

Summertime herbivory of coastal mesozooplankton and metazoan microplankton in the northern Baltic

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ABSTRACT: Size-specific grazing by the coastal zooplankton community in the northern Baltic was studied during the summer. Experiments on grazing by mesozooplankton and metazoan microplankton, fractionated by filtration through 140 and 40 μm mesh, were carried out in the laboratory with two ^{14}C -labelled algae cultures, *Brachiomonas submarina* (size 10 to 15 μm) and *Pavlova lutheri* (size 4 to 6 μm). Zooplankton grazing on 2 size groups (>10 μm and 2 to 10 μm) of naturally occurring phytoplankton was also estimated. Mesozooplankton was composed of copepods *Acartia* spp. and *Eurytemora affinis*, the cladoceran *Bosmina longispina maritima*, rotifers *Synchaeta* spp. and meroplankton; metazoan microplankton consisted mostly of copepod nauplii and rotifers. Mesozooplankton had greater biomass and higher community clearance rate (CCR) when feeding on *B. submarina* than had metazoan microplankton. For mesozooplankton, the CCR on *B. submarina* was dependent on successional changes of total biomass of copepods and cladocerans, whereas the CCR on *P. lutheri* was variable, probably because of less efficient grazing by copepods. The CCR of metazoan microplankton on the test algae was variable and unpredictable, possibly because of the varying biomass specific clearance rates (BSCR) of rotifers and different naupliar stages of copepods. The mean CCR on *P. lutheri* did not differ between mesozooplankton and metazoan microplankton, because of the higher mean BSCR of the latter. The daily grazing of mesozooplankton on naturally occurring phytoplankton was estimated to average 9% of the daily primary production when rotifers, meroplankton or copepods were predominant, but 42% when *B. longispina maritima* was predominant. The integrated grazing of the mesozooplankton and metazoan microzooplankton was estimated to account for 13 and 6%, respectively, of primary production during summer.

KEY WORDS: Zooplankton grazing · Northern Baltic Sea · Tracer feeding technique

INTRODUCTION

The particle size of available food influences the grazing efficiency of many metazooplankton species, including mesozooplankton and metazoan microplankton. The optimal food size of different developmental stages of copepods is reported to increase with increasing body size of the grazer (Paffenhöfer 1971, Berggreen et al. 1988). Cladocerans graze more effectively on smaller food particles than do copepods (Peters & Downing 1984). The food preferences of rotifers vary widely, some species being highly selective, others consuming a range of particles, from bacteria to other rotifers (Bogdan & Gilbert 1982, Arndt et al. 1990).

Metazoan microplankton, such as copepod nauplii, have higher biomass specific grazing rates and meta-

bolic rates than larger mesozooplankton (Moloney & Field 1989, White & Roman 1992). Body size influences the grazing efficiency of different species and ultimately the grazing impact of whole zooplankton communities (Cyr & Pace 1993). Thus, species composition, size structure and biomass of a metazooplankton community are important factors affecting its grazing pressure on available food, where this food consists of different sized food particles. However, the size selectivity of zooplankton grazing and its ecological consequences have not been studied at the community level, but rather single zooplankton species have been used, mostly in artificial laboratory conditions (see Turner & Tester 1989 for critique). Laboratory experiments reveal important information on species-specific grazing characteristics, but the interpretation of natural

communities in the light of laboratory measurements is ambiguous, because many temporally and spatially changing abiotic and biotic factors influence species' grazing behaviour in nature.

In this study, the size selectivity and grazing efficiency of the coastal communities of mesozooplankton and metazoan microzooplankton was investigated during summer in the sea area off Tvärminne, on the southwest coast of Finland. The area is suitable for such studies, because species diversity is relatively low and successional changes in metazooplankton communities are clear. The rotifer *Synchaeta* spp. is common in early summer and its biomass occasionally increases in late summer (Kivi 1986). Calanoid copepods, especially *Acartia* spp. (mostly *Acartia bifilosa* Giesbr.) and *Eurytemora affinis* (Poppe), and the cladoceran *Bosmina longispina maritima* (P. E. Müller) often predominate in the summer (Forsskåhl & Sundberg 1981, Vuorinen & Ranta 1987).

In the grazing experiments, a modified version of Haney's (1971) method was used, but the experiments were carried out in the laboratory. Two cultures of different sized autotrophic nanoflagellates were used as tracer food particles, because naturally occurring phytoplankton of the study area is often dominated by nanoflagellates during summer (Niemi 1973, Forsskåhl & Sundberg 1981, Huttunen & Kuparinen 1986). The specific hypothesis tested during summer 1988 was that successional changes in the structure and biomass influence the size selectivity and grazing efficiency of mesozooplankton and metazoan microplankton communities. The potential consequences of the zooplankton grazing for primary production, and for the size structure of naturally occurring nanophytoplankton, are discussed.

MATERIALS AND METHODS

Size fractionation of the zooplankton community.

Grazing measurements of zooplankton were based on the fractionation of the zooplankton community into different size fractions after the grazing experiments (cf. Mazumder et al. 1990). For these purposes, preliminary studies of the zooplankton size structure were carried out by fractionating 4 l zooplankton samples through nylon filters with mesh sizes of 200, 140, 100, 80, 40 and 20 μm . The efficiency of these filters was examined in a filter fractionation device, constructed with plexiglas funnels (Nalgene) installed on a tripod one above the other. The 140, 100 and 40 μm filters were most suitable for fractionation of the zooplankton community into 3 categories: mesozooplankton (copepods, cladocerans, rotifers and meroplankton); large metazoan microplankton (copepod nauplii,

smallest rotifers and meroplankton passing the 140 μm filter); and small metazoan microplankton (mostly copepod nauplii).

Preparation of algal cultures. Clearance and ingestion rates of zooplankton were measured using two ^{14}C -labelled algal cultures: *Brachiomonas submarina* Bohlin (Chlorophyceae) and *Pavlova lutheri* (Droop) Green (Prymnesiophyceae). The diameters of these species varied from 10 to 15 μm and from 4 to 6 μm respectively, corresponding to mean volumes of 500 and 60 μm^3 . The algal cultures were labelled with ^{14}C (1 $\mu\text{Ci NaH}^{14}\text{CO}_3 \text{ ml}^{-1}$), and incubated in a shaker for 24 h under a light intensity of 40 to 60 $\mu\text{E cm}^{-2} \text{ s}^{-1}$. The final mean radioactivities of the cultures were 0.89 $\mu\text{Ci } \mu\text{gC}^{-1}$ for *B. submarina* and 0.78 $\mu\text{Ci } \mu\text{gC}^{-1}$ for *P. lutheri*. Cell concentrations of unlabelled controls of algal cultures were determined by counting at least 500 cells (3 replicates) on a hemocytometer. The mean final concentration of cells added was 4144 ml^{-1} for *B. submarina* and 4109 ml^{-1} for *P. lutheri*, with carbon contents of 0.228 $\mu\text{gC ml}^{-1}$ and 0.027 $\mu\text{gC ml}^{-1}$ respectively. The carbon content for the test algal cultures was calculated from their specific biovolumes, assuming a carbon percentage of 11% of the cell plasma volume (Edler 1979).

Grazing experiments. A composite water sample of 35 l was taken from a depth of 5 m and transferred to the laboratory for the grazing experiments. First, a phytoplankton subsample of 500 ml was taken and preserved with acid Lugol's solution. To determine the composition of the fractionated zooplankton community in each grazing experiment, 2 or 3 water subsamples of 4 l were taken from the composite sample and fractionated through a series of filters of 140, 100 and 40 μm before the grazing experiments. These filters were placed into separate 20 ml bottles that were then filled with filtered sea water and preserved with formalin. For enumeration of organisms, the filters were placed carefully on the inside wall of separate sedimentation chambers (volume 100 ml, length 10 cm), into which the preserved zooplankton was rinsed from the bottles and filters with filtered sea water. Examination with a microscope showed that the rinsing was sufficient to remove the animals from the nylon filters. The zooplankton and phytoplankton samples were counted using the Utermöhl technique (1958). The biovolumes of the species were converted to organic carbon assuming carbon percentages of 5.2 for metazooplankton (Mullin 1969) and 11 for phytoplankton and ciliates (Edler 1979).

To avoid some of the potential errors associated with metazooplankton grazing experiments (Gulati 1985), the experiments were conducted with the unconcentrated samples of naturally occurring zooplankton. These were fractionated into mesozooplankton and metazoan microplankton immediately after the experi-

ments, without preservation or sorting of zooplankton individuals. For the grazing experiments with both test algae, 5 zooplankton subsamples of 2 l were taken from the same composite sample from which samples for zooplankton biomass determinations were taken. The water in the experimental units was stabilised for several hours at the *in situ* temperature before carrying out the experiments. At the beginning of the experiments, 0.5 to 4 ml of the radiolabelled culture of *Brachiomonas submarina* and *Pavlova lutheri* were added to separate experimental units of 2 l (4 replicates for each test alga) to give a final concentration of about 4000 cells ml⁻¹. The concentrations of test algae were fixed at the same numerical level, because metazooplankton probably experience phytoplankton food mainly in terms of cell numbers, rather than particle biomass (cf. Turner & Tester 1989). In the experiments, the concentrations of test algae and natural phytoplankton were at the lower end of the critical food concentration for metazooplankton reported by Peters (1984 and references therein).

Incubation times for the experimental units were approximately 0, 10, 25 and 45 min for the experiments with both test algae. To prevent the egestion of tracer food during filtration, the zooplankton community was anaesthetised by adding soda water (1/10) to the experimental units, after which the water was passed through a series of filters (140, 100 and 40 µm). The filters were put directly into 20 ml scintillation vials for radioactivity measurements. Inorganic ¹⁴C was evaporated for 24 h after adding 100 µl 1N HCl (Niemi et al. 1983). Seven millilitres of PCS liquid scintillation cocktail (Amersham, UK) were added to the bottles, and because of the high dissolving impact of the PCS's xylene, no other solubilizer was needed. Radioactivity measurements were performed with a Wallac 1219 Rack Beta liquid scintillation counter (LKB-Wallac Co., Turku, Finland). The experiments were run 6 times during summer between 16:00 and 19:00 h. Since the zooplankton fractions on 100 and 40 µm filters appeared to be very similar, both containing mostly copepod nauplii and *Synchaeta* spp., their biomass as well as the ¹⁴C results of grazing experiments were combined together to form only one size fraction of metazoan microplankton, to be compared with the >140 µm mesozooplankton. In later examinations, only these 2 fractions are considered.

Because the added algal cultures included a small amount of inorganic ¹⁴C, the additional intake of ¹⁴C from sources other than test algae (incorporation of inorganic ¹⁴C and grazing on natural phytoplankton labelled during the experiments) was checked in the 2 zooplankton size fractions on one occasion in August. In these control experiments, 5 µCi NaH¹⁴CO₃ l⁻¹ was used, but without the addition of algal cultures. The

Table 1 Regression analysis of the biomass specific intake rate (dpm µg C⁻¹ min⁻¹) of the free tracer (5 µCi NaH¹⁴CO₃ l⁻¹) in 2 zooplankton size fractions. *t*: time in minutes

Size fraction	r ²	p	n
>140 µm 0.7052 - 0.0101t + 0.0003t ²	67%	<0.05	8
40 to 140 µm 2.5127 - 0.0441t + 0.0018t ²	93%	<0.001	8

amount of inorganic ¹⁴C in the experimental units with *Brachiomonas submarina* was between 22 and 36% of the level used in the control experiment, and between 4 and 35% in the units with *Pavlova lutheri*. The biomass specific intake rate of ¹⁴C (dpm µg C⁻¹ min⁻¹) was calculated by regression analysis including linear and quadratic coefficients, because the radioactivity increase of zooplankton is a parabolic function of time (Daro 1978) (Table 1). In the experiments with *B. submarina*, the intake of additional ¹⁴C was at most 7% of the total label intake (intake of test alga + labelled phytoplankton + incorporation of inorganic ¹⁴C) in the 40 to 140 µm zooplankton size fraction. The level usually remained below 1% for all size fractions in experiments with both test algae, due to the short experimentation time (10 to 50 min). The community clearance rate (CCR; ml l⁻¹ h⁻¹) was then calculated with the equation:

$$\frac{\text{dpm}_{t_A} - \text{dpm}_{t_0} - \text{dpm}_{t_B}}{\text{dpm}_x} \times \frac{1}{V} \times \frac{1}{t} \times 60$$

where dpm_{tA} is total activity of the filtered biomass at time *t*; dpm_{t0} is activity of the filtered biomass at time *t*₀; dpm_{tB} is activity of the filtered biomass due to intake of additional ¹⁴C; dpm_x is activity of the tracer in ml; *V* is volume of the bottles (2 l); and *t* is incubation time in minutes.

The CCR of both zooplankton size fractions was calculated as a mean of the clearance rate values (*n* = 3), corresponding to the points of the linear accumulation of ¹⁴C of both tracer foods at times *t*₁ to *t*₃. To determine an overall grazing efficiency, the biomass specific clearance rate (BSCR; ml µg C⁻¹ h⁻¹) was calculated by dividing community clearance rate by community biomass.

The grazing of zooplankton on naturally occurring phytoplankton was estimated using the measured CCR on the test algae. Data from the natural phytoplankton samples were divided into 2 groups: cells larger than 10 µm, and cells from 2 to 10 µm, corresponding to the cell sizes of >500 µm³ and 60 µm³, respectively, of the ¹⁴C-labelled algae, *Brachiomonas submarina* and *Pavlova lutheri*. Grazing on the larger

phytoplankton category was estimated using the CCRs of meso- and microzooplankton when feeding on *B. submarina*, and grazing on the smaller phytoplankton using the CCRs on *P. lutheri*. The biomass of *Aphanizomenon flos-aquae* (L.) Ralfs was not included in the larger phytoplankton group, because metazooplankton do not feed effectively on large filamentous blue-green algae (cf. Webster & Peters 1978). All other species were assumed to be palatable to zooplankton.

RESULTS

Zooplankton succession

In the study area, the mean biomass of mesozooplankton exceeded that of metazoan microzooplankton in summer (2-sample *t*-test for whole log-transformed data set; $p = 0.000$, $n = 24$) (Fig. 1). An increase in rotifer and meroplankton (mostly lamellibranch larvae) biomass produced a mesozooplankton biomass maximum in June. One-third of rotifer biomass was accounted for by *Synchaeta monopus* Plate, the rest being formed by *S. baltica* Ehrenberg. In the middle of July, this community was replaced by calanoid copepods *Eurytemora*

affinis and *Acartia* spp. and the biomass decreased. Later on, the cladoceran *Bosmina longispina maritima* was predominant, along with copepodite and adult stages of the copepod *Acartia* spp.

In June, the biomass of metazoan microzooplankton was composed of *Synchaeta* spp. and meroplankton. *Acartia* spp. and *Eurytemora affinis* nauplii were equal in biomass in the first 3 experiments, but later on, 80% of naupliar biomass was composed of *Acartia* spp. On average, 7% of naupliar biomass was composed of *Temora longicornis* and <1% of *Cyclops* spp. Peritrich and tintinnid ciliates were found on the 40 μm filter, but their biomass was quite low. The coefficient of variation (CV, %) between duplicate zooplankton biomass subsamples averaged 9% for both mesozooplankton and metazoan microzooplankton.

Grazing experiments

The hourly CCR of mesozooplankton varied between 1 and 6 ml l^{-1} , and BSCR between 0.01 and 0.19 $\text{ml } \mu\text{gC}^{-1}$. For metazoan microzooplankton, the corresponding values were 0.5 to 5 ml l^{-1} and 0.05 to 0.47 $\text{ml } \mu\text{gC}^{-1}$ (Fig. 2A, B). The CCR of mesozooplankton feeding on

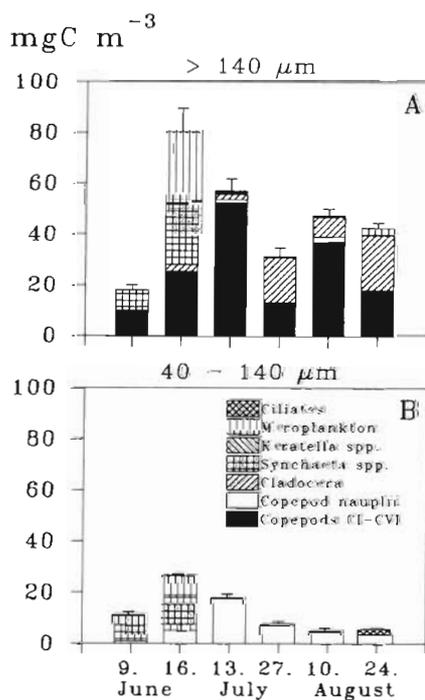


Fig. 1. Zooplankton biomass (mg C m^{-3}) at 5 m depth in the sea area off Tvärminne in 1988: (A) Mesozooplankton of the > 140 μm size fraction (bar shading as in B); (B) metazoan microzooplankton and ciliates of the 40 to 140 μm size fraction. Error bars indicate the variation between duplicate samples

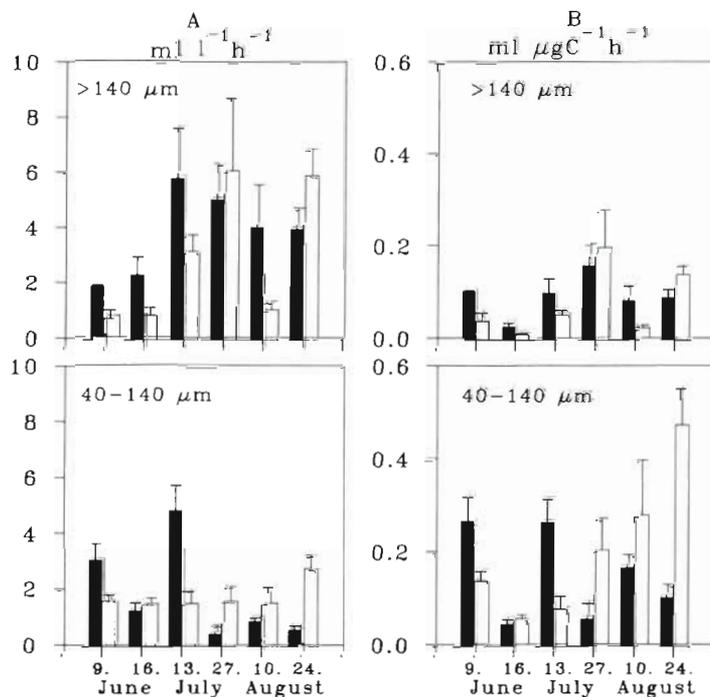


Fig. 2. (A) Community clearance rates (CCR, $\text{ml l}^{-1} \text{h}^{-1}$), and (B) biomass specific clearance rates (BSCR, $\text{ml } \mu\text{gC}^{-1} \text{h}^{-1}$) on *Brachiomonas submarina* (black bars) and *Pavlova lutheri* (white bars) of the > 140 μm and 40 to 140 μm zooplankton size fractions. Error bars indicate 1 standard deviation of the 3 replicated experiments

both test algae increased after June, following the biomass growth of mesozooplankton, but the CCR and BSCR on *Pavlova lutheri* varied more than on *Brachiomonas submarina*. For metazoan microplankton, the CCR varied more when feeding on *B. submarina* than on *P. lutheri*, but the highest temporal variations appeared in the BSCR on *P. lutheri*. The CV between 3 replicates averaged 22 and 25% for grazing experiments with *B. submarina* and 38 and 26% for experiments with *P. lutheri* for mesozooplankton and metazoan microplankton, respectively. The mean CCR on *B. submarina* was higher in mesozooplankton than in metazoan microplankton ($p = 0.0004$), but no difference was found in the BSCR ($p = 0.13$) when the whole log-transformed data set ($n = 36$) was tested with a 2-sample *t*-test. In contrast, there was no difference in the mean CCR on *P. lutheri* between mesozooplankton and metazoan microplankton ($p = 0.49$); this was because the mean BSCR of metazoan microplankton was much higher than that of mesozooplankton ($p = 0.0005$).

To study the grazing efficiency of mesozooplankton communities dominated by different species, the data sets of 6 experiments were pooled to form 3 entities. The first and second experiments were combined to reflect the grazing of a *Synchaeta*-meroplankton-*Acartia* assemblage (SMA); the third and fifth experiments, a copepod assemblage; and the fourth and sixth experiments, a cladoceran assemblage. The SMA and copepod assemblages both had significantly higher BSCR when feeding on *Brachiomonas submarina* than on *Pavlova lutheri* (Wilcoxon signed rank test; $p = 0.04$, $n = 12$), but no such difference was found for the cladoceran assemblage ($p = 0.4$, $n = 12$). It was not reasonable to test the BSCR of 2 metazoan microplankton assemblages (*Synchaeta*-meroplankton and copepod nauplii), because there were high variations in BSCR on the test algae between zooplankton communities with similar community structures.

In the experiments with both test algae, a positive correlation between temperature and CCR was found for mesozooplankton (Table 2). The biomass of *Synchaeta* spp. correlated negatively with the mesozooplankton CCR on *Brachiomonas submarina*, but the total copepod and cladoceran biomass showed a positive correlation. The biomass of *Bosmina longispina maritima* correlated positively with the CCR on *Pavlova lutheri*. For metazoan microzooplankton, BSCR on *P. lutheri* correlated negatively with meroplankton and total metazooplankton biomass. A posi-

Table 2. Spearman's correlation coefficients between temperature, biomass ($\mu\text{g C l}^{-1}$) of different zooplankton taxa and the mean CCR and BSCR of the 2 zooplankton size fractions when feeding on *Brachiomonas submarina* and *Pavlova lutheri* ($n = 6$). * $p < 0.05$; ** $p < 0.01$

	Expt with <i>B. submarina</i>		Expt with <i>P. lutheri</i>	
	CCR	BSCR	CCR	BSCR
Mesozooplankton: size fraction >140 μm				
Temperature	0.89*	0.43	0.94**	0.71
<i>Bosmina longispina maritima</i>	0.46	0.20	0.87*	0.72
<i>Synchaeta</i> spp.	-0.89*	-0.60	-0.37	-0.54
Copepods and cladocerans	0.83*	-0.14	0.49	0.20
Metazoan microplankton: size fraction 40 to 140 μm				
Temperature	-0.43	-0.26	0.03	0.26
Meroplankton	-0.58	-0.06	-0.53	-0.93**
Metazooplankton	0.60	-0.14	-0.60	-0.94**
Ciliates	-0.54	0.09	0.77	0.89*

tive correlation was also found between ciliate biomass and BSCR of the 40 to 140 μm size fraction.

Extrapolation of the grazing measurements to the natural pelagic ecosystem of the study area

In the study area, primary production varied between 8 and 52 $\text{mg C m}^{-3} \text{d}^{-1}$ at a depth of 5 m during the summer (R. Lignell pers. comm.) (Fig. 3A). Nanoflagellates dominated the biomass of autotrophic phytoplankton. Phytoplankton >10 μm consisted mostly of *Eutreptiella gymnastica* Thronsen, *Pseudopedinella elastica* Skuja, *Katodinium rotundatum* (Lohmann) Fott, *Chaetoceros wighamii* Brightwell and *Skeletonema costatum* (Greville) Cleve. Phytoplankton 2 to 10 μm included *Chrysochromulina* spp., *Cryptomonas* spp., *Pyramimonas* spp. and *Pedinella tricornata* Rouchijainen (Fig. 3B). The biomass of the filamentous blue-green alga *Aphanizomenon flos-aquae* increased at the end of August.

The estimated daily grazing on naturally occurring phytoplankton varied between 1 and 6 $\text{mg C m}^{-3} \text{d}^{-1}$ for mesozooplankton and between 1 and 4 $\text{mg C m}^{-3} \text{d}^{-1}$ for metazoan microzooplankton (Fig. 3C). The daily grazing of mesozooplankton exceeded that of metazoan microplankton, except in early June. Mesozooplankton were estimated to graze 4 to 14% of phytoplankton biomass daily, and metazoan microplankton, 2 to 7%. The daily biomass specific grazing efficiency on naturally occurring phytoplankton (% of zooplankton C) varied between 3 and 14% for mesozooplankton and 5 and 35% for metazoan microplankton (Table 3). The estimated daily grazing of mesozooplankton varied between 7 and 54% of the daily primary production, and of metazoan microplankton between 2 and 15%. Integrated over the whole study period, the cor-

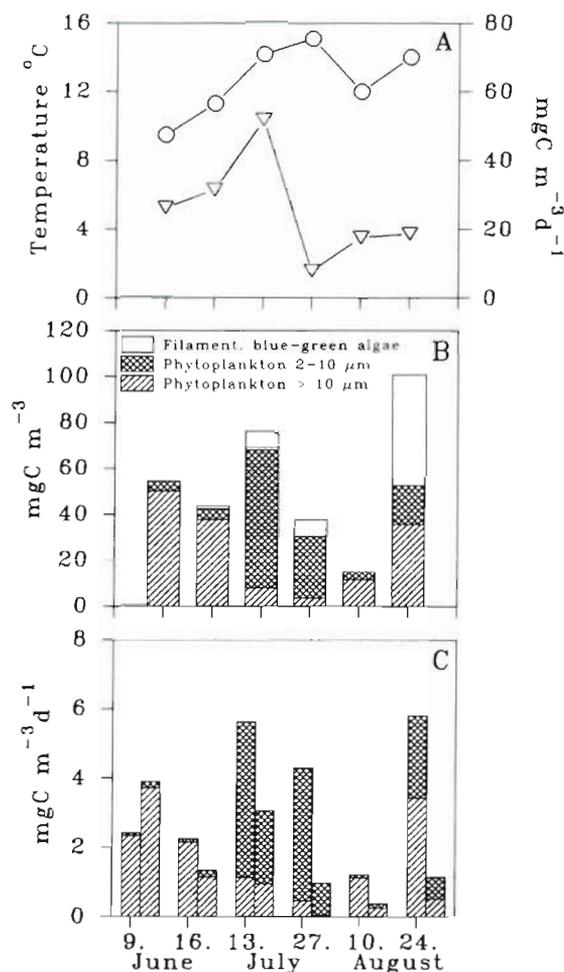


Fig. 3. Summary of environmental parameters and grazing estimates at the study area. (A) Temperature (°C, circles) and primary production (mg C m⁻³ d⁻¹, triangles) (R. Lignell unpubl.); (B) biomass of phytoplankton (mg C m⁻³); (C) daily grazing of zooplankton (mg C m⁻³ d⁻¹), where the left column denotes mesozooplankton, and the right column, metazoan microplankton (bar shading in B)

responding percentages are 13% for mesozooplankton and 6% for metazoan microplankton. In these estimations, zooplankton were assumed to feed continuously throughout the 24 h cycle, without significant vertical migration, as has been found to be the case in the southern Baltic (Nicolajsen et al. 1983).

DISCUSSION

Factors affecting grazing efficiency during summer

Mesozooplankton

Changes in community structure and biomass influenced the grazing efficiency of mesozooplankton dur-

ing summer. The CCR on *Brachiomonas submarina* was dependent, in an almost linear manner, on total biomass of copepods and cladocerans, but the CCR on *Pavlova lutheri* was more variable because of the lower grazing efficiency of copepods on *P. lutheri*. This agrees with other studies where adults and copepodite stages of copepods were found to prefer particles >10 µm as food both *in situ* (Dam & Peterson 1991, Bautista & Harris 1992) and in laboratory experiments (Berggreen et al. 1988). The grazing of communities dominated by *Bosmina longispina maritima* was non-selective, but they seemed to graze more effectively on *P. lutheri* than did other mesozooplankton. *B. longispina maritima* has been found to graze effectively on particles ranging from <5 to 25 µm (Hessen et al. 1986), especially on small nanoflagellates, which are not available to larger mesozooplankton (DeMott & Kerfoot 1982).

The BSCR of mesozooplankton decreased in June, although the community structure did not change remarkably, and biomass increased. Assuming a rough gross growth efficiency of 30% (cf. Riemann et al. 1990) for mesozooplankton biomass, the integrated grazing on naturally occurring phytoplankton could fulfil, at most, 8% of the community's carbon demand. If meroplankton is excluded from this calculation, the percentage is still as low as 13%. *Synchaeta* spp. and *Acartia* spp. (Lindholm 1981, Tiselius 1989, Arndt et al. 1990) are known to feed on ciliates in the Baltic. Thus, feeding on protozooplankton may have satisfied a considerable proportion of the nutritive demand of mesozooplankton in early June. The grazing may also have been constrained in the crowded zooplankton community with the maximum biomass in the middle of June.

Mesozooplankton communities dominated by *Bosmina longispina maritima* had the highest BSCR on *Pavlova lutheri* in late summer. This cladoceran becomes abundant when temperatures rise during summer in the northern Baltic (Kankaala 1983), as was the case in this study. The increase in *B. longispina maritima* biomass was also associated with the decline of the smaller phytoplankton of size 2 to 10 µm, which corresponds to the size of *P. lutheri* and other nanoflagellates found to be palatable for *B. longispina maritima* (DeMott & Kerfoot 1982, Hessen et al. 1986). The results of this study fit well with the findings of Kankaala & Wulff (1981) and Kankaala (1983), who assumed food conditions and temperature to be the main limiting factors for *B. longispina maritima* during the summer in the northern Baltic Sea. With its higher grazing efficiency on algae <10 µm, *B. longispina maritima* may be superior to copepods in its use of late summer phytoplankton, which is dominated by small flagellates in the study area.

Table 3. Estimated daily biomass specific grazing efficiency (% of zooplankton C) of mesozooplankton and metazoan microplankton in the sea area off Tvärminne during summer 1988, compared with other *in situ* measurements with naturally occurring phytoplankton. Chl *a* concentrations were converted to C assuming a carbon:chl *a* ratio of 40. F: adult females

	Daily grazing (% of zooplankton C)	Sea area	Temp. (°C)	Food conc. (µg C l ⁻¹)	Source
Mesozooplankton					
SMA assemblage	3–13	Coastal N Baltic Sea	10–11	43–55	This study, Expts 1 & 2
Copepod assemblage	3–10	Coastal N Baltic Sea	12–14	15–68	This study, Expts 3 & 5
<i>Bosmina longispina</i> <i>maritima</i> assemblage	13–14	Coastal N Baltic Sea	14–15	30–53	This study, Expts 4 & 6
<i>Centrophages hamatus</i> F	3–12	Øresund	1–12	8–1140	Nicolajsen et al. (1983)
<i>Pseudocalanus</i> sp. F	0.2–14	Øresund	1–12	8–1140	Nicolajsen et al. (1983)
<i>Temora longicornis</i> F	18	Kattegat-Skagerrak	2	192	Kjørboe et al. (1985)
<i>Acartia</i> spp. F	25	Kattegat-Skagerrak	2	76	Kjørboe et al. (1985)
<i>Acartia</i> spp. CI–CVI	44–92	E North Sea estuary		300–420	Tackx et al. (1990)
<i>Eurytemora</i> spp. CI–CVI	137–645	E North Sea estuary		800–2200	Gulati & Doornekamp (1991)
<i>Acartia tonsa</i> CI–CVI	58–183	Chesapeake Bay	15–26	180–1620	White & Roman (1992)
<i>A. tonsa</i> F	74–85	Narragansett Bay	13	200	Durbin et al. (1990)
<i>Eurytemora</i> spp. CI–CVI	8	Chesapeake Bay	4–15	180–1620	White & Roman (1992)
Cladoceran	42	Chesapeake Bay	15–17	180–1620	White & Roman (1992)
Rotifer	37	Chesapeake Bay	4–26	180–1620	White & Roman (1992)
Metazoan microplankton					
<i>Synchaeta</i> -meroplankton assemblage	5–35	Coastal N Baltic Sea	10–11	43–55	This study, Expts 1 & 2
Copepod nauplii assemblage	8–29	Coastal N Baltic Sea	12–15	15–68	This study, Expts 3 to 6
<i>Acartia</i> spp. nauplii	28–52	E North Sea estuary		300–420	Tackx et al. (1990)
<i>Acartia</i> spp. nauplii	79–280	Chesapeake Bay	15–26	180–1620	White & Roman (1992)

Metazoan microplankton

The grazing efficiency of metazoan microplankton was variable and unpredictable, even between communities with almost the same community structure. Metazoan microplankton was composed of mero-plankton and *Synchaeta* spp. in June, which grazing efficiency probably decreased for the same reasons as in mesozooplankton. The varying grazing efficiencies of copepod nauplii may have caused the variability in July and August. In this study, the naupliar biomass of *Acartia* spp. and *Eurytemora affinis* was equal in the middle of July, when the BSCR of metazoan microplankton was higher when feeding on *Brachiomonas submarina* than on *Pavlova lutheri*. The preferences seemed to be opposite when the biomass of *Acartia* spp. nauplii exceeded approximately 5 times the biomass of *E. affinis* nauplii later in the summer. In the northern Baltic, *Acartia bifilosa* and *E. affinis* occur at the same time during summer, which suggests that they do not compete for food resources (Viitasalo 1994). Differences in naupliar feeding may be one reason the species are able to coexist.

The irregular feeding and variation in the food size selectivity of different stages of copepod nauplii may have also caused variability in the BSCR and CCR. The naupliar stage NI of many species has been found to be non-feeding (Huntley & Brooks 1982, Uye et al. 1990, Zánkai 1991), and the feeding of some crustaceans can cease or be depressed before moulting to the next stage (Lasker 1966, Paffenhöfer 1971). Bergreen et al.

(1988) found the optimum food sizes for the naupliar stages NII to NIV of *Acartia tonsa* to be 7 µm, with subsequent stages preferring particles of 14 µm in size, corresponding to the sizes of *Pavlova lutheri* and *Brachiomonas submarina* respectively in this study. The BSCR of metazoan microplankton dominated by *Acartia* spp. nauplii increased when feeding on *P. lutheri* during July and August, and this may have been caused by varying naupliar feeding efficiency and food size selectivity, if successive communities were dominated by different naupliar stages. Ciliates occurring on the 40 µm filter could possibly also have increased the BSCR on *P. lutheri* in the last experiment.

Mesozooplankton versus metazoan microplankton

Because of its larger mean biomass, mesozooplankton mean CCR exceeded 2-fold that of the metazoan microplankton, at least when *Brachiomonas submarina* was used as food. However, the mean BSCR of microzooplankton on *Pavlova lutheri* was approximately 3 times higher than that of mesozooplankton, which reduces the differences in mean CCR between mesozooplankton and metazoan microplankton on *P. lutheri* to non-significant levels. Regarding separate experiments conducted during summer, the CCR on both test alga seemed to be even higher in metazoan microplankton than in mesozooplankton. Based on allometric predictions calculated for freshwater crustacean zooplankton in 90 lakes, Cyr & Pace (1993) suggested

that, of 2 communities with equal community biomass, the one dominated by smaller zooplankton should graze more than the other. In the northern Baltic, the biomass of metazoan microplankton is usually smaller than that of mesozooplankton in summer (cf. Vuorinen & Ranta 1987). However, having higher BSCR, metazoan microplankton may occasionally graze more on nanoflagellates < 10 µm than does mesozooplankton.

Effects of temperature and food concentration

Temperature increase is known to have a positive effect on mesozooplankton grazing, especially on that of copepods (Dam & Peterson 1988, Durbin & Durbin 1992). In this study, *in situ* temperatures used in grazing experiments (Fig. 3A) correlated significantly with the CCRs of the mesozooplankton (Table 2). However, this was not found for BSCR, which could be considered the most valid indicator of the effects of changing temperature. Thus, the possible direct effect of temperature on CCR cannot be distinguished from the effects of the changes in community structure and biomass, which may in turn have been influenced indirectly by the effects of temperature, food quality and quantity, and inter- and intraspecific interactions. The estimated daily biomass specific grazing efficiencies (% of community C) of mesozooplankton and metazoan microplankton dominated by different species were similar to those measured at approximately the same temperatures and food concentrations of naturally occurring phytoplankton (Table 3). Higher temperatures and especially food concentrations could produce higher biomass specific grazing efficiencies for mesozoan species *in situ*, an effect which has been shown for copepods in many laboratory studies (cf. Durbin & Durbin 1992 and references therein).

Zooplankton grazing and primary production

The estimated ratio between daily mesozooplankton grazing and daily primary production varied between 7 and 11% for communities dominated by copepods or *Synchaeta* spp. and meroplankton. The ratios are within the range of those measured for copepods or for copepod dominated communities by Tiselius (1988) in the southern Baltic (5 to 48%), Morales et al. (1993) in the north-east Atlantic (1 to 22%), White & Roman (1992) in Chesapeake Bay (12 to 103%), Tackx et al. (1990) in an estuary of the southwestern Netherlands (11 to 18%), and Conover & Mayzaud (1984) in an inlet in Nova Scotia, Canada (10 to 30%). In this study, the highest grazing percentages of 54% and 31% coincided with the presence of communities dominated by *Bosmina longispina*

maritima after the decline in primary production associated with diminishing phytoplankton biomass at the end of July. High grazing efficiencies are reported by Vadstein et al. (1989) and Markager et al. (1994) for freshwater cladoceran communities.

The ratio between daily grazing by metazoan microplankton and daily primary production varied between 2 and 15% during summer. This range is comparable with those calculated for microzooplankton (tintinnids, oligotrich ciliates and rotifers) by Riemann et al. (1990) in the southern Baltic (7 to 11%) and for copepod nauplii by White & Roman (1992) in Chesapeake Bay (1 to 23%). The measured ratio between zooplankton grazing and primary production may vary widely due to differences in methods used, season, time of day, depth of water and study area.

The integrated grazing by metazooplankton was estimated to account for 19% of primary production in summer, which exceeds the percentage found by Lignell et al. (1993) for the preceding spring in the same area. They estimated that the proportion of primary production grazed by metazooplankton was only 2% during the growing phase of the bloom and 12% during the declining phase. The small-sized *Synchaeta littoralis* accounted for most of the grazing during the former phase and, together with the copepod *Acartia* spp., during the latter. In this study, the grazing by metazooplankton dominated by *Synchaeta* spp., meroplankton and copepods accounted for 15% of primary production in the first half of the experiment and 24% during the second half, but the efficiency of the grazing varied widely because of the relative predominance of *Bosmina longispina* *maritima* or copepods.

Reliability of the grazing estimates

In this study, the grazing experiments conducted with the cultured nanoflagellates *Brachiomonas submarina* and *Pavlova lutheri* are likely to provide a reasonable estimate for the zooplankton grazing on autotrophic nanoplankton, which is dominated by nanoflagellates at a depth of 5 m in the study area during summer. However, by using only 2 test algae, these estimations will be quite crude, because phytoplankton attributes other than size, such as shape or chemical properties, are also considered to influence food selection (DeMott 1989).

The community structure of mesozooplankton and metazoan microplankton used in the grazing experiments corresponded with that found in the euphotic zone of the study site (A. Uitto unpubl.). Ciliates may have increased the BSCR of the metazoan microplankton size fraction in August, and thus the grazing may be slightly overestimated in the last experiment. Graz-

ing estimations based on measurements made with naturally occurring zooplankton communities remove some of the uncertainty associated with extrapolation from laboratory experiments, but reveal the grazing at only one depth and time of day. Primary production, the community structure and biomass of auto- and heterotrophs, and the grazing efficiency of zooplankton may vary even at different depths in the euphotic zone (Lambert & Taylor 1985). An experimental frequency of twice a month may also be too low to recover all temporal changes potentially connected to metazooplankton grazing dynamics. However, this study gives the first estimate based on real measurement of mesozooplankton and metazoan microplankton in the study area, and the estimated daily grazing efficiencies fit well with earlier measurements conducted in the southern Baltic and other sea areas.

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LITERATURE CITED

- Arndt H, Schröder C, Schnese W (1990) Rotifers of the genus *Synchaeta* — an important component of the zooplankton in the coastal waters of the southern Baltic. *Limnologia* 21:233–235
- Bautista B, Harris RP (1992) Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Mar Ecol Prog Ser* 82:41–50
- Berggreen U, Hansen B, Kjørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Mar Biol* 99:341–352
- Bogdan KG, Gilbert JJ (1982) Seasonal pattern of feeding by natural populations of *Keratella*, *Polyarthra*, and *Bosmina*: clearance rates, selectivities, and contributions to community grazing. *Limnol Oceanogr* 27:918–934
- Conover RJ, Mayzaud P (1984) Utilization of phytoplankton by zooplankton during the spring bloom in a Nova Scotia inlet. *Can J Fish Aquat Sci* 41:232–244
- Cyr H, Pace ML (1993) Allometric theory: extrapolations from individual to communities. *Ecology* 74:1234–1245
- Dam HG, Peterson WT (1988) The effect of temperature on the gut clearance rate constant of planktonic copepods. *J Exp Mar Biol Ecol* 123:1–14
- Dam HG, Peterson WT (1991) *In situ* feeding behaviour of the copepod *Temora longicornis*: effects of seasonal changes in chlorophyll size fractions and female size. *Mar Ecol Prog Ser* 71:113–123
- Daro MH (1978) A simplified ^{14}C method for grazing measurements on natural planktonic populations. *Helgoländer Wiss Meeresunters* 31:241–248
- DeMott WR (1989) Optimal foraging theory as a predictor of chemically mediated food selection by suspension-feeding copepods. *Limnol Oceanogr* 34:140–154
- DeMott WR, Kerfoot WC (1982) Competition among cladocerans: nature of the interaction between *Bosmina* and *Daphnia*. *Ecology* 63:1949–1966
- Durbin AG, Durbin EG, Włodarczyk E (1990) Diel feeding behaviour in the marine copepod *Acartia tonsa* in relation to food availability. *Mar Ecol Prog Ser* 68:23–45
- Durbin EG, Durbin AG (1992) Effects of temperature and food abundance on grazing and short-term weight change in the marine copepod *Acartia hudsonica*. *Limnol Oceanogr* 37:361–378
- Eidler L (1979) Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. *Baltic Marine Biologists Publ* 5:1–36
- Forsskåhl M, Sundberg A (1981) Abundance, biomass, species composition of phyto- and zooplankton and their interrelations at the entrance of the Gulf of Finland. *Meri* 9:43–55
- Gulati R (1985) Zooplankton grazing methods using radioactive tracers: technical problems. *Hydrobiol Bull* 19:61–69
- Gulati R, Doornekamp A (1991) The spring-time abundance and feeding of *Eurytemora affinis* (Poppe) in Volkerak-Zoommeer, a newly-created freshwater lake system in the Rhine delta (The Netherlands). *Hydrobiol Bull* 25:51–60
- Haney JF (1971) An *in situ* method for measurement of zooplankton grazing rates. *Limnol Oceanogr* 16:971–977
- Hessen DO, Nilssen JP, Eriksen TO (1986) Food size spectra and species replacement within herbivorous zooplankton. *Int Rev Ges Hydrobiol* 71:1–10
- Huntley M, Brooks ER (1982) Effects of age and food availability on diel vertical migration of *Calanus pacificus*. *Mar Biol* 71:23–31
- Huttunen M, Kuparinen J (1986) Species succession and productivity of ultraphytoplankton in the pelagic off Tvärminne, SW coast of Finland. *Ophelia Suppl* 4:73–83
- Kankaala P (1983) Resting eggs, seasonal dynamics, and production of *Bosmina longispina maritima* (P. E. Müller) (Cladocera) in the northern Baltic proper. *J Plankton Res* 5:53–69
- Kankaala P, Wulff F (1981) Experimental studies on temperature-dependent embryonic and postembryonic rates of *Bosmina longispina maritima* (Cladocera) in the Baltic. *Oikos* 36:137–146
- Kjørboe T, Møhlenberg F, Riisgård HU (1985) *In situ* feeding rates of planktonic copepods: a comparison of four methods. *J Exp Mar Biol Ecol* 88:67–81
- Kivi K (1986) Annual succession of pelagic protozoans and rotifers in the Tvärminne Storfjärden, SW coast of Finland. *Ophelia Suppl* 4:101–110
- Lambert W, Taylor B (1985) Zooplankton grazing in a eutrophic lake: impacts of diel vertical migration. *Ecology* 66:68–82
- Lasker R (1966) Feeding, growth, respiration, and carbon utilization of an euphasiid crustacean. *J Fish Res Bd Can* 23:1291–1317
- Lignell R, Heiskanen AS, Kuosa H, Gundersen K, Kuoppo-Leinikki P, Pajuniemi R, Uitto A (1993) Fate of a phytoplankton spring bloom: sedimentation and carbon flow in the planktonic food web in the northern Baltic. *Mar Ecol Prog Ser* 94:239–252
- Lindholm T (1981) On the ecology of *Mesodinium rubrum* (Lohmann) (Ciliata) in a stagnant brackish basin on Åland, SW Finland. *Kieler Meeresforsch, Sonderh* 5:117–123
- Markager S, Hansen B, Søndergaard M (1994) Pelagic carbon metabolism in a eutrophic lake during a clear-water phase. *J Plankton Res* 16:1247–1267

- Mazumder A, McQueen DJ, Taylor WD, Lean DRS, Dickman MD (1990) Micro- and mesozooplankton grazing on natural pico- and nanoplankton in contrasting plankton communities produced by planktivore manipulation and fertilisation. *Arch Hydrobiol* 118:257–282
- Moloney CL, Field JG (1989) General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. *Limnol Oceanogr* 34: 1290–1299
- Morales CE, Harris RP, Head RN, Tranter PRG (1993) Copepod grazing in the oceanic Northeast Atlantic during 6 week drifting station: the contribution of size classes and vertical migrants. *J Plankton Res* 15:185–211
- Mullin MM (1969) Production of zooplankton in the ocean: the present status and problems. *Oceanogr Mar Biol A Rev* 7:293–310
- Nicolajsen H, Møhlenberg F, Kjørboe T (1983) Algal grazing by the planktonic copepods *Centropages hamatus* and *Pseudocalanus* sp. diurnal and seasonal variation during the spring phytoplankton bloom in the Øresund. *Ophelia* 22:15–31
- Niemi, Å (1973) Ecology of phytoplankton in the Tvärminne area, SW coast of Finland. I. Dynamics of hydrography, nutrients, chlorophyll a and phytoplankton. *Acta Bot Fenn* 100:1–68
- Niemi M, Kuparinen J, Uusi-Rauva A, Korhonen K (1983) Preparation of ¹⁴C-labelled algal samples for liquid scintillation counting. *Hydrobiologia* 106:149–156
- Paffenhöfer GA (1971) Grazing and ingestion of nauplii, copepods and adults of marine planktonic copepod *Calanus helgolandicus*. *Mar Biol* 11:286–298
- Peters RH (1984) Methods for the study of feeding, grazing and assimilation by zooplankton. In: Downing JA, Rigler FH (eds) A manual for the assessment of secondary productivity in fresh waters. IBP Handbook 17 Blackwell, Oxford, p 337–413
- Peters RH, Downing JA (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol Oceanogr* 29: 763–789
- Riemann B, Sørensen HM, Bjørnsen PK, Horsted SJ, Jensen LM, Nielsen TG, Søndergaard M. (1990) Carbon budgets of the microbial food web in estuarine enclosures. *Mar Ecol Prog Ser* 65:159–170
- Tackx MLM, Bakker C, van Rijswijk P (1990) Zooplankton grazing pressure in the Oosterschelde (The Netherlands). *Neth J Sea Res* 25:405–415
- Tiselius P (1988) Effects of diurnal feeding rhythms, species composition and vertical migration on the grazing impact of calanoid copepods in the Skagerrak and Kattegat. *Ophelia* 28:215–230
- Tiselius P (1989) Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. *Mar Ecol Prog Ser* 56:49–56
- Turner JT, Tester PA (1989) Zooplankton feeding ecology: nonselective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pilca-tus* Giesbrecht in the plume of the Mississippi River. *J Exp Mar Biol Ecol* 126:21–43
- Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt Int Verein Theor Angew Limnol* 29:117–126
- Uye S, Huang C, Onbe T (1990) Ontogenetic diel vertical migration of the copepod *Calanus sinicus* in the Inland Sea of Japan. *Mar Biol* 104:389–396
- Vadstein O, Harkjerr O, Jensen A (1989) Cycling of organic carbon in the photic zone of a eutrophic lake with special reference to the heterotrophic bacteria. *Limnol Oceanogr* 34:840–855
- Viitasalo M (1994) Seasonal succession and long-term changes of mesozooplankton in the northern Baltic Sea. *Finn Mar Res* 263:3–39
- Vuorinen I, Ranta E (1987) Dynamics of marine mesozooplankton at Seili, northern Baltic Sea, in 1967–1975. *Ophelia* 28:31–48
- Webster KE, Peters RH (1978) Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnol Oceanogr* 23:1238–1245
- White JR, Roman MR (1992) Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Mar Ecol Prog Ser* 86:251–261
- Zánkai NP (1991) Feeding of nauplius stages of *Eudiatomus gracilis* on mixed plastic beads. *J Plankton Res* 13:437–453

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