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Development and application of zooplankton-based paleoecological methods with special focus on Danish brackish lakes

PhD thesis

Susanne Lildal Amsinck

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Susanne Lildal Amsinck
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Development and application of zooplankton-based paleoecological methods with special focus on Danish brackish lakes

Background

In Denmark, brackish lakes are widespread and contribute significantly to the total lake area. The lakes are situated along the coasts, having either evolved naturally or been artificially constructed by land reclamation. The lakes are valuable for tourism and recreational purposes and are as well nationally and internationally important areas of conservation. Some lakes are thus recognised by the Ramsar Convention and under the EC Bird Directive as Special Protection Areas, an example being the Vejlerne Nature Reserve in northern Jutland.

Trophic structure and differences from freshwater lakes

Like many freshwater lakes, several coastal brackish lakes in Northern Europe are in a eutrophic, turbid state (Bales et al. 1993, Moss 1994, Aaser et al. 1995, Jeppesen et al. 1997, Jensen et al. 2002). Yet, contrary to freshwater lakes, little detailed information is available on the long-term development, past conditions, biological structure and trophic dynamics, as most studies of brackish lakes are of recent origin or based on field enclosure studies of short duration. The contemporary studies unambiguously demonstrate that brackish food web structure and trophic interactions, as well as biological responses to nutrient loading, markedly diverge from the patterns observed in freshwater systems.

First of all, the predation pressure on zooplankton is higher in eutrophic brackish lakes than in comparable freshwater lakes. This is partly due to dominance of small-sized three- and nine-spined sticklebacks (*Gasterosteus aculeatus*, *Pungitius pungitius*), which produce offspring several times annually (Jeppesen et al. 1994, 1997). By contrast, in eutrophic freshwater lakes the dominant fish species roach (*Rutilus rutilus*) and bream (*Abramis brama*) reproduce only once a year (Persson et al. 1988, Jeppesen et al. 1994, 2000). As particularly the predation pressure by fish fry on zooplankton is high (He & Wright 1992, Søndergaard et al. 1997), the sticklebacks may potentially exert a continuously high top-down control on zooplankton. In addition, densities of the mysid shrimp *Neomysis integer*, found to be the dominant invertebrate predator in eutrophic brackish lakes at salinities of 0.5-18‰ (Moss 1994, Jeppesen et al. 1994, Aaser et al. 1995, Irvine et al. 1990, 1995, Søndergaard et al. 2000) increase with increasing nutrient levels (Jeppesen et al. 1994, 1997), whereas the densities of the most common invertebrate predators in freshwater lakes, *Leptodora kindtii* and *Chaoborus* (Hanazato 1990, Jeppesen et al. 1991), decline at high nutrient levels (> 250 µg P l^{-1}) (Jeppesen et al. 1997). Moreover, *Neomysis* primarily preys upon large-bodied zooplankton (Arndt & Jansen 1986, Irvine et al. 1995), while *Leptodora* and *Chaoborus* primarily prey upon small and medium-bodied cladocerans (Hanazato 1990). Hence, as large-bodied zooplankton are the most efficient phytoplankton grazers (Gliwicz 1977, 1990), the zooplankton capacity to control phytoplankton through grazing is most likely lower in eutrophic brackish lakes than in comparable freshwater lakes. In support of this view, significantly lower zooplankton/phytoplankton biomass ratios have been found in brackish lakes (Jeppesen et al. 1994, 1997). Moreover, sticklebacks and *Neomysis* are frequently abundant within the littoral zone (Muus 1967, Jeppesen et al. 1997), potentially diminishing the value for zooplankton of using the macrophytes as a daytime refuge against predation. This may, in addition, be a contributing factor to the circumstance that eutrophic brackish lakes remain turbid even at extensive abundance of submerged macrophytes (Moss et al. 1994, Jeppesen et al. 1997). By contrast, in freshwater lakes, macrophytes presumably serve as an effective daytime refuge for zooplankton against predation (Timms & Moss 1984, Lauridsen & Buenk 1996) as e.g. roach feed more effectively in open water than in complex structure habitats such as macrophyte beds (Irvine et al. 1990). Hence, turbidity due to low grazing control in

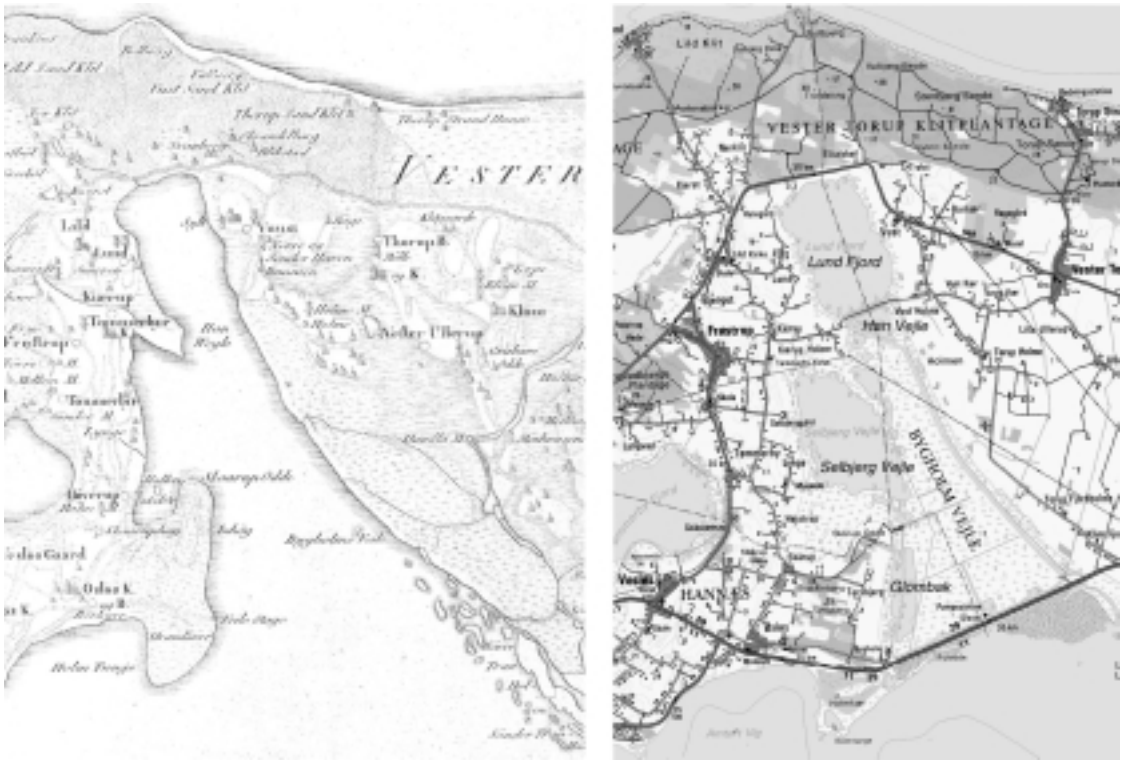

Figure 1. Before land reclamation in the mid-1870s, the Vejlerne nature reserve consisted of shallow branches of the Limfjord (map to the left, Videnskabernes Kort 1787). Around 1916, land reclamation, involving draining and damming, was abandoned, and brackish lakes, reed swamps and meadows evolved. Today, the reserve covers approx. 6000 ha, of which 40 % is covered by brackish lakes (map to the right, Danmarks Topografiske Kortværk 2000, © Kort og Matrikelstyrelsen). Only the eastern part of the reserve is shown.

freshwater lakes is usually confined to lakes in which submerged macrophytes are almost absent (Jeppesen et al. 1999).

Secondly, salinity influences zooplankton species richness and community structure (Hammer 1986, Frey 1993, Bos 1999, Wolfram & al. 1999, Boronat et al. 2001) due to different physiological capacities among the zooplankton (Aladin 1991). The large-bodied cladoceran *Daphnia*, being the key grazer of phytoplankton in freshwater lakes (Carpenter & Kitchell 1993), occurs primarily at salinities below 2‰ (Jeppesen et al. 1994). By contrast, the small-bodied cladoceran *Bosmina longirostris*, the calanoid copepods *Eurytemora affinis* and *Acartia* spp., and the rotifer *Brachionus*, all less efficient algal grazers compared to *Daphnia*, tend to dominate at salinities above 2‰ (Jeppesen et al. 1994, 1997, 2002). Thus, the algal grazing capacity is most likely lower in brackish lakes (> 2‰) than in freshwater lakes, irrespective of the nutrient regime. In agreement with these observations, Jeppesen et al. (1994) found a significantly lower grazing pressure on algae along a gradient of total phosphorus (TP) in brackish lakes (0.5-36‰) compared to corresponding freshwater lakes.

Long-term lake development and use of paleoecological methods

Even though the present turbid state of the brackish lakes may be explained in part by the low top-down control of phytoplankton, as mentioned above, the long-term development still remains to be elucidated. However, the substantial differences between brackish and freshwater lakes, makes transference of knowledge obtained from long-term development in freshwater lakes adverse. In the Norfolk Broads, England, shifts from a clearwater to a turbid state have been observed in brackish lakes having undergone eutrophication during the last century (Moss & Leah 1982, Moss 1994). A number of questions may be raised regarding the development of brackish Danish lakes: Did similar shifts occur here? If so, when? Which biological changes were involved? How substantial were they? Did intermediate states appear? Given the lack of long-term development, and with it the lack of information on pre-disturbed lake conditions, how do we define suitable targets to

be implied in future management strategies for Danish brackish lakes?

In freshwater lakes, paleoecological investigations have proven to be a successful tool to elucidate similar kinds of questions and they provide valuable information on reference states, which may serve as targets for lake restoration projects. Especially zooplankton subfossils recovered from lake sediments are useful indicators of eutrophication-related changes in fish predation (Kitchell & Kitchell 1980, Sanford 1993, Hann et al. 1994, Jeppesen et al. 1996, 2001a) and of changes in the relative importance of different habitats, such as macrophytes, sediments and the pelagic zone (Whiteside 1970, Frey 1986, Hann 1990, Jeppesen et al. 2001b, Shumate et al. 2002). Recently, statistical methods such as weighted-average calibration models have been developed, allowing reconstruction of planktivorous fish densities (Jeppesen et al. 1996) and submerged macrophyte coverage (Jeppesen 1998) based on pelagic zooplankton and macrophyte-associated cladocerans, respectively. In addition, models for inference of TP based on sedimentary chydorids have been evolved (Brodersen et al. 1998). The application of zooplankton subfossils to infer past abundances of fish and macrophytes is particularly useful, as fish (bones, scales etc.) and macrophyte remains (seeds, reproductive structures, tissues etc.) can only provide qualitative information on factors such as absence and presence. Moreover, analyses of fish remains usually involve methodological problems in that excessively large volumes of sediment are required to recover the scarce fish remains (Jeppesen et al. 2001b).

Aim of this thesis

The overall aim was to develop and apply zooplankton-based paleoecological methods to describe long-term development and to detect changes in biological structure and trophic interactions in Danish brackish lakes.

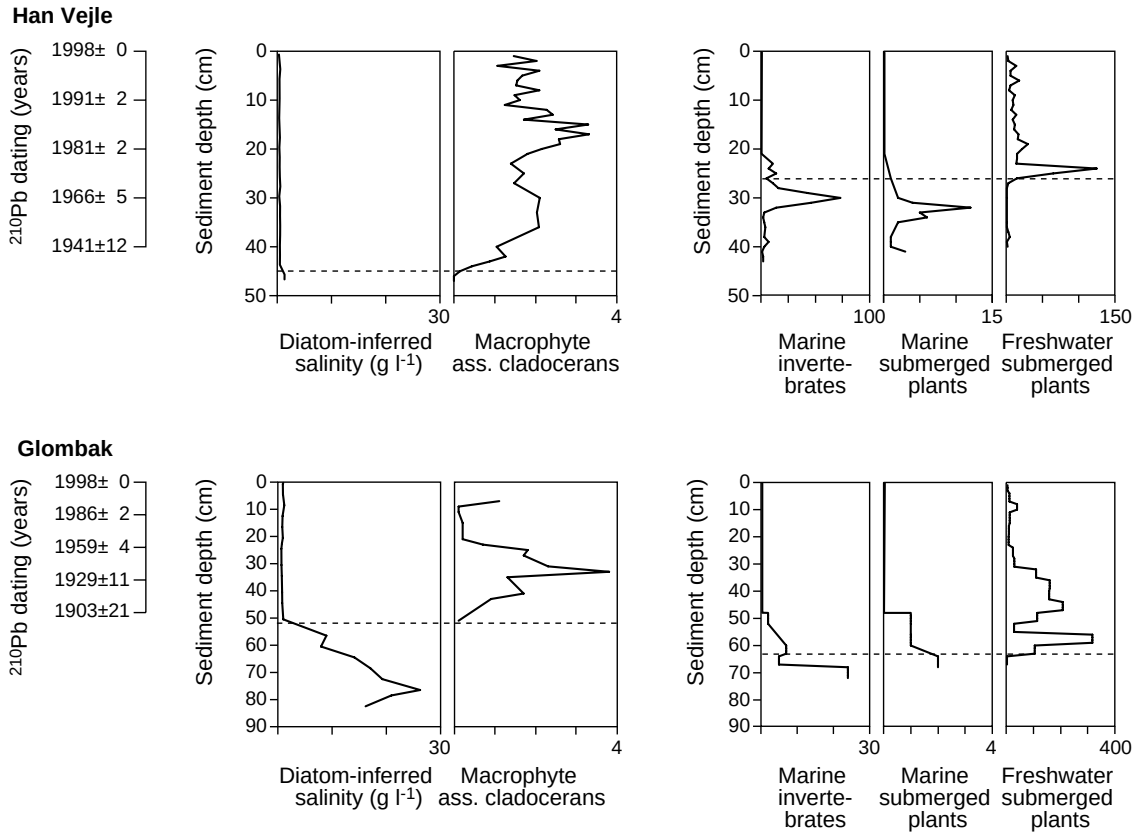

Figure 2. The overall development trends of salinity and marine invertebrates, marine submerged plants and freshwater submerged plants indicated by subfossils assemblages in sediment cores of Han Vejle and Glombak. Horizontal lines indicate transition from marine to brackish - freshwater conditions. ^{210}Pb dating, analyses of diatoms and cladoceran subfossils conducted on one core, macrofossils on another. Cladoceran subfossils expressed as relative weighted abundance (*paper I, figure 3*) and macrofossils as no. of remains pr. 20 ml wet weight sediment. (Macrofossil analysis conducted by Ole Bennike, diatom-inferred salinity reconstructions by David Ryves, unpublished data, shown with permission).

Specific objectives were to:

- elucidate the use-value of zooplankton subfossils as indicators of past changes in biological structure of Danish brackish lakes.
- describe the development of Danish brackish lakes with special emphasis on eutrophication-related biological changes.
- elucidate the importance of different environmental variables determining zooplankton community structure and species richness and evaluate interactions between variables.
- develop inference models for reconstruction of environmental variables important to the zooplankton community structure and evaluate the reliability of model performance.
- apply the inference models to describe past changes in Danish brackish lakes and compare the reconstructions with known historical documentary sources and findings obtained by qualitative paleoecological methods.

Summary of thesis papers and results

Paper I describes past changes in the biological structure having occurred since 1870 in two shallow coastal brackish lakes, Glombak and Han Vejle, located in the Vejlerne nature reserve, Denmark. The two lakes have evolved simultaneously following abandoned land reclamation in the mid-1870s (Figure 1). Yet, the present-day diverging environmental states of the lakes, Glombak being turbid and Han Vejle clear, suggest that the lakes have developed along different environmental tracks.

Zooplankton subfossils (*Cladocera*, *Foraminifera*) were recovered and identified from ^{210}Pb dated sediment cores. Stratigraphic changes from foraminifer to cladoceran dominance indicated an abrupt shift from marine to slightly brackish (Glombak) and freshwater conditions (Han Vejle) coinciding with the land reclamation. In Glombak, the subfossil cladoceran record suggested an increase in fish predation and a subsequent major decline in macrophytes around the mid-1960s (Figure 2). In Han Vejle, a high and almost constant macrophyte abundance (Figure 2) and only minor changes in fish predation seem to have prevailed throughout most of the 20th century. The cladoceran community structure indicated different exposures to salinity and eutrophication, and most likely also different sensitivities to water level changes, factors that may have contributed to today's distinctly different trophic environmental state of the lakes.

The results are consistent with trends and patterns in the sediment records of diatoms and macrofossils (macrophytes and invertebrates) (Figure 2) as well as with historical

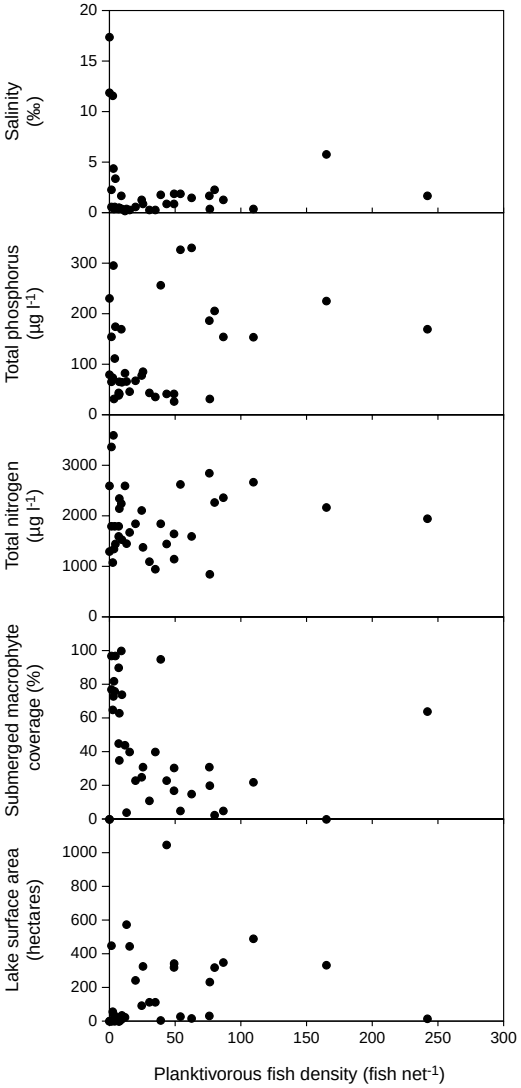

Figure 3. Salinity, epilimnion total phosphorus, epilimnion total nitrogen, coverage of submerged macrophytes and total lake surface area vs. the density of planktivorous fish (PL-CPUE) caught in multiple mesh size gill nets in 36 Danish shallow brackish lakes. (Data from *paper II*).

information and recent contemporary data.

Paper II describes the calibration data set and transfer functions developed from zooplankton subfossils recovered from surface sediments and corresponding contemporary environmental variables (salinity, TP, total nitrogen, macrophyte abundance and planktivorous fish densities) from 36 coastal shallow brackish lakes located in north-western Jutland, Denmark.

The species composition of the zooplankton subfossils showed a significant relationship with salinity, TP and planktivorous fish densities (PL-CPUE), the latter being the only independent environmental variable (Figure 3). Cladoceran species richness was negatively related to both salinity and nutrients. Predictive models for inference of PL-CPUE were developed for 1) all the zooplankton taxa identified, and 2) for specific taxa significantly related to PL-CPUE according to Spearman´s rank correlation. A two-component weighted-averaging-least-partial-squares regression model (WA-PLS) based upon all identified zooplankton taxa provided the most reliable model for PL-CPUE reconstruction with the highest coefficient of determination and lowest jack-knifed root-mean-squared-error of prediction. Yet, residual distribution showed a significant bias (Figure 4). The inference models were applied to subfossil records from Han Vejle and Glombak. In Han Vejle, the reconstructions indicated low and constant levels of PL-CPUE, while in Glombak, PL-CPUE seemed to have increased during the 20th century (Figure 5). Correspondence analyses (CA) based on the species abundances of the subfossil records and of the calibration data set were conducted to qualitatively describe the past changes in environmental conditions of Glombak and Han Vejle.

The patterns identified between zooplankton species distribution, community structure and richness and the environmental variables studied agree with contemporary observations from both saline and brackish lakes. The findings of the PL-CPUE reconstructions are consistent with the size-selective predation on zooplankton indicated by the qualitative paleoecological studies (*paper I*) and with currently measured PL-CPUE values in the two lakes.

Paper III describes the historical changes having occurred during the last century in the biological structure of Lake Flade, a shallow coastal brackish lake located in north-western Jutland, Denmark. The lake has evolved by post glacial land uplift and land-filling by shifting sand, and during the last two centuries it has been markedly affected by anthropogenic activities (Figure 6). During the 20th century Lake Flade was an important site for fishery, first for eel catches and later for pike-perch angling. However, the lake has experienced several fish kill incidents during the last century and is today in a eutrophic, turbid state.

Zooplankton (*Cladocera*, *Rotifera, Foraminifera*) assemblages were analysed in a ^{210}Pb dated sediment core retrieved from Lake Flade. Planktivorous fish densities were reconstructed by the two-component WA-PLS model (*paper II*) to evaluate the potential of identifying known fish kill incidents using sedimentary subfossils. In addition, past changes in environmental conditions were qualitatively described by CA using the calibration data set (*paper II*). The stratigraphic changes in the cladoceran assemblages indicated a shift towards decreased water transparency, a decline in macrophyte abundance and an increase in the size-selective predation pressure on cladocerans during the 20th century. In agreement with this, the reconstructions of PL-

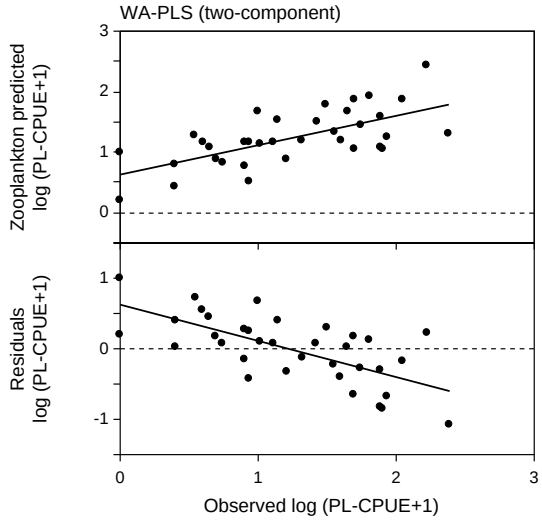

Figure 4. Zooplankton predicted PL-CPUE and residual distribution vs. observed PL-CPUE. Predicted values calculated after jack-knifing (9999 iterations) for the WA-PLS (two-component) model based on 23 zooplankton taxa (22 cladocerans, 1 rotifer) and 35 lakes. (*paper II, figure 5*).

CPUE showed an increasing trend (Figure 5). The results point towards progressive eutrophication with additional impact of salinity. Unfortunately, reduced temporal resolution of the sediment record made identification of fish kill incidents difficult.

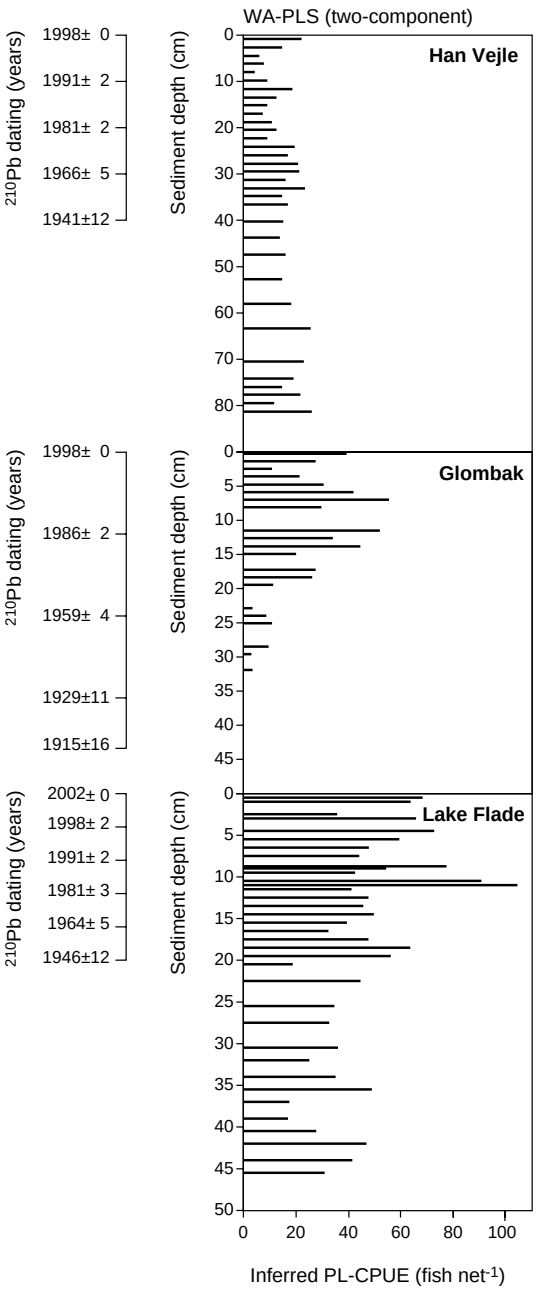

Figure 5. Reconstruction of the historical development in PL-CPUE (based on the two-component WA-PLS model, *paper II*) in Han Vejle, Glombak (*paper II*) and Lake Flade (*paper III)*. In the least eutrophic, brackish clearwater lake (Han Vejle), inferred PL-CPUE maintained low regimes, while in the slightly more eutrophic, brackish turbid lake (Glombak) inferred PL-CPUE increased during the 20th century. In Lake Flade (*paper III*), being the most eutrophic, brackish turbid lake, inferred PL-CPUE was high throughout most of the period covered by the core and even increased further during the 20th century.

The estimated historical changes in biological structure are in accordance with the sparse anecdotal observations and past fish investigations as well as with recent contemporary data.

Paper IV describes methods for reconstructing PL-CPUE and *Daphnia* mean size from the relationships between the sizes of *Daphnia* ephippia in surface sediments and contemporary data. The study included 52 freshwater lakes located in Denmark (30), Greenland (15) and New Zealand (7) with contrasting densities of planktivorous fish and nutrients.

Contemporary PL-CPUE was inversely related to the mean size of sedimentary *Daphnia* ephippia. When including epilimnion TP as a secondary independent variable, the relationship became even stronger. In addition, the contemporary summer mean body weight of *Daphnia* in the pelagial was also significantly related to the size of sedimentary *Daphnia* ephippia. Within the contemporary data set, the size of the ephippia-bearing *Daphnia* females and the size of the ephippia were significantly related. Based on these relationships, multiple regression equations were established for inference of PL-CPUE, summer mean body weight of *Daphnia* and the mean size of ephippia-bearing *Daphnia* from the size of sedimentary *Daphnia* ephippia. The equations were subsequently applied to subfossil records of four lakes (Lake Stigsholm, Lake Søgaard, Lake Langesø, Lake Søbygaard) with diverging contemporary TP levels. The estimated variables corresponded well with contemporary data and past information on fish stocks, fish kill incidents, nutrient loading etc., as well as with sedimentary records of diatoms and macrofossils.

The estimation of PL-CPUE based on *Daphnia* ephippia size provides a less time-consuming, though less accurate method, compared to that of Jeppesen et al. (1996).

Paper V elucidates relationships between zooplankton subfossils of the three pelagic genera *Bosmina*, *Daphnia* and *Ceriodaphnia*, recovered from surface sediments, and associated contemporary data. The study included 135 freshwater lakes located in Greenland (39), the Faroe Islands (25), Denmark (53) and New Zealand (18), cov-

ering a substantial gradient in climate and trophic state.

The relative abundances of *Bosmina* spp. and *Daphnia* spp. ephippia in the surface sediments were significantly related to the same genera in the pelagial zone during summer, while the abundance of *Ceriodaphnia* was higher in the sediment than in the water. Multiple regressions showed a significant inverse relationship between the abundance of sedimentary *Daphnia* ephippia and PL-CPUE when TP was included as a co-variable. Yet, the relationship was somewhat weaker when compared to the relationship based on *Daphnia* ephippia size versus PL-CPUE and TP (*paper IV*). The average ratio between *Bosmina* ephippia and the sum of *Bosmina* ephippia and carapaces was significantly inversely related to summer mean air temperature and most likely then also to lake water temperature.

Despite being based on only three cladoceran genera, the study demonstrates that subfossil analyses provide valuable information on past zooplankton community structure, fish abundance and temperature in freshwater lakes. As in *paper V*, the methods represent time-saving alternatives to the formerly developed methods.

Paper VI describes the trophic structure in the pelagial with focus on interactions between fish and crustaceans (*Cladocera*, *Lepidurus arcticus*). In addition, relationships between crustaceans sampled in the pelagial and recovered in surface sediments are elucidated. The study was conducted in 13 high arctic oligotrophic shallow freshwater lakes located in north-east Greenland.

The crustacean communities were species-poor with marked differences in community structure between fishless lakes (7) and lakes (6) with fish (*Salvelinus alpinus*). In the fishless lakes *Daphnia pulex* and *Lepidurus* were abundant, while in lakes with fish *Daphnia* and *Lepidurus* were absent. Consistent with the contemporary data, *Daphnia* and *Lepidurus* subfossils recovered from surface sediments were either absent or found in low numbers in lakes with fish, while they were abundant in all fishless lakes. Benthic chydorids (*Alona* sp. and *Macrothrix hirsuticornis*) and *Chydorus sphaericus* were more abundant in sediment samples compared to pelagial samples and no significant differences between presence or absence of the three taxa were found between lakes with or without fish. However, the densities of benthic chydorid subfossils were significantly higher in lakes with fish. No significant differences were found in chlorophyll *a*, TP, TN, conductivity or temperature between the 13 lakes, suggesting that the community structure of crustaceans is primarily driven by the top-down control exerted by fish.

The study indicates that crustacean subfossils preserved in sediments of high arctic lakes are useful for elucidating historical changes in top-down control by fish.

Figure 6. During 1868-1875 the lake basin of Lake Flade-Ørum was drained to create farmland (map at top, Høje Målebordsblade M20, 1871-1883, © Kort og Matrikelstyrelsen). Around 1882, the land reclamation was abandoned and Lake Flade-Ørum re-established (map in the middel, Topografisk Kort A1402, 1917, © Kort og Matrikelstyrelsen). In the mid-1950s, embankments were build isolating Lake Flade-Ørum into the present-day Lake Flade (4.3 km^2), Lake Ørum (4.3 km^2) and Lake Roddenbjerg (0.2 km^2) (map at the bottom, Danmarks Topografiske Kortværk 2000 © Kort og Matrikelstyrelsen).

Methodological considerations

Several methodological problems are connected with the use of paleoecological tools in the analysis of brackish lakes.

First, the shallow depth and the wind-stressed nature of Danish brackish lakes potentially increase resuspension, reducing the accuracy of radiometric dating and the ecological resolution of the sediment records (*paper III*).

Second, the different salinity tolerance of the *Daphnia* and *Bosmina* genera renders interpretation difficult, as absence of *Daphnia* and presence of *Bosmina* under high salinity regimes may be more directly linked to salinity than to size-selective fish predation. Thus, the methods found to be useful for estimating fish predation pressure in freshwater lakes (Kitchell & Kitchell 1980, *paper IV*, and *paper V*) are presumably less valid for brackish lakes.

Third, the established calibration data set is mainly based on low salinity lakes (median 0.9 ‰, gradient 0.2 - 17.4 ‰) with low PL-CPUE values (18 fish net^{-1}, gradient 0 – 242 fish net^{-1}) (Figure 3, *paper II*). Hence, the inclusion of more lakes with high salinity and high PL-CPUE levels will most likely improve the data set as well as strengthen the application of the transfer function. In addition, the number of lakes with high macrophyte abundance (> 45%) was only 14 (Figure 3), which may have contributed to the finding that macrophytes were only of minor importance to zooplankton community structure.

Fourth, the transfer function developed for estimation of PL-CPUE is based on all zooplankton taxa identified. Yet, Spearman's correlation showed that the taxa possessed different tolerances to PL-CPUE, *Ctenodaphnia* spp. being more sensitive than *Ceriodaphnia* spp., as an example (*paper II*). Expectably, transfer functions based solely on taxa with a significant relationship to PL-CPUE, as established for freshwater lakes (Jeppesen et al. 1996), will improve the accuracy of the PL-CPUE inference. However, for brackish lakes weighted averaging (WA) models based solely on taxa (n = 6) significantly related to PL-CPUE turned out be less valid compared with the models based on all the recorded zooplankton taxa (n= 23) (*paper II*). Again, the different tolerance to salinity may indicate potential problems in the development of models based on only few taxa for brackish lakes, examples being *Ctenodaphnia* spp. and *Bosmina longirostris* that are significantly related to PL-CPUE but exhibit different salinity tolerances.

Fifth, the two-component WA-PLS model for inference of PL-CPUE performed best in terms of the coefficient of determination and the jack-knifed root-mean-squared-error of prediction (*paper II*). Yet, the residuals showed a significant bias in structure (Figure 4). This conflicts with one of the main assumptions of regression models, i.e. that residuals are normally distributed error terms with a mean of zero, thus suggesting reduced applicability of the inference models. However, bias in the inferred values and hence in residuals is a general problem of WA-based methods (the so-called ´edge-effects´) (Birks 1998). One way to overcome this problem is to use ´analogue´ statistics (see "Future research perspectives").

Finally, contemporary PL-CPUE values, used for the establishment of the transfer function, are encumbered with uncertainties owing to, for instance, large spatial and interannual variations in catches (Mortensen et al. 1991, Jeppesen et al. 1996). Moreover, the multiple-mesh-sized gill nets tend to overestimate large fish living in the littoral zone and underestimate large fish living in the pelagic zone (NERI, unpublished data).
Validation is essential to circumvent the methodological problems and uncertainties. Yet, long-term survey studies in brackish lakes are extremely rare. In Denmark, for instance, only 4 brackish lakes were intensively monitored in the National Monitoring Programme of the Aquatic Environment and only during a 6 year period (1998-2003). Regional inspections conducted by the local counties may provide some information about the environmental state; however, data are commonly only available for the last one-three decades. Alternatively, information from anecdotal reports and past investigations may be useful when evaluating results obtained by paleo-ecological investigations, although the differences in methods applied must be borne in mind. Furthermore, sampling sites and sampling periods may not be identical, which makes the

comparisons between investigations less valid. In addition, anecdotal data sources may rely on subjective rather than objective observations.

Future research perspectives

Without recorded historical environmental data, being the most powerful means of validation of the reconstructions, the need and importance for conducting multi-proxy studies increases. These allow indirect validation or invalidation of a given proxy by other independent proxies and herewith approach an evaluation of the reliability of a given proxy.

Predictive models for inference of salinity based on sedimentary diatoms recovered from 35 Danish brackish lakes are currently being developed (D. Ryves unpublished). In addition, preliminary analyses of stable isotopes (N, C) of zooplankton subfossils recovered from Glombak sediment cores have produced promising results (S. Drew, unpublished). In the Baltic Sea, stable isotope analyses have been used to estimate past changes in the dietary composition and trophic position of *Bosmina* subfossils (Struck et al. 1998). Stable isotopes may thus prove to be useful for describing temporal interactions within the food webs (Jeppesen et al. 2001b). Moreover, sedimentary algae pigments, used for describing past algae community structures in freshwater lakes (Leavitt et al. 1989), may provide an exiting future tool, especially if pigments, associated with the toxic *Prymnesium parvum* can be isolated and compiled to PL-CPUE reconstructions and used for detection of fish kill incidents. Analysis of sedimentary pollen, allowing in-lake responses (recorded by analyses of zooplankton subfossils, diatoms etc.) to be compared to catchment changes (e.g. agricultural activity) is also an interesting tool to be used in the future, especially in the description of eutrophication-related changes in brackish lakes.

Another promising future target is ´analogue´ statistics optimising the accuracy of statistical methods used for quantitative estimations. The basic idea of ´analogue´ methods is establishment of ´dynamic calibration data sets´, which include a selected number of surface samples (e.g. 10 - 20), being most similar (analogue) to each individual sample in the sediment core. Hence, only a short environmental gradient is covered by the individual ´dynamic calibration data set´, minimising the undesirable ´edge effects´ inherent in uni-model-based WA methods and may further allow the use of linear-based techniques (Birks 1998). Yet, use of ´analogue´ methods requires large calibration data sets; thus, the present calibration data set used for inference of PL-CPUE should be expanded considerably to allow an ´analogue´ statistic analysis.

Concluding remarks

The presented papers *(I-III)* demonstrate the powerful potential of using zooplankton-based paleoecological methods to obtain information on long-term lake development in Danish brackish waters. Given the lack of long-term surveys and sparse historical information, paleoecological methods may in fact be the sole tool for obtaining insight into past changes in biological structure and trophic interactions. In addition, in contrast to most data obtained from historical sources, paleoecological reconstructions of lake development are based on a uniform method describing the entire study period. The developed methods may serve as a useful alternative to labour- and time-consuming surveys, at least if the aim is to present a general picture of lake conditions rather than produce an exact estimate, taking into consideration the lower ecological resolution of the sediment records. Hopefully, future research efforts will lead to the development of effective multi-proxy methods and inference models suitable not only for elucidating lake histories in detail, but also for future management, conservation and restoration purposes.

Acknowlegdements

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Paper 1
Journal of Paleolimnology **29:** 495–507, 2003. 495

Cladoceran stratigraphy in two shallow brackish lakes with special reference to changes in salinity, macrophyte abundance and fish predation

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Key words : Brackish lakes, Cladoceran remains, Diatoms, Eutrophication, Fish predation, Paleoecology

Abstract
Sub-fossils of *Cladocera* and *Foraminifera* were used to reconstruct changes since 1870 in the trophic dynamics of two brackish lakes, Glombak and Han Vejle, located in the Vejlerne nature reserve, Denmark, a site of international conservation importance. After creation of the lakes in the mid-1870s following land reclamation, the two lakes have developed quite differently; today Glombak is turbid, while Han Vejle is clear. In both lakes, stratigraphic changes in the assemblages of foraminifers and cladocerans indicate an abrupt shift from marine to brackish conditions at the end of the 19th century, coinciding with land reclamation. However, the composition of the fossil invertebrate assemblages in the 20th century implies differences in the exposure to salinity, in fish predation and in habitat diversity. In Glombak, the cladoceran record suggests relatively saline conditions in the first quarter of the last century and high macrophyte abundance followed by lower salinities and subsequently a major decrease in macrophyte abundance and an increase in fish predation during the past ca. 40 years. By contrast, in HanVejle low salinity, high abundance of macrophytes and only minor changes in fish predation seem to have prevailed throughout most of the 20th century. The results are consistent with recent contemporary data, the few historical records, as well as with trends in the records of diatoms and macrofossils. This study highlights
the potential of using crustacean remains as indicators of long-term changes in the trophic dynamics of brackish lakes.

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Paper 2, accepted by Journal of Paleolimnology

Relationships between environmental variables and zooplankton subfossils in the surface sediments of 36 shallow coastal brackish lakes with special emphasis on the role of Fish

by

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Key words: zooplankton subfossils, brackish lakes, weighted-averaging models, salinity, planktivorous fish

Abstract

Sub-fossil zooplankton assemblages (*Cladocera* 22 taxa, *Rotifera* 1 taxon) were identified from the surface sediments of 36 Danish shallow (median depth 0.7m) coastal brackish lakes differing in epilimion salinity (SAL, range 0.2–17.4‰), summer mean total phosphorus (TP, 0.027-0.327mg l^{-1}) and total nitrogen (TN, 0.850–2.629mg l^{-1}), as well as in submerged macrophyte coverage and planktivorous fish density. Canonical correspondence analysis (CCA) showed that 34‰ of the variation in species data was explained by the five measured environmental variables of which the first two significant axes accounted for 64% of the total species variation. Forward selection and variance partitioning within the CCA analysis revealed that SAL, TP and PL-CPUE were significant, accounting for 18.4‰ of the species variation observed. Even within a narrow salinity range of 0.2 - 2‰, salinity significantly contributed to the variance observed in the species data. PL-CPUE was identified to be the only independent variable, while SAL was correlated to nutrients and macrophyte coverage. Cladoceran species richness declined significantly with increasing SAL, TP and TN, while no significant correlation was found to either PL-CPUE, macrophyte coverage or lake surface area. Predictive models to infer PL-CPUE were developed using variance weighted-averaging procedures. A two-component WA-PLS provided the most reliable model for PL-CPUE reconstruction with the highest coefficient of determination (jack-knifed $r^2 = 0.44$) and lowest jack-knifed root-mean-squared-error of prediction (RMSEP = 0.46). However, the residual distribution showed a significant bias with a tendency to overestimation at low PL-CPUE and underestimation at high PL-CPUE. The inference models were applied to fossil records of two coastal brackish lakes (Glombak, Han Vejle). Moreover, correspondence analyses (CA), with the fossil records as passive samples, were undertaken. The inferred historical changes (*ca.* 1870 - 1998) were consistent with the few historical records and recent contemporary data.

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Paper 3, submitted

RECONSTRUCTION OF PAST CHANGES IN ZOOPLANKTON COMMUNITY STRUCTURE AND PLANKTIVOROUS FISH DENSITIES FROM SEDIMENTARY SUBFOSSILS – A STUDY IN BRACKISH LAKE FLADE, DENMARK, SUBJECTED TO MAJOR FISH KILL INCIDENTS DURING THE PAST CENTURY

by

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Key words: zooplankton subfossils, brackish lakes, planktivorous fish, weighted-averaging models

ABSTRACT

To describe past changes in trophic structure, analyses were conducted of zooplankton (*Cladocera*, *Rotifera*) assemblages recovered in a ^{210}Pb dated sediment core from Lake Flade, a Danish shallow brackish lake exposed to several fish kill episodes during the 20th century. A weighted-averaging partial least square (WA-PLS) zooplankton-based transfer function was applied to reconstruct planktivorous fish densities (PL-CPUE) and to elucidate the potential of identifying fish kill incidents using sedimentary subfossils. The stratigraphical record showed a shift during the 20th century. The cladoceran community structure changed from high abundance of macrophyte-associated taxa and chydorids, characteristic of clearwater conditions, towards a community composed mainly by sediment-associated taxa and small-sized pelagic taxa and rotifers and chydorids, characteristic of eutrophic turbid conditions. Coinciding with this, the mean size of *Daphnia* ephippia decreased while inferred PL-CPUE increased, the latter being substantial also prior to the increase. The results point towards progressive eutrophication with additional impact of salinity. Reduced temporal resolution of the sediment record made identification of fish kill incidents difficult. The indications of high fish planktivory and a decline in macrophyte abundance are consistent with anecdotal observations and past fish investigations as well as with recent contemporary data. The study demonstrates the usefulness of applying zooplankton subfossils to detect past changes in the trophic structure of brackish lakes, the results of sediment record analysis being, however, less valid for highlighting temporary events, such as fish kills, in shallow wind-impacted lakes.

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Paper 4

Journal of Paleolimnology **27:** 133–143, 2002.

Reconstructing the historical changes in *Daphnia* mean size and planktivorous fish abundance in lakes from the size of *Daphnia* ephippia in the sediment

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Key words: fish, palaeoecology, trophic structure, zooplankton fossils, top-down control, ephippia, sediment, shallow lakes

Abstract
The zooplankton community structure in lakes is highly influenced by size-selective predation by fish, with small zooplankton species dominating at high predation pressure. Remains of cladocerans are preserved in the sediment and may be used to trace historical changes in fish predation. We determined how contemporary data on planktivorous fish were related to the size of *Daphnia* ephippia (dorsal length) in the surface sediment (0–1 cm) of 52 mainly shallow lakes with contrasting densities of fish and nutrients (TP: 0.002–0.60 mg P l^{-1}). Density of fish expressed as catch per unit effort, in terms of numbers in multiple mesh-sized gill nets ($CPUE_n$), decreased significantly with increasing mean size of ephippia. The relationship was improved by adding TP as an independent variable, now explaining 90% of the variation in $CPUE_n$ on the full data set covering lakes in Denmark, Greenland and New Zealand, and 78% if only data on Danish lakes were used. CPUE by weight of planktivorous fish and mean weight of *Daphnia* in the pelagial during summer were also related to ephippial size. By including contemporary data on established relationships between the sizes of egg-bearing female *Daphnia* and ephippia, we inferred changes in the $CPUE_n$, mean size of ephippia-bearing *Daphnia* and summer mean body weight of *Daphnia* from ephippial size in four lakes during the past 1–2 centuries. In a hypertrophic lake subject to periodic fish kills, *Daphnia* mean body weight was high and $CPUE_n$ was low compared with those in two eutrophic lakes, while $CPUE_n$ was low and *Daphnia* body weight was high in the least eutrophic, clearwater lake. Estimated $CPUE_n$ and *Daphnia* mean weight in the surface sediment of these four lakes corresponded well with contemporary data. Only small changes in ephippial size with time were observed in the clearwater lake and in one of the lakes that had suffered early eutrophication, while major changes occurred in the two other lakes that had been subjected to a major increase in nutrient input or fish kills. We conclude that *Daphnia* ephippia preserved in the surface sediments of lakes may be a useful and efficient method to quantify the present-day abundance of planktivorous fish and *Daphnia* mean size. The method is particularly valid in surveys aimed to give a general picture of the fish stock and the ecological state in a set of lakes in a region rather than a precise estimate for a single lake. Though some evidence is provided, more work is needed to evaluate whether the equations are valid for hind-casting in down-core palaeoecological studies.

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Paper 5

Hydrobiologia **491:** 321–330, 2003.
E. van Donk, M. Boersma & P. Spaak (eds), Recent Developments in Fundamental and Applied Plankton Research.

Sub-fossils of cladocerans in the surface sediment of 135 lakes as proxies for community structure of zooplankton, fish abundance and lake temperature

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Key words: zooplankton, surface sediment, zooplankton remains

Abstract
To elucidate the possibilities of using zooplankton remains in the surface sediment to describe present-days community structure and population dynamics of zooplankton, fish abundance and temperature, we compared contemporary data sampled in the pelagial during summer with the sediment record from the upper 1 cm of the sediment in 135 lakes covering a latitude gradient from Greenland in the north to New Zealand in the south. The abundance of three genera *Bosmina*, *Daphnia* and *Ceriodaphnia* of the total pool of ephippia was significantly related to the total abundance of the same taxa in the pelagic zone. However, in most lakes the abundance of *Ceriodaphnia*was higher in the sediment than in the water, which may be attributed to the overall preference by this genus for the littoral habitat. Using contemporary data from 27 Danish lakes sampled fortnightly during summer for 10 years, we found substantial inter-annual variations in the abundance of *Daphnia* spp., *Ceriodaphnia* spp., *B. longirostris* and *B. coregoni*. Yet, the sediment record mimicked the medium level well for most of the lakes, which suggests that the sediment record provides an integrated picture of the pelagic cladoceran community, which otherwise can be obtained only by long-term frequent contemporary sampling for several years. The contribution of *Daphnia* to the sum of *Daphnia* and *Bosmina* ephippia was negatively correlated with the abundance of fish expressed as catch per night in multi-mesh sized gill nets (CPUE). Yet, region-specific differences occurred, which partly could be eliminated by including nutrient state expressed as total phosphorus (TP) in a multiple regression. The average ratio of ephippia to the sum of ephippia and carapaces of *Bosmina* varied 40-fold between the sampling regions and was significantly negatively related to summer mean air temperature, and for Danish lakes also, albeit weakly, to fish CPUE but not to chlorophyll *a*. Apparently, temperature is the most important factor determining the ratio of parthenogenetic to ephippia producing specimens of *Bosmina*. We conclude that the sediment record of cladocerans is a useful indicator of community structure of pelagic cladocerans and the abundance of fish and temperature.

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Paper 6

Hydrobiologia **442:** 329–337, 2001.
M. Boersma & K.H. Wiltshire (eds), Cladocera.

Fish and crustaceans in northeast Greenland lakes with special emphasis on interactions between Arctic charr (*Salvelinus alpinus*), *Lepidurus arcticus* and benthic chydorids

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Key words: Arctic lakes, trophic structure, Arctic charr (*Salvelinus alpinus*), *Lepidurus*, fish, zooplankton, pelagic-benthic coupling, benthic chydorids

Abstract
We studied the trophic structure in the pelagial and crustacean remains in the surface 1 cm of the sediment of 13 shallow, high arctic lakes in northeast Greenland (74_ N). Seven lakes were fishless, while the remaining six hosted a dwarf form of Arctic charr (*Salvelinus alpinus).* In fishless lakes, *Daphnia pulex* was abundant, while no daphnids were found in the pelagial of lakes with fish. In fish lakes, the zooplankton community was dominated numerically by cyclopoid copepods and rotifers. Both lake sampling and analysis of remains in the top 1 cm of the sediment indicated that the phyllopod, *Lepidurus arcticus*, occurred in all fishless lakes, but was either absent or present in low densities fromlakes with fish. Adult *Lepidurus* aremainly predators and forage in the top layer of the sediment. An analysis of surface sediment revealed low abundance of the benthic chydorids *Alona* sp. and *Macrothrix* sp. in lakes with *Lepidurus*, while they were abundant in lakes with fish. The low abundance in fishless lakes could not be explained by damage of crustacean remains caused by *Lepidurus* feeding in the sediment, because remains of the more soft-shelled, pelagic-living *Daphnia* were abundant in the sediment of these lakes. No significant differences between lakes with and without fish were found in chlorophyll *a*, total phosphorus, total nitrogen, conductivity or temperature, suggesting that the observed link between *Lepidurus arcticus* and the benthic crustacean community is causal. Consequently, remains of crustaceans in high arctic lake sediments may be useful for detecting the impact of past climate change on top-down control by fish. Not only remains of pelagic species, but also of *Lepidurus* and some benthic chydorids, may be used to detect changes in fish abundance and predation pressure in the past.

National Environmental Research Institute

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NERI's tasks are primarily to conduct research, collect data, and give advice on problems related to the environment and nature.

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Publications:
NERI publishes professional reports, technical instructions, and the annual report.
A R&D projects' catalogue is available in an electronic version on the World Wide Web.
Included in the annual report is a list of the publications from the current year.

Development and application of zooplankton-based paleoecological methods with special focus on Danish brackish lakes

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