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Diurnal and vertical grazing activity of mesozooplankton during summer on the SW coast of Finland

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Diurnal and vertical grazing activity of the most dominant mesozooplankton species was studied during the summer 1987 in the coastal area of the SW Finland. The samples for gut fluorescence measurements (Chl-*a* + phaeopigments) were taken from five depths between the surface and 35 m depth four times a day. Chl-*a* concentration was higher in the upper water layer of 10 m than at 20 m depth, and higher in the daytime (1300 and 1900 hrs samplings) than by night (0100 and 0700 hrs samplings). The ambient Chl-*a* concentration explained 34% to 90% of the variation in the gut pigment contents of *Eurytemora affinis*, *Bosmina longispina maritima* and *Synchaeta* spp., when the whole data was examined using the linear regression analysis. In *Acartia* spp. this relation was insignificant. The gut pigment contents of copepods, *B. longispina maritima* and *Synchaeta* spp. were higher in the upper water layer (0 to 10 m) than in the deeper layer (20 to 35 m), but only by night. Diurnal variation was not found within either of the water layers or vertically between the layers in the daytime. The gut pigment content of the cladocerans *Podon/Pleopsis* spp. and *Evadne nordmanni* exceeded several times that of copepods and *B.longispina maritima*. The estimated daily specific ingestion rate (ingestion% of body carbon) varied from 2% to 12% in *Acartia* spp. and 3% to 28% in *E. affinis*, the highest percentages being found in the upper water layer. For *Pseudocalanus minutus enlongatus*, which was mostly found in the deeper depths, the corresponding percentage was only 4%. Carbon originating from other sources than phytoplankton was likely to be important for the nutrition of copepods.

Introduction

The behaviour of many copepod species is known to follow circadian rhythms. The grazing is shown to be connected to the nightly vertical migrations, when copepods ascend to the phytoplankton-rich surface layer (Baars and Oosterhuis 1984, Mackas and Bohrer 1976, Tiselius 1988). The grazing ac-

tivity can also be bimodal at dusk and dawn (Dagg and Grill 1980, Simard *et al*. 1985). Several internal and external factors are reported to affect the grazing activity, such as periodic starvation, vertical gradients of food, light and temperature (Head *et al*. 1985, Simard *et al*. 1985, Stearns 1986, Napp *et al*. 1988, Fragopoulu and Lykakis 1990), the size of the food particles and the grazers (Bautista and Harris 1992, Morales *et al*. 1991) and the predation avoidance during light periods (Zaret and Suffern 1976, Bollens and Frost 1989). Thus, grazing activity of mesozooplankton can vary considerably at short time intervals, being influenced by variable abiotic and biotic factors.

In the southern Baltic Sea, the grazing of adult or later stage copepods increases during vertical migrations by night (Kiørboe *et al*. 1985, Tiselius 1988), but the grazing activity has been shown to increase also when the copepods did not migrate (Nicolajsen *et al*. 1983). In the northern Baltic Sea the vertical migration and grazing pattern of mesozooplankton is poorly known. In a 24-hour study conducted in the coastal area of the Gulf of Finland, Burris (1980) found abundant copepod, cladoceran and rotifer species to perform vertical migration mostly within the upper water layer in the mid-summer. He suggests that the midnight light conditions at 60°N would be the reason to the low mesozooplankton migration activity. Vuorinen *et al*. (1983) found that the predation avoiding ovigerous *Eurytemora affinis* females migrated below the depth of 20 m at noon, while the non-reproducing individuals were also found in the surface layer in the northern Baltic Sea.

Seasonal variation of mesozooplankton community composition, abundance and biomass is well documented on the SW coast of Finland (Forsskåhl and Sundberg 1981, Viitasalo *et al*. 1995, Uitto 1996, Koski *et al*. 1999). In general, rotifers are most abundant after the spring phytoplankton bloom in early June, while copepods and clacocerans dominate in mid- and late summer. These communities are known to have different feeding selectivity and grazing impact on phytoplankton (Uitto 1996, Uitto *et al*. 1997). However, virtually nothing is known about the diurnal and vertical dynamics of these communities.

This study presents new information on the variations in diurnal and vertical grazing activity of dominating mesozooplankton species in a coastal area of the northern Baltic Sea during summer. The potential role of available phytoplankton in copepod nutrition is also estimated and discussed. The gut fluorescence method was used, which has not been previously applied *in situ* to study zooplankton grazing in the area. This method has mainly been used to measure the grazing of copepods (Båmstedt *et al*. 2000), but Landry *et al*. (1994) also measured the grazing of euphausiids, ostracods, pteropods and thaliaceans, which implies that the method can be applied to many metazoan species. In the present study the grazing activity of the most abundant copepod, cladoceran and rotifer species and meroplanktonic bivalvia larvae, was measured.

Material and methods

The study site is located in an open sea area off Tvärminne (59°47´N, 23°30´E), SW coast of Finland, where the water depth varies between 40 and 46 m. Salinity is around 6 PSU and the water column lacks a permanent halocline. Temperature varies annually between 0 and about 20 °C, and the thermocline is usually formed at 10 to 30 m depth during the summer, but can be interrupted by vertical mixing of the water masses, which originate from upwellings and strong wind conditions (Niemi 1975, Haapala 1994).

The samples for chorophyll *a* (Chl-*a*) and mesozooplankton gut fluorescence analysis were collected from the depths of 0, 5, 10, 20, and 35 m, four times a day (1300, 1900, 0100 and 0700 hrs) and at four occasions during the summer 1987. Water was sampled three times from each depth with a 6.5-l tube sampler, and combined in a container of 20 litres. First a 250-ml subsample for Chl-*a* measurement was taken. Then, depending on the abundance of zooplankton, two 7 to 14-l subsamples were taken from the combined sample and filtered immediately through a 150 µm nylon filter. The filters were put inside plastic dishes, covered with an aluminium foil, frozen with CO_2-spray and kept in dry ice in darkness before transfer into the freezer.

Chl-*a* samples were measured with a Turner 111 fluorometer. Duplicate 50-ml subsamples from the 250-ml sample were filtered onto a Whatman GF/F glass fibre filter, ultrasonicated

for 5 min and extracted in 96% ethanol at room temperature for 24 h in the darkness in the laboratory. The results were calculated according to the recommendations of Baltic Marine Biologists (Edler 1979).

To analyse the gut pigment content of the dominat mesozooplankton taxa, individuals from the frozen nylon filters were picked under a dissection microscope. When possible, at least 50 individuals of each species were picked from each filter; for the most abundant species (*Acartia* spp.) with the lowest gut fluorescence 100 individuals were taken. For *Acartia* spp., *Eurytemora affinis* (Poppe), and *Pseudocalanus minutus elongatus* Boeck, only the copepodite stages CIV-CVI were analysed. Other analysed groups were *Bosmina longispina maritima* (P. E. Müller), *Evadne nordmanni* (Lovén), *Podon*/*Pleopsis* spp., *Synchaeta* spp. and meroplanktonic larvae of the benthic bivalve *Macoma baltica* L. The filters of the gut fluorescence analysis were measured within 2 months of the samplings. During sorting, only cool light was used. The samples were extracted in 5 ml 96% ethanol, and treated further as those for the ambient Chl-*a*. The gut pigment content was expressed as ng pigment ind.$^{-1}$, (Chl-*a* + phaeopigments), calculated with the eqautions:

$$\text{Chl-}a\ (\text{ng ind.}^{-1}) = K(F_o - F_a)/N$$

$$\text{Phaeopigments (ng ind.}^{-1}) = [K(RF_a - F_o)/N] \times 1.5$$

where K is an instrument calibration constant and F_o and F_a are fluorescence readings before and after acidification with 1 N HCl. N is the number of animals and *R* the acidification ratio for the instrument. The potential degradation of pigments to non-fluorescent compounds (Wang and Conover 1986, Lopez *et al.* 1988, Dam and Peterson 1991) was not measured. Thus, following Atkinson (1996) and Båmstedt *et al.* (2000), the measured gut-pigments were multiplied by 1.5 which was taken as a correction factor representing approximately the average of a wide range of pigment degradation values found in the literature. The individual gut pigment content is expressed as the mean (ng ind.$^{-1}$) calculated of two replicate samples from each depth.

The gut pigment contents were converted into ingestion rates using the average gut passage time (45 min), measured by Uitto (1996) for mesozooplankton in the same study area: $I = G \times k$, where I = the ingestion rate of Chl-*a* ind.$^{-1}$ h^{-1}, G = mean gut pigment content per species individual and k = gut clearance constant (1.33 h^{-1}). The specific daily ingestion rates of each species at different depths and times of the day were estimated by converting total pigment values to algal carbon, by assuming a rough carbon to Chl-*a* ratio of 72% for the depths 0 and 5 m, and 35% for deeper depths (from Kuosa 1990). The biomass of mesozooplankton species was calculated using the species-specific biovolumes (Finnish Institute of Marine Research, Helsinki, Finland). The values were converted to carbon using the 5.2% carbon percentage (Mullin 1969). The sufficiency of algal carbon to the growth of copepods was calculated by estimating the daily biomass specific grazing rate (ingested carbon/body carbon × 100).

Results

During the summer the concentration of Chl-*a* varied between 0.7 and 9.6 µg l^{-1} water (Fig. 1). The concentration was usually significantly higher at 0 and 5 m depths than at 20 m, except in late August, when no differences were found (Kruskal-Wallis one-way ANOVA, followed by Tukey's type comparisons, $p < 0.05$; Zar 1984). The concentration reached the highest level in the day-time but decreased by night in June and late August (day-time values; pooled data of 1300 and 1900 hrs samplings, night-time values, pooled data of 0100 and 0700 hrs samplings), when analysed with Mann-Whitney's *U*-test, $p < 0.05$.

The gut pigment content of *Acartia* spp. varied between 0.01 and 0.28 ng pigment ind.$^{-1}$ and that of *E. affinis* 0.06 to 0.77 ng pigment ind.$^{-1}$ (Fig. 2). In *E. affinis* the grazing activity was most varing; in early August the gut pigment content was largest at 0700 hrs, but in late August at 1900 hrs. The gut pigment content of *Synchaeta* spp. varied between 0.05 and 0.37 ng pigment ind.$^{-1}$ in June–July and that of *B. longispina maritima* 0.02 to 0.39 ng pigment ind.$^{-1}$ in August (Fig. 2). The highest gut contents were found in *E. nordmanni* (up to 1.4 ng pigment ind.$^{-1}$) and in *Podon*/*Pleopsis* spp. (up to 1.1 ng pigment ind.$^{-1}$), collected in late August at 1900 hrs and 0100 hrs, respectively (Fig. 3).

P. minutus elongatus was not found above the depth of 20 m, and its abundance (20 to 95 ind.

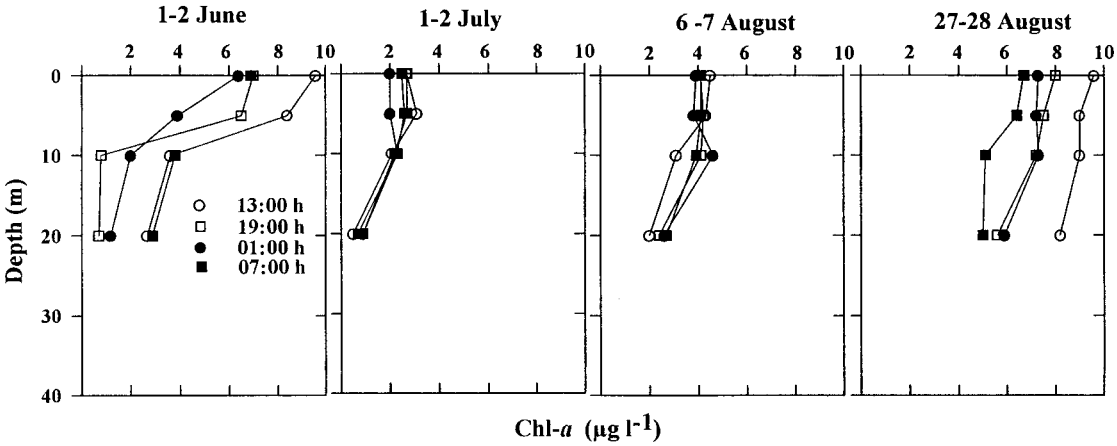

Fig. 1. Diurnal and vertical variation in the concentration of chlorophyll *a* (µg Chl-*a* l^{-1}) at the depths of 0, 5, 10 and 20 m sampled at 1300 and 1900 hrs and at 0100 and 0700 hrs in the Tvärminne sea area on four occasions during 1987.

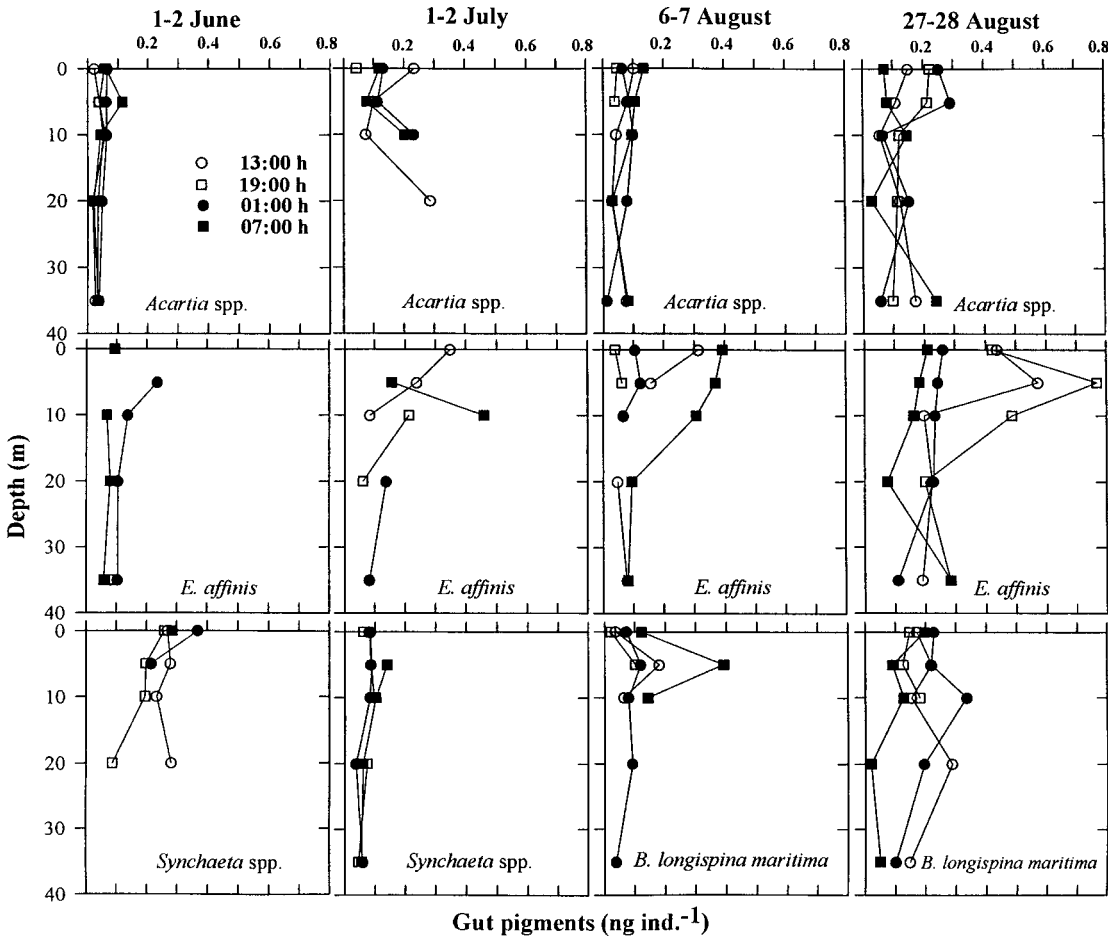

Fig. 2. Diurnal and vertical variation in the gut pigment contents (ng pigments $ind.^{-1}$) of *Acartia* spp., *E. affinis*, *Synchaeta* spp. and *B. longispina maritima.*

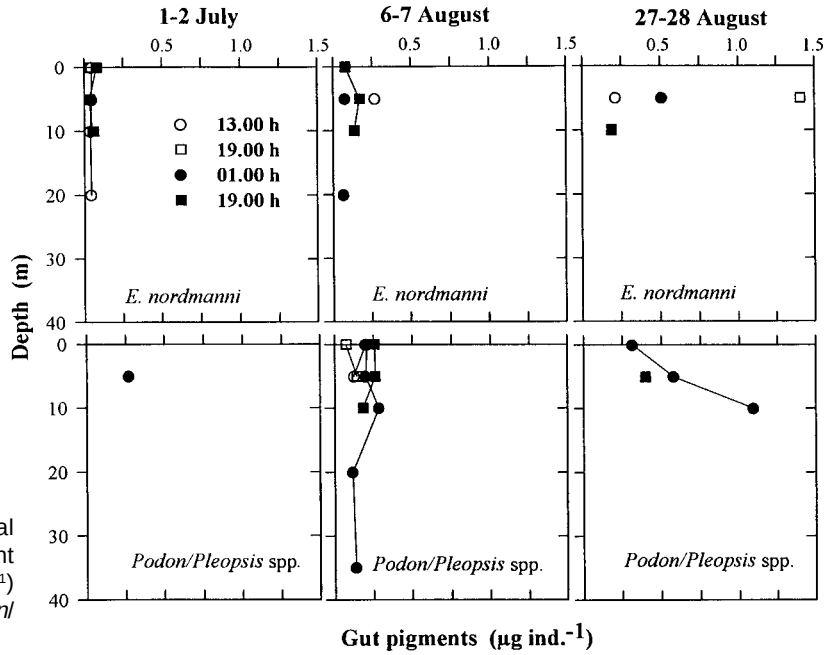

Fig. 3. Diurnal and vertical variation in the gut pigment contents (ng pigments ind.$^{-1}$) of *E. nordmanni* and *Podon/Pleopsis* spp.

sample^{-1}) was high enough only in early July to carry out the fluorescence measurements. In early July the species was found at the depths of 20 and 35 m during all samplings. The gut pigment content of *P. minutus elongatus* varied generally between 0.03 to 0.09 ng pigment ind.$^{-1}$; only in early July was the species found at 10 m depth, where the gut content was 0.39 ng pigment ind.$^{-1}$. For the larvae of *M. baltica*, the gut pigment content varied between 0.18 to 0.50 ng pigment ind.$^{-1}$, but measurable numbers of individuals were found only in early July at the depth of 10 m.

Because the species were often absent or occurred at low densities at the depths of 20 and 35 m, appropriate statistical comparisons of the vertical variation of the gut pigment content could be carried out only with the pooled data sets. To compare overall diurnal variation, the samples were combined to cover two time periods, the first comprising samples taken at 1300 hrs and 1900 hrs (day-time samples), the second those collected at 0100 hrs and 0700 hrs (night-time samples). To compare overall diurnal variation within two water layers (the layer 1: 0, 5, and 10 m and the layer 2: 20 and 35 m) during the summer, all day-time and night-time samples were both combined to form four groups, comprising the four sampling occasions. To study variation between the two layers, all samples were pooled into four separate groups, forming four groups: Layer 1-day, Layer 1-night, Layer 2-day, Layer 2-night (Table 1).

In all species, the overall diurnal difference between the day-time and night-time gut pigment contents was insignificant, when all data was analysed with Mann-Whitney's *U*-test. No significant overall diurnal variation between the four sampling occasions was found within the two water layers either (Kruskal-Wallis one-way ANOVA). Vertically, the gut pigment content of all species was significantly higher in layer 1 than in the layer 2, but only by night (Mann-Whitney's *U*-test; Table 1).

For *Acartia* spp. no significant relationship between the gut pigment content and the Chl-*a* concentration was found, when log-transformed (log n + 1) data were analysed with linear regression (Fig 4A). The gut pigment contents of *E. affinis*, *Synchaeta* spp. and *B. longispina maritima* were related to the ambient Chl-*a* concentration, explaining 34 to 90% of the variation (Fig. 4B–D). The coefficient of determination (r^2) was higher in the regressions where the day-time and the night-time values were analysed separately than in those where the whole data was used. In *E. affinis* and *B. longispina maritima*, this value was also very low (Fig. 4).

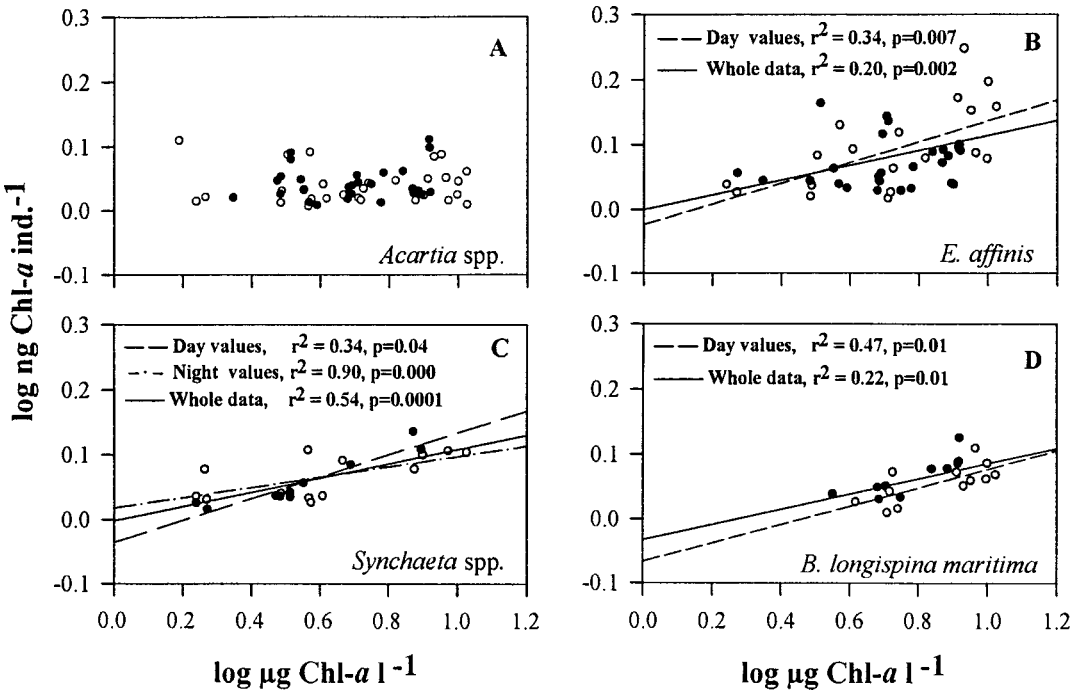

Fig. 4. Linear regressions between ambient chlorophyll *a* concentrations (µg Chl-*a* l^{-1}) and gut pigment content (ng pigments $ind.^{-1}$) of *Acartia* spp., (A), *E. affinis* (B), *Synchaeta* spp. (C) and *B. longispina maritima* (D), calculated from the (log n + 1) transformed whole data set and pooled day-time (1300 and 1900 hrs; white symbols) and night-time (0100 and 0700 hrs; black symbols) data sets.

For copepods, the specific ingestion rate (% of body carbon d^{-1}) was estimated to be highest in *E. affinis*, being on average 18% (range 10% to 28%) in the upper water layer and 4% (range 2% to 6%) in the deeper layer. For *Acartia* spp. the corresponding values were 9% (range 4% to 12%) and 4% (range 2% to 7%). The specific ingestion rate of *P. minutus elongatus* was on average 4%

Table 1. The average gut pigment contents (ng pigments $ind.^{-1}$) of mesozooplankton species in the two depth layers (layer 1 = pooled data of 0, 5, and 10 m over the summer), (layer 2 = pooled data of 20 and 35 m over the summer), calculated from the day-time values (1300 and 1900 hrs) and night-time values (0100 and 0700 hrs). Differences are tested using Mann-Whitney two-tailed *U*-test, n = number of measurements, ns = not significant.

	Day values	Night values	Day values	Night values
	Acartia spp.		*Synchaeta* spp.	
layer 1	0.087	0.116	0.159	0.155
layer 2	0.034	0.069	0.110	0.048
p	ns	0.006	ns	0.009
n1,n2	22, 11	24, 12	10, 4	8, 4
	E. affinis		*B. longispina maritima*	
layer 1	0.202	0.223	0.115	0.157
layer 2	0.128	0.107	0.196	0.078
p	ns	0.002	ns	0.044
n1, n2	16, 9	21, 12	11, 2	12, 6

(range 1% to 15%), The highest value was found on one occasion (0100 hrs) in early July when measurable numbers of the species was found at 10 m depth.

Discussion

Diurnal and vertical grazing activity

The comparison of the pooled day-time and night-time values of gut fluorescence measurements indicate that the grazing activity of the dominant species (*Acartia* spp., *E. affinis*, *Synchaeta* spp. and *B. longispina maritima*) was higher in the upper water layer than in the lower one, but only by night. In general, the increased nocturnal grazing activity of copepods has been connected to diurnal vertical migration in a vertically stratified food environment (Gauld 1953, Mackas and Bohrer 1976). The lower grazing activity in the daytime is linked to the vertical migration when avoiding visually predating zooplanktivores (Zaret and Suffern 1976). In the northern Baltic Sea, pelagic fish (herring and sprat) and invertebrate species (mysid shrimps) consume most of the mesozooplankton production (Rudstam *et al*. 1994), which indicates severe predation pressure on mesozooplankton. However, in the Tvärminne archipelago area, Burris (1980) found the copepods *Acartia bifilosa* and *Eurytemora hirundoides* (syn. *E.affinis*, cf. Busch and Brenning 1992), the rotifer *Synchaeta baltica* and the cladoceran *E.nordmanni* to show only moderate vertical migration, while in other cladocerans and in *Keratella* spp. the migration pattern was not clear. In the present study, measurable numbers of dominant species were usually found in the upper water layer (0–10 m) throughout the diurnal cycle, which indicates that at least a part of the species populations did not migrate vertically between the euphotic and aphotic layers.

Many factors, such as the light intensity, also influence the grazing activity of copepods (Stearns 1986). Even if mesozooplankton species did not migrate vertically, they may have diminished their activity in the illuminated water layer in the daytime, if visually predating top-predators were present (Zaret and Suffern 1976). However, grazing activity can also increase without significant vertical migration (Dagg and Grill 1980, Nicolajsen *et al*. 1983, Christoffersen and Jespersen 1986, Stearns 1986). The grazing pattern can also be regulated by internal factors. Based on their laboratory experiments, Durbin *et al*. (1990) stated that the grazing activity of the copepod *Acartia tonsa* is mostly endogenous, because they found the same diurnal feeding rhythm to prevail in different food concentration, temperature, and light conditions, and with different levels of starvation.

In the present study, the larger amount of edible food within the euphotic layer was apparently one important reason to the higher grazing activity of the dominant mesozooplankton species in the upper water layer. Dam and Peterson (1991) and Landry *et al*. (1994) found copepod gut pigment content to be related to the Chl-*a* concentration, which agrees with the present results. However, in *Acartia* spp., the independence of the gut pigment content of ambient Chl-*a* indicates that other food sources than algal carbon was important in its diet. The species is known to be able to change its feeding type from ambush to suspension-feeding (Jonsson and Tiselius 1990, Saiz and Kiørboe 1995). As ambush feeder *Acartia* spp. catches motile prey, such as microzooplankton. Indeed, ciliates have found to comprise about half of the food for *Acartia bifilosa* (Kivi *et al*. 1996) and the mesozooplankton community in general (Uitto *et al*. 1997) in the study area. The clear dependence of the gut pigment content of *E.affinis*, *Synchaeta* spp. and *B. longispina maritima* on ambient Chl-*a* suggest that these species were more herbivorous suspension-feeders than *Acartia* spp.

The gut pigment content of rotifers, cladocers and bivalvia larvae

The gut pigment contents of *Synchaeta* spp., *B. longispina maritima*, *E. nordmanni*, *Pleopsis/ Podon* spp. and the larvae of *M. baltica* have not previously been reported. The gut content of these species, except for *E. nordmanni* and *Pleopsis/ Podon* was similar to that of copepods. In the study area the abundance and biomass of *Synchaeta* spp. and the larvae of *M. baltica* are able to exceed that of copepods in spring and early summer (Forsskåhl and Sundberg 1981, Uitto 1996, Viitasalo *et al*. 1995, Koski *et al*. 1999). Thus,

while abundant, these taxa may contribute to a significant part of the metazooplankton community grazing in the study area, especially in early summer (Uitto 1996). The annual production of *Synchaeta* spp. approaches that of copepods (Koski *et al.* 1999), indicating their importance in the pelagic food web dynamics. In general, *Synchaeta* spp. are able to feed on particles of a wide size range, but flagellates are reported to be the most important food in the southern Baltic (Arndt *et al.* 1990).

The feeding modes of *E. nordmanni* and *Podon/Pleopsis* spp. have been largely unknown. The gut pigment contents of these species were surprisingly high, exceeding those of other species in August. The species of the genus *Podon* are considered to be predatory in the Caspian Sea (Mordukhai-Boltovskoi and Rivier 1971). However, Jagger *et al.* (1988) and Kim *et al.* (1989) found mainly diatom remains in the faecal pellets of *Podon* spp. In an enclosure experiment on the west coast of Sweden, Turner and Granéli (1992) found *Podon/Pleopsis* spp. to graze on phytoplankton microflagellates and diatoms. Nielsen (1991) found polyphemoids to be favoured by a high abundance of dinoflagellates. In the Gulf of Finland the late summer phytoplakton is usually dominated by the cyanobacteria *Aphanizomenon flos-aquae* and *Nodularia spumigena* (Forsskåhl and Sundberg 1981, Kononen *et al.* 1996). Because *Podon/Pleopsis* spp. are able to ingest microplankton (Turner and Granéli 1992, Nielsen 1991), they may have predated also ciliates that occur in the study area in late summer (Kivi 1986).

In terms of the seasonal change, higher gut pigment contents in all species were found in late August. The gut pigment content of *E.affinis*, *E. nordmanni*, and *Pleopsis/Podon* spp., were especially high at 5 m depth at this time. Obviously there was a lot of edible food for these species in the upper water layer in late August. The strong thermocline situated at 5 m depth in the study area (c.f. Haapala 1994) may have concentrated the food particles within a narrow food layer, thus making intense grazing possible.

Ingestion rates of copepods

The estimated mass specific ingestion rates of *Acartia* spp. were similar to the range of 3% to 10% found by Uitto (1996) in the same study area for a natural mesozooplankton community dominated by copepods, when the community grazing was measured with ^{14}C-labelled algae. The values for *Acartia* spp. are also similar to those found in Øresund for adult females of *Centropages hamatus* (3%–12%, Nicolajsen *et al.*, 1983), *Temora longicornis* (18%), and for *Acartia* spp. (25%) in Kattegat-Skagerrak (Kiørboe *et al.* 1985). Nicolajsen *et al.* (1983) found the ration to be as much as 14% for *P. minutus elongatus.* In the Tvärminne sea area this species was usually found in the depths of 20 m and 35 m. The copepodite stages of *P. minutus elongatus* is known to favour deep water in the Baltic Sea, even the depths of 50 m (Ackefors and Hernroth 1972). The low gut pigment content of this species reflects the low ambient Chl-*a* concentration in the deeper depths.

In the study site, the Chl-*a* concentration, gut pigment content of the species and the estimated carbon rations of dominant copepods were higher in the upper water layer. Thus, the copepods probably got more algal carbon for their growth in this euphotic zone than in the depths below 10 m. According to Marshall and Orr (1966) and Marshall (1973), the daily specific respiration for routine metabolism is about 5% to 10% of body weight for calanoid copepod species below the temperatures of 15 °C, and 15% to 25% at a temperature of 20 °C. The long-term data of Haapala and Alenius (1994) shows that the summer temperatures within the upper water layer (0 to 10 m) often exceed 15 °C during mid-summer in the Gulf of Finland. In spite of the higher potential respiration loss in the warmer water, it may have been advantageous for copepods to ascend to feed in the euphotic layer. Using the 5% to 10% percentage to estimate the carbon need for the routine metabolism, the copepods would have nearly starved in the deeper water layer, if no other food source than algal carbon was available, or if the species did not ascend to the euphotic layer to feed.

Especially in *Acartia* spp., a considerable amount of alternative food sources should be consumed for maintenance and growth, because herbivory only could hardly sustain the carbon need for routine metabolism. Nicolajsen *et al.* (1983) and Christoffersen and Jespersen (1986) also found the daily ingestion rate of copepods to

be low when ingestion was measured with the gut fluorescence method. They suggest that the reason for the relatively low rates was that gut fluorescence method underestimate copepod grazing. When the mesozooplankton community grazing rates were measured using radiotracer methods in the SW coast of Finland (Uitto 1996), herbivory was estimated to fulfil only half of carbon need of metazooplankton communities during the summer (Uitto *et al*. 1997). Thus, the rates may not been underestimated, but instead indicate the importance of omnivory in copepod nutrition in the coastal areas of the Baltic Sea.

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