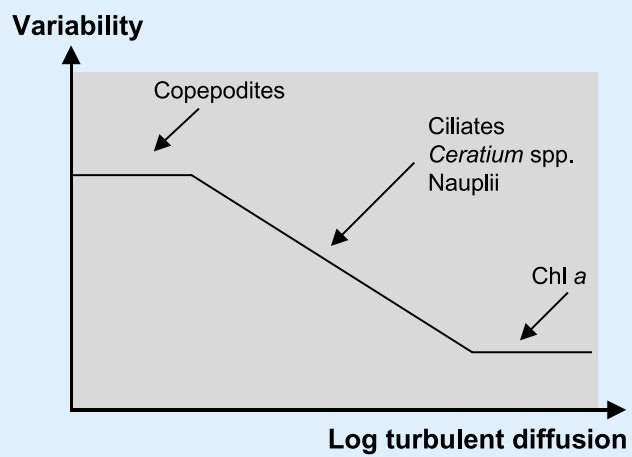




# Distributions of zooplankton in relation to biological-physical factors

*Ph.D. thesis*  
*Marie Maar*



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**National Environmental Research Institute**  
Ministry of the Environment · Denmark

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# Distributions of zooplankton in relation to biological-physical factors

*PhD thesis*  
2003

*Marie Maar*  
Department of Marine Ecology  
National Environmental Research Institute

Department of Marine Ecology  
Institute of Biological Sciences, Faculty of Science,  
University of Aarhus

## Data sheet

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Abstract:	Distributions of zooplankton organisms occurring on different scales were investigated in relation to biological-physical factors. A high seasonal variability in the structure and function of the pelagic food web was found during the spring bloom and in late summer in the Skagerrak. The spring bloom was characterised by a high potential vertical flux of phytoplankton aggregates and a relatively low secondary production within a short period of time. In the more prolonged summer period, secondary production was considerably higher and this season is therefore essential for fuelling fish in the Skagerrak. In addition, the spatial-temporal variability of zooplankton biomass and growth on the scale of km or hours was analysed during the spring bloom in the Skagerrak. Here, the presence of different water masses and diurnal biological rhythms contributed significantly to the observed variability. On the microscale, we found that the variability in the vertical distribution of weak swimmers, the microzooplankton, decreased dramatically with increasing turbulent diffusion levels in the N Aegean and the Skagerrak. This is in contrast to the variability in the vertical distribution of copepodites, that was independent of the measured turbulent diffusion because the copepodites are stronger swimmers. Finally, discarded appendicularian houses was found to be an important microscale food source for copepods in the Skagerrak.
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## Forord (Preface)

Dette ph.d.-studie blev udført på Afdeling for Marin Økologi, Aarhus Universitet (AU) og Afdeling for Marin Økologi, Danmarks Miljøundersøgelser (DMU, Roskilde). Studiet er et bidrag til projektet KEYCOP (Key Coastal Processes in the mesotrophic Skagerrak and the oligotrophic Northern Aegean: a comparative study) finansieret af EU (MAST III: MAS3-CT97-0148).

Formålet med dette studie var at undersøge fordelingen af zooplanktonorganismer i forhold til biologiske-fysiske faktorer på forskellig skala. Data blev indsamlet på KEYCOP-togter i Skagerrak og det nordlige Ægæer hav, Grækenland, samt under 2 workshops på Kristinebergs Marinbiologiske Feltstation, Sverige. Alle KEYCOP-deltagerne takkes for deres sociale og faglige engagement, som har været meget motiverende for mit arbejde.

Min interne vejleder var Professor Katherine Richardson (AU) og min eksterne vejleder var Professor Torkel Gissel Nielsen (DMU). Jeg takker Torkel Gissel Nielsen for hans aldrig svigtende entusiasme, støtte og inspirerende diskussioner. Jeg er taknemmelig for Katherine Richardsons grundige og værdifulde kommentarer samt sproglige rettelser til tidligere versioner af de vedlagte artikler samt for hendes opbakning gennem hele studieforløbet.

Desuden vil jeg gerne takke alle mine medforfattere for givtige diskussioner og et godt samarbejde.

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Til sidst vil jeg gerne takke Peter og Emmeline for deres tålmodighed og opbakning til at gennemføre studiet. Emmelines bedsteforældre takkes for deres pasnings-garanti.





# Summary

The aim of the present thesis was to investigate the temporal and spatial distribution patterns of zooplankton organisms in relation to biological-physical factors occurring on different scales. The thesis is based on field observations and laboratory experiments on scales covering the large- (basin or seasonal), intermediate- (km or hours) and microscales (cm or sec).

## Seasonal variability

### *The Skagerrak*

We found a high seasonal variability in the structure and function of the pelagic food web in the Skagerrak (Paper I and V). The spring bloom was characterised by a high potential vertical export to the sea floor and a relatively low copepod production within a short period of time (3-4 weeks). In the more prolonged, stratified, summer period, copepod production was considerably higher and this season is considered to be essential for fuelling fish in the Skagerrak. The traditional belief that the spring bloom represents the most important period for pelagic secondary production should, therefore, be reconsidered.

### *Grazing impact*

In both seasons, the grazing impact of ciliates and heterotrophic dinoflagellates exceeded that of copepods. Pelagic tunicates (appendicularians) had, on some occasions, a grazing impact comparable to that of copepods despite the lower biomass (Paper V). Thus, other grazers as well as copepods should be considered as being potentially important in deeper waters, where the presence of an overwintering copepod population has resulted in the assumption that large copepods dominate grazing.

## Variability on the scale of km or hours

### *Water masses*

A high degree of patchiness in several biological parameters was recorded in the Skagerrak on a scale of km or hours (Paper I). However, when analysing the data, we found that up to 41% of the patchiness could be explained by the presence of three different water masses (Paper I). In the Gullmarfjord, considerable changes in zooplankton abundance were also related to the intrusion of a surface water mass from the Skagerrak (Paper II). In addition, diurnal rhythms of copepod feeding and bacterial production contributed to the observed variability in the Skagerrak (Paper I). We therefore recommend that data are sampled and analysed in relation to water masses and biological diurnal rhythms.

## Microscale variability

### *Appendicularian houses*

We found that discarded appendicularian houses were full of phyto-detritus and therefore serve as a potential microhabitat and food source for a variety of organisms including copepods (Paper III and

V). Accordingly, mesozooplankton grazing was responsible for the removal of 36-70% of the produced houses within the euphotic zone (Paper II and V).

#### *Microscale distributions*

The variability in the vertical distribution of weak swimmers (microzooplankton: ciliates, *Ceratium* spp. and copepod nauplii) on microscale (cm), decreased dramatically with increasing turbulent mixing due to dispersion (Paper IV). Variability in the microscale distributions of copepodites was, on the contrary, independent of turbulent diffusion and also exceeded that of microzooplankton because the copepodites are stronger swimmers. The ability of zooplankton to detect and remain within microscale food patches is essential for their growth and survival under food limiting conditions, for example, during summer in the Skagerrak or in the N Aegean.

#### **Perspectives**

Knowledge about the variability of the pelagic food web structure on different scales can be used to understand and quantify changes in the ecosystem over time as a function of either natural or anthropogenically mediated environmental changes. It is also important in order to design appropriate future sampling programs and experiments.

## Dansk resumé (Summary in Danish)

Formålet med dette ph.d.-studie var at undersøge den tidslige og rumlige variabilitet i fordelingsmønstret af planktonorganismer i forhold til biologiske-fysiske faktorer på forskellig skala. Afhandlingen er baseret på feltmålinger sammenholdt med laboratorieeksperimenter på en tidslig eller rumlig skala som strækker sig fra storskala (bassin eller årstid), over de mellemliggende skalaer (km eller timer) til mikroskala (cm eller sekunder).

### Årstidsvariabilitet

*Skagerrak*

Vi fandt en høj årstidsvariabilitet i strukturen og funktionen af det pelagiske fødenet i Skagerrak (Appendix I og V). Forårsopblomstringen var karakteriseret ved en høj, potentiel vertikal transport til havbunden og en relativ lav vandloppeproduktion indenfor en kort tidsperiode (3-4 uger). I den længerevarende, lagdelte sommerperiode var vandloppeproduktionen derimod væsentlig højere end under forårsopblomstringen. Sommerperioden må derfor anses for at være essentiel for sekundærproduktionen i Skagerrak. Den traditionelle antagelse af forårsopblomstringen som den mest betydningsfulde periode for sekundærproduktionen bør derfor genovervejes.

*Græsningstrykket*

Ciliaters og heterotrofe dinoflagellaters græsningstryk var tilsammen højere end vandloppernes på begge årstider. Halesøpungenes (appendiculariernes) græsningstryk var i nogle tilfælde af samme størrelse som vandloppernes selvom deres biomasse var mange gange mindre. Derfor bør andre potentielt vigtige græssere end vandlopper også tages i betragtning i dybtvandede områder, hvor det tidligere har været antaget at den overvintrende vandloppepopulation dominerer græsningen.

### Variabilitet på en skala af km eller timer

*Vandmasser*

En høj grad af patchiness af adskillige biologiske parametre blev fundet i Skagerrak på en skala af km eller timer (Appendix I). Ved analyse af data viste det sig at op til 41% af variabiliteten kunne forklares ud fra forekomsten af forskellige vandmasser. I Gullmarfjorden kunne væsentlige forandringer i densiteten af zooplankton også forklares ud fra indtrængningen af overfladevand fra Skagerrak (Appendix II). Desuden bidrog døgnrytmer i vandloppegræsning og bakterieproduktion også til den observerede variabilitet i Skagerrak (Appendix I). Vi anbefaler derfor, at data bliver indsamlet og analyseret i forhold til vandmasser og biologiske døgnrytmer.

### Mikroskala variabilitet

*Appendicularhuse*

Vi fandt at afkastede appendicularhuse (1-2 mm) var fyldt med phytodetritus og derfor var et potentielt egnet mikrohabitat og fødekilde for en mængde forskellige organismer deriblandt vandlopper (Appendix III og V). Mesozooplanktongræsningen var også ansvarlig for

at 36-70% af de producerede appendicularhuse blev nedbrudt indenfor den eufotiske zone (Paper II and V).

### *Mikroskala fordelinger*

Variabiliteten af den vertikale fordeling af svage svømmere (mikrozooplanktonet: ciliater, *Ceratium* spp. og vandloppe nauplii) på mikroskala (cm) blev drastisk formindsket med forøget turbulent diffusion fordi de blev spredt (Appendix IV). Variabiliteten af mikroskala fordelinger af vandlopper var derimod uafhængig af den turbulente diffusion og mere udtalt end for mikrozooplanktonet. Dette skyldes formodentligt at vandlopper er bedre svømmere end mikrozooplanktonet. Zooplanktonets evne til at lokalisere og forblive i lokale fødetoppe er vigtige for deres vækst og overlevelse under fødebegrænsende forhold som f.eks. om sommeren i Skagerrak og i det nordlige Ægærrhav.

### **Perspektivering**

Kendskab til variabiliteten af det pelagiske fødenets struktur på forskellig skala kan anvendes til at forstå og kvantificere ændringer i økosystemet over tid som følge af enten naturlige eller antropogene påvirkninger af miljøet. Det er også vigtigt for at kunne designe fremtidige prøvetagningsprogrammer og eksperimenter.

# 1 Introduction

The great majority of primary producers in the oceans are microscopic, planktonic algae, collectively called phytoplankton. They convert solar energy, carbon dioxide, water and nutrients into organic compounds by the process of photosynthesis and are the basis of most marine food webs (Figure 1). The phytoplankton grazers are the zooplankton (animal plankton) consisting of the protozooplankton (flagellates and ciliates) and the mesozooplankton (e.g. copepods and appendicularians).

## *Fate of primary production*

The fate of primary production depends on the structure of the zooplankton community and its ability to utilise the phytoplankton species as a food source. While the grazed phytoplankton are channelled up through the food web to higher trophic levels such as fish, the ungrazed phytoplankton will, eventually, sediment to the seafloor. In addition, zooplankton waste-products are also of importance for the vertical flux of organic matter. The sedimented matter fuels the benthic community and contributes to the removal of surplus anthropogenic CO<sub>2</sub> from the atmosphere through burial of organic compounds.

Thus, the zooplankton occupies a key position in shaping the pelagic food web. However, the mechanisms behind the magnitude of energy- (carbon), and nutrient flow through the pelagic food web are only partly understood. In order to understand and describe the effects of fisheries, eutrophication, and climatic changes in pelagic ecosystems, it is necessary to gain knowledge about the temporal and spatial structure and functioning of the pelagic food web

## *Aim of the study*

The aim of this study was to investigate the temporal and spatial distribution patterns of zooplankton organisms in relation to biological-physical factors occurring on different scales. The thesis is based on field observations together with laboratory experiments on scales covering the large- (basin or seasonal), the intermediate- (km or hours) and microscales (cm or sec).



## 2 Plankton ecology

The energy transfer from primary producers to fish production is determined by the structure of the pelagic food web. At each trophic level in the food web, energy is respired (lost) and less energy is then available for fish production. Short food chains are therefore considered as more efficient with respect to energy transfer than large and complex food webs. However, the “match-mismatch” between phytoplankton growth and zooplankton grazing pressure is also important as it determines the fate of primary production. A so-called “match” implies an efficient utilisation of primary production as opposed to the “mismatch” scenario where a large fraction of primary production is left ungrazed by the zooplankton and, thus, unavailable to higher trophic levels in the pelagic food web.

### *The classical food chain*

The classical type of pelagic food webs is a short food chain consisting of large phytoplankton, copepods and fish (Figure 1) (Cushing 1989). This classical food chain is fuelled by new production (sensu Dugdale and Göering 1967) i.e. input of new nutrients to the euphotic zone by upwelling, precipitation, N<sub>2</sub>-fixation or river inflow. During blooms of large phytoplankton, the classical food chain will dominate leading to a high fish production. In most cases, however, copepods only graze a small fraction of the bloom resulting in a high sedimentation of organic matter to the sea floor as a potential food source to the benthos (Smetacek 1985, Wassmann 1991).

### *Microbial food web*

During the 1980's, it became clear that, along with the classical food web, there exists a microbial food web (Figure 1). This microbial type of food web consists of small phytoplankton grazed upon by the protozooplankton. The protozooplankton can be grazed upon by copepods. Thus, energy can be channelled through protozooplankton back to the classical food chain. In addition, bacteria utilise dissolved organic carbon (DOC) leaking from the phytoplankton. Thereby, energy is channelled through a “microbial loop” from bacteria to the protozooplankton before it becomes available to the copepods (Azam et al. 1983). This kind of food web is characterised by a high recycling of nutrients and organic matter and sedimentation is accordingly low (Wassmann 1998).

### *Protozooplankton*

While the size relationship between most zooplankton and their prey is 10:1, some heterotrophic dinoflagellates can ingest prey larger than themselves (Figure 1). They can either envelop the prey with a pseudopodium or suck the cell content out of the prey (Hansen 1991). Thus, the heterotrophic dinoflagellates can ingest large diatoms and, thereby, compete with copepods for food. In addition, some heterotrophic dinoflagellates and ciliates are mixotrophic e. g. they can both ingest prey and carry out photosynthesis. This makes it difficult to interpret their trophic role in the food web (Hansen 1991).

### *Appendicularians*

Another important, but often ignored, group of mesozooplankton is the pelagic tunicates, namely the appendicularians. They are common in coastal waters (Gorsky et al. 2000) and often occur in a high abundance during phytoplankton blooms (Nielsen and Hansen 1999).

They filter bacteria and small phytoplankton by pumping water through a unique mucus house (Flood and Deibel 1998). This makes it possible for appendicularians to feed on a prey size range unavailable to other mesozooplankton grazers. One can say, that they “take a short-cut” in the pelagic food web (Figure 1).

Thus, the pelagic food web can be very complex and difficult to describe. According to (Legendre and Rassoulzadegan 1995), there exist a continuum of pelagic food webs between systems dominated by the classical food chain and those dominated by the microbial loop.

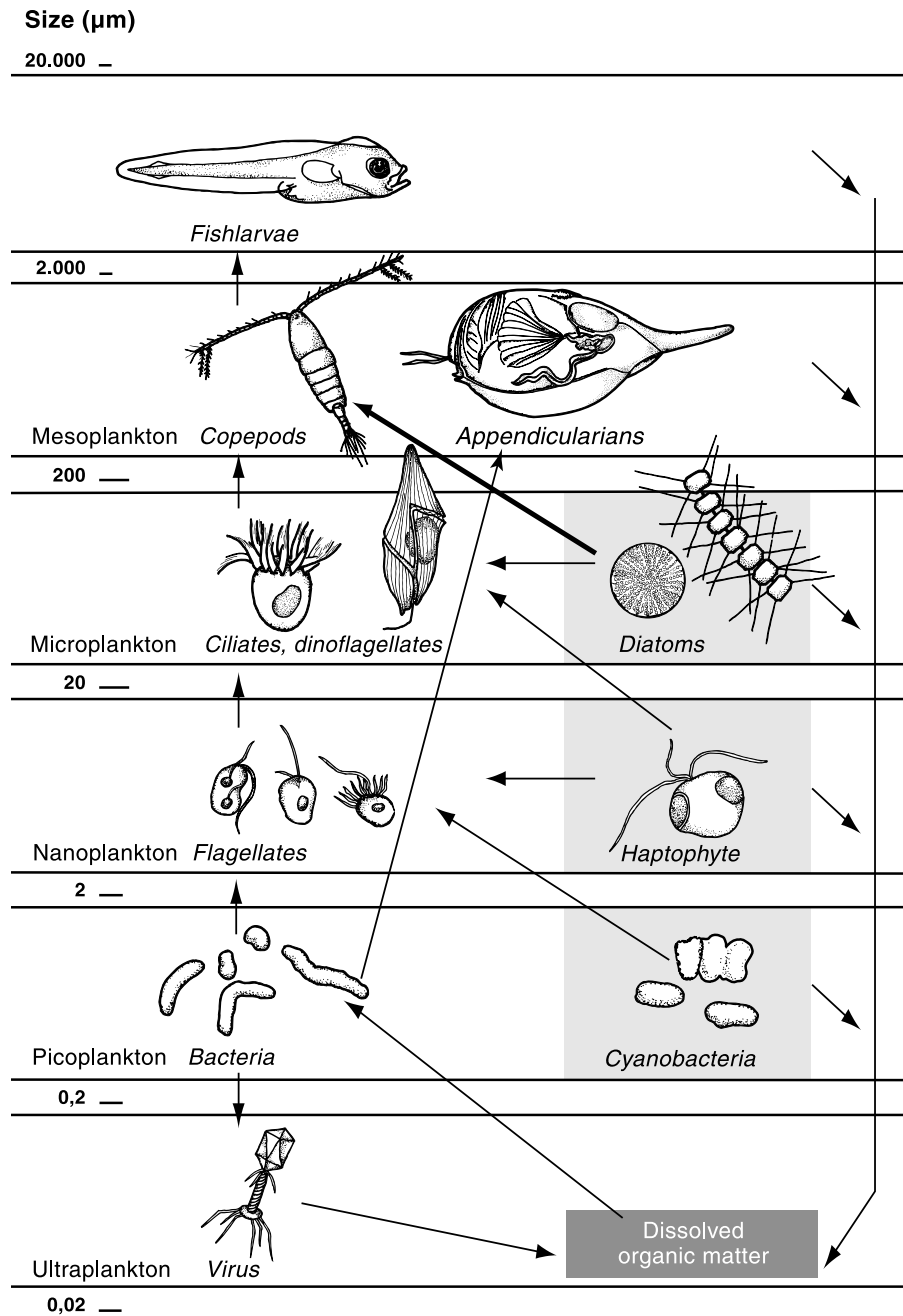


Figure 1. Pelagic food web structure. The bold arrow is the “classical” food chain. Phytoplankton organisms are indicated with a shaded background. Modified from Nielsen and Hansen 1999.



### 3 Study areas

KEYCOP

This thesis is a contribution from the EU-project KEYCOP (Key Coastal Processes in the mesotrophic Skagerrak and the oligotrophic Northern Aegean: a comparative study). The overall objective of the KEYCOP project was to understand and model the processes that determine the vertical and horizontal fluxes of carbon, nutrients and trace substances in the water column and sediment in different hydrographic regimes.

The studies were conducted during six KEYCOP-cruises, one during spring and one in late summer in the following areas: the Skagerrak (Denmark), the N. Aegean (Greece) and the Gullmarsfjord (Sweden), the latter including experimental work at the Kristineberg Marine Research Station.

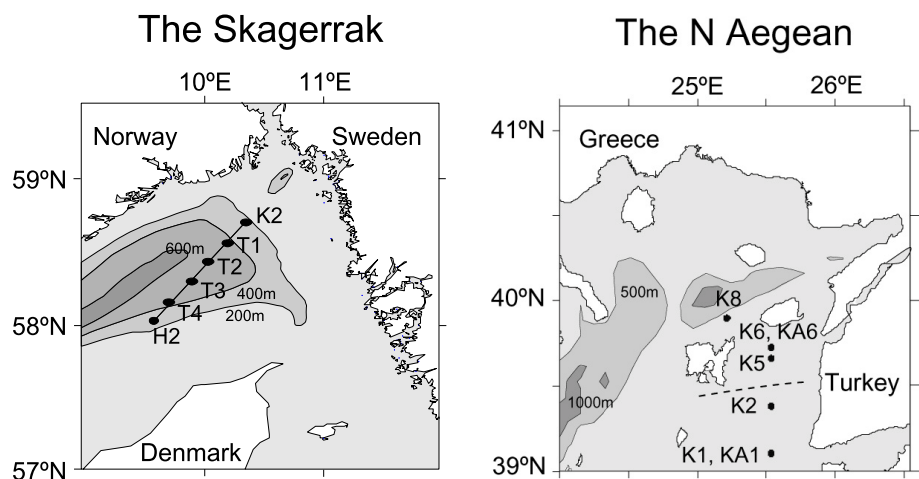


Figure 2. The sampling stations in the Skagerrak and the N. Aegean. In the N. Aegean Sea, Stns. K5, K6/KA6 and K8 were located in the front, whereas Stns. K1/KA1 and K2 were located outside the frontal area indicated with a dotted line.

#### 3.1 The Skagerrak

*Hydrodynamics*

The Skagerrak is a mesotrophic sea area located between Denmark, Sweden and Norway and it is the transition area between the brackish Kattegat-Baltic Sea and the North Sea (Figure 2). The surface water masses form a large cyclonic circulation and consist of the incoming Jutland Current, which together with the Baltic Current forms the outgoing Norwegian Coastal Current (Rohde 1998). The core of the cyclonic circulation consists of water from the central/northern North Sea. During summer, the circulation of water masses forms the characteristic “dome-shaped” pycnocline across the Skagerrak. The mean depth is 200 m with a maximum depth of 700 m in the Norwegian Trench and a sill to the south at 270 m giving it a fjord character.

The Skagerrak acts as a sink for organic and inorganic suspended matter transported by the currents. It is estimated that 50-70% of all suspended matter transported via North Sea water to the Skagerrak is deposited in the Skagerrak (Norwegian Trench) and the Kattegat (Van Weering et al. 1987). The Skagerrak is an important fishing area and the dominant fish species are herring, cod and plaice.

#### *The Gullmarfjord*

The Gullmarfjord is the largest fjord in Sweden and situated on the NW coast of Sweden in the Skagerrak. The fjord is 30 km long and 3 km wide with a maximum depth of 120 m and a sill depth of 45 m. The river, Örekilsälven, is the main source of nutrient inputs and the fjord is considered as mesotrophic. The water column is always stratified and consists of three layers. The top layer is of Baltic Current origin, the intermediate layer of Skagerrak origin and the bottom water in the deep basin is from the North Sea (Lindahl and Hernroth 1983). The area is a marine reservation with no industrial pollution, mining, dumping or dredging, and potentially harmful agricultural runoff is negligible.

### **3.2 The N. Aegean**

#### *Hydrodynamics*

The N. Aegean is subsystem of the oligotrophic Mediterranean and is situated between Greece and Turkey (Figure 2). The water column is stratified most of the year due to the inflow of brackish water from the Black Sea with a layer thickness of about 20 m. Surface water masses form, in general, a cyclonic circulation directing the Black Sea water north-west along the northern coast of the island Lemnos. In summer, the prevailing strong, cold and dry northerly winds (Etesians) lead the Black Sea water to a south-western direction along the East coast of Lemnos. The intermediate water column layer consists of modified Black Sea water (app. 20-100 m depth) followed by a mixture of Levantine intermediate water and South Aegean water (app. 100-300 m depth). Bottom water consists of the N. Aegean Deep Water (Zervakis et al. 2000). The N. Aegean is characterised by a relatively extensive shelf and a series of three aligned depressions extending down to 1600 m that constitutes the so-called N. Aegean trough.

The N. Aegean Sea is enriched with organic and inorganic matter from the Black Sea and rivers (Polat and Tugrul 1996) and is the most important fishing area in Greece. The dominant pelagic fish species are sardine, anchovy, mackerel and horse mackerel.

## 4 Patchiness of zooplankton organisms

### *Patches*

Plankton are per definition passive drifters in the sea. Nevertheless, zooplankton are not homogeneously distributed but occur in “patches”, i. e. positions of individual organisms deviate significantly from a random distribution within a given region. The scale of patches is defined as the distance or time over which the patch remains significantly unchanged. However, spatial and temporal scales are ultimately linked through the mean flow velocity in advective systems, and processes acting on a certain time scale imply an associated spatial scale.

### 4.1 The question of scales

### *Hierarchy of scales*

There exists a hierarchy in spatial and temporal scales among body size, doubling time and trophic position in marine organisms (Sheldon 1972) (Figure 3). Larger-sized organisms have a larger life span in time and space than smaller ones. Hence, small-scale disturbances may have dramatic effects on the dynamics of smaller species, but may not even be registered by larger ones and vice versa.

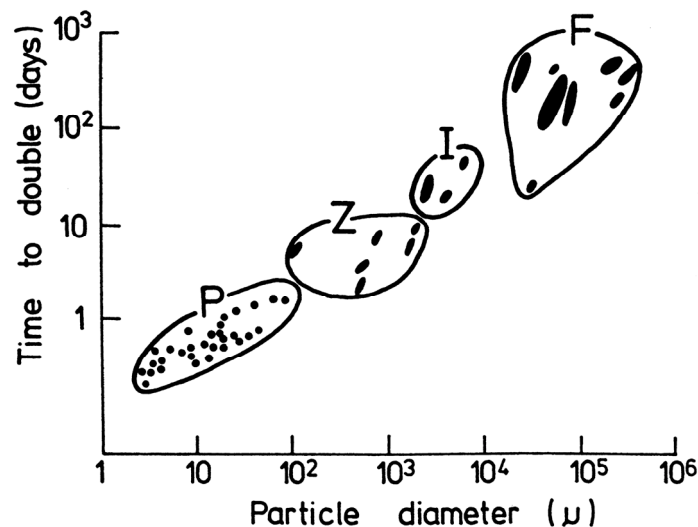


Figure 3. The relationship between organism (particle) size expressed as spherical diameter and doubling time from data for phytoplankton (P), herbivores (Z), invertebrate carnivores (I) and fish (F) from Sheldon et al. 1972 modified in Lenz (2000).

### *Upscaling*

As the energy in pelagic food webs is transferred up through the food web from smaller to larger organisms, the associated variability at each trophic level should affect those higher up in the food web. Thereby, the variability of the individual is scaled up to population, community and, finally, ecosystem level.

*Downscaling*

Likewise, the variability on the global scale will affect processes on smaller scales. Climatic changes, for example, may cause alteration in wind effects and, therefore, change the magnitude of turbulence. This might then affect the growth conditions of phytoplankton and encounter rates between copepods and their prey.

*Linkages between scales*

The understanding of linkages between scales is, however, a major problem in marine ecology. For instance, measurements of specific egg production are estimated for some selected copepods species sampled at different time intervals and positions in a specific study area. But is it appropriate to extrapolate these measurements to a daily, seasonal or annual production of the whole copepod community and to the whole study area? To answer this question, it is necessary to know the variability on each scale in space and time for the investigated parameters before the extrapolation can be done probably. Thus, there is a need for more information of the scale dependent variability of primary and secondary producers before any conclusions can be drawn on, for example, ecosystem level (Marine Zooplankton Colloquium 1 1989).

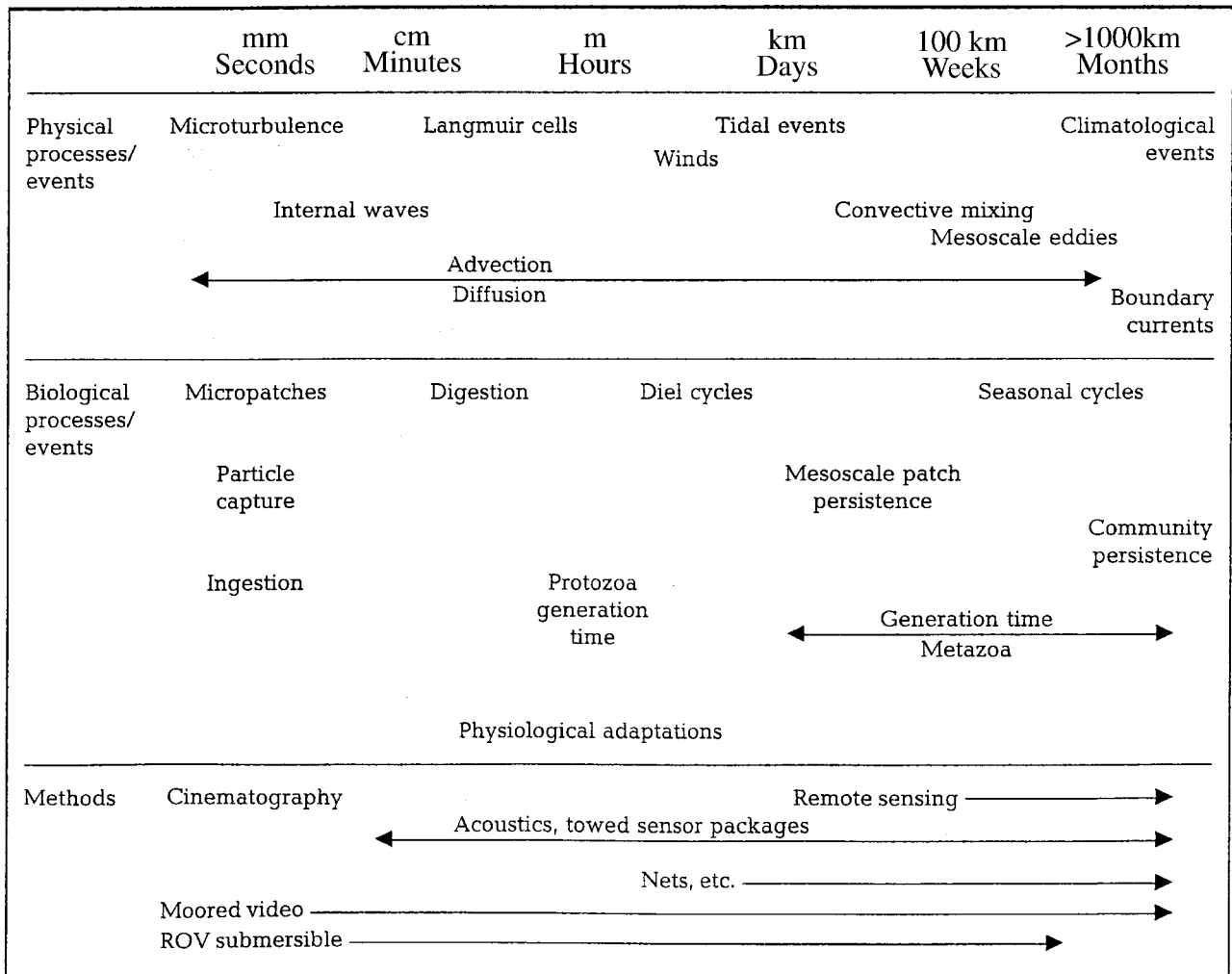


Figure 4. Spatial/temporal scales of biological-physical processes or events affecting plankton distributions and methods to study the latter. Modified from Marine Zooplankton Colloquium 1 (1989).

The two main mechanisms behind the observed patchiness of zooplankton are biological and physical processes. As these processes are scale-dependent operating on a continuum of spatio-temporal scales from mm or seconds to thousands of km or months, different processes are important for creating patchiness on different trophic levels in the marine ecosystem (Figure 4).

The relative importance of biological versus physical processes in creating these patches has been a matter of much discussion in the scientific literature (e.g. Daly and Smith 1993, Folt and Burns 1999). The main hypothesis is that, at microscales, biologic processes dominate while at large scales, physical processes are the dominant forces (Figure 5) (Daly and Smith 1993, Pinel-Alloul 1995).

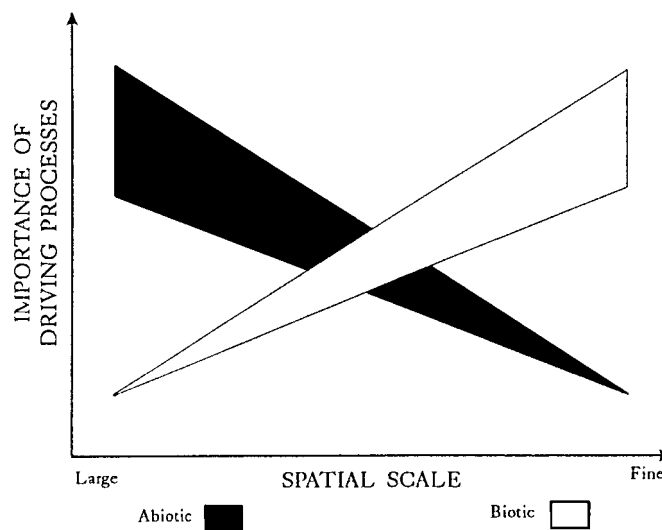


Figure 5. Hypothetical model of relations between sampling spatial scale and the relative importance of abiotic and biotic processes controlling zooplankton spatial heterogeneity in marine ecosystems from Pinel-Alloul 1995.

In Chapter 5, the seasonal variability in the Skagerrak is discussed, followed by examples of important biological-physical processes working on intermediate scales (Chapter 6). Chapter 7 focuses on the microscale variability of food patches and zooplankton organisms. Finally, the overall conclusions and perspectives from this study are presented in Chapter 8.



## 5 Seasonal variability in the Skagerrak

In temperate areas, there is seasonal variability in the pelagic food web structure due to the seasonal changes in hydrography, nutrient availability and light irradiance in the upper mixed layer. During winter, the water column is totally mixed and light irradiance is too low for phytoplankton growth. In early spring the water column becomes stratified and the increased light irradiance and nutrient availability in the euphotic zone is beneficial for phytoplankton growth. During the summer months, the water column remains stratified and surface temperature and light irradiance increases. The surface nutrients are, however, depleted due to utilisation by the spring diatom bloom. In autumn, wind induced mixing events of the water column introduce new nutrients to the euphotic zone, while the light irradiance decreases towards winter levels.

### *Study periods*

The thesis focuses on the two most important periods of the pelagic cycle in temperate areas: the spring bloom (Paper I) and late summer (Paper V). The spring bloom represents the most intense period with new production, while the late summer is the culmination of the pelagic cycle with a peak in zooplankton biomass often co-occurring with blooms of large dinoflagellates.

Previous investigations in the Skagerrak have been conducted in early summer (Kjørboe et al. 1990, Rosenberg et al. 1990, Tiselius et al. 1991, Bjørnson et al. 1993), while information on the structure of the pelagic food web is lacking from spring and late summer. The obtained carbon budgets of those two periods for the open, central part of the Skagerrak are presented in Figure 6.

### *Copepods*

In the Skagerrak, the copepod community is a mixture of large, oceanic (*Calanus finmarchicus*, *Pseudocalanus* spp.) and smaller, neritic (*Acartia* spp.) species reflecting the influence of both North Sea water and brackish Kattegat/Baltic Sea water in the area. *C. finmarchicus* overwinters in the deep coastal basins until spring, where they migrate up to the surface to exploit the bloom. It has therefore been assumed that the Skagerrak resembles the deeper part of the North Sea (Tiselius 1988), where a substantial fraction of the spring bloom is grazed by copepods (Williams and Lindley 1980). Likewise, copepods are assumed to be important during summer after the build up of copepod biomass and because the higher temperatures increase growth rates. However, the grazing impact by other zooplankters such as ciliates, heterotrophic dinoflagellates and nanoflagellates, appendicularians, rotifers and meroplankton have, generally, been ignored in the Skagerrak and other deep waters hosting an overwintering copepod population.

### 5.1 The spring bloom

#### *Grazing impact*

During the spring diatom bloom in the Skagerrak, specific egg production rates were below maximum and copepods grazed less than 3% of primary production. This study suggests that the year-round

stratification of the water column here makes it possible for the spring bloom to initiate early in March, i.e., before the copepod population is well established. In addition, smaller copepods were not able to graze efficiently on the large chain-forming diatoms leaving the majority of the spring bloom ungrazed. Other mesozooplankton grazers (meroplankton and rotifers) were of minor importance for energy flow in the pelagic food web. The grazing impact of ciliates and heterotrophic dinoflagellates, on the other hand, exceeded that of copepods with a factor of 3 to 4. The zooplankton community, in total, grazed 17% of the primary production at the time of the spring bloom.

#### *Sedimentation*

Therefore, the majority of the phytoplankton biomass produced during the spring bloom will eventually form large, fast-sinking aggregates and leave the euphotic zone ungrazed, as a potential food source for the benthos (Smetacek 1985, Kiørboe et al. 1994).

#### *Mismatch*

In shallow, temperate, coastal waters such as the adjacent Kattegat and the southern North Sea, there also is a mismatch between phytoplankton growth and copepod grazing pressure, while the protozooplankton peaks together with the spring bloom (Nielsen and Richardson 1989, Kiørboe and Nielsen 1994). Consequently, the food web in the Skagerrak during the spring bloom resembles that of shallow, coastal waters despite the presence of an overwintering population of *C. finmarchicus*.

## 5.2 Late summer

#### *Phytoplankton*

In late summer, the large dinoflagellate *Ceratium furca* dominated the pelagic food web and masked the structure suggested by Kiørboe et al. (1990), where large phytoplankton species dominated the margins and small cells the centre of the Skagerrak. Nevertheless, the nutrient input to the mixed, coastal station K2 gave a higher primary production, copepod biomass and sedimentation here compared to the more stratified, central stations. At the central stations, deep chl *a* maxima (DCM) were present and accounted for up to 95% of total water column primary production (Richardson et al. in press.).

#### *Copepod growth and feeding*

The measured copepod specific egg production rates were less than maximum and indicate food limitation (Peterson et al. 1991, Kiørboe and Nielsen 1994). The daily specific ingestion rate ranged between 22-50% body-C and the degree of herbivory was 17-100%. Other potential food sources than chl *a* are ciliates, heterotrophic dinoflagellates, fecal pellets and aggregates. Coprophagy (i.e. feeding on fecal pellets) was studied in copepod grazing experiments by comparison of long- and short-term incubations of fecal pellet production. Here, all the examined copepod species (calanoids and cyclopoids) potentially exploited 37-88% of the produced fecal pellets. Field data also indicated that degradation of fecal pellets was significant as only 41% of the fecal pellets produced daily were recovered in the 30 m-traps. Appendicularian mucus houses were another potential food item and 36% of the produced houses of *Oikopleura dioica* were recycled in the euphotic zone. Overall, copepods grazed 23% of primary production, where chl *a*, protozooplankton, copepod fecal pellets and appen-



dicularian houses each contributed with 46, 35, 10 and 9%, respectively, to the copepod diet.

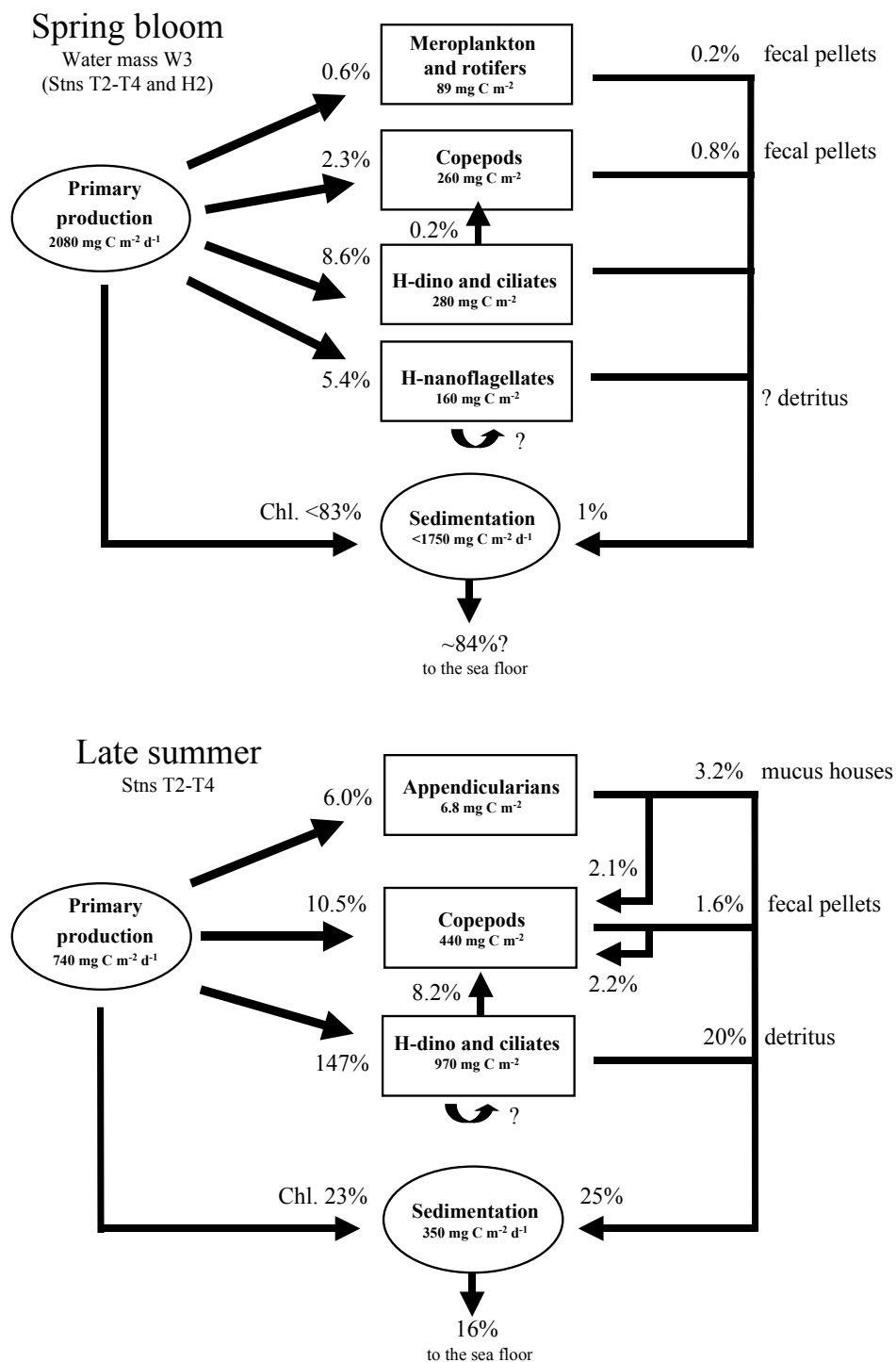


Figure 6. Carbon budgets from the spring bloom (Paper I) and late summer in the Skagerrak (Paper V). Arrows give the percentage of primary production (100%) that is channelled through the different compartments in the pelagic food web. Squared boxes are carbon biomass and round boxes are rates of production or sedimentation. Sedimentation to the sea floor during the spring bloom depends on the respiration of phytoplankton aggregates.

### *Oikopleura dioica*

In late summer, *O. dioica* was, generally, low in biomass, but this organism can clear a large volume of water through their mucus houses. The daily specific ingestion of small phytoplankton and bacteria was 219% body-C, which is much higher than for copepods. *C. furca* was too large to pass the inlet filters of the houses and was therefore not ingested by *O. dioica*. *C. furca* was, however, removed from the suspension because they were trapped on the houses as phytodetritus. The removal of small phytoplankton, *C. furca* and bacteria from the suspension corresponded to 6% of primary production.

### *Grazing impact*

Ciliate and heterotrophic dinoflagellate biomass was high and combined they could potentially exploit 147% of primary production. Hence, a high fraction of primary production was channelled through the protozooplankton up to copepods. The grazing impact of the zooplankton community was then 177% of primary production and hence, considerably more than during the spring bloom. This is also reflected in the relatively lower sedimentation rate (48% of primary production) at 30 m with an equal contribution of chl *a* and zooplankton waste products.

### *Sedimentation*

However, only 16% of primary production actually reaches the sea floor as detritus because there is a high degradation of organic matter in the mid-water column by microorganisms (Paper V, Richardson et al. in press.). Thus, fast-sinking copepod fecal pellets and appendicularian houses have the highest potential for reaching the sea floor in late summer in comparison to during the spring bloom, where the majority of sedimenting matter consists of fast-sinking phytoplankton aggregates.

## 5.3 Summary

### *Seasonal production*

In conclusion, ciliates and heterotrophic dinoflagellates are more important grazers of primary production than copepods during spring (Paper I), early summer (Bjørnsen et al. 1993) and late summer in the Skagerrak (paper V). Appendicularians can on some occasions have a grazing impact comparable to that of copepods despite their lower biomass. Other grazers as well as copepods should therefore be considered in deeper waters, where the presence of an overwintering copepod population has resulted in the assumption that large copepods dominate grazing.

The mesozooplankton are, nevertheless, the direct link to higher trophic levels such as fish and it is therefore still important to estimate their production. The potential daily production of mesozooplankton was actually higher in late summer, 74 mg C m<sup>-2</sup>, than during the spring bloom, 22 mg C m<sup>-2</sup>, and early summer, 55 mg C m<sup>-2</sup> (recalculated from Bjørnsen et al. 1993) assuming a growth efficiency of 33% (Hansen et al. 1997).

### *Conclusion*

The present study confirms a high seasonal variability of the pelagic food web in the Skagerrak. The spring bloom occurs over a relatively short period of time (3-4 weeks) and is characterised by a high potential export to the sea floor and a relatively low pelagic, secondary

production. In the more prolonged, stratified, summer period, new production is of the same order of magnitude (Richardson et al. in press.) and secondary production considerably higher than that occurring during the spring bloom. Consequently, the summer period must be considered as the most important season for pelagic secondary production in the Skagerrak. Thus, the traditional belief that the spring bloom represents the most important season for fuelling higher trophic levels such as fish should be reconsidered.



## 6 Variability on intermediate scales

The variability of pelagic food webs on the oceanic, basin or seasonal scale has been studied thoroughly during the last 40 years (Mann and Lazier 1996). However, few studies have considered the close coupling between biological patchiness and physical processes on the intermediate scale of km or hours (Kiørboe et al. 1990). As sampling of many biological parameters occurs on this scale, it is important to know the degree of variability, to apply an appropriate sampling or monitoring program.

### 6.1 Biological-physical processes

#### *Physical processes*

Entrainment of nutrient-rich water to the depleted surface layer by physical processes occurs by coastal or equatorial upwelling, in frontal or tidal zones, by eddy formation, or turbulent mixing. This is essential for new primary production and the “classical” food chain. In addition, the retention of phytoplankton in the euphotic zone by stratification of the water column is important for optimum phytoplankton growth (Mann and Lazier 1996). Hence, physical processes shape the pelagic food web on the scale of hours to weeks occurring over a few to hundreds of km.

#### *Water masses*

Water masses are natural boundaries for the distribution of zooplankton populations and they often vary considerably in the occurrence of different taxonomic species (Maucline 1998). However, the diel vertical migration of zooplankton brings them in contact with different water masses moving in different directions. Mixing of water masses also contributes to this exchange of zooplankton populations.

#### *Turbulent mixing*

Turbulent mixing in the water column redistributes plankton organisms and, hence, reduces patchiness (Haury et al. 1990). However, copepods might react to changes in vertical turbulence profiles by avoiding the most turbulent part of the water column, thereby creating patchiness (Mackas et al. 1993, Visser et al. 2001).

#### *Zooplankton*

The generation time of copepods is on the order of weeks and they develop from hatched eggs through six successive nauplii stages followed by six successive copepodite stages (Mauchline 1998). Copepod grazing, growth and mortality varies with species, developmental stage, food availability, season, temperature, microscale turbulence and the presence of predators. The match-mismatch between zooplankton grazing pressure and phytoplankton growth, shapes the pelagic food web on the scale of km or hours (Kiørboe 1998).

### 6.2 Observed variability

#### *Sampling program*

The spatio-temporal variability of biological parameters was investigated in the Skagerrak and the Gullmarsfjord. Sampling was conducted every 6 hours for two days at two stations, K2 and H2, and

once at 4 stations on a 100 km-transect across the Skagerrak during the spring bloom (Figure 2, Paper I). In the Gullmarfjord, sampling was conducted every 6 hours over a 28 hour period in October and almost every day during a week in March (Paper II).

#### *Water masses*

Three different surface water masses could be identified by their physical (temperature and salinity) and biochemical (nutrients, chl *a*) properties during the spring diatom bloom in the Skagerrak (Paper I). The water masses were Skagerrak water (W1 and W3) and Baltic water outflow (W2).

#### *Explained patchiness*

In the Skagerrak, there was a high degree of patchiness of several biological parameters quantified as the coefficient of variation ( $CV = SD/mean \times 100\%$ ) with CV-values up to 134% (Paper I). However, when analysing the data, we found that up to 41% of the patchiness could be explained by the presence of the different water masses. The Koster and transect stations exhibited the highest degree of patchiness due to the presence of two water masses (Figure 7). During early spring in the Gullmarfjorden, considerable changes in zooplankton abundance were also related to the intrusion of a surface water mass from the Skagerrak (Paper II). Thus, the water masses appear to set the physical frame within which the plankton organisms can interact with one another and small-scale physical processes.

#### *Diurnal rhythms*

Diurnal rhythm of copepod feeding with increased activity at night was observed at the Hirtshals station in the Skagerrak, which was influenced by the water mass W3 (Figure 7c, Paper I). This agrees well with other studies (Tiselius 1988, Visser 2001). In addition, there was a diurnal rhythm in bacterial production (Figure 7b), which correlated positively with copepod feeding. Bacteria utilise dissolved organic carbon (DOC) leaking from phytoplankton or from fecal pellets, excretion and sloppy feeding by copepods (Rosenberg et al. 1990, Strom et al. 1997, Møller and Nielsen 2001). During blooms of large cells, copepod grazing activity is assumed to be the most important source of leaking DOC (Møller and Nielsen 2001) as observed in the present study.

#### *Diel vertical migration*

Copepods can exhibit diel vertical migration to avoid visual predators in the surface layer during the day or to conserve energy in the cold, deeper layers (Mauchline 1998). During the spring bloom, only *Metridia* spp. exhibited diel vertical migration. This organism contributed, however, only slightly to total biomass and did not affect the overall distribution pattern of copepod biomass (Paper I). In late summer, no diel vertical migration was observed at both areas, and the observed differences in copepod biomass between day and night at the same station was probably due to advection (Paper I & II).

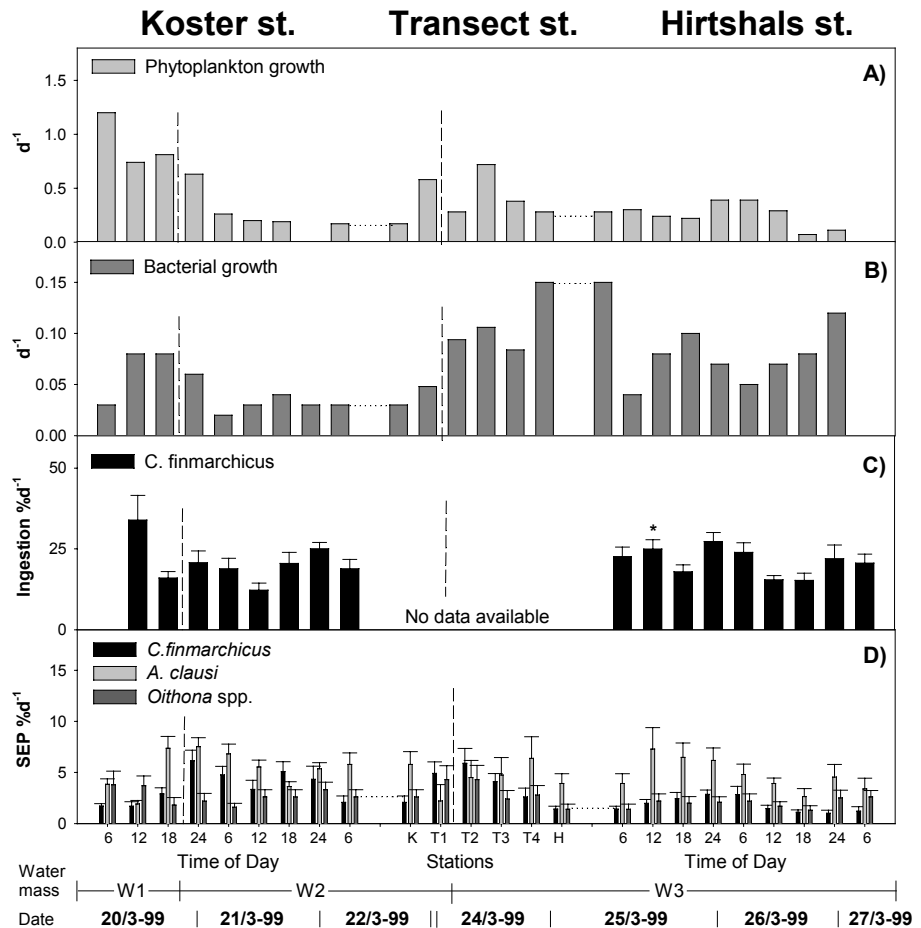


Figure 7. The community-specific growth rates (0-20 m) for A) phytoplankton and B) bacteria, C) specific ingestion by *Calanus finmarchicus* and D) the specific egg production (SEP) for *C. finmarchicus*, *Acartia clausi* and *Oithona similis*. The separation into water masses (W1, W2 and W3) is indicated with vertically dashed lines (Paper I). The value marked with \* was not included in the test of diel cycles.

### Conclusion

In this study, sampling across different water masses was one of the important sources for the observed patchiness in the distribution of biological parameters and water masses should be taken into account during sampling and analysing of data in future studies. Even within the same water mass, however, there was a considerable variability in biological parameters due to diurnal rhythms and other unidentified sources of natural variability. This complicates sampling strategy and extrapolation of data to ecosystem level.





## 7 Microscale variability

Microscale variability in the distribution and activity of individuals occurs on the scale of mm/cm or sec/min. To fully understand the distribution patterns and production of zooplankton, it is necessary to study the interactions between different organisms and the environment on the same (micro-) scale as that of the organisms.

Here, two types of microscale variability are discussed; discarded appendicularian mucus houses as potential microscale food source for copepods (Paper II, III and V) and the vertical distribution of zooplankton in relation to turbulent diffusion (Paper IV).

### 7.1 Biological-physical processes

#### *Physical processes*

Microscale turbulence, internal waves and Langmuir circulation are physical processes operating on the scale of seconds to hours occurring over mm-m. Microscale turbulence increases the encounter rate between predator and prey and, thus, increases growth of the predator. However, depending on magnitude, microscale turbulence can also disperse food patches or stress the copepods and cause decreased survival success and growth (Davis et al. 1991, Saiz and Kiørboe 1995).

#### *Zooplankton behaviour*

Swimming or sinking by zooplankton allows them to alter position to the optimum depth for growth in the water column. They can detect food patches, mates and predators by chemo- or mechanoreception (Buskey 1984, Tiselius 1992). Local turbulent diffusion, however, counteracts the directed swimming behaviour of zooplankton and can at high levels prevent aggregation. Zooplankton shift between different types of prey in response to food quality, quantity, and turbulence and this changes the distribution pattern of the prey (Kiørboe 1998).

#### *Food patches*

In food limited environments, microscale patches of food are essential for the survival success and growth of zooplankton. Such food patches can be thin layers of subsurface chlorophyll peaks (Richardson et al. 1998, Deksheniaks et al. 2002), local patches of microzooplankton (Tiselius 1991, Mackas et al. 1993) or large aggregates consisting of phytoplankton, fecal pellets, detritus or appendicularian houses (Alldredge 1976, Lampitt 1996). The exploitation of these patches by zooplankton depends on their ability to detect and stay within them.

### 7.2 Appendicularian houses

#### *Clearance*

The appendicularian *Oikopleura dioica* produces unique mucus houses to filter particles in the size range from bacteria to nanoplankton for feeding (Figure 8). The tail pump sucks water into the house through two coarse inlet filters allowing particles less than 15-30  $\mu\text{m}$  to enter the house (Fenaux 1986). Hereafter, the particles are collected on the

internal food concentration filter. The particles are, then, sucked into the mouth on the pharyngeal filter and, finally, this filter including the food particles are digested in the gut (Flood and Deibel 1998).

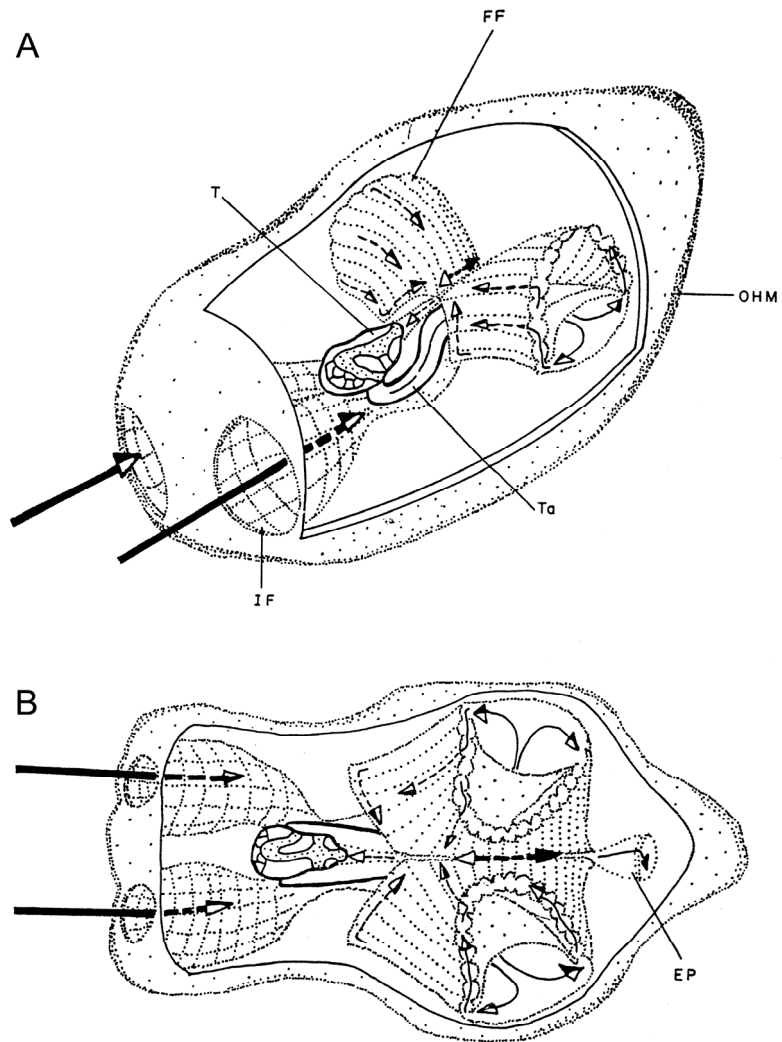


Figure 8. Example of the morphology of an appendicularian (Oikopleuridae) house illustrating the water flow through the house. Arrows indicate the direction of flow, black arrows: flow of water only, white arrows: flow of food particles and black-white arrows: flow of both water and food. A) Cut-away lateral view of the house. B) Cut-away dorsal view of the house. (IF) inlet filters, (FF) food concentration filter, (T) trunk, (Ta) tail, (OHM) outer house membrane and (EP) excurrent passage. From Alldredge 1977.

### *Marine snow*

Some of the particles are not ingested, however, but get stuck to the inlet or internal filters. When clearance is prevented due to clogging of the filters, the house is discarded. Thereafter a new house is inflated and clearance proceeds. The discarded houses are filled with phytodetritus, fecal pellets and other trapped particles and are an important constituent of "marine snow", i.e. suspended immotile aggregates with a size  $>0.5$  mm, in the oceans. Marine snow is believed to be the main vehicle for transport of organic matter to the sea floor (Lampitt 1996). In addition, they are potential "hot spots" of pelagic microbial activity in an otherwise diluted environment (Alldredge 1976).

### House clogging

Previous studies have shown that ~30% of small particles entering the house are not ingested but trapped on the internal filters (Gorsky and Fenaux 1998). House clogging of *O. dioica* due to exposure to different sizes of algae was investigated in Paper III. Here, filtration of the edible *Rhodomonas baltica* and *Thalassiosira weissflogii* caused internal clogging of the houses probably due to high cell surface stickiness. Consequently, 23-75% of the removed algae was trapped in the houses corresponding to 0.3-0.8  $\mu\text{g C house}^{-1}$  at a food concentration of 100  $\mu\text{g C}$ .

### *Ceratium* spp.

The large dinoflagellates *Ceratium* spp. (45-100  $\mu\text{m}$ ), on the other hand, were not collected on the inlet filters. *O. dioica* could probably back flush the houses at the relatively low encounter rate experienced of 41 *Ceratium*  $\text{house}^{-1}$  (Paper III). During the late summer in the Skagerrak, the encounter rate between *Ceratium furca* and houses was considerably higher, 95-102 cells  $\text{house}^{-1}$  (Paper V). Consequently, *O. dioica* was apparently not able to prevent clogging of *C. furca* on the inlet filters and *C. furca* was efficiently removed from the suspension. The trapped cells corresponded to  $1.3 \pm 0.2 \mu\text{g C house}^{-1}$ . In comparison, the carbon content of a freshly produced house is 0.2  $\mu\text{g C}$  (Sato 2001). The carbon content (POC) of discarded appendicularian houses with detritus can also be calculated from the equation  $\text{POC} = 1.09 \times \text{volume}^{0.39}$  (Alldredge 1998). This gives 0.9-1.9  $\mu\text{g C house}^{-1}$  by using a radius of 0.5-1 mm and assuming a spherical shape.

### Recycling of houses

The house aggregates are, therefore, full of organic matter. Consequently, they can serve as a microhabitat and food source for a variety of organisms attached to the surface or embedded in the mucus matrix. Bacterial activity in the aggregates supports the growth of a high number of protozoa and also contribute to the degradation of aggregates with a turnover time of 8-9 days (Plough et al. 1999).

### Mesozooplankton grazing

However, the most important contribution to the degradation of house aggregates is probably mesozooplankton grazing with a turnover time of 1-4 days (Kiørboe 2000). Different mesozooplankton grazers such as the copepods *Microsetella norvegica* and *Oncaea* spp., Nematodes and polychaete larvae have all been observed to feed on aggregates (Alldredge 1972, Shanks and Edmondson 1990, Bochdansky et al. 1992, Green and Dagg 1997). In the Skagerrak, the abundance of *Microsetella norvegica* correlated with the recycling of houses. This indicates that they were important for the degradation of house aggregates (Paper V). The mesozooplankton are suggested to be responsible for the 20-70% degraded aggregates within the euphotic zone (Kiørboe 2000, Paper II and V).

### Conclusion

In conclusion, marine snow aggregates can be an important component of the zooplankton diet. In addition, the grazing on aggregates by zooplankton reduces the vertical flux and thereby retains organic carbon and nutrients for recycling in the euphotic zone (Kiørboe 1998).

### 7.3 Microscale distributions of zooplankton

#### *Predator/prey encounter*

Turbulence influences the encounter rate between predator and prey. Hence, at low turbulence levels, zooplankton swimming can overcome dispersion and utilise the food patches. In a model by Davis et al. (1991), intermediate turbulence levels erode food patches and zooplankton growth decreases in comparison to low turbulence conditions. However, at higher turbulence, the encounter rate between predator and prey increases and zooplankton growth is restored to original values. At the very highest levels of turbulence, the copepods are stressed and growth rates are reduced (Saiz and Kjørboe 1995). Thus, zooplankton will try to alter their position in the water column to the most beneficial depth for growth and avoid the most turbulent parts of the water column (Mackas et al. 1993, Visser et al. 2001).

#### *Turbulent diffusion*

Turbulent eddy diffusivity is herein referred to as “turbulent diffusion” and is a measure of the efficiency of the turbulent eddies to disperse particles. The ability of zooplankton to aggregate at the optimal depth depends on their swimming strength with respect to local turbulent diffusion.

Microscale distributions of proto- and mesozooplankton in relation to turbulent diffusion were investigated using a vertical high-resolution sampler during cruises in the Skagerrak and N. Aegean (Paper IV). It was hypothesised, that the variability of the vertical distribution of zooplankton organisms would be independent of turbulent diffusion up to a certain threshold where dispersion overwhelms the swimming ability of the organism and variability decreases.

#### *Results*

The hypothesis was confirmed by the obtained results as the variability of the vertical distribution (patchiness) of weak swimmers, microzooplankton (ciliates, *Ceratium* spp. and copepod nauplii), decreased dramatically with increasing turbulent diffusion (Figure 9). At the pycnocline, microscale patchiness of microzooplankton was also significantly higher than in the upper mixed layer, where the turbulent diffusion was much higher. Microscale patchiness of stronger swimmers represented by copepodites was, on the contrary, independent of turbulent diffusion and also exceeded that of microzooplankton (Paper IV).

#### *Swimming speeds*

We used a model to evaluate the swimming speed required to maintain a 15-cm drifting food patch (Paper IV). In the upper mixed layer, an organism must swim  $0.1 \text{ cm s}^{-1}$  to maintain the patch in contrast to  $0.03 \text{ cm s}^{-1}$  in the pycnocline. Recorded swimming speeds range between  $0.02\text{-}0.3 \text{ cm s}^{-1}$  for microzooplankton and  $0.1\text{-}4 \text{ cm s}^{-1}$  for copepods (Jonsson 1989, Mauchline 1998). Thus, the calculated swimming speeds necessary to create the observed patchiness in this study are realistic.

#### *Conclusion*

In conclusion, this study demonstrates that a range of planktonic organisms have the abilities and behavioural adaptations that allow them to form and remain within vertical patches of higher food concentrations, thereby increasing their overall survival success.

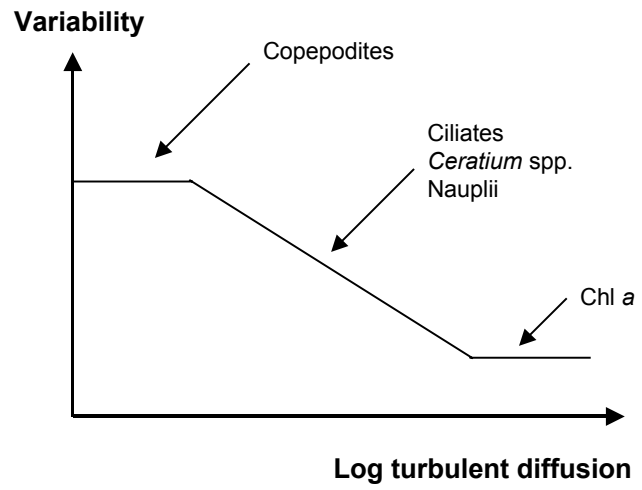


Figure 9. A hypothetical model of the variability of plankton distributions in relation to turbulent diffusion.



## 8 Conclusion and perspectives

The oceans cover 71% of the earth's surface and have a mean depth of 3.8 km, creating the largest environment of the world. The majority of plankton live in the euphotic zone with a maximum depth of 75-200 m, and, consequently, most of the production occurs in about 5% of the ocean by volume (Lalli and Parsons 1993). The movement of zooplankton by advection, turbulence, or swimming, together with their small size makes them difficult to sample properly and, therefore, relatively little is known about their distribution of biomass, production and mortality at various temporal and spatial scales.

The present thesis contributes with new knowledge on the relevant scales and processes affecting zooplankton distributions. This potentially creates a better basis for designing an appropriate sampling schedule in connection with monitoring programs or field experiments. Additionally, a better understanding of linkages between scales makes it possible to extrapolate data in space and time, which is relevant for the understanding, description and modelling of pelagic ecosystems.

### *Variability in the Skagerrak*

The data presented here confirmed a high temporal (hours, daily, seasonal) and spatial (1-100 km) variability in the structure and function of the pelagic food web in the Skagerrak. We recommend, therefore, that the measured biological parameters are sampled and analysed in relation to season, water masses, hydrography and diurnal rhythms. However, even when the mentioned sources of variability were taken into account, there was still a considerable variability of several biological parameters. This complicates the design of an appropriate sampling program and extrapolation of data from km or hours to basin- and annual scale.

### *Remote sensing*

The appropriate technology to study zooplankton distributions depends on the scale of interest (Figure 4). Remote sensing can be used to identify areas with elevated chl *a* levels, where it is interesting to investigate the structure and production of the pelagic food web. This could be, for example, during blooms of large phytoplankton species (diatoms and dinoflagellates) or toxic algae (cyanobacteria), which have implications for zooplankton growth.

### *Continuous plankton recorder*

To study long-term changes in the pelagic food web in open Danish waters, the use of a continuous plankton recorder (CPR) is a possibility. The CPR is a plankton-sampling instrument equipped with a CTD-sensor designed to be towed from merchant ships on their normal sailing. As a near-surface monitoring system the CPR is efficient because it can survey large areas during a cruise (Sameoto et al. 2000). The CPR has been applied regularly during the last 70 years in the North Atlantic, the North Sea and, recently, the Baltic Sea.

### *Monitoring stations*

More detailed information on the vertical structure, production and species composition of the pelagic food web can be obtained by regular cruises to a series of geographically fixed, monitoring sta-

tions. These stations should be chosen according to water mass and hydrography and be representative for Danish waters (Skjoldal et al. 2000).

#### *Microscale distributions*

Microscale distributions of individual plankton organisms (size range: 10  $\mu\text{m}$  to 2 cm) can be revealed by the use of the Video Plankton Recorder (VPR). This method is, however, limited by the lack of an *in situ* calibration and that the size range of taxonomic identification is 500  $\mu\text{m}$  to 100 mm (Foote 2000). By the use of a more conventional method, a vertical high-resolution sampler, we found that the measured turbulent diffusion could have important effects on the microscale patchiness of zooplankton (Paper IV). This is important for the understanding of exploitation of food patches and the, consequently, higher survival success and growth by zooplankton in food limiting environments.

#### *Recycling*

Relatively little is known about the fate of marine snow in deep waters even though this snow is considered as the most important factor for sedimentation. We found that mesozooplankton grazing activity was, apparently, important in reducing vertical fluxes of fecal pellets and house aggregates (Paper II and V). In addition, a high microbial degradation of organic matter in the mid-water column layer in the deep, central part of the Skagerrak was observed. Thus, the recycling of organic matter in the water column with emphasis on the role of detritus feeders (*Microsetella norvegica*, *Oncaea* spp. and *Corycaeus* spp.) should be given emphasis in future studies.

#### *Modelling*

The data obtained in this study will, eventually, contribute to the development and application of coupled biological-physical models that allow transfer of information from the individual- to population- and, ultimately, the ecosystem scale (Marine Zooplankton Colloquium 2 2001).



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# Appendix I

## **Spatial and temporal variability of food web structure during the spring bloom in the Skagerrak**

Maar, M, Nielsen, TG, Richardson, K, Christaki, U, Hansen, OS,  
Zervoudaki, S, and Christou, ED.

Mar Ecol Prog Ser, 239: 11-29 (2002)

# Appendix II

## **Importance of copepods versus appendicularians in vertical carbon fluxes in a Swedish fjord**

Vargas, C, Tönnesson, K, Sell, A, Maar, M, Møller, EF,  
Zervoudaki, S, Giannakourou, A, Christou, ED, Satapoomin, S,  
Petersen, JK, Nielsen, TG and Tiselius, P.

Mar Ecol Prog Ser, 241: 125-138 (2002)



# Appendix III

## Functional response of *Oikopleura dioica* to house clogging due to exposure to algae of different sizes

Tiselius, P, Petersen, JK, Nielsen, TG, Maar, M, Møller, EF, Satapoomin, S, Tönnesson, K, Zervoudaki, S, Christou, ED, Giannakourou, A, Sell, A, and Vargas, C.

Mar Biol, 142: 253-26 (2003)

# **Appendix IV**

## **Microscale distribution of zooplankton in relation to turbulent diffusion**

Maar, M, Nielsen, TG, Stips, A and Visser, AW.

Limnol Oceanogr, 48: 1312-1325 (2003)

# Appendix V

**The trophodynamic function of copepods,  
appendicularians and protozooplankton in the  
late summer zooplankton community in the  
Skagerrak**

Maar, M, Nielsen, TG, Gooding, S, Tønnesson, K, Tiselius, P,  
Zervoudaki, S, Christou, ED, Sell, A and Richardson, K.

Submitted to Mar Biol

# The trophodynamic function of copepods, appendicularians and protozooplankton in the late summer zooplankton community in the Skagerrak

MARIE MAAR, TORKEL GISSEL NIELSEN, SASKIA GOODING, KAISA TÖNNESSON, PETER TISELIUS, SULTANA ZERVOUDAKI, EPAMINONDAS D. CHRISTOU, ANNE SELL, AND KATHERINE RICHARDSON

**Abstract.** The study was carried out in the Skagerrak during late summer when population development in the pelagic cycle culminated in the yearly maximum in zooplankton biomass. The cyclonic circulation of surface water masses created the characteristic “dome-shaped” pycnocline across the Skagerrak. The large dinoflagellate, *Ceratium furca*, dominated the phytoplankton biomass. Ciliates and heterotrophic dinoflagellates were the major grazers and, potentially, consumed 111% of daily primary production. The grazing impact of copepods was estimated from specific egg production rates and grazing experiments. The degree of herbivory differed between species (17-110%), but coprophagy (e.g. feeding on fecal pellets) and ingestion of microzooplankton were also important. The appendicularian *Oikopleura dioica* was present in lower numbers than copepods, but cleared a large volume of water. Consequently, the grazing impact of copepods and *O. dioica* was equivalent to 24 and 11% of daily primary production, respectively. Sedimentation of organic material (30 m) varied between 169-708 mg C m<sup>-2</sup> d<sup>-1</sup> and the contribution from the mesozooplankton (copepod fecal pellets and mucus houses with attached phytodetritus of *O. dioica*) was 5-33% of this sedimentation. Recycling of fecal pellets and mucus houses in the euphotic zone was 59 and 36%, respectively. However, there was a high respiration of organic material by microorganisms in the mid-water column and 34% of the sedimenting material, actually, reached the benthic community in the deep, central part of the Skagerrak.

## Introduction

The Skagerrak is a hydrodynamical complex area where water masses from the North Sea and the shallow, brackish Kattegat meet and mixes. The cyclonic circulation of the water masses creates the characteristic “dome-shaped” pycnocline across the Skagerrak by mixing the water column at the periphery, while the central part is stratified most of the year (Rohde 1998). Accordingly, small phytoplankton cells and a microbial food web would be expected to dominate the central part, while a herbivorous food chain based on large phytoplankton cells, copepods and fish would dominate the margins of the Skagerrak (Legendre 1981).

Pelagic food web structure and production in the Skagerrak have been investigated during the spring bloom (Maar et al. 2002) and as well in early summer (Kiørboe et al. 1990, Rosenberg et al. 1990, Bjørnsen et al. 1993). In both seasons, protozooplankton (heterotrophic dinoflagellates and ciliates) appeared to be the major grazers compared to copepods, despite the presence of an overwintering *Calanus*-population. However, more information of the different zooplankton grazers is needed from late summer, which represents the culmination of population development in the pelagic cycle with a yearly maximum in zooplankton biomass.

The appendicularians *Oikopleura dioica* and *Fritilaria borealis* are also common species in coastal waters (Gorsky et al. 2000) and very abundant during late summer (Nielsen and Hansen 1999). They feed on small phytoplankton and bacteria by filtering water through their mucus houses and their grazing impact can exceed that of copepods (Landry et al. 1994, Nakamura et al. 1997, Hopcroft et al. 1995). They are, nevertheless, often ignored in field studies because they are very fragile and difficult to sample (Gorsky and Fenaux 1998).

Protozooplankton are also important grazers during summer in shallow waters (Smetacek 1981, Nielsen and Kiørboe 1994) and as well in deeper waters (Levinsen et al. 1999, Strom et al. 2001) because they have a relatively high growth rate (Hansen et al. 1997). However, simultaneous measurements of the relative grazing impact of copepods, appendicularians and protozooplankton have, to our knowledge, not been conducted.

The degree of stratification of the water column (which controls the introduction of new nutrients (sensu Dugdale and Goering, 1967) to the euphotic zone determines the potential sedimentation of particulate organic carbon (POC) to the sea floor (e.g. Wassmann 1991). Consequently, a relatively low sedimentation is expected at the central part of the Skagerrak in comparison with the well-mixed coastal area. However, the amount, quality and composition of sedimenting matter are modified by the pelagic food web (Kiørboe 1998, Wassmann 1998).

The aim of the present study is to quantify the relative importance of the different components of the late summer zooplankton community (copepods, appendicularians and protozooplankton) for grazing and vertical flux in the Skagerrak under various hydrodynamic regimes.

## Materials and methods

**Study area.** Sampling took place during a cruise with RV Dana (Danish Institute for Fisheries Research, DIFRES) from August 25 to September 3, 2000 in the Skagerrak. The cruise track was roughly parallel to the Danish coast and was comprised of 6 stations (Figure 1). The stations K2 (Koster), T2 and H2 (Hirtshals) were sampled twice (a and b) while the remaining stations were only visited once (Table 1).

Table 1. Sampling schedule of pelagic parameters and sediment trap deployments across the transect.

	Stn K2-a	Stn K2-b	Stn T1	Stn T2-a	Stn T2-b	Stn T3	Stn T4	Stn H2-a	Stn H2-b
<b>Water column Depth (m)</b>	185	185	400	560	560	500	400	305	305
<b>Date</b>	26 August	26 August	27 August	28 August	29 August	1 September	31 August	30 August	31 August
<b>Pelagic sampling Day/night</b>	Day	Night	Night	Day	Night	Day	Night	Day	Night
<b>Trap deployment (local time)</b>	16:10-21:40	-	22:30-5:30	13:55-21:15	00:15-9:15	10:30-15:15	01:30-9:10	13:30-21:40	8:45-18:30
<b>Duration (hours)</b>	5:30	-	Sediment samples lost	6:20	9:00	4:45	7:40	8:10	9:45

**Hydrography.** Profiles of temperature, salinity and fluorescence were taken from surface to 100 m using a Seabird CTD System (911 plus) equipped with a Dr. Haardt fluorometer. *In situ* fluorescence measurements were calibrated against chlorophyll *a* (chl *a*) determinations (Richardson et al. in press.). Nutrient ( $\text{NO}_2^-$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^-$  and  $\text{SiO}_4^{3-}$ ) samples were taken at the surface, at 15 m, the deep chlorophyll *a*-maximum (DCM), at 50 and at 100 m. Nutrient concentrations were determined at the DIFRES using methods described by Grasshoff (1976).

**Phytoplankton and primary production.** For size-fractionated chl *a* determinations, 100 ml triplicates of seawater were filtered onto GF/F, 10, 45 and 200  $\mu\text{m}$  filters, extracted in 5-ml 96% ethanol for 6-24 h and measured before and after acidification on a Turner Designs Model 700 fluorometer (Yentsch and Menzel 1963). Samples for phytoplankton identification were collected at the surface and from the DCM and preserved in 1% acidified Lugol's solution (final concentration). The phytoplankton was counted and measured after 24 h of settling using inverted microscopy at 200x magnification (Utermöhl 1958). Primary production was measured at two depths (3 m and the DCM) using the  $^{14}\text{C}$ -method and incubated in an artificial light incubator (for further details: Richardson et al. in press.) Specific growth rate was calculated as the primary production divided by the depth-integrated chl *a* and the estimated C/chl *a*-ratio.

**Bacteria and protozooplankton.** Samples for bacterial biomass and production were taken at the surface (5 m), DCM (15-27 m), 15 and 30 m. Bacterial abundance was estimated by flow cytometry (Gasol and Georgio 2000). Cell concentrations were converted to carbon by assuming 20 fg C cell<sup>-1</sup> (Lee and Fuhrman 1987). Bacterial production was estimated by the thymidine method (Fuhrman and Azam 1980). Triplicate samples (10 ml) were incubated with 10 nM  $^3\text{H}$ -thymidine (25 Ci mmol<sup>-1</sup>) at 15°C for 1 h in the dark. The incubations were stopped by the addition of buffered formalin (2% final concentration). Blanks were prepared by the addition of formalin prior to addition of isotope. Bacterial production was estimated from the

$^3\text{H}$ -thymidine incorporation rates by using a conversion factor of  $1.1 \times 10^{18}$  cells  $(\text{mol } ^3\text{H-thymidine})^{-1}$  (Riemann et al. 1987).

Samples for protozooplankton (dinoflagellates and ciliates) were taken at the surface, DCM and 30 m and preserved with 2% acidified Lugol's solution (final concentration). The protozooplankton were counted and measured after 24 h of settling using inverted microscopy at 200x magnification. *Ceratium furca* was counted at 100x magnification. Cell volumes ( $\mu\text{m}^3$ ) were estimated assuming simple geometrical shapes. The dinoflagellates were assigned as hetero-, mixo- or autotrophic species according to Nielsen and Hansen (1999). Carbon biomass was calculated according to Menden-Deuer and Lessard (2000) and the daily carbon demand was calculated assuming a log-log linear relationship between maximum ingestion rate and cell volume (Hansen et al. 1997).

**Mesozooplankton biomass.** Mesozooplankton biomass in the upper 100 m were collected using a submersible pump ( $3000 \text{ l min}^{-1}$ ) equipped with a  $45 \mu\text{m}$  net. Five depth strata were sampled: 0-10, 10-25, 25-40, 40-60 and 60-100 m. However, the pump damaged the fragile appendicularians and additional sampling with a WP-2 net (mesh size  $200 \mu\text{m}$ ) was conducted at five stations. The depth-integrated abundance (0-60 m) of appendicularians was therefore estimated from a net/pump-ratio of  $6.2 \pm 2.8$  ( $n=5$ ). The depth-distribution (0-10, 10-25, 25-40, 40-60 and 60-100 m) was estimated from pump-values in percentage and multiplied with the calibrated total abundance. On deck, the samples were concentrated on a  $30\text{-}\mu\text{m}$  sieve and fixed in 2% buffered formalin (final concentration). In the laboratory, copepods, appendicularians and other mesozooplankton groups were counted and their lengths measured (copepod stages:  $n=10$ , appendicularians:  $n=147$ , and other groups:  $n=10$ ). The biomass of copepods was calculated from the abundance and the weight:length relationship according to literature values (Klein Breteler et al. 1982, Berggreen et al. 1988, Hay et al. 1991, Hirche and Mumm 1992, Karlson and Bömstedt 1994, Sabatini and Kiørboe 1994, Satapoomin 1999). The biomass of each of the appendicularians *Oikopleura dioica* and *Fritilaria borealis* was calculated from the ash free dry weight-length regression in Paffenhöfer (1975) and assuming carbon to be 45% of dry weight.

**Egg and fecal pellet production (24 h).** Copepods for egg and fecal pellet production experiments were collected from the upper 25 m using the WP-2 net with a large non-filtering cod end. The contents of the cod end were transferred to a thermobox with surface water and immediately brought to the laboratory. Females were transferred to the 600-ml polycarbonate bottles containing  $45\text{-}\mu\text{m}$  filtered seawater for *Acartia clausi*, *Paracalanus parvus* and *Oithona similis* and  $200\text{-}\mu\text{m}$  filtered seawater for *Calanus finmarchicus/helgolandicus* and *Centropages typicus*. Five replicate bottles, each containing 2 females of *Calanus spp.* or *C. typicus*, 4 females of *A. clausi* or *P. parvus*, or 12 females of *O. similis* (only fecal pellet production) were incubated for 24 hours at  $15^\circ\text{C}$  in dark on a rotating plankton wheel (2 rpm). After incubation, the spawned eggs and produced fecal pellets were counted. The length of females and the diameter of eggs were measured. The specific egg production rate (SEP, % body C  $\text{d}^{-1}$ ) was calculated from the carbon content of females and assuming a carbon content of  $0.14 \text{ pg C } \mu\text{m}^{-3}$  for all eggs (Kiørboe et al. 1985).

Copepod secondary production was estimated as SEP for *Calanus spp.*, *C. typicus*, *A. clausi* and *P. parvus* multiplied with the respective biomass (0-40 m) plus the mean SEP multiplied with the remaining copepod biomass assuming that SEP was representative for all stages and species (Berggreen et al. 1988). Total ingestion by copepods (0-40 m) was calculated as the total secondary production divided by a growth efficiency of 33% (Hansen et al. 1997).

**Short-term fecal pellet production.** To evaluate the effect of long-term incubations (24 h) on the fecal pellet production, short-term (2.5-4 hours) experiments were conducted at the stations T2, T3, T4 and H2. During long-term incubations, the fecal pellet production rate is assumed to be affected by 1) changes in the natural diet composition and 2) potential modification of fecal pellets by copepods. Five replicate bottles, each containing 1 female of *Calanus* spp. or *Centropages typicus*, 2-4 females of *Acartia clausi* or *Paracalanus parvus*, or 9-10 females of *Oithona similis* were incubated in 100-ml blue cap bottles with 45- or 200- $\mu\text{m}$  filtered seawater under the same conditions as for the 24 h incubations. The length and width of pellets were measured and the volume of fecal pellets was calculated assuming a cylindrical shape. The specific fecal pellet production rate (SFP, % body C  $\text{d}^{-1}$ ) was calculated from the carbon content of females and fecal pellets. A recent study has shown that 33% of fecal pellet carbon is lost to the surrounding water through leaking within 1.5 hours (Møller et al. submitted.). Therefore, fecal pellet carbon content was assumed to be  $0.076 \text{ pg C } \mu\text{m}^{-3}$ , which is  $0.057 \text{ pg C } \mu\text{m}^{-3}$  for sedimented (24 h) fecal pellets estimated by González et al. (1994) plus the 33%. Total fecal pellet production was estimated as the SFP for *Calanus* spp., *Centropages* spp., *Acartia* spp., *Paracalanus* spp. and *Oithona* spp. multiplied by the respective biomass plus the mean SFP multiplied by the remaining copepod biomass.

**Grazing experiments.** At Stn T2-a, chl *a*-concentrations were measured during the 24 h incubations (three replicates) in order to estimate the grazing activity of *Calanus* spp., *Centropages typicus*, *Acartia clausi*, *Paracalanus parvus* and *Oithona similis*. Three control bottles containing 45- $\mu\text{m}$  or 200- $\mu\text{m}$  filtered seawater were incubated under the same conditions as for grazing bottles.

Grazing and house production rates were estimated for the appendicularian, *Oikopleura dioica*, at Stn T2-a, T3 and H2a-b. *O. dioica* was sampled by vertical hauls using a 1-m ring net (90- $\mu\text{m}$ ) equipped with a zip-on 30 l Plexi glass cod end, which was immediately brought to the laboratory after retrieval. *O. dioica* with houses were gently transferred with a wide-mouth pipette to the 600-ml incubation bottles. Five replicate bottles with 45- $\mu\text{m}$  or 200- $\mu\text{m}$  filtered seawater each containing 1-3 individuals were incubated for 24 h. Three control bottles with 45- $\mu\text{m}$  or 200- $\mu\text{m}$  filtered seawater were incubated under the same conditions as for grazing bottles. Chl *a* concentrations were measured and the number of produced houses was counted at the end of the incubation period. A few replicates with a negative clearance rates were omitted from further analysis assuming that the animals were stressed.

**Sedimentation.** Vertical flux of particulate organic matter and pigments was measured with sediment traps during the cruise (Table 1). The sediment traps were deployed at 15 and 30 meters depth for 5 to 10 h. The traps consisted of two cylindrical Plexi-glas tubes with a diameter of 7.2 cm and an aspect ratio of  $>6.0$  (KC Instruments, Denmark). They were deployed without baffles or preservatives. After retrieval, the upper 20% of the trap volume were siphoned off using a j-shaped tube to reduce mixing and discarded. The supernatant was, then, siphoned off into a bottle and assumed to represent concentrations of the estimated parameters (see below) in the water surrounding the trap. The remaining trap contents with the sedimented matter were transferred to another bottle. Each bottle was mixed 3 times and subsamples of 100-200 ml for pigments, 200-300 ml for fecal pellets and appendicularian houses and 200-400 ml for particulate organic -carbon (POC) and -nitrogen (PON) analysis were taken.



Water samples for pigment determinations were filtered onto GF/F filters (Whatmann) and extracted in 5-ml 96% ethanol, kept in the dark and refrigerated for 24 hours. The samples were kept frozen until analysis. Chl *a* and phaeophytin (Pha) concentrations were measured on a Turner Designs Model 700 fluorometer before and after acidification (Yentsch and Menzel 1963).

Samples for estimation of fecal pellets and appendicularian houses were preserved in 4% buffered formalin (final concentration) and counted under a dissecting microscope. The length and width of the fecal pellets were measured and the volumes estimated assuming a cylindrical shape for copepod pellets and ellipsoidal shape for appendicularian pellets. Carbon content of pellets was calculated using the ratios 0.057 pg C  $\mu\text{m}^3$  for copepods and 0.042 pg C  $\mu\text{m}^3$  for appendicularians (González et al. 1994) and corrected (+33%) for leaking dissolved organic carbon (see above). Only fecal pellets with volumes  $<5 \times 10^6 \mu\text{m}^3$  were considered as they represent the maximum size of fecal pellets for the copepods used in the present study. Carbon content of fresh appendicularian houses was estimated as 15.3% of body C (Sato et al. 2001) using an average body length of appendicularians caught on the cruise. Any other organisms present were noted, such as copepods and appendicularians.

The POC- and PON samples were filtered onto precombusted GF/F filters (Whatmann) and stored frozen until analysis. The filters were dehydrated at 80°C for 12h before analysis on a CE Instruments CHNS-Elemental Analyser (Model EA 1110).

The sedimentation rates  $f$  ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) of chl *a*, phaeophytin, fecal pellets, mucus houses, POC and PON were corrected for background concentrations in the surrounding water and calculated as:

$$(1) \quad f = (C - C_0) V (A t)^{-1} \times 24 \text{ h}$$

where:  $C$  and  $C_0$  are the sample- and background concentrations ( $\text{mg l}^{-1}$ ),  $V$  sample volume (l),  $A$  trap area ( $\text{m}^2$ ) and  $t$  incubation time (h). The coefficient of variation ( $\text{CV} = \text{SD}/\text{mean}$ ) between trap replicates were below 22% for POC, 27% for PON, 30% for Chl *a*, 39% for pha, 47% for fecal pellets, and 95% for mucus houses. The  $C/\text{chl } a$ -ratio and the POC/PON-ratio of the suspended and sedimented matter were estimated as the slope in linear regression models using data from both the 15 and 30 m traps to achieve a higher significance.

**Statistical analyses.** For testing the difference between means, a two-way ANOVA was used with a significance level of 5%. The mean values are indicated with  $\pm$  the standard deviation (SD) in text and tables. Regression analyses were conducted using a significance level of 5% and the  $r^2$  and number ( $n$ ) of replicates are indicated in the text. All statistical tests were conducted using Statistical Package of Social Science (SPSS, version 10.0) for Windows.

## Results

### Hydrography

Temperature and salinity profiles displayed the characteristic “dome shaped” pycnocline across the Skagerrak (Fig. 2a, b) due to the large cyclonic circulation of the surface currents (Rohde 1998). The warm surface water mass (temperature  $>11^\circ\text{C}$ , salinity  $<34.5$  psu) covered

most of the area and extended to 10-15 meters depth in the central Skagerrak (Stns T2-T4). At the stations close to the Norwegian coast (Stns K2 and T1), the Baltic Coastal Current was present and deepened the surface layer down to 45 meters depth. On the Danish site (Stn H2), a surface water mass with lower salinity (<30 psu) occurred and the surface layer and extended to 20 meters depth.

Surface (5 m) concentrations of N (nitrate and nitrite) were significantly higher ( $0.39\pm 0.06 \mu\text{M}$ ) at the coastal stations (K2, T1 and H2) than at the central stations ( $0.22\pm 0.11 \mu\text{M}$ ) (Table 2). Surface P (phosphate)- concentrations were similar across the transect with an average of  $0.12\pm 0.02 \mu\text{M}$ . Surface concentrations of silicate were highest at Stns K2 and T1 ( $0.83\text{-}1.56 \mu\text{M}$ ).

## Phytoplankton

Surface (5 m) chlorophyll *a* (chl *a*) concentrations were between  $2\text{-}5 \mu\text{g l}^{-1}$  and decreased with depth at the stations K2 and T1 (Figure 2c, 3). At the central stations, surface chl *a* concentrations were below  $3 \mu\text{g l}^{-1}$  and several deep chl *a* maxima (DCM) were recorded during the cruise. The most pronounced DCM occurred at Stn T2-a with a chl *a* concentration of  $20 \mu\text{g l}^{-1}$  at 23-27 m depth.

Generally, the size-fraction 45-200  $\mu\text{m}$  dominated chl *a* with  $55\pm 16\%$  of total and correlated with the abundance of *Ceratium furca* ( $n=15$ ,  $r^2=0.92$ ,  $p<0.05$ ). Microscopy revealed that the size-fractions 0-10  $\mu\text{m}$  and 10-45  $\mu\text{m}$  were dominated by nanoflagellates and diatoms, respectively. The C/chl *a*-ratio, pha/chl *a*-ratio and the POC/PON-ratio of the suspended matter were estimated to 108 ( $r^2=0.41$ ,  $n=12$ ,  $p<0.05$ ), 0.18 ( $r^2=0.27$ ,  $n=14$ ,  $p<0.06$ ) and 6.6 ( $r^2=0.68$ ,  $n=12$ ,  $p<0.05$ ), respectively. Primary production varied between  $475\text{-}2071 \text{ mg C m}^{-2} \text{ d}^{-1}$  (Table 2) and was highest at the stations influenced by the Baltic Coastal Current (Stns K2 and T1).

Table 2. The sampled stations with surface (5 m) nitrate-, nitrite- and silicate concentrations, potential primary production (water column), depth-integrated (0-40 m) chl *a* concentrations, phytoplankton growth rate, depth-integrated (0-40 m) bacterial biomass and production. C/chl=108.

	Stn K2-a	Stn K2-b	Stn T1	Stn T2-a	Stn T2-b	Stn T3	Stn T4	Stn H2-a	Stn H2-b
$\text{NO}_3^- + \text{NO}_2^-$ (5 m) ( $\mu\text{M}$ )	0.34	0.36	0.36	0.07	0.20	0.34	0.26	0.42	0.49
$\text{Si}(\text{OH})_3$ (5 m) ( $\mu\text{M}$ )	1.56	1.49	0.83	0.37	0.34	0.57	0.55	0.53	0.66
Primary production ( $\text{mg C m}^{-2} \text{ d}^{-1}$ )	2071	1083	2011	1068	745	668	471	725	665
Chl <i>a</i> ( $\text{mg chl } a \text{ m}^{-2}$ )	74	83	129	181	160	79	93	70	69
Bacterial biomass ( $\text{mg C m}^{-2}$ )	508	766	1012	793	795	916	741	1004	961
Bacterial production ( $\text{mg C m}^{-2} \text{ d}^{-1}$ )	292	196	223	202	270	245	220	273	271

## Bacteria and protozooplankton

Bacterial abundance decreased slightly with depth from  $1.2\pm 0.2 \times 10^6 \text{ cells ml}^{-1}$  at the surface to  $0.8\pm 0.2 \times 10^6 \text{ cells ml}^{-1}$  at 30 m. Bacterial biomass and production (0-40 m) were quite stable across the transect with an average of  $833\pm 160 \text{ mg C m}^{-2}$  and  $244\pm 35 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,

respectively (Table 2). Ciliate abundance was highest at the surface with 1560-8800 cells l<sup>-1</sup> (Figure 4) and was dominated by the aloricate genera, *Strombidium* spp. and *Strombilidium* spp. Heterotrophic dinoflagellates responded to the DCM at the central stations with a higher abundance and a maximum of 36,800 cells l<sup>-1</sup>. Protozooplankton biomass (0-40 m) was generally higher at the central stations and varied between 459-1216 mg C m<sup>-2</sup> across the transect (Figure 5a). Heterotrophic dinoflagellates dominated the protozooplankton biomass with 90±4%. The most important species were *Gyrodinium spirale*, *Protoperidinium* spp., *Polykrikos schwartzii*, *Prorocentrum micans* and *Dinophysis norvegica*.

## Mesozooplankton

The two most abundant copepod species were *Oithona similis* and *Microsetella norvegica* with up to 9,600 ind. m<sup>-3</sup> at Stn T2-b and 23,400 ind. m<sup>-3</sup> at Stn K2-a, respectively. *O. similis*, *M. norvegica* and nauplii were located in the upper 40 meters of the water column (Figure 6). Calanoid copepods were present in the surface mixed layer above the 12°C–isotherm with the highest abundance at Stn K2. Depth-integrated (0-40 m) copepod biomass was highest (1216-1798 mg C m<sup>-2</sup>) at Stn K2 (Figure 5b) compared to the other stations (268-809 mg C m<sup>-2</sup>). The dominant species were *Calanus finmarchicus/helgolandicus*, *Centropages typicus*, *Temora longicornis*, *Acartia clausi*, *Paracalanus parvus*, *O. similis* and *M. norvegica*.

The abundance of *Oikopleura dioica* was highest at Stn K2 with up to 1200 ind. m<sup>-3</sup> and the depth-distribution followed the 10°C- isotherm (Figure 6e). The depth-integrated biomass was 3-68 mg C m<sup>-2</sup> (0-40 m) (Fig. 5c). *Fritilaria borealis* occurred at Stn T2-a with 170 ind. m<sup>-3</sup> and at stns T2-b, T3 and T4 with 2-9 ind. m<sup>-3</sup>. Larvae of bivalves, polychaetes, echinoderms and gastropods were also present with <3000 ind. m<sup>-3</sup>.

Mean specific egg production rates (SEP) ranged between 7.3-16.0% body C d<sup>-1</sup> for the different stations with an overall mean of 10.6±3.1% body C d<sup>-1</sup> (Table 3). The mean SEP was highest for *C. typicus* with 16.8±5.1 8% body C d<sup>-1</sup> and lowest for *A. clausi* with 7.4±4.0% body C d<sup>-1</sup>. SEP by *A. clausi* correlated with maximum chl *a* (>10 µm) –values in the upper 25 meters across the transect (n=9, r<sup>2</sup>=0.42, p<0.05). There were no correlations between SEP for the other copepod species and different size-fractions of chl *a* or protozooplankton. Specific ingestion rates were calculated from SEP of the different species and assuming a growth yield of 33% (Hansen et al. 1997). The length of females were 2294±25 µm, 1337±12 µm, 844±10 µm, 702±7 µm and 457±8 µm for *Calanus* spp., *C. typicus*, *A. clausi*, *P. parvus*, and *O. similis*, respectively.

Table 3. Specific egg production rate (% body C d<sup>-1</sup>) of four copepod species. The mean specific egg production rates for the different species are shown as % body C d<sup>-1</sup> and eggs female<sup>-1</sup> day<sup>-1</sup>. The overall mean specific egg production rate for the stations was 10.6 (3.1) % body C d<sup>-1</sup>. Standard deviations are given in the parenthesis.

	Stn K2-a	Stn K2-b	Stn T1	Stn T2-a	Stn T2-b	Stn T3	Stn T4	Stn H2-a	Stn H2-b	Mean %body C d <sup>-1</sup>	Mean eggs f <sup>-1</sup> d <sup>-1</sup>
<i>Calanus</i> spp.	4.5 (1.1)	5.2 (5.7)	7.1 (4.0)	8.8 (3.3)	12.7 (9.4)	-	-	12.2 (9.3)	5.5 (3.8)	8.0 (3.4)	20.5 (8.6)
<i>Centropages typicus</i>	21.6 (6.8)	14.3 (7.4)	11.6 (4.8)	15.6 (3.6)	23.1 (5.1)	14.6 (7.8)	22.5 (3.0)	9.0 (9.8)	18.6 (7.5)	16.8 (5.1)	88.7 (26.7)
<i>Acartia clausi</i>	1.7 (1.2)	6.0 (1.1)	6.8 (2.7)	6.3 (4.5)	5.0 (1.9)	16.1 (3.1)	10.0 (4.7)	7.8 (0.6)	7.4 (2.4)	7.4 (4.0)	9.2 (4.9)
<i>Paracalanus parvus</i>	8.4 (2.1)	3.9 (2.0)	4.3 (0.9)	8.0 (2.8)	9.8 (5.4)	17.4 (5.0)	10.8 (4.5)	5.2 (1.4)	8.2 (4.5)	8.3 (3.9)	10.9 (5.3)
Mean	9.0 (8.9)	7.3 (4.7)	7.4 (3.1)	9.7 (4.1)	12.7 (7.9)	16.0 (1.4)	14.4 (7.0)	8.5 (2.9)	9.9 (5.9)		

## Fecal pellet production

The daily production rate of fecal pellets per individual was significantly higher in short- versus long-term incubations. Changes in the natural diet composition and decrease in food concentration during the long-term incubations could result in a lower fecal pellet production here. However, the reduction of chl *a* corresponded to 3-24% of the initial chl *a* concentration (Stn T2) and did probably not affect feeding and defecation rate (Båmstedt et al. 2000). Since the investigated copepod species mainly were herbivores except for *Centropages typicus* (Table 5), the potential change in food composition and concentration did probably not cause the relatively lower fecal pellet production during the long-term incubations.

Thus, we assume that the ratio between long- and short-term incubations indicates the degree of fecal pellet removal from the suspension due to modification by copepods. The modification could be either coprophagy (ingestion of fecal pellets) or coprorhexy (fragmentation of fecal pellets) (Table 4). *Oithona similis* had the lowest ratio (0.12) and, thus, removed nearly all the produced fecal pellets during 24 hours. *Acartia clausi* and *Paracalanus parvus* also removed their own fecal pellets efficiently (0.28-0.39), while this was less important for *Calanus* spp. and *Centropages typicus* (0.59-0.63). The long-term incubations, thus, underestimated the fecal pellet production rate and, therefore, the short-term values were used for estimation of the weight-specific fecal pellet production rate (SFP).

The SFP ranged between 2.5–7.0% body C d<sup>-1</sup> for the different stations with an overall mean of 4.6±1.3% body C d<sup>-1</sup> (Table 4). Total fecal pellet production rate across the transect could then be estimated as the SFP multiplied with the copepod biomass at each station. The average size of fecal pellets (×10<sup>5</sup> μm<sup>3</sup>) was 13.6±4.3 (n=43) for *Calanus* spp., 7.6±3.6 (n=39) for *Centropages typicus*, 2.0±0.5 (n=14) for *Acartia clausi*, 1.2±0.7 (n=49) for *Paracalanus parvus*, and 0.5±0.1 (n=4) for *Oithona similis*. Overall, there was a linear correlation of SEP versus SFP for the four calanoid species (SEP=1.64×SFP+3.26, n=32, r<sup>2</sup>=0.38, p<0.05).

Table 4. Short term (2.5-4 h) mean specific faecal pellet production rate (% body C d<sup>-1</sup>) for five copepod species. Standard deviations in parenthesis are based on 5-10 replicates. The overall mean specific faecal pellet production rate was 4.5±1.3% body C d<sup>-1</sup>. The ratio of faecal pellets produced ind<sup>-1</sup> d<sup>-1</sup> between long- and short-term incubations are the mean from 6 experiments. \*The production rates for Stn K2 and T1 are based on long term incubations and corrected with the long/short-term incubations ratio.

	Stn K2-a*	Stn K2-b*	Stn T1*	Stn T2-a	Stn T2-b	Stn T3	Stn T4	Stn H2-a	Stn H2-b	Long/short incubation
<i>Calanus</i> spp.	1.6 (1.6)	2.2 (1.3)	2.5 (1.5)	3.6 (1.0)	-	-	3.4 (1.5)	2.2 (2.1)	1.9 (1.0)	0.63 (0.24)
<i>Centropages typicus</i>	6.7 (2.8)	2.4 (2.2)	5.0 (2.4)	6.7 (2.4)	4.6 (3.6)	5.3 (2.8)	5.0 (2.0)	7.1 (1.4)	9.0 (7.0)	0.59 (0.22)
<i>Acartia clausi</i>	1.9 (1.7)	1.4 (0.9)	2.7 (1.6)	2.1 (2.8)	2.7 (1.0)	8.2 (4.6)	3.8 (3.0)	2.0 (0.7)	4.6 (3.2)	0.28 (0.16)
<i>Paracalanus parvus</i>	4.7 (1.6)	3.9 (2.4)	5.4 (3.5)	3.7 (2.4)	3.6 (1.7)	7.3 (2.7)	8.0 (3.8)	2.0 (0.6)	5.1 (3.3)	0.39 (0.25)
<i>Oithona similis</i>	8.5 (2.1)	-	12.6 (1.3)	6.6 (4.9)	3.2 (1.1)	-	-	5.5 (1.6)	1.8 (0.5)	0.12 (0.04)
Mean	4.7 (3.0)	2.5 (1.0)	5.6 (4.1)	4.5 (2.0)	3.5 (0.8)	7.0 (1.5)	5.1 (2.1)	3.7 (2.4)	4.5 (2.9)	

## Grazing experiments

All of the investigated copepods ingested chl *a* comparable to a daily ratio of 9-53% body C d<sup>-1</sup> (Table 5). The degree of herbivory (%) was estimated as chl *a*-ingestion relative to total ingestion, which was calculated from the weight-specific egg production rate (SEP) and a growth yield of 33% (Hansen et al. 1997). *Acartia clausi* was herbivorous (97%), while *Calanus*

spp., *Centropages typicus* and *Paracalanus parvus* were omnivorous (17-68%). Unfortunately, there were no measurements of SEP for *Oithona similis*. Instead, SEP of *O. similis* was estimated from the linear regression model of SEP versus the weight-specific fecal pellet production (SFP) for the calanoid species (see above). This gives a total ingestion of 42% body C d<sup>-1</sup>. *O. similis* ingested chl *a* comparable to a daily ratio of 46% body C d<sup>-1</sup> of and the degree of herbivory was, therefore, 110%.

Table 5. Mean ( $\pm$ SD) clearance rate and ingestion rate of chlorophyll *a* by five copepod species at Stn T2-

	Replicates n	Filtration $\mu$ m	Clearance rate (ml ind <sup>-1</sup> d <sup>-1</sup> )	Ingestion rate of chl <i>a</i> (% body C d <sup>-1</sup> )	Herbivory %	Coprophagy %	Microzoopl. %
<i>Calanus</i> spp.	3	<200	103 (19)	16 (3)	68	5.4	27
<i>Centropages typicus</i>	3	<200	7 (1)	9 (1)	17	5.4	78
<i>Acartia clausi</i>	3	<45	10 (4)	22 (8)	97	6.8	-3.8
<i>Paracalanus parvus</i>	3	<45	4 (16)	15 (65)	58	9.2	33
<i>Oithona similis</i>	3	<45	3 (1)	46 (10)	110*	13.8	-24

a. The number of replicates (n) and the size-fraction ( $\mu$ m) of filtered incubation water are indicated. The degree of herbivory in percent was estimated as the chl *a* ingestion rate relative to the total ingestion calculated from the SEP and a growth efficiency of 33%. The potential contribution (%) of fecal pellets to the diet (coprophagy) was calculated from Table 4. The potential contribution (%) of microzooplankton to the diet was calculated as 100% subtracted the % herbivory and coprophagy. The initial chl *a* concentrations were 2.3 and 1.0  $\mu$ g l<sup>-1</sup> in the <200  $\mu$ m and <45  $\mu$ m incubations, respectively. C/chl=108. \*See text for estimation of total ingestion by *Oithona* spp.

The degree of coprophagy was estimated from the fecal production multiplied by (1-the long/short-incubation ratio) of each species in Table 4 assuming that all the removed pellets were ingested. Coprophagy, then, contributed 5.4-13.8% to the copepod diet. The remaining part of ingested material was, finally, assumed to consist of microzooplankton. This shows that microzooplankton potentially contributed 27-78% to the diet of *Calanus* spp., *C. typicus* and *P. parvus*.

Average clearance by *Oikopleura dioica* was 26 $\pm$ 4 ml ind<sup>-1</sup> d<sup>-1</sup> in the <45- $\mu$ m incubations (0.9 $\pm$ 0.1  $\mu$ g chl *a*), which corresponded to a chl *a* ingestion of 165 $\pm$ 18% body C d<sup>-1</sup> (Table 6). We assume that all chl *a* <45  $\mu$ m was ingested because the major part of this size-fraction consisted of cells <10  $\mu$ m (Figure 3). In the <200  $\mu$ m-incubations, clearance by *Oikopleura dioica* was 37 $\pm$ 2 ml ind<sup>-1</sup> d<sup>-1</sup> and significantly higher than in the 45  $\mu$ m incubations (n=3, df=2, p<0.05). *Oikopleura dioica* removed 493 $\pm$ 105% body C d<sup>-1</sup> of chl *a*, which was considerably more than in the <45- $\mu$ m incubations. The size-fraction 45-200  $\mu$ m mainly consisted of *Ceratium furca* but cells larger than 30  $\mu$ m cannot pass through the incurrent filters of the mucus house (Fenaux 1986). The algae were, therefore, not ingested but probably stuck to the mucus house. The carbon content of trapped cells on the houses was estimated as the removal of chl *a* in the size-fraction 45-200  $\mu$ m divided by the number of produced houses. This results in a carbon content of 1.3 $\pm$ 0.2  $\mu$ g C house<sup>-1</sup> and is referred to here as “house detritus”. Individual house production rates (HP) were 3.3 $\pm$ 0.9 and 3.8 $\pm$ 0.9 houses ind<sup>-1</sup> d<sup>-1</sup> in the <45  $\mu$ m- and <200  $\mu$ m incubations, respectively (paired *t*-test, n=6, p=0.08). However, house production also increased with increasing chl *a* (<200  $\mu$ m) concentration on log scale (n=3, r<sup>2</sup>=0.99, p<0.05). We can therefore conclude that potential clogging of houses led to higher house production rates when *Ceratium* was present. This relationship was used to estimate HP from the mean chl *a* (0-

25 m) concentration at each station. Total house production across the transect could, then, be estimated as HP multiplied by the biomass of *O. dioica*.

It was not possible to estimate fecal pellet production of *O. dioica* in the experiment because the pellets were disintegrated into fluffy material. The average length of *O. dioica* was  $470 \pm 160 \mu\text{m}$  and the average carbon content was  $1.48 \pm 1.55 \mu\text{g C ind}^{-1}$  ( $n=127$ ). The carbon content of fresh mucus houses was  $0.2 \mu\text{g C}$ .

Table 6. *Oikopleura dioica*: clearance, removal rate (ingested+trapped chl *a*) and house production in the <45  $\mu\text{m}$ - and <200  $\mu\text{m}$  incubations. Trapped chl *a* on the houses was calculated as the difference between removal rates in the two incubations. Average house detritus was calculated as trapped chl *a* divided by house production and multiplied by the specific biomass of *O. dioica*. C/chl *a*-ratio=108. Abundance of *Ceratium* spp. was estimated from the chl *a* (45-200  $\mu\text{m}$ ) using a linear regression model (see text). Standard deviations are given in the parenthesis.

Incubation		Exp. 1	Exp. 2	Exp. 3	Mean
<45 $\mu\text{m}$	Number of replicates	4	4	4	4
	Chl <i>a</i> concentration ( $\mu\text{g l}^{-1}$ )	1.0	0.9	0.9	0.9 (0.1)
	Clearance rate ( $\text{ml ind.}^{-1} \text{d}^{-1}$ )	22 (13)	30 (11)	25 (14)	26 (4)
	Removal rate (% body C $\text{d}^{-1}$ )	145 (81)	189 (95)	160 (55)	165 (22)
	House production (houses $\text{ind.}^{-1} \text{d}^{-1}$ )	4.0 (1.6)	2.3 (0.8)	3.5 (2.1)	3.3 (0.9)
<200 $\mu\text{m}$	Number of replicates	5	5	5	5
	Chl <i>a</i> concentration ( $\mu\text{g l}^{-1}$ )	2.2	1.4	2.3	2.0 (0.5)
	<i>Ceratium</i> spp. (cells $\text{l}^{-1}$ )	17900	7800	19500	15100
	Clearance rate ( $\text{ml ind.}^{-1} \text{d}^{-1}$ )	37 (12)	38 (21)	34 (27)	37 (2)
	Removal rate (% body C $\text{d}^{-1}$ )	567 (173)	373 (197)	540 (425)	493 (105)
	Trapped chl <i>a</i> (% body C $\text{d}^{-1}$ )	422	184	380	329 (127)
	House production (houses $\text{ind.}^{-1} \text{d}^{-1}$ )	4.3 (2.3)	2.7 (0.8)	4.3 (2.3)	3.8 (0.9)
	House detritus ( $\mu\text{g C house}^{-1}$ )	1.4	1.0	1.3	1.3 (0.2)

## Sedimentation

Sedimentation rates of POC and chl *a* were significantly higher in the 15 m traps than in the 30 m traps (paired t-test, two-tailed,  $df=6$ ,  $p<0.05$ ) (Figure 7). POC-sedimentation at 30 m depth decreased across the transect from Stn K2 with  $710 \text{ mg C m}^{-2} \text{d}^{-1}$  to Stn H2 with  $169\text{-}176 \text{ mg C m}^{-2} \text{d}^{-1}$ . For sedimented matter, the C/chl-ratio was 124 ( $r^2 = 0.65$ ,  $n=12$ ,  $p<0.05$ ), the pha/chl-ratio was 0.23 ( $r^2=0.55$ ,  $n=14$ ,  $p<0.05$ ) and the C/N-ratio was 8.3 ( $r^2=0.70$ ,  $n=12$ ,  $p<0.05$ ), which were all higher than for the suspended matter. The relative contribution of chl *a* to POC-sedimentation (30 m) was lowest at the coastal stations (K2 and H2) with 17-36% compared to 45-67 % at the central stations. Sedimentation of POC as percent of primary production was, likewise, lower at the coastal stations with 23-34% than for the central stations (39-59%).

Mesozooplankton activity contributed to the vertical flux with fecal pellets and appendicularian mucus houses (Figure 8). Total mesozooplankton-mediated vertical flux (15 and 30 m) was most important at Stn H2 with 24-34% of total POC, while it only contributed 5-15% of total POC for the other stations.

Sedimentation of fecal pellets was relatively low with  $10 \pm 6 \text{ mg C m}^{-2} \text{d}^{-1}$  at 15 m depth and  $13 \pm 5 \text{ mg C m}^{-2} \text{d}^{-1}$  at 30 m depth. There was, however, no significant difference between the two depths (paired t-test, two-tailed,  $df=6$ ,  $p>0.05$ ) and the contribution of fecal pellets to POC-sedimentation at 30 m was  $4 \pm 2\%$ . Appendicularian fecal pellets contributed less than 6% to the fecal pellet flux and was, therefore, regarded as insignificant. The proportion of recovered fecal

pellets in the 30 m-sediment traps was 41% indicating that 59% of the produced fecal pellets were recycled in the water column (Table 7).

The carbon content of sedimented houses was estimated as the carbon content of fresh mucus houses (0.2  $\mu\text{g C}$ ) plus the carbon content of house detritus (1.3  $\mu\text{g C}$ ). House sedimentation (including detritus) varied over the transect with 14-87 (mean:  $42\pm 24$ )  $\text{mg C m}^{-2} \text{d}^{-1}$  at 15 m and 11-43 (mean:  $28\pm 13$ )  $\text{mg C m}^{-2} \text{d}^{-1}$  at 30 m. House sedimentation decreased significantly with depth with the exception of Stn T3 (paired t-test, two-tailed,  $df=5$ ,  $p<0.05$ ). Sedimentation of houses was 64% of house production, so therefore 36% of the produced houses were recycled in the water column (Table 7). Recycling of houses in the water column correlated non-linearly with the abundance (0-40 m) of *Microsetella norvegica* (Figure 9), but not with other copepod species.

Table 7. Production and sedimentation rates ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) and recycling efficiency (%) of copepod fecal pellets (FP) and appendicularian houses (H).

	Stn K2-a	Stn K2-b	Stn T1	Stn T2-a	Stn T2-b	Stn T3	Stn T4	Stn H2-a	Stn H2-b	Mean ( $\pm$ SD)
<b>FP production</b>	79.8	29.8	31.2	18.4	22.4	18.4	20.0	17.7	33.1	30.1 (19.6)
<b>FP sedimentation</b>	20.5	-	-	9.5	9.1	18.5	9.0	7.3	14.0	12.6 (5.2)
<b>%FP recycling</b>	74	-	-	48	59	-	55	58	58	59 (9)
<b>H production</b>	13.0	45.7	17.4	2.4	3.1	5.7	6.0	5.1	9.5	12.0 (13.5)
<b>H sedimentation</b>	5.6	-	-	1.7	1.6	4.8	2.9	4.6	6.0	3.9 (1.8)
<b>%H recycling</b>	57	-	-	28	48	17	52	10	37	36 (18)

## Discussion

### Hydrography and plankton distributions

Physical processes in the ocean shape the pelagic food web structure on a continuum of scales from the oceanic (Legendre 1984) via the mediate, basin scales (Kiørboe et al. 1990, Maar et al. 2002) to microscale (Owen 1989, Maar et al. 2003). Food web structure and production have previously been shown to be greatly influenced by the hydrodynamics in the Skagerrak (Pingree et al. 1982, Kiørboe et al. 1990, Tiselius et al. 1991, Bjørnsen et al. 1993, Maar et al. 2002, Richardson et al. in press.). In the present study, coastal water masses deepened the pycnocline at Stns K2, T1 and H2 and introduced new nutrients to the surface waters. This was reflected in the higher phytoplankton growth rates here compared to the stratified central stations. Especially Stn K2 was characterised by a strong surface advection of outflowing Baltic Water resulting in variable profiles of temperature and salinity (Richardson et al. in press.). Phytoplankton was, in general, dominated by the large dinoflagellates *Ceratium furca*, which is a common late summer feature in temperate, stratified waters (Nielsen 1991, Peterson et al. 1991). Diatoms were only present in low numbers except for Stns K2, T1 and for the deep chl *a* maximum (DCM) at Stn T2, where silicate concentrations were high. The general dominance of *Ceratium furca* in late summer masked the pelagic food web structure suggested by Kiørboe et al. (1990), where large species dominated the margins and small phytoplankton cells the centre of the Skagerrak.

The assumed dominance of small cells and the microbial food web in the central part was only partly confirmed in the present study. Protozooplankton biomass was generally higher at the central stations, while bacterial biomass increased slightly across the transect from Stn K2 to H2. The biomass of copepods and the appendicularian *Oikopleura dioica* was, in general, highest at the coastal stations (K2, T1 and H2). Here, calanoid copepods dominated the biomass with  $70\pm 10\%$  compared to at the central stations ( $49\pm 11\%$ ). In contrast, the cyclopoid copepod *Oithona similis* and the harpacticoid copepod *Microsetella norvegica* became relatively more important at the central stations (Stns T2-T4). Overall, the biomass of small copepod species (calanoids, cyclopoids and harpacticoids) exceeded that of the larger species such as *Calanus finmarchicus/helgolandicus* and *Centropages typicus*. The observed differences in depth of mixed layer and plankton community structure across the transect will have implications for the production and the fate of biogenic carbon through zooplankton grazing activity or sedimentation (Kiørboe 1998, Wassmann 1998).

### Copepod egg production and grazing

The overall average specific egg production rate (SEP) of copepods was  $10.6\pm 3.1\%$  body  $C\ d^{-1}$  and similar to the measured SEP rate during a *Ceratium* spp. bloom in these waters (Peterson et al. 1991, Kiørboe and Nielsen 1994). SEP varied little across the transect for the examined species but was, on average, higher at the central stations (Stns T2-T4). SEP rates were, however, less than maximum and indicate food limitation (Kiørboe et al. 1990, Peterson et al. 1991, Kiørboe and Nielsen 1994). Mean specific ingestion rates ranged between 22-50% body  $C\ d^{-1}$  (calculated from SEP of each species) and the degree of herbivory differed among species. *Oithona similis*, *Acartia clausi* and *Paracalanus parvus* were mainly herbivorous and the SEP by *A. clausi* also correlated with chl *a*  $> 10\ \mu m$ . The larger copepods, *Calanus* spp. and *Centropages typicus*, are able to graze efficiently on *Ceratium* spp. (Nielsen 1991) and the proportion of chl *a* in their diet was 68 and 17%, respectively. In general, however, the copepods must graze on other particles than phytoplankton to sustain their estimated daily carbon demand.

Ingestion of microzooplankton can be a major contribution to the copepod diet during the stratified summer period (Nielsen et al. 1993, Kiørboe and Nielsen 1994, Levinsen et al. 2000). Ciliate biomass was low  $< 5\ \mu g\ C\ l^{-1}$  but heterotrophic dinoflagellate biomass was higher with up to  $50\ \mu g\ C\ l^{-1}$ . In grazing experiments, microzooplankton potentially contributed 0-78% to the diet of copepods. The biomass of available food including ciliates, heterotrophic dinoflagellates and chl *a* (10-45  $\mu m$ ) was well below food saturation of 500 and 200  $\mu g\ C\ l^{-1}$  for *Acartia tonsa* (Berggreen et al. 1988) and *Oithona* spp. (Sabatini and Kiørboe 1994), respectively, and could not alone meet the carbon demand of copepods.

Another possibility for meeting the carbon demand is through coprophagy (i.e. feeding on fecal pellets). This has been reported for both calanoid and cyclopoid copepods (Paffenhöfer and Knowles 1979, Dagg 1993, Gonzáles and Smetacek 1994). Comparison of our long- and short-term fecal pellet production experiments showed that all the examined species exploited fecal pellets to different degrees. The cyclopoid copepod, *Oithona similis* removed nearly all the produced fecal pellets as observed by Gonzáles and Smetacek (1994). For calanoid copepods, the fecal pellet production rate was 28-63% lower in the long-term experiments. However, it is not possible to distinguish between coprophagy and coprorhexy (fragmentation of fecal pellets). Coprorhexy can also result in fewer fecal pellets in the suspension because the fragmented fecal



pellets are disintegrated (Lampitt et al. 1990, Noji et al. 1991). It has been suggested that calanoid copepods only feed on fecal pellets when phytoplankton is sparse (González and Smetacek 1994). Coprophagy might therefore have been important for the diet of both calanoid and cyclopoid species under the present food limiting conditions.

The field data also indicate that ingestion/degradation of fecal pellets was significant as only 41% d<sup>-1</sup> of the produced fecal pellets were recovered in the 30 m-traps. Viitasalo et al. (1999) and Riser et al. (2001) found an even higher recycling of fecal pellets (>98%) while recycling was quite low (16%) in a Swedish fjord (Vargas et al. 2002). *Oithona* spp. have been suggested to function as coprophagous filters in the upper mixed layer (Gonzalez and Smetacek 1994, Svensen and Nejstgaard in press.). There was, however, no correlation between the abundance of *Oithona similis* and recycling of fecal pellets. Thus, the whole copepod community probably contributed to this recycling. Accordingly, sedimentation of fecal pellets was low with an average of 13±5 mg C m<sup>-2</sup> d<sup>-1</sup> at 30 m corresponding to 4±2% of POC sedimentation. This contribution is even less if the loss through leaking dissolved organic carbon (Urban-Rich 1999, Møller et al. submitted). Sedimentation of copepod fecal pellets has been suggested to be insignificant in areas with a dominance of smaller copepod species in agreement with the present study (Viitasalo et al. 1999). For example, the percentage of fecal pellets to POC sedimentation was 5% in the Kattegat (Olesen and Lundsgaard 1995) and <0.05% in the northern Baltic Sea (Viitasalo et al. 1999). However, fecal pellets have a considerably higher sinking rate than single phytoplankton cells or amorphous detritus and they might, therefore, be more important for sedimentation in deep waters (see discussion below).

## Appendicularian grazing and house production

The appendicularian *Oikopleura dioica* is a small filter feeder with a unique mucus house that collects particles in sizes ranging from bacteria to nanoplankton (Flood and Deibel 1998). The potential food sources offered in our experiments in the fraction <45 µm were phytoplankton with 101±4 µg C l<sup>-1</sup> and bacteria with 26±5 µg C l<sup>-1</sup> given a total of 127 µg C l<sup>-1</sup>. Clearance of small phytoplankton by *O. dioica* was slightly lower, 26 ml ind<sup>-1</sup> d<sup>-1</sup>, than observed in previous studies, 29-31 ml ind<sup>-1</sup> d<sup>-1</sup>, at the same food concentration consisting of *Isochrysis galbana* (Acuña and Kiefer 2000, Tiselius et al. (2003)). The present ingestion was 219% body C d<sup>-1</sup>, which is below the maximum ingestion of 394% body C d<sup>-1</sup> indicating that the animals were food limited (Tiselius et al. 2003).

The difference between removal rate in the two size-fractionated incubations were used for calculation of the amount of trapped chl *a* on the houses assuming that the condition of animals was similar in both incubations. This shows that *Ceratium furca* (chl *a* 45-200 µm) was efficiently removed from the suspension by *O. dioica* and probably trapped on the inlet filters of the houses. Clearance (of the fraction 0-200 µm) was, therefore, 11±4 ml ind<sup>-1</sup> d<sup>-1</sup> higher as opposed to the incubation with small cells. This could be due to adhesion of *C. furca* to the house surface during encounter caused by small-scale turbulence or sinking (Hansen et al. 1996). Sinking velocity was low with 7.9±5.2 m d<sup>-1</sup> and coagulation due to scavenging could therefore be ignored. The volume cleared per house due to shear coagulation was calculated according to Hansen et al. (1996) assuming the size of houses and of *C. furca* to be 2 and 0.15 mm, respectively, a shear rate of 0.1-1 s<sup>-1</sup> and a residence time of 24 h (=incubation time). This gave a clearance of 0.5-5 ml house<sup>-1</sup> and could only partly explain the higher clearance rate. Another possibility would be that the animals increased clearance to compensate for a lower

food supply. If small cells to some extent were hindered to enter the houses due to clogging by *C. furca*, *O. dioica* would experience a lower food supply than for the incubations with small cells only. Previous studies found lower ingestion rates of the animals only (not including particles trapped in the houses) during blooms of large cells probably due to obstruction (Knoechel and Steel-Flynn 1989, Acuña et al. 1999).

In the study by Tiselius et al. (2003), *O. dioica* was on the other hand able to back-flush the houses and prevent trapping of *Ceratium* cells on the inlet filters. However, there was a higher concentration of *C. furca* (7900-19500 l<sup>-1</sup>) in the present study compared to the initial concentration of *C. tripos* (6000 l<sup>-1</sup>) in the study by Tiselius et al. (2003). The encounter rate of *C. furca* with houses of *O. dioica* was 95-102 cells house<sup>-1</sup> in the present study calculated from the clearance rate in the <45 µm incubations and house production in the presence of *C. furca*. In comparison, the encounter rate was 41 cells house<sup>-1</sup> in the study by Tiselius et al. (2003) using a clearance of 31 ml ind<sup>-1</sup> d<sup>-1</sup> and a house production of 4.5 houses d<sup>-1</sup>. Thus, the back-flush mechanism might not be efficient at the high encounter rates found in this study.

The average amount of trapped chl *a* (45-200 µm) on the houses was 1.3±0.2 µg C (C/chl ratio=108). Other studies have also observed numerous diatoms, autotrophic flagellates, protozooplankton and fecal pellets attached to the abandoned mucus houses of *Oikopleura* spp. (Taguchi 1982, Alldredge and Silver 1988, Hansen et al. 1996). The carbon content of discarded appendicularian houses has been reported as: 6.9 µg C (Alldredge 1976), 1-10 µg C (Taguchi 1982) and 0.9-4.3 µg C by using the equation POC=1.09×V<sup>0.39</sup>, a radius of 0.5-2 mm and assuming a spherical shape (Alldredge 1998). The estimated carbon content of discarded houses then falls within the expected range, but was probably underestimated because the contribution from fecal pellets, small phytoplankton cells and other microorganisms was not considered (Gorsky and Fenaux 1998). Sedimentation of *O. dioica* houses with detritus (30 m) was, on average, 28±13 mg C m<sup>-2</sup> d<sup>-1</sup> or 18,500±8600 houses m<sup>-2</sup> d<sup>-1</sup> and is within the range of earlier measurements of 5,800 houses m<sup>-2</sup> d<sup>-1</sup> in a Swedish fjord (Vargas et al. 2002) and 55,000 houses m<sup>-2</sup> d<sup>-1</sup> in a shallow fjord on the west coast of the USA (Hansen et al. 1996). Sedimentation of houses with detritus exceeded that of copepod fecal pellets and was most important at Stn H2, where they contributed with 17-29% of sedimented POC.

One third of the produced appendicularian houses was not recovered in the sediment traps, indicating a pronounced recycling in the euphotic zone. It has been suggested that invertebrate zooplankton grazing activity is responsible for the 20-70% of aggregate carbon that is degraded within the upper 50 m of the euphotic zone (Kjørboe 2000, Vargas et al. 2002). In the present study, there was a non-linear relationship between the recycling of mucus houses and the abundance of the harpacticoid copepod *Microsetella norvegica*. The relationship gave a daily recycling of 0.04-0.09 house ind.<sup>-1</sup> corresponding to 11-24 ind. house<sup>-1</sup> using an abundance of 1-4×10<sup>5</sup> ind m<sup>-2</sup>. *M. norvegica* have been observed embedded in the mucus matrix of appendicularian house aggregates with up to 14 ind. aggregate<sup>-1</sup> (Green and Dagg 1997) and to consume particles trapped in the houses (Alldredge 1972). There are only a few studies that focus on *M. norvegica* despite the fact that it is a common and widely distributed species (Nielsen and Andersen 2002, Uye et al. 2002).

A relatively low growth rate compared to calanoid species was found for *M. norvegica* from the Inland Sea of Japan (Uye et al. 2002). Specific ingestion rate of *M. norvegica* was 10% body C d<sup>-1</sup> by using the equation in Uye et al. (2002) at 15°C and assuming a growth yield of 33% (Hansen et al. 1997). Recycling of houses with detritus in the present study was 0.06-13 µg C ind<sup>-1</sup> d<sup>-1</sup> and corresponds to a specific ingestion rate of 13-28% body C d<sup>-1</sup> by *M. norvegica*.

This is probably overestimated because, firstly, the aggregates will disintegrate before all of it has been fully ingested, secondly, because not all individuals of *M. norvegica* might be associated with houses, and, finally, other organisms such as microorganisms and other invertebrates potentially feed on the house aggregates (Alldredge 1972, Green and Dagg 1997, Ploug et al 1999). Other loss factors apart from degradation could be advection or under-sampling by sediment traps. Nevertheless, there seems to be a close relationship between the recycling of houses and the presence of *M. norvegica*.

## Grazing impact and sedimentation

Total grazing impact by the zooplankton community (copepods, *Oikopleura dioica*, heterotrophic dinoflagellates and ciliates) was 70-219% of primary production and ranged between 1019-1524 mg C d<sup>-1</sup> with maximum values at Stn K2 (Table 8). Traditionally, ecological studies have focused on copepods, because they are abundant and a trophic link between large phytoplankton and fish (Steele 1974). In the present study, however, copepod grazing only contributed with 17±8% of total grazing impact. Instead, a large fraction of primary production was cycled through the protozooplankton to higher trophic levels.

Table 8. Grazing or removal rates (mg C m<sup>-2</sup> d<sup>-1</sup>) by copepods, *Oikopleura dioica* and protozooplankton and the daily loss rates (%) of primary production (PP) and chl *a*. Grazing rates of copepods were estimated from the depth-integrated biomass (0-40 m), SEP and a growth yield of 33%. For *O. dioica*, the average specific removal rate was estimated from the house production multiplied by 1.3 µg C house<sup>-1</sup> (Table 6). Grazing rates were, then, estimated from the depth-integrated biomass (0-40 m) multiplied by the specific ingestion rate of 219% body C d<sup>-1</sup>. Grazing rates by protozooplankton were estimated from the depth-integrated biomass (0-40 m) and a maximum ingestion rate according to Hansen et al. (1997). Total (1) is the amount of carbon removed (grazed and trapped on houses) from the suspension and total (2) is the amount of carbon grazed by the zooplankton community. Parenthesis gives the relative contribution (%) of total grazing impact.

	Stn K2-a	Stn K2-b	Stn T1	Stn T2-a	Stn T2-b	Stn T3	Stn T4	Stn H2-a	Stn H2-b
<b>Copepods</b>	493 (32)	270 (21)	139 (10)	121 (8)	246 (17)	130 (11)	192 (19)	114 (11)	239 (20)
<i>O. dioica</i> (removed)	132 (9)	432 (33)	150 (11)	22 (2)	28 (2)	57 (5)	59 (6)	51 (5)	96 (8)
<b>Protozooplankton</b>	898 (59)	591 (46)	1122 (79)	1297 (90)	1178 (81)	1031 (84)	780 (75)	854 (84)	842 (72)
<b>Total (1)</b>	1524	1293	1411	1441	1452	1218	1032	1019	1177
<b>% of PP</b>	74	119	70	135	195	182	219	141	177
<i>O. dioica</i> (ingested)	51	149	42	7	9	21	22	20	38
<b>Total (2)</b>	1443	1010	1303	1426	1432	1182	994	987	1118
<b>% of PP</b>	70	93	65	134	192	177	211	136	168
<b>% of chl <i>a</i></b>	18	11	9	7	8	14	10	13	15

Thus, the protozooplankton (heterotrophic dinoflagellates and ciliates) appear to be the major grazers in the Skagerrak in late summer (75±14%). This has also been observed to be the case during the spring bloom (Maar et al. 2002) and early summer in the Skagerrak (Bjørnsen et al. 1993). While the higher grazing impact of protozooplankton relative to copepods has often been demonstrated in shallow coastal waters (Hirst et al. 1999, Nielsen and Kjørboe 1994, Smetacek 1981, Dagg 1995), there are relatively few studies examining this possibility in deeper waters, where the presence of a *Calanus*-population has resulted in the assumption that large copepods dominate grazing (Nielsen and Hansen 1995, Hansen et al. 1999). Our study

shows that the grazing impact by the protozooplankton may also be important over the entire seasonal cycle in deeper waters hosting an overwintering copepod population.

The contribution from another, often ignored, grazer, *O. dioica*, was  $9\pm 10\%$  of total grazing impact and includes both the ingested and trapped phytoplankton. Despite the low biomass of *O. dioica*, the high removal rate resulted in a grazing impact comparable to that of copepods. *Oikopleura* spp. have earlier been reported to be major grazers on the plankton community where their contribution frequently exceeded that of copepods (Landry et al. 1994, Nakamura et al. 1997, Hopcroft et al. 1995). However, only 40% of the removed chl *a* from the suspension by *O. dioica* was actually ingested. The rest was associated with house detritus that eventually settles to the sea floor. Hence, the percentage of primary production that was actually ingested was below 100% at Stns K2 and T1, while it was  $>134\%$  at the other stations (Table 8). This is also reflected in a higher sedimentation rate at Stn K2 compared to the other stations. Sedimentation rates ranged between  $169\text{--}708\text{ mg C m}^{-2}\text{ d}^{-1}$  (30 m) and were similar to those observed during early summer in the Skagerrak by Rosenberg et al. (1990),  $160\text{--}888\text{ mg C m}^{-2}\text{ d}^{-1}$ . Potential sedimentation out of the euphotic zone during the summer period was  $32\text{--}53\text{ g C m}^{-2}$  (3-5 months) using an average of  $350\text{ mg C m}^{-2}\text{ d}^{-1}$ . In comparison, the potential sedimentation rate during the spring bloom was  $<52\text{ g C m}^{-2}$  (1-month) assuming that  $<17\%$  of primary production was grazed by the zooplankton community (Maar et al. 2002).

At the central stations (T2, T3 and T4), a higher percentage of POC-sedimentation consisted of chl *a*, and the relative loss of primary production to sedimentation was also higher (39-59%) than at the stations at the periphery. Phytoplankton stuck to appendicularian houses only contributed with  $9\pm 4\%$  of sedimenting chl *a* and could not explain the high chl *a*-sedimentation at the central stations. Another explanation could be that phytoplankton at these stations was more nutrient limited and that senescent algae were sedimenting out of the water column. The overall higher C/chl *a*-ratio, pha/chl *a*-ratio and POC/PON-ratio in the sedimented matter than for suspended matter also indicate that the settling chl *a* consisted of phytodetritus. The origin of phytodetritus could probably be assigned to the surface phytoplankton community as the potential photosynthetic capacity and nitrate concentrations were lower here than at the DCM's (Richardson et al. In press.). This is also supported by the fact that sedimentation rates of chl *a* decreased with depth and that surface nitrate and silicate concentrations were significantly lower at the central stations compared to the coastal stations. Another possibility was that chl *a* in the sediment traps could originate from vertical migrating dinoflagellates (Lundsgaard et al. 1999). However, there was no difference in chl *a* sedimentation between day or night indicating that this was probably not the case.

The unidentified, remaining detritus fraction (sedimented POC without chl *a*, fecal pellets and houses with detritus) could originate from dead organisms, collapsed houses of *Fritilaria borealis*, sloppy feeding by copepods or detritus from the protozooplankton (Lundsgaard and Olesen 1997). The detritus fraction corresponded to  $14\pm 2\%$  of protozooplankton ingestion, except at Stn K2 with 47%, and agrees well with an assimilation ratio of 70-82% for ciliates (Stoecker 1984). If the detritus fraction is assigned to the protozooplankton, their contribution to the vertical flux would be  $4.1\pm 2.7$  times higher than that of the mesozooplankton (fecal pellets and appendicularian houses with detritus). However, the average sinking velocities of fecal pellets ( $58\pm 25\text{ m d}^{-1}$ ) and appendicularian houses ( $7.9\pm 5.2\text{ m d}^{-1}$ ) are higher than the detritus fraction ( $0.9\pm 0.7\text{ m d}^{-1}$ ) and chl *a* ( $0.6\pm 0.3\text{ m d}^{-1}$ ). Theoretically, fecal pellets will reach the seafloor after 7 days and houses after 7 weeks as opposed to the 1-2 years for detritus and chl *a* in a 400-m water column. The degradation time of fecal pellets and marine snow aggregates are

6-9 days (Hansen et al. 1996, Plough et al. 1999). Depending on the depth of the water column, some of the fecal pellets and appendicularian houses might in fact reach the bottom.

To evaluate how much of the sedimented material that potentially reaches the sea floor, the sedimentation rates at 30 m were compared with the POC-input to the sediment measured during the same campaign (Ståhl et al. in press.). The POC-input to the sediment was estimated as the sum of measured (*in-situ* with a benthic lander) benthic organic carbon oxidation rates, DOC fluxes and organic carbon burial rates at all stations (Ståhl et al. in press). At the relatively shallow (app. 200 m) coastal Stns K2 and H2, 64 and 100% of POC-sedimentation, respectively, reached the sea floor. In comparison, only 34% of POC-sedimentation reached the sea floor at the deeper (560 m), central Stn T2. The majority of zooplankton was located in the upper 40 meters and grazing on the sedimenting material was presumably insignificant below the euphotic zone. Microbial degradation of organic material, on the other hand, was important in the mid-water column where an oxygen minimum layer was found below the depths of the DCM (Richardson et al. in press). The amount of degraded material in this layer was 180-360 mg C m<sup>-2</sup> d<sup>-1</sup> assuming that the layer was build up over 10-20 days (Richardson et al. in press.). This is in agreement with the reduction of 255±1 mg C m<sup>-2</sup> d<sup>-1</sup> in sedimentation rates between 30 m and bottom at Stns K2 and T2. However, the comparison between the two types of sedimentation rates should be interpreted cautiously, because they are operating on different time-scales and because lateral advection also disturbs the pattern (Ståhl et al. in press.).

The export ratio (sedimentation/primary production) of the euphotic zone was estimated to 23-39% at the stations K2, T2 and H2. This is in agreement with the estimated *f*-ratio (new/total primary production) of 18-36%, which indicates the potential export ratio of organic material (Richardson et al. in press.). The export ratio during summer in the Skagerrak was higher than in the Gulf of Riga and the Kattegat with 9-22% (Lundsgaard and Olesen 1997, Lundsgaard et al. 1999), but lower than during the spring bloom in boreal shelf and coastal areas with 46±35% (Wassmann 1991).

Thus, despite the relatively high sedimentation of biogenic carbon out of the euphotic zone, only a fraction of this actually reaches the sea floor and potentially benefits the benthic community. The quality, quantity and type of food provided to the benthos are, however, modified over the year through different processes in the pelagic food web. While protozooplankton grazing was most important for the trophic transfer of energy within the pelagic food web in late summer, mesozooplankton waste products (copepod fecal pellets and appendicularian houses) were important for the vertical flux of biogenic carbon to the sea floor.

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## Figure legends

1. Map of the study area with the position of the sampling stations.
2. Depth profiles of a) salinity, b) temperature and, c) chl *a* across the transect.
3. Size-fractionated chl *a* at the surface and the deep chl *a* maximum (DCM). The depth positions of DCM are indicated.
4. Abundance of protozooplankton (ciliates and heterotrophic dinoflagellates) at the surface and the DCM.
5. Depth-integrated biomass (0-40 m) of a) protozooplankton, b) copepods, and c) appendicularians across the transect.
6. Depth-distributions of the abundance (ind. l<sup>-1</sup>) of a) nauplii, b) *Oithona* spp., c) *Microsetella* spp., d) calanoid copepods, and e) *Oikopleura dioica*. Data points for the different depths intervals are: 5 m (0-10m), 17.5 m (10-25 m), 32.5 m (25-40 m), 50 m (40-60 m) and 80 m (60-100 m).
7. Sedimentation of POC divided into chl *a* and detritus (POC – chl *a*) at a) 15 m and b) 30 m depth and the percentage POC-sedimentation of primary production (PP) at 30 m are indicated.
8. Mesozooplankton mediated sedimentation given as fecal pellets, appendicularian houses and house detritus and indicated with the percentage of total POC-sedimentation at a) 15 m and b) 30 m depth.
9. A non-linear regression model of house recycling versus abundance of *Microsetella* spp.

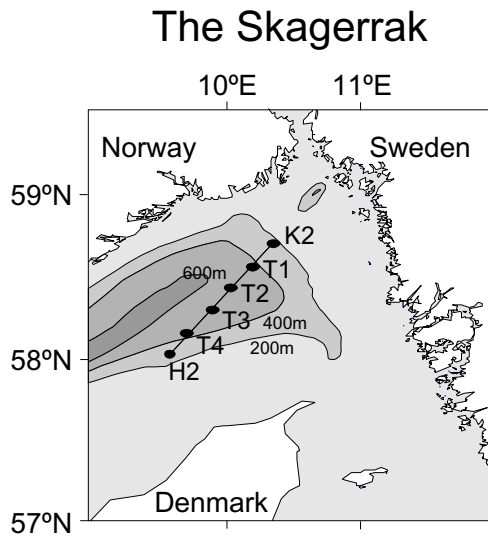


Figure 1.

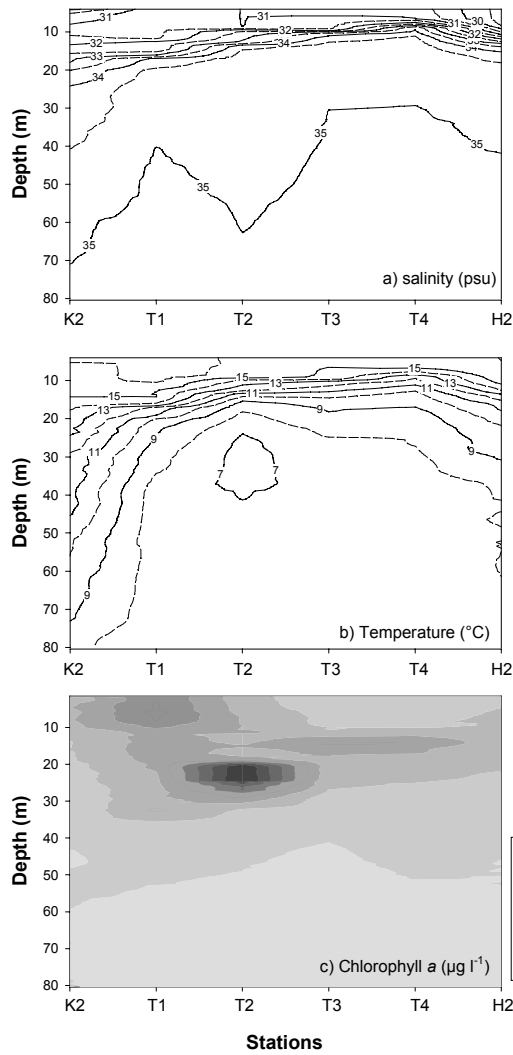


Figure 2.

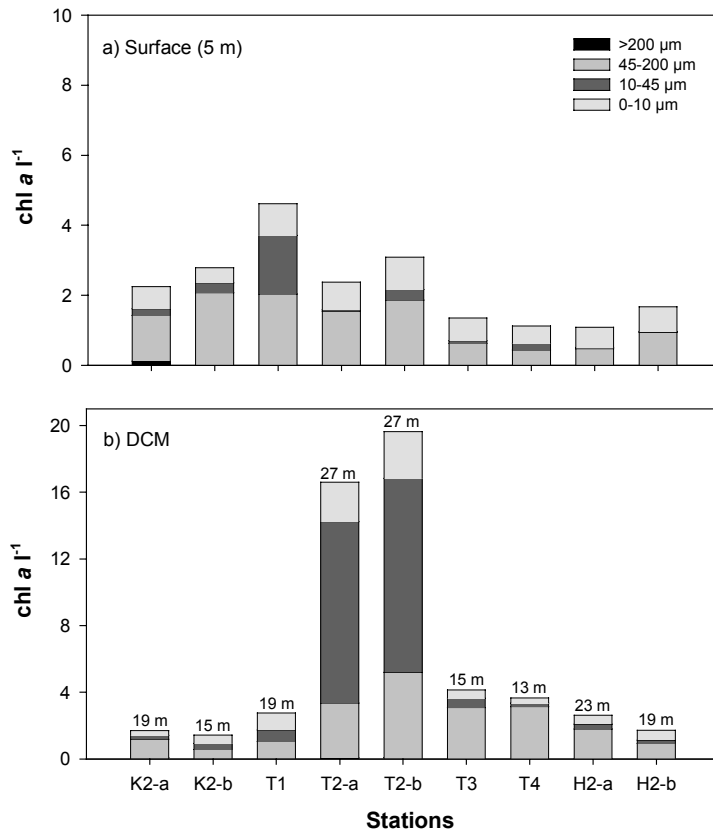


Figure 3.

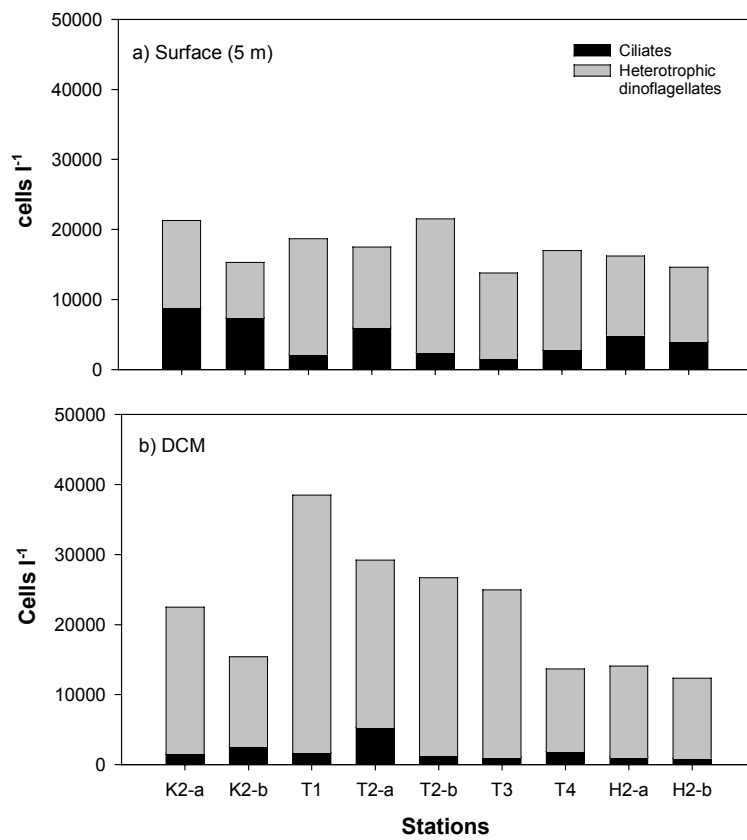


Figure 4.

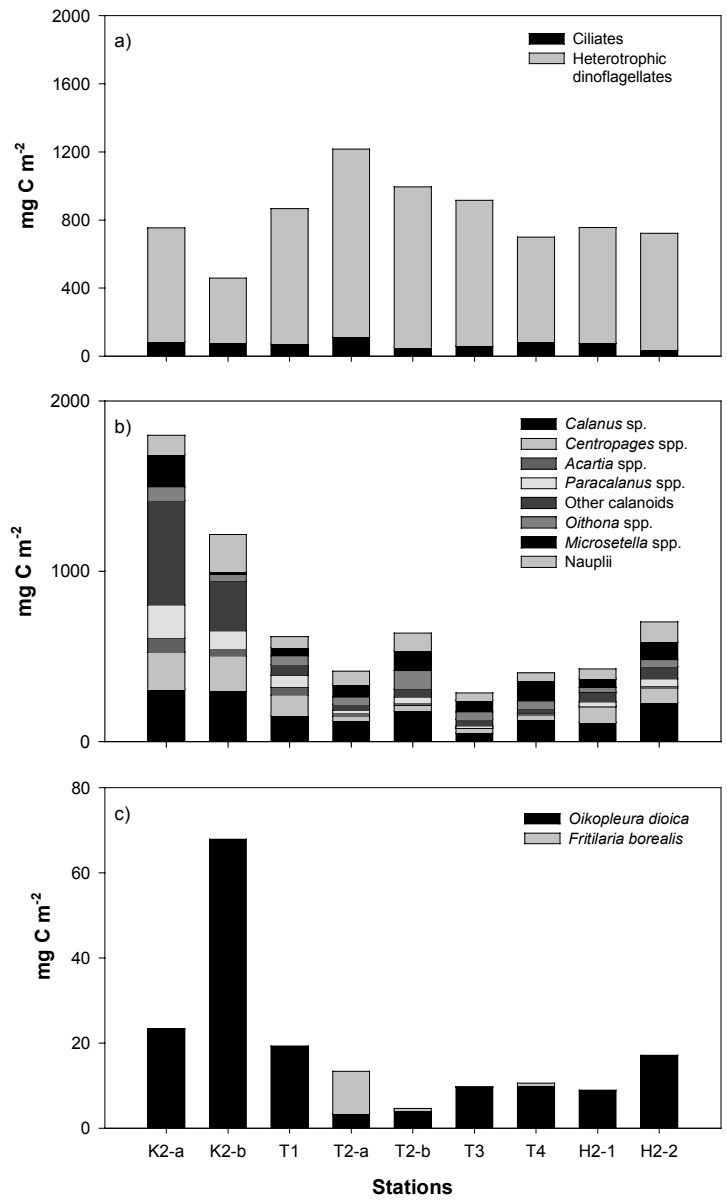


Figure 5.

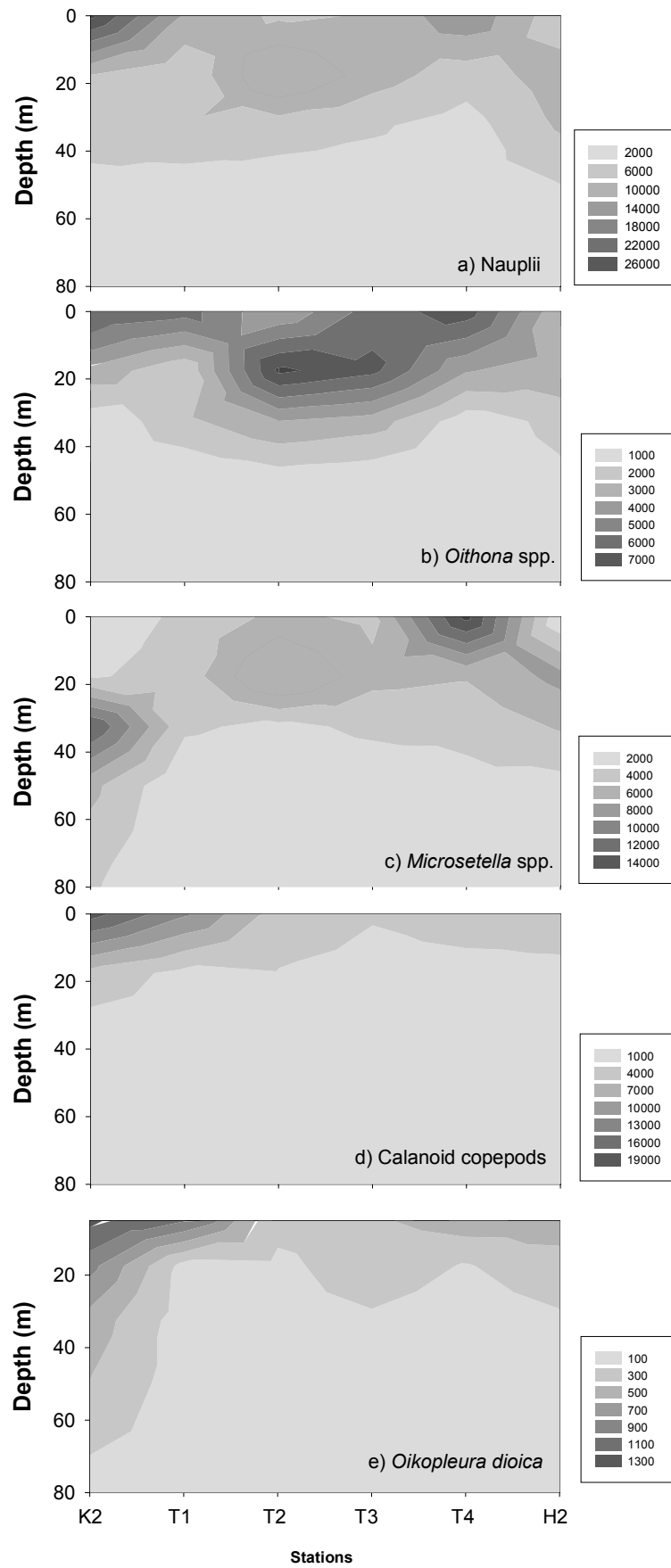


Figure 6.

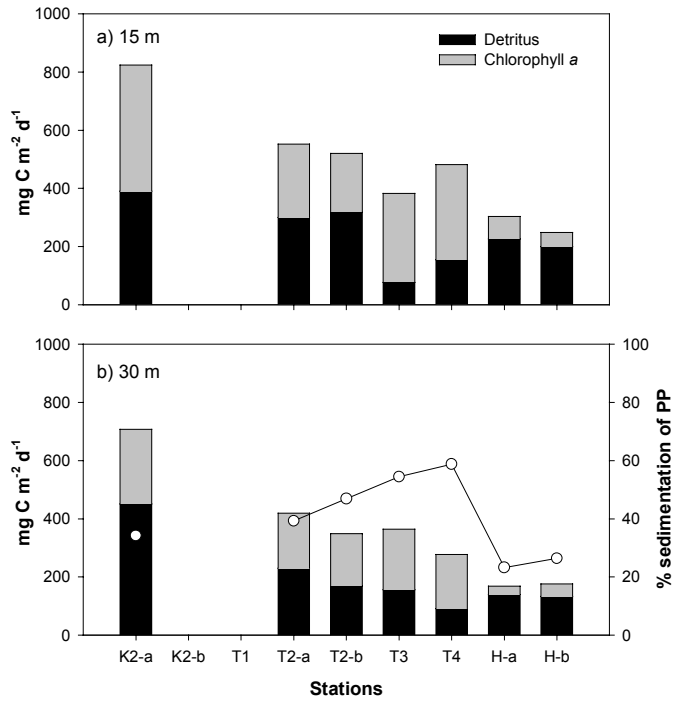


Figure 7.

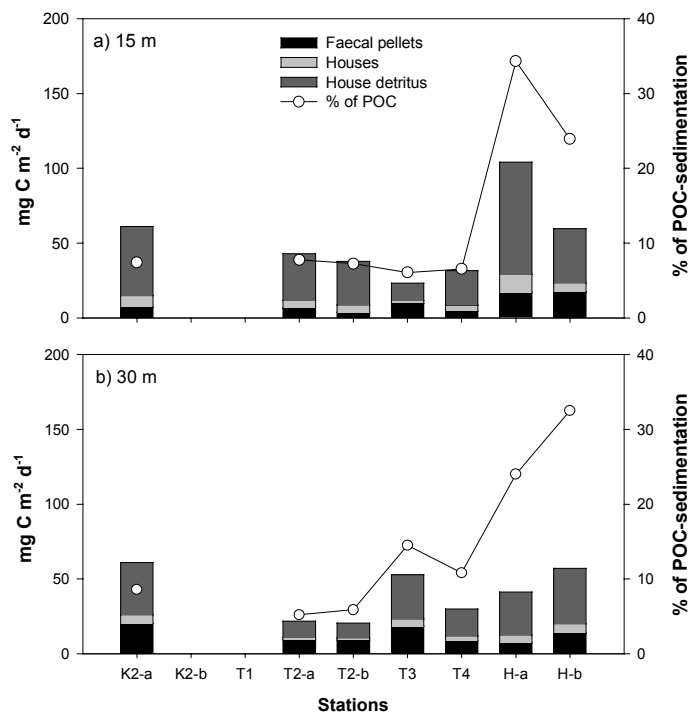


Figure 8.



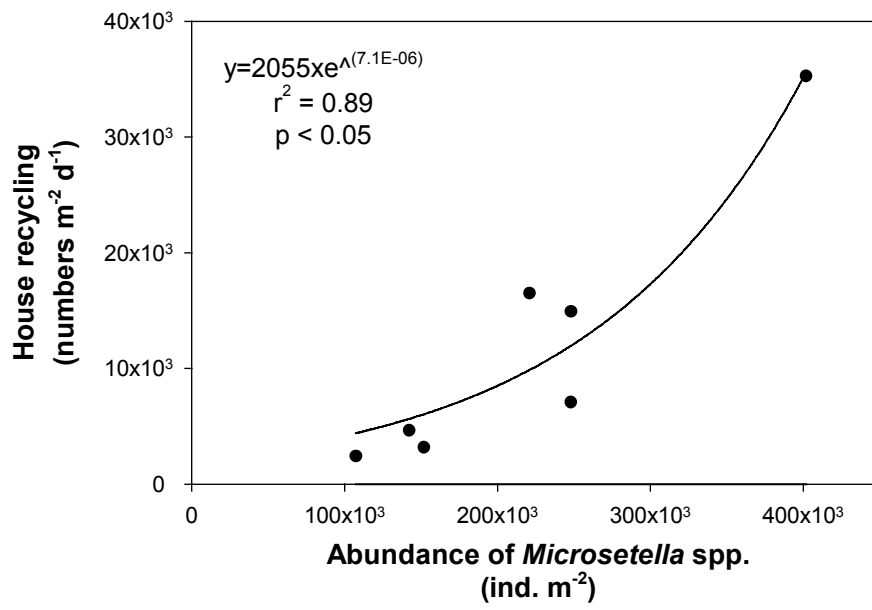


Figure 9.

# National Environmental Research Institute

The National Environmental Research Institute, NERI, is a research institute of the Ministry of the Environment. In Danish, NERI is called *Danmarks Miljøundersøgelser (DMU)*. NERI's tasks are primarily to conduct research, collect data, and give advice on problems related to the environment and nature.

## 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 Policy Analysis*  
*Department of Atmospheric Environment*  
*Department of Marine Ecology*  
*Department of Environmental Chemistry and Microbiology*  
*Department of Arctic Environment*  
*Project Manager for Quality Management and Analyses*

National Environmental Research Institute  
Vejløsøvej 25  
PO Box 314  
DK-8600 Silkeborg  
Denmark  
Tel: +45 89 20 14 00  
Fax: +45 89 20 14 14

*Environmental Monitoring Co-ordination Section*  
*Department of Terrestrial Ecology*  
*Department of Freshwater Ecology*  
*Project Manager for Surface Waters*

National Environmental Research Institute  
Grenåvej 12-14, Kalø  
DK-8410 Rønde  
Denmark  
Tel: +45 89 20 17 00  
Fax: +45 89 20 15 15

*Department of Wildlife Ecology and Biodiversity*

## 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.

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Distributions of zooplankton organisms occurring on different scales were investigated in relation to biological-physical factors. A high seasonal variability in the structure and function of the pelagic food web was found during the spring bloom and in late summer in the Skagerrak. The spring bloom was characterised by a high potential vertical flux of phytoplankton aggregates and a relatively low secondary production within a short period of time. In the more prolonged summer period, secondary production was considerably higher and this season is therefore essential for fuelling fish in the Skagerrak. In addition, the spatial-temporal variability of zooplankton biomass and growth on the scale of km or hours was analysed during the spring bloom in the Skagerrak. Here, the presence of different water masses and diurnal biological rhythms contributed significantly to the observed variability. On the microscale, we found that the variability in the vertical distribution of weak swimmers, the microzoo-plankton, decreased dramatically with increasing turbulent diffusion levels in the N Aegean and the Skagerrak. This is in contrast to the variability in the vertical distribution of copepodites, that was independent of the measured turbulent diffusion because the copepodites are stronger swimmers. Finally, discarded appendicularian houses was found to be an important microscale food source for copepods in the Skagerrak.

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