «dilution curve» assuming non-stratified conditions.

2.3. Delay in recovery

Data describing the recovery phase following a reduction in P-loading is available for 27 Danish lakes. The loading reduction ranged from 34 to 94%, although in most cases was above 70%. The resilience of these lakes is illustrated by figure 3A where the reduction in the ratio of in-lake P-concentration (RED$_{lake}$) to the reduction in P-loading (RED$_{load}$) is shown *versus* the number of years following loading reduction. If we assume that the Vollenweider equation is valid, which seems to be the case for Danish lakes (Kristensen *et al.* 1990), then a new steady state will be reached when this ratio approaches unity. In most of the case studies RED $_{lake}$:Red$_{load}$ was well below one (Fig. 3A) even as many as 4-16 years after loading had been reduced, thus indicating a high degree of resilience, a finding that is in accordance with other studies od lake recovery (Fig. 3B, Cullen & Forsberg 1988; Sas 1989; Marsden 1989). The factors which are most likely to account for the delay in recovery, namely dilution effects and internal nutrient loading on one hand, and homeostasis of biological structure on the other, are discussed below.

2.3.1. Dilution and internal loading

In lakes with a relatively long hydraulic retention time, simple dilution effects may account for much of the delay. Assuming that the lake can be expressed as an homogeneous system without any nutrient exchange between sediment and water, then the time required to reduce the surplus pool of phosphorus in the lake water by 95% by simple flushing will be three times the hydraulic retention time (Sas 1989). Consequently, even longer would be required for a new steady state to be reached. However, in most Danish lakes with a high tw, the reduction in P-lake occurred faster than could be predicted from simple dilution, which implies that a part of the excess phosphorus in the lake water settled out as particulate P, subsequently becoming immobilized in the sediment.

In lakes with a low tw, marked resilience was observed, the delay being 10-300 times higher than could be explained by dilution and seeming to increase with decreasing tw (Fig. 3A). Thus in contrast to what would be expected from the dilution theory, the recovery period was not inversely related to tw, but was in fact of comparable duration for lakes with a low and with a high tw (Fig. 3A). In order to illustrate that the behavior of the Danish lakes is general, data from abroad (Cullen & Forsberg 1988) is shown together with our data in figure 3B.

That internal loading is long-lasting in lakes with a low tw can partly be attributed to the fact that the sediment P-pool is greater because of the higher external P loading (Fig. 4, Tab. 2). Hence, for 131 Danish lakes P-loading decreased significantly with increasing tw and increasing mean depth (Fig. 4A and Tab. 2). However, a higher external

P-loading may not necessarily result in the increased accumulation of P in the sediment because the percentage of P retained in the lakes is also related to tw and generally increases with increasing tw (Vollenweider 1976; Dillon & Rigler 1974). Nevertheless, if we correct for the differences in the proportion retained using the Vollenweider equation, the normalized P-loading still decreases with increasing tw and increasing mean depth (Fig. 4B and Tab. 2). Accordingly, the P content of both the upper 5 cm and upper 20 cm of sediment also decreased significantly with increasing tw (Figs 4C, 4D and Tab.2).

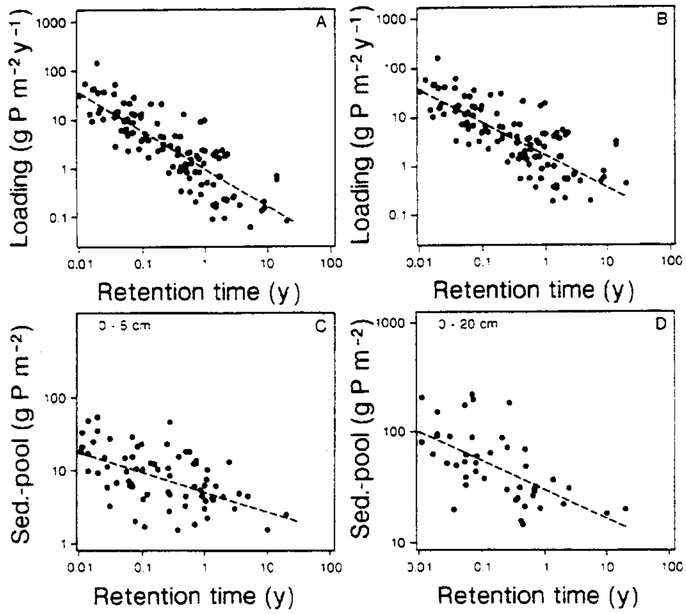

Fig. 4. Relationships between hydraulic retention time and the P-loading (A,B) and the accumulated P in the sediment (C, D). A: P-loading normalized by correcting for differences in P-retention according to the Vollenweider equation (Vollenweider 1976); C: P-pool 0-5 cm; D: P-pool 0-20 cm.

Although the P content of the uppermost layer of sediment may give some indication as to the extent of internal loading during recovery, the actual P-release from sediment is influenced by several factors (Boström *et al.* 1982). In the study of 15 Danish lakes, it was found that the iron:P ratio in the sediment has a major impact on P-release: irrespective of the size of the sediment P-pool, aerobic P-release decreased significantly when the iron:P ratio (by weight) increased above 15

(Jensen *et al.* 1991 a). At ratios below 15, there was no correlation: P-release was in fact correlated, albeit weakly, to the NH_4Cl-extractable fraction of the P-pool and total P in the sediment. The positive relationships between the P and iron content in the sediment of Danish lakes (Tab. 2; Jensen *et al.* 1991 a), may therefore lead to a reduction of the impact of the accumulated P-pool on internal loading and thus on the resilience in recovery.

Tab. 2. Regression analysis on P-loading (P-load), normalized P-loading (NP-load=P-load/(1-Rp), where Rp is the P retention coefficient according to Vollenweider 1976). P-pool in the uppermost 5 cm and uppermost 20 cm versus hydraulic retention time (tw, y^{-1}), mean depth (Z, m) and the iron-pool, in the sediment layer concerned (Fe-pool, g Fe m^{-2}) using GLM (SAS 1990) on log-transformed data.

P-load	(g P m^{-2} y^{-1})=	1.0 $tw^{-0.78}$	$r^2=0.81$	$P<0.0001$	n=122
P-load	(g P m^{-2} y^{-1})=	0.34 $tw^{-0.99}$ $Z^{0.73}$	$r^2=0.82$	$P<0.0001$	n=122
NP-load	(g P m^{-2} y^{-1})=	1.89 $tw^{-0.63}$	$r^2=0.65$	$P<0.0001$	n=122
NP-load	(g P m^{-2} y^{-1})=	0.70 $tw^{-0.83}$ $Z^{0.75}$	$r^2=0.74$	$P<0.0001$	n=122
P-pool	(0-5 cm, g P m^{-2})	5.3 $tw^{-0.27}$	$r^2=0.29$	$P<0.0001$	n= 71
P-pool	(0-5 cm, g P m^{-2})	1.4 $tw^{-0.16}$ Fe-$pool^{0.51}$	$r^2=0.47$	$P<0.0001$	n= 49
P-pool	(0-20 cm, g P m^{-2})	31.2 $tw^{-0.27}$	$r^2=0.39$	$P<0.0001$	n= 44
P-pool	(0-20 cm, g P m^{-2})	8.8 $tw^{-0.23}$ Fe-$pool^{0.37}$	$r^2=0.37$	$P<0.0009$	n= 32

Besides being due to differences in the exchangeable P-pool, the higher resilience of lakes (expressed in number of tw) with low tw may be partly attributable to the slow process of P diffusion from the deeper layers of the sediment to the water: Although P diffusion increases with decreasing tw because the P concentration in the lake, and hence the gradient between sediment and water, is affected by the P-efflux from the lake, this increase is most likely less than the corresponding decrease in tw, thereby prolonging the recovery phase.

Seasonal variation in tw may also have contributed to the resilience. In several of the fast-flushed lakes, although mean annual tw was high in summer, when internal loading and hence the P concentration was high, and low in winter (unpub. results). Thus the large part of the released P may have returned to the sediment before the autumn when tw again decreased. This may have prolonged the recovery phase as compared with that in lakes with a similar mean annual tw but little seasonal variation in tw (e.g. lakes with a high infiltration of groundwater).

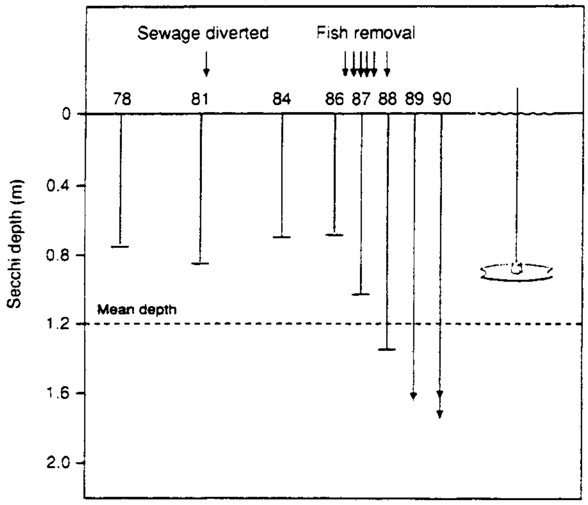

Fig. 5. Changes in the summer mean Secchi-depth (May-October) in Lake Væng following sewage diversion 1981 and fish manipulation in 1986-1988, where 50% of the biomass of planktivorous fish was removed. Arrows indicate that Secchi-depth reached the bottom at some of the sampling dates, thus mean values are higher.

2.3.2. Biological structure

Homeostasis in the biological structure may also delay the recovery of eutrophic lakes following a reduction in loading. Planktivorous and benthivorous fish may make a major contribution to the resilience of the lake, partly because feeding activity may result in an increase in the concentration of suspended matter (Meijer *et al.* 1990) and enhancement of phosphorus release from the sediment (Andersson *et al.* 1978, 1988) and partly because a high density of these fish may, by preventing re-occurrence of large cladocerans, decrease the grazing pressure on phytoplankton. These factors may delay improvement of the light climate and delay the colonization of submerged macrophytes, which could otherwise have stimulated a shift to a clearwater stage (Timms & Moss 1984; Scheffer 1989, 1990; Jeppesen *et al.* 1990c).

That the community could effect homeostatic control of the biological structure of a lake was documented in the biomanipulation experiment in Lake Væng (Figs 5 and 6; Søndergaard *et al.* 1990; Jeppesen *et al.* 1990b). Although the sewage water input to the lake was diverted in 1982, there were no decrease in phosphorus level in the lake water and no increase in transparency during the subsequent 4 year period (Fig. 5). Furthermore, the phytoplankton community remained dominated by cyanobacteria during summer. However, immediately after a 50% reduction in the planktivorous fish biomass in November 1986 to June 1988, a number of marked and self-perpetuating changes occurred during the subsequent two year period (Figs 5 and 6):

1) phytoplankton biomass decreased by 86% to 10 μg chl*a* l^{-1}, and cyanobacteria, which had previously been dominant, almost disappeared. Consequently the Secchi-depth in summer increased from 0.7-0.9 m to more than the maximun depth in the lake in 1989-1990.

2) The density of cladocerans increased seven fold from 1986 to 1987 then decreased steadily during the next years reflecting the decrease in total and edible phytoplankton biomass (Fig. 6; Søndergaard *et al.* 1990).

3) The phosphorus level decreased by 55% to 70 μg total P l^{-1}.

4) The submerged macrophytes increased slowly during 1987-1988 and then rapidly in 1989 and 1990 such that maximun coverage of the lake surface area was 40-50% and 80%, respectively. Simultaneously, the concentration of total N decreased, mainly due to an enhancement of denitrification (unpublished data).

5) The fish catch per unit effort (CPUE) in multiple mesh size gill nets (14 mesh sizes) decreased by 67% and the relative proportion in terms of number of perch (*Perca fluviatilis*) and pike (*Esox lucius*) increased from 18 to 56%.

6) The coot (*Fulica atra*) density increased markedly in 1989 to a maximum of about 20 ind ha^{-1}, and the density of mute swans (*Cygnus olor*) rose from zero to 0.4 ha^{-1}, in both cases reflecting the significant increase in submerged macrophytes in 1989.

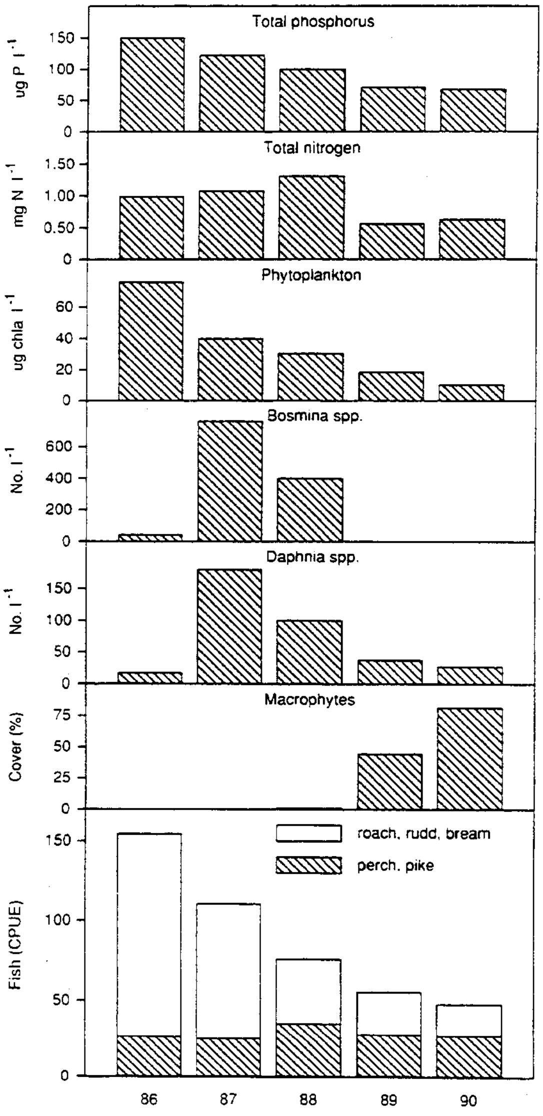

Fig. 6. Changes in summer mean values of total phosphorus, total nitrogen, phytoplankton volume, numbers of *Bosmina* and *Daphnia* following fish manipulation during 1986-1988 in Lake Væng. Also shown is the maximum cover of submerged macrophytes (mainly *Elodea canadensis* and *Potamogeton crispus*) and catch per net in terms of numbers of the dominating fish species. Using a standard testfishing programme with 15 survey gillnets of 14 mesh sizes each.

The cascading effect (*sensu* Carpenter *et al.* 1987) of the fish manipulation thus demonstrate that planktivorous fish contribute significantly to the resilience of eutrophic lakes following a marked reduction in external loading. The case-study also demonstrates the interdependence of internal nutrient loading and biological structure.

A delay in recolonization by submerged macrophytes, attributable to enhanced turbidity, changes in the sediment composition and grazing by birds, may also contribute to the resilience of eutrophic lakes (Moss & Leah 1982; Moss 1990). Maintenance of enhanced turbidity following loading reduction may, as described above, be partly attributable to homeostatic control of the biological structure by the fish stock. However, wind-induced resuspension of the fine particulate matter, accumulated in the sediment during the period prior to loading reduction, may also lead to increased turbidity (Meijer *et al.* 1990). The impact of resuspension on resilience probably increases with decreasing mean depth, as the effect of resuspension on lake water turbidity was found to be inversely proportional to approximately the square root of mean depth in shallow, eutrophic lakes (Kristensen *et al.* 1991). Furthermore, because sediment resuspension increases with increasing lake size due to the relationship between resuspension and fetch (Carper & Bachmann 1984), and because a high fetch may reduce the ability of the plants to become rooted in the loose sediment, resilience of eutrophic lakes may also increase with lake size.

The enhanced content of organic matter in the sediment and the concurrent changes in sediment density might be expected to affect the growth of macrophytes and thereby their recolonization rate. However, although Barko & Smart (1983) found a reduction in growth of *Myriophyllum* sp. in sediment with high organic content, several other studies contradict this view (Jupp & Spence 1977; Duarte & Kalff 1986; Nichols & Shaw 1986) and translocation experiments in Lake Væng showed that the submerged macrophytes grew well on both sandy sediments from exposed littoral areas and on mud at the lake center and from sheltered littoral areas. In fact, the macrophyte growth rate was higher on the mud at the center of the lake (Lauridsen 1990), indicating that sediment quality could not have played a major role in the two year delay in colonization of this lake following fish manipulation (Fig. 6).

The delay in macrophyte recolonization may also be due to grazing by birds (Moss 1990). Experiments in Lake Væng and Lake Stigsholm showed that macrophyte growth increased markedly when enclosures were erected to protect the macrophytes from bird grazing (Lauridsen 1990; Olofsson, unpubl.). The growth was high even in areas where the natural vegetation was scarce and where plants outside the enclosures had been eliminated by grazing. In those lakes *Fulica atra* was the major bird grazer. Enhanced biomass development in enclosures has also been observed in other shallow lakes (Jupp & Spence 1977; Moss & Leah 1982; Moss 1990). The impact of bird grazing appears to be highest in the early phase of colonization and near to reed belts which are used by coots for nesting and refuge (Lauridsen 1990).

2.4. Methods for reducing recovery time following loading reduction

In an attempt to reduce recovery time after a reduction in external loading of shallow, fully mixed Danish lakes, three additional measures have been applied in Denmark, i.e. sediment dredging, chemical treatment of sediment and biomanipulation. Since sediment removal is 1-2 orders of magnitude more costly than biomanipulation, a comprehensive study was undertaken in order to examine the perspectives and limitations of using manipulation of fish stock to overcome the homeostasis of biological structure that contributes to resilience of eutrophic lakes.

This study included three whole-lake experiments and a detailed analysis of data from 300 shallow Danish lakes (Jeppesen *et al.* 1990b, 1990c; Søndergaard *et al.* 1990; Riemann *et al.* 1990).

The biological structure of shallow lakes was found to be extremely dependent on in-lake P concentration, as illustrated by figure 7. At low P-concentration (0-50 µg total P l^{-1}) the fish community (>10 cm) was dominated by piscivores, submerged macrophytes colonized to relative deep maximum depths (often the maximum depth of the lake), phytoplankton biomass was low and dominated by algae other than blue green and green, and the Secchi-depth was high. At slightly higher P-concentration the character of the fish community changed to a higher proportion of planktivores, and the maximum colonization depth of submerged macrophytes decreased. Hence, in the range 80 to 150 µg total P l^{-1} about 80% of the fish stock (>10 cm) consisted of planktivores, the maximum macrophyte colonization depth was reduced to 1-1.5 m and cyanobacteria dominated in 20% of samples taken during summer (May-September). At phosphorus concentrations between 250-1000 µg total P l^{-1}, submerged macrophytes were absent, the fish stock totally dominated by planktivores and cyanobacteria now the dominant

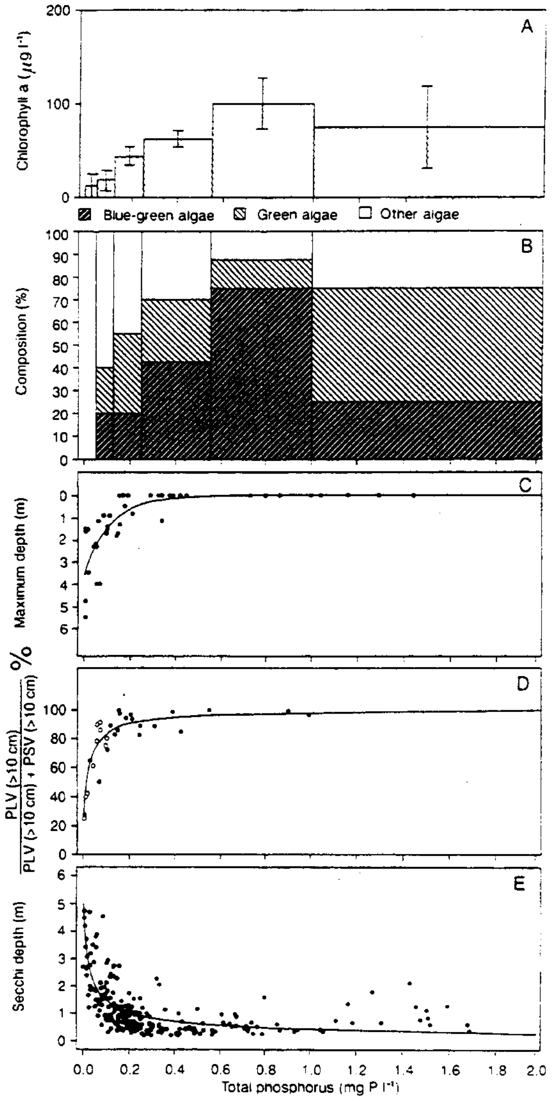

Fig. 7. The relationships between the concentration of total phosphorus in the lake water (May-September) and A: algal biomass (July-September); B: the percentage distribution of dominating species and genera of some phytoplankton classes (July-September); C: maximum colonization depth of submerged macrophytes; D: planktivorous fish (PLV) population in percent of the total population of PLV and piscivorous (PSV), larger than 10 cm caught during standardized testfishing with survey gill nets of multiple mesh sizes. • = Danish lakes; ○ = data from Lessmark 1983, where piscivores included only perch and planktivores only roach; E:

phytoplankton group.

At P-concentrations above 1000 µg total P l^{-1}, the biological structure become unstable and easily influenced by marked variations in the density and age composition of the fish stock due to fish kill and marked variation in the recruitment an survival of the offspring of the dominant planktivores (Jeppesen *et al.* 1990c; Mortensen *et al.* unpubl.). Furthermore, there was often a shift between from green algal dominance and turbid water when the grazing pressure at phytoplankton was low to cryptophyte dominance and clear water when the grazing pressure was high.

2.4.1. Fish manipulation

Based on the above mentioned analysis, Jeppesen *et al.* (1990c) suggested that fish manipulation, as a supplement to loading reduction in shallow lakes not severely limited to nitrogen, would:

1) be most effective below the threshold area of 80-150 µg total P l^{-1}, where marked changes *per* unit of phosphorus reduction were seen (Fig. 6);

2) be least effective, even on a short term, in lakes in which cyanobacteria dominate (250-1000 µg total P l^{-1}) because the cyanobacteria, by negatively influencing the population increase of cladocerans of high densities, may counterbalance the effect of reduced cladoceran predation by fish;

3) be effective in eutrophic lakes dominated by green algae, at least in the short term, whereas the long term effect is uncertain because of the high probability of returning to a fish stock dominated by planktivores.

The three whole-lake experiments support the hypothesis. Marked and self-perpetuating changes occurred in Lake Væng, which had P-level in the threshold area, whereas only minor changes occurred in the strongly cyanobacteria-dominated Frederiksborg Castle Lake. In Lake Søbygård which is dominated by green algae, marked short term changes occurred in spite of the facts that the fish manipulation mainly consisted of reduced recruitment of planktivorous fish during a four year period and that the fish biomass remained high (Jeppesen *et al.* 1990b, 1990c; Søndergaard *et al.* 1990; Riemann *et al.* 1990).

Fish stock manipulation by partial removal of planktivores has now been undertaken in six Danish lakes. A long term effect has only been seen in lakes in which P-concentration was below the threshold of 80-150 µg total P l^{-1} (Nielsen 1977; Jeppesen *et al.* 1990b; County of Viborg, unpubl.; Town of Skanderborg, unpubl.) Additional experiments, in which fish stock is manipulated by the stocking the piscivores pike instead of removal of planktivores, are now being undertaken in two lakes in Central Jutland. Furthermore, a large scale biomanipulation study, combining removal of planktivores with stocking of piscivores (pike and maybe zander (*Stizostedion lucioperca*)) (County of Storstrøm) will be initiated in 1991 in the 8 km^2 Lake Maribo (with P below the threshold-level).

2.4.2. Macrophyte refuges

In lakes in which part of the resilence is due to extensive bird grazing on submerged macrophytes, recovery time may be reduced by establishing protected macrophyte colonies in cages. This might, by enhancing the dispersal of vegetative parts, fruit and turions, enhance macrophyte colonization of the whole lake area. During the growing season the protected macrophyte colonies can either be fully separated from the lake e.g. by the use of tarpaulins or kept open to the lake water. The main advantage of a closed environment is that it provides better light conditions for plant growth: because fish fry are prevented from entering, the density of filter feeding zooplankton may increase thus increasing grazing pressure on phytoplankton. Growth of phytoplankton may be further limited by the fact that import of nutrients from external sources is eliminated. Finally, closed environments may also provide shelter against wave action and, possibly, a higher impact of allelophatic substances (Vermaat *et al.* 1990). A disadvantage of closed systems is that nutrients, in particular nitrogen and perhaps also carbon, may become limiting for plant growth (Ozimek *et al.* 1990; T.V. Madsen, pers. comm.). This problem could be overcome by building meshed windows in the closed systems such that the water can exchange freely with the surrounding lake water. A second disadvantage is that large closed systems are expensive, because thick walls are needed in order to avoid damage by wave action.

The advantage of using wire netting for macrophyte colony protection are that the method is cheap and that it does not hinder the dispersal of vegetation parts, turions and fruits to the lake during the growing season. Furthermore, the submerged macrophyte colony can act as a refuge for piscivorous fish and zooplankton, which may lead to improvement of water quality. The major disadvantage is the high turbidity resulting from the influx of algae and the low algal grazing by zooplankton (because planktivorous fish can enter from the lake) affords poor light conditions, and thus poor growth conditions for the macrophytes. Nevertheless, in a recent investigation of protected macrophyte colonies in shallow Lake Stigsholm, a high macrophyte growth rate was obtained in open wire cages despite a high turbidity, whereas growth in foil covered cages was more variable despite clear water conditions (Olofssen, unpublished observation). This indicates that protected macrophyte colonies in open wire cages may serve as a useful supplement to loading reduction in cases where the nutrient level is closed to or below the P-threshold at which colonization by submerged macrophytes is feasible, i.e. 80-150 μg total P l^{-1} (Fig. 6).

Macrophyte manipulation may also be an alternative to fish manipulation in lakes in which fish stock regulation cannot be undertaken (Moss 1990).

2.4.3. Dredging and chemical treatment

In shallow lakes with a P concentration above the suggested threshold for fish and submerged macrophyte manipulation, dredging and chemical treatment of the sediment may be used to supplement loading reduction. Dredging may be undertaken in order to remove the uppermost P-rich layer of sediment (Björk 1985; Cook *et al.* 1986) and in shallow lakes, also to increase their mean depth. In Denmark, dredging has been used for both purposes in a number of small lakes. Recently a large scale dredging project started in Lake Brabrand (surface area 1.5 km^2, tw 10-20 days), the aim of which is to remove 400,000 m^3 sediment during a six year period. However, because the external P-loading has not been reduced adequately yet, no improvement in lake water quality has yet occurred despite removal of 80,000 m^3 (J. Windolf, pers. comm.).

Chemical treatment of the water and sediment with the iron salts, aluminium and calcium has been used in attempts to reduce lake water

P concentration and internal P-loading (e.g. Cooke *et al.* 1986). Of these elements the most used is aluminium because phosphate binds tightly to aluminium salts over a wide ecological range, including at low redox conditions (EPA 1988). In Denmark aluminium sulfate treatment was undertaken in 1974 in the shallow Lake Lyngby: only a short term effect on the P-concentration was obtained however, and in 1975 the P-concentration had returned to the pre-treatment level, mainly reflecting the high external P-loading (Norup 1975). In other countries long-lasting effects of aluminium treatment have been obtained in a number of deep lake and ponds, whereas the method has been less promising for shallow lakes (EPA 1988). In addition to the problem of efficacy, aluminium may have the negative side effect of being toxic for aquatic biota (EPA 1988; Boers *et al.*, submitted). Iron treatments has therefore been suggested as an alternative restoration measure for shallow, fully mixed lakes with an aerobic sediment surface (Boers *et al.*, submitted). The ability of iron treatment to reduce internal P-loading in such lakes is supported by laboratory experiments and, on a short term scale, by a whole-lake *in situ* experiment (Boers *et al.*, submitted). Further evidence is the observation of reduced P-release from the sediment of Danish lakes when sediment iron:P ratio was above 15 (Jensen *et al.*, 1991 a). It should be remembered however, that iron treatment is risky because the high redox sensitivity makes the P-pool accumulated during treatment a potential time bomb. All that is needed to detonate the bomb is for the iron:P ratio in the surface sediment (either through accumulation of external derived P or due to differential reallocation of iron and P from deep to superficial sediment) to become too low to prevent P-release. Thus iron treatment may sometimes do more harm than good, particularly in lakes which have a low tw and high P-loading and where much of the P, were it not for the treatment would have been flushed through the outlet rather than being accumulated. Following termination of treatment these lakes may suffer from an enhanced P release reflecting the higher P retention and thus P accumulation during treatment. Iron treatment must therefore be used with caution.

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REFERENCES

Ahlgreen, I. 1980. A dilution model applied to a system of shallow eutrophic lakes after diversion of sewage effluents. *Arch. Hydrobiol.*, 89: 17-32.

Andersson, G. H. Berggren, G. Cronberg & C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia*, 59: 9-15.

Andersson, G., W. Granéli & J. Stenson. 1988. The influence of animals on phosphorus cycling in lake ecosystems. *Hydrobiologia*, 170: 267-284.

Arresøgruppen. 1989. Restaurering og fremtiding tilstand af Arresø. *Rapport til Hovedstad-rådet* (in Danish).

Baagø, J. & F. Køplin Ravn. 1896. Exkursion til Jydske søer og vandlob. *Bot. Tidsskrift*, 20: 288-326 (in Danish).

Barko, J.W. & R.M. Smart. 1983. Effect of organic matter additions to sediment on the growth of aquatic plant. *J. Ecol.*, 71: 161-175.

Benndorf, J. 1987. Food web manipulation without nutrient control: a useful strategy in lake restoration? *Schweiz. z. Hydrol.*, 49: 237-248.

Benndorf, J. 1990. condition for effective biomanipulation: conclusion derived from whole-lake experiments in Europe. *Hydrobiologia*, 200/201: 187-204.

Björk, S. 1987. Lake restoration techniques. In: Vismara *et al.* (Eds), *Lake pollution and recovery*. Proceedings Int. Cong. Rome, 1985: 281-291.

Boers, P.C.M., M.P. Queah, J. van der Does & J.C. van der Flugt. (1991). Phosphorus fixation with ferrichloride: a new method to combat internal loading in shallow lakes. *Hydrobiologia*, (submitted).

Boström, B., M. Jansson & C. Forsberg. 1982. Phosphorus release from lake sediments. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, 18: 5-59.

Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer, X. He & C.N. von Ende. 1987. Regulation of lake primary production by food web structure. *Ecology*, 68: 1863-1876.

Carper, G.L. & R.W. Bachmann. 1984. Wind resuspension of sediment in a praire lake. *Can. J. Fish. aquat. Sci.*, 41: 1763-1767.

Cooke, G.D., E.B. Welch, S.A. Peterson & P.R. Newroth. 1986. *Lake and reservoir restoration*. Butterworth Publ., Boston.

CowiConsult. 1989. Økologisk Baggrundstilsand og udviklingshistorie i fem søer. *Rapport til Hovedstadsrådet. Københavns amt, Frederiksborg amt og Roskilde amt* (in Danish).

Cullen, P. & C. Forsberg. 1988. Experience with reducing point sources of phosphorus to lakes. *Hydrobiologia*, 170: 321-336.

Dillon, P.J. & F.H. Rigler. 1974. A test of simple nutrient budget model of predicting the phosphorus concentration in lake water. *J. Fish. Res. Bd Canada*, 31: 1771-1778.

Duarte, C.M. & J. Kalff. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. *Limnol. Oceanogr.*,

EPA. 1988. The lake and reservoir restoration guidance manual. *EPA*, 440/5-88-002.

Jensen, H.S., P. Kristensen, E. Jeppesen & A. Skytthe. (1991 a). Iron:Phosphorus ratio in surface sediment as an indicator of phosphorus release from aerobic sediments in shallow lakes. *Hydrobiologia*, (submitted).

Jensen, J.P., E. Jeppesen, P. Kristensen, P.B. Christensen & M. Søndergaard. (1991 b). Nitrogen loss and denitrification as studied in relation to reduction of nitrogen loading in a shallow, hypertrophic lake (Lake Søbygaard, Denmark). *Int. Revue ges. Hydrobiol.*, (in press).

Jeppesen, E. M. Søndergaard, O. Sortkjær, E. Mortensen & P. Kristensen. 1990a. Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study of phytoplankton collapses in Lake Søbygård, Denmark. *Hydrobiologia*, 191: 149-164.

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H.J. Jensen, J.P. Müller, O. Sortkjær, J.P. Jensen, K. Christoffersen, S. Bosselmann & E. Dall. 1990b. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. I. Cross-analysis of three Danish case-studies. *Hydrobiologia*, 200/201: 205-218.

Jeppesen, E., J.P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik. 1990c. Fish manipulation as a lake restoration tool in shallow, europhic, temperate lakes. II. Threshold levels, long-term stability and conclusions. *Hydrobiologia*, 200/201: 219-227.

Jupp, B.P. & D.H.N. Spence. 1977. Limitations of macrophytes in a eutrophic lake, Loch Leven. J. *Ecol.*, 65: 431-446.

Kristensen, P., B. Kronvang, E. Jeppesen, P. Græsbøll, M. Erlandsen, A. Rebsdorf, A. Bruhn & M. Søndergaard. 1990. *Ferske vandområder - vandløb kilder og søer*. Vandmiljøplanens Overvågningsprogram 1989. Danmarks Miljøundersøgelser, 1990: 130 pp.

Kristensen, P., M. Søndergaard & E. Jeppesen. (1991). Resuspension in a shallow hypertrophic lake. *Hydrobiologia*, (in press).

Lauridsen, T. 1990. *Omgivelsernes indflydelse på væksten og udbredelseshastighed af makrofyter i den biomanipulerede, lavvandede Væng sø*. M. Sc. Thesis: 93 pp.

Lessmark, O. 1983. *Influence of abiotic and biotic factors on the structure of perch and roach populations in thirteen Swedish lakes, with special reference to interspecific competition*. Ph. D. Thesis, University of Lund, Sweden: 135-172.

Marsden, M.W. 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. *Freshw. Biol.*, 21: 139-162.

Meijer M.L., W. de Haan, A.W, Breukelaar & H. Buiteveld. 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? *Hydrobiologia*, 200/201: 303-316.

Moss, B. & R.T. Leah. 1982. Changes in the ecosystem of a guanotrophic and brackish shallow lake in Eastern England: Potential problems in its restoration. *Int. Revue ges. Hydrobiol.*, 67: 625-659.

Moss, B. 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia*. 200/201: 367-378.

Nichols, S.A. & B.H. Shaw. 1986. Ecological life histories of three aquatic nuisance plants *M. spicatum, P. crispus, E. canadensis. Hydrobiologia*, 131: 3-21.

Nielsen. E. 1977. The development of the fishery in Lake Arreso with special reference to bream population (Abramis brama L.). In: Hunding C. (Ed.). *Danish limnology, reviews and perspectives*. Fol. Limnol. Scand., 17: 27-36.

Norup, B. 1975. *Lyngby Sø 1974-75*. Rapport til Lyngby-Tårbæk Kommune (in Danish): 21 pp.

Ozimek, T., R.D. Gulati & E. van Donk. 1990. Can macrophytes be useful in biomanipulation of lakes?. *Hydrobiologia*, 200/201: 399-408.

Riemann, B., K. Christoffersen, H.J. Jensen, J.P. Müller, C. Lindegaard & S. Bosselmann. 1990. Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. *Hydrobiologia*, 200/201: 241-250.

Sas, H. (Ed.) 1989. *Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation*. Acad. Ver. Richardz Gmbh.: 497 pp.

SAS. 1990. SAS language, version 6. SAS Institute Inc., NC. U.S.A.

Scheffer, M. 1989. Alternative stable states in eutrophic shallow freshwater system: a minimal model. *Hydrobiol. Bull.*, 23: 73-89.

Scheffer, M. 1990. Multiplicity of stable states in freshwater systems. *Hydrobiologia*, 200/201: 475-486.

Shapiro, J. 1990, Biomanipulation: the next phase - making it stable. *Hydrobiologia*. 200/201: 13-27.

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen & O. Sortkjær. 1990. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. *Hydrobiologia*, 200/201: 229-240.

Timms, R.M. & B. Moss. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorour fish in a shallow wetland ecosystem. *Limnol. Oceanogr.*, 29: 472-486.

Vermaat, J.E., M.J.M. Hootsmans & G.M. van Dijk. 1990. Ecosystem development in different types of littoral enclosures. *Hydrobiologia*. 200/201: 391-398.

Vollenweider, R.A. 1976. Advance in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. ital. Idrobiol.*, 33: 53-83.

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Impact of a trophic cascade on heterotrophic bacterioplankton production in two shallow fish-manipulated lakes

By ERIK JEPPESEN, OLE SORTKJÆR, MARTIN SØNDERGAARD
and MOGENS ERLANDSEN

With 5 figures and 1 table in the text

Abstract

Heterotrophic bacterioplankton production (BP) in two shallow Danish lakes, one eutrophic and one hypertrophic, was studied for a period of 5-6 years. Average BP, determined by the 3H-thymidine-method, was highest in the hypertrophic lake. However, despite a 9-fold difference in the average summer chlorophyl a concentration and a 6-fold difference in phytoplankton production (PP) of the 2 lakes, there was only a 2-fold difference in BP. Major trophic cascade induced by a reduction in the fish stock density only slightly altered BP in both lakes: despite a 70-140 fold increase in cladoceran biomass and a 4-6 fold reduction in PP, BP, only increased 2-fold. The BP:PP-ratio consequently increased substantially from 2.5 to 9% in the hypertrophic lake, Lake Søbygård, and from 4 to 52% in the eutrophic lake, Lake Væng. The increase was coincident with an increase in cladoceran grazing pressure, except in 1989-90 in Lake Væng, when the BP:PP ratio was higher than expected, probably because of the high biomass of submerged macrophytes. Average bacterioplankton cell volume decreased and the specific bacterial growth rate increased in both lakes, probably reflecting size-selective grazing on large bacteria by cladocerans, and a cladoceran-mediated reduction in the number of small bacteria-feeding flagellates and ciliates. Evidence is provided that BP is stimulated to a greater extent by *Bosmina longirostris* than by *Daphnia* spp., a finding in accordance with the fact that *Daphnia* is the most efficient bacteria-feeder; hence although *Daphnia* spp. are able to stimulate BP when grazing on algae, they are also able to exert top-down control on bacteria. A tentative model is proposed to explain how a trophic cascade elicited by changes in the fish stock can alter BP and the BP:PP-ratio in shallow eutrophic and hypertrophic lakes.

Introduction

Fish play an important role in structuring the pelagic ecosystem of shallow lakes. This is evidented by the fact that a substantial reduction of the planktivorous fish stock often results in a trophic cascade (CARPENTER et al. 1985) i.e. a marked increase in macrozooplankton grazing pressure and a consequent reduction in phytoplankton biomass and production (e.g. HRBACEK et al. 1961, SHAPIRO et al. 1975, BENNDORF 1987, CARPENTER et al. 1987 and JEPPESEN et al. 1990a, b). Although much is known regarding phytoplankton, little is known about the impact of such a trophic cascade on

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the pelagic microbial community (PACE & FUNKE 1991), and the information that is available is often contradictory. For example, in short-term enclosure experiments in eutrophic Lake Hylke fish removal was without effect on the bacterioplankton production but caused a marked reduction in biomass (GEERTZ-HANSEN et al. 1987). In contrast, short term enclosure experiments in eutrophic Frederiksborg Castle Lake revealed a substantial reduction in both bacterial production and biomass when fish was excluded from the enclosures (RIEMANN 1985, RIEMANN & SØNDERGAARD 1986), whereas long-term experiments in the same lake revealed a marked lower bacterial biomass in the fish free enclosures but a similar bacterial production in enclosures with and without fish (CHRISTOFFERSEN et al., submitted). The different response in the two experiments in Frederiksborg Castle lake could probably be attributable to the different time scale of the experiments and in general, enclosure experiments cannot simply be transferred to the whole-lake system (CARPENTER 1989).

In the present paper we describe the long term impact of trophic cascade on heterotrophic bacterioplankton production, biomass and cell volume in both a eutrophic lake and a hypertrophic lake following substantial alteration in the planktivorous fish stock. Only average summer values are included here while the seasonal dynamics will be modelled and described in detail elsewhere.

Study area

The investigation was conducted in two shallow Danish lakes, one eutrophic and one hypertrophic, both of which had short hydraulic retention times.

The eutrophic lake, Lake Væng has a surface area of 16 ha, a mean and maximum depth of 1.2 and 2.2 m, respectively, and a hydraulic retention time of 15-25 days. Summer average total P is 50-150 μ l^{-1}. In order to reduce the recovery period after sewage diversion, the biomass of planktivorous fish (mainly roach and bream) was reduced by 50% during 1987 and 1988. This initiated a self-perpetuating process which further reduced planktivorous fish biomass to about 25% of the 1986-level in 1989 and 1990. The lake and biomanipulation experiments are described in detail elsewhere (SØNDERGAARD et al. 1990a, JEPPESEN et al. 1990a, b, and 1991).

The hypertrophic lake, Lake Søbygård has a surface area of 40 ha, a mean and maximum depth of 1.0 and 1.9 m, respectively, and a hydraulic retention time of 15-20 days. Summer average total P is 550-1,000 μ l^{-1}. Large natural changes have occurred in the fish stock as a result of major fish kill in the late seventies, and low recruitment since 1984 (particularly during 1984-1987), due to outstanding high pH during the spawning period (up to pH 11.2). In addition, 4.3 tons of planktivorous fish (mainly roach and rudd) which is equivalent 17% of the standing stock in 1986 was removed during 1986-88 by commercial fishermen. Further detail about this lake and the oscillations in its biological structure and its chemical environment are given in JEPPESEN et al. (1990a, c), SØNDERGAARD et al. (1990b) and HANSEN & JEPPESEN (1992).

Materials and methods

Lake Væng was studied during the 5 year period 1986-1990 and Lake Søbygård during the 6 year period 1985-1990. Heterotrophic bacterioplankton production was measured in situ every 2-7 days from May to October, either on a mid-lake sample pooled from the depths 0.2, 0.8 and 1.25 m or on separate samples from each of the three depths. The approach followed was basically that described by FUHRMANN & AZAM (1982), only minor changes being made. Triplicate 25 ml transparent Jena flasks and triplicate formalin killed blanks (1% final concentration) were incubated in situ with 12.5 nM 3H-methyl-thymidine for 15-60 min depending on lake temperature. The reaction was then stopped by addition of formalin and 7-10 ml of each sample filtered separately on 25 mm Sartorius cellulose acetate filters (0.2 μm) and rinsed 8 times with 1 ml ice-cold 5% TCA not later than 24 h after sampling. The radioactivity retained on the filters was counted not later than 48 hours after sampling, the external-channels-ratio method being used to correct for quenching. Bacterial production was calculated from 3H-methyl-thymidin using the following conversion factors: 2×10^9 cells nmol-thymidine^{-1} (RIEMANN et al. 1982) and 25 fg C cell^{-1} (R. BELL, pers. comm.).

Enumeration of bacteria was undertaken using the method of HOBBIE et al. (1977) with only minor modification. Water from the sampling depths given above was added to 25 ml Jena flasks (triplicate) and fixed with formalin at a final concentration of 2%. Prior to enumeration 0.5-1.0 ml of each sample was stained with a 50-100 μl acridine orange solution (1:1,000 citrate buffer, pH 6.6), diluted after 2 min with 3 × 2 ml sterile distilled water and then filtered through 0.2 μm Nucleopore filters prestained with irgalan black. Enumeration was undertaken at × 1560 magnification using a Leitz epifluorescence microscope equipped with a 75 W mercury lamp. At least 500 cells were counted on 2-3 different fields. Bacterial cell dimensions were measured using an eyepiece micrometer at × 1560 magnification (each micrometer unit = 0.7 μm). Cells were divided into rods (8 size classes), cocci (4 classes) and half-circle-formed rods (4 classes) and cell volume calculated using standard geometric formulae.

Phytoplankton production (PP), corrected for dark fixation, was estimated from the photosynthesis vs. irradiance relationship determined from laboratory incubations, and integrated over depth and time using observations of Secchi depth (converted to a light extinction coefficient) and the time-variation of surface irradiance at a station situated 30-40 km from the lakes. Sampling frequency was as described for bacterioplankton.

The procedures used for sampling and analysis of phytoplankton and zooplankton are described by JEPPESEN et al. (1990a, c) and those used for chemical analysis by SØNDERGAARD et al. (1990a, b).

Statistical analyses of the changes in summer averages (May to October) in some variables during the investigation period were undertaken using multiple regression. Firstly we fitted a model with lake-dependent levels (intercepts) and yearly changes (slopes), and secondly we tested between inter-lake equality of the yearly changes (slopes (Table 1)).

Results

In both Lake Væng and Lake Søbygård the average bacterioplankton production during summer (May-Oct.) displayed only minor inter-annual variation despite a marked variation in the cladoceran biomass and the phytoplankton production and biomass (Figs. 1-3). In eutrophic Lake Væng, bacterioplankton production only varied from $15\text{-}25 \times 10^7$ cells l^{-1} h^{-1} despite a 70-fold variation in cladoceran biomass (0.04 to 2.8 mg DW l^{-1}), a 7-fold variation in chlorophyll *a* (11 to 79 μg l^{-1}) and a 6-fold variation in phytoplankton production (0.3 to 1.9 g C m^{-2} d^{-1}) (Fig. 1). Similarly, in hypertrophic Lake Søbygård bacterioplankton production only varied from $37\text{-}53 \times 10^7$ cells l^{-1} h^{-1} despite a 150 fold variation in the cladoceran biomass (0.008 to 1.2 mg DW l^{-1}), a 5.5 fold variation in chlorophyll *a* (137 to 748 μg l^{-1}) and 3.7 fold variation in primary production (3 to 11 g C m^{-2} d^{-1}) (Fig. 2).

Table 1. Changes in summer average (May to October) of some variables (Figs. 3-4) during the investigation period calculated by means of a regression analysis. The slope and the significance level (in paranthesis) are shown.
* = only data from 1986-1988 were included in this analysis.

	BP:PP (%)	CLA:PHYT (-)	Spec. growth rate of bacteria h^{-1}	Volume of bacteria μm^3
Lake Væng	6.42* (p=0.003)	0.33* (p=0.023)	0.00062 (p=0.51)	-0.0050 (p=0.18)
Lake Søbygård	1.13 (p=0.037)	0.013 (p=0.73)	0.0027 (p=0.005)	-0.0031 (p=0.27)
Test for equality between lakes	(p=0.008)	(p=0.032)	(p=0.11)	(p=0.67)

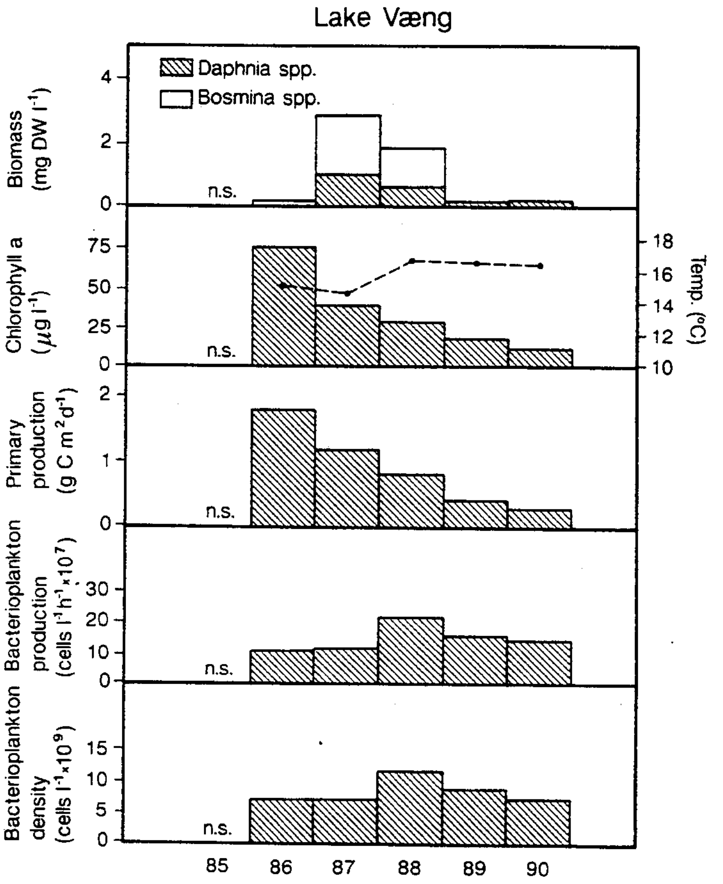

Fig. 1. Average summer values (1 May - 1 Oct.) of cladoceran biomass, chlorophyll *a*, water temperature, C14-primary production, heterotrophic bacterioplankton production and bacterial density in eutrophic Lake Væng during a 5 year period (1986-90). The planktivorous fish stock, mainly roach (*Rutilus rutilus*) and bream (*Abramis brama*) was reduced by 50% in 1987 and 1988. n.s. = no sampling.

Bacterioplankton production in Lake Søbygård was significantly greater in 1990 than in the preceding years, ($p<0.001$, t-test), the increase coinciding with a shift in the dominant cladoceran from *Daphnia longispina* to *Bosmia longirostris*. As an average for the five years bacterioplankton production in Lake Søbygård was significantly greater than in less eutrophic Lake Væng ($p<0.01$, t-test).

The variation in bacterioplankton density observed in both lakes was less than 2-fold, density ranging from 6.6 to 11.5×10^9 cells l^{-1} in Lake Væng, and from 8.1 to 16.3×10^9 cells l^{-1} in Lake Søbygård. Whereas the inter-annual variation in bacterioplankton density closely followed that of bacterioplankton production in Lake Væng, being high when the production was high and vice versa (Fig. 1), no clear relationship was found for Lake Søbygård (Fig. 2).

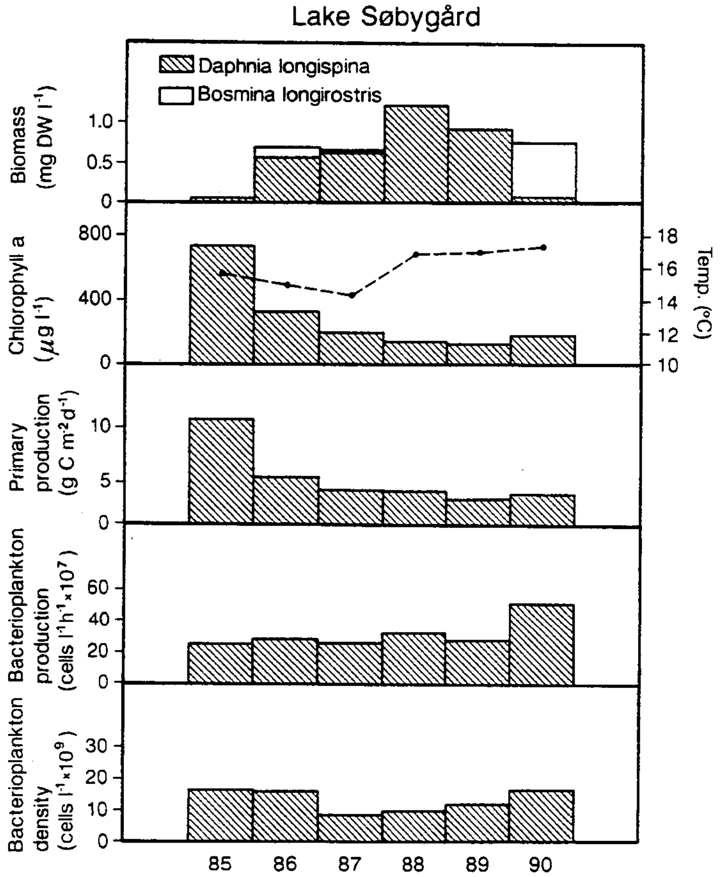

Fig. 2. Average summer values (1 May - 1 Oct.) of cladoceran biomass, chlorophyll *a*, water temperature, C14-primary production, heterotrophic bacterioplankton production and bacterial density in hypertrophic Lake Søbygård during a 6 year period (1985-90). Major natural changes in the predation pressure from fish occurred throughout this period, mainly due to fluctuating spawning success of roach (*Rutilus rutilus*) and rudd (*Scardinius erythropthalmus*). It should be noted that the scales on the vertical axes differ from those in Fig. 1.

The ratio of bacterioplankton production to phytoplankton production, BP:PP, increased significantly during the study in both lakes. In Lake Væng BP:PP increased from 4.1% in 1986 prior to fish-manipulation, to 52% in 1990, whereas in Lake Søbygård BP:PP only increased from 2.5% in 1985 to 8.9% in 1990 (Fig. 3). The significantly steeper increase of BP:PP in Lake Væng initially coincided with a significant higher increase in the ratio of cladoceran to phytoplankton biomass (CLA:PHYT-ratio) (Table 1, Fig. 3); in 1989-90, however, BP:PP-ratio in Lake Væng was high despite a relative low CLA:PHYT-ratio (Fig. 3), probably because of the high and rapidly expanding submerged macrophyte coverage (Fig. 3). In Lake Søbygård CLA:PHYT-ratio had a slight but significant increase (Table 1) whereas no submerged macrophytes appeared (Fig. 3).

Concurrent with the increase in the BP:PP-ratio in both lakes there was a slight, although not significant decrease (Table 1), in the average cell volume of bacteria, from 0.082 μm^3 in 1986 to 0.062 μm^3 in 1990 in Lake Væng, and from 0.077 μm^3 in 1985 to 0.054 μm^3 in 1990 in Lake Søbygård (Table 1, Fig.4). Simultaneously the specific growth of the bacteria increased significantly from 0.016 to 0.034 h^{-1} (generation time 20-43 h) in Lake Søbygård and there was a tendency to an increase from 0.017 to 0.020 h^{-1} (generation time 34-40 h) in Lake Væng (Table 1, Fig. 4).

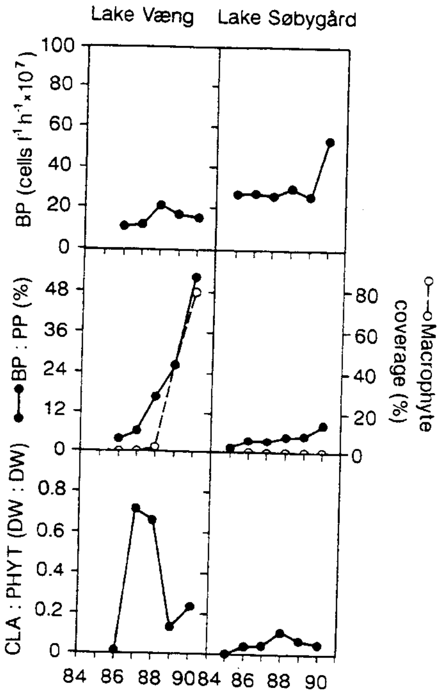

Fig. 3. Average summer values (1 May - 1 Oct.) of bacterioplankton production, the ratio of bacterioplankton production to the C14-primary production (BP:PP), the coverage of submerged macrophytes and the ratio of cladoceran biomass to phytoplankton biomass (CLA:PHYT) (estimated from chlorophyll *a* assuming a conversion factor of 45 μg C(μg Chl *a*)$^{-1}$) in eutrophic Lake Væng (left) and hypertrophic Lake Søbygård (right) during a 5-6 year period with major changes in fish predation pressure on zooplankton.

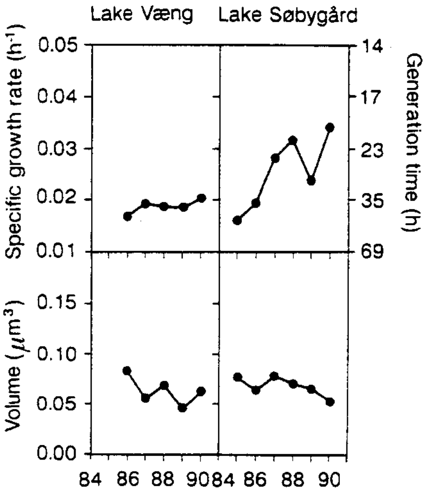

Fig. 4. Average summer values (1 May - 1 Oct.) of the specific growth and generation time of bacteria and average cell volume in eutrophic Lake Væng (left) and hypertrophic Lake Søbygård (right) during a 5-6 year period with major changes in fish predation pressure on zooplankton.

Discussion

Bacterioplankton production was significantly higher in hypertrophic Lake Søbygård than in eutrophic Lake Væng (Fig. 3), whereas the ratio of bacterioplankton production to phytoplankton production was substantially higher in Lake Væng. These findings are in accordance with recent comparative studies which suggest an association between increasing eutrophication and increasing bacterioplankton production, and a decreasing ratio of bacterioplankton biomass and production to chlorophyll *a* (BIRDS & KALFF 1984, HARDY et al. 1986, COLE et al. 1988, WHITE et al. 1991).

The relative importance of the bacterioplankton in lake ecosystems seems to vary markedly, bacterioplankton contribution anywhere from 2% to >80% of primary production. However, some of this variation may be due to differences in the conversion factors used in the various studies. BELL et al. (in prep.), who used the same conversion factors as those used in the present study found that bacterioplankton accounted for approximately 25% of phytoplankton production of three eutrophic and one oligotrophic lake in which there was a 100-fold variation in algal biomass. Compared to these data, the values found in Lake Søbygård prior to the enhancement of zooplankton biomass, and in Lake Væng prior to fish-manipulation, i.e. 2.5% and 4%, respectively, are relatively low. Assuming a growth yield of 50%, then only 5 and 8%, respectively, of the phytoplankton production was channeled through the bacterioplankton. We interpret the low values obtained in the present study as reflecting partly the shallowness and short hydraulic retention time of the two lakes studied; because the settling distance is short algal loss through sedimentation is higher than in deeper lakes and because the retention time is short algal loss through the outlet is high. As a consequence the interval during which exudates from algae can be released, and subsequently consumed by bacteria, is short. This interpretation is supported by sedimentation measurements in Lake

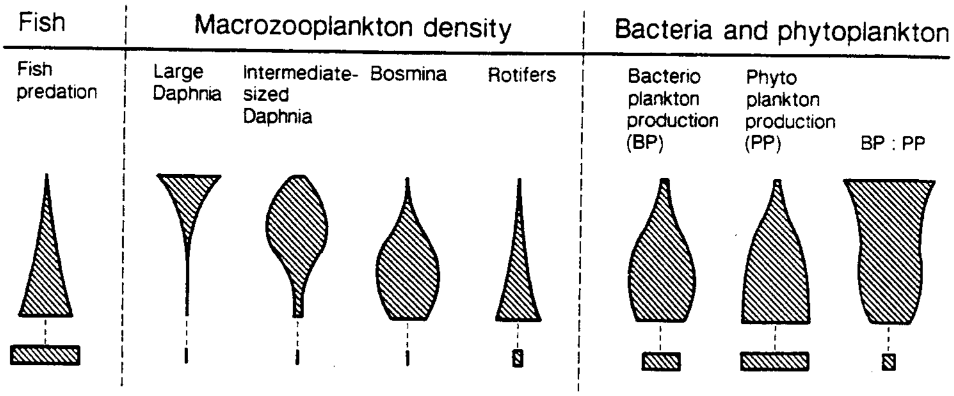

Fig. 5. A tentative model to explain how changes in fish predation pressure in eutrophic to hypertrophic shallow lakes are propagated to the phytoplankton and heterotrophic bacterioplankton level via their impact on zooplankton community structure. The upper part represents lakes with pH <10.5 and the lower part lakes in which pH frequently is above 10.5 (e.g. Lake Søbygård in 1985).

Søbygård in 1985 which revealed that average summer daily loss through sedimentation was 20% of phytoplankton biomass and 40% of daily production (Kristensen & Jensen 1987, Jeppesen et al. 1990a). Mass balance studies showed that an additional 5% of the biomass and 10% of the production were exported (unpublished observation). Thus only 50% of the production was available for algal respiration, zooplankton grazing and bacterioplankton consumption. Nevertheless, despite a 50% reduction the proportion of BP are still low in the two lakes compared to values of Bell et al. (in prep.) and Cole et al. (1988), but they are in agreement with the 0.3-16.8%, mean = 2%) from hypertrophic lake Hartbeespoort Dam (Roberts & Wichs 1990). Maybe the low grazing impact on phytoplankton and thus low turn over of phytoplankton in the very eutrophic-hypertrophic lakes contribute to the low BP:PP-ratios in these lakes.

Bacterioplankton production in both lakes was only slightly affected by the trophic cascade, even though there was major reduction in chlorophyll *a* and phytoplankton production (Figs. 1-3). Therefore, the percentage of the total phytoplankton production, which was channelized through the bacterioplankton increased with increasing grazing pressure on phytoplankton (Fig. 3). Although a number of studies have shown a tight coupling between bacterioplankton production and phytoplankton production in lakes ranging from oligotrophic to eutrophic (Riemann et al. 1982, Bell & Kuparinen 1984, Güde et al. 1985, Simon & Tilzer 1987), most of these studes were carried out during periods in which cladoceran density was low (e.g. the spring). In accordance with the present findings, a much weaker relationship between bacterioplankton production and phytoplankton production was observed when the cladoceran density was relatively high (Simon & Tilzer 1987, Güde 1988).

As discussed in the following the overall increase in the BP:PP ratio with increasing grazing pressure in Lake Væng and Lake Søbygård is interpreted as being mainly due to direct and indirect effects of the cladocerans. In Lake Væng the changes in submerged macrophyte coverage also played a role.

Cladocerans may have a dual impact on the bacterioplankton. They may stimulate bacterioplankton production in different ways. First, by feeding on algae, cladocerans may enhance the release of organic matter (excretion and sloppy feeding) which can serve as a food source for the bacterioplankton (LAMPERT 1978). Second, they may reduce the top-down control on bacteria by reducing the density of more efficient bacteria feeders, such as rotifers, through competition or interference, and the density of microheterotrophs, such as ciliates and flagellates, through cropping or competition. Third, by indirectly reducing loss through sedimentation, they enhance pelagic retention of organic matter of algal origin which via excretion, either by the zooplankton themselves, or when channelized through the pelagic food-web, will then gradually become available as a source for bacterioplankton growth. As discussed above, this enhanced retention is of particular importance to bacterioplankton in shallow lakes, where the risk of loss through sedimentation is high.

Cladocerans may also exert negative effects on the bacterioplankton community, however. Both laboratory and field studies have revealed that bacteria can be grazed by several species of cladocerans (GELLER & MÜLLER 1981, DE MOTT 1985), although there are contrasting reports on the short term impact of cladoceran grazing on bacterioplankton biomass and production: RIEMANN (1985), GEERTZ-HANSEN et al. (1987) and PACE et al. (1990) all found a close impact of grazing, while others reported negligible effects (e.g. PETERSON et al. 1978, PEDROS-ALIO & BROCK 1982, 1983, SANDERS et al. 1989). In addition, by grazing algae, cladocerans may reduce the phytoplankton production (as has been demonstrated in the two lakes studied) and thereby reduce the amount of algal exudates for bacterial growth.

When considering the average summer values, the stimulatory impact of cladocerans on bacterioplankton either balanced or slightly exceeded the negative impact in both lakes (Figs. 1 and 2). Concurrently, as the primary production decreased, the BP:PP ratio increased when cladoceran biomass increased, the increase being highest in the lake in which the CLA:PHYT ration, and thus grazing pressure on algae increased most i.e. Lake Væng (Fig. 3). The specific growth rate of bacterioplankton also increased (Fig. 4), probably reflecting enhanced substrate availability mediated mainly by the increase in cladoceran grazing pressure on algae, but possibly also by the reduction in average bacterial cell volume. The latter may, in turn, reflect enhanced size-selective predation by cladocerans on large bacteria. In addition, the reduction in the density of flagellates and ciliates that is known to occur in eutrophic lakes with high densities of cladocerans (RIEMANN 1985, GÜDE 1988, CHRISTOFFERSEN et al. submitted, JÜRGENS 1992) may further reduce the predation pressure on small bacteria (SHIKONO et al. 1990) and thus further enhance their competitive capacity. However, the possibility that changes in water temperature may also have contributed cannot be excluded: temperature was higher in 1988-1990 than in the preceding years (Figs. 1-2) and cell volume is known to decrease with increasing temperature, even in a predator free environment (CHRZANOWSKI et al. 1988).

The results from 1989-90 in Lake Væng deviated from the overall pattern in that there was a sustained increase in the BP:PP ratio despite a reduction in grazing pressure (Fig. 3). This increase coincided with a marked increase in coverage of submerged macrophytes; as macrophyte production is not included in PP, it is likely that organic matter released from the plants and their associated biofilm was responsible for the increase in BP:PP in those 2 years. This is supported by the fact that bacterioplankton consumption, assuming a growth yield of 50%, exceeded algal production in 1990 which strongly suggest, that organic substrate derived from other sources than phytoplankton production was important. In addition to macrophyte-derived organic matter, grazing by sessile filter feeders associated with the macrophyte community (cladocerans, mussels etc.) may have further enhanced the turnover of organic matter derived from algae, thereby further stimulating bacterioplankton production.

The high bacterioplankton production in Lake Søbygård in 1990, which was almost twice that of the preceding five years, occurred simultaneously with a shift from *D. longispina* to *B. longirostris* (Fig. 2). This may reflect a difference in the ability of these two species to efficiently crop bacteria, and hence in their ability to create top-down control of bacterioplankton biomass and production: whereas some *Daphnia* species, including *D. longispina*, efficiently feed on bacteria, although less efficiently than on larger sized particles such as algae (e.g. PETERSON et al. 1978, GELLER & MÜLLER 1981, DE MOTT 1985, NAGATA & OKHAMOTO 1988), *Bosmina* are much less efficient at feeding on free-living bacteria (SCHOENBERG & MACCUBIN 1985). The different impact of the two cladocerans is supported by studies of the seasonal dynamics in the two lakes and a number of grazing experiments in Lake Søbygård (E. JEPPESEN, unpubl. observations).

Based on our findings in eutrophic Lake Væng and hypertrophic Lake Søbygård, we have established a tentative model to explain how changes in fish predation in the two shallow eutrophic lakes are propagated to the phytoplankton and bacterioplankton level via their impact on the zooplankton structure (Fig. 5): when fish predation on zooplankton is low, large daphnids dominate and occur in high density. By grazing, the daphnids are able to suppress the biomass and production of both algae and bacterioplankton. The BP:PP ratio is high because most of the algae produced is mineralized in the water via grazing and the pelagic microbial loop, and because only a small amount is lost through sedimentation when algal biomass is low. When fish predation increases there is a shift to intermediate-sized daphnids and grazing pressure on both algae and bacteria thus decreases. As a consequence, biomass and production of both algae and bacterioplankton increases, the higher algal biomass resulting in a higher loss through sedimentation and thereby a decrease in the BP:PP ratio. With a further increase in fish predation, there is a shift to the less efficient bacteria feeder *Bosmina* spp.; this results in a significant increase in bacterioplankton production and an intermediate increase in the BP:PP-ratio. At even higher fish predation the BP:PP-ratio decreases again reflecting a shift to rotifer dominance and consequently, to a further decrease in algal grazing, an increase in algal biomass and enhanced algal loss through sedimentation. At extremely hypertrophic conditions phytoplankton production may cause pH to rise to such high levels (i.e. 10.5-11.2) that the cladocerans and rotifers prevailing under such conditions suffer and the biomass of filter feeding zooplankton thus falls abruptly (JEPPESEN et al. 1990c, HANSEN et al. 1991). Grazing will be low and algal biomass and loss through sedimentation will then be high, and the BP:PP-ratio will consequently be low. Whether this tentative model can be transferred to shallow eutrophic lakes in general have to be elucidated.

In summary, a reduction in planktivorous fish predation on the macrozooplankton community of two shallow eutrophic lakes had only a minor effect on bacterioplankton production, despite a substantial increase in the bacterioplankton:phytoplankton production ratio, an increase in the specific growth of bacterioplankton and a tendency to a reduction in bacterioplankton cell volume. By enhancing organic turnover and reducing loss through sedimentation, cladocerans had a major impact on bacterioplankton populations dynamics and hence on the microbial loop. Species specific differences were observed however: whereas *Bosmina longirostris* usually stimulated bacterioplankton production, *Daphnia* spp. frequently exerted a major top-down control on bacteria. Thus, the extent of fish predation on zooplankton by determining the relative abundance of these two species, may influence the impact of a trophic cascade on bacterioplankton.

If one only considers summer average of biomass and production, then top-down control was strong at the top of the food-chain (Figs. 1-2), became gradually weaker at lower trophic levels, and was almost negligible at the bacterioplankton level. These results are in accordance with the hypothesis proposed by McQueen et al. (1986). However, if one considers the functional response (e.g. BP:PP and specific growth rate), then top-down control of bacterioplankton was not weak. Differences in the scale of the analysis undertaken may therefore influence the conclusions drawn about the control mechanisms.

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References

Bell, R.T. & Kuparinen, J. (1984): Assessing phytoplankton and bacterioplankton production during early spring in Lake Erken, Sweden. - Appl. Environ. Microbiol. **48:** 1221-1230.

Benndorf, J. (1987): Food web manipulation without nutrient control: A useful strategy in lake restoration? - Schweiz. Z. Hydrol. **49:** 237-248.

Bird, D.F. & Kalff, J. (1984): Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. - Can. J. Fish. Aquat. Sci. **41:** 1015-1023.

Carpenter, S.R. (1989): Replication and treatment strength in whole-lake experiments. - Ecology **70:** 453-463.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985): Cascading trophic interactions and lake productivity. - BioScience **35:** 634-639.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, D., He, X. & von Ende, C.N. (1987): Regulation of lake primary productivity food web structure. - Ecology **68:** 1863-1876.

Christoffersen, K., Riemann, B., Klysner, A. & Søndergaard, M. (submitted): Potential role of natural populations of zooplankton on plankton community structure in eutrophic lake water. - Limnol. Oceanogr.

Chrzanowski, T.H., Crotty, R.D. & Hubbarb, G.J. (1988): Seasonal variation in cell volume of epilimnetic bacteria. - Microb. Ecol. **16:** 155-163.

Cole, J.J., Findlay, S. & Pace, M.L. (1988): Bacterial production in fresh and saltwater ecosystems: a cross-system overview. - Mar. Ecol. Progr. Ser. **43:** 1-10.

DeMott, W.R. (1985): Relations between filter mesh-size, feeding mode, and capture efficiency for cladocerans feeding on ultrafine particles. - Arch. Hydrol., Beih. Ergebn. Limnol. **21:** 125-134.

Fuhrmann, J.A. & Azam, F. (1982): Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. - Mar. Biol. **66:** 109-120.

Geertz-Hansen, O., Olesen, M., Bjørnsen, P.K., Larsen, J.B. & Riemann, B. (1987): Zooplankton consumption of bacteria in a eutrophic lake and in experimental enclosures. - Arch. Hydrobiol. **110,4:** 553-563.

Geller, W. & Müller, H. (1981): The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. - Oecologia **49:** 316-321.

Güde, H. (1988): Direct and indirect influences of crustaceran zooplankton on bacterioplankton of Lake Constance. - Hydrobiologia **159:** 63-73.

Güde, H., Haibel, B. & Müller, H. (1985): Development of bacterial planktonic populations in a water column of Lake constance (Bodensee-Obersee). - Arch. Hydrobiol. **105:** 59-77.

Hansen, A.-M., Christensen, J.V. & Sortkjær, O. (1991): Effect of high pH on zooplankton and nutrients in fish-free encolusures. - Arch. Hydrobiol. **123:** 143-164.

Hansen, A.-M. & Jeppesen, E. (1992): Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. - J. Plank. Res. **14:** 591-605.

Hardy, F.J., Shortreed, K.S. & Stockner, J.G. (1986): Bacterioplankton, phytoplankton and zooplankton communities in a British columbia coastal lake before and after nutrient reduction. - Can. J. Fish. Aquat. Sci. **43:** 1504-1514.

Hobbie, R., Daly, J. & Jasper, S. (1977): Use of nuclepore filters for counting bacteria by fluorescence microscopy. - Appl. Environ. Microbiol. **33:** 1225-1228.

Hrbacek, J., Dvorakova, M., Korinek, V. & Prochazkova, L. (1961): Demonstration of the effect of fish stock on the species composition and the intensity of metabolism of the whole plankton association. - Verh. Internat. Verein. Limnol. **14:** 192-195.

Jeppesen, E., Søndergard, M., Mortensen, E. Kristensen, P., Riemann, B., Jensen, H.J., Müller, J.P., Sortkjær, O., Jensen, J.P., Christoffersen, K., Bosselmann, S. & Dall, E. (1990a): Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. - Hydrobiologia **200/201:** 205-218.

Jeppesen, E., Jensen, J.P., Kristensen, P., Søndergaard, M., Mortensen, E., Sortkjær, O. & Olrik, K. (1990b): Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. - Hydrobiologia **200/201:** 219-227.

Jeppesen, E., Søndergaard, M., Sortkjær, O., Mortensen, E. & Kristensen, P. (1990c): Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. - Hydrobiologia **191:** 139-148.

Jeppesen, E., Kristensen, P., Jensen, J.P., Søndergaard, M., Mortensen, E. & Lauridsen, T. (1991): Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. - Mem. Ist. Ital. Idrobiol. **48:** 127-148.

Jürgens, K. (1992): Is there plenty of food for bactivorous flagellates in eutrophic waters? - Arch. Hydrobiol., Beih. Ergebn. Limnol. **37:** 195-205.

Kristensen, P. & Jensen, P. (1987): Sedimentation and resuspension in Lake Søbygård [Sedimentation og resuspension i Søbygård Sø]. - M.Sc.thesis. Freshwater Laboratory, Silkeborg, & Botanical Institute, University of Aarhus, Denmark, 176 pp. [in Danish].

Lampert, W. (1978): Release of dissolved organic carbon by zooplankton grazing. - Limnol. Oceanogr. **23:** 831-834.

McQueen, D.J., Post, J.R. & Mills, E.L. (1986): Trophic relationships in freshwater pelagic ecosystems. - Can. J. Fish. Aquat. Sci. **43:** 1571-1581.

Nagata, T. & Okamoto, K. (1988): Filtering rates on natural bacteria by *Daphnia longispina* and *Eodiaptomus japonicus* in Lake Biwa. - J. Plank. Res. **10:** 835-850.

Pace, M.L., Porter, K.G. & Feig, Y.S. (1983): Species and age specific differences in bacterial utilization by two co-occurring cladocerans. - Ecology **64:** 1145-1156.

PACE, M.L., MCMANUS, G.B. & FINDLAY, S.E.G. (1990): Plankton community structure determines the fate of bacterial production in a temperate lake. - Limnol. Oceanogr. **35**: 795-808.

PACE, M.L. & FUNKE, E. (1991): Regulation of planktonic microbial communities by nutrients and herbivores. - Ecology **72**,3: 904-914.

PEDROŚ-ALÍO, C. & BROCK, T.D. (1982): Assessing biomass and production of bacteria in eutrophic Lake Mendota, Wisconsin. - Appl. Environ. Microbiol. **44**: 203-218.

— — (1983): The impact of zooplankton feeding on the epilimnic bacteria of an eutrophic lake. - Freshw. Biol. **13**: 227-239.

PETERSON, B.J., HOBBIE, J.E. & HARVEY, J.F. (1978): *Daphnia* grazing on natural bacteria. - Limnol. Oceanogr. **23**: 1039-1044.

RIEMANN, B. (1985): Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. - Appl. Environ. Microbiol. **50**: 187-193.

RIEMANN, B., SØNDERGAARD, M., SCHIERUP, H.-H., BOSSELMANN, S., CHRISTENSEN, G., HANSEN, J. & NIELSEN, B. (1982): Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossø. - Int. Rev. Ges. Hydrobiol. **67**: 145-185.

RIEMANN, B. & SØNDERGAARD, M. (1986): Regulation of bacterial secondary production in two eutrophic lakes and in experimental enclosures. - J. Plank. Res. **8**: 519-536.

ROBERTS, R.D. & WICKS, R.J. (1990): Heterotrophic bacterial production and its dependence on autotrophic production in a hypertrophic African reservoir. - Can. J. Fish. Aquat. Sci. **47**: 1027-1037.

SANDERS, R.W., PORTER, K.G., BENNETT, S.J. & DEBIASE, A.E. (1989): Seasonal patterns of bacterivory by flagellates, ciliates, rotifers and cladocerans in a freshwater planktonic community. - Limnol. Oceanogr. **34**: 673-687.

SCHOENBERG, S.A. (1990): Short-term productivity responses of algae and bacteria to zooplankton grazing in two freshwater lakes. - Freshw. Biol. **23**: 395-410.

SCHOENBERG, S.A. & MACCUBIN, A.E. (1985): Relative feeding rates on free and particle bound bacteria by freshwater macrozooplankton. - Limnol. Oceanogr. **30**: 1084-1090.

SHAPIRO, J., LAMARRA, V. & LYNCH, M. (1975): Biomanipulation: an ecosystem approach to lake restoration. - In: BREZONIK, P.L. & FOX, J.L. (Ed.): Water Quality Management through Biological Control. - Report No. ENV-07-75-1, University of Florida, Gainesville (1975), pp. 85-96.

SHIKANO, S., LUCKINBILL, L.S. & KURIHARA, Y. (1990): Changes of traits in a bacterial population associated with protozoal predation. - Microb. Ecol. **20**: 75-84.

SIMON, M. & TILZER, M.M. (1987): Bacterial response to seasonal changes in primary production and phytoplankton biomass in Lake Constance. - J. Plank. Res. **9**: 535-552.

SØNDERGAARD, M., JEPPESEN, E., KRISTENSEN, P. & SORTKJÆR, O. (1990a): Interactions between sediment and water in a shallow hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. - Hydrobiologia **191**: 149-164.

SØNDERGAARD, M., JEPPESEN, E., MORTENSEN, E., DALL, E., KRISTENSEN, P. & SORTKJÆR, O. (1990b): Phytoplankton biomass reduction after plantivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. - Hydrobiologia **200/201**: 229-240.

WHITE, P.A., JACOB, K., RASMUSSEN, J.B. & GASOL, J.M. (1991): The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. - Microb. Ecol. **21**: 99-118.

Address of the authors: E. JEPPESEN, O. SORTKJÆR, M. SØNDERGAARD and M. ERLANDSEN, National Environmental Research Institute, Department of Freshwater Ecology, Vejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark.

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Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ?

E. Jeppesen, M. Søndergaard, E. Kanstrup, B. Petersen, R. B. Eriksen, M. Hammershøj, E. Mortensen, J. P. Jensen & A. Have*
*National Environmental Research Institute, Department of Freshwater Ecology, Vejlsøvej, 25, P.O. Box 314, DK-8600 Silkeborg, Denmark; *Ringkøbing County Council, Domstrædet 2, DK-6950 Ringkøbing, Denmark*

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Abstract

The effects of nutrients on the biological structure of brackish and freshwater lakes were compared. Quantitative analysis of late summer fish, zooplankton, mysid and macrophyte populations was undertaken in 20–36 shallow brackish lakes of various trophic states and the findings compared with a similar analysis of shallow freshwater lakes based on either sampling (fish) or existing data (zooplankton, mysids and macrophytes). Special emphasis was placed on differences in pelagic top-down control. Whereas the fish biomass (CPUE, multiple mesh-size gill nets) rose with increasing P-concentration in freshwater lakes, that of brackish lakes was markedly reduced at P-concentrations above *ca.* 0.4 mg P l^{-1} and there was a concomitant shift to exclusive dominance by the small sticklebacks (*Gasterosteus aculeatus and Pungitius pungitius*); as a result, fish density remained relatively high. Mysids (*Neomysis integer*) were found at a salinity greater than 0.5‰ and increased substantially with increasing P-concentration, reaching levels as high as 13 ind. l^{-1}. This is in contrast to the carnivorous zooplankton of freshwater lakes, which are most abundant at intermediate P levels. The efficient algal controller, *Daphnia* was only found at a salinity below 2‰ and *N. integer* in lakes with a salinity above 0.5‰. Above 2‰ the filter-feeding zooplankton were usually dominated by the less efficient algal controllers *Eurytemora* and *Acartia*. In contrast to freshwater lakes, no shift to a clearwater state was found in eutrophic brackish lakes when submerged macrophytes became abundant. We conclude that predation pressure on zooplankton is higher and algal grazing capacity lower in brackish eutrophic-hypertrophic lakes than in comparable freshwater lakes, and that the differences in trophic structure of brackish and freshwater lakes have major implications for the measures available to reduce the recovery period following a reduction in nutrient loading. From the point of view of top-down control, the salinity threshold dividing freshwater and brackish lakes is much lower than the conventionally defined 5‰.

Introduction

The biological structure and internal biological control mechanisms of shallow freshwater lakes are highly affected by lake water nutrient level and by the extent of nutrient loading (Gulati *et al.*, 1985; Moss, 1990; Jeppesen *et al.*, 1991a). At low P-concentrations, freshwater lakes are usually in a clearwater stage; submerged macrophytes are abundant, potential piscivores are present in large numbers and predation pressure on zooplankton is consequently low. At somewhat higher P-concentrations there is a shift to a turbid stage; submerged macrophytes disappear and the fish stock changes towards exclusive dominance by cyprinids. This leads to a reduction in the ratio of filter-feeding zooplankton to phytoplankton, and a consequent reduction of the capacity of zooplankton to control algal growth. Because of the initiation of self-perpetuating processes, the shift to the turbid stage is often abrupt (Scheffer, 1990; Moss, 1990; Jeppesen *et al.*, 1991a, Scheffer *et al.*, 1993).

To what extent shallow brackish lakes are affected by changes in nutrient concentrations and nutrient load is unclear, little information being available. However, several studies indicate that there are major differences in the response of freshwater and brackish lakes (Moss & Leah, 1982; Hansson *et al.*, 1990; Heerkloss *et al.*, 1991; Moss *et al.*, 1991).

The aim of the present study was to further elucidate changes in the biological structure of shallow brackish lakes with different lake water nutrient concentration. The findings are compared with similar observations in freshwater lakes based partly on sampling and partly on existing data, special emphasis being placed on the differences in top-down control.

Materials and methods

Fish

Pelagic fish stock composition and abundance was estimated in 37 freshwater lakes and in 8 brackish lakes by means of standardized test-fishing (Mortensen *et al.*, 1991) with multiple mesh-size survey gill nets (6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, 75 mm). The length and depth of each section was 3 m and 1.5 m, respectively. Between 6 and 64 nets were used depending on size, depth distribution and shore line development. In addition, a reduced test-fishing programme was conducted in 11 brackish lakes using only 2 nets – one placed parallel to the shore at a distance of 20 m, the other placed perpendicular to the shore at a distance of 30–70 m. In 4 lakes a 4 mm section was included in the gill nets. As only minor differences have previously been found between CPUE (catch per grill net) in the littoral and the pelagical zones of shallow lakes with a uniform depth (unpublished data), such as those included in the present analysis, the two nets are assumed to provide representative information about the composition or the pelagical fish stock in the littoral zone. Test-fishing was conducted once in each lake between August 15 and September 15. Both fish number and biomass were analyzed.

Mysids

The mysid *Neomysis integer* was studied in 31 brackish lakes. In the day time replicate vertical hauls were made using a 1 mm mesh net (diameter 0.5 m or 0.6 m, length 1 m) at 3–5 randomly selected stations situated between 20 and 100 m from the shore. In order to allow individuals near the bottom to distribute over the net surface, the nets were allowed to rest on the bottom for 2 minutes (1991) or 1 min (1992) before undertaking the vertical haul. As there is no difference in *N. integer* density whether the nets are allowed to rest 1 to 5 min (Åser, H., personal communication), the samples are comparable. Sampling was undertaken once between late July and early September. The samples were fixed in 70% ethanol, counted and the number of individuals per litre estimated using the water depth at the sampling stations. Shore data tend to overestimate the average density of the lake: Arndt & Jansen (1986) found a twofold higher density along the shore than in open water. On the other hand, daytime sampling underestimate the actual population by a factor of 3–4 (B. Moss & H. Åser, personal comments), because most animals stay near the bottom during the day and do not colonize the net properly during incubation. In 18 of the lakes 5–10 breder traps (Breder, 1960) were incubated at the sediment surface for two hours in the same area as where the vertical hauls were drawn. Fish species were counted separately and the mysids were fixed in ethanol and later counted in the laboratory.

Zooplankton
Carnivorous and herbivorous zooplankton densities were determined using depth-integrated water samples, these comprising pooled samples from 1–3 stations taken using a 3.3 l Patalas sampler. Sampling was undertaken 1–3 times in each lake between late July and early September and 10 times between May and October every year (1989–1991) in Lake Lemvig. The pooled samples were filtered through a 20 μm net and fixed in Lugol's iodine (1 ml, 100 ml tap water). All zooplankton retained on a > 140 μm net were counted, individual zooplankton < 140 μm being filtered on a 20 μm net and counted in strips in fifteen 2.9 ml chambers in an inverted microscope. At least 100 individuals of the dominant zooplankton species were counted. Biomass of the different species was calculated from the density (ind. l^{-1}) and the average mass of one individual using length-weight relationships obtained from a number of Danish locations (unpublished observations). The biomass of copepod nauplii, copepodites, males and females were calculated separately. The findings were compared with similar freshwater data (Kristensen *et al.*, 1991).

Grazing
Crustacean grazing was calculated by assuming that copepods and cladocerans ingested 50% and 100% of their biomass per day, respectively (Hansen *et al.*, 1992) and that their prey exclusively consisted of phytoplankton. The grazing pressure was then determined as the time-weighted average consumption during summer by zooplankton divided by the average algal biomass. This method was preferred to averaging daily percentages, because the latter often is biased by a few extremely high grazing percentages found during short term clearwater phases. Phytoplankton biomass (dry weight, DW) was estimated from chlorophyll *a* (pooled sample from the photic zone, ethanol extractions) using a chl*a*:C-ratio of 30 and a DW:C ratio of 2.2 or from phytoplankton volume using a DW:WW ratio of 0.29. Phytoplankton volume, in turn, was estimated by inversed microscope counting (5 ml lugol subsample of a pooled sample from the photic zone) converted to biovolume by means of appropriate geometric figures.

Macrophytes
Information on submerged macrophyte coverage was obtained from a large number of technical reports from various Danish survey programmes, and the lakes assigned to one of two categories: coverage more than, or less than, 30% of lake area.

Results

The 36 brackish lakes included in the analysis are characterized in Table 1. The lakes were generally shallow and covered a wide range of surface areas (1.5–29500 ha), total phosphorus levels (0.034–1.64 mg P l^{-1}) and salinities (0.19–35.6‰), albeit the majority were relatively small eutrophic lakes with low salinity levels (Table 1).

Fish

The composition of the pelagic fish stock in the littoral zone of brackish lakes was markedly dependent on salinity and total P (Figs 1–2). In lakes with a low P-concentration and a salinity below 8‰, the fish biomass was exclusively dominated by typical freshwater fish (roach *Rutilus rutilus*, bream *Abramis brama*, perch *Perca fluviatilis*, rudd *Scardinius erythrophtalmus*) (Fig. 1).

Table 1. Morphometric data, total phosphorus and salinity of the lakes included in the analysis. The chemical data represent mean values of all data collected during the summer (May–Oct.).

	Mean	Median	Min.	Max.	N
Surface area (ha)	1134	94	1.5	29500	36
Mean depth (m)	0.9	0.8	0.3	2.9	30
Maximum depth (m)	1.9	1.4	0.6	7.0	29
Total phosphorus (mg P l^{-1})	0.35	0.17	0.034	1.64	36
Salinity (‰)	6.4	4.7	0.19	35.6	36

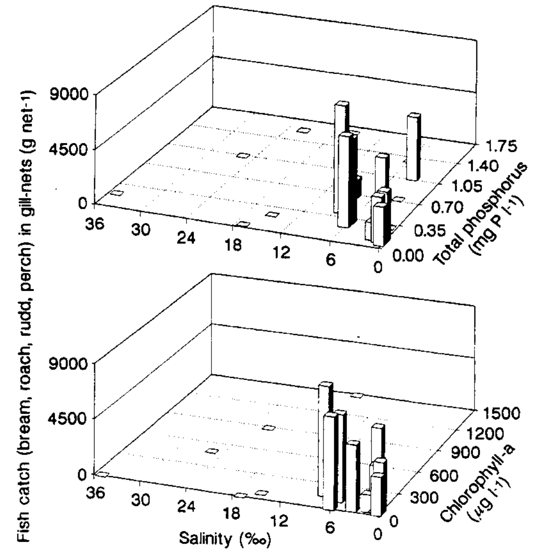

Fig. 1. Total catch (gill-nets, 14 meshes from 6.5 to 75 mm) of bream (*Abramis brama*), roach (*Rutilus rutilus*), rudd (*Scardinius erythropthalmus*) and perch (*Perca fluviatilis*) in relation to lake water salinity and total phosphorus (upper panel) and chlorophyll *a* (lower panel). Each column represents one lake.

However, at P-concentrations above 0.7 mg P l^{-1}, these four species disappeared completely and were instead replaced by sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*). (One exception was a lake with a low nitrogen concentration and hence a low chlorophyll *a* concentration *i.e.* which was less eutrophic than indicated by the P-concentration). Typical freshwater fish were not observed at chlorophyll concentrations above 464 μg P l^{-1} (Fig. 1), and were also absent in lakes with a salinity above 8.3‰, irrespective of the P level.

At salinities between 8–22‰, oligohaline-euhaline species such as smelt (*Osmerus eperlanus*), herring (*Clupea sp.*) and whitefish (*Coregonus laveretus*) contributed markedly to the fish biomass. At high P-concentrations, these species were almost completely replaced by sticklebacks (*G. aculeatus* and *P. pungitius*) (Fig. 2). At the highest salinities (> 22‰) the pelagic fish stock was exclusively dominated by sticklebacks, irrespective of the P level.

In the freshwater lakes and at low P-concentrations in brackish lakes the total and the planktivorous fish biomass (CPUE) rose with increasing P to maximum values of 10–18 kg net^{-1} (Fig. 3 A,C). Using all freshwater data and data for brackish lakes below 0.4 mg P l^{-1}, the following relationship was established:

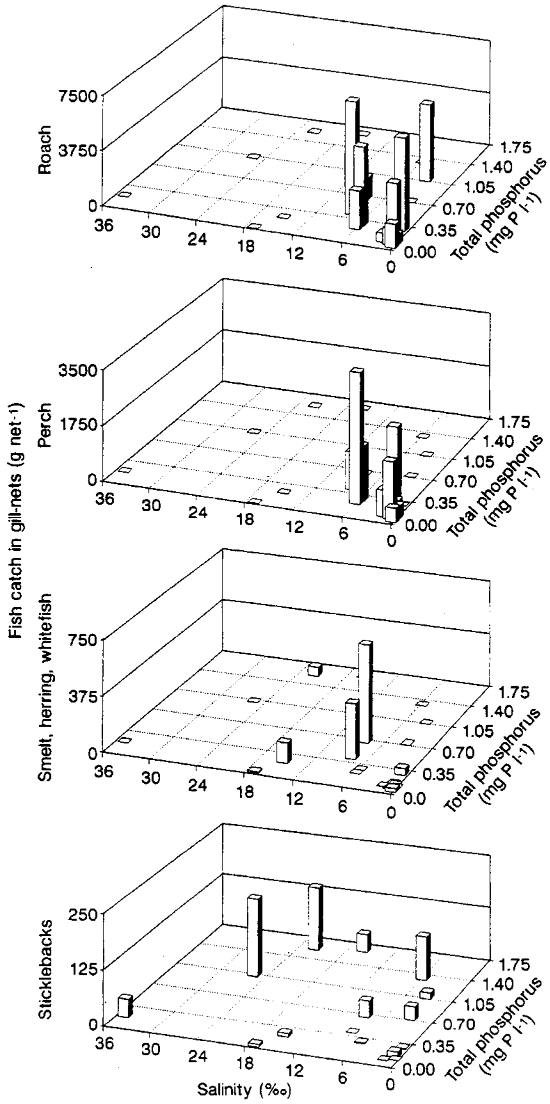

Fig. 2. Total catch (gill-nets, 14 meshes from 6.5 to 75 mm) of roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), smelt (*Osmerus eperlanus*), herring (*Clupea sp.*) and whitefish (*Coregonus lavaretus*), and sticklebacks (*Gasterosteus aculeatus*), in relation to lake water salinity and total phosphorus. Each column represents one lake.

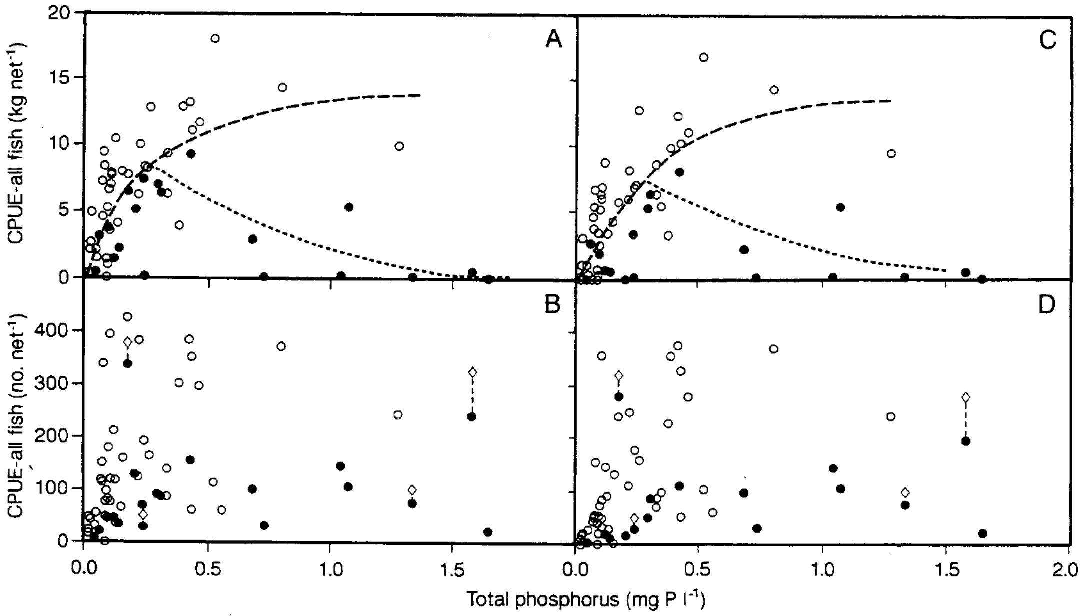

Fig. 3. Total catch (gill-nets, 14 meshes from 6.5 to 75 mm) of fish in freshwater lakes (○) and brackish lakes (●, salinity $>0.2‰$) (A, B) and planktivorous fish (C, D) in relation to lake water total phosphorus. Each point represents one lake. In A and C the broken lines are the linear regression of biomass and $\log_{10}$ (tot P) for all data from freshwater lakes and for brackish lakes below 0.4 mg P l^{-1} and the dotted lines are for brackish lakes above 0.4 mg P l^{-1}. The diamonds indicate the catch when a 4 mm section is added to the gill net (data for 4 lakes only). The catch with and without the 4 mm net is interconnected by a broken line.

$$\text{Total biomass (kg net}^{-1}) = 12.7 + 3.17 \ln (\text{tot P, mg l}^{-1}), \quad (p<0.0001,\ r^2 = 0.43)$$

$$\text{Planktivorous biomass (kg net}^{-1}) = 12.0 + 3.02 \ln (\text{tot P, mg l}^{-1}), \quad (p<0.0001,\ r^2 = 0.47).$$

At total P-concentrations greater than 0.4 mg P l^{-1} the total and planktivorous fish biomass of the brackish lakes decreased, on the contrary, to extremely low levels in the most hypertrophic lakes (0.04–0.1 kg net $^{-1}$) (Fig. 3 A, C); the relationship being:

$$\text{Total biomass (kg net}^{-1}) = 2.2 - 5.2 \ln (\text{tot P, mg l}^{-1}), \quad (p<0.05,\ r^2 = 0.52)$$

$$\text{Planktivorous biomass (kg net}^{-1}) = 2.0 - 4.4 \ln (\text{tot P, mg l}^{-1}), \quad (p<0.007,\ r^2 = 0.46).$$

In the freshwater lakes there was a tendency to a similar but markedly less dramatic biomass reduction (CPUE) at the highest P-concentration (Fig. 3 A, C).

In terms of number of all fish caught, CPUE was relatively low (<60 fish net^{-1}) at P-concentrations below 0.05 mg P l^{-1} (Fig. 3 B, D). At levels above 0.05 mg P l^{-1} the CPUE data were highly scattered, ranging from 31 and 430 fish net^{-1} without there being any clear relationship to total P and without there being any clear differences between brackish and freshwater lakes. The number of planktivorous fish caught was somewhat lower at low P values ($<$ 0.3 mg P l^{-1}), but similar at higher P-concentration, *i.e.* the fish stock becomes exclusively dominated by planktivores.

Mysids

The density of *N. integer* (vertical hauls) was markedly dependent on nutrient level and salinity (Fig. 4). It was absent at salinities below 0.5‰ irrespective of the P-concentration, and in some brackish lakes with a low P-concentration. Linear regression analysis (GLM, SAS Institute, 1990) of $\log(n+1)$ transformed data revealed a significant, positive relationship between *N. integer* density (both ind. l^{-1} and ind. m^{-2}) and total P ($p<0.001$), and a negative (although insignificant) relationship between total fish biomass and *N. integer* density (indiv. l^{-1}: $p=0.06$, ind. m^{-2}: $p=0.08$). The maximum density recorded was 12.8 ind. l^{-1} or 10400 ind. m^{-2}. Following $\log(n+1)$ transformation, *N. integer* caught with breder traps were linearly related to the density obtained with vertical hauls ($r^2=0.67$, $p<0.001$) (Fig. 5). Thus it can be excluded that the density increase with increasing total-P just reflects that mysids are easier to catch because a gradually larger proportion of mysids occur in the pelagic when water turbidity increases.

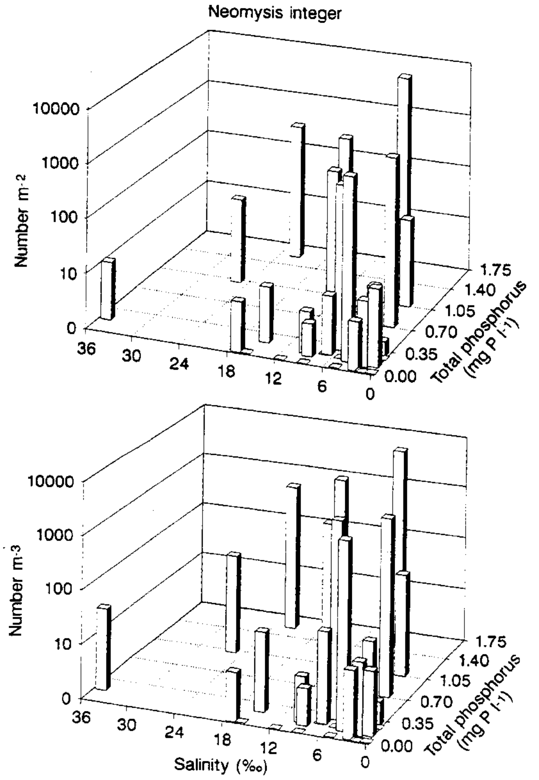

Fig. 4. Density of *Neomysis integer* (A: number m^{-2}, B: number m^{-3}) in relation to salinity and lake water total phosphorus. Each column represents one lake.

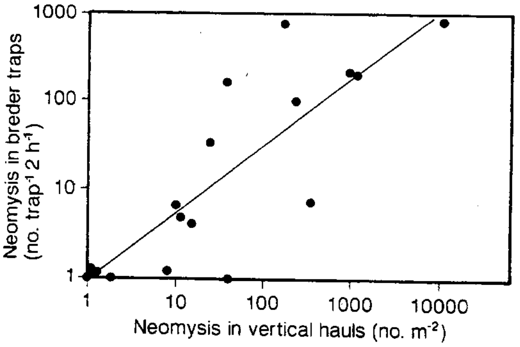

Fig. 5. Comparisons of the $\log(n+1)$ transformed abundance of *Neomysis* in breder traps (incubated at the bottom for two hours) and those obtained by obtained by vertical hauls (0.5 m or 0.6 m nets, 1 mm meshes).

Macrozooplankton

A shift in zooplankton composition and abundance occurred at increasing salinity: the typical freshwater cladocerans gradually became of less importance with increasing salinity, *Daphnia* spp. disappearing completely at salinities above 2‰ and other cladocerans at salinities above 7.2‰, the exception being *Bosmina* spp. which occurred, albeit in small numbers at a salinity of 15.9‰ (Fig. 6). Although the marine cladocerans, *Podon* sp. and *Evadne* sp. were present at salinities above 15.9‰, they never constituted more than 2.2% of the total crustacean biomass. The cladocerans were replaced by calanoid copepods: the freshwater species *Eudiaptomus* spp. disappeared at salinities above 2‰, *E. affinis* was present in lakes with salinities between 0.2 and 15.9‰, and was particularly dominant in the range 1–8‰; *Acartia* was present at salinities above 0.5‰ and was particulary dominant above 6‰ (Fig. 6).

Further evidence of the structuring impact of salinity on the zooplankton community is provided by Lake Lemvig. When the salinity of the surface water increased from a summer mean of

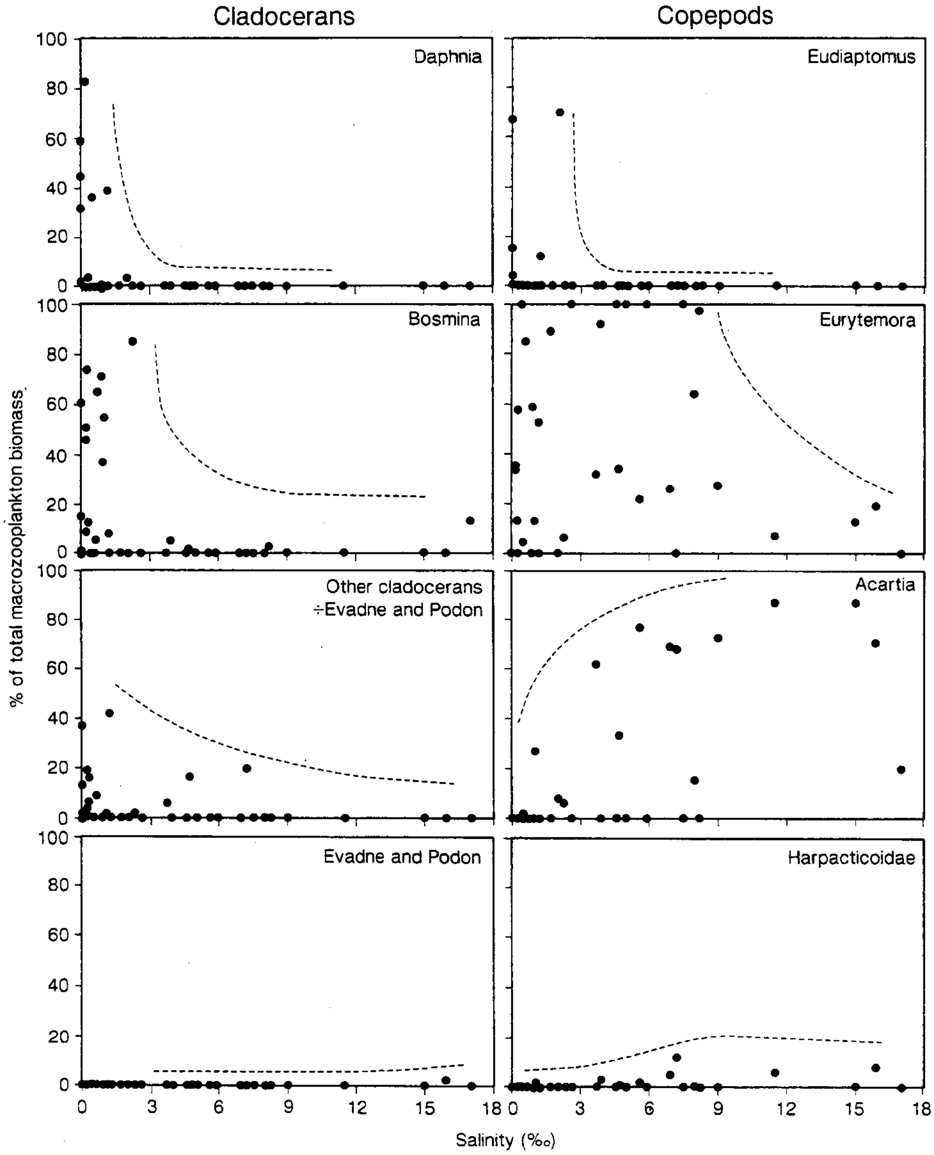

Fig. 6. Relative contribution of different groups to total macrozooplankton biomass in relation to salinity. Each point represents one lake.

0.9‰ in 1989 (maximum 2.1‰) to 3.5‰ in 1990 (maximum 4.0‰) as a result of the entry of salt water from Lemvig Bay in Feb – Mar 1990, the crustacean community shifted from being dominated by cladocerans (*Daphnia spp.*, *Bosmina longirostris*), cyclopoid copepods (*Cyclops vicinus*, *Mesocyclops leuckartii*) and calanoid copepods (*Eudiaptomus graciloides*) to being exclusively dominated by *E. affinis* (Fig. 7). Conversely, when the salinity decreased again to a summer mean of 0.7‰ in 1991 (maximum 1.5‰), the community structure seen in 1989 was restored except that *E. affinis* remained in the lake (albeit in low density).

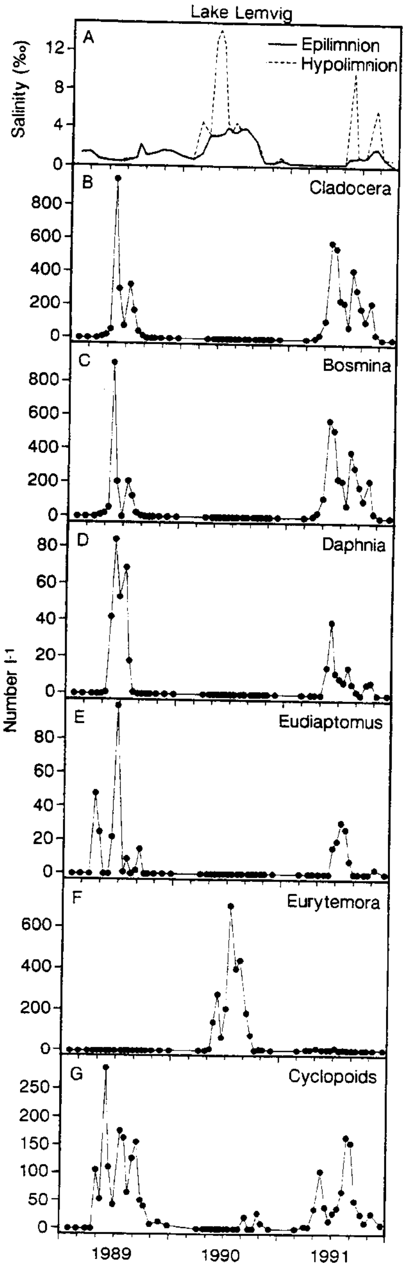

Fig. 7. Changes in density of various zooplankton groups in Lake Lemvig over a three year period during which there was a marked variation in salinity (upper panel).

Following log–transformation there was a significant linear decline in the estimated grazing pressure with increasing total P in both freshwater and brackish lakes ($p<0.02$ and $p<0.05$, respectively). While the slope for the two sets of data was not significantly different ($p>0.95$), the intercepts were ($p<0.001$) *i.e.* the grazing pressure was 5.1 times higher in the freshwater lakes.

Submerged macrophytes

The Secchi depth decreased with increasing P-concentration in both freshwater and brackish lakes (Fig. 9). Whereas freshwater lakes with submerged macrophyte coverage above 30% generally had a higher Secchi depth than lakes with little or no submerged macrophyte coverage, no differences were found in the case of brackish lakes. Submerged macrophytes coverage of freshwater lakes >3 ha was only high (above 30%) when the P-concentration was below 0.15 mg P l^{-1}; in contrast, high coverage was observed in brackish lakes at all P-concentrations between 0.04–1.6 mg P l^{-1}.

Discussion

Top-down control

With increasing P-concentration the fish biomass of the freshwater lakes rose (Fig. 3), and in accordance with previous studies (Hartmann, 1977; Lessmark, 1983; Persson *et al.*, 1988, Jeppesen *et al.*, 1990, 1991a) there was a shift from a system dominated by pike (*Esox lucius*) and perch (*P. fluviatilis*) to one exclusively dominated by planktivorous-benthivorous fish, mainly bream (*A. brama*) and roach (*R. rutilus*) (Jeppesen *et al.*, 1990). At high P-concentrations (>1 mg P l^{-1}) biomass had a tendency to fall (one lake), this perhaps being related to fish kill in hypertrophic lakes because of ice cover during winter and occasionally during the summer as a result of oxygen depletion or high pH (Barica, 1975; Jeppesen *et al.*, 1990, 1991a). In such lakes fish kill may be accompanied by a short-term or even long-lasting shift to clearwater conditions (Jeppesen *et al.*, 1991a).

In the brackish lakes, the CPUE fish biomass also increased with increasing P-concentration, but only at low concentrations; at concentrations above 0.4 mg P l^{-1} there was a marked reduction in fish biomass to extremely low levels (in most lakes) and a concomitant shift towards exclusive dominance by sticklebacks (*G. aculeatus* and *P. pungitius*) (Figs 1–3).

Due to differential net selectivity, differences in CPUE may not necessarily reflect differences in ambient fish abundance or biomass. Corrections for net selectivity have not been undertaken on the full data set. However, to justify that the fish biomass is substantially lower in hypertrophic brackish lakes than in comparable freshwater lakes, a correction was made using the iteration methods of Jensen (1990) on *G. aculeatus* in two hypertrophic lakes, where this species exclusively dominated the gill net catches (a 4 mm mesh size section being included in the gill nets used), and on roach (*R. rutilus*) in one eutrophic freshwater lake, roach often being the dominant planktivore in Danish eutrophic lakes. The analysis revealed a 45% higher abundance and a 66% higher biomass of *G. aculeatus* in one of the hypertrophic brackish lakes after corrections for net selectivity and for the absence of the 4 mm mesh size section were made, the figures being 55% and 45% in the other hypertrophic lake. The comparable data for roach were 110% and 54%, respectively. It therefore seems reasonable to conclude that as regards species caught in nets differences in net selectivity cannot explain the major difference in the observed pelagical fish biomass (CPUE) in hypertrophic freshwater lakes and brackish lakes.

However, *P. pungitius* is not caught in the nets used in the standardized programme (≥ 6.25 mm mesh size), and the total stickleback biomass may consequently be somewhat underestimated. The importance of this species can be evaluated from the breder trap catches. In the 18 lakes where breder traps were used, including all hypertrophic lakes in the study, the total *P. pungitius* density was low, averaging 3.2% (0–28%) of the total number of sticklebacks (*P. pungitius* and *G. aculeatus*). Thus if the breder traps do not strongly select against *P. pungitius*, this species would not contribute significantly to the total biomass most of the lakes under study. When comparing data obtained by breder traps in the brackish estuary Kertinge Nor with catches in drop-nets, it was revealed that the efficiency of catching *P. pungitius* in breder traps was only 12% lower than that of *G. aculeatus* (Mortensen, E., unpublished results). It can therefore be concluded that the number of *P. pungitius* (and hence the biomass) was low in the lakes included in the analysis and in terms of biomass the fish CPUE decline in eutrophic-hypertrophic lakes is consequently real and not an artifact related to the fishing methods used.

Although the low fish biomass in brackish eutrophic lakes may be interpreted as indicating that fish predation on zooplankton is low, this is probably not the case. From freshwater lakes it is known that the predation pressure in eutrophic lakes (>0.1 mg P l^{-1}) is related to CPUE in terms of fish number (gill-net catch) rather than to the fish biomass (Jeppesen *et al.*, 1991b; E. Jeppesen & J. P. Jensen, unpublished results) and that predation pressure is high when the CPUE exceeds 50–100 ind. (Jeppesen *et al.*, 1991b; E. Jeppesen & J. P. Jensen, unpublished results). The density of sticklebacks (CPUE) always exceeded 25 ind. and was only below 75 ind. in two of the hypertrophic brackish lakes of the present study (Fig. 3). Actual density may be even higher, it being known that the density of small sticklebacks is somewhat underestimated in comparison with that of other fish species; hence adding a 4 mm section to the gill nets (data only available for 3 lakes) increased CPUE by an average of 48% (range 12–72%) (Fig. 3). Sticklebacks prey voraciously on zooplankton and are able to eliminate large cladocerans completely when rapidly colonizing fish-free pools (Pont *et al.*, 1991). They also prey on copepods (Worgan & FitzGerald, 1981), including the species most abundant in brackish lakes, *Eurytemora affinis*, (Delbeek & Williams, 1987; Williams & Delbeek, 1989), and may even havea major top-down impact on this species (Castionguay & FitzGerald, 1990). It can therefore reasonably be assumed that fish predation on zooplankton is potentially high in hypertrophic brackish lakes despite the low fish biomass. Although this is in contradiction with the conceptual model of Moss *et al.* (1991), it is in accordance with an earlier model by Moss & Leah (1982).

Besides fish, carnivorous zooplankton and mysids may also exert a top-down influence on zooplankton. In the brackish lakes (> 0.2‰) the mysid *N. integer* was often abundant, while the typical freshwater species *Chaoborus* and *Leptodora* were absent. With increasing eutrophication (total P) *N. integer* density increased substantially (Fig. 4). This probably reflects changes in food availability, *N. integer* being omnivorous, feeding on zooplankton, detritus, periphyton and, to a lesser extent, on phytoplankton (Rudstam *et al.*, 1986; Irvine *et al.*, 1990), most of which are more abundant in eutrophic than in oligotrophic lakes. The density of *N. integer* seems, in turn, to be influenced by fish predation. Although Irvine *et al.* (1990) suggest that *N. integer* is likely to be relatively free from predation because of its ability to escape, and although Moss *et al.* (1991) predicted a weak impact of fish on *N. integer* in hypertrophic Hickling Broad, Bremer & Vijverberg (1982) showed that *N. integer* is an important food source for smelt, perch, juvenile pike-perch and ruffe in the Frisian lakes, and Timola (1980) showed that *Neomysis* contributed significantly to the food of smelt in the northeastern Bothnian Bay – particularly among older fish. Furthermore, in Lake Wolderwejd, Meijer *et al.* (1994) observed a major increase in *N. integer* density in the first year after removal of 75% of the planktivorous fish biomass, and an abrupt decline in the second year following the return of young-of-the-year perch. In the present study, the relationship between fish biomass and *N. integer* density tended to be negative, a finding in accordance with the fact that with increasing eutrophication the fish stock shifted from a community with a high fish biomass comprising species which prey on all sizes of *N. integer*, to a community with a low biomass of sticklebacks, which only prey on juvenile *N. integer* (M. Søndergaard *et al.*, unpublished results), a change which spares the reproductively active specimens. The conflicting observations concerning the impact of fish on *Neomysis* may therefore reflect differences in the fish stock composition of the lakes studied.

Although the possibility cannot be excluded that the negative relationship between fish and *N. integer* found in the present study is an artifact attributable to the interplay between fish and eutrophication, combining our findings with those of the studies described above suggests that the substantial increase in *N. integer* density in eutrophic brackish lakes may reflect not only the increase in abundance of food, but also the shift in fish stock composition, *i.e.* from species which efficiently prey on *N. integer*, to the less efficient sticklebacks.

Like other mysids, *N. integer* preys efficiently on cladocerans (Richard *et al.*, 1975). It is probably a more efficient predator than the typical freshwater carnivorous zooplankton, *Leptodora* and *Chaoborus* (Hanazato, 1990) since it preys on all sizes of cladocerans, including the reproductively active specimens (Bremer & Vijverberg, 1982; Hollebeek *et al.*, 1993), whereas *Leptodora* and *Chaoborus* prey mainly on small and intermediate-sized zooplankton (Hanazato, 1990). In fact, cladocerans disappeared completely in a eutrophic Japanese lake during spring and autumn, when the density of *N. intermedius* was as low as 0.025 ind. l^{-1}, and in the summer, when *N. intermedius* density was greater than 0.5 ind. l^{-1}. Similarly, rotifers became scarce at a *N. intermedius* density of 0.25 ind. l^{-1} and cyclopoid copepods at a density of 3–4 ind. l^{-1}. The higher selectivity for cladocerans is in accordance with the findings of Murtaugh (1981) and Goldman *et al.* (1979) that copepods are only rarely found in the stomach of mysids. However, several studies indicate that *N. integer* preys on copepods when the latter are abundant (Hanazato & Yasuno 1988; Bremer & Vijverberg, 1982; Arndt & Jansen, 1986; Irvine *et al.*, 1990). Laboratory experiments have shown that *N. integer* may ingest *E. affinis*, the zooplankton species most abundant in brackish lakes, at a rate of 6–82 nauplii and 0.2–30 copepods per hour (Irvine *et al.*, 1990). It therefore seems reasonable to assume that in shallow brackish eutrophic lakes, in which *N. integer* occurs in high densities (up to 13 ind. l^{-1}), it may, like the planktivorous fish, exert major top-down control on the zooplankton community.

In Denmark, the carnivorous zooplankton *Chaoborus* and *Leptodora* are particularly abundant in shallow mesotrophic and slightly eutrophic freshwater lakes (Jeppesen *et al.*, 1991b) while carnivorous zooplankton density is low in the more eutrophic-hypertrophic lakes, despite high food abundance. This probably indicates an abundance of fish that prey efficiently on carnivorous zooplankton. In contrast to the suggestion for brackish lakes eutrophic-hypertrophic lakes, the top-down impact of carnivorous zooplankton on herbivorous zooplankton is consequently weak in freshwater eutrophic-hypertrophic lakes. It is therefore likely that the top-down control of zooplankton is particularly important in brackish eutrophic-hypertrophic lakes, since not only fish, but also mysids (*i.e. N. integer*) prey on the larger zooplankton. This may explain why the overall grazing pressure on algae at eutrophic and hypertrophic conditions was 5.1 times higher in the freshwater lakes (Fig. 8). The shift from cladoceran dominance in freshwater lakes to calanoid copepod dominance in brackish lakes may further weaken the top-down control. Although a high daily consumption per unit biomass (daily ration) has been found for *E. affinis* in a brackish eutrophic lake (Gulati & Doornekamp, 1991), the species does not seem to have the capacity of large cladocerans to control the phytoplankton in a predation-free environment in eutrophic lakes (Irvine *et al.*, 1990; H. Åser, unpublished results). This may reflect the small size of *E. affinis* and the more restricted sized spectrum of food particles it selects compared with large cladocerans. In general, large size seems to be a key factor in the ability of zooplankton to control phytoplankton (Carpenter & Kitchell, in press).

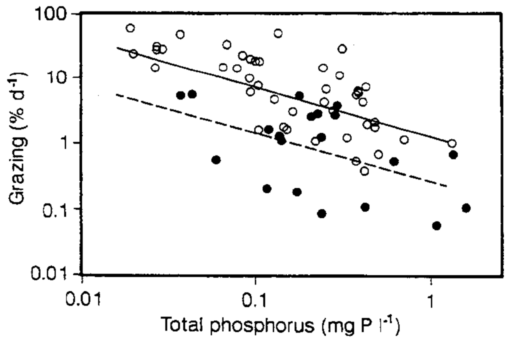

Fig. 8. Calculated grazing pressure (GP – % of phytoplankton biomass d^{-1}) of crustacean zooplankton in relation to total phosphorus (TP, mg P l^{-1}). ○ freshwater lakes, ● brackish lakes (> 0.5‰). The regression lines for the two sets of data are also shown. Freshwater lakes: $\log_{10}$ GP = 0.12-0.77 $\log_{10}$ TP. brackish lakes: $\log_{10}$ GP = -0.59-0.77 $\log_{10}$ TP.

In summary, we hypothesize that top-down control of zooplankton in brackish eutrophic-hypertrophic lakes is high and is higher than in comparable freshwater lakes. The latter reflects the fact that whereas fish are the only important predator in freshwater hypertrophic lakes, both fish and *Neomysis* occur in high densities in comparable brackish lakes. Because of this, and because of the shift from cladocerans to copepods and the resultant reduction in zooplankton size, the capacity to control phytoplankton is particularly low in brackish eutrophic-hypertrophic lakes.

Impact of submerged macrophytes

The difference in the impact of submerged macrophytes on the turbidity of brackish and freshwater lakes may also be attributable to differences in top-down control (Fig. 9). In freshwater lakes, moderately high macrophyte coverage favours piscivorous fish such as pike and perch at the expense of planktivorous fish such as roach and bream; this reduces predation on cladocerans and thereby enhances algal grazing and transparency in a self-perpetuating manner (Moss, 1990; Jeppesen *et al.*, 1990). Moderately high macrophyte-coverage may also provide valuable daytime refuge for cladocerans against predation, thereby further reducing predation pressure and consequently enhancing transparency (Timms & Moss, 1984). In contrast, the water in brackish eutrophic lakes is turbid despite submerged macrophyte coverage of up to 100%. In such

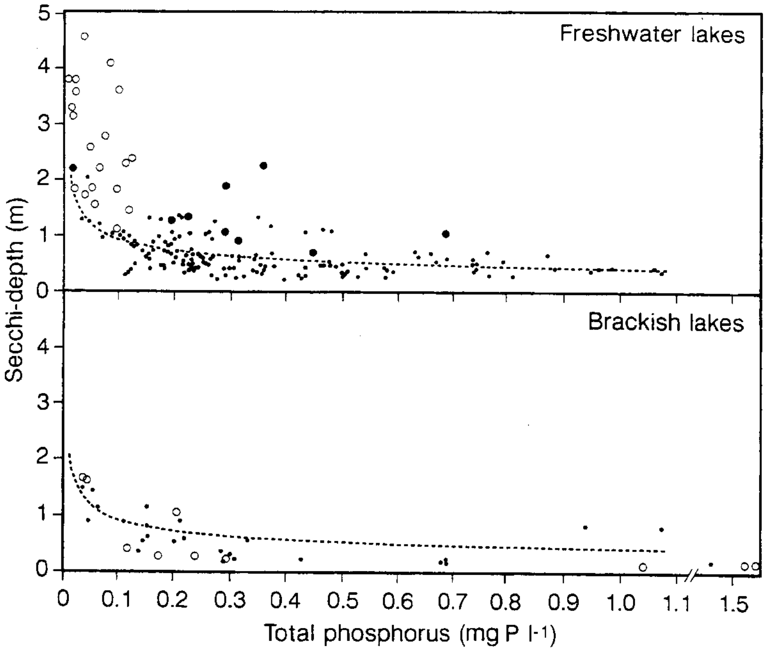

Fig. 9. Secchi depth in relation to lake water total phosphorus for a number of shallow freshwater lakes (A) and brackish lakes (B). O: lakes with more than 30% submerged macrophyte coverage and a surface area >3 ha; ●: lakes with more than 30% submerged macrophyte coverage and a surface area <3 ha; • lakes with little coverage (<30%) or an unknown submerged macrophyte coverage. Each point represents one lake and is a time-weighted average of all data collected between 1st May and 1st October. The exponential curve and the equation developed by Kristensen *et al.* (1991) on data from lakes with low submerged macrophyte coverage are shown. Upper panel is from Jeppesen *et al.* (1990).

lakes cladocerans are either absent or only occur in low densities (Fig. 5). The positive impact of macrophytes on cladocerans may therefore be of less importance or even non-existent in brackish lakes. In addition, the density of *N. integer* and sticklebacks appears to be particularly high within the vegetation (Muus, 1967; P. Hollebeek, personal communication) this being attributable to several factors: (1) *N. integer* and sticklebacks may use the vegetation to shelter from predation by larger fish; (2) by feeding on periphyton on plant surfaces *N. integer* may survive in large numbers in periods with low zooplankton density (Moss *et al.*, 1991), thereby preserving a potentially high predation pressure on zooplankton; (3) nine-spined sticklebacks use the plants for nesting and (4) high plant-coverage may reduce the territorial demands of sticklebacks. Enhanced macrophyte coverage may therefore lead to a higher density of sticklebacks and *N. integer* and hence to higher predation on zooplankton. In contrast to the conditions pertaining in freshwater lakes, high macrophyte coverage in brackish lakes may therefore lead to a lower zooplankton density and consequently a lower algal grazing pressure. Hence, as was in fact observed (Fig. 9), lake water transparency would be expected to remain unchanged, or even diminish.

Salinity threshold

In the present study the typical freshwater fish, mainly roach and perch, but occasionally also bream and rudd, were found in brackish lakes with a salinity below 8.3‰ (Figs 1–2), which is close to the threshold of 10‰ described for perch by Lutz (1972) and the 10–12‰ threshold described by Larsen (1962) for freshwater fish in general. As some of the freshwater fish, e.g. perch, zander (*Stizostedion lucioperca*) and bream are even better adapted to slightly brackish water than to freshwater (Oliphan, 1940; Ribi, 1992) the disappearance of the freshwater fish at low salinities, but at high P-concentrations, cannot by solely related to the salinity. Moreover, oligohaline-euhaline species such as smelt, herring and whitefish also disappeared or their biomass was markedly reduced at high P-concentrations (Fig. 2). A possible explanation is fish kill in connection with high abundance of the ichthyotoxic flagellate *Prymnesium parvum*, this having been observed in several eutrophic lakes (Moss *et al.*, 1991), including some of the lakes in the present study (Otterstrøm & Steeman-Nielsen, 1940; Olrik, 1985). However, whether this is the only reason for the shift to exclusive dominance by sticklebacks in hypertrophic brackish lakes remains to be elucidated.

That *N. integer* was absent in the freshwater lakes (Fig. 4), but present in brackish lakes at all salinities between 0.5 and 36‰ confirms earlier laboratory observations by Arndt *et al.* (1986) of a salinity tolerance range for *N. integer* of between 1 and 32‰. Kuhlman (1984) found a significant increase in *N. integer* mortality when salinity exceeded 25‰, and a substantial increase above 30‰, whereas Kaiser (1978) as well as Tattersall & Tattersall (1951) in a survey of large number of Danish and British brackish lakes reported that *N. integer* was only occasionally present at salinities above 18‰, the lower threshold for *N. integer* being 0.10–0.14‰ (Tattersall & Tattersall, 1951; Bremer & Vijverberg, 1982). In the present study, *N. integer* was only found at a density above $0.1\,\mathrm{l}^{-1}$ when salinity was between 4 and 22‰. *N. integer* may therefore be of great potential importance as a predator over a wide range of salinities.

Cladocerans decreased markedly with increasing salinity, *Daphnia spp.* being absent above 2‰ and other cladocerans (*B. longirostris*) above 16‰ (Fig. 6). They were instead replaced by calanoid copepods – *Eurytemora affinis* at relatively low salinities, and *Acartia spp.* at higher salinities. Whereas Moss *et al.* (1991) found that cladocerans were present in eutrophic Martham Broad at a salinity of 1.8‰, but were absent at a salinity of 3–4‰ in eutrophic Hickling Broad (Moss, 1994), Hansson *et al.* (1990) found that *Bosmina coregoni maritime* occurred at higher salinities (6–7‰) in the Northern Baltic Sea. In the present study *B. longirostris* was found at 16‰, while it disappeared completely in Lake Lemvig when the salinity exceeded 3–4‰ (Fig. 7). These conflicting results may reflect that not only physiological factors, but also a number of other factors are involved e.g. top-down and bottom-up forces.

The shift in the copepod community seen in the present study (Fig. 6) is in concert with earlier observations; *Eurytemora* was present at a wide range of salinities (0.5–30‰) in San Francisco Bay although abundance was highest below 5‰ and, as in the present study, *Acartia* was the dominant copepod at somewhat higher salinities (10 and 35‰) (Ambler *et al.*, 1985). Roddie *et al.* (1984) found that the survival rates of *Eurytemora affinis* adults and copepodites were highest at salinities between 3 and 10‰, which is in accordance with our finding that this species constituted more than half of the biomass in 71% of the lakes with a salinity between 2.6–8.3‰, but only in 30% of the lakes with a salinity between 0.2–2.6‰. It was not present in any of the lakes with a salinity above 8.3‰ (calculated from Fig. 6). Similarly, Heerkloss *et al.* (1991) found that *E. affinis* was the exclusively dominant macrozooplankter in the Darss-Zingst-Estuary and the Vistula Lagoon, where the salinities ranged from 1.5–8.5‰ and from 0.7–4.5‰, respectively. The shift from *Eurytemora* to the smaller *Acartia* at high salinities may further reduce the capacity of the zooplankton to control the phytoplankton.

By convention the threshold between freshwater and brackish lakes is defined as 5‰ (Remane & Schlieper, 1971). However, from a top-down control point of view this definition is far from optimal; whereas the appearance of *N. integer* (above 0.5‰) and the disappearance of *Daphnia* (above 2‰) cause major shifts in lake trophic structure and dynamics, no major changes occur at 5‰. Thus considering the pelagical trophic interactions and taking into account the structuring importance of *N. integer*, a threshold of <2‰ seems to be much more appropriate for Northern European lakes.

Lake restoration measures

The major differences in the biological structure of freshwater and brackish lakes may have important implications for the response of lakes to reduced nutrient loading and for the selection of additional restoration measures. As is the case with bream and roach in freshwater lakes, stickleback predation on zooplankton in brackish lakes may prevent improvement in the light climate and thereby prevent the appearance of the visible hunting piscivores such as perch and pike (*E. lucius*). In addition, as sticklebacks eat roach eggs (Otterstrøm, 1930), they may delay the recovery of species which spawn in the lake. The delay in lake recovery is further influenced by the fact that the return of submerged macrophytes in eutrophic brackish lakes does not lead to a clearwater stage (Fig. 9 and Moss *et al.*, 1991), and hence does not stimulate the recovery of visible hunters, e.g. perch and pike.

Fish manipulation may be a valuable tool with which to reduce the biological resilience of eutrophic lakes following a reduction of nutrient levels. However, reducing the number of planktivorous fish, a measure which has led to a short or long-term clearwater stage in many freshwater lakes (Gulati *et al.*, 1990), is unlikely to be adequate in brackish lakes because *N. integer* would probably become abundant and prevent the return of large zooplankton as observed in Lake Wolderwijd by Meijer *et al.* (1994). It may be more valuable to stock with fish that prey on *N. integer* and sticklebacks, e.g. the robust rainbow trout or perch, and perhaps even roach. Experience in this field is limited, however.

An alternative proposed by Moss *et al.* (1991), is to enhance the zooplankton grazing capacity by reducing salinity to apr. 1.8‰, and thereby stimulating a shift from calanoid copepods to cladocerans. The present study supports this concept in that the threshold for the appearance of *Daphnia* was close to 2‰ (Figs 6–7). Another possibility is to markedly enhance salinity in areas where it is held artificially low for agricultural purposes e.g. by dams and sluices. The aim of salinity enhancement – e.g. to above 20–25‰ – would be (1) to enhance water exchange with the marine environment and hence the efflux of nutrients accumulated in water and sediment (2) to reduce the importance of *N. integer* and (3) to improve conditions for mussels and other benthic filter feeders, thereby stimulating a shift from pelagical to benthic control. However, if water exchange is insufficient, the result might be dense benthic macroalgal growth and periodical oxygen depletion, such as has been seen in many Danish lagoons and coves (e.g. Ærtebjerg *et al.*, 1991).

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References

Ambler, J. W., J. E. Cloern & A. Hutchinson, 1985. Seasonal cycles of zooplankton from San Francisco Bay. Hydrobiol. 129: 177–197.

Arndt, E. A. & W. Jansen, 1986. *Neomysis integer* (Leach) in the chain of boddens Darss/Zingst (Western Baltic) – ecophysiology and population dynamics. Ophelia. Suppl. 4: 1–15.

Barica, J., 1975. Collapses of algal blooms in prairie pothole lakes: their mechanism and ecological impact. Verh. int. Ver. Limnol. 19: 606–615.

Breder, C. N., 1960. Design for a fry trap. Zoologica 45: 155–160.

Bremer, P. & J. Vijverberg, 1982. Production, population biology and diet of *Neomysis integer* (leach) in a shallow Frisian lake (The Netherlands). Hydrobiologia 93: 41–51.

Carpenter, S. R. & J. F. Kitchell (eds) (in press). The trophic cascade in lakes. Cambridge University Press.

Castionguay, M. & G. J. Fitzgerald, 1990. The ecology of the calanoid copepod *Eurytemora affinis* in salt marsh tide pools. Hydrobiologia 202: 125–133.

Delbeek, J. C. & D. D. Williams, 1987. Food resource partitioning between sympatric populations of brackishwater sticklebacks. J. anim. Ecol. 56: 949–967.

Goldman, C. R., M. D. Morgan & S. T. Threlkeld, 1979. A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. Limnol. Oceanogr. 24: 289–297.

Gulati, R. D., K. Siewertsen & G. Postema, 1985. Zooplankton structure and grazing activities in relation to food quality and concentration in Dutch lakes. Arch. Hydrobiol. Beih. 21: 91–102.

Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer & E. Van Donk (eds), 1990. Biomanipulation – Tool for Water Management. Developments in Hydrobiology 61. Kluwer Academic Publishers, Dordrecht, x + 628 pp. Reprinted from Hydrobiologia 200–201.

Gulati, R. D. & A. Doornekamp, 1991. The spring-time abundance and feeding of *Eurytemora affinis* (poppe) in Volkerak-Zoommeer, a newly-created freshwater lake system in the Rhine Delta (The Netherlands). Hydrobiol. Bull. 25: 51–60.

Hanazato, T., 1990. A comparison between predation effects on zooplankton communities by *Neomysis* and *Chaoborus*. Hydrobiologia 198/Dev. Hydrobiol. 60: 33–40.

Hanazato, T. & M. Yasuno, 1988. Impact of predation of *Neomysis intermedia* on a zooplankton community in Lake Kasumigaura. Verh. int. Ver. Limnol. 23: 2092–2098.

Hansen, A. M., E. Jeppesen, S. Bosselmann & P. Andersen, 1992. Zooplankton i søer – metoder og artsliste. [Zooplankton in Lakes – methods and list of species] Miljøprojekt 205. Miljøministeriet, 114 pp. (in Danish).

Hansson, S., U. Larsson & S. Johansson, 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J. Plankton Res. 12: 1099–1116.

Hartmann, P. 1977. Fishereiliche Veränderungen in kulturbedingt eutrophierenden Seen. Schw. Zeit für Hydrol. 39: 243–54.

Heerkloss, R., W. Schnese & Adamkiewicz-Chojnacka, 1991. Seasonal variation in the biomass of zooplankton in two shallow coastal water inlets differing in their stage of eutrophication. Int. Revue ges. Hydrobiol. 76: 397–404.

Irvine, K., M. T. Bales, B. Moss, J. H. Stansfield & D. Snook, 1990. Trophic relations in Hickling Broad – a shallow and brackish eutrophic lake. Verh. int. Ver. Limnol. 24: 576–579.

Jensen, J. W., 1990. Comparing fish catches taken with gill nets of different combinations of mesh sizes. J. Fish. Biol. 37: 99–104.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik, 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 219–227.

Jeppesen, E., P. Kristensen, J. P. Jensen, M. Søndergaard, E. Mortensen & T. Lauridsen, 1991a. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. Mem. Ist. ital. Idrobiol. 48: 127–148.

Jeppesen, E., E. Mortensen, M. Søndergaard, A. M. Hansen & J. P. Jensen, 1991b. Dyreplanktonet som miljøindikator. [Zooplankton as environmental indicator.] Vand og Miljø 8: 394–98 (in Danish).

Kaiser, E. W., 1978. Storkrebs (*Malacostraca*) fra Indvande i Thy og Vester-Hanherred, Zootopografiske undersøgelser i Thy 14. [Malacostraca from inland waters in Thy and Vester-Hanherred, zootopographic investigations in Thy]. Flora og Fauna 84: 3–28 (in Danish).

Kristensen, P., J. P. Jensen, E. Jeppesen, 1991. Simple empirical lake models. In: Miljøstyrelsen (Ed.) Nitrogen and phosphorus in fresh and marine water. Abstracts: 125–145.

Kristensen, P., J. P. Jensen, E. Jeppesen & M. Erlandsen, 1991. Ferske vandområder – søer. Vandmiljøplanens Overvågningsprogram 1990. Danmarks Miljøundersøgelser, 104 pp. (in Danish).

Kuhlmann, D., 1984. Effects of temperature, salinity, oxygen and ammonia on the mortality and growth of *Neomysis integer* Leach. Limnologica (Berlin) 15: 479–485.

Lessmark, O., 1983. Influence of abiotic and biotic factors on the structure of perch and roach populations in thirteen Swedish lakes, with special reference to interspecific competition. Part of Ph. D. thesis, University of Lund, Sweden: 135–172.

Lutz, P. L., 1972. Ionic and body compartment responses to increasing salinity in the perch, *Perca fluviatilis*. Comp. Biochem. Physiol. 42: 711–717.

Meijer, M.-L., E. H. van Nes, E. H. R. R. Lammens, R. D. Gulati, M. P. Grimm, J. Backx, P. Hollebeek, E. M. Blaauw & A. W. Breukelaar, 1994. The consequences of a drastic fish stock reduction in the large and shallow Lake Wolderwidj, The Netherlands. Can we understand what happened? Hydrobiologia 275–276/Dev. Hydrobiol. 94: 31–42.

Mortensen, E., H. J. Jensen & J. P. Müller, 1991. Retningslinjer for standardiseret forsøgsfiskeri i søer og en beskrivelse af fiskeredskaber og -metoder. [Guidelines for standardized testfishing in lakes and a description of fish gears and methods]. National Environmental Research Institute, 60 pp. (in Danish).

Moss, B. & R. T. Leah, 1982. Changes in the ecosystem of a guanotrophic and brackish shallow lake in Eastern

England: Potential problems in its restoration. Int. Revue ges. Hydrobiol. 67: 625–659.

Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 367–378.

Moss, B., M. Bales & K. Irvine, 1991. Food web and water quality relationships in the saline broads of the River Thurne, Norfolk. Mem. Ist. ital. Idrobiol. 48: 345–362.

Moss, B., 1994. Brackish and freshwater lakes – different systems or variations on the same theme? Hydrobiologia 275–276/Dev. Hydrobiol. 94: 1–14.

Murtaugh, P. A., 1981. Selective predation by *Neomysis mercedis* in Lake Washington. Limnol. Oceanogr. 26: 445–453.

Muus, B. J., 1967. The fauna of Danish estuaries and lagoons. Meddr. Danmarks Fiskeri. og Havundersøgelser N. S. 5: 316 pp.

Oliphan, V. I., 1940. Contributions to the physiological ecology of the eggs and larvae of fishes. I. The effects of salinity on early developmental stages of *Abramis brama* L, *Lucioperca lucioperca*, L. and *Caspialosa volgensis* Berg. Zool. Zh. 19: 73–98.

Olrik, K., 1985. Miljøtilsyn i Flade Sø 1985. [Environmental survey in Lake Flade, 1985]. Report to the County Council of Ringkøbing, 9 pp. (in Danish).

Otterstrøm, C. V., 1930. De danske skallearter. [The Danish roach species]. Vid. Medd. 90: 87–311 (in Danish).

Otterstrøm, C. V. & E. Steemann-Nielsen, 1940. Two cases of extensive mortality in fishes caused by the flagellate *Prymnesium parvum* Carter. Rept. Danish Biol. Sta. 44: 5–24.

Persson, L., G. Anderson, S. F. Hamrin & L. Johansson, 1988. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. in S. R. Carpenter (ed.), Complex interactions in lake communities. Springer Verlag: 45–65.

Pont, D., A. J. Crivelli & F. Guillot, 1991. The impact of three-spined sticklebacks on the zooplankton of a previously fish-free pool. Freshwat. Biol. 26: 149–163.

Remane, A & C. Schlieper, 1971. The biology of brackish water. Die Binnengewasser 2nd (English) Edn. 25: 1–37.

Ribi, G.,1992. Perch larvae (*Perca fluviatilis* l.) survive better in dilute sea water. Aqua. Sciences 54: 85–90.

Richards, R. C., C. R. Goldman, T. C. Frantz & R. Wickwire, 1975. Where have all the *Daphnia* gone? The decline of a major cladoceran in Lake Tahoe, California-Nevado. Verh. int. Ver. Limnol. 19: 835–842.

Roddie, B. D., R. J. G. Leakey & J. Berry, 1984. Salinity-temperature tolerance and osmoregulation in *Eurytemora affinis* (Poppe) (Copepoda: Calanoida) in relation to its distribution in the zooplankton of the upper reaches of the Forth Estuary. J. exp. mar. Biol. Ecol. 79: 191–211.

Rudstam, L. G., S. Hansson & U. Larsson, 1986. Abundance, species composition and production of Mysid shrimps in a coastal area of the northern Baltic proper. Ophelia, Suppl. 4: 225–238.

SAS, 1990. SAS language version 6. Sas Institute Inc. NC. USA.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 475–486.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in Shallow Lakes. TREE 8: 275–279.

Tattersall, W. M. & O. S. Tattersall, 1951. The British Mysidaces. Ray Society, London, 460 pp.

Timms, R. M. & B. Moss, 1984. Prevention of growth of potentially dense phytoplankton grazing in the presence of zooplanktivorous fish in a shallow wetland ecosystem. Limnol. Oceanogr. 29: 472-486.

Timola, O., 1980. The diet of the smelt, *Osmerus eperlanus eperlanus* L., in the northeastern Bothnian Bay. Bothnian Bay Reports 2: 9–16.

Williams, D. D. & J. Charles Delbeek, 1989. Biology of the threespined stickleback, *Gasterosteus aculeatus*, and the blackspotted stickleback, *G. wheatlandi*, during their marine pelagic phase in the Bay of Fundy, Canada. Envir. Biol. Fishes 24, No. 1: 33–41.

Worgan, J. P. & J. Fitzgerald, 1981. Diel activity and diet of three sympatric sticklebacks in tidal salt marsh pool. Can. J. Zool. 59: 2375–2379.

Ærtebjerg, G., P. Sandbeck, S. Lundøer, F. Jakobsen, B. Løkkegaard, J. N. Jensen, P. B. Christensen & O. L. Jensen, 1991. Marine områder – Fjorde, kyster og åbent hav. Vandmiljø-planens overvågningsprogram 1990. [The marine environment – Fiords, coastal areas and the sea. The Nation-wide Danish Monitoring Programme 1990]. National Environmental Research Institute, 132 pp. (in Danish).

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Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibration data set from shallow lakes

ERIK JEPPESEN, ESBEN AGERBO MADSEN, JENS PEDER JENSEN
Department of Lake and Estuarine Ecology, National Environmental Research Institute, Vejlsøvej 25, DK-8600 Silkeborg, Denmark

N. JOHN ANDERSON
Department of Geobotany Geological Survey of Denmark and Greenland, Thoravej 8, DK-2400 Copenhagen NV, Denmark

SUMMARY

1. As quantitative information on historical changes in fish community structure is difficult to obtain directly from fish remains in lake sediments, transfer function for planktivorous fish abundance has been developed based on zooplankton remains in surface sediment (upper 1 cm). The transfer function was derived using weighted average regression and calibration against contemporary data on planktivorous fish catch per unit effort (PF-CPUE) in multiple mesh size gill nets. Zooplankton remains were chosen because zooplankton community structure in lakes is highly sensitive to changes in fish predation pressure. The calibration data set consisted of thirty lakes differing in PF-CPUE (range 18–369 fish net^{-1}), epilimnion total phosphorus (range 0.025–1.28 mg P l^{-1}) and submerged macrophyte coverage (0–57%).

2. Correlation of log-transformed PF-CPUE, total phosphorus and submerged macrophyte coverage *v* the percentage abundance in the sediment of the dominant cladocerans and rotifers revealed that the typical pelagic species correlated most highly to PF-CPUE, while the littoral species correlated most highly to submerged macrophyte coverage. Consequently, only pelagic species were taken into consideration when establishing the fish transfer function.

3. Canonical correspondence analysis (CCA) revealed that the pelagic zooplankton assemblage was highly significantly related to PF-CPUE (axis 1), whereas the influence of total phosphorus and submerged macrophyte coverage was insignificant. Predicted PF-CPUE based on weighted average regression without (WA) and with (WA(tol)) downweighting of zooplankton species tolerance correlated significantly with the observed values ($r^2 = 0.64$ and 0.60 and RMSE = 0.54 and 0.56, respectively). A marginally better relationship ($r^2 = 0.67$) was obtained using WA maximum likelihood estimated optima and tolerance.

4. It is now possible, quantitatively, to reconstruct the historical development in planktivorous fish abundance based on zooplankton fossil records. As good relationships exist between contemporary PF-CPUE data and indicators such as the zooplankton/phytoplankton biomass ratio, Secchi depth and the maximum depth distribution of submerged macrophytes, it is now also possible to derive information on past changes in lake water quality and trophic structure. It will probably prove possible

further to improve the transfer function by including other invertebrate remains, e.g. chironomids, *Chaoborus*, snails, etc., and its scope could be widened by including deeper lakes, more oligotrophic lakes, more acidic lakes and lakes with extensive submerged macrophyte coverage (in the latter case to enable use of the information in the fossil record on plant-associated cladocerans).

Introduction

Analysis of the relative composition of zooplankton remains in lake sediments has been extensively used to describe historical development in lake biological community structure and productivity (Frey, 1986; Anderson & Battarbee, 1992). Research conducted during the last decade has demonstrated the importance of fish for lake biological community structure and dynamics (Hrbáček, 1969; Persson *et al.*, 1988; Gulati *et al.*, 1990; Carpenter & Kitchell, 1993; Jeppesen *et al.*, 1994; Jeppesen *et al.* in press). From empirical studies, enclosure experiments and full-scale manipulation it is known that zooplankton composition and size structure are markedly affected by the density of planktivorous fish (e.g. Brooks & Dodson, 1965; Hrbáček, 1969; Kerfoot, 1981). A change from dominance by calanoid copepods or *Daphnia* at low fish predation to successive dominance by small cladocerans, cyclopoid copepods and rotifers occurs at higher fish predation pressure (e.g. Gulati, Sivertsen & Postema, 1985; Jeppesen *et al.*, 1992). Thus zooplankton fossils can also serve as an indicator of past changes in fish predation, as demonstrated by Kerfoot (1974), Kitchell & Kitchell (1980), Kitchell & Carpenter (1987), Leavitt, Carpenter & Kitchell (1989), Kitchell & Sanford (1992) and Sanford (1993). Such analyses improve knowledge of the structure and function of lake ecosystems as they describe changes over a longer period of time than covered by existing monitoring series and full-scale experiments. An example is the studies of Leavitt *et al.* (1989) and Leavitt *et al.* (1994a) demonstrating how changes in fish communities due to stocking, rotenone treatment and winter fish kill produce long-lived changes in the zooplankton community that cascade to the phytoplankton level.

Former analyses of zooplankton remains in sediment only provide a qualitative picture of changes in fish predation pressure; however, it was not previously possible to transfer information directly from contemporary data sets to the sediment records. The problem is that the various zooplankton species are not deposited and preserved in the sediment in the same proportion as they appear in the lake water (Leavitt *et al.*, 1994a). Thus relationships derived from zooplankton and fish based on contemporary data (Jeppesen *et al.* in press, E. Jeppesen, unpublished data) do not necessarily apply to sediment zooplankton assemblages. Recently, however, methods have been developed that allow quantitative reconstruction of environmental variables based on calibration of zooplankton remains deposited in the surface sediment of lakes differing in the variables in question. These methods include multiple linear regression, weighted least square analyses (ter Braak & van Dam, 1989) or weighted averaging partial least square regression (ter Braak & Juggins, 1993). Application of the latter method to diatoms has enabled reconstruction of changes in, for example, lake pH, dissolved organic carbon, total phosphorus and summer mean temperature (e.g. Birks *et al.*, 1990; Kingston & Birks, 1990; Walker & Smol, 1990; Fritz *et al.*, 1991; Stevenson *et al.*, 1991; Hall & Smol, 1992; Anderson, Rippey & Gibson, 1993; Anderson, 1993; Bennion, 1994).

Hitherto, however, no one has employed the surface sediment calibration technique to reconstruct lake trophic structure. The first calibration data set is now presented allowing reconstruction of planktivorous fish abundance based on the zooplankton fossil record in lake sediments.

Materials and methods

The study included thirty mainly shallow meso-hypertrophic Danish lakes (Table 1). Sediment samples were taken with a core sampler (5.2 cm diameter) in the deepest part of lakes or at a mid-lake station in the case of uniform shallow lakes. The upper 1 cm of the surface sediment was sampled and wet weight, dry weight and ash-free dry weight determined on a 5 ml aliquot. Approximately 5 ml sediment was used for quantifying the zooplankton remains. The samples were weighed and boiled in 25 ml 10% KOH for 20 min. Matter retained on a 140 μm plastic filter was

Table 1 Descriptive statistics of the variation in mean depth, planktivorous fish CPUE in multiple mesh size gill nets, percentage coverage of submerged macrophytes, epilimnion total phosphorus and the percentage contribution of each of the five different zooplankton species used in the CANOCO and WA analyses

	Mean	Median	25%	75%	Min.	Max.
Mean depth (m)	3.7	2.5	1.2	4.3	0.9	16.3
Planktivorous fish CPUE (no. net^{-1})	115	76	42	159	19	369
Submerged macrophytes (%)	8.3	0	0	2.5	0	57
Total phosphorus (mg P l^{-1})	0.24	0.15	0.08	0.37	0.025	1.28
% *Daphnia*	9	4	1	12	0	43
% *Leptodora* sp.	17	10	2	26	0	82
% *Bosmina coregoni*	6	4	0.5	10	0	30
% *Bosmina longirostris*	24	23	9	30	0	66
% Rotifers	44	50	28	66	0	77

examined with the aid of a stereomicroscope and a total count made of large remains and resting eggs. Subsamples of smaller remains retained on a 80 µm filter were counted using an inverted microscope.

Remains of cladocerans and rotifers were identified from exoskeleton fragments (postabdominal claws, carapaces, caudal cerca) and resting eggs. The minimum number of individuals represented by the exoskeleton fragments was calculated for each taxa according to the method of Frey (1986). As reported in previous studies (e.g. Frey, 1986), exoskeleton fragments of copepods and rotifers were found not to be well preserved in the lake sediments. In addition, though, it was found that this was also the case for *Daphnia* and *Ceriodaphnia*, a finding in concert with previous studies of shallow lakes (e.g. Stansfield, Moss & Irvine, 1990), but in contrast to that in some deep lakes (Leavitt *et al.*, 1989; Leavitt *et al.*, 1994a,b). This difference may reflect the greater degree of disturbance and fragmentation of zooplankton remains caused by resuspension in shallow lakes. As a consequence the present abundance estimates for *Daphnia*, rotifers and *Ceriodaphnia* are based solely on resting eggs. For *Bosmina*, both carapaces and resting eggs were counted, and in addition we conducted a head pore analysis (Frey, 1959, 1986) together with analysis of the presence or absence of a mucros on at least 100 individuals per lake in order to estimate the percentage contribution of *B. longirostris*, *B. coregoni* and *B. longispina*. Only the former two species were used in the final analyses as *B. longispina* proved only to be present in the surface sediment of a single lake. Finally, a count was made of postabdomens of abundant chydorids, i.e. *Acroperus*, *Graptoleberis*, *Leydigia*, *Eurycercus* and *Alonopsis*, as well as of *Leptodora* caudal cerca.

The composition and relative abundance of the pelagic fish stock in the thirty lakes were determined by standardized test-fishing (Mortensen, Jensen & Müller, 1991) with multiple mesh size gill nets (6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, 75 mm), the length and depth of each section being 3 and 1.5 m, respectively. Between six and sixty-four nets were used, depending on lake size and morphometry. Test-fishing was conducted once in each lake between 15 August and 15 September, previous test-fishing having indicated that the fish population distribution was most even during that period (Mortensen *et al.*, 1991). The nets were set late in the afternoon and retrieved the next morning. Catch per unit effort (CPUE) of planktivorous fish was calculated as mean catch per net. The planktivorous fish catch usually comprised bream (*Abramis brama*), silver bream (*Bjoerkna blicca*), roach (*Rutilus rutilus*), smelt (*Osmerus eperlanus*), whitefish (*Coregonus lavaretus*), crucian carp (*Carassius carassius*), *Leucaspius delineatus*, and bleak (*Alburnus alburnus*), with bream and roach being dominant in most lakes.

To determine macrophyte coverage and the plant volume infested (PVI), the macrophyte belt was divided into a number of sub-areas (typically fifteen to twenty-two), each having similar macrophyte coverage. If the macrophyte depth limit in a sub-area was less than 1.5 m, total macrophyte coverage was determined at ten randomly selected spots at depth intervals of 25 cm reaching from the shore to the macrophyte boundary; otherwise a depth interval of 50 cm was used. Coverage was determined from a boat using a water glass or by diver. The following categories were used: < 1, 1–5, 5–25, 25–50, 50–75, 75–90 and 90–100%. Macrophyte average height was measured at each spot and area-specific plant volume

Table 2 Pearson correlation for log-transformed values of planktivorous fish CPUE (no. net^{-1}) in multiple mesh size gill nets (LOGFISH), % coverage of submerged macrophytes (LOGMAC) and epilimnion total phosphorus (LOGTP) *v* the percentage contribution of the different variables examined. Cladoceran and rotifer remains in the upper 1 cm of the sediment, i.e. resting eggs of *Daphnia* (DAPH), *Leptodora* (LEP). rotifers (ROT), *Bosmina* (BOS_L), *B. coregoni* (BOS_C) and *Ceriodaphnia* (CER); postabdomen of *Sida*, (SIDA), *Acroperus* (ACRO), *Eurycercus* (EURY), *Graptoleberis* (GRAP), *Alonopsis* (ALON) and *Leydigia* (LEY%) and the caudal cerca of *Leptodora* (LEP)

	LOGMAC	LOGTP	DAPH%	LEP%	ROT%	BOS_L%	BOS_C%	CER%	SIDA%	ACRO%	EURY%	GRAP%	ALON%	LEY%
LOGFISH	-0.65	0.66	0.29	0.43101	0.66	0.57	0.22	–0.48	–0.41518	–0.60	–0.54	–0.43	–0.40	0.13
	(0.0006)	(0.0002)	(0.13)	(0.0196)	(0.0001)	(0.0013)	(0.26)	(0.008)	(0.025)	(0.0007)	(0.0027)	(0.021)	(0.03)	(0.48)
LOGMAC		–0.51	0.069	–0.06	–0.54	–0.45	–0.27	0.67	0.57	0.85	0.77	0.63	0.44	–0.23
		(0.0154)	(0.75)	(0.75)	(0.0074)	(0.032)	(0.21)	(0.0004)	(0.0042)	(0.0001)	(0.0001)	(0.0012)	(0.033)	(0.30)
LOGTP			–0.12	–0.36	0.38	0.37	–0.23	–0.32	–0.36	–0.46	–0.37	–0.28	–0.22	0.41
			(0.47)	(0.09)	(0.50)	(0.05)	(0.26)	(0.10)	(0.07)	(0.015)	(0.056)	(0.16)	(0.27)	(0.034)

Table 3 Ecological tolerances *t* and deshrinking updated species optima *v* calculated by means of weighted averaging WA and maximum likelihood ML. The tolerance-weighted planktivorous fish estimate in log-scale is $x = \sum_k y_k v_k t_k^{-2}/\sum_k y_k t_k^{-2}$ where *y* is the percentage contribution of the species in question (Birks *et al.*, 1990)

		Daphnia	Rotifers	*B. longirostris*	*B. coregoni*	*Leptodora*
WA	*v*	2.879	5.321	5.251	3.279	2.798
	t	0.673	0.830	0.847	0.691	0.692
ML	*v*	3.082	5.119	6.210	3.439	3.291
	t	0.890	1.403	1.311	0.610	0.773

(PV) determined as coverage × plant height/100. Average coverage (COV) and PV were calculated for each sub-area (ii), while COV% and (PVI%) were calculated for the whole lake as:

$$COV\% = \frac{\sum_{ii=1}^{n} COV_{ii} \times area_{ii}}{total\ lake\ area}, \quad PVI\% = \frac{\sum_{ii=1}^{n} PV_{ii} \times area_{ii}}{total\ lake\ volume}$$

In three lakes COV and PVI% were estimated from coverage and plant height measurements at a number of stations located along transects covering the entire lake area (Lauridsen, Jeppesen & Søndergaard, 1994).

Total phosphorus was measured as orthophosphate using the ascorbic acid–molybdenum method (Murphy & Riley, 1972) following persulphate digestion according to the method of Koroleff (1970). Chlorophyll *a* was estimated spectrophotometrically following extraction with ethanol by the method of Holm-Hansen & Riemann (1978).

Initial exploratory data analysis was accomplished using both the canonical correspondence analyses (CCA) and the correspondence analysis (CA) (ter Braak, 1987b) routines in the program CANOCO 3.10 (ter Braak, 1990a,b). Weighted averaging (WA) regression was used to estimate species optima in relation to planktivorous fish $u_k = \Sigma_i\, y_{ik}\, x_i/y_{+k}$, where y_{ik} is the percentage contribution of zooplankton species k in lake i, + indicates summation over the current index, and x_i is the planktivorous fish CPUE in lake i. Inverse deshrinking regression was used to obtain the final prediction formula for estimating planktivorous fish CPUE $x_0 = \Sigma_k\, y_{0\,k}\, v_k/y_{0+}$ where $v_k = a + bu_k$ are the deshrinking updated species optima (Birks *et al.*, 1990; ter Braak & Juggins, 1993), and zero symbolizes an arbitrary lake. WA calibration was made both with and without zooplankton species ecological tolerance downweighting (WA and WA(tol), respectively), using the program WACALIB 3.3. (Line, ter Braak & Birks, 1994). The WA calibration with inverse deshrinking was also carried out with maximum likelihood (ML) estimated optima and tolerances (ML (tol)) in a Gaussian unimodal regression model (ter Braak, 1987b; Birks *et al.*, 1990). The root mean square of the error (RMSE) and the coefficient of determination r^2 was calculated for comparison of the predictive ability of the WA, WA(tol) and ML(tol) methods.

Results

The thirty lakes in the calibration data set covered a wide range of summer mean total phosphorus concentrations (0.025–1.280 mg P l^{-1}), planktivorous fish CPUE (18–369 net^{-1}) and submerged macrophyte coverage (0–57%) (Table 1).

Pearson correlation for log-transformed planktivorous fish CPUE, total phosphorus and submerged macrophyte coverage *v* the percentage contribution to the surface sediment (upper 1 cm) zooplankton assemblage of rotifer and the abundant cladocerans revealed that the CPUE best correlated to the typical pelagic species, as represented by *Leptodora* caudal cerca and *Daphnia* resting eggs, *Bosmina longirostris, B. coregoni* and rotifers. With *Daphnia* and *B. coregoni* the correlation was not significant, however ($P > 0.05$, Table 2) and the data plots (Fig. 1) tended towards a unimodal relationship, as was also the case for *Leptodora*. The percentage contributions of the various littoral cladocerans as represented by the postabdomens of *Sida, Acroperus, Eurycercus, Graptoleberis* and *Alonopsis* best correlated to submerged macrophyte coverage ($P < 0.0001$ to $P = 0.03$) (Table 2, Fig. 2). A high correlation to submerged macrophyte coverage was also found for the semi-littoral *Ceriodaphnia* (resting eggs), whereas the percentage contribution of the mud-associated *Leydigia* (postabdomen) best correlated to epilimnion total phosphorus (Table 2, Fig. 2).

Based on the correlation analysis, the plots given in Fig. 1 and an initial correspondence analysis (CA), we decided to develop the transfer function for planktivorous fish solely taking into consideration the pelagic zooplankton (cladocerans and rotifers). The CA analysis on the pelagic species revealed a significant relationship (*F*-test, $P = 0.001$) between the first species CA axis and log-transformed planktivorous fish (CPUE), while no significant relationship was found between submerged macrophyte coverage (%) and mean summer epilimnion total phosphorus concentration ($P = 0.08$ and 0.58, respectively). The percentage of variance accounted for was 61%. This analysis suggests that the planktivorous fish CPUE is sufficient to predict the variation in zooplankton species composition represented by the first ordination axis (ter Braak, 1987b). Reverse regression of planktivorous fish CPUE on all the CA ordination axes revealed that only the first CA ordination axis was significant, thus suggesting that planktivorous fish CPUE relates only to the first axis.

In the more robust CANOCO Monte Carlo permutation test (CANOCO 3.10, forward selection, ter Braak, 1990a,b) of the full data set there was a significant correlation with planktivorous fish CPUE ($P = 0.001$), but not for submerged macrophyte coverage or epilimnion total phosphorus ($P = 0.6$ and $P = 0.7$, respectively). Planktivorous fish CPUE was highly correlated with CCA axis 1 ($r^2 = 0.71$) (Fig. 3), suggesting that WA calibration of planktivorous fish abundance is possible. The location of the individual zooplankton species in the constraint ordination diagram follows the pattern known from contemporary data; thus the zooplankton most vulnerable to predation such as *Leptodora, Daphnia* and *B. coregoni* occur at low planktivorous fish densities, while the less vulnerable *B. longirostris* and rotifers occur at high fish densities. In the WA and ML calibrations the deshrinking updated species optima ranged from 2.8 to 5.3 and from 3.1 to 6.2 log units, respectively, being particularly high for rotifers and *B. longirostris* (Table 3). The ecological tolerance of the five zooplankter included in the analysis was quite similar in the WA calibration, ranging from 0.67 to 0.85 log units, again being higher for rotifers and *B. longirostris*. The latter was also the case in the ML calibration, albeit that the variation tended to be greater: 0.61–1.40 (Table 3).

Both WA and WA(tol) predicted planktivorous fish CPUE were closely related to the observed CPUE (r^2 = 0.60 and 0.56; RMSE = 0.64 and 0.54, respectively) (Fig. 4). However, the WA(tol) calibration that includes maximum likelihood estimated optima and tolerance appeared marginally better ($r^2 = 0.67$ and RMSE = 0.52). There were no substantial outliers. However, in lakes with high submerged macrophyte coverage the predicted CPUE tended to be somewhat too high (Fig. 3).

Discussion

Our results suggest that it is possible to establish a transfer function between planktivorous fish abundance (CPUE in multiple mesh size gill nets) and zooplankton remains in lake surface sediments. The three calibration methods WA, WA(tol) and ML(tol) appear very similar, although RMSE was marginally better with the theoretically more rigorous maximum likelihood approach (0.52 *v* 0.56 and 0.54), and r^2 was higher (0.67 *v* 0.60 and 0.64). This is in concert with the observation of ter Braak (1987a), who found that the weighted averaging method approximated the approach of maximum likelihood method in a Gaussian unimodal model. Inverse deshrinking regression (RMSE) tends to underestimate the predictive variance. More reliable estimates are available from bootstrapping, split-sampling or cross-validation methods (Birks *et al.*, 1990) and ought to be taken into account in further, more refined, analyses on a larger data set. The WA regression estimates of ecological

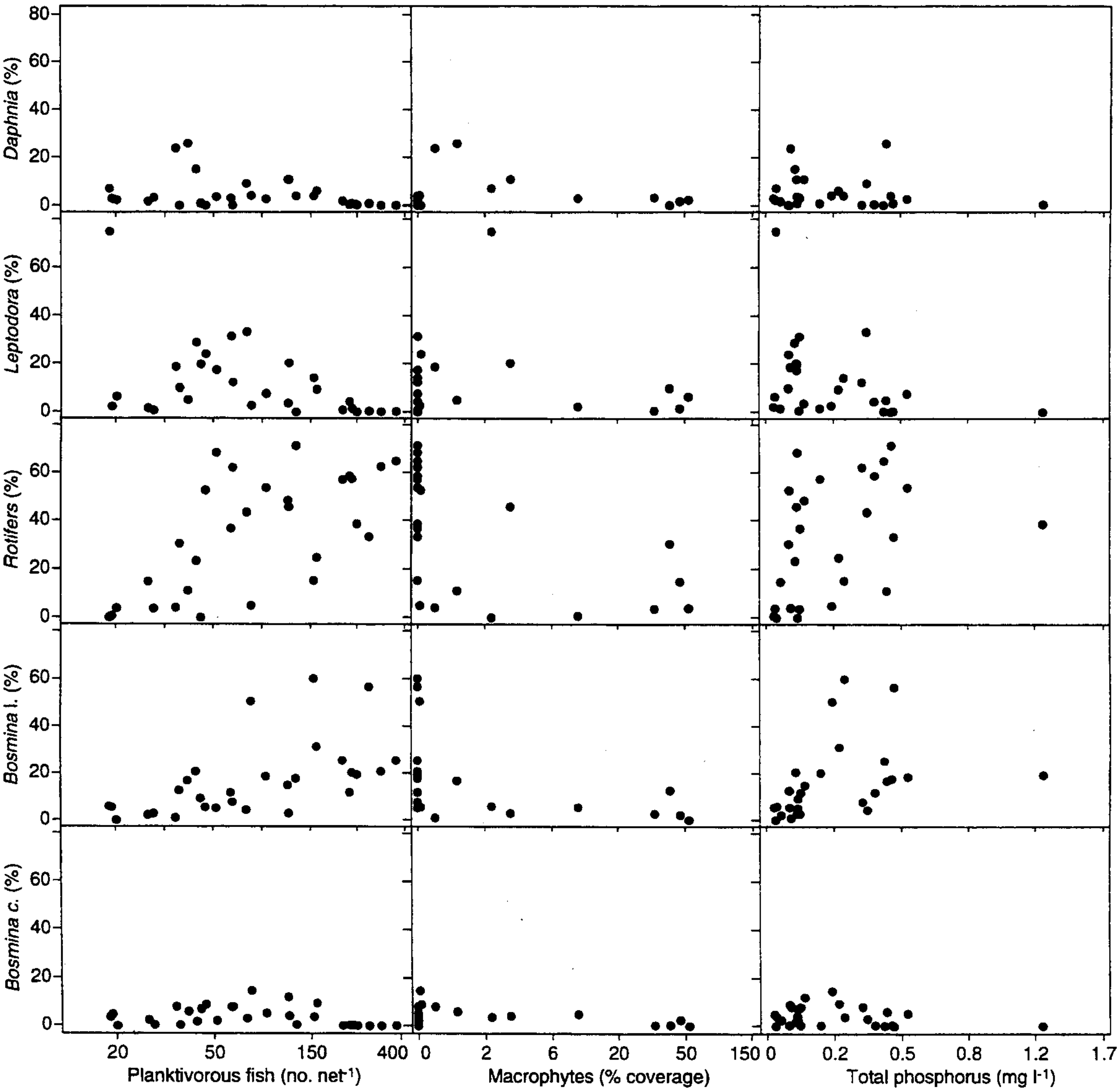

Fig. 1 Percentage contribution of *Leptodora* caudal cerca and resting eggs of *Daphnia* spp., *Bosmina longirostris*, *Bosmina coregoni* and rotifers to the total fossil assemblage present in surface sediment (upper 1 cm) of thirty Danish lakes *v* planktivorous fish CPUE in multiple mesh size gill nets (left), percentage coverage of submerged macrophytes at biomass maximum (centre), and mean epilimnion total phosphorus concentration.

tolerance hardly varied between the various zooplankton species (Table 3), implying that the predicted planktivorous fish CPUE derived by WA and WA(tol) are similar. The species optima were generally higher when estimated by maximum likelihood regression compared with WA regression estimated optima (Table 3), but tolerance was also higher and more variable. High planktivorous fish abundance appeared to be more precisely predicted by the maximum likelihood method (Fig. 3). It could be argued that the CPUE used should have been expressed in terms of biomass rather than fish number. However, we found a much better relationship between CPUE expressed in terms of fish number *v* both contemporary zooplankton as well as fossil data (not shown here).

The scatter in the relationship between fish and the

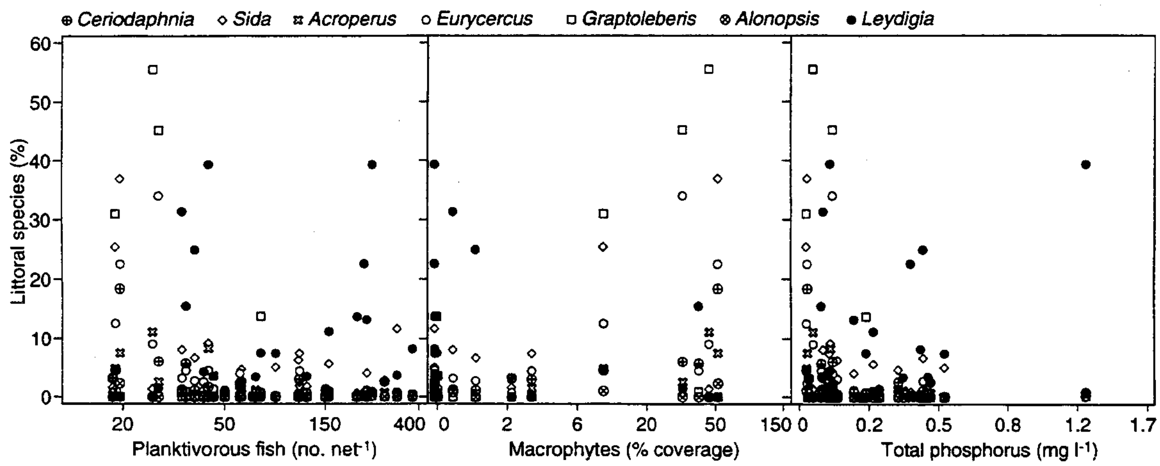

Fig. 2 The percentage contribution of *Ceriodaphnia* resting eggs and postabdomens of *Sida, Acroperus, Eurycercus, Graptoleberis, Alonopsis,* and *Leydigia* to the total assemblage in surface sediment (upper 1 cm) of thirty Danish lakes *v* the density of planktivorous fish caught in multiple mesh size gill nets (left), the percentage coverage of submerged macrophytes at biomass maximum (centre), and mean total phosphorus concentration in the epilimnion.

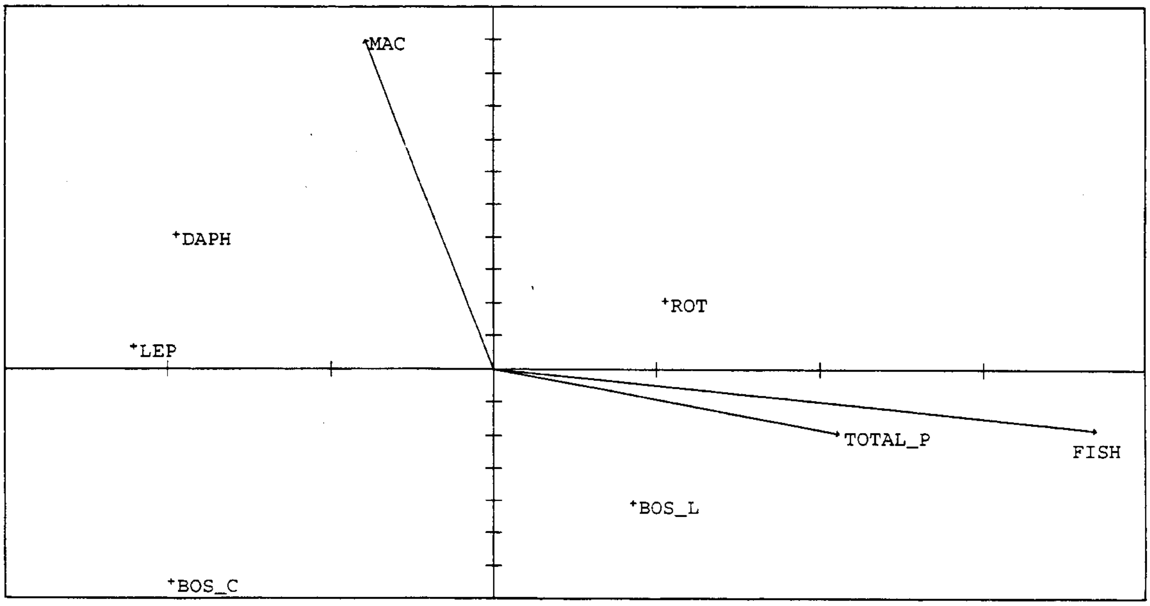

Fig. 3 Ordination diagram based on canonical correspondence analysis (CCA) of the environmental and species variables included in the analysis. For explanation of abbreviations, see Table 2.

zooplankton is attributable to a number of factors, of which uncertainty in the estimation of fish abundance may be considered the most important. First, there may be large spatial and interannual variation in the catches (Mortensen *et al.*, 1991; unpublished data). In addition, the age structure of the fish may differ, thereby influencing the per capita specific predation rate. Secondly, the CPUE estimates are based on survey fishing during August–September, and although the 0 + class (YOY) is represented in the nets this may give rise to scatter as variability in recruitment and YOY survival seen during the first 1–2 months after hatching will have stabilized by that time and hence will not be recorded. This is relevant because YOY fish are particularly important for predation pressure on zooplankton during mid-summer (Mills & Forney,

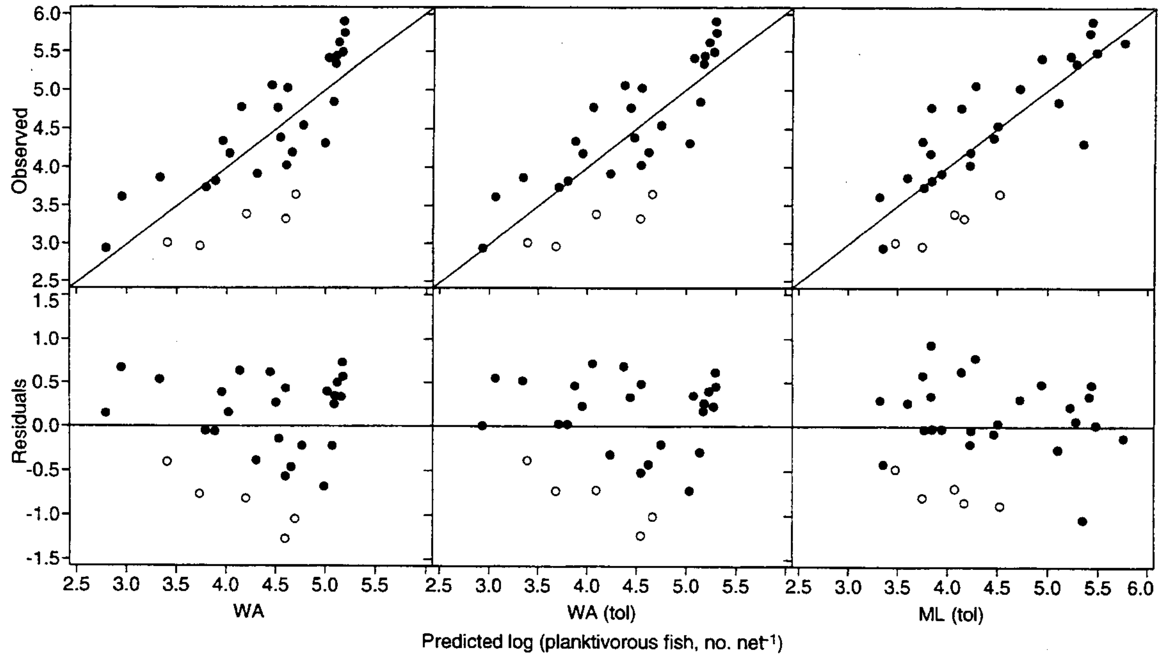

Fig. 4 Observed *v* predicted log-transformed density of planktivorous fish caught in multiple mesh size gill nets and the residuals obtained by weighted average calibration with (WA(tol) and without (WA) zooplankton genus or species ecological tolerance downweighting, and with maximum likelihood estimated optima and tolerance (ML(tol)).

1983; Cryer, Peirson & Townsend, 1986; Luecke *et al.*, 1990; Jeppesen *et al.* in press). Thirdly, as the test fishing is conducted during a limited period, short-term variation in weather conditions (water temperature, etc.) may influence catch number and hence sample representativeness. Other problems include net selectivity (Jensen, 1986) and mixing in the upper layers of sediment, in the latter case because fish and zooplankton data sets may not then be fully synchronous.

In view of the above-mentioned problems involved in the estimation of fish abundance and predation pressure and the fact that fish surveys are only made during a limited period of the year, one cannot expect the modelled relationship to be as precise as that between diatoms and total phosphorus. Accordingly, r^2 values for the fish–zooplankton relationships are about 0.10–0.15 lower than for diatom–total phosphorus and diatom–pH relationships (e.g. Birks *et al.*, 1990; Stevenson *et al.*, 1991; Anderson *et al.*, 1993). In addition the lower precision may be attributable to the fact that only five zooplankton species or genera are included in the reconstruction *v* upwards of 100 species in most diatom relationships. Finally, that resting eggs of *Daphnia, Bosmina* and rotifers were used instead of body parts may have introduced a further uncertainty as resting eggs are only produced during unfavourable environmental conditions, and hence do not necessarily accurately reflect abundance.

Predicted planktivorous fish CPUE tended to be too high in lakes with high submerged macrophyte coverage (> 10%) (Fig. 4). However, macrophytes do not encourage the species responsible for the predicted planktivorous fish abundance being higher than the observed abundance; the opposite is true, in fact, as large zooplankton such as *Daphnia*, seek shelter in the vegetation because it provides protection against fish predation (Timms & Moss, 1984; Winfield, 1986; Irvine, Moss & Stansfield, 1990; Schriver *et al.*, 1995). *Daphnia*, thus, tolerate a higher fish density in macrophyte-rich lakes (Schriver *et al.*, 1995). Another possible explanation for the high predicted fish density could be that gill net surveys are more efficient in open water than in the vegetation because fish forage more slowly in vegetation, thereby lowering the possibility of their being caught in the nets. That macrophytes protect juvenile fish against predation from larger fish (Bohl, 1980; Winfield *et al.*, 1983; Jakobsen & Johnsen, 1987;

Persson & Eklöv, 1995) may also play a role as does the density of juvenile fish which is often being higher in macrophyte-rich lakes (Werner *et al.*, 1983; Carpenter & Lodge, 1986). As juvenile fish are not caught efficiently by multiple mesh size gill nets (Jensen, 1986), CPUE may therefore be slightly underestimated in macrophyte-rich lakes, thus explaining the difference between predicted and observed CPUE in such lakes.

The transfer function so far developed is based solely on pelagic zooplankton, littoral cladocerans showing a higher correlation to submerged macrophyte coverage than to planktivorous fish CPUE (Table 2). Plant-associated cladocerans, which offer the advantage of being well-preserved in sediment (Frey, 1986), are also affected by changes in fish predation. The relationship is less straightforward than with pelagic zooplankton, however, because the vulnerability of plant-associated cladocerans in macrophyte beds depends on plant density (Schriver *et al.*, 1995) and fish composition (Persson, 1991). In addition, the protection provided by the various plant species may differ (Diehl, 1988; Engel, 1988). Unfortunately, as few of the lakes studied had extensive submerged macrophyte communities it has not been possible to include plant-associated species in the analysis. Nevertheless, preliminary findings suggest that with a more comprehensive data set it might be possible to include plant-associated species (either untransformed or normalized to macrophyte coverage) in the reconstruction of past changes in planktivorous fish abundance (E. Jeppesen *et al.* unpublished findings).

It is also likely that the transfer function for planktivorous fish might be improved by including other indicators of fish predation For example, a low mean carapace and mucros length of *Bosmina* together with

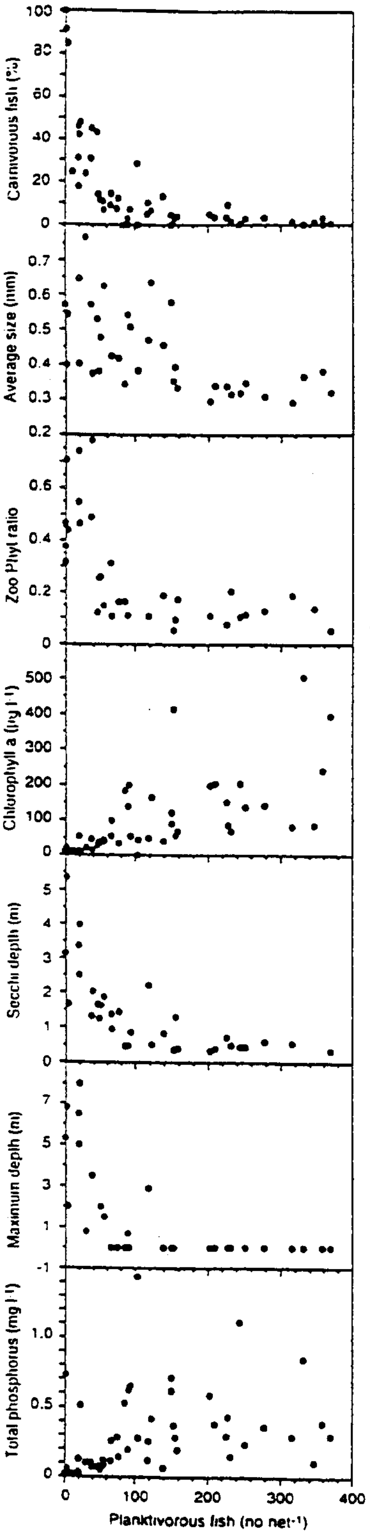

Fig. 5 Percentage carnivores in multiple mesh size gill net catch, average size of cladocerans, zooplankton:phytoplankton biomass ratio, epilimnion chlorophyll *a* concentration, Secchi depth, maximum depth of submerged macrophytes and epilimnion total phosphorus concentration *v* planktivorous fish CPUE in multiple mesh size gill nets in a number of Danish lakes. Fish were surveyed between 15 August and 15 September, and submerged macrophytes in July–August at biomass maximum. All other data are summer averages (1 May–1 October). Zooplankton and phytoplankton summer averages were calculated before estimating the ratio. (Partly after Jeppesen *et al. in press.*)

a low proportion of cornuta to straight-form attennules indicates high fish predation (Nilssen & Sandøy, 1990; Sanford, 1993; Leavitt *et al.*, 1994). Information on the species composition of *Chaoborus* remains may also yield information on fish predation (Uutala, 1990); for instance, the non-migratory *C. americanus* only occurs in fishless lakes, while migrating species such as *C. flavicans* coexist with fish even when the latter are abundant (Pope, Carter & Power, 1973; Christoffersen, 1990), an exception being shallow lakes with high abundance of planktivorous fish (J.P. Jensen & E. Jeppesen, unpublished findings). Moreover, it seems highly probable that inclusion of remains of soft-bodied benthic invertebrates like snails, molluscs and ostracods would yield valuable information as such invertebrates are generally highly sensitive to changes in fish predation (Brönmark & Weisner, 1992). The effects on benthic invertebrates have been confirmed by numerous studies of benthivorous fish stock reduction, the response being a highly significant increase in benthic invertebrate abundance and major changes in community structure (Kornijow & Gulati, 1992; Berg *et al.*, 1994). A multi-fossil approach will therefore undoubtedly improve the accuracy of fish community reconstruction.

The transfer function developed predicts only planktivorous fish CPUE. At present, it is not possible to convert this to the area-specific or volume-specific fish density or fish biomass as concurrent data sets for gill net CPUE and estimates based on marking–recapture methods are only available for five of the lakes. Even though survey fishing with gill nets may result in bias due to differential selectivity, both in relation to fish size and species composition, the multiple mesh size gill nets used in the present investigation seem to yield an adequate description of the changes in fish stock composition and density along a trophic gradient (Persson *et al.*, 1988; Quiros, 1990; Jeppesen *et al.*, 1990 and, in press). This interpretation is further supported by the very reliable correlations found between CPUE expressed in terms of planktivorous fish number and such indicators of predation pressure as the piscivorous/planktivorous fish ratio, cladoceran average size and the zooplankton/phytoplankton biomass ratio (Fig. 5). The cascading effects of these changes in the form of changes in the phytoplankton biomass (chlorophyll *a*), Secchi depth and the maximum depth distribution of submerged macrophytes are therefore also related to planktivorous fish CPUE, albeit to a varying degree (Jeppesen *et al. in press*) (Fig. 5). A reconstruction of planktivorous fish abundance from the zooplankton fossil record in different layers of lake sediments will therefore provide information not only on fish stock development, but also on water quality and trophic interactions in lake systems. A precondition, though, is that there is no differential degradation of the different zooplankton remains included in the transfer function. Unfortunately, few zooplankton time series exist that are sufficiently long to allow comparison with fossil records, although a relatively good relationship between *Bosmina* density and fossil concentrations has been reported for a 19-year period in a Canadian lake by Hann, Leavitt & Chang (1994). As the carapace of *Bosmina* and the resting eggs of the cladocerans used in the analysis are thick-walled it can be assumed that they are well-preserved in recent sediments. However, it is an open question whether or not rotifer resting eggs and *Leptodora* caudal cerca undergo degradation in sediment. Analysis of sediment cores from a lake where the fish stock is known to have been dominated by planktivorous fish in the 1920s has revealed a high accumulation of rotifer resting eggs in the layers corresponding to that period (E. Jeppesen *et al.* unpublished findings), thus indicating good preservation. It is therefore unlikely that differential degradation will present a major problem for the reconstruction of fish and trophic structure, although further studies on degradation are needed.

The lakes used in the analysis cover an epilimnion summer mean total phosphorus range of 0.025–1.28 mg P l^{-1} and pH was higher than 6.5. The data set therefore lack oligotrophic lakes, in which the zooplankton community is often dominated by calanoid copepods that are rarely found in the sediment (Frey, 1986; Hann, Leavitt & Chang, 1994). Furthermore, the data set does not cover acidified lakes, in which pH-mediated changes in the zooplankton community structure are known to be partly unrelated to fish stock alterations (Nilssen & Sandøy, 1990). In addition, various carnivorous invertebrates play an important structuring role for the zooplankton in acidified lakes (Uutala, 1990). A satisfactory reconstruction of planktivorous fish abundance in acidified lakes would probably require the study of some of the other sediment remains mentioned above, e.g. fossils of invertebrates such as chironomids, *Chaoborus*, etc.

In conclusion, a transfer function for predicting planktivorous fish abundance has been developed (CPUE in gill nets) from the relative abundance of pelagic zooplankton fossils in lake surface sediment (upper 1 cm) based on data sets from thirty shallow mesotrophic to hypertrophic lakes. Assuming that degradation of different zooplankton fossils in the sediment does not differ, then the transfer function can be applied to sediment core fossil samples to reconstruct past planktivorous fish abundance (CPUE). The transfer function may also provide quantitative and qualitative information on lake water quality and the development of trophic structure, either alone or in combination with other transfer functions and multiple relationships currently being developed.

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References

Anderson N.J. (1993) Natural vs. anthropogenic change in lakes: The role of the sediment record. *Trends in Ecology and Evolution*, **8**, 356–361.

Anderson N.J. & Battarbee R.W. (1992) Aquatic community persistence and variability: A palaeolimnological perspective. *Aquatic Ecology—Scale, Patten and Process* (ed. P. Giller), pp. 223–259. Blackwell Scientific Publications, London.

Anderson N.J., Rippey B. & Gibson C.E. (1993) A comparison of sedimentatry and diatom inferred phosphorus profiles: Implications for defining predisturbance nutrient conditions. *Hydrobiologia*, **253**, 357–366.

Bennion H. (1994) A diatom–phosphorus transfer function for shallow, eutrophic ponds in southeast England. *Hydrobiologia*, **275/276**, 391–410.

Berg S., Jeppesen E., Søndergaard M. & Mortensen E. (1994) Environmental effects of introducing whitefish *Coregenus lavaretus* (L.) in Lake Ring. *Hydrobiologia*, **275/276**, 71–79.

Birks H.J.B., Line J.M., Juggins S., Stevenson A.C. & ter Braak C.J.F. (1990) Diatoms and pH reconstruction. *Land*, **327**, 263–278.

Bohl E. (1980) Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia*, **44**, 368–375.

Brooks J.L. & Dodson S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.

Brönmark C. & Weisner S. (1992) Indirect effects of fish community structure on submerged vegetation in shallow, eutrophic lakes: An alternative mechanism. *Hydrobiologia*, **243/244**, 293–301.

Carpenter S.R. & Kitchell J.F. (1993) *The Trophic Cascade in Lakes*. Cambridge University Press, New York.

Carpenter S.R. & Lodge D.M. (1986) Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany*, **26**, 341–370.

Christoffersen K. (1990) Evaluation of *Chaoborus* predation on natural populations of herbivorous zooplankton in a eutrophic lake. *Hydrobiologia*, **200/201**, 459–466.

Cryer M., Peirson G. & Townsend C.R. (1986) Reciprocal interactions between roach (*Rutilus rutilus* L.) and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. *Limnology and Oceanography*, **31**, 1022–1038.

Diehl S. (1988) Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. *Oikos*, **53**, 207–214.

Engel S. (1988) The role and interactions of submerged macrophytes in a shallow Wisconsin lake. *Journal of Freshwater Ecology*, **3**, 329–341.

Frey D.G. (1959) The taxonomic and phylogenetic significance of the head pores of the Chydoridae (Cladocera). *Internationale Revue der Gesamten Hydrobiologie*, **44**, 27–50.

Frey D.G. (1986) Cladocera analysis. *Handbook of Holocere Palaeoecology and Palaeohydrology* (ed. B.E. Berglund), pp. 667–692. John Wiley & Sons, New York.

Fritz S.C., Juggins S., Battarbee R.W. & Engstrom D.R. (1991) Reconstruction of past changes in salinity and climate using a diatom-based transfer function. *Nature*, **352**, 706–708.

Gulati R.D., Sivertsen K. & Postema G. (1985) Zooplankton structure and grazing activities in relation to food quality and concentration in Dutch lakes. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **21**, 91–102.

Gulati R.D., Lammens E.H.R., Meijer M-L. & van Donk E. (1990) Biomanipulation tool for water management. *Hydrobiologia*, **200/201**, 557–566.

Hall R.I. & Smol J.P. (1992) A weighted-averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. *Freshwater Biology*, **27**, 417–434.

Hann B., Leavitt P.R. & Chang P.S.S. (1994) Cladocera community response to experimental eutrophication in lake 227 as recorded in laminated sediments. *Canadian Journal of Fisheries and Aquatic Science*, **51**, 2312–2321.

Holm-Hansen D. & Riemann B. (1978) Chlorophyll *a* determination: Improvements in methods. *Oikos*, **30**, 438–447.

Hrbáček J. (1969) On the possibility of estimating predation pressure and nutrition level of populations of *Daphnia* from their remains in sediments. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **17**, 262–274.

Irvine K., Moss B. & Stansfield J. (1990) The potential of artificial refugia for maintaining a community of large-bodied cladocera against fish predation in a shallow eutrophic lake. *Hydrobiologia*, **200/201**, 379–380.

Jakobsen P.J. & Johnsen G.H. (1987) The influence of predation on horizontal distribution of zooplankton species. *Freshwater Biology*, **17**, 501–508.

Jensen J.W. (1986) Gillnet selectivity and the efficiency of alternative combinations of mesh sizes for some freshwater fish. *Journal of Fish Biology*, **28**, 637–646.

Jeppesen E., Sortkjær O., Søndergaard M. & Erlandsen M. (1992) Impact of a trophic cascade on bacterioplankton production and biomass in two fish-manipulated lakes. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **37**, 219–231.

Jeppesen E., Jensen J.P., Kristensen P., Søndergaard M., Mortensen E., Sortkjær O. & Olrik K. (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. *Hydrobiologia*, **200/201**, 219–227.

Jeppesen E., Søndergaard M., Kanstrup E., Petersen B., Henriksen R.B., Hammershøj M., Jensen J.P. & Have A. (1994) Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? *Hydrobiologia*, **275/276**, 233–242.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T., Pedersen L.J. & Jensen L. (in press) Top-down regulation in freshwater lakes: The role of fish, submerged macrophytes and water depth. *Hydrobiologia.*

Kerfoot W.C. (1974) Net accumulation rates and the history of cladoceran communities. *Ecology*, **55**, 51–61.

Kerfoot W.C. (1981) Long-term replacement cycles in cladoceran communities: A history of predation. *Ecology*, **62**, 216–233.

Kingston J.C. & Birks H.J.B. (1990) Dissolved organic carbon reconstruction from diatom assemblages in PIRLA project lakes. North America. *Philosophical Transactions of the Royal Society of London*, **327**, 279–288.

Kitchell J.A. & Kitchell J.F. (1980) Size-selective predation, light transmission, and oxygen stratification: Evidence from recent sediments of manipulated lakes. *Limnolology and Oceanography*, **25**, 389–40.

Kitchell J.F. & Carpenter S.R. (1987) Piscivores, planktivores, fossils, and phorbins. *Predation: Direct and Indirect Impacts on Aquatic Communities* (eds W.C. Kerfoot and A. Sih), pp. 132–146. University Press of New England, Hanover, New England.

Kitchell J.F. & Sanford P.R. (1992) Paleolimnology and evidence of food web dynamics in lake Mendota. *Food Web Management—A Case Study of Lake Mendota* (ed. J.F. Kitchell), pp. 31–48. Springer-Verlag, New York.

Kornijów R. & Gulati R.D. (1992) Macrofauna and its ecology in Lake Zwemlust, after biomanipulation. I. Bottom fauna. *Archiv für Hydrobiologie*, **123**, 337–347.

Koroleff F. (1970) *Determination of total phosphorus in natural waters by means of persulphate oxidation.* Interlab Report No. 3 Cons. int. Explor. Mer.

Lauridsen T., Jeppesen E. & Søndergaard M. (1994) Colonization and succession of submerged macrophytes in shallow Lake Vængduring the first five years following fish manipulation. *Hydrobiologia*, **275–276**, 33–42.

Leavitt P.R., Carpenter S.R. & Kitchell J.F. (1989) Whole lake experiments: The annual record of fossil pigments and zooplankton. *Limnolology and Oceanography*, **34**, 700–717.

Leavitt P.R., Sanford P.R., Carpenter S.R. & Kitchell J.F. (1994a) An annual fossil record of production, planktivory and piscivory during whole-lake manipulations. *Journal of Paleolimnology*, **11**, 133–149.

Leavitt P.R., Hann B.J., Smol J.P., Zeeb B.A., Christie C.E., Wolfe B. & Kling H.J. (1994b) Paleolimnological analysis of whole-lake experiments: an overview of results from Experimental Lakes Area Lake 227. *Canadian Journal of Fisheries and Aquatic Science*, **51**, 2322–2332.

Line J.M., ter Braak C.J.F. & Birks H.J.B. (1994) WACALIB version 3.3—a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. *Journal of Paleolimnology*, **10**, 147–152.

Luecke C., Vanni M.J., Magnuson J.J., Kitchell J.F. & Jacobson P.J. (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the clearwater phase. *Limnology and Oceanography*, **35**, 1718–1733.

Mills E.L. & Forney J.L. (1983) Impact on *Daphnia pulex* on predation by yellow perch in Oneida Lake, New York. *Transactions of the American Fisheries Society*, **112**, 154–161.

Mortensen E., Jensen H.J. & Müller J.P. (1991) *Retningslinjer for standardiseret forsøgsfiskeri i søer og en beskrivelse af fiskeredskaber og—metoder* (in Danish). National Environmental Research Institute, Silkeborg.

Murphy J. & Riley J.R. (1972) A modified single solution method for the determination of phosphate in natural waters. *Analytical Chemistry Acta*, **27**, 21–26.

Nilssen J.P. & Sandøy S. (1990) Recent lake acidification and cladoceran dynamics: Surface sediment and core analyses from lakes in Norway, Scotland and Sweden. *Philosophical Transactions of the Royal Society of London B*, **327**, 299–309.

Persson L. (1991) Behavioural response to predators reverses the outcome of competition between prey species. *Behavioural Ecology. Sociobiology*, **28**, 101–108.

Persson L. & Eklöv P. (1995) Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology*, **76**, 70–81.

Persson L., Anderson G., Hamrin S.F. & Johansson L. (1988) Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. *Complex Interactions in Lake Communities* (ed. S.R. Carpenter), pp. 45–65. Springer-Verlag, New York.

Pope G.F., Carter J.C.H. & Power G. (1973) The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density larvae in the Matamek River system, Quebec. *Transactions American Fisheries Society*, **102**, 707–714.

Quiros R. (1990) Predictors of relative fish biomass in lakes and reservoirs of Argentina. *Canadian Journal of Fisheries and Aquatic Science*, **47**, 928–939.

Sanford P.R. (1993) *Bosmina longirostris* antennule morphology as an indicator of intensity of planktivory by fish. *Bulletin of Marine Sciences*, **53**, 216–227.

Schriver P., Bøgestrand J., Jeppesen E. & Søndergaard M. (1995) Impact of submerged macrophytes on the interactions between fish, zooplankton, and phytoplankton: Large-scale enclosure experiments in a shallow lake. *Freshwater Biology*, **33**, 255–270.

Stansfield J., Moss B. & Irvine K. (1990) The loss of submerged plants with eutrophication III. Potential role of organochlorine pesticides: A palaeoecological study. *Freshwater Biology*, **22**, 109–132.

Stevenson A.C., Juggins S., Birks H.J.B., Anderson D.S., Anderson N.J., Battarbee R.W., Berge F., Davis R.B., Flower R.J., Haworth E.Y., Jones V.J., Kingston J.C., Kreiser A.M., Line J.M., Munro M.A.R. & Renberg I. (1991) *The Surface Waters Acidification Project Palaeolimnology Programme: Modern Diatom/Lake-water Chemistry Data-set.* Ensis Ltd, London.

ter Braak C.J.F. (1987a) *Unimodal models to relate species to environment.* PhD thesis, University of Wageningen, the Netherlands.

ter Braak C.J.F. (1987b) Ordination. *Data Analysis in Community and Landscape Ecology* (eds R.H.G. Jongman, C.J.F. ter Braak and O.F.R. van Tongeren), pp. 91–173. Pudoc, Wageningen.

ter Braak C.J.F. (1990a) *CANOCO—A Fortran Program for Canonical Community Ordination.* Microcomputer Power, Ithaca, NY.

ter Braak C.J.F. (1990b) *Update Notes: CANOCO Version 3.10.* Agricultural Mathematics Group, University of Wageningen, the Netherlands.

ter Braak C.J.F. & van Dam H. (1989) Inferring pH from diatoms: A comparison of old and new calibration methods. *Hydrobiologia*, **178**, 209–233.

ter Braak C.J.F. & Juggins S. (1993) Weighted averaging partial least squares regression (WA-PLS): An improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia*, **269/270**, 485–502.

Timms R.M. & Moss B. (1984) Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish in a shallow wetland ecosystem. *Limnology and Oceanography*, **29**, 472–486.

Uutala A.J. (1990) *Chaoborus* (Diptera: Chaoboridae) mandibles—paleolimnological indicators of the historical status of fish populations in acid-sensitive lakes. *Journal of Paleolimnology*, **4**, 139–151.

Walker I.R. & Smol J.P. (1990) An assessment of chironomidae as quantitative indicators of past climatic change. *Canadian Journal of Fisheries and Aquatic Science*, **48**, 975–987.

Werner E., Gilliam E.J.F., Hall D.J. & Mittelbach G.G. (1983) An experimental test of the effect of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.

Winfield I.J. (1986) The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophtalmus*, and perch, *Perca fluviatilus*. *Journal of Fish Biology*, **29**, 37–48.

Winfield I.J., Peirson G., Cryer M. & Townsend C.R. (1983) The behavioural basis of prey selection by under yearling bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)) *Freshwater Biology*, **13**, 139–149.

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Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a long-term study in shallow hypertrophic Lake Søbygaard

Erik Jeppesen, Martin Søndergaard, Jens Peder Jensen, Erik Mortensen and Ole Sortkjær

National Environmental Research Institute, Department of Lake and Estuarine Ecology, 25 Vejlsøvej, DK-8600 Silkeborg, Denmark

Abstract. The impact of fish-mediated changes on the structure and grazing of zooplankton on phytoplankton and bacterioplankton was studied in Lake Søbygaard during the period 1984–92 by means of *in vitro* grazing experiments (^{14}C-labelled phytoplankton, ^{3}H-labelled bacterioplankton) and model predictions. Measured zooplankton clearance rates ranged from 0–25 ml l^{-1} h^{-1} on phytoplankton to 0–33 ml l^{-1} h^{-1} on bacterioplankton. The highest rates were found during the summer when *Daphnia* spp. were dominant. As the phytoplankton biomass was substantially greater than that of bacterioplankton throughout the study period, ingestion of phytoplankton was 26-fold greater than that of bacterioplankton. Multiple regression analysis of the experimental data revealed that *Daphnia* spp., *Bosmina longirostris* and *Cyclops vicinus*, which were the dominant zooplankton, all contributed significantly to the variation in ingestion of phytoplankton, while only *Daphnia* spp. contributed significantly to that of bacterioplankton. Using estimated mean values for clearance and ingestion rates for different zooplankters, we calculated zooplankton grazing on phytoplankton and bacterioplankton on the basis of monitoring data of lake plankton obtained during a 9 year study period. Summer mean grazing ranged from 2 to 4% of phytoplankton production and 2% of bacterioplankton production to maxima of 53 and 88%, respectively. The grazing percentage decreased with increasing density of planktivorous fish caught in August each year using gill nets and shore-line electrofishing. The changes along a gradient of planktivorous fish abundance seemed highest for bacterioplankton. Accordingly, the percentage contribution of bacterioplankton to the total ingestion of the two carbon sources decreased from a summer mean value of 8% in *Daphnia*-dominated communities at lower fish density to 0.7–1.1% at high fish density, when cyclopoid copepods or *Bosmina* and rotifers dominated. Likewise, the percentage of phytoplankton production channelled through the bacteria varied, it being highest (5–8%) at high fish densities. It is argued that the negative impact of zooplankton grazing on bacterioplankton in shallow lakes is highest at intermediate phosphorus levels, under which conditions *Daphnia* dominate the zooplankton community.

Introduction

It has long been recognized that zooplankton grazing can be an important loss factor for phytoplankton in lakes (Gulati *et al.*, 1982; Bergquist *et al.*, 1985; Kerfoot, *et al.*, 1988), especially when *Daphnia* are dominant and present in high density. In fact, *Daphnia* are considered to play a key role in the top-down control of phytoplankton in such lakes (Carpenter and Kitchell, 1993). In recent years, it has become apparent that large *Daphnia* may also have a significant effect on the microbial community, including bacterioplankton (Riemann, 1985; Riemann and Søndergaard, 1986; Güde, 1988; Christoffersen *et al.*, 1993; Jürgens, 1994; Jürgens *et al.*, 1994), although the results are not unequivocal (Pace and Funke, 1991; Vaqué and Pace, 1992). The key role of *Daphnia* is attributable to their ability to filter particles in a wide range of size: from bacterioplankton to relatively large phytoplankton.

A change in fish predation affects the biomass, structure and average size of the zooplankton community. In shallow eutrophic lakes, increased fish predation leads to a shift from a community dominated by *Daphnia* to one dominated by *Bosmina* and cyclopoid copepods, and, at high fish predation, to one dominated by rotifers and cyclopoid copepods (Gulati, 1990; Jeppesen *et al.*, 1992, 1996b). *Bosmina*, cyclopoid copepods and many rotifers select for particles larger than bacterioplankton, including bacterioplankton-consuming protozoans (DeMott and Kerfoot, 1982; Arndt, 1983; Sanders *et al.*, 1989). It could, therefore, be hypothesized that a shift towards dominance of small-bodied zooplankton as a result of an increase in fish predation will alter the grazing pressure in the direction of a relatively higher pressure on phytoplankton and hence an increase in the percentage of carbon channelled from phytoplankton to bacterioplankton.

To elucidate the impact of fish-mediated changes in the zooplankton grazing on phytoplankton and bacterioplankton in Lake Søbygaard, we conducted 32 *in vitro* community grazing experiments on ^{3}H-labelled bacterioplankton and 34 experiments on ^{14}C-labelled phytoplankton during years with contrasting fish densities and accordingly contrasting zooplankton community structure. Further, using regression models developed from these data, we calculated the seasonal and inter-annual variation in grazing during a 9 year investigation period. Finally, we compared estimated grazing with data on phytoplankton and bacterioplankton production and biomass.

Study area

Lake Søbygaard is a shallow lake with a surface area of 40 ha, a mean and maximum depth of 1.0 and 1.9 m, respectively, and a hydraulic retention time of 15–20 days. During the study period (1984–92), summer average total P ranged from 550 to 1000 μg l^{-1}. During the 9 year study period, the abundance of the fish community changed markedly and was exclusively dominated by roach (*Rutilus rutilus*), rudd (*Scardinius eryptropthalmus*) and bream (*Abramis brama*) throughout the study. The fish stock changes were the result of major episodes of fish kill in the late 1970s and low recruitment since 1984 (particularly from 1984 to 1988) due to exceedingly high pH (up to pH 11.2) during the spawning period (E.Mortensen *et al.*, unpublished observation). Moreover, during the period 1986–88, a commercial fishery removed 4.3 tonnes of roach and rudd from the lake, equivalent to 17% of the 1986 standing stock of ~660 kg ha^{-1}.

During the first part of the study in 1984–86, when the majority of the grazing experiments were carried out, the crustacean zooplankton consisted exclusively of *Cyclops vicinus*, *Daphnia longispina*, *Daphnia galeata* and *Bosmina longirostris*, while the rotifer community mainly consisted of *Brachionus calyciflorus* and *B.urceolaris rubens*. The latter subsequently became more diverse. The phytoplankton community was exclusively dominated by centric diatoms in the spring, and by green algae, diatoms and cryptophytes during the summer.

The dynamics of the Lake Søbygaard zooplankton, phytoplankton and bacterioplankton communities is described in detail in Jeppesen *et al.* (1990a,b), Hansen and Jeppesen (1992) and Jeppesen *et al.* (1992, 1996a).

Method

Grazing experiments

The clearance rate of zooplankton (CR) was determined for both phytoplankton and bacterioplankton using the *in vitro* grazing method of Bjørnsen *et al.* (1986). A total of 32–34 experiments were undertaken during the years 1984–86 and 1991. For each experiment, water samples were first filtered through a 50 μm mesh net to remove zooplankton and then incubated with either [^{14}C]bicarbonate NaOH^{14}CO$_3$ or [^{3}H]methyl-thymidine at *in situ* temperatures for 18 h in daylight (^{14}C-labelled phytoplankton) or 2–3 h in darkness (^{3}H-labelled bacterioplankton). In order to reduce the labelling of flagellates and small ciliates, the incubation times were reduced from October 1985 onwards to 2–3 h for phytoplankton and 1 h for bacterioplankton. To obtain the same labelling of the plankton as before October 1985, we enhanced the ^{14}C and ^{3}H activity during incubation. Following the reduction in incubation time, we observed no significant reduction in the specific clearance rate of the zooplankton community (E.Jeppesen, unpublished results).

The zooplankton sampling for the grazing experiments was conducted at a mid-lake station with a Patalas sampler, and consisted of a pooled sample (60–70) from depths of 0.5 and 1.5 m. Triplicate 200 ml ^{14}C-labelled and triplicate 200 ml non-labelled phytoplankton were then added to 800 ml subsamples from the composite water samples of the incubated bacterioplankton. The procedure was the same for bacterioplankton, except that 100 ml labelled and non-labelled bacterioplankton were added to 900 ml water samples. The labelled triplicates were incubated *in vitro*, usually for 15–20 min, depending on water temperature. On a few occasions during winter, the incubation time was longer in order to obtain sufficient labelling (30–60 min). (It could be argued that the latter represents assimilation rather than ingestion; however, exclusion of these samples did not alter the results shown in Table III significantly; E.Jeppesen, unpublished results.) After incubation, the plankton were filtered on a 140 μm net followed by a 50 μm (1984) or a 20 μm net (1985, 1986 and 1991). The non-labelled samples were used as 'time zero' controls. Tracer was added to these and the bottles were shaken for 10 s and treated as the labelled samples. The zooplankton retained on the net were washed six times in lake water by rapid back-filtration, whereafter the filter was dried on a filter paper and transferred to glass vials containing 10 ml Ready-solv Hp/b (Beckmann). After 24 h, the radioactivity was counted on an LKB-WALLAC 1210 liquid scintillation counter. Quenching was determined by the external standard channels ratio method. The ^{14}C activity of phytoplankton and the ^{3}H activity of bacterioplankton in the incubated samples and the non-incubated controls were determined on 10 ml aliquots filtered on cellulose nitrate filters (0.45 μm) for phytoplankton and 25 mm Sartorius acetate filters (0.2 μm) for bacterioplankton. To estimate tracer activity in the incubated samples, 3–5 samples were taken at both the start and at the end of the experiments, and the measured activities were averaged. The filters were dissolved in Ready-solv and counted as described above. In the laboratory, the filters were transferred to glass vials, dissolved in Ready-solv and ^{3}H or ^{14}C activity determined as described above. In most of the experiments, the ^{14}C and ^{3}H activities of the incubated 50–140 and 20–140 μm zooplankton fractions were not significantly different from those in the controls, reflecting relatively high 'time zero' control activity in combination with low uptake of labelled substrate in the fractions, and large variation among replicates (E.Jeppesen, unpublished results). We have therefore elected to present only results obtained with zooplankton >140 μm.

Zooplankton were counted on triplicate 1 l non-labelled samples taken from the composite samples, filtered through a 140 μm net, and the biomass determined from length–weight relationships as described in Jeppesen *et al.* (1990a), except that *C.vicinus* numbers were converted to biomass assuming 7.38, 12.85, 4.76 and 0.14 mg dry weight (DW) indiv.$^{-1}$ for males, females, copepodites and nauplii, respectively. These weight factors are averages for the *C.vicinus* population in the lake (Hansen and Jeppesen, 1992; A.-M.Hansen, unpublished observation).

Chlorophyll *a* (<50 μm) was measured in triplicate in water from the composite samples after ethanol extraction (Holm-Hansen and Riemann, 1978), and converted to carbon content using a conversion factor of ×35.

Specific clearances rates of the zooplankton community (SCR; ml mg^{-1} C h^{-1}) were determined as CR divided by the zooplankton biomass in terms of carbon. Zooplankton ingestion rates (IR; mg C l^{-1} h^{-1}) for phytoplankton and bacterioplankton were determined from CR by multiplying by chlorophyll *a* converted to carbon and the bacterial biomass in terms of carbon, respectively. The daily ration (DR; mg C mg^{-1} body C day^{-1}) was determined as IR × 24 divided by the biomass of zooplankton in terms of carbon.

Clearance rate correction factor

The grazing method for determining ingestion rate has recently been criticized by Jarvis and Hart (1993), who demonstrated that 'time zero' controls may not fully compensate for adsorption to particles because adsorption increases with the duration of exposure to radiolabelled compounds. They found that adsorption errors were often attributable to abundant colonies of cyanobacteria (*Microcystis*). However, since cyanobacteria accounted for <0.1% of the phytoplankton biomass in Lake Søbygaard, we consider adsorption errors to have been of minor importance in our experiments.

Several authors have observed a loss of ingested labelled material when handling zooplankton samples, especially with cladocerans (Downing and Peters, 1980; Gulati *et al.*, 1982; Holtby and Knoechel, 1982; DeMott, 1985; Gulati, 1985; Lampert and Taylor, 1985; Nagata and Okamoto, 1988; Mourelatos *et al.*, 1992). However, since the animals were not handled and analysed individually in the present experiments, the loss of labelled material is likely to have been much lower than in most of the previous studies carried out. Nevertheless, there could have been some loss during the 2 h period between the end of the incubation and the time scintillation fluid (Ready-solv) was added and scintillation counting started. Experiments were therefore conducted by adding 3–5 filters directly to the scintillation fluid after *in vitro* incubation (grazing), and the samples mixed and counted <30 min later until constant counts were obtained. Another set of 3–5 filters was treated according to the procedure followed in this study (i.e. a 2 h delay). We observed no significant change in ^{3}H-labelled zooplankton (t-test, $P > 0.89$), while a significant (t-test, $P < 0.05$) 15 ± 2% (mean ± SD, $n = 2$) reduction was found for ^{14}C-labelled zooplankton. We accounted for the ^{14}C loss in the calculations.

Zooplankton and phytoplankton density and biomass

The abundance and biomass of phytoplankton and zooplankton (>20 μm) in the lake were determined on composite samples taken at depths of 0.5 and 1.5 m with a Patalas sampler at a mid-lake station, and, in the case of zooplankton, also at an eastern and a western station. The samples were counted and converted to biomass as described above. Phytoplankton biovolume was determined on some of the collected samples by the use of simple geometric formulae (Olrik, 1991), and converted to carbon content (C) assuming a DW of 24% and a DW : C ratio of 2.2. In the present analysis, we distinguished between total phytoplankton and grazeable phytoplankton defined as those passing a 50 μm filter. Chlorophyll *a* (ethanol extraction, see above) in the composite water sample from the mid-lake station was determined more frequently ($n = 644$) than phytoplankton biomass ($n = 310$). Carbon content derived by conversion of chlorophyll *a* values was therefore used in the grazing calculations for the entire study period. To determine grazeable phytoplankton, we multiplied chlorophyll *a* by interpolated values of the ratio of phytoplankton biovolume <50 μm to total phytoplankton biovolume.

Bacterioplankton and phytoplankton production

Bacterioplankton production was measured by the [^{3}H]methyl-thymidine method basically as described by Fuhrmann and Azam (1982) with minor changes (Jeppesen *et al.*, 1992) and converted to cells and carbon production using the following conversion factors: 2×10^{9} cells nmol^{-1} thymidine (Riemann *et al.*, 1982) and 25 fg C cell^{-1} (R.Bell, personal communication). In total, 351 measurements were conducted from 1985 to 1992.

Bacterioplankton were counted according to Hobbie *et al.* (1977) with only minor modifications (Jeppesen *et al.*, 1992) and converted to biomass as described above. Bacterioplankton cell dimensions were measured using an eyepiece micrometer at ×1560 magnification (each micrometer unit = 0.7 μm), and half-circle formed rods (four classes) and cell volume calculated using standard geometric formulae (Jeppesen *et al.*, 1992). Density and biomass were measured on 302 samples from 1985 to 1992.

Phytoplankton production corrected for dark fixation was estimated from the photosynthesis versus irradiance relationship determined from laboratory incubation conducted at each sampling date, and integrated over depth and time using observations of Secchi depth (converted to a light extinction coefficient) and the time variation of surface irradiation at a station situated 30–40 km from the lakes. Sampling frequency was the same as that described for bacterioplankton. In total, 324 measurements of phytoplankton production were conducted between 1984 and 1992.

Fish

Fish stock measurements were conducted in autumn each year from 1987 to 1992 using a standardized monitoring programme adapted for Danish lakes (Mortensen *et al.*, 1991). The lake was divided into six sections. In each section 300 m along the shoreline was electrofished and three multi-mesh size gill nets (16 different mesh sizes ranging from 6.25 to 75 mm) were set overnight (from about 16.00 p.m. to 09.00 a.m.). One gill net was set perpendicular to the shoreline, another parallel with and ~25 m from the shoreline, and the third was set at about half the distance to the middle of the lake. The catch by electrofishing in each section was considered as a single sample. Likewise, the catch in each gill net was considered as a single sample and defined as one effort. From the catches, arithmetic mean catch per unit effort (CPUE) for each species, in terms of numbers and biomass, was calculated for gill nets ($\mathrm{CPUE_{net}}$, $n = 18$) and 300 m shoreline electrofishing ($\mathrm{CPUE_{el}}$, $n = 6$), and pooled. As no electrofishing data were available for 1991, we calculated $\mathrm{CPUE_{el}}$ as the average of that in 1990 ($\mathrm{CPUE_{el}} = 66$) and in 1992 ($\mathrm{CPUE_{el}} = 39$).

Statistical analyses

The paired *t*-test was used to test differences in clearance rates on phytoplankton and bacterioplankton (Statistical Analysis Systems Institute, 1989). Multiple regression was used to estimate SCR and DR of *Bosmina*, *Daphnia*, cyclopoid copepods and rotifers from all the 32–34 community grazing experiments (Table III). CR and DR were adjusted to 15°C according to Gulati *et al.* (1982) before the analysis was performed. Estimated SCR and DR at 15°C were then applied to calculate grazing on bacteria and phytoplankton during the entire study period using the monitoring data on zooplankton, bacterioplankton, phytoplankton and temperature (see further below).

Results

Grazing experiments

During autumn 1984 and throughout 1985 when the biomass of filter-feeding zooplankton was low, the CR of zooplankton (>140 μm) on both bacterioplankton and phytoplankton was low, averaging 0.7 $\mathrm{ml\ l^{-1}\ h^{-1}}$ (range 0–4 $\mathrm{ml\ l^{-1}\ h^{-1}}$) and 0.6 $\mathrm{ml\ l^{-1}\ h^{-1}}$ (range 0.04–2.7 $\mathrm{ml\ l^{-1}\ h^{-1}}$), respectively (Figure 1). Concurrently with the increase in the biomass of *Daphnia* spp. during the summer of 1986 (Figure 1), there was a marked increase in CR on both phytoplankton and bacterioplankton to maximum levels of 25 $\mathrm{ml\ l^{-1}\ h^{-1}}$ for phytoplankton and 33 $\mathrm{ml\ l^{-1}\ h^{-1}}$ for bacterioplankton. High CR values (14–25 $\mathrm{ml\ l^{-1}\ h^{-1}}$) were also found in two phytoplankton experiments conducted in 1991 when *B.longirostris* was dominant and present in high density. Paired *t*-test on grazing data from the 32 experiments on both phytoplankton and bacterioplankton grazing revealed that CR was 13% higher on bacterioplankton than on phytoplankton ($P < 0.02$). Moreover, CR differed significantly ($P < 0.05$) in 14 of the 32 experiments, in 12 cases there being higher CR for bacterioplankton.

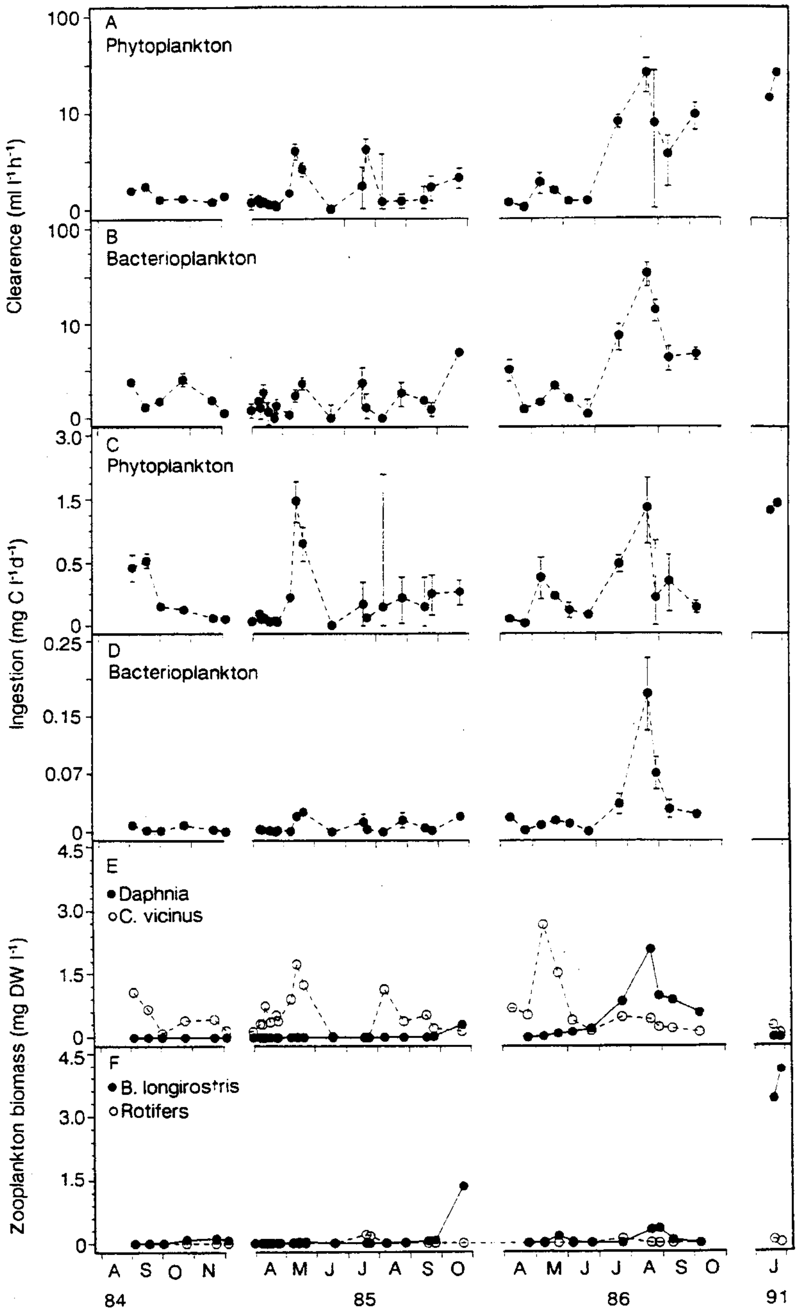

Fig. 1. Zooplankton (>140 μm) clearance and ingestion rates on phytoplankton (**A**, **C**) and bacterioplankton (**B**, **D**) measured in Lake Søbygaard, shown together with the biomass of *Daphnia* spp. and cyclopoid copepods (*C.vicinus*) (**E**) and *B.longirostris* and rotifers (**F**).

The IR largely followed the variation in CR, except that IR on phytoplankton was relatively high in autumn 1984, and in the spring of 1985 and 1986, when the phytoplankton biomass was particularly high (Figure 1). Maximum IR on phytoplankton was 0.5 mg C l^{-1} day^{-1} in 1984, and between 1.4 and 1.5 mg C l^{-1} day^{-1} in 1985, 1986 and 1991, and on bacterioplankton it was 0.008, 0.02 and 0.18 mg C l^{-1} day^{-1} in 1984, 1985 and 1986, respectively, with no data being available for 1991. As the phytoplankton biomass was substantially higher throughout the investigation period than that of bacterioplankton, ingestion of bacterioplankton-C only accounted for an average of 3.7% (range 0.2–28%) of total C uptake from the two sources (Figure 2).

The DR of the zooplankton (defined as daily carbon intake per unit body carbon of zooplankton) averaged 0.82 for phytoplankton and 0.03 for bacterioplankton of 1.00 and 0.04, respectively, when adjusting DR to 15°C at each date as described by Gulati *et al.* (1982) (Table I).

In 1984 and 1985, the ingestion of bacterioplankton was much lower than both ambient bacterioplankton biomass and production (Figure 3). Thus, ingestion of bacterioplankton amounted to 0.3–3.7% day^{-1} (mean 1.8% day^{-1}) of the biomass in late autumn 1984 and 0.8–9.5% day^{-1} (mean 1.7% day^{-1}) in 1985, while ingestion as a percentage of daily production amounted to 0.6–13% (mean 11.8%) and 0.4–19.2% (mean 5.4%), respectively. Relatively low percentages were found in 1986 until August, when ingestion increased and peaked at 80% of bacterioplankton biomass day^{-1} and 190% of daily production. This occurred simultaneously with a pronounced peak in the abundance of *Daphnia* spp. (Figure 1). In 1986, the sampling average of bacterioplankton ingestion amounted to 14% day^{-1} of biomass and 43% of daily production.

A pattern similar to that of bacterioplankton was observed for phytoplankton ingestion (Figure 3). In 1984–85, the ingestion amounted to 0.1–6.5% day^{-1} (mean 2.5% day^{-1}) of phytoplankton biomass and 0.4–32% (mean 8%) of daily production. As with bacterioplankton, ingestion increased in August 1986 to a maximum of 51% of biomass day^{-1} and 136% of daily production. High values were also recorded in 1991 (28% and 53% biomass day^{-1}; 33% and 80% of daily production; Figure 3), at which time *B.longirostris* density was high (Figure 1). In 1986, the sampling average of phytoplankton ingestion amounted to 11% day^{-1} of biomass and 30% of daily production.

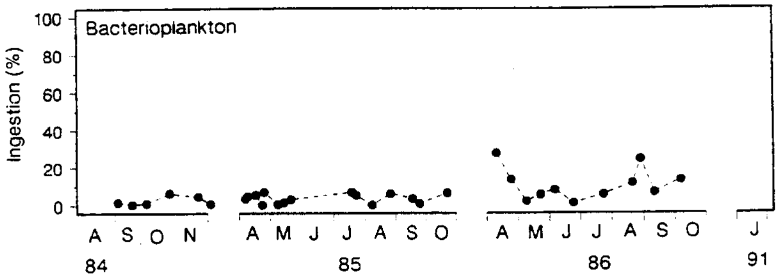

Fig. 2. Ingestion of bacterioplankton-C expressed as a percentage of total carbon ingestion of bacterioplankton and phytoplankton sources.

Table I. Daily ration (average specific ingestion: mg C mg^{-1} C day^{-1} ± SE) of phytoplankton and bacterioplankton ingested by zooplankton >140 μm in 32–34 *in vitro* grazing experiments in Lake Søbygaard. The ration at 15°C, adjusted according to Gulati *et al.* (1982), is also shown

Daily ration	*n*	Measured	Adjusted to 15°C
Phytoplankton	34	0.82 ± 0.13	1.00 ± 0.16
Bacterioplankton	32	0.03 ± 0.006	0.04 ± 0.006

n, number of experiments.

Stepwise multiple linear regression of IR versus the biomass of different zooplankton species revealed that whereas *Daphnia* spp., *B. longirostris* and *C. vicinus* contributed significantly to IR on phytoplankton, rotifers (>140 μm) did not (Table II), the slope (DR) being 0.88, 0.89, 1.02 and 2.38, respectively. In contrast, only *Daphnia* spp. contributed significantly to IR on bacterioplankton, the slope

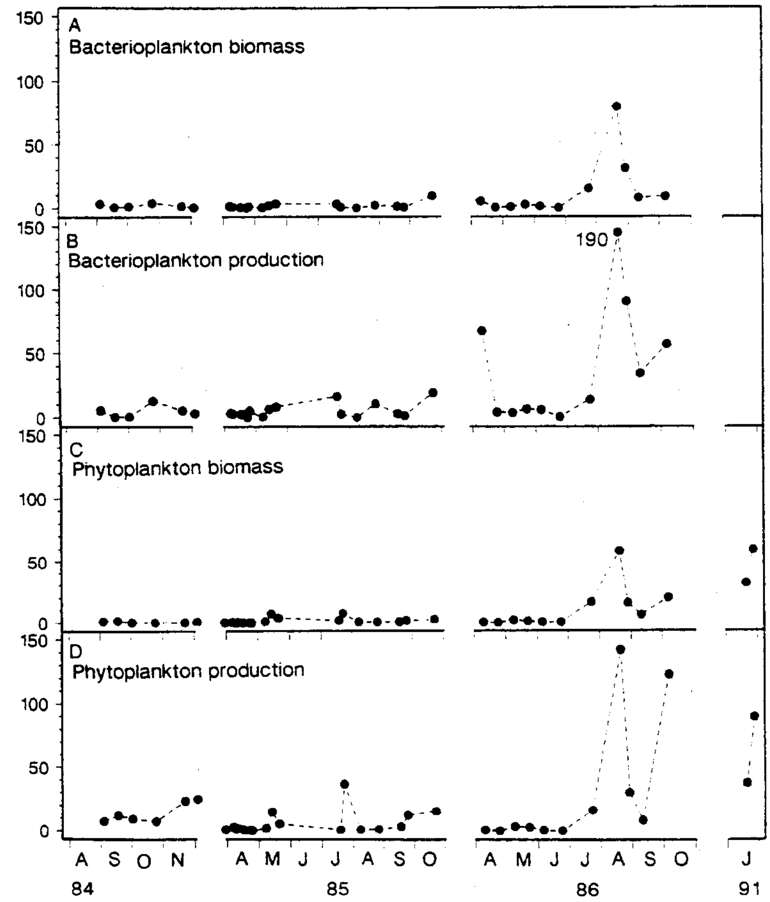

Fig. 3. Zooplankton ingestion rate on bacterioplankton and phytoplankton expressed as a percentage of biomass (**A**, **C**) and production (**B**, **D**).

Table II. Multiple regression of clearance rate (CR, ml l^{-1} h^{-1}, 15°C) and ingestion rate (IR, mg^{-1} C l^{-1} day^{-1}, 15°C) on data obtained from *in vitro* zooplankton (>140 μm) grazing experiments on ^{14}C-labelled phytoplankton and ^{3}H-labelled bacterioplankton versus the biomass of various zooplankters (mg C l^{-1}). The slopes approximately represent the specific clearance rate (SCR; ml mg^{-1} body C h^{-1}) in (A, C) and daily ration (mg C mg^{-1} body C day^{-1}) in (B, D).

		F value	Pr > *F*
(A) CR on phytoplankton			
Intercept	−0.58 ± 0.73		0.44
Slope ± SE			
B.longirostris	10.8 ± 1.1	96.8	0.0001
Daphnia spp.	19.8 ± 2.3	75.4	0.0001
C.vicinus	10.6 ± 18	0.8	0.37
Rotifers	16.4 ± 20.7	0.6	0.43
Regression model: $r^2 = 0.85$, $F = 42.4$, $P < 0.0001$, $n = 34$			
(B) IR on phytoplankton			
Intercept	−0.04 ± 0.09		0.58
Slope ± SE			
B.longirostris	0.88 ± 0.13	46.8	0.0001
Daphnia spp.	1.02 ± 0.27	14.5	0.0041
C.vicinus	0.89 ± 0.21	17.8	0.0072
Rotifers	2.38 ± 2.43	1.0	0.3355
Regression model: $r^2 = 0.68$, $F = 16.46$, $P < 0.0001$, $n = 34$			
(C) CR on bacterioplankton			
Intercept	−0.5 ± 0.7		0.46
Slope ± SE			
Daphnia spp.	28.1 ± 2.1	172.8	0.0001
C.vicinus	1.3 ± 1.6	0.66	0.42
B.longirostris	2.9 ± 3.9	0.54	0.47
Rotifers	1.5 ± 19.1	0.01	0.93
Regression model: $r^2 = 0.87$, $F = 48.8$, $P < 0.0001$, $n = 32$			
(D) IR on bacterioplankton			
Intercept	−0.003 ± 0.004		0.45
Slope ± SE			
Daphnia spp.	0.15 ± 0.01	161.53	0.0001
C.vicinus	0.016 ± 0.009	2.99	0.095
B.longirostris	0.011 ± 0.02	0.24	0.63
Rotifers	0.034 ± 0.11	0.10	0.75
Regression model: $r^2 = 0.87$, $F = 44.5$, $P < 0.0001$, $n = 32$			

being 0.15; *C.vicinus*, *B.longirostris* and rotifers being ~0.02, 0.01 and 0.03, respectively. Regression analysis of CR on phytoplankton revealed slopes (SCR) of ~11–20 ml mg^{-1} C h^{-1} for the four zooplankton groups, with that for *C.vicinus* being lowest (Table II). The slope for bacterioplankton was low for *C.vicinus*, *B.longirostris* and rotifers (1.3–2.9 ml mg^{-1} C h^{-1}) and high for *Daphnia* spp. (28 ml mg^{-1} C h^{-1}).

Model predictions

The SCR and DR obtained from the regression analysis on grazing experiments (Table II) (whether significant or not) were used to calculate both summer mean

(Table III) and annual mean (Table IV) zooplankton grazing on bacterioplankton and phytoplankton for the entire investigation period (1984–92) by using monitoring data for the biomass of zooplankton, phytoplankton and bacterioplankton, e.g. for phytoplankton as:

$$\text{SCR-grazing} = \mathrm{SCR}_{\mathrm{Rot}}\mathrm{Phyt} + \mathrm{SCR}_{\mathrm{Daph}}\mathrm{Phyt} + \mathrm{SCR}_{\mathrm{Cyc}\,+}\,\mathrm{Phyt} + \mathrm{SCR}_{\mathrm{Bos}}\mathrm{Phyt}$$
$$\text{DR-grazing} = \mathrm{DR}_{\mathrm{Rot}}\mathrm{Bio}_{\mathrm{Rot}} + \mathrm{DR}_{\mathrm{Daph}}\mathrm{Bio}_{\mathrm{Daph}} + \mathrm{DR}_{\mathrm{Cyc}}\mathrm{Bio}_{\mathrm{Cyc}} + \mathrm{DR}_{\mathrm{Ros}}\mathrm{Bio}_{\mathrm{Bos}}$$

where Phyt is phytoplankton biomass (mg C l^{-1}) and Bio is the total biomass of the different zooplankton groups (mg C). All SCR and DR were adjusted to actual temperature according to Gulati *et al.* (1982). As the carbon content of phytoplankton was lower than the incipient limiting level (ILL) for *Daphnia* (~0.2 mg C l^{-1}; Lampert and Muck, 1985) during short periods only, totalling 1.8% of the investigation period (E.Jeppesen, unpublished observation), and as detritus

Table III. Calculated summer mean (linear interpolation: 1 May–1 October) zooplankton grazing (crustaceans and rotifers) on phytoplankton and bacterioplankton obtained using multiple regression models based on specific ingestion rates (daily ration) (A) and specific clearance rate (B) (Table II). Grazing is shown as a percentage of the total measured production and biomass together with total zooplankton biomass, the relative contribution to the biomass of *Daphnia*, *Bosmina*, cyclopoid copepods and rotifers, and the bacterioplankton:phytoplankton production ratio

	1984	1985	1986	1987	1988	1989	1990	1991	1992
(A) Based on daily ration									
Phytoplankton grazing									
(μg C l^{-1} day^{-1})	259	415	1222	1085	1978	1727	1632	1447	859
% of production	2	4	15	26	47	53	40	25	14
% of biomass (% day^{-1})	0.7	1	8	12	27	28	20	17	9
Bacterioplankton grazing									
(μg C l^{-1} day^{-1})	3	3	77	68	169	124	13	38	63
% of production	2.0	1.9	45	45	88	77	4	12	39
% of biomass (% day^{-1})	–	0.7	22	24	67	44	3	8	16
% of phytoplankton grazing	1.1	0.7	6	6	9	7	0.8	5	9
(B) Based on specific clearance rate									
Phytoplankton grazing									
(μg C l^{-1} day^{-1})	421	531	1844	1056	1767	1479	1089	1446	1637
% of production	3	5	23	25	42	45	27	11	21
% of biomass (% day^{-1})	1	1	12	11	24	24	13	7	14
Bacterioplankton grazing									
(μg C l^{-1} day^{-1})	–	5	114	68	179	130	24	92	80
% of production	–	3	67	46	92	81	7	29	49
% of biomass (% day^{-1})	–	1	36	24	70	46	5	20	21
% of phytoplankton grazing	–	0.9	6	6	10	9	2	6	5
Total zooplankton biomass									
(mg DW l^{-1})	0.6	0.6	2.2	1.9	2.7	2.5	1.8	2.3	1.3
% *Daphnia* spp.	0.9	2	47	51	74	63	2	18	60
% *Bosmina longirostris*	0.5	4	6	0.8	0.3	0.0	39	32	0.0
% Cyclopoid copepods	94	64	46	43	22	28	13	28	39
% Rotifers	4	29	2	6	3	9	46	22	0.8
Bacterio:phytoplankton production ratio (%)	–	2	2	4	5	5	8	6	3
Minimum number of samples	11	46	45	41	52	53	20	19	16

Table IV. Calculated annual mean (linear interpolation) zooplankton grazing (crustaceans and rotifers) on phytoplankton and bacterioplankton obtained by using the multiple regression models for specific ingestion rates (daily ration) (Table II). Grazing is shown as a percentage of the total measured production and biomass together with total zooplankton biomass, the relative contribution to the biomass of *Daphnia*, *Bosmina*, cyclopoid copepods and rotifers, and the bacterioplankton:phytoplankton production ratio

	1984	1985	1986	1987	1988	1989	1990	1991	1992
Phytoplankton grazing									
(μg C l^{-1} day^{-1})	205	264	573	526	901	835	786	817	545
% of production	3	5	14	24	39	39	27	24	15
% of biomass (% day^{-1})	0.9	1.4	7	9	18	11	9	11	8
Bacterioplankton grazing									
(μg C l^{-1} day^{-1})	3	4	35	32	75	57	6	18	40
% of production	–	5	40	40	75	61	4	11	43
% of biomass (% day^{-1})	–	1	13	15	33	21	2	8	14
% of phytoplankton grazing	–	2	6	6	8	7	1	2	7
Total zooplankton biomass									
(mg DW l^{-1})	0.6	0.6	1.1	1.0	1.4	1.4	0.9	1.3	1.1
% *Daphnia* spp.	0.5	6	41	48	66	53	2	21	58
% *Bosmina longirostris*	4	40	5	0.6	0.2	0.0	36	29	0.0
% Cyclopoid copepods	94	43	53	46	31	39	18	31	42
% Rotifers	2	12	2	6	3	8	44	20	0.4
Bacterio:phytoplankton									
production ratio (%)	–	2	2	4	4	4	6	5	2
Minimum number of samples	18	75	86	79	89	91	34	19	17

might have been available during this period, we have ignored it to account for a decline in SCR and DR during these periods. When using DR values, we assumed that the relative contribution of bacterioplankton in the diet during the investigation period was the same as during the grazing experiments (1984–86), although minor changes occurred in relation to changes in the zooplankton grazing (Tables III and IV). We finally assumed that estimated DR and SCR for rotifers >140 μm were also valid for small rotifers.

Interpolated summer mean (1 May – 1 October) and annual mean grazing and related factors are shown in Tables III and IV, respectively. Calculated summer mean phytoplankton grazing based on DR varied ~8-fold from a minimum of 259 μg C l^{-1} day^{-1} (equivalent to 259 mg C m^2 day^{-1} as mean depth = 1 m) in 1984 to 1978 μg C l^{-1} day^{-1} in 1988. Phytoplankton grazing was low when the zooplankton biomass was low and dominated by cyclopoid copepods (1984–85), intermediate in years with an intermediately high biomass when dominated by *B.longirostris* or a mixed community of *Daphnia*, *Bosmina*, rotifers and copepods, and high in years with a high biomass of *Daphnia* spp. (1988–89) (Table IV). However, as estimated SCR did not differ essentially with respect to the cyclopoid copepods, *Daphnia* and *Bosmina* (Table III), the changes in phytoplankton grazing largely reflect changes in the zooplankton biomass.

Calculated summer mean phytoplankton grazing, expressed as a percentage of production and biomass, varied markedly: from 2 to 53% of daily production and from 0.7 to 28% day^{-1} of biomass. The variation in annual mean grazing was slightly less than that seen for summer mean grazing (Table IV). Thus, phytoplankton grazing only varied 4-fold, from 205 to 901 μg C l^{-1} day^{-1}. Likewise, the variation in grazing pressure was smaller, ranging from 3 to 39% of the production and 0.9 to 18% of the biomass.

Calculated summer mean bacterioplankton grazing varied seven times more than that of phytoplankton grazing (i.e. 58-fold), ranging from 3 μg C l^{-1} day^{-1} in 1985 to 169 μg Cl^{-1} day^{-1} in 1988. It was particularly low in 1984–85, when cyclopoid copepods were dominant, and in 1990–91, when *Bosmina* and rotifers were abundant, whereas it was comparatively high during years with *Daphnia* dominance, it being especially high in 1988 and 1989 when the biomass of *Daphnia* was high. Zooplankton grazing on bacterioplankton was substantially less than that on phytoplankton, ranging from 0.7 to 9% of phytoplankton grazing (Table III). On an annual basis, bacterioplankton grazing only varied 26-fold, from 3 to 75 μg C l^{-1} day^{-1} (Table IV). The inter-annual variation in the grazing pressure on bacteria was greater than for phytoplankton, ranging from 1.9 to 88% of bacterioplankton production and to 0.7–67% day^{-1} of biomass during summer (Table III). On an annual basis, zooplankton grazing reached a maximum of 75% of daily bacterioplankton production and 33% day^{-1} of biomass (Table IV). The grazing pressure on bacterioplankton was highest in years with high densities of *Daphnia*, and particularly low in years dominated by cyclopoid copepods (1984–85) and *Bosmina* and rotifers (1990–91).

In general, low differences were found between the grazing rates calculated on the basis of the SCR and DR values obtained by multiple regression on data from the grazing experiments (Table III). Based on CR, grazing on phytoplankton ranged from 421 to 1844 μg C l^{-1} day^{-1}, corresponding to 3–45% of daily production and 1–24% day^{-1} of biomass, while grazing on bacterioplankton ranged from 5 to 179 μg C l^{-1} day^{-1}, corresponding to 3–92% of daily production and 1–70% of biomass day^{-1}. In addition, inter-annual variation in grazing rates calculated on the basis of SCR was roughly the same as for the rates calculated on the basis of DR. In the following discussion, we therefore concentrate on grazing rates based on DR.

The changes in grazing pressure on phytoplankton and bacterioplankton, and in the relative abundance of various zooplankter, were related to changes in the abundance (CPUE) of fish as determined by survey gill nets and electrofishing along the shore (Figures 4 and 5). A negative linear relationship was found between CPUE of fish in terms of numbers and grazing in percentage of both phytoplankton and bacterioplankton biomass and production, and between CPUE of fish and zooplankton biomass. However, only the relationship for bacterioplankton was significant ($P < 0.05$). Grazing expressed as percentages of biomass and production was markedly higher for bacterioplankton than for phytoplankton at low fish density, and lower or similar at high densities (Figure 4). Among the filter-feeding zooplankton, a shift occurred from *Daphnia* dominance at low CPUE to *Bosmina* and rotifer dominance at the highest CPUE (Figure 5).

Discussion

Grazing experiments

As revealed by the grazing experiments, there was considerable inter-annual and seasonal variation in CR and grazing pressure on phytoplankton and

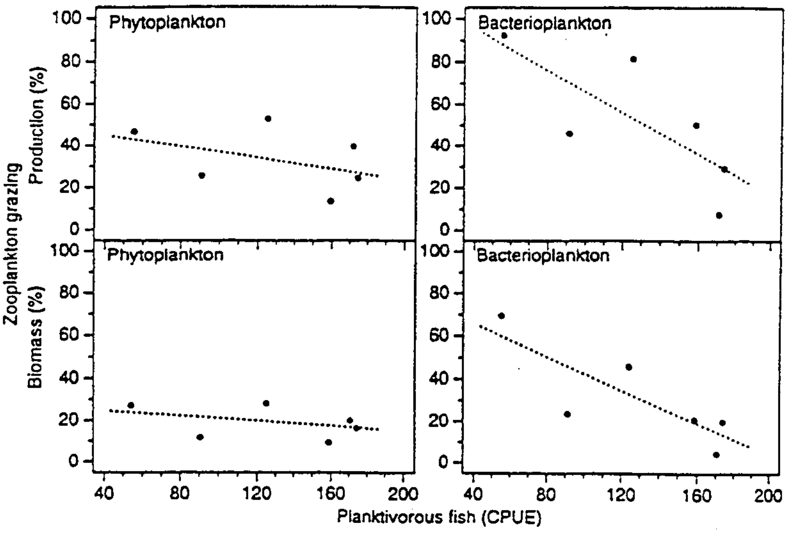

Fig. 4. Calculated summer average zooplankton grazing as a percentage of the production and biomass of phytoplankton (**left**) and bacterioplankton (**right**) versus the catch per unit effort in terms of numbers of planktivorous fish caught by gill netting in the open water and electrofishing along the shore.

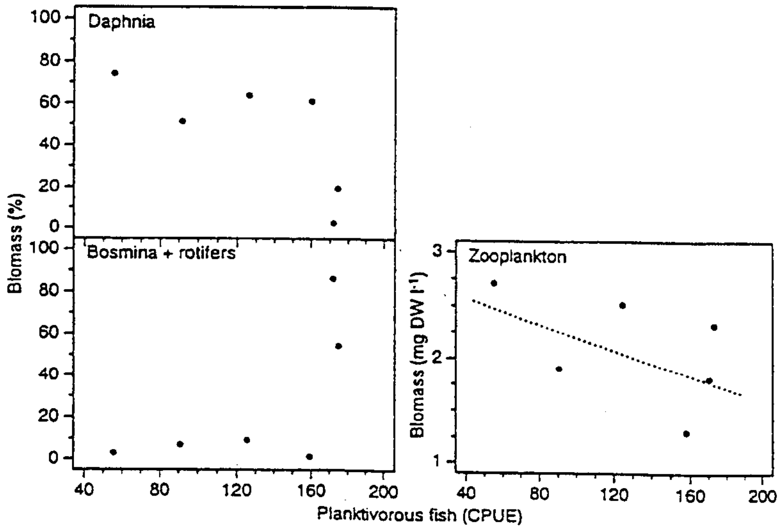

Fig. 5. The contribution of *Daphnia* and *Bosmina* + rotifers to the total biomass of zooplankton (**left**) and total zooplankton biomass (**right**) versus the catch per unit effort in terms of numbers of planktivorous fish caught by gill netting in the open water and electrofishing along the shore.

bacterioplankton. CR on bacterioplankton was only high when *Daphnia* spp. were dominant and abundant (1986), while CR on phytoplankton was high when cyclopoid copepods, *Daphnia* spp. or *B.longirostris* were dominant and abundant

(Figure 1). However, grazing pressure on phytoplankton expressed as a percentage of production was only high when *Daphnia* and *Bosmina* were dominant (1986, 1991).

Multiple regression analysis revealed that *B.longirostris*, *Daphnia* spp. and *C.vicinus*, which most frequently dominated the Lake Søbygaard pelagic zooplankton community, each contributed significantly to the variation in IR on phytoplankton, while only *Daphnia* spp. were significantly related to IR on bacterioplankton. The validity of applying multiple regression analysis at the community level to separate the impact of the species present can be questioned because of the risk of autocorrelation and misinterpretation of the impact of less abundant species. In the present study, it is suggested to be a minor problem because of the low number of species present and the long intervals separating periods of dominance by specific zooplankton grazers (Figure 1). Multiple regression analysis revealed no significant difference in *Daphnia* SCR on bacterioplankton and phytoplankton ($P > 0.05$). Low selectivity has also been found in a number of other studies (Hebert, 1978; DeMott, 1982, 1985). Cyclopoid copepods seemed to select for phytoplankton, although the variability of SCR in the regression was high. Herbivorous feeding by cyclopoids and particularly by *C.vicinus* is well known (e.g. Tóth and Zánkai, 1985; Adrian, 1991; Hansen and Santer, 1995), and further evidence is provided by the study on the population dynamics of *C.vicinus* in Lake Søbygaard (Hansen and Jeppesen, 1992). Bacterioplankton ingestion, however, was observed in most of the grazing experiments in which cyclopoids were exclusively dominant, albeit IR was low. This apparently contradicts the results from other studies. Thus, using a microsphere technique, Sanders *et al.* (1989) observed a lack of clearance of small-sized particles by calanoid and cyclopoid species during a single season in eutrophic Lake Oglethorpe. The same conclusion has also been reached by others, e.g. Bogdan and Gilbert (1987) and Vanderploeg and Paffenhöffer (1985). The apparent (albeit low and not significant) bacterioplankton ingestion by cyclopoid copepods in our study is therefore most likely caused by predation on labelled bacterivores, flagellates or ciliates, rather than on bacteria.

Bosmina longirostris did not contribute significantly to the SCR on bacterioplankton either, the SCR regression coefficient being four times lower than for *Daphnia* spp. This is in accordance with the finding of DeMott and Kerfoot (1982) that *Bosmina* strongly select against bacterioplankton (4- to 16-fold higher SCR on *Chlamydomonas* than on *Aerobacter*), and that adult *Bosmina* presented with a pure culture of *Aerobacter* even stop feeding. Similarly, Hart and Jarvis (1993) found a 4-fold higher SCR on phytoplankton than on bacterioplankton for *Bosmina*. That the SCR of *Bosmina* on bacterioplankton is low in Lake Søbygaard is further supported by the fact that both bacterioplankton biomass and production were particularly high in years and periods when *Bosmina* was dominant (Jeppesen *et al.*, 1992, 1996a).

Zooplankton DR feeding on phytoplankton averaged 0.82, or 1.0 when adjusted to 15°C according to Gulati *et al.* (1982), while DR on bacterioplankton was 0.03 (0.04 at 15°C) (Table I). In a comprehensive study of mesotrophic Lake Vechten, Gulati *et al.* (1982) found that the zooplankton community DR (^{14}C-labelled seston < 33 μm) ranged from 0.26 to 0.61 on an annual basis and from 0.45 to 1.28 during summer. In subsequent investigations in a large number of shallow lakes, annual DR (adjusted to 15°C) was found to range from 0.65 to 3.7, and in most cases from 1 to 2, with the highest ratios being found in lakes in which algal biomass was high and small cladocerans dominant (Gulati, 1990). Compared with these ratios, and taking into account that the more slow-growing cyclopoids most often dominated the crustacean biomass in Lake Søbygaard during the time of the grazing experiments, the zooplankton DR of 1.0 at 15°C found in the present study seems probable, although it is at the low end of the scale determined by Gulati (1990). The generally higher DR values found in Gulati's experiments may reflect the fact that ingestion in his study comprised the total seston pool, i.e. also detritus, the latter often being high in shallow lakes because of resuspension. In contrast, in our experiments and the other experiments cited, only phytoplankton ingestion was measured.

DR for *B.longirostris* (0.88) was low compared with the value of 2–3 on the total seston pool reported by Gulati (1990), but was close to the DR of 1.0 on phytoplankton reported by Johnson and Börsheim (1988). The cyclopoid copepod DR corresponds to some of the values found in the literature on eutrophic lakes. For example, Adrian (1991) reported average phytoplankton ingestion by *C.vicinus* of 7.3 (4.5–10.6) μg DW indiv.$^{-1}$ day^{-1} for females and 8.7 μg DW indiv.$^{-1}$ day^{-1} for males in hypertrophic Lake Heiliger See, while Tóth and Zánkai (1985) reported a value of 8.1 μg DW indiv.$^{-1}$ day^{-1} for adult *C.vicinus* in Lake Balaton. Assuming an individual biomass equivalent to those found in Lake Søbygaard, these ingestion rates correspond to a DR of 0.6, 1.2 and 0.8, respectively, or to a mean of 0.8, which is comparable with the DR of 0.89 at 15°C determined for *C.vicinus* by regression analysis in the present study (Table II). DR was, however, somewhat higher than values obtained at high food concentrations (*Chlamydomonas*) in laboratory experiments conducted by Santer and van den Bosch (1994). Contrary to most other cyclopoid copepods, *C.vicinus* can undergo its whole life cycle as a herbivore (Santer and van den Bosch, 1994).

Model estimates of grazing

Except for the DR values of Gulati (1990), which were based on a total seston uptake, the DR values we determined by regression analysis fit relatively well with those reported by others for the zooplankton species in question. We have therefore used the SCR and DR values obtained from the regression analysis to calculate grazing for the whole study period (1984–92). We thus assume that all phytoplankton <50 μm are edible. This is supported by the fact that cladoceran fecundity was generally high, except for short periods (<2% of the summer 1984–92) with extremely high grazing pressure during which the phytoplankton collapsed (Jeppesen *et al.*, 1990a; E.Jeppesen, unpublished observation).

Phytoplankton grazing expressed as a percentage of phytoplankton biomass ranged between 0.8 and 14% day^{-1} on an annual basis (0.7–28% day^{-1} in summer), which is comparable to that found in the majority of other studies (Cyr and Pace, 1992). Carney and Elser (1990) argued that the crustacean grazing pressure on phytoplankton is highest in mesotrophic lakes and decreases markedly towards hypertrophic lakes due to a shift to dominance by less palatable and less nutritious phytoplankton. However, in hypertrophic Lake Søbygaard, the grazing pressure was low in, for instance, 1984–85 despite dominance by edible phytoplankton (mainly *Scenedesmus*). Several authors have emphasized the importance of fish in the determination of the grazing pressure on phytoplankton in eutrophic lakes (e.g Leipold, 1989; Gulati *et al.*, 1990; Sarnelle, 1992; Carpenter and Kitchell, 1993; Mortensen *et al.*, 1994). This is further supported by data from 39 shallow Danish lakes showing that the potential phytoplankton grazing pressure on zooplankton was significantly inversely related to the density of planktivorous fish (CPUE, multiple mesh size gill nets) and that this relationship was not influenced significantly by whether edible or inedible phytoplankton dominated (Jeppesen *et al.*, 1996b). Fish also seem to play a key role in Lake Søbygaard. In the period 1987–92, both zooplankton biomass and phytoplankton grazing on algae were negatively related (although not significantly so) to the CPUE of fish in terms of numbers caught with gill nets and electrofishing. Moreover, when fish density was highest, a shift occurred from *Daphnia* dominance to dominance by *Bosmina* and rotifers. Unfortunately, routine investigation of fish density was not initiated until 1987, a mark–recapture study, however, being undertaken in 1986 (E.Mortensen *et al.*, unpublished data). The latter, which also included age determination on the basis of scale analyses, showed that fish biomass was high in 1986 (660 kg ha^{-1}), and that the stock was totally dominated by roach and rudd larger than 12 cm (3^+ or older), whereas only few 0^+–2^+ fish were caught. It is, therefore, reasonable to conclude that the abundance of planktivorous fish was high in 1984 and decreasing until 1986, which may explain the particularly low grazing pressure on phytoplankton in 1984–85 (Tables III and IV). Analyses of seasonal variations in zooplankton (Jeppesen *et al.*, 1990) and experimental *in situ* investigations in the lake (Hansen *et al.*, 1991) suggest, however, that high pH (>10.5) mediated indirectly by the low grazing pressure on phytoplankton (low grazing means high phytoplankton production and accordingly high pH) in a self-amplifying manner has added to the low grazing pressure in 1984 and 1985.

How trophic structure affects zooplankton grazing on bacterioplankton is less well known. Evidence from enclosure experiments in eutrophic lakes indicates that fish stock alterations may markedly affect the grazing rate on bacterioplankton. For example, Riemann (1985) found a zooplankton grazing rate of 4.6% of bacterial production when fish density in the enclosures approximately corresponded to that in the lake under study, while removal of fish from the enclosures led to an increase in grazing rate to 48–51% of production. Geertz-Hansen *et al.* (1987) found even higher grazing rates (55–114%) in fish-free enclosures, and biomanipulation studies in a German lake revealed that *Daphnia* consistently consumed >95% of the bacterioplankton production during late summer (Jürgens, 1994; Jürgens *et al.*, 1994). The present study supports the concept that grazing on bacterioplankton is high in eutrophic lakes when fish predation is low (Figure 4, Tables IV and V), the key organism being *Daphnia*, as in other studies (Jürgens, 1994). Daily mean grazing rates thus reached maxima of 77–88% of the daily bacterioplankton production during the summers of 1988–89 and 44–67% of the biomass. However, at higher planktivorous fish densities, at which the zooplankton community was dominated by the less efficient bacterioplankton feeders *B.longirostris*, rotifers and *C.vicinus*, the zooplankton grazing rates calculated for Lake Søbygaard were below 5% of bacterioplankton production and 2% day^{-1} of biomass. In shallow lakes, the zooplankton community at natural fish densities typically changes from one dominated by calanoid copepods at low total P to *Daphnia* dominance at intermediate total P, and finally to dominance by *Bosmina* or cyclopoid copepods and rotifers at high total P (Gulati *et al.*, 1985; Jeppesen *et al.*, 1992). As calanoid copepods are inefficient grazers on bacterioplankton-sized food (Horn, 1985), it is likely that the zooplankton grazing pressure on bacterioplankton at natural fish densities is highest at intermediate total P levels, i.e. when the contribution of *Daphnia* to total biomass is highest.

The response to changes in the abundance of planktivorous fish was markedly higher for bacterioplankton than for phytoplankton (Figure 3), which reflects the fact that a shift occurs at increasing fish density towards higher abundance of inefficient bacteria, but comparatively efficient phytoplankton grazers. High zooplankton grazing percentages at low fish densities suggest low protozoan grazing on bacteria. This corresponds to the results from other investigations (Christoffersen *et al.*, 1993; Jürgens, 1994), showing that *Daphnia* in high densities not only affect the bacterioplankton, but exploit the whole microbial community. No data on flagellates were available from the investigation period in Lake Søbygaard, but a strong negative relationship was found between the *Daphnia* biomass and bacterioplankton biomass (Jeppesen *et al.*, 1996a) as well as ciliate density (E.Jeppesen, unpublished results). In addition, the grazing pressure, expressed as a percentage of production and biomass, was markedly higher on bacterioplankton than on phytoplankton in the *Daphnia*-dominated situations. This does not necessarily mean, however, that the impact of grazing is highest on bacterioplankton. In fact, the biomass of phytoplankton decreased 5-fold from 1984–85 to 1988–89, while only a 2-fold reduction was found for bacterioplankton (Jeppesen *et al.*, submitted). This may be explained by the fact that in addition to grazing, phytoplankton loss by sedimentation was high in this green algae-dominated lake (in 1985, ~50% of the production per day during summer) (Jeppesen *et al.*, 1990b; P. Kristensen and P. Jensen, unpublished) and even increased markedly with increasing grazing pressure due to a simultaneous 10-fold increase in the average volume of phytoplankton (Jeppesen *et al.*, 1990, and E. Jeppesen, unpublished results). Consequently, grazing enhanced phytoplankton loss by sedimentation and thereby the overall loss in the lake. A similar effect is not to be expected for bacterioplankton as high *Daphnia* grazing normally results in dominance by small bacteria (Jürgens, 1994).

The observed fish-mediated changes in zooplankton grazing rate also seem to affect the relative levels of grazing on phytoplankton and bacterioplankton, as well as the bacterioplankton:phytoplankton production ratio. Thus, annual bacterioplankton grazing in terms of C amounted to 1–2% of phytoplankton grazing when inefficient bacterioplankton feeders such as *C.vicinus* and *B.longirostris* were dominant at high fish predation pressure, and despite a higher grazing pressure than on phytoplankton it increased to 6–8% at relatively low fish predation pressure when *Daphnia* spp. were dominant (Table IV). Likewise, the bacterioplankton:phytoplankton production ratio changed from 2% when cyclopoid copepods dominated to 2–4% and 5–6% when *Daphnia* and *Bosmina*, respectively, were dominant and present in high densities. The relatively low importance of bacterioplankton to the zooplankton diet is in concert with the findings of numerous other studies (Börsheim and Andersen, 1987; Hart and Jarvis, 1993). It primarily reflects the fact that bacterioplankton biomass is usually much lower than phytoplankton biomass, although in some lakes the difference is further enhanced because the zooplankton actively select against bacterioplankton. An exception is humic lakes, in which bacterioplankton grazing may be higher than phytoplankton grazing (Hessen, 1985; Kankaala, 1988). Our findings indicate that changes in fish predation pressure may also have an impact on the relative importance of bacterioplankton to the zooplankton diet, as well as on the bacterioplankton:phytoplankton production ratio, mainly as a result of fish-mediated changes in the composition of the zooplankton community.

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References

Adrian,R. (1991) Filtering and feeding rates of cyclopoid copepods feeding on phytoplankton. *Hydrobiologia*, **210**, 217–223.

Arndt,H. (1993) Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates ciliates) – a review. *Hydrobiologia*, **255/256**, 231–246.

Bergquist,A.M., Carpenter,S.R. and Latino,J.C. (1985) Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. *Limnol. Oceanogr.*, **30**, 1037–1045.

Bjørnsen,P.K., Larsen,J.B., Geertz-Hansen,O. and Olsen,M. (1986) A field technique for the determination of zooplankton grazing on natural bacterioplankton. *Freshwater Biol.*, **16**, 245–253.

Bogdan,K.G. and Gilbert,J.J. (1987) Quantitative comparison of food niches in some freshwater zooplankton. A multitracer approach. *Oecologia (Berlin)*, **72**, 331–340.

Börsheim,K.Y. and Andersen,S. (1987) Grazing and food size selection by crustacean zooplankton compared to production of bacteria and phytoplankton in a shallow Norwegian mountain lake. *J. Plankton Res.*, **9**, 367–379.

Carney,H.J. and Elser,J.J. (1990) Strength of zooplankton-phytoplankton coupling in relation to trophic state. In Tilzer,M.M.(ed.), *Ecology of Large Lakes*. Springer, New York, pp. 616–631.

Carpenter,S.R. and Kitchell,J.R. (1993) Cascading trophic interactions and lake productivity. *BioScience*, **35**, 634–639.

Christoffersen,K., Riemann,B., Klysner,A. and Søndergaard,M. (1993) Potential role of natural populations of zooplankton on plankton community structure in eutrophic lake water. *Limnol. Oceanogr.*, **38**, 561–573.

Cyr,H. and Pace,M.L. (1992) Grazing by zooplankton and its relationship to community structure. *Can. J. Fish. Aquat. Sci.*, **49**, 1455–1465.

DeMott,W.R. (1982) Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnol. Oceanogr.*, **23**, 518–527.

DeMott,W.R. (1985) Relations between filter mesh-size, feeding mode, and capture efficiency for cladocerans feeding on ultrafine particles. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **21**, 125–134.

DeMott,W.R. and Kerfoot,W.C. (1982) Competition among cladocerans: Nature of the interaction between *Daphnia* and *Bosmina*. *Ecology*, **63**, 1949–1966.

Downing,J.A. and Peters,R.H. (1980) The effect of body size and food concentration on the in situ filtering rates of *Sida crystalina*. *Limnol. Oceanogr.*, **25**, 883–895.

Fuhrmann,J.A. and Azam,F. (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: Evaluation and field results. *Mar. Biol.*, **66**, 109–120.

Geertz-Hansen,O., Olesen,M., Bjørnsen,P.K., Larsen,J.B. and Riemann,B. (1987) Zooplankton consumption of bacteria in a eutrophic lake and in experimental enclosures. *Arch. Hydrobiol.*, **110**, 553–563.

Güde,H. (1988) Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. *Hydrobiologia*, **159**, 63–73.

Gulati,R.D. (1985) Zooplankton grazing methods using radioactive tracers: technical problems. *Hydrobiol. Bull.*, **19**, 61–69.

Gulati,R.D. (1990) Structural and grazing responses of zooplankton community to biomanipulation of some Dutch water bodies. *Hydrobiologia*, **200/201**, 99–118.

Gulati,R.D., Siewertsen,K. and Postema,G. (1982) The zooplankton: its community structure, food and feeding, and role in the ecosystem of Lake Vechten. *Hydrobiologia*, **95**, 127–163.

Gulati,R.D., Siewertsen,K. and Postema,G. (1985) Zooplankton structure and grazing activities in relation to food quality and concentration in Dutch lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **21**, 91–102.

Gulati,R.D., Lammens,E.H.R.R., Meijer,M.-L. and van Donk,E. (1990) Biomanipulation–Tool for water management. *Hydrobiologia*, **200/201**, 1–628.

Hansen,A.-M. and Jeppesen,E. (1992) Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. *J. Plankton Res.*, **14**, 591–605.

Hansen,A.-M. and Santer,B. (1995) The influence of food resources on the development, survival and reproduction of the two cyclopoid copepods: *Cyclops vicinus* and *Mesocyclops leuckarti*. *J. Plankton Res.*, **17**, 631–646.

Hansen,A.-M., Christensen,J.V. and Sortkjær,O. (1991) Effect of high pH on zooplankton and nutrients in fish-free enclosures. *Arch. Hydrobiol.*, **123**, 143–164.

Hart,R.C. and Jarvis,A.C. (1993) *In situ* determinations of bacterial selectivity and filtration rates by five cladoceran zooplankters in a hypertrophic subtropical reservoir. *J. Plankton Res.*, **15**, 295–315.

Hebert,P.D. (1978) The population biology of *Daphnia* (Crustacea, Daphnidae). *Biol. Rev.*, **53**, 387–426.

Hessen,D.O. (1985) Filtering structures and particle size selection in coexisting Cladocera. *Oecologia (Berlin)*, **66**, 368–372.

Hobbie,R., Daly,J. and Jasper,S. (1977) Use of nuclepore filters for counting bacteria by fluorescence microscopy. *Appl. Environ. Microbiol.*, **33**, 1225–1228.

Holm-Hansen,O. and Riemann,B. (1978) Chlorophyll *a* determination: improvements in methods. *Oikos*, **30**, 438–447.

Holtby,L.B. and Knoechel,R. (1981) Zooplankton-filtering rates: error due to loss of radio isotopes label in chemically preserved samples. *Limnol. Oceanogr.*, **26**, 774–780.

Horn,W. (1985) Investigations into the food selectivity of the planktic crustaceans *Daphnia hyalina*, *Eudiaptomus gracilis* and *Cyclops vicinus*. *Int. Rev. Ges. Hydrobiol.*, **70**, 603–612.

Jarvis,A.C. and Hart,R.C. (1993) Determining *in situ* bacterial filtration rates by zooplankton : improvements to the [methyl-^{3}H]thymidine labelling technique. *J. Plankton Res.*, **15**, 277–294.

Jeppesen,E., Søndergaard,M., Sortkjær,O., Mortensen,E. and Kristensen,P. (1990a) Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study on phytoplankton collapses in Lake Søbygaard, Denmark. *Hydrobiologia*, **191**, 139–148.

Jeppesen,E., Søndergaard,M., Mortensen,E., Kristensen,P., Riemann,B., Jensen,H.J., Müller,J.P., Sortkjær,O., Jensen,J.P., Christoffersen,K., Bosselmann,S. and Dall,E. (1990b) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: Cross-analysis of three Danish case-studies. *Hydrobiologia*, **200/201**, 205–218.

Jeppesen,E., Sortkjær,O., Søndergaard,M. and Erlandsen,M. (1992) Impact of a trophic cascade on heterotrophic bacterioplankton production in two shallow fish-manipulated lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **37**, 219–231.

Jeppesen,E., Erlandsen,M. and Søndergaard,M. (1996a) Can simple empirical equations describe the seasonal dynamics of bacterioplankton in lakes: A long-term study in shallow hypertrophic and biological highly oscillating lake Søbygaard, Denmark. *Microb. Ecol.*, in press.

Jeppesen,E., Jensen,J.P., Søndergaard,M., Lauridsen,T., Pedersen,L.J. and Jensen,L. (1996) Top-down control in freshwater lakes: the role of fish, submerged macrophytes and water depth. *Hydrobiologia*, in press.

Johnson,G.H. and Børsheim,K.V. (1988) Functional response and food selection of the water flea, *Bosmina longispina*. *J. Plankton Res.*, **10**, 319–325.

Jürgens,K. (1994) Impact of *Daphnia* on planktonic microbial food webs – A review. *Microb. Food Webs*, **8**, 295–324.

Jürgens,K., Arndt,H. and Rothhaupt,K.O. (1994) Zooplankton mediated changes of microbial food web structure. *Microb. Ecol.*, **5**, 27–42.

Kankaala,P. (1988) The relative importance of algae and bacteria as food for *Daphnia longispina* (Cladocera) in polyhumic lake. *Freshwater Biol.*, **19**, 285–296.

Kerfoot,C.W., Levitan,C. and DeMott,W.R. (1988) *Daphnia*-phytoplankton interactions: density-dependent shifts in resource quality. *Ecology*, **69**, 1806–1825.

Lampert,W. and Muck,P. (1985) Multiple aspects of food limitation in zooplankton communities: the *Daphnia Eudiaptomus* example. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **21**, 311–322.

Lampert,W. and Taylor,B.E. (1985) Zooplankton grazing in a eutrophic lake: Implications of diel vertical migration. *Ecology*, **66**, 68–82.

Leipold,M.A. (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.*, **134**, 922–949.

Mortensen,E., Jensen,H. and Müller,J.P. (1991) Retningslinier for standardiseret forsøgsfiskeri i søer og en beskrivelse af fiskeredskaber og -metoder. [Guidelines for standardized test-fishing in lakes and a description of fish gears and methods.] National Environmental Research Institute, 60 pp. (in Danish).

Mortensen,E., Jeppesen,E., Søndergaard,M. and Kamp Nielsen,L. (eds) (1994) Nutrient dynamics and biological structure in shallow freshwater and brackish lakes. *Hydrobiologia*, **275–276**, 1–507.

Mourelatos,S., Rougier,C. and Lacroix,G. (1992) Radiotracer losses due to freezing in formalin of ^{14}C-labelled cladocerans. *Arch. Hydrobiol.*, **126**, 239–253.

Nagata,T. and Okamoto,K. (1988) Filtering rates on natural bacteria by *Daphnia longispina* and *Eodiaptomus japonicus* in Lake Biwa. *J. Plankton Res.*, **10**, 835–850.

Olrik,K. (1991) Planteplankton-metoder. Prøvetagning, bearbejdning og rapportering ved undersøgelseri søer og marine områder. Miljøprojekt nr. 187. Miljøstyrelsen, Miljøministeriet, 108 pp. (in Danish).

Pace,M.L. and Funke,E. S(1991) Regulation of planktonic microbial communities by nutrients and herbivores. *Ecology*, **72**, 904–914.

Riemann,B. (1985) Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. *Appl. Environ. Microbiol.*, **50**, 187–193.

Riemann,B. and Søndergaard,M. (1986) Regulation of bacterial secondary production in two eutrophic lakes and in experimental enclosures. *J. Plankton Res.*, **8**, 519–536.

Riemann,B., Søndergaard,M., Schierup,H.-H., Bosselmann,S., Christensen,G., Hansen,J. and Nielsen,B. (1982) Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossø. *Int. Rev. Ges. Hydrobiol.*, **67**, 145–185.

Sanders,R.W., Porter,K.G., Bennett,S.J. and DeBiase,A.E. (1989) Seasonal patterns of bacterivory by flagellates, ciliates, rotifers and cladocerans in a freshwater planktonic community. *Limnol. Oceanogr.*, **34**, 673–687.

Santer,B. and van den Bosch,F. (1994) Herbivorous nutrition of *Cyclops vicinus*: the effect of a pure algal diet on feeding, development, reproduction and life cycle. *J. Plankton Res.*, **16**, 171–195.

Sarnelle,O. (1992) Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology*, **73**, 551–560.

Statistical Analysis Systems Institute (1989) *SAS/STAT User's Guide*, Version 6, 4th edn, Vols 1 and 2. SAS Institute Inc., Cary, NC, 943, and 846 pp.

Tóth,L.G. and Zánkai,N.P. (1985) Feeding of *Cyclops vicinus* (Uljanin) (Copepoda: Cyclopoida) in Lake Balaton on the basis of gut content analyses. *Hydrobiologia*, **122**, 251–260.

Vanderploeg,H.A. and Paffenhöfer,G.-A. (1985) Modes of algal capture by the freshwater copepod *Diaptomus sicilis* and their relation to food-size selection. *Limnol. Oceanogr.*, **30**, 871–885.

Vaqué,D. and Pace,M.L. (1992) Grazing on bacteria by flagellates and cladocerans in lakes of contrasting food-web structure. *J. Plankton Res.*, **14**, 307–321.

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Can Simple Empirical Equations Describe the Seasonal Dynamics of Bacterioplankton in Lakes: An Eight-Year Study in Shallow Hypertrophic and Biologically Highly Dynamic Lake Søbygård, Denmark

E. Jeppesen, M. Erlandsen, M. Søndergaard

Dept. of Lake and Estuarine Ecology, National Environmental Research Institute, Vejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark

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ABSTRACT

Seasonal variation in bacterioplankton abundance, biomass, and bacterioplankton production was studied over eight years in hypertrophic Lake Søbygård. Biologically, the lake is highly variable; this is due mainly to large interannual variation in fish recruitment. Bacterioplankton production was low during winter, typically 1–3 × 10^7 cells l^{-1} h^{-1}, and high during summer, albeit greatly fluctuating with maximum rates typically ranging from 60 to 90 × 10^7 cells l^{-1} h^{-1} (or 0.4 to 0.6 mg C l^{-1} day^{-1}). Less pronounced variations were found in bacterioplankton abundance, which typically ranged from 3–8 × 10^9 cells l^{-1} in winter to 15–30 × 10^9 cells l^{-1} during summer. The specific growth rate of bacterioplankton varied from 0.02–0.2 d^{-1} in winter to 0.5–2.3 day^{-1} during summer. Interpolated mean bacterioplankton production, in terms of carbon, ranged from 0.08 to 0.16 mg C l^{-1} day^{-1}, corresponding to 1.6–5.5% of the phytoplankton production, while biomass ranged from 0.28 to 0.36 mg C l^{-1}, corresponding to 1.9–4.6% of the phytoplankton biomass. We conducted regression analysis, relating the bacterioplankton variables to a number of environmental variables, and evaluated the interannual parameter variability. Chlorophyll *a* and phytoplankton production contributed less to the variation in the bacterioplankton variables than in most previous analyses using data from less eutrophic systems. We suggest that the proportion of phytoplankton production that is channelized through bacterioplankton in lakes decreases with increasing trophic state and decreasing mean depth. This probably reflects a concurrent increase in fish predation on macrozooplankton and loss by sedimentation. An important part of the residual variation in the equations hitherto proposed in the literature could be explained by variation in macrozooplankton biomass and pH > 10.2. A negative effect of high pH on bacterioplankton production was confirmed by laboratory experiments. The impact of different zooplankton varies considerably, with *Daphnia* seeming to have a negative impact on bacterioplankton abundance and, thereby, indirectly on bacterioplankton production, while *Bosmina*, rotifers, and cyclopoid copepods seem to stimulate both abundance and production. *Bosmina* apparently also stimulate the bacterioplankton specific growth rate.

Correspondence to: E. Jeppesen.

Introduction

Bacterial abundance and production vary seasonally [6, 18, 48], as well as along a trophic gradient [8, 13]. Attempts have been made to develop empirical equations relating bacterioplankton abundance, production (measured as ^{3}H-thymidine uptake), and specific growth rate to a number of physicochemical and biological variables, e.g., temperature, chlorophyll *a*, and phytoplankton production [8, 13, 14, 56]. These equations indicate that bacterioplankton abundance increases with increasing chlorophyll *a* [8, 14], and that bacterioplankton production increases with either increasing phytoplankton production or chlorophyll *a* and with bacterioplankton abundance [13, 56]. However, a subject of much debate is the size of the slope of these relations [14, 16] and, consequently, the proportion of the phytoplankton production being channelized to the bacterioplankton. Water temperature also has a positive impact on both production and specific growth rate, the latter being positively related to the interaction between temperature and chlorophyll *a* and mean bacterioplankton cell volume [56].

The equations previously developed are based mainly on summer data from a large number of aquatic systems worldwide. Few investigations have tried to develop equations for seasonal variation in bacterioplankton variables, and few investigations extend beyond one year [18]. Moreover, these equations fail to address the impact of the zooplankton on the bacterioplankton dynamics, even though macrozooplankton are able both to stimulate bacterioplankton production (e.g., by fueling the bacterioplankton with organic matter released during phytoplankton grazing [35] or by grazing on potential bacterioplankton predators such as ciliates and flagellates) and directly suppress bacterioplankton production by cropping. The balance between the two processes seems to vary with zooplankton composition and grazing pressure [21, 29]. Numerous enclosure experiments (e.g., [43, 12, 32, 34]) and full-scale experiments [28] have shown major decreases in bacterioplankton abundance and production in eutrophic lakes following changes in fish density. This phenomenon is attributable mainly to increases in the abundance of large-sized cladocerans (*Daphnia*). In concert with this, Jeppesen et al. [28] found a twofold increase in bacterioplankton production and specific growth rate in a shallow lake following a shift in zooplankton dominance from *Daphnia* to the less efficient bacterioplankton feeder, *Bosmina*. Thus, it seems likely that some of the residual variance in the simple "bottom-up" equations of Bird and Kalff [8], Cole et al. [13], White et al. [56], and Currie [14] might be attributable to variation in zooplankton composition and abundance.

In this paper, we describe the seasonal variation in bacterioplankton dynamics during an eight-year period (295–358 data sets), in shallow, hypertrophic Lake Søbygård, which, during the study, underwent major changes in its biological structure, mainly reflecting changes in the density of planktivorous fish. We conducted regression analyses on bacterioplankton abundance, production, and specific growth rate versus various environmental variables, and compared estimated parameters with those advanced on a multilake data set. In addition, we analyzed interannual parameter variations and present new equations that incorporate the effect of crustaceans, rotifers, and high pH.

Materials and Methods

Study Area

Lake Søbygård has a surface area of 40 ha, a mean and maximum depth of 1.0 and 1.9 m, respectively, and a hydraulic retention time of 15–20 days. Summer average total P is 550–1,000 μg l^{-1}, and the lake is hypertrophic. Large natural changes have occurred in the fish stock as a result of major fish kills in the late 1970s and low recruitment since 1984 (particularly from 1984 to 1987), due to high pH during the spawning period (up to pH 11.2). In addition, 4.3 tn of planktivorous fish (mainly roach [*Rutilus rutilus*] and rudd [*Scardinius erythrophtalmus*])—equivalent to 17% of the standing stock in 1986—were removed by commercial fishermen between 1986 and 1988. Further details about the lake and the variations in its biological structure are given in Jeppesen et al. [27, 28, 29] and Hansen and Jeppesen [22].

Sampling, Measurements, and Calculations

For enumeration of zooplankton, 6.6–7.2 liters lake water from each of 1–3 stations was sampled with a Patalas sampler, filtered through a 20-μm mesh net, and fixed with 1 ml Lugol solution in 100 ml tap water. The samples were pooled from 0.5 and 1.0 m. During periods of peak zooplankton density, 2–3 samples were enumerated; otherwise only one sample (mid-lake station) was enumerated. Zooplankton larger than 140 μm were counted at a magnification of ×40, while subsamples of a 20- to-140-μm fraction were counted in an inverted microscope at a magnification of ×100. In periods when suspended particulate content was high, it was necessary to dilute the samples five- to tenfold before enumeration, in which case zooplankton larger than 140 μm were enumerated on subsamples. The percentage of sample volume enumerated on each sampling date ranged from 2 to 100%. Ciliates were enumerated on unfiltered 100-ml subsamples from a composite 6.6-l sample taken with a Patalas sampler at depths of 0.5 and 1.5 m and fixed in Lugol solution.

Bacterioplankton production was measured using the approach of Fuhrman and Azam [19], with minor changes. Triplicate samples or formalin-killed blanks (1% final concentration) were incubated in Jena flasks in situ with 12.5 nM ^{3}H-methylthymidine for 15–60 min, depending on lake water temperature. The reaction was stopped by adding formalin. Within 2 h after sampling, 7–10 ml of each sample was filtered on a 25-mm cellulose acetate filter (0.2 μm) and rinsed 8 times with 1 ml ice-cold 5% TCA. The radioactivity retained on the filters was counted within 48 h after sampling; quench correction was made using the external channels ratio method. Bacterial production was calculated from ^{3}H-methylthymidine incorporation using the following conversion factors: 2×10^9 cells (nmol thymidine)$^{-1}$ [43] and 25 fg C cell^{-1} (R. Bell, personal communication).

Enumeration of bacteria was undertaken using the method of Hobbie et al. [24] with only minor modification [29] at ×1,560 magnification using a Leitz epifluorescence microscope equipped with a 75-W mercury lamp. At least 500 cells were enumerated on two to three different fields. Bacterial cell dimensions were measured using an eyepiece micrometer at ×1,560 magnification (each micrometer unit = 0.7 μm). Cells were divided into rods (8 size classes), cocci (4 size classes), and half-circle formed rods (4 classes), and cell volume calculated using standard geometric formulas. Biomass, in terms of carbon, was determined from cell production, as described for bacterioplankton production.

Phytoplankton ^{14}C production corrected for dark fixation was estimated from the photosynthesis vs. irradiance relationship determined from laboratory incubation [27], and integrated over depth and time using observations of Secchi depth (converted to a light extinction coefficient) and the time variation of surface irradiance at a station situated 30–40 km from the lake. Lake water chlorophyll *a* was determined spectrophotometrically, after ethanol extraction [26].

Statistical Analyses

The data were analyzed by multiple regression methods using the SAS statistical package [47]. We first made regressions on equations comparable to those developed by Bird and Kalff [8], Cole et al. [13], White et al. [56], Currie [14], and combinations thereof. Subsequently, new equations were developed using stepwise regression procedures on possible explanatory variables; the equations were verified by forward and backward procedures. The final regression equations were analyzed for outliers by examining deletion residuals and high leverage points [5]. In order to compare the different equations, we calculated the root mean square error (RMSE) between the untransformed observation (y) and the mean corrected backtransformed prediction ($\hat{\mu}$) for each equation. $\hat{\mu}$ is obtained as follows: let $\hat{y}$ denote the backtransformed prediction of y and let s^2 denote the residual variance from the regression equation, and define the correction factor $\mathrm{CF} = \exp(\frac{1}{2} s^2)$ (logarithm, base e) or $\mathrm{CF} = \mathrm{antilog}_{10}(1.1513\ s^2)$ (logarithm, base 10), then $\hat{\mu} = \mathrm{CF} \times \hat{y}$ [36]. With this notation we have $\mathrm{RMSE} = (1/n\Sigma(y - \hat{\mu})^2))^{1/2}$, where n is the number of observations. Note that RMSE has the same dimension as y. Bivariate plots of the response variables versus the explanatory variables indicated that data should be log transformed (base e, unless otherwise stated), except for water temperature and pH. Since only high pH values were believed to influence bacterioplankton production, we compared several cutoff points, assuming no pH effect below the cutoff point and a linear decrease above, i.e., using a variable of the form pH(cutoff point) = max(pH − cutoff point, 0).

Abbreviations used: BACPRO = bacterioplankton production (μg C l^{-1} day^{-1}, unless otherwise stated); ABUND = bacterioplankton abundance (10^9 cells l^{-1}); TEMP = water temperature (°C); SGR = bacterioplankton specific growth rate (day^{-1}); CHLA = chlorophyll *a* (μg l^{-1}); MVOL = bacterioplankton mean cell volume (μm^3); PP = phytoplankton production (μg C l^{-1} day^{-1}); PHYTBIO = phytoplankton biomass (μg C l^{-1}); CYC, DAPH, BOS, ROT = biomass (mg DW l^{-1}) of cyclopoid copepods (mainly *Cyclops vicinus*), *Daphnia* spp., *Bosmina longirostris*, and rotifers, respectively.

Results

Seasonal Dynamics and Correlations

There was considerable seasonal and interannual variation in bacterioplankton production, abundance, and specific growth rate in Lake Søbygård during the study period (Fig. 1). Bacterioplankton production was generally low during winter (minimum typically 1–3 × 10^7 cells l^{-1} h^{-1} or 0.006–0.018 mg C l^{-1} day^{-1}), and high during summer, although fluctuating markedly without any repeated seasonal pattern (Fig. 1). The major fluctuations in bacterioplankton production generally paralleled those in phytoplankton production, chlorophyll *a*, and water temperature (Fig. 1). During summer, phytoplankton production and chlorophyll *a* were, in turn, inversely related, in general, to the biomass of filter-feeding macrozooplankton (*Daphnia longispina*, *B. longirostris*, and rotifers). Maximum bacterioplankton production typically ranged from 60 to 100 × 10^7 cells l^{-1} h^{-1} or 0.4 to 0.6 mg C l^{-1} day^{-1}. Interpolated annual mean bacterioplankton production varied between 0.08 and 0.16 mg C l^{-1} day^{-1} (~0.08–0.16 g C m^{-2} day^{-1}) (Table 1), being particularly high in 1990 and 1991 when *Bosmina* and rotifers occurred in high density during summer (Fig. 1). This bacterioplankton production corresponds to 1.6–5.5% of phytoplankton production.

The variation in bacterioplankton abundance was less pronounced than for bacterioplankton production (Fig. 1), typically ranging from 3–8 × 10^9 cells l^{-1} in winter to a maximum of 15–30 × 10^9 cells l^{-1} during summer, often coinciding with the variation in bacterioplankton production. The peak recorded was 48 ×10^9 cells l^{-1} in June 1986. Bacterioplankton abundance fluctuated markedly during summer. Annual mean bacterioplankton biomass varied between 0.22 and 0.36

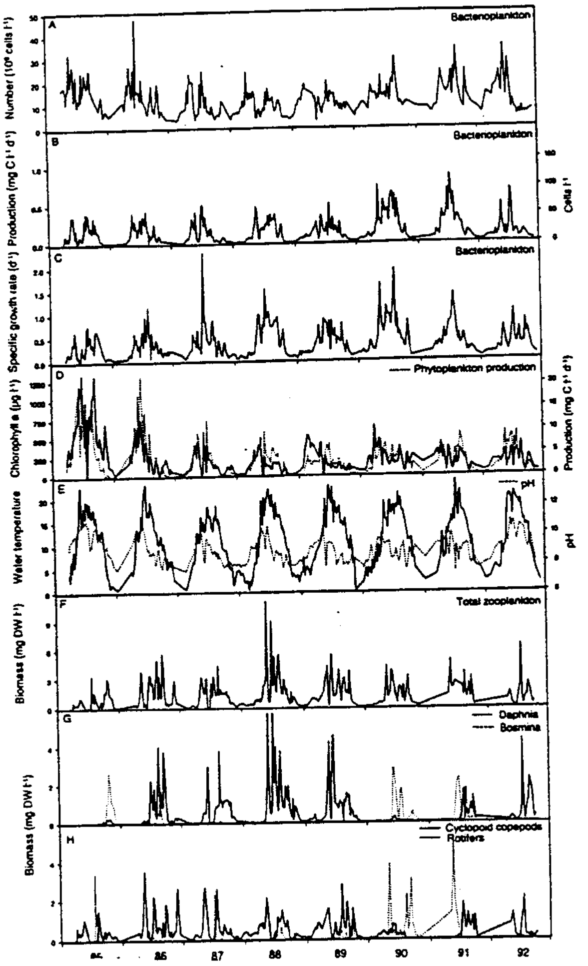

Fig. 1. Seasonal variation in bacterioplankton abundance (A), ^{3}H-thymidine production (B), and calculated specific growth rate (C) in Lake Søbygård during the period 1985–1992 together with chlorophyll *a* and phytoplankton ^{14}C production (D), water temperature and pH (E), total zooplankton biomass (F), the biomass of *Daphnia* spp. and *Bosmina longirostris* (G), and of cyclopoid copepods (~biomass of *Cyclops vicinus*) and rotifers (H).

mg C l^{-1}, or between 1.9 and 4.6% of phytoplankton biomass (Table 1). Bacterioplankton specific growth rate typically varied from around 0.02–0.2 day^{-1} during winter to a maximum of around 0.5–1.5 day^{-1} during summer, although values as high as 2.3 day^{-1} were recorded. Summer fluctuation was also observed in bacterioplankton specific growth rate, which occasionally reached values as low as 0.03 day^{-1}. The hypertrophic state of the lake was evident from the high maximum levels of phytoplankton production (22 mg C l^{-1} day^{-1} [22 g C m^{-2} day^{-1}]) and chlorophyll *a* (1,313 μg l^{-1}).

Correlation analysis revealed that log-transformed bacterioplankton production, bacterioplankton abundance, and bacterioplankton specific growth rate correlated significantly and positively with water temperature and log-transformed values of chlorophyll *a* and phytoplankton production ($P < 0.0001$), an exception being that bacterioplankton specific growth rate did not correlate with chlorophyll *a* ($P > 0.05$) (Table 2, Fig. 2). The relationship to temperature was particularly strong (Fig. 2). Moreover, the data suggest a decrease in bacterioplankton production and calculated specific growth rate at high pH.

Correlation between the three bacterioplankton variables and biomass (log-transformed) of the various zooplankton in the lake varied markedly (Table 2, Fig. 3). Bacterioplankton abundance correlated significantly and negatively with *Daphnia* ($P < 0.0001$), while the correlations between bacterioplankton production, abundance, and specific growth rate, and the biomass of *Bosmina*, cyclopoid copepods, and rotifers were all significant and positive ($P < 0.05$ to $P < 0.0001$). There was a significant, albeit weak, positive correlation between ciliate volume versus bacterioplankton production ($P < 0.05$) and specific growth rate ($P < 0.05$), but, otherwise, the correlations to ciliate volume and number were insignificant (Table 2). The ciliate data sets were considerably smaller than the macrozooplankton data sets, however (Table 2).

Regression Analysis

Regression analysis revealed the following significant relationship between bacterioplankton abundance versus chlorophyll *a* and phytoplankton production, respectively (Eqs. 1 and 2, Table 3):

$$\log_{10} \mathrm{ABUND} = 0.42 + 0.29 \log_{10} \mathrm{CHLA} \ (r^2 = 0.42) \quad \text{(Eq. 1)}$$

$$\log_{10} \mathrm{ABUND} = 1.00 + 0.19 \log_{10} \mathrm{PP} \ (r^2 = 0.41) \quad \text{(Eq. 2)}$$

The slope in Eq. 1 was significantly lower ($P < 0.001$) than the 0.76 in the equation of Bird and Kalff [8] advanced on less eutrophic lakes (0.84 if marine data were included), but comparable to the 0.33 in the Currie equation [14]. Our equation overestimated summer abundance, and vice versa during winter (Fig. 4). The relationship could be improved slightly by including water temperature (Fig. 4), albeit the temperature coefficient was low (Q10 of 1.08) (Table 3). The relationship to phytoplankton production (Eq. 2) could,

Table 1. Interpolated annual mean production and biomass[a]

	1985	1986	1987	1988	1989	1990	1991	1992
PP (mg C l^{-1} day^{-1})	5.1	4.2	2.2	2.3	2.1	2.9	3.4	3.8
BACPRO (mg C l^{-1} day^{-1})	0.08	0.09	0.08	0.10	0.09	0.16	0.16	0.09
BACPRO:PP (%)	1.6	2.1	3.6	4.3	4.3	5.5	4.7	2.4
PHYTBIO (mg C l^{-1})	19.2	8.9	5.8	5.1	7.9	9.2	7.4	6.5
BACBIO (mg C l^{-1})	0.36	0.29	0.22	0.22	0.28	0.31	0.34	0.30
BACBIO:PHYTBIO (%)	1.9	3.3	3.8	4.3	3.5	3.4	4.6	4.6
ZOOBIO (mg C l^{-1})	0.3	0.5	0.5	0.6	0.6	0.4	0.6	0.5

[a] pp, Phytoplankton; BACPRO, bacterioplankton production; PHYTBIO, phytoplankton biomass; BACBIO, bacterioplankton biomass; ZOOBIO, zooplankton biomass

Table 2. Pearson correlation coefficients[a]

	BACPRO	ABUND	SGR	*n*
TEMP	0.70****	0.35****	0.69****	(376, 296, 296)[b]
CHLA	0.21****	0.50****	0.01^{nsc}	(375, 297, 297)
PP	0.44****	0.52****	0.26****	(359, 286, 286)
DAPH	0.10^{ns}	−0.25****	0.25****	(324, 289, 289)
BOS	0.20**	0.15*	0.22****	(330, 295, 295)
CYC	0.35****	0.30****	0.26****	(305, 281, 281)
ROT	0.25****	0.18**	0.21***	(316, 281, 281)
CILVOL	0.21*	0.06^{ns}	0.23*	(109, 109, 109)
CILNUM	0.16^{ns}	0.15^{ns}	0.10^{ns}	(129, 120, 120)

* $P < 0.05$; ** ; *** $P < 0.001$; **** 0.0001

[a] BACPRO, log-transformed bacterioplankton production; ABUND, log-transformed bacterioplankton abundance; SGR, log-transformed bacterioplankton specific growth rate; TEMP, water temperature; CHLA, log-transformed values of chlorophyll *a*; PP, log-transformed values of phytoplankton production; DAPH, log-transformed values of *Daphnia* spp. biomass; BOS, log-tranformed values of *Bosmina longirostris*; CYC, log-transformed values of cyclopoid copepod biomass; ROT, log-transformed values of rotifer biomass; CILNUM, log-transformed values of ciliate number; CILVOL, log-transformed values of ciliate volume

[b] Number of samples in each data set is given in parentheses in corresponding order

[c] ns, Not significant

however, not be improved by including water temperature (Table 3). The slope and the intercept varied markedly and significantly from year to year (Table 4). The slope for chlorophyll *a* ranged between 0.08 and 0.39, being particularly low in 1985 when pH was high, and in 1990–1991 when *Bosmina* and rotifers dominated the zooplankton community (Table 4, Fig. 1). In Eq. 3, the slope on temperature ranged between 0 and 0.02 (Q10 of 1–1.2) (Table 4), i.e., the temperature dependency was low during all years if chlorophyll *a* was included in the model.

Regression analysis revealed a weak relationship between bacterioplankton production and chlorophyll *a* (Fig. 4), and a somewhat stronger relationship with phytoplankton production and bacterioplankton abundance (Eqs. 5–7, Table 5).

$$\log_{10} \text{BACPRO} = 1.20 + 0.37 \log_{10} \text{CHLA} \ (r^2 = 0.15) \quad \text{(Eq. 5)}$$

$$\log_{10} \text{BACPRO} = 1.89 + 0.44 \log_{10} \text{PP} \ (r^2 = 0.42) \quad \text{(Eq. 6)}$$

$$\log_{10} \text{BACPRO} = 0.60 + 1.33 \log_{10} \text{ABUND} \ (r^2 = 0.39) \quad \text{(Eq. 7)}$$

The slopes of Eqs. 5 and 6 were significantly ($P < 0.05$) lower than in the equations obtained by White et al. [56] and Cole et al. [13], being 0.49 and 0.8, respectively, while the slope of Eq. 7 was higher than the 0.8 in the White et al. equation [56]. The relationships given in Eqs. 5 and 6 could be markedly improved by including water temperature and bacterioplankton abundance (Table 5, Fig. 4), accounting for up to 70–71% of the variation in bacterioplankton production. A substantial number of outliers were found when the pH was >10 (Fig. 4).

An analysis of the interannual variations in parameters was conducted on Eqs. 6, 10, and 11 (Table 4). In the most

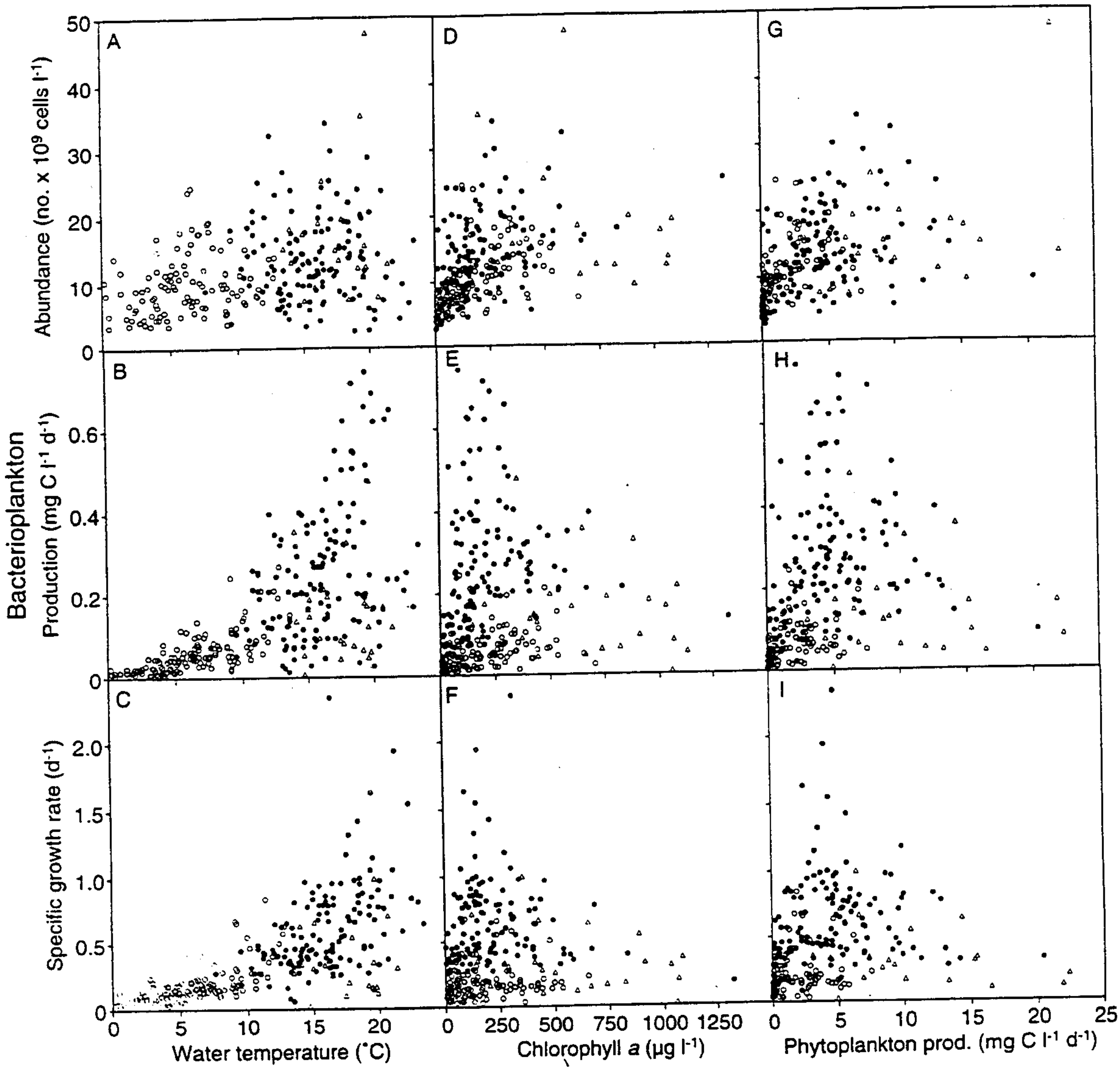

Fig. 2. Bacterioplankton abundance, ^{3}H-thymidine production, and calculated specific growth rate versus and water temperature, chlorophyll *a*, and phytoplankton phytoplankton production during 1985–1992. (•) summer values (1 May–1 Oct) (△) values with pH > 10; (○) others.

simple of the equations (Eq. 6), the intercept ranged only between 1.7 and 2.1, albeit the year-to-year variation was significant ($P = 0.013$). The intercept was particularly high in 1990 and 1991, when *Bosmina* and rotifers dominated. The interannual variation in slope was low (0.34–0.62) and insignificant ($P > 0.09$), and, during all years, lower than in the Cole et al. [13] equation. As expected, the interannual variation due to autocorrelation increased when more variables were included in the equation (Table 4). The temperature coefficient varied between 0.02 and 0.07 (Q10 = 1.2–2.0), and that of bacterioplankton abundance between 0.3 and 1.1, and between 0.02 and 0.32 when bacterioplankton abundance was included in the equation (Table 4). The variation in both intercept and slope was markedly higher when phytoplankton production was substituted by chlorophyll *a* (data not shown).

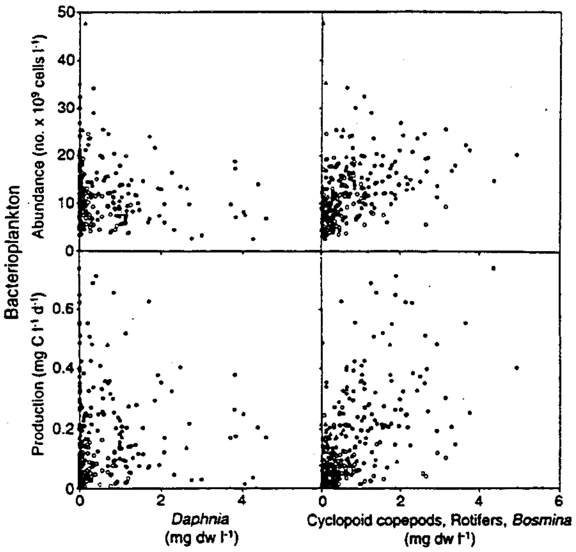

Fig. 3. Bacterioplankton abundance, ^{3}H-thymidine production versus biomass of *Daphnia* spp. and the total biomass of rotifers, *Bosmina longirostris*, and cyclopoid copepods during 1985–1992. Symbols as in Fig. 2.

While no relationship was found between chlorophyll *a* and SGR (Fig. 4), a highly significant relationship was found between the specific growth rate and water temperature (Table 6, Fig. 4):

$$\log_{10} \mathrm{SGR} = -1.04 + 0.046\ \mathrm{TEMP}\ (r^2 = 0.51) \qquad \text{(Eq. 12)}$$

The slope was ($P < 0.001$) and 49% higher than in the equation of White et al. [56]. White et al. [56] obtained a better prediction by including the interactions between chlorophyll *a* and water temperature. This interaction term did not contribute greatly to the variation in our data (Table 6). However, by excluding data with pH > 10.2, the interaction term became significant and positive, as in the White et al. equation [56], indicating that the effect of temperature on the data set increases with increasing chlorophyll *a*. As in White et al. [56], the relationship could be further improved by including mean bacterioplankton volume, i.e., SGR increases with increasing mean volume (Table 6).

Influence of Zooplankton and High pH

The data in Figs. 1–4 and the correlation matrices indicate that it was possible to improve the empirical equations further by including zooplankton and pH in the equations. This was confirmed by stepwise regression analyses (Table 7, Fig. 4). Accordingly, besides being positively related to chlorophyll *a*, as in the Bird and Kalff [8] and Currie [14] equations, bacterioplankton abundance was negatively influenced by *Daphnia* biomass, and positively so by phytoplankton production and the biomass of *Bosmina*, rotifers, and cyclopoid copepods (Eq. 17, Table 7, Figs. 4 and 5). This extended equation accounted for 59% of the variation in bacterioplankton abundance, i.e., 13% more than in the most accurate of the simpler equations (Eq. 3, Table 3).

$$\begin{aligned} \log \mathrm{ABUND} = {} & 1.64 + 0.11 \log \mathrm{PP} + 0.12 \log \mathrm{CHLA} \\ & - 0.23 \log \mathrm{DAPH} + 0.23 \log \mathrm{BOS} \\ & + 0.45 \log \mathrm{ROT} + 0.38 \log \mathrm{CYC}, \\ & (r^2 = 0.59) \qquad \text{(Eq. 17)} \end{aligned}$$

Besides being positively related to water temperature, chlorophyll *a* and bacterioplankton abundance, as in the White equation, bacterioplankton production was negatively influenced by high pH (>10.2), and positively so by *Bosmina longirostris*, rotifers, and cyclopoid copepods (Eq. 11, Table 7, Figs. 4 and 5). The equation accounted for 84% of the variation in bacterioplankton production, i.e., 13% more than the most accurate of the simple equations (Eq. 11. Table 5).

$$\begin{aligned} \log \mathrm{BACPRO} = {} & 0.65 + 0.12\ \mathrm{TEMP} + 0.55 \log \mathrm{ABUND} \\ & - 2.65 \max (\mathrm{pH} - 10.2, 0) \\ & + 0.22 \log \mathrm{CHLA} + 0.43 \log \mathrm{BOS} \\ & + 0.36 \log \mathrm{ROT} + 0.27 \log \mathrm{CYC}, \\ & (r^2 = 0.84) \qquad \text{(Eq. 18)} \end{aligned}$$

As with the White equation, water temperature, chlorophyll *a*, and bacterioplankton mean cell volume had a positive influence on bacterioplankton specific growth rate. In addition, *Bosmina longirostris* contributed significantly to the variation in bacterioplankton specific growth rate, while pH > 10.2 contributed negatively (Eq. 12, Figs. 4 and 5). This equation accounted for 72% of the variation in bacterioplankton specific growth rate, i.e., 18% more than Eq. 15 (Table 6).

$$\begin{aligned} \log \mathrm{SGR} = {} & -1.75 + 0.12\ \mathrm{TEMP} - 2.91 \max \\ & (\mathrm{pH} - 10.2, 0) + 0.08 \log \mathrm{CHLA} + 0.42 \log \\ & \mathrm{MVOL} + 0.38 \log \mathrm{BOS},\ (r^2 = 0.72) \qquad \text{(Eq. 19)} \end{aligned}$$

Table 3. Multiple regression of bacterioplankton abundance (10^9 cells l^{-1} in the water of Lake Søbygård[a]

	Intercept	$\log_{10}$ CHLA (μg l^{-1})	$\log_{10}$ PP (μg C l^{-1} day^{-1})	TEMP (°C)	r^2	RMSE	CF	Residual SD	Source	Equation
$\log_{10}$ ABUND	0.428 (0.043)	0.286 (0.020)			0.42	5.2	1.08	0.17	This study	1
	−0.13	0.78			0.88				Bird & Kalff [8]	–
	−0.2	0.33							Currie [15]	–
$\log_{10}$ ABUND	1.00 (0.01)		0.19 (0.01)		0.41	5.03	1.08	0.17	This study	2
$\log_{10}$ ABUND	0.37 (0.04)	0.27 (0.02)		0.008 (0.002)	0.46	5.04	1.07	0.16	This study	3
$\log_{10}$ ABUND	1.03 (0.03)		0.21 (0.02)	$-0.003^{n.s.}$ (0.002)	0.41	5.03	1.08	0.17	This study	4

[a] SE in parentheses; CHLA, chlorophyll *a*; PP, phytoplankton production; TEMP, water temperature; RMSE, root mean square error; CF, correction factor ns, Not significant

Various pH cutoff points between 9 and 10.5 were tested, but pH 10.2 was found to be the optimum value in both equations (Eqs. 18 and 19). Ciliate abundance or volume did not contribute significantly to variation in bacterioplankton abundance, production, or specific growth rate in these equations derived by stepwise regression.

A laboratory experiment was conducted to test the impact of high pH on bacterioplankton thymidine uptake (Table 8). The uptake was significant (*t*-test, $P < 0.001$) and 60% higher at natural pH than at pH 10.5. It was, however, also low in samples in which pH was raised to 10.5 and subsequently lowered to lake pH level, and not significantly ($P > 0.05$) different from the uptake at pH 10.5, albeit there was a tendency toward a small recovery in uptake (13%).

Discussion

The three main findings of the Lake Søbygård study can be summarized as follows. First, the percentage of phytoplankton production channelized through bacterioplankton was generally low, an observation which, together with findings published in the literature (see later) suggests that the percentage generally decreases with increasing eutrophication. Second, both bacterioplankton production and specific growth rate seem to be highly temperature dependent. Third, a major part of the residual variance in earlier equations could be explained by variations in biomass and relative composition of the zooplankton, and by pH when higher than 10.2.

Bacterioplankton production and abundance were high in Lake Søbygård, compared to the majority of reported values for lakes and marine environments [13, 18, 56]. This probably reflects the hypertrophic state of the lake. The bacterioplankton production:phytoplankton production ratio was low, however, ranging from 1.6 to 5.5% on an annual basis (Table 1) and from 2 to 8% during summer (data not shown). Assuming a growth yield of 50%, then 3–11% of the phytoplankton production was channelized through the bacterioplankton on an annual basis. This is low compared to most studies from less eutrophic lakes [50], but comparable to that reported for other hypertrophic shallow lakes [1, 44]. The low percentage of phytoplankton production channelized to the bacterioplankton in Lake Søbygård and other hypertrophic lakes may be partly attributable to low zooplankton grazing pressure on the phytoplankton. This lack of grazing pressure could be due to high predation from fish [28]. This means a lower grazing-mediated release of substrates, which, in lakes with high grazing density, has been shown to be more important for bacterioplankton growth than organic carbon released from phytoplankton [11, 31, 52]. The impact of fish on macrozooplankton grazers seems to be particularly high in shallow lakes [30]. The importance of grazers in shallow Lake Søbygård is apparent from the fact that the bacterioplankton production:phytoplankton production ratio seems to increase with increasing zooplankton biomass (Table 1), in return, reflecting a concomitant reduction in the density of planktivorous fish [29]. Another contributory factor to the low percentage of phytoplankton production channelized to the bacterioplankton is the high loss by sedimentation, reflecting the low turnover by grazing, a short settling distance (low mean depth), and dominance by algae with high specific settling rates [27, 29]. Much of the organic material that is produced in the water phase is, therefore, mineralized in the sediment.

This study confirmed several empirical relations between

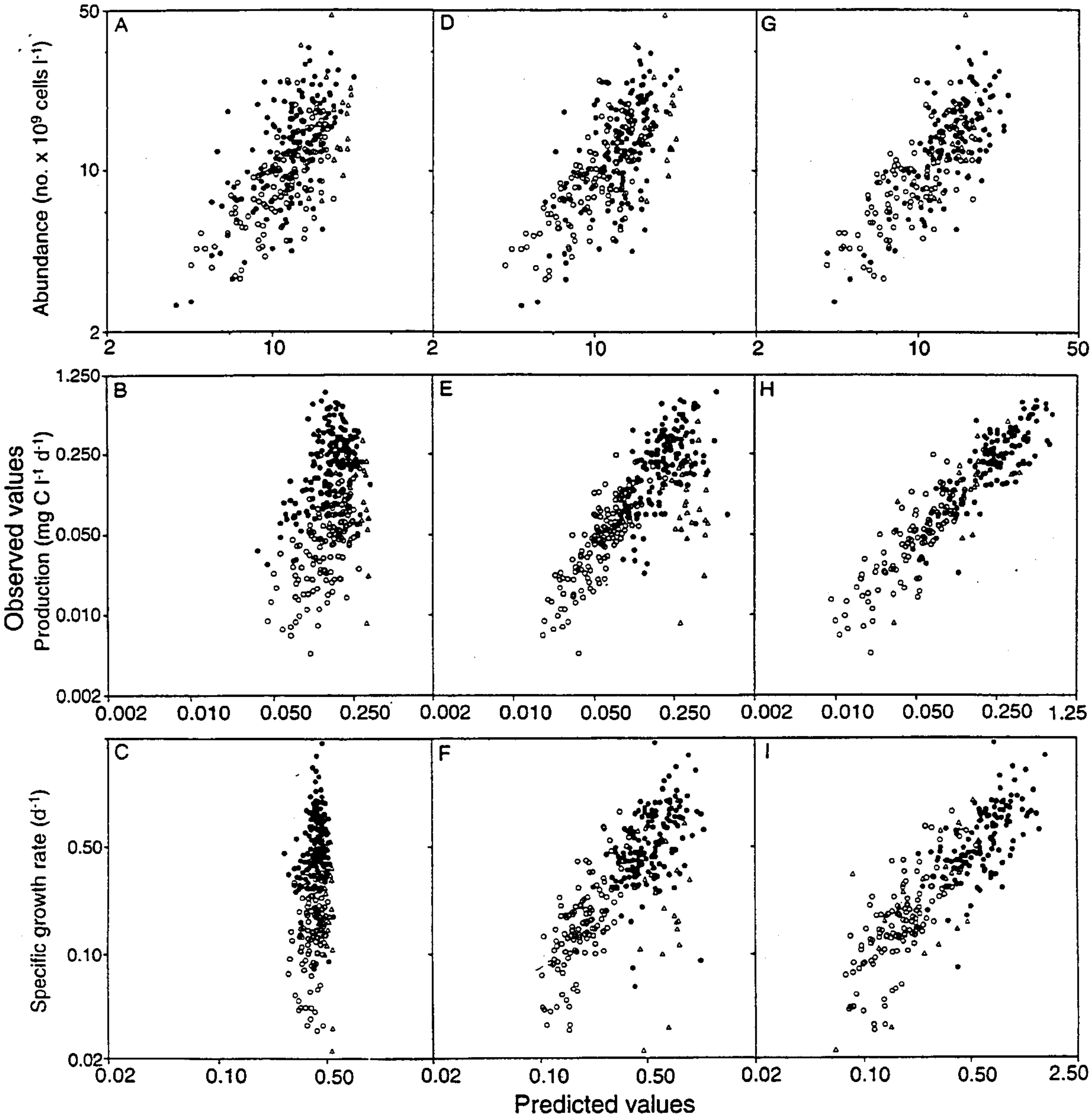

Fig. 4. Observed bacterioplankton abundance, ^{3}H-thymidine production, and calculated specific growth rate versus predicted values obtained from various equations. A and B are versus chlorophyll *a* (Eqs. 1 and 5), D and E versus chlorophyll *a* and temperature (Eqs. 3 and 8), and G, H, and I the final equations (Eqs. 17–19). C and F show, respectively, the relationship to chlorophyll *a* and water temperature (Eq. 12). Symbols as in Fig. 2.

Table 4. Multiple regression of bacterioplankton abundance and production versus various explanatory variables showing interannual parameter variations[a]

	Bacterioplankton abundance (10^9 cells l^{-1})			Bacterioplankton production (μg C l^{-1} day^{-1})			
Year	Intercept	Log_{10} CHLA	TEMP	Intercept	log_{10}PP	TEMPV	log_{10} ABUND
1985	0.98	0.08		1.71	0.34		
1986	0.20	0.39		1.91	0.35		
1987	0.27	0.34		1.90	0.45		
1988	0.43	0.28		1.93	0.54		
1989	0.36	0.31		1.88	0.54		
1990	0.73	0.16		2.04	0.61		
1991	0.97	0.07		2.10	0.35		
1992	0.20	0.38		1.81	0.62		
(P<)	(0.0007)	(0.0026)		(0.01)	(0.09)		
1985	0.96	0.04	0.010	1.52	0.18	0.023	
1986	0.18	0.32	0.015	1.38	0.14	0.051	
1987	0.25	0.33	0.003	1.46	0.29	0.041	
1988	0.43	0.28	−0.001	1.43	0.32	0.043	
1989	0.22	0.35	0.005	1.58	0.42	0.037	
1990	0.60	0.11	0.019	1.27	0.04	0.075	
1991	0.81	0.02	0.024	1.49	0.11	0.056	
1992	0.30	0.30	0.006	1.54	0.47	0.018	
(P<)	(0.02)	(0.0002)	(0.0021)	(0.44)	(0.02)	(0.002)	
1985				0.39	0.07	0.019	1.05
1986				0.95	0.06	0.049	0.43
1987				0.70	0.13	0.044	0.77
1988				0.33	0.10	0.055	1.03
1989				0.32	0.15	0.042	1.11
1990				1.02	0.02	0.070	0.29
1991				0.69	0.10	0.035	0.92
1992				1.07	0.32	0.022	0.54
(P<)				(0.36)	(0.83)	(0.005)	(0.28)

[a] P-values testing the significance of the interannual variation in parameters are in parentheses. For further information and units see Table 3

bacterioplankton and environmental variables advanced on the basis of multilake comparisons (e.g., [8, 13, 14]). There were, however, certain differences. In the equations relating bacterioplankton production to chlorophyll *a* and phytoplankton production, the slopes were 24 and 45% lower, respectively, than in the equations by White et al. [56] and Cole et al. [13] that are based on less eutrophic, and mainly deeper, lakes. The interannual analysis revealed that the slopes were low during all years in Lake Søbygård (Table 5 and data not shown). Likewise, the slope of the bacterioplankton abundance–chlorophyll *a* relationship in Lake Søbygård (0.29, interannual variation 0.08–0.39) was significantly lower than the slopes of 0.8 reported by Bird and Kalff [8] and Cole et al. [13]. However, it was similar to the slope of 0.2–0.3 reported by Simon et al. [50] for relationships between bacterioplankton and phytoplankton. Simon et al. [50] argued that the difference in slope between their study and that of Bird and Kalff [8] is presumably attributable to the use of C units rather than chlorophyll *a*, and to the fact that they accounted for the cell size-dependent C:volume ratio. However, as they included more data from eutrophic lakes than Bird and Kalff [8] and Cole et al. [13], the lower slope could also be interpreted as reflecting a decrease in slope with increasing eutrophication. In fact, the study of Currie [14] that covered a chlorophyll *a* range of 0.2–100 μg l^{-1} revealed slopes of 0.2–0.4, averaging 0.33 on their most extensive data set. The latter is close to the mean value for Lake Søbygård, where the chlorophyll *a* range was 3–1,313 μg l^{-1}, and to the value of 0.27 found by del Giorgio and Peters [16]. Although lower slopes are to be expected in relationships advanced on the basis of a single lake than from the multilake models, the tendency to a decrease in slope with increasing nutrient range in the multilake models and our results indicate that the bacterioplankton production:phytoplankton production and bacterioplankton:phytoplankton biomass ratios decrease from oligotrophic to hypertrophic lakes.

Temperature seems to play a major role in bacterioplank-

Table 5. Multiple regression of bacterioplankton production ($\mu g\ C\ l^{-1}\ day^{-1}$) in the water of Lake Søbygård[a]

	Intercept	$\log_{10}$ CHLA	$\log_{10}$ PP	$\log_{10}$ ABUND	TEMP	r^2	RMSE	CF	Residual SD	Source	Equation
$\log_{10}$ BACPRO	1.14	0.40				0.18	152	1.59	0.42	This study	5
	(0.11)	(0.05)									
	1.90	0.49				0.20				White et al. [56]	–
$\log_{10}$ BACPRO	1.89		0.44			0.42	138	1.36	0.34	This study	6
	(0.02)		(0.03)								
	1.94		0.8							Cole et al. [13]	–
$\log_{10}$ BACPRO	0.60			1.33		0.39	133	1.43	0.37	This study	7
	(0.10)			(0.096)							
	0.95			0.81		0.21				White et al. [56]	–
$\log_{10}$ BACPRO	0.77	0.27			0.054	0.62	131	1.24	0.29	This study	8
	(0.08)	(0.03)			(0.003)						
	0.48	0.06$^{n.s.}$		0.78	0.048	0.70	122	1.19	0.28	This study	9
	(0.08)	(0.04)		(0.09)	(0.003)						
$\log_{10}$ BACPRO	1.45		0.23		0.042	0.64	124	1.24	0.25	This study	10
	(0.04)		(0.03)		(0.003)						
	0.68		0.08	0.74	0.044	0.71	118	1.19	0.25	This study	11
	(0.10)		(0.03)	(0.09)	(0.003)						

[a] For further information including units see Table 3

Table 6. Multiple regression of bacterioplankton specific growth rate (day^{-1})[a]

	Data included	Intercept	TEMP	TEMP × $\log_{10}$ CHLA[b]	$\log_{10}$ MVOL[c] ($\mu m^3\ cell^{-1}$)	r^2	RMSE	CF	Residual SD	Model	Equation
$\log_{10}$ SGR	All data	−1.08	0.046			0.51	0.26	1.20	0.26	This study	12
		(0.035)	(0.003)								–
		−1.04	0.031							White et al. [56]	–
$\log_{10}$ SGR	All data	−1.08	0.054	−0.004		0.52	0.26	1.20	0.26	This study	13
		(0.035)	(0.006)	(0.002)							
	If pH<10.2	−1.12	0.04	0.007		0.69		1.12	0.21	This study	14
		(0.03)	(0.005)	(0.002)							
	All data	−1.15	0.027	0.17						White et al. [56]	–
$\log_{10}$ SGR	All data	−1.28	0.060	−0.007	3.55	0.54	0.26	1.18	0.25	This study	15
		(0.063)	(0.006)	(0.003)	(0.98)						
	If pH<10.2	−1.22	0.04	0.005	1.96	0.70		1.12	0.21	This study	16
		(0.05)	(0.006)	(0.002)	(0.83)						
	All data	−2.22	0.036	0.018	7.28	0.84				White et al. [56]	–

[a] For further information including units see Table 3

[b] TEMP × $\log_{10}$ CHLA, interaction between water temperature and chlorophyll *a*

[c] MVOL, bacterioplankton mean volume

ton production and bacterioplankton specific growth rate (Fig. 4, Tables 5 and 6). The apparent impact of temperature on bacterioplankton production is in accord with a number of studies [39], although some have found the relationship to temperature to be weak at high temperatures [25, 39, 57], this being ascribed to an increased limitation of substrate availability [39]. A weak relationship may, however, also reflect grazer control on bacterioplankton during summer. Thus, in Lake Søbygård, temperature dependency increased considerably when macrozooplankton biomass was included in the equation (Tables 5 and 7); this suggests that grazers may be an important contributory factor to the weak relationship at high temperatures, as they were typically abundant during summer (Fig. 1). Temperature alone accounted for 51% of the variation in bacterioplankton specific growth rate, which is similar to the finding of White et al. [56]. In contrast to their results, however, we found no significant additional effect of the interaction between water temperature and chlorophyll *a* on the full data set ($P > 0.05$). This may be due to the strong negative effect of high pH on

Table 7. Stepwise multiple regressions on data from Lake Søbygård[a]

	Inter- cept	TEMP	log ABUND	max (pH −10.2, 0)	log PP	log CHLA	log MVOL	log DAPH	log BOS	log ROT	log CYC	r^2	RMSE	CF	Residual SD	Equa- tion
log ABUND	1.64 (0.18)				0.11 (0.02)	0.12 (0.04)		−0.23 (0.06)	0.23 (0.10)	0.45 (0.08)	0.38 (0.07)	0.59	4.7	1.06	0.339	17
log BACPRO	0.65 (0.15)	0.12 (0.006)	0.55 (0.08)	−2.65 (0.28)		0.22 (0.04)			0.43 (0.13)	0.36 (0.12)	0.27 (0.10)	0.84	85	1.11	0.45	18
log SGR	−1.73 (0.47)	0.12 (0.005)		−2.91 (0.27)		0.08 (0.03)	0.42 (0.13)		0.38 (0.14)			0.72	0.2	1.11	0.46	19

[a] DAPH, BOS, ROT, and CYC represent biomass (DW l^{-1}) of *Daphnia*, *Bosmina*, rotifers, and cyclopoid copepods, respectively. For an explanation of other variables and units see Tables 3, 5, and 6. Log is base e

bacterioplankton specific growth rate (Table 6). Thus, if data containing pH above the optimum cutoff point was excluded, the interaction term contributed positively and significantly to the variation in bacterioplankton specific growth rate (Table 6). In accordance with White et al. [56], bacterioplankton mean volume contributed significantly to the variation in specific growth rate, and, in this enlarged equation, the interaction between chlorophyll *a* and water temperature contributed greatly, albeit negatively. Again, if data where the pH exceeded 10.2 was excluded, the contribution became positive (Table 6). An increase in growth rate with increasing mean cell volume was also found by White et al. [56], and corresponds with other laboratory and field results [14, 20]. Likewise, Billen et al. [7] observed an increase in cell size with increasing bacterioplankton production when compiling data from a large number of freshwater and marine localities. However, like White et al. [56], we cannot exclude the possibility that the impact of cell volume in our study is an artifact related to the use of a fixed-carbon-per-cell conversion factor (29 μg $cell^{-1}$), rather than one dependent on cell size.

As in the multilake cross analyses, considerable residual variance remains to be explained in the equations previously found for Lake Søbygård. Currie [14] and del Giorgio and Peters [16] found that the bacterioplankton abundance equation improved if total P was used instead of chlorophyll *a*, thus suggesting that other factors related to changes in total P play a role. Thus competition for phosphorus between phytoplankton and bacterioplankton has been observed in several studies in oligotrophic lakes [15]. However, phosphorus cannot have controlled bacterioplankton production in the hypertrophic Lake Søbygård, since both total P and ortho P were high throughout the study period [27 and unpublished observations]. Alternatively, dissolved organic carbon (DOC) could be responsible, as DOC increases with increasing productivity (total P). No relationship between residual variance and DOC was found for Lake Søbygård (data not shown). Likewise, del Giorgio and Peters [16] and Søndergaard [53] found no relationships between DOC and bacterioplankton abundance and production, respectively. The nonexisting relationship to DOC may reflect the fact that DOC consists largely of substances that are slowly degraded [54].

An alternative explanation of the residual variance could be differences in grazing by zooplankton: Zooplankton may either stimulate the bacterioplankton through cropping of potential predators and fueling substrate during feeding, or negatively influence the bacterioplankton through direct cropping and elimination of potential substrates (e.g., by negatively affecting phytoplankton production) [31, 32]. The stepwise multiple regressions revealed that *Bosmina*, rotifers, and cyclopoid copepods contributed significantly and positively to the variation in both production and abundance of bacterioplankton, while only *Bosmina* contributed to the variation in the specific growth rate (Table 7). Contrary to *Bosmina*, *Daphnia* apparently had a significant negative influence on bacterioplankton abundance, but no impact on the production when the equation included abundance and chlorophyll *a*, and no impact on the specific growth rate. While regression equations must be interpreted with caution, the lake included in our study is characterized by dominance of a few zooplankton species, and the proportion and significance of these species varied markedly both seasonally and interannually (Fig. 1). Thus, the regression most likely mirrors the different effects of the various types of zooplankton. The negative impact of *Daphnia* on bacterioplankton abundance corresponds well to in vitro grazing experiments conducted in the lake using ^{3}H-thymidine-labeled bacterioplankton. These experiments revealed that consumption by macrozooplankton was high during periods of high *Daphnia* density (the summer average grazing at high *Daphnia* density being up to 67% of the biomass and 88% of the production

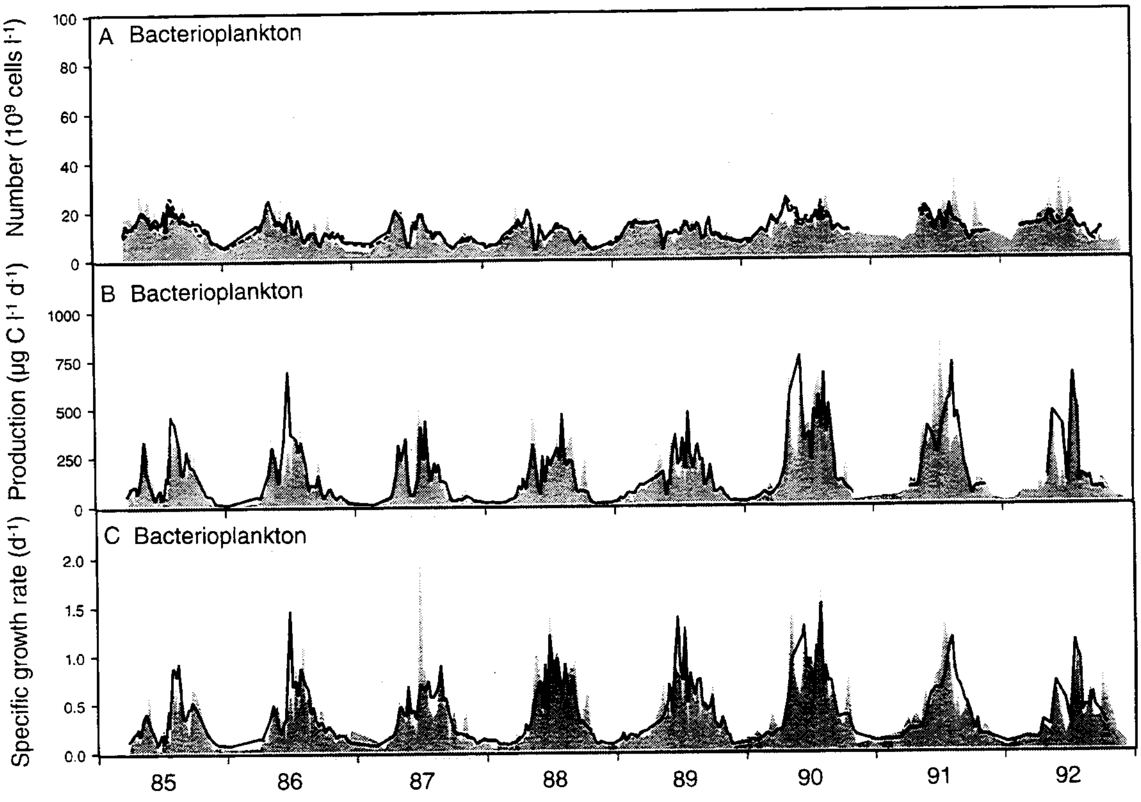

Fig. 5. Measured (hatched) and predicted (Eqs. 17–19, Table 7) variations in bacterioplankton abundance, ^{3}H-thymidine production, and calculated specific growth rate.

Table 8. Short-term experiments showing the effect on ^{3}H-thymidine bacterioplankton production of altered pH[a]

	Lake pH (10.0)	pH 10.5	pH 10 → 10.5 → 10[b]
Bacterioplankton production (cell l^{-1} h^{-1} × 10^7)	34.7 ± 2.9	21.6 ± 1.0	24.4 ± 2.1

[a] Mean ± SE, *n* = 5

[b] The results of experiments in which pH was raised to 10.5 and subsequently reduced to lake pH (10.0) before measuring production

day^{-1}) [29]. A negative impact of *Daphnia* has also been found in several other eutrophic lakes and enclosure experiments with relatively low abundance of planktivorous fish [12, 32, 42], as well as during the early summer clearwater phase of some lakes [21]. Size-selective predation, leading to dominance of small, relatively slowly growing bacteria, has been suggested to reduce bacterioplankton production [32], and several studies have shown that mean bacterioplankton cell size decreases when *Daphnia* peak [21, 34, 37]. The same was found in Lake Søbygård and another shallow lake by Jeppesen et al. [28]. An alternative explanation of the negative impact of *Daphnia* could be that they reduce phytoplankton production directly, through grazing. This may result in loss of phytoplankton exudates and, hence, in bacterioplankton production, although the loss may be partly compensated for by excretion [32]. In our study, however, bacterioplankton specific growth rate was unaffected by *Daphnia*. The low bacterioplankton production at high *Daphnia* density seems, therefore, to be due simply to a *Daphnia*-mediated reduction in bacterioplankton abundance. Only a few other studies have shown such a strong negative impact of *Daphnia* [33, 37, 41]. Most studies of less eutrophic lakes have found *Daphnia* to have little or no effect [10, 40]. It may suggest that the impact of *Daphnia* on bacterioplankton abundance and production is potentially highest in hypertrophic lakes.

In accordance with earlier suggestions [28], the present analysis predicts a strong positive impact of *Bosmina* on bacterioplankton specific growth rate and abundance. A high abundance when *Bosmina* dominates the zooplankton community has also been found in a Czech reservoir [51]. *Bosmina* consumes phytoplankton more efficiently than it does bacterioplankton. Thus, the phytoplankton clearance rate for *Bosmina* is typically 4–15 times that for bacterioplankton [17, 23], and regression analyses on data from grazing experiments in Lake Søbygård suggest a fourfold higher rate [29]. The low predation on bacterioplankton, together with the release of fueling substrates when feeding on phytoplankton, may explain the high positive impact of *Bosmina* on bacterioplankton, albeit that *Bosmina* predation on bactivorous flagellates and ciliates may also have played a role.

The predicted positive impact of cyclopoid copepods and rotifers on bacterioplankton production and abundance is also in accordance with grazing experiments undertaken at Lake Søbygård since, like *Bosmina*, they both consumed phytoplankton more efficiently than bacterioplankton [29]. However, the impact was less than with *Bosmina*. In the case of rotifers, this may be because, although they fuel the bacteria, some rotifer species also prey on them (e.g., [2, 9]). Such a dual impact of rotifers has, in fact, been demonstrated in chemostat experiments with *Brachionus* [4], which is the predominant rotifer in Lake Søbygård.

The total ciliate volume was only weakly related to bacterioplankton production and specific growth rate. However, neither abundance nor volume of heterotrophic flagellates (data not shown, $n = 25$) or ciliates contributed significantly to any of the bacterial parametres in the stepwise multiple regression, including the various zooplankton. At first glance, this may seem unusual as a number of ciliates and heterotrophic flagellates have been shown to predate on the bacterioplankton [46, 49], and ciliates may also have an indirect impact on bacterioplankton via predation on flagellates [3, 55]. As for ciliates, it may, however, be due to the fact that no distinction was made between herbivorous and bactivorous species. Another explanation may be that zooplankton not only influence the bacterioplankton directly (fueling, predation, cropping phytoplankton), but also affect the abundance of ciliates and flagellates (e.g., [4, 45, 57], and thereby weaken the direct coupling between the latter two and the bacterioplankton [32]. This has been shown as for *Daphnia* [12, 32, 42], but our results also seem to indicate that the same is true for other zooplankton groups; zooplankton thus have a superior regulative influence on bacterioplankton as compared with ciliates and heterotrophic flagellates. This will be consistent with field studies that have shown only a weak coupling between bacterioplankton and heterotrophic flagellates [38, 55, 58]. In our case, we cannot exclude, however, that the apparently low importance of flagellates may reflect the low number of samples.

When above 10.2, pH had a strong negative influence on bacterioplankton production and specific growth rate, but not on abundance (Fig. 3, Tables 6 and 7). In 1985, during a prolonged period in June–July when pH was higher than 10.2, bacterioplankton production and specific growth rate both decreased to winter levels (Fig. 1). In concert with the regression analyses, laboratory experiments showed that an increase in pH from a lake level of 10.0 to 10.5 resulted in a significant, and, in the short term, irreversible decrease in thymidine uptake (40%), as a subsequent reduction in pH to lake level did not lead to a significant recovery in uptake (Table 8). The experiments do not, however, allow us to make conclusions on whether the bacterioplankton community may adapt to a high pH level. Further studies are needed to determine the mechanisms behind the negative impact of high pH.

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References

1. Ahlgren I, Sörensen F, Waara T, Vrede K (1994) Nitrogen budgets in relation to microbial transformation in lakes. Ambio 23:367–377.

2. Arndt H (1993) Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates)—a review. Hydrobiologia 255/256:231–246.
3. Arndt H, Nixdorf B (1991) Spring clear-water phase in a eutrophic lake: control by herbivorous zooplankton enhanced by grazing on components of the microbial web. Verh Int Verein Limnol 24:879–883.
4. Arndt H, Güde H, Macek M, Rothhaupt KO (1992) Chemostats used to model the microbial food web: evidence for the feedback effect of herbivorous metazoans. Arch Hydrobiol Beih Ergebn Limnol 37:187–194.
5. Atkinson AC (1987) Plots, transformations and regression. Claradon Press, Oxford
6. Bell RT, Kuparinen J (1984) Assessing phytoplankton and bacterioplankton production during early spring in Lake Erken, Sweden. Appl Environ Microbiol 48:1221–1230.
7. Billen G, Servais P, Becquevort S (1990) Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom-up or top-down control? Hydrobiologia 207:37–42.
8. Bird DF, Kalff J (1984) Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Can J Fish Aquat Sci 41:1015–1023.
9. Bogdan KG, Gilbert JJ (1980) In situ clearance rates of planktonic rotifers. Hydrobiologia 73:73–77.
10. Brett MT, Wiackowski K, Lubner FS, Mueller-Solger A, Elser JJ, Goldman CR (1994) Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle Lake, California. Ecology 75:2243–2254.
11. Christoffersen K, Riemann B, Hansen LR, Klysner A, Sørensen HB (1990) Qualitative importance of the microbial loop and plankton community structure in a eutrophic lake during a bloom of cyanobacteria. Microb Ecol 20:253–272.
12. Christoffersen K, Riemann B, Klysner A, Søndergaard M (1993) Potential role of natural populations of zooplankton on plankton community structure in eutrophic lake water. Limnol Oceanogr 38:561–573.
13. Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1–10.
14. Currie DJ (1990) Large-scale variability and interactions among phytoplankton, bacterioplankton, and phosphorus. Limnol Oceanogr 35:1437–1455.
15. Currie DJ, Kalff J (1984) A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. Limnol Oceanogr 29:298–310.
16. del Giorgio PA, Peters RH (1993) The influence of DOC on the bacteria-chlorophyll relationship in lakes. Verh Int Verein Limnol 25:359–362.
17. DeMott W, Kerfoot WC (1982) Competition among cladocerans: nature of the interaction between *Daphnia* and *Bosmina*. Ecology 63:1949–1966.
18. Ducklow HW, Shiah FK (1993) Bacterial production in estuaries. In: Ford TE (ed) Aquatic microbiology. Blackwell Scientific Publications, Boston, pp 261–287.
19. Fuhrman JA, Azam F (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar Biol 66:109–120.
20. Gilmour CC, Leavitt ME, Shiaris MP (1990) Evidence against incorporation of exogenous thymidine by sulfate-reducing bacteria. Limnol Oceanogr 35:1401–1409.
21. Güde H (1988) Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. Hydrobiologia 159:63–73.
22. Hansen AM, Jeppesen E (1992) Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. J Plank Res 14:591–605.
23. Hart RC, Jarvis AC (1993) In situ determination of bacterial selectivity and filtration rates by five cladoceran zooplankters in a hypertrophic reservoir. J Plank Res 15:295–315.
24. Hobbie R, Daly J, Jasper S (1977) Use of nucleopore filters for counting bacteria by fluorescence microscopy. Appl Environ Microbiol 33:1225–1228.
25. Hoch MP, Kirchmann (1993) Seasonal and inter-annual variability in bacterial producton and biomass in a temperate estuary. Mar Ecol Prog Ser 98:283–295.
26. Holm-Hansen O, Riemann B (1978) Chlorophyll *a* determination: improvements in methods. Oikos 30:438–447.
27. Jeppesen E, Søndergaard M, Mortensen E, Kristensen P, Riemann B, Jensen HJ, Müller JP, Sortkjær O, Jensen JP, Christoffersen K, Bosselmann S, Dall E (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes. 1. Cross analysis of three Danish case-studies. Hydrobiologia 200/201:205–218.
28. Jeppesen E, Sortkjær O, Søndergaard M, Erlandsen M (1992) Impact of a trophic cascade on heterotrophic bacterioplankton production in two shallow fish-manipulated lakes. Arch Hydrobiol Beih 37:219–231.
29. Jeppesen E, Jensen JP, Søndergaard M, Mortensen E, Sortkjær O (1996) Fish mediated changes in macrozooplankton grazing on phytoplankton and bacterioplankton: a nine year study in shallow hypertrophic lake Søbygård. J Plank Res 18:1605–1625.
30. Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L (1997) Top-down control in freshwater lakes: the role of nutrients, submerged macrophytes and water depth. Hydrobiologia
31. Jumars PA, Penry DL, Baross JA, Perry MJ, Frost BW (1989) Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep Sea Res 36:483–495.
32. Jürgens K (1994) Impact of *Daphnia* on planktonic microbial food webs—a review. Mar Microb Food Webs 8:295–324.
33. Jürgens K, Güde H (1994) The potential importance of grazing-resistant bacteria in planktonic systems. Mar Ecol Prog Ser 112:169–188.
34. Jürgens K, Arndt H, Rothhaupt KO (1994) Zooplankton mediated changes of microbial food web structure. Microb Ecol 27:27–42.
35. Lampert W (1978) Release of dissolved organic carbon by zooplankton grazing. Limnol Oceanogr 23:831–843.
36. Land CE (1972) An evaluation of approximate confidence

interval estimation methods for lognormal means. Technometrics 14:145–158.

37. Markošová R, Jeržek J (1993) Bacterioplankton interactions with Daphnia and algae in experimental enclosures. Hydrobiologia 264:85–99.
38. Nagata T (1988) The microflagellate-picoplankton food linkage in the water column of Lake Biwa. Limnol Oceanogr 33:504–517.
39. Ochs CA, Cole JJ, Likens GE (1995) Population dynamics of bacterioplankton in an oligotrophic lake. J Plank Res 17:365–391.
40. Pace ML, Funke E (1991) Regulation of planktonic microbial communities by nutrients and herbivores. Ecology 72:904–914.
41. Rao S, Kwiatkowski RE, Jurkovic AA (1979) Distribution of bacteria and chlorophyll *a* at a nearshore station in Lake Ontario. Hydrobiologia 66:33–39.
42. Riemann B (1985) Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. Appl Environ Microbiol 50:187–193.
43. Riemann B, Søndergaard M, Schierup HH, Bosselmann S, Christensen G, Hansen J, Nielsen B (1982) Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossø. Int Rev Ges Hydrobiol 67:145–185.
44. Robarts RD, Wicks RJ (1990) Heterotrophic bacterial production and its dependence on autotrophic production in a hypertrophic African reservoir. Can J Fish Aquat Sci 47:1027–1037.
45. Sanders RW, Porter KG, Bennett SL, DeBiase AE (1989) Seasonal patterns of bactivory by flagellates, ciliates, rotifers and cladocerans in a freshwater planktonic community. Limnol Oceanogr 34:673–687.
46. Sanders RW, Leepers DA, King CH, Porter KG (1994) Grazing by rotifers and crustacean zooplankton on nanoplanktonic protists. Hydrobiologia 288:167–181.
47. SAS Institute, Inc. (1989) SAS/STAT user's guide, version 6, 4th edn, vols 1 and 2. SAS Institute, Inc., Cary, North Carolina
48. Scavia D, Laird GA (1987) Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. Limnol Oceanogr 32:1917–1033.
49. Sherr EB, Sherr BF (1988) Role of microbes in pelagic food webs: a revised concept. Limnol Oceanogr 33:1225–1227.
50. Simon M, Byong CC, Azam F (1992) Significance of bacterial biomass in lakes and the ocean: comparison to phytoplankton biomass and biogeochemical implications. Mar Ecol Prog Ser 86:103–110.
51. Straškrabová V, Komárková J, Macek M, Seďa, Šimek K, Vrba J, Vyhnálek V (1994) Microbial-algal-crustacean interactions in a reservoir under different fish stock. Arch Hydrobiol Beih 40:209–221.
52. Søndergaard M, Riemann B, Jørgensen NOG (1985) Extracellular organic carbon (EOC) released by phytoplankton and bacterial production. Oikos 45:323–332.
53. Søndergaard M (1993) Organic carbon pools in two Danish lakes: flow of carbon to bacterioplankton. Verh Int Verein Limnol 25:593–598.
54. Søndergaard M, Middelboe M (1995) A cross-system analysis of labile dissolved organic carbon. Mar Ecol Prog Ser 118:283–294.
55. Weisse T (1991) The annual cycle of heterotrophic freshwater nanoflagellates: role of bottom-up versus top-down control. J Plank Res 13:167–185.
56. White PA, Jacob K, Rasmussen JB, Gasol JM (1991) The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habits. Microb Ecol 21:99–118.
57. Wiachowski K, Brett MT, Goldman R (1994) Differential effects of zooplankton species on ciliate community structure. Limnol Oceanogr 39:486–492.
58. Wright RT, Coffin RB (1984) Measuring microzooplankton grazing on planktonic marine bacteria by its impact on bacterial production. Microb Ecol 19:137–149.

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Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth

Erik Jeppesen, Jens Peder Jensen, Martin Søndergaard, Torben Lauridsen,
Leif Junge Pedersen & Lars Jensen
Dept. of Lake and Estuarine Ecology, National Environmental Research Institute, Vejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark.

Key words: top-down control, shallow lakes, trophic structure, trophic cascade, macrophytes, zooplankton, fish, biomanipulation

Abstract

Based on data from 233 Danish lakes, enclosure experiments, full-scale experiments and published empirical models we present evidence that top-down control is more important in shallow lakes than in deep lakes, excepting lakes with a high abundance of submerged macrophytes. The evidence in support is: (1) That at a given epilimnion total phosphorus concentration (TP) the biomass of fish per m^2 is independent of depth, which means that biomass per m^3 is markedly higher in shallow lakes. (2) That the biomass of benthic invertebrates is higher in shallow lakes, which means that the benthi-planktivorous fish are less dependent on zooplankton prey than in deep lakes. By their ability to shift to zoobenthos predation their density can remain high even in periods when zooplankton is scarce and they can thereby maintain a potentially high predation pressure on zooplankton. (3) That the possibilities of cladocerans to escape predation by vertical migration are less. (4) That the zooplankton:phytoplankton mass ratio per m^2 is lower and presumably then also the grazing pressure on phytoplankton. (5) That nutrient constraints appear to be weaker, as evidenced by the fact that at a given annual mean TP, summer TP is considerably higher in shallow lakes, especially in eutrophic lakes lacking submerged macrophytes. (6) That negative feedback on cladocerans by cyanobacteria is lower as cyanobacterial dominance is less frequent in shallow lakes and more easily broken (at least in Northern temperate lakes), and (7) That top-down control by benthi-planktivorous fish is markedly reduced in lakes rich in submerged macrophytes because the plants serve as a refuge for pelagic cladocerans and encourage predatory fish at the expense of prey fish. We conclude that manipulation of fish and submerged macrophytes may have substantial impact on lake ecosystems, in particular in shallow eutrophic lakes. On the contrary, if the conditions for more permanent changes in plant abundance or fish community structure are lacking the feed-back mechanisms that endeavour a return to the original turbid state will be particularly strong in shallow lakes.

Introduction

Until recently most lake research concentrated on deep lakes, even in Denmark (Hunding, 1977) in which the majority of lakes are shallow (Jeppesen et al., 1991). During the last ten-twenty years, however, shallow lakes and the littoral zone of deeper lakes have come into focus (e.g. Gulati et al., 1990; Mortensen et al., 1994). This may due to the increasing attention now paid to trophic interactions and top-down versus bottom-up control: Since alteration of the nutrient balance and biological system of shallow lakes often results in marked structural changes, they are particularly suitable for identifying interactions and feedback mechanisms (e.g. Gulati et al., 1990; Mortensen et al., 1994). Moreover, shallow lakes are easier to manipulate than deep lakes. A second reason for the increasing interest in shallow lakes is that lake restoration by means of biological manipulation seems more effective than in deep lakes (Lammens et al., 1990; Jeppesen et al., 1990b; McQueen, 1990). This is partly attributable to the fact that submerged macrophytes are able to colonize relatively large areas in shallow lakes and the potential for obtaining clearwater effects of macrophytes is consequently greater in these lakes (e.g. Scheffer et al., 1993). However, biomanipulation of shallow lakes may have marked effects even without the establishment of submerged macrophytes (Jeppesen et al., 1997). In the present report based on experience and data from Danish lakes and published empirical equations (Hanson & Leggett, 1982; Zdanowski, 1982; Hanson & Peters 1984, Pridmore et al., 1985; Downing et al., 1990), we provide evidence that top-down control is in fact potentially higher in shallow lakes. How this can be exploited in lake management is discussed, special emphasis being placed on the role of fish and submerged macrophytes.

Top-down control: shallow versus deep lakes

Is the importance of fish higher in shallow lakes?

At increasing nutrient levels significant changes in fish abundance, biomass and composition take place in temperate lakes. Fish biomass and density per unit of lake area increase with increasing total phosphorus concentration (TP) (Hanson & Leggett, 1982; Quiros, 1990; Table 1) and the percentage contribution of piscivorous fish decreases (Persson et al., 1988; Jeppesen et al., 1990b, 1994; Figure 1). At the same time, the predation pressure on zooplankton increases as evidenced by a reduction in the zooplankton:phytoplankton biomass ratio (Figure 1), which means that the grazing pressure on phytoplankton most likely decreases. There are several indications suggesting that the top-down effect of these changes is greatest in shallow lakes. Cross analysis of data from 29 lakes covering a wide range of phosphorus levels (TP = 0.008-0.54 mg P l^{-1}) and mean depth (2.4-148 m) revealed that fish biomass per unit area is negatively related to mean depth (Hanson & Leggett, 1982): Fish biomass decreased from 239 to 46 kg ww ha^{-1} when mean depth increased from 1 to 10 m corresponding to a difference as high as 48-fold in mean biomass per unit volume (24 and 0.5 mg ww fish l^{-1}, respectively). The reduction in biomass per unit area may be a coincidence related to a difference in the nutrient state of the lakes included in the analysis, since depth dependence disappears if TP is included in the analysis (Table 1). Downing et al. (1990) also found that the fish biomass could be related to TP and that depth did not contribute significantly to the relationship. The two studies thus

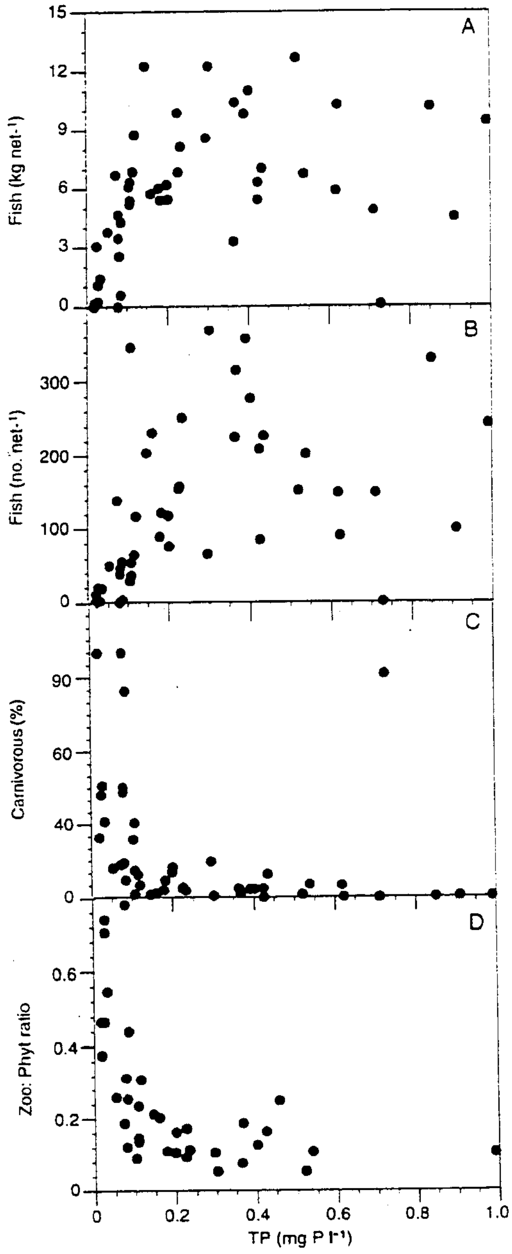

Figure 1. Biomass (A) and density (B) of planktivorous fish and contribution of carnivorous fish (%) (C) to the total number of fish caught in multiple mesh sized gill-net surveys conducted between 15 August and 15 September, and the ratio of zooplankton to phytoplankton biomass (D) versus the concentration of total phosphorus in the epilimnion. Each point represents one lake. The outlier in panel C represents a lake in which TP is high due to former sewage discharge, but where external N and P loading is presently low (from Jeppesen, unpubl. data).

Table 1. Regression equations relating fish biomass (FISHBIO, kg ww ha^{-1}) to total phosphorus concentration (TP, μg P l^{-1}) and mean depth (Z_{mean}, m) (From Hanson & Leggett, 1982).

	Intercept	Log_{10} TP	Log_{10} Z_{mean}	r^2	P^a
Log_{10} FISHBIO	2.38	–	−0.72	0.27	<0.02
Log_{10} FISHBIO	0.774	0.708	n.s.	0.75	<0.001

[a] *T*-test

show that fish biomass per unit volume at fixed TP reduces proportionately with mean depth. In very shallow lakes the biomass can be considerably higher than the above-mentioned maximum of 24 mg l^{-1}. Thus, in bream and carp dominated lakes, biomass has been reported to be as high as 600-1,000 kg ww ha^{-1} (Meijer et al., 1990; Jeppesen et al., 1990b; Grimm & Backx, 1990), corresponding to 60-100 mg l^{-1}.

Although it is likely, a higher density of fish per unit volume in shallow lakes does not necessarily indicate a higher predation pressure on zooplankton, as the biomass (and then probably also production) of prey zooplankton per unit volume is also higher in shallow lakes. Thus using data covering a broad spectrum of water depth (maximum 1.8-397 m) and TP levels (0.004–0.2 mg P l^{-1}), Hanson & Peters (1984) found that zooplankton biomass increased with increasing TP and decreased with maximum depth (Table 2). At a TP of 0.1 mg P l^{-1}, for example, biomass decreases from 1.23 to 0.86 mg dw l^{-1} (or 30%) when maximum depth increases from 1 to 10 m and accordingly zooplankton biomass per unit area markedly increases with depth. It is a prerequisite for these calculations that the data in Hanson & Peters (1984) investigation represents the entire water column, which cannot be evaluated. A similar slope on mean depth similar to the one of Hanson & Peters on maximum depth has, however, been obtained with survey data from 35 Danish lakes sampled fortnightly during summer for six years in a way that integrates the entire water column (Table 3).

The lower biomass of zooplankton per unit area in shallow lakes may indicate higher fish predation pressure than in deep lakes. Accordingly, the grazing pressure on phytoplankton can be expected to be lower, as in fact seems to be the case. Like zooplankton, chlorophyll *a* in the photic zone of lakes increases with increasing TP and decreases with increasing mean depth. The slope of the depth relationship is higher than was the case with zooplankton, however, the estimate for Danish lakes, for instance, being −0.26 (Table 3). Using this equation we find that at a TP of 0.1 mg P l^{-1} chlorophyll *a* decreases from 46 μg l^{-1} at a mean depth of 1 m to 25 μg l^{-1} at 10 m (54%). Accordingly phytoplankton biomass per unit area only increases 5-fold as compared with a 7-fold increase for zooplankton (Figure 2, Table 3). We obtained a similar slope on chlorophyll *a* using regression analysis of data from Polish lakes published by Zdanowski (1982) (Table 3), while Pridmore et al. (1985) found a somewhat higher slope using data on New Zealand lakes (Table 4). The generally higher slope of the depth relationship for chlorophyll *a* than for zooplankton thus shows that the zooplankton:phytoplankton per unit area ratio – and hence most likely also the grazing pressure on phytoplankton – increases with increasing mean depth (Figure 2). In practice the zooplankton:phytoplankton ratio will most likely increase more than shown in Figure 2, as the calculations imply that chlorophyll a measurements represent the whole water column. This is often not the case in stratified lakes, in which chlorophyll *a* is often lower in the hypolimnion. As samples usually cover the epilimnion only, the increase of chlorophyll-*a* per unit of area towards depth will therefore be less significant, implying a higher zooplankton:phytoplankton ratio.

Several factors may explain a higher fish predation in shallow lakes. Firstly, the possibilities for crustacean zooplankton to employ vertical migration as a means of avoiding predation – a phenomenon known to be important in deep lakes (Ringelberg, 1991; Lampert, 1993) – are probably considerably less in shallow lakes. Secondly, benthiplanktivorous fish such as bream (*Abramis brama* (L.)), roach (*Rutilus rutilus* (L.)), and rudd (*Scardinius erythrophthalmus* (L.)) may rely more on benthic feeding in shallow lakes since benthic invertebrate biomass (Hanson & Peters, 1984) (Table 2, Figure 2) and production (Lindegaard, 1994) at a given TP level are both higher than in deep lakes. Thus plankti-benthivorous fish are less likely to be as sensitive to variations in zooplankton abundance as in deep lakes. Accordingly, their density may remain comparatively high even in periods when zooplankton

Table 2. Regression equations relating zooplankton biomass (ZOOPL, μg dw l^{-1}) and zoobenthos biomass (ZOOBEN, g ww m^{-2}) to total phosphorus concentration (TP, μg l^{-1}), and maximum or mean depth (Z_{max} and Z_{mean}, m). The equations are developed from 38–49 lakes from NorthAmerica, Europe and Africa (from Hanson & Peters, 1984).

	Intercept	$\log_{10}$ TP	$\log_{10} Z_{max}$	$\log_{10} Z_{mean}$	r^2
$\log_{10}$ ZOOPLB	1.13	0.98	−0.16	–	0.75
$\log_{10}$ ZOOBEN	−0.38	0.65	−0.22	–	0.54
$\log_{10}$ ZOOBEN	+ 0.38	0.65	–	−0.22	0.54

Table 3. Regression equations relating zooplankton biomass (ZOOPLB, mg dw l^{-1}), chlorophyll *a* (CHLA, μg l^{-1}) and Secchi depth (SECCHI, m) to total phosphorus (TP, mg P l^{-1}), total nitrogen (TN, mg N l^{-1}) and mean depth (ZMEAN, m) in Danish lakes (TP-range: 0.017–1.91 mg P l^{-1}, mean depth range: 0.7–16.5 m) and Polish lakes (TP-range 0.020–0.94 mg P l^{-1}, mean depth range: 11–39 m). Also are shown r^2, root mean square error (RMSE) and the number of lakes, n. Both data sets concurrently show that chlorophyll *a* markedly reduces and Secchi depth markedly increases with increasing mean depth.

	Intercept	$\log_e$ TP	$\log_e$ TN	$\log_e Z_{mean}$	r^2	RMSE	n
Danish lakes							
$\log_e$ ZOOPLB	0.65 ± 0.02****	0.47 ± 0.08****	–	−0.14 ± 0.10$^{n.s.}$	0.59	0.46	35
$\log_e$ ZOOPLB	0.39 ± 0.005****	0.39 ± 0.10***	0.17 ± 0.1$^{n.s.}$	−0.16 ± 0.10$^{n.s.}$	0.60	0.46	35
$\log_e$ CHLA	5.78 ± 0.17****	0.85 ± 0.08****	–	−0.26 ± 0.10**	0.72	0.61	60
$\log_e$ CHLA	5.16 ± 0.26****	0.65 ± 0.10****	0.46 ± 0.16**	−0.26 ± 0.10**	0.74	0.58	59
$\log_e$ SECCHI	−1.23 ± 0.11****	−0.45 ± 0.05****	–	0.42 ± 0.06****	0.76	0.38	59
$\log_e$ SECCHI	−0.83 ± 0.16****	−0.33 ± 0.06****	−0.31 ± 0.10**	0.42 ± 0.06****	0.79	0.35	59
Polish lakes$^{\diamond}$							
$\log_e$ CHLA	5.38 ± 0.26****	0.84 ± 0.12****	–	−0.34 ± 0.13*	0.62	0.74	67
$\log_e$ CHLA	4.56 ± 0.44****	0.67 ± 0.14****	0.77 ± 0.33*	−0.25 ± 0.14$^{n.s.}$	0.65	0.71	65
$\log_e$ SECCHI	−1.36 ± 0.18****	−0.41 ± 0.08****	–	0.50 ± 0.08****	0.67	0.48	65
$\log_e$ SECCHI	−0.98 ± 0.30**	−0.33 ± 0.10**	−0.34 ± 0.22$^{n.s.}$	0.46 ± 0.10****	0.66	0.66	64

$^{\diamond}$ Data from Zdanowski, 1982

* $p<0.05$, ** $p<0.01$, *** $p<0.001$, **** $p<0.0001$, $^{n.s.}$ = not significant

is scarce; and being able to shift to zooplankton predation, they can maintain a continuously higher capacity to control zooplankton than in deep lakes. Thirdly, as zoobenthos biomass generally decreases and zooplankton biomass per unit area conversely increases with depth, the zooplankton:zoobenthos biomass ratio increases markedly with increasing mean depth (Figure 2). The same seems to apply to production, Lindegaard (1994) having found that zoobenthic production constituted as much as 86% of the total zoobenthic + zooplankton production in two shallow (mean depth 1.9–2.3 m) lakes, but only 47% and 32% in two deep lakes (mean depth 13.5 m and 34.1 m, respectively) with comparable nutrient levels. A shift from benthic to pelagic feeding – for example during times when prey zooplankton density is high – is therefore likely to have a substantially greater impact on zooplankton in shallow lakes. The higher zoobenthos biomass and production in shallow lakes may reflect higher sedimentation mediated by the lower settling distance (Jeppesen et al., 1990a), as well as the lower grazing pressure on phytoplankton due to the higher fish predation. Moreover, the nutritive value of the settled material is probably higher in shallow lakes since the retention time in the water column is lower. An exception may be large shallow lakes in which frequent resuspension enhances retention and decomposition in the water, thereby reducing the availability of settled material for deposit-feeding zoobenthos.

While it can be surmised that fish predation pressure on zooplankton is highest in shallow lakes, experiments involving fish manipulation indicate that if predation pressure is reduced, the capacity of zooplankton to control phytoplankton will be especially high in shallow lakes (Lammens et al., 1990; Jeppesen et al., 1990b, Moss, 1990). One reason may be that

Table 4. Regression equations relating chlorophyll *a* (CHLA, $\mu g\ l^{-1}$) to total phosphorus (TP, $\mu g\ l^{-1}$), total nitrogen (TN, $\mu g\ l^{-1}$), and mean depth (Z_{mean}, m) in 16 New Zealand lakes. TP ranged from 10-153 μg P l^{-1}, mean depth from 2–97 m and chlorophyll *a* from 0.6–54 μg $^{-1}$ (from Pridmore et al., 1985).

	Intercept	$\log_{10}$ TP	$\log_{10}$ TN	$\log_{10}$ Z_{mean}	r^2
$\log_{10}$ CHLA	−1.26	1.50	–	–	0.73
$\log_{10}$ CHLA	−1.43	1.40	0.11	–	0.73
$\log_{10}$ CHLA	−0.11	1.00	–	−0.50	0.80

large *Daphnia* spp. like fish, use the settled seston and epipelon as alternative food sources in shallow lakes. If that is the case, the zooplankton will be able to maintain a potentially high grazing pressure on the phytoplankton even during periods in which the phytoplankton density is so low that starvation followed by a decline in zooplankton biomass would otherwise have occurred. In support of this view typical zooplankton-phytoplankton predator-prey oscillations do not often occur in nutrient-rich shallow lakes in the absence of fish. Algal biomass remains continuously low during the major part of the summer, while the biomass of large *Daphnia* (*D. magna* Straus, *D. pulex* Baird) – although fluctuating – remains high (Barica, 1975; Fott et al., 1980; Carvalho, 1994; Jeppesen, unpubl. data). In addition, enhanced phytobenthos growth, due to *Daphnia* grazing-mediated improved light conditions, may directly by phytobenthos uptake and indirectly by changing the chemical environment in the sediment reduce the nutrient release from the sediment as observed in laboratory experiments by Hansson (1989) and Jansson (1989). This will further help *Daphnia* in controlling phytoplankton because of the consequent greater nutrient constraints on phytoplankton (increased bottom-up control).

Fish may influence both bottom-up and top-down control via their search for food at the bottom. Benthivorous fish, in particular carp (*Cyprinus carpio* (L.)) and bream, stir up sediment when searching for food; at high fish density the concentration of suspended organic and inorganic matter increases markedly. Results from shallow fish-manipulated lakes (Meijer et al., 1990) and from pond experiments (Breukelaar et al., 1994) with varying densities of benthivorous fish revealed a highly significant linear relationship between the abundance of inorganic suspended matter and carp and bream biomass, Secchi depth thus being considerably lower when the biomass of these fish was high. At reduced transparency the food capture efficiency of visually hunting predators such as perch (*Perca fluviatilis* L.) most likely decreases, thus reducing their capacity to control planktivorous prey fish with a negative feedback on the large-bodied zooplankton grazers, i.e. the daphnids. In addition, a high concentration of suspended matter may negatively influence the growth of *Daphnia* spp. (and thus top-down control of phytoplankton) as their assimilation efficiency is reduced (Arruda et al., 1983; Hart, 1988). Moreover, it may lower their competitiveness compared to rotifers (Kirk & Gilbert, 1990; Kirk 1991), which are less efficient grazers on large phytoplankton (Bogdan & Gilbert, 1984; Arndt, 1993). As consequence, the capacity to control phytoplankton is further reduced.

The impact of benthivorous fish on resuspension is believed to increase with decreasing mean depth, partly because the sediment stirred up by fish is distributed within a smaller water volume, and partly because wind forces in shallow lakes more easily hold resuspended sediment in suspension. In addition, wind-induced resuspension is more likely to occur in shallow lakes. That water depth and benthivorous fish are important is supported by empirical relationships developed for Danish lakes (Windolf et al., 1993): In shallow lakes the concentration of suspended matter increased with increasing TP concentration and lake area (the latter being a substitute for wind impact) and decreases with mean depth and increasing grazing pressure on phytoplankton. Even when these variables were included the bream biomass still made a significant contribution to the relationship. In deep lakes, however, bream and lake area did not make a significant contribution to the variation in suspended matter. Fish-induced resuspension of sediment not only has a negative impact on top-down control forces, it probably also reduces the nutrient constraint on phytoplankton growth as a result of nutrient release (Havens, 1991; Søndergaard et al., 1992). On the other hand, the reduction in light conditions may negatively affect the phytoplankton growth

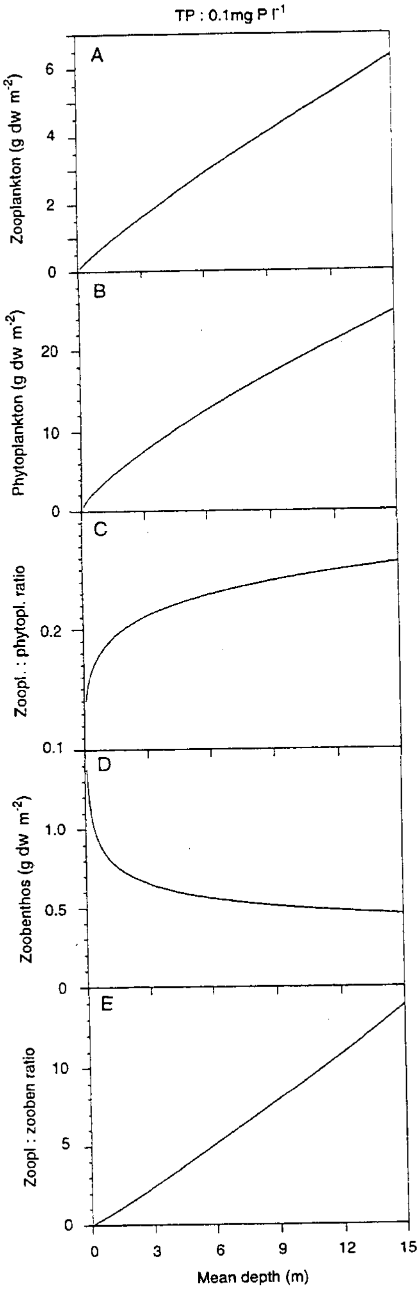

Figure 2. Biomass per unit area of zooplankton (A) and phytoplankton (B), zooplankton:phytoplankton per unit area ratio (C), zoobenthos biomass (D) and the zooplankton:zoobenthos ratio (E) in lakes with an epilimnion total phosphorus concentration of 0.1 mg P l^{-1} and different mean depths. The curves in A and B are based on the equations from Danish lakes shown in Table 3, while that in D is based on the equation by Hanson & Peters (1984), shown in Table 2. The equations used are those including total phosphorus and mean depth.

(Hoyer & Jones, 1983). Accordingly, while high resuspension does not necessarily imply high phytoplankton growth, it always results in lower water transparency.

How important are YOY fish? In order to facilitate the development of methods to combat top-down control by fish it is important to know the relative contribution of small and large fish to predation on zooplankton. In recent years it has been established that young-of-the year (YOY) fish play a far more important structuring role in lake ecosystem than previously believed (Mills & Forney, 1983; Cryer et al., 1986; Mills et al., 1987; Whiteside, 1988; Gliwicz & Pijanowska, 1989, Hewett & Steward, 1989). Some studies indicate that YOY are responsible for the mid-summer decline in zooplankton (Luecke et al., 1990), a phenomenon previously attributed to the increased density of inedible phytoplankton such as cyanobacteria (e.g. Bernardi & Guissani, 1990). The importance of YOY seems, however, to decrease with increasing TP as indicated by the seasonal dynamics in zooplankton grazing pressure on phytoplankton (Figure 3). Thus, in mesotrophic lakes there is a gradual change from a high pre-summer and, in some of the lakes, a high autumn grazing pressure on phytoplankton to a low grazing pressure all year round in the most hypertrophic lakes (Figure 3). The latter probably reflects that due to a high biomass planktivorous fish maintain a high predation pressure on zooplankton resulting in a low grazing pressure on phytoplankton throughout the season irrespective of the number of YOY. The low grazing pressure in hypertrophic lakes cannot be due to lack of edibility or palatibility of the phytoplankton as most of these lakes were dominated by edible green algae (Jeppesen et al., 1990a, 1990b; Jensen et al., 1994). Likewise, the low grazing pressure during mid-summer at lower TP levels cannot be primarily due to negative feedback from cyanobacteria since the decline occurs every year irrespective of whether or not cyanobacteria are present (Jeppesen, unpubl. data). The potential role og zooplankton grazing may be higher than indicated in Figure 3, however, as the zooplankton was sampled during the day; because even though the samples integrate the whole water column, zooplankton seeking refuge at the sediment surface may have escaped sampling (Jeppesen, unpubl. data). Nevertheless, grazing pressure on pelagic phytoplankton seems very low during summer, at least during the day.

Although the question of whether or not YOY fish are particularly important in shallow lakes remains to be clarified, the findings indicate that YOY-fish play

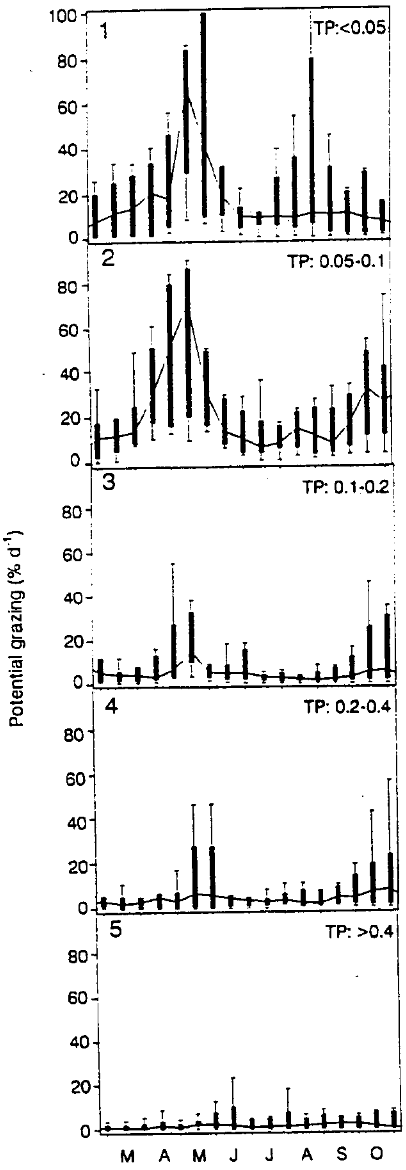

Figure 3. Seasonal variation in the zooplankton potential grazing pressure on phytoplankton (% of the phytoplankton biomass ingested per day) at five different phosphorus categories (mg P l^{-1}). The curve indicates the median, the thick bars the 25–75% percentiles, and the thin bars the 10–90% percentiles. Each phosphorus category includes 6–10 lakes. The potential grazing pressure is calculated assuming that cladocerans and copepods ingest phytoplankton corresponding to 100% and 50%, respectively, of their biomass per day (from Jeppesen, unpubl. data).

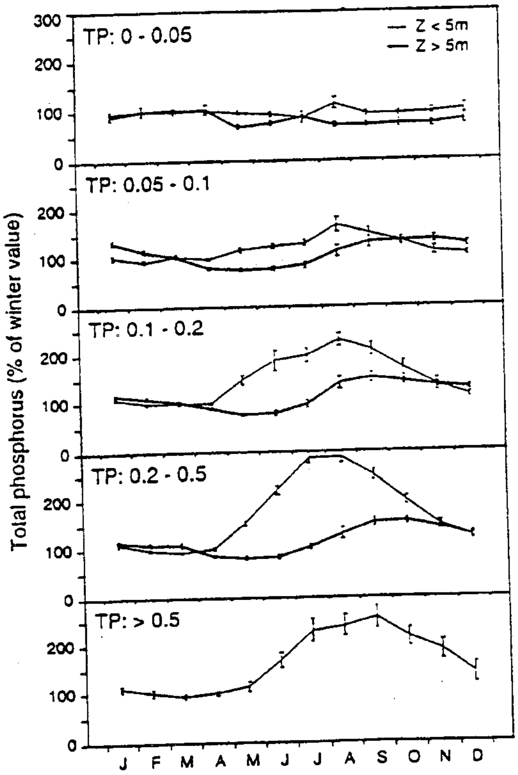

Figure 4. Seasonal variation in epilimnion total phosphorus concentration, expressed in per cent of winter values (monthly mean ± SD) in Danish lakes in different categories of mean annual TP (mg P l^{-1}). The data set is divided into lakes with a mean depth < 5 m ($n = 191$) and > 5 m ($n = 42$).

an important role for the overall predation pressure in mesotrophic and slightly eutrophic shallow lakes. In hypertrophic shallow lakes YOY-fish are probably less important because older fish seem to maintain a high predation pressure throughout the year anyway.

Are nutrient constraints less important in shallow lakes? The importance of top-down control is also influenced by the strength of bottom-up factors, and these seem to be weaker in shallow lakes. The shallow lake is typically fully mixed throughout the year, whereas most deep lakes are summer-stratified. This affects nutrient availability for the phytoplankton. Due to nutrient loss to the hypolimnion through sedimentation TP typically decreases in stratified lakes in late spring, thereafter to gradually increase to an autumn peak in connection with the thermocline being forced downwards and eventually broken (Figure 4). In shallow mesotrophic and macrophyte-rich Danish lakes (<0.05 mg P l^{-1}) there is also a tendency towards a slight decrease in TP in late spring followed by a minor peak in August. In the more nutrient-rich shallow lakes, in contrast, there is a marked increase in TP during summer that peaks in August. The summer–winter difference in TP levels increases markedly with increasing nutrient level, TP being 2.5–3-fold greater during summer than winter in hypertrophic lakes. The increasing amplitude may reflect increased internal loading during summer. In a number of the lakes with short residence time, however, it also reflects increased TP concentration in the water inlets because of the reduced groundwater input to inflowing rivers in summer and the resultant increased proportion of sewage in the inlet water (Kristensen et al., 1991). As phosphorus is often the growth-limiting nutrient in lakes, this suggests that nutrient constraint (bottom-up control) is comparatively weak in shallow lakes.

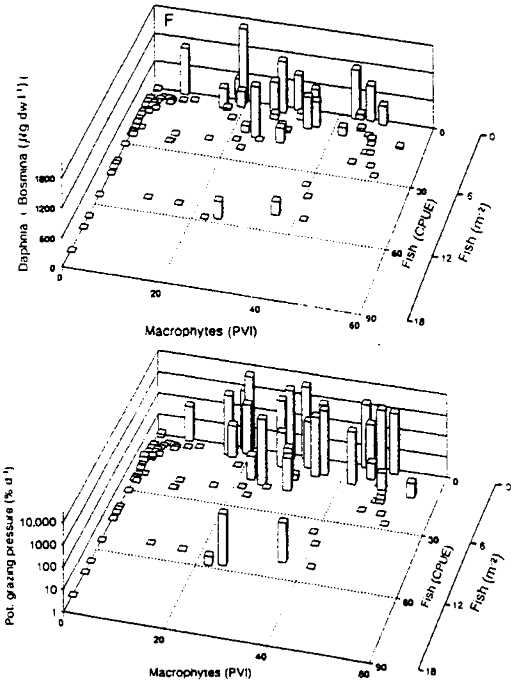

Figure 5. Biomass of the dominant pelagic cladocerans (*Bosmina* + *Daphnia*; upper panel) and their potential grazing pressure on phytoplankton (estimated 24 h ingestion by *Bosmina* + *Daphnia* in % of phytoplankton biomass; lower panel) versus the abundance of 0+ and 1+ roach and three-spined sticklebacks (CPUE in traps) and macrophyte plant volume ingested, PVI (%) in Lake Stigsholm enclosure experiments involving manipulation of plants (mainly *Potamogeton* species) and fish density (modified from Schriver et al., 1995).

Is the competitive capacity of cyanobacteria lower in shallow lakes? Although fish thus seem to be the main cause of the decrease in zooplankton grazing pressure from mesotrophic to eutrophic lakes, large and in particular filamentous algae can also have a negative impact on grazing capacity and thereby weaken the top-down control of phytoplankton. This is particularly the case with cyanobacteria in freshwater lakes (Bernardi & Giussani, 1990). Thus large cyanobacteria may affect the filtration capacity of zooplankton by interference and be less edible, less nutritious, and sometimes toxic (Bernardi & Guissani, 1990). Cyanobacteria are often dominant during summer in eutrophic shallow lakes (Sas, 1989) but appear to contribute less to biomass at relatively low and high TP in shallow non-stratified lakes than in deep stratified lakes – at least in the Northern temperate region. Thus, analysis of data from 178 Danish lakes (Jeppesen et al., 1990b; Jensen et al., 1994) showed that cyanobacteria dominate at intermediate TP levels (0.1–0.5 mg P l^{-1}), while green algae usually dominate in the most hypertrophic lakes and a mixed community is found at TP levels below 0.1 mg P l^{-1}. Green algal dominance of shallow hypertrophic lakes has also been observed elsewhere (Nygaard, 1949; Pavoni, 1963; Leah et al., 1980). In contrast, the majority of deep lakes are dominated by cyanobacteria at TP levels above some 0.02–0.05 mg P l^{-1} (Sas, 1989). Cyanobacteria are S-strategist and have a low specific settling rate, among other reasons, because of a high buoyancy (Reynolds, 1984). This makes them competitive in stratified systems where loss by sedimentation is critical because, as discussed above, the nutrients do not immediately return to epilimnion. In fully mixed lakes, in contrast, nutrients are rapidly returned from the sediment (Søndergaard et al., 1990a) and TP is often higher during summer (Figure 4), thereby rendering nutrient loss by sedimentation less critical. In addition, due to temporal fluctuations in temperature on a seasonal and diurnal scale as well as wind-induced resuspension nutrient release to the photic zone probably fluctuates more in shallow lakes, thus enabling R-strategists to compete more easily with S-strategists (Sommer, 1985) such as cyanobacteria. It therefore seems reasonable to assume that the overall negative influence which cyanobacteria may have on the top-down control forces is more important in deep lakes.

How is the impact of submerged macrophytes on top-down control? Several studies have shown that submerged macrophytes have a stabilizing effect on lake ecosystems and, if abundant, contribute to maintaining a clearwater state even at high nutrient concentrations (Canfield et al., 1984; Jeppesen et al., 1990b; Scheffer et al., 1993; Moss et al., 1994; Meijer et al., 1994). The reasons for this are numerous, as discussed by e.g. Moss (1990), Scheffer (1990), Jeppesen et al. (1991) and Scheffer et al. (1993). We will concentrate on macrophytes as a refuge for pelagic cladocerans as submerged macrophytes protect pelagic and plant-associated cladocerans from fish predation (Timms & Moss, 1984), thereby helping to maintain a higher grazing pressure on phytoplankton produced in the plant-covered areas or which have drifted in from the pelagic with the water current (Schriver et al., 1995). The efficacy of the macrophyte as a refuge for pelagic cladocerans depends on plant density (Crowder & Cooper, 1979; Winfield, 1986; Diehl, 1988) and type (Irvine et al., 1990), as well as on the density and composition of the planktivorous fish present in the vegetation (Persson, 1991). For example, Schriver et al. (1995) found a poor refuge effect of macrophytes even at low densities of 0+ and 1+ planktivorous fish (three-spined sticklebacks (*Gasterosteus aculeatus* (L.)) and roach if the plant volume infested (PVI) (Canfield et al., 1984) of filamentous *Potamogeton* species was lower than 10-15%, but a high refuge effect at higher PVI provided that fish density was low (Figure 5). In the latter case the estimated grazing pressure on phytoplankton was extremely high, phytoplankton biomass consequently being low and dominated by grazing-tolerant forms. If fish density was higher than about 4 fish per m^2 the grazing pressure on phytoplankton again fell drastically to values so low that the zooplankton could no longer control the phytoplankton. Although the experiments were based on calculated grazing pressure (see legend to Figure 5), subsequent in vitro grazing experiments with ^{14}C-labelled phytoplankton have confirmed the results (Jeppesen, unpubl. data).

A factor that contributes to the stabilization is that pelagic cladocerans primarily use the macrophytes as a daytime refuge against predation from fish. During night they, migrate into the open water where they contribute to control of pelagic phytoplankton (e.g. Timms & Moss, 1984). Macrophyte refuges are therefore comparable to vertical migration and compensate for the poor possibilities for cladocerans for using the vertical alternative in shallow lakes. This daytime migration to the plant beds takes place despite the fact that submerged macrophytes may have a repellent effect on pelagic cladocerans which may be attributable to chemical cues (Hasler & Jones, 1949; Pennak, 1966, 1973; Quade, 1969). Regarding zooplankton this seems reasonable as the open water among the plants in dense macrophyte beds is frequently poor in phytoplankton and microorganisms due to high grazing pressure by plant-associated cladocerans, etc. (Jeppesen et al., unpubl. data). Pelagic cladocerans are also influenced by chemical cues from planktivorous fish (Dodson, 1988; De Meester, 1993; Loose et al., 1993; Lauridsen & Lodge, 1996), however, and the net result of these two contradictory cues is that migration to macrophyte beds occurs during the day – at least in shallow eutrophic lakes with high fish densities (Lauridsen et al., 1996; Lauridsen & Buenk, 1996). Aggregation of pelagic cladocerans seems to be especially important in the case of small macrophyte beds (Lauridsen et al., 1996) since pelagic cladocerans mainly appear in

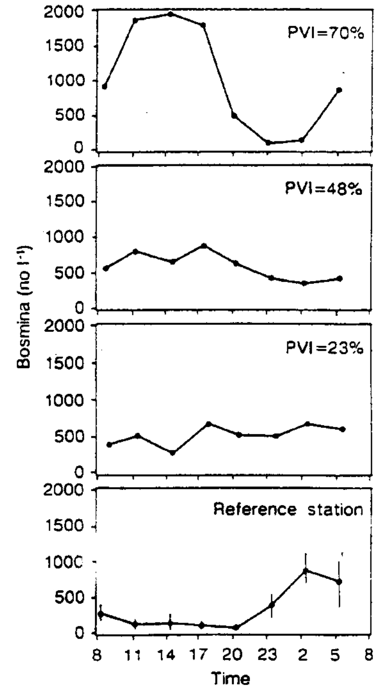

Figure 6. Diel variation in the density of *Bosmina* spp. (mainly *B. longirostris*) in exclosures with various macrophyte densities (PVI) and at a reference station (including SD, $n = 3$) located in a plant-free part of Lake Stigsholm. Average density and diel amplitude (high during day and low during night) are highest at high PVI. At the reference station, in contrast, the highest density occurred at night (Pedersen, unpubl. data).

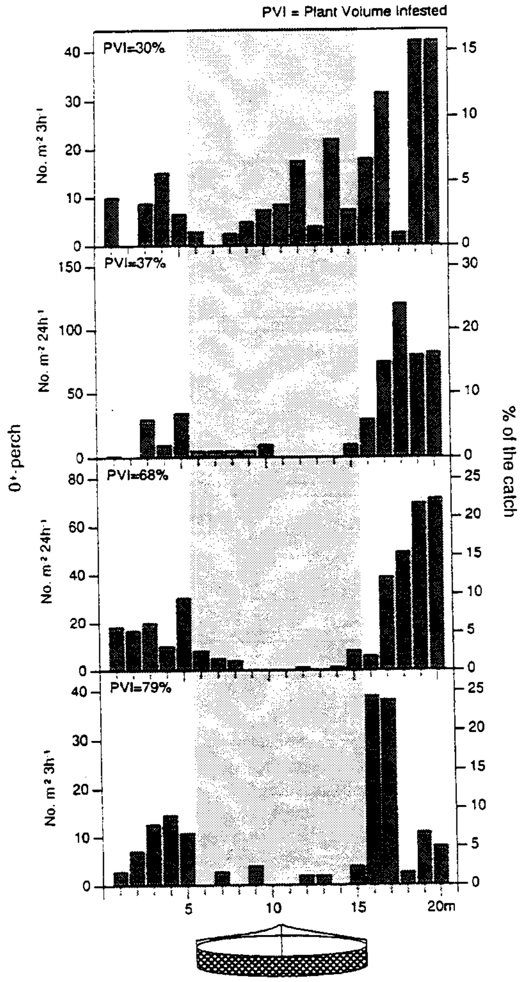

Figure 7. Diel variation in gill net (8 mm mesh size) catches of the predominant 0+ fish (perch) along a 20 m transect running through and 5 m at either side of 10 m enclosures differing in submerged macrophyte (hatched area) plant volume infested (PVI). Each column represents the catch in a 1 m section of the gill net. It can be seen that 0+ perch avoided dense macrophyte beds (above 30% PVI) consisting of mainly *Potamogeton pusillus* and *P. pectinatus* (Jensen, unpubl. data).

the transitional zone between the macrophyte belt and open water (Lauridsen & Buenk, 1996). Aggregation also appears to be especially high in dense macrophyte beds (Figure 6 and Stansfield et al., 1997), partly because the zooplanktivorous fish tend to avoid these areas (Engel, 1988; Phillips et al., 1995; Figure 7), and partly because they provide better protection against fish predation (Winfield, 1986; Engel, 1988; Schriver et al., 1995; Figure 5).

Apart from influencing the phytoplankton in the macrophyte beds during the day, night-time migration to the open water may also have a significant effect on the pelagic system. On the basis of migration data from densely vegetated 2 m beds Lauridsen et al. (1996) calculated that only 3% coverage of lake area was needed for an increase of the average night-time concentration of cladocerans 2-fold in the entire water column of shallow lake Stigsholm (mean depth: 1 m; surface area: 21 ha). Establishment of even small numbers of small, dense macrophyte beds may therefore markedly enhance the capacity of the pelagic zooplankton to control phytoplankton in the open water. This is further strengthened by the fact that submerged macrophytes favour piscivorous fish such as perch and pike (*Esox lucius* L.) at the expense of planktivorous fish such as roach and bream (Winfield, 1986; Grimm & Backx, 1990) and thereby indirectly the large pelagic cladocerans and grazing pressure on phytoplankton. Submerged macrophytes therefore compensate for the overall higher predation risk in shallow lakes.

Management implications (biomanipulation)

Fish and submerged macrophytes seem to play an important role in shallow lakes, and lake manipulation of these two compartments may thus have substantial impact on the ecosystem. Conversely, it also implies that if the conditions for more permanent changes in plant density or fish stock are not present the feed-back mechanisms that endeavour to return lake systems to their original turbid state will be particularly strong in shallow lakes. It is important to bear this in mind when undertaking biomanipulation in shallow lakes.

Several management-oriented biological restoration methods have been developed (e.g. Moss, 1990). Selective removal of planktivorous fish is one of the methods that may enhance top-down control of phytoplankton, and several experiments have been conducted with varying degrees of success (e.g. Shapiro & Wright, 1984; Benndorf, 1987; Gulati et al., 1990; De Melo et al., 1992; Reynolds, 1994; Meijer et al., 1994). An alternative or supplementary method is stocking of predatory fish, e.g. pikeperch (Benndorf et al., 1988), perch (Riemann et al., 1990) or YOY pike (Prejs et al., 1994). In Denmark we have experimented with the stocking of large numbers of YOY pike, the idea being that they would forage on newly hatched roach and bream since the YOY of these two species seem to maintain a high predation pressure on pelagic zooplankton during summer (Figure 2). The Danish studies (Berg et al., 1997) and those of a Polish lake (Prejs et al., 1994) have shown that at high density YOY pike may have a highly significant negative impact on the density of YOY prey fish, and that this cascades to the lower trophic levels resulting in a shift to large-bodied zooplankton, a decrease in chlorophyll *a* and TP and an increased Secchi depth (Søndergaard et al., 1997). Due to cannibalism among pike during winter the long-term effect is poor, however, although repeated stocking of pike can be used during a transitional period following nutrient loading reduction in order to maintain a high transparency and thereby stimulate growth of submerged macrophytes (Søndergaard et al., 1997).

Since the first experiments involving fish manipulation in Denmark were initiated in 1986 (Riemann et al., 1990; Søndergaard et al., 1990b; Jeppesen et al., 1990a, 1990b), 14 additional experiment have been undertaken. The results indicate that the method will have a long-term effect in shallow lakes if nutrient loading has been reduced to levels so low that the TP concentration in the future state of equilibrium will be below 0.05-0.1 mg P l^{-1} (Jeppesen & Søndergaard, unpubl. data) which is somewhat lower than the 0.08-0.15 mg P l^{-1} given by Jeppesen et al. (1991). However, if nitrogen loading is low a positive result may also be obtained at higher phosphorus concentrations. Although it has been claimed that fish manipulation is most likely to be successful in lakes with a surface area <0.04 km^2 (Reynolds, 1994), this is not in accordance with our experience. Thus a marked trophic cascade has taken place in lake Arreskov (3 km^2) after natural fish kill, resulting in a shift to a clearwater stage (Fyns Amtskommune, 1995), and following fish manipulation of lake Christina (16 km^2) (Hanson & Butler, 1994) and lake Finjasjön (11 km^2) (Annedotter et al., personal comments) the lakes became clear with extensive growth of submerged macrophytes. Also cyanobacteria have been reported to render it difficult to initiate a shift to the clearwater state as they negatively influence the zooplankton in various ways (Bernardi & Guissani, 1990). Again, however, this is not in accordance with our experience (e.g. Søndergaard et al., 1990b; Jeppesen et al., 1997). Further evidence is given by cross-analyses of survey data from Danish lakes showing that low grazing pressure on phytoplankton during summer in eutrophic lakes rather reflects a high fish predation pressure on zooplankton (especially by YOY) than it is a result of negative cyanobacterial feedback (Jeppesen, unpubl. data). Fish manipulation methods still need to be further developed, but will undoubtedly become an important lake restoration tool, especially in the case of shallow lakes as a follow-up to a reduction in external nutrient loading.

Plant refuges, protecting submerged macrophytes against waterfowl grazing may be an alternative or supplementary method to increase the top-down control of phytoplankton, especially in cases where grazing by waterfowl, such as coot and mute swans, delays the establishment of submerged macrophytes such as has frequently been observed at low plant densities (Lauridsen et al., 1993, 1994; Van Donk et al., 1994; Søndergaard et al., 1996, but see Perrow et al., 1997). The refuges serve two purposes: They enable the plants to grow in a predation-free environment from where they can spread vegetatively or via seeds from to the remaining part of the lake, and they increase the daytime refuge possibilities for pelagic cladocerans. As described above, the migration intensity of pelagic cladocerans is probably greatest in small, dense macrophyte beds. The refuges must therefore be adapted accordingly. They can be simple, consisting of wooden poles covered by open mesh wire fencing, etc.. The use of plant refuges as a restoration tool is probably limited to the same nutrient interval as fish manipulation because it is in this nutrient interval that colonization of submerged macrophytes is most likely to succeed (Jeppesen et al., 1990b, 1991). We predict that the method will be most efficient in small lakes, because coot density is relatively higher in these lakes (Brøgger-Jensen & Jørgensen, 1992; Søndergaard et al., 1996).

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References

Arndt, H., 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 255/256: 231–246.

Arruda, J.,A., G. R. Marzolf & R. T. Faulk, 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. Ecology 65: 1225–1235.

Barica, J., 1975. Collapses of algal blooms in prairie pothole lakes: Their mechanisms and ecological impact. Verh. int. Ver. Limnol. 19: 606–615.

Benndorf, J., 1987. Food web manipulation without nutrient control: A useful strategy in lake restoration? Schweiz. Z. Hydrol. 49: 237–248.

Benndorf, J., H. Schultz, A. Benndorf, R. Unger, E. Penze, H. Kneschke, K. Kossatrz, R. Dumke, U. Hornic, R. Kruspe & S. Reichels, 1988. Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypertrophic Bautzen Reservoir. Limnologica 19: 97–110.

Berg, S., E. Jeppesen & M. Søndergaard, 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng (Denmark). Hydrobiologia 342/343: 311–318.

Bernardi, R. de & G. Guisanni, 1990. Are blue-green algae suitable food for zooplankton? An overview. Hydrobiologia 200/201: 29–41.

Bogdan, K. G. & J. J. Gilbert, 1984. Body size and food size in freshwater zooplankton. Proc. natn. Acad. Sci. U.S.A. 81: 6427–6431.

Breukelaar, A. W., E. H. R. Lammens, J. P. G. Klein Breteler & I. Tatrai, 1994. Effects of benthivorous bream (*Abramis brama* L.) and carp (*Cyprinus caprio* L.) on sediment resuspension and concentration of nutrients and chlorophyll *a*. Freshwat. Biol. 32: 113–121.

Brøgger-Jensen, S. & H. E. Jørgensen, 1992. Vandfugle og søers miljøtilstand [The environmental state of waterfowl and lakes]. Miljøprojekt nr. 200. Danish Environmental Protecton Agency, Copenhagen, 64 pp.

Canfield, D E., J. V. Shireman, D. E. Colle, W. T. Haller, C. E. Watkins, & M. J. Maceina, 1984. Prediction of chlorophyil *a* concentrations in Florida lakes: Importance of aquatic macrophytes. Can. J. Fish. aquat. Sci. 44: 497–501.

Carvalho, L., 1990. Top-down control of phytoplankton in a shallow hypertrophic lake: Little Mere (England). Hydrobiologia 200/201: 53–64.

Crowder, L. B. & W. E. Cooper, 1979. Structural complexity and fish-prey interactions in ponds: A point of view. In Johnson, D. L. & R. A. Stein (eds), Response of fish to habitat structure in standing water. North Central Division. Am. Fish. Soc. Spec. Pub. 6: 1–10.

Cryer, M., G. Pierson & C. R. Townsend, 1986. Reciprocal interactions between roach *Rutilus rutilus*, and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31: 1022–1038.

De Meester, L., 1993. Genotype, fish-mediated chemicals, and planktonic behaviour in *Daphnia magna*. Ecology 74: 1467–1474.

De Melo, R., R. France & D. J. McQueen, 1992. Biomanipulation: Hit or myth? Limnol. Oceanogr. 37: 192–207.

Diehl, S., 1988. Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. Oikos 53: 207–214.

Dodson, S., 1988. The ecological role of chemical stimuli for the zooplankton: the predator-avoidance behaviour in *Daphnia*. Limnol. Oceanogr. 33: 1431–1439.

Downing, J. A., C. Plante & S. Lalonde, 1990. Fish production correlated with primary productivity and the morphoedaphic index. Can. J. Fish. aquat. Sci. 47: 1929–1936.

Engel, S., 1988. The role and interactions of submersed macrophytes in a shallow Wisconsin lake. J. Freshwat. Ecol. 4: 329–340.

Fott., J., L. Pechar & M. Prazakowa, 1980. Fish as a factor controlling water quality in ponds. In Barica, J. & L. R. Mur (eds), Hypertrophic Ecosystems, Developments in Hydrobiology 2. Dr W. Junk Publishers, The Hague: 255–261.

Fyns Amtskommune, 1995. Vandmiljøovervågning - Arreskov Sø 1994 [Environmental Survey - Lake Arreskov Sø 1994]. Fyns Amt, 123 pp.

Gliwicz, Z. M. & J. Pijanowska, 1989. The role of predation in zooplankton succession. In Sommer, U. (ed.), Plankton Ecology. Springer Verlag, London: 253–296.

Grimm, M. P. & J. J. G. M. Backx, 1990. The restoration of shallow eutrophic lakes and the role of northern pike, aquatic vegetation and nutrient concentration. Hydrobiologia 200/201: 557–566.

Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer & E. van Donk, 1990. Biomanipulation, tool for water management. Hydrobiologia, 200/201: 1–628.

Hanson, J. M. & M. G. Butler, 1994. Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lakes. Can. J. Fish. aquat. Sci. 51: 1180–1188.

Hanson, J. M. & W. C. Leggett, 1982. Empirical prediction of fish biomass and weight. Can. J. Fish. aquat. Sci. 39: 257–263.

Hanson, J. M. & R. H. Peters, 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. Can. J. Fish. aquat. Sci. 41: 439–445.

Hansson, L. A., 1989. The influence of a periphytic biolayer on phosphorus exchange between substrate and water. Arch. Hydrobiol. 115: 21–26.

Hart, P. C., 1988. Zooplankton feeding rates in relation to suspended sediment content: Potential influences on community structure in a turbid reservoir. Freshwat. Biol. 19: 123–139.

Hasler, A. & F. Jones, 1949. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30: 359–364.

Havens, K. E., 1991. Fish-induced sediment resuspension: Effects on phytoplankton biomass and community structure in a shallow hypereutrophic lake. J. Plankton. Res. 13: 1163–1176.

Hewett, S. W. & D. J. Stewart, 1989. Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal and historical patterns. Trans. am. Fish. Soc. 118: 581–596.

Hoyer, M. V. & J. R. Jones, 1983. Factors affecting the relation between phosphorus and chlorophyll *a* in Midwestern reservoirs. Can. J. Fish. Aquat. Sci. 40: 192–199.

Hunding, C., (ed.) 1977. Danish Limnolgy. Reviews and Perspectives. Folia limnol. scand. 17, 136 pp.

Irvine, K., B. Moss & J. Stansfield, 1990. The potential of artificial refugia for maintaining a community of large-bodied cladocera against fish predation in a shallow eutrophic lake. Hydrobiologia 200/201: 379–389.

Jansson, M., 1989. Role of benthic algae in transport of nitrogen from sediment to lake water in a shallow clearwater lake. Arch. Hydrobiol. 89: 101–109.

Jensen, J. P., E. Jeppesen, K. Olrik & P. Kristensen, 1994. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorococcal green algal dominance in shallow Danish lakes Can. J. Fish. aquat. Sci. 51: 1692–1699.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjaer & K. Olrik, 1990b. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. Hydrobiologia 200/201: 219–227.

Jeppesen, E., P. Kristensen, J. P. Jensen, M. Søndergaard, E. Mortensen & T. Lauridsen, 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: Duration, regulating factors and methods for overcoming resilience. Mem Ist. ital. Idrobiol. 48: 127–148.

Jeppesen, E. M. Søndergaard, E. Kanstrup, B. Petersen, R. B. Henriksen, M. Hammershøj, E. Mortensen, J.P. Jensen & A. Have, 1994. Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia 275/276: 15–30.

Jeppesen, E., M. Søndergaard, B. Kronvang, J. P. Jensen, L. M. Svendsen & T. Lauridsen. Lake and catchment management in Denmark, 1997. In Harper, D., B. Brierley, A. Ferguson, G. Phillips & J. Madgwick (eds), The ecological basis for lake and reservoir management. J. Wiley & Sons.

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H. J. Jensen, J. P. Müller, O. Sortkjaer, J. P. Jensen, K. Christoffersen, S. Bosselmann & E. Dall, 1990a. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: Cross-analysis of three Danish case-studies. Hydrobiologia 200/201: 205–218.

Kirk, K. L., 1991. Inorganic particles alter competition in grazing plankton: the role of selective feeding. Ecology 72: 915–923.

Kirk, K. L. & J. J. Gilbert, 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. Ecology 71: 1741–1755.

Kristensen, P., J. P. Jensen & E. Jeppesen, 1991. Simple empirical lake models. Nitrogen and phosphorus in fresh and marine waters. NPo forskning fra Miljøstyrelsen. C-abstracts. Danish Environmental Protection Agency, Copenhagen, 125–145.

Lammens, E. H. R. R., D. Gulati, M-L. Meijer & E. van Donk, 1990. The first biomanipulation conference: A synthesis. Hydrobiologia 200/201: 619–627.

Lampert, W., 1993. Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39: 79–88.

Lauridsen, T., E. Jeppesen & M. Søndergaard, 1994. Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish-manipulation. Hydrobiologia 275/276: 233–242.

Lauridsen T. & D. Lodge, 1996. Avoidance by *Daphnia magna* Straus of fish and macrophytes: Chemical cues and predator-mediated use of macrophyte habitat. Limnol. & Oceanogr. 41: 794–798.

Lauridsen, T. & I. Buenk, 1996. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two eutrophic shallow lakes. Arch. Hydrobiol. 137: 161–176.

Lauridsen, T., L. Junge Pedersen, E. Jeppesen & M. Søndergaard, 1996. The importance of macrophyte bed size for composition and horizontal migration of cladocerans in a shallow lake. J. Plankton Res. 18: 2283–2294.

Lauridsen. T. L., E. Jeppesen & F. Ø. Andersen, 1993. Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: Impact of sediment composition and water fowl grazing. Aquat. Bot. 46: 1–15.

Leah, R. T., B. Moss & D. E. Forrest, 1980. The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. Int. Rev. ges. Hydrobiol. 65: 223–247.

Lindegaard, C., 1994. The role of zoobenthos in energy flow in two shallow lakes. Hydrobiologia 275/276: 313–322.

Loose, C. J. E., von Elert & P. Dawidowicz, 1993. Chemically induced diel vertical migration in *Daphnia*: A new bioassay for kairomones exuded by fish. Arch. Hydrobiol. 126: 329–337.

Luecke, C., M. J. Vanni, J. J. Magnuson, J. F. Kitchell & P. J. Jacobson, 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the clearwater phase. Limnol. Oceanogr. 35: 1718–1733.

McQueen, D. J., 1990. Manipulating lake community structure: Where do we go from here? Freshwat. Biol. 23: 613–620.

Meijer, M. L, W. de Haan, A. W. Breukelaar & H. Buiteveld, 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia 200/201: 303–316.

Meijer, M. L., E. Jeppesen, E. van Donk., B. Moss, M. Scheffer, E. H. R. R. Lammens, E. Van Nes, J. A. Berkum, G. J. de Jong, B. A. Faafeng & J. P. Jensen, 1994. Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five year results of four biomanipulation cases in the Netherlands and Denmark. Hydrobiologia 275/276: 457–466.

Mills, E. L. & J. L. Forney, 1983. Impact on *Daphnia pulex* of predation by yellow perch in Oneida Lake, New York. Trans. am. Fish. Soc. 112: 154–161.

Mills, E. L., J. L. Forney & K. J. Wagner, 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In Kerfoot, W. C. & A. Sih (eds), Predation: Direct and indirect effects on aquatic communities. University Press of New England, Hanover, New Hampshire: 118–131.

Mortensen, E., E. Jeppesen, M. Søndergaard & L. Kamp Nielsen (eds), 1994. Nutrient Dynamics and Biological Structure in Shallow Freshwater and Brackish Lakes. Developments in Hydrobiology 94. Kluwer Academic Publishers, Dordrecht, 507 pp. Reprinted from Hydrobiologia 275/276.

Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201: 367–378.

Moss, B., S. McGowan & L. Carvalho, 1994. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland Meres. Limnol. Oceanogr. 39: 1020–1029.

Nygaard, G., 1949. Hydrobiological studies on some Danish ponds and lakes. Biol. Skr. K. Dan. Vidensk. Selsk. 7: 1–239.

Pavoni, M., 1963. The importance of nanoplankton compared to netplankton. Schweiz. Z. Hydrol. 25: 219–341.

Pennak, R. W., 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. Trans. am. microsc. Soc. 85: 329–349.

Pennak, R. W., 1973. Some evidence for aquatic macrophytes as repellents for a limnetic species of *Daphnia*. Int. Revue. ges. Hydrobiol. 58: 569–576.

Perrow, M. R., J. Schutten, J. R. Howes, T. Holzer, F. J. Madgwick & A. J. D. Jowitt, 1997. Interactions between coot (*Fulica atra*) and submerged macrophytes: the role of birds in the restoration process. Hydrobiologia 342/343: 241–255.

Persson, L., 1991. Behavioural response to predators reverses the outcome of competition between prey species. Behav. Ecol. Sociobiol. 28: 101–105.

Persson, L., G. Anderson, S. F. Hamrin & L. Johansson, 1988. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. In Carpenter, S. R. (ed.), Complex interactions in lake communities. Springer Verlag, New York: 45–65.

Phillips, G. L., M. Perrow & J. Stansfield, 1996. Manipulating the fish-zooplankton interaction in shallow lakes: a tool for restoration. In S. P. R. Greenstreet & M. L. Tasker (eds), Aquatic predators and their prey. Blackwell Scientific Publications, Oxford: 174–183.

Prejs, A., A. Martyniak, S. Boron, P. Hliwa & P. Koperski, 1994. Food web manipulation in a small eutrophic Lake Wirbel, Poland: Effect of stocking with juvenile pike on planktivorous fish. Hydrobiologia 275/276: 65–70.

Pridmore, R. D., W. N. Vant & J. C. Rutherford, 1985. Chlorophyll-nutrient relationships in North Island lakes (New Zealand). Hydrobiologia 121: 181–189.

Quade, H. W., 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. Ecology 50: 170–179.

Quiros, R., 1990. Predictors of relative fish biomass in lakes and reservoirs of Argentina. Can. J. Fish. aquat. Sci. 47: 928–939.

Reynolds, C. S., 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, 384 pp.

Reynolds, C. S., 1994. The ecological basis for the successful biomanipulation of aquatic communities. Arch. Hydrobiol. 130: 1–33.

Riemann, B., K. Christoffersen, H. J. Jensen, J. P. Müller, C. L. Lindegaard & S. Bosselmann, 1990. Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. Hydrobiologia 200/201: 241–250.

Ringelberg, J., 1991. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). J. Plankton Res. 13: 17–25.

Sas, H. (Ed.), 1989. Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation. Acad. Ver. Richardz Gmbh. 497 pp.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 475–486.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. Trends in ecology and evolution (TREE) 8: 275–279.

Schriver, P., J. Bøgestrand, E. Jeppesen & M. Søndergaard, 1995. Impact of submerged macrophytes on the interactions between fish, zooplankton and phytoplankton: Large-scale enclosure experiments in a shallow lake. Freshwat. Biol. 33: 255–270.

Shapiro, J. & D. I. Wright, 1984. Lake restoration by biomanipulation. Round Lake, Minnesota – the first two years. Freshwat. Biol. 14: 371–383.

Sommer, U., 1985. Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. Limnol. Oceanogr. 30: 335–346.

Søndergaard, M., E. Jeppesen & S. Berg, 1997. Pike (*Esox lucius*) stocking as a biomanipulation tool, 2. Effects on lower trophic levels in Lake Lyng, Denmark. Hydrobiologia 342/343: 319–325.

Søndergaard, M., E. Jeppesen, P. Kristensen & O. Sortkjær, 1990a. Interactions between sediment and water in a shallow hypertrophic lake: A study on phytoplankton collapses in Lake Søbygard, Denmark. Hydrobiologia 191: 149–164.

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen & O. Sortkjær, 1990b. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: A combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200/201: 229–240.

Søndergaard, M., P. Kristensen & E. Jeppesen, 1992. Phosphorus release from resuspended sediment in the shallow and wind exposed Lake Arresø, Denmark. Hydrobiologia 228: 91–99.

Søndergaard, M., L. Olufsen, T. Laundsen, E. Jeppesen & T. Vindbæk Madsen, 1996. The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. Aquat. Bot. 53: 73–84.

Stansfield, J. H., M. R. Perrow, L. D. Tench, A. J. D. Jowitt & A. A. L. Taylor, 1997. Submerged macrophytes as refuges for grazing Cladocera against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. Hydrobiologia 342/343: 229–240.

Timms, R. M. & B. Moss, 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceanogr. 29: 472–486.

Van Donk, E., E. De Deckere, J. G. P. Klein Breteler & J. Meulemans, 1994. Herbivory by waterfowl and fish on macrophytes in a biomanipulated lake: Effects on long-term recovery. Verh. int. Ver. Limnol. 25: 2139–2143.

Whiteside, M. C., 1988. 0+ fish as major factors affecting abundance patterns of littoral zooplankton. Verh. int. Ver. Limnol. 23: 1710–1714.

Windolf, J., E. Jeppesen, M. Søndergaard, J. P. Jensen & L. Sortkjær, 1993. Vandmiljøplanens Overvågningsprogram 1992. Ferske vandområder - Søer. [The Action Plan on the Aquatic Environment 1992. Freshwater area - Lakes]. National envir. Res. Inst., 129 pp.

Winfield, L. J., 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. J. Fish. Biol. 29: 37–48.

Zdanowski B., 1982. Variability of nitrogen and phosphorus contents and lake eutrophication. Pol. Arch. Hydrobiol. 29: 3–4.

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Do planktivorous fish structure the zooplankton communities in New Zealand lakes?

ERIK JEPPESEN*
TORBEN LAURIDSEN*
STUART F. MITCHELL
CAROLYN W. BURNS
Department of Zoology
University of Otago
P. O. Box 56
Dunedin, New Zealand

*Present address: National Environmental Research Institute, Department of Lake and Estuarine Ecology, P. O. Box 314, Vejlsøvej 25, DK–8600 Silkeborg, Denmark.

Abstract We critically evaluate the prevailing view that the species composition of zooplankton communities in New Zealand lakes, and the abundance and size distribution of the zooplankton, are more commonly controlled by food and temperature than by predation. We conclude that predation may play a far more important role than was hitherto thought. This conclusion is based first on the seasonal zooplankton dynamics of several New Zealand lakes being similar to those in Danish lakes, in which fish predation has been shown to have major effects. Second, the indigenous planktivorous fish fauna in New Zealand lakes is dominated by larvae of benthic fish with a long breeding season (bullies) and other small potent zooplanktivores such as smelt and larvae of galaxiids. Patterns of diurnal vertical migration of zooplankton in several New Zealand lakes during summer are also consistent with it being a mechanism to escape from predation. Third, the dominant piscivorous fish (brown trout and rainbow trout) are only facultative piscivores and are therefore probably weaker predators on the planktivores than the more obligate piscivores in many north-temperate lakes. Although various other explanations have been offered for the low ratio of zooplankton-to-phytoplankton biomass observed in New Zealand lakes, this phenomenon is equally consistent with high rates of predation. Re-analyses of data from earlier investigations in Tomahawk Lagoon No. 2, provide evidence for a periodically high predation pressure on zooplankton during summer, which was further supported experimentally. We call for further investigation of top-down control of zooplankton in New Zealand lakes. It is important not only for scientific understanding, but potentially also for lake management.

Keywords top-down control; fish; zooplankton; cascading effects; fish predation

INTRODUCTION

It has been widely accepted that the structure, size, and abundance of the zooplankton communities in New Zealand lakes are determined mainly by the abundance and quality of food, and by temperature, whereas predation plays only a minor role (Chapman et al. 1975; Chapman et al. 1985; Burns & Xu 1990; Burns 1992). This view of mainly bottom-up control of zooplankton (sensu McQueen et al. 1986) is based on a variety of observations. The instantaneous birth rates and death rates and the clutch sizes of the crustacean zooplankton are often low (Chapman et al. 1985; Burns 1992). Likewise, clutch sizes have been found to be positively correlated with chlorophyll *a* levels and temperature in some studies (Burns 1979, 1992) and the breeding activity of calanoid copepods in seven North Island lakes was inversely related to the population density (Chapman et al. 1985). The hypothesis that predation pressure on zooplankton is low is also based partly on the fact that many of the common northern lake pelagic invertebrate predators like *Chaoborus* and *Leptodora* are missing and that obligate planktivorous fish are not widespread (e.g., Chapman et al. 1985; Burns 1992).

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If the hypothesis of mainly bottom-up control on zooplankton is true, then New Zealand lakes deviate from the many northern temperate lakes for which there is strong evidence that fish play a major role in structuring the zooplankton communities and regulating their grazing pressure on phytoplankton (e.g., Reinartsen & Olsen 1984; Gulati et al. 1990; Carpenter & Kitchell 1993; Mortensen et al. 1994), particularly in eutrophic and hypertrophic lakes (Leipold 1989; Sarnelle 1992; Jeppesen et al. 1990b, 1994, 1997).

The fish fauna of New Zealand lakes is characterised by a mixture of native species including galaxiids (*Galaxias* spp.), bullies (*Gobiomorphus* spp.), smelt (*Retropinna retropinna*), eels (*Anguilla* spp.), and more recently introduced species such as brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), perch (*Perca fluviatilis*), mosquito fish (*Gambusia*), a few other salmonids, and a few less widespread species (McDowall 1990). Whether such fish communities indicate a low predation pressure on zooplankton in comparison with similar northern temperate lakes is debatable. The planktivores consist of larvae and adults of smelt and trout, and larvae of bullies and koaro (*Galaxias brevipinnis*) (McDowall 1990; Rowe 1993) and the densities may be high. Thus the almost ubiquitous bullies have been reported to occur in the pelagic with abundances as high as 114 m^{-2} to 208 m^{-2} of mainly 0^+ fish (Staples 1975b; Rowe & Chisnall in press). These densities are higher than those found in many northern temperate or subtropical lakes (Chick & McIvor 1994; Hoyer & Canfield 1996; Stansfield et al. 1997). In addition, bullies may spawn over an extended period from mid winter to late summer (Stephens 1982) which may keep the pelagic larval density high over a more prolonged period than in most northern freshwater lakes, where spawning of the dominant planktivores is usually restricted to late spring and early summer. It is striking that those eutrophic northern lakes in which the dominant fish have extended spawning (brackish lakes dominated by sticklebacks) have unusually low ratios of zooplankton to phytoplankton (Jeppesen et al. 1994), in common with New Zealand lakes (Malthus & Mitchell 1990). This may reflect a higher predation pressure by fish (Jeppesen et al. 1994). The reported high maximum densities of larval fish in the pelagic (Staples 1975b; Rowe & Chisnall in press) along with the extended breeding period of the widespread bullies and a low zooplankton-to-phytoplankton biomass ratio (Malthus & Mitchell 1990) suggest a high, rather than a low, predation pressure on zooplankton in New Zealand lakes.

The suggested high predation pressure on zooplankton may also reflect a comparatively low mortality of zooplanktivorous fish. Brown trout and rainbow trout, the dominant top carnivores in many New Zealand lakes, are omnivores, with a large component of benthic invertebrates in their diets (authors' unpubl. data). They may therefore be weaker piscivores than the more obligate piscivorous fish such as pike (*Esox lucius*) and large perch that dominate in lowland lakes in Northern Europe (Persson et al. 1988; Grimm & Backx 1990; Jeppesen et al. 1990b) or the largemouth bass (*Micropterus salmoides*) of North America (Carpenter & Kitchell 1993).

It seems therefore reasonable to hypothesise that predation pressure on zooplankton is potentially high in New Zealand lakes. Until now, however, only Maly (1984) and Rowe (1994) have argued against the pure bottom-up control idea. In this paper we present several examples that give further evidence of a relatively high top-down control on zooplankton by fish in some New Zealand lakes. The examples are based on existing New Zealand literature, a preliminary experiment we conducted in one New Zealand lake, and comparisons with data from Danish lakes.

METHODS

An enclosure experiment with presence-absence of larvae of common bully was conducted at a water depth of 0.6 m in Tomahawk Lagoon No. 2 (46°S) in Nov–Dec 1995. The enclosures consisted of circular 80 cm diameter polyethylene tubes folded at each end over a steel ring and kept in place by a stainless steel hose clip. The upper ring was attached to polystyrene floats keeping the upper ring 25 cm above the water surface. The lower ring sank into the substratum. The entire enclosure was secured in position with two steel rods, 3 m long, that were passed through lugs on the outside of both rings and pushed into the substratum. The enclosures were designed by Ogilvie (1989). Four common bullies (*Gobiomorphus cotidianus*) (4.2–5.2 cm long) were then added to each of three enclosures (8 bullies m^{-2}), whereas the remaining three served as controls. The density of large zooplankton was adjusted initially to obtain similar densities in all enclosures and to mimic the lake concentration, by adding zooplankton collected with 0.5 mm mesh net. Zooplankton were sampled three times over the next 8 days in each enclosure with a core sampler (7.4 cm diam.) that samples the entire water column from the surface to c. 3 cm above the bottom (Lauridsen et al. 1996). Then, four additional bullies of a smaller size (2.0–2.1 cm) were added to the enclosures with fish, and zooplankton samples were taken on four occasions during the following 2 weeks. To obtain representative samples from the enclosures, water was gently mixed with the core before sampling. Zooplankton from a 2-litre subsample were counted under a stereo microscope at ×40–100 magnification.

The methods used in the Danish lakes are described by Jeppesen et al. (1994, 1997). Briefly, zooplankton were sampled at three stations (integrated for the entire water column) and phytoplankton at a mid-lake station. An estimate of fish density (catch per unit effort, CPUE) was obtained from overnight catches in multiple mesh-sized gill nets (14 sizes between 6.25 and 75 mm, 1.5 × 3 m sections) placed in open water and the littoral zone. The number of nets used varied from 6 to 64, depending on lake size and morphometry. The fish investigation was conducted in late summer when the fish were most evenly distributed in the lakes and young-of-the-year had become large enough to be caught in the nets.

RESULTS AND DISCUSSION

We present five examples that appear to suggest a high impact of predation by fish on zooplankton in New Zealand lakes.

Example 1

Staples (1975a, 1975b, 1975c) conducted a comprehensive study on the upland bully (*Philypnodon breviceps*) in the smaller of the Spectacles lakes (Canterbury) during 1969–70. The lake is shallow, mesotrophic (Table 1) and has a high coverage of submerged macrophytes. Upland bullies were the only fish present although the lake had earlier been stocked with trout (Staples 1975a). Using a mark-recapture technique and quantitative sampling with push-nets corrected for net selectivity, Staples (1975b) found maximum densities of bullies ranging from 208 m^{-2} in February 1969 to 21 m^{-2} in March 1970. Behaviour studies and stomach analysis revealed that the fish were mainly planktivorous during the first few months after hatching, after which they gradually shifted to benthic feeding. Zooplankton remained, however, a part of the diet of the subsequent two year classes. Densities of 21–208 m^{-2} of even partially zooplanktivorous fish would indicate a high predation pressure on zooplankton. In experiments with various densities of 0^+ and 1^+

Table 1 Morphometric and chemical data from the lakes of Fig. 3–4. Total phosphorus and chlorophyll *a* are annual means.

	Surface area (km^2)	Mean depth (m)	Total phosphorus (μg P l^{-1})	Chlorophyll *a* (μg l^{-1})
New Zealand				
Lake Hayes	2.0	19	55	10
Lake Mahinerangi	16.2	6.2	25	7
Lake Johnson	0.2	17	85	25
Tomahawk Lagoon	0.1	1.0	140	1–42
Small Spectacles Lake	0.06–0.09	0.5–3[1]	–	–
Denmark				
Ravnsø	1.8	15	35	8
Lake Tystrup	6.6	9.9	257	24
Furesø	7.4	16.5	238	21
Lake Faarup	1.0	5.6	92	35
Lake Søholm	0.3	6.5	78	21
Lake Arresø	42	2.9	463	383
Dons Nørresø	0.4	1.0	189	217

[1] Maximum depth.

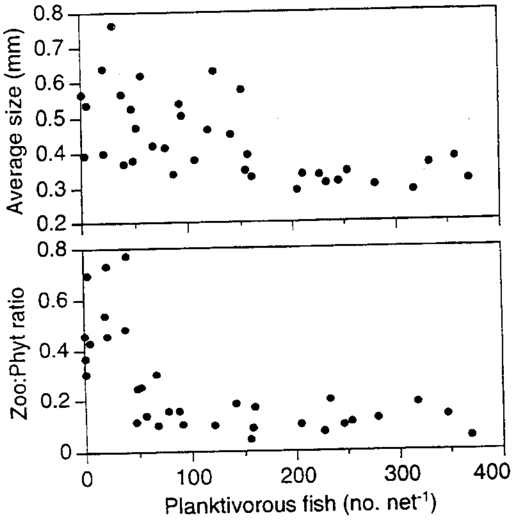

Fig. 1 Average length of cladocerans during summer (1 May–1 Oct) and the ratio of zooplankton to phytoplankton biomass versus catch per unit effort (CPUE, no. per net) of fish caught in multiple mesh-sized gill nets (14 mesh sizes ranging from 6–25 to 75 mm). Fish surveys were conducted in late summer (15 Aug–15 Sep) and the nets were placed overnight in the pelagic and littoral zone according to the Danish standardised test survey programme (Mortensen et al. 1991). Each point represents one lake (modified from Jeppesen et al. 1996).

three-spined sticklebacks *(Gasterosteus aculeatus)* and roach (*Rutilis rutilis*) in 100 m^2 enclosures placed at a depth similar to the depth in the small Spectacles Lake, Schriver et al. (1995) found that *Daphnia galeata* disappeared in enclosures with high macrophyte cover at fish densities above 2 m^{-2}, whereas densities of the smaller cladocerans *Ceriodaphnia* spp. and *Bosmina longirostris* decreased to low densities at fish densities above 4 m^{-2}. In the absence of macrophytes the required fish density to meet these thresholds was 1–2 orders of magnitude lower. In accordance with these results the zooplankton community in the smaller Spectacles Lake was dominated by small forms (Staples 1975a).

Example 2

Investigations in several Danish lakes suggest that a low biomass ratio of zooplankton to phytoplankton (ZOO:PHYT) reflects high fish predation on zooplankton (Jeppesen et al. 1997, unpubl. data). Thus, a close inverse relationship was obtained between the catch of planktivorous fish in multiple mesh-sized gill nets (14 mesh-sizes from 6.25 to 75 mm) and the summer mean ZOO:PHYT ratio (Fig. 1). In addition, the mean size of cladocerans decreased with increasing fish abundance (Fig. 1). That these relationships are causal is supported by results from 17 whole-lake fish manipulation experiments in Denmark in which the ZOO:PHYT ratio and the mean cladoceran size increased markedly in all the lakes when the density of planktivorous fish was markedly reduced (Jeppesen et al. 1990a; Søndergaard et al. 1990, 1997; E. Jeppesen & M. Søndergaard, unpubl. data).

An analysis of data from 19 New Zealand lakes by Malthus & Mitchell (1990) revealed that the ratios of ZOO:PHYT, ZOO-to-total-phosphorus and ZOO-to-chlorophyll-*a* were all substantially lower than in northern temperate lakes, with only a few exceptions. The authors rejected the predation hypothesis and argued that the low ZOO:PHYT ratios most likely reflected an apparent tendency for dominance of large phytoplankton forms that are not likely to be directly available as food for zooplankton. In addition, they argued that poor nutritional quality of the food as a result of low nitrogen input to New Zealand lakes might have contributed to lower zooplankton biomass, although later experimental work did not support the hypothesis that zooplankton growth is less efficient on N-deficient algae than on P-deficient ones (Mitchell et al. 1992). Although dominance of large phytoplankton may have played a role, the evidence is not conclusive, and the authors concede that two of the lakes with low ratios were in fact dominated by small phytoplankton.

It has been argued that filamentous heterocystous Cyanobacteria are more dominant in New Zealand lakes than in Northern European lakes because of a lower nitrogen input to the former (Malthus & Mitchell 1988) and Cyanobacteria are commonly considered to be less edible, less nutritious, and less palatable than most eukaryotic phytoplankton (e.g., de Bernardi & Guisanni 1990). In theory, therefore, widespread dominance of Cyanobacteria could contribute to the lower ZOO:PHYT ratio in New Zealand lakes. Consistent with this view is the preference of several *Boeckella* species for algae in mixtures of algae and filamentous Cyanobacteria at high concentrations (Burns & Hegarty 1994), although *Boeckella* can survive and reproduce on a pure diet of various filamentous Cyanobacteria (Burns & Xu 1990).

Many of the northern European lakes with higher ZOO:PHYT ratios than in the New Zealand lakes are also dominated by large filamentous Cyanobacteria. In these lakes no relationship was found between the contribution of Cyanobacteria to the total phytoplankton biomass and the ZOO:PHYT ratio. The contribution of Cyanobacteria did not add significantly either to the relationship between fish and the ZOO:PHYT ratio (Jeppesen et al. 1997, unpubl. data). Therefore it seems unlikely that cyanobacterial dominance by itself can explain the particularly low ZOO:PHYT ratio in New Zealand lakes.

Example 3

Based on data from a 19-month study of the population dynamics of crustacean zooplankton in mesotrophic Lake Mahinerangi, Burns (1992) concluded, in concert with Malthus & Mitchell (1990), that predation had no or negligible effect on the zooplankton in the lake. She based the conclusion with respect to *Boeckella hamata* on the fact that clutch was positively related to concentration of chlorophyll *a* plus phaeopigments (CHL). In addition, the fecundity of female *B. hamata* was significantly positively related to temperature and CHL. These factors are consistent with bottom-up control of this species. The study revealed, however, a high and unexplained death rate throughout the summer that in prolonged periods exceeded the birth rate (Burns 1992). The high death rate may have reflected enhanced predation by fish as it coincided with the appearance of fish larvae in the pelagic zone in other South Island lakes (McDowall 1990; Dodds 1991; authors' unpubl. data). The potential planktivores in this lake include galaxiids, larval bullies, and larval perch (Burns 1992). Fish larvae have recently been shown to have a major impact on zooplankton community structure and abundance in several studies outside New Zealand (Mills & Forney 1983; Cryer et al. 1986; Luecke et al. 1990; Jeppesen et al. 1997; Søndergaard et al. 1997).

If predation by fish is significant we would expect the contribution of large cladocerans (*Daphnia*) to the total cladoceran density to be low (Brooks & Dodson 1965). As cyclopoid copepods seem to be less vulnerable to fish predators than calanoid copepods (Soto & Hurlbert 1991) we would also expect the calanoid-to-cyclopoid ratio to be low. Accordingly, in both deep and shallow Danish lakes the percentage *Daphnia* and percentage calanoid copepods decreased with increasing density of planktivorous fish, expressed as catch per unit effort (CPUE, no. net^{-1}) in multiple mesh-sized gill nets, and approached zero at the highest density (Fig. 2). These data also indicate a decline during mid summer at low to moderately high CPUE, whereas the percentages remain low throughout the season at the highest densities. The relationship between the ratios and planktivorous fish is supported by 17 fish manipulation experiments undertaken in Danish lakes: in the lakes in which a marked reduction of the planktivorous fish stock was obtained, the two ratios increased significantly, although percentage calanoid copepods declined again at extremely high *Daphnia* densities (Søndergaard et al. 1997; E. Jeppesen & M. Søndergaard unpubl. data), probably reflecting competition for food between calanoids and *Daphnia*.

If we compare the results from Lake Mahinerangi (Burns 1992) and two other intensively studied eutrophic, southern lakes (Lake Hayes and Lake Johnson, data from Burns & Mitchell 1980) with those of Danish lakes, similarities as well as differences are evident. In Lake Hayes there was a spring peak (September–November) of percentage *Daphnia* (Fig. 3) similar to that found in Danish lakes with low to medium high CPUE (Fig. 1 and 2). In Lake Mahinerangi, *Daphnia* abundance in 1981 reached 50% and peaked earlier (30 June 1981) than in Lake Hayes, whereas the percentages in Lake Johnson were close to zero throughout the year. The 50% and near-0% correspond to the level found in Danish lakes with a moderately high and very high fish density, respectively (Fig. 1 and 2). The seasonal variation in percentage *Daphnia* was, however, more pronounced in Lake Mahinerangi than in the Danish lakes. A possible explanation may be that *Daphnia carinata*, the dominant *Daphnia* species in New Zealand lakes, is a relatively large-bodied species and probably more vulnerable to predation by 0$^+$ fish than many of the small *Daphnia* species that occur in northern European lakes. The period with low percentage *Daphnia* in Lake Hayes and Lake Mahinerangi was also longer than in the Danish lakes. This is to be expected if zooplankton-feeding fish larvae in New Zealand lakes are produced over an extended breeding season, as is known for bullies (Stephens 1982). The pattern in the New Zealand lakes of percentage calanoids decreasing in autumn, after the reduction in percentage *Daphnia*, is also consistent with the hypothesis of intense, size-selective predation. The percentage calanoids does

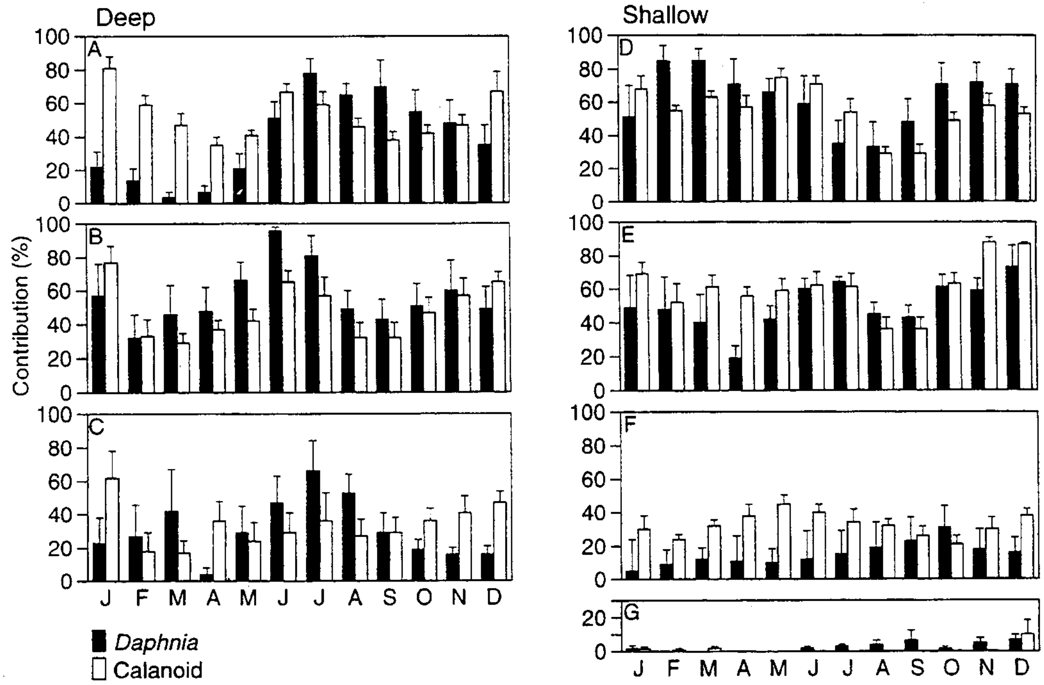

Fig. 2 Seasonal variation in the percentage contribution of *Daphnia* (left columns in each panel) and calanoid copepods to total cladoceran and copepod abundance, respectively, in some deep (left panel) and shallow Danish lakes with contrasting densities of planktivorous fish expressed as CPUE (no. per net, see legend of Fig. 1). The columns show monthly averages over 6 years (+ SE). **A**, Ravnsø (CPUE = 20 per net); **B**, Lake Tystrup (CPUE = 37 per net); **C**, Furesø (CPUE = 119 per net); **D**, Lake Faarup (CPUE = 37 per net); **E**, Lake Søholm (CPUE = 51 per net); **F**, Arresø (CPUE = 154 per net); **G**, Dons Nørresø (CPUE = 369 per net). The deep lakes have mean depths of 10–15 m and the shallow lakes have mean depths of 1–6.5 m.

not entirely follow the pattern of the Danish lakes, in which it generally follows the percentage *Daphnia* (Fig. 3). The reason for this difference is not clear, but it is known that cyclopoid copepods are scarce in New Zealand lakes (Jolly & Chapman 1977; Chapman & Green 1987) which may explain the generally higher percentage of calanoids in the three New Zealand lakes than in Danish lakes with similar percentage *Daphnia*.

Example 4

The zooplankton dynamics in shallow, eutrophic Tomahawk Lagoon No. 2 have been studied during several periods over the last 30 years (Nayar 1968; Mitchell et al. 1988; Dodds 1991). Mitchell et al. (1988) found that the zooplankton show marked, albeit irregular, seasonal variations between years in both abundance and the relative contributions of *D. carinata* and other crustaceans like *Bosmina meridionalis* and *Boeckella hamata,* and argued that fish predation may have been responsible for a regular summer decline in *D. carinata*. In most years *D. carinata* have a spring peak (up to 150 animals per litre) and then almost disappear in early summer, when bully and perch larvae are present in the pelagic. Small *B. hamata* and *B. meridionalis* tended to dominate the summer zooplankton. Dodds (1991) found that the density of *D. carinata* remained below 1 per litre from late December 1988 to late July 1989, despite periodically high fecundity in the population—indicating a high death rate that cannot be explained by food limitation.

Our enclosure experiments in the lagoon in November–December 1995 revealed no significant differences ($P > 0.28$, repeated measures ANOVA) between enclosures with and without fish in the

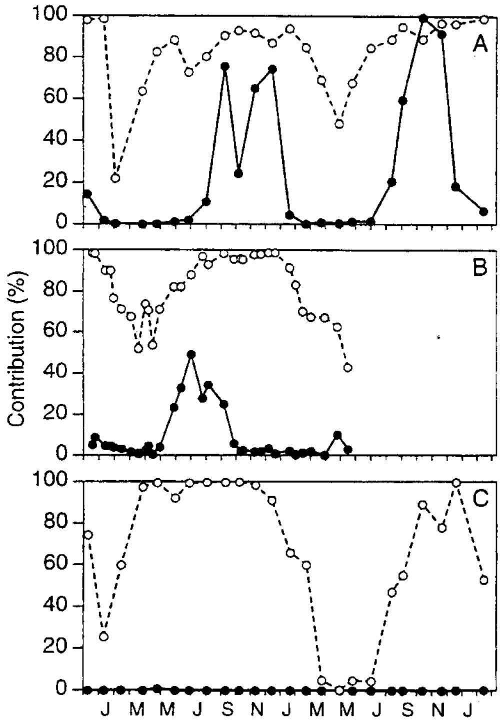

Fig. 3 Seasonal variation in the percentage contribution of *Daphnia* (•) to total cladoceran abundance and calanoid copepods (o) to total copepod abundance, respectively, in three New Zealand lakes. **A**, Lake Hayes (data from Burns & Mitchell 1980); **B**, Lake Mahinerangi (data from Burns 1992); **C**, Lake Johnson (data from Burns & Mitchell 1980). Alternating months are indicated on the horizontal axis.

abundance of the various zooplankton species during the first eight days following the addition of 8 m^{-2} large bullies (length 4.5 cm) (Fig. 4). Following the addition of 8 m^{-2} small bullies (length 2 cm) significant differences (repeated measures ANOVA) were observed for *Daphnia* ($P < 0.04$) and adults and copepods of *B. hamata* ($P < 0.006$ and $P < 0.002$, respectively), whereas no significant differences were found for nauplii and rotifers ($P > 0.4$). These results are consistent with the fact that larger bullies are mainly benthivorous, and 2 cm bullies are zooplanktivorous (Staples 1975a; Rowe & Chisnall in press).

Experiments conducted by Clare (1978) in the same lagoon support our findings. In two experiments, he observed a larger decline in *D. carinata* in enclosures with 28–42 bullies m^{-2} than in controls without fish, particularly during the first days of the experiments. At the end of his 14–18 day experiments daphnid density was relatively low in all enclosures, but between 12 and 74% lower in those with bullies than in the controls. In addition, the mean size of *D. carinata* was substantially smaller and the contribution of rotifers substantially higher in enclosures containing bullies.

These changes all suggest a predation impact from fish. Although the bully densities in these experiments were high compared with earlier observations from Tomahawk Lagoon No. 2 (Dodds 1991; S. F. Mitchell unpubl. data) they were substantially lower than the maximum densities of upland bully in small Spectacles Lake of 208 m^{-2} (Staples 1975b) and of common bully (114 m^{-2}) recorded by Rowe & Chisnall (in press) in North Island lakes. Moreover, the fish used by Clare (1978) consisted of size-classes that according to Staples (1975c) and Rowe & Chisnall (in press) are mainly benthivores. The results from the Tomahawk Lagoon No. 2 enclosure experiments therefore provide further evidence of high predation pressure on zooplankton in a New Zealand lake.

Example 5

North Island lakes generally show less seasonality in zooplankton than South Island lakes, most likely because the milder winters in the North allow continuous recruitment of zooplankton (Chapman et al. 1987) and perhaps also because of a prolonged breeding season for fish. This makes it more difficult to detect from existing data any potential predation impacts of fish on zooplankton in North Island lakes. A study of Lake Rotongaio (Forsyth et al. 1983) provides one example, however. The dominant *Boeckella propinqua* population declined in December 1974 in this lake despite only minor changes in clutch size, before gradually recovering in May 1975. *Ceriodaphnia dubia* showed a similar pattern, while the small *B. meridionalis* showed only a temporary decline in December–January, and rotifers increased in number during summer (Forsyth et al. 1983: fig. 6–8). These changes are also consistent with a hypothesis of high predation from larval and juvenile fish during summer. Partly in accordance with this hypothesis, Forsyth et al. (1990) argued for a top-down structuring effect of fish predation in concert with negative effects of Cyanobacteria as major driving factors for zooplankton abundance and composition in Lake Rotongaio. The marked seasonality in the

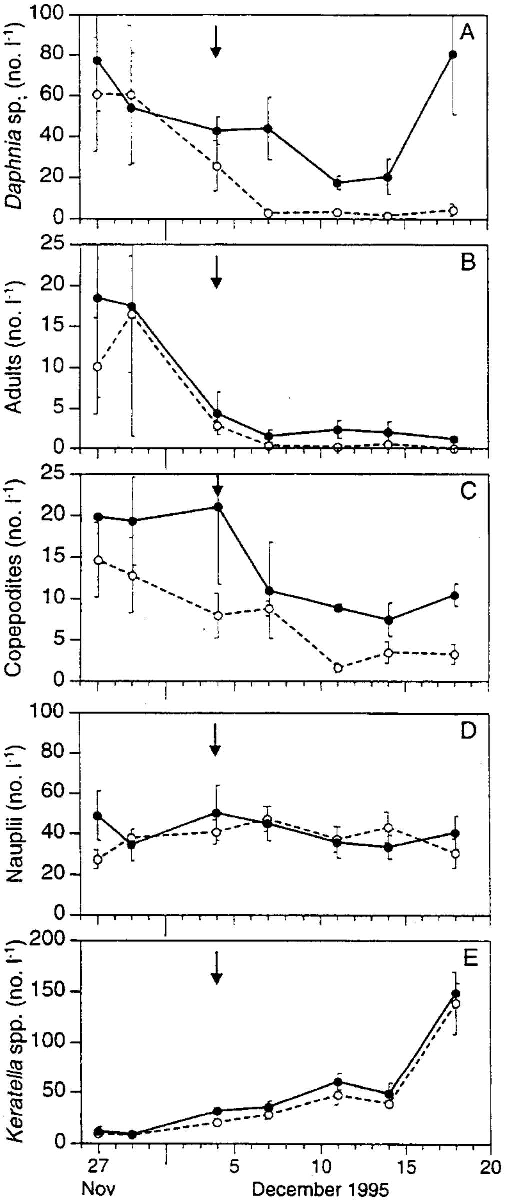

Fig. 4 Changes in abundance of *Daphnia carinata* (**A**), adults, copepodites and nauplii of *Boeckella hamata* (**B, C, D**) and rotifers (*Keratella* spp.) in enclosures with (o) and without (•) common bullies (*Gobiomorphus cotidianus*) in Tomahawk Lagoon No. 2. Four bullies (4.2–5.2 cm total length (TL)) were added to the first enclosures 6 days before the first sampling and an additional 4 bullies (2.0–2.1 cm TL) on 4 Dec (arrows).

zooplankton abundance compared with that in the adjacent and inter-connected large and deep Lake Taupo (Forsyth & McCallum 1980) suggests that shallow Lake Rotongaio may act as a nursery area for juvenile fish from Lake Taupo, as seen in other studies in northern lakes (B. Auer pers. comm.). The shallowness of Lake Rotongaio may also have contributed to the difference as fish predation pressure appears to increase with decreasing mean depth (Jeppesen et al. 1997).

Crustacean zooplankton undergo diurnal vertical migration in several deep North Island lakes (Chapman et al. 1987). Recent studies have provided convincing evidence that diel migration of zooplankton between surface and deeper water is often an antipredator defence mechanism (Ringelberg 1991; Lampert 1993). New Zealand lakes are characterised by a lack of most pelagic invertebrate predators such as *Chaoborus* and *Leptodora* (Chapman & Green 1987), and predation pressure of the water mite *Piona* on zooplankton seems to be low (Burns 1992; Butler & Burns 1993). The vertical migration observed in New Zealand lakes is therefore most likely to be a defence mechanism against predation by fish. Accordingly, Rowe (1994) found that the upper 20–40 m of some North Island lakes were occupied by planktivorous fish segregated into an upper layer with juvenile smelt, followed successively by layers of larval bullies and large smelt—suggesting a high risk of predation for the crustacean zooplankton.

It is therefore likely that fish predation pressure on zooplankton is important also in North Island lakes. It may be even higher than in South Island lakes due to the more prolonged breeding period of fish and the more widespread distribution of smelt and introduced planktivorous fish such as *Gambusia* in the North Island (McDowall 1990). Maly (1984) similarly argued for a high risk of fish predation in the North Island to account for his observations on interlake variations in the ratio of small to large calanoid copepod species.

CONCLUSION

In summary, at least some New Zealand lakes have fish densities that would be sufficiently high to have major effects on the zooplankton biomass and size structure, as in similar northern lakes. The low ZOO:PHYT ratios in the 19 New Zealand lakes considered by Malthus & Mitchell (1990) are similar to the ratios in those Danish lakes in which fish predation strongly influences zooplankton biomass. We have further shown that in four New Zealand lakes (Lakes Hayes, Johnson, Mahinerangi, and Rotongaio) seasonal changes in biomass and size structure of the zooplankton are consistent with high predation by larval fish over the extended fish breeding seasons. An experimental study and field data also indicate at least intermittently high fish predation on zooplankton in Tomahawk Lagoon No. 2. The annual ZOO:PHYT ratio in this lake is highly variable, ranging from 30 to 300% of the values observed in typical northern lakes (Mitchell et al. 1988). This variation might reflect the large year-to-year variations in the bully population revealed by an annual sampling for post-larval bullies over 25 years (C. W. Burns & S. F. Mitchell unpubl. data).

The experiments and examples thus suggest that fish predation may have a major impact on the species composition, size structure, and abundance of zooplankton in New Zealand lakes; it seems unlikely that the impact of predation by fish on zooplankton in New Zealand lakes is substantially lower than in Northern temperate lakes. It may even be higher. Our aim has not been to shift opinion from a simple bottom-up to a simple top-down control way of thinking. Both effects are important. Their relative contributions may vary over the seasons and between lakes, and are often interlinked. Constraints by food limitation may, for instance, reduce the growth rate and thus enhance the risk for a zooplankton population to be eliminated by fish.

ACKNOWLEDGMENTS

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REFERENCES

de Bernardi, R.; Guisanni, G. 1990: Are blue-green algae suitable food for zooplankton? An overview. *Hydrobiologia 200/201*: 29–41.

Brooks, J. L.; Dodson, S. I. 1965: Predation, body size and composition of plankton. *Science 150*: 28–35.

Burns, C. W. 1979: Population dynamics and production of *Boeckella dilatata* (*Copepoda:Calanoida*) in Lake Hayes, New Zealand. *Archiv für hydrobiologie, supplement 54*: 409–465.

Burns, C. W. 1992: Population dynamics of crustacean zooplankton in a mesotrophic lake, with emphasis on *Boeckella hamata* Brehm (*Copepoda:Calanoida*). *Internationale revue der gesamten hydrobiologie 77*: 553–577.

Burns, C. W.; Hegarty, B. 1994: Diet selection by copepods in the presence of cyanobacteria. *Journal of plankton research 16*: 1671–1690.

Burns, C. W.; Mitchell, S. F. 1980: Seasonal succession and vertical distribution of zooplankton in Lake Hayes and Lake Johnson. *New Zealand journal of marine and freshwater research 14*: 189–204.

Burns, C. W.; Xu, Z. 1990: Utilization of colonial cyanobacteria and algae by freshwater calanoids: survivership and reproduction of adult *Boeckella* spp. *Archiv für hydrobiologie 117*: 257–270.

Butler, M. I; Burns, C. W. 1993: Water mite predation on planktonic *Cladocera*: parallel curve analysis of functional responses. *Oikos 66*: 5–16.

Carpenter, S. R; Kitchell, J. F. (eds.) 1993: The trophic cascade in lakes. Cambridge, Cambridge University Press. 385 p.

Chapman, M. A.; Green, J. D. 1987: Zooplankton ecology. *In*: Viner, A. B *ed*. Inland waters of New Zealand. *DSIR bulletin 241*, Wellington, New Zealand, pp. 225–263.

Chapman, M. A.; Green, J. D; Jolly, V. H. 1975: Zooplankton. *In*: Jolly, V. H.; Brown, J. M. A. *ed*. New Zealand lakes. Auckland, Auckland University Press, pp. 209–230.

Chapman, M. A.; Green, J. D; Jolly, V. H. 1985: Relationships between zooplankton abundance and trophic state of seven New Zealand lakes. *Hydrobiologia 123*: 119–136.

Chick, J.; McIvor, C. C. 1994: Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. *Canadian journal of fisheries and aquatic sciences 51*: 2873–2882.

Clare, D. C. 1978: Some effects of zooplankton grazing and bully predation inside enclosures in Tomahawk lagoon No. 2. Unpublished thesis, University of Otago, Dunedin, New Zealand. 55 p.

Cryer, M.; Peirson, G.; Townsend, C. R. 1986: Reciprocal interactions between roach *(Rutilus rutilus* L.) and zooplankton in a small lake: prey dynamics and fish growth and recruitment. *Limnology and oceanography 31*: 1022–1038.

Cryer, M. 1988: Predatory impact of New Zealand smelt on natural populations of zooplankton. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie 23*: 1778–1783.

Dodds, A. 1991: Effects of food limitation,allelopathy and predation by juvenile bullies on a *Daphnia carinata* population. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand. 82 p.

Forsyth, D. J.; McCallum, L. 1980: Zooplankton of Lake Taupo. *New Zealand journal of marine and freshwater research 14*: 65–69.

Forsyth, D. J.; Downes, M. T.; Gibbs, M. M.; Kemp L.; McCallum, L.; MacKenzie, L.; Payne, G. 1983: Aspects of the limnology of Lake Rotongaio. *New Zealand journal of marine and freshwater research 17*: 423–435.

Forsyth, D. J.; James, M. R.; Cryer, M. 1990: Alteration of seasonal and diel patterns in vertical migration of zooplankton by *Anabaena* and planktivorous fish. *Archiv für hydrobiologie 117*: 385–404.

Grimm, M. P.; Backx, J. J. G. M. 1990: The restoration of shallow eutrophic lakes and the role of northern pike, aquatic vegetation and nutrient concentration. *Hydrobiologia 200/201*: 557–566.

Gulati, R. D.; Lammens; E. H. R. R.; Meijer, M.-L.; van Donk, E. *ed.* 1990: Biomanipulation tool for water management. *Hydrobiologia 200/201*: 1–628.

Hoyer, M. V.; Canfield, D. E. 1996: Large-mouth bass abundance and aquatic vegetation in Florida lakes: An empirical analysis. *Journal of aquatic plant management 34*: 23–32.

Jeppesen, E.; Jensen, J. P.; Kristensen, P.; Søndergaard, M.; Mortensen, E.; Sortkjær, O.; Olrik, K. 1990b: Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. 2. Threshold levels, long-term stability and conclusions. *Hydrobiologia 200/201*: 219–227.

Jeppesen, E.; Jensen, J. P.; Søndergaard, M.; Lauridsen, T.; Pedersen, L. J.; Jensen, L. 1997: Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia.*

Jeppesen, E.; Madsen, E. A.; Jensen, J. P.; Anderson, N. J. 1996: Reconstruction of the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface calibration data set from shallow lakes. *Freshwater biology 36*: 115–127.

Jeppesen, E.; Søndergaard, M.; Mortensen, E.; Kristensen, P.; Riemann, B.; Jensen, H. J.; Møller, J. P.; Sortkjær, O.; Jensen, J. P.; Christoffersen, K.; Bosselmann, S.; Dall, E. 1990a: Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. 1. Cross-analysis of three Danish case-studies. *Hydrobiologia 200/201*: 205–218.

Jeppesen, E.; Søndergaard, M.; Mortensen, E.; Kristensen, P.; Riemann, B.; Jensen, H. J.; Møller, J. P.; Sortkjær, O.; Jensen, J. P.; Christoffersen, K.; Bosselmann, S.; Dall, E. 1990a: Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. 1. Cross-analysis of three Danish case-studies. *Hydrobiologia 200/201*: 205–218.

Jeppesen, E.; Søndergaard, M.; Kanstrup, E.; Petersen, B.; Henriksen, R. B., Hammershøj, M.; Jensen, J. P.; Have, A. 1994: Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? *Hydrobiologia 275/276*: 15–30.

Jolly V. H.; Chapman, M A. 1977: The comparative limnology of some New Zealand lakes. 2. Plankton. *New Zealand journal of marine and freshwater research 11*: 307–340.

Lampert, W. 1993: Ultimate causes of diel migration of zooplankton: new evidence for predator avoidance hypothesis. *Ergebnisse der limnologie 39*: 79–88.

Lauridsen, T.; Pedersen, L. J.; Jeppesen, E.; Søndergaard M. 1996: The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *Journal of plankton research 18*: 2283–2294.

Leipold, M. A. 1989: Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American naturalist 134*: 922–949.

Luecke, C.; Vanni, M. J.; Magnuson, J. J.; Kitchell, J. F.; Jacobson, P. J. 1990: Seasonal regulation of *Daphnia* populations by planktivorous fish: implications for the clearwater phase. *Limnology and oceanography 35*: 1718–1733.

Malthus, T. J.; Mitchell, S. F. 1988: Agricultural development and eutrophication of Lake Mahinerangi, New Zealand. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie 23*: 1028–1031.

Malthus, T. J.; Mitchell, S. F. 1990: On the occurrence, causes and potential consequences of low zooplankton to phytoplankton ratios in New Zealand lakes. *Freshwater biology 22*: 383–394.

Maly, E. J. 1984: Dispersal ability and relative abundance of *Boeckella* and *Calamoecia* (*Copepoda*: *Calanoida*) in Australian and New Zealand waters. *Oecologia 62*: 173–181.

McDowall, R. M. 1990: New Zealand freshwater fishes. A natural history and guide. Auckland, New Zealand, Heinemann Reed. 553 p.

McQueen, D. J.; Post, J. R; Mills, E. L. 1986: Trophic relationship in freshwater pelagic ecosystems. *Canadian journal of fisheries and aquatic sciences 43*: 1571–1581.

Mills, E. L.; Forney, J. L 1983: Impact on *Daphnia pulex* predation by yellow perch in Oneida Lake, New York. *Transactions of the American Fisheries Society 112*: 154–161.

Mitchell, S. F; Hamilton, D. P.; MacGibbon, W. S: Nayar, P. K., Reynolds, R. N. 1988: Interrelations between phytoplankton, submerged macrophytes, black swans (*Cygnus atratus*) and zooplankton in a shallow New Zealand lake. *Internationale Revue der gesamten Hydrobiologie 73*: 145–170.

Mitchell, S. F.; Trainor, F. R.; Rich, P. H.; Goulden, C. E. 1992: Growth of *Daphnia magna* in the laboratory in relation to the nuritional state of its food species, *Chlamydomonas reinhardtii. Journal of plankton research 14*: 379–391.

Mortensen, E.; Jensen, H.; Müller, J. P. 1991: Retningslinier for standardiseret forsøgsfiskeri i søer og en beskrivelse af fiskeredskaber og - metoder. [Guidelines for standardized test-fishing in lakes and a description of fish gears and methods]. National Environmental Research Institute. 60 p. (In Danish).

Mortensen, E.; Jeppesen, E.; Søndergaard, M.; Kamp-Nielsen, L. *ed.* 1994: Nutrient dynamics and biological structure in shallow lakes. *Hydrobiologia 275/276*: 1–564.

Nayar, P. K. B. 1968: Zooplankton of Tomahawk Lagoon No 2. Unpublished BSc thesis, University of Otago, Dunedin, New Zealand.

Ogilvie, B. G. 1989: The dynamics and biological effects of nutrients released from sediments of shallow lakes by wave action. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand. 157 p.

Persson, L.; Andersson, G.; Hamrin, S. F.; Johansson, L. 1988: Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. *In*: Carpenter, S.R. *ed.* Complex interactions in lake communities. New York, Springer Verlag: 45–65.

Reinartsen, H.; Olsen, Y. 1984: Effects of fish elimination on the phytoplankton community of a eutrophic lake. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie 22*: 649–657.

Ringelberg, J. 1991: Enhancement of phototactic reaction in *Daphnia hyalina* by a chemical mediated signal by juvenile perch (*Perca fluviatilis*). *Journal of plankton research 13*: 17–25.

Rowe, D. K. 1993: Disappearance of koaro, *Galaxias brevipinnis*, from Lake Rotopounamu, New Zealand, following the introduction of smelt, *Retropinna retropinna. Environmental biology of fishes 36*: 329–336.

Rowe, D. K. 1994: Vertical segregation and seasonal changes in fish depth distribution between lakes of contrasting trophic status. *Journal of fish biology 45*: 87–800.

Rowe, D. K.; Chisnall, B. L. in press: Size-related differences in diel feeding activity, prey selection and nocturnal migration strategy of the planktonic larvae of *Gobiomorphus cotidianus* in Lake Rotoiti (NI), New Zealand. *Hydrobiologia.*

Sarnelle, O. 1992: Nutrient enrichment and grazer effect on phytoplankton in lakes. *Ecology 73*: 551–560.

Schriver, P.; Bøgestrand, J.; Jeppesen, E.; Søndergaard, M. 1995: Impact of submerged macrophytes on the interactions between fish, zooplankton and phytoplankton: Large-scale enclosure experiments in a shallow lake. *Freshwater biology 33*: 255–270.

Soto, D.; Hurlbert, S. H. 1991: Long-term experiments on calanoid-cyclopoid interactions. *Ecological monographs 61*: 245–265.

Stansfield, J. H.; Perrow, M. R.; Tench, L. D.; Jowitt, A. J. D.; Taylor, A. A. L. 1997: Submerged macrophytes as refuges for grazing Cladocera against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. *Hydrobiologia.*

Staples, D. J. 1975a: Production biology of the upland bully *Philypnodon breviceps* Stokell in a small New Zealand lake I. Life history, food, feeding and activity rhythms. *Journal of fish biology 7*: 1–24.

Staples, D. J. 1975b: Production biology of the upland bully *Philypnodon breviceps* Stokell in a small New Zealand lake II. Population dynamics. *Journal of fish biology 7*: 25–45.

Staples, D. J. 1975c: Production biology of the upland bully *Philypnodon breviceps* Stokell in a small New Zealand lake III. Production, food consumption and efficiency of food utilisation. *Journal of fish biology 7*: 47–69.

Stephens, R. T. T. 1982: Reproduction, growth and mortality of common bully, *Gobiomorphus cotidianus* McDowall, in a eutrophic, New Zealand lake. *Journal of fish biology 20*: 259–270.

Søndergaard, M.; Jeppesen, E.; Mortensen, E.; Dall, E.; Kristensen, P.; Sortkjær, O. 1990: Phytoplankton biomass reduction after planktivorous fish reduction in a shallow lake. *Hydrobiologia 200/201*: 229–240.

Søndergaard, M.; Jeppesen, E.; Berg, S. 1997: Pike stocking as a biomanipulation tool, 2. Effects on the lower trophic levels in Lake Lyng, Denmark. *Hydrobiologia 342/343*: 319–325.

28. Macrophytes and Turbidity in Brackish Lakes with Special Emphasis on the Role of Top-Down Control

Erik Jeppesen, Martin Søndergaard, Jens Peder Jensen,
Eva Kanstrup, and Birgitte Petersen

Introduction

Evidence from both empirical studies (Canfield et al., 1984; Jeppesen et al., 1990; Faafeng and Mjelde, this volume, Chapter 27) and numerous experimental field studies (see e.g., Gulati et al., 1990; van Donk et al., 1990; Mortensen et al., 1994) indicates that in freshwater lakes extensive growth of submerged macrophytes may lead to clearwater conditions, even at high nutrient concentrations. Several factors seem to be involved, including both increased zooplankton grazer control and nutrient constraint on phytoplankton, alterations in the physical environment that result in less wind-induced and fish-induced resuspension, and possibly also allelophatic effects (Jeppesen et al., 1990; Moss, 1990; Scheffer et al., 1993). A cross-analysis of survey data from 35 Danish brackish lakes revealed a significant decrease in Secchi depth with increasing concentrations of total phosphorus (TP); in contrast to freshwater lakes, however, transparency was independent of whether submerged macrophytes were present at high density (Jeppesen et al., 1994). Similarly, Moss (1994) found that nutrient-rich brackish lakes with extensive growth of submerged macrophytes tend to be in a turbid state. By using both empirical data and field experiments conducted in several brackish and freshwater shallow Danish lakes, we examine here how differences in top-down control may influence the turbidity of freshwater and brackish lakes in the macrophyte state.

Materials and Methods

The analysis is based on survey data from 50–100 freshwater lakes and 35 brackish lakes. Fish population estimates are based on fish caught overnight in gill nets (3 × 1.5-m sections, 14 different mesh sizes from 6.25 to 75 mm) expressed as catch per unit effort (CPUE = fish/net/19 h). Most of the sampling procedures and methods are described by Jeppesen et al. (1994) and Aaser et al. (1995), and only additional methods are presented here. *Leptodora kindti* was counted on zooplankton samples taken at equidistant intervals from the surface to the bottom at one–three stations in the pelagic zone. *Chaoborus* spp. density was estimated from their abundance (n/m^2) in sediment samples collected during the day in autumn or spring, and we assumed that they were evenly distributed in the pelagic zone at night. Between 3–10 samples were taken with a Kajak sampler (diameter, 5.2 cm) in each lake on one–five occasions during winter or spring. The estimate is thus conservative, as summer densities of *Chaoborus* are higher (e.g., Christoffersen, 1990).

Sampling of *Neomysis integer* in shallow Lake Ørslevkloster (40 ha; mean depth, about 2 m; max depth, about 4 m; salinity, 2–4‰) was conducted at 16 stations by vertical hauling with a 0.5-mm net (diameter, 0.5 m) according to Aaser et al. (1995). Fish sampling in this lake was conducted by using 1.5 × 32-m sinking gill nets (eight 4-m sections; each including 1-m sections of 6.25-, 8-, 10-, and 12.5-mm mesh size, respectively), four nets being placed overnight in the littoral zone running parallel to the shore and two in the pelagic at a mid-lake station. Physico-chemical data were obtained by sampling at mid-lake stations (pooled samples from the entire water column).

Results and Discussion

A plot of TP versus Secchi depth in Danish lakes shows that nutrient-rich brackish lakes are turbid even when macrophyte densities are high (Fig. 28.1). Chlorophyll *a* was significantly linearly related to TP and unrelated to submerged macrophyte coverage (Fig. 28.2). These results indicate that zooplankton grazing on phytoplankton is unaffected by the presence or absence of macrophytes in brackish lakes. In eutrophic freshwater lakes, by contrast, the macrophyte state is generally associated with high transparency (Fig. 28.1) and usually, but not always (Meijer et al., 1994), with a high zooplankton/phytoplankton biomass ratio and hence a potentially high grazing pressure on phytoplankton (Moss et al., 1994; Jeppesen et al., 1997; Van den Berg et al., this volume, Chapter 25). Lower zooplankton grazing in brackish lakes may partly reflect differences in zooplankton community structure. Although large-bodied *Daphnia* (e.g., *D. magna*), which play a key role in grazer control of phytoplankton in freshwater lakes (Carpenter and Kitchell, 1993), may become dominant in slightly brackish lakes (Jürgens and Stolpe, 1995), they most frequently disappear above salinities of 2–4‰ (Jeppesen et al., 1994; Moss, 1994). Instead, the lakes are dominated by the copepods, *Eurytemora* spp. and

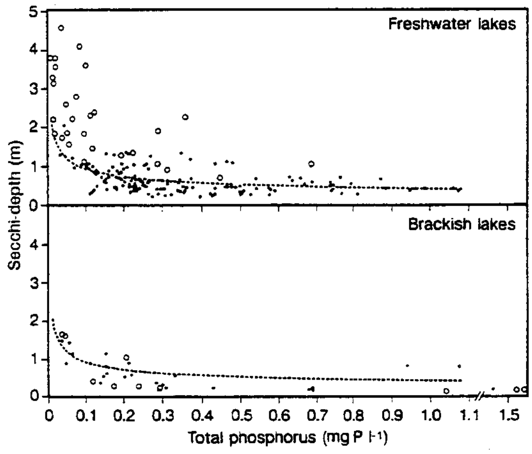

Figure 28.1. Secchi depth in relation to lake water total phosphorus in shallow freshwater (upper panel) and brackish lakes (lower panel). ○ lakes with more than 30% submerged macrophyte coverage; ● lakes with a low (< 30%) or unknown submerged macrophyte coverage. Each point represents one lake and is a time-weighted average of all data collected between May 1 and October 1. The broken line indicates an exponential curve developed by Kristensen et al. (1991) on the basis of data from freshwater and brackish lakes with low submerged macrophyte coverage. (From Jeppesen et al., 1994. Published with permission from Kluwer Academic Publishers.)

Acartia spp., and occasionally by rotifers (Jeppesen et al., 1994), which are probably less efficient in controlling phytoplankton than large-bodied cladocerans. In addition, the zooplankton/phytoplankton ratio is low in brackish lakes (Jeppesen et al., 1994).

Lake Ørslevkloster is an example of how a salinity-mediated shift in trophic structure may reduce grazer control on phytoplankton in macrophyte-rich brackish lakes. The lake shifted from a brackish state (1–3‰) dominated by *Eurytemora affinis* and rotifers to a slightly brackish state (0.5–1‰) dominated by *Daphnia galeata* (Fig. 28.3). Chlorophyll *a* was 2.5–3.5-fold higher in the brackish state

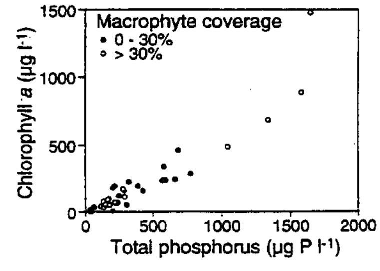

Figure 28.2. Summer mean chlorophyll *a* versus total phosphorus in some Danish shallow brackish lakes with submerged macrophyte coverage in the range 0–30% (●) or greater than 30% (○).

(1993 and 1994) during summer than in the slightly brackish state and 17–23-fold higher during autumn. Correspondingly, Secchi depth was 20–50% and 10–12% lower during summer and autumn, respectively (Fig. 28.4). Despite the fact that external loading did not change (Viborg County, 1995), lake water TP was highest in the brackish state, which is probably due to internal loading caused by FeS formation and a resultant release of iron-bound phosphorus as demonstrated in the nearby Hjarbæk Fjord (H. Jensen, unpublished results). The higher chlorophyll *a* in the brackish state may therefore partly reflect the higher P concentration. However, the chlorophyll *a*/TP ratio during summer and autumn also tended to be higher, which may indicate lower zooplankton grazing on phytoplankton. This is supported by the substantially lower zooplankton/phytoplankton biomass ratio in the brackish state during summer (0.02–0.06 versus 0.49 in the slightly brackish state) (Fig. 28.3). The shifts in turbidity and zooplankton/phytoplankton biomass ratios in Lake Ørslevkloster thus follow the predictions of the established empirical relations, but we cannot, however, exclude the possibility that the shift is caused by other factors. Changes in the recruitment of fish unrelated to changes in salinity may, for instance, also have played a role, but sufficient data to elucidate this are not available.

The low zooplankton/phytoplankton biomass ratio in the brackish state in Lake Ørslevkloster (Fig. 28.3) and in other Danish brackish lakes (Jeppesen et al., 1994) cannot simply be explained by lack of edible phytoplankton. Green algae and diatoms, which are a common food source for the dominant zooplankton (*Eurytemora affinis* and rotifers), are abundant in most eutrophic brackish lakes (Balls et al., 1993; J.P. Jensen et al., unpublished observation), as well as in Lake Ørslevkloster (Nielsen, 1995). Another explanation is top-down control via invertebrates and fish. In North European eutrophic brackish lakes, *Neomysis integer* is a major invertebrate predator (Irvine et al., 1990; Moss, 1994; Aaser et al., 1995), and mysid density increases with increasing TP, particularly above 400 μg P/L (Fig. 28.5), reaching densities as high as 13/L (Jeppesen et al., 1994). The marked increase in mysid density coincides with a shift in the fish community from dominance by roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), whitefish (*Coregonus* spp.), smelt (*Osmerus* spp.), etc., to exclusive dominance by small-sized sticklebacks (*Gasterosteus* spp.) (Jeppesen et al., 1994). The latter coexist with *N. integer*, probably because unlike the larger fish, sticklebacks prey selectively on smaller stages of mysids rather than on ovigorous females (Jeppesen et al., 1994; Kanstrup, 1996). By contrast, the maximum density of the pelagic invertebrate predators in freshwater lakes (*Leptodora kindti* and *Chaoborus* spp.) occurs at 100–200 μg P/L, and they almost disappear at high TP (Fig. 28.5). This is probably due to increased fish predation because large-sized fish such as roach and bream (*Abramis brama*) dominate in north European hypertrophic lakes (Persson et al., 1988; Jeppesen et al., 1990). Although *N. integer* is omnivorous (Arndt and Jansen, 1986) as opposed to the more strict carnivorous *Chaoborus* and *Leptodora* found in freshwater lakes, the predation pressure on zooplankton by pelagic invertebrate predators is probably higher in hypertrophic brackish lakes than in comparable freshwater lakes because of the very high predator density that *Neomysis* may reach in the brackish lakes.

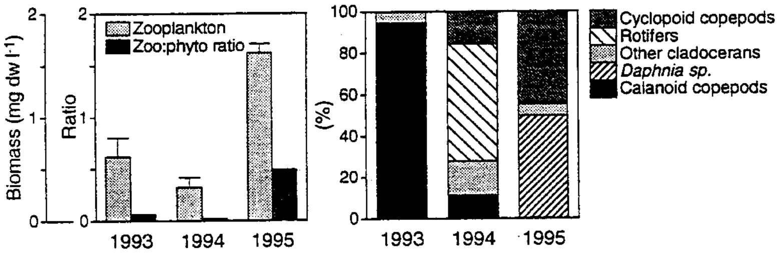

Figure 28.3. Zooplankton biomass and zooplankton/phytoplankton biomass ratio (A) and percentage of biomass accounted for by the various zooplankton groups (B) in shallow Lake Ørslevkloster in 1993, 1994, and 1995. No quantitative data are available for 1986, but high density of *Daphnia hyalina* was observed in littoral fauna samples (Viborg County, 1988), thus indicating that the lake was then in a cladoceran state.

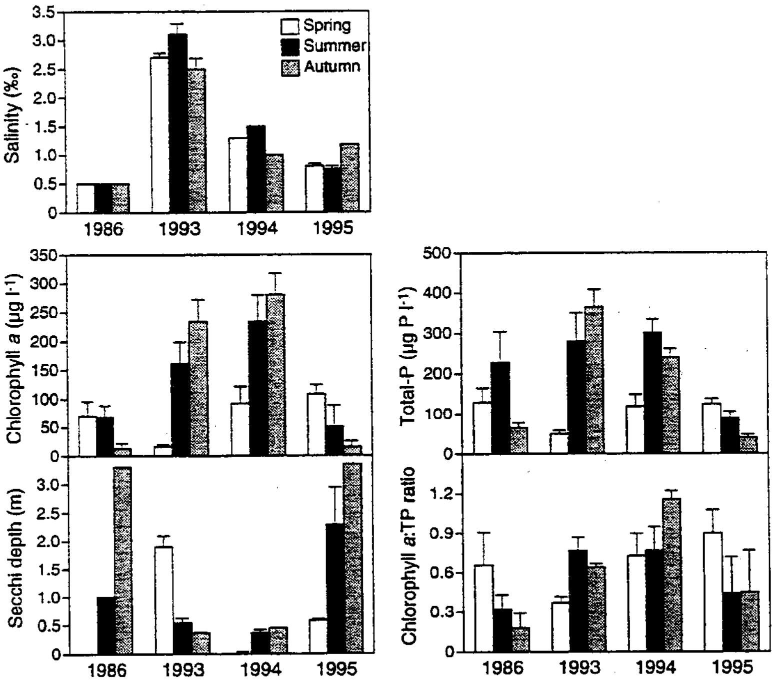

Figure 28.4. Spring (Jan 1–May 1), summer (May 1–Oct 1) and autumn (Oct 1–Jan 1) mean (±SE) values of chlorophyll *a*, Secchi depth, total phosphorus and chlorophyll *a*/total phosphorus ratio in Lake Ørslevkloster during 4 years differing in salinity (upper panel).

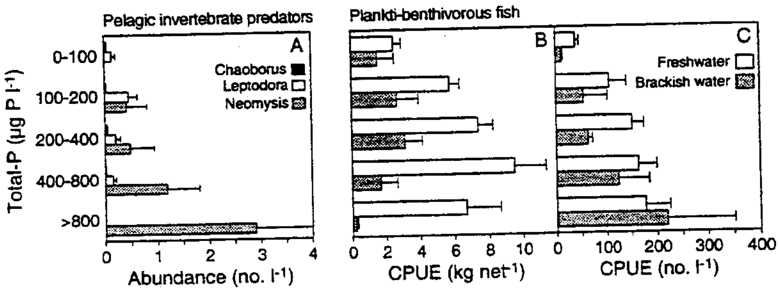

Figure 28.5. Summer (May 1–Oct 1) mean abundance of some invertebrate predators in Danish freshwater and brackish lakes (A). CPUE of planktivorous fish in terms of biomass (B) and number (C) (multiple mesh size gill netting in late July–August, 14 different mesh sizes, 6.25–75 mm), each versus summer mean lake water total phosphorus.

Planktivorous fish significantly affect zooplankton abundance, composition, and the zooplankton/phytoplankton biomass ratio in Danish shallow eutrophic freshwater lakes (Jeppesen et al., 1997). The biomass of planktivorous fish caught in multiple mesh-sized gill nets in brackish lakes is lower than in freshwater lakes, particularly at higher TP, when small-sized sticklebacks dominate (Fig. 28.5; for discussion about net selectivity, see Jeppesen et al., 1994). In terms of numbers, however, CPUE was not lower at high TP concentrations. The data from the freshwater lakes therefore suggest that the predation pressure on zooplankton should be high also in eutrophic brackish lakes (Jeppesen et al., 1994). In addition, sticklebacks produce offspring several times during the summer and autumn. Predation pressure on zooplankton by fish fry is particularly high (e.g., He and Wright, 1992; Søndergaard et al., 1997; Jeppesen et al., 1997), suggesting that there is more likely a continuously high fish predation pressure on zooplankton in eutrophic brackish lakes than in comparable freshwater lakes. This idea of higher invertebrate and fish predation is further supported by the lower zooplankton/phytoplankton biomass ratio in brackish lakes (Fig. 28.3; Jeppesen et al., 1994).

Aggregation of *G. aculeatus* and *N. integer* in the littoral zone (Arndt and Jensen, 1986) may be a contributory factor to the higher turbidity of macrophyte-rich brackish lakes, as it may diminish the ability of the pelagic zooplankton to use macrophytes as a daytime refuge. In Lake Ørslevkloster, the gill net catch of sticklebacks was about sevenfold higher in the littoral zone than in the open water during November–August, and 10–25-fold higher during the summer (Kanstrup, 1996; Fig. 28.6). After August, the pattern changed, however, with the number of stickleback caught being highest in the open water. Correspondingly, the annual mean concentration of *N. integer* was 120-fold higher in the littoral zone than in the pelagic zone (Fig. 28.6), or 30-fold higher per unit area. An experiment involving partial harvesting of macrophytes in the littoral zone of the same lake

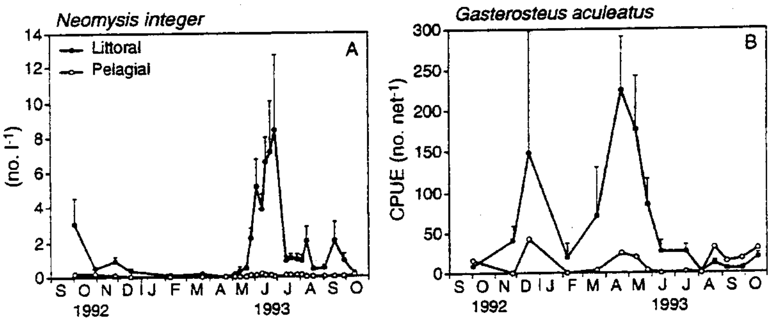

Figure 28.6. Seasonal variation in the density (±SE) of *Neomysis integer* (A) and gill net CPUE of three-spined stickleback (*Gasterosteus aculeatus*) (B) in the littoral and pelagic zone of Lake Ørslevkloster in 1992/93.

showed an 80% higher mysid density inside the plant beds than at similar depths outside (Petersen, 1994). The suggested low refuge effect of macrophytes in brackish lakes may contribute to the low zooplankton control of phytoplankton and hence to the high turbidity of macrophyte-rich lakes, as the possibility of seeking daytime refuge in the vegetation has been shown to be a key factor for the survival of pelagic cladocerans in macrophyte-rich freshwater lakes with a high density of planktivorous fish (Jeppesen et al., this volume, Chapter 5; Lauridsen et al., this volume, Chapter 13).

Nutrient release by *N. integer* may also contribute to a different response of the two lake types. Experiments conducted in two shallow brackish lakes thus showed a considerably higher TP in enclosures containing mysids than in controls devoid of mysids (Aaser et al., 1995; Nielsen, 1995). The results indicated that mysids enhance nutrient release from the sediment, perhaps because some of the nutrients ingested when feeding on sediment detritus and benthic invertebrates are subsequently released to the pelagic. This, in turn, may stimulate phytoplankton growth, thereby contributing to the low Secchi depth in brackish lakes.

Although we are beginning to understand the mechanisms behind the high turbidity of eutrophic macrophyte-rich brackish lakes, more research is needed before any firm conclusions can be drawn. Further studies are important not only from a basic science point of view but also with regard to lake management. Thus, the difference in trophic structure and dynamics of the two different lake types has important implications when transferring the ecotechnological restoration methods known from freshwater lakes to brackish lakes (Jeppesen et al., 1994; Moss, 1994).

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References

Aaser, H.F.; Jeppesen, E.; Søndergaard, M. Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake. Mar. Ecol. Prog. Ser. 127:47–56; 1995.

Arndt, E.A.; Jansen, W. *Neomysis integer* (Leach) in the Chain of Boddens south of Darss/Zingst (Western Baltic). Ecophysiology and population dynamics. Ophelia 4:1–15; 1986.

Balls, M.; Moss, B.; Phillips, G.L.; Irvine, K.; Stansfield, H. The changing ecosystem of a shallow, brackish lake, Hickling Broad, Norfolk II. Long-term trends in water chemistry and ecology and their implications for restoration of the lake. Freshwat. Biol. 29:141–165; 1993.

Canfield, D.E.; Shireman, J.V.; Colle, D.E.; Haller, W.T.; Watkins, C.E.; Maceina, M.J. Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes. Can. J. Fish. Aquat. Sci. 41:497–501; 1984.

Carpenter, S.R.; Kitchell, J.F., eds. The trophic cascade in lakes. New York: Cambridge University Press; 1993.

Christoffersen, K. Evaluation of *Chaoborus* predation on natural populations of herbivorous zooplankton in a eutrophic lake. Hydrobiologia 200/201:459–466; 1990.

Gulati, R.D.; Lammens, E.H.R.R.; Meijer, M.-L.; van Donk, E. Biomanipulation, tool for water management. Hydrobiologia 200/201:1–628; 1990.

He, X.; Wright, R. An experimental study of piscivore–planktivore interactions: population and community responses to predation. Can. J. Fish. Aquat. Sci. 49:1176–1185; 1992.

Irvine, K.; Bales, M.T.; Moss, B.; Stansfield, J.H.; Snook, D. Trophic relations in Hickling Broad—a shallow and brackish eutrophic lake. Verh. Int. Verein. Limnol. 24:576–579; 1990.

Jeppesen, E.; Jensen, J.P.; Kristensen, P.; Søndergaard, M.; Mortensen, E.; Sortkjær, O.; Olrik, K. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. Hydrobiologia 200/201: 219–227; 1990.

Jeppesen, E.; Søndergaard, M.; Kanstrup, E.; Petersen, B.; Eriksen, R.B.; Hammershøj, M.; Mortensen, E.; Jensen, J.P.; Have, A. Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia 275/276: 15–30; 1994.

Jeppesen, E.; Jensen, J.P.; Søndergaard, M.; Lauridsen, T.L.; Junge Pedersen, L.; Jensen, L. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342/343:151–164; 1997.

Jürgens, K.; Stolpe, G. Seasonal dynamics of crustacean zooplankton, heterotrophic flagellates and bacteria in a shallow eutrophic lake. Freshwat. Biol. 33:27–38; 1995.

Kanstrup, E. Trepigget hundestejles *Gasterosteus aculeatus* L. betydning for de biologiske interaktioner i en lavvandet, eutrof brakvandssø (in Danish). [The influence of three-spined stickleback *Gasterosteus aculeatus* on the biological interactions in a shallow eutrophic brackish lake.] MSc thesis, National Environmental Research Institute and the University of Aarhus, Aarhus; 1996.

Kristensen, P.; Jensen, J.P.; Jeppesen, E. Simple empirical lake models. In: Nitrogen and phosphorus in fresh and marine water. Danish Environmental Protection Agency Abstracts, Copenhagen; 125–145; 1991.

Meijer, M-L.; Jeppesen, E.; van Donk, E.; Moss, B.; Scheffer, M.; Lammens, E.; van Nes, E.; van Berkum, J.A.; de Jong, G.J.; Faafeng, B.A.; Jensen, J.P. Long-term response to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in the Netherlands and Denmark. Hydrobiologia 275/276:457–466; 1994.

Mortensen, E.; Jeppesen, E.; Søndergaard, M.; Kamp Nielsen, L., eds. Nutrient dynamics and biological structure in shallow freshwater and brackish lakes. Hydrobiologia 275/276:1–507; 1994.

Moss, B. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201:367–378; 1990.

Moss, B. Brackish and freshwater lakes—different systems or variations on the same theme? Hydrobiologia 275/276:367–378; 1994.

Moss, B.; McGowan, S.; Carvalho, L. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. Limnol. Oceanogr. 39:1020–1029; 1994.

Nielsen, F. Græsning af copepoder *Eurytemora affinis* i to eutrofe søer (in Danish). [*Eurytemora affinis* grazing in two eutrophic lakes.] MSc thesis, National Environmental Research Institute, Silkeborg, and the University of Aarhus, Aarhus; 1995.

Persson, L.; Anderson, G.; Hamrin, S.F.; Johansson, L. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. In: Carpenter, S.R., ed. Complex interactions in lake communities. New York: Springer-Verlag; 1988: 45–65.

Petersen, B. *Neomysis integers* økologiske rolle i en lavvandet, eutrof brakvandssø (in Danish). [The ecological role of *Neomysis integer* in a shallow eutrophic brackish lake.] MSc thesis, National Environmental Research Institute, Silkeborg, and the University of Aarhus, Aarhus; 1994.

Scheffer, M.; Hosper, S.H.; Meijer, M.-L.; Moss, B.; Jeppesen, E. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8:275–279; 1993.

Søndergaard, M.; Jeppesen, E.; Berg, S. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 2. Effects on lower trophic levels in Lake Lyng (Denmark). Hydrobiologia 342/343:319–325; 1997.

van Donk, E.; Grimm, M.P.; Gulati, R.D.; Klein, J.P.G. Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. Hydrobiologia 200/201:275–289; 1990.

Viborg County. Miljøtilstand i Ørslevkloster Sø 1986–1987 (in Danish). [The environmental state of Lake Ørslevkloster 1986–1987.] Viborg, Denmark; 1988.

Viborg County. Ørslevkloster Sø 1994. Belastning, fysisk-kemiske forhold, vegetation samt fiskebestand (in Danish). [Lake Ørslevkloster 1994. Loading, physico-chemical interactions, vegetation and fish stock.] Viborg, Denmark; 1995.

5. Impact of Submerged Macrophytes on Fish–Zooplankton Interactions in Lakes

Erik Jeppesen, Torben L. Lauridsen, Timo Kairesalo, and
Martin R. Perrow

Introduction

Fish have a major structuring impact on the zooplankton communities in lakes (Hrbaček et al., 1961; Brooks and Dodson, 1965) that may cascade to the lower trophic levels and chemical environment (Carpenter et al., 1985; Carpenter and Kitchell, 1993). Ample evidence is available from enclosure experiments (e.g., Christoffersen et al., 1993), whole-lake experiments (e.g., Shapiro et al., 1975; Benndorf, 1987; Gulati et al., 1990; Carpenter and Kitchell, 1993), and empirical analyses (Jeppesen et al., 1990, 1997). More recently, it has become evident that 0^+ fish may play a key role in zooplankton population dynamics (Cryer et al., 1986; Mills et al., 1987), and some studies suggest that fish larvae are responsible for the midsummer decline in zooplankton (Luecke et al., 1990; Jeppesen et al., 1997), a phenomenon that is often attributed to increased density of inedible phytoplankton such as cyanobacteria (e.g., De Bernardi and Guisanni, 1990). Whole-lake (Søndergaard et al., 1997) and enclosure (He and Wright, 1992) experiments support the structuring role of 0^+ fish. How the importance of top-down control of zooplankton by fish varies along a trophic gradient is debated extensively. McQueen et al. (1986) suggested that the cascading effect of zooplanktivorous fish is stronger in oligotrophic lakes than in eutrophic lakes, but a growing body of literature argues that the cascading effect of fish is greater in eutrophic and hypertrophic lakes with respect to the food web in the classic sense

(Jeppesen et al., 1990, 1997; Leibold, 1990; Sarnelle 1992) and the microbial web (Jeppesen et al., 1992; Jürgens 1994; Jürgens and Jeppesen, this volume, Chapter 16).

In addition to nutrient-dependent fish effects, the role of fish seems also to change with lake depth. A cross-analysis of data and existing empirical relations suggests that plankti-benthivorous fish have a higher impact on the zooplankton in macrophyte-free shallow lakes than in corresponding deep lakes (Jeppesen et al., in press). This is because fish biomass per unit of area at any given nutrient level does not change with mean depth (Hanson and Leggett, 1982; Downing et al., 1990), implying that the biomass per unit of volume, and thus probably also the predation on zooplankton, increases with decreasing mean depth. In addition, vertical migration as an antipredator defense mechanism (Lampert, 1993) is less effective in shallow lakes. Furthermore, the availability of alternative food sources for the fish, such as sediment and bottom fauna, is higher in shallow lakes than in deep lakes because of detritus and thus of higher quality for the benthos of shallow lakes. In lakes with low oxygen in the hypolimnion, parts of the sediment may furthermore be inaccessible to the fish. Consequently, the shallow lake zooplanktivorous fish biomass may be sustained at high levels by additional alternative food sources, and they can therefore maintain a higher predation pressure on zooplankton than in deep lakes (Jeppesen et al., 1997). In shallow lakes, however, submerged macrophytes may cover large areas, and if abundant, this may alter the interaction strength between fish and pelagic zooplankton as zooplankton may use macrophytes as refuge against predation from fish. The interactions are, however, complex, as the presence of macrophytes also influences the mutual interaction between piscivorous fish and prey fish. For instance, small planktivores use macrophytes as an antipredator defense mechanism. Macrophytes may also influence the competition between various predatory species and, at the juvenile stages, competition between prey fish and predators (see Persson and Crowder, this volume, Chapter 1). Yet, we far from fully understand how the interactions between fish and zooplankton are influenced by macrophytes. However, certain patterns are emerging.

We first briefly describe the zooplankton communities in macrophyte beds. Thereafter, we discuss how macrophytes may influence the interactions between fish and zooplankton and show how these interactions may have cascading effects on phytoplankton, protozoans, and bacterioplankton. Then, we present a tentative model describing how fish–zooplankton interactions may alter along a nutrient gradient, and finally, we suggest future research needs. We intend to highlight key issues emerging particularly from our own results rather than present a full literature review. In this chapter, the term *littoral zone* does not only comprise the nearshore areas but all areas with plants and nearby open water. Thus, in very shallow lakes the littoral zone may extend to the lake center.

Zooplankton Community in Macrophyte Beds

Crustacean and rotifer communities in plant beds consist of epiphytic, benthic, and pelagic forms. Most plant-associated species in the littoral zone can be categorized as scrapers on solid substrate (e.g., *Eurycercus*), suckers (some rotifers), or graspers (cyclopoid copepods) (Gliwicz and Rybak, 1976). Some forms such as *Sida* collect seston by filtration while fixed to the plants, but they do show a certain plasticity, as they periodically appear free-swimming, especially at night (Vuille, 1991). Others are probably facultative filter feeders (e.g., *Chydorus, Eurycercus,* and *Acroperus*), and others are predators (*Polyphemus*). The ecological role of these plant-associated cladocerans is, however, virtually unknown.

Most, if not all, pelagic zooplankton species may periodically occur in the plant beds. It is characteristic that if a littoral zone is present, cladocerans such as *Ceriodaphnia* spp., *Chydorus sphaericus, Diaphanosoma brachyurum,* and cyclopoid copepods are often more abundant here than in the pelagic zone, whereas rotifer and calanoid copepod densities show the opposite pattern (Gliwicz and Rybak, 1976; Vuille, 1991; Lauridsen et al., 1996). In particular, *Ceriodaphnia* spp. and *D. brachyurum* seem well adapted to plant beds, probably because they are efficient microfiltrators (of bacterioplankton, etc.) (Gliwicz and Rybak, 1976; DeMott, 1986). In addition, *Ceriodaphnia* tolerates low-oxygen conditions (Gliwicz and Rybak, 1976).

The study by Jeppesen et al. (unpublished results) illustrates how habitat choice depends on plant density. In fish-free enclosures in which zooplankton could select between open water and three different plant densities (artificial plastic plants), major differences in relative zooplankton composition and total abundance were found. *Bosnuna longirostris* preferred open water. *Daphnia* spp. were widespread at all plant densities and in open water. *D. brachyurum* abundance was highest at intermediate plant volume infested (PVI), and *Ceriodaphnia* spp. and cyclopoid copepods abundance was highest in the most dense vegetation (Fig. 5.1). In accordance with these results, a cross-analysis of data from 13 lakes conducted by Cyr and Downing (1988) revealed a negative relationship between the abundance of *B. longirostris* and plant density but a positive one with the density or biomass of cyclopoid copepods and other cladocerans. Other studies, however, showed high abundance of *B. longirostris* in the vegetation (Pennak, 1966; Gliwicz and Rybak, 1976; Jakobsen and Johnsen, 1987; Lauridsen et al., 1996). These differences may reflect variations in fish predation pressure (see below). The relative contribution of pelagic zooplankton may also depend on plant bed size, being lower in large beds (Lauridsen et al., 1996) as pelagic zooplankton often aggregate in the transitional zone between plant beds and open water (Lauridsen and Buenk, 1996). In addition. light intensity and water currents may influence the zooplankton distribution (e.g., Kairesalo and Penttilä, 1990). In accordance with Figure 5.1, the abundance (Cyr and Downing, 1988; Paterson, 1993; Phillips et al., 1996) and biomass (Cyr and Downing, 1988) of microcrustaceans often increase with plant biomass but to a varying degree depending on plant type (Paterson, 1993). In the study by Paterson (1993), the number of microcrustaceans per unit of area was an order of magnitude higher in the plant beds (0.5×10^6 m^2) than in open water and plant-free sediment in the littoral zone. Likewise, the average size of the different species is often larger inside the vegetation than outside (Vuille and Maurer, 1991; Lauridsen and Buenk, 1996).

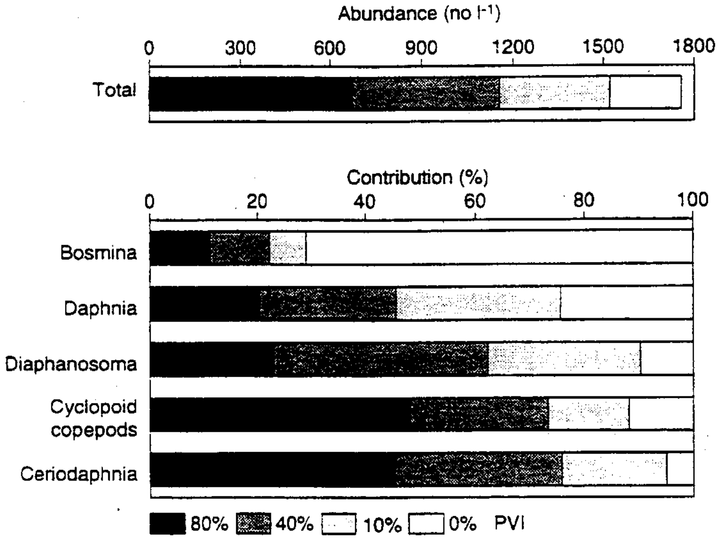

Figure 5.1. (Upper panel) Total abundance and (lower panel) percentage distribution in terms of numbers of various zooplankton in fish-free enclosures with contrasting densities of artificial plants (ivy imitations) (0, 10, 40, and 80% plant volume infested [PVI]) in Lake Stigsholm July 1995. The data represent a day–night average. (Modified from Jeppesen et al., in preparation.)

Increasing invertebrate density with increasing plant density and high densities per square meter in the plant beds have also been observed in the case of macroinvertebrates (Cyr and Downing, 1988; Diehl and Kornijów, this volume, Chapter 2).

Diel Horizontal and Littoral Vertical Migration of Zooplankton

The presence of planktivorous fish in both the pelagic and the littoral zone may alter the horizontal distribution of zooplankton. Some recent studies show daytime aggregation of pelagic zooplankton in the littoral zone (Lauridsen and Buenk, 1996; Stansfield et al., 1997), whereas other studies support the "shore avoidance hypothesis" proposed by Hutchinson (1967). These differences seem to be highly dependent on season, reflecting differences in density and horizontal distribution of fish. Cryer and Townsend (1988) studied the horizontal distribution of pelagic zooplankton during 2 years with contrasting densities of 0^+ fish and found that in July densities of *Daphnia hyalina* and *B. longirostris* were an order of magnitude higher in the pelagic than the littoral zone in the low-fish year but up to 100-fold more abundant in the littoral than in the pelagic zone when fish density was high (*D. hyalina*). Likewise, Jakobsen and Johnson (1987) recorded an even distribution in the pelagic and littoral zones of *Daphnia longispina* and *Bosmina longispina* in Lake Kvernavatn, Norway, early in the season, but a segregation took place when sticklebacks aggregated in the littoral zone, *D. longispina* moving to the pelagic zone, while *B. longispina*, being smaller and less predation vulnerable, moved to the littoral zone.

The horizontal distribution of zooplankton also varies from day to night. Based on zooplankton studies in shallow Hoveton Great Broad, Timms and Moss (1984) proposed that pelagic zooplankton move into macrophyte beds during daytime, using it as spatial refuge against fish predation, but migrate into open water at night to feed on phytoplankton. Since this study, the existence of diel horizontal migration (DHM) has been confirmed by several studies (Davies, 1985; De Meester et al., 1993; De Stasio, 1993; Lauridsen and Buenk, 1996; Lauridsen et al., 1996; Jeppesen et al., 1992; Lauridsen et al., this volume, Chapter 13). Diel and seasonal studies undertaken in the littoral zone by Kairesalo (1980), Lehtovaara and Sarvala (1984), Walls et al. (1990), and Stansfield et al. (1992) lend further support to DHM. Studies undertaken in several lakes with varying fish densities suggest that the extent of DHM is positively related to the density of planktivorous fish in the pelagic zone (Lauridsen et al., this volume, Chapter 13). Likewise, fish density seems to decide the migrating species and size classes. In Lake Ring, Denmark, where the abundance of planktivorous fish was low, Lauridsen and Buenk (1996) thus found that *Daphnia magna* showed higher levels of DHM than the smaller *Daphnia galeata*. In the more fish-rich Lake Stigsholm, even small species such as *B. longirostris* and *Ceriodaphnia* spp. migrated (Lauridsen et al., 1996; Jeppesen et al., submitted) (Fig. 5.2). In addition, other studies have shown that it is the largest individuals of the various species in particular that undergo DHM (Lauridsen and Buenk, 1996; Pedersen, unpublished results). All these observations are in accordance with the size-efficiency hypothesis (Brooks and Dodson, 1965). The empirical evidence of fish-mediated horizontal migration is confirmed by controlled laboratory and field experiments. Laboratory experiments by Lauridsen and Lodge (1996) showed that the presence of fish (*Lepomis cyanellus*) or kairiomone cue in open water initiated a migration of *D. magna* toward the plant bed. A preliminary experiment in 80 m^2 enclosures in Lake Stigsholm showed that in the presence of planktivorous fish in high densities (13–16 m^2) *Daphnia* spp. sought refuge in the vegetation (Jacobsen et al., 1997). Later, more detailed enclosure studies in this lake have shown that addition of 0^+ perch (*Perca fluviatilis*) to fishless enclosures resulted in a differential degree of habitat shift of zooplankton, dependent on species and development stage (copepods), being particularly high for *Daphnia* spp. (Jeppesen et al., in preparation). DHM can also be an antipredator defense mechanism against invertebrate predators such as *Chaoborus flavicans* (Kvam and Kleiven, 1995), involving chemical cues (Kleiven et al., 1996). Reverse migration (highest densities in the plant beds at night) may be observed if plant-associated invertebrate predators such as odonates are important, as discussed by Lauridsen et al. (this volume, Chapter 13). DHM induced by invertebrate predators will probably be most important in lakes with low fish densities.

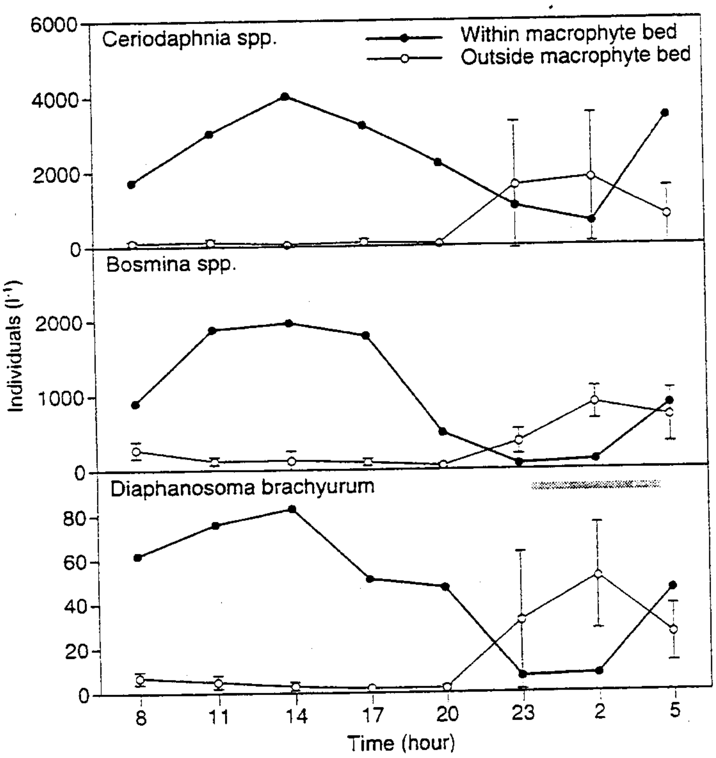

Figure 5.2. Diel variations in the abundance of various cladocerans in a 2-m exclosure (open to small fish and zooplankton) with dense coverage of submerged macrophytes and at a reference station outside the macrophyte bed in Lake Stigsholm in August. Hatched area shows the dark period. (Modified from Lauridsen et al., 1996, by permission of Oxford University Press.)

Macrophytes may also have a repellent effect on various pelagic zooplankters (Hasler and Jones, 1949; Pennak, 1966; Pennak, 1973; Dorgelo and Heykoop, 1985; Lauridsen and Lodge, 1996). This seems appropriate as the plant beds host several plant-associated facultative filtrators that most likely are superior competitors to pelagic zooplankton in a plant community in which the production of periphytic algae is substantially higher than that of phytoplankton (Wetzel, 1975; Wetzel and Søndergaard, this volume, Chapter 7). Habitat choice of pelagic zooplankton therefore seems to be a trade-off between the risk of predation and optimum food conditions that at least partly seem to be regulated by chemical cues from either fish or plants.

Diel vertical migration in the pelagic zone (DVM) is well documented and is most frequently interpreted as being an antipredator defense against predation

(Ringelberg, 1991; Lampert, 1993) that may involve chemical cues (von Elert and Loose, 1996). DVM of both pelagic and benthic crustaceans (e.g., Szlaur, 1963; Whiteside, 1974) may also occur in the plant-rich littoral zone, and various explanations have been offered. In some studies, it has been interpreted as a night-time escape from low oxygen concentrations within the macrophyte beds (Meyers, 1980; Timson and Laybourn-Parry, 1985). Others have argued that DVM in the littoral zone reflects diel variation in predation risk, the predation pressure being released at night due to reduced visibility and offshore migration by fish (Jeppesen et al., in preparation). Further evidence for the importance of fish for DVM is given by De Stasio (1993), who showed that fish removal in a lake almost eliminated DVM in the pelagic as well as in the littoral zone. Likewise, Jeppesen et al. (in preparation) have shown that in the littoral zone especially large-bodied predation-vulnerable zooplankton such as *Daphnia* spp. and adult cyclopoid copepods exhibited DVM, whereas smaller forms such as nauplii and rotifers did not. As expected, DVM was higher in the macrophyte-free area than in the plant bed. In addition, the degree of DVM increased with increasing density of planktivorous fish and decreasing plant density. The studies by De Stasio (1993) and Jeppesen et al. (in preparation) showed substantial DVM despite the samples integrating the entire water column except the lower few centimeters. This suggests that the zooplankton in the littoral zone sought refuge at the sediment surface and in plant beds perhaps also close to plant surfaces.

DVM in the littoral zone has, however, also been observed in the absence of fish by Paterson (1993), who argued that DVM of plant-associated forms was lower in fishless lakes than in fish-rich lakes, which may indicate a lower predation pressure on zooplankton by invertebrate predators than fish. Accordingly, Paterson (1994) found only marginal differences in the density of cladocerans and cyclopoid copepods in experiments run at different densities of some important littoral invertebrate predators (*Odonata, Acari, Tanypodinae*). Also, Johnson et al. (1987) and Blois-Heulin et al. (1990) failed to detect a strong impact of large odonates on cladocerans. By contrast, others have found negative effects of water mites (Kajak et al., 1968) and *Procladius* (Dusoge, 1980).

Refuge Effect in Relation to Structural Complexity and Fish Density

Like zooplankton, small fish may seek refuge in the vegetation to avoid predatory fish and birds (e.g., Carpenter and Lodge, 1986; Gliwicz and Jachner, 1992; Persson and Crowder, this volume, Chapter 1). The prey fish often prefer sparse vegetation (Engels, 1988; Phillips et al., 1996; Jeppesen et al., 1992, 1997; Stansfield et al., 1997), which may reflect that the foraging efficiency of fish decreases with increasing plant density (e.g., Crowder and Cooper, 1982; Savino and Stein, 1982; Anderson, 1984; Diehl, 1988), although there are exceptions to this rule (Winfield, 1986; Persson and Crowder, this volume, Chapter 1). The study in Cromes Broad (Phillips et al., 1996) is an example of aggregation and high predation on zooplankton by planktivorous fish in sparse vegetation (Fig. 5.3). Accordingly,

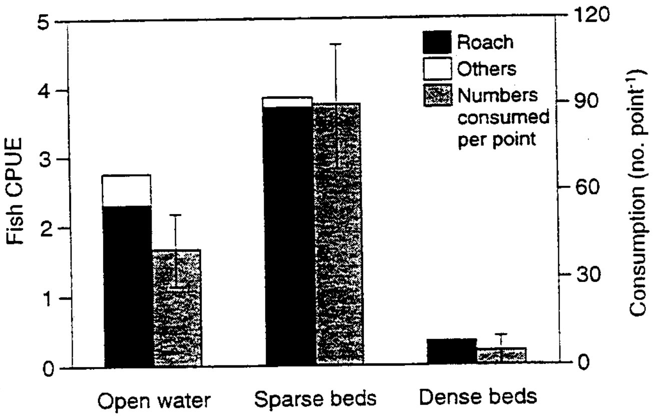

Figure 5.3. Fish community structure in various habitats in Cromes Broad (1993) shown by the mean number of fish captured using point sample electrofishing (left column) and index of point predation (mean ± SE) on zooplankton derived by multiplication of fish density with the mean number of zooplankton in the fish guts. (Data from Phillips et al., 1996.)

zooplankton density was highest in the dense vegetation. Likewise, Lehtovaara and Sarvala (1984) and Kairesalo and Penttilä (1990) found higher fish densities at low density of *Equisetum* than at high density of this plant, with corresponding inverse effects on zooplankton densities.

The presence of predatory fish in the vegetation may further complicate the interaction between planktivorous fish and zooplankton in the littoral zone. On the one hand, the predation pressure on zooplankton may be reduced as the planktivorous fish reduce their activity level (Bean and Winfield, 1995; Jacobsen et al., 1997; L. Jacobsen, unpublished data) or switch to alternative food sources as a consequence of a restricted habitat use (Persson, 1993). As an example, Persson (1993) found that roach in the absence of predators fed on mainly *Bosmina* sp. but switched to detritus/algae in the presence of piscivorous perch. This, in turn, led to an increase in *Bosmina* density. On the other hand, a high predation risk may drive the prey fish to move into even the most dense vegetation (Savino and Stein, 1982; Werner et al., 1983; Persson et al., 1991; Persson and Eklöv, 1995) and accordingly a loss of refuge for large-sized zooplankton may occur (Jeppesen et al., in preparation).

The role of fish density was studied by Schriver et al. (1995), who conducted experiments in 100-m^2 enclosures with varying PVI and density of 0^+ and 1^+ planktivorous fish (three-spined sticklebacks [*Gasterosteus aculeatus*] and roach [*Rutilus rutilus*]) in Lake Stigsholm, Denmark. They showed a refuge effect when PVI was >15–20% if fish density was below ca. 2/m^2 (Fig. 5.4). At lower PVI, the zooplankton were dominated by cyclopoid copepods. At fish densities of 2–4/m^2 and PVI at >15–20%, zooplankton shifted to small cladocerans, and at even higher

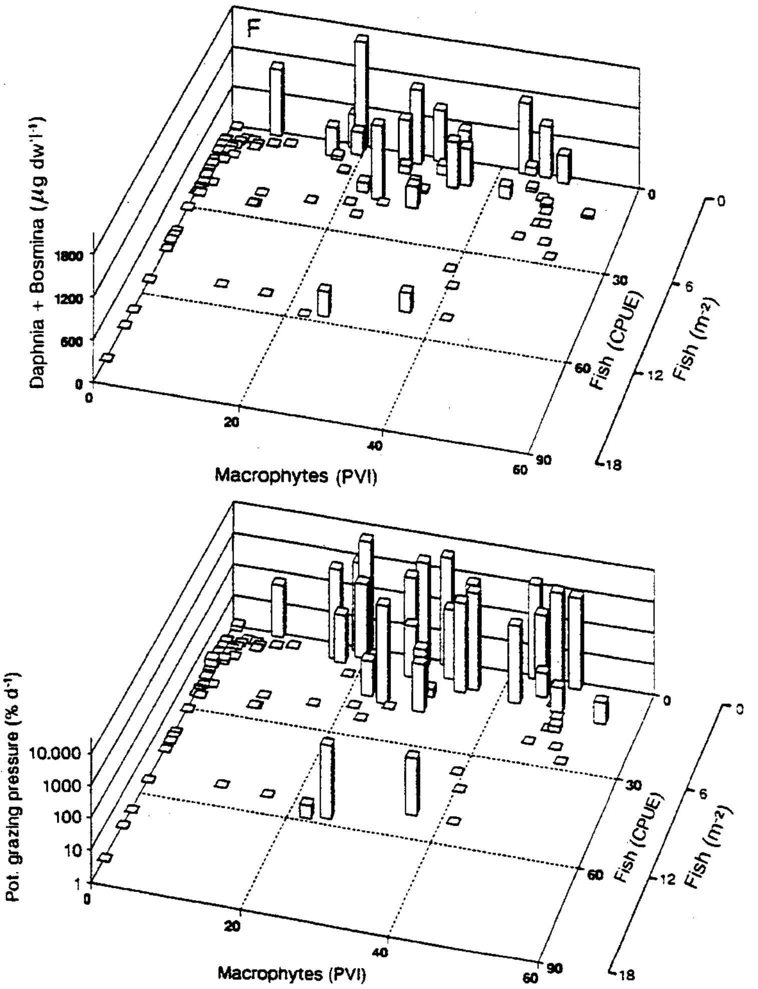

Figure 5.4. Biomass of the dominant pelagic cladocerans (*Bosmina* + *Daphnia:* upper panel) and their potential grazing pressure on phytoplankton (estimated 24-hour ingestion by *Bosmina* + *Daphnia* in % of phytoplankton biomass; lower panel) versus the abundance of 0^+ and 1^+ roach and three-spined sticklebacks (catch per unit effort [CPUE] in traps) and macrophyte PVI (%) in Lake Stigsholm enclosure experiments involving manipulation of plants (mainly *Potamogeton* species) and fish density. (From Schriver et al., 1995, published with kind permission of Blackwell Science Ltd.)

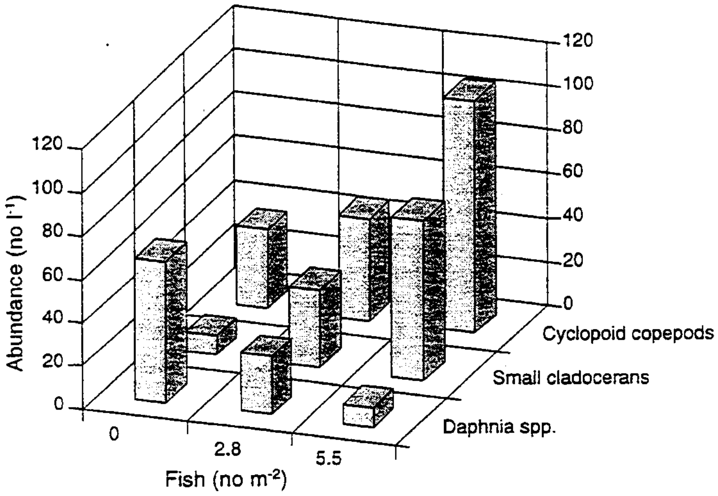

Figure 5.5. Average concentration of various zooplankton in enclosure experiments with high plant biomass (87–165 g/DW/m^2) and contrasting fish densities (0 to 5.5 10–12-cm perch m^2). The experiment was conducted in hypertrophic Little Mere, England. (Data from Table 2, Beklioglu and Moss, 1996.)

fish densities, to cyclopoid copepods and rotifers. Thus, submerged macrophytes acted as refuge for zooplankton against fish predation if PVI was >15–20%, but the refuge effect almost disappeared—even for small-sized cladocerans—if fish density exceeded a certain threshold level, in this example ca. 4 fish/m^2. Low refuge effect and dominance by small zooplankton were also observed in the same lake in another experiment with a mixed community of 0$^+$ perch and roach (3/m^2) and a PVI of 24% (Jeppesen et al., in preparation). A partial loss of refuge for large-sized zooplankton within the vegetation has been observed in other studies. In enclosure experiments with a plant density of 87–165 g dry weight (DW)/m^2, Beklioglu and Moss (1996) found a significant reduction in *D. hyalina* and *Daphnia cuculata* at densities of 2.8 perch/m^2 (10–12 cm in length) and a further reduction of daphnids at a fish density of 5.5/m^2 while the densities of small cladocerans (*Ceriodaphnia* spp., *B. longirostris, Chydorus ovalis*) and cyclopoid copepods increased (Fig. 5.5). No data on total zooplankton biomass are available from this study, but a marked increase in chlorophyll *a* as fish densities increased indicates reduced zooplankton control of phytoplankton. A further evidence of loss of refuge effect for zooplankton is offered by Persson and Eklöv (1995), who used artificial plants with a stem density of 280 m^2 in enclosures and a fish density of 2.1 m^2 0$^+$ perch and 1$^+$ roach (1:1). During a 48-day experiment, crustacean zooplankton were reduced 40–100-fold to densities <1.6 ind/L, with large *D. longispina,* as well as large plant-associated cladocerans such as *Eurycercus* sp.

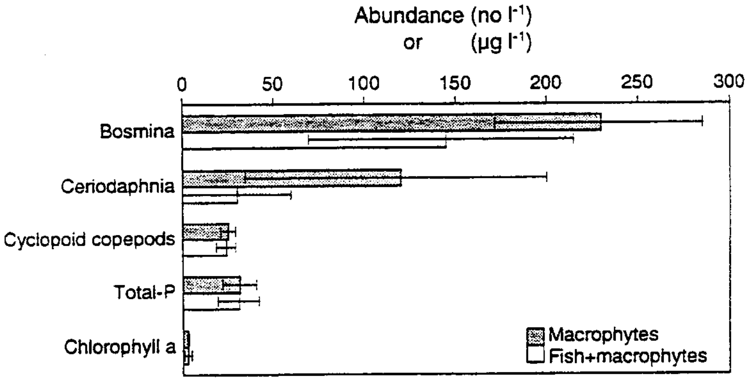

Figure 5.6. Abundance of *Bosmina* spp., *Ceriodaphnia* spp., cyclopoid copepods, total phosphorus, and chlorophyll *a* in macrophyte-rich enclosures (*Elodea canadensis*, 216 g DW m^{2}) without and with fish (3 m^{2} 0^{+} perch). The results stem from the last sampling date of the 21-day-long experiment. (Data from Kairesalo et al., in press.)

reduced to near-zero. In these experiments, no differences were observed whether plants were present or not. Effects of fish presence were also demonstrated by Kairesalo et al. (in press), who found that addition of 3/m^{2} of 0^{+} perch to enclosures with dense beds (216 g DW/m^{2}) of *Elodea canadensis* resulted in a major reduction in the density of *Bosmina* spp. (mainly *B. longispina*) and especially *Ceriodaphnia* spp. (mainly *C. pulchella*) compared with controls without fish, but densities of cyclopoid copepods did not differ (Fig. 5.6).

These last few examples all show that the refuge effect for *Daphnia* spp.—and occasionally also for small-sized cladocerans—even at relatively high plant densities may be partly or totally lost if the density of potentially planktivorous fish exceeds <2–5/m^{2}. It is, however, yet to be demonstrated if the same threshold levels also occur in nature. The enclosure size of these experiments was highly variable, ranging from 0.7 m^{2} (Beklioglu and Moss, 1996) to 100 m^{2} (Schriver et al., 1995), but common to all these studies is that they do not allow discernible diel migration of zooplankton and fish between the littoral zone and open water. Lake Stigsholm experiments indicate that such a migration may reduce the strength of the interactions between fish and zooplankton in the vegetation (Jeppesen et al., unpublished data). Both roach and perch fry migrate to open water at night, which in itself may reduce the predation pressure in the littoral zone. This is strengthened by the fact that, for instance, perch feed especially at dusk and dawn outside the littoral zone and are less active during the day (Gliwicz and Jachner, 1992). Thus, in practice, the threshold for loss of refuge effect at high plant density may be higher than indicated by the experiments described above. In sparse beds the fish threshold for loss of refuge effect may be substantially lower (Schriver et al., 1995; Stansfield et al., 1997). The study by Stansfield et al. (1997) suggests, for example,

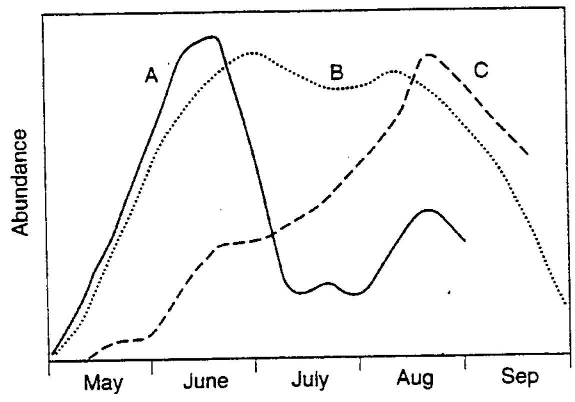

Figure 5.7. Diagrammatic curves that show abundance of littoral zooplankton during the summer months in some northern temperate lakes. Curve A, in which there is a midsummer decline, is the most frequently reported. (From Whiteside, 1988, published with kind permission of E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart.)

a loss of refuge for *Daphnia* spp. at a density of 0.25 0^+ fish/m^2. As densities of 0^+ fish are often higher than 0.25–5/m^2 during the summer (Lehtovaara and Sarvala, 1984; Chick and McIvor, 1994), it is likely that the fish may often have a major structuring impact on zooplankton in the littoral zone. This is supported by the studies of the seasonal patterns of microcrustaceans in the littoral zone. Based on several studies, Whiteside (1988) identified three seasonal patterns (Fig. 5.7): A, a presummer peak followed by low densities during July and by a minor peak in August; B, an almost unimodal pattern with a midsummer maximum; and C, only an autumn peak. Pattern A is very similar to the one observed in the pelagic zone of lakes highly influenced by fish predation (Jeppesen et al., 1997). Whiteside (1988) claimed that predation is responsible for the summer and autumn declines, as there were no arguments in favor of deteriorated food conditions. The bimodal curve (A) is most frequently observed (Whiteside, 1988), indicating that the littoral refuge effect often tends to disappear during midsummer. Subsequent investigations by others support Whiteside's suggestions. Vuille (1991) found a major decline in zooplankton and plant-associated cladocerans in a year with high littoral fish densities and found minor reductions in the preceding year when fish density was low.

Fish-mediated loss of refuge in the littoral zone does not necessarily mean that the predation pressure on zooplankton in the total lake per se is high, because unless the density of older planktivorous fish is high, a predator-mediated aggregation of young fish in the vegetation may lead to a major reduction in the predation on zooplankton in open water. Thus, Boikova (1986) found a reverse migration of crustaceans, with daytime densities being 10–100-fold higher in the pelagic zone than in a dense *Elodea canadensis* plant bed, whereas the crustaceans were more evenly distributed at night. The frequently observed avoidance of the littoral zone (Hutchinson, 1967; Siebeck, 1969, 1980) also indicates that predation pressure in the littoral zone is often higher than in the pelagic zone (Gliwicz and Rybak, 1976; Evans et al., 1980).

Implications for the Lower Trophic Levels

Due to the aggregation of small fish in the littoral zone and the frequently low depth, presumably the overall predation pressure on zooplankton in the plant-free littoral zone may be higher than in the pelagial. Accordingly, the grazing pressure of zooplankton on phytoplankton, protozoans, and bacterioplankton is likely to be lower than in the pelagial. Conversely, if plant density is high and fish are not forced into the vegetation, the cascading effects of grazers may be high due to low fish predation and the daytime aggregation of pelagic zooplankton in the plant beds. The spatial differences in grazing pressure of zooplankton between dense plant beds and open water in the littoral zone are, therefore, expected to be particularly large. This is supported by a few investigations undertaken so far. Jeppesen et al. (in preparation) found that in shallow eutrophic Lake Stigsholm, the daily clearance rates of phytoplankton ranged from very low values of 2% in the littoral zone outside the plant beds to 3.2% in sparse vegetation (PVI = 24%) and to values as high as 300% in dense vegetation (PVI = 50%), whereas the corresponding figures for bacterioplankton clearance were 2.5, 4, and 219%, respectively (Fig. 5.8). The clearance rates were thus 144-fold (phytoplankton) and 88-fold (bacterioplankton) higher in the dense beds than in the macrophyte-free littoral. Such high clearance rates in dense vegetation had significant cascading effects on the trophic structure within the bed. For example, the densities of ciliates, phytoplankton, flagellates, and bacterioplankton were 75-, 4.4-, 4-, and 3-fold, respectively, lower inside than outside the beds (Fig. 5.8) (see also Jeppesen et al., submitted; Søndergaard and Moss, this volume, Chapter 6; Søndergaard et al., this volume, Chapter 15). The significant role played by zooplankton in the determination of these differences was confirmed by size fractionation experiments (Jürgens and Jeppesen, this volume, Chapter 16). Earlier empirical data from experiments involving dense beds of submerged macrophytes and low fish densities have also shown high zooplankton:phytoplankton biomass ratios, suggesting a great cascading impact on the lower trophic levels (Irvine et al., 1989; Moss et al., 1994; Schriver et al., 1995; see also Søndergaard and Moss, this volume, Chapter 6), whereas high fish densities resulted in low ratios inside and especially outside the littoral vegetation (Schriver et al., 1995). The high cascading effect on the lower trophic level within the dense plant beds may not necessarily reflect the role of aggregating pelagic zooplankton. The beds host plant-associated filter feeders such as *Sida*, which may have a potentially high grazing impact (Stansfield et al., 1997). The plant beds also host several filter-feeding macroinvertebrates including mussels with high filtering capacity (Ogilvie and Mitchell, 1995). In addition, the plants and epiphytes may help control the phytoplankton by shading (Straskraba and Pieczynska, 1970) or cause nutrient

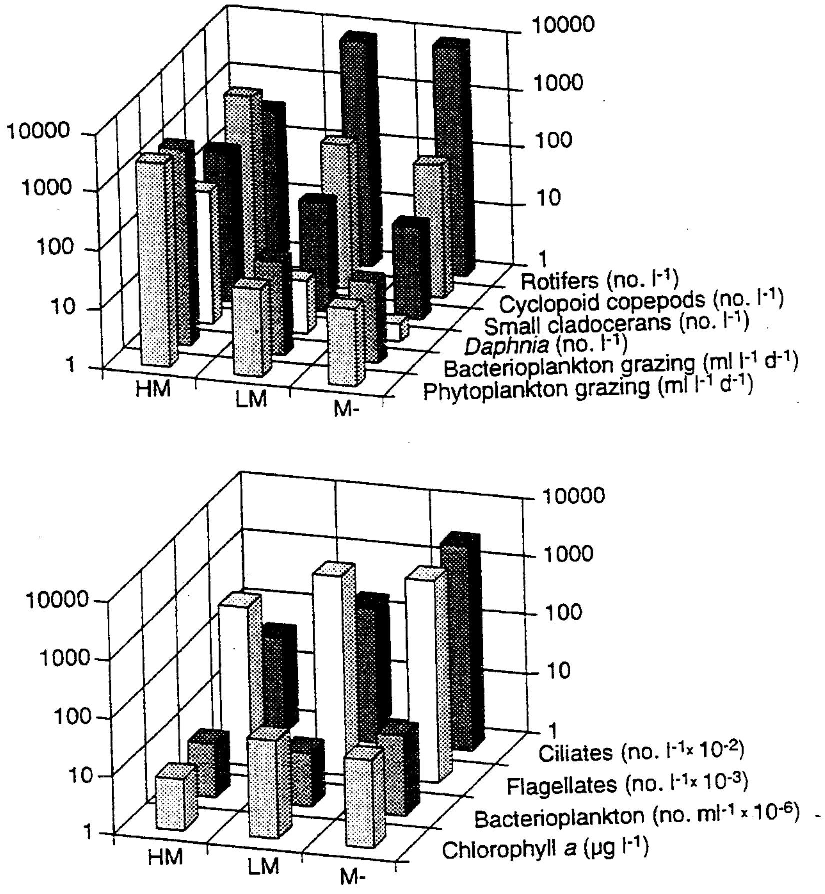

Figure 5.8. Abundance (no. L^{-1}) of various zooplankton and microbial components, chlorophyll *a* (μg L^{-1}), and zooplankton (>140 μm) clearance (ml/L/day) of phytoplankton and bacterioplankton in Lake Stigsholm enclosures with contrasting densities of submerged macrophytes (HM, plant volume infested (PVI) = 50%; LM, PVI = 24%; M-, without macrophytes). Note the logarithmic scale. (Data from Jeppesen et al., submitted.)

limitation (Kairesalo et al., in press). Multiple factors may thus contribute to the relatively high zooplankton:phytoplankton biomass ratio and the stronger top-down control of phytoplankton in the dense plant beds with low fish densities.

Although aggregation of zooplankton in the vegetation has a substantial impact on both the trophic structure and phytoplankton biomass within the plant bed, we do not know the extent to which night-time migration to the pelagic zone will influence open water phytoplankton. Lauridsen et al. (1996) estimated that a 3% coverage of the lake surface area with 2-m diameter patches of dense *Potamogeton pectinatus* beds is sufficient for a night-time doubling of the density of *Ceriodaphnia* spp. and *B. longirostris* in Lake Stigsholm with a low natural plant coverage, and this must be assumed to have a great impact on the phytoplankton grazing pressure. It does, however, require that the zooplankton are widely spread throughout the pelagic zone during night. There are still no measurements of how far zooplankton migrate horizontally. DVM studies have shown night-time migration of >30 m (e.g., Geller et al., 1992) and a mean migration velocity of 0.2 cm/sec for large-sized *Daphnia* species and at maximum speed as much as .5–2 cm/sec (S.I. Dodson, personal communication). If these figures can be transferred to DHM, the zooplankton may be able to exploit the entire pelagic zone in many shallow lakes. An additional consideration is that plants in shallow lakes are often not restricted to the nearshore area but can be found in patches in large parts or in somewhat deeper areas of the lake, further increasing the possibilities of night-time exploitation of the pelagic zone. We, therefore, predict that in many shallow lakes the possibility of seeking refuge in the vegetation during the day increases grazer control of the phytoplankton in open water and thus contributes to maintaining those lakes with comprehensive and dense macrophyte coverage in the clearwater state. The establishment of macrophyte refuges protected from waterfowl grazing has been proposed as a restoration measure to complement nutrient-loading reductions in shallow lakes (Moss, 1990; Jeppesen et al., 1991). Establishment of numerous small and dense refuges should therefore result in much higher densities of migrating cladocerans than a few large refuges. The higher density of cladocerans will ensure a greater filtering capacity within the beds during the day and in open water during the night. Per unit area, small and dense macrophyte refuges may be better able to promote a shift to a clearwater stage than larger ones with low macrophyte density (Lauridsen et al., 1996; Jeppesen et al., 1997).

Changes in Interactions Along a Nutrient Gradient

Changes in nutrient levels affect both the abundance and composition of macrophytes (Wetzel, 1975) and fish (Persson et al., 1991; Jeppesen et al., 1997), which will alter the zooplankton refuge efficiency of the plants against fish predation. Empirical data are scarce, but we propose various hypotheses that may help initiate future discussions and tests. We restrict ourselves to northern European lakes.

With increasing nutrient levels, the depth limit of submerged macrophytes decreases (Chambers and Kalff, 1985), but at the same time the biomass per unit of area and stem density of plants increase (Wetzel, 1975). This supposedly leads to a reduction of the total refuge area for zooplankton, but in the remaining plant-filled areas the refuge effect will increase. Whether increased density compensates for lower area coverage is open to debate, but with the step-like increases observed by Schriver et al. (1995) in the refuge effect at high plant density, it may be presumed that this is indeed the case. At the highest nutrient levels, submerged macrophytes most often totally disappear due to light limitation caused by phytoplankton (but see Moss et al., 1997), leaving only floating-leaved plants and reed belts, which often have a comparatively low refuge effect (Gliwicz and Rybak, 1976; Winfield, 1986; Venugopal and Winfield, 1993) due to low stem density. Presumably, therefore, the refuge effect at a fixed density of planktivorous fish is greatest in slightly eutrophic lakes in which plant density is high and the area covered not yet severely reduced.

Simultaneously with the changes in density and distribution of plants, there are also plant composition changes. In northern temperate lakes, the succession is often from characeans to elodeids in hardwater lakes and from isotids to elodeids in softwater lakes. Isoetids are small dense rosette plants that may act as an efficient refuge among the leaves. However, due to small stature, their general effect as a refuge is probably poor. Characeans often form dense beds with a high areal biomass. Potentially, they may therefore act as an efficient refuge against predation by fish: Diehl (1988) has shown that high density of characeans results in high density of macroinvertebrates. We do not, however, know if this is true for zooplankton. Elodeids may also appear in high densities, but the biomass per unit volume is often smaller than that of characeans (Diehl, 1988), indicating that characeans potentially may act as a better refuge than elodeids.

The picture is further complicated by changes in the density and the relative contribution of some fish species along the nutrient gradient in lakes (Persson et al., 1988; Jeppesen et al., 1990). In eutrophic and hypereutrophic lakes, plankti-benthivorous fish such as roach and bream dominate, being the most efficient fouragers in the pelagic habitat. The preference for the pelagial may be further strengthened by the fact that plant-associated pike (*Esox lucius* L.) is often the dominant piscivore in such lakes (Grimm and Backx, 1990), making it less favorable for prey fish to forage in the vegetation. The pattern will be different if the dominant species is the pelagic forager zander (*Stizostedion lucioperca*), but this species is often not abundant in lakes with extensive growth of submerged macrophytes. Thus, the efficiency of plant beds as a refuge for zooplankton will often be high in eutrophic lakes. The aggregation of zooplankton is further strengthened by the high risk of predation in the pelagic zone.

In less eutrophic to mesotrophic lakes, the impact of predatory fish increases, perch become more important, and the foraging conditions for predatory fish improve due to, for instance, increased transparency. Prey fish thus seek refuge in the vegetation. As planktivorous fish density is relatively high, it is expected that aggregation of young planktivorous fish in the vegetation will be particularly high

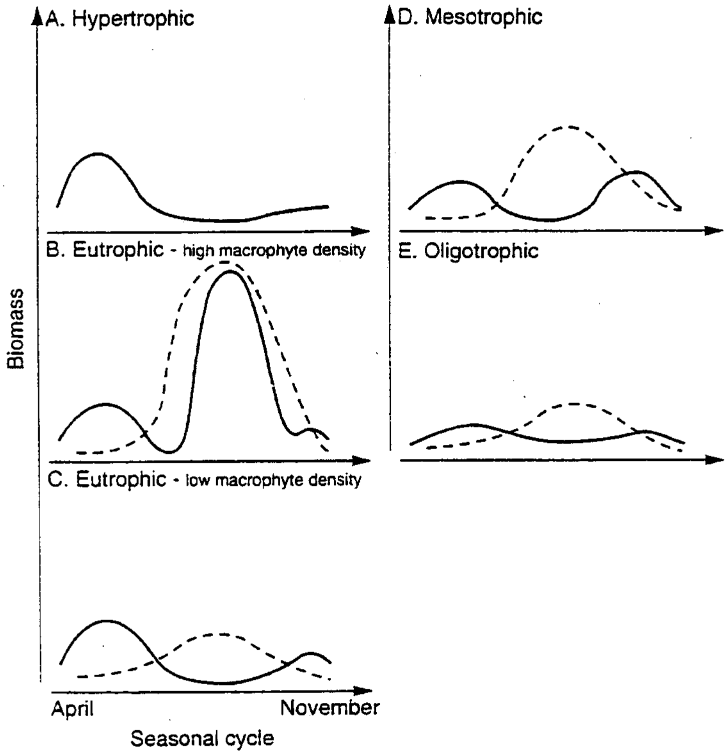

Figure 5.9. Conceptual model showing how the seasonal dynamics of microcrustacean biomass (solid line) in the littoral zone is expected to vary under different nutrient conditions. The broken line represents the average biomass of submerged macrophytes in plant-covered areas.

and the refuge effect correspondingly low. In mesotrophic-oligotrophic lakes, the predator control of planktivorous fish increases. The aggregation is expected to remain high due to a larger share of predatory fish, but the lower abundance of planktivores and lower fish density counteract the effect. The question is if the refuge effect at a given plant density will be higher or lower than in slightly eutrophic lakes. In oligotrophic lakes, the refuge effect for prey fish due to low plant density and plant height will probably be poor, so that the refuge effect for zooplankton may increase.

It is difficult to combine these multiple and complex interactions into a common conceptual model, but we tentatively predict (Fig. 5.9) that

- In hypertrophic lakes without submerged macrophytes, the refuge effect for zooplankton in the littoral zone dominated by reeds is poor throughout the

summer. The density of zooplankton and to a lesser extent plant-associated crustaceans is low and dominated by small forms (Fig 5.9A).
- In eutrophic lakes with high areal coverage of submerged macrophytes and high PVI, the refuge effect will be high throughout the summer period, during which planktivorous fish stay in the pelagic zone or in the sparse vegetation. The density of macrocrustaceans in the plant bed will be high, apart from a period during early summer before macrophyte density has become high. (Fig. 5.9B).
- In eutrophic lakes with low PVI, the pattern approaches the one suggested for hypereutrophic lakes (Fig. 5.9C).
- In meso-slightly eutrophic lakes, 0^+ fish seek refuge in the vegetation during mid-summer, and Whiteside's type A (bimodal) or C (unimodal with autumn maximum) response of microcrustacean density (see Fig. 5.7) can be observed, depending on whether the abundance of planktivorous fish (≥ 1 year) is low or high. Very high plant density (e.g., of characeans) may result in a response resembling that of eutrophic lakes. (Fig. 5.9D).
- In oligotrophic lakes, the refuge effect will often be low due to low plant height (Fig. 5.9E).

The patterns described cannot be applied to brackish lakes in northern Europe that deviate substantially in trophic structure and dynamics from freshwater lakes (Leah et al., 1978; Jeppesen et al., 1994, this volume, Chapter 31). Several factors indicate that the refuge effect for zooplankton in nutrient-rich brackish lakes is poor due to aggregation of both sticklebacks and *Neomysis* in the plant beds (Jeppesen et al., this volume, Chapter 31).

Future Research Needs

Although much new information has appeared during recent years about the impact of macrophytes on fish–zooplankton interactions, there are still several unclarified questions. We know that DHM does occur in lakes, but little is known about the distances covered by the zooplankton. This is interesting from a theoretical point of view, but it also has practical implications. As mentioned, the use of macrophyte implantations has been suggested as a restoration tool in lakes. To ensure optimum placement of these macrophyte enclosures to obtain the highest night-time grazing effect of zooplankton in the pelagic zone, more information on the potential migration distances is needed. Also, we know little about how the zooplankton find their way back from the pelagic to the plant-covered areas during the daytime. Moreover, it is unknown what the migration pattern would look like if zooplankton are influenced by both fish and invertebrate predators inhabiting spatially segregated areas (e.g., fish in the pelagic zone and odonates, water mites, etc., in the littoral zone). In addition, cost–benefit analyses are required. When will horizontal migration be cost-efficient and how do such estimates alter along a gradient in food supply and predation risk in the vegetation and the pelagic zone?

What influence does the size of the plant-filled areas have? To answer these questions, we suggest both intensive laboratory and field studies, including detailed studies of zooplankton population dynamics and the use of a modeling approach.

Most of the former studies of the interactions between fish, macrophytes, and zooplankton were undertaken with only one or two species of prey fish and typically one species of predatory fish. Because interactions between a given fish species and zooplankton may change in the presence of other species (Persson and Eklöv, 1995), there is a great need for multispecies experiments. A better insight into the interactions between fish and zooplankton also requires a more thorough knowledge of the feeding behavior of the various zooplanktivorous fish. This is crucial because it is not possible from data on distribution alone to determine where and when the interactions between fish and zooplankton are particularly strong.

It is necessary to undertake investigations under more natural conditions than hitherto has been the case. This means on a scale that allows horizontal migration for both zooplankton and fish (i.e., a large scale and whole-lake basis). Empirical studies of seasonal and diel variations in fish and zooplankton in the pelagic and littoral zones, with contrasting nutrient levels, fish communities, and macrophyte abundance and composition, may contribute to the understanding of natural interactions. Also, the inclusion of quantitative paleoecological investigations, including reconstruction of fish and submerged macrophytes (Jeppesen et al., 1996), will add to our understanding, and it may increase our knowledge about long-time perturbations, factors that are poorly elucidated from the existing short monitoring series and short-term enclosure and whole-lake experiments (Anderson, 1995). We need to know more about the role of plant-associated microcrustaceans and their interactions with zooplankton staying temporarily or permanently in the open water among the plants. Stable isotope (^{13}C and ^{15}N) analyses and grazing measurements on radio-labeled periphyton may be useful methods in such studies. Finally, there is a great need for studies of how density and composition of submerged macrophytes affect the interaction between fish, *Neomysis*, and zooplankton in brackish lakes.

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References

Anderson, N.J. Temporal scale, phytoplankton ecology and palaeoecology. Freshwat. Biol. 34:367–378; 1995.

Anderson, O. Optimal foraging by largemouth bass in structured environments. Ecology 65:851–861; 1984.

Bean, C.W.; Winfield, I.J. Habitat use and activity patterns of roach (*Rutilus rutilus*), rudd (*Scardinius erythrophtalmus* (L.)), perch (*Perca fluviatilis*) and pike (*Esox lucius*) in the laboratory: the role of predation threat and structural complexity. Ecol. Freshwat Fish 4:37–46; 1995.

Beklioglu, M.; Moss, B. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants with the structure of phytoplankton and zooplankton communities. Freshwat. Biol. 36:315–325; 1996.

Benndorf, J. Food web manipulation without nutrient control: a useful strategy in lake restoration? Schweiz. Z. Hydrol. 49:237–248; 1987.

Blois-Heulin, C.; Crowley, P.H.; Arrington, M.; Johnson, D.M. Direct and indirect effects of predators on the dominant invertebrates of two freshwater littoral communities. Oecologia 84:295–306; 1990.

Boikova, O.S. Horizontal distribution of crustaceans in Lake Glubokoe. Hydrobiologia 141:113–123; 1986.

Brooks, J.L.; Dodson, S.I. Predation, body size and composition of plankton. Science 150:28–35; 1965.

Carpenter, S.R.; Kitchell, J.F., eds. The trophic cascade in lakes. Cambridge: Cambridge University Press; 1993.

Carpenter, S.R.; Lodge, D.M. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26:341–370; 1986.

Carpenter, S.R.; Kitchell, J.F.; Hodgson, J.R. Cascading trophic interactions and lake productivity. BioScience 35:635–639; 1985.

Chambers, P.A.; Kalff, J. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 47:1929–1936; 1985.

Chick, J.H.; McIvor, C.C. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. Can. J. Fish. Aquat. Sci. 51:2873–2882; 1994.

Christoffersen, K.; Riemann, B.; Klysner, A.; Søndergaard, M. Potential role of zooplankton in structuring a plant community in eutrophic lake water. Limnol. Oceanogr. 38:561–573; 1993.

Crowder, L.B.; Cooper, W.E. Habitat structural complexity and the interaction between bluegill and their prey. Ecology 63:1802–1813; 1982.

Cryer, M.; Townsend, C.R. Spatial distribution of zooplankton in a shallow eutrophic lake, with a discussion of its relation to fish predation. J. Plankton Res. 10:487–501; 1988.

Cryer, M.; Pierson, G.; Townsend, C.R. Reciprocal interactions between roach *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. Limnol. Oceanogr. 31:1022–1038; 1986.

Cyr, H.; Downing, J.A. Empirical relationships of phytomacrofaunal abundance to plant biomass and macrophyte bed characteristics. Can. J. Fish. Aquat. Sci. 45:976–984; 1988.

Davies, J. Evidence for a diurnal horizontal migration in *Daphnia hyalina lacustris* Sars. Hydrobiologia 120:103–105; 1985.

De Bernardi, R.; Guisanni, G. Are blue-green algae suitable food for zooplankton? An overview. Hydrobiologia 200/201:29–41; 1990.

De Meester, L.; Maas, S.; Dierckens, K.; Dumont, H.J. Habitat selection of patchiness in *Scapholeberis:* horizontal distribution and migration of *S. mucronata* in a small pond. J. Plankton Res. 15:1129–1139; 1993.

DeMott, W.R. The role of taste in food selection by freshwater zooplankton. Oecologia 69:224–240; 1986.

De Stasio, B.T., Jr. Diel vertical and horizontal migration by zooplankton: population budgets and the diurnal deficit. Bull. Mar. Sci. 53:44–64; 1993.

Diehl, S. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53:207–214; 1988.

Dorgelo, J.; Heykoop, M. Avoidance of macrophytes by *Daphnia longispina*. Verh. Int. Verein. Limnol. 22:3369–3372; 1985.

Downing, J.A.; Plante, C.; Lalonde, S. Fish production correlated with primary productivity and the morphoedaphic index. Can. J. Fish. Aquat. Sci. 47:1929–1936; 1990.

Dusoge, K. The occurrence and role of the predatory larvae of Procladius Skuse (Chironomidae, Diptera) in the benthos of Lake Sniardy. Ekol. Pol. 28:155–186; 1980.

Engels, S. The role and interactions of submersed macrophytes in a shallow Wisconsin lake. J. Freshwat. Ecol. 4:329–340; 1988.

Evans, M.S.; Bethany, E.H.; Sell, D.W. Seasonal features of zooplankton assemblages in the nearshore area of southeastern Lake Michigan. J. Great Lakes Res. 6:275–289; 1980.

Geller, W.; Pinto-Coelho, R.; Pauli, H.-R. The vertical distribution of zooplankton (Crustacea, Rotatoria, Ciliata) and their grazing over the diurnal and seasonal cycles in Lake Constance. Arch. Hydrobiol. Beih. Ergebn. Limnol. 35:79–85; 1992.

Gliwicz, Z.M.; Jachner, A. Diel migration of juvenile fish: a ghost of predation past or present. Arch. Hydrobiol. 124:385–410; 1992.

Gliwicz, Z.M.; Rybak, J.I. Zooplankton. In: Pieczynska, E., ed. Selected problems of lake littoral ecology. Warsaw: University of Warsaw; 1976:69–96.

Grimm, M.P.; Backx, J.J.G.M. The restoration of shallow eutrophic lakes, and the role of northern pike, aquatic vegetation and nutrient concentration. Hydrobiologia 200/201: 557–566; 1990.

Gulati, R.D.; Lammens, E.H.R.R.; Meijer, M.-L.; van Donk, E. Biomanipulation tool for water management. Hydrobiologia 200/201:1–628; 1990.

Hanson, J.R.; Leggett, W.C. Empirical prediction of fish biomass and weight. Can. J. Fish. Aquat. Sci. 39:257–263; 1982.

Hasler, A.D.; Jones, E. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30:359–364; 1949.

He, X.; Wright, R. An experimental study of piscivore–planktivore interactions: population and community responses to predation. Can. J. Fish. Aquat. Sci. 49:1176–1185; 1992.

Hrbaček, J.; Dvorakova, M.; Korinek, M.; Prochazkova, L. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Int. Verein. Limnol. 14:192–195; 1961.

Hutchinson, G.E. A treatise on limnology II. New York: J. Wiley & Sons; 1967.

Irvine, K.; Moss, B.; Balls, H. The loss of submerged plants with eutrophication II. Relationships between fish and zooplankton in a set of experimental ponds, and conclusions. Freshwat. Biol. 22:89–107; 1989.

Jacobsen, L.; Perrow, M.R.; Landkildehus, F.; Hjørne, M.; Lauridsen, T.L.; Berg, S. Interactions between piscivores, zooplanktivores and zooplankton in submerged macrophytes: preliminary observations from enclosure and pond experiments. Hydrobiologia 342/343:197–205; 1997.

Jakobsen, P.J.; Johnsen, G.H. The influence of predation on horizontal distribution of zooplankton species. Freshwat. Biol. 17:501–507; 1987.

Jeppesen, E.; Jensen, J.P.; Kristensen, P.; Søndergaard, M.; Mortensen, E.; Sortkjær, O.; Olrik, K. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. 2: Threshold levels, long-term stability and conclusions. Hydrobiologia 200/201: 219–227; 1990.

Jeppesen, E.; Kristensen, P.; Jensen, J.P.; Søndergaard, M.; Mortensen, E.; Lauridsen, T.L. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. Mem. Ist. Ital. Idrobiol. 48:127–148; 1991.

Jeppesen, E.; Sortkjær, O.; Søndergaard, M.; Erlandsen, M. Impact of a trophic cascade on heterotrophic bacterioplankton production and biomass in two shallow fish-manipulated lakes. Arch. Hydrobiol. Ergebn. Limnol. 37:219–231; 1992.

Jeppesen, E.; Søndergaard, M.; Kanstrup, E.; Petersen, B.; Henriksen, R.B.; Hammershøj, M.; Mortensen, E.; Jensen, J.P.; Have, A. Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia 275/276: 15–30; 1994.

Jeppesen, E.; Agerbo Madsen, E.; Jensen, J.P.; Anderson, N.J. Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibration data set from shallow lakes. Freshwat. Biol. 36:115–127; 1996.

Jeppesen, E.; Jensen, J.P.; Søndergaard, M.; Lauridsen, T.; Pedersen, L.J.; Jensen, L. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342/343:151–164; 1997.

Johnson, D.M.; Pierce, C.L.; Martin, T.H.; Watson, C.N.; Bohanan, R.E.; Crowley, P.H. Prey depletion by odonate larvae: combining evidence from multiple field experiments. Ecology 68:1459–1465; 1987.

Jürgens, K. Impact of *Daphnia* on planktonic microbial food webs—a review. Microb. Food Webs 8:295–324; 1994.

Kairesalo, T. Diurnal fluctuations within a littoral plankton community in oligotrophic Lake Pääjärvi, southern Finland. Freshwat. Biol. 10:533–537; 1980.

Kairesalo, T.; Penttilä, S. Effect of light and water flow on the spatial distribution of littoral *Bosmina longispina* Leydig (Cladocera). Verh. Int. Verein. Limnol. 24:682–687; 1990.

Kairesalo, T.; Tátrai, I.; Luokkanen, E. Impacts of waterweed (*Elodea canadensis* Michx) on plankton-fish interactions in lake littoral. Verh. Int. Verein. Limnol. (in press).

Kajak, Z.; Dusoge, K.; Stanczykowska, A. Influence of mutual relations of organisms, especially Chironomidae, in natural benthic communities, on their abundance. Ann. Zool. Fenn. 5:49–56; 1968.

Kleiven, O.T.; Larssen, P.; Hobæk, A. Direct distributional response in *Daphnia pulex* to a predator kairomone. J. Plankton Res. 18:1341–1348; 1996.

Kvam, O.V.; Kleiven, O.T. Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. Hydrobiologia 307:177–184; 1995.

Lampert, W. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39:79–88; 1993.

Lauridsen, T.L.; Buenk, I. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. Arch. Hydrobiol. 137:161–176; 1996.

Lauridsen, T.L.; Lodge, D. Avoidance by *Daphnia magna* fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. Limnol. Oceanogr. 41:794–798; 1996.

Lauridsen, T.L.; Pedersen, L.J.; Jeppesen, E.; Søndergaard, M. The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. J. Plankton Res. 18:2283–2294; 1996.

Leah, R.T.; Moss, B.; Forrest, D.E. Experiments with large snails in a fertile, shallow, brackish lake. Hickling Broad, United Kingdom. Int. Rev. Ges. Hydrobiol. 63:291–310; 1978.

Lehtovaara, A.; Sarvala, J. Seasonal dynamics of total biomass and species composition of zooplankton in the littoral of an oligotrophic lake. Verh. Int. Verein. Limnol. 22:805–810; 1984.

Leibold, M.A. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. Am. Nat. 134:922–949; 1990.

Luecke, C.; Vanni, M.J.; Magnuson, J.J.; Kitchell, J.F.; Jacobson, P.J. Seasonal regulation of *Daphnia* populations by planktivorous fish: implications for the clearwater phase. Limnol. Oceanogr. 35:1718–1733, 1990.

McQueen, D.J.; Post, J.R.; Mills, E.L. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43:1571–1581; 1986.

Meyers, D.G. Diurnal vertical migration in aquatic microcrustaceans: light and oxygen responses of littoral zooplankton. In: Kerfoot, W.C., ed. Evolution and ecology of zooplankton communities. Hanover, NH: University Press of New England; 1980: 80–90.

Mills, E.L.; Forney, J.L.; Wagner, K.J. Fish predation and its cascading effect on the Oneida Lake food chain. In: Kerfoot, W.C.; Sih, A., eds. Predation: direct and indirect effects on aquatic communities. Hanover, NH: University Press of New England; 1987:118–131.

Moss, B. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201:367–378; 1990.

Moss, B.; McGowan, S.; Carvalho, L. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland Meres. Limnol. Oceanogr. 39:1020–1029; 1994.

Moss, B.; Beklioglu, M.; Carvalho, L.; Kilinc, S.; McGowan, S.; Stephen, D. Vertically challenged limnology: contrasts between deep and shallow lakes. Hydrobiologia 342/343:257–267; 1997.

Ogilvie, S.H.; Mitchell, S.F. A model of mussel filtration in a shallow New Zealand lake, with reference to eutrophication control. Arch. Hydrobiol. 133:471–482; 1995.

Paterson, M. The distribution of microcrustacea in the littoral zone of a freshwater lake. Hydrobiologia 263:173–183; 1993.

Paterson, M. Invertebrate predation and seasonal dynamics of microcrustaceans in the littoral zone of a fishless lake. Arch. Hydrobiol. 99:1–36; 1994.

Pennak, R.W. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. Trans. Am. Microsc. Soc. 85:329–349; 1966.

Pennak, R.W. Some evidence for aquatic macrophytes as repellents for a limnetic species of *Daphnia*. Int. Rev. Ges. Hydrobiol. 58:569–576; 1973.

Persson, L. Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. Oikos 68:12–22; 1993.

Persson, L.; Eklöv, P. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76:763–784; 1995.

Persson, L.; Anderson, G.; Hamrin, S.F.; Johansson, L. Predation regulation and primary production along the productivity gradient of temperature lake ecosystems. In: Carpenter, S.R., ed. Complex interactions in lake communities. New York: Springer-Verlag; 1988:45–65.

Persson, L.; Diehl, S.; Johanson, L.; Andersson, G.; Hamrin, S.F. Shifts in fish communities along the productivity gradient of temperate lake-patterns and the importance of size-structured populations. J. Fish Biol. 38:281–293; 1991.

Phillips, G.L.; Perrow, M.R.; Stansfield, J. Manipulating the fish–zooplankton interaction in shallow lakes: a tool for restoration. In: Greenstreet, S.P.R.; Tasker, M.L., eds. Aquatic predators and their prey. Oxford: Blackwell Scientific Publications; 1996:174–183.

Ringelberg, J. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). J. Plankton Res. 13:17–25; 1991.

Sarnelle, O. Nutrient enrichment and grazer effects of phytoplankton in lakes. Ecology 73:551–560; 1992.

Savino, J.; Stein, R.A. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111:255–266; 1982.

Schriver, P.; Bøgestrand, J.; Jeppesen, E.; Søndergaard, M. Impact of submerged macrophytes on the interactions between fish, zooplankton and phytoplankton: large-scale enclosure experiments in a shallow lake. Freshwat. Biol. 33:255–270; 1995.

Shapiro, J.; Lamarra, V.; Lynch, M. Biomanipulation: an ecosystem approach to lake restoration. In: Brezonik, P.L.; Fox, J.F., eds. Water quality management through biological control. Gainesville, FL: University of Florida; 1975:85–96.

Siebeck, O. Spatial orientation of planktonic crustaceans. 1. The swimming behaviour on a horizontal plane. Verh. Int. Verein. Limnol. 17:831–840; 1969.

Siebeck, O. Optical orientation of pelagic crustaceans and its consequence in the pelagic and the littoral zones. In: Kerfoot, W.C., ed. Evolution and ecology of zooplankton communities. Hanover, NH: University Press of New England; 1980:28–38.

Søndergaard, M.; Jeppesen, E.; Berg, S. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 2. Effects on lower trophic levels in lake Lyng (Denmark). Hydrobiologia 342/343:319–325; 1997.

Stansfield, J.H.; Perrow, M.R.; Tench, L.D.; Jowitt, A.J.D.; Taylor, A.A.L. Submerged macrophytes as refuges for grazing *Cladocera* against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. Hydrobiologia 342/343:229–240; 1997.

Straskraba, M.; Pieczynska, E. Field experiments on shading effect by emergents on littoral phytoplankton and periphyton production. Rozpravy Ceskoslovenské Akademie Vêd. ĺada Matematickych a Píirodnich Vêd. 80:7–30; 1970.

Szlauer, L. Diurnal migrations of minute invertebrates inhabiting the zone of submerged hydrophytes in a lake. Schweiz. A. Hydrol. 25:56–64; 1963.

Timms, R.M.; Moss, B. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceanogr. 29:472–486; 1984.

Timson, S.; Laybourn-Parry, J. The behavioural responses and tolerance of freshwater benthic cyclopoid copepods to hypoxia and anoxia. Hydrobiologia 127:257–263; 1985.

Venugopal, M.N.; Winfield, I.J. The distribution of juvenile fishes in a hypereutrophic pond: can macrophytes potentially offer a refuge for zooplankton? J. Freshwat. Ecol. 8:389–396; 1993.

von Elert, E.; Loose, C.J. Predator-induced diel vertical migration in *Daphnia:* enrichment and preliminary chemical characterization of a kairomone exuded by fish. J. Chem. Ecol. 22:885–895; 1996.

Vuille, T. Abundance, standing crop and production of microcrustacean populations (*Cladocera, Copepoda*) in the littoral zone of Lake Biel, Switzerland. Arch. Hydrobiol. 123:165–185; 1991.

Vuille, T.; Maurer, V. Body mass of crustacean zooplankton in Lake Biel: a comparison between pelagic and littoral communities. Verh. Int. Verein. Limnol. 24:938–942; 1991.

Walls, M.; Rajasilta, M.; Sarvala, J.; Salo, J. Diel changes in horizontal microdistribution of littoral cladocera. Limnologica 20:253–258; 1990.

Werner, E.E.; Gilliam, J.F.; Hall, D.J.; Mittelbach, G.G. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548; 1983.

Wetzel, R.G. Limnology. Philadelphia: W.B. Saunders; 1975.

Whiteside, M.C. Chydorid (*Cladocera*) ecology: seasonal patterns and abundance of populations in Elk Lake, Minnesota. Ecology 55:538–550; 1974.

Whiteside, M.C. 0^+ fish as major factors affecting abundance patterns of littoral zooplankton. Verh. Int. Verein. Limnol. 23:1710–1714; 1988.

Winfield, I.J. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. J. Fish Biol. 29:37–48; 1986.

Submitted

Cascading trophic interactions in the littoral zone of a shallow lake

Erik Jeppesen(1), Martin Søndergaard(1), Morten Søndergaard(2), Kirsten Christoffersen(2), Jon Theil-Nielsen(2), Klaus Jürgens(3); Susanne Bosselmann(2) and Louise Schlüter(4)

(1) National Environmental Research Institute, Vejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark
(2) The Freshwater Biological Laboratory, University of Copenhagen, Helsingørsgade 51, DK-3400 Hillerød, Denmark
(3) Max-Planck Institute for Limnology, P.O. Box 165, 24302 Plön, Germany
(4) Water Quality Institute, Agern Allé 11, DK-2970 Hørsholm, Denmark

Abstract

1. The influence of submerged macrophyte density on trophic structure and interactions was elucidated in a series of diel studies in 20 m^2 enclosures established in the littoral zone of a shallow eutrophic lake. The experiment was conducted at two different plant densities (24% and 50% plant volume infested, PVI) of *Potamogeton* spp., and in plant-free controls. The experimental design allowed approximate natural fish densities differing among treatments. 0^+ perch (*Perca fluviatilis*) and 0^+ and 1^+ roach (*Rutilus rutilus*) were abundant (2.5-4 m^{-2}) at low PVI and in the controls and scarce (0-0.2 m^{-2}) at high PVI.

2. In the plant-free controls and at low PVI , the zooplankton were dominated by rotifers and cyclopoid copepods, while the density of *Daphnia* spp. was # 8 l^{-1} as a diel average for the study period. Zooplankton clearance of phytoplankton and bacterioplankton was low (<54 ml l^{-1} d^{-1}), and chlorophyll *a* and the abundance of ciliates, heterotrophic nanoflagellates (HNF), bacterioplankton and picoalgae were high. At high PVI large-sized zooplankton dominated, the average density of *Daphnia* spp. being 160 indiv. l^{-1}. Likewise, the zooplankton clearance rate of phytoplankton and bacterioplankton increased substantially to 2200-3000 ml l^{-1} d^{-1} and accordingly chlorophyll *a* and the abundance of ciliates, HNF and bacterioplankton decreased to 25%, 1.4%, 25% and 33%, respectively, of the level in the plant-free enclosures.

3. Addition of 0^+ perch (4 m^{-2}) to the high PVI enclosures tended to shift the trophic structure in direction of small-sized zooplankton and higher chlorophyll *a*, indicating that it is the naturally low fish density that determines the dominance by large-sized zooplankter and the high clearance rates at high PVI.

4. Despite a low water depth of 0.6 m, density of large-sized zooplankton was substantially higher at night, particularly when fish were abundant and the plant density low. No diel variation was found for cyclopoid nauplii and rotifers. Large-sized zooplankton apparently sought refuges during day at the sediment surface and maybe also close to the plant surfaces.

5. We conclude that plant density-dependent variations in fish abundance may have a substantial effect on the efficacy of plant beds as a refuge for zooplankton and consequently on the entire pelagic food web structure and dynamics in the littoral zone of eutrophic lakes.

Introduction

Several studies have shown that alterations in the pelagic fish community may cascade down the food-web to phytoplankton (e.g. Carpenter, Kitchell & Hodgson, 1985; Carpenter & Kitchell 1993, Gulati et al. 1990), protozoans and bacterioplankton (Pace & Funke 1991; Pace 1993; Christoffersen et al. 1993). McQueen et al. (1986) forwarded the hypothesis that the cascading effect is particularly strong in oligotrophic lakes. A number of recent studies suggest, however, that the effect may be more significant in eutrophic and hyper-eutrophic lakes for both the phytoplankton (Leibold 1989; Sarnelle 1992; Jeppesen et al. 1997) and the microbial community (Riemann 1985; Christoffersen et al. 1993, Jürgens 1994). In addition, the cascading effect seems to be particularly strong in shallow lakes (e.g. Gulati et al. 1990; Jeppesen et al. 1997).

Submerged macrophytes may significantly alter the top-down control in shallow lakes. In Northern European lakes the presence of plants may favour piscivorous perch (*Perca fluviatilis*) and pike (*Esox lucius*) over plankti-benthivorous roach (*Rutilus rutilus*) and bream (*Abramis bream*) (Persson 1991). Predator control of planktivorous fish releases the predation on zooplankton (Jeppesen et al. 1997). In addition, the plants may act as a refuge for zooplankton against predators during the day (Timms & Moss 1984; Lauridsen et al. 1996), thereby enhancing survival of large-bodied zooplankton. Via their night-time migration to open water (Lauridsen et al. 1996) zooplankters may contribute to an overall higher grazing pressure on open-water phytoplankton than if macrophytes were absent (Lauridsen et al. 1996; Jeppesen et al. 1998). Young fish may, however, also use submerged macrophytes as a refuge against predators (e.g. Savino & Stein 1982; Werner et al. 1983; Persson & Eklöv 1995). The prey fish often prefer sparse plant beds (Engels 1988; Phillips, Perrow & Stansfield, 1996; Stansfield et al. 1997; Jeppesen et al. 1997), probably reflecting the fact that foraging efficiency of many fish species decreases with increasing structural complexity (e.g. Savino and Stein 1982; Anderson 1984). Predator fish density may, however, become so high that prey fish seek refuge in the most dense vegetation (Jacobsen et al. unpubl.), thereby reducing the efficiency of the plants as a refuge for zooplankton and plant-associated cladocerans, seemingly in a step-wise manner when a certain fish threshold is reached (Schriver et al. 1995; Phillips, Perrow & Stansfield, 1996; Stansfield et al. 1997). How the fish density threshold for loss of zooplankton refuge depends on habitat structure, plant and fish composition are, however, virtually unknown (Jeppesen et al. 1998).

The major daytime aggregation of zooplankton in dense plant beds in lakes with high density of planktivorous fish and low percentage of piscivores (Jeppesen et al. 1998) suggest that grazing may be intensive in the beds. Correspondingly, Schriver et al. (1995) found that the zooplankton:phytoplankton biomass ratio was much higher within dense macrophyte beds than in open water if fish density in the plant beds was low. Likewise, Moss, McGowan & Carvalho (1994) found a high zooplankton:phytoplankton biomass ratio in macrophyte-rich lakes. Apart from zooplankton, the plant beds also host a number of plant-associated filter-feeding crustaceans and benthic invertebrates (e.g. molluscs) that may contribute to low phytoplankton densities (e.g. Ogilvie & Mitchell 1996). It can therefore be hypothesized that grazer control of phytoplankton, and probably also of protozoans and bacterioplankton, have the potential of being particularly strong in dense plant beds.

Until now only few studies have dealt with how fish-macrophytes relations affect the trophic structure in plant beds, and none has included both the classic and the microbial food webs or measured the grazing rates. In this study we have looked at the trophic interactions at contrasting densities of submerged macrophytes and fish in the littoral zone of shallow, eutrophic Lake Stigsholm (Denmark). We demonstrate that variations in zooplankton abundance and size composition may have substantial effects on phytoplankton, protozoans and bacterioplankton in dense macrophyte beds, the effect being considerably lower in sparse beds and macrophyte-free patches. We argue that this difference is most likely determined by differences in fish abundance. In related papers, Søndergaard et al. (1998) discuss bacterioplankton dynamics and carbon sources and Jürgens and Jeppesen (1998) the structuring impact of zooplankton on the microbial food web based on size fractionation experiments.

Study area

The study was conducted in July-August 1993 and 1994 in eutrophic Lake Stigsholm, Central Jutland, Denmark. The surface area of the lake is 21 ha and its maximum and mean depth are 1.2 and 0.8 m, respectively. Mean total P was 100 μg P l^{-1} during May to October in 1993 and 1994, while the corresponding figures for total N and chlorophyll *a* were 1.6 mg l^{-1} and 46 μg l^{-1}, respectively. Summer mean Secchi depth was 0.86 m in 1993 and 0.89 m in 1994, and maximum areal coverage of submerged macrophytes at biomass maximum was 5.8% in 1993 and 2.1% in 1994.

Materials and methods

Four enclosures with a diameter of 5 m were established in April 1993 and six in May 1994 approx. 20 m from the shore at a mean water depth of 0.6 m. The enclosures were made by moveable polyethylene sheets that were kept in place at the bottom by a steel ring and fixed at the top to another steel ring mounted on poles. A moveable ladder with runners fixed to a pole in the centre of the enclosure and running on the steel ring allowed sampling all over the enclosures without disturbance. An outer polyethylene sheet (diameter 10 m) with a sewn-in iron ring (5 kg m^{-2}) supported by sixteen wooden poles served as protection against waves and undermining. The inner and outer sheets were mounted above the water surface on a releasable loop allowing full exchange of water with the surroundings prior to the experiment. Every second enclosure was kept free from plants by frequent manual harvesting, while plants were allowed to grow in the other enclosures.

In late July 1993, the inner sheets were lowered 3 h before the first sampling was undertaken by releasing the loop at a distance of 5 m to avoid disturbance of fish. Sampling was conducted once during day and night for three days in two enclosures with and two without plants (at 1-2 p.m. and 1-2 a.m., respectively). At the end of the 1993 experiments (in the following termed E2) fish densities in the enclosures were estimated using transparent perspex traps (Breder 1960). Five traps were placed randomly in each enclosure from 8 to 12 a.m. The catches were converted to no. m^{-2} using a relationship between the average catch per trap and absolute density measurements based on repeated seine nettings and electrofishing undertaken as part of an experiment conducted in the same lake area in the weeks following our experiment (L. Jacobsen unpublished results). The calculated density per m^{-2} of perch and roach (mainly 0^+ and a few 1^+) averaged 4.1 ± 2 (SE) m^{-2} in the plant-free and 2.5 ± 0 m^{-2} in the plant-filled enclosures.

In late July 1994, the inner sheet was lowered 2 days before the experiment and all fish were removed by electrofishing and trapping. The before density of 0^+ and 1^+ perch and roach (*Rutilus rutilus*) amounted to a total of 0.1 ± 0.1 (SE) m^{-2} in the enclosures with plants and to 3.7 ± 2.5 m^{-2} in the plant-free enclosures. Sampling was conducted for 9 days. After 6 days, 0^+ perch (*Perca fluviatilis*) (4 m^{-2}) were added to each enclosure. The fish were pre-adapted in a net cage in the lake. In the following this experiment is termed E1.

Water samples were collected randomly with a core sampler (diameter = 7.4 cm) covering the entire water column except the lower 3 cm. Ten to fifteen samples from each enclosure were pooled in a plastic container (~ 40 l). A subsequent subsampling included: 5-6 l for zooplankton, 100 ml for phytoplankton and ciliates and 20 ml for heterotrophic nanoflagellates (HNF), picoalgae and bacterioplankton analyses. The zooplankton samples were filtered on a 20 µm filter and fixed with Lugol's solution. Phytoplankton and ciliates samples were fixed with Lugol's solution without filtration. Samples for HNF, picoalgae and bacterioplankton analyses were fixed in glutaraldehyde (1.5% final concentration) and stained with DAPI within 24 h and subsequently filtered onto 0.8 µm and 0.2 µm black membrane filters, respectively. The filters were kept frozen (-20° C) until the counting.

Phytoplankton were identified to genus or species level and counted using an inverted microscope. The biomass was calculated by fitting each taxon to simple geometric figures. Chlorophyll *a* (>50 µm) was measured in triplicates from the composite water samples after ethanol extraction (Jespersen & Christoffersen 1987) and converted to carbon using 30 mg C (mg chlorophyll $a)^{-1}$. At least 100 individuals of the dominant zooplankton species were counted at 40-100x magnification on each sampling date. The biomass was estimated from length-weight measurements of 50 individuals of each species based on formula in Botrell et al. (1976) and Culver et al. (1985). Copepods were separated into nauplii, copepodids, males and females.

Ciliates were counted using the Utermöhl technique, and HNF and picoalgae in an epifluorescence microscope fitted with a UV filter and a blue filter, respectively. Only 2-10 µm HNF were considered and at least 50 cells were counted from each filter. Linear dimensions were measured and converted to cell volumes using standard geometric formulae and to carbon using 0.154 pg C μm^{-3} (Geller & Müller 1993) for ciliates, 0.12 pg C μm^{-3} for HNF (Hansen & Christoffersen 1995) and 0.24 pg C μm^{-3} for picoalgae (Reynolds 1983) assuming a cell diameter of 1.5 mm. Bacterioplankton was counted by epifluorescence microscopy after DAPI staining. At least 500 cells were counted. Individual bacterial cells (at least 25) were sized from enlarged micrographs and the biovolume was calculated as spheres or rods with hemispheres and converted to biomass using the factor 0.10 pg C μm^{-3} (Theil-Nielsen & Søndergaard submitted). In 1993, bacterial production was measured with the leucine method (Simon & Azam 1989) and converted to carbon by 3.1 µg C mol^{-1} (Kirchman 1993). As saturation in leucine uptake at the added concentration (200 nM) was not present in all samples, the thymidine method (Furhman & Azam 1980) was used in 1994. ^{3}H-thymidine was added to a final and saturating concentration of 20 nM, incubated for 30 minutes and stopped with TCA (5% final conc.). Cell production was calculated using the empirical factor 2×10^{18} cells (mol thymidine)$^{-1}$ (Smits & Riemann 1988) and converted to carbon using mean volume and 0.1 pg C μm^{-3}.

Phytoplankton production corrected for dark fixation was estimated from ^{14}C-photosynthesis-irradiance relationships determined on the basis of laboratory incubation and interpolated over depth and time using observations of chlorophyll *a* (converted to a light extinction coefficient) and surface radiation data from a nearby station. In the calculations, we did not account for light attenuation by macrophytes so the calculated production for the macrophyte enclosure may be somewhat overestimated.

The zooplankton clearance rates of phytoplankton and bacterioplankton were determined using an *in vitro* grazing method described in detail by Jeppesen et al. (1996). Briefly, water samples from enclosures with and without plants (treated separately) were first filtered through a 50 µm mesh net to remove zooplankton and then incubated with either [^{14}C] bicarbonate $NaOH^{14}CO_3$ or [^{3}H] methyl-thymidine at *in situ* temperatures for 4 h in daylight (phytoplankton) or 2-3 h in darkness (bacterioplankton) and then re-filtered through 50 µm mesh nets. Labelled samples were then mixed with the composite water samples (5 replicates) from each enclosure and incubated *in vitro* for 10 min and subsequently filtered through a 140 µm net and, in one of the experiments, also through a 50 µm net. Five samples were used as 'time zero' controls.

Grazing by heterotrophic nanoflagellates (HNF) on bacteria was measured according to Christoffersen (1994) using fluorescently labelled bacteria (FLB).

Table 1: Some key variables (mean ± SD) for the first 3 diel periods in the high PVI-experiment in 1994 (E1) and low PVI-experiment in 1993 (E2) (+ with and - without macrophytes). Also shown are the results of a repeated measures ANOVA testing of differences between plant-containing and plant-free enclosures with time as repeated variable. *,**,*** represent $p<0.05$, $p<0.01$ and $p<0.001$, respectively. N.D. = no data. N.S. = not significant. - no tests performed.

	E1-	E1+	E2-	E2+	E1-:E1+	E2-:E2+
Zooplankton						
Daphnia spp. (no l^{-1})	1.3±0.9	160±60	2±1	8±8	***	N.S.
Ceriodaphnia (no l^{-1})	0.8±0.4	286±177	10±4	30±24	*	*
Diaphanosoma (no l^{-1})	1.3±1.4	20±7	0.2±0.2	3±3	**	*
Bosmina (no l^{-1})	0.3±0.5	0	18±3	12±2	*	*
Other cladocerans (no l^{-1})	0.8±0.2	46±24	10±2	19±10	***	*
Cyclopoid copepods (no l^{-1})	328±12	1296±622	176±15	277±70	**	**
Rotifers (no l^{-1})	17856±2791	300±37	8380±3481	7461±148	***	N.S.
Total biomass (µg C l^{-1})	170±12	1350±415	83±26	130±35	***	N.S.
Ciliates						
Abundance (no l^{-1} x 10^3)	236±40	3.2±0.2	139	195	***	N.S.
Mean volume (µm^3 cell^{-1})	4247±439	8877±2080	4619±226	4157±249	**	N.S.
Heterotrophic nanoflagellates (HNF)						
Abundance (no l^{-1} x 10^3)	1940±442	499±105	2910±14	2495±332	***	*
Mean volume (µm^3 cell^{-1})	25±6	17±4	48±9	30±7	**	N.S.
Bacterioplankton						
Abundance (cells ml^{-1} 10^6)	24±1.5	8.4±1.6	14±3	8.8±0.5	*	N.S.
Production (µg C l^{-1} d^{-1})	117	126	71±29	73±14	**	N.S.
Mean volume (µm^3)	0.058±0.005	0.061±0.011	0.324±0.129	0.335±0.120	N.S.	N.S.
Phytoplankton						
Chlorophyll *a* < 50 µm (µg l^{-1})	35±9	9.5±4.2	32±2	50±3	***	***
% > 20 µm, < 50 µm	36±18	10±5	N.D.	N.D.	-	-
% 2-20 µm	27±8	60±23	N.D.	N.D.	-	-
% < 2 µm	36±23	30±18	43±3	38±2	-	-
Picoalgae (µg C l^{-1})	4.4	1.0	8.5	8.1	-	-
Total production (µg C l^{-1} d^{-1})	879±205	223±99	838±68	1374±45	**	***

Briefly described, bacteria from Lake Stigsholm were concentrated by reverse filtration and incubated with 5-(5-,6-dichlorotriazin-2-yl) aminofluorescein (DTAF) for 2 hours at 50°C. The suspension was centrifuged and washed with phosphate-buffered saline solution, sonicated and finally filtered through a membrane filter to remove large aggregations. Grazing experiments were performed *in situ* using 20 ml water samples incubated with FLB. The final concentration of FLB was kept at approx. 5% of the natural bacterial abundance. The 1993 grazing experiments were based on fixed grazing periods of 0 and 15 min., while the 1994 experiments were based on time series (0 to 30 min). Grazing was terminated by adding acid Lugol's solution (0.03% final concentration) and subsequently glutaraldehyde (1.25% final concentration) and thiosulphate (0.015% final concentration). The samples were filtered within 24 h and stored and analyzed according to Christoffersen (1994).

In each sampling period, percent coverage of submerged macrophytes and plant height were measured. Coverage was measured at 50 cm intervals along 8 transects running from the centre of the enclosures to the edge (80 points) by means of a water glass with a diameter of 0.3 m. Macrophyte density was expressed as PVI (Canfield et al. 1984) - in our study calculated as the product of the per cent coverage and plant height divided by the water depth at each measuring point. The dominant macrophytes were *Potamogeton pectinatus, P. pusillus* and *P. berchtoldii.*

We concentrated our data analysis on the three diel periods of 1993 and the first 3 diel periods before and the first two after the perch stocking in 1994, i.e. the days when both daytime and night-time sampling was undertaken. To test for differences in abundance of pelagic biota and process rates in enclosures with and without submerged macrophytes, we used repeated measures ANOVA with time as repeated variable. To test for differences in diel variations in abundance of various zooplankton, we used ANOVA on night/(night+day) ratios where night and day represented averages for the different sampling periods.

Results

Biological structure and processes at high macrophyte density (E1, 1994 experiments).

In the macrophyte enclosures, per cent volume infested (PVI) was 50±3% (mean ± SE, n=3). Substantial differences were found in the pelagic community structure in enclosures with (E1+) and without (E1-) submerged macrophytes from the first day and until 0^+ perch were stocked six days later (Fig. 1; Table 1). Within the plant beds, the zooplankton community was dominated by large forms. The density of *Daphnia* spp. (mainly *D. galeata* and *D. hyalina*), other cladocerans (mainly *Ceriodaphnia* spp. and *Diaphanosoma brachyurum*) and cyclopoid copepods were 120-, 110- and 60-fold higher than in the controls, while rotifer density was 60-fold higher in E1-. Total zooplankton biomass averaged 1.35 mg C l^{-1} in E1+ and 0.17 mg C l^{-1} in E1- (Fig. 2), reflecting differences in both abundance (Fig. 1, Table 1) and the individual biomass of the various crustaceans, the highest per capita biomass being found in E1+ (data not shown).

The consequence of the major difference in zooplankton were reflected in phytoplankton and the microbial community. Chlorophyll *a* was 4.4-fold higher (35 mg l^{-1}) in E1-. The three selected size-classes of phytoplankton were evenly represented in E1-, while intermediate-sized phytoplankton (2-20 µm) and picoalgae (< 2 µm) dominated in E1+ (Table 1). The densities of ciliates, HNF and bacterioplankton in E1- were 74-, 3.9- and 2.9-fold higher than in E1+. In addition, the mean volume of ciliates was 2.2-fold larger in E1+ (8,877 µm^3 indiv.$^{-1}$), while that of HNF was 1.5-fold larger in E1- (25 µm^3 indiv.$^{-1}$). No significant differences in bacterioplankton mean volume were found, the average being 0.059 µm^3 cell $^{-1}$.

These results suggest a substantially stronger cascading effect of zooplankton on phytoplankton and the microbial community in E1+ than in E1-, which was supported by the grazing experiments (Fig. 3; Table 2). The zooplankton (>140 µm) mean clearance rates on phytoplankton and bacterioplankton were 3027 and 2192 ml l^{-1} d^{-1} in E1+, respectively, which were 56- and 99-fold higher than in E1-. Assuming that zooplankton grazed the different size classes of phytoplankton <50 µm non-selectively, phytoplankton ingestion was 3.8 times higher than phytoplankton production in E1+ and only 7%

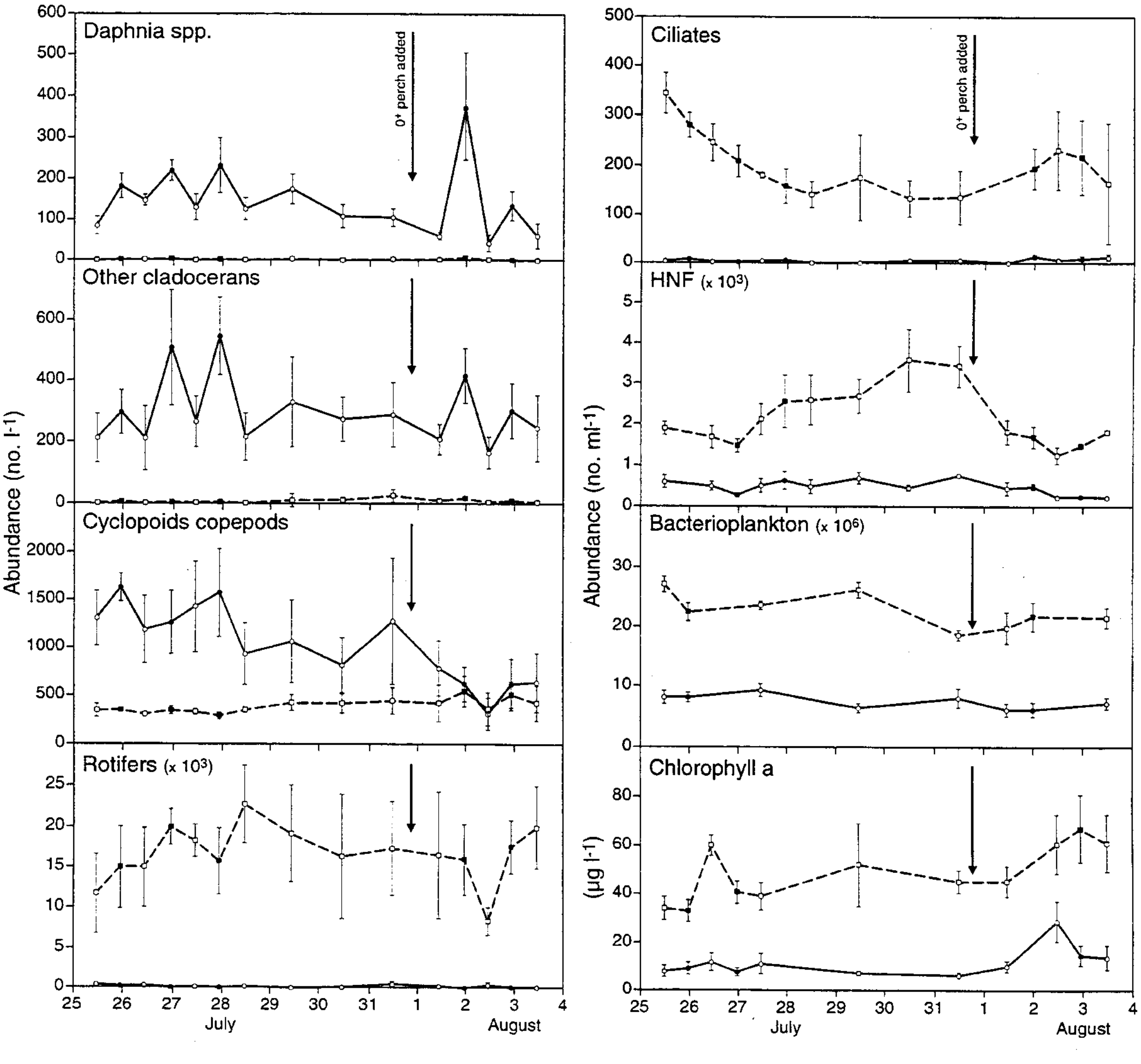

Fig. 1. Experiment 1 (E1) showing mean ± SE (n = 3) of various biological variables in enclosures with (PVI = 50%, E1+) and without (E1-) submerged macrophytes - before and after the stocking of 0+ perch (*Perca fluviatilis*) (4 m^{-2}). Dark and open symbols indicate night and day samples, respectively.

Table 2: Mean ±SD of key processes for the first diel period of the high PVI-experiment in 1994 (E1) and for the first 3 diel periods of the low PVI-experiment in 1993 (E2). Daily ration is the daily amount ingested in percentage of zooplankton and HNF (heterotrophic nanoflagellates) biomass, respectively. See also the legend of Table 1.

	E1-	E1+	E2-	E2+	E1-:E1+	E2-:E2+
Zooplankton (>140 µm) grazing						
Bacterioplankton						
Clearance (ml l^{-1} d^{-1})	22±5	2192±493	27±2	49±21	***	N.S.
Ingestion (µg C l^{-1} d^{-1})	3	114	12	14	-	-
% of bacterioplankton production	3	90	17	19	-	-
Daily ration (%)	4	9	26	13	-	-
Phytoplankton						
Clearance (ml l^{-1} d^{-1})	54±38	3027±1036	25±6	41±18	***	N.S.
Ingestion (µg C l^{-1} d^{-1})	57	863	25	64	-	-
% of phytoplankton production	7	387	3	5	-	-
Daily ration (%)	77	71	81	80	-	-
Heterotrophic nanoflagellate grazing						
Bacterioplankton						
Clearance (ml l^{-1} d^{-1})	127	39	178	143	*	*
Ingestion (µg C l^{-1} d^{-1})	18	2	82	41	-	-
% of bacterioplankton production	15	2	115	56	-	-
Picoplankton						
Clearance (ml l^{-1} d^{-1})	N.D.	N.D.	690	500	***	N.S.
Ingestion (µg C l^{-1} d^{-1})	N.D.	N.D.	6	4	-	-

of the production in E1-. Zooplankton ingestion of bacterioplankton was approximately similar to bacterioplankton production in E1 and only 2.5% of the production in E1-. Total estimated daily ingestion of phytoplankton plus bacterioplankton by zooplankton >140 µm in per cent of their biomass (in the following termed "daily ration") equalled 81% in E1- and 80% in E1+, respectively (Table 2).

HNF clearance of bacterioplankton was 127 ml l^{-1} d^{-1} in E1- and significantly lower in E1+ (39 ml l^{-1} d^{-1}) (Table 2). The rate was six times higher than the corresponding rates for zooplankton >140 µm in E1- and only 2% of the zooplankton clearance rate in E1+. HNF ingested 13% of the bacterioplankton biomass d^{-1} in E1- and 4% in E1+.

Effects of 0^+ perch stocking at high macrophyte density (1994 experiment).

In both E1+ and E1-, there was a tendency towards a decline over time in the densities of *Daphnia* and cyclopoid copepods when stocking 0^+ perch (4 m^{-2}) (Fig. 1). Accordingly, macrozooplankton (>140 µm) clearance of phytoplankton and bacterioplankton showed a decreasing trend (Fig. 3). Ciliates and chlorophyll *a* showed an increasing trend, while HNF decreased in both E1+ and E1-. No changes seemed to occur in the abundance of bacterioplankton. The duration of the period after stocking perch was too short to allow statistical tests on changes.

During this part of the experiment we also measured clearance of phytoplankton and bacterioplankton by small zooplankton (50 - 140 µm) in rotifer-dominated E1-, the values being 143 ml l^{-1} d^{-1} (phytoplankton) and 28 ml l^{-1} d^{-1} (bacterioplankton), respectively. The total estimated ingestion of phytoplankton and bacterioplankton by zooplankton >50 µm in E1 corresponded to 25% of the phytoplankton production and 11% of the bacterioplankton production. Including the small zooplankton fraction (50-140 µm) total grazing thus increased considerably in E1-, although it far from reached the clearance rates of large-sized zooplankton in E1+.

Biological structure and grazing at low macrophyte density (E2, 1993 experiment).

The plant volume infested was 24±2% (mean ± SE, n=2) in E2+. Only minor differences were found in biota and processes between E2 and E2+ The trophic structure in both E2+ and E2- was comparable to that of the plant-free enclosures in E1, and accordingly deviated substantially from the one of E1+ (Fig. 4 and 5; Table 1 and 2). Mean *Daphnia* spp. density was low amounting to only 0.7-5% of the density in E1+. (Table 1). The density of other cladocerans (mainly *Ceriodaphnia* spp. and *Bosmina* spp.) and cyclopoid copepods was 68% and 57% higher in E2+ than in E2-, respectively, but only 18% and 21% of the density in E1+. Despite a higher zooplankton biomass, chlorophyll *a* and phytoplankton production were somewhat higher in E2+ than in E2-.

The zooplankton clearance rates of phytoplankton and bacterioplankton were below 50 ml l^{-}d^{-1} (Fig. 5; Table 2). These rates were comparable to the E1-rates, but were substantially lower than the ones of E1+. Calculated ingestion only amounted to 3-5% of phytoplankton production and 17-19% of bacterioplankton production (Table 2). The ingestion of bacterioplankton plus phytoplankton represented a daily ration for zooplankton >140 µm of 81% in E2- and 72% in E2+ and was thus comparable to the percentages found in the E1 experiment (Table 2).

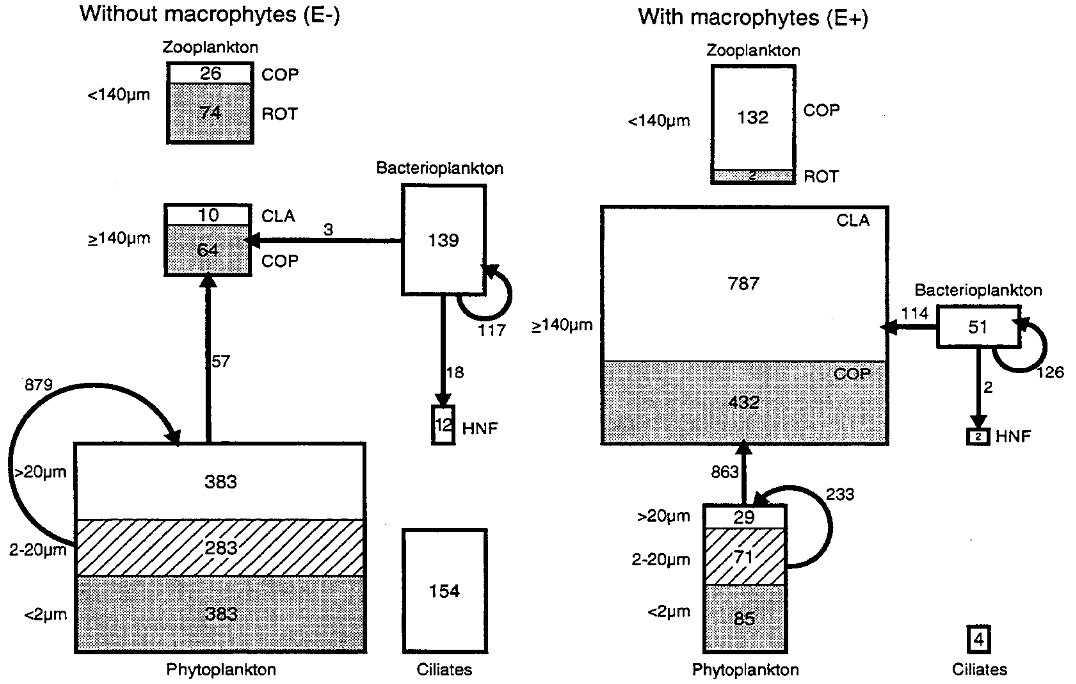

Fig. 2 Carbon budget (µg l^{-1}) for the first 3 diel periods in Experiment 1 (E1+, PVI = 50%) and controls (E1-). The boxes represent the biomass (µg C l^{-1}) of different trophic components and the arrows the measured fluxes (µg C l^{-1} d^{-1}). COP = copepods (mainly cyclopoids), ROT = rotifers, CLA = cladocerans.

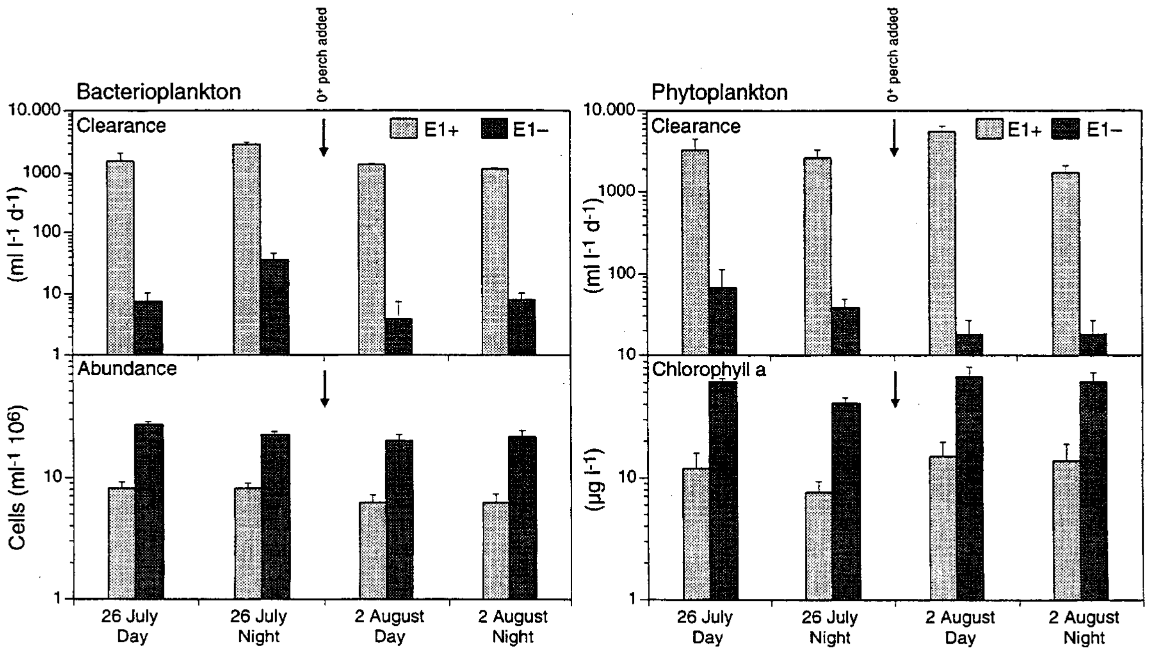

Fig. 3. Experiment 1 showing diel variations in zooplankton (>140 µm) clearance rate (mean ± SE, n = 3) on bacterioplankton and phytoplankton (upper panels) in enclosures with (dark, PVI = 50%) and without macrophytes before (left two sets of columns) and after introduction of 0^+ perch. The lower panels show the corresponding abundance of bacterioplankton and concentration of chlorophyll *a*, respectively.

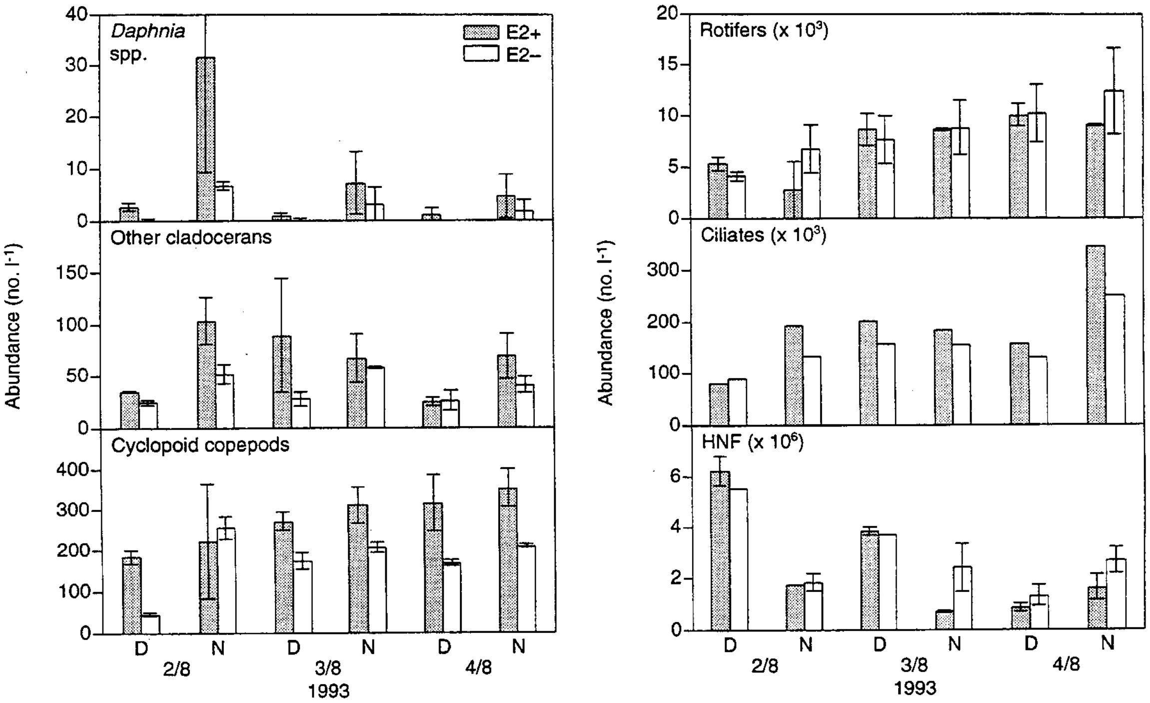

Fig. 4. Experiment 2 showing mean ± SE (n = 2) of various biological variables in enclosures with (dark, PVI = 24%, E2+) and without (E2-) submerged macrophytes. D = day and N = night.

Mean HNF clearance of bacterioplankton was 178 ml l^{-1} d^{-1} in E2- and 143 ml l^{-1} d^{-1} in E2+ (Fig. 5, Table 2), which is 3.5- and 7-fold higher than for macrozooplankton. The corresponding figures for HNF clearance of picoalgae were 690 and 500 ml l^{-1} d^{-1}. Calculated ingestion of bacterioplankton amounted to 56% (E2+) and 115% (E2-) of production.

Diel vertical migration of zooplankton.

Pronounced night (n) to day (d) differences in zooplankton abundance were found for several zooplankton species (Fig. 6). The n:(n+d) ratio was selected as indicator instead of n:d due to some zero values found during the day. In E2+ with fish, the ratio was high for several zooplankters. *Scapholeberis* and *Sida* were only found in night-time samples (ratio = 1). The *Daphnia* ratio was 0.82±0.09 (mean ±SE) and 0.8 for female and male cyclopoid copepods, suggesting a major night-time migration from the sediment or plants to the water column between the plants. Somewhat lower ratios were found for *Ceriodaphnia* (0.75±0.08), cyclopoid copepods (0.72±0.12) and *Diaphanosoma* (0.62±0.18), while the ratios for nauplii and rotifers were close to and not significantly (t-test, $p > 0.05$) different from 0.5, indicating no diel variation. The same patterns can be observed for E1+ after fish stocking, although the ratios were generally somewhat lower than in E2+. In E1+ however, the ratios for *Scapholeberis* (0.62±0.03), *Sida* (0.55±0.08) and *Daphnia* (0.63±0.006) were significantly ($p < 0.05$) lower before than after fish stocking (Fig. 6).

The pattern in the plant-free enclosures more or less corresponds the one found in the plant beds, there being, however, a tendency towards higher ratios (higher diel migration) even for rotifers and nauplii than in enclosures with plants. Only the difference in male and female cyclopoids between E1+ and E1- was, however, significant ($p < 0.01$).

Discussion

Trophic structure and dynamics.

Despite the fact that the experiments were undertaken at the same time of the year in 1993 and 1994, there was a substantial between year difference in plant bed zooplankton composition and abundance, while only minor differences were observed in the plant-free enclosures and in the lake (Table 1 and 2). In 1993, small species dominated at low plant density (PVI = 24%, E2), while the abundance of predator-sensitive species such as *Daphnia* was low. A similar structure was found in the macrophyte-free controls in 1994, while large zooplankton dominated in E1+ (PVI = 50%). This difference in zooplankton structure and abundance is reflected the food-web. In the absence of macrophytes when the zooplankton was dominated by small forms, zooplankton grazing on phytoplankton and bacterioplankton was low, while chlorophyll *a* and the abundance of ciliates, HNF and bacterioplankton were accordingly high. Slightly higher zooplankton grazing on phytoplankton and bacterioplankton was observed in the sparse vegetation (PVI = 24%), while the major structural shift that occurred in the dense plant beds (PVI = 50%) resulted in an extremely high grazing pressure on both phytoplankton and bacterioplankton, low biomass of phytoplankton and low densities of ciliates, flagellates and bacterioplankton. These changes suggest differential cascading effects of zooplankton in E1+ and E1-, which were confirmed by size-fractionation experiments (Jürgens & Jeppesen, 1998). Twentyfour h after the zooplankton > 20 µm were removed, there was a 3- and 9-fold increase in heterotrophic bacteria and nanoflagellate abundance in E1+ as compared with the zooplankton-containing controls, and major increases in chlorophyll *a*, picoplankton and ciliate abundance were observed during the subsequent four days. On the contrary, removal of zooplankton in E1- did not affect the microbial food community (ciliates, flagellates and bacterioplankton), except for a minor increase in the density of filamentous bacterioplankton (Jürgens & Jeppesen 1998).

In the grazer dominated E1+, phytoplankton was dominated by relatively small algae (<20 µm), while a more evenly distribution of size-classes were found in E1- (Table 1). In previous enclosure experiments in Lake Stigsholm, Schriver et al. (1995) found a shift from dominance by cyanobacteria and dinoflagellates at low zooplankton densities (high fish densities) to dominance by grazer-tolerant fast-growing cryptomonads and *Chlamydomonas* at high zooplankton densities. This is consistent with our experiment where *Cryptomonas* and *Rhodomonas* dominated at high, and *Microcystis, Dictyosphaerium* and picoalgae at low

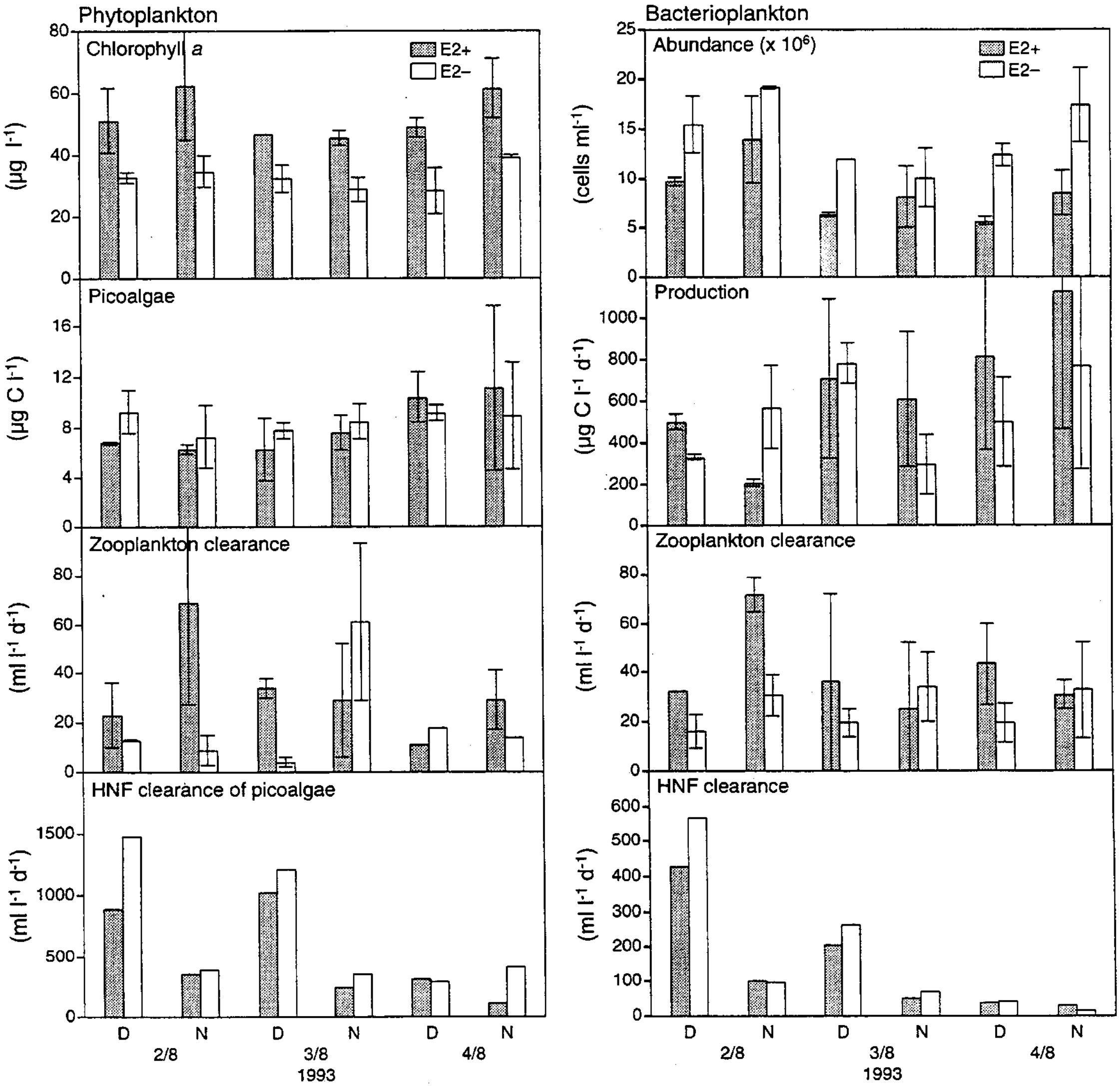

Fig. 5. Right panel: Experiment 2 showing diel variation in abundance, production and specific growth rate of bacterioplankton and zooplankton > 140 µm and HNF clearance of bacterioplankton in enclosures with (dark, PVI = 24%, E2+) and without (E2-) submerged macrophytes. Left panel: Corresponding diel variation in chlorophyll *a* < 50 µm, ^{14}C-labelled phytoplankton production, zooplankton clearance, picoalgae biomass and HNF clearance of picoalgae (all: mean ± SE, n = 2) in enclosures with (dark) and without submerged macrophytes.

Table 3. Daytime abundance of zooplankton at a mid-lake station in late summer 1993 and 1994.

	Abundance (no l^{-1})	
	9 Aug. 1993	19 July 1994
Daphnia spp.	0	2
Bosmina spp.	0	0
Ceriodaphnia spp.	0.8	0.2
Other cladocerans	3.7	0.1
Calanoid copepods	2	26
Cyclopoid copepods	274	131
Rotifers	14,792	14,234

zooplankton grazing pressure (Søndergaard & Moss, 1998; Søndergaard et al. unpublished data). Although several investigations have shown that enhanced grazing leads to an increase in phytoplankton size (Bergquist & Carpenter 1986), our results and those of others (e.g. Kerfoot, 1987; Schriver et al. 1995) suggest that small, fast-growing algae are predominant when the grazing pressure is high.

In the microbial web, particularly ciliates were affected by the trophic cascade, the density being 74-fold higher in E1- than in E1+. The differences are thus at the same order of magnitude as for cladocerans. *Daphnia* are considered to be a key-indicator of top-down control in mesotrophic and eutrophic lakes (Carpenter & Kitchell 1985) and perhaps ciliates have a similar status in the microbial web (see also Jürgens & Jeppesen 1998). The low abundance of ciliates and HNF at high *Daphnia* densities follows the pattern found in numerous studies of the pelagic zone (e.g., Christoffersen et al. 1993; Jürgens 1994). Despite high zooplankton grazing in E1+, however, the ciliate mean volume was 2-fold higher in E1+ than in E1-, E2+ and E2-, reflecting a higher proportion of large hypotrich species that probably are part-time associated with the plants (Jürgens and Jeppesen 1998) and thereby may escape interference and predation by pelagic grazers.

The significant, negative effect of zooplankton on abundance of bacterioplankton in E1+ contradicts previous reports from the pelagial of oligo- and mesotrophic lakes (Pace & Funke 1991; Brett et al. 1994), but is in accordance with results from eutrophic lakes (Jeppesen et al. 1991; Markosova & Jerñek 1993; Jürgens, Arndt & Rothaupt. 1994). Despite a 3-fold higher density, bacterioplankton production did not, however, differ significantly between E1+ and E1-. Thus the specific growth rate was higher in the plant-rich enclosures (Søndergaard et al. 1997). Perhaps the different response reflects that bacterioplankton in E1+ use organic matter released from the plant-periphyton community as the carbon uptake by bacterioplankton in E1+ could not be balanced by release within the pelagic food web (Søndergaard et al, 1997). Release of organic matter from the macrophyte-periphyton community has earlier been suggested to modulate the top-down zooplankton control on bacterioplankton in lakes with high macrophyte densities (Jeppesen et al. 1992).

Cascading trophic interactions in the pelagic zone mediated by changes at the fish level have been observed in many studies (e.g. Gulati et al. 1990; Carpenter & Kitchell 1993; Christoffersen et al. 1993). Using the experience from the pelagial as a starting point, our results indicate a high fish predation pressure in the control enclosures (E2- and E1-) and the low density plant beds, while the predation pressure seemed low in high density plant beds (E1+). These observations agree well with the fish stock estimations. While the number of zooplanktivorous fish ranged from 2.5 to 4.1 m^{-2} in E2 and before fish removal in E1-, the level was low before fish removal in E1+ (0.1 m^{-2}). The results suggest a sudden decline in the densities of 0^+ and 1+ fish and a corresponding steep increase in zooplankton grazing control of phytoplankton and the microbial food-web, when PVI increases from 24% to 50%. The experiments at low and high PVI densities are, however, not necessarily comparable, as the experiments were undertaken in two different years. Two circumstances suggest, though, that the experimental conditions were fairly similar in the two years: First, fish investigations conducted in the lake using gill nets showed high abundance of zooplanktivorous fish in both 1993 and 1994 (S. Berg, unpublished results), and the zooplankton community at a mid-lake station was accordingly dominated by small forms in approximately equal densities in both years (Table 3). Second, at the initiation of the experiment, fish density as well as zooplankton composition and abundance in the macrophyte-free enclosures were similar in 1993 and 1994. We therefore conclude that the data sets from 1993 and 1994 are comparable.

The suggested higher fish predation in sparse plant beds than in dense beds accords with earlier studies of fish distribution in the littoral zone of the lake. Jeppesen et al. (1997) showed that roach and perch concentrated outside the open circular experimental areas when PVI was above 37%, but were evenly distributed in and outside the plant beds at <30% PVI. This suggests a stepwise increase in the refuge effect for zooplankton, which is supported by enclosure studies previously undertaken in the lake. In the experiments by Schriver et al. (1995) submerged macrophytes served as efficient refuges as long as prey fish were below 2 m^{-2} (0^+ and 1^+ sticklebacks (*Gasterosteus aculeatus*) and 0^+ roach) and PVI>10-15%, resulting in dominance by *Daphnia* and a high calculated grazing pressure on phytoplankton as in our 1994 experiment. When the number of fish exceeded 2-4 m^{-2}, zooplankton dominance changed to small-sized forms, and the calculated grazing pressure on phytoplankton decreased to levels comparable to our E2+, E2- and E1- clearance rates. Other studies also suggest a

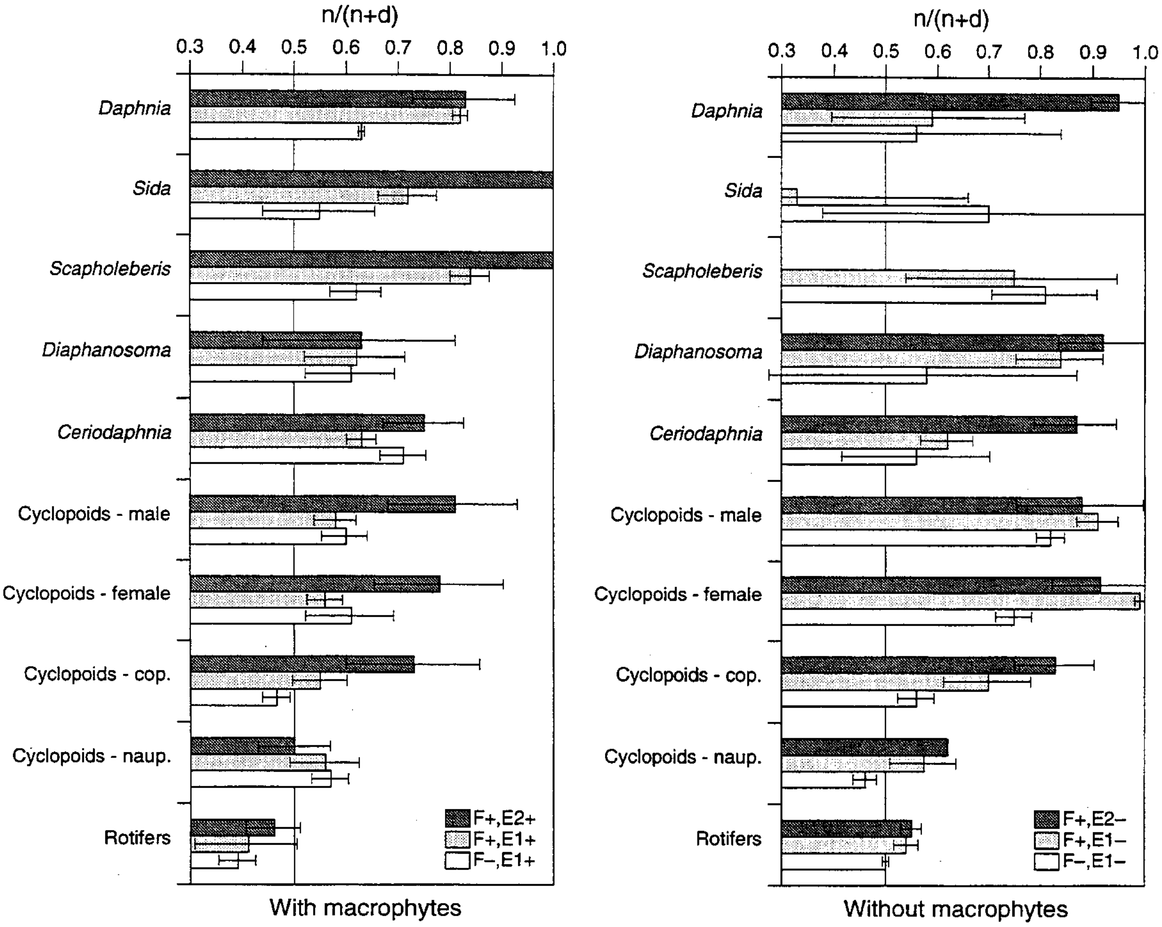

Fig. 6. Night (n) to day (d) (n:(n+d) variation in density of various zooplankter in enclosures with contrasting densities of submerged macrophytes. Left panel shows data from macrophyte beds, and right panel controls without macrophytes. F+, F-: with (2.5-4 m^{-2}) and without fish, respectively. E2: Low PVI experiment (PVI = 24%). E1: High PVI-experiment (PVI 50%). Mean ± SE (n = 2, 1993, and n = 3, 1994) are given.

loss of refuges for large-sized zooplankton in dense plant beds at fish densities of 2-6 fish m^{-2} in eutrophic lakes (Beglioglu & Moss 1996; Kairesalo et al. in press), while the density threshold of fish is substantial lower in sparse beds (Stansfield et al. 1997; Jeppesen et al. 1998). Moreover the interaction strength between fish and zooplankton in the littoral zone may change along a nutrient gradient (Jeppesen et al,1998).

The substantial trophic cascade at the high macrophyte density generally follows the pattern found in the pelagic zone of eutrophic lakes following fish removal (Leibold 1989; Sarnelle 1992; Jeppesen et al. 1997), although it seems to be particularly strong in the macrophyte beds. High zooplankton:phytoplankton biomass ratios and thereby a potentially high grazing pressure on phytoplankton have also been found in other studies of dense plant beds (Moss, McGowan & Carvalho 1994; Schriver et al. 1995). It would be too simple to explain the apparently higher grazer control in the plant beds by the daytime aggregation of pelagic zooplankton in the plant beds, since several investigations in eutrophic lakes have shown continuously high densities of large-bodied *Daphnia* and high zooplankton:phytoplankton biomass ratios in fish-free macrophyte-rich enclosures in which diel migration was restricted (Irvine et al. 1989; Schriver et al. 1995). An explanation may be that the zooplankton also feed on epiphyton and benthic organic matter. The macrophyte beds also host benthic and plant-associated microcrustacean filter-feeders that may contribute significantly to the grazing (Stansfield et al. 1997). Likewise, plant bed density and filtration capacity of mussels may be high (Ogilvie & Mitchell 1995). A complex set of factors may thus be responsible for the strong cascading effects observed in dense macrophyte beds. Due to aggregation of 0^+ fish and the low water depth in the littoral zone the predation pressure on zooplankton in areas with no or sparse vegetation may be higher than in the pelagic zone as evidenced by the "shore avoidance" of large zooplankton in many lakes (e.g., Gliwicz & Rykowska 1992) and the low zooplankton grazing pressure on phytoplankton and bacterioplankton in the plant-free and sparsely vegetated beds of the present study. Small variations in plant density may therefore yield substantial differences in structure and zooplankton grazing pressure in the littoral zone.

Vertical migration of zooplankton.
Pronounced diel variation in density of large-sized zooplankton such as *Daphnia* and adult cyclopoid copepods was observed during both years. Variations for small-sized cladocerans and cyclopoid copepodites were intermediate, while no diel variation was observed for rotifers and nauplii (Fig. 5). Apparently, the strength of vertical migration is determined by the differential risk of predation. This inference is supported by the fact that the night:day ratio was particularly high when fish were abundant and overall higher in the plant-free enclosures than in the more protected environment in the plant bed. As the zooplankton sampler integrated the entire water column (except for the lower 3 cm above the sediment), large-sized zooplankton must have been concentrated close to the sediment surface during day in these shallow areas (mean depth: 0.6 m). These inferences were visually confirmed. Similar observations have been made by de Stasio (1993). Vertical migration occurs in the pelagic zone of many deep lakes and has often been interpreted as being an anti-predator defence mechanism (Lampert 1993). Vertical migration has also been found in studies of the littoral zone (e.g. Szlauer 1963; Whiteside 1974), but the causal factors are less well-studied. Some authors have interpreted it as night-time escape from low oxygen concentrations in the vegetation (Meyers 1980; Timson & Laybourn-Parry 1985), while others have perceived it as diel variation in predation pressure by fish (e.g. Whiteside 1988; de Stasio 1993) or invertebrates (Paterson 1994).

Conclusion

The study has shown that the cascading effect of release of fish predation on zooplankton, phytoplankton and heterotrophic microorganisms can be as high or even higher in the littoral zone than in the pelagial of eutrophic lakes. In the natural system, the cascading effect seemed affected by plant density increasing abruptly from 24% to 50% plant volume infested most likely reflecting variations in habitat preference by young planktivorous fish. Furthermore, in the presence of fish diel vertical migration of large-sized zooplankton was substantial despite low water depth. The present study allowed no horisontal migration of fish and zooplankton that may be substantial. It is important that future studies on the trophic dynamics in the littoral zone include the effects of such migrations.

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References

Beklioglu, M. & Moss, B. 1996. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants with the structure of phytoplankton and zooplankton communities. Freshwater Biology **36**: 315-325.

Bergquist, A.M. & Carpenter, S.R. 1986. Limnetic herbivory: effects on phytoplankton populations and primary production. Ecology **67**: 1351-60.

Botrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. &Weglenska T. 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology **24**: 419-456.

Breder, C.M. 1960. Design for a fish trap. Zoologica, N.Y. **45**: 155-159.

Brett, M.T., Wiackowski, K., Lubnow, F.S., Müller-Solger, A., Elser, J.J., & Goldman, C.R. 1994. Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle Lake, California. Ecology **75**: 2243-2254.

Canfield , D.E., Shireman, J.V., Colle, D.E., Haller, W.T., Watkins, C.E. & Maceina, M.J., 1984. Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes. Canadian Journal of Fisheries and Aquatic Science **41**: 497-501.

Carpenter, S.R. & Kitchell, J.f. [eds.]. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge.

Carpenter, S.R. & Lodge, D.M. 1986. Effects of submerged macrophytes on ecosystem processes. Aquatic Botany **26**: 341-370.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience **35**: 635-639.

Chick, J.H. & McIvor, C.C. 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. Canadian Journal of Fisheries and Aquatic Science **51**: 2873-2882.

Christoffersen, K., Riemann, B., Klysner, A. & Søndergaard, M. 1993. Potential role of zooplankton in structuring a plankton community in eutrophic lake water. Limnology and Oceanography **38**: 561-573.

Christoffersen, K. 1994. Variations of feeding activities of heterotrophic nanoflagellates on picoplankton. Marine Microbial Food Webs **8**: 111-123.

Culver, D.A., Bourcherle, M.M., Bean, D.J. & Fletcher, J.W. 1985. Biomass of freshwater Crustacean zooplankton from lenght-weight regressions. Canadian Journal of Fisheries and Aquatic Science **42**: 1380-1390.

De Stasio JR., B.T. 1993. Diel vertical and horizontal migration by zooplankton: Population budgets and the diurnal deficit. Bulletin of Marine Sciences **53**: 44-64.

Diehl, S. 1988. Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. Oikos **53**: 207-214.

Fuhrman, J.A., & Azam, F. 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. Applied and Environmental Microbiology **39**: 1085-1095.

Geller; W., & Müller, H. 1993. Maximum growth rates of aquatic ciliated protozoa: the dependence on body size and temperature reconsidered. Archiv für Hydrobiologie 126: 315-327.

Gliwicz, Z.M., & Rybak, J.I. 1976. Zooplankton. *In* E. Pieczynka [ed.], Selected problems of lake littoral ecology. University of Warsaw:69-96.

Gliwicz, Z.M. & Jachner, A. 1992. Diel migration of juvenile fish: a ghost of predation past of present. Archiv für Hydrobiologie **124**: 385-410.

Gliwicz, Z.M. & Rykowska, A. 1992. 'Shore avoidance' in zooplankton: a predator-induced behaviour or predator-induced mortality? Journal of Plankton Research **14**: 1331, 1342.

Gulati, R.D., Lammens, H.R.R, Meijer, M.-L. & Van Donk, E. (eds). 1990. Biomanipulation tool for water management. Hydrobiologia **200/201**: 1-628.

Hansen, B., & Christoffersen, K. 1995. Specific growth rates of heterotrophic plankton organisms in a eutrophic lake during a spring bloom. Journal of Plankton Research **17**: 413-430.

Irvine, K., Moss, B. & Balls, H. 1989. The loss of submerged plants with eutrophication II. Relationships between fish and zooplankton in a set of experimental ponds, and conclusions. Freshwater Biology. **22**: 89-107.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Pedersen, L.J. & Jensen, L. 1997. Top-down control in freshwater lakes: the role of nutrients, submerged macrophytes and water depth. Hydrobiologia 342/343: 151-164.

Jeppesen, E., Lauridsen, T.L., Kairesalo, T. & Perrow, M.R. 1998. Impact of submerged macrophytes on fish-zooplankton-interactions in lakes. *In* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard and K. Christoffersen [eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies Series **131**:91-114, Springer, New York.

Jeppesen, E., Søndergaard, M., Jensen, J.P., Mortensen, E. & Sortkjær, O. 1996. Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a 9 year study in shallow hypertrophic Lake Søbygård. Journal of Plankton Research **9**: 1605-1625.

Jeppesen, E., Sortkjær, O., Søndergaard, M. & Erlandsen, M. 1992. Impact of trophic cascade on bacterioplankton production and biomass in two fish-manipulated lakes. Archiv für Hydrobiologie Ergebnisse der Limnologie 37: 219-231.

Jespersen, A.-M., & Christoffersen, K. 1987. Measurements of chlorophyll *a* from phytoplankton using ethanol as extraction solvent. Archiv für Hydrobiologie **109**: 445-454.

Jürgens, K. 1994. The impact of *Daphnia* on microbial food webs - a review. Marine Microbial Food Webs **8**: 295-324.

Jürgens, K., Arndt, H. & Rothaupt, K.O. 1994. Zooplankton-mediated changes of bacterial community structure. Microbial Ecology **27**: 27-42.

Jürgens, K., & Jeppesen,E. 1997. Cascading effects on microbial food web structure in a dense macrophyte canopy. *In* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard and K. Christoffersen [Eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies Series **131**: 262-277. Springer, New York.

Kairesalo, T., Tátrai, I. & Luokkanen, E. Impacts of waterweed (*Elodea canadensis* Michx) on plankton-fish interactions in lake littoral. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie (in press).

Keerfoot, W.C. 1987. Cascading effects and indirect pathways, p57-70. In Kerfoot, W.C. & Sid, A.˙ [eds.], Predation: Direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Kirchman, D.L. 1993. Leucine incorporation as a measure of biomass production by heterotrophic bacteria, p. 509-512. *In* P.F. Kemp, B.F. Sherr, E.B. Sherr and J.J. Cole [eds.], Handbook of methods in aquatic microbial ecology. Lewis Publ., Boca Raton.

Lampert, W. 1993. Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. Archiv für Hydrobiologie Beih. Ergebnisse der Limnologie **39**: 79-88.

Lauridsen, T. & Buenk, I. 1996. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. Archiv für Hydrobiologie **137**: 161-176.

Lauridsen, T., Junge Pedersen, L., Jeppesen, E. & Søndergaard, M. 1996. The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. Journal of Plankton Research **12**: 2283-2294.

Lehtovaara, A. & Sarvala, J. 1984. Seasonal dynamics of total biomass and species composition of zooplankton in the littoral of an oligotrophic lakes. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie **22**: 895-810.

Leibold, M.A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist **134**: 922-949.

MarkoÓova, R. & Jerñek, J. 1993. Bacterioplankton interactions with *Daphnia* and algae in experimental enclosures. Hydrobiologia **264**: 85-99.

McQueen, D.J., Post, J.R. Mills, E.L. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Science **43**: 1571-1581.

Meyers, D.G. 1980. Diurnal vertigal migration in aquatic microcrustaceans: light and oxygen responses of littoral zooplankton, p. 80-90. *In* W.C. Kerfoot, W.C. [ed.], Evolution and ecology of zooplankton communities. The University Press of New England.

Moss, B., McGowan & Carvalho, L. 1994 Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. Limnology and Oceanography **39**: 1020-1029.

Ogilvie, S.H. & Mitchell, S.F. 1995. A model of mussel filtration in a shallow New Zealand lake, with reference to eutrophication control. Archiv für Hydrobiologie **133**: 471-482.

Pace, M.L. 1993. Heterotrophic microbial process, p. 252-277. *In* S.R. Carpenter and J.F. Kitchell [eds.], Cascading trophic interactions. Cambridge University Press.

Pace, M.L. & Funke, E.S. 1991. Regulation of planktonic microbial communities by nutrients and herbivores. Ecology **72**: 904-914.

Paterson, M.J. 1994. Invertebrate predation and the seasonal dynamics of microcrustacea in the littoral zone of a fishless lake. Archiv für Hydrobiologie **99**: 1-36.

Persson, L. 1991. Behavioural response to predators reverses the outcome of competition between prey species. Behav. Ecol. Sociobiol. **28**: 101-105.

Persson, L. & Eklöv, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology **76**: 763-784.

Phillips, G.L., Perrow, M. & Stansfield, J. 1996. Manipulating the fish-zooplankton interaction in shallow lakes: a tool for restoration, p. 174-183. *In* S.P.R. Greenstreet and M.L. Tasker [eds.], Aquatic predators and their prey. Blackwell Scientific Publications.

Riemann, B. 1985. Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. Applied and Environmental Microbiology **50**: 187-193.

Sarnelle, O. 1992. Nutrient enrichment and grazer effects of phytoplankton in lakes. Ecology **73**: 551-560.

SAS Institute, 1989. SAS/STAT User's Guide, Version 6, 4th ed. Vols 1 and 2. SAS Institute Inc.

Savino, J., & Stein, R.A. 1982. Predator-prey interaction between Largemouth Bass and Bluegills as influenced by simulated, submersed vegetation. Trans. American Fisheries Society **111**: 255-266.

Schriver, P., Bøgestrand, J., Jeppesen, E. & Søndergaard, M. 1995. Impact of submerged macrophytes on the interactions between fish, zooplankton and phytoplankton: large-scale enclosure experiments in a shallow lake. Freshwater Biology **33**: 255-270.

Simon, M. & Azam, F. 1989. Protein content and protein synthesis rates of planktonic marine bacteria. Marine Ecology Progress Series **51**: 201-213.

Smits, J. & Riemann, B. 1988. Cell production derived from ^{3}H-thymidine incorporation using freshwater bacteria. Applied and Environmental Microbiology **54**: 2213-2219.

Stansfield, J.H., Perrow, M.R., Tench, L.D., Jowitt, A.D.J. & Taylor, A.A.L. 1997. Submerged macrophytes as refuges for grazing *Cladocera* against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. Hydrobiologia **342/343**: 229-240.

Szlauer, L. 1993. Diurnal migrations of minute invertebrates inhabiting the zone of submerged hydrophytes in a lake. Schweizerische Zeitschrift für Hydrobiologie **25**: 56-64.

Søndergaard, M., Søndergaard, M., Jeppesen, E. & Christoffersen, K. 1998. Bacteria and carbon turnover in a dense macrophyte canopy. *In* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard and K. Christoffersen [eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies Series **131**:250-261, Springer, New York.

Theil-Nielsen, J. & Søndergaard, M. Submitted. A note on bacterial carbon biomass calculated from biovolumes.

Timms, R.M. & Moss, B. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnology and Oceanography **29**: 472-486.

Timson, S. & Laybourn-Parry, J. 1985. The behavioral responses and tolerance of freshwater benthic cyclopoid copepods to hypoxia and anoxia. Hydrobiologia **127**: 257-263.

Vuille, T. 1991. Abundance, standing crop and production of microcrustacean populations (*Cladocera, Copepoda*) in the littoral zone of Lake Biel, Switzerland. Archiv für Hydrobiologie **123**: 165-185.

Werner; E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**: 1540-1548.

Wetzel, R.G. 1992. Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems. Hydrobiologia **229**: 181-198.

Wetzel, R.G. & Søndergaard, M. 1998. The role of submerged macrophytes for the microbial community and dynamics of siddovled organic carbon in aquatic ecosystems. In E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard and K. Christoffersen [eds.9, The structuring role of submerged macrophytes in lakes. Ecological Studies Series **131**: 133-148, Springer, New York.

Whiteside, M.C. 1988. 0$^+$ fish as major factors affecting abundance patterns of littoral zooplankton. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie **23**: 1710-1714.

Winfield, I.J. 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. Journal of Fish Biology **29**: 37-48.

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Changes in nitrogen retention in shallow eutrophic lakes following a decline in density of cyprinids

Erik Jeppesen[1], Jens Peder Jensen[1], Martin Søndergaard[1],
Torben Lauridsen[1], Poul Hald Møller[2] and Kjeld Sandby[3]

With 5 figures and 6 tables in the text

Abstract: To study how changes in biomass of cyprinids (mainly roach, *Rutilus rutilus* L., and bream, *Abramis brama* L.) affect nitrogen retention in shallow lakes, we conducted mass balances of total nitrogen for 6–11 years in four eutrophic lakes in which the fish biomass changed markedly, either from natural causes or due to manipulation. The decline in cyprinids led to a shift from a turbid to a clearwater state in three of the four lakes. In these lakes total nitrogen (N) concentrations decreased and the percentage of N retained in the sediment, or lost by denitrification ($N_{ret\%}$) increased substantially. In Lake Væng, summer $N_{ret\%}$ increased from 19-37% before to 58–70% after the biomass of cyprinids had been reduced by 50%. $N_{ret\%}$ temporarily decreased to 40% during a short-term return to the turbid state. In Lake Engelsholm, a 90% reduction in cyprinids resulted in an increase in summer mean $N_{ret\%}$ from 13–50% to 58–60%, and in Lake Arreskov the annual mean $N_{ret\%}$ increased from −4–34% before a major fish kill to 54–59% after. A comparison with data from 16 non-manipulated lakes revealed that these changes could not be ascribed to natural interannual variations. No significant changes in N concentrations or $N_{ret\%}$ were found in Lake Søbygård, which remained turbid and maintained a relatively high biomass of cyprinids. In the three lakes that shifted to a clearwater state, $N_{ret\%}$ was significantly inversely related to chlorophyll-a, but independent of the abundance of submerged macrophytes and biomass of N-fixing cyanobacteria. The increase in $N_{ret\%}$ might have resulted from 1) a decrease in organic N in the lake and the outlet due to the decrease in phytoplankton biomass and thus phytoplankton-N, which was not compensated by an increase in inorganic N, 2) reduced resuspension, probably reflecting both a decrease in the number of fish foraging in the sediment and a suggested increase in benthic algal growth, 3) higher denitrification in the sediment, reflecting less competition between denitrifiers and phytoplankton for nitrate, enhanced N retention by phyto- and zoobenthos and enhanced sediment nitrification due to

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[1] **Authors' addresses:** Dept. of Lake and Estuarine Ecology, National Environmental Research InstituteVejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark.

[2] County of Vejle, Damhaven 12, DK-7100 Vejle, Denmark.

[3] County of Funen, Amtsgården, Ørbækvej 100, 5220 Odense SØ, Denmark.

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higher oxygen concentrations, the latter reflecting lower sedimentation, higher density of zoobenthos and higher oxygen production by benthic algae. More research is needed to elucidate the relative importance of these mechanisms. It may, however, be concluded that fish manipulation or phosphorus-loading reduction leading to a shift from a turbid to a clearwater state in eutrophic lakes may markedly enhance lake $N_{ret\%}$ and consequently reduce the transfer of nitrogen to coastal waters.

Introduction

Lakes act as nitrogen filters (ANDERSEN 1974, SEITZINGER 1988, JENSEN et al. 1990) due to denitrification and nitrogen accumulation in the sediment; the former process is usually the more important one (ANDERSEN 1974). The retention of total nitrogen (N_{ret}) in lakes has often been shown to increase with increasing N loading (e.g. BACHMANN 1984, FLEISCHER & STIBE 1991), although there are exceptions, particularly from oligotrophic lakes (BERGE et al. 1997). The percentage of N loading retained or lost in the lakes ($N_{ret\%}$) usually increases with increasing hydraulic retention time (OECD 1982, BACHMANN 1984, LIJKLEMA et al. 1989, MOLOT & DILLON 1993) and decreasing mean depth (JENSEN et al. 1990, WINDOLF et al. 1996). Most of the empirical models of nitrogen retention have been developed for eutrophic lakes that are characterized by high biomasses of planktivorous and benthivorous cyprinids and low abundance of submerged plants (LIJKLEMA et al. 1989, JENSEN et al. 1990, WINDOLF et al. 1996). Fish manipulation experiments conducted in four shallow lakes in The Netherlands and Denmark in which the biomass of bream (*Abramis brama* L.), carp *(Cyprinus carpio* L.) and roach *(Rutilus rutilus* L.) were reduced, have, however, all shown a substantial decrease in summer N concentrations (VAN DONK et al. 1990, JEPPESEN et al. 1991, VAN DONK et al. 1993, MEIJER et al. 1994), which implies that $N_{ret\%}$ increased. Similarly, long-term studies of lakes alternating between a clear-water state with extensive growth of submerged macrophytes and a turbid state without extensive macrophytes, showed low N in the clearwater state (BLINDOW et al. 1992). Submerged macrophytes may enhance $N_{ret\%}$ by taking up nutrients from the water for growth or by stimulating denitrification (CHRISTENSEN & SØRENSEN 1986, WEISNER et al. 1994). However, several other ecosystem changes that follow fish manipulation, could lead to an increase in $N_{ret\%}$. A reduction in phytoplankton biomass (SHAPIRO & WRIGHT 1984) means lower particulate N in the lake and its outlet; reduced fish-mediated resuspension (ANDERSSON et al. 1978, MEIJER et al. 1990) may have the same effect; enhanced biomass of macroinvertebrates (GILES et al. 1989) enhances denitrification (PELEGRI et al. 1994, SVENSSON & LEONARDSON 1996) and increased benthic algal growth due to improved light conditions may enhance denitrification (RISGAARD-

PETERSEN et al. 1994) and reduce N release from the sediment (JANSSON 1980, VAN LUIJN et al. 1995).

To further study the effect of changes in fish abundance on N retention we conducted N mass balance studies on four lakes before and after a reduction in the abundance of plankti-benthivorous fish. As the lakes developed differently following the changes in the fish community, the data allowed us partly to distinguish between the effects of fish, macrophytes, sediment and phytoplankton on N retention. By comparing results with those from 16 unmanipulated shallow lakes we could additionally evaluate the responses of the four lakes against the natural variation that occurs from year to year.

Study areas

Lake Væng is small, shallow and eutrophic and has a short hydraulic retention time (Table 1). 90 % of the inlet water is derived from springs along the shore or from subsurface inflow. The lake has one outlet. Sewage was diverted from the lake in 1982 without producing any improvement in lake water quality in terms of reduced phytoplankton biomass or increased water transparency. Therefore, the biomass of cyprinids (mainly roach and bream) was reduced by 50 % to 150 kg ha^{-1} from December 1986 to June 1988. This reduction initiated a self-perpetuating process that further reduced the planktivorous fish biomass to about 25 % of the 1986-level in 1989 and 1990, which in turn resulted in an increased zooplankton grazing pressure on phytoplankton, colonization of submerged macrophytes and enhanced water transparency (SØNDERGAARD et al. 1990, JEPPESEN et al. 1990, 1991 and in press, LAURIDSEN et al. 1994).

Lake Engelsholm is small and eutrophic and has a moderately high hydraulic retention time and depth (Table 1). From April 1992 to September 1994, cyprinids were removed by netting. In total 19.2 t, or 438 kg WW ha^{-1} were removed (66 % of the stock in 1990), of which bream constituted 85 %. 11.5 t were removed in 1992, 2 t in 1993 and 5.7 t in 1994. In 1994, there was a significant increase in the number and average size of *Daphnia* and a marked reduction in chlorophyll-a (JENSEN et al. 1994, County of Vejle 1996).

Table 1. Lake surface data, mean hydraulic retention time and annual mean total phosphorus of the four lakes studied.

	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Retention time (days)	Total phosphorus (μg P l^{-1})
Lake Væng	16	1.2	1.9	15–25	50–150
Lake Engelsholm	44	2.6	6.1	65–88	66–124
Lake Arreskov	317	1.9	3.7	510–770	97–230
Lake Søbygård	40	1.0	1.9	14–20	550–1000

Lake Arreskov is large, shallow and eutrophic and has a comparatively long hydraulic retention time (Table 1). A major fish kill occurred in the autumn and winter of 1991. This resulted in a substantial increase in the abundance and average size of *Daphnia* and a marked reduction in phytoplankton biomass (County of Funen 1996). Additional 4 t cyprinids were removed in 1995 and during 1993 and 1995 the lake was stocked with 0^+ pike amounting to totally 141 ind. ha^{-1}. Cyprinid biomass was calculated as 172 kg ha^{-1} in 1987 and 71 kg ha^{-1} in 1995 (County of Funen 1996).

Lake Søbygård is small, shallow and hypertrophic and has a short hydraulic retention time (Table 1). During 1986–88, 4.3 t of cyprinids (mainly roach and rudd), equivalent to 17 % of the 1986 standing stock of 670 kg ha^{-1}, were removed by commercial fishermen. Variations in fish abundance have resulted in major interannual variations in phytoplankton grazing by zooplankton and thus in chlorophyll-a (JEPPESEN et al. 1990, 1996). N retention has been measured for a 12-year period and the quarterly budgets from the first 8 years have been described elsewhere (JENSEN et al. 1992). During this period, N loading decreased by approx. 30 % due to the closing-down of a local slaughterhouse. In the present study, we concentrate on the period after the N loading reduction and fish manipulation (1988–1995).

Materials and methods

Slightly different methods were used to determine mass balances in the three lakes. In Lake Engelsholm and Lake Arreskov the sampling procedure followed the standardized guidelines of the Danish Nationwide Monitoring Programme (KRISTENSEN et al. 1990, KRONVANG et al. 1993). For the nutrient analysis, the main inlet of each lake was sampled 18–26 times annually, depending on seasonal variation in discharge, while the minor inlets were sampled less frequently, depending on their relative contribution to the total hydraulic and nutrient loading. Outlet samples were collected fortnightly during summer and monthly during winter, i.e. 19 times annually. Total N and nitrate + nitrite was measured as nitrite, the former after potassium persulphate digestion according to the method of SOLÓRZANO & SHARP (1980).

Total discharge in the main inlets and outlets (Q_m) of the two lakes was measured monthly with an OTT-propeller. The water level (H) in the inlet and outlet streams was automatically and continuously recorded during the entire study period. Daily discharge (Q_d) was calculated by use of the relationship obtained for H and Q_m in the inlet and the outlet, respectively. In minor inlets discharge (q) was measured with an OTT-propeller and daily discharge values were calculated from q/Q_d relationships.

Monthly water balances were calculated for each lake using the following equation:

$$Q_{inm} + Q_{inu} + Prec = Vol_{dif} + Q_{outm} + Q_{outu} + Evap \qquad (1)$$

where Q_{inm} and Q_{outm} are the total discharge measured in inlets and outlets, respectively. Evap and Prec are total monthly evaporation and precipitation obtained from meteorological stations situated in the vicinity of the lakes and Vol_{dif} is the monthly change in lake volume. Q_{inu} and Q_{outu} are the unmeasured input from the catchment without stream inlets to the lake and the output (seepage) from the lake, respectively.

The net value of Q_{inu} and Q_{outu} was determined monthly by adjusting the mass balance, if $vol_{dif} + Q_{outm} + Evap > Q_{inm} + Prec$, then Q_{inu} equals the difference; otherwise, Q_{outu} equal to the difference.

Daily N concentrations were calculated by linear interpolation between observed values. N transport was then estimated for each inlet and outlet as the product of daily water discharge and N concentration. We assumed that the N concentration of the unmeasured discharges to and from the lake equalled the Q-weighted concentrations in the measured inlets and outlets. Atmospheric deposition on the lake surface was added using an average rate for Denmark of 15 kg N ha^{-1} $year^{-1}$ (Hovmand et al. 1993).

Outlet discharge measurements from Lake Søbygård followed the procedure described above. Frequent measurements of the discharge in the main inlet to Lake Søbygård in 1984–85 and again in 1993 showed that it accounted for 80–90 % of the total hydraulic loading of the lake (Jensen et al. 1992), while the remaining water was derived from groundwater-fed small streams along the shores. Only minor seasonal variations in discharge and N loading were found in these small streams. The main inlet discharge was calculated by deducting minor inlet contributions from the outflow, taking into account also precipitation and evaporation. Otherwise, the sampling frequency for the former two lakes was followed.

In Lake Væng, 89 % of the hydraulic loading was derived from subsurface inflow of groundwater or small springs. The remaining 11 % came from a small stream. The annual outlet discharge was constant, averaging 116±4 (SE) l s^{-1} (n=22) from October 1 to May 1 and 124±10 l s^{-1} (n=18) for the summer. Discharge was therefore measured less frequently than in the three other lakes. N concentration was measured periodically in the springs and the main inlet. There was no apparent seasonal variation at any of the sites. The average concentrations implied an external N loading of 118 mg N m^{-2} d^{-1}, including atmospheric deposition. Sewage input before diversion in 1981 was 30 mg N m^{-2} d^{-1} (County of Vejle, unpubl. data). As the first two years of study had revealed no significant differences in the concentration of the various N species between the lake and the outlet, samples were taken only occasionally from the outlet and export was calculated from N in depth-integrated lake samples.

In Lake Væng, submerged macrophyte coverage was measured along 14 transects covering the whole lake surface. Along each transect macrophyte coverage and height were registered one (1989) to ten times annually at 6 to 12 stations, with the number of stations depending on transect length. Vegetation coverage was assigned to one of five categories: 1–5, 5–25, 25–50, 50–75 and 75–100 %. Macrophyte height was measured by lowering a Secchi disc to the top of the macrophytes and then to the lake bottom. If macrophytes were not visible due to turbid water, coverage was estimated by using a rake and height by measuring the length of the macrophytes that were pulled up from the lake. Mean coverage and mean height were used as representative values for the whole lake. The biomass (g DW m^{-2}) was estimated using the linear regression for non-canopy forming exclusive stands of *Elodea* by Rørslett et al. (1986), $B = -28.4 + 407.5\,H$ (H = height in m) multiplied by mean coverage. We chose this relation because *Elodea* dominated the macrophyte community and because 30 measurements of biomass gave values similar to our predictions (T. Lauridsen, unpubl. observations). A conversion factor of 39 mg N g DW^{-1} was used, which is the average value derived from 36 plant measurements in the lake described in detail by Lauridsen et al. (1993).

A somewhat different procedure was used in Lake Arreskov. The macrophyte bed was divided into a number of sub-areas (typically 15–22), each having approximately the same macrophyte coverage. If the macrophyte depth limit in a sub-area was less than 1.5 m, total macrophyte coverage was determined at ten randomly selected spots at depth intervals of 25 cm reaching from the shore to the macrophyte boundary; otherwise a depth interval of 50 cm was used. Coverage was determined from a boat using a water glass or by diver. The following categories were used: <1, 1–5, 5–25, 25–50, 50–75, 75–95, 95–100 %. Macrophyte average height was measured at each spot and area-specific plant volume (PV) determined as coverage multiplied by plant height/100. Average coverage (COV) and PV were calculated for each sub-area (i), while COV% and PVI% were calculated for the whole lake as:

$$\text{Cov }\% = \frac{\sum_{i=1}^{n} Cov_i \times area_i}{total\ lake\ area} \qquad \text{PVI }\% = \frac{\sum_{i=1}^{n} PV_i \times area_i}{total\ lake\ volume} \tag{9}$$

We used the same conversion factor from biomass to nitrogen as for Lake Væng. No submerged plants were found in Lake Søbygård and Lake Engelsholm during the study period.

Fish N-content was estimated according to PENCZAK (1983) assuming a dry weight (DW) to wet weight ratio of 0.25 and a total N : DW ratio of 0.106. In-lake concentrations of chlorophyll-a (ethanol extraction, JESPERSEN & CHRISTOFFERSEN 1987), total N, ammonium and nitrite + nitrate were measured 19 times annually on depth-integrated composite samples from a mid-lake station. Ammonium was determined by the phenate method (APHA 1985). Nitrite + nitrate was determined as nitrite using a flow injection analyzer, and inorganic N (N_{inorg}) was calculated as the sum of ammonium, nitrite, and nitrate. Organic N was estimated as $TN - N_{inorg}$. Suspended solids were analyzed according to standard methods (APHA 1985).

Linear regressions (SAS Institute 1989) on log-transformed data were used in the analysis of relationships between relevant variables and the t-test when testing differences in slope and intercept before and after fish manipulation.

N retention (N_{ret}) was calculated as:

$$N_{ret} = \text{Total input} - \text{storage} - \text{total output}$$

and the retention percentage ($N_{ret\%}$) as:

$$N_{ret}\,\% = \frac{100 \times N_{ret}}{\text{Total input} + \text{Lake N-pool}}$$

Results

Lake Væng

Annual data are available for only a few years, so we chose to concentrate on summer results. Summer mean $N_{ret\%}$ increased from 19 % before sewage was diverted in 1981 to 37 % in 1986–1987 (Fig. 1, Table 2). After the fish manipulation that was followed by low chlorophyll-a during summer and high Secchi depths, $N_{ret\%}$ increased to 58–70 %, except in 1992 when it temporarily decreased to 40 % concurrently with an almost total disappearance of plants

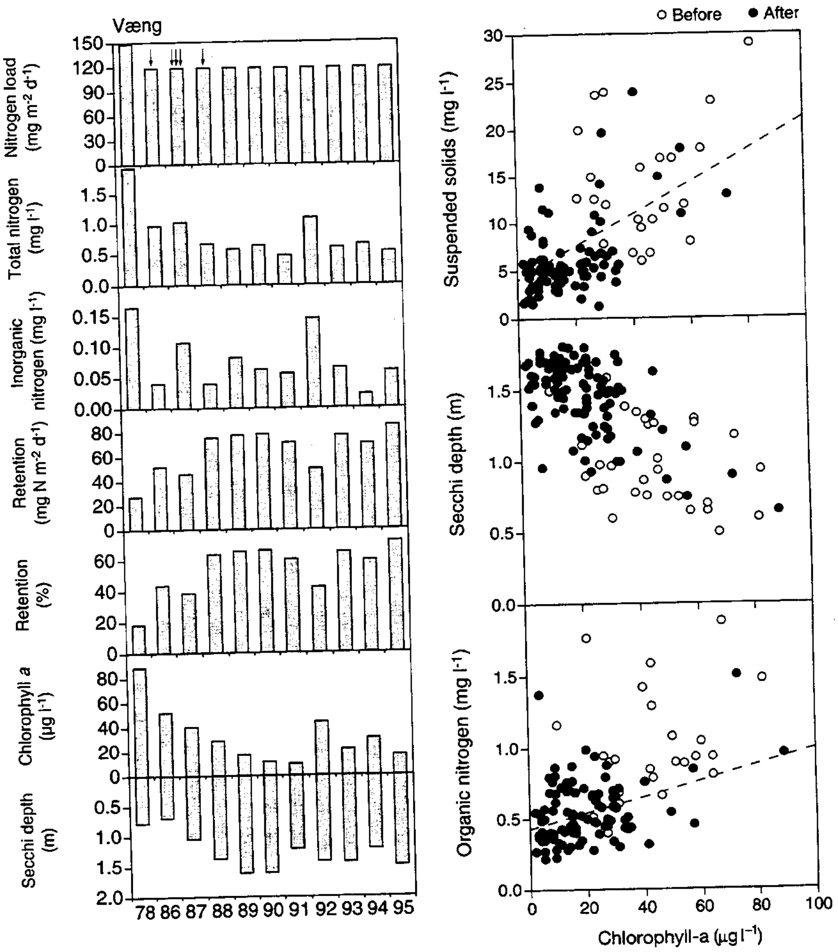

Fig. 1. Left: Summer mean external N loading, lake water total N and inorganic N concentrations, N retention and retention percentage, chlorophyll-a and Secchi depth in Lake Væng. 50 % of the fish biomass was removed from Dec. 1986 to June 1988 (shown by arrows). Right: suspended solids and Secchi depth and organic nitrogen vs. chlorophyll-a. ○: before (1978–1986) and ●: after (1988–1995) the fish removal. Broken lines show the regression lines after fish manipulation.

from the lake and a temporary increase in chlorophyll-a. N_{ret} ranged between 33 and 86 mg N m^{-2} d^{-1}. Summer mean N_{inorg} ranged between 0.02 and 0.16 mg l^{-1}. There was a tendency towards a negative relationship between N_{inorg} and $N_{ret\%}$ ($p=0.07$), while no relationship was found between N_{inorg} and chlorophyll-a ($p>0.47$).

Table 2. Mass balance of nitrogen in Lake Væng (summer mean, 1 May–1 Oct.). N_{load} = loading, N_{water} = changes in the lake water pool, N_{out} = export from the lake, N_{ret} = net retention in the lake (denitrification and net accumulation in submerged macrophytes and sediments). N_{ret} (%) = total net retention during summer in percentage of total $N_{load} + N_{pool}$. CHLA = chlorophyll-a, N_{inorg} = inorganic lake water N. PLANTS = net accumulation in plants. N_{ret}–PLANTS = net retention corrected for net accumulation in submerged plants. N_{ret}–PLANTS (%) = N_{ret}–PLANTS (%) in percentage of $N_{load} + N_{pool}$.

	Before fish removal			After fish removal							
	1978	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
N_{load} (mg N m^{-2} d^{-1})	148	118	118	118	118	118	118	118	118	118	118
N_{water} (mg N m^{-2} d^{-1})	−18	1	0.2	−1	1	−1	1	3	0.4	1	−2
N_{out} (mg N m^{-2} d^{-1})	133	65	72	44	39	41	32	66	41	46	34
N_{ret} (mg N m^{-2} d^{-1})	33	52	46	75	78	79	85	50	77	71	86
N_{ret} (%)	19	37	37	62	64	65	70	40	63	58	70
PLANTS (mg N m^{-2} d^{-1})		0	0	0	7	54	15	−9	3	71	46
N_{ret}–PLANTS (mg N m^{-2} d^{-1})	33	52	46	75	71	25	70	59	74	−0.1	40
N_{ret}–PLANTS (%)	19	37	37	62	57	11	46	48	60	0	31
CHLA (µg l^{-1})	75	52	40	29	17	11	10	44	22	31	17
N_{inorg} (mg N l^{-1})	0.16	0.04	0.11	0.04	0.08	0.07	0.06	0.15	0.07	0.02	0.06

Suspended solids and organic nitrogen were positively related to chlorophyll-a, but there was no difference in slope or intercept from the pre- to the post-manipulation period ($p > 0.05$). The scatter of data was, however, large, which may reflect accidental inclusion of plant-associated particulate matter in years with high macrophyte coverage. Supporting this view, we found a significantly ($p < 0.03$) higher Secchi depth per unit of chlorophyll-a after fish manipulation, indicating a reduction in suspended solids.

Net uptake by submerged macrophytes during summer ranged between −9 and 71 mg N m^{-2} d^{-1} (Table 2). In years with high macrophyte biomass (1990, 1994 and 1995) the uptake amounted to 68–100% of N_{ret}, while it was <18% in the remaining years.

In total, 116 kg N were removed by fish manipulation during 1986–1988. The 1987 catch is equivalent to a N-removal of 0.4 mg N m^{-2} d^{-1} or 1% of the daily retention during summer, whereas the percentage was lower than 0.8 in the other two years.

Lake Engelsholm

On an annual basis, mean N_{load} ranged from 94–136 mg N m^{-2} d^{-1}, N_{ret} from 14–58 mg N m^{-2} d^{-1} and $N_{ret\%}$ from 10–43% (Fig. 2). Summer mean $N_{ret\%}$ ranged from 13–50% before the fish were removed (13–45 mg N m^{-2} d^{-1}). It was 29–47% during 1992–1993, when 13.6 t of fish were removed, but increased to 58–60% in the subsequent two summers when a shift occurred to

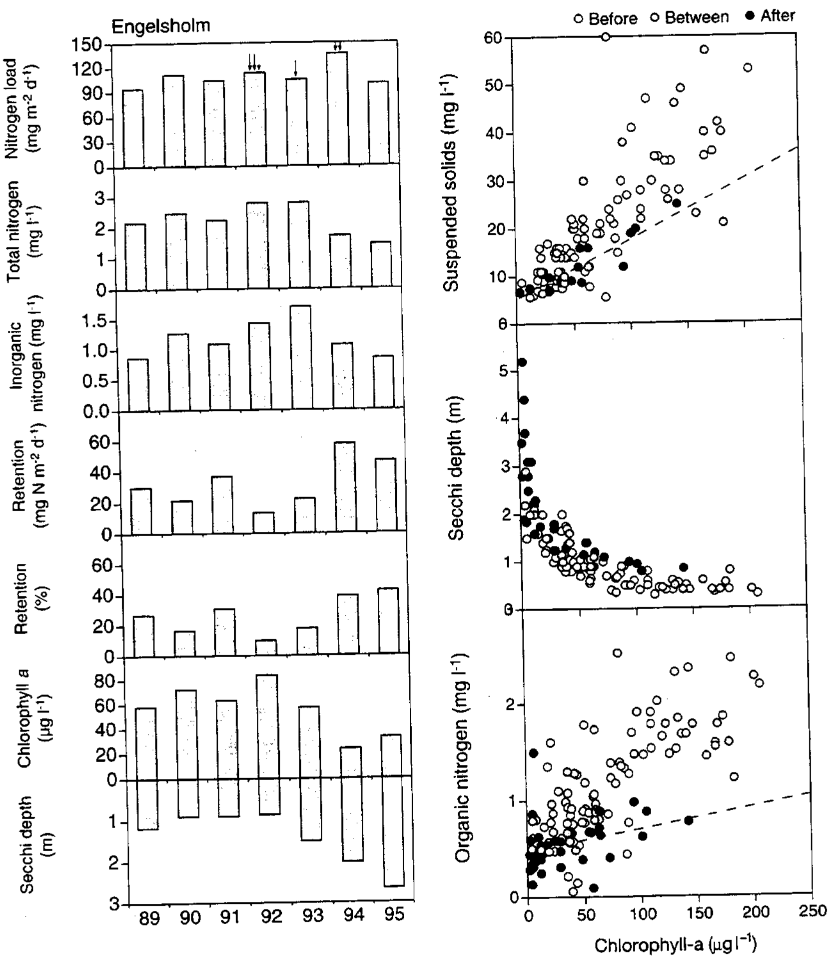

Fig. 2. Left: Annual mean external N loading, lake water total N and inorganic N concentrations, N retention and retention percentage, chlorophyll-a and Secchi depth in Lake Engelsholm. 90% of the cyprinid biomass was removed in 1992–1994 (shown by arows). Right: suspended solids and Secchi depth and organic nitrogen vs. chlorophyll-a. O: before (1989–1991), O: between (1992–1993), and ●: after (1994 and 1995) the fish removal. Broken lines show the regression lines after fish manipulation.

high densities of *Daphnia* (not shown), low chlorophyll-a and high Secchi depths (Fig. 2, Table 3). Summer mean N_{inorg} ranged between 0.22 and 0.71 mg N l^{-1} (Table 3). The lowest values were found in 1994–95. Accordingly, N_{inorg} was significantly negatively related to $N_{ret\%}$ ($p<0.05$) and tended to be positively related to chlorophyll-a ($p = 0.08$).

Table 3. Mass balance of total nitrogen in Lake Engelsholm (summer mean, 1 May–1 Oct.) Abbreviations as in Table 2.

	Before fish removal			During fish removal		After fish removal	
	1989	1990	1991	1992	1993	1994	1995
N_{load} (mg N m^{-2} d^{-1})	67	63	60	60	60	74	69
N_{water} (mg N m^{-2} d^{-1})	2	−24	−20	−49	−16	−2	-9
N_{out} (mg N m^{-2} d^{-1})	53	52	36	59	47	25	28
N_{ret} (mg N m^{-2} d^{-1})	13	34	45	50	29	51	50
N_{ret} (%)	13	33	50	47	29	58	60
CHLA (μg l^{-1})	77	112	69	122	110	38	51
N_{inorg} (mg N l^{-1})	0.30	0.51	0.39	0.54	0.71	0.22	0.25

Significant differences ($p < 0.0003$) were found in the relationship between suspended solids and chlorophyll-a before, during and after the fish manipulation. The slope was 67 % higher before and 58 % higher during fish manipulation than after. No significant changes ($p > 0.90$) were found in the intercepts. The relationships between chlorophyll-a and Secchi depth and organic nitrogen also changed (Fig. 2). The slope of the regression of organic N on chlorophyll was 4.4 times higher ($p < 0.001$) before fish manipulation than after and 3 times higher during it.

In total, 360 kg N were removed during the fish manipulation. The 1992 catch is equivalent to an average N-removal of 1.9 mg N m^{-2} d^{-1} or 1.5 % of N_{ret}. The equivalent figure was <0.5 % in the other two years.

Lake Arreskov

Due to the long hydraulic retention time (1.4–2.1 y) only annual mass balances have been conducted for this lake. Annual daily mean N_{load} was low in 1989 (29 mg N m^{-2} d^{-1}), after which it fluctuated between 37 and 63 mg N m^{-2} d^{-1} without any clear trend (Table 4, Fig. 3). Annual mean $N_{ret\%}$ ranged between −4 (1989) and 34 % in the two years before the fish kill in 1991. It was 49 % in 1991, and between 54 and 59 % after the fish kill. N_{ret} ranged between −2 and 23 mg N m^{-2} d^{-1} before to 28–39 mg N m^{-2} d^{-1} after fish kill. Mean summer N_{inorg} ranged between 0.05 and 0.34 mg N l^{-1} (Table 4) and was not significantly correlated with annual mean $N_{ret\%}$ ($p > 0.47$) or chlorophyll-a ($p > 0.68$). The fish kills were also followed by a major decrease in chlorophyll-a and an increase in Secchi depth (Table 4, Fig. 3).

The results suggest a reduction in resuspension and particulate organic N following the fish kill (Fig. 3). Suspended solids were positively related to chlorophyll-a, but the intercept was 5.4-fold higher ($p < 0.05$) before than after

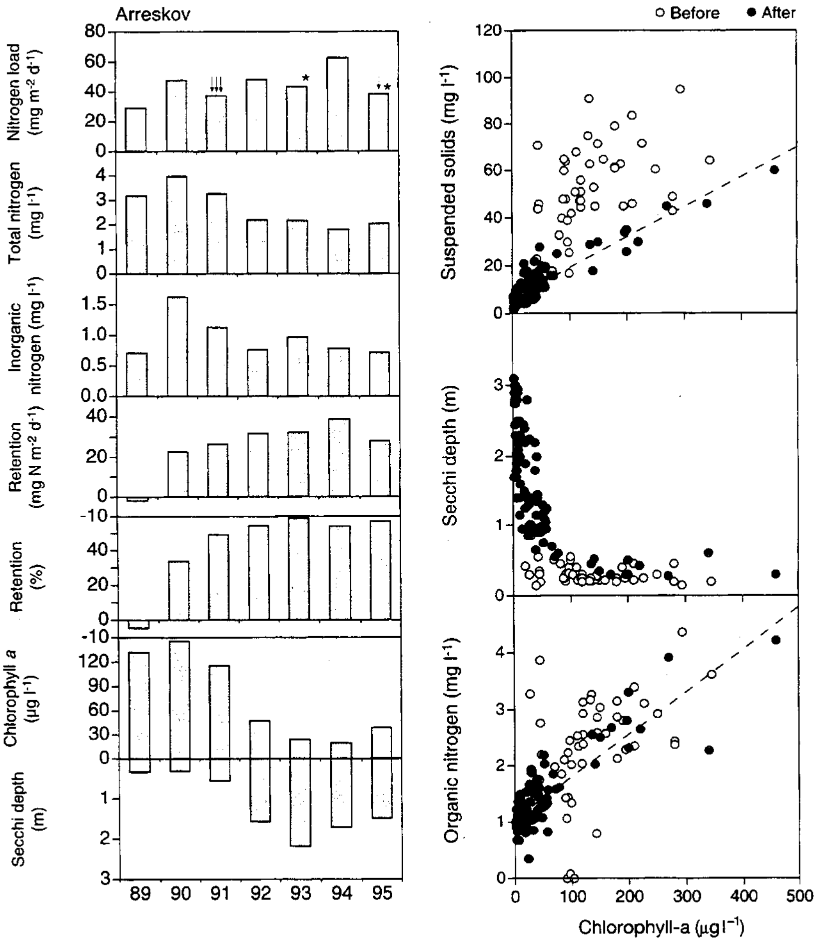

Fig. 3. Left: Annual mean external N loading, lake water total N and inorganic N concentrations, N retention and retention percentage, chlorophyll-a and Secchi depth in Lake Arreskov during 1989–1995. A major fish kill occurred in mid-summer and autumn 1991 and a minor fish removal in 1995 (shown by arrows). 0+ pike were stocked in 1993 and 1995 (shown by an asterisk). Right: suspended solids and Secchi depth and organic nitrogen vs. chlorophyll-a. O: before (1989–1990) and ●: after (1992–1995) the fish kill in 1991. Broken lines show the regression lines after fish manipulation.

the fish kill. Accordingly, the Secchi depth vs. chlorophyll-a relationship deviated significantly, with transparency being higher per unit of chlorophyll-a after the fish kill. Substantial scatter was found in the organic N vs. chloro-

Table 4. Mass balance of total nitrogen in Lake Arreskov (annual mean). Abbreviations as in Table 2. N_{inorg} is summer mean.

	Before fish kill		Fish kill	After fish kill			
	1989	1990	1991	1992	1993	1994	1995
N_{load} (mg N m^{-2} d^{-1})	29	48	37	48	44	63	38
N_{water} (mg N m^{-2} d^{-1})	14	−7.5	−7.2	2.9	−3.9	−0.1	−6.9
N_{out} (mg N m^{-2} d^{-1})	17	33	18	14	15	24	17
N_{ret} (mg N m^{-2} d^{-1})	−2	23	27	32	32	39	28
N_{ret} (%)	−4	34	49	54	59	54	57
CHLA (μg l^{-1})	132	146	116	48	24	20	38
N_{inorg} (mg N l^{-1})	0.05	0.27	0.34	0.26	0.26	0.21	0.12

Table 5. Mass balance of total nitrogen (N) in Lake Søbygård (summer mean, 1 May–1 Oct.) Abbreviations as in Table 2.

	1988	1989	1990	1991	1992	1993	1994	1995
N_{load} (mg N m^{-2} d^{-1})	185	168	109	135	133	179	129	244
N_{water} (mg N m^{-2} d^{-1})	9	6	6	3	0.5	9	−1	5
N_{out} (mg N m^{-2} d^{-1})	54	44	74	64	82	58	86	96
N_{ret} (mg N m^{-2} d^{-1})	122	118	39	68	50	112	44	143
N_{ret} (%)	61	65	32	46	34	58	31	54
CHLA (μg l^{-1})	145	127	175	189	207	137	265	299
N_{inorg} (mg N l^{-1})	0.70	0.56	0.31	0.42	0.63	0.73	0.46	0.43

phyll-a relationship, but the intercept was significantly ($p < 0.03$) and 35 % lower after the fish kill.

Following the improved light conditions submerged macrophytes appeared in the lake. The maximum biomass in 1994 and 1995 was estimated to be 0.3 and 3.8 g DW m^{-2} or 12 and 148 mg N m^{-2}. Assuming a growth season of 3 months, this corresponds to a net uptake of 0.1 and 1.6 mg N m^{-2} d^{-1} during the growing season or 0.3 and 6 % of the annual daily mean N_{ret}, respectively.

Lake Søbygård

The annual daily mean N_{load} ranged from 197 to 302 mg N m^{-2} d^{-1}. N_{ret} ranged from 49 to 119 mg N m^{-2} d^{-1} and $N_{ret\%}$ between 21 and 44 % (Fig. 4). During summer (1 May–1 Oct.), $N_{ret\%}$ ranged between 31 and 65 %. Annual and summer mean $N_{ret\%}$ were not correlated with chlorophyll-a ($p > 0.30$ and $p > 0.15$, respectively). Summer mean N_{inorg} ranged between 0.31 and 0.73 mg N l^{-1} (Table 5) and was not significantly correlated with chlorophyll-a ($p > 0.21$) or $N_{ret\%}$ ($p > 0.38$).

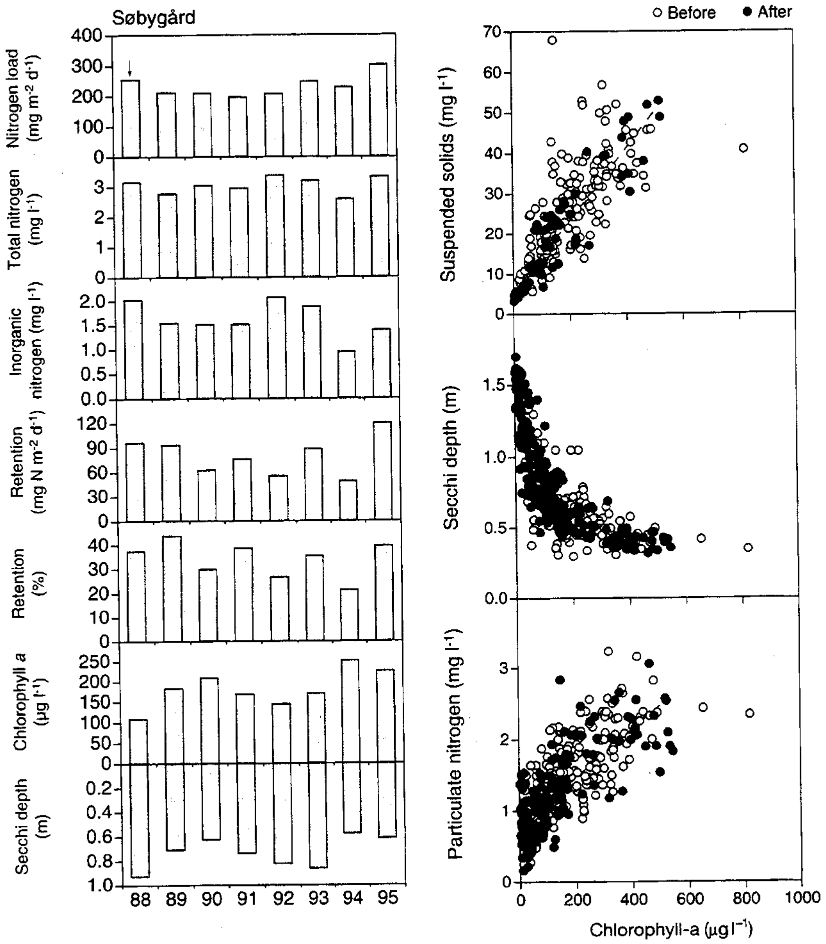

Fig. 4. Left: Annual mean external N loading, lake water total N and inorganic N concentrations, N retention and retention percentage, chlorophyll-a and Secchi depth in Lake Søbygård during 1988–1995. From 1986–1988, 17 % of the 1986 standing stock of cyprinids was removed (shown by arrows). Right: suspended solids and Secchi depth and organic nitrogen vs. chlorophyll-a. ●: years with low chlorophyll-a (1988–89, 1993), ○: other years. Broken lines show the regression lines after fish manipulation.

No significant difference $(p > 0.4)$ was found in the relationship between chlorophyll-a and suspended solids, Secchi depth or organic N in years with low (1988, 1989, 1993) and high chlorophyll-a (other years) (Fig. 4). The fish removal during 1986–1988 corresponded to 227 mg N m^{-2} y^{-1} or 0.2 mg N m^{-2} d^{-1} which was less than 0.4 % of the annual daily mean N_{ret} in the lake.

The role of cyanobacteria

In Lake Væng, log-transformed summer mean N_{ret} was significantly negatively related to summer mean total cyanobacteria volume (log-transformed) ($p < 0.05$), but not to the volume of heterocystous cyanobacteria ($p > 0.10$), while no relationship between N_{ret} and the volume of all or heterocystous cyanobacteria were found for any of the other lakes ($p > 0.10$).

Discussion

In the three lakes that had a large reduction in cyprinid biomass, $N_{ret\%}$ increased significantly. Various factors may contribute to an increase in $N_{ret\%}$ after fish removal or fish kill, and our results provide some insight into their relative importance.

The importance of submerged macrophytes

Following fish removal, submerged macrophytes may return to shallow lakes shifting from the turbid to the clear-water state (MEIJER et al. 1994, HANSON & BUTLER 1994). Macrophytes may take up nutrients from the water during the growth season, particularly when the leaves to surface root area is large (OZIMEK et al. 1993). Macrophytes may also stimulate denitrification. CHRISTENSEN & SØRENSEN (1986) suggested that oxygen release from roots in the sediment stimulated the coupled nitrification-denitrification and WEISNER et al. (1994) found a substantially higher denitrification in plant beds (*P. pectinatus L.*) than on bar sediments, in particular when plants were extensively colonized by epiphytes and in the dark, when O_2 concentration was low. The latter suggests that denitrification may occur in the biofilm on plant surfaces. High nitrogen loss caused by processes in the plant biofilm has also been found in streams and ponds (PRAHL et al. 1991, ERIKSSON & WEST 1996, 1997). The concentration of organic N in the lake water may also decrease because plants promote sedimentation and reduce resuspension (JAMES & BARKO 1990, DIETER 1990, HAMILTON & MITCHELL 1996). Macrophyte establishment may therefore result in an increase in $N_{ret\%}$.

Extensive growth of submerged macrophytes was found only in Lake Væng in which summer N_{ret} increased by 0–29 mg N m^{-2} d^{-1} (mean = 20 mg N m^{-2} d^{-1}) after cyprinid reduction. The plant net incorporation of N varied between 0 and 71 mg N m^{-2} d^{-1}. In summers with high plant growth (exclusively *E. canadensis* L.), net uptake therefore exceeded the N_{ret} increase and amounted to as much as 68–100 % of total N_{ret}. Potentially, macrophytes may therefore have had a high impact on $N_{ret\%}$ as *Elodea* is able to use nutrients from the water column for growth (RØRSLETT et al. 1985, OZIMEK et al. 1990, 1993). We found, however, no correlation ($p>0.4$, $n=8$) between the biomass of submerged macrophytes and $N_{ret\%}$. Instead, summer mean $N_{ret\%}$ was significantly negatively related to chlorophyll-a, suggesting that the general increase in $N_{ret\%}$ in Lake Væng following fish manipulation reflects the shift to a clear-water state rather than an increase in the abundance of submerged macrophytes. The results from Lake Arreskov and Lake Engelsholm provide further evidence. In these lakes, $N_{ret\%}$ increased markedly following the shift to the clear-water state despite absence or low densities of plants. The results therefore suggest that if plants incorporate a considerable proportion of nutrients for growth from the water phase, other N retention processes diminish, thereby precluding a particularly high $N_{ret\%}$ in those lakes that have become both clear and colonized by submerged macrophytes.

Reduction in benthivorous and zooplanktivorous cyprinids

Benthic-feeding cyprinids enhance nutrient release from sediment to water as a result of sediment resuspension and fish excretion (ANDERSSON et al. 1978, TATRAI & ISTVANOVICS 1986, MEIJER et al. 1990, PERSSON 1997). Removal of cyprinids may therefore enhance $N_{ret\%}$. In addition, release from predation may result in an increase in the abundance of benthic invertebrates (GILES et al. 1989), which may enhance sediment denitrification as demonstrated by PELEGRÍ et al. (1994), RYSGAARD et al. (1995) and SVENSSON & LEONARDSON (1996), and suggested from mass balances on total nitrogen by ANDERSEN (1977) and ANDERSEN & JENSEN (1991). Furthermore, release of predation on zooplankton may enhance $N_{ret\%}$ due to a grazer-mediated reduction in phytoplankton and thus in loss of particulate N through the outlet. A lower phytoplankton biomass means lower sedimentation and thus lower mineralization in the surface sediment, which might increase the depth of the aerobic zone and stimulate the coupled nitrification-denitrification (RYSGAARD et al. 1995). Finally, by removing cyprinids, N is exported from the lakes.

We can exclude a major effect of N removed by fish in the three fish-manipulated lakes as it amounted to <1.5 % of N_{ret}. The fish manipulation or fish kill were followed by a marked decrease in chlorophyll-a in three of the lakes (SØNDERGAARD et al. 1990, County of Funen 1996, County of Vejle 1996). Organic N in the lakes and outlets therefore decreased. In Lake Arreskov and Lake Engelsholm, the reduction in the concentrations of organic N and suspended matter were higher than expected from the decrease in chlorophyll-a, probably reflecting reduced bioturbation by fish (MEIJER et al. 1990, BREUKELAAR et al. 1994). Reduced resuspension leads to reduced export of particulate N. It also has a more indirect effect on the N loss as Secchi depth improves which results in a potentially higher growth of benthic algae (see below). The impact of changes in the abundance of benthic invertebrates on N_{ret} cannot be evaluated as sufficient data on their abundance was not available. In addition, it is difficult to assess the significance of reduced phytoplankton sedimentation on sediment N release and N turnover. In Lake Søbygård, $N_{ret\%}$ did not increase significantly in the years with lower phytoplankton biomass, suggesting that this effect was unimportant. However, in Lake Søbygård chlorophyll-a and phytoplankton sedimentation were high even in the "low chlorophyll-a years" (Fig. 4) (JENSEN et al. 1990), which makes it difficult to transfer the results to the lakes that cleared up after fish manipulation.

Microbenthic or filamentous algae

Increased water clarity may stimulate growth of microbenthic algae and thus enhance oxygen production of the surface sediment. This may stimulate denitrification through coupled nitrification-denitrification (CHRISTENSEN et al. 1990, RISGAARD-PETERSEN et al. 1994, RYSGAARD et al. 1995, VAN LUIJN et al. 1995) depending on the concentration of N_{inorg} in the overlying water (RYSGAARD et al. 1995). Several studies have emphasized that the release of nutrients from the sediment is reduced markedly, when microbenthic algae are abundant, and particularly in the light (HENRIKSEN et al. 1980, JANSSON 1980, HANSSON 1989, VAN LUIJN et al. 1995).

In three of the lakes, transparency increased substantially following the reduction in suspended matter (Figs 1–3). Due to the low water depth it is to be presumed that large parts of the lake bottom became colonized by benthic algae (which was confirmed visually), which has most likely led to a decrease in nitrogen release from the sediment and to a higher denitrification.

Competition between phytoplankton and nitrifying and denitrifying bacteria

When phytoplankton biomass is high, much N_{inorg} may be used for phytoplankton growth. Phytoplankton-bound nitrogen exported from the lake is therefore not available as substrate for denitrification, the coupled nitrification-denitrification in the surface sediment or for other biota. A lower phytoplankton biomass may therefore release more N_{inorg} for the other processes.

There was no significant increase in summer mean N_{inorg} as chlorophyll-a decreased. In Lake Engelsholm, N_{inorg} was even significantly negatively correlated with $N_{ret\%}$, and in Lake Væng the relation was almost significant, suggesting a higher loss of N_{inorg} after fish manipulation than before. The sediment therefore seemed capable of absorbing the surplus N_{inorg} appearing following the reduction in chlorophyll-a, and may even enhance removal of N_{inorg} after fish removal or fish kills.

Nitrogen fixation

Fish removal may result in a reduction both in the total phytoplankton biomass and the relative contribution of cyanobacteria, including nitrogen-fixing species (VAN DONK et al. 1990, SØNDERGAARD et al. 1990). Any decrease in N_2-fixation will increase the values of $N_{ret\%}$ as N fixation is not included in the input-output mass balances.

In the lakes in which major changes in cyprinid abundance occurred, cyanobacteria decreased from 14–15 $mm^3\ l^{-1}$ before the fish kill to 1–8 $mm^3\ l^{-1}$ in the three succeeding years in Lake Arreskov (County of Funen 1996), from 16–39 $mm^3\ l^{-1}$ to 7 $mm^3\ l^{-1}$ in Lake Engelsholm (County of Vejle 1996) and from 25 $mm^3\ l^{-1}$ to <5 mm^3 in Lake Væng (SØNDERGAARD et al. 1990 and unpubl. results). A decrease in N_2-fixation might therefore have contributed to the increase in $N_{ret\%}$ in these lakes. No data on N_2-fixation is available, but a review by HOWARTH et al. (1988) revealed rates between 0 and 2.2 $g N m^{-2} y^{-1}$ in temperate lakes (or max 6 $mg\ m^{-2}\ d^{-1}$), but typically below 1 $g\ N\ m^{-2}\ y^{-1}$. In Lake Væng and Lake Arreskov the maximum value (2.2 $g\ N\ m^{-2}\ y^{-1}$) would result in only 20–30 % of the N_{ret} increase following fish manipulation and about approx. 50 % in Lake Engelsholm. No relationship was, however, found between $N_{ret\%}$ and cyanobacterial biovolume for the lakes except for total cyanobacteria but not heterocystous cyanobacteria in Lake Væng. This suggests a minor influence of changes in N fixation on N_{ret}. We can, however, not fully exclude that reduced N fixation may have contributed to the increase in $N_{ret\%}$.

Comparison with multi-lake mass balances

During 1989–1995, N mass balance studies were conducted in 16 turbid shallow Danish lakes following the same methods as described for Lake Arreskov and Lake Engelsholm (Table 6 and WINDOLF et al. 1996). These data allow comparison of the response by the four lakes with the natural inter-annual variations. The annual mean N loading in these lakes ranged between 106 and 230 $g\ N\ m^{-2}\ yr^{-1}$ and was particularly low in 1989. In 1989, $N_{ret\%}$ was relatively high (39 %). During the next four years $N_{ret\%}$ was constant (29–31 %) followed by two years with lower $N_{ret\%}$ (23–24 %). The same pattern was found for the median, 25 % and 75 % quartiles (Table 6). It is therefore unlikely that higher $N_{ret\%}$ in Lake Arreskov after the fish kill in mid-summer 1991 (Table 4) reflects natural interannual variations. Also the increase in Lake Engelsholm in 1994 in the second year after the fish manipulation does not follow the multi-lake pattern. The results from the 16 lakes therefore support our conclusion that the changes in $N_{ret\%}$ were related directly or indirectly to the changes in the fish community. The annual mean (or summer mean, Lake Væng) lake N concentration in the three lakes that shifted from a turbid to a

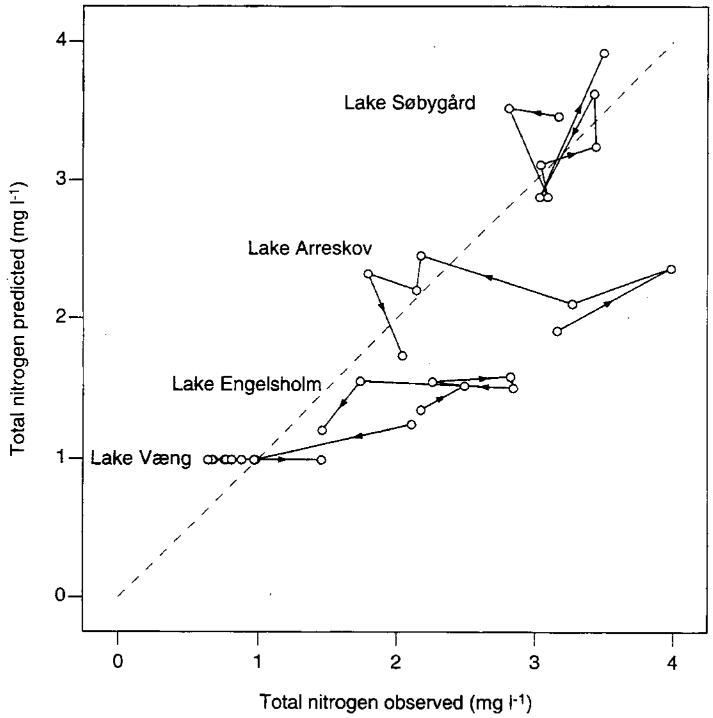

Fig. 5. Changes in observed annual mean N-concentrations (summer mean for Lake Væng) in the four lakes during the study period vs. concentrations estimated from the equations on 16 Danish lakes (WINDOLF et al. 1996).

clear-water state following fish manipulation approached the predicted values based on an equation developed by WINDOLF et al. (1996) on data from 16 lakes (Fig. 5).

Conclusions

It can be concluded that fish manipulation in shallow eutrophic lakes leading to a shift from the turbid to the clear-water state results in a major reduction of the total nitrogen concentrations and an increase in the retention percentage. The increase seems independent of the establishment of submerged macrophytes, as corresponding changes occurred in macrophyte-free lakes shifting to the clear-water state. The results indicate that the most important factors are increased sediment loss of nitrogen via denitrification (possibly coupled with

Table 6. Annual mean total nitrogen mass balances from 16 shallow Danish lakes during 7 years (based on data from WINDOLF et al. (1996) and JENSEN et al. (1995)). For abbreviations see Table 2.

	N_{load}	N_{ret}	$N_{ret\%}$			
	(mg N m^{-2} d^{-1})	(mg N m^{-2} d^{-1})	mean	75%	median	25%
1989	270	88	39	52	40	24
1990	454	107	29	35	27	23
1991	359	93	31	42	28	18
1992	468	124	31	44	26	18
1993	487	102	29	43	23	14
1994	560	107	24	34	18	12
1995	376	88	23	37	29	13

nitrification) conditioned by reduced sedimentation, lower phytoplankton biomass, and maybe increased bioturbation by benthic invertebrates and reduced competition with pelagic organisms for available inorganic nitrogen. In addition, increased growth of benthic algae and other sediment biota may have reduced the nitrogen release from the sediment. More research is, however, needed to elucidate the causal mechanisms. Irrespective of the mechanisms involved the results have shown that lake restoration, including fish manipulation, leading to a shift from a turbid to a clear-water state will result in a major increase in nitrogen retention in shallow lakes and consequently a decline in the transfer of nitrogen to downstream aquatic ecosystems. The results presented all originate from relatively eutrophic lakes. Studies of Norwegian lakes (BERGE et al. 1997) indicate that oligotrophic lakes do not always have the same high capacity to retain nitrogen as eutrophic lakes. One should therefore be cautious when transferring our results to less nutrient-enriched conditions.

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References

ANDERSEN, F. Ø. & JENSEN, H. S. (1991): The influence of chironomids on decomposition of organic matter and nutrient exchange in a lake sediment. – Verh. Int. Verein. Limnol. **24**: 3051–3055.

ANDERSEN, J. M. (1974): Nitrogen and phosphorus budgets and the role of sediments in six shallow Danish lakes. – Arch. Hydrobiol. **74**: 528–550.

– (1977): Importance of the denitrification process for the rate of degradation of organic matter in lake sediments. – In: GOLTERMAN, H. L. (ed): Interaction between sediment and freshwater. – Dr. W. Junk, The Hague–Boston–London, pp. 216–226.

ANDERSSON, G., BERGGREN, H., CRONBERG, G. & GELIN, C. (1978): Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. – Hydrobiologia **59**: 9–15.

APHA (1985): Standard methods for the examination of water and waste water. 16th edition. – American Public Health Association, New York, 1268 p.

BACHMANN, R. W. (1984): Calculation of phosphorus and nitrogen loadings to natural and artificial lakes. – Verh. Int. Verein. Limnol. **22**: 239–243.

BERGE, D., FJELD, E., HINDAR, O. & KASTE, Ø. (1997): Nitrogen retention in two Norwegian watercourses of different trophic status. – Ambio **26**: 282–288.

BLINDOW, I., ANDERSSON, G., HARGEBY, A. & JOHANSSON, S. (1992): Long-term patterns of alternative stable states in two shallow eutrophic lakes. – Freshwat. Biol. **30**: 159–167.

BREUKELAAR, A. W., LAMMENS, E. H. R. R., KLEIN BRETELER, J. G. P. & TATRAI, I. (1994): Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll-a. – Freshwat. Biol. **32**: 113–121.

CHRISTENSEN, P. B., NIELSEN, L. P., SØRENSEN, J. & REVSBECH, N. P. (1990): Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism. – Limnol. Oceanogr. **35**: 640–651.

CHRISTENSEN, P. B. & SØRENSEN, J. (1986): Temporal variation of denitrification activity in plant-covered littoral sediment from Lake Hampen, Denmark. – Appl. Envir. Microbiol. **51**: 1174–1179.

County of Funen (1996): Arreskov Sø, 1995. Vandmiljøovervågning. (Lake Arreskov. Monitoring of the Aquatic Environment), 111 pp. (in Danish).

County of Vejle (1996): Engelsholm Sø 1995. Vandmiljøovervågning. (Lake Engelsholm. Monitoring of the Aquatic Environment), 66 pp. (in Danish).

DIETER, C. D. (1990): The importance of emergent vegetation in reducing sediment resuspension in wetlands. – J. Freshw. Ecol. **5**: 467–473.

ERIKSSON, P. G. & WEISNER, S. E. B. (1996): Functional differences in epiphytic microbial communities. – Freshwat. Biol. **36**: 555–562.

– – (1997): Nitrogen removal in a wastewater reservoir: The importance of denitrification by epiphytic biofilms on submersed vegetation. – J. Environ. Qual. **26**: 905–910.

FLEISCHER, S. & STIBE, L. (1991): Drainage basin management – reducing river transported nitrogen. – Verh. Int. Verein Limnol. **24**: 1753–1755.

GILES, N., STREET, M., WRIGHT, R., PHILLIPS, V. & TRAILL-STEVENSON, J. A. (1989): Food for wildfowl increases after fish removal. – Game Cons. Ann. Rev. **20**: 137–140.

HAMILTON, D. P. & MITCHELL, S. F. (1996): An empirical model for sediment resuspension in shallow lakes. – Hydrobiologia **317**: 209–220.

Hansson, L. A. (1989): The influence of a periphytic biolayer on phosphorous exchange between substrate and water. – Arch. Hydrobiol. **115:** 21–26.

Hanson, M. A. & Butler, M. G. (1994): Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lake. – Can. J. Fish. Aquat. Sci. **51:** 1180–1188.

Henriksen, K. J., Hansen, J. & Blackburn, T. H. (1980): The influence of benthic in fauna on exchange rates of inorganic nitrogen between sediment and water column. – Ophelia **1:** 249–256.

Hovmand, M. F., Grundahl, L., Runge, E. M., Kemp, K. K. & Aistrup, W. (1993): Atmosfærisk deposition af kvælstof og fosfor. (Atmospheric deposition of nitrogen and phosphorus) – Faglig rapport fra DMU nr. 91. Danmarks Miljøundersøgelser (in Danish).

Howart, R. W., Marino, R. & Lane, J. (1988): Nitrogen fixation in freshwater, estuarine, and marine ecosystems. 1. Rates and importance. – Limnol. Oceanogr. **33:** 669–687.

James, W. F. & Barko, J. W. (1990): Macrophyte influences on the zonation of sediment accretion and composition. – Arch. Hydrobiol. **120:** 120–129.

Jansson, M. (1980): Role of benthic algae in transport of nitrogen from sediment to lake water in a shallow clear-water lake. – Arch. Hydrobiol. **89:** 101–109.

Jensen, J. P., Jeppesen, E., Kristensen, P., Christensen, P. B. & Søndergaard, M. (1992): Nitrogen loss and denitrification as studied in relation to reductions in nitrogen loading in a shallow, hypertrophic lake (Lake Søbygård, Denmark). – Int. Rev. ges. Hydrobiol. **77:** 29–42.

Jensen, J. P., Jeppesen, E., Olrik, K. & Kristensen, P. (1994): Impact of nutrients and physical factors on the shift from cyanobacterial to chlorococcal green algal dominance in shallow Danish lakes. – Can. J. Fish. Aquat. Sci. **51:** 1692–1699.

Jensen, J. P., Jeppesen, E., Søndergaard, M., Windolf, J., Lauridsen, T. & Sortkjær, L. (1995): Ferske vandområder – søer. Vandmiljøplanens Overvågningsprogram 1994. Danmarks Miljøundersøgelser. – Faglig rapport fra DMU nr. 139. 116 pp.

Jensen, J. P., Kristensen, P. & Jeppesen, E. (1990): Relationships between N loading and in-lake N concentrations in shallow Danish lakes. – Verh. Int. Verein. Limnol. **24:** 201–204.

Jeppesen, E., Jensen, J. P., Kristensen, P., Søndergaard, M., Mortensen, E., Sortkjær, O. & Olrik, K. (1990): Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. – Hydrobiologia **200/201:** 219–227.

Jeppesen, E., Jensen, J. P., Søndergaard, M., Mortensen, E. & Sortkjær, O. (1996): Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a 9 year study in shallow hypertrophic Lake Søbygård. – J. Plank. Res. **18:** 1605–1625.

Jeppesen, E., Kristensen, P., Jensen, J. P., Søndergaard, M., Mortensen, E. & Lauridsen, T. (1991): Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. – Mem. Ist. Ital. Idrobiol. **48:** 127–148.

JEPPESEN, E., SØNDERGAARD, M., KRONVANG, B., JENSEN, J. P., SVENDSEN, L. M. & LAURIDSEN, T. (in press): Lake and catchment management in Danmark. – To be published in: HARPER, D., FERGUSON, A., BRIERLEY, B. & G. PHILLIPS (Eds.): Ecological basis for lake and reservoir management. – J. Wiley & Sons.

JESPERSEN, A.-M. & CHRISTOFFERSEN, K. (1987): Measurements of chlorophyll-a from phytoplankton using ethanol as extraction solvent. – Arch. Hydrobiol. **109**: 445–454.

KRISTENSEN, P., JENSEN, J. P. & JEPPESEN, E. (1990): Simple empirical lake models. – In: Miljøstyrelsen (ed): Nitrogen and phosphorus in fresh and marine waters. – C-abstract: 125–145.

KRONVANG, B., ÆRTEBJERG, G., GRANT, R., KRISTENSEN, P. HOVMAND, M. & KIRKEGAARD, J. (1993): Nationwide monitoring of nutrients and their ecological effects: state of the Danish aquatic environment. – Ambio **22:** 176–187.

LAURIDSEN, T. L., JEPPESEN, E. & ANDERSEN, F. Ø. (1993): Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: Impact of sediment composition and water fowl grazing. – Aquat. Bot. **46:** 1–15.

LAURIDSEN, T., JEPPESEN, E. & SØNDERGAARD, M. (1994): Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish-manipulation. – Hydrobiologia **275/276:** 233–242.

LIJKLEMA, L., JANSEN, H. & ROIJACKERS, R. M. M. (1989): Eutrophication in the Netherlands. – Wat. Sci. Tech. **21:** 1899–1902.

MEIJER. M.-L., DE HAAN, M. W., BREUKELAAR, A. W. & BUITEVELD, H. (1990): Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? – Hydrobiologia **200/201:** 303–315.

MEIJER, M.-L., JEPPESEN, E., VAN DONK, E., MOSS, B., SCHEFFER, M., LAMMENS, E., VAN NES, E., BERKUM, J. A., DE JONG, G. J., FAAFENG, B. A. & JENSEN, J. P. (1994): Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five year results of four biomanipulation cases in the Netherlands and Denmark. – Hydrobiologia **275/276:** 233–242.

MOLOT, L. A. & DILLON, P. J. (1993): Nitrogen mass balances and denitrification rates in central Ontario lakes. – Biogeochemistry **20:** 195–212.

OECD (1982): Eutrophication of waters. Monitoring, assessments and control. – OECD, Paris. 210 pp.

OZIMEK, T., GULATI, R. D. & VAN DONK, E. (1990): Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. – Hydrobiologia **200/201:** 399–407.

OZIMEK, T., VAN DONK, E. & GULATI, R. D. (1993): Growth and nutrient uptake by two species of *Elodea* in experimental conditions and their role in nutrient accumulation in a macrophyte-dominated lake. – Hydrobiologia **251:** 13–18.

PELEGRÍ, S. P., NIELSEN, L. P. & BLACKBURN, T. H. (1994): Denitrification in estuarine sediment stimulated by the irrigation activity of the amphipod *Corophium volutator*. – Mar. Biol. Ecol. Pro. Ser. **105:** 285–290.

PENCZAK, T. (1983): Phosphorus, nitrogen and carbon cycling by fish populations in two small lowland rivers in Poland. – Hydrobiologia **120:** 159–165.

PERSSON, A. (1997): Effects of fish predation and excretion on the configuration of aquatic food webs. – Oikos **79:** 137–146.

PRAHL, C., JEPPESEN, E., SAND-JENSEN, K. & IVERSEN, T. M. (1991): Continuous-flow system for measuring *in vitro* oxygen and N metabolism in separated stream communities. – Freshwat. Biol. **26:** 495–506.

RISGAARD-PETERSEN, N., RYSGAARD, S., NIELSEN, L. P. & REVSBECH, N. P. (1994): Diurnal variation of denitrification in sediments colonized by benthic microphytes. – Limnol. Oceanogr. **39:** 573–579.

RYSGAARD, S., CHRISTENSEN, P. B. & NIELSEN, L. P. (1995): Seasonal variation in nitrification and denitrification in estuarine sediment colonized by benthic microalgae and bioturbating infauna. – Mar. Ecol. Prog. Ser. **126:** 111–121.

RØRSLETT, B., BERGE, D. & JOHANSEN, S. W. (1985): Mass invasion of *Elodea canadensis* in a mesotrophic, South Norwegian lake – impact on water quality. – Verh. Int. Verein. Limnol. **22:** 2920–2926.

– – – (1986): Lake enrichment by submersed macrophytes: a Norwegian whole lake experience with *Elodea canadensis*. – Aquat. Bot. **26:** 325–340.

SAS Institute (1989): SAS/STAT User's Guide, vers. 6, 4th edition.

SEITZINGER, S. P. (1988): Denitrification in freshwater and coastal marine ecosystems: Ecological and geochemical significance. – Limnol. Oceanogr. **33:** 702–724.

SHAPIRO, J. & WRIGHT, D. I. (1984): Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. – Freshwat. Biol. **14:** 371–383.

SOLÓRZANO, L. & SHARP, J. H. (1980): Determination of total dissolved nitrogen in natural waters. – Limnol. Oceanogr. **25:** 751–754.

SØNDERGAARD, M., JEPPESEN, E., MORTENSEN, E., DALL, E., KRISTENSEN, P. & SORTKJÆR, O. (1990): Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. – Hydrobiologia **200/201:** 229–240.

SVENSSON, J. M. & LEONARDSON, L. (1996): Effects of bioturbation by tube-dwelling chironomid larvae on oxygen uptake and denitrification in eutrophic lake sediments. – Freshwat. Biol. **35:** 289–300.

TATRAI, I. & ISTVANOVICS, V. (1986): The role of fish in the regulation of nutrient cycling in lake Balaton, Hungary. – Freshwat. Biol. **16:** 417–424.

VAN DONK, E., GRIMM, M. P., GULATI, R. D. & KLEIN BRETELER, J. P. G. (1990): Whole-lake food-web manipulation as a mean to study community interactions in a small ecosystem. – Hydrobiologia **200/201:** 275–289.

VAN DONK, E., GULATI, R. D., IEDEMA, A. & MEULEMANDS, J. T. (1993): Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. – Hydrobiologia **251:** 19–26.

VAN LUIJN, F., VAN DER MOLEN, D. T., LUTTMER, W. J. & BOERS, P. C. M. (1995): Influence of benthic diatoms on the nutrient release from sediments of shallow lakes recovering from eutrophication. – Wat. Sci. Tech. **32:** 89–97.

WEISNER, S., ERIKSSON, G., GRANÉLI, W. & LEONARDSON, L. (1994): Influence of macrophytes on nitrate removal in wetlands. – Ambio **23:** 363–366.

WETZEL, R. G. (1983): Limnology. – Saunders College Publishing, New York, 767 pp.

WINDOLF, J., JEPPESEN, E., JENSEN, J. P. & KRISTENSEN, P. (1996): Modelling the seasonal variation in in-lake concentration and retention of nitrogen in 16 shallow lakes: a four-year mass balance study. – Biogeochemistry **33:** 25–44.

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ECOSYSTEMS

Cascading Trophic Interactions from Fish to Bacteria and Nutrients after Reduced Sewage Loading: An 18-Year Study of a Shallow Hypertrophic Lake

Erik Jeppesen,[1]* Martin Søndergaard,[1] Jens Peder Jensen,[1] Erik Mortensen,[1] Anne-Mette Hansen,[1] and Torben Jørgensen[2]

[1]Department of Lake and Estuarine Ecology, National Environmental Research Institute, Vejlsøvej 25, DK-8600 Silkeborg; and [2]Århus County, Environmental Office, Lyseng Allé 1, DK-8230 Højbjerg, Denmark

ABSTRACT

The effects of major reductions in organic matter, total phosphorus (TP), and total nitrogen (TN) loading on the chemical environment, trophic structure, and dynamics of the hypertrophic, shallow Lake Søbygård were followed for 18 years. After the reduction in organic matter loading in 1976, the lake initially shifted from a summer clear-water state, most likely reflecting high grazing pressure by large *Daphnia* species, to a turbid state with extremely high summer mean chlorophyll *a* (up to 1400 μg L^{-1}), high pH (up to 10.2), and low zooplankton grazing. Subsequently, a more variable state with periodically high grazing rates on phytoplankton and bacteria was established. Changes in zooplankton abundance and grazing could be attributed to variations in cyprinid abundance due to a fish kill (probably as a consequence of oxygen depletion) and pH-induced variations in fish recruitment and fry survival. The results suggest strong cascading effects of fish on the abundance and size of zooplankton and phytoplankton and on phytoplankton production. A comparatively weak cascading effect on ciliates and bacterioplankton is suggested. Due to high internal loading, only minor changes were observed in lake-water TP after a reduction in external TP loading of approximately 80% in 1982; net retention of TP was still negative 13 years after the loading reduction, despite a short hydraulic retention time of a few weeks. TN, however, decreased proportionally to the TN-loading reduction in 1987, suggesting a fast N equilibration. Only minor improvement in the environmental state of the lake has been observed. We suggest that another decade will be required before the lake is in equilibrium with present external P loading.

Key words: recovery; top-down control; bottom-up control; loading reduction; internal loading; fish; zooplankton; phytoplankton; ciliates; bacteria; size distribution; production.

INTRODUCTION

Eutrophication has resulted in a deterioration of lake ecosystems worldwide (OECD 1982; Sas 1989; Kristensen and Hansen 1994). In many countries, attempts to restore lakes by reducing external nutrient loading (Sas 1989) have in some cases resulted in a new equilibrium within a few years (Kristensen and others 1990). Many lakes, however, are resistant to recovery (Ryding 1981; Cullen and Forsberg 1988; Marsden 1989; Sas 1989; Jeppesen and others 1991; Cooke and others 1993; Van der Molen and Boers 1994). Delayed response to restoration measures is not restricted to lakes with a long hydraulic

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Dr. Hansen's current address: Odense University, Institute of Biology, Campusvej 55, DK-5230 Odense M, Denmark.

**Corresponding author. e-mail:* ej@dmu.dk retention time. Some shallow lakes with a water renewal time of only a few weeks may respond in 10–15 years (Jeppesen and others 1991). Apart from dilution (renewal of the water mass), delayed recovery may be attributed to phosphorus (P) release from the accumulated sediment pool (internal loading). Internal P loading seems to be an important factor in the long term (Ryding 1981), while internal nitrogen (N) loading following N-loading reduction appears important only in the short term (Jensen and others 1992).

Resistance may also be related to a delay in biological changes, for example, in the fish community or in the appearance of submerged macrophytes (Gulati and others 1990; Moss 1990; Lauridsen and others 1993). Biomanipulation experiments show that active combating of biological resistance will often reduce internal nutrient loading (Shapiro and Wright 1984; Jeppesen and others 1998), suggesting that chemical and biological resilience are highly interlinked (Boers and others 1991; Carpenter and others 1992). Recent studies suggest that the structuring role of fish in the entire pelagic ecosystem is most significant in eutrophic lakes (Leibold 1989; Sarnelle 1992) and generally more so in shallow lakes (Jeppesen and others 1997b). The duration, course, and outcome of the transient phase in shallow, eutrophic lakes after an external nutrient-loading reduction are particularly affected. The majority of detailed lake-recovery studies following nutrient-loading reduction describe the early, short-term effects; only a few cover more than a decade [for example, see Sas (1989), Edmonson (1985), Cullen and Forsberg (1988), Welch and Cooke (1995), Lathrop and others (1996) and Hosper (1997)]. To our knowledge, no long-term recovery studies have investigated the entire pelagic, biological community from bacteria to fish in combination with nutrient dynamics.

We followed the recovery phase of shallow hypertrophic Lake Søbygård for 18 years and more intensively for the past 12 years. The study consisted of N and P mass balances (Jensen and others 1992; Søndergaard and others 1993), internal P loading (Søndergaard and others 1990, 1993), and changes in pelagic trophic structure from bacteria to fish (Jeppesen and others 1990b, 1990c, 1992, 1996, 1997a; Hansen and Jeppesen 1992; Mortensen and others unpublished data). Phytoplankton and bacterioplankton production and zooplankton grazing were also measured (Jeppesen and others 1996, 1997a). In this report, we present an analysis of data from the entire study period, with special emphasis on biotic changes in the pelagial. We demonstrate how profoundly the recovery process in shallow hypertrophic lakes may be affected by perturbations in the fish community, mediated by both external factors and internal feedback mechanisms.

STUDY AREA

The study was conducted in Lake Søbygård, a small (0.39 km^2) shallow (mean depth, 1.0 m; and maximum depth, 1.9 m) lake in Jutland, Denmark. The hydraulic retention time is short, with an annual mean of 18–27 days and a summer mean of 23–34 days. The lake catchment area is 12 km^2, consisting of grassland, areas under intense agricultural cultivation, and forest. The lake shoreline is forested, except to the west, where it is exposed to the prevailing westerly wind. Emergent and floating-leaved macrophytes are sparsely developed, and submerged vegetation is absent.

The lake receives from 80% to 90% of its water from an inlet that also receives sewage effluent from a small town, while iron-rich groundwater represents approximately 10% of the water input. The lake received large amounts of primary treated sewage water during the 1960s and early 1970s. In 1976, biological treatment was initiated at the sewage plant, and this led to a threefold to tenfold reduction in organic matter loading to the lake. In 1982, P stripping was introduced at the plant and, in 1987, external N-loading was reduced by closing down a local slaughterhouse.

MATERIALS AND METHODS

Chemical Variables

Water samples were collected fortnightly or more often (between 1000 and 1200 h) with a Patalas sampler at a midlake station at 0.5-m and 1.5-m depth. Mixed total P (TP) was determined as molybdate-reactive P (Murphy and Riley 1962) after persulfate digestion (Koroleff 1970). Total N (TN) was determined as nitrites + nitrate after potassium persulfate digestion (Solórzano and Sharp 1980). Nitrites and nitrate were determined as nitrite on a Tecator 5012 flow-injection analyzer supplied with a copper–cadmium reductor column. Chlorophyll *a* was determined spectrophotometrically after ethanol extraction [according to the method described by Jespersen and Christoffersen (1987)], except for 1978–81, when acetone extraction was used. Because acetone extraction of chlorophyll *a* in green algae is inefficient, chlorophyll *a* before 1982 was most likely underestimated.

Mass Balances

The study of Lake Søbygård was initiated in 1978 and a more intensive program began in 1984. To estimate N and P loading and retention, water was sampled manually in the main inlet and in the outlet in 1978 and in 1981 and with an automatic sampler from 1984 to 1995. In 1978 and in 1981, discrete samples were taken monthly in the inlet and outlet. Beginning in 1984, 3–4 samples were taken during each 24-h period. Before analysis, samples were pooled to represent either a 1-day or 7-day average. Additional water samples were taken 2–8 times in 1985 from other small streams entering the lake. Discharge (Q) of the lake inlet was measured 46 times during the study period. In the lake outlet, discharge was calculated from automatically recorded data of water level (H) by using a derived relationship between H and Q. In the small spring-fed streams along the lake shore, discharges were also measured 2–8 times during 1985. These sources accounted for approximately 10% of the total water input to the lake throughout the season. Daily values of Q inlet could therefore be calculated as Q-outlet minus Q-springs. Daily total N and P concentrations were calculated by linear interpolation of observed values. N and P transport in the main inlet, in the outlet, and in the springs entering the lake was calculated by multiplying daily water discharge values with interpolated daily N and P concentrations. N and P precipitation on the lake surface was considered to be constant during the investigation period (5 mg N m^{-2} d^{-1} and 0.04 mg P m^{-2} d^{-1}) (Hovmand and others 1993). Monthly retention of P and N was then calculated by using the mass balance model of Messer and Brezonik (1978): retention = total input + storage − total output. N fixation was not included, but is considered of minor importance because cyanobacteria biomass was low during 1984–95.

Biological Variables

The abundance and biomass of phytoplankton and zooplankton were determined on composite samples from a midlake station and, in the case of zooplankton, also at an eastern station and a western station on occasion. For enumeration of zooplankton, 6.6–7.2 L of water from each station was filtered through a 50 µm (1984) or 20 µm (1985–95) mesh sieve and then fixed with 1 mL Lugol's solution in 100 mL tap water. Subsamples were counted at 40- to 100-fold magnification, depending on zooplankton size. Between 2% and 100% of the sample volume was counted on each sampling date, depending on zooplankton abundance. During periods with peak zooplankton densities, all samples were counted; otherwise, only one sample (midlake station) was analyzed. Phytoplankton were counted in an inverse microscope, and biovolume was determined for each species or subspecies by using geometric formulae (Olrik 1991). We used 0.24 pg C μm^{-3} (Reynolds 1984) to convert biovolume to carbon.

Ciliates were counted from the phytoplankton samples. At least 100 individuals per sample were counted, if possible, and maximum length measured on a minimum of 50 cells. Species determination was not performed.

Bacterioplankton production was estimated according to the method described by Fuhrmann and Azam (1982), with only minor changes (Jeppesen and others 1992). Triplicate 25-mL samples and controls (formalin killed) were incubated in situ with 12.5 nM ^{3}H-methylthymidine for 15–60 min, depending on lake-water temperature. Production was calculated from ^{3}H-methylthymidine by using the following conversion factors: 2×10^9 cells nmol thymidine^{-1} (Riemann and others 1982) and 25 tg C cell^{-1} (R. Bell personal communication). Bacteria were enumerated according to the method described by Hobbie and colleagues (1977), with minor modifications (Jeppesen and others 1992) at 1560× magnification by using a Leitz epifluorescence microscope equipped with a 75-W mercury lamp. At least 500 cells were counted on 2–3 different fields, and cell dimensions recorded. Cells were divided into rods (8 size classes) and cocci (8 classes), and cell volume was calculated by using standard geometric formulae.

Phytoplankton production corrected for dark fixation was estimated from the photosynthesis-versus-irradiance relationship determined from laboratory incubation with $H_2{}^{14}CO_3$ at six different light intensities. From this relationship, a 24-h integrated value of areal production was then calculated by using observations of lake Secchi depth (converted to a light-extinction coefficient) and hourly data of surface irradiance at a station situated 30–40 km from the lake. Zooplankton community grazing on phytoplankton and bacteria was estimated according to the method described by Jeppesen and colleagues (1996). In total, 32 grazing experiments were carried out during 1984–86 and 1992 by using ^{3}H-thymidine-labeled bacterioplankton and ^{14}C-labeled phytoplankton. Specific clearance rate and daily ingestion of the different zooplankton species, which were temperature corrected to 15°C according to the method described by Gulati and colleagues (1982) and corrected for isotope loss (Jeppesen and others 1996), were estimated by multiple regression. Total daily ingestion for the entire study period was then calculated by multiplying the calculated biomass-specific daily ingestion, adjusted to actual water temperature, with the biomass of the different zooplankton.

Density, biomass, and age structure of fish populations were estimated by mark–recapture and scale analysis in midsummer 1986 (Mortensen and others unpublished manuscript). Beginning in 1987, an annual gill-net survey was conducted (Mortensen and others unpublished manuscript) between 15 August and 15 September (November in 1988) at a time when fish fry could be included in the catches. The lake was divide into six sections, and in each section three multi-mesh-size gill nets (14 different mesh sizes ranging form 6.25 to 75 mm) were set overnight (from about 1600 to 0900 h). One gill net was set perpendicular to the shoreline, another was set parallel with and about 25 m from the shoreline, and the third was set at about half the distance from the center of the lake.

All chemical and biological variables, except fish, are interpolated summer (1 May–1 October) or annual means of 10–91 samples based on fortnightly or more frequent samplings.

RESULTS

Nutrient Loading, Water Chemistry, and Secchi Depth

Since 1982, P removal measures at the treatment plant have resulted in a loading reduction from 28–33 g P m^{-2} y^{-1} in 1978–81 to 2–7 g P m^{-2} y^{-1} (Figure 1). Annual mean TP concentrations in the main inlet decreased from 1–3 mg P L^{-1} to 0.15–0.25 mg P L^{-1} (Søndergaard and others 1993). Comparatively minor changes were observed in inlake mean summer TP ranging from 0.9–1.6 mg P L^{-1} before the P-loading reduction to 0.4–1.0 mg P L^{-1} after the reduction (Figure 2). However, linear regression with time as the independent variable revealed a significant decline in summer mean TP from 1978 to 1995 ($P < 0.04$, $r^2 = 0.25$, $n = 15$). The minor response to the P-loading reduction reflects high internal loading. Accordingly, lake retention of TP shifted from positive values before 1982 to negative values after. Net release ranged between 1.9 and 5.4 g P m^{-2} y^{-1} during 1983–95 without showing any declining trend over time. Net release was, however, positively related to annual mean lake-water chlorophyll *a* (log-transformed data, $r^2 = 0.54$, $P < 0.02$, $n = 12$) after the P-loading reduction. The observed annual mean inlake TP (TP_{lake}) was lower than predicted from the Vollenweider (1976) equation ($TP_{lake} = [TP_{in}[1/(1 + \sqrt{tw})]]$, TP_{lake}, where *tw* is the hydraulic retention time (years) and TP_{in} is the annual mean inlet TP concentration). Following the reduction, the observed TP_{lake} was substantially higher than the predicted values (Figure 3). Closing the slaughterhouse in July 1987 resulted in a reduction in N loading from 350–498 mg N m^{-2} d^{-1} during 1984–86 to 195–299 mg N m^{-2} d^{-1} during 1988–95 (Figure 1). N retention ranged from 137–200 mg N m^{-2} d^{-1} before 1987 to 55–118 mg N m^{-2} d^{-1} after the N-loading reduction. Between 22% and 40% of the loading was retained (including loss by denitrification) in the lake, and there was no tendency toward a temporary reduction in the retention percentage after the TN-loading reduction. The lake summer mean TN averaged 4.0 mg N L^{-1} before and 2.2 mg N L^{-1} after the N-loading reduction in 1987 (Figure 2).

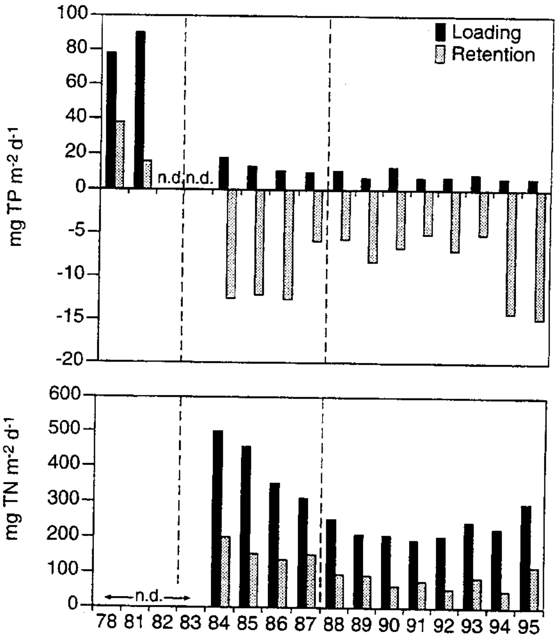

Figure 1. Estimated annual mean external loading of total phosphorus, total nitrogen and net retention from 1978–1995. External sewage loading of phosphorus and nitrogen was reduced in 1982 and in 1987, respectively (shown by broken lines). n.d. = no data.

The changes observed in annual mean inlake TN (TN_{lake}) closely followed those predicted by Windolf and colleagues (1996) for 16 shallow Danish lakes [$TN_{lake} = 0.27\, TN_{in}\, tw^{-0.22}\, z^{0.12}$, where TN_{in} is annual mean inlet concentration and *z* is mean lake depth (in meters)] (Figure 3). The TN–TP ratio was low, ranging from 3.5–7.8 (mean, 5.4), before 1987 to 3.0–6.0 after 1987 (mean, 4.2) (Figure 2).

Despite the relatively small changes in TP and TN in the lake, chlorophyll *a*, water transparency, and pH changed markedly (Figure 2). Mean summer chlorophyll *a* was relatively low (50 µg L^{-1}) in 1978, two years after biological treatment was implemented at the upstream sewage plant, and in 1981 chlorophyll *a* then increased, peaking in 1984 (840

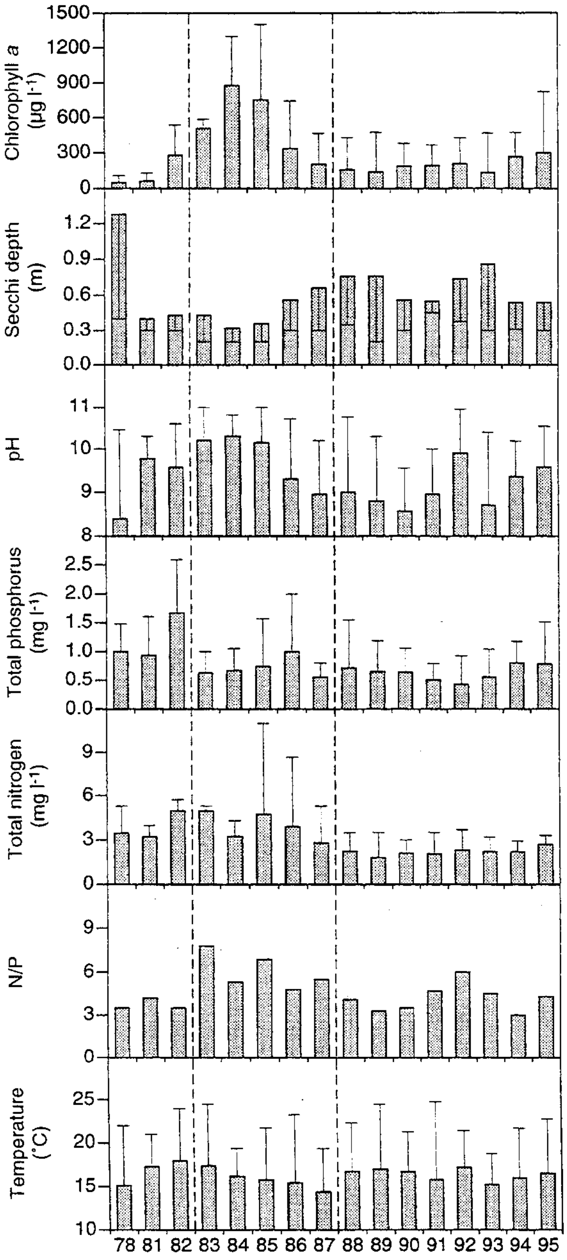

Figure 2. Interpolated summer (1 May–1 October) mean chlorophyll *a*, Secchi depth, pH, total phosphorus (P), total nitrogen (N), N–P ratio, and lake-water temperature during 1978–95. Minimum Secchi depth and maximum values of the other variables, except for the N–P ratio, are also shown.

µg L^{-1}), two years after the external P-loading reduction caused by P stripping at the plant. Thereafter, chlorophyll *a* decreased to 139 µg L^{-1} in 1989 and has since fluctuated between 133 and 299 µg L^{-1} without any distinct pattern. Maximum chlorophyll *a* varied from 110 µg L^{-1} in 1978 to as much as 1400 µg L^{-1} in 1985. Concurrent with the changes in chlorophyll *a*, summer mean Secchi depth decreased from more than 1.20 m in 1978 to 0.31 m in 1984 and has since fluctuated between 0.55 and 0.84 m. Mean pH increased from 8.3 in 1978 to 10.2 in 1984–85, after which it ranged between 8.6 and 9.9. Maximum recorded pH was as high as 11 in 1985. The diel variation in pH was typically less than 0.3 (Søndergaard and others 1990).

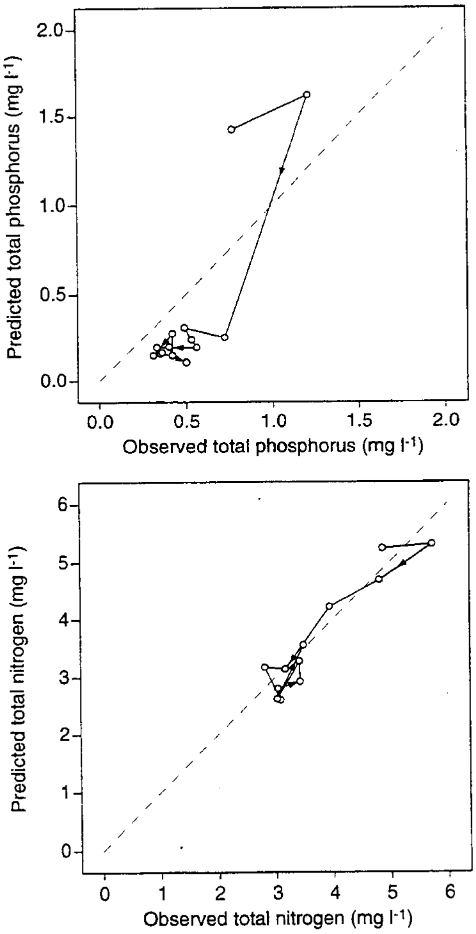

Figure 3. Observed annual mean total phosphorus and total nitrogen concentrations compared with predicted values based on equations developed by Vollenweider (1976) and Windolf and colleagues (1996), respectively.

Phytoplankton and Zooplankton

The major changes in chlorophyll *a* were accompanied by changes in the phytoplankton community structure (Figure 4). In 1978, when chlorophyll *a* was low, cyanobacteria (primarily *Aphanizomenon flos–aqua*) and small spherical green algae (mainly

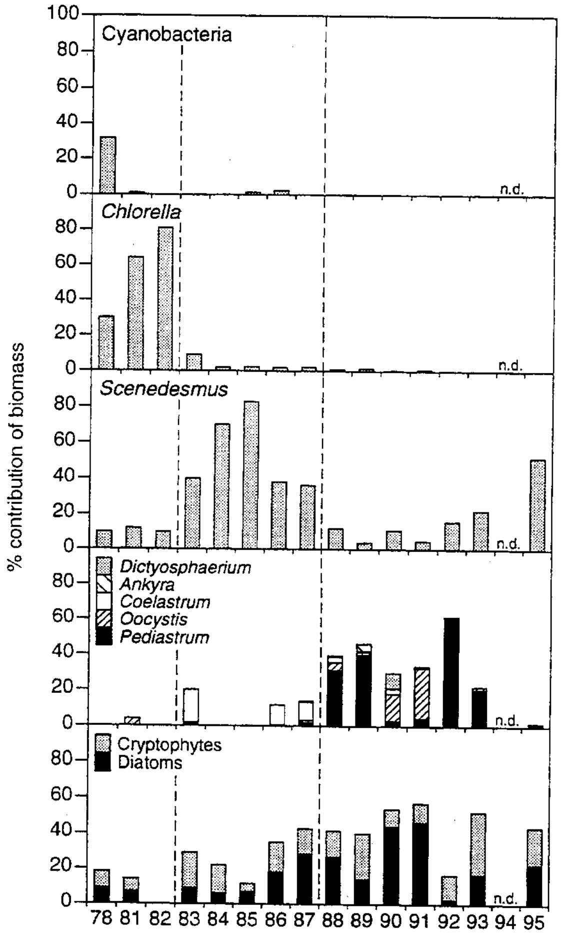

Figure 4. Percentage contribution to the biovolume of various lake-water phytoplankton groups during 1978–95. The percentages are estimated from interpolated summer mean values (n.d., no data).

Chlorella) were most abundant, each constituting about 30% of the total volume. Following the major increase in chlorophyll *a* during 1981–85, cyanobacteria almost disappeared, while first *Chlorella* in 1981–82 and subsequently *Scenedesmus* spp. in 1984–85 became exclusively dominant, constituting 64%–82% and 70%–83% of the total volume, respectively. The decline in chlorophyll *a* during 1986–92 corresponded with an increase in the abundance of large or gelatinous green algae. Subsequently, *Scenedesmus* increased again to 52% in 1995. In addition, the contribution of diatoms and cryptophytes to the total biovolume (summer means) increased significantly with time (linear regression, $P < 0.01$, $r^2 = 0.43$, $n = 14$).

Changes in phytoplankton mean volume were accompanied by significant changes in light-saturated phytoplankton production (P_{max}). P_{max} had a significant positive relationship to phytoplankton volume and temperature, but declined with increasing phytoplankton mean volume (Table 1). Accordingly, volume-specific chlorophyll *a* declined significantly with increasing mean volume. However, P_{max} per unit of chlorophyll *a* increased slightly with phytoplankton mean volume, indicating a "chlorophyll *a* package effect" (Elser and others 1986) that partly compensated for the reduction in volume-specific P_{max}. Nevertheless, total biomass and total primary production decreased with increasing phytoplankton mean volume (Figure 5).

From the foregoing data, it is obvious that the major changes in chlorophyll *a* and the phytoplankton community and its size distribution cannot be explained by changes in nutrient concentrations. On the other hand, these changes suggest major top-down control variations mediated by changes in zooplankton abundance, size distribution, and grazing. The macrozooplankton community consisted of only a few species. *Daphnia longispina* and *Bosmina longirostris* completely dominated the cladoceran community, contributing 95%–100% of the cladoceran biomass. No calanoid copepods were found, and the cyclopoids were exclusively dominated by *Cyclops vicinus*, whose mean summer density ranged between 200 and 492 individuals L^{-1} (Figure 6), except for 1990, when low densities were recorded. Maximum densities of *C. vicinus* exceeded 2000 individuals L^{-1} (Hansen and Jeppesen 1992). During the study period, the number of rotifer taxa identified in a given year ranged between 6 and 31. Species of *Brachionus* were exclusively dominant in 1984–86 and again in 1995. In other years, the rotifer community was diverse, with species of *Keratella, Synchaeta, Filinia, Polyathra,* and *Asplanchna* dominating the rotifer biomass (unpublished data).

The structure and abundance of filter-feeding zooplankton changed markedly (Figure 6). In the early 1980s, densities of *B. longirostris* were high: in 1981, the mean abundance was 200 indiv L^{-1}. In 1983, it was 850 indiv L^{-1}, and maximum densities as high as 10,000 were recorded, while chlorophyll *a* was relatively low (data now shown). However, *Bosmina* almost disappeared in June 1983, and phytoplankton became abundant. Low cladoceran density and biomass were also recorded in 1984 and 1985 (Figures 5 and 6), when summer mean chlorophyll *a* was at its highest. Concurrently with the subsequent decline in chlorophyll *a* and algal biomass during 1986–89, cladoceran biomass increased with *Daphnia longispina* dominating (Figures 2 and 6). At the same time, *Scenedesmus* spp. were replaced by less-grazing-sensitive species (Figure 4). Among

Table 1. Multiple-Regression Analysis Relating Light-Saturated Phytoplankton ^{14}C Production (P_{max}, mg C L^{-1} d^{-1}) During Summer (1 May–1 October) to Chlorophyll *a* (Chl*a*, µg l^{-1}), Mean Phytoplankton Volume (M_{vol} µm^3 Cell^{-1}), Phytoplankton Volume (T_{vol}, mm^3 l^{-1}), and Water Temperature (Temp. °C) for the Entire Study Period. All, Except Temperature, Are Log$_e$ Transformed, SE in Parenthesis

	Intercept	Log$_e$ (Chl*a*)	Log$_e$ (T_{vol})	Log$_e$ (M_{vol})	Temp	$P<$	r^2	n
Log$_e$ (P_{max})	−5.3****	0.93***	—	0.15***	—	0.0001	0.87	137
	(0.2)	(0.03)		(0.04)				
Log$_e$ (P_{max})	−5.9****	0.91****	—	0.09*	0.04***	0.0001	0.88	134
	(0.2)	(0.03)		(0.04)	(0.01)			
Log$_e$ (P_{max})	−3.5****	—	0.82****	−0.21****	—	0.0001	0.79	137
	(0.1)		(0.04)	(0.05)				
Log$_e$ (P_{max})	−4.4****	—	0.81****	−0.27****	0.05***	0.0001	0.80	134
	(0.3)		(0.04)	(0.05)	(0.01)			

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*, **, ***, **** are $P < 0.05, 0.01, 0.001, 0.0001$, respectively.

these, *Coelastrum* spp. dominated in 1986–87, and *Pediastrum boryanum* and *Ankyra judayi* dominated in 1988–89 (Figure 4). Thereafter, the zooplankton community shifted to a dominance by *B. longirostris* and rotifers in 1990–91, with an accompanying increase in intermediate-sized green algae, such as *Oocystis* and *Dictyosphaerium* sp. In 1992, *D. longispina* was again the most abundant filter feeder, and the large *P. boryanum* returned as the dominant green algae.

Accordingly, mean sizes of phytoplankton and zooplankton changed markedly. Cladoceran mean size increased threefold from approximately 0.4 mm in 1984–85 to 1.1–1.2 mm in 1988–89, and the phytoplankton mean volume simultaneously increased five- to eightfold to 1140–1230 µm^3 (Figure 5). Intermediately low phytoplankton mean volumes were found in 1990–91. Linear regression revealed a significant positive relationship between the mean size of phytoplankton compared with total cladoceran biomass, total zooplankton biomass, and the estimated zooplankton-grazing pressure on phytoplankton (Table 2), and between mean phytoplankton volume (M_{vol}) compared with mean size of cladocerans (C_{size}) [M_{vol} (µm^3) $= -0.1 + 1.0 * C_{size}$ (µm) ($r^2 = 0.55$, $P < 0.01$, $n = 10$)].

A grazing equation for the lake based on 31 measurements of clearance rates on ^{14}C-labeled phytoplankton during 1984–91 (Jeppesen and others 1996) revealed the importance of grazing. Zooplankton ingested 1%–2% of the phytoplankton biomass d^{-1} during summer in 1984–85 (2%–4% of phytoplankton production), increasing to 20%–27% (40%–53% of production) in 1988–90. In the subsequent years, it varied between 9% and 22 % of the biomass d^{-1} (Figure 5). Linear regression revealed a significant negative relationship between estimated zooplankton grazing compared with total phytoplankton biomass and grazing compared with phytoplankton production (Table 2).

Ciliates and Bacterioplankton

The summer mean abundance of ciliates ranged from 299 mL^{-1} in 1985 to 117 mL^{-1} in 1990 (Figure 7). The average maximum length of ciliates ranged from 14.5 to 24 µm and was highest (18–24 µm) in years when *Bosmina longirostris* and rotifers dominated, and was particularly high (24 µm) in 1990 when the biomass of cyclopoid copepods was low.

The biomass of bacterioplankton ranged between 0.21 and 0.41 g C m^{-2}. It was particularly high in years with low zooplankton biomass or high biomass of rotifers and *B. longirostris* (1985, 1990, and 1991). Small bacteria dominated, the average volume ranging from 0.050 µm^3 cell^{-1} to 0.074 µm^3 cell^{-1}, with the lowest volumes occurring when *Bosmina* and rotifers were abundant. Bacterioplankton production was relatively constant (0.15–0.22 g C m^{-2} d^{-1}) during most years, but somewhat higher in 1990–91 (0.31–0.32 g C m^{-2} d^{-1}).

The impact of zooplankton on bacterioplankton was further elucidated by a grazing equation developed by Jeppesen and colleagues (1996) on the basis of grazing experiments in the lake with ^{3}H-thymidine-labeled bacterioplankton. The calculated ingestion was low in 1985 (less than 0.7% of bacterioplankton biomass), but increased to a maximum of 67% of bacterioplankton biomass and 88% of bacterioplankton production in 1988. Bacterio-

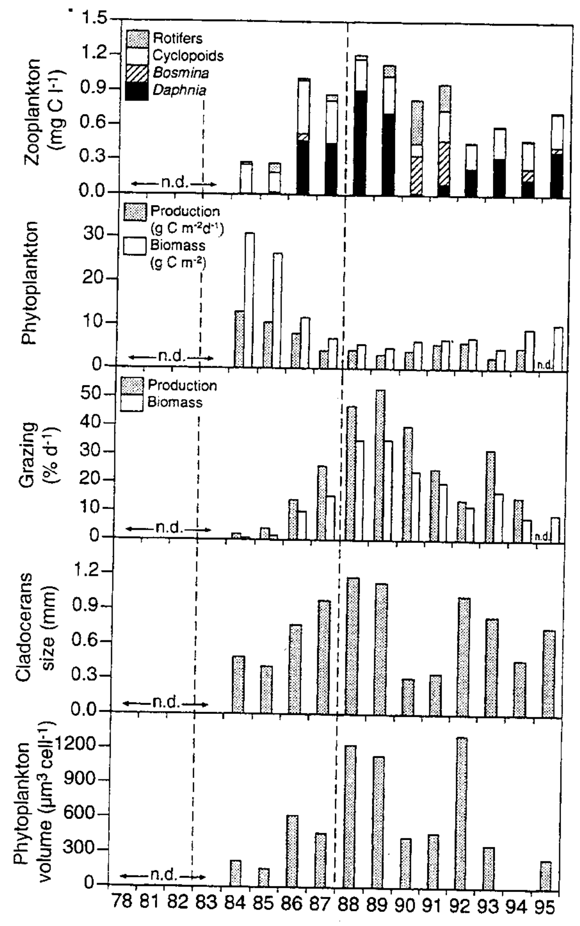

Figure 5. Interpolated summer means of the biomass of various zooplankton, phytoplankton production, and biomass, estimated macrozooplankton grazing in percentage of phytoplankton production and biomass, average size of cladocerans, and average biovolume of phytoplankton during 1984–95 (n.d., no data).

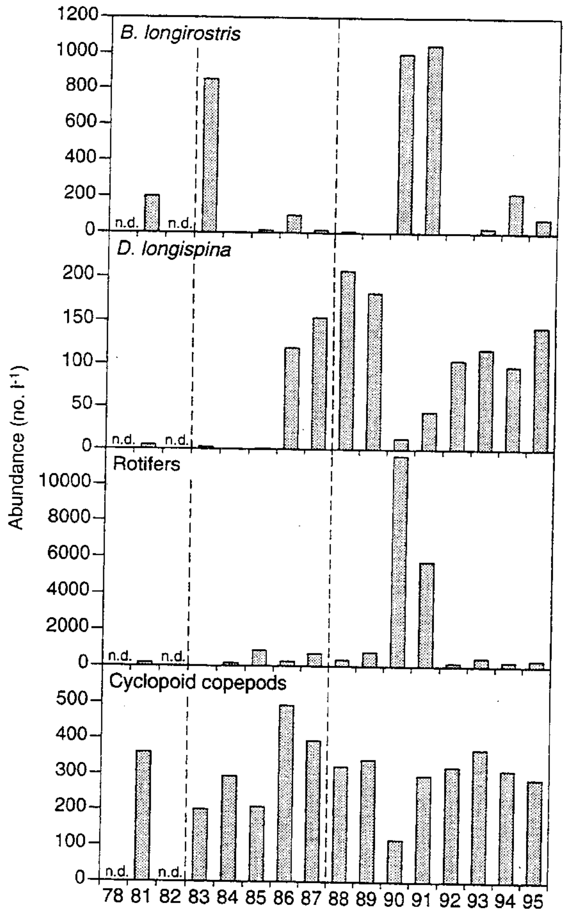

Figure 6. Interpolated summer mean abundance of various zooplankton during 1981–95 (n.d., no data).

plankton biomass was depressed the same year (Figure 7). Low grazing and high biomass of bacterioplankton were found in 1990–91 (*B. longirostris* and rotifer dominance). However, no significant relationship was found between estimated zooplankton grazing on bacterioplankton compared with either biomass, production, or size of bacterioplankton (Table 2).

Fish

The major changes in the zooplankton community structure and size distribution suggest large variations in fish predation. Quantitative information on fish is available from 1986 to 1996. In 1986, the total biomass of the planktivorous fish population was estimated as 67 g wet weight m^{-2}. Roach (*Rutilus rutilus*), rudd (*Scardinius erypthrophtalmus*), and bream (*Abramis brama*) constituted 63%, 34%, and 3% of the biomass and 53%, 46%, and 1% of the planktivorous fish density, respectively. For these three species, the age classes 2+ and 8+ represented more than 80% of the fish population in terms of numbers, while fish younger than 2–3 years and older than 8 years were almost absent.

Major changes in catches per net (that is, catch per unit effort, CPUE) in multiple-mesh-sized gill nets were observed since 1987 (Figure 8). The CPUE for roach in terms of numbers ranged from 34 to 205. Rudd and three-spined sticklebacks (*Gasterosteus aculeatus*) were particularly abundant in 1989–90. CPUE of the potentially carnivorous perch was less than 3, but there was a tendency toward increasing abundance from 1988 to 1995. CPUE, as biomass, fluctuated less. Mean CPUE of the fish

Table 2. Linear Regression Relating Various Phytoplankton and Bacterioplankton Variables to Cladoceran Biomass and Estimated Zooplankton-Grazing Rates (All Data Are Interpolated, Log-Transformed Summer Means), SE in parenthesis

	Log$_e$ (Cladoceran Biomass, mg C L^{-1})					Log$_e$ (Zooplankton Biomass, mg C L^{-1})					Log$_e$ (Zooplankton Grazing, mg C L^{-1} d^{-1})				
	Intercept	Slope	$P<$	r^2	n	Intercept	Slope	$P<$	r^2	n	Intercept	Slope	$P<$	r^2	n
Log$_e$ (phytoplankton biomass, mg C L^{-1})	1.86 (0.13)	−0.32 (0.06)	0.0002	0.76	11	1.97 (0.18)	−0.89 (0.27)	0.01	0.51	11	2.32 (0.115)	−0.82 (0.19)	0.002	0.64	11
Log$_e$ (phytoplankton production, mg C L^{-1} d^{-1})	1.33 (0.06)	−0.22 (0.06)	0.006	0.59	10	1.44 (0.12)	−0.56 (0.18)	0.03	0.42	10	1.66 (0.11)	−0.57 (0.19)	0.02	0.50	10
Log$_e$ (phytoplankton mean volume, μm^3)	6.59 (0.23)	0.27 (0.10)	0.03	0.43	10	6.55 (0.22)	0.88 (0.34)	0.04	0.42	10	6.22 (0.16)	0.78 (0.26)	0.02	0.49	10
Log$_e$ (bacterioplankton production, mg C L^{-1} d^{-1})	−1.56 (0.14)	0.07 (0.09)	NS	0.06	10	−1.58 (0.11)	0.16 (0.19)	NS	0.08	10	−1.90 (0.25)	−0.10 (0.08)	NS	0.14	10
Log$_e$ (bacterioplankton biomass, mg C L^{-1})	−1.26 (0.13)	−0.13 (0.08)	NS	0.23	10	−1.17 (0.11)	−0.17 (0.18)	NS	0.09	10	−1.47 (0.23)	−0.13 (0.08)	NS	0.25	10
Log$_e$ (bacterioplankton mean volume, μm^3 $cell^{-1}$)	−2.84 (0.05)	−0.05 (0.03)	NS	0.26	10	−2.81 (0.04)	−0.12 (0.07)	NS	0.28	10	−2.82 (0.10)	−0.02 (0.03)	NS	0.03	10

NS, not significant.

community ranged between 9.0 and 16.9 kg net^{-1} in 1990 and 1994–95 (Figure 8), respectively, mainly due to roach (CPUE, 8.1–15.4 kg net^{-1}) and rudd. The biomass of predatory fish was less than 3%. Linear regression revealed a significant negative relationship between total cladoceran biomass and mean length of *Daphnia* spp. compared with cyprinid CPUE numbers and between mean length of *Daphnia* compared with CPUE, while a weak negative relationship between CPUE and the estimated zooplankton grazing on bacterioplankton was observed (Table 3). No significant relationships between CPUE in terms of biomass and any of these variables were found (data not shown).

DISCUSSION

Prolonged Internal Loading of Total Phosphorus

Most studies of recovery following P-loading reduction have shown negative net retention of P for 0–5 years (Sas 1989; Van der Moelen and Boers 1994). Despite the low hydraulic retention time of a few weeks, net retention of P in Lake Søbjård has remained negative for 13 years now (or 204 water renewal times). Even in 1995, P concentrations still exceeded five times the value predicted by the equation developed by Vollenweider (1976). The high and persistently negative retention reflects a high-P pool in the sediment amounting to 240 g P m^{-2} of the upper 23 cm of sediment as measured in 1990 (Søndergaard and others 1993). Immediately following the external loading reduction, TP was released from the surface sediment, but at present it is being released from the 18- to 23-cm sediment level (Søndergaard and others 1993 and unpublished results). Based on iron–TP ratios in the upper sediment, Søndergaard and colleagues (1993) argued that at least 26 g P m^{-2} was expected to be released after 1990 before a new equilibrium based on the present P-loading could be obtained. From 1990 to 1995, the net release has been 17 g P m^{-2}.

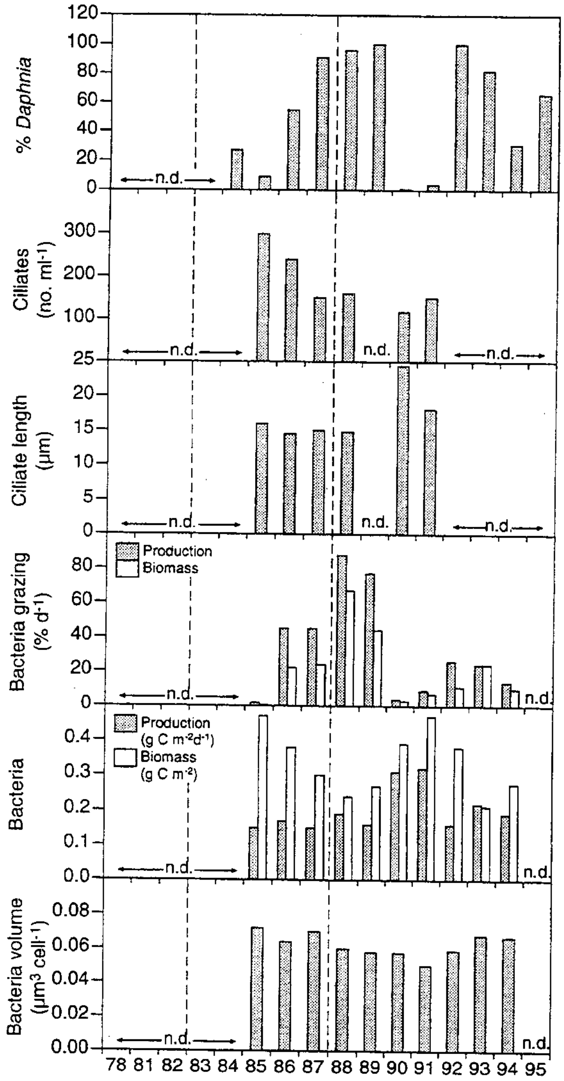

Figure 7. Summer means of the contribution of *Daphnia* as a percentage of total cladoceran abundance (calculated from interpolated means), abundance and mean length of ciliates, estimated zooplankton grazing on bacterioplankton as a percentage of bacterioplankton biomass and production, and mean bacterioplankton volume during 1984–95. (n.d., no data.)

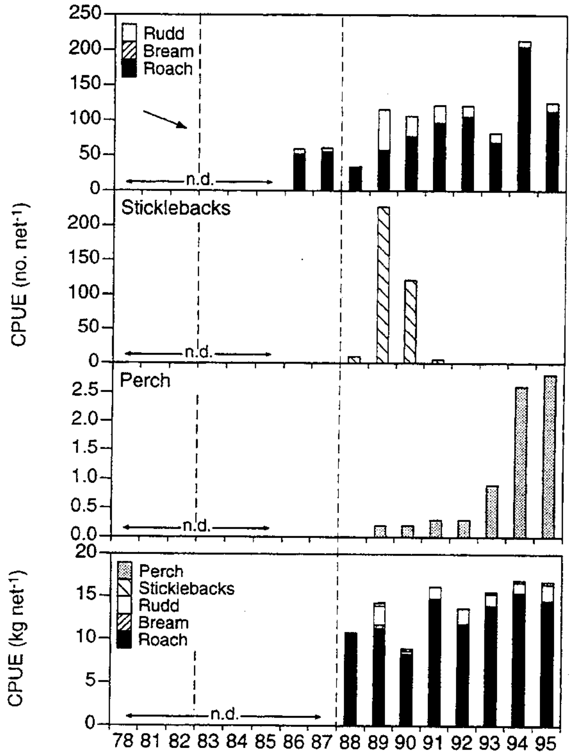

Figure 8. Average catch per unit effort (CPUE) of predominant fish species caught in multiple mesh-sized gill nets (14 sizes between 6.25 and 75 mm; 18 nets) during 16 h (overnight) between 15 August and 15 September of each year (November in 1988). CPUE in terms of numbers and biomass are given; roach, *Rutilus rutilus*, bream, *Abramis brama*, rudd, *Scardinius erythrophthalmus*, perch, *Perca fluviatilis*, stickleback (three-spined), *Gasterosteus aculeatus*. No fish data (n.d.) exist before 1986, but mark–recapture experiments from 1986 suggest higher numbers during the early 1980s, as indicated by the *arrow*. (n.d., no data.)

Predictions based on a dynamic P model suggest that another decade will pass before the equilibrium is reached (Jensen and others 1994a).

Net P release was positively related to chlorophyll *a* during 1983 to 1995, indicating benthic–pelagic coupling. The higher net release in years with high chlorophyll *a* was probably caused by higher oxygen consumption in the sediment mediated by a higher sedimentation of phytoplankton. The importance of microbial metabolism for P release from sediments in shallow lakes has been demonstrated in several studies [for example, see Gächter and colleagues (1988) and Boström and colleagues (1988)], including Lake Søbygård (Jensen and Andersen 1992). In the years with high chlorophyll *a*, pH was also high. High pH reduced P binding to iron hydroxides in the lake sediments, thereby enhancing P release to the overlying water [for example, see Boström and colleagues (1982)]. Jensen and Andersen (1992) confirmed that high pH may cause an increase in the P-release rate from the sediment in Lake Søbygård in early spring, but that the pH effect is less important compared with the microbial-mediated release during summer. Lower net internal loading due to a grazer-mediated reduction in chlorophyll *a* has also been found in several fish manipulation studies [for example, see

Table 3. Linear Regression of Some Zooplankton Variables and Estimated Grazing on Phytoplankton and Bacterioplankton Compared with the Average Number of Cyprinids Caught in Multiple-Mesh-Size Gill Nets (14 Different Mesh Sizes, 6.25–75 mm) During 16 Hours in Early Autumn (15 August–15 September). The *y*-Variables Are Interpolated Summer Means. All Data Are Log_e Transformed to Stabilize Variance. SE in Parenthesis

	Log_e (CPUE of Cyprinids, No Net^{-1})				
	Intercept	Slope	$P<$	r^2	n
Log_e (cladoceran biomass, mg C L^{-1})	1.72 $(1.01)^{NS}$	−0.57 (0.04)	0.04	0.45	9
Log_e (zooplankton biomass, mg C L^{-1})	1.77 (0.76)	−0.45 (0.17)	0.03	0.48	9
Log_e (*Daphnia* mean size, mm)	0.90 (0.31)	−0.21 (0.07)	0.02	0.53	9
Log_e (*Bosmina* mean size, mm)	−0.89 (0.22)	−0.05 (0.05)	NS	0.11	8
Log_e (grazing on phytoplankton, mg C L^{-1} d^{-1})	1.55 $(0.94)^{NS}$	−0.31 (0.21)	NS	0.22	9
Log_e (grazing on bacterioplankton, mg C L^{-1} d^{-1})	1.26 $(1.93)^{NS}$	−0.94 (0.43)	0.06	0.41	8

CPUE, catch per unit effort; NS, not significant.

Reinartsen and Olsen (1984, Shapiro and Wright (1984), Søndergaard and others (1990), and Benndorf (1990)].

In contrast to P, the N-loading reduction did not appear to affect the TN retention percentage, suggesting fast equilibration. This suggests that a large part of the N was denitrified, resulting in little accumulation of inorganic N in the sediment (Jensen and others 1992). The observed annual mean TN closely matched the one predicted by the equation of Windolf and colleagues (1996) for 16 shallow Danish lakes (Figure 3). According to this model, water TN is related to discharge-weighted inlet concentrations, hydraulic retention, and mean depth.

The Vollenweider equation predicts that TP_{lake} in equilibrium with the present loading will be 0.105 mg P L^{-1}, which is 21% of the 1995 level. The equilibrium concentration of TP is so high that the lake, in all probability, will remain in a turbid state. Diversion of sewage and a reduction in the diffuse loading from arable land may be necessary to shift the lake to the clear-water state with extensive growth of submerged macrophytes, which characterized the lake in the previous century, as suggested by paleoecological studies of lake sediment (Anderson and others unpublished; Jeppesen and others unpublished).

Strong Cascading Effects of Fish on Zooplankton

The marked changes found in trophic dynamics, pH, and Secchi depth could largely be attributed to the major variations in the fish population structure and abundance rather than to changes in the external loadings of organic matter, P, and N. The variation in fish abundance most likely reflects variations in oxygen concentration and pH (Figure 9).Hence, the low abundance of fish recruited before 1979 can be attributed to the frequent and severe summer fish kills in the 1970s (Andersen and others 1979; Mathiesen and Christensen 1981), most likely caused by oxygen depletion due to high organic loading as seen in other studies of hypertrophic lakes (Barica 1975; Carvalho 1994). Following the introduction of biological sewage treatment in 1976, the oxygen concentration increased, and the last major fish kill occurred in 1978. Likewise, the low CPUE of rudd and roach during 1986–88 compared with 1989–95 (Figure 8) can be mainly ascribed to the near absence of fish recruitment from 1984 to 1987. This poor recruitment may have resulted from high pHs in those years. In support of this theory, Timmermann (1987) showed that the 1986 spawning of roach and rudd was delayed 1–2 months, and spawning occurred simultaneously with a pH reduction caused by a major phytoplankton collapse. It cannot, however, be excluded that the low CPUE during 1986–88 was influenced by large commercial harvests of roach and rudd that corresponded to 17% of the biomass estimate from 1986.

Changes in the age structure and density of the planktivorous fish population were discernible in zooplankton structure and abundance. We have no quantitative zooplankton data from the 1970s when fish kills were observed. However, the large cladoceran, *D. magna*, occurred in high densities during summer and dominated the efflux of organic matter from the lake (Holm and Tuxen-Pedersen 1975). Furthermore, sediment analyses revealed a high abundance of resting eggs of large daphnids (*D. magna* or *D. pulex*) deposited in the 1970s (Jeppesen and others unpublished data). Large daphnids were apparently abundant in 1978, when chlorophyll *a* was low from late May to September (Andersen and others 1979), the year of the last fish kill.

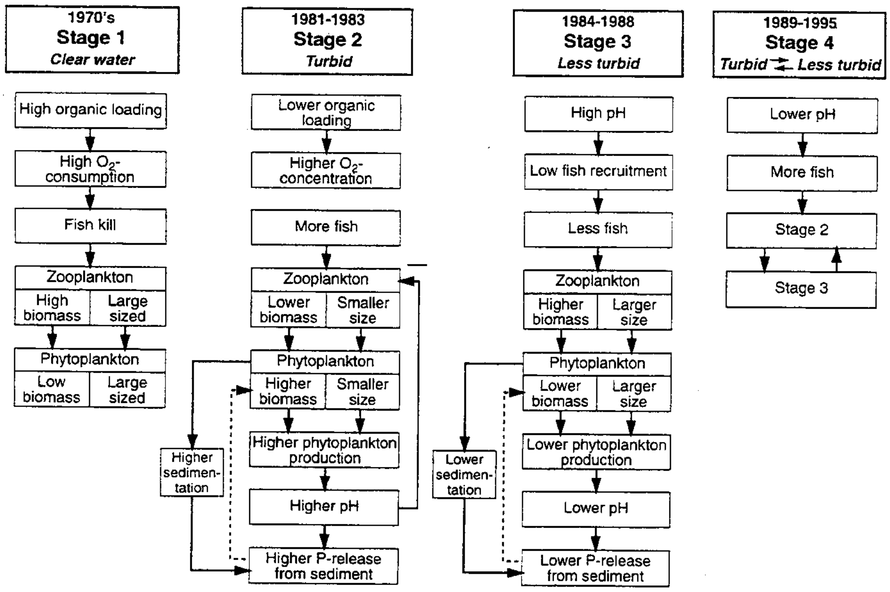

Figure 9. A conceptual model for how organic loading and pH are suggested to have affected the trophic structure and dynamics in the pelagial of Lake Søbygård during 2 decades.

The major changes in zooplankton community structure and size with changes in CPUE numbers of planktivorous fish are in accord with the size-efficiency hypothesis (Brooks and Dodson 1965). The shifts occurred despite relatively minor changes in CPUE biomass, however, which underlines the importance of young fish in structuring zooplankton communities (Cryer and others 1986; Mills and others 1987; He and Wright 1992; Søndergaard and others 1997; Jeppesen and others 1997b). The significant negative relationship between cladoceran biomass and mean size of *D. longispina* to cyprinid CPUE numbers, but not biomass, provides further evidence.

Effects of High pH on Trophic Dynamics

Besides being influenced by fish, the extremely low abundance of cladocerans in 1984 and 1985 may be attributed to high pH. Midmorning pH was above 10.5 approximately half of the time during the summers of 1984 and 1985 [data in Jeppesen and others (1990c)], and field experiments in the lake (Hansen and others 1991) have shown a negative effect on *D. longispina* survival when pH is greater than 10.5. Likewise, laboratory experiments by Vijverberg and colleagues (1996) showed enhanced mortality of juvenile and adult *D. galeata* at pH above 10.5 and of eggs and neonates at pH above pH 10. The pH effect is self-perpetuating, as a pH-mediated reduction in cladoceran abundance reduces the zooplankton-grazing pressure on phytoplankton (Figure 9). This reduction facilitated an increased growth of phytoplankton and higher pH with negative feedback on cladocerans. Results from the enclosure experiments also indicate that high pH may increase the P release from the sediment and inhibit nitrification and accordingly uncouple nitrification–denitrification leading to increased ammonium release (Hansen and others 1991), which, in turn, may potentially stimulate phytoplankton growth. As just described, however, high pH seemed to have a negative influence on the spawning success of the fish (Mortensen and others unpublished manuscript). Reduced abundance of fish resulted in lower predation on cladocerans. In 1986, cladoceran densities reached high enough densities to reduce phytoplankton biomass and production, as well as pH values. The resultant lower pH levels, in turn, improved conditions for fish recruitment, which caused enhanced predation on cladocerans (Figure 9). Accordingly, the marked variations in the biological structure in Lake Søbygård seemed partly influenced by pH-mediated effects on biological structure and nutrients: pH-provoked variations at the top (fish and zooplankton) and at the bottom (N and P) of the food web that, at least for the former, influenced phytoplankton and Secchi depth.

Strong Cascading Effect of Zooplankton on Phytoplankton

The fish-mediated and pH-mediated changes in zooplankton had a major impact on the phytoplankton composition, size distribution, and production. Our data strongly suggest that the marked interannual variations in the contribution of the various phytoplankton species to the total biovolume were largely determined by the changes in zooplankton composition, size, and grazing pressure. When cladoceran biomass was low, *Scenedemus* dominated. When small *B. longirostris* and rotifers became abundant, a shift occurred to small or intermediate-sized green algae (mainly *Chlorella* spp. and *Oocystis*). When intermediate-sized *Daphnia* (*D. longispina*) dominated, algae shifted to intermediate-sized *Pediastrum* spp. Finally, when large *D. magna* dominated, there was a shift from large flake-forms of *Aphanizomenon flos–aqua*, as observed in other studies of highly eutrophic lakes (Lynch 1980; Fott and others 1980; Andersson and Cronberg 1984). The shift to large algae caused a marked decrease in the volume-specific P_{max} and total phytoplankton production. These changes all support the trophic cascade hypothesis (Carpenter and others 1985). However, strong support for the hypothesis has only been found in some cases (Carpenter and Kitchell 1993). Kerfoot (1987) demonstrated a tendency toward a unimodal relationship between grazing pressure and algal size, large algae being dominant at intermediate *Daphnia* densities. Our data indicate that phytoplankton mean volume correlated more strongly with zooplankton size than with zooplankton-grazing pressure (Figure 5).

The high cascading effect of fish on zooplankton contradicts "the intermediate hypothesis" (Carney and Elser 1990; Carney 1990), which claims that herbivory declines from mesotrophic to hypertrophic lakes because the phytoplankton community becomes dominated by less nutritious and less palatable algae. Our results show that, in hypertrophic Lake Søbygård, the phytoplankton community was dominated by edible green algae and that the intensity of herbivory seems mainly influenced by changes in the abundance of planktivorous fish. This is in accord with results from a cross-analysis of data from 39 shallow Danish lakes showing a close negative relationship between the zooplankton–phytoplankton biomass ratio and the abundance of planktivorous fish, while percent cyanobacteria in terms of biovolume did not contribute significantly to the relationship (Jeppesen and others 1997b). Moreover, in eutrophic Danish lakes alternately dominated by blue-green and green algae, the zooplankton–phytoplankton biomass ratio showed no significant year-to-year variation (Jeppesen and others unpublished), suggesting that top-down control is the key factor in such lakes. Leibold (1989) and Sarnelle (1992) have already suggested that fish play a key role for herbivory in eutrophic lakes.

In 1983–85, when the phytoplankton biomass reached extremely high values (maximum chlorophyll *a*, 1400–1500 μg L^{-1}), the phytoplankton community was completely dominated by small algae (*Scenedesmus* spp. and *Chlorella* sp.). Small green algae have been reported to dominate in many other hypertrophic, freshwater lakes with dense phytoplankton communities (Nygaard 1949; Pavoni 1963; Leah and others 1980; Jensen and others 1994b). These results are not in agreement with the hypothesis of Agustí and Kalff (1989), Duartes and colleagues (1990), and Agustí (1991) that predicts that the average size of phytoplankton generally increases with increasing phytoplankton biomass. There may be several advantages of being small in dense, shallow lake communities. First, small algae have a higher chlorophyll content per unit of volume (Reynolds 1984; Enriquez and others 1996), maximizing light exploitation in a light-limited system. Second, the small size facilitates nutrient uptake (Hein and others 1995), which may be important in an environment characterized by pulse loading of nutrients as normally occurs in shallow lakes due to, for instance, wind-induced resuspension and diel changes in water temperature. The data from Lake Søbygård suggest that a shift to larger algae occurs only when larger zooplankton dominate (Figure 5). Low grazing pressure mediated by high fish predation may thus contribute to the frequently observed dominance by small algae in hypertrophic freshwater lakes, although exceptions can be found from less eutrophic, cyanobacteria-dominated lakes [for example, see Barica (1975) and Gulati and others (1992)].

Phytoplankton and Nutrients

According to most studies, the environmental conditions found in Lake Søbygård [high pH, low N–P ratios, low euphotic–mixing zone ratios (low Secchi depth) (Figure 2), and periodically low inorganic N concentrations (see below)] should favor cyanobacteria (Schindler 1977; Smith 1983; Shapiro 1990; Van Liere and Gulati 1992; Scheffer and others 1997). In addition, Sterner and colleagues (1992) and Hessen (1997) argued that cyanobacteria are favored in lakes with low *Daphnia*–copepod ratio, because the TN–TP ratio of matter excreted by copepods is lower than for *Daphnia*. Except in 1978, the phytoplankton community was, however, dominated by green algae and diatoms, even in years with a low biomass ratio of cladocerans–copepods. This pattern can be observed in many temperate shallow hypertrophic lakes (Jeppesen and others 1990a; Jensen and others 1994b). In previous reports, we have argued that high external loading of nutrients along with a high internal loading of CO_2 and nutrients from the sediment may explain the dominance of green algae in these lakes (Jeppesen and others 1990b; Jensen and others 1994b).

The slight reduction in lake TN and TP during the study may have influenced phytoplankton succession. The reduction in TP concentrations and organic matter loading after the implementation of biological waste water treatment (Holm and Tuxen-Pedersen 1974) may have caused the shift in the early 1980s from *Chlorella* sp. to *Scenedesmus* spp. Both genera are favored in nutrient-rich and often highly organically loaded ponds and lakes (Jeppesen and others 1990b; Jensen and others 1994b), but *Chlorella* sp. seems more tolerant of high ammonia concentrations and is better adapted to utilize organic substances for growth (Niewolak 1971). The shift to dominance by *Scenedesmus* spp. occurred concomitantly with a major decrease in the density of *Bosmina* and this could potentially indicate an interdependent relationship. However, *Chlorella* sp. densities did not increase after the return of *Bosmina* dominance in 1990–91, suggesting that changes in nutrients and organic loading are more likely to be the decisive factor for the decreased abundance of *Chlorella* sp. Likewise, the gradual increase in importance of diatoms may reflect a reduction in nutrient concentrations. The duration of the period with low inorganic N concentrations (below, for instance, 50 $\mu g\ L^{-1}$ during summer) increased from an average of 8 days in 1984–87 to 38 days in 1989–95 (unpublished results), and average TN-TP ratio decreased from 3–7 before 1987 to 2–5 after (Figure 2). This may have improved the competitive capacity of diatoms. Enrichment experiments with natural phytoplankton from the hypertrophic Grosser Binnensee (Sommer 1989) revealed that the Monod saturation coefficient for inorganic N was 6–10 times higher for *Scenedesmus* than for *Stephanodiscus*, which is the most abundant diatom genus in Lake Søbygård. Accordingly, the phytoplankton species composition in Lake Søbygård seems influenced by the reduction in nutrient loading and nutrient concentration. Superimposed upon that, however, substantial fluctuations occurred, reflecting changes propagated from fish via zooplankton.

Modest Cascading Effects on the Microbial Community

The cascading effects of fish-stock changes seemed less significant on the abundance of ciliates and bacterioplankton than on zooplankton and phytoplankton, supporting several observations that cascading effects diminish downward through the food web (McQueen and others 1986; Pace 1993). The response in 1990–91, when *B. longirostris* and rotifers dominated the zooplankton community, was significantly different from the other years. Bacterioplankton biomass and especially production were high, average bacteria volume was low, and ciliate mean size was high, particularly in 1990–91 (Figure 7). A multiple-regression analysis on summer data from 1985 to 1992 showed that bacterioplankton abundance and production were positively related to the biomass of rotifers, *B. longirostris*, and cyclopoid copepods and negatively related to the biomass of *D. longispina* (Jeppesen and others 1997a). The apparent positive effect of the small cladocerans, rotifers, and cyclopoid copepods may be explained by increased organic substrate for bacteria through excretion in combination with predation on potential bactivores, flagellates, and ciliates. As for *Daphnia*, predation seems to overrule the potential positive effects on bacterioplankton, as demonstrated in other studies of eutrophic lakes (Riemann 1985; Christoffersen and others 1993; Jürgens 1994; Christoffersen and Bosselmann 1997). Annual bacterioplankton production amounted to only 2%–6% of phytoplankton production, the highest percentages being obtained in 1990 and 1991 when *B. longirostris* and rotifers dominated (Jeppesen and others 1997a). The low values compared with Cole and colleagues' (1988) mean of 17% for a number of aquatic systems may be attributed to high loss by sedimentation due to the shallowness of the lake (low mean depth) and to dominance of phytoplankton with high specific settling rates (Kristensen and Jensen 1987) and low grazing rates in some years (Jeppesen and others 1997a). Our results support the conclusion by Cole and colleagues (1988) that the bacterioplankton–phytoplankton production ratio declines from oligotrophic to eutrophic lakes.

The multiple regression analysis also showed a significant negative effect of pH on bacterioplankton production, when pH was higher than 10.2. This effect was supported by laboratory experiments (Jeppesen and others 1997a) and implies that recycling of dissolved organic matter back to the food web via bacteria is reduced at high pH. Pace and Cole (1996) found a similar negative effect of pH on bacterioplankton production at low pH.

In conclusion, the results from the long-term study of Lake Søbygård suggest that shallow hypertrophic lakes with short retention times may be highly resistant to external P-loading reduction. In addition, sewage-loading reduction may create substantial perturbations at the top of the food web that may have major cascading effects on zooplankton and phytoplankton community structure, biomass, size, and production, with more minor effects on the pelagial microbial community. Changes in oxygen concentration and pH mediated by changes in external loading of organic matter and internal biological processes seemed to be the most important factors determining the perturbations. The results obtained are in accord with the trophic cascade hypothesis (Carpenter and others 1985), but can not confirm (a) that dense phytoplankton communities are dominated by large phytoplankton (Agustí and Kalff 1989), (b) that herbivory declines from mesotrophic to hypertrophic lakes because of an increase in biomass of large cyanobacteria (Carney and Elser 1990), or (c) that cyanobacteria are favored at low N–P ratios and high pH (Smith 1983; Shapiro 1990). In contrast, small green algae dominated when zooplankton-grazing pressure was low and phytoplankton biomass extremely high, large green algae dominated at higher grazing pressure, and herbivory seemed mainly influenced by the abundance of planktivorous fish.

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REFERENCES

Agustí S. 1991. Light environment within dense algal populations: cell size influences on shelf-shading. J Plankton Res 13:863–71.

Agustí S, Kalff J. 1989. The influence of growth conditions on the size dependence of maximal algal density and biomass. Limnol Oceanogr 34:1104–8.

Andersen JM, Jensen J, Kristensen Aa, Kristensen K. 1979. Investigation of the environmental state of Lake Søbygård in 1978 [In Danish]. Århus (Denmark): Report from Århus County, 29 p.

Andersson G, Cronberg G. 1984. *Aphanizomenon flosaqua* and *Daphnia*: an interesting plankton association in hypertrophic waters. In: Bösheim S, Nicholls M, editors. Interactions between different trophic levels in freshwater [In Norwegian]. Oslo (Norway): Norsk Limnologförening, Blindern. p 63–76.

Barica J. 1975. Collapses of algal blooms in prairie pothole lakes: their mechanisms and ecological impact. Verh Int Ver Limnol 19:606–15.

Boers P, Van Ballegooijen L, Uunk J. 1991. Changes in phosphorus cycling in a shallow lake due to food web manipulations. Freshwater Biol 25:9–20.

Benndorf J. 1990. Conditions for effective biomanipulation: conclusions derived from whole-lake experiments in Europe. Hydrobiologia 200–201:187–203.

Boström B, Andersen JM, Fleischer S, Jansson M. 1988. Exchange of phosphorus across the sediment-water interface. Hydrobiologia 170:457–74.

Boström, Jansson M, Forsberg C. 1982. Phosphorus release from lake sediments. Ergeb Limnol 18:5–59.

Brooks JL, Dodson SI. 1965. Predation, body size and composition of plankton. Science 150:28–35.

Carney HJ. 1990. A general hypothesis for the strength of food web interactions in relation to trophic state. Verh Int Ver Limnol 24:487–92.

Carney HJ, Elser JJ. 1990. The strength of zooplankton–phytoplankton coupling in relation to trophic state. In: Tilzer MM, editor. Ecology of large lakes. New York: Springer-Verlag. p 613–31.

Carpenter SR, Cottingham KL, Schindler DE. 1992. Biotic feedbacks in lake phosphorus cycles. TREE 7:332–6.

Carpenter SR, Kitchell JF, editors. 1993. The trophic cascade in lakes. Cambridge: Cambridge University. 385 p.

Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. Bioscience 35:634–9.

Carvalho L. 1994. Top-down control of phytoplankton in a shallow hypertrophic lake: Little Mere (England). Hydrobiologia 275–276:53–64

Christoffersen K, Bosselmann S. 1997. Zooplankton: growth, grazing and interactions with fish. In: Sand-Jensen K, Pedersen O, editors. Freshwater biology: priorities and development in Danish research. Copenhagen (Denmark): GEC GAD p 162–82.

Christoffersen K, Riemann B, Klysner A, Søndergaard M. 1993. Potential role of zooplankton in structuring a plankton community in eutrophic lake water. Limnol Oceanogr 38:561–73.

Cole JJ, Findlay S, Pace ML. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1–10.

Cooke GD, Welch EB, Peterson SA, Newroth PR. 1993. Restoration and management of lakes and reservoirs. Boca Raton (FL): Lewis.

Cryer M, Peirson G, Townsend CR. 1986. Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. Limnol Oceanogr 31:1022–38.

Cullen P, Forsberg C. 1988. Experience with reducing point sources of phosphorus to lakes. Hydrobiologia 170:321–36.

Duartes CE, Agustí S, Canfield DE. 1990. Size plasticity of freshwater phytoplankton: implications for community structure. Limnol Oceanogr 35:1846–51.

Edmonson WT. 1985. Recovery of Lake Washington from eutrophication. In: Proceedings from lakes pollution and recovery, Rome, 15–18 April 1985. p 228–34.

Elser JJ, Elser MM, Carpenter SR. 1986. Size fractionation of algal chlorophyll, carbon fixation and phosphatase activity: relationships with species-specific size distributions and zooplankton community structure. J Plankton Res 8:365–83.

Enriquez S, Duarte CM, Sand-Jensen K, Nielsen SL. 1996. Broad-scale comparison of photosynthetic rates across phototrophic organisms. Oecologia 108:197–206.

Fott J, Pechar L, Prazaková M. 1980. Fish as a factor controlling water quality in ponds. In: Barica J, Mur LR, editors. Hypertrophic ecosystems. Dev Hydrobiol 2:255–61.

Fuhrmann JA, Azam F. 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar Biol 66:109–20.

Gächter R, Meyer JS, Mares A. 1988. Contribution of bacteria to release and fixation of phosphorus in lake sediments. Limnol Oceanogr 33:1542–58.

Gulati RD, Lammens EHHR, Meijer M-L, van Donk E. 1990. Biomanipulation, tool for water management. Hydrobiologia 200–201:1–628.

Gulati RD, Ooms-Willems AL, Tongeren OFR, Postma G, Siwertsen K. 1992. The dynamics and role of limnetic zooplankton in Loosdrecht lakes (The Netherlands). Hydrobiologia 233:69–86.

Gulati RD, Siewertsen K, Postema G. 1982. The zooplankton: its community structure, food and feeding, and the role in the ecosystem of Lake Vechten. Hydrobiologia 95:127–63.

Hansen A-M, Christensen JV, Sortkjær O. 1991. Effect of high pH on zooplankton and nutrients in fish-free enclosures. Arch Hydrobiol 123:143–64.

Hansen A-M, Jeppesen E. 1992. Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. J Plankton Res 14:591–605.

He X, Wright R. 1992. An experimental study of piscivore–planktivore interactions: population and community responses to predation. Can J Fish Aquat Sci 49:1176–83.

Hein M, Pedersen MF, Sand-Jensen K. 1995. Size-dependent nitrogen uptake in micro- and macroalgae. Mar Ecol Prog Ser 118:247–53.

Hessen DO. 1997. Stochiometry in food webs: Lotka revisited. Oikos 79:195–200.

Hobbie R, Daly J, Jasper S. 1977. Use of nuclepore filters for counting bacteria by fluorescence microscopy. Appl Environ Microbiol 33:1225–8.

Holm TF, Tuxen-Pedersen F. 1975. River Gudenåen 1974 [in Danish]. Århus (Denmark): Report from the Laboratory of Physical Geography, Geological Institute, University of Århus, Denmark. 108 p.

Hosper H. 1997. Clearing lakes: an ecosystem approach to the restoration and management of shallow lakes in the Netherlands [PhD dissertation]. Lelystad (The Netherlands): RIZA. 168 p.

Hovmand MF, Grundahl L, Runge EM, Kemp KK, Aistrup W. 1993. Atmospheric deposition of nitrogen and phosphorus [In Danish]. Roskilde (Denmark): National Environmental Research Institute, research report no. 91, 65 p.

Jensen HS, Andersen F.Ø. 1992. Importance of temperature, nitrate and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. Limnol Oceanogr 37:577–89.

Jensen JP, Jeppesen E, Bøgestand J, Roer Petersen A, Søndergaard M, Windolf J, Sortkjær L. 1994a. Action Plan for the Aquatic Environment; Survey Programme 1993; Freshwater; Lakes (In Danish). Roskilde (Denmark): National Environmental Research Institute, Research Report no. 121, 93 p.

Jensen JP, Jeppesen E, Kristensen P, Christensen PB, Søndergaard M. 1992. Nitrogen loss and denitrification as studied in relation to reductions in nitrogen loading in a shallow, hypertrophic lake (Lake Søbygård, Denmark). Int Rev Gesamten Hydrobiol 77:29–42.

Jensen JP, Jeppesen E, Olrik K, Kristensen P. 1994b. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. Can J Fish Aquat Sci 51:1692–9.

Jeppesen E, Erlandsen M, Søndergaard M. 1997a. Can simple empirical equations describe the seasonal dynamics of bacterioplankton in lakes? An eight year study in shallow hypertrophic and biologically highly dynamic Lake Søbygård Denmark. Microb Ecol 34:11–26.

Jeppesen E, Jensen JP, Kristensen P, Søndergaard M, Mortensen E, Sortkjær O, Olrik K. 1990a. Fish manipulation as a lake restoration tool in shallow eutrophic lakes. 2. Threshold levels, long-term stability and conclusions. Hydrobiologia 200–201: 219–27.

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen TL, Møller PH, Sandby K. 1998. Changes in nitrogen retention in shallow eutrophic lakes following a decline in density of cyprinids. Arch Hydrobiol. Forthcoming.

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L. 1997b. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342–343:151–64.

Jeppesen E, Jensen JP, Søndergaard M, Sortkjær O. 1996. Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a long-term study in shallow hypertrophic Lake Søbygård. J Plankton Res 18:1605–25.

Jeppesen E, Kristensen P, Jensen JP, Søndergaard M, Mortensen E, Lauridsen T. 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. Mem Ist Ital Idrobiol 48:127–48.

Jeppesen E, Søndergaard M, Mortensen E, Kristensen P, Riemann B, Jensen HJ, Møller JP, Sortkjær O, Jensen JP, Christoffersen K, Bosselmann S, Dahl E. 1990b. Fish manipulation as a lake restoration tool in shallow eutrophic lakes. 1. Cross-analysis of three shallow, eutrophic temperate lakes. Hydrobiologia 200–201:205–18.

Jeppesen E, Søndergaard M, Sortkjær O, Kristensen P. 1990c. Interactions between phytoplankton, zooplankton and fish in a shallow hypertrophic lake: a study on short term changes in the trophic relationships in Lake Søbygård, Denmark. Hydrobiologia 191:149–64.

Jeppesen E, Sortkjær O, Søndergaard M, Erlandsen M. 1992. Impact of a trophic cascade on heterotrophic bacterioplankton production in two shallow fish-manipulated lakes. Arch Hydrobiol 37:219–31.

Jespersen A-M, Christoffersen K. 1987. Measurements of chlorophyll *a* from phytoplankton using ethanol as extraction solvent. Arch Hydrobiol 109:445–54.

Jürgens K. 1994. The impact of *Daphnia* on microbial food webs: a review. Mar Microb Food Web 8:295–324.

Kerfoot WC. 1987. Cascading effects and indirect pathways. In: Kerfoot WC, Sid A, editors. Predation: direct and indirect impacts on aquatic communities. Hanover (NH): University Press of New England. p 57–70.

Koroleff F. 1970. Determination of total phosphorus in natural water by means of the persulphate oxidation. Cons Int Explor Mer; Interlaboratory Report 3.

Kristensen P, Hansen HO, editors. 1994. European rivers and lakes: assessment of their environmental state. Copenhagen (Denmark): European Environment Agency. 122 p.

Kristensen P, Jensen P. 1987. Sedimentation and resuspension in Søbygård Lake [MSc thesis] [in Danish]. Silkeborg (Denmark): National Agency of Environmental Protection, Freshwater Laboratory. 152 p.

Kristensen P, Jensen JP, Jeppesen E. 1990. Simple empirical lake models. In: Miljøstyrelsen, editor. Nitrogen and phosphorus in fresh and marine waters. C-abstract. Copenhagen (Denmark): Environmental Protection Agency. p 125–45.

Lauridsen TL, Jeppesen E, Andersen F.Ø. 1993. Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: impact of sediment composition and water fowl grazing. Aquat Bot 46:1–15.

Lathrop RC, Carpenter SR, Rudstam LG. 1996. Water clarity in Lake Mendota since 1900: responses to differing levels of nutrients and herbivory. Can J Fish Aquat Sci 53:2250–61.

Leah RT, Moss B, Forres DE. 1980. The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. Int Rev Gesamten Hydrobiol 65:223–47.

Leibold MA. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. Am Nat 134:922–49.

Lynch M. 1980. *Aphanizomenon* blooms: alternate control and cultivation by *Daphnia pulex*. In: American Society of Limnology and Oceanography Special Symposium. Volume 3. Hanover (NH): University Press of New England. p 299–305.

Marsden S. 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshwater Biol 21:139–62.

Mathiesen H, Christensen J. 1981. The Gudenå investigation. Characteristics of the Lakes [in Danish]. Århus (Denmark): Botanical Institute, Århus University.

McQueen DJ, Post JR, Mills EL. 1986. Trophic relationships in freshwater pelagic ecosystems. Can J Fish Aquat Sci 43: 1571–81.

Messer JJ, Brezonik PL. 1978. Denitrification in the sediments of lake Okeechobee. Verh Int Ver Limnol 20:2207–16.

Mills EL, Forney JL, Wagner KJ. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In: Kerfoot WC, Sih A, editors. Predation: direct and indirect effects on aquatic communities. Hanover (NH): University Press of New England. p 118–31.

Moss B. 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200–201:367–78.

Murphy J, Riley JP. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:21–6.

Niewolak S. 1971. The influence of living and dead cells of *Chlorella vulgaris* and *Scenedesmus obliquus* on aquatic microorganisms. Pol Arch Hydrobiol 18:43–54.

Nygaard G. 1949. Hydrobiological studies on some Danish ponds and lakes. Biol Skr K Vidensk Selsk 7:1–239.

OECD. 1982. Eutrophication of waters: monitoring, assessments and control. Paris: OECD. 210 p.

Olrik K. 1991. Phytoplankton methods for lakes and marine areas. Copenhagen (Denmark): Environmental Protection Agency, Ministry of Environment, Environmental Project no. 187, 108 p.

Pace ML. 1993. Heterotrophic microbial process. In: Carpenter SR, Kitchell JF, editors. Cascading trophic interactions. Cambridge: Cambridge University. p 252–77.

Pace ML, Cole JJ. 1996. Regulation of bacteria by resources and predation tested in whole-lake experiments. Limnol Oceanogr 41:1448–60.

Pavoni M. 1963. The importance of nannoplankton compared to netplankton. Schweiz Z Hydrol 25:219–341.

Reinertsen H, Olsen Y. 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. Verh Int Ver Limnol 22:649–57.

Riemann B. 1985. Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. Appl Environ Microbiol 50:187–93.

Riemann B, Søndergaard M, Schierup HH, Bosselmann S, Christensen G, Hansen J, Nielsen B. 1982. Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossø. Int Rev Gesamten Hydrobiol 67:145–85.

Reynolds CS. 1984. The ecology of freshwater phytoplankton. Cambridge: Cambridge University. 384 p.

Ryding S-O. 1981. Reversibility of man-induced eutrophication: experiences of a lake recovery study in Sweden. Int Rev Gesamten Hydrobiol 66:189–207.

Sarnelle O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. Ecology 73:551–60.

Sas H, editor. 1989. Lake restoration by reduction of nutrient loading: expectation, experiences, extrapolation. Sankt Augustin: Acad Ver Richardz. 497 p.

Scheffer M, Rinaldi S, Gragnani A, Mur LR, van Nes EH. 1997. On the dominance of filamentous cyanobacteria in shallow turbid lakes. Ecology 78:272–82.

Schindler DW. 1977. Evolution of phosphorus limitation in lakes. Science 195:260–2.

Shapiro J. 1990. Current beliefs regarding dominance by blue-greens: the case for the importance of CO_2 and pH. Verh Int Ver Limnol 24:38–54.

Shapiro H, Wright DI. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwater Biol 14:371–83.

Smith VH. 1983. Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. Can J Fish Aquat Sci 43:1101–12.

Solórzano L, Sharp JH. 1980. Determination of total dissolved nitrogen in natural waters. Limnol Oceanogr 25:751–4.

Sommer U. 1989. Nutrient status and nutrient competition in a shallow, hypertrophic lake. Limnol Oceanogr 34:1162–73.

Søndergaard M, Jeppesen E, Berg S. 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 2. Effects on lower trophic levels in Lake Lyng, Denmark. Hydrobiologia 343–343:319–25.

Søndergaard M, Jeppesen E, Kristensen P, Sortkjær O. 1990. Interactions between sediment and water in a shallow and hypertrophic lake: a study on short term changes in the trophic relationships in Lake Søbygård, Denmark. Hydrobiologia 1991: 139–48.

Søndergaard M, Kristensen P, Jeppesen E. 1993. Eight years of internal phosphorus loading and changes in the sediment phosphorus profile of Lake Søbygård, Denmark. Hydrobiologia 253:345–56.

Sterner RW, Elser JJ, Hessen DO. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry 17:49–67.

Timmermann M. 1987. Lacking reproduction of roach (Rutilus rutilus (L.)), bream (Abramis brama (L.)) and perch (Perca fluviatilis (L.)) in Lake Søbygård and the density and growth of fish fry in Lake Væng [in Danish]. Silkeborg (Denmark): the

Freshwater Laboratory, Agency of Environmental Protection; Publication 85. 81 p.

Van der Molen DT, Boers PCM. 1994. Influence of internal loading on phosphorus concentration in shallow lakes before and after reduction of external loading. Hydrobiologia 275/276:479–92.

Van Liere L, Gulati RD, editors. 1997. Restoration and recovery of shallow eutrophic lake ecosystems in the Netherlands. Hydrobiologia 233:1–287.

Vijverberg J, Kalf DF, Boersma M. 1996. Decrease in *Daphnia* egg viability at elevated pH. Limnol Oceanogr 41:789–94.

Vollenweider RA. 1976. Advance in defining critical loading levels for phosphorus in lake eutrophication. Mem Ist Ital Idrobiol 33:53–83.

Welch EB, Cooke GD. 1995. Internal phosphorus loading in shallow lakes: importance and control. Lake Reservoir Manage 11:273–81.

Windolf J, Jeppesen E, Jensen JP, Kristensen P. 1996. Modelling the seasonal variation in in-lake concentration and retention of nitrogen in 16 shallow lakes: a four-year mass balance study. Biogeochemistry 33:25–44.

Chapter 29 in: D. Harper, B. Brierley, A. Ferguson, G. Phillips & J. Madgewick (Eds.), **Ecological Basis for Lake and Reservoir Management,** ***Hydrobiologia,*** **1998.**

Lake and Catchment Management in Denmark

Erik Jeppesen, Martin Søndergaard, Brian Kronvang1), Jens P. Jensen, Lars M. Svendsen & Torben L. Lauridsen2)
1)National Environmental Research Institute, Vejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark.
2)Department of Lake and Estuarine Ecology.

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Abstract

The majority of Danish lakes are highly eutrophic due to high nutrient input from domestic sources and agricultural activities. Reduced nutrient retention and shorter water residence time in catchments as a result of agricultural drainage of wetlands and lakes and channelization or culverting of streams also play a role. Attempts have recently been made to reduce nutrient loading on lakes by intervening at the source level and by improving the retention capacity of lake catchment areas. The former measures includes phosphorus-stripping and nitrogen removal at sewage works, increased use of phosphate-free detergents, and regulations concerning animal fertilizer storage capacity, fertilizer application practices, fertilization plans and green cover in winter. In order to improve nutrient retention capacity of lake catchments, wetlands and lakes have been re-established and channelised streams have been remeandered. In addition, cultivation-free buffer strips have been established alongside natural streams and there has been a switch to manual weed control. These measures have resulted in a 73% reduction of the mean total phosphorus concentration of point-source polluted streams since 1978; in contrast, there has been no significant change in the total nitrogen concentration. Despite the major reduction in stream phosphorus concentration, lake water quality has often not improved. This may reflect too high external or internal phosphorus loading or biological resistance. Various physico-chemical restoration measures have been used, including dredging and oxidation of the hypolimnion with nitrate and oxygen. Biological restoration measures have been employed in 17 Danish lakes. The methods include reducing the abundance of cyprinids, stocking with 0^+ pike (*Esox lucius*) to control 0+ cyprinids, and promoting macrophyte recolonization by protecting germinal submerged macrophyte beds against grazing waterfowl and transplanting out macrophyte shoots. In several lakes marked and long-lasting improvements have been obtained. The findings to date indicate that fish manipulation has a long-term effect in shallow lakes provided that nutrient loading is reduced to a level so low as to ensure an equilibrium lake water phosphorus concentration of less than 0.05-0.1 mg P l^{-1}. If nitrogen loading is low, however, positive results may be obtained at higher phosphorus concentrations. Macrophyte refuges and transplantation seem to be most successful as restoration measures in the same phosphorus regime as fish manipulation.

Action plans to combat eutrophication

Danish lakes are typically small, shallow, fast-flushed and highly eutrophic (Table 1). Eutrophication is largely attributable to high point-source loading in the past, and high nutrient input from arable land at present. In order to combat eutrophication, the Danish government has implemented a number of action plans. These have two objectives:

- To reduce external nutrient loading (Table 2)
- To improve nutrient retention and removal by wetlands (Table 3).

Table 1. Morphometric and environmental parameters for 200-283 Danish lakes.

	Mean	Median	Minimum	Maximum
Catchment area (km^2)	89	11	0.11	1500
Surface area (km^2)	0.88	0.14	0.00031	42
Maximum depth (m)	5.7	3.7	0.3	37.7
Mean depth (m)	2.9	2.0	0.3	16.5
Hydraulic retention time (years)	1.1	0.27	0.0010	21
Total phosphorus (mg P l^{-1})*	0.37	0.21	0.017	2.4
Total nitrogen (mg N l^{-1})*	2.4	2.1	0.21	9.0
Chlorophyll *a* (µg chl *a* l^{-1})*	73	57	2	445
Secchi depth (m)*	1,2	1.4	0.2	6.1

* Summer mean values (May 1 - Oct 1)

Table 2. Major measures implemented in Denmark to reduce nutrient loading of the aquatic environment.

Incorporation of P-stripping at sewage works (>500-5,000P.E.)
Incorporation of N-removal at sewage works (>15,000 P.E.)
Increased use of phosphate-free detergents
Regulations on the amount of fodder used in fish farms
Regulations on livestock density (1.7 - 2.3 livestock units ha^{-1})
Regulations on utilization of liquid and solid manure (30-45% fertilization efficiency, depending on type)
Increased storage capacity for animal manure
Preparation of fertilization budgets/plans and regulations concerning application practices for manure (no use of liquid manure from harvest to spring ploughing after spreading)
Mandatory regulations on set-aside and green cover in winter
Increased afforestation
Cessation of subsidies for drainage
Establishment of 2 m wide cultivation-free riparian buffer strips along natural streams and rivers

The reason for the latter is that wetland area has been reduced considerably over the past 150 years due to land reclamation and drainage.

The major environmental plans are the 1987 "Action Plan on the Aquatic Environment", which is a national plan aimed at reducing land-based nitrogen and phosphorus loading of the aquatic environment by 50% and 80%, respectively. The reduction target for nitrogen was reiterated in the 1991 "Action Plan on Sustainable Agricultural Development". These plans are supplemented with recipient quality objectives stipulated in each Danish county's "Region Plan". The recipient quality plans are differentiated plans adapting catchment loading reductions to the specific water quality objectives set for each water body and to the sensitivity of the environment. These plans were first elaborated by the Counties in the 1980s and have subsequently been revised every five years. Several other more recent plans may also help reduce nutrient loading of the aquatic environment, e.g. the afforestation plan, aimed at doubling the forest area in Denmark during the next 60-80 years (5,000 ha y^{-1}), the "Strategy on Marginal Lands", aimed at restoring 20,000 ha of former wetlands (equivalent to 10% of the drained area) over the next 10-20 years, and finally, the EU Set-Aside scheme, which required that 9% of Danish farmland was removed from production in 1994 (Skotte-Møller, 1995).

Table 3. Major measures implemented in Denmark to improve nutrient retention and removal by wetlands.

A switch to gentle weed clearance and reduced dredging in many public streams
Remeandering of channelized streams
Re-establishment of wetlands, streams and lakes
Biomanipulation of lakes

Several attempts have been or are currently being made to reduce external loading of nutrients (Table 2). The Action Plan on the Aquatic Environment requires that phosphorus-stripping be incorporated at sewage works with a capacity exceeding 5,000 person equivalents (PE), and nitrogen removal at works with a capacity exceeding 15,000 PE. In many of the recipient quality plans, however, phosphorus stripping is required at works with a capacity exceeding 500 PE. As sewage works are usually centralized, sewage from many communities of less than 500 PE will also be subjected to phosphorus stripping and nitrogen removal. These measures, and increased use of phosphate-free detergents on a voluntary basis, have led to a 75% reduction in total phosphorus loading from point sources to freshwater systems during 1989-94 (Madsen, 1995). Multiple measures have been implemented to reduce nutrient loading from arable soils, including requirements on the following:

- Storage capacity for animal fertilizer on farms with more than 31 livestock units and application practices
- Preparation of fertilizer budgets/plans
- Establishment of uncultivated buffer strips along all natural streams
- Maintenance of green cover of fields in winter
- Set-aside of agricultural land (EU-directive) (Table 2). Set-aside will hopefully be concentrated in environmentally sensitive areas in future.

During the last 150 years, a substantial percentage of Danish wetlands, lakes and streams have disappeared due to land reclamation (Iversen et al., 1993). Moreover, to enhance drainage capacity most of the remaining streams were culverted or channelised, and hard-handed maintenance was introduced (dredging and mechanical weed control). In addition, stream beds were lowered and stream width enhanced to diminish the risk of flooding (Iversen *et al.*, 1993). These steps have resulted in a significant reduction in hydraulic retention time, and the overall capacity for temporary or more permanent retention and removal of nutrients by wetlands has consequently decreased.

Table 4. National tally of re-establishment of wetlands and other natural areas over the period 1989-94 (Skotte-Møller, 1995).

Lakes	1,700 ha
Small ponds	1,600
Channelized or culverted streams	60 km
Salt marshes	2,200 ha
Freshwater meadows	2,300 ha
Bogs	2,000 ha
Heathland	4,800 ha
Grassland	1,300 ha
Natural forest	100 ha

Table 5. Total nitrogen and total phosphorus removal and retention in various Danish aquatic ecosystems.

	Denitrification (kg N ha^{-1} y^{-1})	Sedimentation adsorption/desorption (kg N ha^{-1} y^{-1})	Sedimentation adsorption/desorption (kg P ha^{-1} y^{-1})
Streams (annual)	5-200 [1]	3-380 [2,5]	0
Streams (summer)	5-1,460 [1]	10-500 [2,5]	2-300 [2,5]
Riparian zones (summer)	?	20-600 [2,5]	8-450 [2,5]
Flooded riparian areas	?	?	12-118 [10,11]
Irrigated riparian areas	30-2725 [7,8,9,12]	?	-30-31 [6,7,8,10,12]
Meadows	42-2170 [7,8,9,12]	?	-9-3 [7,8,12,13]
Lakes	- - - - - - - - - - - - - - 65 - 220 [3,4] - - - - - - - - - -		2.7-5 [14]

1) Christensen *et al.*, 1991 2) Svendsen & Kronvang, 1993 3) Jensen, J.P. *et al.*, 1991 4) Windolf *et al.* (1996) 5) Svendsen *et al.*, in press 6) Hoffmann *1996,1997* 7) Rebsdorf *et al.*, 1994 8) Hoffmann *et al.*, 1993 9) Hoffmann, 1997 and unpublished observations 10) Iversen *et al.*, 1995 11) Larsen *et al.*, 1995 12) Paludan and Hoffmann, 1996 13) Hoffmann, 1998 14) Windolf *et al.*, 1993.

On the basis of the 1989 Nature Conservation Act a number of projects have been initiated aimed at re-establishing wetlands, streams, ponds and lakes, at remeandering channelized streams (Table 4), and at speeding up the restoration of lakes showing resilience following a reduction in external nutrient loading. In addition, there has been a shift towards more environmentally sound maintenance practices, weed control now being undertaken manually with scythes in many public streams (Madsen, 1995).

The latter significantly increases the nutrient retention capacity of streams during summer, an investigation undertaken in the river Gjern showed that net retention of total phosphorus was highly positively related to the size of the riparian zone and macrophyte coverage as well as being positively related to the concentration and negatively so to the water velocity, (Box 1 and Svendsen et al., in press). While temporary retention in streams does not affect annual total phosphorus transport to lakes, it is of significance for their overall environmental state during summer, especially in the case of fast-flushed lakes (the typical Danish lake type) that are heavily influenced by the immediate nutrient input from the catchment streams (Kristensen et al., 1990).

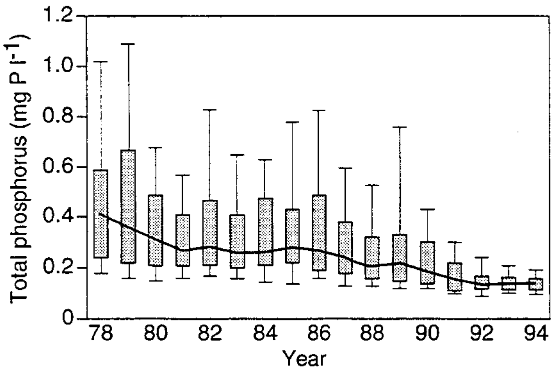

Figure 1. Trend in annual mean concentration of total phosphorus in Danish streams during 1978-94. Mean quartiles and 5 and 95 percentiles (5% and 95%) are also shown.

The new more environmentally sound weed-clearance practices together with the remeandering of streams and the raising of stream beds have increased the frequency of flooding, thereby increasing hydraulic retention time and hence nitrogen loss by denitrification. Flooding also increases retention of the particulate phosphorus being transported by the streams (Table 5), thereby significantly affecting phosphorus transport since particulate phosphorus typically constitutes 35-77% of the total phosphorus transport in Danish streams (Svendsen et al., 1995; Kronvang, 1992). The potential retention capacity of the flooded riparian zones is illustrated by the river Gjern study, where a 0.5 ha riparian area in the lower part of the 114 km^2 catchment retained 94 kg P ha^{-1} flooded area from November 1992 to March 1993, which corresponds to a phsphorus loss from a 300-fold greater area of agricultural land (Iversen et al., 1995; Kronvang et al., in press, b).

Phosphorus loading of freshwaters has decreased considerably since the implementation of the various

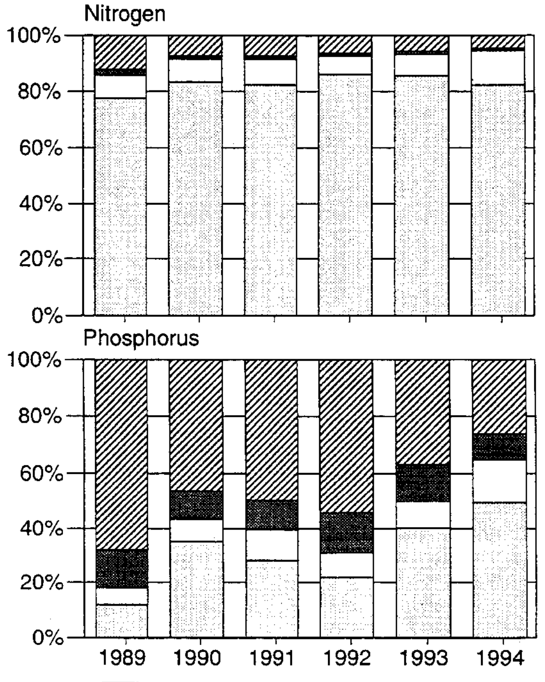

Figure 2. Trend in source apportionment of total phosphorus and total nitrogen inputs to Danish streams during 1989-94.

Action Plans. Thus, stream TP concentrations have fallen 73% from 1978 to 1993, when the annual discharge-weighted mean was 0.14 mg P l^{-1} (Figure 1). The decline is mainly attributable to improved sewage treatment. Thus the percentage of total phosphorus input to freshwaters accounted for by point sources has fallen from 68% in 1989 to only 26% in 1994; conversely, the percentage accounted for by arable land has increased from 15% to 49% (Figure 2). Even though point-source nitrogen loading of freshwaters has been reduced by 42% since 1981-88 (Larsen et al., 1995), there has been no significant change in stream nitrogen transport, which is completely dominated by the input from arable land (88% in 1989 and 95% in 1994) (Kronvang et al., 1995). Export coefficient models for diffuse nutrient losses have been developed based on the 1989-94 data from approximately 80 small, representative catchments encompassed by the Danish Nationwide Monitoring Programme under the Action Plan on the Aquatic Environment (Kronvang et al., 1995). The models estimate catchment losses of total nitrogen and total phosphorus by use of simple predictor variables (run-off, proportion of arable land and soil type). The models can be used to estimate diffuse nutrient loading of lakes from otherwise non-monitored areas, as well as to assess measures taken to diminish diffuse nutrient loading by reducing the area of arable land under cultivation.

The impact of the reduction in external loading on lake environmental conditions can be evaluated by using loading response models originally developed by Vollenweider et al. (1976), and subsequently a-

Box 1. Nutrient retention in the river Gjern

Temporal and more permanent retention of particulate matter and associated nutrients has been measured by *in situ* sampling techniques in different stream environments and in riparian zones at 35 stream reaches in the 114 km^2 river Gjern catchment (Svendsen et al., in press). Phosphorus and nitrogen retention was low on coarse stream bed substrates, but high within macrophyte patches and in vegetated riparian zones (Table 6). Dividing the Gjern river system into four stream orders revealed that median total sediment phosphorus (TSP) retention during the low-flow period mid-March to mid-August 1994 increased significantly with increasing stream order ($p>0.0001$, Wilcoxon ranksum test (Table 7). Net catchment TSP retention in stream beds and riparian zones during the same period amounted to 850±20 kg P, corresponding to 25% of gross total P export from the watershed during the period and 12% of 1994 annual total P export (or 0.65 kg P ha^{-1}) (Svendsen et al., in press). Phosphorus retention mainly results from the sedimentation of particulate matter-associated phosphorus, although dissolved P adsorbed to sediment or assimilated by macrophytes, benthic algae, etc. may also contribute. In the main channel of the river Gjern up to 80% of dissolved reactive P (DRP) was adsorbed or assimilated during spring (Svendsen & Kronvang, 1993). The pools of particulate N and P retained during summer are flushed out of the stream system following weed clearance (usually during August and September) or during the first major autumn storm events (Svendsen & Kronvang, 1993, Svendsen et al., 1995 and Kronvang et al., in press, b). Thus, net TSP resuspension in September 1987 and October/November 1987 amounted to 77% and 20%, respectively, of particulate P export from the river Gjern system during these two periods. The corresponding figures for total suspended N were 20% and 15%, respectively (Svendsen & Kronvang, 1993). On the other hand during a low flow period from September 1994 to March 1995 resuspension of retained nutrients contributed 78% of retained N and 80% of retained P, thereby indicating that more permanent retention of N and P took place in the streams and the riparian zones during 1994/95 (Kronvang et al., in press, b). Reduced stream maintenance, remeandering of stream channels and cutting of drains before entering the riparian zone will increase water residence time within stream systems, thereby increasing temporary retention of particulate matter and associated substances (nutrients, pesticides and heavy metals), prolonging the period with positive net retention within the stream system and increasing the frequency of flooding of riparian areas (thus enhancing permanent retention of particulate matter).

Table 6. Mean P and N retention measured during summer (June-August) in different types of stream bed and in riparian zones. Values are the average of five different stream reaches in the Gjern river system. Mean accumulation during winter was 3.4 g m^{-2} (after Svendsen & Kronvang, 1993 and Svendsen, unpublished).

Retention g m^{-2}	Type of stream bed				Riparian zone
	Gravel	Sand	*Batrachium pel.*	*Sparghanium emers.*	*Sparghanium erectum*
Phosphorus	4	8	18	18	29
Nitrogen	4	9	20	20	32

Table 7. Median and net watershed total sediment phosphorus (TSP) retention in the river Gjern during mid-March 1994 to mid-August 1994 apportioned by stream order (sensu Strahler, 1957). For median TSP retention the 25% and 75% percentiles are given in parentheses. SD = standard deviation. Modified from Svendsen *et al.* (1997).

Stream order	No. of reaches	Stream bed and riparian zone area (1,000 m^{-2})	Median TSP retention (kg P km^{-1})	Net TSP (kg ±SD)
1st order	12	59	3.9 (2.1-7.8)	220 ±74
2nd order	11	38	8.3 (5.3-12)	180 ±5.7
3rd order	5	19	29 (23-30)	150 ±8.7
4th order	7	48	31 (21-35)	300 ±8.3
River system	35	164	-	850 ±20

Box 2. Impact of remeandering the river Gelså on nutrient retention

Numerous formerly channelized Danish streams and rivers have been remeandered by regional authorities over the last 5-10 years. Habitat diversity and hence biodiversity have been documented to increase following remeandering, an example being the remeandering of a 1,850 m reach of the river Gelså in 1989 (Kronvang et al., 1994). Following an initially unsteady period with excessive erosion of the newly excavated watercourse, macroinvertebrate density and species composition increased, as did the number of submerged and emergent macrophyte species (Friberg et al., 1994; Kronvang et al., 1996). Remeandering of rivers also influences their sediment and nutrient retention capacity, which increases due to an increase in the total area of riparian zones and restoration of hydrological contact between the river and its riparian area. Re-establishment of temporarily flooded wet meadows thus results in the removal of large quantities of nitrate nitrogen by denitrification, as well as the retention of sediment and sediment-associated phosphorus during flooding. In the case of the river Gelså, the mass balance for the restored reach and an upstream reference reach revealed a decrease in nitrate loss to the river of 80 kg N ha^{-1} wet meadow (Kronvang et al., 1994). The restored reach of river Gelså also acted as a sink for suspended sediment and phosphorus during the second year following remeandering, probably due to the significant reduction in discharge capacity and hence increased flooding of riparian zones and riparian areas (Kronvang et al., 1996). Excessive loss of sediment and phosphorus during the first year following restoration of the river channel was succeeded by a net retention of 42 kg suspended sediment and 67 kg P per km restored river channel during the second study year.

dapted for Danish lakes by Kristensen et al. (1990, 1991). Such calculations have been made for the 37 lakes included in the Nationwide Monitoring Programme (Figure 3). The lakes are considered representative of Danish lakes with respect to loading, size and mean depth. The scenarios, run over 1989-94, show that fulfilment of sewage plant treatment requirements is insufficient to bring many of the lakes into the clearwater state that is the aim for most lakes in the Region Plans (Figure 3). Not even a cut-off of the sewage contribution by diversion will suffice. The aim can only be achieved if efficient measures are taken against the diffuse sources.

Lake restoration measures

External phosphorus loading of some Danish lakes is now so low that a shift to the clearwater state ought to have taken place. However, resilience to recovery is sometimes observed due to both chemical and biological factors.

Phosphorus release (internal loading) from the phosphorus pool accumulated in the lake sediments during the time when loading was high may counteract the reduction of external loading. The duration of resilience depends on conditions such as the magnitude and duration of loading, hydrological retention time and iron input (Cullen & Forsberg, 1988; Sas, 1989; Jeppesen et al., 1991; Jensen et al., 1991). The period of resilience may be long-lasting, even in rapidly-flushed lakes (Jeppesen et al., 1991). A good example is shallow Lake Søbygaard (retention time 15-25 days), in which internal loading was still so high thirteen years after a 90% reduction in external loading that it exceeded external phosphorus loading (Figure 4). Phosphorus is now released from a sediment depth of 20-25 cm, and it is estimated that a further 10-20 years will pass before the lake reaches equilibrium at the present level of external P loading (Søndergaard et al., 1993).

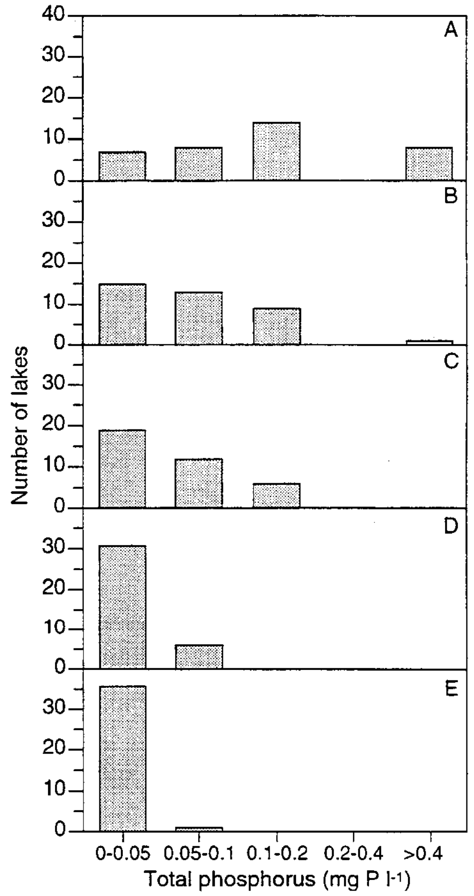

Figure 3. Effects of various measures aimed at lowering annual average phosphorus loading of 37 Danish lakes (representative for Danish lakes): a) recorded averages for the period 1989-95, b) when the lakes are in equilibria at the current level of loading according to Vollenweider's retention models (Vollenweider, 1976), c) cut-off of all loading point-sources, excluding the contribution from scattered dwellings, d) cut-off of point-sources and reduction of diffuse loading by 50%, e) as d, but a 70% reduction of diffuse loading. The results show that effective measures need to be taken against diffuse loading, if the phosphorus level of Danish lakes is to be reduced to a level so low that a shift to the clearwater state may take place (see Figure 7).

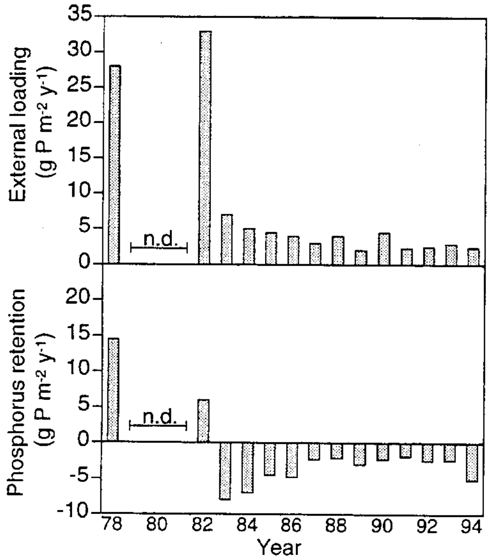

Figure 4. Trend in phosphorus loading and net retention in Lake Søbygaard during 1978-94.

In Denmark, various physical and chemical methods have been employed to combat internal phosphorus loading in order to speed up the recovery of lakes following a reduction in external loading. The methods include sediment dredging and oxygenation of the hypolimnion by pure oxygen or nitrate. The most extensive dredging restoration project so far undertaken in Denmark was that at shallow Lake Brabrand (surface area 1.5 km^2, mean depth 1 m). Approx. 500,000 m^3 of phosphorus-rich sediment were removed to prevent the lake silting up and to reduce internal phosphorus loading. Although this significantly reduced internal loading, quality of the lake water is still poor due to high external loading and high density of planktivorous fish (particularly bream) (Jørgensen, submitted)

Hypolimnic oxidation with pure oxygen has been undertaken for the last ten years in Lake Hald (surface area 3.4 km^2, mean depth 13.1 m and max depth 31 m) to supplement the reduction in external P loading, which has been reduced to 0.7 g P m^2 y^{-1} from approx. 1.3 g P m^2 y^{-1} before restoration (Rasmussen, submitted). The main objective was to ensure the survival of an endangered chironomid (*Chironomus anthracinus*) and to reduce internal nutrient loading. Hypolimnic oxidation markedly reduced internal phosphorus loading, which together with the reduction in external loading, significantly lowered the average summer epilimnion phosphorus concentration from 0.13 mg P l^{-1} to 0.03 mg P l^{-1}. As a consequence, algal biomass has decreased and transparency has improved considerably (Rasmussen, submitted.). Oxidation is now gradually being phased out.

Nitrate treatment of lake sediment (Ripl, 1976) or the hypolimnion (Erlandsen *et al.*, 1988) may be a valuable alternative oxidation method to the use of pure oxygen. An experiment recently initiated in Lake Lyng (10 ha, max depth 7.6 m) has confirmed earlier observations that nitrate treatment of the hypolimnion may significantly reduce phosphorus release from iron-rich sediment (M. Søndergaard and E. Jeppesen unpublished observation). The findings, together with those of Erlandsen *et al.* (1988), indicate that nitrate treatment of the hypolimnion is a feasible alternative to the far more expensive and technically demanding sediment treatment method developed by Ripl (1976). Like oxygen, the nitrate serves two purposes: In the short-term it improves sediment redox conditions, thereby diminishing the phosphorus release in the transitional phase following a reduction in external loading; in the long-term, it stimulates aerobic mineralization of organic matter, thereby enhancing the sediment retention capacity for phosphorus.

Biological homeostasis is another factor affecting internal P loading. Thus planktivorous and benthivorous fish seem to contribute significantly to biological resilience in shallow eutrophic lakes. By feeding on large zooplankton and stirring up sediment when foraging on benthic invertebrates, they prevent efficient grazer control of phytoplankton, thereby keeping the lake in the turbid state despite a reduction in external loading. A shift to the clear-water state may therefore be prevented or delayed (Jeppesen et al., 1990; Hosper and Jagtman, 1990; Scheffer, 1990; Scheffer et al., 1993). To overcome such biological resilience, various fish manipulation methods have been and are currently being developed. One such method is the enhancement of top-down control of phytoplankton by the selective removal of planktivorous fish, a method that has been employed with varying degrees of success in many parts of the world (Shapiro and Wright, 1984, Benndorf, 1990; De Melo et al., 1992; Meijer et al., 1994; Gulati et al., 1995; Phillips et al., 1996).

An alternative or supplementary method to fish removal is to stock high numbers of 0+ pike (1,500-3,000 ha^{-1}) to control newly hatched planktivorous fish such as roach, bream and bleak (Prejs, 1994; Søndergaard et al., 1997; Berg et al., in press) (see Box 3). However, stocking has to be repeated every year until macrophytes have become established, it not usually being possible to maintain a sufficiently high pike density to control the young-of-the-year (YOY) due to cannibalism among the pike (see Box 3).

The first Danish full-scale experiments involving fish manipulation were initiated in 1986, and fourteen additional experiments have since been undertaken. Lake Væng is an example of a successful restoration (see Box 4). The findings to date indicate that the method will have a long-term effect in shallow lakes if nutrient loading has been reduced to a level where the TP concentration in the future state of equilibrium will be below 0.05-0.1 mg P l^{-1} (E. Jeppesen and M. Søndergaard, unpublished obser-

Box 3. Fish manipulation by stocking of 0^+ pike (Esox lucius) in Lake Lyng.

Lake Lyng has a surface area of 10 ha, a mean depth of 2.4 m and a maximum depth of 7.6 m. Approximately 10% of the lake area has a depth above 5 m and stratifies during summer. The lake has no surface inlets except during periods of heavy precipitation, and the hydraulic retention time is estimated to be more than one year. It is eutrophic and in 1989, before pike stocking began, mean summer Secchi depth was 0.72 m and total phosphorus 0.79 mg P l^{-1} (epilimnion). In spring 1990-93 stocking of juvenile pike (mean length: 2-6 cm) was undertaken in densities ranging from 500 to 3,600 ind. ha^{-1} $year^{-1}$. Catch per unit effort of the dominant species, roach, varied from 17 to 272 during the period 1989-94. YOY (young of the year roach) density was high in years with little or no stocking, but was low in years with high stocking. There were corresponding marked changes in the abundance and relative composition of zooplankton, and the percentage contribution of *Daphnia* to total cladoceran density was highest and rotifer density lowest in years with low YOY density (Figure 5). Mean summer chlorophyll *a* correlated significantly with YOY density, suggesting an impact of stocking at the phytoplankton level. Finally, total phosphorus concentration was positively related to YOY density, irrespective of the fact that no changes were observed in the external P loading. It is concluded that pike stocking can be used as a lake restoration tool to increase lake water transparency; however, the effect only lasts for the season in which stocking is undertaken. The method is therefore considered to be most useful in shallow, turbid lakes in which nutrient loading has been reduced sufficiently to permit substantial and permanent macrophyte coverage if clearwater conditions are established. Further information about the pike stocking trials is given in Berg et al. (1997) and Søndergaard et al. (1997).

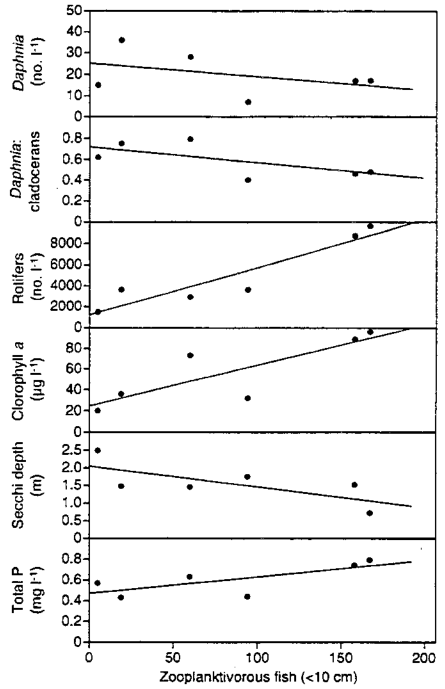

Figure 5. *Daphnia* abundance, contribution of *Daphnia* to total cladoceran density, rotifer abundance, chlorophyll *a*, Secchi depth and total phosphorus versus abundance of planktivorous fish (<10 cm) caught in multiple mesh size gill-nets in Lake Lyng in August during 6 years with different levels of stocking of 0^+ pike (0-3,620 indiv. ha^{-1}).

vation), a level somewhat lower than the threshold of 0.08-0.15 mg P l^{-1} given by Jeppesen et al. (1990). However, if nitrogen loading is low, fish manipulation may have a positive impact at higher phosphorus concentrations. The threshold of 0.05-0.1 mg P l^{-1} is in accordance with the results of a survey of 65 Danish lakes (Figure 7) as it is within this range that major changes in lake biological structure are usually observed: The biomass of planktivorous fish decreases and the percentage of predator fish increases, thus indicating greater control of prey fish by the carnivorous fish. Moreover, the zooplankton:phytoplankton ratio increases, thus indicating greater grazer control of phytoplankton, and chlorophyll *a* declines and transparency increases. Fish manipulation may cascade to the nutrient levels as well. A 30-50% reduction in lake concentrations of total nitrogen and total phosphorus has been found in the most successful fish manipulation experiments in Denmark, even in cases where macrophytes were absent (Jeppesen *et al.*, 1998). Consequently, lake nutrient retention capacity increases and loading of the marine areas decreases. Fish manipulation methods are still being developed, but there is little doubt that they will become an important tool to promote the restoration of eutrophic lakes once external nutrient loading reduction has been reduced.

A further factor contributing to resilience following a reduction in nutrient loading is grazing by waterfowl, in particular coot (*Fulica atra*) and mute swan (*Cygnus olor*), which have been reported to delay recolonization by submerged macrophytes (Lauridsen et al., 1993, 1994; van Donk et al., 1994; Søndergaard et al., 1996). The construction of refuges to protect macrophytes against grazing has therefore been employed as an alternative or supplementary restoration tool. The refuges need only be simple, e.g. wooden poles surrounded by garden fencing or chicken wire. The refuges enable the macrophytes to grow in a grazer-free environment from where they may spread and colonize the remainder of the lake.

In addition, macrophyte refuges serve as a daytime refuge for pelagic zooplankton (*Daphnia*, etc.), thereby enabling them to avoid fish predation (Timms & Moss, 1984; Phillips *et al.*, 1996; Schriver *et al.*, 1995; Lauridsen and Lodge, 1996). At night, when predation risk is lower, the zooplankton migrate into open water in search of food. Macrophyte refuges thus help augment grazing pressure on phytoplankton, thereby enhancing water transparency and further improving growth conditions for the macrophytes. Experiments undertaken in Denmark show that zooplankton density is highest in areas of high macrophyte density (Jeppesen et al., 1997), this being in accordance with

Box 4. Fish manipulation by removal of planktivorous fish in Lake Væng

Lake Væng covers 15 ha, has a mean depth of 1.2 m, a maximum depth of 1.8 m and a hydraulic retention time of 15-25 days. Groundwater contributes 95% of the inflow, and biologically treated sewage effluent from a small village was discharged into the lake until 1981. No changes in biological structure and Secchi depth were observed during the first five years following cessation of sewage discharge. The fish stock was dominated by plankti-benthivorous fish and the zooplankton biomass was low, while the phytoplankton biomass was high and dominated by cyanobacteria.

From October 1986 to July 1988, 50% of the plankti-benthivorous fish biomass was removed, thereby causing a trophic cascade resulting in low phytoplankton biomass and low percentage of cyanobacteria. Secchi depth increased significantly from a summer mean of approx. 0.6 m and peaked in 1989-90 (Figure 6). After an initial delay that was probably attributable to grazing by waterfowl, submerged macrophytes colonized the lake and the concentration of nitrogen, and in most years also of phosphorus, decreased. The piscivore:plankti-benthivore ratio increased to 50%, thereafter fluctuating between 30% and 60%. The macrophytes almost disappeared during the winter of 1991-92. However, expect for a short-term deterioration in late summer (a few weeks), the lake stayed clear, supposedly due to the high density of piscivorous fish. The macrophytes reappeared in 1993 and have since increased their coverage. Thus the lake has stayed clear for seven years following the fish manipulation initiative. The Lake Væng case study is a good illustration of biological resilience caused by the plankti-benthivorous fish, as well as of the efficacy of fish removal in cases where the conditions for such an intervention are fulfilled (see text).

It also shows a cascading effect on the nitrogen and phosphorus levels in the lake, in particular following the appearance of submerged macrophytes. Further information about the study can be found in Søndergaard et al. (1990), Jeppesen et al. (1990, 1991 and 1998) and Lauridsen et al. (1993, 1994).

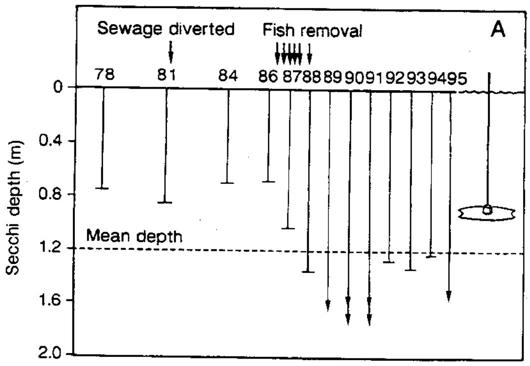

Figure 6a. Trend in the summer mean Secchi depth (May-October) in Lake Væng following the cessation of sewage discharge in 1981 and fish manipulation in 1986-88 involving removal of 50% of the planktivorous fish biomass. Arrows indicate that Secchi depth reached the bottom at some of the sampling dates; the mean values are therefore higher.

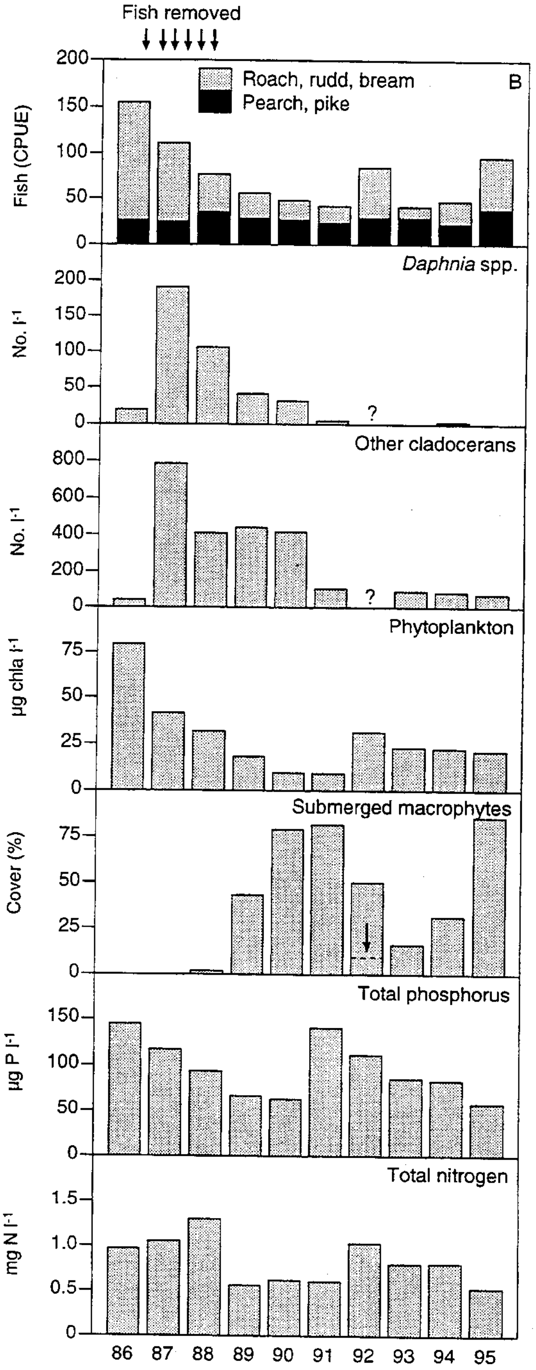

Figure 6b. Trend in catch per unit effort (numbers of fish caught in multiple mesh size gill-nets) of the dominant fish species in Lake Væng following fish manipulation. Also shown are summer mean *Daphnia* and *Bosmina* abundance, chlorophyll *a*, lake water total phosphorus and total nitrogen concentrations, and maximum submerged macrophyte coverage during summer.

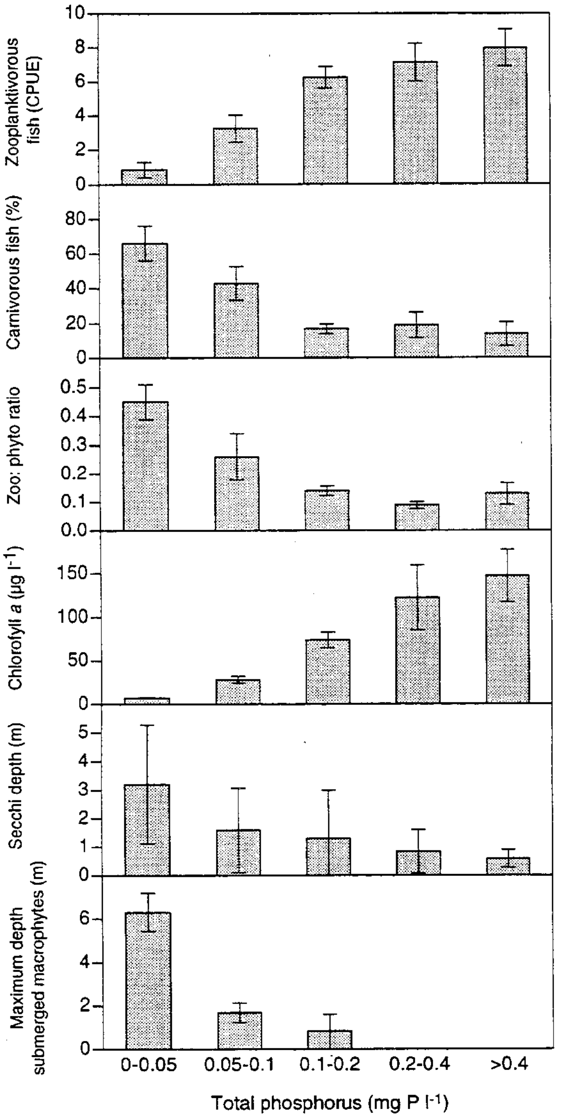

Figure 7. Catch per unit effort (CPUE) in terms of biomass of plankti-benthivorous fish in multiple mesh-sized gill nets (14 different mesh sizes 6.25-75 mm) sampled between 15 August and 15 September in all Danish lakes on which information about fish CPUE and zooplankton is available (n = 65). Also shown are the percentage of carnivorous fish, summer mean of zooplankton:phytoplankton biomass ratio, epilimnion chlorophyll *a* concentration, Secchi depth and the maximum depth of submerged angiosperm macrophytes versus total phosphorus. Mean ± SD of the five total phosphorus groups is shown. Note that the x-axis is not linear. The impact of changes in total phosphorus on biological structure and physico-chemical variables is thus particularly high at low phosphorus levels.

the fact that fish tend to avoid such areas (Winfield; 1986; Engel, 1988; Phillips et al., 1996; Jeppesen et al., 1997). Moreover, the number of zooplankton migrating into open water at night was highest from dense macrophyte refuges (Jeppesen et al., 1997), just as daytime concentration and night-time migration of zooplankton per unit area at fixed macrophyte density were highest from small refuges (Lauridsen et al., 1996). The latter may be attributable to the fact that migratory pelagic zooplankton seem to prefer the transitional zone between plants and open water, for which reason their density is greatest in refuges having a high perimeter:area ratio (Lauridsen & Buenk, 1996). Small, dense macrophyte beds thus seem to have the highest flux of migrating zooplankton per unit area, and hence probably have the greatest grazing impact on the open water phytoplankton. The usefulness of plant refuges as a restoration tool is probably limited to the same nutrient level as the fish manipulation methods (Jeppesen et al., 1997), and their effect is probably greatest in small lakes (Søndergaard et al., 1996; Jeppesen et al., 1997) where coot density in the absence of plants is highest (Brøgger-Jensen & Jørgensen, 1992).

Conclusions

The Danish findings indicate that even if population density is high and agricultural activity intensive, then lake eutrophication problems can still be remedied. This demands a multiple approach encompassing measures aimed at reducing point source and diffuse loading, as well as enhancing nutrient retention and removal in the catchment, e.g. by re-establishing lost wetlands, remeandering streams and changing stream maintenance practice. To speed up lake recovery following a reduction in nutrient loading, lake restoration measures may be used. At relatively low nutrient concentrations, particularly in shallow lakes, recovery may be enhanced by biomanipulation. At high nutrient concentrations, however, sediment dredging and hypolimnic oxidation with pure oxygen or nitrate may be more valuable. Danish experience also indicates that cooperation between state and regional authorities on the exchange of know-how, data and models can ensure an efficient and scientifically sound approach to the lake eutrophication problem.

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References

Benndorf, J. (1990). Condition for effective biomanipulation: Conclusion derived from whole-lake experiments in Europe, *Hydrobiologia,* 200/201, 187-204.

Berg, S., E. Jeppesen & M. Søndergaard (1997). Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng (Denmark), *Hydrobiologia.,* 342/343, 311-318.

Brøgger-Jensen, S. & H.E. Jørgensen (1992). Vandfugle og søers miljøtilstand. Miljøprojekt nr. 200 [Waterfowl versus the environmental state of lakes. Environmental Project no. 200], Danish Environmental Protection Agency, Copenhagen, 64 pp. (In Danish).

Christensen, P.B., L.P Nielsen & N.P. Revsbech (1991). Denitrification i våd- og vandområder [Denitrification in wetlands, lakes, rivers and fjords]. In: J.-O. Frier & J.R. Christensen*: Kvælstof, fosfor og organisk stof i jord- og vandmiljøet* [Nitrogen, phosphorus and organic matter in land and water environment]. Rapport fra konsensuskonference 31. januar, 1. og 4. februar 1991, Danish Environmental Protection Agency, 10-24. (In Danish)

Cullen, P. & C. Forsberg (1988). Experience with reducing point sources of phosphorus to lakes. *Hydrobiologia,* 170, 321-336.

De Melo, R., R. France & D.J. McQueen (1992). Biomanipulation: Hit or myth? *Limnology & Oceanography,* 37, 192-207.

Engel, S. (1988). The role and interactions of submersed macrophytes in a shallow Wisconsin lake. *Journal of Freshwater Ecology,* 4, 329-340.

Erlandsen, H., P. Breetum, J.E. Løvik, S. Markager & T. Källqvist (1988). Kolbotnvatnet. Sammenstilling av resultater fra perioden 1984-89. Report from Norsk Institut for Vannforskning, NIVA, Oslo, Norge, 118 pp. (In Norwegian).

Friberg, N., B. Kronvang, L.M. Svendsen, H.O. Hansen & M.B. Nielsen (1994). Restoration of a channelized reach of the River Gelså, Denmark: Effects on the macroinvertebrate community. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 3, 73-92.

Gulati, R., 1995. Manipulation of fish population for lake recovery from eutrophication in the temperate regions (Chapter 4). In: R. De Bernardi & G. Guissani (Eds.), *Biomanipulation in lakes and reservoirs management. Guidelines of lake management,* 7, 53-79.

Hoffmannn, C.C., M. Dahl, L. Kamp-Nielsen & H. Stryhn (1993). Vand- og stofbalance i en natureng [Water and nutrient mass balance in a meadow]. Danish Environmental Protection Agency, Copenhagen, 152 pp. (In Danish).

Hoffmannn, C.C. (1996). Fate of phosphate, nitrate and other elements during short-term flooding of a riparian meadow. In: Kronvang B., Svendsen, L.M. & Sibbesen, E. (Eds.) (1996): Sediment and phosphorus. Erosion and delivery, transpor and fate of sediments and sedimentassociated nutrients in waterheds. Proceedings from an international workshop held in Silkeborg, Denmark, October 9-12, 1995. Ministry of Environment and Energy. NERI Technical Report. No. 178, 135-142.

Hoffmannn, C.C. (1997). Nitrate removal in a regularly flooded riparian meadow. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie.* (In press).

Hoffmann, C.C. (1998). Nutrient retention in wet meadows and fens. Phd-thesis. National Environmental Research Institute, Denmark, pp 134.

Hosper, S.H. & E. Jagtman (1990). Biomanipulation additional to nutrient control for restoration of shallow lakes in the Netherlands, *Hydrobiologia,* 200/201, 523-534.

Iversen, T.M., B. Kronvang, B.L. Lauge, P.N. Markmann & M.B. Nielsen (1993). Re-establishment of Danish streams: restoration and maintenance measures. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 3, 73-92.

Iversen, T.M., B. Kronvang, C.C. Hoffmannn, M. Søndergaard & H.O. Hansen (1995). Restoration of aquatic ecosystems and water quality. In: Skotte-Møller, H. (ed.), *Nature restoration in the European Union.* Proceedings from a seminar in Denmark 29-31 May 1995. Ministry of Environment and Energy, The National Forest and Nature Agency, 63-69.

Jensen, J.P., P. Kristensen & E. Jeppesen (1991). Relationships between nitrogen loading and in-lake nitrogen concentrations in shallow Danish lakes. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie,* 24, 201-204.

Jensen, H.S., P. Kristensen, E. Jeppesen & A. Skytthe (1991). Iron:phosphorus ratio in surface sediment as an indicator of phosphorus release from aerobic sediments in shallow lakes. *Hydrobiologia,* 235/236, 731-743.

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H.J. Jensen, J.P. Müller, O. Sortkjær, J.P. Jensen, K. Christoffersen, S. Bosselmann & E. Dall, 1990a: Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. – *Hydrobiologia,* 200/201: 205-218.

Jeppesen, E., J.P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik (1990b). Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. *Hydrobiologia,* 200/201, 219-227.

Jeppesen, E., P. Kristensen, J.P. Jensen, M. Søndergaard, E. Mortensen & T. Lauridsen (1991). Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: Duration, regulating factors and methods for overcoming resilience. *Memorie dell'Istituto Italiono di Idrobiologia,* 48, 127-148.

Jeppesen, E., J.P. Jensen, M. Søndergaard, T. Lauridsen, L.J. Pedersen & L. Jensen (1997). Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia,* 342/343, 151-164.

Jeppesen, E., J.P. Jensen, J. Windolf, T.L. Lauridsen, M. Søndergaard, K. Sandby & P.H. Møller (1998). Changes in nitrogen retention in four shallow eutrophic lakes following a decline in density of cyprinids. *Archiv für Hydrobiologie,* 142, 129-152.

Jørgensen, T.B. (Submitted) Brabrand sø (Lake Brabrand) in Danish.

Kristensen, P., J.P. Jensen & E. Jeppesen (1990). Eutrofieringsmodeller for søer. [Eutrophication models for lakes]. NPo-forskning fra Miljøstyrelsen C9, C-abstracts. Danish Environmental Protection Agency, Copenhagen, 120 pp. (In Danish).

Kristensen, P., J.P. Jensen & E. Jeppesen (1991). Simple empirical lake models. Nitrogen and phosphorus in fresh and marine waters. NPo-forskning fra Miljøstyrelsen, C-abstracts. Danish Environmental Protection Agency, Copenhagen, 125-145.

Kronvang, B. (1992). The export of particulate matter, particulate phosphorus and dissolved phosphorus from two agricultural river basins: Implications for estimating the non-point phosphorus load. *Water Research,* 26, 1347-1358.

Kronvang, B., P. Græsbøll, L.M. Svendsen, N. Friberg, A.B. Hald, G. Kjellson, M.B. Nielsen, B.D. Petersen & O. Ottosen (1994). Restaurering af Gelså ved Bevtoft – miljømæssig effekt i vandløb og de vandløbsnære arealer. [Restoration of the river Gelså at Bevtoft – environmental effect in streams and riparian zones. National Environmental Research Institute. Scientific Report no. 110]. Faglig rapport fra DMU nr. 110, 87 pp. (In Danish).

Kronvang, B., R. Grant, S.E. Larsen, L.M. Svendsen & P. Kristensen (1995). Non-point-source nutrient losses to the aquatic environment in Denmark: Impact of agriculture. *Marine Freshwater Research,* 46, 167-77.

Kronvang, B., L.M. Svendsen, O. Ottosen, M.B. Nielsen & L. Johannesen (1997). Remeandering of rivers: short-term implications for sediment and nutrient transport. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie.* (In press).

Kronvang, B, C.C. Hoffmann, L.M. Svendsen, J. Windolf, J.P. Jensen & J. Dørge (1998): Retention of nutrients in river basins, Aquatic Ecology. (In press, b).

Larsen, S.E., J. Erfurt, P. Græsbøll, B. Kronvang, E. Mortensen, C.A. Nielsen, N.B. Ovesen, C. Paludan, Aa. Rebsdorf, L.M. Svendsen & Per Nyegaard (1995). Ferske vandområder – Vandløb og kilder. Vandmiljøplanens Overvågningsprogram 1994. [Freshwater areas – streams and springs. The Aquatic Monitoring Programme 1994. National Environmental Research Institute. Scientific Report no. 140]. Danmarks Miljøundersøgelser. Faglig rapport fra DMU nr. 140, 196 pp. (In Danish).

Lauridsen, T.L., E. Jeppesen & F.Ø. Andersen (1993). Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: Impact of sediment composition and water fowl grazing. *Aquatic Botany,* 46, 1-15.

Lauridsen, T.L., E. Jeppesen & M. Søndergaard (1994). Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish-manipulation. *Hydrobiologia,* 275/276, 233-242.

Lauridsen, T. & I. Buenk (1996). Diel changes in the horizontal distribution of zooplankton in the littoral zone of two eutrophic shallow lakes. *Archiv für Hydrobiologie,* 137, 161-176.

Lauridsen T. & D. Lodge (1996). Avoidance by *Daphnia magna* Strauss of fish and macrophytes: Chemical cues and predator-mediated use of macrophyte habitat. *Limnology & Oceanography,* 41, 794-798.

Lauridsen, T., L. Junge Pedersen, E. Jeppesen & M. Søndergaard (1996). The importance of macrophyte bed size for composition and horizontal migration of cladocerans in a shallow lake. *Journal of Plankton Research.* 18, 2283-2294

Madsen, B.L. (1995). Danish watercourses – ten years with the new Watercourse Act. Miljønyt no. 11, Danish Environmental Protection Agency, Copenhagen, 206 pp.

Meijer, M-L., E. Jeppesen, E. van Donk., B. Moss, M. Scheffer, E. Lammens, E. Van Nes, J.A. Berkum, G.J. de Jong, B.A. Faafeng & J.P. Jensen (1994). Long-term responses to fish-stock reduction in small shallow lakes: Interpretation of five year results of four biomanipulation cases in the Netherlands and Denmark. *Hydrobiologia,* 275/276, 457-466.

Paludan, C. & C.C. Hoffmann (1996); Fate of phosphorus in a Danish minerotrophic wetland. In: Kronvang B., Svendsen, L.M. & Sibbesen, E. (Eds.) (1996): Sediment and phosphorus. Erosion and delivery, transpor and fate of sediments and sedimentassociated nutrients in waterheds. Proceedings from an international workshop held in Silkeborg, Denmark, October 9-12, 1995. Ministry of Environment and Energy. NERI Technical Report. No. 178, 123-129.

Phillips, G.L., M. Perrow & J. Stansfield (1996). Manipulating the fish-zooplankton interaction in shallow lakes: a tool for restoration. In: S.P.R. Greenstreet and M.L. Tasker (Eds.), *Aquatic Predators and Their Prey.* Blackwell Scientific Publications, Oxford, 174-183.

Prejs, A., A. Martyniak, S. Born, P. Hliwa & P. Koperski (1994). Food web manipulation in a small eutrophic Lake Wirbel, Poland: Effect of stocking with juvenile pike on planktivorous fish. *Hydrobiologia,* 275/276, 65-70.

Rasmussen, K. (submitted). Restaurering af Hald Sø. [Restoration of lake Hald]. (In Danish)

Rebsdorf, AA., N. Friberg, C.C. Hoffmannn & B. Kronvang (1994). Ånære arealers samspil med vandløb. [The interaction of riparian zones with streams]. Danish Environmental Protection Agency, Copenhagen, 140 pp. (In Danish).

Riemann, B., K. Christoffersen, H.J. Jensen, J.P. Müller, C. Lindegaard & S. Bosselmann, 1990. Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. *Hydrobiologia,* 200/201, 241-250.

Ripl, W. (1976). Biochemical oxidation of polluted lake sediment. A new restoration method. *Ambio,* 5, 409-452.

Sas, H. (Ed.), 1989. *Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation.* Acad. Ver. Richardz Gmbh., 497 pp.

Scheffer, M. (1990). Multiplicity of stable states in freshwater systems. *Hydrobiologia,* 200/201, 475-486.

Scheffer, M., S.H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen (1993). Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution (TREE),* 8, 275-279.

Schriver, P., J. Bøgestrand, E. Jeppesen & M. Søndergaard (1995). Impact of submerged macrophytes on fish, zooplankton and phytoplankton interactions: Large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology*, 33, 255-270.

Shapiro, J. & D.I. Wright (1984). Lake restoration by biomanipulation. Round Lake, Minnesota – the first two years. *Freshwater Biology*, 14, 371-383.

Skotte-Møller, H., 1995. Nature restoration in Denmark – status and perspectives. In: Skotte-Møller, H. (ed.), *Nature restoration in the European Union*. Proceedings from a seminar in Denmark 29-31 May 1995. Ministry of Environment and Energy, The National Forest and Nature Agency, 63-69.

Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. *American Geophysical Union Transactions*, 38, 913-920.

Svendsen, L.M. & B. Kronvang (1993). Retention of nitrogen and phosphorus in a Danish lowland river system: Implications for the export from the watershed. *Hydrobiologia*, 251, 123-135.

Svendsen, L.M., B. Kronvang, P. Kristensen & P. Græsbøll (1995). Dynamics of phosphorus compounds in a lowland river system: Importance of retention and non-point sources. *Hydrobiological Processes*, 9, 119-142.

Svendsen, L.M., B. Kronvang, A.R. Laubel, S.E. Larsen & B. Andersen (1998). Phosphorus retention in a Danish lowland river system. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*. (In press).

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen & O. Sortkjær (1990). Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: A combined effect of reduced internal P-loading and increased zooplankton grazing. *Hydrobiologia*, 200/201, 229-240.

Søndergaard, M., P. Kristensen & E. Jeppesen (1993) Eight years of internal phosphorus loading and changes in the sediment phosphorus profile of Lake Søbygaard, Denmark. *Hydrobiologia*, 253, 345-356.

Søndergaard, M., L. Olufsen, T. Lauridsen, E. Jeppesen & T. Vindbæk Madsen (1996). The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. *Aquatic Botany*, 53, 73-84.

Søndergaard, M., E. Jeppesen & S. Berg (1997). Pike *(Esox lucius)* stocking as a biomanipulation tool, 2. Effects on lower trophic levels in Lake Lyng, Denmark. *Hydrobiologia*, 342/343, 319-325.

Timms, R.M. & B. Moss (1984). Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnology & Oceanography*, 29, 472-486.

Van Donk, E., E. De Deckere, J.G.P. Klein Breteler & J. Meulemans (1994). Herbivory by waterfowl and fish on macrophytes in a biomanipulated lake: Effects on long-term recovery. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 25, 2139-2143.

Vollenweider, R.A. (1976). Advance in defining critical loading levels for phosphorus in lake eutrophication. *Memorie dell'Istituto Italiono di Idrobiologia*, 33, 53-83.

Windolf, J., E. Jeppesen, M. Søndergaard, J.P. Jensen & L. Sortkjær (1993). Ferske vandområder – søer. Vandmiljøplanens Overvågningsprogram 1992. [Freshwater areas – lakes. The Aquatic Monitoring Programme 1992. National Environmental Research Institute. Scientific Report no. 90]. Danmarks Miljøundersøgelser. Faglig rapport fra DMU, nr. 90, 130 pp. (In Danish)

Windolf, J. E. Jeppesen, J.P. Jensen & P. Kristensen (1996). Modelling the seasonal variation in in-lake concentration and retention of nitrogen in 16 shallow lakes: a four-year mass balance study. *Biogeochemistry*, 33, 25-44.

Winfield, I.J. (1986). The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. *Journal of Fish Biology*, 29, 37-48.

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Jens Peder Jensen, Erik Jeppesen, Peter Kristensen, Peter Bondo Christensen and Martin Søndergaard

National Environmental Research Institute, Division of Freshwater Ecology,
25 Vejlsøvej, DK - 8600 Silkeborg, Denmark

Nitrogen Loss and Denitrification as Studied in Relation to Reductions in Nitrogen Loading in a Shallow, Hypertrophic Lake (Lake Søbygård, Denmark)

key words: nitrogen, shallow lakes, reduced loading, budgets, burial, denitrification, models

Abstract

A detailed mass balance on nitrogen was carried out in shallow and hypertrophic Lake Søbygård during 4.5 years before through 2.5 years after a 36 % reduction in nitrogen loading. Annual mean loss rate of nitrogen was 159–229 mg N m^{-2} d^{-1} before the loading reduction and 125 mg N m^{-2} d^{-1} after. In spite of a short hydraulic retention time (18–27 days) the proportion of nitrogen loading lost in the lake was high (38–53 %) and not affected by changes in loading. Calculated denitrification accounted for 86–93 % of the loss rate, while 7–14 % was permanently buried. Marked seasonal variations in the loss percentage were found during the season, ranging from 23 % in first quarter to 65 % in third quarter. The seasonal variation in the loss percentage of nitrogen showed a hysteresis like relationship to temperature, with a high percentage in fourth quarter. This suggests that the amount of available substrate, which mainly consists of sedimentated phytoplankton, accumulated during summer, is an important regulating factor. The ability of various published input-output models to predict the observed changes in in-lake nitrogen concentration in Lake Søbygård was tested. This study has further confirmed that small lakes with short retention and high nitrogen loading may significantly reduce the nitrogen loading of downstream aquatic environments.

Contents

1. Introduction

Several authors have stressed the importance of freshwater aquatic ecosystems as a sink in the transport of anthropogenic, land based nitrogen to coastal areas (e.g. SEITZINGER, 1988). Highly variable percentage reductions have been obtained for streams and rivers, ranging from less than 2 % in shallow Danish streams (JEPPESEN *et al.*, 1987; CHRISTENSEN and SØRENSEN, 1988) to more than 70 % in slow-running and heavily organic loaded rivers in Central Europe (BILLEN *et al.*, 1986). Similar high ranges have been found when considering all sizes and eutrophication levels of lakes and estuaries (8 to 81 %, SEITZINGER, 1988). However, remarkably constant and high relative loss rates have been found in 69 shallow, eutrophic Danish lakes with short retention time (43 % ± 6 %, 95 % C.L., JENSEN *et al.*, in press[1]). Relative constant loss percentages have also been obtained for six estuaries with various nitrogen loadings (SEITZINGER, 1988).

In order to test whether the proportion of nitrogen loss was affected by changes in nitrogen loading to shallow lakes with short retention time, we carried out a comprehensive mass balance study of hypertrophic Lake Søbygård during 4.5 years before through 2.5 years after a 36 % reduction in nitrogen loading. In this paper the annual balances are discussed in details, while the seasonal trends are only crudely evaluated. Furthermore, we compare the ability of various published input-output models to predict the observed changes in Lake Søbygård. A more detailed discussion of the seasonal variations and determining factors of the nitrogen dynamics in Lake Søbygård will appear elsewhere.

2. Materials and Methods

2.1. Study area

The study was carried out in Lake Søbygård which is small (0.39 km^2), shallow (mean depth of 1.0 m and maximum depth of 1.9 m) and alkalic (1 to 2.6 meq l^{-1}). The lake is situated in the central part of Jutland, Denmark. The retention time is short; 18 to 27 days as an annually mean and 23 to 34 days in average during summer. The catchment area is 11.6 km^2 and consists of grassland, intensive agricultivated areas and forest. The lake is almost entively surrounded by forest. One exception is to the west, and the lake is therefore exposed to westerly wind which is the dominating wind in Denmark. Emergent and floating-leaved macrophytes are sparsely developed while submerse vegetation is totally absent.

The lake receives 80 to 90 % of the water from one main inlet containing sewage water from the nearby situated town, Hammel. Groundwater fed, iron rich springs are responsible for the remaining 10 to 20 % of the inlet water to the lake. During the sixties and early seventies, the lake received large amounts of only mechanical treated sewage water. In 1976, a biological treatment was established at the plant, which caused a 3 to 10 fold reduction in organic loading. In 1982, phosphorus removal was additionally established which reduced the phosphorus loading from 28–33 to 4–7 g P m^{-2} y^{-1}, corresponding to a reduction in annual mean phosphorus concentration in the main inlet from 1–3 to 0.15–0.25 mg P l^{-1} (SØNDERGAARD *et al.*, 1987). Due to internal loading of the lake, however, in-lake phosphorus concentration did not change accordingly. Thus, since 1982 mean concentration of total phosphorus has been relatively constant ranging from 0.35 to 0.64 mg P l^{-1} as annual means and from 0.50 to 0.90 mg P l^{-1} in summer (JEPPESEN *et al.*, 1990b).

2.2. Sampling

An extensive study was undertaken in 1978, while during 1984 and the following five years, the lake was studied intensively. To estimate loading and retention of nitrogen, water was sampled in the main inlet and in the outlet during 1978 manually and during 1984–89 with automatically

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[1] Here and following pages: instead "JENSEN *et al.*, in press" read "1991".

devices (Manning sampler). In 1978 point samples were taken in inlet lake and outlet 12 times during the season. During 1984 to 1989 three to four samples were taken during each 24 h. Before analysis, samples were pooled to represent either a 24 h mean or a weekly mean. Samples were additionally taken 2 to 8 times annually in springs entering the lake. Lake water was sampled with a 3.3 l Friedinger sampler either daily or 1 to 2 times weekly at a midlake station. Samples from 0.5 m and 1.5 m depths were mixed to represent the water column.

2.3. Discharge and nitrogen loading

Discharge (Q) in the inlet of the lake was measured 46 times during the study period. In the outlet of the lake, discharge was calculated from automatically recorded data of water level (H) and by use of relationship between H and Q, established from synchronous monthly measurements of discharge (OTT-propeller) and water level. In the major springs along the lake shore, discharges were additionally measured 2–8 times during 1985. No seasonal variation was found in the discharge from springs which accounted for approximately 10 % of the total water inlet to the lake. Daily values of Q-inlet could therefore be calculated as Q-outlet–Q-springs.

Daily total nitrogen concentrations were calculated by lineary interpolation of observed values. Nitrogen transport in the main inlet, in the outlet and in the springs entering the lake were calculated by multiplying of the daily values of water discharge and values of total nitrogen concentrations. This method gives the best estimation according to Bruhn and Kronvang (1989).

Nitrogen precipitation on the lake surface was considered to be constant during the investigation and a value of 5 mg N m^{-2} d^{-1} was obtained from The National Agency of Environmental Protection (1984).

2.4. Nitrogen burial and denitrification

Assuming that iron (Fe) can be regarded as a conservative tracer, annual net sedimentation of nitrogen was calculated from mass balances of total iron in the lake and a N : Fe ratio of permanently accumulated sediment. Total iron in the water phase was measured at the same frequency as nitrogen measurements. The annual iron loading ranged from 109 to 159 mg Fe m^{-2} d^{-1} during 1984 to 1989, and 62 to 80 % (mean = 73 %) of this loading was retained in the lake. The Fe : N-ratio in the sediment ranged from 3.7 in the upper 0–1 cm to 5.8, 6–10 cm below the sediment surface. Between 10 and 20 cm the ratio was almost constant (6.9 ± 0.2 (mean ± S.E.), $n = 21$). The latter is assumed to represent the ratio in permanently buried material. Thereby mean net sedimentation of nitrogen for 1984–1989 could be calculated to 15 mg N m^{-2} d^{-1}. If, instead, the lowest Fe : N-ratio observed in the surface and still decomposing sediment (upper 0–1 cm) was used, the estimate would have been 26 mg N m^{-2} d^{-1}.

Internal storage of nitrogen was calculated as differences in nitrogen content of the lake water during well defined periods (yearly or quarterly). Denitrification was then estimated according to the mass balance model presented by Messer and Brezonik (1978): Denitrification = Total input – (Total outlet + Storage + Burial).

2.5. Analyses

Ammonium was determined by the phenate method (Apha, 1985). Nitrite + nitrate was determined as nitrite on a Tecacor 5012 flow injection analyzer, supplied with a copper-cadmium reductor column. Total nitrogen was measured as nitrite + nitrate after potassium persulphate digestion according to Solorzano and Sharp (1980). Total phosphorus was determined as orthophosphate (Murphy and Riley, 1962) after persulphate digestion in an autoclave at 200 kPa for 30 minutes according to Koroleff (1970). Total iron was measured according to Heaney and Davison (1977) and Mackereth *et al.* (1978) after oxidation with potassium persulphate.

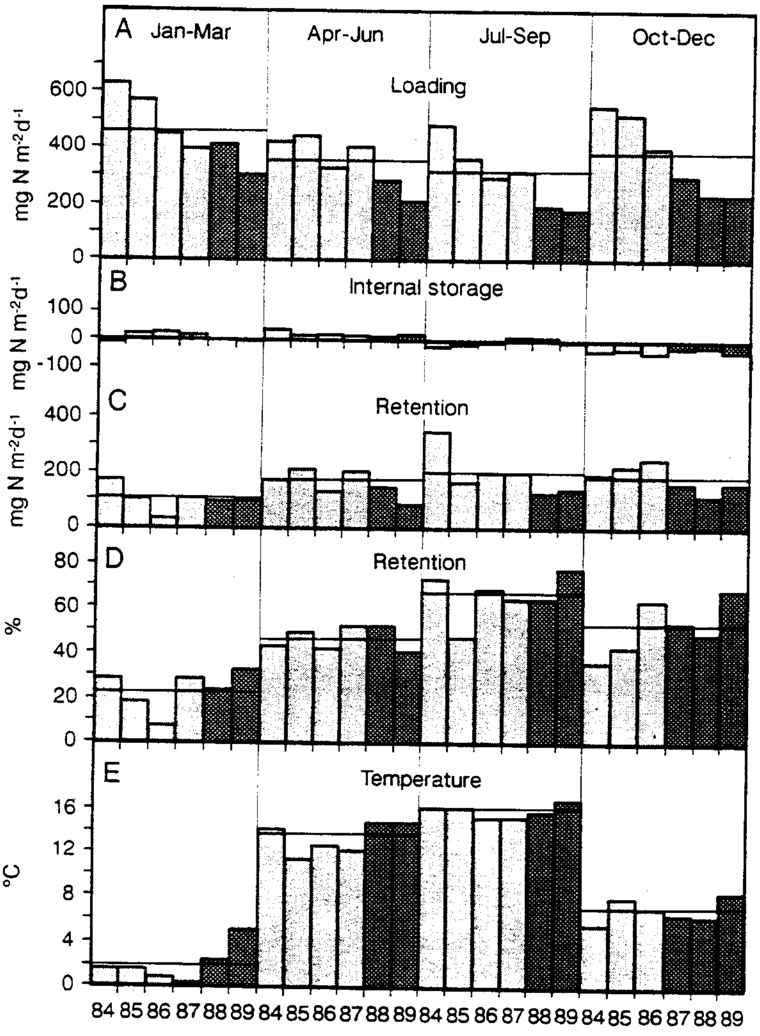

Figure 2. Quarterly nitrogen budget of and temperature in Lake Søbygård during 1984–1989. *A*: External loading, *B*: Internal storage in the lake water, *C*: Net retention, *D*: Net retention in percentage of external loading, *E*: Mean water temperature. The horizontal lines represent average values for each quarter during 1984–1989.

The mean loss in the lake was 23 % in the first quarter. The loss percentage was not significantly different in second and fourth quarters, 47 % and 52 % respectively, but significantly higher (65 %) in the third quarter (Fig. 2D). The loss percentage was similar in the second and fourth quarter in spite that the mean temperature differed significantly between the two periods (13.4 and 7.1 °C, respectively; Fig. 2). Internal storage and burial of nitrogen in the lake contributed to the total nitrogen loss by less than 10 %. Denitrification was therefore the most important process in the removal of nitrogen in Lake Søbygård. The seasonal variation in activity demonstrated that other factors than the temperature also were of importance in the control of the process.

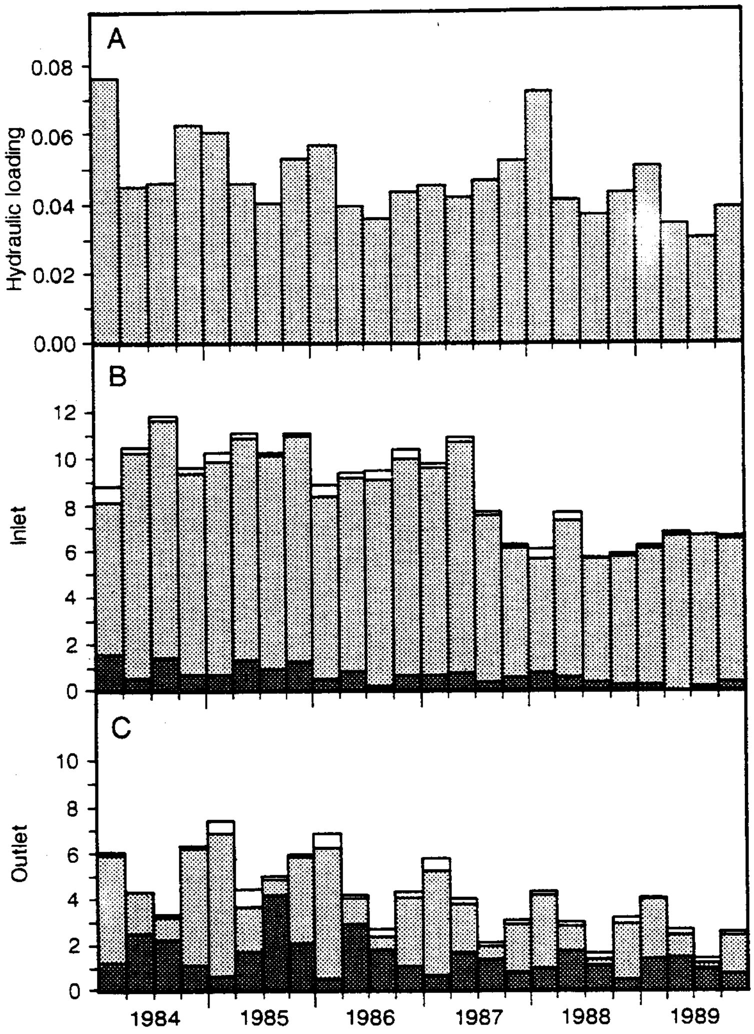

Figure 1. The quarterly mean hydraulic loading ($m^3\ m^{-2}\ d^{-1}$) (*A*), mean nitrogen concentration in inlet ($mg\ N\ l^{-1}$) (*B*) and outlet ($mg\ N\ l^{-1}$) (*C*) of Lake Søbygård during 1984–1989. Nitrogen is divided into organic nitrogen (dark shading), Nitrite + nitrate nitrogen (light shading) and ammonia nitrogen (open signature).

In general, highest nitrogen concentrations were measured in the first quarter (Jan to Mar) while the lowest values were found in the third quarter (Jul to Sep). Nitrate was the dominating nitrogen source in the inlet during all seasons (Fig. 1B). In contrast, organic nitrogen was a significant nitrogen source in the outlet water, in particular during summer where organic nitrogen constituted a major fraction of the total nitrogen (Fig. 1C).

Nitrogen loss showed a marked seasonal variation as significant higher rates ($P < 0.05$) were found in the last three quarters compared to the first quarter of the year (Fig. 2). A mean value of 214 and 135 mg N $m^{-2}\ d^{-1}$ was thus found for quarter 2 to 4 before and after reductions in nitrogen loading, respectively, compared to 121 and 97 mg N $m^{-2}\ d^{-1}$ for the first quarter.

3. Results

3.1. Annual balances

The total nitrogen loading of Lake Søbygård varied from 358 to 523 mg N m^{-2} d^{-1} until 1988. After closing down the slaughterhouse in August 1987, the nitrogen loading was significantly reduced by approximately 36 % in the following years to a value of 237 to 285 mg N m^{-2} d^{-1} (Table 1).

Table 1. Annual hydraulic loading (l m^{-2} d^{-1}) and annual nitrogen balance (mg N m^{-2} d^{-1}) of Lake Søbygård.

	1978	1984	1985	1986	1987	1988	1989
Hydraulic loading	40	58	50	44	47	49	39
Total nitrogen loading	359	523	476	369	358	285	237
Total nitrogen in outlet	175	300	293	209	174	160	114
Lake retention:							
– Internal storage	~0	−6	1	1	9	1	−2
– Loss	184	229	181	159	175	124	125
– Loss (% of loading)	51	44	38	43	49	43	53
– Burial	15	15	15	15	15	15	15
– Estimated denitrification	169	214	166	144	160	109	110
– Denitrification (% of loading)	47	41	35	39	45	38	46

Nitrogen concentrations in the springs entering the lake were constant throughout the seasons (data not shown) and the springs were estimated to contribute 25 mg N m^{-2} d^{-1}, corresponding to 5 to 10 % of the total external loading. Nitrogen loading from precipitation contributed less than 1 % of total loading. Nitrogen fixation was considered insignificant since cyanobacteria were almost absent in the lake (Jeppesen *et al.*, 1990a; Jeppesen *et al.*, 1990b). Diffuse sources and sewage water thus accounted for the remaining nitrogen-loading.

The net nitrogen loss in the lake varied from 159 to 229 mg N m^{-2} d^{-1} (annual mean) before reduction in nitrogen loading. Upon reduction, the average net loss was reduced to approximately 125 mg N m^{-2} d^{-1}. Expressed in percentage of loading, however, the nitrogen loss was comparable ranging between 38 to 53 % and these figures were not affected by reductions in nitrogen loading. Denitrification was responsible for 86 to 93 % of the net loss (corresponding to a denitrification rate of 109–214 mg N m^{-2} d^{-1}). Burial of nitrogen in the sediment was of minor importance and accounted only for 7 to 14 % of the net loss (approximately 15 mg N m^{-2} d^{-1}, Table 1).

3.2. Seasonal variation

The seasonal variation in hydraulic loading was low, indicating a constant input of sewage water and ground water (Fig. 1A). Also, the inlet nitrogen concentration was relative constant throughout the season. The reduction in nitrogen loading was reflected in the quarterly mean nitrogen concentration which markedly changed in the fall of 1987 from a mean value of 10.2 to 6.6 mg N l^{-1} (Fig. 1B). Similarly the mean outlet nitrogen concentration decreased from 5.0 to 2.8 mg N l^{-1} after the reduction in nitrogen loading (Fig. 1C).

Although nitrogen concentrations were relative constant in the lake inlet, marked seasonal variations were found in the quarterly mean outlet concentration (Fig. 1B and C).

4. Discussion

4.1. Denitrification activity

Denitrification rates in Lake Søbygård were high compared to rates reported from oligotrophic lakes and coastal areas (Abdelmoneim *et al.*, 1986; Christensen and Sørensen, 1986; Seitzinger, 1988). The rates were, however, comparable to rates obtained in other shallow, eutrophic lakes (Andersen, 1977; Jensen *et al.*, in press), in reservoirs (Admiraal and van der Vlugt, 1988) in streams (Edwards and Rolley, 1965; Jeppesen *et al.*, 1987; Christensen and Sørensen, 1988) and in shallow, eutrophic estuaries (Jørgensen and Sørensen, 1988).

Denitrification activities in shallow aquatic environments may greatly be stimulated by resuspension events. In Lake Søbygård, resuspension occurs almost twice a week (Kristensen and Jensen, 1987). In larger (42 km^2) and less wind protected lakes, resuspension events have been reported to occur every second day (Gons *et al.*, 1986; Kristensen *et al.*, submitted), which in one of the lakes (Lake Arresø), caused a suspension of the upper 3 mm of the sediment during 50 % of the time as an annual mean (Kristensen *et al.*, submitted). In undisturbed sediments, denitrification is restricted to a narrow zone of only 0.5 mm in depth located immediately below the oxic surface layer. The oxic surface layer constitutes a major diffusion barrier for NO_3^--diffusion to the denitrification zone and the depth of this layer is therefore an important controlling factor for the total NO_3^--flux for denitrification (Christensen *et al.*, 1989; Christensen *et al.*, 1990; Nielsen *et al.*, 1990). By suspending sedimentated material, resuspension events may introduce both O_2 and NO_3^- into deeper sediment layers. Increased availability of NO_3^- in the deeper sediment layer may greatly enhance denitrification activity since the denitrification potential in those layers is comparable to the potential in the uppermost surface layers. Introduction of O_2 into the deeper layers may initially inhibit denitrification activity but may, however, also stimulate denitrification in an expanded area of the sediment due to a coupling of the nitrification and denitrification processes. Similar results have been reported in bioturbated and vegetated sediments where fauna and plant activity provide a route of O_2 and NO_3^--transport to deeper sediment layers which supported denitrification to considerable depths in the sediment (Chatarpaul *et al.*, 1980; Christensen and Sørensen, 1986; Grundmanis *et al.*, 1977).

4.2. Loss percentage and recovery

Nitrogen loading and total activity of denitrification varied from year to year in Lake Søbygård. It was therefore remarkable that the percentage of nitrogen loss due to denitrification was relatively constant throughout the years of investigation (35 to 47 %, Table 1) and that the proportion lost was not affected by reduction in nitrogen loading. As a mean for all seven years, 40 % of the nitrogen loading was lost due to denitrification. The process accounted for approximately 90 % of total loss in the lake. Similar results have recently been reported for six estuaries which differed considerably in nitrogen loading (Seitzinger, 1988). In all estuaries, a nitrogen amount equivalent to 40–50 % of the nitrogen input was removed by denitrification. By calculating annual nitrogen budgets for 69 shallow, Danish lakes, Jensen *et al.* (in press) also demonstrated a very significant and relatively constant nitrogen loss for all lakes, and denitrification removed about 33 % of the nitrogen loading as a mean.

In Jensen *et al.* (in press) three simple empirical models relating annual mean in-lake nitrogen concentration to annual mean nitrogen loading and morphometric parameters were developed on the data from the 69 lakes. These models reflected the relative constant loss percentage of nitrogen found in this study (Fig. 3), since nitrogen loading was the far most important independent variable accounting for 50 % of the variation in in-lake concentration of nitrogen, while hydraulic retention time and mean depth accounted for additionally only 11 %, 2 %, respectively (JENSEN *et al.*, in press). The three models and additionally three models from the literature were applied to the data from Lake Søbygård to test the ability of the models to predict in-lake concentration in Lake Søbygård upon the marked changes in nitrogen loading. Predictions of the annual mean in-lake nitrogen concentration and thus the annual nitrogen loss was in close agreement with the actual measured concentrations for all the models developed by JENSEN *et al.* (in press). The most simple model (model 1), which only included inlet nitrogen as independent variable predicted the level of the observed in-lake concentration with a high accuracy (mean deviation: -4 %), while the two models including retention time and mean depth deviated 21 % and 14 %, respectively. The model by LIJKLEMA *et al.* (1989) showed a mean deviation of the same order as for the later two models (15 %), but in contrast to the Danish models, the slope of the regression line between predicted and observed in-lake concentration was significantly different from 1 (Fig. 3 B, $P < 0.0001$). The two other models tested predicted higher (32 %; OECD, 1982) and lower (-23 %; BACHMANN, 1984) in-lake concentration than observed.

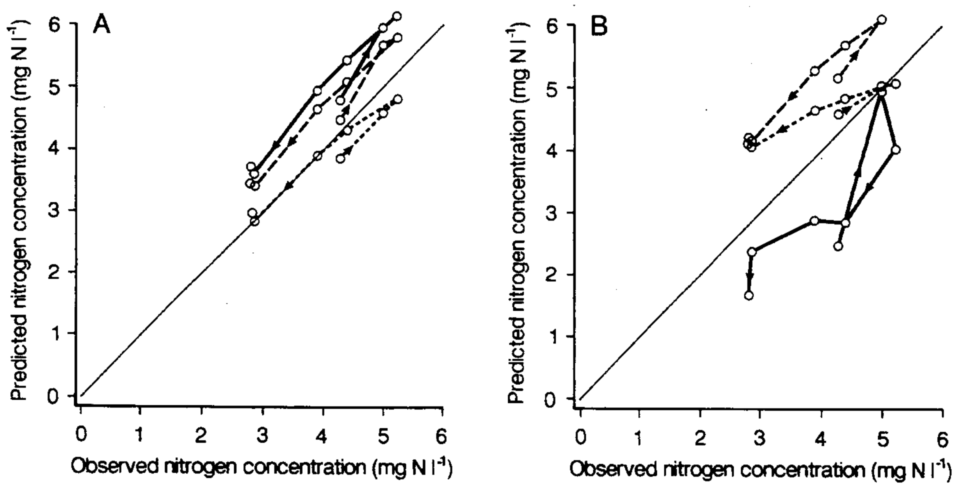

Figure 3. Comparison of observed and predicted in-lake total nitrogen concentrations in Lake Søbygård (1978, 1984–1989).

a) Models from JENSEN *et al.* (in press):

(----) Model 1: $[N]\ \lambda = 0.45 \cdot [N]_i$

(——) Model 2: $[N]\ \lambda = 0.42 \cdot [N]_i \cdot \tau\omega^{-0.11}$

(- - -) Model 3: $[N]\ \lambda = 0.34 \cdot [N]_i \cdot \tau\omega^{-0.16} \cdot Z^{0.17}$

b) Models from

(----) LIJKLEMA *et al.* (1989): $[N]\ \lambda = 2.06 \left(\frac{[N]_i}{1+\tau\omega}\right)^{0.42}$

(——) BACHMANN (1984): $[n]\ \lambda = \exp(\log(LN) - 0.859 \cdot \log(Z) - 0.77 \cdot \log(\tau\omega))$

(- - -) OECD (1982): $[n]\ \lambda = 5.34 \left(\frac{[n]_i}{1+\tau\omega}\right)^{0.78}$

Abbrevations: $[N]\ \lambda$: In-lake nitrogen conc. (mg N l^{-1}), $[n]\ \lambda$: In-lake nitrogen conc. (µg N l^{-1}), $[N]_i$: Inlet nitrogen conc. (mg N l^{-1}), $[n]_i$: Inlet nitrogen conc. (µg N l^{-1}), LN: Areal nitrogen loading (mg N m^{-2} d^{-1}), $\tau\omega$: retention time (years), Z: Mean depth (m)

The difference in the predictions of the level of nitrogen among the models may reflect a difference in the lake types used during model development. While the Danish models included data from lakes comparable to Lake Søbygård concerning both morphometry and nutrient loading, the three other models were established on data from lakes with larger variation in nutrient loading and especially in the morphometry.

The three Danish models predict a loading independent loss percentage of nitrogen for lakes, while the models by OECD (1982) and LIJKLEMA *et al.* (1989) predict a decreasing loss percentage with decreasing nitrogen loading (Fig. 3). This difference could be real reflecting differences in the importance of nitrogen-fixing cyanobacteria in the lakes studied by the different authors. Hence, SCHINDLER *et al.* (1987) and BENGTSSON (1978) found a reduced loss percentage upon loading reduction in nitrogen loading. SCHINDLER *et al.* (1987) claimed that the reduction most likely was due to an increased importance of nitrogen derived from nitrogen fixing by cyanobacteria (not included in the budgets) rather than due to internal loading of nitrogen from the sediment. Furthermore, BENGTSSON (1978) showed that the significant increase in nitrogen fixation in Lake Södra Bergundasjöen upon reduction in nitrogen loading could account for the minor loss percentage of nitrogen. Changes in the importance of nitrogen fixation may therefore explain the decrease in loss percentage predicted by OECD (1982) and LIJKLEMA *et al.* (1989), since nitrogen fixation most often is not included in the nitrogen budgets. On the contrary the constant loss percentage in Lake Søbygård and the 69 Danish lakes studied by JENSEN *et al.* (in press) may reflect the low importance of nitrogen fixing cyanobacteria in those lakes probably due to the overall high loading of nutrients and the short retention time of the lakes included (JENSEN *et al.*, in press; JEPPESEN *et al.*, 1990a and c).

The relatively constant annual loss percentage of nitrogen in Lake Søbygård both before and upon the 36 % reduction in nitrogen loading indicates that the transient phase is short (less than a year) before a steady state condition concerning loading and removal of nitrogen was obtained. A short response time was also found by AHLGREN (1980) after loading reduction in four Swedish lakes. These results indicate that internal loading of nitrogen is not an important resilience factor in lake recovery in contradiction to what is often found for phosphorus (e.g. SAS, 1989). The transient state after a phosphorus loading reduction in Lake Søbygård in 1982 was thus far from being finished in 1989, where the lake still exported more phosphorus than it received (SØNDERGAARD *et al.*, 1987 and unpubl. results).

Planktonic uptake of inorganic nitrogen caused a significant change in the nitrogen composition of inlet and outlet water (Fig. 1). In many lakes and estuaries the N : P ratio in the water column often reflects the N : P ratio of phytoplankton cells (7 : 1) and the nitrogen in the outlet water can be restricted to organic bound nitrogen (ANDERSEN, 1974; SEITZINGER, 1988). In highly productive systems where denitrification is not limited by organic substrate, it may be hypothesized that the nitrogen loss percentage is controlled by the difference in N : P ratio between inlet and outlet water. Surplus nitrogen which is not taken up by the phytoplankton is thus most likely denitrified in the sediment. In estuaries and bays a decrease in N : P ratios from 10 : 1 and 14 : 1 to 7 : 1 has been reported (NIXON and PILSON, 1984; SEITZINGER, 1987) and this reduction may almost explain a loss percentage of 30–50 %, respectively (SEITZINGER, 1988). Data from six highly loaded and fast-flushed Danish lakes (ANDERSEN, 1977) showed a similar increase in the loss percentages with increasing N : P ratio in the inlet water. Oligotrophic lakes (e.g. lakes with a low phosphorus-loading) may deviate from this hypothesis since availability of organic substrate can be a limiting factor for the removal of nitrogen by denitrification. BENNDORF and PÜTZ (1987) thus found increasing nitrogen loss percentages with decreasing N : P ratios in the inlet water of 19 "slightly loaded" dams and lakes.

The idea of a relationship between the N : P ratio in the external loading and the loss percentage is not supported by results in the present study or by the work of JENSEN *et al.*

(in press), who found a relatively constant loss percentage for 69 eutrophic Danish lakes although the N : P ratio of the inlet water varied considerably. Several factors may, however, blur this relationship. First, the internal phosphorus loading is often high in shallow Danish lakes and may therefore significantly affect the N : P ratio of the total loading. Secondly, the growth of algae was not limited by phosphorus in the major part of the lakes studied by JENSEN *et al.* (in press) due to high phosphorus levels in the Danish, eutrophic lakes. All available phosphorus was therefore not consumed by the algae and the nitrogen consumption was correspondingly lower than expected from the N: P ratio in the inlet. More nitrogen was consequently available as a source for denitrification and the nitrogen loss percentage higher than expected. There seems to be some evidence for a relationship between the N : P ratio in the inlet water and the nitrogen loss percentage in the lakes but detailed analysis of existing data and further studies are needed before general conclusions can be drawn.

4.3. Seasonal variations

The nitrogen loss rate in Lake Søbygård, which mainly was due to denitrification, was proportional to nitrate concentration considering each quarter separately (Table 1 and 2). This suggested a first order relationship between nitrogen removal and NO_3^--concentration. Similar results have been obtained by laboratory experiments with organic rich sediment incubated with aerobic conditions in overlying water (e.g. ANDERSEN, 1977; MADSEN, 1979). In Lake Søbygård the loss rate was, however, even stronger correlated to both the total nitrogen concentration of the lake water and the external nitrogen loading (Table 2), which suggested that the total nitrogen content of the water column was a more important controlling factor for the nitrogen loss compared to the in-lake nitrate concentration. Laboratory experiments and mass-balance techniques may thus lead to different conclusions since sedimentation is not considered in the laboratory experiments. At high sedimentation rates denitrifiers may partly benefit from nitrate derived from nitrification of mineralized ammonia. In this situation, down-mixing or diffusion of nitrate from the overlying water may be of minor importance. Several facts support this view. First, results from trap experiments in Lake Søbygård in 1985 showed annually mean gross

Table 2. Quarterly estimated slope (β) in the relationships: *a*) Nloss (mg N m^{-2} d^{-1}) = β * Nload (mg N m^{-2} d^{-1}) *b*) Nloss (mg N m^{-2} d^{-1}) = β * in-lake nitrate concentration (mg N l^{-1}) *c*) Nloss (mg N m^{-2} d^{-1}) = β * in-lake total nitrogen concentration (mg N l^{-1})

	Quarter	Slope (β)	S.E of β	*F*-value	*P*-value
a)	1th	0.2266	0.03458	42.94	< 0.0012
	2nd	0.4722	0.01937	594.0	< 0.0001
	3rd	0.6536	0.04490	211.9	< 0.0001
	4th	0.4734	0.04975	90.55	< 0.0002
b)	1th	20.98	5.268	15.86	< 0.0105
	2nd	107.4	7.061	231.4	< 0.0001
	3rd	295.4	28.44	107.8	< 0.0001
	4th	58.55	8.633	46.01	< 0.0011
c)	1th	17.35	3.717	21.80	< 0.0055
	2nd	44.27	3.450	164.7	< 0.0001
	3rd	61.89	12.70	23.74	< 0.0046
	4th	41.96	4.785	76.88	< 0.0003

sedimentation rates of 350 mg N m^{-2} d^{-1} and 550–800 mg N m^{-2} d^{-1} in summer (KRISTENSEN and JENSEN, 1987 and unpubl. results). These rates are of the same order or higher than the external loading and underscore the importance of sedimentation as a nitrogen sink between water and sediment and as a potential source for a coupled nitrification and denitrification in the sediment. Secondly, high loss rates were also found during periods where nitrate was below detection level (10 µg N l^{-1}) and where denitrification governed by nitrate diffusion from overlaying water therefore was low (JENSEN *et al.*, in prep.). Thirdly, release rates of inorganic nitrogen of 220 mg N m^{-2} d^{-1} were found in laboratory experiments with undisturbed sediment in July 1987 (JENSEN and ANDERSEN, 1990) and furthermore net release rates of 90 to 220 mg N m^{-2} d^{-1} were observed in Lake Søbygård during short term clear water periods in which sedimentation was of minor importance (SØNDERGAARD *et al.*, 1990). These rates are 2 to 8 times lower than the gross sedimentation rates, which suggest that a large part of the sedimented nitrogen is retained or lost in the sediment. Since burial as an annual average only accounted for 15 mg N m^{-2} d^{-1} this loss thus must be interpreted as denitrification. A coupled nitrification-denitrification therefore must be an important contributor to the overall nitrogen loss in Lake Søbygård, especially during summer when the ambient nitrate concentration was low.

The nitrogen loss rates changed significantly during season and showed no simple relationship with temperature even after correction for differences in loading (Fig. 3 and Table 1). Weak or insignificant relationships to temperature were also found by ANDERSEN (1977), CHRISTENSEN and SØRENSEN (1988) and SEITZINGER (1988) because ambient nitrate concentration, organic substrate and size of the aerobic zone were more important governing factors than temperature. The results from Lake Søbygård suggest a hysteresis-like relationship to temperature (Fig. 2), with relative high rates in fourth quarter. A similar response pattern, with relatively high loss percentages in fourth quarter can be obtained when combining nitrogen budget data from six Danish lakes (ANDERSEN, 1974). This probably reflects changes in the pool of available organic substrate in the sediment which is suggested to increase during summer, when gross sedimentation of algae is extremely high and thereâfter gradually decreases following mineralisation during autumn and winter.

The suggested importance of available substrate for the seasonal pattern in loss rate is also supported by NIEWOLAK (1970), who measured the density of denitrifiers in the sediment of some Polish lakes. While a strong relationship to temperature was found in sediment with low inorganic content, only minor seasonal changes were observed in the lake with organic rich sediment.

We therefore conclude that available substrate and total nitrogen loading were more important controlling factors for the seasonal variation in nitrogen loss rates in Lake Søbygård than temperature. However, the relatively low rates in the first quarters may also have been significantly influenced by temperature, because denitrification has been shown to be very sensitive to low temperatures and decreases markedly below 5 °C (LEWANDOWSKI, 1982) and the mean temperatures in Lake Søbygård in first quarter ranged between 0.3 °C and 5.1 °C.

5. Conclusions

This paper has given further evidence for a high nitrogen removal primarily due to denitrification in shallow eutrophic lakes with a low hydraulic retention time. The loss by denitrification was not related to nitrate concentration in the lake water but more closely related to inlet and in-lake total nitrogen. It is suggested that nitrate provided by nitrification of ammonia released from mineralisation of organic matter originating from sedimentation (coupled nitrification-denitrification) and nitrate introduced into the sediment during resuspension events especially during summer are more important N-sources for denitrification in the sediment in shallow lakes than is nitrate diffusion. The loss percentage of nitrogen was not affected by a major reduction in nitrogen loading, which suggests that internal nitrogen loading is not an important delay factor for lakes recovery as often demonstrated for phosphorus. Therefore simple empirical loading-concentration models derived from a large number of lakes in steady state also predicted closely the annual in-lake nitrogen concentration during the transition from high to low nitrogen loading. The seasonal variation in loss percentage of nitrogen showed a hysteresis-like relationship to temperature most likely reflecting the variations in the pool of organic substrate for denitrification in the top-layer of the sediment. Despite that the loss percentage varied during the season a major conclusion is that shallow eutrophic lakes with a short retention time may contribute significantly to the nitrogen loss of load and consequently reduce the loading of downstream aquatic environments.

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7. References

ABDELMONEIM, M. A., J. OLAH and P. SZABO, 1986: Denitrification in water bodies and sediments of Hungarian shallow waters.–Aquacultura Hungarica **5**: 133–146.

ADMIRAAL, W., and J. C. VAN DER VLUGT, 1988: High rates of denitrification in a storage reservoir fed with water of the river Rhine.–Arch. Hydrobiol. **113**: 593–605.

AHLGREN, I., 1980: A dilution model applied to a system of shallow eutrophic lakes after diversion of sewage effluents.–Arch. Hydrobiol. **89**: 17–32.

ANDERSEN, J. M., 1974: Nitrogen and phosphorus budgets and the role of sediments in six shallow Danish lakes.–Arch. Hydrobiol. **74**: 528–550.

ANDERSEN, J. M., 1977: Rates of denitrification of undisturbed sediment from six lakes as function of nitrate concentration, oxygen and temperature.–Arch. Hydrobiol. **80**: 147–159.

APHA, 1985: Standard methods for the examination of water and wastewater.–16th edition. American Public Health Association, New York. 1268 pp.

BACHMANN, R. W., 1984: Calculation of phosphorus and nitrogen loadings to natural and artificial lakes.–Verh. int. Verein. Limnol. **22**: 239–243.

BENNDORF, J., and K. PÜTZ, 1987: Control of eutrophication of lakes and reservoirs by means of pre-dams–1. Mode of operation and calculation of the nutrient elimination capacity.–Water Res. **21**: 829–838.

BENGTSSON, L., 1978: Effects of sewage diversion in lake Södra Bergundasjöen 1: Nitrogen and phosphorus budgets.–Vatten **1**: 2–9.

BILLEN, G., C. LANCELOT, E. DEBECKER SOMVILLE and P. SERVAIS, 1986: The terrestrial-marine interface: Modelling nitrogen transformations during its transfer through the Scheldt River system and its estuarine zone.–*In* J. C. J. NIHOUL (Ed.): Marine Interfaces Ecohydrodynamics. Elsevier Oceanograph Series 42. Elsevier, p. 429–452.

BRUHN, A., and B. KRONVANG, 1989: Load estimation in streams. Methods of estimation and sampling frequency.–The Ministry of the Environment, National Environmental Research Institute. 62 pp. + supplements. (in Danish).

CHATARPAUL, L., J. B. ROBINSON and N. K. KAUSHIK, 1980: Effects of tubificid worms on denitrification and nitrification in stream sediment.–Can. J. Fish. Aquat. Sci. **37**: 656–663.

Christensen, P. B., and J. Sørensen, 1986: Temporal variation of denitrification activity in plant covered littoral sediments (Lake Hampen, Denmark).–Appl. Environ. Microbiol. **51**: 1174–1178.

Christensen, P. B., and J. Sørensen, 1988: Denitrification in sediment of lowland streams: Regional and seasonal variation in Gelbæk and Rabis Bæk, Denmark.–FEMS Microbiol. Ecol. **53**: 335–344.

Christensen, P. B., L. P. Nielsen, N. P. Revsbech and J. Sørensen, 1989: Microzonation of denitrification activity in stream sediments as studied with a combined oxygen and nitrous oxide microsensor.–Appl. Environ. Microbiol. **55**: 1234–1241.

Christensen, P. B., L. P. Nielsen, J. Sørensen and N. P. Revsbech, 1990: Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism.–Limnol. Oceanogr.

Edwards, R. W., and H. L. J. Rolley, 1965: Oxygen consumption of river muds.–J. Ecol. **53**: 1–22.

Gons, H. J., R. Veeningen and R. van Keulen, 1986: Effects of wind on a shallow lake ecosystem: resuspension of particles in the Loosdrecht Lakes.–Hydrobiol. Bull. **20**: 109–120.

Grundmanis, V., and J. W. Murray, 1977: Nitrification and denitrification in marine sediments from Puget Sound.–Limnol. Oceanogr. **22**: 804–813.

Heaney, S. I., and N. Davison, 1977: The determination of ferrous iron in natural water with 2.2-bipyridyl.–Limnol. Oceanogr. **22**: 753–760.

Jensen, H., and F. Ø. Andersen, 1990: Internal phosphorus loading in shallow eutrophic lakes.–NPO-report No. C 4. The National Agency of Environmental Protection. 99 pp. (in Danish).

Jensen, J. P., P. Kristensen and E. Jeppesen, 1991: Relationships between nitrogen loading and in-lake nitrogen concentrations in shallow Danish lakes.–Verh. int. Verein. Limnol.: 201–204.

Jeppesen, E., N. Thyssen, C. Prahl, K. Sand Jensen and T. M. Iversen, 1987: Nitrogenaccumulation and transformation in streams with basis in investigations in Suså and Gryde å.–Vand og Miljø **3**: 123–129. (in Danish).

Jeppesen, E., M. Søndergaard, O. Sortkjær and P. Kristensen, 1990a: Interactions between phytoplankton, zooplankton and fish in a shallow hypertrophic lake: A study on short term changes in the trophic relationships in Lake Søbygård, Denmark.–Hydrobiologia **191**: 149–164.

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H. J. Jensen, J. P. Müller, O. Sortkjær, J. P. Jensen, K. Christoffersen, S. Bosselmann and E. Dahl, 1990b: Fish manipulation as a lake restoration tool in shallow eutrophic lakes 1: Cross-analysis of three shallow, eutrophic temperate lakes.–Hydrobiologia **200/201**: 205–218.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær and K. Olrik, 1990c: Fish manipulation as a lake restoration tool in shallow eutrophic lakes 2: Threshold levels, long-term stability and conclusions.–Hydrobiologia **200/201**: 219–227.

Jørgensen, K. S., and J. Sørensen, 1988: Two annual maxima of nitrate reduction and denitrification in estuarine sediment (Norsminde Fjord, Denmark).–Mar. Ecol. Prog. Ser. **24**: 65–74.

Koroleff, F., 1970: Determination of total phosphorus in natural water by means of the persulphate oxidation.–An. Interlab. report No. 3, Cons. Int. pour l'Explor de la Mer.

Kristensen, P., and P. Jensen, 1987: Sedimentation and resuspension in Lake Søbygård.–M. sc.-thesis. National Agency of Environmental Protection, The Freshwater laboratory, Silkeborg Denmark. 152 pp. (in danish).

Kristensen, P., M. Søndergaard and E. Jeppesen, submitted: Resuspension in a shallow hypertrophic lake.– Hydrobiologia.

Lewandowski, Z., 1982: Temperature dependence of biological denitrification with organic materials addition.–Water Res. **16**: 19–22.

Lijklema, L., J. H. Jansen and R. M. M. Roijackers, 1989: Eutrophication in the Netherlands.–Wat. Sci. Tech. **21**: 1899–1902.

Mackereth, F. H. J., J. Heron and J. F. Talling, 1978: Water analysis: Some revised methods for limnologists. Freshwater Biological Association, Scientific publication No. **36**. 120 pp.

Madsen, P. P., 1979: Seasonal variation in denitrification rate in sediment determined by use of ^{15}N.–Water Res. **13**: 461–465.

Messer, J. J., and P. L. Brezonik, 1978: Denitrification in the sediments of Lake Okeechobee.–Verh. int. Verein. Limnol. **20**: 2207–2216.

Murphy, J., and J. P. Riley, 1962: A modified single solution method for the determination of phosphate in natural waters.–Analyt. Chem. Acta **27**: 21–26.

NIELSEN, L. P., P. B. CHRISTENSEN, N. P. REVSBECH and J. SØRENSEN, 1990: Denitrification and oxygen respiration in biofilms studied with a microsensor for nitrous oxide and oxygen.–Microbiol. Ecol. **18**.

NIEWOLAK, S., 1970: Seasonal changes of nitrogen-fixing and nitrifying and denitrifying bacteria in the bottom deposits of the Ilawa lakes.–Pol. Arch. Hydrobiol. **17**: 509–523.

NIXON, S. W., and M. E. Q. PILSON, 1984: Estuarine total system metabolism and organic exchange from nutrient ratios: An example from Narragansett Bay.–*In* V. S. KENNEDY (ed.): "The Estuary as a Filter". Academic. p. 261–290.

OECD, 1982: Eutrophication of waters. Monitoring, assessment and control.–OECD, Paris. 210 pp.

SAS, H. (Ed.), 1989: Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation.–Acad. Ver. Richarz Gmbh. 497 pp.

SCHINDLER, D. W., R. H. HESLEIN and M. A. TURNER, 1987: Exchange of nutrients between sediments and water after 15 years of experimental eutrophication.–Can. J. Fish. Aquat. Sci. **44**, suppl. 1: 26–33.

SEITZINGER, S. P., 1987: Nitrogen biochemistry in an unpolluted estuary: The importance of benthic denitrification.–Mar. Ecol. Progr. Ser. **41**: 177–186.

SEITZINGER, S. P., 1988: Denitrification in freshwater and coastal marine ecosystems: Ecological and geochemical significance.–Limnol. Oceanogr. **33**: 702–724.

SOLÓRZANO, L., and J. H. SHARP, 1980: Determination of total dissolved nitrogen in natural waters.–Limnol. Oceanogr. **25**: 751–754.

SØNDERGAARD, M., E. JEPPESEN and O. SORTKJÆR, 1987: Lake Søbygård: A shallow lake in recovery after a reduction in phosphorus loading.–GeoJournal **14**: 381–384.

SØNDERGAARD, M., E. JEPPESEN, P. KRISTENSEN and O. SORTKJÆR, 1990: Interactions between sediment and water in a shallow and hypertrophic lake: A study on short term changes in the trophic relationships in Lake Søbygård, Denmark.–Hydrobiologia **191**: 139–148.

The National Agency of Environmental Protection, 1984: The NPo-statement. 218 pp. (in Danish).

Impact of Nutrients and Physical Factors on the Shift from Cyanobacterial to Chlorophyte Dominance in Shallow Danish Lakes

J.P. Jensen, E. Jeppesen, K. Olrik,[1] and P. Kristensen

National Environmental Research Institute, Division of Freshwater Ecology, 25 Vejlsøvej, P.O. Box 314, DK-8600 Silkeborg, Denmark

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Phytoplankton dominance (as biomass) by heterocystous cyanobacteria, nonheterocystous cyanobacteria, and chlorophytes was studied along a trophic gradient (0.011–2.2 mg P·L^{-1}) by analyzing regularly collected semiquantitative data from 178 shallow Danish lakes (mean depth <3 m) and quantitative data from 32 lakes. Heterocystous cyanobacteria were dominant at low total P (TP) (<0.25 mg P·L^{-1}) and nonheterocystous cyanobacteria at intermediate TP (0.25–0.8 mg P·L^{-1}), while chlorophytes often were dominant at high TP (>1 mg P·L^{-1}). In contrast with many earlier findings, heterocystous cyanobacteria were not dominant at low total N (TN):TP or low inorganic N concentrations; chlorophytes were dominant at extremely high pH, and the shift from cyanobacterial to chlorophyte dominance could not be explained by a change in the photic zone to mixing zone ratio. We suggest that chlorophyte dominance in hypertrophic shallow lakes is attributable to continuous input of nutrients and carbon from the sediment and external sources. This renders the fast-growing chlorophytes a superior competitor compared with the relatively slow-growing cyanobacteria, even when inorganic nutrient concentration is low and pH high. New predictive models relating phytoplankton dominance to TP in shallow lakes were developed, as former models failed to predict our observations satisfactorily.

On a étudié les espèces dominantes de phytoplancton (en termes de biomasse), soit les cyanobactéries hétérocystiques, les cyanobactéries non hétérocystiques et les chlorophycophytes le long d'un gradient trophique (0,011–2,2 mg P·L^{-1}) en analysant des données semi quantitatives recueillies régulièrement dans 178 lacs danois peu profonds (profondeur moyenne <3 m) et des données quantitatives provenant de 32 lacs. Les cyanobactéries hétérocystiques étaient dominantes à une faible concentration de P total (PT) (<0,25 mg P·L^{-1}) et les cyanobactéries non hétérocystiques aux concentrations intermédiaires de PT (0,25–0,8 mg P·L^{-1}), et les chlorophytes dominaient souvent à des concentrations élevées de PT (>1 mg P·L^{-1}). Contrairement à de nombreux résultats obtenus auparavant, les cyanobactéries hétérocystiques n'étaient pas dominantes à un faible rapport N total (NT):PT ou à de faibles concentrations de N inorganique; les chlorophytes étaient dominants à des pH extrêmement élevés, et le changement de dominance des cyanobactéries au profit des chlorophytes ne pouvait s'expliquer par une modification du ratio zone euphotique à zone de mélange. Nous sommes d'avis que la dominance des chlorophytes dans les lacs hypertrophiques peu profonds est attribuable à un apport continu de nutriments et de carbone provenant des sédiments et de sources externes. Les chlorophytes qui croissent plus rapidement sont donc des concurrents plus sérieux que les cyanobactéries dont la croissance est relativement lente, même à une faible concentration de nutriments inorganiques et à un pH élevé. De nouveaux modèles prévisionnels mettant en relation les espèces dominantes de phytoplancton et la concentration de PT dans les lacs peu profonds ont été élaborés, car les anciens modèles ne permettaient pas de prévoir nos observations de façon satisfaisante.

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Major changes in phytoplankton community structure are known to take place along the trophic gradient, and large cyanobacteria have been found to dominate at high nutrient levels in several lakes. This is also reflected in the predictive models by Trimbee and Prepas (1987) and Seip (1988) who found that cyanobacterial dominance increased with increasing total P (TP). Various explanations of cyanobacterial dominance at high nutrient levels have been proposed, e.g., changes in the availability of P and the relative availability of P and N (total N (TN):TP ratio, light conditions, pH/CO_2 conditions, and zooplankton grazing pressure) (e.g., Smith 1986; Pick and Lean 1987; Shapiro 1990). The relative importance of these factors is, however, still subject to considerable debate (Shapiro 1990; Smith 1990).

Although the majority of studies suggest that cyanobacteria are the dominant phytoplankton in eutrophic lakes, there are a few reports on exclusive dominance by chlorophytes, particularly in shallow hypertrophic lakes and ponds (e.g., Nygaard 1949; Pavoni 1963; Leah et al. 1980; Bucka 1989; Jeppesen et al. 1990b, 1990c, 1991), even under conditions that, according to Shapiro (1990) and Smith (1990), should favour cyanobacterial growth (high pH, low TN:TP, CO_2, and light). Analyses of data from a number of shallow Danish lakes have revealed that the dominance of chloro-

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[1] Present address: The Environmental Biology Laboratory, 5 Baunebjergvej, DK-3050 Humlebæk, Denmark.

TABLE 1. Some characteristics of the lakes studied (n = 178). Morphometric data and hydraulic retention time were calculated on a yearly basis, while the remaining parameters were calculated for the summer (May 1 – Oct. 1).

	Mean	Median	Min.	Max.
Surface area (km^2)	0.85	0.25	0.001	41.0
Mean depth (m)	1.5	1.4	0.5	3.0
Maximum depth (m)	2.4	2.0	0.6	10.1
Hydraulic retention time (yr)	0.46	0.25	0.006	4.3
TP (mg P·L^{-1})	0.52	0.38	0.011	2.2
TN (mg N L^{-1})	2.8	2.2	0.20	10.9
Secchi depth (m)	0.70	0.55	0.20	3.0
pH	8.2	8.1	6.3	10.1

phytes at high TP levels was the rule rather than the exception (Jeppesen et al. 1990a, 1991). Jeppesen et al. (1990b) argued that the chlorophyte dominance in hypertrophic Lake Søbygård may reflect the circumstance that phytoplankton, besides using incoming nutrients, also use nutrients and CO$_2$ released at high rates from the lake sediment during summer, a source which is not important for phytoplankton growth in the epilimnion in stratified lakes.

It is commonly believed that especially heterocystous cyanobacteria are particularly abundant in eutrophic lakes with a low content of inorganic N or low N:P in the external loading (Schindler 1977; Smith 1983). However, in shallow Danish lakes, they (typically *Anabaena* and *Aphanizomenon*) dominate in early summer when nitrate concentration is high and the concentration of inorganic P is low in contrast with late summer when nonheterocystous cyanobacteria (typically *Microcystis*) often are dominant (J.P. Jensen, unpublished data). *Microcystis* dominance at low inorganic N concentrations has also been observed elsewhere (Gelin 1975; Gelin and Ripl 1978; Vincent 1989; Takamura et al. 1992). It therefore appears that it is not the low concentration of inorganic N that determines the shift from dominance by nonheterocystous cyanobacteria or chlorophytes to heterocystous cyanobacteria.

In the present paper, we further evaluate the shift from cyanobacterial to chlorophyte dominance and the shift from dominance by heterocystous to dominance by nonheterocystous species of cyanobacteria in shallow lakes. Using semiquantitative data from 178 Danish lakes and quantitative data from 32 lakes, we seek to answer the following questions: Do cyanobacteria or chlorophytes dominate at high nutrient levels, high pH, and low light conditions? Are heterocystous cyanobacteria more dominant at low inorganic N concentrations and low TN:TP ratios than nonheterocystous cyanobacteria and chlorophytes or are other environmental factors more important for the differences in dominance structure? And finally, are the regression models relating cyanobacterial dominance to TP valid for temperate shallow lakes? If not, can we develop new predictive models for this type of lake?

Materials and Methods

Study Area

The main characteristics of the 178 lakes included in the study are given in Table 1. The lakes were mainly small (mean surface area 0.85 km^2) and shallow (mean depth 1.5 m) with a low hydraulic retention time (0.46 yr). Most of the lakes had high external nutrient loading, and although nutrient levels varied widely (0.011–2.2 mg P·L^{-1} and

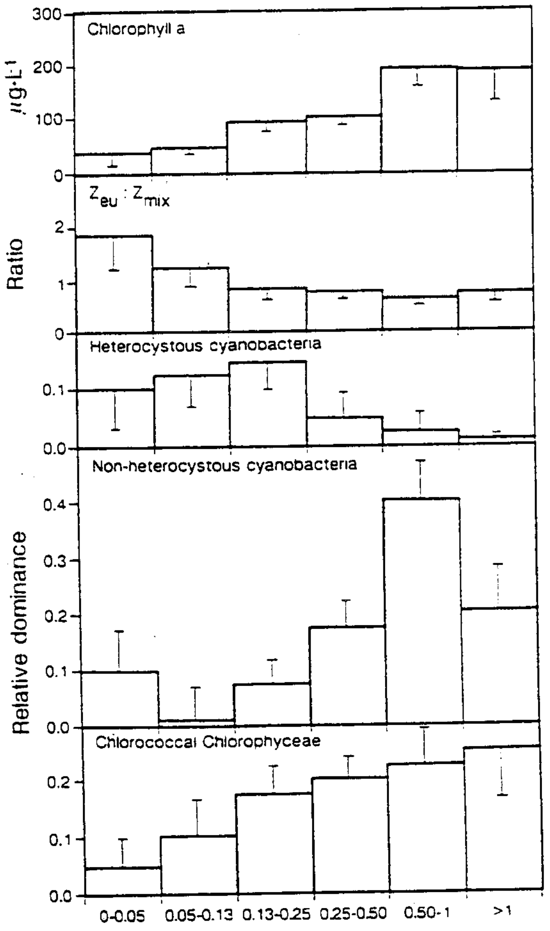

FIG. 1. Chlorophyll a, Z_{mix}:Z_{eu}, and relative cyanobacterial and chlorophyte dominance (±heterocysts) in the six groups of lakes as classified by P (summer mean values, May 1 – Oct. 1). Vertical bars indicate SE of the mean in each group.

TABLE 2. Correlations between cyanobacterial (±heterocysts) and chlorophyte dominance and selected environmental parameters (summer mean values, May 1 – Oct. 1) for the semiquantitative data set. The upper value represents Spearman's rank correlation coefficient (r_s) (Sokal and Rohlf 1981) and the parenthetical value the corresponding significance level ($P(r_s = 0)$) ($n = 178$).

	TP	TN	Secchi depth	pH	Z_{mean}	Z_{eu}:Z_{mix}
Cyanobacteria	0.15	−0.04	−0.21	0.05	0.18	−0.32
(nonheterocysteous)	(0.05)	(0.62)	(0.01)	(0.08)	(0.03)	(0.00)
Cyanobacteria	−0.15	−0.02	−0.17	0.00	−0.05	−0.16
(heterocysteous)	(0.04)	(0.86)	(0.03)	(0.96)	(0.84)	(0.06)
Chlorophyceae	0.19	0.06	−0.07	0.25	0.02	−0.06
(chlorococcales)	(0.01)	(0.42)	(0.39)	(0.00)	(0.86)	(0.50)

0.20–10.9 mg N·L^{-1}) the mean concentration of P and N was high (0.52 mg P·L^{-1} and 2.8 mg N L^{-1}). Because of the high nutrient levels, chlorophyll *a* tended to be high and exceeded 200 μg·L^{-1} when the TP concentration was above 0.5 mg P·L^{-1} (Fig. 1). Mean Secchi depth was low (0.70 m). The euphotic zone to mixing zone ratio Z_{eu}:Z_{mix} decreased with increasing TP concentration (Fig. 1), but was relatively constant at concentrations above 0.125 mg P·L^{-1}.

Sampling and Analyses

Composite epilimnion sampling was undertaken by local water authorities. The samples were analyzed for various physical and chemical parameters and for phytoplankton composition. TP was measured as orthophosphate using the method of Murphy and Riley (1972) following persulphate digestion (Koroleff 1970). Ammonium was determined by the phenate method (APHA 1985). Nitrite + nitrate was determined as nitrate using a flow injection analyzer, and inorganic N was calculated as the sum of ammonium, nitrite, and nitrate. TN was measured as nitrate + nitrite after potassium persulphate digestion according to the methods of Solórzano and Sharp (1980). The pH of the samples was measured with a pH meter either in the field or in the laboratory. Temperature was measured in the field with either a thermometer or a thermistor with a precision greater than 0.5°C; when temperature gradients were present in the water column, the measurements were made at minimum intervals of 1 m. The euphotic zone was calculated from the Secchi depth (Z_{eu} = 1.7·Secchi depth; Reynolds 1984). The mixing zone was defined as the water column mean depth when there was no temperature gradient and as the zone from the surface to the depth where the temperature gradient exceeded 1°C·m^{-1} in stratified lakes (Ruttner 1963).

Phytoplankton were enumerated on Lugol-fixed sedimented water samples using an inverted microscope (Ütermöhl 1958; Rott 1981). Phytoplankton abundance and "biomass" were rated using six categories: absent, present in low numbers, moderately high density and "biomass", high density and "biomass", subdominant in terms of "biomass", and dominant in terms of "biomass" (Olrik 1981). In a few cases (<15%), only four categories were used: absent, present, subdominant in terms of "biomass", and dominant in terms of "biomass". "Biomass" is put in quotation marks because its determination is based on the importance of each individual group as judged from the projected picture in the inverted microscope and not from actual biomass determination. This implies that the importance of, for instance, large spherical species is somewhat underestimated. To ensure that the present analysis represents biomass dominance, only the category "dominant" is used. Systematic classification of phytoplankton was undertaken according to the method of Christensen (1966, 1980), the main identification references being Hüber-Pestalozzi (1933–83), Komárek (1958), and Bourrelly (1966, 1968, 1970). In the present study, we only include chlorococcal green algae in the term chlorophytes, as this group characterizes eutrophic waters (Reynolds 1984), while other greens, e.g., desmids, are found in a larger nutrient spectrum, the latter being particularly abundant under oligotrophic conditions (Nygaard 1949).

For each environmental parameter analyzed, data were arranged in numerical order and then divided into six groups of equal size (approximately 30 lakes in each group). The relative dominance of the three phytoplankton groups was calculated as the proportion of samples in each class of the environmental parameter analyzed in which a given phytoplankton group was dominant in terms of biomass (summer (May–October) means a minimum of four samples). This nonlinear method of data presentation was necessary because of the use of a rating scale to assess the response variable. Basic statistical testing when undertaken according to the method of Sokal and Rohlf (1981) using the SAS statistical package (SAS Institute Inc. 1989), the exception being phytoplankton "biomass" rating versus environmental parameters which was performed by means of logistic regression, this being a more appropriate and powerful statistical method than ordinary linear regression for testing rating scale responses (Hosmer and Lemeshow 1989). Different junctions of the explanatory parameters, e.g., logarithmic, exponential, and polynomial equations, were tested in the logistic procedure. The fitting of the logistic equations was undertaken according to the "logistic procedure" of the SAS/STAT statistical package (SAS Institute Inc. 1989).

In the verification data set from 32 lakes the phytoplankton species composition was determined by counting and the specific volume calculated by fitting the different species and genera to geometric forms (Ütermöhl 1958; Edler 1979; Rott 1981). The chemical and physical parameters were determined as described above.

Results

Correlation analysis on semiquantitative data revealed that dominance by heterocystous cyanobacteria, nonheterocystous cyanobacteria, and chlorophytes was significantly correlated to TP concentration (Table 2). However, whereas dominance by nonheterocystous cyanobacteria (mainly *Microcystis*) and chlorophytes (mainly *Scenedesmus* and *Pediastrum*) increased significantly with increasing TP ($P < 0.05$

TABLE 3. Correlations between cyanobacterial (±heterocysts) and chlorophyte dominance and selected environmental parameters (summer mean values, May 1 – Oct. 1) for the quantitative data set. The upper value represents Spearman's rank correlation coefficient (r_s) (Sokal and Rohlf 1981) and the parenthetical value the corresponding significance level ($P(r_s = 0)$) ($n = 32$).

	TP	TN	Secchi depth	pH	Z_{mean}	$Z_{cu}:Z_{mix}$
Cyanobacteria	0.18	0.11	−0.35	0.35	0.24	−0.46
(nonheterocysteous)	(0.32)	(0.54)	(0.05)	(0.06)	(0.17)	(0.00)
Cyanobacteria	−0.29	−0.04	0.12	−0.10	−0.03	−0.10
(heterocysteous)	(0.10)	(0.84)	(0.53)	(0.59)	(0.86)	(0.59)
Chlorophyceae	0.88	0.75	−0.72	0.65	0.08	−0.73
(chlorococcales)	(0.00)	(0.00)	(0.00)	(0.00)	(0.65)	(0.00)

and $P < 0.01$, respectively), dominance by heterocystous cyanobacteria (mainly *Anabaena* and *Aphanizomenon*) decreased ($P < 0.05$). In contrast, there was no significant correlation between dominance by the three phytoplankton groups and the concentration of TN. In each case, there was a negative correlation with Secchi depth, although this was only significant for the cyanobacteria (both heterocysteous and nonheterocysteus). Dominance by chlorophytes increased significantly with increasing pH whereas the relationship between pH and cyanobacteria was less clear. Even though the range of mean depth was rather narrow (<3 m), a positive correlation could be demonstrated between dominance by nonheterocystous cyanobacteria and mean depth. When $Z_{eu}:Z_{mix}$ increased, dominance by nonheterocystous and heterocystous cyanobacteria decreased, there being no significant correlation in the case of chlorophytes (Table 2). The correlation matrix was similar for the less extensive quantitative data set (Table 3), suggesting that the consistency conclusions for the semiquantitative data below apply to the quantitative data as well.

More detailed analysis of the semiquantitative and quantitative data revealed nonlinear relationships (Fig. 1 and 2). Below 0.5 mg $P \cdot L^{-1}$, nonheterocystous cyanobacteria became increasingly dominant with increasing TP whereas above 1 mg $P \cdot L^{-1}$, dominance was reduced significantly ($P < 0.0041$: Mann–Whitney *U*-test) (Sokal and Rohlf 1981). The relationship between the probability of dominance and TP for the semiquantitative data set was unimodal with a maximum at 0.82 mg $P \cdot L^{-1}$ ($P < 0.0063$), as described by the logistic regression equation

(1) $P(\text{dominance}) = 1/(1 + \exp(1.9 - 4.6 \cdot \text{TP} + 2.8 \cdot \text{TP}^2))$.

Dominance by nonheterocystous cyanobacteria was also significantly inversely related to $Z_{eu}:Z_{mix}$ ($P < 0.0089$):

(2) $P(\text{dominance}) = 1/(1 + \exp(1.7 + 1.6 \cdot \log(Z_{eu}:Z_{mix})))$.

Heterocystous cyanobacteria tended to dominate at relatively low TP with a maximum between 0.06 and 0.25 mg $P \cdot L^{-1}$ (Fig. 1 and 2). However, an exponentially declining relationship to TP gave the best regression ($P < 0.0063$):

(3) $P(\text{dominance}) = 1/(1 + \exp(1.2 + 1.4 \cdot \text{TP}))$.

The relationship between dominance by heterocystous cyanobacteria and $Z_{eu}:Z_{mix}$ was only tenuous ($P < 0.0514$), but as with the nonheterocystous cyanobacteria, dominance decreased when the ratio increased:

(4) $P(\text{dominance}) = 1/(1 + \exp(0.7 + 1.4 \cdot (Z_{eu}:Z_{mix})))$.

Dominance by chlorophytes increased with increasing TP, in particular above 1 mg $P \cdot L^{-1}$ (Fig. 1 and 2). The best fit was obtained using a square root (sqrt) function ($P < 0.0098$):

(5) $P(\text{dominance}) = 1/(1 + \exp(1.5 - 1.4 \cdot \text{sqrt(TP)}))$.

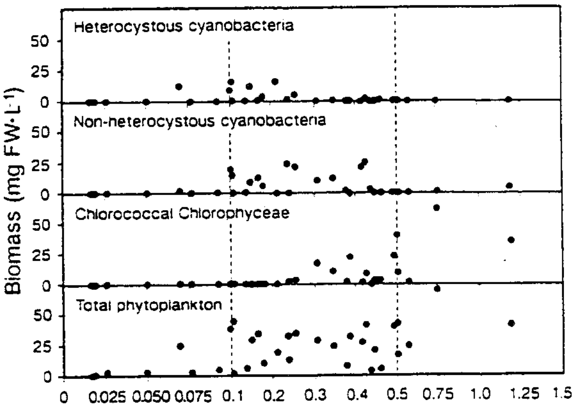

FIG. 2. Biomass of cyanobacteria, chlorophytes, and total phytoplankton in relation to summer TP concentration (mean values, May 1 – Oct. 1).

In contrast with the cyanobacteria, there was no significant relationship between dominance by chlorophytes and $Z_{eu}:Z_{mix}$ ($P > 0.3035$). All three groups of phytoplankton were generally more dominant at high pH values (Fig. 3) although dominance by cyanobacteria tended to decrease at the highest pH (pH > 9). The TP–phytoplankton models developed in the present study (equations 1, 3, and 5) deviated markedly from the predictions of Trimbee and Prepas (1987) and Seip (1988) (Fig. 4); cyanobacterial dominance was somewhat lower in our models, and there was no decrease in relative cyanobacterial dominance at high TP. However, the models of Trimbee and Prepas (1987) and Seip (1988) only cover TP up to 0.2 and 1 mg $P \cdot L^{-1}$, respectively.

As with the correlation with TN (Table 3), the relationship between dominance and TN:TP was less clear (Fig. 5). The nonheterocystous cyanobacteria were most frequently dominant at TN:TP less than 8, although no significant relationship could be established ($P > 0.072$). In contrast with Smith (1983), dominance by heterocystous cyanobacteria gradually increased up to a TN:TP of about 32. They were only occasionally dominant above this level. Cumulative distribution of dominance in relation to inorganic N (Fig. 6) suggests

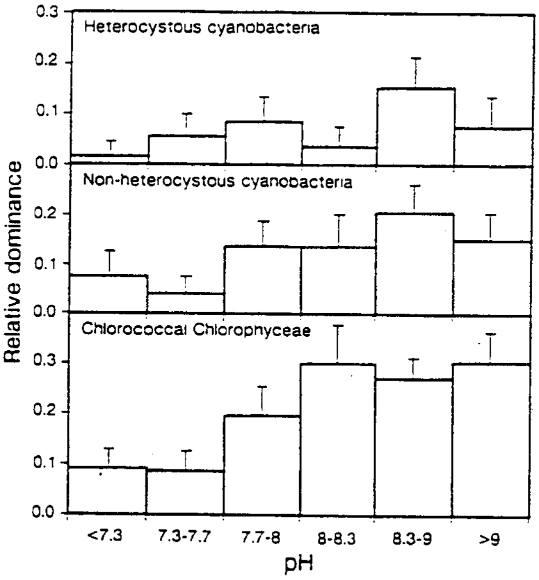

Fig. 3. Relative dominance of cyanobacteria (±heterocysts) and chlorophytes in relation to pH (summer mean values, May 1 – Oct. 1). Vertical bars indicate SE of the mean in each group.

that nonheterocystous cyanobacteria (as well as chlorophytes) were more frequently dominant at low inorganic N concentrations than were heterocystous cyanobacteria. Chlorophytes were only occasionally dominant at TN:TP above 32 (Fig. 5), although in this case, no significant trend could be detected at ratios below this threshold ($P > 0.15$). However, as the median TP and TN values in the six TN:TP groups were 1.2, 0.6, 0.4, 0.2, 0.1, and 0.03 mg P·L^{-1} and 1.8, 1.6, 2.4, 1.6, 2.9, and 2.2 mg N·L^{-1}, respectively, changes in TN:TP, and hence the relationship between TN:TP and phytoplankton, may instead reflect changes in TP.

Discussion

The general finding of the present study that cyanobacteria become increasingly dominant towards eutrophic conditions is in accordance with numerous other studies (Olrik 1978; Reynolds 1984; Smith 1986; Pick and Lean 1987; Reynolds 1987; Smith et al. 1987; Trimbee and Prepas 1987; Sas et al. 1989). However, there have been few other reports of a shift to dominance by chlorophytes at hypertrophic conditions (Nygaard 1949; Pavoni 1963; Leah et al. 1980; Bucka 1989), probably because most comparative studies have dealt with lakes that are deeper or have less extreme nutrient concentrations, conditions which as discussed below are less favourable for chlorophyte dominance. Thus, whereas chlorophytes are characterized by high growth and loss rates and hence have high demand for nutrients (C-strategist, sensu Reynolds 1988), cyanobacteria have lower growth and loss rates and hence a lower demand for nutrients (S-strategist, sensu Reynolds 1988). The balance between the rates of net growth and loss may be one of the keys to understanding why chlorophytes are usually able to outcompete cyanobacteria at high TP in shallow, nonstratified lakes, but not in deep, stratified lakes. In eutrophic–hypertrophic lakes, nutrient turnover as a result of zooplankton grazing is usually low because of high fish predation (E. Jeppesen et al., personal observation). This means that the turnover of nutrients in the water column is low. The nutrient balance in such lakes is consequently very sensitive to loss by sedimentation unless the nutrients are returned to the photic zone with little or no delay. The latter is the case in nonstratified lakes where sediment nutrient release continuously recycles nutrients lost through sedimentation back to the photic zone. For example, maximum release rates as high as 240 mg P·m^{-2}·d^{-1} and summer averages of 100 mg P·m^{-2}·d^{-1} have been observed in hypertrophic chlorophyte-dominated Lake Søbygaard (Søndergaard et al. 1990; Jensen and Andersen 1992) in which daily sedimentation loss comprises 20% of the biomass and 40% of the primary production (Kristensen and Jensen 1987; Jeppesen et al. 1990c). P release from the sediment was more than 10 times the external loading despite a short hydraulic retention time (15–25 d) (Jensen and Andersen 1992). This example, together with the findings from other shallow Danish lakes (Jensen and Andersen 1992), underlines the importance of the sediment as a major source of nutrients for phytoplankton growth in shallow lakes. In addition, the high sediment release rates may help to explain why many hypertrophic lakes are dominated by chlorophytes, even when the concentration of inorganic nutrients is low. In stratified lakes, in contrast, nutrients lost by sedimentation are trapped in the hypolimnion, thereby discouraging growth of algae with high loss rates; nevertheless, chlorophytes may still become dominant during periods of high grazing pressure and hence high nutrient turnover in the photic zone (Sommer 1985; Vanni and Temte 1990).

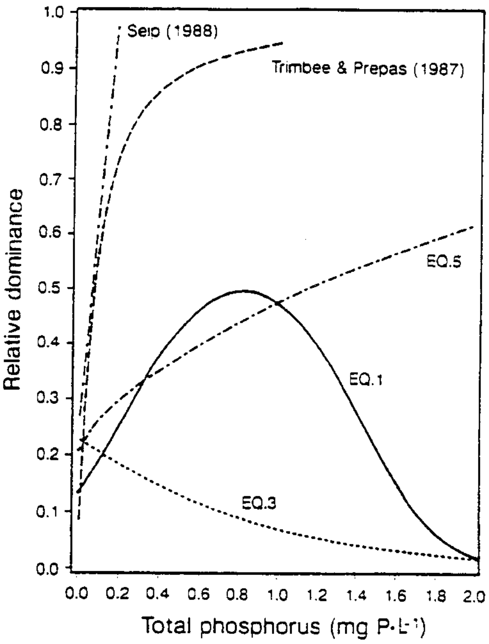

Fig. 4. Comparison of different models relating the relative dominance of phytoplankton to TP. EQ.1, EQ.3, and EQ.5 are the equations for nonheterocystous cyanobacteria, heterocystous cyanobacteria, and chlorophytes, respectively. The equations of Trimbee and Prepas (1987) and Seip (1988) are also shown.

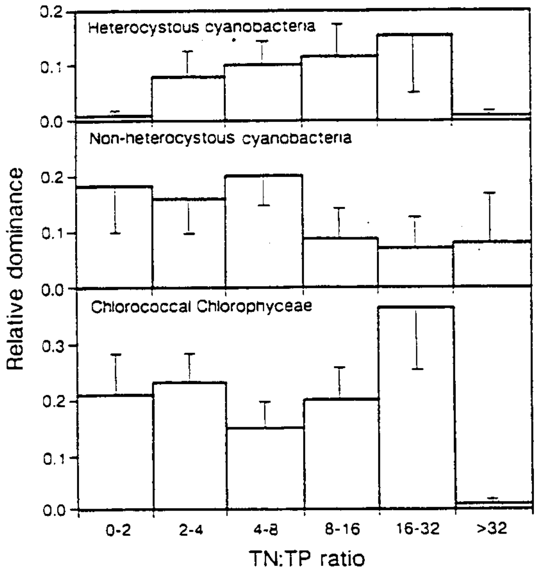

FIG. 5. Relative dominance of cyanobacteria (±heterocysts) and chlorophytes in relation to TN:TP (summer mean values, May 1 – Oct. 1). Vertical bars indicate SE of the mean in each group.

Apart from nutrients, the outcome of the competition between cyanobacteria and chlorophytes may be influenced by Z_{eu}:Z_{mix}, cyanobacteria generally being better adapted to low light conditions than chlorophytes (Zewenboom and Mur 1980). Although this may explain the inverse relationship between dominance and Z_{eu}:Z_{mix} seen with both groups of cyanobacteria, it cannot explain the major shift to chlorophytes in hypertrophic lakes (>0.8 mg P·L^{-1}), since the ratio was just as low as in the cyanobacteria-dominated lakes.

Physical stability of the water in the photic zone may also influence phytoplankton dominance. Thus, as in the deep stratified lakes, stable water column conditions favour growth of cyanobacteria in eutrophic lakes (e.g., Reynolds and Walsby 1975; Steinberg and Hartmann 1988). Hence, the frequent physical disturbance of the photic zone seen in shallow lakes may disfavour cyanobacteria and may, by causing the pulsed release of nutrients from sediment (e.g., by resuspension), enhance the competitiveness of chlorophytes, as has been demonstrated in the laboratory (Sommer 1985).

Variations in zooplankton grazing pressure have been shown to affect the relative phytoplankton composition in many lakes, and large phytoplankton species are often favoured in lakes with high grazing pressure (e.g., Bergquist et al. 1985). It may, therefore, be argued that the low zooplankton grazing pressure in hypertrophic lakes as a result of high fish predation may be a prerequisite for the dominance of small-sized edible chlorophytes instead of large inedible cyanobacteria. In contradiction to this view, however, results from a number of Danish hypertrophic lakes have shown that increasing grazing pressure on phytoplankton due to a reduction in fish predation on zooplankton leads to a shift from dominance by small-sized to dominance by large-sized chlorophytes (typically from *Scenedesmus* or *Chlorella* to *Pediastrum* or *Oocystis*, etc.) (Jeppesen et al. 1990b; E. Jeppesen et al., personal observation). Only at almost fish-free conditions was a shift to dominance by grazerblade forms of *Aphanizomenon* found, as also observed in other studies (Fott et al. 1980; Lynch 1980; Andersson and Cronberg 1984).

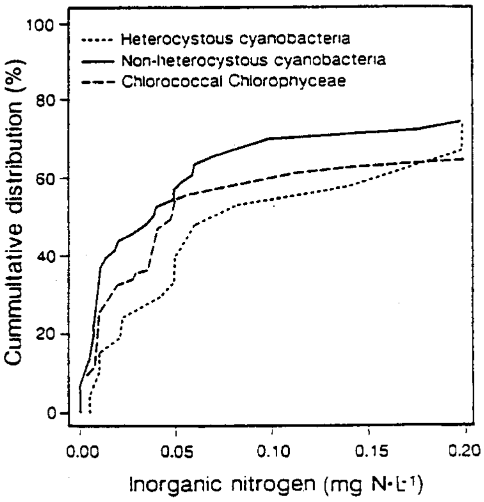

FIG. 6. Cumulative distribution of cyanobacterial (±heterocysts) and chlorophyte dominance in relation to summer inorganic N concentration (May 1 – Oct. 1) up to 0.2 mg N·L^{-1}.

Several authors have stressed the fact that cyanobacteria are favoured at high pH/low CO_2 because of their lower half-saturation constant for CO_2 uptake (King 1970; Talling 1976; Shapiro 1984). Shapiro (1990) even claimed that "if the pH/CO_2 hypothesis is correct it alone could go a long way towards explaining blue-green dominance in lakes, and changes in that dominance". In contrast, DeNoyelles and O'Brien (1978) found that chlorophytes dominated at pH values above 10.5 in enriched experimental ponds and they were apparently able to take up sufficient C for growth under these conditions. These results are in accordance with the findings of the present study, since chlorophyte dominance was more positively correlated with pH than was cyanobacterial dominance (Fig. 3). Furthermore, exclusive dominance by chlorophytes has even been observed at pH values as high as 11.2 (Jeppesen et al. 1990a). These contradictory findings may be attributable to a difference in the input of atmospheric CO_2, the input in shallow lakes being greater per unit of volume than in deeper lakes because of the higher surface area to volume ratio (Olrik 1981). In addition, and probably more importantly, shallow nonstratified lakes are continuously supplied with CO_2 from the sediment.

The ability of heterocystous cyanobacteria to fix atmospheric N should be advantageous when the ambient inorganic N concentration is low (Paerl 1988) or when TN:TP is low (Smith 1983). In the present study, cyanobacteria were seldom dominant at TN:TP above 32, a level close to the threshold of 29 proposed by Smith (1983) for differentiating cyanobacteria-dominated lakes (Fig. 5). However, the negative relationship between increasing TN:TP and cyanobacterial dominance proposed by Smith (1985) was not found and, in fact, heterocystous cyanobacterial dominance increased with TN:TP up to a ratio of 32. Moreover, heterocystous cyanobacteria were not the superior competitors at low inorganic N concentrations (Fig. 6); they mainly occurred in early summer, when inorganic N concentration was relatively high and ortho-P low as compared with later in the summer (J.P. Jensen, unpublished data). Our findings are more in accordance with the conclusions of Trimbee and Prepas (1987) who, by recompiling the data of Smith (1985), concluded that the shift to cyanobacterial dominance at low TN:TP was caused by the increase in TP rather than the decrease in TN:TP. Whether the energetically rather costly N_2-fixation is important at low inorganic N concentrations in shallow nonstratified lakes is therefore open to question. Leonardson (1984), who studied N_2-fixation of heterocystous cyanobacteria in two shallow eutrophic lakes, concluded that N_2-fixation is generally a minor N contributor to phytoplankton growth in such lakes. In analogy with P release, the sediment N flux may be an important N source in shallow lakes (Søndergaard et al. 1990), thereby rendering shallow lakes less favourable to atmospheric N_2-fixation than deeper lakes. In addition, whereas shallow eutrophic lakes are often highly supersaturated with O_2 throughout the water column, this probably inhibiting the strictly anaerobic N_2-fixation process, cyanobacteria in deep lakes may reach areas of low O_2 during the night, e.g., in the metalimnion. Our data strongly suggest that the outcome of competition between heterocystous and nonheterocystous cyanobacteria in the lakes of the present study is determined by higher P affinity of the former rather than by variation in the ability to fixate atmospheric N.

In some aspects, our findings were discordant with those of Trimbee and Prepas (1987), and also of Seip (1988), whose models predicted a higher relative cyanobacterial dominance in eutrophic lakes than did our models and no decrease in cyanobacterial dominance at high TP (Fig. 4). This discrepancy might be attributable to differences in the lake types studied, the analysis of Trimbee and Prepas (1987) covering lakes with a mean depth ranging from 1.1 to 313 m, the majority being deep (mean 27 m), while that of Seip (1988) mainly included deep lakes, the precise depths of which were not given. Accordingly, their model predictions fit well with observations from other deep lakes (Sas et al. 1989; Faafeng et al. 1990), TP threshold for cyanobacterial dominance being about 10 $\mu g\ P \cdot L^{-1}$, there being no upper limit for cyanobacteria dominance, and no shift to chlorophytes at high TP such as found in the shallow lakes of the present study.

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References

Andersson, G., and G. Cronberg. 1984. *Aphanizomenon flos-aquae* and *Daphnia*. An interesting plankton association in hypertrophic waters, p. 63–76. *In* Bosheim and Nicholls [ed.] Interaksjoner mellom trofiske nivåer i ferskvann. Norsk Limnologförening, Blindern, Oslo, Norway.

APHA. 1985. Standard methods for the examination of water and waste water. 16th edition. American Public Health Association. New York. 1268 p.

Bergquist, A.M., S.R. Carpenter, and J.C. Latino. 1985. Shift in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. Limnol. Oceanogr. 30: 1037–1045.

Bourrelly, P. 1966. Les algues d'eau douce. 1. Les algues vertes. M. Boubée & Cie, Paris. 572 p.

Bourrelly, P. 1968. Les algues d'eau douce. 2. Les algues jaunes et brunes. M. Boubée & Cie, Paris. 438 p.

Bourrelly, P. 1970. Les algues d'eau douce. 3. Les algues bleues et rouges, les eugléniens, peridiniens et cryptomonadines. M. Boubée & Cie, Paris. 512 p.

Bucka, H. 1989. Ecology of selected planktonic algae causng water blooms. Acta Hydrobiol. 31: 207–258.

Christensen, T. 1966. Alger. Botanik 2:1 Munksgaard. Copenhagen. 180 p. (In Danish)

Christensen, T. 1980. Algae, a taxonomic survey. Fasc. 1. AIO Tryk. Odense. 228 p.

DeNoyelles, F. Jr., and W.J. O'Brien. 1978. Phytoplankton succession in nutrient enriched experimental ponds as related to changing carbon, nitrogen and phosphorus conditions. Arch. Hydrobiol. 84: 137–165.

Edler, L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Baltic Marine Biologists Working Group 9. 38 p.

Faafeng, B., P. Brettum, and D. Hessen. 1990. Nationwide investigation of the trophic conditions in 355 lakes in Norway (Landsomfattende undersøkelse av trofitilstanden i 355 innsjøer i Norge). Niva Rapp. 389/90. Niva, Oslo. 57 p. (In Norwegian)

Fott, J., L. Pechar, and M. Prazaková. 1980. Fish as a factor controlling water quality in ponds. *In* J. Barica and L.R. Mur [ed.] Hypertrophic ecosystems. Dev. Hydrobiol. 2: 255–261.

Gelin, C. 1975. Nutrients, biomass and primary productivity of nanoplankton in a eutrophic lake. Oikos 22: 230–234.

Gelin, C., and G. Ripl. 1978. Nutrient decrease and response of various phytoplankton size fractions following the restoration of Lake Trummen, Sweden. Arch. Hydrobiol. 81: 339–367.

Hosmer, D.W., and S. Lemeshow. 1989. Applied logistic regression. Wiley series in probability and mathematical statistics. John Wiley & Sons, New York, N.Y. 307 p.

Hüber-Pestalozzi, G. [Ed.] 1933–83. Das Phytoplankton des Süßwassers. *In* Tienemans Binnengewässer 16. E. Schweizerbartche Verlagsbuchhandlung, Stuttgart.

Jensen, H.S., and F.Ø. Andersen. 1992. Importance of temperature, nitrate, and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. Limnol. Oceanogr. 37(3): 577–589.

Jeppesen, E., J.P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, E. Sortkjær, and K. Olrik. 1990a. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia 200/201: 219–227.

Jeppesen, E., P. Kristensen, J.P. Jensen, M. Søndergaard, E. Mortensen, and T. Lauridsen. 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors, and methods for overcoming resilience. Mem. Ist. Ital. Idrobiol. 48: 128–148.

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kristensen, B. Riemann, H.J. Jensen, J.P. Müller, O. Sortkjær,, J.P. Jensen, K. Christoffersen, S. Bosselmann, and E. Dall. 1990b. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. Hydrobiologia 200/201: 205–218.

Jeppesen, E., M. Søndergaard, O. Sortkjær, E. Mortensen, and P. Kristensen. 1990c. Interactions between phytoplankton, zooplankton and fish in a shallow hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. Hydrobiologia 191: 149–164.

King, D.L. 1970. The role of carbon in eutrophication. J. Water Pollut. Control Fed. 42: 2035–2051.

Komárek, J. 1958. Die taxonomische Revision der planktischen Blaualgen der Tschechoslowakei. Algologische Studien. Verl. der Tschechoslowakischen Akademie der Wissenschaften. 10–206.

Koroleff, F. 1970. Determination of total phosphorus in natural water by means of persulphate oxidation. An. Interlab. Rep. No. 3, Cons. Int. pour l'Explor. de la Mer.

Kristensen, P., and P. Jensen. 1987. Sedimentation and resuspension in Lake Søbygård (Resuspension og sedimentation i Søbygård Sø). M.Sc. thesis, Freshwater Laboratory, Silkeborg & Botanical Institute, University of Aarhus. 176 p. (In Danish)

Leah, R.T., B. Moss, and D.E. Forrest. 1980. The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. Int. Rev. Gesamten Hydrobiol. 65: 223–247.

Leonardson, L. 1984. Does N_2 fixation meet the nitrogen requirements of heterocystous blue-green algae in shallow eutrophic lakes? Oecologia (Berl.) 63: 398–404.

Lynch, M. 1980. *Aphanizomenon* blooms: alternate control and cultivation by *Daphnia pulex*. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3: 299–305. University Press of New England, Hanover, N.H.

Murphy, J., and J.P. Riley. 1972. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27: 21–26.

Nygaard, G. 1949. Hydrobiological studies on some Danish ponds and lakes. Biol. Skr. K. Dan. Vidensk. Selsk. 7: 1–239.

Olrik, K. 1978. Cyanophyceae and environmental factors in 15 Danish lakes. Verh. Int. Limnol. 20: 690–695.

Olrik, K. 1981. Succession of phytoplankton in response to environmental factors in Lake Arresø, North Zealand, Denmark. Schweiz. Z. Hydrol. 43: 6–19.

Paerl, H.W. 1988. Growth and reproductive strategies of freshwater blue-green algae (cyanobacteria), p. 261–315. *In* C.D. Sandgren [ed.] Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge.

Pavoni, M. 1963. The importance of nannoplankton compared to netplankton. Schweiz. Z. Hydrol. 25: 219–341.

Pick, F.R., and D.R.S. Lean. 1987. The role of macronutrients (C, N, P) in controlling cyanobacterial dominance in temperate lakes. N.Z. J. Mar. Freshwater Res. 21: 425–434.

Reynolds, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge. 384 p.

Reynolds, C.S. 1987. Cyanobacterial water-blooms. Adv. Bot. Res. 13: 67–143.

Reynolds, C.S. 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton, p. 388–433. *In* C.D. Sandgren [ed.] Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge.

Reynolds, C.S., and A.E. Walsby. 1975. Water blooms. Biol. Rev. 50: 437–481.

Rott, E. 1981. Some results from phytoplankton counting intercalibrations. Schweiz. Z. Hydrol. 43: 34–62.

Ruttner, F. 1963. Fundamentals of limnology. 3rd ed. University of Toronto Press, Toronto, Ont. 295 p.

Sas, H. [ed.] 1989. Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation. Acad. Ver. Richardz Gmbh. 497 p.

SAS Institute Inc. 1989. SAS/STAT® user's guide version 6, 4th ed. Vol. 2. SAS Institute Inc., Cary, N.C. 846 p.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., D.C.) 195: 260–262.

Seip, K.L. 1988. A system for identifying lakes response to reductions in phosphorus loading. Part II. Occurrence of bluegreen algae (cyanobacteria) (Et regelsystem for å identifisere innsjøers respons på redusjoner fosforbelastning. Del II. Forekomst av blågrønn-alger (cyanobacteria)). Limnos 3: 8–12. (In Norwegian)

Shapiro, J. 1984. Blue-green dominance in lakes: the role and management significance of pH and CO_2. Int. Rev. Gesamten Hydrobiol. 69: 765–780.

Shapiro, J. 1990. Current beliefs regarding dominance by blue-greens: the case for the importance of CO_2 and pH. Verh. Int. Ver. Limnol. 24: 38–54.

Smith, V.H. 1983. Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. Science (Wash., D.C.) 221: 669–671.

Smith, V.H. 1985. Predictive models for the biomass of blue-green algae in lakes. Water Resour. Bull. 21: 433–439.

Smith, V.H. 1986. Light and nutrient effect on the relative biomass of blue-green algae in lake phytoplankton. Can. J. Fish. Aquat. Sci. 43: 148–153.

Smith, V.H. 1990. Phytoplankton responses to eutrophication in inland waters, p. 231–249. *In* I. Akatsuka [ed.] Introduction to applied phycology. Academic Publishing bv, The Hague, The Netherlands.

Smith, V.H., E. Willén, and B. Karlsson. 1987. Predicting the summer peak biomass of four species of blue-green algae (Cyanophyta/Cyanobacteria) in Swedish lakes. Water Resour. Bull. 23: 397–402.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. The principles of statistics in biological research. 2nd ed. W.H. Freeman & Co., New York, N.Y. 859 p.

Solórzano, L., and J.H. Sharp. 1980. Determination of total dissolved nitrogen in natural waters. Limnol. Oceanogr. 33: 702–724.

Sommer, U. 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnol. Oceanogr. 30: 335–346.

Steinberg, C., and H. Hartmann. 1988. Planktonic bloom-forming cyanobacteria and the eutrophication of lakes and rivers. Freshwater Biol. 20: 279–287.

Søndergaard, M., E. Jeppesen, P. Kristensen, and O. Sortkjær. 1990. Interactions between sediment and water in a shallow and hypertrophic lake: a study on short term changes in the trophic relationships in Lake Søbygård, Denmark. Hydrobiologia 191: 139–148.

Takamura, N., A. Otsuki, M. Aizaki, and Y. Nojiri. 1992. Phytoplankton species shift accompanied by a transition from nitrogen dependence to phosphorus dependence of primary production in lake Kasumigaura, Japan. Arch. Hydrobiol. 124: 129–148.

Talling, J.F. 1976. The depletion of carbon dioxide from lake water by phytoplankton. J. Ecol. 64: 79–121.

Trimbee, A.M., and E.E. Prepas. 1987. Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. Can. J. Fish. Aquat. Sci. 44: 1337–1342.

Utermöhl, H. 1958. Zur Vervollkomnung der quantitativen Phytoplankton-Methodik. Mitt. Int. Ver. Limnol. 9: 1–38.

Vanni, M.J., and J. Temte. 1990. Grazing and nutrient limitation of phytoplankton in a eutrophic lake: seasonal pattern. Limnol. Oceanogr. 35: 697–709.

Vincent, W.F. 1989. Cyanobacterial growth and dominance in two eutrophic lakes — review and syntheses. Arch. Hydrobiol. Beih. Ergebn. Limnol. 32: 239–254.

Zewenboom, W., and L.R. Mur. 1980. N_2-fixing cyanobacteria: why do they not become dominant in Dutch, hypereutrophic lakes. Dev. Hydrobiol. 2: 123–130.

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The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake

Torben L.Lauridsen, Leif Junge Pedersen, Erik Jeppesen and Martin Søndergaard

National Environmental Research Institute, Department of Lake and Estuarine Ecology, Vejlsøvej 25, PO Box 314, DK-8600 Silkeborg, Denmark

Abstract. Cladoceran composition and diel horizontal migration were studied in 2, 10 and 25 m diameter macrophyte exclosures established in the littoral zone of shallow Lake Stigsholm, Denmark. The exclosures were protected from waterfowl grazing, but open to fish. The macrophyte community comprised *Potamogeton pectinatus*, *Potamogeton pusillus* and *Callitriche hermaphroditica*. Cladocerans were sampled randomly every third hour inside and outside the macrophyte exclosures during a 24 h period. In the 2 m exclosure, the pelagic species *Ceriodaphnia* spp. and *Bosmina* spp. dominated during the day, mean density being as high as 3430 indiv. l^{-1}. During the night, density decreased to 10–20% of the daytime density, thus indicating diel horizontal migration. In the 10 and 25 m exclosures, the daytime mean density of *Ceriodaphnia* spp. was 865 and 202 indiv. l^{-1}, respectively, and did not decrease at night. In contrast to the pelagic species, the density of macrophyte-associated species tended to be higher in the 10 and 25 m exclosure than in the 2 m exclosure. In the daytime, *Eurycercus lamellatus* density in the 2, 10 and 25 m macrophyte exclosures was 7, 28 and 16 indiv. l^{-1}, respectively, while that of *Simocephalus vetulus* was 11, 171 and 92 indiv. l^{-1}, respectively. There was no day–night difference in the density of macrophyte-associated species. We conclude that cladoceran community composition varies with macrophyte bed size, and that the edge zone between the bed and open water is an important daytime refuge for potentially migrating pelagic cladocerans.

Introduction

Submerged macrophytes can have an important stabilizing effect on the clear-water stage in eutrophic freshwater lakes (Moss, 1990; Scheffer, 1990; Jeppesen *et al.*, 1991). One of the reasons is that the macrophyte beds act as a spatial daytime refuge for cladocerans (Timms and Moss, 1984; Davies, 1985; Lauridsen and Buenk, 1996; Lauridsen and Lodge, 1996), thereby enabling the zooplankton to survive despite the presence of fish, and hence maintain a high grazing pressure on the phytoplankton.

In many eutrophic lakes, however, submerged vegetation is lacking due to the low transparency. Attempts to restore macrophytes by reducing external nutrient loading are often thwarted by resilience caused by internal nutrient loading or biological resistance (Ryding, 1981; Sas, 1989; Jeppesen *et al.*, 1991). One approach used to reduce the recovery period is fish manipulation (Gulati *et al.*, 1990; Jeppesen *et al.*, 1990), a measure that in some lakes has led to the reappearance of submerged macrophytes within 1 or 2 years (Ozimek *et al.*, 1990; Van Donk *et al.*, 1990; Hanson and Butler, 1994; Meijer *et al.*, 1994). In other cases, however, the response time has been longer (Lauridsen *et al.*, 1993), the delay being attributable to factors such as a lack of seeds or other propagules, resistance related to sediment composition (Barko and Smart, 1986) and waterfowl grazing (Lauridsen *et al.*, 1993; Søndergaard *et al.*, 1996). In such cases, it would be relevant to promote macrophyte growth actively, for instance by improving conditions for a sparse natural stand, e.g. by fencing in the potential growth areas or by transplantation.

Such measures may also have implications for the survival of cladocerans seeking refuge in the plant beds. The findings of Lauridsen and Buenk (1996) indicate that the boundary zone between macrophyte beds and the open water is particularly important as a refuge for cladocerans. This suggests that a high macrophyte bed edge: area ratio would favour migrating cladocerans, while a low edge:area ratio would favour the non-migrating littoral species that usually dominate in macrophyte-covered shallow areas (e.g. Quade, 1969; DiFonzo and Campbell, 1988; Paterson, 1993). In the present study, we have therefore evaluated how macrophyte bed size affects the composition and diel migration of a number of pelagic and littoral cladoceran species.

Study area

The study was undertaken in shallow eutrophic Lake Stigsholm situated in central Jutland, Denmark. The lake area is 21 ha and it has a maximum and mean depth of 1.2 and 0.8 m, respectively. In the period 1988–1992, average summer (May–October) total phosphorus (P) ranged from 105 to 151 μg P l^{-1}. The vegetation was dominated by submerged macrophytes until the 1950s, but has since been alternately dominated by macrophytes and phytoplankton. At the time of the study, the fish stock was dominated by roach (*Rutilus rutilus* L.) and perch (*Perca fluviatilis* L.), which comprised 79 and 18%, respectively, of the total number of fish caught in multiple mesh size survey nets (Schriver *et al.*, 1995).

Method

The study was conducted in August 1992 as part of a larger project. Triplicate circular macrophyte exclosures with diameters of 2, 10 and 25m, respectively, were established ~15 m from the shore in the littoral region of the lake bed. However, the macrophyte development in the exclosures deviated substantially among the replicates. Since the importance of macrophytes as a refuge for cladocerans is highly dependent on the per cent plant volume infested (PVI) (Schriver *et al.*, 1995; Jeppesen *et al.*, 1996), we decided to concentrate this study on three exclosures (one of each diameter) with identical and high PVI (60–70%).

Water depth in each of the three exclosures ranged from ~0.6 to 0.9 m. The exclosure fencing consisted of 60 mm mesh polyethylene netting projecting 1.6 m above the sediment surface, thereby preventing the macrophytes from being grazed by the lake waterfowl [mainly coot (*Fulica atra* L.) and mute swan (*Cygnus olor* Gmelin)] and large fish, but leaving the exclosures open to lake water and sediment. The macrophytes in the exclosures were left to grow naturally. A 10–20 m wide macrophyte-free zone was cleared around the exclosures to create a sharp demarcation between the macrophyte beds and the open water. The dominant macrophytes present were *Potamogeton pectinatus* L., *Potamogeton pusillus* L. and *Callitriche hermaphroditica* L. Macrophyte coverage, height and water depth were measured 1 week before the study at 5, 10 or 25 locations equidistant along the diameter of the three exclosures, the number depending on exclosure size. Macrophyte density was expressed as PVI (Canfield *et al.*, 1984) calculated as the product of per cent coverage and height divided by the water depth. The macrophyte beds and the adjacent open-water reference areas were sampled every 3 h during a 24 h period using a core sampler (diameter 7.2 cm) to collect an entire water column. The method only allows sampling of animals inhabiting the water between the macrophytes together with individuals shaken off the plants during sample collection. The number of macrophyte-associated species is therefore likely to be underestimated. Samples for cladoceran enumeration were collected randomly at four locations within each macrophyte bed and at three open-water reference stations located 5–10 m from each exclosure. The composite exclosure and reference samples (6–12 l) were filtered through an 80 μm mesh net and fixed in acid Lugol's solution. Cladocerans >140 μm were determined to genus or species level and counted using a stereomicroscope. Dense samples were subsampled, but at least 100 individuals of the dominant species were counted. A zooplankton sample was also taken in the open water of the central part of the lake on 11 August in connection with routine lake sampling.

Because of the lack of replicates, we tested horizontal migration from the macrophyte beds by comparing day data (mean density at 11 a.m., 2 p.m.and 5 p.m.) with night data (8 p.m., 11 p.m. and 1 a.m.) using Student's *t*-test. Eight p.m. was included as 'night' because zooplankton densities generally resembled night more than day at that time (Figure 1). Such a test can only give a rough estimate of the difference, as the triplicate samples cannot be assumed to be mutually independent. However, the reference samples are true replicates. Student's *t*-test was also used when testing for differences in cladoceran density between macrophyte-covered and open areas.

Results

Macrophyte composition was identical in the three exclosures, with *C.hermaphroditica* covering the bottom, and PVI being mainly accounted for by *P.pectinatus* and *P.pusillus*. PVI in the 2, 10 and 25 m macrophyte exclosures was 70, 60 and 61%, respectively.

As the diameter of the macrophyte exclosures increased, daytime cladoceran mean density decreased: from 5527 indiv. l^{-1} in the 2 m exclosure to 1864 indiv. l^{-1} in the 10 m exclosure, and 894 indiv. l^{-1} in the 25 m exclosure (Table I). This was mainly attributable to a marked decrease in the number of *Ceriodaphnia* spp. and *Bosmina* spp. with increasing macrophyte exclosure size (Table I, Figure 1). Most other cladocerans in fact increased in density, but as they were only present in small numbers, this could not compensate for the decrease in the two dominant species (Table I, Figure 1). Total cladoceran daytime mean density at the reference and mid-lake stations was 243 and 121 indiv. l^{-1}, respectively, *Ceriodaphnia* spp. and *Bosmina* spp. being completely dominant (Table I).

Ceriodaphnia spp. and *Bosmina* spp. accounted for 96% of total cladoceran numbers in the 2 m macrophyte exclosure, 62% in the 10 m exclosure and 26% in the 25 m exclosure (Table I). The corresponding figures for the reference and mid-lake stations were 89 and 94%, respectively. *Diaphanosoma brachyurum* accounted for 4% of the mid-lake population, 1% of the total cladoceran numbers

Table I. Cladoceran daytime mean densities (±95% CL) and percentage of total cladoceran numbers in macrophyte exclosures of diameter 2, 10 and 25 m ($n = 3$), at the open-water reference stations (all sampled 5–6 August; $n = 9$) and at the mid-lake station (sampled 11 August; $n = 1$)

	2m exclosure		10 m exclosure		25 m exclosure		Reference stations		Mid-lake	
	No. l^{-1}	%	No. l^{-1}	%	No. l^{-1}	%	No. l^{-1}	%	No. l^{-1}	%
Ceriodaphnia spp.	3430	62	865	46	202	23	99 ± 38	41 ± 16	92	76
Bosmina spp.	1876	34	300	16	28	3	118 ± 45	48 ± 18	22	18
Diaphanosoma brachyurum	70	1	278	15	138	15	3 ± 1	1 ± 0.3	5	4
Sida crystallina	1	0	10	0.5	10	1	0,1 ± 0,1	0 ± 0	0	0
Eurycercus lamellatus	7	0.1	28	1.5	16	2	0,1 ± 0,1	0 ± 0	0	0
Simocephalus vetulus	11	0.2	171	9	92	11	0 ± 0	0 ± 0	0	0
Pleuroxus sp.	109	2	72	4	82	9	16 ± 13	7 ± 5	0	0
Chydorus sphaericus	23	0.4	140	8	325	36	7 ± 4	3 ± 2	2	2
Total no. l^{-1}	5527	100	1864	100	893	100	243	100	121	100

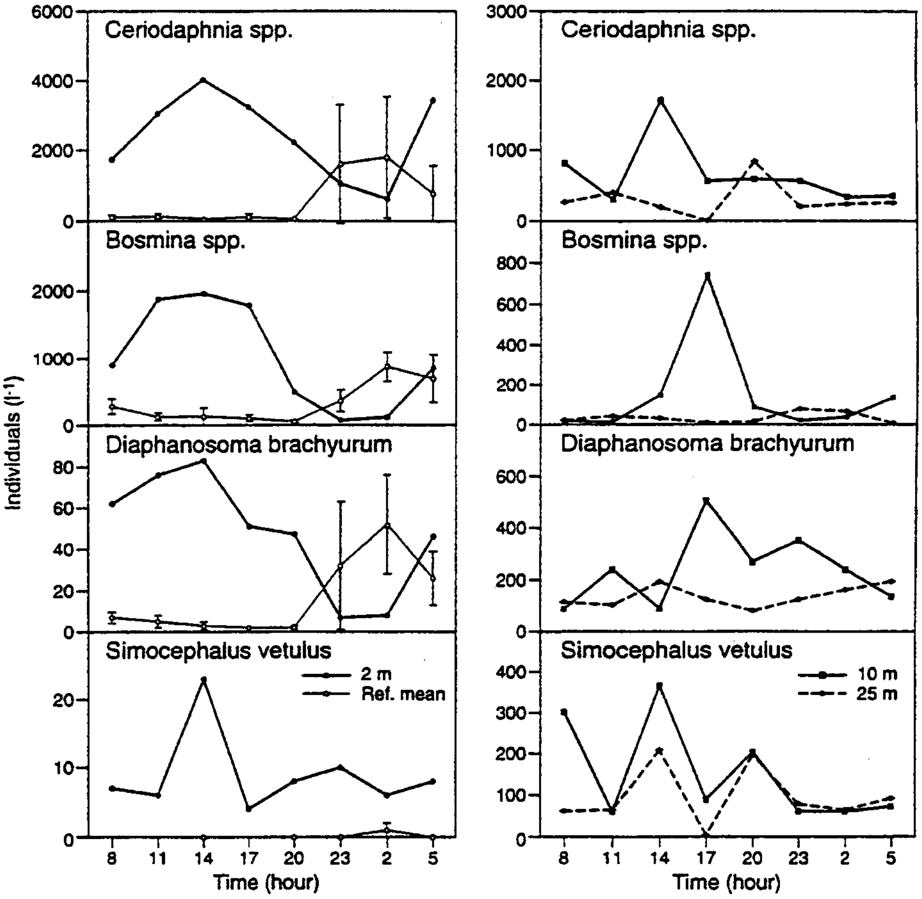

Fig. 1. Cladoceran density in macrophyte exclosures of three sizes during a 24 h period (5–6 August). **Left panel:** 2 m diameter exclosure (●), reference station mean value ± 95% CL (○). **Right panel:** 10 m diameter exclosure (■) and 25 m diameter exclosure (◆).

in the 2 m exclosure, and 15% in the 10 and 25 m exclosures. The percentage of the macrophyte-associated species *Sida crystallina*, *Eurycercus lamellatus* and *Simocephalus vetulus* increased with size, comprising 0.3, 11 and 14% of the total cladoceran numbers in the 2, 10 and 25 m exclosures, respectively (Table I).

Daytime mean densities of *Ceriodaphnia* spp. and *Bosmina* spp. in the 2 m exclosure were significantly ($P = 0.0078$ and $P = 0.00008$) higher (340 and 1876 indiv. l^{-1}, respectively) than in the reference area (99 and 118 indiv. l^{-1}, respectively) and at the mid-lake station (92 and 22 indiv. l^{-1}, respectively) (Table I and Figure 2). At night, no difference was found, density being ~1000 and 300 indiv. l^{-1}, respectively (Figure 2). In the 10 m macrophyte exclosure, both *Bosmina* spp. and *Ceriodaphnia* spp. density did not differ from that at the reference stations, either during the day or during the night. However, in the 25 m macrophyte exclosure, *Bosmina* spp. density was lower during the day ($P = 0.035$) than at the

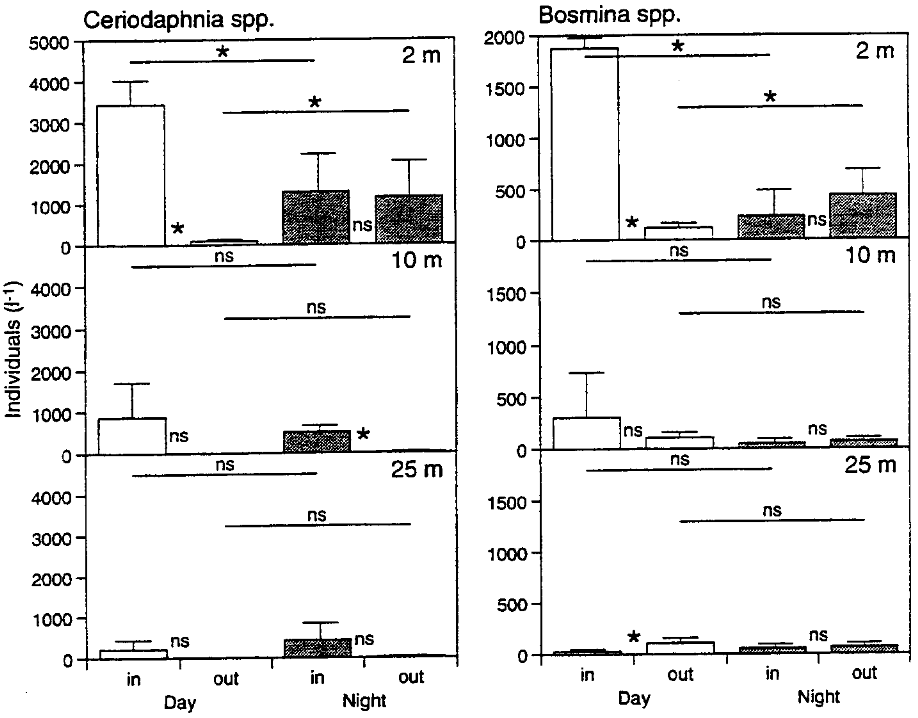

Fig. 2. Mean daytime and night-time density of *Ceriodaphnia* spp. and *Bosmina* spp. inside and outside macrophyte exclosures of diameter 2, 10 and 25 m. Statistically significant differences are indicated by an asterisk (see the text for *P* values; ns, not significant). The vertical bars indicate 95% CL ($n = 3$–9).

reference stations. Moreover, the daytime density of *Ceriodaphnia* spp. was significantly higher in the 2 m macrophyte exclosure (3430 indiv. l^{-1}) than in the 10 m ($P = 0.008$) and the 25 m ($P = 0.0002$) macrophyte exclosures (865 and 202 indiv. l^{-1}, respectively) (Table I and Figure 2). No consistent pattern was found for *D.brachyurum*. The density was significantly higher during the day than at night in the 2 m macrophyte exclosure ($P = 0.04$). During the night, a significantly higher density was found in the 10 and 25 m macrophyte exclosures than at the reference stations, while no differences were found between the 2 m macrophyte exclosure and the reference stations, except during the day ($P = 0.02$). There was a tendency towards higher densities in the 10 and 25 m exclosures than in the 2 m exclosure: 278 and 138 indiv. l^{-1}, respectively, versus 70 indiv. l^{-1} (Table I, Figure 3). At the mid-lake station, the density was only 5 indiv. l^{-1}.

Sida crystallina daytime density was <1 indiv. l^{-1} both inside and outside the 2 m exclosure, whereas in the 10 and 25 m exclosures it was 10 indiv. l^{-1} and substantially greater ($P = 0.003$ and 0.04, respectively) than at the reference stations (Table I, Figure 3). During the night, no significant difference was found in the density between the macrophyte beds and the reference stations. Neither was any significant day–night difference in *D.brachyurum* and *S.crystallina* density found

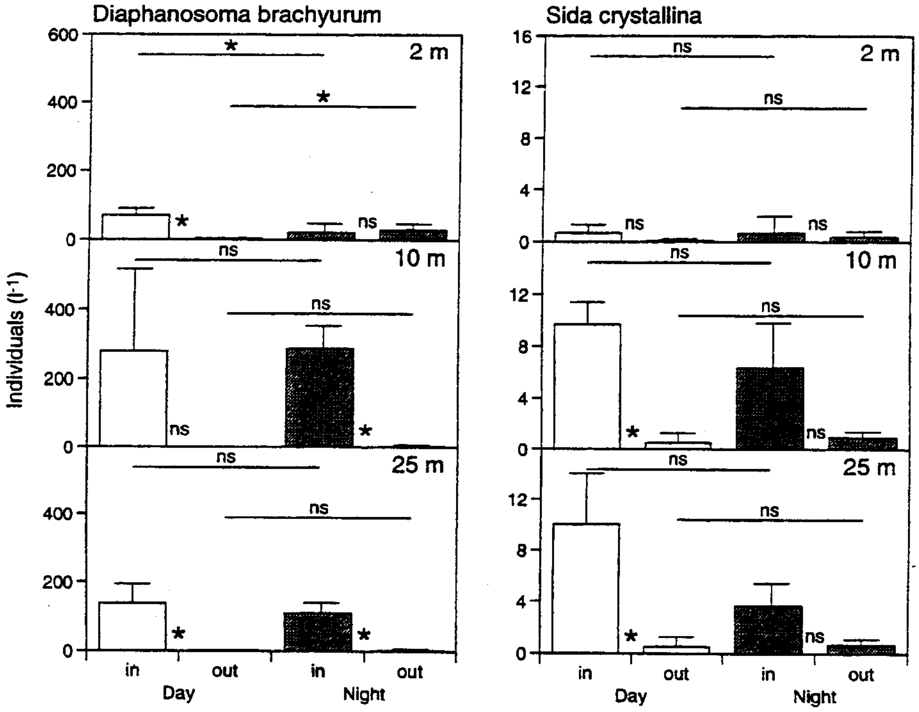

Fig. 3. Mean daytime and night-time density of *Diaphanosoma brachyurum* and *Sida crystallina* inside and outside macrophyte exclosures of diameter 2, 10 and 25 m. See Figure 2 for further information.

within the different macrophyte exclosures. However, the density of *S.crystallina* in the 10 and 25 m exclosures was significantly higher (P = 0.002, P = 0.022 and P = 0.035, P = 0.028) than in the 2 m exclosure during both the day and night (Table I and Figure 3). *Eurycercus lamellatus* was found in significantly higher densities in the 10 and 25 m exclosures than at the reference stations (Table I, Figure 4) during both the day and night, mean daytime density of *E.lamellatus* in the 2, 10 and 25 m exclosures being 7, 28 and 16 indiv. l^{-1}, respectively. *Simocephalus vetulus* showed the same, although not as pronounced, tendency as *E.lamellatus*. The mean daytime density in 2, 10 and 25 m macrophyte exclosures was 11, 171 and 92 indiv. l^{-1}, respectively. Moreover, *E.lamellatus* and *S.vetulus* density was higher in the 10 and 25 m exclosures than in the 2 m exclosure, albeit only significant for *E. lamellatus*. For the two species, no day–night change was found. The density at the reference stations was <1 indiv. l^{-1} and both species were absent at the mid-lake station.

Pleuroxus spp. and *Chydorus sphaericus* showed the same diel pattern as *E.lamellatus* and *S.vetulus*, the density of both being higher inside the macrophyte exclosures irrespective of exclosure size and time of sampling (Figure 5). Only during the night were significant variations found in the mean density between the macrophyte beds and the reference stations. Mean density in the macrophyte beds tended to be less at night than during the day, but the difference was not

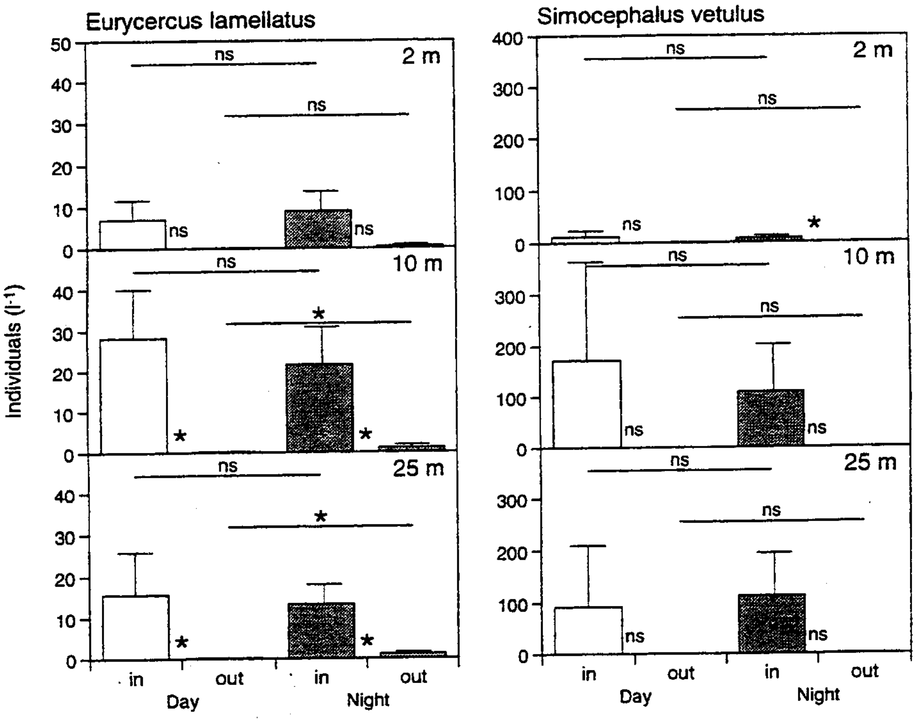

Fig. 4. Mean daytime and night-time density of *Eurycerus lamellatus* and *Simocephalus vetulus* inside and outside macrophyte exclosures of diameter 2, 10 and 25 m. See Figure 2 for further information.

significant. At the reference and mid-lake stations, no consistent day–night pattern was found and the daytime density of *Pleuroxus* spp. and *C.sphaericus* at the mid-lake station was 0 and 2 indiv. l^{-1}, respectively. *Pleuroxus* spp. and *C.sphaericus* density did not differ significantly between the various exclosure sizes.

Discussion

The present study suggests that the macrophyte bed cladoceran community changes in composition depending on bed size. Thus, pelagic and horizontally migrating species dominated in the small macrophyte bed, and littoral non-migrating species in the larger beds. Moreover, diel horizontal migration to and from open water was greatest in the case of a small macrophyte bed.

A reservation about our study, though, is the lack of replicates of the macrophyte bed size because of the accidental, large difference in development of macrophytes within triplicate exclosures. There are nevertheless two good reasons for believing that the conclusion drawn about the impact of macrophyte bed size on cladoceran community composition and diel migration is valid. Firstly, a recent study in the same lake revealed little inter-bed variation in triplicate 5 m macrophyte exclosures, e.g. SE on total abundance for the different species included in

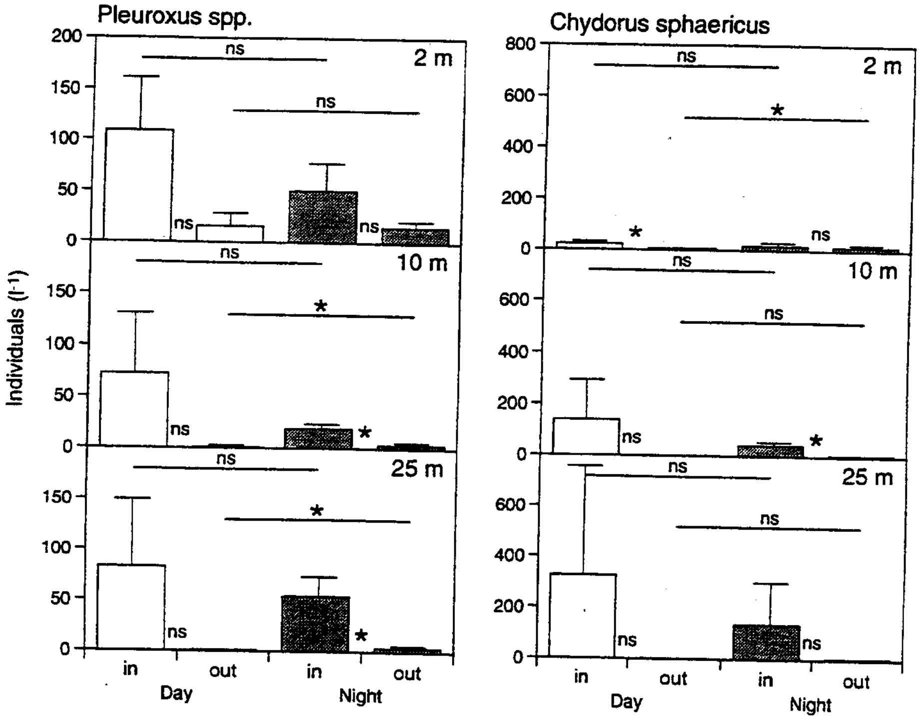

Fig. 5. Mean daytime and night-time density of *Pleuroxus* spp. and *Chydorus sphaericus* inside and outside macrophyte exclosures of diameter 2, 10 and 25 m. See Figure 2 for further information.

the present study averaged 24% (E.Jeppesen, unpublished data), which is substantially lower than the major inter-bed and diel density variations found in the present study for several of the species. Secondly, the 95% CL was low for our reference stations.

Ceriodaphnia spp. and *Bosmina* spp. were both found in very high concentrations in the small macrophyte bed during the day, at which time they totally dominated the cladoceran community. The density of these two species was much less in the larger macrophyte beds, albeit greater than at the reference and the mid-lake stations. At night, the density of both *Bosmina* and *Ceriodaphnia* in the small bed decreased to ~10–20% of the daytime level, and there was a corresponding increase at the reference stations, thus suggesting that both species undergo diel horizontal migration between the macrophyte-covered area and open water. An increase in night-time density of *Bosmina* in open littoral areas has also been reported by DiFonzo and Campbell (1988). *Ceriodaphnia* spp. and *Bosmina* spp. are often found in the pelagic (Lair, 1991; Vuille, 1991; Bast and Seitz, 1993; Paterson, 1993), especially when predation pressure by fish is high. Predation by 0^+ fish was probably high in Lake Stigsholm, thus *Daphnia* spp. and *Eudiaptomus graciloides*, which were both present in high densities in late spring, disappeared almost completely in mid-June when 0^+ fish appeared (L.Jensen, unpublished data), and the zooplankton community became dominated by small cladocerans, cyclopoid copepods and rotifers (Søndergaard *et al.*, 1993). Thus, the substantial diel horizontal migration seen with the 2 m exclosure probably reflects a reaction to high fish predation pressure (Lauridsen and Lodge, 1996).

Diaphanosoma brachyurum was abundant within the two larger macrophyte exclosures. Like *Bosmina* and *Ceriodaphnia*, *D.brachyurum* was observed to migrate from the 2 m exclosure to open water at night. This coincided with the fact that *D.brachyurum* is found in the pelagic zone in many lakes (Jarvis *et al.*, 1987; Vuille, 1991) as well as in Lake Stigsholm (Table I).

Sida crystallina, *E.lamellatus* and *S.vetulus* were found to be closely associated with macrophytes, as has been reported by others (e.g. Quade, 1969; Fairchild, 1981; Lehtovaara and Sarvala, 1994; Paterson, 1994). All three species were present in low density in the small macrophyte exclosure and high density in the large exclosures, but were absent at the mid-lake station. Moreover, for *E.lamellatus* and *S.vetulus* there was no diel variation in density in either the macrophyte exclosures or at the reference stations, indicating that they do not migrate between macrophyte beds and open water. For *S.crystallina*, there was a tendency towards migration from the large macrophyte exclosures as significantly higher density was found in the exclosure than at the reference station during the day, but not during the night. However, there was not any day to night difference in density within the various macrophyte exclosures.

Our study also suggests that *Chydorus sphaericus* and *Pleuroxus* spp. in Lake Stigsholm were mainly macrophyte-associated, showing no diel horizontal migration, although the association is not as close as for *E.lamellatus* and *Simocephalus*. This corresponds well with the fact that *Pleuroxus* spp. is found in surface sediment (DiFonzo and Campbell, 1988) and that *C.sphaericus* occurs in the pelagic zone of many lakes (e.g. Boikova, 1986; Cryer and Townsend, 1988), including Lake Stigsholm (Table I).

Although we registered a major shift from dominance by pelagic species (*Bosmina* spp. and *Ceriodaphnia* spp.) in the small macrophyte exclosure to a higher contribution of macrophyte-associated species in the larger macrophyte exclosures, the density of pelagic species were nevertheless equal to or larger than that of the macrophyte-associated species even in the 25 m exclosures. This may be due to methodological underestimation of macrophyte-associated species. Thus, when comparing open-water samples taken among macrophytes, Vuille (1991) found that *S.crystallina* density was underestimated by a factor of 2–5 in relation to the density in a sample including macrophytes.

The present study thus suggests that per unit area, small-sized macrophyte beds are more important as a daytime refuge for horizontally migrating cladocerans than large-sized beds. This is in concert with the finding of Lauridsen and Buenk (1996) that *Daphnia magna* and *Daphnia hyalina/galeata* favour the edge zone between macrophytes and open water as a daytime refuge rather than the whole bed area. In a parallel study, Jeppesen *et al.* (in press) found that the daytime density in the beds and the migration intensity increased with increasing macrophyte density.

That night-time migration may markedly enhance the density of pelagic cladocerans, even when the macrophyte-covered area is small, can be illustrated by data from the 2 m exclosure. The reduction in density for *Bosmina* and *Ceriodaphnia* from day to night amounted to 1600 and 2500 l^{-1}, respectively, which is ~35-fold higher than the concentration in mid-lake samples. This means that a 3% coverage of small, dense macrophyte beds (2 m in diameter, 60–70% PVI) may lead to a doubling of cladoceran density in open water during the night. Consequently, a large macrophyte-covered area is not a prerequisite for achieving a significant increase in zooplankton grazing capacity in open water at night.

The establishment of macrophyte refuges protected from waterfowl grazing has been proposed as a restoration measure to supplement loading reductions in shallow lakes (Moss, 1990; Jeppesen *et al.*, 1991). The implication of the present study, therefore, is that establishing numerous small refuges should result in a much higher density of migrating cladocerans than establishing a single or few large refuges. This, in turn, will ensure a greater filtration capacity within the beds during the day and in the open water during the night. Per unit area, small and dense macrophyte refuges may be better able to promote a shift to a clearwater stage than larger ones with low macrophyte density.

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References

Barko,J.W. and Smart,R.M. (1986) Sediment related mechanisms and growth limitations in submersed macrophytes. *Ecology*, **67**, 1328–1340.

Bast,S. and Seitz,A. (1993) Differential horizontal distribution during a day-night vertical migration of some cladocerans in a hypereutrophic lake. *Arch. Hydrobiol. Beih.*, **39**, 187–198.

Boikova,O.S. (1986) Horizontal distribution of crustaceans in Lake Globukoe. *Hydrobiologia*, **141**, 113–123.

Canfield,D.E., Shireman,J.V., Haller,W.T., Watkins,C.E. and Maceina,M.J. (1984) Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes. *Can. J. Fish. Aquat. Sci.*, **41**, 497–501.

Cryer,M. and Townsend,C.R. (1988) Spatial distribution of zooplankton in a shallow eutrophic lake, with a discussion of its relation to fish predation. *J. Plankton Res.*, **10**, 487–501.

Davies,J. (1985) Evidence for a diurnal horizontal migration in *Daphnia hyalina lacustris* Sars. *Hydrobiologia*, **120**, 103–105.

DiFonzo,C.D. and Campbell,J.M. (1988) Spatial partitioning of microhabitats in littoral cladoceran communities. *J. Freshwater Ecol.*, **4**, 303–313.

Fairchild,G.W. (1981) Movement and microdistribution of *Sida crystallina* and other littoral microcrustacea. *Ecology*, **62**, 1341–1352.

Gulati,R.D., Lammens,E.H.R.R., Meijer,M.-L. and van Donk,E. (1990) Biomanipulation, tool for water management. *Hydrobiologia*, **200/201**, 1–628.

Hanson,M.A. and Butler,M.G. (1994) Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lake. *Can. J. Fish. Aquat. Sci.*, **51**, 1180–1188.

Jarvis,A.C., Robert,C.H. and Combrink,S. (1987) Cladoceran feeding on size fractioned *Microcystis* colonies and *Chlorella* in a hypertrophic lake (Hartbeespoort Dam, South Africa): implications to resource utilization and cladoceran succession. *J. Plankton Res.*, **9**, 1231–1249.

Jeppesen,E., Søndergaard,M., Mortensen,E., Kristensen,P., Riemann,B., Jensen,H.J., Muller,J.P., Sortkjær,O., Jensen,J.P., Christoffersen,K., Bosselmann,S. and Dall,E. (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes. 1: Cross analysis of three Danish case studies. *Hydrobiologia*, **200/201**, 205–218.

Jeppesen,E., Kristensen,P., Jensen,J.P., Søndergaard,M., Mortensen,E. and Lauridsen,T. (1991) Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Mem. Ist. Ital. Idrobiol.*, **48**, 127–148.

Jeppesen,E., Jensen,J.P., Søndergaard,M., Lauridsen,T., Pedersen,L.J. and Jensen,L. (1996) Top-down control in freshwater lakes: the role of fish, submerged macrophytes and water depth. *Hydrobiologia*, in press.

Lair,N. (1991) Grazing and assimilation rates of natural populations of planktonic cladocerans in a eutrophic lake. *Hydrobiologia*, **215**, 51–61.

Lauridsen,T.L. and Buenk,I. (1996) Diel changes in the horizontal distribution of zooplankton in two shallow eutrophic lakes. *Arch. Hydrobiol.*, **137**, 161–176.

Lauridsen,T.L. and Lodge,D.M. (1996) Avoidance of *Daphnia magna* by fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. *Limnol. Oceanogr.*, **41**, 794–798.

Lauridsen,T.L., Jeppesen,E. and Andersen, F.Ø. (1993) Colonization of submerged macrophytes in shallow manipulated Lake Væng: impact of sediment composition and waterfowl grazing. *Aquat. Bot.*, **46**, 1–15.

Lehtovaara,A. and Sarvala,J. (1984) Seasonal dynamics of total biomass and species composition of zooplankton in the littoral of an oligotrophic lake. *Verh. Int. Ver. Limnol.*, **22**, 805–810.

Meijer,M.-L., Jeppesen,E., Van Donk,E., Moss,B., Scheffer,M., Lammens,E., Van Nes,E., Van Berkum,J.A., de Jong,G.J., Faafang,B.A. and Jensen,J.P. (1994) Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia*, **275/276**, 457–466.

Moss,B. (1990) Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia*, **200/201**, 367–377.

Ozimek,T., Gulati,R.D. and Van Donk,E. (1990) Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. *Hydrobiologia*, **200/201**, 399–407.

Paterson,M. (1993) The distribution of microcrustacea in the littoral zone of a freshwater lake. *Hydrobiologia*, **263**, 173–183.

Paterson,M. (1994) Invertebrate predation and the seasonal dynamics of microcrustacea in the littoral zone of a fishless lake. *Arch. Hydrobiol. Suppl.*, **99**, 1–36.

Quade,H.W. (1969) Cladoceran faunas associated with aquatic macrophytes in some lakes in Northwestern Minnesota. *Ecology*, **50**, 170–179.

Ryding,S.O. (1981) Reversibility of man-induced eutrophication. Experience of a lake recovery study in Sweden. *Hydrobiologia*, **66**, 449–503.

Sas,H. (ed.) (1989) *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations*. Academia Verlag, St Augustin, 497pp.

Scheffer,M. (1990) Multiplicity of stable states in freshwater systems. *Hydrobiologia*, **200/201**, 475–486.

Schriver,P., Bøgestrand,J., Jeppesen,E. and Søndergaard,M. (1995) Impact of submerged macrophytes on fish-cladoceran-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biol.*, **33**, 255–270.

Søndergaard,M., Bøgestrand,J., Schriver,P., Lauridsen,T., Jeppesen,E., Berg,S. and Hald,P. (1993) Betydningen af fisk, fugle og undervandsplanter for vandkvalitet: biomanipulationsforsøg i Stigsholm Sø. National Environmental Research Institute Technical Report no. 77, 68 pp. (in Danish).

Søndergaard,M., Bruun,L., Lauridsen,T.L., Jeppesen,E. and Madsen,T.V. (1996) The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. *Aquat. Bot.*, **53**, 73–84.

Timms,R.M. and Moss,B. (1984) Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.*, **29**, 472–486.

Van Donk,E., Gulati,R.D. and Grimm,M.P. (1990) Restoration by biomanipulation in a small hypertrophic lake: first-year results. *Hydrobiologia*, **191**, 285–295.

Vuille,Th. (1991) Abundance, standing crop and production of microcrustacean populations (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. *Arch. Hydrobiol.*, **123**, 165–185.

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E. Mortensen et al. (eds). Nutrient Dynamics and Biological Structure in Shallow Freshwater and Brackish Lakes.

Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark

M-L. Meijer[1], E. Jeppesen[2], E. van Donk[3], B. Moss[4], M. Scheffer[1], E. Lammens[1], E. van Nes[1], J. A. van Berkum[5], G. J. de Jong[6], B. A. Faafeng[7] & J. P. Jensen[2]
[1] *RIZA, P.O. Box 17, 8200 AA, Lelystad, The Netherlands;* [2] *National Environmental Research Institute, P.O. Box 314, DK 8600, Silkeborg, Denmark;* [3] *Agricultural University, P.O. Box 8080, 6700 DD, Wageningen, The Netherlands;* [4] *Dept of Environmental and Evolutionary Biology, University of Liverpool, P.O. Box 147, Liverpool L89 3BX, United Kingdom;* [5] *Waterboard of West Overijssel, P.O. Box 60, 8000 AB, Zwolle, The Netherlands;* [6] *Waterboard of Schieland, P.O. Box 4059, 3006 AB, Rotterdam, The Netherlands;* [7] *Norwegian Institute for Water Research, P.O. Box 69, Korsvoll, 0808 Oslo 8, Norway*

Abstract

The effects of fish stock reduction have been studied in 3 Dutch lakes (Lake Zwemlust, Lake Bleiswijkse Zoom and Lake Noorddiep) and 1 Danish lake (Lake Væng) during 4–5 years. A general response is described. The fish stock reduction led in general to a low fish stock, low chlorophyll-*a*, high Secchi-disc transparency and high abundance of macrophytes. Large *Daphnia* became abundant, but their density decreased, due to food limitation and predation by fish. The total nitrogen concentration became low due to N-uptake by macrophytes and enhanced denitrification. In Lake Bleiswijkse Zoom the water transparency deteriorated and the clear water state was not stable. The fish stock increased and the production of young fish in summer was high. Clear water occurred only in spring. Large daphnids were absent in summer and the macrophytes decreased.

In Lake Zwemlust, Lake Væng and Lake Noorddiep the water remained clear during the first five years. In summer of the sixth year (1992) transparency decreased in Lake Zwemlust (with high P-concentration of 1.0 mg P l^{-1}). Also in Lake Væng (with a low nutrient concentration of 0.15 mg P l^{-1}) a short term turbid stage (1.5 month) occurred in summer 1992 after a sudden collapse of the macrophytes. Deterioration of the water quality seems to start in summer and seems related to a collapse in macrophytes. At a low planktivorous fishstock (e.g. Lake Væng) the duration of the turbid state is shorter than in presence of a high planktivorous fish biomass (e.g. Lake Zwemlust, and later years of Lake Bleiswijkse Zoom).

Introduction

Fish stock reduction may cause a shift from turbid water to clear water (Reinertsen & Olsen, 1984; Van Donk *et al.*, 1990). Reduction of planktivorous fish may lead to an increase of large daphnids (Shapiro *et al.*, 1975), while reduction of benthivorous fish causes a decrease in resuspension of the sediment (Meijer *et al.*, 1990) and a reduction in P-release of the sediment (Andersson *et al.*, 1978). Although many experiments have clearly demonstrated these short-term effects, there is still much controversy on the long-term stability of the clear water state. The stability is likely to be related to the nutrient concentrations; the highest stability is expected at low nutrient levels (Bendorff, 1987; Scheffer, 1990; Jeppesen *et al.*, 1990; Sarnelle, 1992).

Data from 300 shallow Danish lakes showed that at P-levels < 0.10 mg P l^{-1} and in small lakes (< 3 ha) at < 0.35 mg P l^{-1} clear water states occur frequently (Jeppesen *et al.*, 1990, 1991): the share of piscivorous fish is often higher, leading to a better control of planktivorous fish and also the abundance of macrophytes is often high. However, Scheffer (1990) showed that theoretically a clear-water state obtained by biomanipulation will always be vulnerable to perturbations. The mere fact that the manipulated lake was turbid under the same external conditions before manipulation implies that the obtained clear state is not the only equilibrium of the ecosystem. Therefore, a sufficient perturbation should always be able to cause a shift back to the turbid state.

This paper is a result of an international workshop on long-term stability of manipulated lakes held in April 1992 in Lelystad, The Netherlands. We have studied three small lakes in The Netherlands and one lake in Denmark during 5 years after reducing the fish biomass. A general pattern will be discussed in this paper and a hypothesis for the mechanisms causing a return to the turbid water state is presented.

Study areas

All four lakes are small and shallow, but their phosphorus levels differ from 0.15 mg P l^{-1} (Lake Væng) to 1.0 mg P l^{-1} (Lake Zwemlust) (Fig. 1g). In the three Dutch lakes the fish stock was drastically reduced during one winter (85–100%), in Lake Væng the fish stock reduction was 50% in 1.5 year. In Lake Væng and Lake Zwemlust no additional fish removal has occurred, in Lake Noorddiep and Lake Bleiswijkse Zoom two and three years after the fish reduction a small additional fishery has been carried out on behalf of the anglers (maximum 3–10% of the original fish stock). In Lake Zwemlust and Lake Bleiswijkse Zoom almost every year young pike were introduced to increase the predation pressure on young-of-the-year cyprinids.

Table 1. Main characteristics of the studied lakes.

Lake	Surface area (ha)	Mean depth (m)	Max. depth (m)	Fish reduction (%)
Væng	15	1.2	2.0	50
Noorddiep	4.5	1.5	2.5	85
Bleiswijk	3.5	1.1	1.5	85
Zwemlust	1.5	1.5	2.5	100

Methods

The summer averages (Denmark: May–October; The Netherlands: April–September) of *Daphnia* (> 0.8 mm), Chlorophyll-*a* concentration, Secchi-disc transparency, % macrophytes cover, total N-, total P-concentration and the estimates of the fish stock at the end of the summer are compared with the previous reference state. In Lake Væng, Lake Zwemlust and Lake Noorddiep, data for the year before the fish reduction are used as reference, in Lake Bleiswijkse Zoom the data of the lake part without a fish reduction are used as a reference.

Concentrations of nitrogen, phosphorus and chlorophyll-*a* (ethanol extraction) were measured according to International standards (ISO). *Daphnia* biomass was calculated using a L-DW relationship from Bottrel *et al.*, (1975). In the Dutch lakes and in 1986 in Lake Væng the fish biomass was estimated with the adjusted Petersen mark-recapture method (Ricker, 1975). In Lake Væng a standardized test fishing was undertaken in August each year using multiple gillnets with 14 different mesh-sizes. Results are expressed in Catch per unit effort (CPUE, kg net^{-1}). For details about method and results see Meijer *et al.*, 1990; Van Donk *et al.*, 1990, Søndergaard *et al.*, 1990; Jeppesen *et al.*, 1990, 1991.

General responses

A general pattern can be found based on the average of the four lakes. In all lakes the fish stock

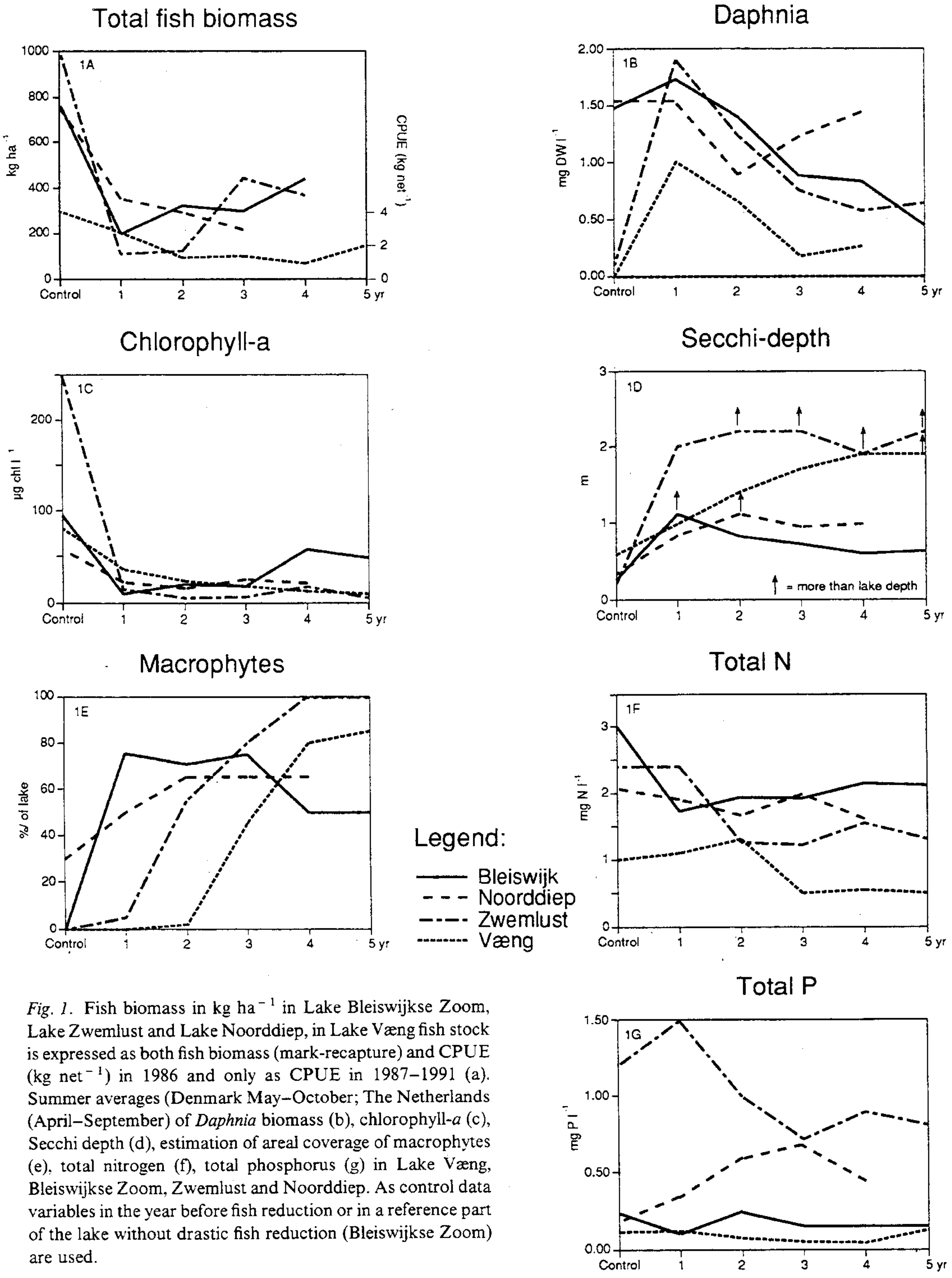


Fig. 1. Fish biomass in kg ha^{-1} in Lake Bleiswijkse Zoom, Lake Zwemlust and Lake Noorddiep, in Lake Væng fish stock is expressed as both fish biomass (mark-recapture) and CPUE (kg net^{-1}) in 1986 and only as CPUE in 1987–1991 (a). Summer averages (Denmark May–October; The Netherlands (April–September) of *Daphnia* biomass (b), chlorophyll-*a* (c), Secchi depth (d), estimation of areal coverage of macrophytes (e), total nitrogen (f), total phosphorus (g) in Lake Væng, Bleiswijkse Zoom, Zwemlust and Noorddiep. As control data variables in the year before fish reduction or in a reference part of the lake without drastic fish reduction (Bleiswijkse Zoom) are used.

has drastically been reduced (Fig. 1a). In two lakes the *Daphnia* biomass was high in the first year after the fish reduction, and afterwards the biomass decreased due to food limitation and predation by fish (Fig. 1b). In the two other lakes, the *Daphnia* biomass was already high before the fish reduction. The Secchi depth increased to maximum values (to the bottom) and the chlorophyll-*a* concentrations became very low (Figs 1c and 1d). As a consequence the lake surface became covered with submerged macrophytes (Fig. 1e). In all lakes the total nitrogen concentration started decreasing not in the year that the fish reduction took place, but in the year that macrophytes covered more than 50% of the lake surface area (Figs 1e and 1f), indicating that macrophytes caused this decrease. The total nitrogen concentration remained low due to uptake by macrophytes and enhanced denitrification (Ozimek *et al.*, 1990; Van Donk *et al.*, 1993, Moss, 1990). Total phosphorus concentration did not show a general pattern (Fig. 1g).

Differences between the lakes

Lake Væng

In Lake Væng the relative fish stock reduction was less drastic than in the Dutch lakes. This might explain why most responses were more gradual in Lake Væng than in the other lakes. In Lake Væng the increase of the Secchi depth to the bottom took 3 years, while in the Dutch lakes this was reached in the first year after the fish reduction. Also the decrease of chlorophyll-*a*, total P and the increase in macrophytes progressed more slowly. The delay in recovery of the macrophytes in Lake Væng was probably caused by the slower increase in Secchi transparency and macrophyte grazing by water fowl (Lauridsen *et al.*, 1994). A drastic decrease in total N was found in the third year when the macrophytes became abundant. The decrease in *Daphnia* biomass was mainly caused by a decrease in *Daphnia* length. The amount of fish caught in the test fishing (CPUE) did not increase in the course of the years, possibly due to the lower nutrient concentration and the high percentage of piscivorous fish (Fig. 4). The water remained continuously clear during these five years.

Lake Zwemlust

The response of Lake Zwemlust was very similar to the general pattern as described above. A strong response in Secchi depth, chlorophyll-*a* and *Daphnia* biomass was found in the first year after the very drastic fish stock reduction. The *Daphnia* biomass decreased in the following years, due to a shift to small *Daphnia* species. A strong increase in macrophytes occurred in the second year, followed by a decrease in nitrogen concentration. The water remained continuously clear during the five years. Incidently large colonies and bluegreen cyanobacteria were found for short periods (van Donk *et al.*, 1990). A small decrease of the coverage of the macrophytes was found, starting in 1990, probably caused by the increased herbivory by birds and rudd (Van Donk *et al.*, in press). The fish stock gradually increased, combined with an increase in planktivorous fish and a decrease in percentage of piscivores (Fig. 4).

Lake Noorddiep

Unlike the response in the other lakes, in Lake Noorddiep the total P-concentration significantly increased after the fish removal. This might be caused by the fact that in Lake Noorddiep more than in the other lakes filamentous macroalgae were present at the bottom, leading to P-release in anaerobic zones. As in Lake Bleiswijkse Zoom, large *Daphnia* were already abundant before fish reduction, because the fish stock was mainly composed of benthivorous fish (e.g. large bream *Abramis brama* and carp *Cyprinus carpio*). In Lake Bleiswijkse Zoom and Lake Noorddiep gut analysis showed that the large brasem and carp almost ate exclusively chironomids.

In Lake Noorddiep the fish biomass rapidly increased in the first year after the fish reduction, from 145 kg ha^{-1} to 300 kg ha^{-1} in October of the first year, but afterwards the fish stock gradually decreased. The Secchi depth remained high in all four studied years.

Lake BLeiswijkse Zoom

Lake Bleiswijkse Zoom is the only lake in which a deterioration can be found during the five years. In the first year Lake Bleiswijkse Zoom was in a clear water state, thereafter a deterioration was found, probably triggered by a repeated inlet with turbid water. The fish stock increased, chlorophyll-*a* concentration increased, Secchi depth decreased and the macrophytes became less abundant.

Detailed observations showed that in Lake Bleiswijkse Zoom the water became turbid only in summer; in spring the water was often clear, due to abundance of large *Daphnia* (Fig. 2).

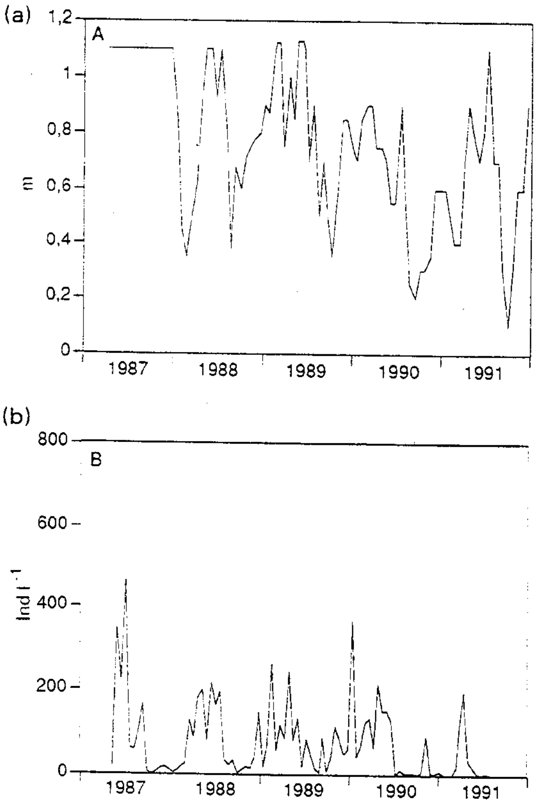


Fig. 2. Individual data on Secchi depth (a) and *Daphnia* density (b) in Lake Bleiswijkse Zoom. In March 1987 the fish stock was drastically reduced. In March and June 1988 and in June 1989 inflow of turbid water (rich in algae and suspended sediment) occurred.

Hypothesis on the change in seasonal cycle

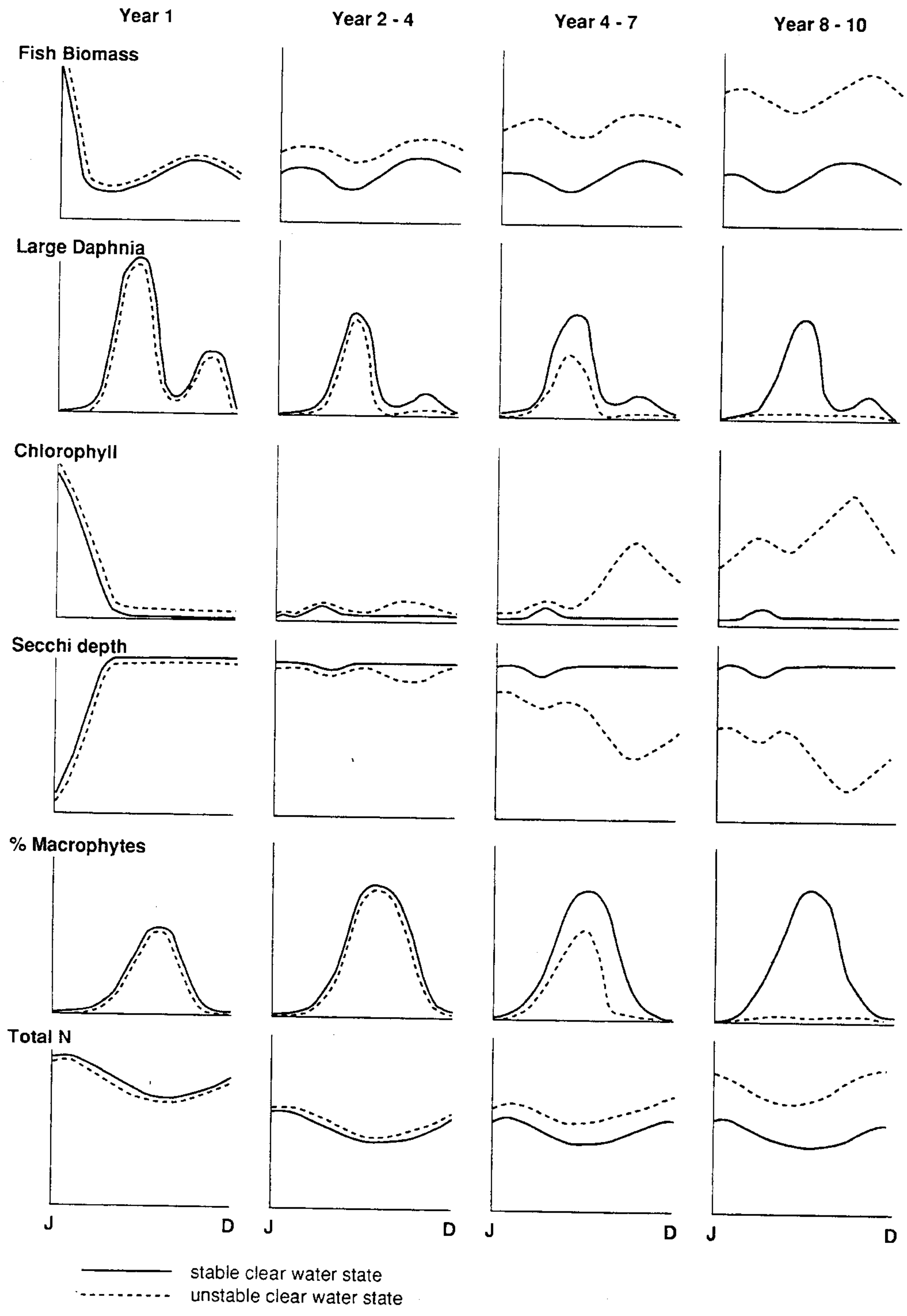
Results from Lake Bleiswijkse Zoom show that the seasonal cycle is important. We formulate a hypothesis on the change in the seasonal cycle in the years after the fish stock reduction. A stable clear water state is compared with a system going back to the turbid state, with emphasis on differences in spring and summer. Deterioration of the light climate starts in summer. The summer differs from spring in many aspects: we paid here mainly attention to the higher predation pressure of young-of-the-year fish on *Daphnia* and the presence of macrophytes, which may cover a substantial part of the lake area.

First two years

In the first two years all systems respond approximately alike. In early spring an algal bloom may occur. In April–June (May–June in Denmark) large *Daphnia* is able to develop exponentially and control algal biomass, because fish predation on zooplankton is low. Due to the reduction in benthivorous fish also the concentration of resuspended bottom material is low and the water becomes clear. Reduction of mainly benthivorous fish may reduce the phosphorus concentration (Havens, 1993), as also can be seen in Lake Bleiswijkse Zoom. However Lake Noorddiep did not show this pattern. Macrophytes start to develop. *Daphnia* decreases in early summer due to food limitation (Gliwicz & Pijanowska, 1989), but recovers in summer when the predation by planktivorous fish remains low. Algal biomass remains low in summer due to grazing by large daphnids. If macrophytes are already abundant in those years, also limitation of the algal growth by macrophytes and associated filterfeeders can be expected (see below).

Later years

Around the third year after the fish reduction differences start to develop between lakes establishing a stable clear water state, and lakes that are returning to the turbid state (Fig. 3).


Year 1
Year 2 - 4
Year 4 - 7
Year 8 - 10
Fish Biomass
Large Daphnia
Chlorophyll
Secchi depth
% Macrophytes
Total N
J
D
J
D
J
D
J
D
stable clear water state
unstable clear water state

To a stable clear water state

Only slight changes occur in the course of the years. The fish stock hardly increases, probably due to a high impact of piscivorous fish. In summer some 0 + planktivorous fish might occur. An early spring algal bloom might occur. In May–June large *Daphnia* reduces the algal biomass. Then the *Daphnia* density decreases due to food limitation as can be seen from fecundity data. In summer *Daphnia* might become abundant again, when the predation by planktivorous fish remains low. In summer the algal biomass is kept low by grazing by large daphnids and the impact of the macrophytes. Macrophytes cause a decrease of the nitrogen concentration directly by uptake and indirectly by creating alternately aerobic and anaerobic zones in the sediment, enhancing denitrification. Because algal productivity under N-limited conditions is low in the summer the grazing pressure needed to control the algal biomass is not high, so a relatively low density of *Daphnia* is able to control the algal biomass. N_2 fixing cyanobacteria which could have compensated for the low nitrogen levels, are not important in these macrophyte rich lakes (Søndergaard *et al.*, 1990; Van Donk *et al.*, 1990). The presence of a dense cover of macrophytes stabilise the clear water state. Short term destabilization may occur along with macrophyte succession due to die-back of a monoculture of e.g. *Elodea* (Lauridsen *et al.*, 1994), fish entrance, or water level alterations (Blindow, 1992). However the percentage piscivorous fish remains high and a return to a clear water stage occurs within months (Lake Væng, unpubl.) to years (Perrow *et al.*, 1994).

Return to a turbid state

In spring of the first year or two large *Daphnia* is still able to develop exponentially and control the algal biomass, because the fish predation on zooplankton is relatively low until the end of June. From then onwards the young-of-the-year fish start feeding on large *Daphnia*.

In summer the production of 0 + fish can reach such high levels that the planktivorous fish stock exceeds a threshold level and large *Daphnia* might disappear in summer (e.g. Lake Bleiswijkse Zoom, Fig. 2). In the first years macrophytes compete with phytoplankton for nitrogen and thus keep the algal biomass low and the transparency high. In later years the Secchi depth gradually decreases during this period. Eventually macrophytes may disappear due to e.g. periphytic growth (Phillips *et al.*, 1978), abrupt die-back of a monoculture of macrophytes (Lauridsen *et al.*, 1994) or external disturbances such as water inlet (Meijer *et al.*, 1990) or increased herbivory (Van Donk *et al.*, in press) and the water becomes turbid. The first years with turbid water in summer, are still followed by clear water in spring (e.g. Bleiswijkse Zoom, Figs 2 and 3). But at some point due to a low percentage of piscivorous fish the planktivorous fish stock will become so high that large *Daphnia* can not reach high densities in spring anymore and the water may remain turbid throughout the year. Also the biomass of benthivorous fish increases, causing higher resuspension of the sediment.

Some lakes may alternate between the turbid and clear water stage over decades (Jeppesen *et al.*, 1990; Perrow *et al.*, 1994). The mechanisms behind the alterations at those lakes are not yet clear.

Signals of deteriorating stability

None of the cases studied has really returned to the permanently turbid state yet, but deterioration in summer and other signs of instability are observed in Lake Bleiswijkse Zoom, and in Lake Zwemlust, such as:

Fig. 3. Hypothesized generalization of developments of fish, *Daphnia*, chlorophyll-*a*, Secchi depth, macrophytes and nitrogen in the long term in stable and unstable clear water states.

- increase of total fish stock, decrease of percentage of predatory fish and an increase of 0 + fish (Fig. 4)
- decrease of mean length of *Daphnia* in August (Lake Bleiswijkse Zoom and Lake Zwemlust, Gulati, 1990)
- increase of periphyton on macrophytes and decrease of areal coverage of macrophytes (Lake Bleiswijkse Zoom, pers. comm. R. W. Doef, RIZA Zwemlust, Van Donk *et al.*, in press)

In Lake Væng and Lake Noorddiep less signs of instability are present (Table 2). According to the Danish data which show that clear water can occur at P-levels of *ca* 0.10 mg P l^{-1} (Jeppesen *et al.*, 1990) only Lake Væng (Fig. 1) seems suitable for a stable clear water state. Indeed in Lake Væng none of the above mentioned indications for a deterioration are observed in first 5 years. However in 1992 also in Væng the water became turbid (Table 2) after the macrophytes almost disappeared in spring, probably reflecting a sudden die-back of a monoculture of *Elodea* sp (Lauridsen *et al.*, 1993). However this return was only temporary (1.5 month) and the percentage piscivorous fish remained high, both in numbers and biomass. In Lake Noorddiep and Lake Bleiswijkse Zoom the surface area and P-levels are close to the range in which stable clear water might be expected (lakes < 3 ha at P-levels of 0.35 mg P l^{-1}). However, the latter lake is deteriorating, probably triggered by a repeated inlet of turbid water. However, in 1990 hardly any and in 1991 no water inlet had taken place, but still the water became turbid in summer due to a decrease of macrophytes and an increase in algal biomass. The production of 0 + fish was very high and large cladocerans were absent in summer (Figs 2 and 4). Each spring the water became clear again. In Lake Noorddiep with the same morphology and nutrient level as in Lake Bleiswijkse Zoom, the increase of the fish stock was much lower. It is not exactly known why in Lake Noorddiep the fish stock is not increasing. The total P-concentrations even increased after the measure, probably due to P-release from the sediment under a dense cover of filamentous macroalgae, and the total nitrogen concentration did not decrease much. Possibly the natural pike population (composed of small individuals) was better able to control planktivorous 0 + recruitment. The nutrient levels, especially P, in Lake Zwemlust were so high that no stable clear water state was expected. Nevertheless the water remained clear for over five years (Van Donk *et al.*, 1993, in press). One reason for the remarkably long period of high transparency might be that in Lake Zwemlust all fish were removed and the lake was stocked with piscivorous fish and some rudd. In addition young pike were added throughout the investigation period. The increasing fish stock and the absence of large *Daphnia* in summer are indications that the clear water situation might not continue, although the results show that the water can stay clear with those high planktivorous fish densities. As in Lake Væng the water became turbid in summer 1992 (Table 2). Here the turbid period lasted longer (still turbid in October 1992) than in Lake Væng,

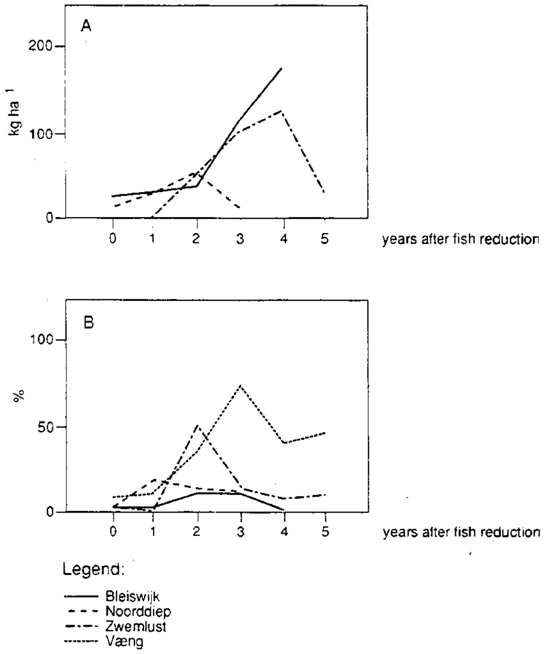


Fig. 4. Total biomass of 0 + planktivorous fish (a) and percentage of piscivores (b) in Lake Væng, Zwemlust, Bleiswijkse Zoom and Noorddiep.

Table 2. Presence of signs of instability in the summer 4–5 years after the fish stock reduction in lake Væng, Noorddiep, Bleiswijkse Zoom and Zwemlust. + = yes, − = no.

	Secchi 4–5 years high	Fish stock decreases	Few 0+ fish	High % pisciv. fish	Daphnia length stays high	Secchi depth Summer 1992 stays high
Væng	+	+	+	+	+	−
Noorddiep	+	+	±	−	±	+
Bleiswijk	−	−	−	−	−	−
Zwemlust	+	−	−	−	−	−

possibly because of the higher biomass of planktivores due to a lower % of piscivorous fish.

Especially in Lake Zwemlust and Lake Bleiswijkse Zoom the amount of small planktivorous fish is increasing (Fig. 4), despite the repeated introduction of 0+ pike in the lakes. In Lake Væng and Lake Noorddiep where the development of planktivorous fish has been less explosive, pike was already present before the fish reduction. There the conditions were already favourable for pike. It seems that a natural pike population is better able to control 0+ fish than a population of stocked 0+ pikes. One explanation for the limited success of introduced pike may be that pike needs a high abundance of emergent vegetation (Grimm & Backx, 1990) and apparently this vegetation does not develop automatically after a fish reduction measure.

An abrupt return to the turbid state, as can be seen in summer in Lake Væng, Lake Zwemlust and Lake Bleiswijkse Zoom seems more related to a decrease in macrophytes than to a high predation by planktivorous fish. However, a high percentage of piscivores associated with a low density of planktivorous fish, makes it more likely that the turbid stage will not last long. An increase in planktivorous fish causing the disappearance of large *Daphnia*, makes the system more vulnerable to sudden changes in macrophyte populations and can lead to a gradual decrease in transparency. Although in Lake Bleiswijkse Zoom, the water becomes clear again in each spring, the transparency in later years was lower than in the first year after the fish removal.

Conclusions

- In small shallow lakes from which fish stocks have been reduced, the water can remain clear irrespective of the nutrient levels for at least five years.
- In Lake Bleiswijkse Zoom the water quality deteriorated from the second year onwards, probably triggered by a perturbation (e.g. inlet of turbid water). In Væng a short term (1.5 month) turbid stage was found in summer 1992 (sixth year). Also in Lake Zwemlust the water became turbid in July 1992, but here the water was still turbid in October 1992.
- The return to the turbid water state starts in summer. At first, the water becomes clear again in next spring. At a low biomass of planktivorous fish the recovery of the system goes faster than in presence with a high biomass of planktivores.
- None of the lakes has yet returned to the turbid water state the whole year around, so we do not know how much time it will take for a system to return to the turbid state permanently, but the more fish is removed the longer the expected longevity of the clear situation.
- Based on those four cases there are some indications that the clear water state is most likely more stable at low nutrient levels. However, more information is needed on the factors that determine the succession in macrophytes and the reasons for a sudden collapse of the macrophyte population. Possibly also the conditions for an efficient predator (pike) population are important.

- The results indicate that macrophytes play a key-role in keeping the water clear in the lakes included in the present analysis. All studied lakes are small and shallow and therefore suitable for abundant growth of submerged macrophytes. Vegetation cannot develop to the same extent in deeper lakes and larger lakes. We, therefore, expect the long-term effects of fish stock reduction described here are only valid for small and shallow lakes.

Acknowledgements

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References

Benndorff, J., 1987. Food-web manipulation without nutrient control: a useful strategy in lake restoration? Schweiz. Z. Hydrol. 49: 237–248.

Blindow, I., 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwat. Biol. 28: 15–27.

Grimm, M. P. & J. J. G. M. Backx, 1990. The restoration of shallow eutrophic lakes, and the role of northern pike, aquatic vegetation and nutrient concentration. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 557–566.

Gulati, R. D., 1990. Structural and grazing response of zooplankton community to biomanipulation in Dutch water bodies. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 99–118.

Havens, K. E., 1993. Response to experimental fish manipulations in a shallow, hypereutrophic lake: the relative importance of benthic nutrient recycling and trophic cascade. Hydrobiologia 254: 73–80.

Jeppesen, E., M. Søndergaard, E. Mortensen, P. Kirstensen, B. Riemann, H. J. Jensen, J. P. Muller, O. Sortkjaer, J. P. Jensen, K. Christoffersen, S. Bosselmann & E. Dall, 1990. Fish manipulation as a lake restoration tool in shallow eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 205–218.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik, 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temporate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 219–227.

Jeppesen, E. P. Kristensen, J. P. Jensen, M. Søndergaard, E. Mortensen & T. Lauridsen, 1991. Recovery resilience following a reduction in external phosphorus loading of shallow eutrophic Danish lakes: duration, regulation factors and methods for overcoming resilience. Mem. Ist. ital. Idrobiol. 48: 127–148.

Lauridsen, T. L., E. Jeppesen & M. Søndergaard, 1994. Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish manipulation. Hydrobiologia 275–276/Dev. Hydrobiol. 94: 233–242.

Meijer, M-L., M. W. de Haan, S. W. Breukelaar & H. Buiteveld, 1990. Is reduction of benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia 200–201/ Dev. Hydrobiol. 61: 303–316.

Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 367–378.

Ozimek, T., E. van Donk & R. D. Gulati, 1990. Can macrophytes be useful in biomanipulation of lakes. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 475–487.

Perrow, M. R., B. Moss & J. Stansfield, 1994. Trophic interactions in a shallow lake following a reduction in nutrient loading: a long-term study. Hydrobiologia 275–276/Dev. Hydrobiol. 94: 43–52.

Phillips, Y., L. Eminson & B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated fresh waters. Aquat Bot. 4: 103–126.

Reinertsen, H. A. & Y. Olsen, 1984. Effects of fish elimination on the phytoplankton community of an eutrophic lake. Verh. int. Ver. Limnol. 22: 649–657.

Sarnelle, O., 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. Ecology 73: 551–560.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 475–486.

Shapiro, J., V. Lamarra & M. Lynch, 1975. Biomanipulation: an ecosystem approach to lake restoration. In: P. L. Brezonik & J. F. Fox (eds), Water Quality management through biological control. Univ. of Florida, Gainesvill, Florida, Usa: 85–96.

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P.Kristensen & O. Sortkjaer, 1990. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 229–240.

Van Donk, E., M. P. Grimm, R. D. Gulati & J. P. G. Klein Breteler, 1990. Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 275–291.

Van Donk, E., R. D. Gulati, A. Iedema & J. T. Meulemans, 1993. Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. Hydrobiologia 251/Dev. Hydrobiol. 82: 19–26.

Van Donk, E., E. de Deckere, J. P. G. Kleine Breteler & J. T. Meulemans (in press). Herbivory by waterfowl and fish on macrophytes in a biomanipulated lake: effects on long-term recovery. Verh. int. ver. Limnol. 25.

Vanni, M. J. & D. L. Findlay, 1990. Trophic cascades and phytoplankton community structure. Ecology 71: 921–937.

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Alternative Equilibria in Shallow Lakes

M. Scheffer, S.H. Hosper, M-L. Meijer,
B. Moss and E. Jeppesen

The turbidity of lakes is generally considered to be a smooth function of their nutrient status. However, recent results suggest that over a range of nutrient concentrations, shallow lakes can have two alternative equilibria: a clear state dominated by aquatic vegetation, and a turbid state characterized by high algal biomass. This bi-stability has important implications for the possibilities of restoring eutrophied shallow lakes. Nutrient reduction alone may have little impact on water clarity, but an ecosystem disturbance like foodweb manipulation can bring the lake back to a stable clear state. We discuss the reasons why alternative equilibria are theoretically expected in shallow lakes, review evidence from the field and evaluate recent applications of this insight in lake management.

The theoretical possibility of ecosystems having more than one equilibrium has long been recognized[1,2]. Support from field data is less easily obtained. However, recent observations in shallow lakes have led aquatic ecologists to suspect that these ecosystems may indeed possess two alternative stable states, a turbid and a clear one[3–7]. Many ecological mechanisms are probably involved, but the whole feedback system is thought to center around the interaction between submerged vegetation and turbidity (Fig. 1). Vegetation tends to enhance water clarity, while a high turbidity, on the other hand, prevents the growth of submerged plants. The adverse impact of turbidity on vegetation growth is simply a matter of light limitation. Submerged plants can only grow down to a certain turbidity-dependent depth (Fig. 2) beyond which the light availability becomes too low[9]. The positive effect of vegetation on water clarity is the result of a number of different mechanisms: resuspension of bottom material is reduced by vegetation[10]; aquatic plants provide a refuge against planktivorous fish for phytoplankton-grazing zooplankton[3]; vegetation suppresses algal growth due to a reduction of nutrient availability[11]; and plants release allelopathic substances that are toxic to algae[12].

M. Scheffer, S. Hosper and M-L. Meijer are at the Institute for Inland Water Management and Waste Water Treatment, PO Box 17, 8200 AA Lelystad, The Netherlands; B. Moss is at the Dept of Environmental and Evolutionary Biology, University of Liverpool, Liverpool, UK L69 3BX; E. Jeppesen is at the Dept of Freshwater Ecology, National Environmental Research Institute, PO Box 314, 25 Vejlsøvej, DK-8600 Silkeborg, Denmark.

Although the quantitative importance of each of these submechanisms is often hard to assess and may vary between lakes, analysis of comprehensive data sets supports the view that there is an overall positive effect of vegetation on water transparency in freshwater lakes. Lakes with a high cover of submerged macrophytes tend to have a higher transparency than lakes with the same nutrient status in which vegetation is sparse or absent (Fig. 3).

Theory of alternative lake equilibria

Whether these ecological mechanisms may indeed be expected to cause alternative stable states has been explored extensively by means of minimal models[5,6]. The basic idea, however, can already be clarified by a simple graphical approach (Fig. 4). Vegetation can stabilize a clear-water state in shallow lakes up to relatively high nutrient loadings, but once the system has switched to a turbid state, it takes a strong nutrient reduction to enable recolonization by plants. This graphical analysis is based on some rather crude simplifications like the assumption that submerged vegetation disappears abruptly at a critical turbidity, but models employing more realistic assumptions[6] produce similar results (an example is given in Box 1).

The stability properties of such systems can be visualized by means of 'marble-in-cup' pictures (Fig. 5). The equilibrium line with 'catastrophe fold' shown at the bottom of the figure is computed from the vegetation–algae model explained in Box 1. The valleys in the stability landscapes correspond to stable

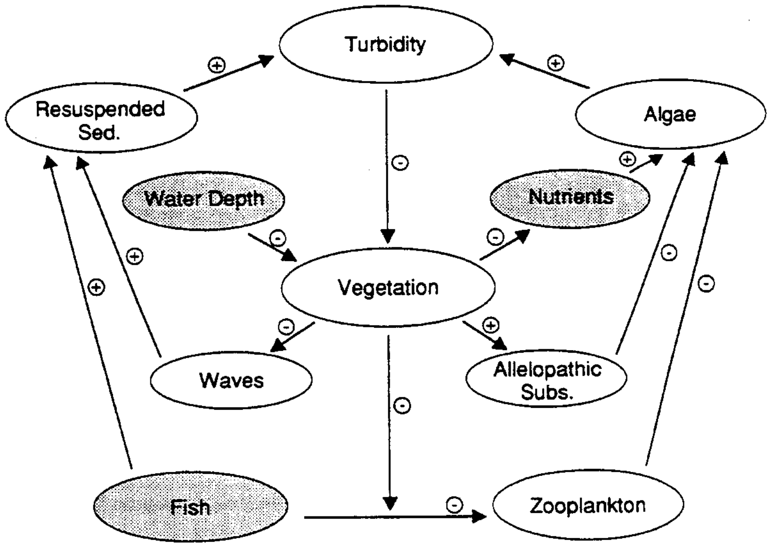


Fig. 1. Main feed-back loops thought to be responsible for the existence of alternative equilibria in shallow lake ecosystems. The qualitative effect of each route in the diagram can be determined by multiplying the signs along the way. In this way it can be seen that both the vegetated and the turbid state are self-reinforcing. The qualitative effect of management measures discussed in this review can be checked in the same way if a 'manager' box with positive or negative arrows pointing to either of the shaded parts of the system is added.

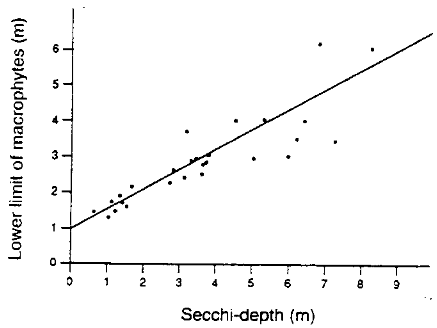


Fig. 2. Relation between transparency ('secchi-depth') and the lower limit of vegetation in 27 Finnish lakes[8].

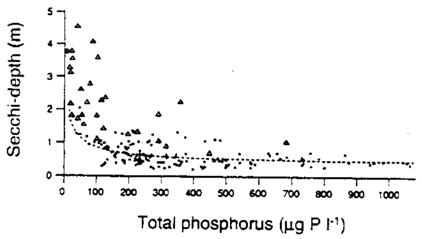


Fig. 3. Summer mean transparency ('secchi-depth') in relation to lake water total phosphorus for shallow Danish lakes with (triangles) and without (dots) high cover of submerged vegetation[7].

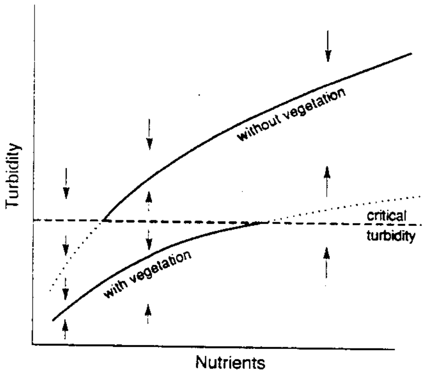


Fig. 4. Alternative equilibrium turbidities related to the presence and absence of aquatic vegetation[9]. Equilibrium turbidity increases with rising nutrient level, but as vegetation reduces turbidity, two different relations apply depending on the presence or absence of vegetation. Vegetation presence itself, however, also depends on turbidity. Light limitation prevents growth below a (turbidity-dependent) depth, and since shallow lakes are often rather homogeneous in depth, the response of the vegetated area to turbidity tends to be discontinuous. To construct this figure we assume the extreme case of total disappearence of vegetation from the lake when the turbidity exceeds a threshold value at which the critical light level for vegetation growth at this depth is reached. Consequently, the 'with vegetation' line applies below the critical turbidity and the 'without vegetation' line above this level. Hence, the dashed parts of the two equilibrium lines do not represent stable states. The emerging picture shows that at low nutrient levels only the vegetated clear equilibrium exists and at high nutrient levels only the turbid vegetationless one. However, over a range of intermediate nutrient concentrations two alternative stable states are possible. Here, the critical turbidity represents the breakpoint of the system separating the attraction areas of these alternative states. Arrows indicate the direction of change in turbidity when the system is out of equilibrium.

parts of the fold curve, and the hill tops to the dashed breakpoint part marking the separation between the basins of attraction. Each picture in the series shows the stability properties at a different nutrient status. The front landscape represents a hypertrophic situation in which just one, turbid, equilibrium exists. The rear picture represents the pristine state of a lake, a low-nutrient situation in which a clear-water equilibrium is the only possible stable state. Between these two extremes there is a range of nutrient levels over which two alternative equilibria exist.

The response of a lake with these stability properties to eutrophication and subsequent restoration efforts can be derived from this representation. Starting at the pristine state, a moderate increase in nutrient level gives rise to an alternative turbid equilibrium, but if no large perturbations occur, the system will remain in the clear state. Continuing enrichment, however, gradually causes the stability of the clear state to shrink to nil, making it more and more vulnerable to perturbations that may bring it within the basin of attraction around the turbid equilibrium. Even in the absence of perturbations the hysteresis period in which the lake hardly responds to nutrient loading will finally end with a catastrophic transition into a turbid state at the inflection point of the catastrophe fold where the clear-water equilibrium disappears.

Obviously, restoration of such a lake by reducing the nutrient level may often have little effect, since the system can show hysteresis again, staying in its current turbid state. However, in this situation a change to the alternative clear-water equilibrium can be achieved in other ways. One way to force a switch is by 'pushing the ball over the hill top', bringing it within the attraction basin of the clear state. More specifically this requires a temporary reduction in the turbidity of the lake, sufficiently large to allow recolonization by submerged vegetation. The other obvious possibility from the theoretical point of view is to 'move the hill top temporarily to the other side of the ball'. The hill top is situated at the critical turbidity for recolonization by submerged vegetation (Fig. 5). Since it is water depth in combination with turbidity that determines whether the underwater light level for vegetation development is met, the hill top can be moved by changing the water level. Lowering the water level causes an increase in critical turbidity and it can be seen from Fig. 5 that this may bring a system from a formerly stable turbid state on the upper equilibrium line into the attraction area of the vegetated state.

A high potential impact of vegetation on the system and a sigmoidal decrease of vegetation with turbidity are important in the proposed mechanisms (Fig. 4 and Box 1). Therefore, the phenomenon of alternative clear and turbid stable states is expected to be restricted to shallow lakes of homogeneous depth, where a major part of the water body can be occupied by plants and small changes in turbidity or water level can have a relatively high impact on vegetation when the light climate is just critical for plant growth at the average lake depth.

Evidence from the field

The theoretical results supply a search image of the symptoms to look for in the real world. For instance, one would expect some sets of shallow lakes to show a bimodality of states, being clear or turbid depending on history rather than physical and chemical conditions. Also, relatively swift transitions from a vegetated clear state to a turbid vegetationless situation and vice versa should occur as a response to disturbances or changes in external factors other than nutrients. The current literature on shallow lakes does indeed provide several observations of these phenomena.

A good example of a set of shallow lakes showing bimodality of state is the Great Linford sand and gravel pit complex in England. The site has 14 lakes excavated over the past 40 years. Some were dry-dug, others wet-dug. The digging method appears to have a pronounced effect on turbidity. Dry digging results in clear lakes, while wet digging results in turbid ones because of a high loading of fine silt. Remarkably, after some decades the wet-dug lakes are still turbid and devoid of vegetation, whereas the dry-dug ones remained clear and richly vegetated[13]. In 1987, part of the fish stock was removed from one of the turbid lakes. This led to a reduction of turbidity, and large weed beds quickly developed in the 25 year old lake, which had no such growth previously[14,15]. The lake has, so far, remained in this state, supporting the view that clear and turbid states are indeed alternative stable equilibria.

Another way to trace bimodality of states is to analyse the history of one lake rather than the current situation in a set of lakes. Some lakes are known to have switched back and forth between a clear vegetated state and a distinct turbid situation repeatedly in the past. Although the information about such switches is often anecdotal, there are some relatively well-documented cases also.

A good example of a switching lake is the shallow Tomahawk Lagoon in New Zealand[16,17], in which phytoplankton and aquatic vegetation have predominated in turn for periods of 1–5 years since 1963. In the clear, vegetation-dominated years phytoplankton production can be reduced by as much as two orders of magnitude. The mechanism inducing the switches has not been explained yet, but the strong contrast between the two states suggests that they are separate equilibria.

A similar situation is found in Lake Takern and Lake Krankesjön, two shallow lakes in the south of Sweden[18]. Periods with clear water and abundant submerged vegetation have alternated with periods of turbid water and sparse submerged vegetation over the past 40–50 years without considerable change in the external nutrient loading. Although the mechanism of change is difficult to reconstruct, there are indications that changes in the water level affecting the performance of submerged macrophytes may have been an important trigger of the switches in these lakes. The best available information comes from Lake Krankesjön[18,19] which showed a marked change from clear to turbid in the early 1970s after an increase in water level. A low water period during 1985 and 1986 seems to have been the onset for a pronounced switch back to a clear state with abundant vegetation growth and waterfowl.

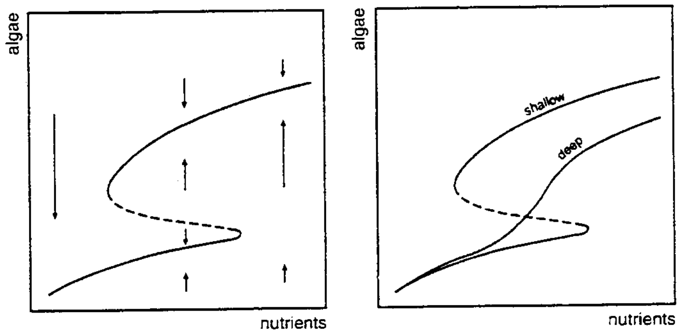
Box 1. A vegetation–algae model

A simple model[6] of the interaction between the growth of planktonic algae (A) and the abundance of vegetation (V) illustrates the potential for alternative equilibria in shallow lakes:

$$\frac{\mathrm{d}A}{\mathrm{d}t} = rA\left(\frac{N}{N+h_N}\right)\left(\frac{h_V}{V+h_V}\right) - cA^2$$

$$V = \frac{h_A^p}{A^p + h_A^p}$$

Algal growth is basically logistic with a maximum intrinsic growth rate (r) and a competition coefficient (c) as parameters. In addition, growth increases in a monod fashion with the nutrient level and decreases in a similar way with vegetation abundance (h_N and h_V being the half-saturation constants). Vegetation abundance is a negative sigmoidal function of algal biomass (h_A being a half-saturation constant again). The value of the power (p) shapes this relation. A high value of p causes it to approach a step function representing the disappearance of vegetation from a shallow lake of homogeneous depth around a critical algal biomass where turbidity makes the average depth of the lake unsuitable for plant growth. If the equilibrium density of phytoplankton ($\mathrm{d}A/\mathrm{d}t = 0$) is plotted against the nutrient level for the shallow lake case, a catastrophe fold arises which is a smooth edged version of the representation derived graphically in Fig. 4.



The response of vegetation to increased turbidity will be less discontinuous in deeper lakes with gradually declining slopes[6]. When we mimic this by decreasing p, the range of nutrient values over which alternative equilibria exist becomes smaller until the alternative equilibria disappear and the response of phytoplankton equilibrium density to nutrient level becomes continuous. Obviously, each depth profile will have its own vegetation–turbidity response, but the result suggests that alternative equilibria arising from the modelled interaction are limited to shallow lakes. Another reason to expect this is that the effect of vegetation on turbidity will be strongest in shallow water where the vegetation structure can fill the whole water column. High vegetation impact can be represented in the model by decreasing the h_V. It appears that such an increase of vegetation impact does indeed increase the tendency of the model to generate alternative stable states.

Obviously, the fact that these observations fit the theory is by no means a proof of its validity. Alternative explanations may exist in any specific case, and it is questionable whether experimental determination of the unique responsible mechanism is feasible at all in ecosystems[20–22]. Nevertheless, the case for the alternative stable state idea appears strong enough to persuade lake managers to aim at forcing turbid shallow lakes into a clear equilibrium with a single perturbation[23].

Application to the management of shallow lakes

The restoration of eutrophied turbid shallow lakes is notoriously difficult. Reduction of the nutrient loading rarely leads to a satisfactory recovery of the clear state in shallow lakes. This can in part be explained from the release of buffered phosphorus from the sediment delaying the response of the actual nutrient level of the water to the reduced external loading[24–27]. However, the current theory of bi-stability suggests an additional explanation. Even if the nutrient level is considerably reduced, this will often be insufficient to restore the clear-water

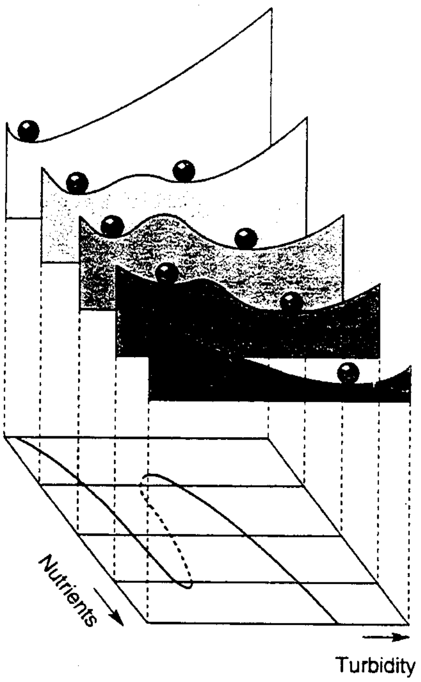


Fig. 5. Stability properties of a shallow lake system at different nutrient levels, as derived from model analyses[6].

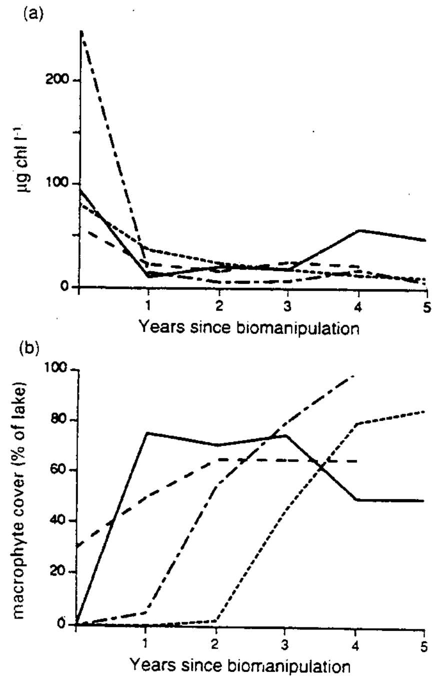


Fig. 6. Sustained effects of biomanipulation on (a) chlorophyll and (b) macrophytes in four shallow lakes[34].

state in bi-stable shallow lakes, as the turbid equilibrium can be (locally) stable down to low nutrient levels (Figs 4,5). In such cases restoration requires an additional 'shock therapy' to bring the ecosystem within the basin of attraction of the alternative clear-water equilibrium.

Recently, reduction of the fish stock ('biomanipulation'[28]) has been successfully applied to several turbid shallow lakes to enforce such a switch[11,29,30]. Two mechanisms seem to be predominantly responsible for the initial increase of clarity after fish stock reduction in shallow lakes (Fig. 1). In the first place, the strongly debated[31,32] trophic cascade effect is observed[11,30]. Reduction of the predation pressure by planktivorous fish allows populations of large-bodied zooplankters to peak and graze down the algal biomass causing clear water in spring[33,34]. At least as important as the trophic cascade, however, is the effect of reduced sediment resuspension in many shallow lakes[29,35]. When the fish community is dominated by species that feed at the bottom like carp (*Cyprinus carpio*) or bream (*Abramis brama*), resuspended bottom material is often the main cause of turbidity, and consequently removal of fish leads to an almost instantaneous increase of transparency.

In shallow lakes, the increase of transparency after biomanipulation is typically followed by a strong development of submerged vegetation in the following years[11,29,30]. Recruitment of the remaining fish is generally good under the new conditions, giving rise to large numbers of young fish in the subsequent years. Such small fish are mainly planktivorous and can potentially exert a huge predation pressure on zooplankton. Nonetheless, the lakes stay clear, presumably because of the manifold stabilizing effect of vegetation on the clear-water situation[36]. An analysis of the long-term response of four particularly well-studied cases[36] shows that these lakes have remained in the obtained clear-water state for at least 4–5 years (Fig. 6). Although changes are still occurring and it is uncertain whether they will all stay clear in the future, the current results support the alternative stable state hypothesis.

As argued, lowering the water level should be another possibility for inducing the switch to a vegetated clear state – an idea that is supported by the likelihood that the pronounced changes in the Swedish lakes Krankesjön and Takern[18,19] are induced by natural water level fluctuations. We are not aware of cases where the water level has been manipulated with the explicit purpose of changing the ecosystem state, but it is known that the effect of such manipulation on the community of shallow lakes can be dramatic. A well documented example is the case of the Swedish Lake Tämnaren[37]. The construction of a dam increased the water level in this shallow (< 2 m) lake by 0.5 m, causing a decrease in vegetated area from 80% to 14% of the lake bed. The large numbers of birds that used to forage in the vegetated lake disappeared, and the water that had been sufficiently clear to see the bottom through the vegetation became turbid because of wind resuspension of the unconsolidated sediment and increased algal growth. A subsequent lowering of the water level would be necessary to check whether the clear and the turbid state are indeed alternative equilibria in this specific case, but the response of the lake illustrates the potential of water level manipulation as a tool for managing the ecosystem state of shallow eutrophic lakes.

Obviously, many of the mechanisms governing the dynamics of shallow lake communities are still poorly understood, and it remains difficult to determine whether an alternative clear equilibrium may be expected in any specific case. Nonetheless, the current experiences are encouraging from a management point of view, since they suggest that shallow lakes which stay turbid despite reduced nutrient loading may be permanently restored by a single perturbation.

References

1 Noy-Meir, I. (1975) *J. Ecol.* 63, 459–483
2 May, R.M. (1977) *Nature* 269, 471–477
3 Hosper, S.H. (1989) *Hydrobiol. Bull.* 23, 5–11
4 Timms, R.M. and Moss, B. (1984) *Limnol. Oceanogr.* 29, 472–486
5 Scheffer, M. (1989) *Hydrobiol. Bull.* 23, 73–85
6 Scheffer, M. (1990) *Hydrobiologia* 200/201, 475–486
7 Jeppesen, E. *et al.* (1990) *Hydrobiologia* 200/201, 219–227
8 Wetzel, R.G. (1975) *Limnology*, Saunders
9 Spence, D.H.N. (1982) *Adv. Ecol. Res.* 12, 37–125

10 James, W.F. and Barko, J.W. (1990) *Arch. Hydrobiol.* 120, 129–142

11 Van Donk, E., Grimm, M.P., Gulati, R.D. and Klein Breteler, J.P.G. (1990) *Hydrobiologia* 200/201, 275–290

12 Wium-Andersen, S. (1987) *Arch. Hydrobiol. Beih.* 27, 167–172

13 Giles, N. (1986) *Game Conservancy Ann. Rev.* 18, 130–133

14 Giles, N. (1988) *Game Conservancy Ann. Rev.* 20, 136–137

15 Wright, R.M. and Phillips, V.E. (1992) *Aquatic Botany* 43, 43–49

16 Mitchell, S.F. *et al.* (1988) *Int. Revue Ges. Hydrobiol.* 73,145–170

17 Mitchell, S.F. (1989) *Aquat. Bot.* 33, 101–110

18 Blindow, I. (1992) *Freshwater Biology* 28, 15–27

19 Andersson, G., Blindow, I., Hargeby, A. and Johansson, S. (1990) *Anser* 29, 53–62

20 Quinn, J.F. and Dunham, A.E. (1983) *Am. Nat.* 122, 602–617

21 Roughgarden, J. (1983) *Am. Nat.* 122, 583–601

22 Scheffer, M. and Beets, J. *Hydrobiologia* (in press)

23 Hosper, S.H. and Jagtman, E. (1990) *Hydrobiologia* 200/201, 523–534

24 Cullen, P. and Forstberg, C. (1988) Hydrobiologia 170, 321–336

25 Sas, H. (1989) *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations,* Academia Verlag

26 Jeppesen, E. *et al.* (1991) *Mem. Ist. Ital. Idrobiol.* 48, 127–148

27 Van Der Molen, D.T. and Boers, P.C.M. *Hydrobiologia* (in press)

28 Gulati, R.D., Lammens, E.H.R.R., Meijer, M-L. and Van Donk, E., eds (1990) *Biomanipulation, Tool for Water Management*, Kluwer

29 Meijer, M-L., de Haan, M.W., Breukelaar, A.W. and Buiteveld, H. (1990) *Hydrobiologia* 200/201, 303–316

30 Søndergaard, M. *et al.* (1990) *Hydrobiologia* 200/201, 229–240

31 DeMelo, R., France, R. and McQueen, D.J. (1992) *Limnol. Oceanogr.* 37, 192–207

32 Carpenter, S.R. and Kitchell, J.F. (1992) *Limnol. Oceanogr.* 37, 208–213

33 Carpenter, S.R. (1988) *Complex Interactions in Lake Communities.* Springer-Verlag

34 Scheffer, M. (1992) *Oikos* 62, 271–282

35 Breukelaar, A.W., Lammens, E.H.R.R., Klein Breteler, J.P.G. and Tatrai, I. *Verh. Internat. Verein. Limnol.* (in press)

36 Meijer, M-L. *et al. Hydrobiologia* (in press)

37 Wallstein, M. and Forsgren, P-O. (1989) *J. Aquat. Plant Manage.* 27, 32–37

Freshwater Biology (1995) 33, 255–270

Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake

PER SCHRIVER, JENS BØGESTRAND, ERIK JEPPESEN* AND MARTIN SØNDERGAARD*
National Environmental Research Institute, Vejlsøvej 25, PO Box 314, DK-8600 Silkeborg, Denmark

* *To whom correspondence should be addressed*

SUMMARY

1. The impact of changes in submerged macrophyte abundance on fish–zooplankton–phytoplankton interactions was studied in eighteen large-scale (100 m^2) enclosures in a shallow eutrophic lake. The submerged macrophytes comprised *Potamotegon pectinatus* L., *P. pusillus* L. and *Callitriche hermaphroditica* L. while the fish fry stock comprised three-spined sticklebacks, *Gasterosteus aculeatus* L., and roach, *Rutilus rutilus* L.
2. In the absence of macrophytes zooplankton biomass was low and dominated by cyclopoid copepods regardless of fish density, while the phytoplankton biovolume was high (up to 38 $mm^3\ l^{-1}$) and dominated by small pennate diatoms and chlorococcales. When the lake volume infested by submerged macrophytes (PVI) exceeded 15–20% and the fish density was below a catch per unit effort (CPUE) of 10 (approx. 2 fry m^{-2}), planktonic cladoceran biomass was high and dominated by relatively large-sized specimens, while the phytoplankton biovolume was low and dominated by small fast-growing flagellates. At higher fish densities, zooplankton biomass and average biomass of cladocerans decreased and a shift to cyclopoids occurred, while phytoplankton biovolume increased markedly and became dominated by cyanophytes and dinoflagellates.
3. Stepwise multiple linear regressions on log-transformed data revealed that the biomass of *Daphnia, Bosmina, Ceriodaphnia* and *Chydorus* were all significantly positively related to PVI and negatively to the abundance of fish or PVI × fish. The average individual biomass of cladocerans was negatively related to fish, but unrelated to PVI. Calculated zooplankton grazing pressure on phytoplankton was positively related to PVI and negatively to PVI × fish. Accordingly the phytoplankton biovolume was negatively related to PVI and to PVI × zooplankton biomass. Cyanophytes and chryptophytes (% of biomass) were positively and *Chlorococcales* and diatoms negatively related to PVI, while cyanophytes and *Chlorococcales* were negatively related to PVI × zooplankton biomass. In contrast diatoms and cryptophytes were positively related to the zooplankton biomass or PVI × zooplankton.
4. The results suggest that fish predation has less impact on the zooplankton community in the more structured environment of macrophyte beds, particularly when the PVI exceeds 15–20%. They further suggest that the refuge capacity of macrophytes decreases markedly with increasing fish density (in our study above approximately 10 CPUE). Provided that the density of planktivorous fish is not high, even small improvements in submerged macrophyte abundance may have a substantial positive impact on the zooplankton, leading to a lower phytoplankton biovolume and higher water transparency. However, at high fish densities the refuge effect seems low and no major zooplankton mediated effects of enhanced growth of macrophytes are to be expected.

This further emphasizes the usefulness of macrophyte refuges as a lake-restoration tool in shallow lakes, but also demonstrates the shortcomings of the method, if the density of planktivorous fish is high.

Introduction

Empirical studies undertaken both in temperate and subtropical areas have shown that water transparency is generally high in lakes with a macrophyte coverage or PVI (per cent volume infested, Canfield *et al.*, 1984) exceeding 30%, irrespective of nutrient concentrations in the lake water (Canfield *et al.*, 1984; Jeppesen *et al.*, 1990; Canfield & Hoyer, 1992). Numerous explanations for the clearwater stage of macrophyte-rich lakes have been suggested, including that grazing pressure on algae (and consequently transparency) is enhanced because cladocerans are able to use the macrophytes as a daytime refuge against predation by fish (Timms & Moss, 1984). In addition it has been argued that increased submerged macrophyte coverage leads to an increase in the number of predatory fish (Grimm & Backx, 1990) which eventually, via an increase in predation on cyprinids, is propagated to the phytoplankton level. However, support for the hypothesis of a higher proportion of piscivorous fish in macrophyte-rich lakes has only been found in some cases (Meijer *et al.*, 1994). Carpenter & Lodge (1986) alternatively argued that fish fry became abundant in macrophyte-rich lakes due to their use of macrophytes both as a refuge and when foraging (Hall & Werner, 1977; Werner *et al.*, 1983) and Canfield & Hoyer (1992) showed that the average size of planktivorous and benthivorous fish decreases with increasing plant coverage and PVI. A high abundance of small fish is generally synonymous with a high predation pressure on zooplankton in both the pelagic (e.g. Cryer, Peirson & Townsend, 1986; Persson *et al.*, 1992; Jeppesen *et al.*, unpublished data) and in the littoral zone (Kairesalo & Seppala, 1987; Whiteside, 1988). However, predation pressure may be somewhat attenuated because the submerged macrophytes concomitantly protect the zooplankton against predation by fish fry foraging in the vegetation (Winfield, 1986; Diehl, 1988). As yet few investigations have focused on the impact on fish–zooplankton interactions in lakes with a structural complexity such as that associated with the presence of macrophytes (Winfield, 1986; Diehl, 1988; Persson, 1993) and most of the studies reported were based on laboratory experiments or in small *in situ* enclosures, neither of which are optimal for simulation of fish behaviour.

Apart from affecting zooplankton and fish, the presence or absence of submerged macrophytes also has a major impact on the structure of the phytoplankton community. Thus the phytoplankton community in macrophyte beds is generally dominated by small and motile forms such as cryptophytes, while the abundance of algae with high sinking rates (e.g. diatoms and green algae) is generally low (Balls, Moss & Irvine, 1989; Van Donk *et al.*, 1990). Although this has been explained by the more quiescent environment within the plant beds favouring algae with low sinking rates (Losee & Wetzel, 1993), the same community structure has also been observed in macrophyte-free lakes with high zooplankton grazing pressure, for instance in biomanipulated lakes in which the planktivorous fish stock has been artificially reduced (e.g. Leah, Moss & Forrest, 1980; Reinartsen & Olsen, 1984; Van Donk *et al.*, 1990; Søndergaard *et al.*, 1990). The high contribution of motile forms to the phytoplankton biomass in macrophyte beds may therefore alternatively reflect reduced fish predation. So far it is unclear whether biological factors or physicochemical factors have the most important structuring effect on the phytoplankton community in macrophyte beds. To our knowledge no studies have elucidated how fish–macrophyte interactions via their impact on zooplankton are propagated to the phytoplankton level.

The objective of the present study was to determine the impact of changes in submerged macrophyte density on fish–zooplankton–phytoplankton interactions in a shallow lake. This was tested by large-scale (100 m^2) enclosure experiments over a 5-month period. Six combinations of macrophytes/fish fry density were studied in triplicates using eighteen enclosures established in the littoral zone of a shallow, eutrophic lake. We addressed the following questions:

- how do simultaneous variations in fish and macrophyte abundance affect zooplankton community structure and abundance?
- how do simultaneous variations in zooplankton and macrophyte abundance affect the phytoplankton community structure and abundance?

Materials and methods

Study area

The experiments were undertaken in the shallow eutrophic Lake Stigsholm situated in central Jutland, Denmark. The area of the lake is 21 ha and its maximum and mean depth is 1.2 and 0.8 m, respectively. Between 1988 and 1992 the average summer (May–October) total P ranged from 0.102 to 0.151 mg l^{-1}. The lake was completely dominated by macrophytes until the 1950s, but has since, for as yet unknown reasons, been alternately dominated by phytoplankton and macrophytes.

Experimental design

The experiment was conducted during a 5-month period from 14 May to 15 October, 1991. Eighteen 100-m^2 enclosures (5 × 20 m, ~50 m^3, 1 m in height) were established in the littoral region of the lake bed comprising a homogeneous sandy slope. The water depth in the enclosures ranged from approximately 0.3 m near the shore to 0.5–0.8 m nearest to the middle of the lake, with depth ranging from 0.4 to 0.6 m. The enclosures consisted of vertical polyethylene sheets secured to poles and kept in place in the lake sediment by a heavy iron chain (5 kg m^{-1}). The enclosed water was isolated from the lake water but open to the sediment. Dissolved KNO_3-N (38 g $week^{-1}$) was added to each enclosure so as to mimic the level of the measured external nitrogen loading to the lake in the previous year (unpublished results). Phosphorus was not added since there was high internal loading from the sediment. The enclosures were divided into three adjacent groups consisting of six enclosures each.

Macrophytes were excluded from six of the enclosures (two randomly selected from each of the three groups) by covering the sediment with a black polypropylene fibre fabric (Fibertex, Elephant Geotextiles) that excluded light, but allowed exchange across the water–sediment interface. The fabric, which was held in place using wire mesh and stones, was perforated in order to facilitate the escape of gas produced in the sediment and to ensure nutrient exchange between sediment and water. All but three enclosures (selected randomly from each of the three groups) were covered with bird netting to prevent the macrophytes being grazed by wildfowl [e.g. coot (*Fulica atra* L.) and mute swans *Cygnus olor* (Gmelin)]. The unprotected set of enclosures was intended to represent intermediate macrophyte density. It may be argued that the use of Fibertex and the waterfowl grazing activity affect the nutrient level, thereby rendering comparison with the results from the remaining enclosures difficult. However, no differences in average total P or total N were found either between enclosures with and without fibertex (ANOVA, $P > 0.6$ and $P > 0.25$, respectively) or between enclosures with and without protection from waterfowl grazing (ANOVA, $P > 0.6$ and $P > 0.5$, respectively).

The dominant macrophytes present were *Potamogeton pectinatus* L, *P. pusillus* L, and *Callitriche hermaphroditica* L. The percentage coverage and height of each macrophyte species in each enclosure was estimated four times during the experiment at twenty equidistant locations along the mid-line stretching from the shallow end to the deep end. Macrophyte density was expressed as per cent volume infested (PVI; Canfield *et al.*, 1984), in our study calculated as the product of percentage coverage and plant height divided by the water depth. During July and August, the average PVI in the eighteen enclosures ranged from 0 to 42%. Macrophyte biomass was measured on 4 September in one of the enclosures by sampling at all twenty sites using a reinforced PVC-tube (177 cm^2). The samples were subsequently sorted, dried (at 105 °C for 24 h) and weighed. PVI in the enclosure was 55%. Total macrophyte biomass was 53 g m^{-2}, of which the filamentous chlorophyte *Oedogonium* sp. accounted for 9 g m^{-2}.

The experiment was initiated by removing all fish from the enclosures by electrofishing and gill netting in May, and then restocking in June with three different densities (0, 30, and 530 individuals per enclosure) of 0+ and 1+ three-spined sticklebacks, (*Gasterosteus aculeatus* L.) and roach (*Rutilus rutilus* L.), the dominant planktivorous species in the lake in the study year (S. Berg, unpublished data). Development of the fish populations was monitored by frequent trapping with Breder fry traps (Breder, 1960). The number of 1+ sticklebacks and both 0+ and 1+ roach was found to decline during the experiment, whereas the number of 0+ sticklebacks increased, this being explicable by differences in survival and reproduction. Trapping was also undertaken in the fish-free enclosures so as to ensure their fish-free status. Fish density was expressed as the mean of time-weighted catch per unit effort (CPUE). During a 2-week period in late September the weight and length of the fish caught in each enclosure were recorded. The fish were not returned to the enclosures so the absolute size of the populations could be estimated on the basis of declining CPUE according to the method of Higgins (1985). CPUE was converted into absolute population density using a linear regression of log-transformed data on the estimated density and time-weighted average CPUE: density (indiv. m^{-2}) = $0.23\,CPUE^{0.96}$, $R^2 = 0.83$. However, only 0+ sticklebacks were numerous enough to be estimated by this method, their number varying between 0.06 and 13 ind. m^{-2} (0.04–4 g m^{-2}). We assumed that trap efficiency was similar for roach. At a final trapping no significant correlation between PVI and the ratio of estimated fish density to CPUE (Spearman $R_S = -0.15$ $P < 0.6$) was found. It is therefore unlikely that trap efficiency was influenced by macrophyte density and the enclosure catches are accordingly directly comparable.

Sampling and analyses

All water samples were collected with a core sampler from a small rubber boat. Each sample comprised an entire water column collected in open water between macrophyte beds. Samples were collected fortnightly from 9 July to 3 September, during which period PVI was relatively constant.

Samples for zooplankton enumeration were collected at five equidistant locations along the mid-line running from the shallow to the deep end of each enclosure. The composite sample (5–10 l) from each enclosure was filtered through a 20-µm net and the specimens fixed with acid Lugol. Zooplankton (> 140 µm) were counted using a stereo microscope. Very dense samples were subsampled, but at least 100 individuals of the two or three dominant species were counted. Cyclopoid copepods were identified as nauplii and older stages; cladocerans were determined to genus or species level. Twenty-five individuals of each cladoceran species/genus were measured in each sample. Individual cladoceran biomass was determined using the length/weight relationships of Dumont, Van de Velse & Dumont (1975) and Culver *et al.* (1985).

Water samples were collected for phytoplankton and chemical analysis in the deepest part of each enclosure. Phytoplankton were counted until SE on the biomass was less than ± 20% using an inverted microscope. Phytoplankton was determined to genus or species level, and phytoplankton biovolume ($mm^3\,l^{-1}$) was obtained by fitting each genus/species to simple geometric figures (Olrik, 1991). The percentage contri-bution of various genera/species to the total biovolume was calculated (RPB%). Phytoplankton biovolume was converted to dry weight (DW) by multiplying by 0.256 (Behrendt, 1990).

A potential grazing pressure index (PGP) was calculated by assuming that planktonic cladoceran (i.e. *Bosmina* and *Daphnia*, see below) daily ration is equivalent to their biomass (Hansen *et al.*, 1992; Jeppesen *et al.*, unpublished data) and that they only feed on phytoplankton. Thus PGP is expressed as the ratio between the biomass of *Daphnia* + *Bosmina* to the phytoplankton biomass (%). PGP is a crude estimate as the filtration rate may vary with food concentrations (Lampert & Muck, 1985). Despite these reservations, we believe that the PGP provides valuable information concerning the potential capacity of cladocerans to control phytoplankton biomass.

Orthophosphate (PO_4^{3-}-P) was analysed by the ascorbic acid/molybdenum blue method [modified from Murphy & Riley (1972)]. Total phosphorus (tot-P) was determined as phosphate after persulphate digestion according to Koroleff (1970). Ammonium (NH_4^+-N) was determined using the phenol hypochlorite method modified from Solórzano (1969), nitrate + nitrite according to the method of Dahl (1974), and total nitrogen (tot-N) after potassium persulphate digestion according to the method of Solórzano & Sharp (1980). Chlorophyll *a* was determined spectrophotometrically following extraction with ethanol according to the method of Holm-Hansen & Riemann (1978). pH was determined potentiometrically.

Statistical analysis

A stepwise regression approach (SAS Institute Inc., 1989) was used, including date and interaction terms as possible predictor variables. Date-related variables were included as 'dummy' variables. Criteria for entry and acceptance were $P < 0.15$ and $P < 0.05$, respectively.

To improve normality, the data [except the relative phytoplankton volume (RPB%)], were log-transformed [$\ln(x+1)$]. RPB% was transformed to logits [ln (RPB%/(100–RPB%)], values less than 1% or greater than 99% being set to 1 and 99%, respectively.

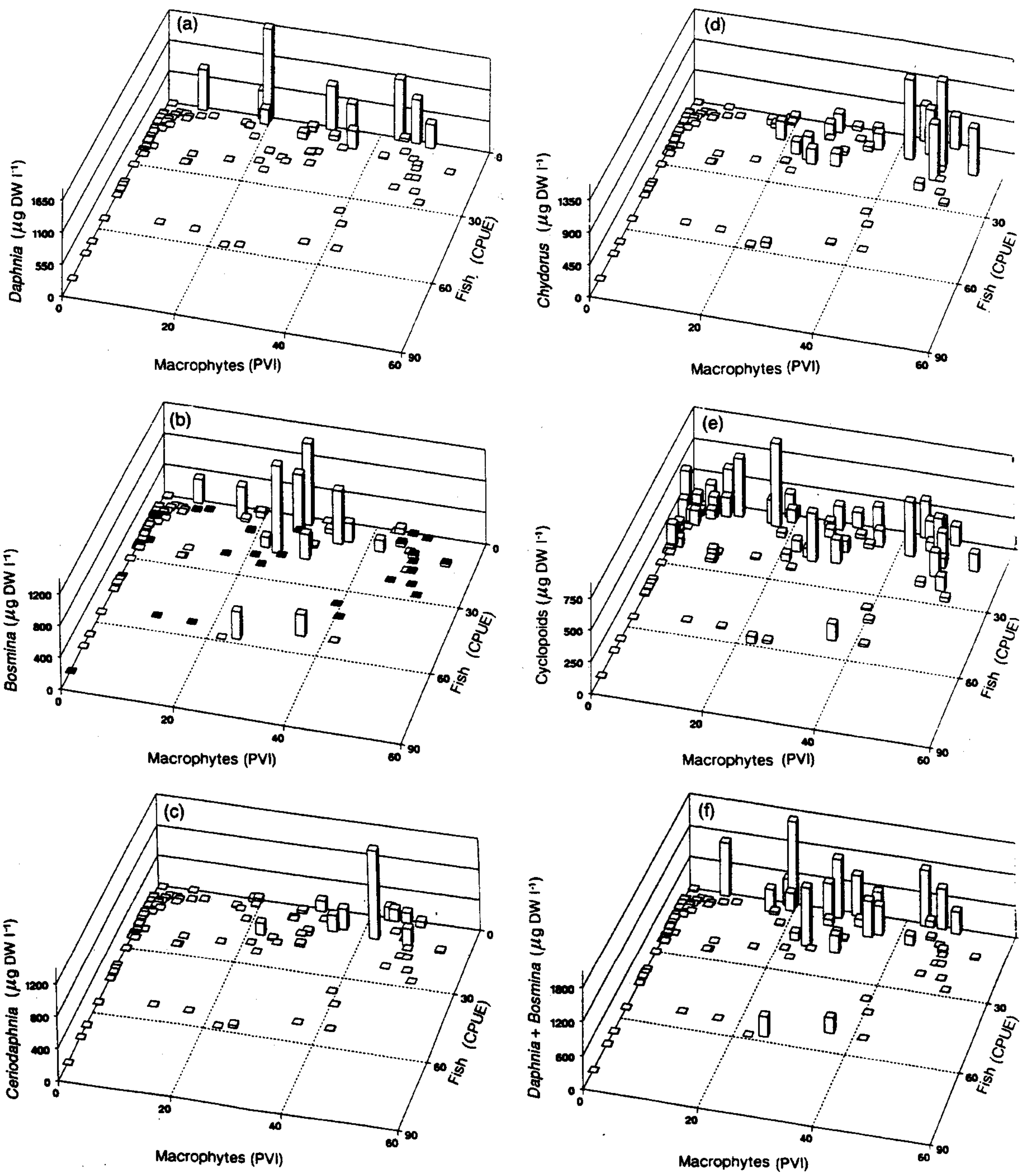


Fig. 1 Biomass of different zooplankton taxa (a–e) and planktonic cladocerans (*Daphnia* and *Bosmina*) (f) in relation to macrophyte per cent volume infested (PVI) and fish abundance (CPUE) at each sampling date. In (b) n represents samples from 20 August and 3 September.

Table 1 Stepwise multiple regression showing the relationship between the log-transformed biomass of various groups of crustaceans (mg DW l^{-1}) versus log-transformed values of fish trap catches (CPUE), per cent volume infested by submerged macrophytes (PVI) and date. *, **, *** represent the 0.05, 0.01, 0.001% significance levels. Fish × date were not significant ($P > 0.05$) for any of the groups. Date 1 = 9 July, date 2 = 23 July, date 3 = 6 August, date 4 = 20 Aug., date 5 = 3 Sep., NS = not significant

	Daphria		*Bosmina*		*Daphnia* +*Bosmina*		*Creiodaphnia*		*Chydorus*		*Cyclopoids*	
Intercept	0.17	$F = 0.9$, NS	0.56	$F = 4^{*}$	0.73	$F = 9^{*}$	−0.16	$F = 0.6$,NS	−2.02	$F = 6^{*}$	5.43	$F = 377^{*}$
Date		NS		NS		NS		NS		NS		NS
PVI	1.59	$F = 130^{***}$		NS		NS		NS	2.01	$F = 54^{***}$		NS
PVI × date		$F = 4.3^{**}$		$F = 15^{***}$		$F = 39^{***}$		$F = 39^{***}$		NS		NS
Date 1	0.37		1.34		2.2		1.26					
Date 2	0.36		0.98		2.09		1.63					
Date 3	0		0.38		1.45		1.38					
Date 4	0		0.16		1.31		1.02					
Date 5			0.11		1.27		1					
Fish		NS		NS		NS		NS	0.58	$F = 5^{*}$	−0.94	$F = 74^{***}$
PVI × fish	−0.5	$F = 199^{***}$	NS	−0.35		$F = 56^{***}$	−0.24	$F = 40^{***}$	−0.32	$F = 12^{**}$	0.14	$F = 30^{***}$
Model R^2	0.79		0.47		0.70		0.49		0.67		0.48	
df83	84		83		83		86		87			

	Biomass of cladocerans (µg ind.$^{-1}$)		Biomass ratio Clad./cyclopoids		PGP (% day^{-1})	
Intercept	0.90	$F = 40^{***}$	−0.80	$F = 3$, NS	−2.95	$F = 486^{***}$
PVI × date		NS		$F = 9^{***}$		$F = 50^{**}$
Date 1			0.98		1.42	
Date 2			0.96		1.35	
Date 3			0.69		0.97	
Date 4			0.68		0.85	
Date 5			0.73		0.83	
Fish	−0.30	$F = 33^{***}$	0.33	$F = 5^{*}$		NS
PVI × fish		NS	−0.18	$F = 13^{***}$	−0.22	$F = 63^{***}$
Model R^2	0.28		0.50		0.75	
df84		78		83		

Table 2 Stepwise multiple regression showing the relationship between the log-transformed values of average cladoceran individual biomass, cladocerans/cyclopoids biomass ratio and PGP (potential grazing pressure), versus log-transformed values of fish trap catches (CPUE), per cent volume infested by submerged macrophytes (PVI) and date. Fish × date were not significant ($P > 0.05$) for any of the groups. See also Table 1

Results

The biomass of all crustacean zooplankton taxa sampled in the open water tended, although not always significantly, to be negatively related to fish density (CPUE) and positively related to macrophyte density (PVI) (Fig.1). Cladocerans showed a much stronger dependence upon macrophyte vegetation than the cyclopoids and they almost disappeared at PVI lower than 5–10% (Fig. 1).

Daphnia seemed to demand both low fish density and at least some macrophyte vegetation. Thus, even at low fish density (0.2 < CPUE < 1), daphnid density was below 1 l^{-1} in the plant-free enclosures (Fig. 1a). At higher macrophyte densities daphnid biomass was primarily affected by fish density and high biomass of *Daphnia* was only found when CPUE was below 10. These observations were supported by the regression model (Table 1) and the isocline plot (Fig. 2) in which the strongly curved isocline reflected the impact of PVI × fish.

Bosmina showed no significant relationship with fish density but was significantly related to PVI, this effect in turn being strongly dependent upon date (Table 1): in early summer *Bosmina* reached a high biomass in enclosures with vegetation, whereas they almost disappeared in August and September independently of the macrophyte cover (Fig. 1b).

Ceriodaphnia showed a similar response as *Daphnia*, but was less affected by fish density. Macrophyte effect was significantly modified by date, reaching a maximum on 23 July (date 2; Table 1). *Chydorus sphaericus* was primarily affected by macrophyte density, but when

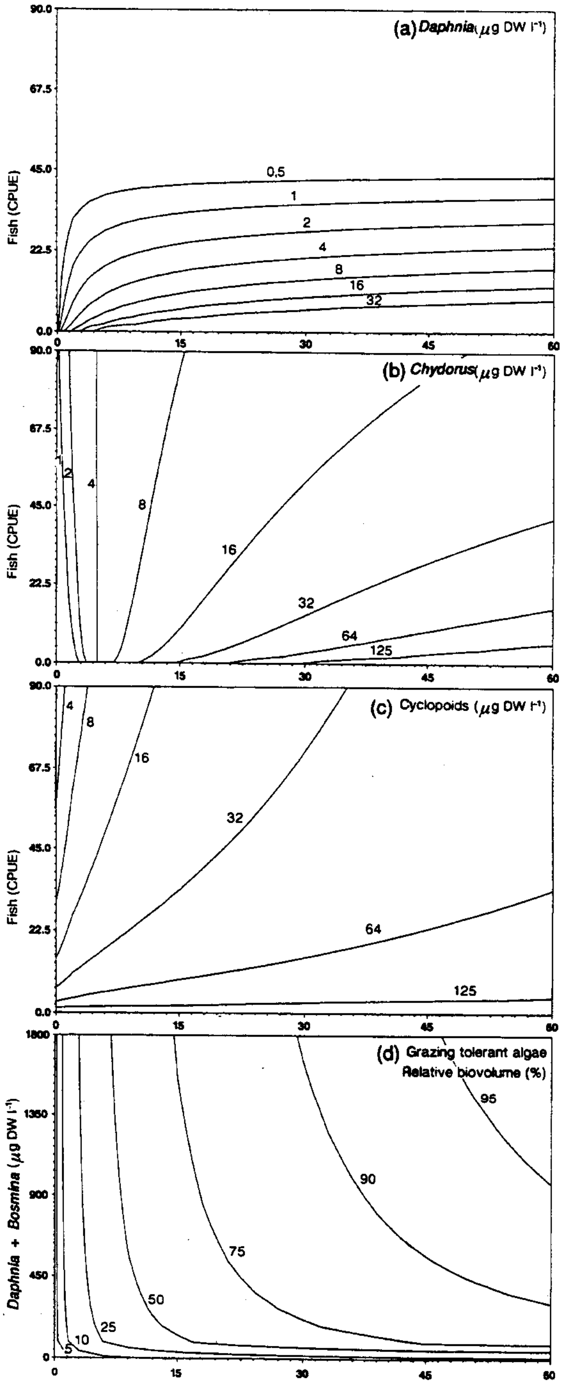


Fig. 2 Isocline plots showing the predicted biomass of *Daphnia* (a), chydorids (b) and cyclopoid copepods (c), and the predicted contribution (%) of grazing-tolerant phytoplankton (*Ankyra judayi*, *Volvocales*, Cryptophytes) to the total biovolume (d), per cent volume infested (PVI) and fish abundance (CPUE).

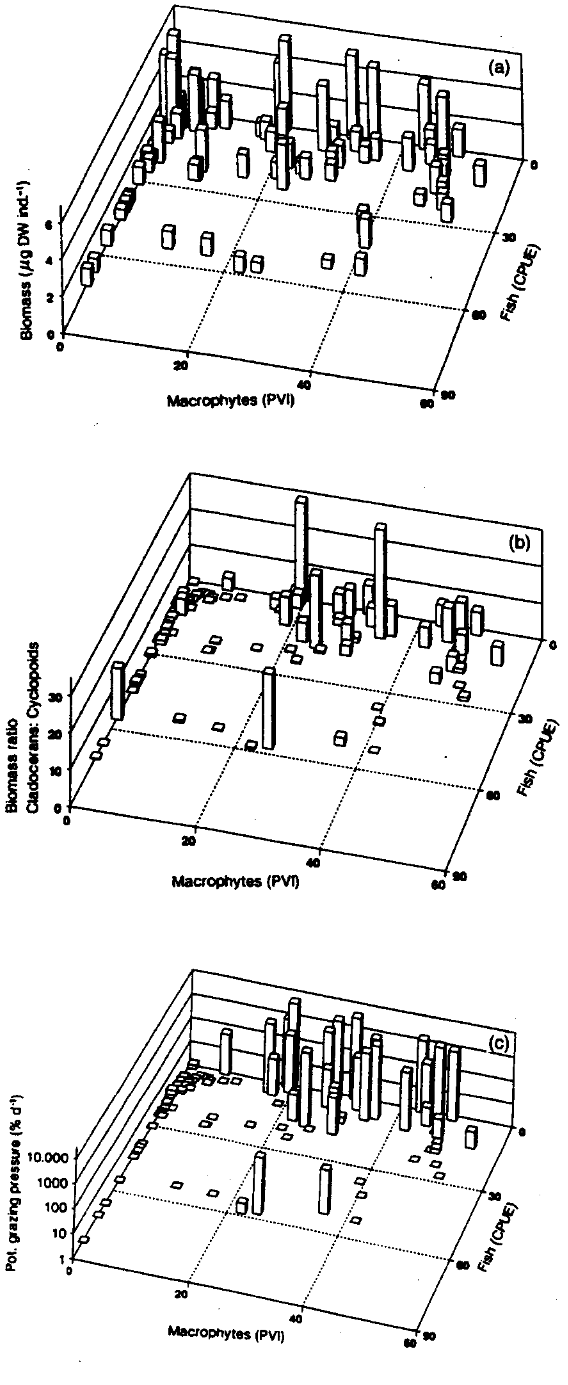


Fig. 3 Average individual biomass of cladocerans (a), the biomass ratio of cladocerans to cyclopoid copepods (b), potential grazing pressure [(*Daphnia* and *Bosmina*):phytoplankton biomass ratio] (c) in relation to changes in per cent volume infested (PVI) and fish abundance (CPUE).

Table 3 Stepwise multiple regression showing the relationship between the biovolume of total phytoplankton ($mm^3\ l^{-1}$) and the grazing tolerant algae defined as the biovolume of *Volvocales*, cryptophytes and *Ankyra* versus the biomass of *Bosmina* + *Daphnia* (Zoo, mg DW l^{-1}), per cent volume infested by submerged macrophytes (PVI) and date. Date, PVI × date, zoo and zoo × date were not significant ($P > 0.05$). See also Table 1

	Total phytoplankton ($mm^3\ l^{-1}$)		Grazing tolerant algae ($mm^3\ l^{-1}$)	
Intercept	2.62	$F = 367^{***}$	-3.35	$F = 62^{**}$
PVI	–0.16	$F = 5^{*}$	0.47	$F = 8^{*}$
PVI × zoo	–0.07	$F = 34^{***}$	0.15	$F = 27^{***}$
Model R^2	0.62		0.52	
df	87		87	

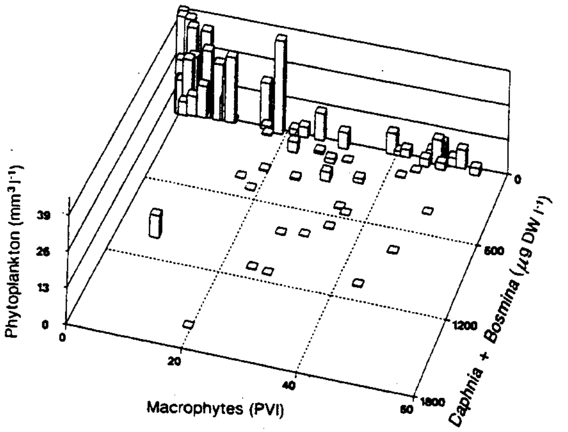


Fig. 4 Phytoplankton biovolume in relation to macrophyte per cent volume infested (PVI) and biomass of planktonic cladocerans (*Daphnia* and *Bosmina*).

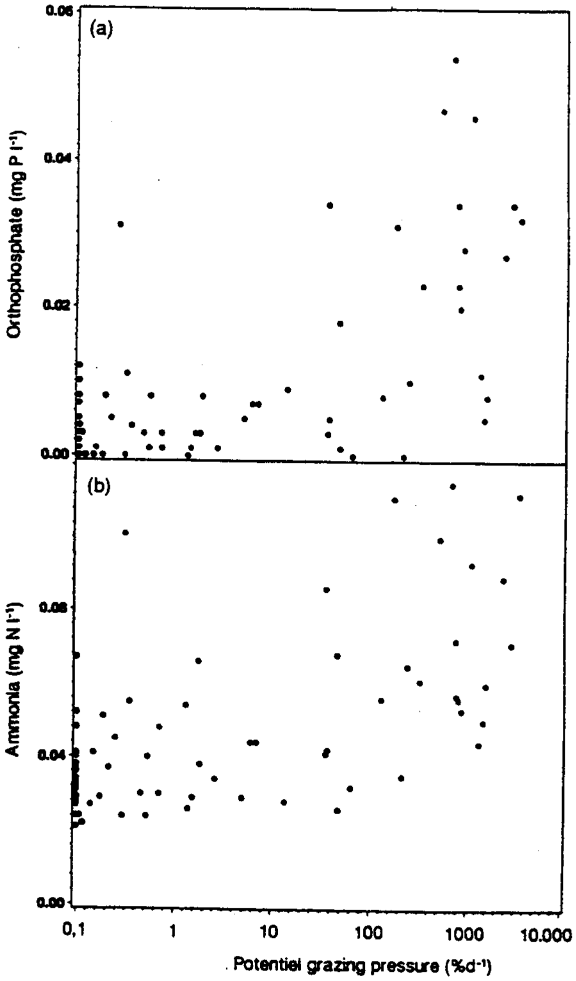


Fig. 5 Concentration of orthophosphate (a) and ammonium (b) in relation to potential grazing pressure (planktonic cladocerans: phytoplankton biomass ratio).

PVI was relatively high, fish density also became important. The cyclopoid copepod biomass in macrophyte-free enclosures was high at low fish density (Fig. 1e) and negatively related to fish density (Table 1). However, the regression model indicates that macrophyte vegetation had a positive effect especially at high fish densities (Table 1).

The average biomass of cladocerans was negatively related to the density of fish, but unrelated to PVI, while the biomass ratio of cladocerans to cyclopoid copepods was positively related to both fish and PVI, albeit negatively to PVI × fish (Table 2, Fig. 3a,b).

The best relationship between total phytoplankton biovolume and PVI, zooplankton biomass, date and interactions was obtained by including only *Daphnia* and *Bosmina* into the zooplankton biomass ($R^2 = 0.62$), this probably being attributable to the facts that advanced stages of cyclopoid copepods are often carnivorous (Brandl & Fernando, 1975) and that *Chydorus sphaericus* and *Ceriodaphnia* spp. select for small particles including bacteria (Geller & Müller, 1981). If all zooplankton were included R^2 would decline to 0.54. The regression model for the sum of the biomass of *Daphnia* and *Bosmina*, in the following called the planktonic cladocerans, showed a significant date-dependent positive response to macrophyte density and a significant negative response to PVI × fish (Table 1).

Phytoplankton biovolume showed a significant negative response to PVI and to PVI × planktonic cladocerans (Table 3). The results indicate a sudden decrease in phytoplankton biovolume as PVI exceeded 15–20% even with low densities of planktonic cladocerans (Fig. 4). Because cladocerans were generally absent when PVI was less than 15%, the relationship between cladocerans and phytoplankton in the absence of macrophytes could not be assessed separately.

The potential grazing pressure (PGP) varied considerably, ranging from 0% day^{-1} to the extremely high level of 3600% day^{-1} and generally being highest (above 100% day^{-1}) when PVI exceeded 15–20% and the fish CPUE was below 10 (Fig. 3c). High PGP was not restricted to communities dominated by *Daphnia*. Communities dominated by *Bosmina* showed PGP well above 100% day^{-1} and phytoplankton biovolume less than 1 mm^3 l^{-1} when the fish density was relatively low (Figs 1 and 3). PGP showed a significant, albeit date dependent, positive relation to PVI, and a negative relationship to PVI × fish (Table 2).

The mean chlorophyll *a* level in the enclosures ranged from 3.8 to 167 $\mu g\ l^{-1}$, the average being 51 $\mu g\ l^{-1}$ (SD = 43 $\mu g\ l^{-1}$). Mean total phosphorus concomitantly ranged from 75 to 235 $\mu g\ l^{-1}$, with the average being 132 $\mu g\ l^{-1}$ (SD = $\mu g\ l^{-1}$) and total N between 1.1 and 3.4 mg N l^{-1} (mean = 1.8 mg N l^{-1}, SD = 0.7). Mean nitrate + nitrite was low, ranging from 2 to 32 $\mu g\ l^{-1}$, with the average being 9 $\mu g\ l^{-1}$(SD = 7.4 $\mu g\ l^{-1}$). The concentration of orthophosphate and ammonium was highly positively related to PGP (Spearman *Rs* were 0.50, $P < 0.0001$ and 0.61, $P < 0.0001$, respectively) (Fig. 5), thus indicating that the shift to low phytoplankton volume at high PGP reflected enhanced grazing rather than enhanced nutrient control of algal growth.

All zooplankton data hitherto described were collected in open water, also in the enclosures with macrophytes. To evaluate whether the data were representative, mid-period sampling was carried out in two macrophyte-rich enclosures, one with (CPUE = 10.2, PVI = 48%) and one almost without fish (CPUE = 0.06, PVI = 47%), both by night and by day (Table 4). As only one pooled sample from each of the two enclosures was collected the data cannot be analysed statistically, but they indicate that open water genera such as *Daphnia* and *Bosmina* were found in higher densities outside macrophyte beds in the daytime as well as during night, while the density of plant-associated groups and genera such as *Chydorids, Pleuroxus* and *Eurycercus* were markedly higher in the vegetation during both day and night. Although there is a tendency towards higher density of several groups during night their relative importance remained the same: *Daphnia* occurred only sporadically in the enclosure with fish, also at night, while they were abundant in the enclosure almost without fish, the opposite being true for *Bosmina*. The daytime sample accordingly seems to be representative of open water conditions, although the number, and thereby also PGP, may be somewhat underestimated.

The composition of the phytoplankton community changed markedly with the density of planktonic cladocerans and macrophytes (Fig. 6). The cyanophytes (*Nostocophyceae*) were represented mainly by *Planktothrix agardii* (Gom.) Angan. et Kom., *Limnothrix planctonica* (Wolosz) Meffert, *Microcystis aeruginosa* (Kütz.) Kütz., and a solitary *Aphanothece* sp. While the relative contribution of cyanophytes to the total phytoplankton biovolume increased notably with increasing macrophyte density, their contribution was small when planktonic cladocerans were abundant, an exception being four samples having high proportions of *Aphanothece* sp. (Fig. 6a). Thus the multiple regression revealed a significant positive relationship to PVI, and a negative one to PVI × zoo (Table 5).

Species of the order *Chlorococcales* mainly comprised *Scenedesmus* spp., *Kirchneriella* spp., an unidentified picoalgae species (2 × 4 μm), and *Ankyra judayi* (G.M.S.M.) Fott. The latter is shown together with the *Volvocales* in Fig. 6(d) because its occurrence was distinctly different to that of other *Chlorococcales*; in fact, it was the only alga in which absolute biovolume increased with increasing planktonic cladoceran biomass. Like most cyanophytes, *Chlorococcales* only constituted a major proportion of the phytoplankton volume in the absence of cladocerans (Fig. 6b). The multiple regression revealed a negative relationship to both PVI and PVI × zoo (Table 5). This relationship is not particularly conspicuous in Fig. 6b because of several overlapping samples with high relative biovolume at low PVI.

The relative contribution of dinoflagellates to the biovolume (mainly *Gymnodinium* sp. and *Peridinium* spp.) was not significantly related to PVI, but was negatively related to planktonic cladoceran biomass and influenced by the sampling date (Table 5). The class was consistently less represented in July and August (Fig. 6c).

Like *Ankyra judayi*, the relative biovolume of the *Volvocales* (primarily *Chlamydomonas* spp.) was highest at high planktonic cladoceran biomass, but was not significantly related to PVI (Table 5 and Fig. 6d). In contrast, the relative importance of cryptophytes (pri-

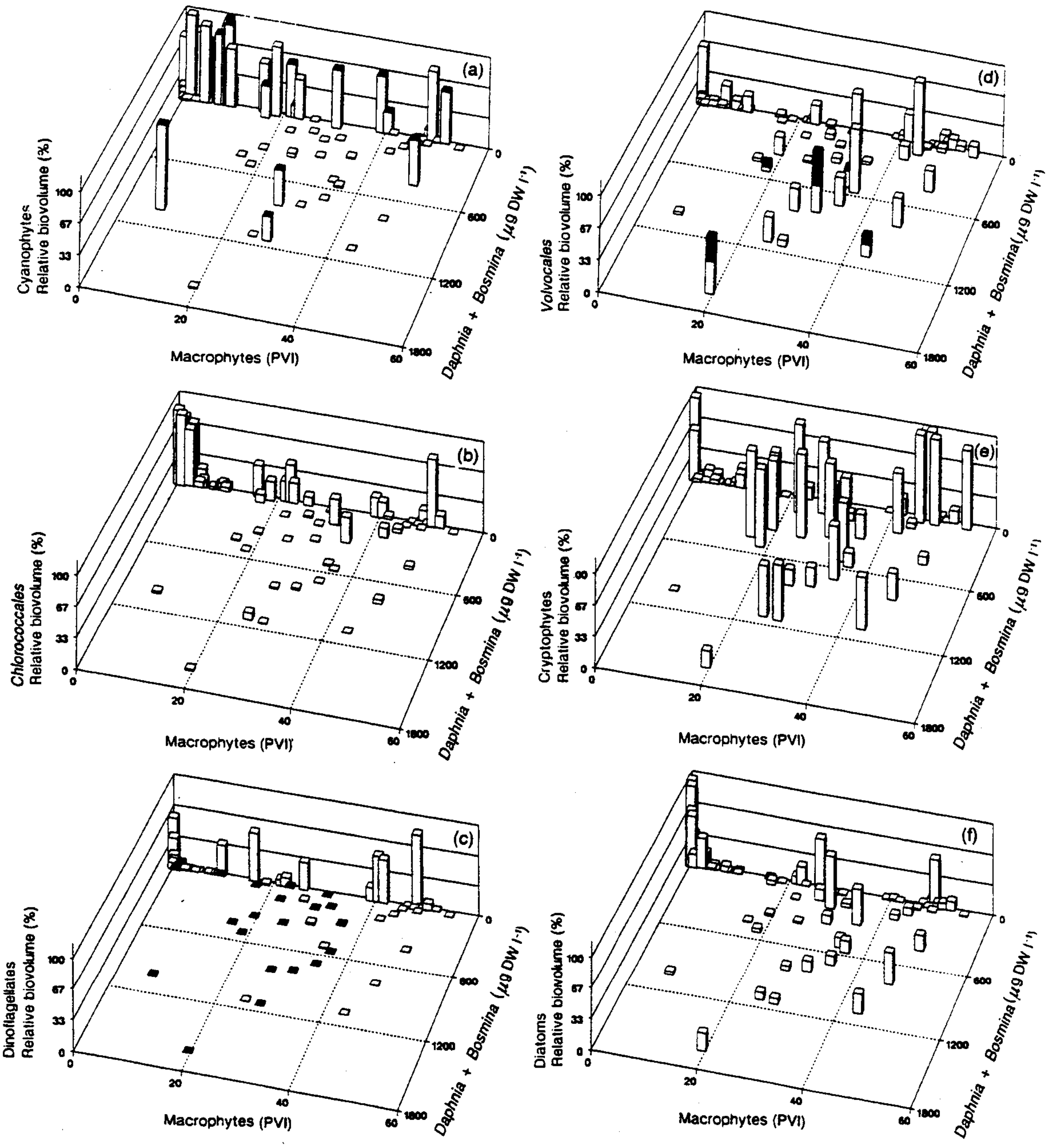


Fig. 6 Relative biomass of different phytoplankton taxa (a–f) in relation to macrophyte percent volume infested (PVI) and biomass of planktonic cladocerans (*Daphnia* and *Bosmina*) at each sampling date. In (a) ▪ represents samples dominated by *Aphanothece*, in (c) samples from July, and in (d) the contribution of *Ankyra judayi*.

marily *Cryptomonas reflexa* Skuja) and grazing tolerant algae defined as the sum of *Volvocales*, cryptophytes and *Ankyra* increased with both PVI and PVI × zoo (Table 3, Table 5 and Fig. 6e). The contribution of diatoms (mainly *Nitzschia* sp.) to the biovolume was highest in the macrophyte-free enclosures and positively related to the planktonic cladoceran biomass (Table 5 and Fig. 6f).

Table 4 The number (no. l^{-1}) of different crustaceans in samples taken inside the plant beds and in the open water outside the beds during day and night in an enclosure almost without fish (CPUE = 0.06) and in one with fish (CPUE = 10.2). The plant volume infested by submerged macrophytes (PVI) was 47 and 48%, respectively.

	Without fish				With fish			
	Daytime		Night-time		Daytime		Night-time	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
Daphnia	34	206	132	346	0	0	0	2
Bosmina	0	0	0	2	116	369	134	266
Ceriodaphnia	22	10	45	25	313	29	245	81
Chydorids	525	32	483	70	2180	185	3259	453
Pleuroxus	116	4	26	1	27	1	22	9
Eurycercus	22	0	13	0	14	1	86	6
Simocephalus	0	0	0	0	14	5	46	0
Copepodites + adult copepods	120	3	77	11	170	15	190	21
Nauplii	151	136	109	112	123	139	117	129

Discussion

Changes in PVI and fish density were accompanied by major changes in the zooplankton community. In accordance with the size-efficiency hypothesis (Brooks & Dodson, 1965), the structure of the crustacean zooplankton community changed with increasing fish density from one dominated by daphnids to one dominated by small cladocerans and, at the highest fish densities, to one most often dominated by cyclopoid copepods (Figs 1 and 3). The threshold level at which these shifts occurred depended on PVI. In the macrophyte-free enclosures cyclopoid copepods dominated even when fish density was low ($0.2 < \text{CPUE} < 1$, roughly 0.04–0.2 m^{-2}). Because the phytoplankton in these enclosures primarily consisted of edible algae with a relatively high biomass, the absence of cladocerans must be attributable to predation by fish, despite the relatively low fish density, probably reflecting the fact that the escape capability of zooplankton is low in such unstructured and shallow environments. Contradicting this view, no significant positive impact of PVI on the size of the mean biomass of cladocerans was observed, which may reflect uncertainty of calculation as only few cladoceran individuals were found in the zooplankton samples at low PVI.

With increasing PVI cladocerans gradually became more important, particularly at levels greater than 15–20% PVI. Moreover, the results suggest that sensitivity to fish predation declined with increasing PVI; thus above a PVI of 15–20% *Daphnia* was still abundant at fish CPUE of 6 (approx. 1.2 fish m^{-2}) (Fig. 1a). The lower impact of fish in the presence of macrophytes is in accordance with the findings of Crowder & Cooper (1979) who further argued that prey capture rates decline uniformly with increasing structural complexity. Similar results were obtained for roach fed on *Daphnia* in laboratory experiments (Winfield, 1986) and for largemouth bass fed on bluegill (Savino & Stein, 1982). In contrast, experimental studies with the littoral species rudd revealed a unimodal relationship between stem density and fish capture rate, the latter being highest at inter-mediate densities, while with perch the prey capture rate tended to increase at the highest stem densities (300–600 m^{-2}) (Winfield, 1986). Our results suggest that with increasing PVI there is a stepwise decrease in susceptibility to predation by a fry community comprised of three-spined sticklebacks and roach.

A key question is whether the protection against fish predation allows zooplankton biomass to increase to a level high enough to control phytoplankton growth, thereby explaining the clearwater conditions often found to be associated with macrophyte beds. The potential grazing pressure by *Daphnia* and *Bosmina* (PGP) was generally higher than 100% when PVI was greater than 15–20% as long as the fish density was below 10 CPUE (roughly 2 fish m^{-2}). These values are so high in comparison with maximum phytoplankton growth rates (Reynolds, 1984a) that it seems reasonable to conclude that grazers were able to control pelagic phytoplankton

Table 5 Stepwise multiple regression showing the relationship between the relative contribution of various groups of phytoplankton (expressed as% of total volume, $mm^3 l^{-1}$) versus the biomass of *Bosmina* and *Daphnia* (Zoo, mg DW l^{-1}), per cent volume infested by submerged macrophytes (PVI) and date. Coefficients of Date 1 to Date 4 were –1.48, –1.06, 0.9, 0.78, respectively, in (¹), 0.14, –0.18, –0.60, –0.66 in (²), and 0.41, 0.34, 0,01, –0.08 in (³). NS = not significant, $P > 0.05$. See also Table 1

	A. judayi		Cyanophytes		*Chlorococcales*		*Volvocales*		Chryptophytes		Dinoflagellates		Diatoms	
Intercept	–4.72	$F = 2811^{***}$	–2.89	$F = 48^{***}$	–0.93	$F = 12^{***}$	–3.48	$F = 278^{***}$	–3.99	$F = 136^{***}$	–2.83	$F = 52^{***}$	–1.87	$F = 36^{***}$
Date		NS		NS		NS				NS		$F = 5^{***1)}$		NS
PVI		NS	0.95	$F = 14^{***}$	–0.35	$F = 7^{*}$		NS	0.43	$F = 6^{*}$		NS	–0.54	$F = 17^{***}$
PVI*Date		NS		$F = 3^{*2)}$		NS		NS		NS		NS		NS
Zoo.	0.11	$F = 17^{***}$		NS		NS	–0.35	$F = 4^{*}$		NS	–0.45	$F = 6^{*}$	0.2	$F = 6^{*}$
Zoo*Date		NS		NS		NS		NS		NS		$F = 3^{*3)}$		NS
PVI*Zoo		NS	–0.15	$F = 13^{*}$	–0.08	$F = 13^{***}$	0.17	$F = 14^{***}$	0.13	$F = 17^{***}$		NS		NS
Model R^2	0.16		0.22		0.39		0.30		0.42		0.40		0.16	
df	88		83		87		87		87		80		87	

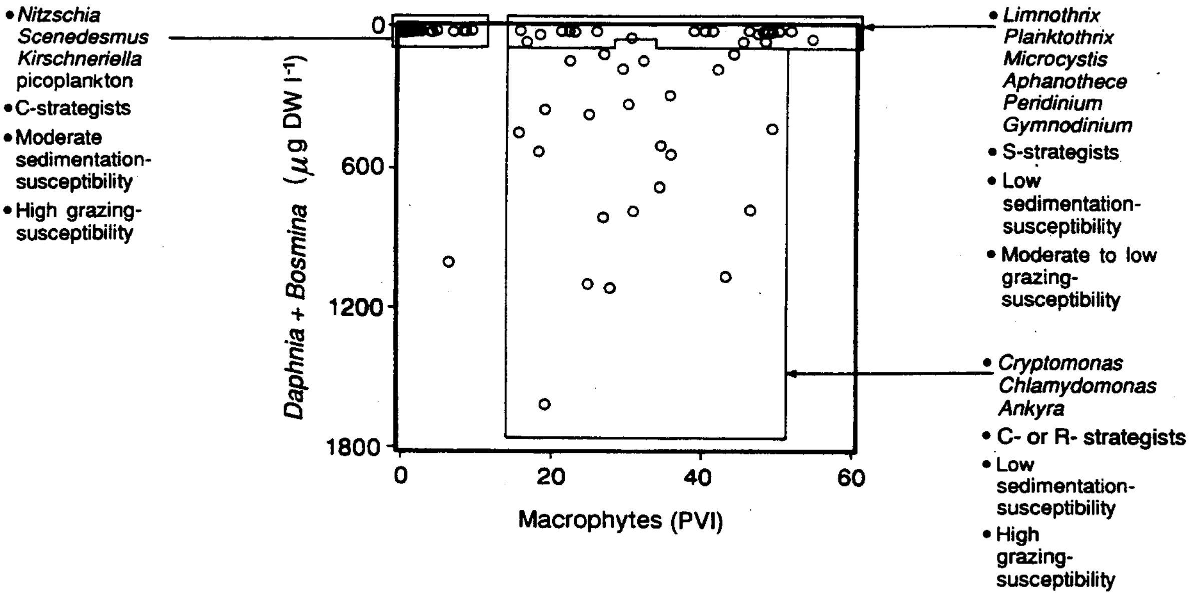


Fig. 7 General scheme of the variation in the phytoplankton community along with changes in macrophyte per cent volume infested (PVI) and biomass of planktonic cladocerans (*Daphnia* and *Bosmina*).

within these macrophyte beds. Further evidence of grazer control is that high PGP and low phytoplankton volume coincided with high orthophosphate and ammonia concentrations (Fig. 5), thus indicating that the low phytoplankton volume was not attributable to nutrient limitation. A PGP ranging from several 100 to 3600% day^{-1} will in practice not be realizable without it leading to elimination of all phytoplankton and subsequent starvation among the zooplankton. It is therefore likely that the zooplankton use alternative food sources such as bacterioplankton [e.g. *Daphnia, Ceriodaphnia, Chydorus* are efficient bacterial feeders (Geller & Müller, 1981; Pace, Porter & Feig, 1983; Hart & Jarvis, 1993)] or they graze the biofilm on plant surfaces and the sediment. Nevertheless, the high PGP values suggest that the potential capacity to control phytoplankton is high. In contrast, when PVI was low (< 15–20%) at low fish densities or when PVI was larger than 15–20% and the fish density above approximately 20 CPUE, PGP tended to be so low (0.5–1%) that it is unlikely that planktonic cladocerans were able to control phytoplankton growth.

The structural changes in the phytoplankton community were closely associated with the changes in macrophyte and zooplankton density (Fig. 7). When *Daphnia* and *Bosmina* were abundant, the phytoplankton community was dominated by fast-growing small flagellates. In the absence of these planktonic cladocerans, but in the presence of macrophytes, cyanophytes and dinoflagellates were dominant, while in the absence of both planktonic cladocerans and macrophytes the community was dominated by fast-growing diatoms and chlorophytes. This is in general agreement with the life-history strategies described by Reynolds (1987). Thus in the turbulent environment of the macrophyte-free enclosures fast-growing algae moderately susceptible to loss by sedimentation were dominant. In contrast, slow-growing algae (i.e. cyanobacteria) were dominant in the more quiescent water among plants, where the risk of settling is supposed to be high (Losee & Wetzel, 1993) and nutrient availability often is relatively low (Van Donk *et al.*, 1990; Sand-Jensen & Borum, 1991). However, with respect to grazing susceptibility the pattern observed contradicts Reynold's classification. Thus cyanophytes with low susceptibility were present at low grazing pressure, while the grazer dominated community consisted of algae with high grazing susceptibility. A similar pattern has been observed in experiments involving a drastic reduction or complete removal of planktivorous fish. As in the present study such manipulations have resulted in a shift from cyano-phyte dominance to *Cryptomonas, Ankyra* and pico-plankton dominance (e.g. Van Donk *et al.*, 1990; Jeppesen *et al.*, 1990; Sanni & Wærvågen, 1990). In contrast, less intensive fish manipulations often showed no or only minor effects on cyanobacterial dominance and in several cases it increased (Benndorf *et al.*, 1988; Riemann *et al.*, 1990). It thus seems reasonable to distinguish between resistance and tolerance to grazing rather than using the classification 'grazing susceptibility', the implication being that grazing-resistant algae (e.g. *Micro-cystis*) are only favoured until grazing pressure increases to a certain limit whereafter the grazing-tolerant algae (e.g. *Cryptomonas*) become dominant.

The generally high PGP and the low algal biomass at high inorganic nutrient concentrations found in the present study, together with the qualitative changes in the phytoplankton community, suggest that grazer control by planktonic cladocerans plays an important role in macrophyte beds at low as well as moderately high fish densities. However, because the phytoplankton volume declined with increasing PVI even when planktonic cladocerans were absent, other factors must also be involved in the control of phytoplankton. Plant-associated filter feeders, e.g. *Simocephalus*, may be of significance. It was in fact observed that plant-associated zooplankton were much more abundant in macrophyte beds than in open water (Table 4). Significant grazing by plant-associated zooplankton may therefore be possible, as previously proposed by Irvine, Moss & Balls (1989). Furthermore, we cannot totally exclude the possibility that competition for nutrients occurred between macrophytes and phytoplankton (low orthophosphate and inorganic nitrogen at high algal biomass, Fig. 6) or allelopathic substances released from the macrophytes have been another contributory factor.

It was demonstrated that the biomass of zooplankton in the open water in between the macrophyte beds and consequently the resultant grazing pressure on phytoplankton was high during daytime when the PVI exceeded approximately 15–20% and fish CPUE was below 10 (approx. 2 fish m^{-2}). At high fish densities the sheltering effect of macrophytes was, however, low. If these results are of general validity, small improvements in the growth of submerged macrophyte might have a substantial and self-perpetuating positive impact on the grazer community and hence lake water transparency, provided that the planktivorous fish density is not high. The self-perpetuating effect is attributable to the fact that zooplankton hiding in the macrophytes during the day may graze phytoplankton in the open water during the night (Timms & Moss, 1984), thereby improving light and hence growth conditions for the submerged macrophytes. The major effect seen with even a relatively low PVI further supports the concept (Moss, 1990, Jeppesen *et al.*, 1991) of using macrophyte refuges (protected against bird grazing) as a lake restoration tool, in shallow lakes following a reduction in nutrient loading to levels at which the submerged macrophytes are likely to appear (0.08–0.15 mg P l^{-1}, Jeppesen *et al.*, 1990, 1991) and the density of planktivorous fish tends to be low (Jeppesen *et al.*, unpublished data). In more nutrient-rich macrophyte-dominated lakes the density of planktivorous fish is often high (Meijer *et al.*, 1994) and based on the results of the present study the function of macrophytes as zooplankton refuge is accordingly assumed to be of minor importance. The experimental design used in our study allowed, however, no diel horizontal migration of fish and zooplankton, which is expected to reduce the strength of fish–zooplankton interactions. Experiments allowing horizontal migration are therefore needed. The abrupt shifts that occur at a PVI of 15–20% and again at planktivorous fish densities above 10 CPUE provide further evidence that changes in the dynamics of shallow lakes are not a smooth function of changes in macrophyte density; small changes in PVI and planktivorous fish CPUE may lead to major changes in the biological structure and thus in water quality.

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References

Balls H., Moss B. & Irvine K. (1989) The loss of submerged plants with eutrophication I. Experimental design, water chemistry, aquatic plant and phytoplankton biomass in experiments carried out in the Norfork Broadland. *Freshwater Biology*, **22**, 71–87.

Behrendt H. (1990) The chemical composition of phytoplankton and zooplankton in a eutrophic shallow lake. *Archiv für Hydrobiologie*, **118**, 129–145.

Benndorf J., Schultz H., Benndorf A., Unger R., Penz E., Kneschke H., Kossatz K., Dumke R., Hornig U., Knispe R. & Reichel S. (1988) Food web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. *Limnologica*, **19**, 97–110.

Brandl Z. & Fernando C.H. (1975) Food consumption and utilization in two freshwater cyclopoid copepods (*Mesocyclops edax* and *Cyclops vicinus*). *Internationale Revue der gesamten Hydrobiologie*, **60**, 471–494.

Breder C.N. (1960) Design for a fry trap. *Zoologica*, **45**, 155–160.

Brooks J.L. & Dodson S.I. (1965) Predation, body size and composition of plankton. *Science*, **150**, 28–35.

Canfield D.E. & Hoyer M.V. (1992) *Aquatic Macrophytes and their Relation to Limnology of Florida Lakes*. Bureau of Aquatic Plant Management, Florida Department of Natural Resources, Florida, 600 pp.

Canfield D.E. Jr., Shireman J.V., Colle D.E., Haller W.T., Watkins C.E. II & Maceina M.J. (1984) Prediction of chlorofyll a concentrations in Florida lakes: importance of aquatic macrophytes. *Canadian Journal of Fisheries and Aquatic Science*, **41**, 497–501.

Carpenter S.R. & Lodge D.M. (1986) Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany*, **26**, 341–370.

Crowder L.B. & Cooper W.E. (1979) Structural complexity and fish-prey interactions in ponds: a point of view. *Response of Fish to Habitat Structure in Standing Water* (eds D.L. Johnson and R.A. Stein), pp. 2–10. Special Publication 6. North Central Division. American Fisheries Society, Bethesda.

Cryer M.G., Peirson G. & Townsend C.R. (1986) Reciprocal interactions between roach (*Rutilus rutilus* L.) and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. *Limnology & Oceanography*, **31**, 1022–1038.

Culver D.A., Boucherle M.M., Bean D.J. & Fletcher J.W. (1985) Biomass of freshwater Crustacean zooplankton from length-weight regressions. *Canadian Journal of Fisheries and Aquatic Science*, **42**, 1380–1390.

Dahl I. (1974) Intercalibrations of methods for chemical analysis of water.V. Results from intercalibrations of methods for determining nitrate and total nitrogen. Vatten 30, 180–186.

Diehl S. (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos, 1988*, 209–214.

Dumont, H.J., I. Van de Velse & S. Dumont, (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from plankton, periphyton and benthos of continental waters. *Oecologia* (Berl.) 1, 75–97.

Geller W. & Müller H. (1981) The filtration apparatus of Cladocera: Filter mesh-sizes and theirimplications on food selectivity. *Oecologia*, **49**, 316–321.

Grimm M.P. & J.J.G.M. Backx, (1990) The restoration of shallow eutrophic lakes, and the role of northern pike, aquatic vegetation and nutrient concentration. *Hydrobiologia*, **200/201**, 557–566.

Hall D.J. & Werner E.E. (1977) Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society*, **106**, 545–555.

Haney J.F. (1987) Field studies on zooplankton-cyanobacteria interactions. *New Zealand Journal of Marine and Freshwater Research*, **21**, 467–475.

Hansen A.M., Jeppesen E., Bosselmann S. & Andersen P. (1992) *Zooplankton i Søer – Metoder og Artsliste*. Miljøprojekt 205. Miljøministeriet, 114 pp. [*Zooplankton in Lakes–Methods and Species List*. Environmental Project no. 205. Danish Ministry of the Environment. In Danish]

Hart R.C. & Jarvis A.C. (1993) In situ determination of bacterial selectivity and filtration rates by five cladoceran zooplankton in a hypertrophic subtropical reservoir. *Journal of Plankton Research*, **15**, 295–315.

Higgins P.J. (1985) An interactive computer program for population estimation using the Zippin method. *Aquaculture and Fisheries Management*, **1**, 287–295.

Holm-Hansen D. & Riemann B. (1978) Chlorophyll *a* determination: improvements in methods. *Oikos*, **30**, 438–447.

Irvine K., Moss B. & Balls H. (1989) The loss of submerged plants with eutrophication II. Relationships between fish and zooplankton in a set of experimental ponds, and conclusions. *Freshwater Biology*, **22**, 89–107.

Jeppesen E., Søndergaard M., Mortensen E., Kristensen P., Riemann B., Jensen H.J., Müller J.P., Sortkjær O., Jensen J.P., Christoffersen K., Bosselmann S. & Dall E. (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. *Hydrobiologia*, **200/201**, 205–218.

Jeppesen E., Kristensen P., Jensen J.P., Søndergaard M., Mortensen E. & Lauridsen T. (1991) Recovery resilience following a reduction in external phosphorus loading of shallow eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Memorie Dell'istituto Italiano Di Idrobiologia*, **48**, 128–148.

Kairesalo T. & Seppala T. (1987) Phosphorus flux through a littoral ecosystem: the importance of cladoceran zooplankton and young fish. *Internationale Revue der gesamten Hydrobiologie*, **72**, 385–403.

Koroleff F. (1970) Determination of total phosphorus in natural water by means of persulphate oxidation. Interlaboratory report No. 3, Cons. Int. pour l'Explor de la Mer.

Lampert W. & Muck P. (1985) Multiple aspects of food limitation in zooplankton communities: the *Daphnia – Eudiaptomus* example. *Archiv für Hydrobiologie Ergebnisse der Limnologie*, **21**, 311–322.

Leah R.T., Moss B. & Forrest D. (1980) The role of predation in causing major changes in the limnology of a hypereutrophic lake. *Internationale Revue der gesamten Hydrobiologie*, **65**, 223–247.

Losee R.F. & Wetzel R.G. (1993) Littoral flow rates within and around submersed macrophyte communities. *Freshwater Biology*, **29**, 7–17.

Meijer M-L., Jeppesen E., van Donk E., Moss B., Scheffer M., Lammens E., van Nes E., van Berkum J.A., de Jong G.J., Faafeng B.A. & Jensen J.P. (1994) Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia*, **275/276**, 457–466.

Moss B. (1990) Engineering and biological approached to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia*, **200/201**, 267–277.

Murphy J. & Riley J.P. (1972) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 21–26.

Olrik K. (1991) *Planteplankton-metoder*. Miljøprojekt nr. 187, Miljøstyrelsen. 108 pp. [Phytoplankton. Environmental Project no. 187. The Danish Ministry of the Environment. In Danish].

Pace M.L., Porter K.G. & Feig Y.S. (1983) Species and age specific differences in bacterial resource utilization by two co-occuring cladocerans. *Ecology*, **64**, 1148–1156.

Persson. L. (1993) Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos*, **68**, 12–22.

Persson L., Diehl S., Johansson L., Andersson G. & Hamrin S. (1992) Trophic interactions in temperate lake ecosystems: a test of food chain therory. *American Naturalist*, **140**, 59–84.

Reinartsen H. & Olsen Y. (1984) Effects of fish elimination on the phytoplankton community of a eutrophic lake. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 649–657.

Reynolds C.S. (1984a) *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, London, 384 pp.

Reynolds C.S. (1984b) Phytoplankton periodicity: the interactions of form, function and environmental variability. *Freshwater Biology*, **14**, 111–142.

Reynolds C.S. (1987) The response of phytoplankton communities to changing lake environments. *Schweizerische Zeitschrift für Hydrobiologie*, **49**, 220–236.

Riemann B., Christoffersen K., Jensen H.J., Müller J.P., Lindegaard C. & Bosselmann S. (1990) Ecological consequences of a manual reduction of roach and bream in a eutrophic, temperate lake. *Hydrobiologia*, **200/201**, 241–250.

Sand-Jensen K. & Borum, J. (1991) Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany*, **41**, 137–175.

Sanni S. & Wærvågen S.B. (1990) Oligotrophication as a result of fish removal with rotenone in the small, eutrophic, Lake Mosvatn, Norway. *Hydrobiologia*, **200/201**, 263–274.

SAS Institute Inc. (1989) *SAS/STAT User's Guide*, Version 6, 4th edn, Vols 1 & 2. SAS Institute Inc., Cary, NC, 943 & 846 pp.

Savino J. & Stein R.A (1982) Predator-prey interaction between largemouth bass and bluegills as influenced by simualted, submersed vegetation. *Transactions of the American Fisheries Society*, **111**, 255–266.

Solórzano L. (1969) Determination of ammonia in natural waters by the phenolhypochlorite methods. *Limnology & Oceanography*, **14**, 799–801.

Solórzano L. & Sharp J.H. (1980) Determination of total dissolved nitrogen in natural waters. *Limnology & Oceanography*, **25**, 751–754.

Søndergaard M., Jeppesen E., Mortensen E., Dall E., Kristensen P. & Sortkjær O. (1990) Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. *Hydrobiologia*, **200/201**, 229–240.

Timms R.M. & Moss B. (1984) Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnology & Oceanography*, **29**, 472–486.

Van Donk E., Grimm M.P., Gulati R.D. & Klein Breteler J.P.G. (1990) Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. *Hydrobiologia*, **200/201**, 275–289.

Werner E., Gilliam E.J.F., Hall D.J. & Mittelbach G.G. (1983) An experimental test of the effect of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.

Whiteside M.C. (1988) 0+ fish as major factors affecting abundance pattern of littoral zooplankton. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **21**, 1710–1714.

Winfield I.J. (1986) The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, Rutilus rutilus, rudd, Scardinius erythrophthalmus, and perch, Perca fluviatilis. *Journal of Fish Biology*, **29**, 37–48.

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Pike (*Esox lucius* L.) stocking as a biomanipulation tool
2. Effects on lower trophic levels in Lake Lyng, Denmark

Martin Søndergaard[1], Erik Jeppesen[1] & Søren Berg[2]
[1]*National Environmental Research Institute, Dept. of Lake and Estuarine Ecology, Vejlsøvej 25, P.O. Box 314, 8600 Silkeborg, Denmark*
[2]*Danish Institute for Fisheries Research, Dept. of Inland Fisheries, Vejlsøvej 39, 8600 Silkeborg, Denmark*

Key words: biomanipulation, pike stocking, top-down control, zooplankton, phytoplankton, nutrients, internal loading

Abstract

In order to study how pike stocking affects trophic structure pike fingerlings (0–3600 ha^{-1}) were stocked during six years in eutrophic Lake Lyng (lake area 10 ha), Denmark. Subsequently, marked changes were recorded in the abundance of zooplanktivorous fish, catch per unit effort of roach, which was the dominant fish species, thus varied from 17 to 272. Simultaneously, marked changes were recorded in the abundance and relative composition of zooplankton. *Daphnia* abundance ranged from 7 to 36 ind. l^{-1} and *Bosmina* from 2 to 99 ind. l^{-1}, mean summer abundance of *Daphnia* being highest and *Bosmina* lowest in years with low fish density. Additionally, cyclopoid copepod and rotifer abundance correlated significantly ($p<0.05$, $r^2=0.70$ and 0.83, respectively) and positively with fish abundance. Mean summer chlorophyll *a* correlated significantly ($p=0.04$, $r^2=0.70$) with the abundance of roach, suggesting an impact on phytoplankton level also, disregarding that the phytoplankton biomass was dominated by filamentous cyanobacteria. Total phosphorus concentration was lowest in years with low zooplanktivorous fish abundance, which is hypothesized to be due to lower sedimentation of organic material and lower phosphorus release from the sediment in years with high zooplankton grazing on phytoplankton. It is concluded that pike stocking can be used as a lake restoration tool to increase lake water transparency by creating a trophic cascade. The effect of stocking, however, seems to last only during the season in which it has been undertaken, the impact being most significant at high stocking densities. The method is therefore regarded to be most useful in shallow, turbid lakes in which the nutrient loading has been sufficiently reduced to allow a substantial and permanent macrophyte coverage if clearwater conditions are established.

Introduction

The importance of top-down versus bottom-up control in lakes and the possibilities of creating a trophic cascade by fish manipulation have been amply discussed in recent years (De Melo et al., 1992; Carpenter et al., 1993; Reynolds, 1994). Numerous enclosure and whole-lake experiments have been conducted to investigate the usefulness of fish manipulation as a restoration tool (e.g. review by De Melo et al., 1992; Meijer et al., 1994; Reynolds, 1994). In most cases the starting point has been a direct reduction or removal of the zooplanktivorous fish with a view to increasing the abundance of large-sized and efficient phytoplankton-filtrating species such as *Daphnia*.

More recently, manipulation experiments have been undertaken at the top level of the food chain by introducing carnivorous fish to reduce the number of zooplanktivorous fish. Most frequently, stocking of piscivores has been used as a supplement to fish removal, but in some cases also as the only measure to induce a trophic cascade (Benndorf et al., 1988; He & Wright, 1992; Prejs et al., 1994). Compared to the more traditional biomanipulation methods mentioned above, stocking of piscivorous fish has several advantages (Berg et al. 1997), among these being less time-consuming and less costly. However, the effect of piscivorous fish stocking in terms of stocking density on lower trophic levels is poorly documented.

In the present paper we evaluate how stocking of pike fingerlings in high densities affects the abundance of zooplankton and phytoplankton and nutrient concentrations. More specifically, we wanted to evaluate the impact of varying stocking densities and observe the long-term effects. The investigation was based on a six-year study of a 10 ha large lake into which pike fingerlings were stocked every spring during the four-year period. In another paper we discuss the direct influence of pike on the fish community (Berg et al., 1997).

Methods

Study area

The investigation was conducted in Lake Lyng situated near Silkeborg, Denmark. Lake Lyng (10 ha) has a mean depth of 2.4 m and a maximum depth of 7.6 m and is stratified during summer. Depth is below approximately 5 m (10% of the lake area), and the lake is anoxic from July to September. The lake has no surface inflows and the hydraulic retention time is estimated to be more than one year. Sewage from the town of Silkeborg was diverted in 1956 and except for periods with heavy rainfall there have been no external sources of nutrients to the lake since then. Before the pike stocking mean summer Secchi depth in 1989 was 0.72 m and total phosphorus 0.79 mg P l^{-1} in the epilimnion. See Berg et al. (1997) for further details.

Pike stocking and fish abundance

Stocking of pike juveniles (mean length: 2–6 cm) was conducted from 1990 to 1993 in densities ranging from 500 to 3600 ha^{-1}. Stocking was undertaken in either May or June. Fish abundance was calculated as catch per unit effort (CPUE) once every August or September using multiple mesh size gill nets. For further details see Berg et al. (1997).

Sampling and analysis

Sampling of zooplankton, phytoplankton, nutrients and chlorophyll *a* was undertaken once or twice monthly during summer (1 May to 1 October).

Zooplankton was sampled at a mid-lake station using a 3.3 l Patalas sampler. Samples taken at 0.5 m, 2.5 m, 4.5 m and 6.5 m were pooled, filtered through a 20 μm net, and the contents fixed in Lugol (1 ml 100 ml^{-1} tap water). Zooplankton retained on a 140 μm net were counted (at least 150 ind. of the most dominant species) using a Wild microscope, whereas those <140 μm were filtered on a 20 μm net and counted in strips using an inverted microscope (at least 100 ind. of the most dominant species). As the vertical distribution probably is restricted to the epilimnion during most of the summer, the actual zooplankton density in the photic zone above the thermocline is underestimated with up to 100%.

Phytoplankton were sampled at the mid-lake station at a depth of 0.5 m (1994) or as a composite sample from 1/2 Secchi depth, Secchi depth and 2 Secchi depth (other years). If 2 Secchi depth was below the epilimnion this sample was omitted. Phytoplankton biomass was estimated by inverted microscope counting (at least 100 ind. of the dominant species) and converted to biovolume by means of appropriate geometric shapes.

Chemical analyses were conducted on a composite 0.5 m and 2.5 m sample (1994) or from the same depth as phytoplankton (other years). Nutrients and chlorophyll *a* were analysed according to Søndergaard et al. (1990), chlorophyll *a* using ethanol extraction, phosphate PO_4-P by the ascorbic acid molybdene blue method, total phosphorus (tot-P) after persulphate digestion, ammonium (NH_4-N) by the phenol hypochlorite method and total nitrogen (tot-N) after potassium persulphate digestion. Particulate phosphorus (part-P) was calculated as the difference between tot-P and PO_4-P.

The number of zooplankton and phytoplankton samplings varied from 5 in 1993 to 20 in 1989. Samplings for Secchi depth, chlorophyll *a* and nutrients varied from 6–8 in 1990 to 10— 25 in 1989.

Statistical analyses

Mean summer (1 May to 1 October) values of zooplankton, Secchi depth, chlorophyll *a* and nutrients for each of the six years were calculated and correlated to catch per unit effort of roach< 10 cm (roach< 10), total roach number (roach-total) or, in a multiple regression, to roach-total and perch< 10 cm. The regression analyses were performed according to SAS (1989) on untransformed or on log-log transformed data.

Table 1. Catch per unit effort of roach < 10 cm (roach<10), total number of roach (roach-total) and perch <10 cm (perch<10). (See Berg et al. (1997) for further details).

	1989	1990	1991	1992	1993	1994
Roach<10	167	60	5	158	19	94
Roach-total	272	97	17	171	43	123
Perch<10	50	76	67	10	61	87

Table 2. Linear regression between mean summer zooplankton abundance, Secchi depth and nutrient concentrations and catch per unit effort of roach<10 and roach-total. In roach-total + perch<10, stepwise multiple regression was performed including catch per unit effort of perch <10 cm. N.s. means no significant improval (significance level = 0.15) of the relationship.

	Roach<10		Roach-total		Roach-total + perch<10	
	p	r^2	p	r^2	p	r^2
Daphnia	0.42	0.16	0.53	0.11	N.s.	
Bosmina	0.06	0.64	0.21	0.37	N.s.	
Daph./cla. ratio	0.13	0.47	0.22	0.34	N.s.	
Cyc. cop.	0.06	0.63	0.04	0.70	N.s.	
Rotifers	0.01	0.86	0.01	0.83	0.01	0.98
Secchi depth	0.12	0.49	0.05	0.67	N.s.	
Chl a	0.04	0.70	0.04	0.70	N.s.	
Tot-P	0.10	0.53	0.09	0.54	N.s.	
Part-P	0.01	0.87	<0.01	0.93	N.s.	

Results

Fish

The CPUE of zooplanktivorous fish varied greatly during the six years. Thus, roach<10 varied from 5 in 1991 to 167 in 1989 and perch<10 from 10 in 1992 to 87 in 1994 (Table 1). Roach $\geq$ 10 was 105 in 1989 and varied between 12 and 37 in 1990 to 1994. For further details see Berg et al. (1997).

Zooplankton

During the whole sampling period large cladocerans were dominated by *Daphnia cucullata* Sars and *D. galeata* Sars, and small cladocerans mainly by *Bosmina longirostris* O. F. Müller. Cyclopoid copepods were dominated by *Mesocyclops leuckarti* Claus, while calanoid copepods almost exclusively consisted of *Eudiaptomus gracilis* Sars. *Keratella cochlearis* Gosse was the dominant rotifer species during all years.

Mean summer density of *Daphnia* decreased with the density of roach<10, from less than 7 ind. l^{-1} in 1994 to 36 ind. l^{-1} in 1993 (Figure 1). Contrarily, the density of *Bosmina* was highest in years with high roach abundance (Figure 1), the mean being below 20 ind. l^{-1} in years with low roach abundance, but up to 100 ind. l^{-1} in years with high roach abundance. Accordingly, the *Daphnia* to total cladoceran ratio was lowest in years with high roach abundance (Figure 1). Rotifer abundance increased with increasing roach abundance (Figure 1) from less than 2000 ind. l^{-1} in 1991, when the abundance of roach was low, to almost 10 000 in 1989 and 1992 when roach abundance was high. The correlation was significant ($p = 0.01$) to both roach<10 ($r^2 = 0.86$) and roach-total ($r^2 = 0.83$, Table 2). Finally, cyclopoid copepod abundance (adults + copepodites) correlated significantly ($p = 0.04$, $r^2 = 0.70$) and positively with roach-total. Regression analyses performed on log-transformed data did not improve the statistical significance of any of the parameters analysed. Only for rotifers an improved relationship to fish abundance could be established by including the number of perch< 10 cm in a multiple regression, r^2, increasing to 0.98 (Table 2).

Phytoplankton and Secchi depth

Phytoplankton biomass was dominated by cyanobacteria from 1989 to 1992, while the community was more diverse in 1993 and 1994 (Table 3). The dominant cyanobacteria were *Anabaena spiroides* Klebahn and *A. flos-aquae* Komarek. *Pediastrum duplex* Meyen and *Dictyosphaerium* sp. were among the dominant green algae in 1989, constituting 24% of the total mean summer biomass. Among the chrysophytes, which were of particular importance for the total phytoplankton biomass in 1991 and 1993, *Syncrypta* sp. (1991) and *Uroglena* sp. (1993) dominated, while picoplankton accounted for a large part of the unspecified phytoplankton biomass in 1994.

A significant ($p = 0.04$, $r^2 = 0.70$) and positive relationship was recorded between chlorophyll *a* and roach<10 and roach-total (Figure 2, Tables 2 and 4). Thus, mean summer chlorophyll *a* varied from 20 μg l^{-1} in 1991 to about 90 μg l^{-1} in 1989 and 1992. Correspondingly, a tendency towards a negative relationship was recorded between Secchi depth and roach< 10 ($p = 0.12$, $r^2 = 0.49$) and roach-total ($p = 0.05$, $r^2 = 0.67$, Figure 2, Table 2).

Table 3. Total phytoplankton biomass ($mm^3\ l^{-1}$) and major phytoplankton classes as % of total biomass.

Year	Total ($mm^3\ l^{-1}$)	Cyanophytes (%)	Cryptophytes (%)	Chrysophytes (%)	Diatoms (%)	Chlorophytes (%)	Others (%)
1989	18.9	61	10	<1	<1	24	5
1990	24.4	89	3	2	<1	1	5
1991	5.1	43	6	27	<1	16	8
1992	20.3	79	16	1	<1	1	3
1993	3.7	4	11	51	<1	18	16
1994	3.9	14	21	2	5	19	39

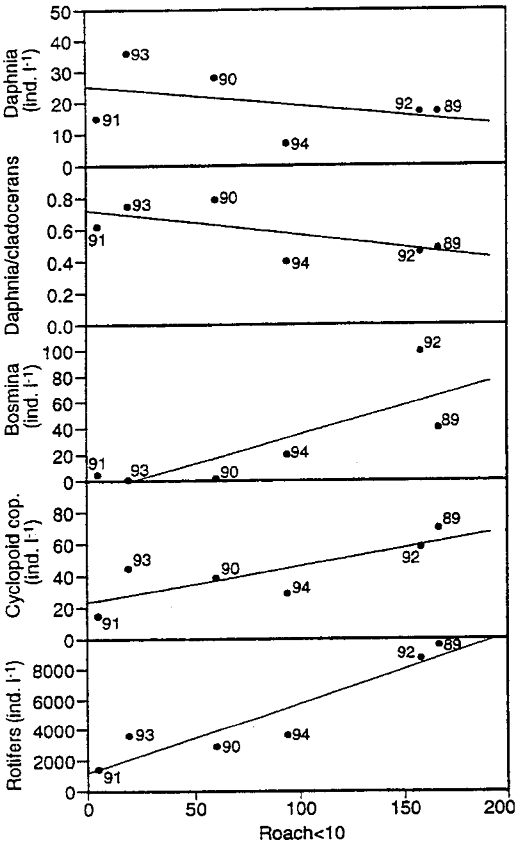

Figure 1. Mean number (1 May to 1 October, 1989–1994) of different zooplankton groups versus catch per unit effort of roach<10.

Table 4. Linear regression between number of cyclopoid copepods (Cyc. Cop., adults+copepodites l^{-1}) rotifers (ind. l^{-1}), chlorophyll a (Chl. *a*, $\mu g\ l^{-1}$) and particulate P (part-P, $\mu g\ P\ l^{-1}$) and roach<10 and roach-total.

Cyc. Cop.	= 21 + 0.18*roach-total,	$p=0.038$, $r^2=0.70$
Rotifers	= 1200+ 45*roach<10,	$p=0.007$, $r^2=0.86$
Rotifers	= 1040 + 33*roach-total,	$p=0.012$, $r^2=0.83$
Chl. *a*	= 24.6 + 0.39*roach<10,	$p=0.039$, $r^2=0.70$
Chl. *a*	= 22.3 + 0.29*roach-total,	$p=0.037$, $r^2=0.70$
Part-P	= 90 + 0.86*roach<10,	$p=0.006$, $r^2=0.87$
Part-P	= 82 + 0.66*roach-total,	$p=0.003$, $r^2=0.94$

Nutrients

Mean summer PO_4-P varied from 0.25 to 0.55 mg P l^{-1} from 1989 to 1994, while minimum summer PO_4-P ranged between 0.071 (1989) and 0.340 (1992) mg P l^{-1}. Summer tot-P and PO_4-P were 2–4 times higher than winter concentrations, suggesting a heavy influence of sediment phosphorus release on lake water concentrations.

Mean summer nitrate concentrations never exceeded 0.01 mg N l^{-1} while NH_4-N varied between 0.040 and 0.096 mg N l^{-1}. Tot-N ranged from 0.90 mg N l^{-1} in 1991 to 1.97 mg N l^{-1} in 1992.

A highly significant ($p=0.01$, $r^2=0.87$) and positive relationship was recorded between particulate phosphorus and roach<10, and between particulate phosphorus and roach-total ($p<0.01$, $r^2=0.93$, Figure 2, Tables 2 & 4). Furthermore, a tendency towards a positive relationship ($p=0.10$, $r^2=0.53$) was recorded between tot-P and roach<10, and between tot-P and roach-total ($p=0.09$, $r^2=0.54$). Tot-N did not correlate to roach <10 ($p=0.4$). Changes in mean summer PO_4-P and NH_4-N did not correlate to changes in roach<10 or roach-total ($p>0.3$).

Discussion

Zooplankton composition and abundance in Lake Lyng along with the changes in the planktivorous fish abundance mediated by the introduction of pike fingerlings

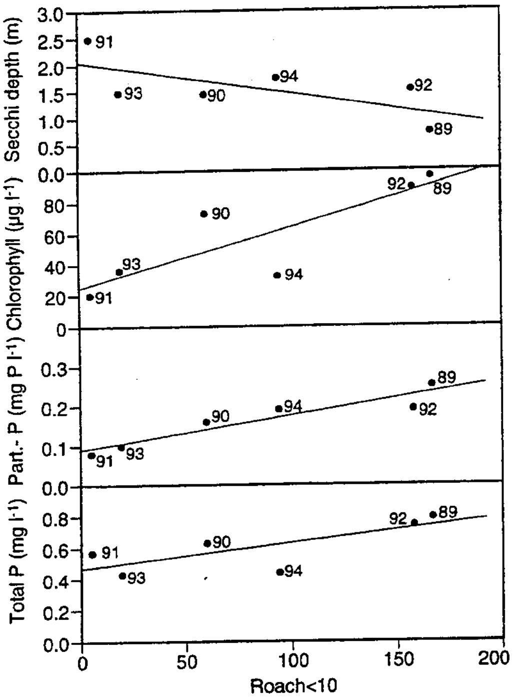

Figure 2. Mean (1 May to 1 October, 1989–1994) Secchi depth, chlorophyll *a* concentration (chla), total phosphorus (total-P) and particulate phosphorus concentration (part-P) versus catch per unit effort of roach<10.

(Berg et al., 1997) showed a number of characteristic features that indicate a marked top-down control in accordance with the classical size-efficiency theory of Brooks & Dodson (1965). Firstly, low planktivorous fish abundance was accompanied by relatively high abundance of *Daphnia*, which generally is considered to be a sign of low grazing pressure by fish (Post & McQueen, 1987; Reinertsen et al., 1990). Secondly, *Bosmina* abundance was high at the highest fish densities. This is typically observed in lakes with a relatively high zooplanktivorous fish stock (Stensson et al., 1978; Benndorf et al., 1988) and is considered to reflect the improved growth conditions for *Bosmina* at low *Daphnia* densities. Consequently, the *Daphnia* to total cladoceran ratio was highest in years with low fish densities. Thirdly, high cyclopoid copepod abundance as in Lake Lyng is also mainly observed in lakes with high fish densities (Benndorf et al., 1988; Hansen & Jeppesen, 1992). Finally, high rotifer abundance, as observed during years with low *Daphnia* abundance in Lake Lyng, is usually associated with a high chlorophyll *a* level (Canfield & Watkins, 1984), and is mainly observed when *Daphnia* density is low as a result of changes in the competition for food and interference (Gilbert, 1985; May & Jones, 1989; Telesh, 1993). Often marked changes in rotifer abundance may be related to changes in fish abundance, the highest abundance of rotifers occurring at the highest fish densities (Reinertsen et al., 1990; Christoffersen et al., 1993; Ronneberger et al., 1993).

Generally, no or only minor improvements were achieved in the correlations by using the total number of roach instead of roach <10 cm. This supports earlier observations (He & Wright, 1992; Jeppesen et al., 1997) that it is the YOY planktivorous fish in particular that create a high predation pressure on the large cladocerans. Furthermore, the lack of impact when including perch<10 cm in the correlation shows that the effect on zooplankton can mainly be ascribed to YOY roach.

The suitability of cyanobacteria and other large-sized algae as a zooplankton food source has been amply investigated and discussed (Hawkins & Lampert, 1989; Bernardi & Giussani, 1990; McQueen, 1990). However, the significant positive relationship recorded in Lake Lyng between roach number and chlorophyll *a* strongly indicates that the effect of changed fish abundance is transferred down to the phytoplankton level. Zooplankton were thus able to suppress phytoplankton abundance in years with low density of planktivorous fish despite dominance of filamentous cyanobacteria during summer, cyanobacteria biomass being, for instance, reduced from 22 mm^3 l^{-1} in 1990 to 2 mm^3 l^{-1} in 1991.

Changes in the planktivorous fish abundance were also accompanied by changes in the nutrient regime, which most likely reflects changes in the biological structure, as changes in external loading were not recorded. As expected, particulate P was highly significantly related to roach abundance, reflecting the correspondingly good correlation to the phytoplankton biomass. However, the substantial year to year variability also in total phosphorus indicates that increasing abundance of zooplanktivores seems able to provoke changes in the internal recycling of phosphorus, causing increased phosphorus concentrations. This suggests a strong cascading effect of changed fish structure all the way down to the nutrient level. Changes in nutrient concentrations were recorded in other biomanipulation experiments. There are various explanations of the phenomenon such as increased sedimentation due to precipitation of calcium carbonate (Andersson et al., 1978), excretion of P below the thermocline by migrating large-bodied zooplankton (Shapiro & Wright, 1984), increased sedimentation of detrital phosphorus (Boers et al., 1991), increased sedimentation of zooplankton and reduced phosphorus release from the sediment because of the lowered pH (Reinertsen et al., 1990), and lower number of cyprinids foraging on the sediment, thereby decreasing release of P from the sediment (Persson & Hamrin, 1994). As the Lake Lyng tot-P concentration in the epilimnion during summer is considerably higher than during winter a substantial internal loading takes place. A decrease in the release of phosphorus from the sediment due to increased sedimentation of organic matter and reduced oxygen demand seems therefore to be the most likely explanation of the reduced tot-P at decreased abundance of zooplanktivorous fish in Lake Lyng. This assumption is supported by the fact that about 50% of the phosphorus in the surface sediment of Lake Lyng is bound to iron and that the phosphorus release rate experimentally has been shown to be very sensible to changes in oxygen and nitrate concentrations (unpubl. data) as has been found in other shallow iron-rich lakes (Jensen et al., 1992). The strong cascading effect down to the nutrient level in this eutrophic lake contradicts the hypothesis of McQueen et al. (1986) that the top-down effect is weak in eutrophic lakes, but it is in accordance with Sarnelle (1992).

Based on the correlation between tot-P and roach it could be argued that the changes in phytoplankton abundance simply reflect changes in the nutrient regime as total phosphorous also increased with density of roach. Orthophosphate, however, was high during the whole experimental period and is therefore not likely to have been a limiting factor for phytoplankton growth. Inorganic nitrogen, on the other hand, may periodically constitute a limiting factor and although mean summer NH_4-N never went below 0.04 mg N l^{-1}, it cannot be excluded that changes in the internal flux of nitrogen, as in phosphorus, may have occurred, which may have influenced the abundance of phytoplankton.

In conclusion, the investigations in Lake Lyng strongly indicate that it is possible to create a top-down control on phytoplankton biomass by introducing pike fingerlings. However, the effects of pike stocking on lower trophic levels seem to last only during the season in which stocking is undertaken. This is in agreement with the finding that the carrying capacity of pikes in lakes is largely determined by the area covered by vegetation (Grimm & Backx, 1990) and in agreement with the finding by Berg et al. (1997) that the autumn pike biomass was not increased by the stocking. To achieve a long-term effect the stocking therefore has to be repeated every year or until more permanent changes in the biological structure have been established. We therefore hypothesize that this management method is most useful in lakes in which changes in other stabilizing elements can be achieved following an increase in water transparency, i.e. particularly in relatively shallow lakes and lakes in which the nutrient loading has been reduced sufficiently to enable the permanent establishment of submerged macrophyte vegetation.

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References

Andersson, G., H. Berggren, G. Cronberg & C. Gelin, 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

Benndorf, J., H. Schulz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, U. Hornig, R. Kruspe & S. Reichel, 1988. Food-web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. Limnologica: 97–110.

Berg, S., E. Jeppesen & M. Søndergaard, 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng, Denmark. Hydrobiologia 342/343: 311–318.

Bernardi, R. de & G. Guissani, 1990. Are blue-green algae a suitable food for zooplankton? An overview. Hydrobiologia 200/201: 29–41.

Boers, P., L. Van Ballegooijen & J. Uunk, 1991. Changes in phosphorus cycling in a shallow lake due to food web manipulations. Freshwat. Biol. 25: 9–20.

Brooks, J. L. & S. I. Dodson, 1965. Predation, body size, and composition of plankton. Science 150: 28–35.

Canfield., D. & C. E. Watkins, 1984. Relationships between zooplankton abundance and chlorophyll *a* concentrations in Florida lakes. J. Fresh. Ecol. 2: 335–343.

Carpenter, S. R., X. He., J. F. Kitchell & P. A. Sorrano, 1993. Whole-lake experiments: is grazer functional response stable? Verh. int. Ver. Limnol. 25: 398–400.

Christoffersen, K., B. Riemann, A. Klysner & M. Søndergaard, 1993. Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. Limnol. Oceanogr. 38: 561–573.

De Melo, R., R. France & D. J. McQueen, 1992. Biomanipulation: Hit or myth? Limnol. Oceanogr. 37: 2–207.

Gilbert, J.J., 1985. Competition between rotifers and *Daphnia*. Ecology 66: 43–50.

Grimm, M. P. & J. J. G. M. Backx, 1990. The restoration of shallow eutrophic lakes, and the role of northern pike, aquatic vegetation and nutrient concentration. Hydrobiologia 200/201: 557–566.

Hansen, A-M. & E. Jeppesen, 1992. Changes in the abundance and composition of cyclopoid copepods following fish manipulation in eutrophic Lake Væng, Denmark. Freshwat. Biol. 28: 183–93.

Hawkins, P. & W. Lampert, 1989. The effect of *Daphnia* body size on filtering rate inhibition in the presence of a filamentous bacterium. Limnol. Oceanogr. 34: 1084–1089.

He, X. & R. Wright, 1992. An experimental study of piscivore-planktivore interactions: population and community responses to predation. Can. J. Fish aquat. Sci. 49: 1176–1183.

Jensen, H. S., P. Kristensen, E. Jeppesen & A. Skytthe, 1992. Iron: phosphorus ratio in surface sediment as an indicator of phosphate release from aerobic sediments in shallow lakes. Hydrobiologia 235-236: 731–743.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, L. J. Pedersen & L. Jensen, 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342/343: 151–164.

May, L. & D. H. Jones, 1989. Does interference competition from *Daphnia* affect populations of *Keratella cochlearis* in Loch Leven, Scotland. J. Plankton Res. 11: 455–461.

McQueen, D. J., 1990. Manipulation lake community structure: where do we go from here? Freshwat. Biol. 23: 613–620.

McQueen, D. J., R. France & C. Kraft, 1992. Confounded impacts of planktivorous fish on freshwater biomanipulation. Arch. Hydrobiol. 125: 1–24.

McQueen, D. J., J. R. Post & E. L. Mills, 1986. Trophic relations in freshwater pelagic ecosystems. Can. J. Fish. aquat. Sci. 43: 1571–1581.

Meijer, M-L., E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, E. Lammens, E. van Nes, J. A. van Berkum, G. J. de Jong, B. A. Faafeng & J. P. Jensen, 1994. Long-term response to fish-stock reduction in small shallow lakes: interpretations of five-year results of four biomanipulation cases in The Netherlands and Denmark. Hydrobiologia 200/201: 457–466.

Meijer, M-L., E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, E. Lammens, E. van Nes, J. A. Persson & S. F. Hamrin, 1994. Effects of cyprinids on the release of phosphorus from lake sediment. Verh. int. Ver. Limnol. 25: 2124–2127.

Persson, A. & S. F. Hamrin, 1994. Effects of cyprinids on the release of phosphorus from lake sediment. Verh. int. Ver. Limnol. 25: 2124–2127.

Post, J. R. & D. J. McQueen, 1987. The impact of planktivorous fish on the structure of a plankton community. Freshwat. Biol. 17: 79–89.

Prejs, A., A. Martyniak, S. Boron, P. Hliwa & P. Koperski, 1994. Food web manipulation in a small eutrophic Lake Wirbel, Poland: effect of stocking with juvenile pike on planktivorous fish. Hydrobiologia 275/276: 65–70.

Reinertsen, H., A. Jensen, J. I. Koksvik, A. Langeland & Y. Olsen, 1990. Effects of fish removal on the limnetic ecosystem of a eutrophic lake. Can. J. Fish aquat. Sci. 47: 166–173.

Reynolds, C., 1994. The ecological basis for the successful biomanipulation of aquatic communities. Arch. Hydrobiol. 130: 1–33.

Ronneberger, D., P. Kasprzak & L. Krienitz., 1993. Long-term changes in the rotifer fauna after biomanipulation in Haussee (Feldberg, Germany, Mecklenburg-Vorpommern) and its relationship to the crustacean and phytoplankton communities. Hydrobiologia 255/256: 297–304.

Sarnelle, O., 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. Ecology 73: 551–560.

Sas Institute Inc., 1989. SAS/STAT User's Guide, Version 6, 4th edn., Vols 1 & 2. SAS Institute Inc., Cary, NC, 943 & 846 pp.

Shapiro, J. & D. I. Wright, 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwat. Biol. 14: 371–383.

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen & O. Sortkjær, 1990. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200/201: 229–240.

Stensson, J. A. E., T. Bohlin, L. Henrikson, B. I. Nilsson, H. G. Nyman, H. G. Oscarson & P. Larsson, 1978. Effects of fish removal from a small lake. Verh. int. Ver. Limnol. 20: 794–801.

Telesh, I., 1993. The effect of fish on planktivorous fish. Hydrobiologia 255/256: 289–296.

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Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake

Henning Fjord Aaser, Erik Jeppesen*, Martin Søndergaard

National Environmental Research Institute, Vejlsøvej 25, PO Box 314, DK-8600 Silkeborg, Denmark

ABSTRACT: The study included field sampling, field experiments in enclosures and laboratory predation experiments. *Neomysis integer*, which underwent 2 generations during the study year (1992), occurred in high density, the maximum being 0.8 ind. l^{-1} or 1250 ind. m^{-2}. Estimated production was 2.2 g DW (dry wt) m^{-2} yr^{-1} and peaked in August at 25 mg DW m^{-2} d^{-1}. The laboratory predation experiments revealed a high predation potential on *Eurytemora affinis*, the maximum predation rates on nauplii and copepodites + adults being 52 and 8 ind. $mysid^{-1}$ h^{-1}, respectively. Stepwise multiple regressions on the data obtained from enclosure experiments conducted at various densities of *N. integer* and three-spined sticklebacks *Gasterosteus aculeatus* revealed that the number of nauplii and the total number of *E. affinis* were significantly negatively related to the densities of both *N. integer* and fish, albeit positively to the interaction between fish density and *N. integer* density. In addition, the density of the advanced stages was significantly negatively related to that of fish, while the chlorophyll *a* concentration was weakly negatively related to *E. affinis* biomass and highly positively related to that of *N. integer*. The results provide further evidence that *N. integer* enhances eutrophication in nutrient-rich brackish lakes, i.e. *N. integer* predation on zooplankton reduces grazing pressure on the phytoplankton. Moreover, the results indicate that mysids also stimulate phytoplankton growth more directly.

KEY WORDS: *Neomysis integer* · *Eurytemora affinis* · Mysid · Copepod · Predation · Brackish · Hypertrophic · Lake

INTRODUCTION

Invertebrate predation may have an important structuring impact on the zooplankton community in brackish as well as freshwater lakes (Hanazato 1990, Branstrator & Lehman 1991), in particular when the abundance of vertebrate predators is low (Gliwicz & Pijanowska 1989). Most mysids belong to the group of invertebrate predators, and prey on all sizes of rotifers, cladocerans and copepods (Arndt & Jansen 1986, Hanazato 1990). Mysids are occasionally found in freshwater lakes, sometimes being artificially introduced to improve conditions for commercial fishing. In brackish lakes, in contrast, they are very common, and often even abundant (e.g. Beattie & de Kruijf 1978, Arndt & Jansen 1986, Moss 1994, Jeppesen et al. 1994).

It is well known from freshwater lakes that the presence of mysids in high density may affect zooplankton composition and abundance (Goldman et al. 1979, Bowers & Vanderploeg 1982, Fulton 1983, Langeland 1988, Hanazato 1990, Meijer et al. 1994), and recent research suggests that this may also be the case in brackish coastal areas (Rudstam et al. 1986, Hansson et al. 1990) and brackish lakes (Moss & Leah 1982, Jeppesen et al. 1994). Jeppesen et al. (1994) found an inverse relationship between the density of fish and that of the mysid *Neomysis integer* (Leach). It was argued that the predation pressure by *N. integer* on zooplankton is particularly high in hypertrophic brackish lakes because fish biomass is low and dominated by sticklebacks, which are inefficient predators on *N. integer*. A

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*Addressee for correspondence. E-mail: fvms@dmu.dk further argument was that the availability of alternative food sources favoured this omnivorous species, thus keeping their density high even during periods of low zooplankton abundance and thereby maintaining a potentially high predation pressure on zooplankton. In contrast to this view, however, studies of a shallow eutrophic lake in the UK suggested that despite being present in high numbers, *N. integer* was unable to control the population of the dominant macrozooplankton, the copepod *Eurytemora affinis* (Irvine et al. 1993).

To further elucidate the structuring impact of *Neomysis integer* on the population of the dominant macrozooplankton *Eurytemora affinis* in a shallow hypertrophic brackish lake, we conducted a number of laboratory and *in situ* enclosure predation experiments and followed the seasonal dynamics of mysids and zooplankton for a 1 yr period. In addition, we studied how the impact of *N. integer* on *E. affinis* was affected by the presence of three-spined sticklebacks *Gasterosteus aculeatus.*

MATERIALS AND METHODS

Study area. The study was undertaken in Lake Ferring, a shallow brackish (salinity 3 to 6‰) lake situated in western Jutland, Denmark (56° N, 8° E), about 100 to 200 m from the North Sea (Fig. 1). The lake area is 3.2 km^2, and the mean and maximum depths are 1.5 and 2.6 m, respectively. The lake is hypertrophic (500 µg total-P l^{-1}) with a high algal biomass and a low Secchi depth, i.e. less than 0.5 m throughout the year, the summer average being 0.25 m (M. Søndergaard unpubl. obs.). The phytoplankton was dominated by small-celled colonies of cyanobacteria, mainly *Aphanothece* spp. which comprised more than 90% of the total phytoplankton biomass. The mean summer phytoplankton biovolume was approximately 50 mm^3 l^{-1}. The fish community was dominated by three-spined sticklebacks *Gasterosteus aculeatus* which, in terms of fish number, accounted for more than 95% of the total catch in a standardized test-fishing conducted in August with multiple mesh-size survey gill nets ranging from 6.25 to 75 mm (Søndergaard et al. unpubl. obs.).

Field sampling. Sampling was undertaken monthly between October and March 1992, and every 2 wk from April to September. Zooplankton were sampled with a 3.3 l Patalas sampler at a mid-lake station, samples from depths of 0.2 and 1 m being pooled.

Mysid density in the lake was estimated by means of day time vertical hauls undertaken with a 500 µm net (diameter 0.6 m) at 21 stations (replicates from each station) positioned so as to represent the whole lake area (Fig. 1). The nets were lowered to the bottom and allowed to rest for 1 min before undertaking the haul. Preliminary investigations showed that mysid density was independent of whether the nets were allowed to rest for 1, 2 or 5 min. The samples were fixed in 96% ethanol.

A diurnal investigation on mysid density was carried out in September, when vertical hauls were made at 7 stations and Perspex Breder traps (Breder 1960) were positioned on the sediment surface at 12 locations for 2 h (4 in each of the transects, Nos. 1 to 3, Fig. 1). Sampling was performed in the afternoon (15:00 h), at night (23:00 h) and in the morning after sunrise (08:00 h).

A qualitative investigation was made of the gut content of 20 mysids caught in net during the diurnal investigation, the food items being identified with the aid of a microscope at a magnification of 100 to 200×.

Production and growth rates. The length-frequency distribution of *Neomysis integer* on each sampling date was estimated from length measurements of 75 mysids selected randomly from a pooled sample of the vertical hauls. Microscope images of the mysids were digitized using a video frame grabber and their length (measured from the tip of their rostrum to the end of their telson) determined on the computer from the digitized image. Mysid growth rates were estimated by studying the change in the average length of *N. inte-*

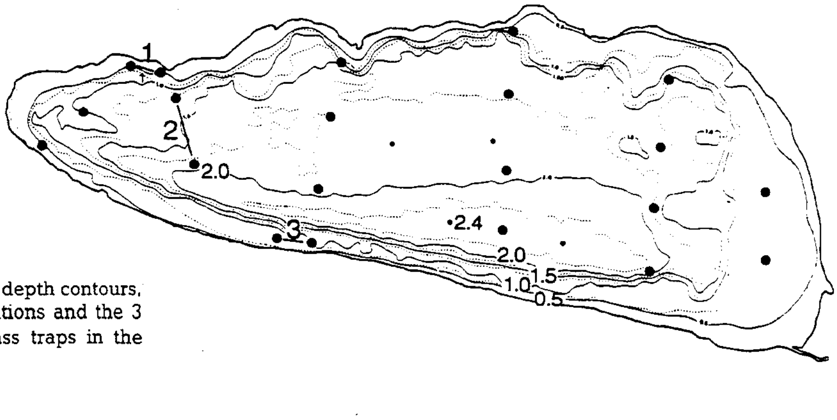

Fig. 1. Map of Lake Ferring showing depth contours, the locations of the 21 sampling stations and the 3 transects for incubation of plexiglass traps in the diurnal study (1 to 3)

ger between sampling dates on cohorts from January to May, from late May to mid-July, and from mid-July to late October. To calculate mysid biomass and production the length-dry weight relationship (24 h at 60°C) of mysids caught in January was used for the January to April samples, while that of mysids caught in August was used for August to December samples. In May and June, when both overwintering and summer generations were present simultaneously, the relationship for the combined data set was used. Mysid production (P, mg DW d^{-1}) (DW: dry wt) was then calculated according to Bremer and Vijverberg (1982) as:

$$P = \sum_{i=1}^{n} P_i,$$

where P is the daily population production, $P_i = \Delta W_i \times N_i$ and is the daily production by the ith size class, n is the number of size classes in the population, W_i is the daily weight increase by the ith size class, and N_i is the population density of the ith size class.

Eurytemora affinis biomass was calculated by applying a dry weight of 6.0 µg $ind.^{-1}$ for females, 5.0 µg $ind.^{-1}$ for males, 2.0 µg $ind.^{-1}$ for copepodites, and 0.5 µg $ind.^{-1}$ for nauplii (Bach et al. 1991). The somatic production (SP) for *E. affinis* was calculated according to Hirche (1992) as

$$SP = [\ln(W) - \ln(0.13)]/10^{(1.9636 - 0.04333T)}$$

where W is the average dry weight of adult copepods (5.5 µg $ind.^{-1}$ assuming equal numbers of females and males) and T is the water temperature (°C).

Field enclosure experiments. Field experiments were carried out in 12 cylindrical enclosures made of tarpaulin sheets attached to a metal ring (diameter 1.5 m, depth 0.75 m). Each enclosure had a water volume of 1.3 m^3 and was open to the sandy sediment at the bottom. The enclosures were organized in 3 sets of 4 enclosures. Prior to initiation of the experiments mysids were removed from one set using 500 µm nets, and the density in the remaining 2 sets adjusted to approximately 0.5 and 1 ind. l^{-1}, respectively. The stickleback *Gasterosteus aculeatus* density was adjusted randomly to one of 3 levels: 0–1, 1–2, and 2–5 ind. m^{-2}. Because of loss due to mortality, mysids were added to the enclosures at each sampling date to maintain the required experimental density.

Enclosure mysid density was determined from vertical hauls as described above, while stickleback density was determined from the catches in Breder traps placed at the bottom for 1 h. We used the Zippin method to convert trap catches to enclosure density (Higgins 1985). In order to quantify zooplankton, 6.6 l of water was sampled in the centre of each enclosure at a depth of 0.2 m using a 3.3 l Patalas sampler. The water was filtered through a 80 µm filter and the specimens fixed in Lugols solution. Samples were taken twice weekly from July 22 to August 20. Backward stepwise multiple regression including date as a dummy variable was performed on all data from July 30 to August 20 (7 samples), thereby excluding the initial transitional phase, i.e. the first 8 d of the experiment. *Eurytemora affinis* was the only macrozooplankton recorded in the enclosures.

Chlorophyll *a* (chl *a*) in the enclosures was measured according to the method of Holm-Hansen & Riemann (1978) using water samples pooled from the same depths and at the same dates as described above.

The results from 3 of the 12 enclosures had to be excluded from the analysis, in 2 cases because the enclosure was damaged during a storm, and in the third case because the 'ecosystem' collapsed (the water became turbid, and all zooplankton and mysids disappeared within the first week).

Predation experiments. Laboratory experiments on *Neomysis integer* predation on *Eurytemora affinis* were carried out in 1 l glass bottles. The mysids and copepods used were collected using 500 and 80 µm nets, respectively. The mysids were allowed to acclimatize for 24 h in plastic holding tanks with approximately 10 l of aerated Lake Ferring water and on a mixed diet of *E. affinis* and trout feed in the form of pellets. About 1 h prior to the experiment, mysids in sets of 3 were transferred to bottles containing 1 l Lake Ferring water pre-filtered through a 50 µm filter to remove copepods. The experiments were initiated by transferring either 100, 200 or 400 nauplii and 100 copepodites + adults to the bottles. Three bottles served as controls. All experiments were conducted in aerated water in subdued light at 15°C and lasted 2 h.

Following incubation the water was filtered through a 50 µm filter and the mysids retained fixed in 96% ethanol and counted. The copepods were fixed in Lugol's solution and counted at a magnification of 25 to 50×. The predation rate (PR, number $mysid^{-1}$ h^{-1}) was calculated as:

$$PR = (C_{start} - C_{end})/(\text{number of mysids} \times \text{incubation time})$$

C_{start} and C_{end} being the number of nauplii and copepodites + adults in the bottles before and after incubation, respectively. Clearance rates (F, l $mysid^{-1}$ h^{-1}) were calculated according to Gauld (1951) as:

$$F = [(\ln C_{start} - \ln C_{end}) \times \text{litres}]/(\text{number of mysids } l^{-1} \times \text{incubation time})$$

and the preference value (S) was estimated according to Chesson (1978) as:

$$S = (R_i/Pt_i)/\sum_{i=1}^{n} (R_i/Pt_i)$$

where R_i is relative abundance of the ith prey type in the food, Pt_i relative abundance of the ith prey type in the environment, and n total number of prey types.

RESULTS

Field data

The average daytime catch of *Neomysis integer* in Lake Ferring increased in late May from a low winter level of approximately 100 ind. m^{-2} to a maximum level of 1250 m^{-2} (0.8 l^{-1}) in July followed by a decrease to a winter mean level of approximately 200 m^{-2} (Fig. 2). These values are conservative, however, as the diurnal investigation undertaken in September revealed that the number of mysids caught by vertical hauls was substantially and significantly ($p < 0.05$, Tukey's *t*-test) higher at night (1 ind. l^{-1}) than in the morning and afternoon (approximately 0.27 ind. l^{-1}) (Table 1). The higher catch during the night largely reflects migration from the bottom to the open water since the lake bottom Breder trap catch of mysids was significantly (2 to 3 times) greater during the day (average 360 ind. $trap^{-1}$) than during the night (Table 1).

The first juvenile mysids were observed in mid-May (Fig. 3). Recruitment continued until the end of October and was most intensive in mid-May, mid-July and mid-August. The mysids were approximately 2 to 3 mm when leaving the female marsupium, whereafter they grew to 17 mm. Three cohorts were identified. From the changes in the average length of the different *Neomysis integer* cohorts (Fig. 4) the following semi-log transformed linear relationship between mysid length (L, mm) and growth rate (GR, mm d^{-1}) was established: January to April cohort: GR = 0.024 ($p < 0.0001$, $n = 5$), May to July cohort: $GR = 3.14 \times 0.567^{L}$ ($r^2 = 0.82$, $p < 0.03$, $n = 5$), August to December cohort: $GR = 2.41 \times 0.538^{L}$ ($r^2 = 0.97$, $p < 0.001$, $n = 7$).

Differential log transformed linear relationships between dry weight (DW, mg) and length (L, mm) were found for the *Neomysis integer* caught in January (the winter generation): $DW = 0.00347\,L^{2.7046}$ ($r^2 = 0.98$, $p < 0.0001$, $n = 50$), and for mysids caught in August (the summer generation): $DW = 0.00621\,L^{2.4873}$ ($r^2 = 0.98$, $p < 0.0001$, $n = 50$). For the combined data set the relationship was $DW = 0.00638\,L^{2.435}$ ($r^2 = 0.98$, $p < 0.0001$, $n = 100$).

Table 1. Average catch of *Eurytemora affinis* (±SD) in Breder traps (n = 12) and vertical hauls (n = 7) in Lake Ferring at 3 different times on 25 and 26 September 1992

Time (h)	Breder traps (mysids $trap^{-1}$)	Vertical hauls (mysids l^{-1})
15:00	360 ± 346	0.26 ± 0.23
23:00	132 ± 78	1.03 ± 0.68
08:00	268 ± 110	0.27 ± 0.19

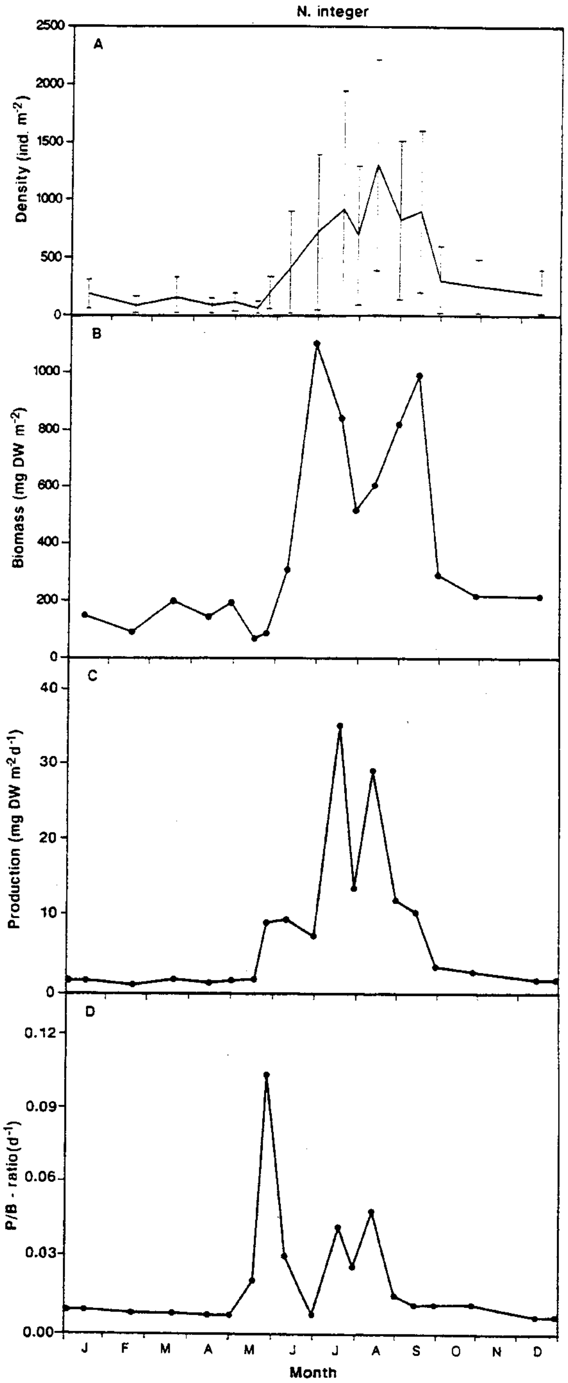

Fig. 2. *Neomysis integer*. Seasonal variation in (A) population density (±SD, n = 21), (B) biomass, (C) calculated production and (D) P/B ratio in Lake Ferring in 1992

Mysid biomass increased from the end of May from low winter values of 100 to 200 mg DW m^{-2} to maximum values of 1000 to 1100 mg DW m^{-2} in the begin-

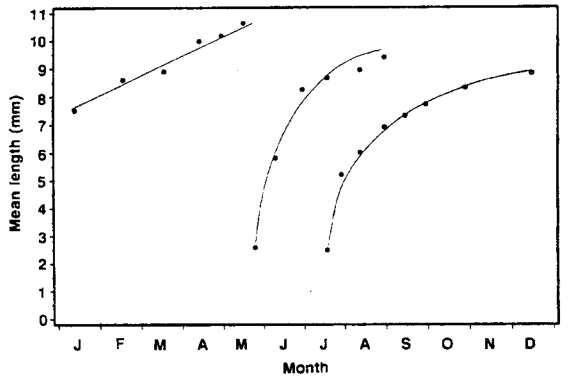

Fig. 4. *Neomysis integer.* Mean length of cohorts in Lake Ferring used for growth rate calculations

ning of July and mid-September (Fig. 2), after which it decreased again to winter levels. In late July and August biomass was 500 to 800 mg DW m^{-2}. Mysid production, based on vertical hauling, increased from winter and spring levels of 0 to 3 mg DW m^{-2} d^{-1} to maximum levels of 35 and 29 mg DW m^{-2} d^{-1} in mid-July and mid-August, (Fig. 2), thereafter decreasing gradually to winter levels. In comparison, calculated production of its potential prey, *Eurytemora affinis,* was less than 10 mg DW m^{-2} d^{-1} during most of the year apart from a short period in June, where it peaked at approximately 55 mg DW m^{-2} d^{-1} (Fig. 5). On an annual basis the total production was calculated to 2.2 g DW m^{-2} for *Neomysis integer* and 2.5 g DW m^{-2} for *E. affinis.*

The density of *Eurytemora affinis,* nauplii and advanced stages was almost equal throughout the year (Fig. 5), winter and spring (January to May) density being 5 to 30 ind. l^{-1} in both cases. A maximum of 72 nauplii l^{-1} and 60 copepodites + adults l^{-1} was reached in mid-June, density then decreasing to winter levels in July and August. In September to December the density was slightly higher than in July and August, the average density being approximately 25 ind. l^{-1} in both cases. As a consequence, copepod biomass was low in spring, the mean value being 60 mg DW m^{-2}. The maximum value of 300 mg DW m^{-2} was recorded in June, while the mean value was 135 mg DW m^{-2} in September to December (Fig. 5). The *Neomysis integer* P/B ratio ranged from 0.004 to 0.10 d^{-1} and the seasonal pattern was bimodal, the maxima being reached in late May and again in July and August (Fig. 2).

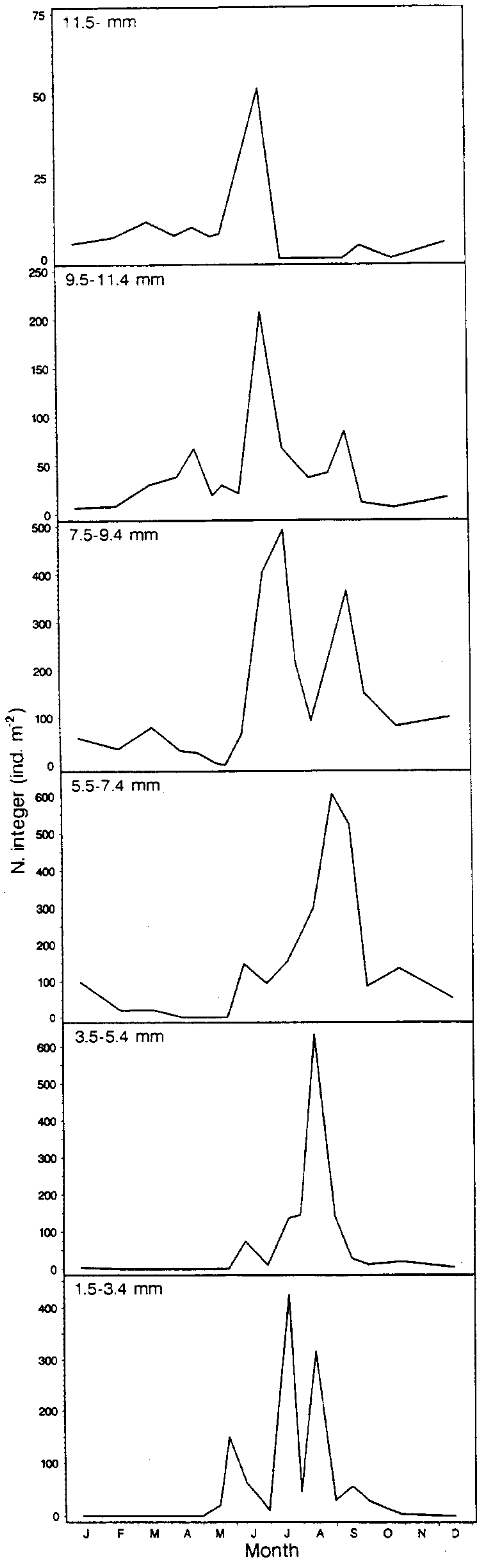

Fig. 3. *Neomysis integer.* Seasonal variations in the density of various size classes in Lake Ferring

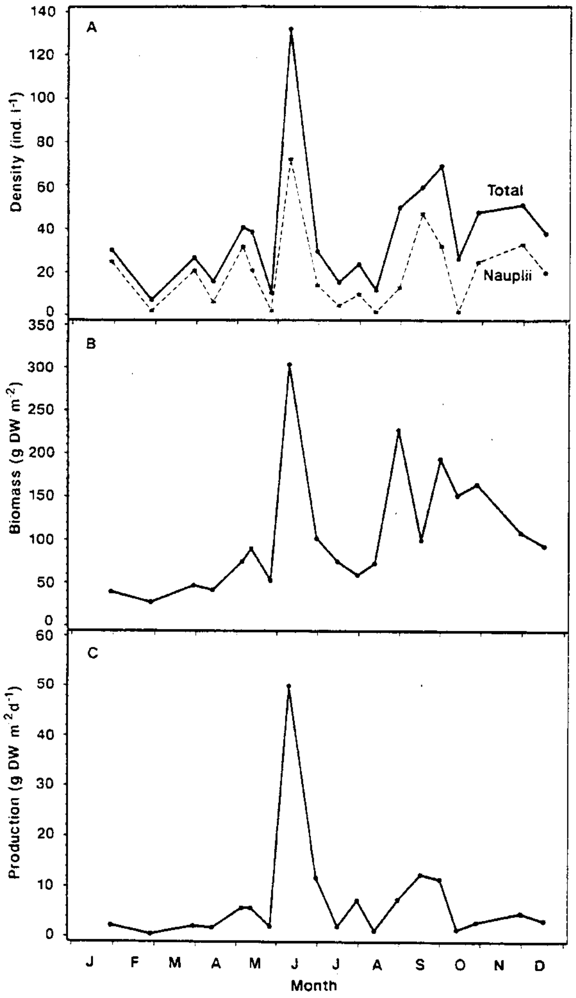

Fig. 5. *Eurytemora affinis*. Seasonal variation of (A) density (both total and naupliar), (B) biomass and (C) calculated production in Lake Ferring in 1992

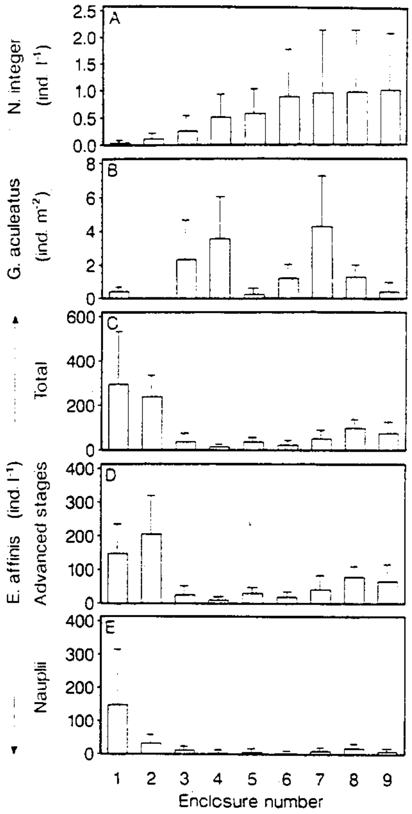

Fig. 6. Mean density (30 July to 20 August 1992) (±SD, n = 7) of (A) *Neomysis integer*, (B) *Gasterosteus aculeatus*, and (C) total *Eurytemora affinis*, (D) *E. affinis* copepodites + adults and (E) *E. affinis* nauplii in the 9 field enclosures ordered by increasing mean *N. integer* density

Enclosure experiments

In the enclosure experiments marked changes in *Eurytemora affinis* density were found that followed changes in the density of *Neomysis integer* and *Gasterosteus aculeatus*. Average copepod density during the 25-day experiment varied from 295 ind. l^{-1} when the density of the mysids and sticklebacks was low (0.04 ind. l^{-1} and 0.4 ind. m^{-2}, respectively), to less than 100 when mysid density was high (>0.25 ind. l^{-1}), in the latter case irrespective of stickleback density, which ranged from 0.25 to 4.2 ind. m^{-2} (Fig. 6). Naupliar density decreased markedly at a mysid density of 0.1 ind. l^{-1}, nauplii accounting for approximately 50% of the *E. affinis* population at the lowest *N. integer* density, but only 10 to 25% at higher *N. integer* densities. In accordance with this, nauplii density was significantly negatively correlated to *N. integer* density [Table 2; log(n+1) transformed data]. In contrast, no relationship was detected between the density of mysids and that of copepodites + adults, although both nauplii and advanced stages of *E. affinis* were negatively correlated to the density of *G. aculeatus*. Stepwise multiple linear regression on log(n+1) transformed data revealed a significant negative influence of *G. aculeatus* and *N. integer* on both *E. affinis* total density and the density of nauplii, while the contribution of fish × mysid was positive. In contrast, the density of the advanced stages of *E. affinis* was alone significantly negatively related to the density of *G. aculeatus* (Table 3).

Correlation analysis [log(n+1) transformed data] revealed a highly positive relationship between chl *a* and the *Neomysis integer* density, but only a moderately negative relationship to *Eurytemora affinis* and no re-

Table 2. Spearman correlation coefficients (with the statistical significance level in parentheses) based on log(n+1) transformed data collected on 7 sampling dates (30 July to 20 August) in 9 field enclosures. *, **, ***, **** represent the 0.05, 0.01, 0.001 and 0.0001 significance levels, respectively. ns: not significant

	Three-spined sticklebacks	*Neomysis integer*	*Eurytemora affinis* number			*E. affinis* Total biomass
			Nauplii	Copepodites + adults	Total	
N. integer	-0.002^{ns}					
E. affinis number						
Nauplii	-0.27^{*}	-0.46^{***}				
Copepodites + adults	-0.62^{****}	0.05^{ns}	0.49^{****}			
Total	-0.59^{****}	-0.06^{ns}	0.67^{****}	0.97^{****}		
E. affinis						
Total biomass	-0.62^{****}	0.04^{ns}	0.52^{****}	0.99^{****}	0.98^{****}	
Chl *a*	-0.03^{ns}	0.49^{****}	-0.32^{*}	-0.02^{ns}	-0.12^{ns}	-0.03^{ns}

lationship to *Gasterosteus aculeatus* density (Table 2). Stepwise multiple linear regression on log(n+1) transformed data revealed a highly significant relationship between chl *a* and *N. integer* density, and a slightly negative one to *E. affinis* density (Table 3).

Predation experiments

The predation experiments showed a positive relationship between naupliar density and the *Neomysis integer* specific predation rate (SPR) ($r^2 = 0.89$, $p < 0.0001$, Pearson's correlation) (Table 4). The SPR on nauplii at 15°C changed from an average of 15 ind. mysid^{-1} h^{-1} at a density of 100 nauplii l^{-1} to an average of 52 ind. mysid^{-1} h^{-1} at a density of 400 nauplii l^{-1}. SPR on the advanced stages of *Eurytemora affinis* was not influenced by changes in naupliar density, and remained constant at an average of 6 ind. mysid^{-1} h^{-1} ($p > 0.3$, Kruskal-Wallis). Moreover, the clearance rates were not influenced by changes in naupliar density ($p > 0.3$, Kruskal-Wallis), probably indicating that the mysids catch the nauplii by 'filter feeding' (Gauld 1951). The average clearance rate was 0.34 l mysid^{-1} h^{-1} for nauplii and 0.08 l mysid^{-1} h^{-1} for copepodites + adults. The mysid preference value was 0.7 for nauplii and for advanced stages 0.3, the values being unaffected by naupliar density ($p > 0.25$, Kruskal-Wallis).

DISCUSSION

Neomysis integer had 2 generations in Lake Ferring during the study year. Recruitment started in May and June when the winter generation reproduced, and the resultant spring-born first generation constituted the

Table 3. Stepwise multiple regression showing the relationship between log(n+1) transformed values of chl *a*, the density of nauplii, copepodites + adults (Cop.+ adults) and all stages of *Eurytemora affinis* versus log(n+1) transformed values of *E. affinis* (only chl *a*), *Neomysis integer* and sticklebacks *Gasterosteus aculeatus* density, as well as date in the enclosure experiments in July and August. *, **, ***, **** represent the 0.05, 0.01, 0.001 and 0.0001 significance levels, respectively. ns: not significant

	Chl *a* (µg l^{-1})	*F*	*Eurytemora affinis* (ind. l^{-1})					
			Nauplii	*F*	Cop.+ adults	*F*	Total	*F*
Intercept	6.16	4544^{****}	3.29	60^{****}	4.46	561^{****}	5.18	426^{****}
E. affinis	−0.05	10^{**}	–		–		–	
Neomysis integer	0.21	19^{****}	−3.42	24^{****}	ns		−1.76	8^{**}
Sticklebacks	ns		−1.28	19^{****}	−1.25	41^{****}	−1.63	43^{****}
N. integer × fish	ns		2.49	9.5^{**}	ns		2.02	8^{**}
Dates		11^{****}		4.4^{**}	ns		ns	
1	0.06		−0.05					
2	−0.11		0.46					
3	0.08		−0.12					
4	0.19		1.63					
5	0.37		1.02					
6	0.25		−0.17					
Model r^2	0.67		0.60		0.40		0.46	
df	61		61		61		61	

Table 4. Mean (±SD) specific predation rates, clearance rates and selectivity coefficient of *Neomysis integer* feeding at 3 different densities of *Eurytemora affinis*. Water volume was 1 l, incubation time 2 h at 15°C in subdued light, and mysid density 3 l^{-1}. NC: density change in controls during the experiment

	Inital density (ind. l^{-1})	NC (ind. l^{-1})	Spec. predation rate (ind. $mysid^{-1}$ h^{-1})	Clearance rate (l $mysid^{-1}$ h^{-1})	Selectivity coefficient
Nauplii	100	2 ± 1	15 ± 2	0.38 ± 0.18	0.65 ± 0.09
Copepodites + adults	100	0 ± 2	8 ± 2	0.11 ± 0.05	0.36 ± 0.09
(n = 3)					
Nauplii	200	2 ± 3	26 ± 6	0.36 ± 0.22	0.75 ± 0.11
Copepodites + adults	100	2 ± 2	5 ± 4	0.08 ± 0.10	0.25 ± 0.11
(n = 9)					
Nauplii	400	3 ± 14	52 ± 11	0.30 ± 0.17	0.70 ± 0.12
Copepodites + adults	100	4 ± 4	6 ± 3	0.07 ± 0.04	0.30 ± 0.12
(n = 6)					

summer generation that together with surviving individuals of the winter generation reproduced in July and August, thus providing the new winter generation. Because of the protracted reproduction period, it was difficult to follow the individual cohorts; however, the seasonal variation in mysid size distribution was identical with that observed for *N. integer* in other brackish lakes, both in Denmark (Kaiser 1978) and elsewhere (Kinne 1955, Mauchline 1971, Borghouts 1978, Mauchline 1980, Bremer & Vijverberg 1982, Arndt & Jansen 1986, Irvine et al. 1993).

Mysid density and biomass in Lake Ferring was high (maximum 0.8 ind. l^{-1}, corresponding to 1250 ind. m^{-2}), the maximum biomass being 1100 mg DW m^{-2}. Similar mysid density was observed by Irvine et al. (1993), whereas much lower values were recorded by Bremer & Vijverberg (1982) and Arndt & Jansen (1986). Even though daytime mysid density in Lake Ferring was high, it was probably considerably underestimated. The diurnal study revealed substantial diel vertical migration of *N. integer*, the catches in Breder traps located at the lake bottom being 2- to 3-fold greater in daytime than at night, and the vertical hauls being conversely 4-fold less in daytime than at night. That mysids in shallow lakes undergo diurnal migration is well documented (Beattie & de Kruijf 1978, Bremer & Vijverberg 1982, Irvine et al. 1993), and the differences found between day and night hauls were comparable to those found in previous investigations (Grossnickle & Morgan 1979, Nero & Davies 1982, Irvine et al. 1993). Estimated mysid density (and hence potential mysid impact on zooplankton) may therefore be underestimated by a factor of 4, the true density probably therefore being nearer 3 ind. l^{-1} at maximum.

The high mysid density in Lake Ferring may reflect the hypertrophic character of the lake and the low predation pressure by fish; the fish biomass is extremely low and exclusively dominated by sticklebacks that mainly prey on copepods and to a minor extent on juvenile *Neomysis integer* (M. Søndergaard & E. Jeppesen unpubl. obs.). High densities of *N. integer* (up to 13 ind. l^{-1}) have been found in other Danish hypertrophic brackish lakes in which fish biomass is low (Jeppesen et al. 1994). Moreover, the relationship between *N. integer* density and the biomass of fish caught in multiple mesh size gill nets is generally negative in Danish shallow brackish lakes (Jeppesen et al. 1994). The importance of fish is also evidenced by fish manipulation experiments undertaken in Lake Wolderwejd, The Netherlands, where removal of 75% of the planktivorous fish biomass resulted in a major increase in *N. integer* density (Meijer et al. 1994).

The estimated growth rates of the various *Neomysis integer* size groups and the seasonal dynamics are similar to those found in previous investigations (Bremer & Vijverberg 1982, Asthorsson & Ralph 1984, Arndt & Jansen 1986). The validity of calculating mysid growth rates from field data was questioned by Asthorsson & Ralph (1984) on the grounds that it is periodically difficult to follow the cohorts. On the other hand, growth rates calculated from laboratory experiments may be influenced by the experimental conditions. In comparison with laboratory growth rates, Arndt & Jansen (1986) found higher rates in natural populations. Mysid production (not corrected for sampling error) was higher than 10 mg DW m^{-2} d^{-1} during most of the summer, reaching 35 mg DW m^{-2} d^{-1} in mid-July. Despite the much higher density in Lake Ferring, the level and seasonal variation in the *N. integer* P/B ratio was comparable to that reported in other studies on *N. integer* (Bremer & Vijverberg 1982, Arndt & Jansen 1986).

As to whether a high density of *Neomysis integer* affects the population structure of its potential prey, *Eurytemora affinis*, the laboratory predation experiments showed that mysids had a selective preference for nauplii and that the predation potential was high, with maximum predation rates on nauplii and copepodites + adults of 52 and 8 ind. mysid^{-1} h^{-1}, respectively. Converted to biomass, this amounts to a daily ration of approximately 360 % d^{-1} (3.6 g DW g^{-1} DW d^{-1}). These rates are similar to observations made in other laboratory studies on *N. integer* (Irvine et al. 1990, 1993). If the *in situ* predation rate was really so high, mysids in Lake Ferring would exterminate the nauplii and copepodite populations in a few days. This also applies to the field enclosures with the highest densities of *N. integer* (0.5 to 1 ind. l^{-1}). However, as the predator and prey species coexist in both the enclosures and the lake as a whole, the predation pressures found in the laboratory experiments must be overestimates. There are various possible explanations for this. Firstly, *E. affinis* may find it more difficult to escape predation in the experimental chambers than in the field. In the lake the *N. integer* seek refuge from fish predation by staying near the bottom during daytime, but at the same time thereby affording the pelagic *E. affinis* a higher chance of survival. Secondly, there are alternative food sources in the lake, *N. integer* being known to be omnivorous and also able to feed on detritus and algae (Mauchline 1971, Bremer & Vijverberg 1982, Arndt & Jansen 1986, Irvine et al. 1993). That this was the case in Lake Ferring was confirmed by qualitative analysis of *N. integer* gut contents; these consisted, apart from copepods, of cyanobacteria, chlorophytes and diatoms, as well as various zooplankton such as ciliates and rotifers. Fragments of vascular plants, pollen and detritus were also detected. Further evidence of omnivory is provided by the fact that *N. integer* would only be able to meet a maximum of 22% and as little as 6% when corrected for sampling error of its food energy requirements from *E. affinis*, if we assume a growth yield of approximately 20% for *N. integer* (as the production of *E. affinis* and *N. integer* was calculated to 2.5 and 2.2 g DW m^{-2} yr^{-1}, respectively). That the predation rates found in the laboratory studies are overestimates is further emphasized by the fact that a daily ration of 360% d^{-1} will result in a growth rate far exceeding that obtained from the lake data (Fig. 2), and considerably greater than that found in several other studies (Cooper & Goldman 1980, Chigby & Sibley 1994). As the mysids used in the laboratory studies were prefed with *E. affinis*, the possibility can be excluded that prestarvation could explain the high predation rates obtained.

The enclosure experiments showed that at natural lake densities, *Neomysis integer* had a significant negative effect on the abundance of nauplii as well as on the total number of *Eurytemora affinis*, but not on the number of copepodites + adults. In contrast, *Gasterosteus aculeatus* had a negative impact on all stages but particularly the advanced stages, as has been reported in many other studies (e.g. Worgan & FitzGerald 1981, Castonguay & FitzGerald 1990, Pont et al. 1991). The contribution of sticklebacks × *N. integer* in the multiple regression was positive for the nauplii (Table 3), however, which may be explained by the fact that *N. integer* seeks refuge from fish predation near the bottom (Meijer et al. 1994), thereby reducing the predation pressure on the nauplii, which typically inhabit pelagic waters.

Since *Neomysis integer* and *Gasterosteus aculeatus* coexist in many hypertrophic brackish lakes, including Lake Ferring, it is therefore likely that the predation pressure on *Eurytemora affinis* in such lakes is particularly high, the *E. affinis* being preyed upon both from 'below' (*N. integer*) and from 'above' (*G. aculeatus*). The coexistence of *N. integer* and sticklebacks may explain why the zooplankton grazing pressure on the phytoplankton is generally lower in hypertrophic brackish lakes, including Lake Ferring, than in corresponding freshwater lakes, where planktivorous fish are the exclusively dominant macropredator (Jeppesen et al. 1994).

In the enclosure experiments a highly positive correlation was found between chl *a* and *Neomysis integer* density. This may in part be explained by predation on the phytoplankton-grazing copepods since chl *a* and nauplii density were negatively correlated (Table 2). However, the correlation to *N. integer* was much stronger than to copepods. Moreover, the stepwise multiple regression showed that *N. integer* contributed highly significantly to residual variation in chl *a* when copepods were included in the model, while sticklebacks did not (Table 3). Similar results were obtained in enclosure experiments in another Danish brackish lake (F. Nielsen & E. Jeppesen unpubl. obs.). These results suggested a more direct stimulation of phytoplankton growth by *N. integer*, perhaps because nutrients consumed when feeding on the sediment surface are subsequently excreted to the water above. In fact, the experiment by Nielsen & Jeppesen (unpubl. obs.) showed markedly higher phosphorus levels in enclosures with *N. integer*. As the density in the enclosures (0.5 to 1 mysid l^{-1}) in Lake Ferring was comparable to that in the lake (Figs. 4 & 5), it seems reasonable to suggest that mysids negatively influenced the environmental state of the lake in terms of higher algal biomass and consequently a lower Secchi depth. In support of this view multiple regression analysis of 3 years' data from the lake showed that besides being significantly negatively related to the total zooplankton biomass, chl *a* was positively related to the *N. integer* density (Nielsen & Jeppesen unpubl. obs.).

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LITERATURE CITED

Arndt EA, Jansen W (1986) *Neomysis integer* (Leach) in the Chain of Boddens south of Darss/Zingst (Western Baltic). Ecophysiology and population dynamics. Ophelia 4:1-15

Asthorsson OS, Ralph R (1984) Growth and moulting of *Neomysis integer* (Crustacea: Mysidacea). Mar Biol 79:55-61

Bach F, Petersen A, Jacobsen H (1991) Metoder ved oparbejdning af plankton i Ferring Sø, Søndervese, Nørrevese, Noret og Hygum Nor 1990. Report to Ringkjøbing County. Danish Health Society, Silkeborg

Beattie DM, de Kruijf H (1978) Population dynamics and biomass production of *Neomysis integer* (Leach) in the Bergumermeer. Verh int Verein theor angew Limnol 20: 2566-2571

Borghouts CH (1978) Population structure and life-cycle of *Neomysis integer* (Leach) (Crustacea, Mysidacea) in two types of inland waters. Verh int Verein theor angew Limnol 20:2561-2565

Bowers JA, Vanderploeg HA (1982) *In situ* predatory behavior of *Mysis relicta* in Lake Michigan. Hydrobiologia 93: 121-131

Branstrator DK, Lehman JT (1991) Invertebrate predation in Lake Michigan: regulation of *Bosmina longirostris* by *Leptodora kindtii*. Limnol. Oceanogr. 36(3):483-495

Breder CN (1960) Design for a fry trap. Zoologica 45:155-160

Bremer P, Vijverberg J (1982) Production, population biology and diet of *Neomysis integer* (Leach) in a shallow Frisian lake (The Netherlands). Hydrobiologia 93:41-51

Castonguay M, FitzGerald GJ (1990) The ecology of the calanoid copepod *Eurytemora affinis* in salt marsh tide pools. Hydrobiologia 202:125-133

Chesson J (1978) Measuring preference in selective predation. Ecology 59(2): 211-215

Chigby P, Sibley TH (1994) Predation by *Neomysis mercedis*: effects of temperature, *Daphnia magna* size and prey density on ingestion rate and size selectivity. Freshwat Biol 32: 39-48

Cooper SD, Goldman CR (1980) Opossum shrimp (*Mysis relicta*) predation on zooplankton. Can J Fish Aquat Sci 37:909-919

Fulton RS III (1983) Interactive effects of temperature and predation on an estaurine zooplankton community. J exp mar Biol Ecol 72:67-81

Gauld DT (1951) The grazing rate of planktonic copepods. J mar biol Ass UK 29:695-706

Gliwicz ZM, Pijanowska I (1989) The role of predation in zooplankton succession. In: Sommer U (ed) Plankton ecology — succession in plankton communities. Springer-Verlag New York, p 253-296

Goldman CR, Morgan MD, Threlkeld ST, Angeli N (197 A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. Limnol Oceanogr 24(2):289-297

Grossnickle NE, Morgan MD (1979) Density estimates of *Mysis relicta* in Lake Michigan. J Fish Res Bd Can 36: 694-698

Hanazato T (1990) A comparison between predation effects on zooplankton communities by *Neomysis* and *Chaoborus*. Hydrobiologia 198:33-40

Hansson S, Larsson U, Johansson S (1990) Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J Plankton Res 12:1099-1116

Higgins PJ (1985) An interactive computer program for population estimation using the Zippin method. Aquacult Fish Mgmt 1:287-295

Hirche HJ (1992) Egg production of *Eurytemora affinis* — effect of k-strategy. Estuar coast Shelf Sci 35:395-407

Holm-Hansen O, Riemann B (1978) Chlorophyll a determination: improvements in methods. Oikos 30:438-447

Irvine K, Bales MT, Stansfield JH, Snook D (1990) Trophic relations in Hickling Broad — a shallow and brackish eutrophic lake. Verh int Verein theor angew Limnol 24: 576-579

Irvine K, Moss B, Bales M, Snook D (1993) The changing ecosystem of a shallow, brackish lake, Hickling Broad, Norfolk, UK. I. Trophic relationships with special reference to the role of *Neomysis integer* (Leach). Freshwat Biol 29:119-139

Jeppesen E, Søndergaard M, Kanstrup E, Petersen B, Eriksen RB, Hammershøj M, Mortensen E, Jensen JP, Have A (1994) Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia 275/276:15-30

Kaiser EW (1978) Storkrebs (Malocostraca) fra indvande i Thy og Vester-Hanherred. Zootopografiske undersøgelser i Thy 14. Flora Fauna 84:3-28

Kinne O (1955) *Neomysis vulgaris* Thompson, eine autökologisch-biologische Studie. Biol Zbl 74:160-202

Langeland A (1988) Decreased zooplankton density in a mountain lake resulting from predation by recently introduced *Mysis relicta*. Verh int Verein theor angew Limnol 23:419-429

Mauchline J (1971) The biology of *Neomysis integer* (Crustacea, Mysidacea). J mar biol Ass UK 51:347-354

Mauchline J (1980) The biology of mysids and euphausiids. In: Blaxter JHS, Russel FS, Yonge M (eds) Advances in marine biology 18. Academic Press, London, p 1-677

Meijer ML, van Nes EH, Lammens EHRR, Gulati RD, Grimm MP, Backx J, Hollebeek P, Blaauw EM, Breukelaar AW (1994) The consequences of a drastic fish stock reduction in the large shallow Lake Wolderwijd, The Netherlands. Can we understand what happened? Hydrobiologia 275/276:457-466

Moss B (1994) Brackish and freshwater shallow lakes — different systems or variations on the same theme? Hydrobiologia 275/276:1-14

Moss B, Leah RT (1982) Changes in the ecosystem of a guanotrophic and brackish shallow lake in eastern England: potential problems in its restoration. Int Revue ges Hydrobiol 67(5):625-659.

Nero RW, Davies IJ (1982) Comparison of two sampling methods for estimating the abundance and distribution of *Mysis relicta*. Can J Fish Aquat Sci 39:349-355

Pont D, Crivelli AJ, Guillot F (1991) The impact of three-spined sticklebacks on the zooplankton of a previously fish-free pool. Freshwat Biol 26:149-163

Rudstam LG, Hansson S, Larsson U (1986) Abundance, species composition and production of mysid shrimps in a coastal area of the Northern Baltic Proper. Ophelia 4:225-238

Worgan JP, FitzGerald GJ (1981) Diel activity and diet of three sympatric sticklebacks in tidal salt marsh pools. Can J Zool 59:2375-2379

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Addresses:

URL: http://www.dmu.dk

National Environmental Research Institute
Frederiksborgvej 399
PO Box 358
DK-4000 Roskilde
Denmark
Tel: +45 46 30 12 00
Fax: +45 46 30 11 14

Management
Personnel and Economy Secretariat
Research and Development Section
Department of Atmospheric Environment
Department of Environmental Chemistry
Department of Policy Analysis
Department of Marine Ecology and Microbiology

National Environmental Research Institute
Vejlsøvej 25
PO Box 413
DK-8600 Silkeborg
Denmark
Tel: +45 89 20 14 00
Fax: +45 89 20 14 14

Department of Lake and Estuarine Ecology
Department of Terrestrial Ecology
Department of Streams and Riparian areas

National Environmental Research Institute
Grenåvej 12, Kalø
DK-8410 Rønde
Denmark
Tel: +45 89 20 17 00
Fax: +45 89 20 15 14

Department of Landscape Ecology
Department of Coastal Zone Ecology

National Environmental Research Institute
Tagensvej 135, 4
DK-2200 København N
Denmark
Tel: +45 35 82 14 15
Fax: +45 35 82 14 20

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