



Seasonal Dynamics of Sublittoral Meiobenthos in Relation to Phytoplankton Sedimentation in the Baltic Sea

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Meiobenthic metazoans (40–500) μm were sampled monthly at a 37 m deep station in the north-western Baltic Sea proper. Nematodes dominated the meiofauna, ranging from 67% of total abundance in February to 91% in September. Harpacticoid copepods were the second most common group, ranging from 2% in September to 15% in February. Total meiofauna shell-free dry weight biomass was lowest in winter (0.9 mg 10 cm⁻² in January), and increased rapidly following the spring bloom, to high values in May–July (peak 1.7 mg 10 cm⁻² in July). As an annual average, ostracods contributed most to biomass, 38%, while nematodes and harpacticoids made up 24 and 15%, respectively. Only nematodes were common below 2 cm depth in the sediment, and few nematodes penetrated below 4 cm. Of Wieser's morphologically based nematode feeding groups, epistrate feeders dominated the surface sediment, and non-selective deposit feeders dominated the deeper layer in May. Total nematode abundance was significantly different among dates, with lowest numbers in winter and spring (October–April), and almost doubled within about 2 months after the spring phytoplankton bloom in March. There was a significant increase in selective deposit feeders and epistrate feeders after the spring bloom. Harpacticoid copepods were almost all of two species, *Pseudobryadia* sp. and *Microarthridion littorale*, both of which differed significantly in abundance among months, and displayed continuous reproduction throughout the year, with a peak in pairs in precopula in winter for *Pseudobryadia* sp. and in ovigerous females in *M. littorale* after the spring bloom. *Pseudobryadia* was significantly more numerous in winter than in other seasons. *Microarthridion littorale* had its highest abundance from July to October. Three species of ostracods were common throughout the year and all differed significantly in numbers among months. Turbellaria, Kinorhyncha were found in lowest numbers during winter and peaked in summer. The peak of newly settled *Macoma balthica* spat in June disappeared rapidly, as predicted from laboratory experiments showing they are eaten by amphipods. The results support the hypothesis that meiobenthic animals react in two ways to phytoplankton sedimentation, with surface feeders directly assimilating sedimented phytoplankton, and increasing markedly following the spring bloom, while subsurface feeders experience a more stable food supply, and rely only indirectly on sedimented phytoplankton.

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Introduction

Seasonal variation of plant and animal populations is the rule in nature, and often quite predictable. In benthic communities, seasonal variation is generally more pronounced intertidally than in deeper waters. A variety of abiotic and biotic variables may account for temporal oscillations in benthic animal populations, but temperature and food availability are the factors most often invoked to explain seasonal changes in abundance.

For the meiobenthos, seasonal and annual variations are normal in intertidal and shallow subtidal areas (see reviews by Hicks & Coull, 1983; Heip *et al.*, 1985). Abundance peaks of harpacticoid copepods commonly coincide with the warmest months of

the year. Hicks and Coull (1983) argue that since reproductive and development rates are known to be positively correlated with temperature (e.g. Heip & Smol, 1976; Feller, 1980; Palmer & Coull, 1980), it is not surprising that most species have their maximum abundance in warmer months. Without manipulative experiments it is, nevertheless, difficult to separate the effects of temperature and food availability, since these variables are often closely linked. For example, many meiobenthic species assimilate sedimented planktonic diatoms (e.g. Decho, 1986; Rudnick, 1989), and spring phytoplankton sedimentation is usually associated with rising temperature. Although meiobenthic populations usually peak in the warm months, individual species may reach their highest abundance at other times of the year (e.g. McIntyre &

Murison, 1973; Bell, 1979). Such patterns may be a result of predation (Sibert, 1979) or competition (Coull & Vernberg, 1975).

A few careful seasonal studies of meiobenthic populations in subtidal areas have failed to detect temporal changes [i.e. Juario, 1975 (35 m); Warwick & Buchanan, 1971 (80 m); Boucher, 1980 (19 m)]; but others have reported significant seasonality in subtidal meiobenthos [e.g. Stripp, 1969 (16–49 m); Soyer, 1971 (35 m); Bovée & Soyer, 1974 (35 m); Faubel *et al.*, 1983 (134 m); Rudnick *et al.*, 1985 (7 m)].

Studies of seasonal change in Baltic soft bottom meiobenthos are few. Arlt *et al.* (1982) and Arlt (1988) studied meiofaunal temporal fluctuations at a number of stations in the central and western Baltic Sea. From these studies, it is difficult to deduce a clear pattern as data were not statistically evaluated.

In the Askö area of the Baltic proper, the spring bloom is fairly predictable, in most years falling between late March and the end of April (Larsson *et al.*, 1991). Elmgren (1978) argued that the sedimentation of organic matter following the spring phytoplankton bloom is the most important food input of the year for the deposit-feeding amphipods that dominate the macrobenthic community over large areas of the Baltic. The Baltic Sea is of particular interest for the discussion on the causation of the summer meiobenthos maximum, in that Baltic water temperature below the summer thermocline tends to preserve winter values all through summer, until autumn storms mix the upper 60–80 m of the water column (Kullenberg, 1981). Even though enhanced mixing and downwelling events complicate this picture in the coastal zone, the sub-thermocline Baltic benthos thus experiences maxima in food input and temperature separated by up to half a year.

Phytoplankton sedimentation after the spring bloom is also likely to affect the meiobenthos, as many species in this area can be classified as diatom or epistrate feeders living close to the sediment surface (see below). Phytodetritus may reach deeper dwelling species later than the surface dweller and hence affect them later in the year. The present paper reports on a study conducted in the north-western Baltic proper, designed to test the following null-hypotheses:

1. There is no difference in the density of major taxa and nematode and harpacticoid species before and after the spring bloom.

and if Hypothesis 1 was not supported, then:

2. There is no difference in the response of surface dwelling species and subsurface dwelling species to the spring bloom.

The authors chose to sample an easily accessible station below the normal summer thermocline, which thus has a relatively small annual variation in temperature, situated where hydrography, phytoplankton and sedimentation are carefully monitored year round.

Materials and methods

Study area and site

Samples were taken from a 37 m deep station (58°48'N, 17°37'E) *c.* 3 km south of the Askö Laboratory field station in the north-western Baltic proper. In this area, the water temperature at 35 m depth may rise to 10 °C in late summer–early autumn (August–October) and fall to near freezing in late winter (March, April) (Figure 1, Ankar & Elmgren, 1976, p. 10). Bottom water salinity is fairly constant through the year, being typically around 7. Average annual pelagic primary production for 1976–89 was 135 gC m⁻² year⁻¹ (Larsson *et al.*, 1991). Before the spring bloom, production is low, but during the bloom it usually reaches 1–2 gC m⁻² day⁻¹ (Larsson *et al.*, 1991), while during summer, typical values are about 0.5 gC m⁻² day⁻¹, with some bloom peaks reaching over 1 gC m⁻² day⁻¹. The sediment was soft, with a dry weight content of carbon and nitrogen in the top 2 cm of between 1.6 and 3.0% C and 0.23–0.58% N, with a C/N ratio of 5.8–7.0, and a loss-on-ignition of 3.0–7.6% (*n*=3 for each of 10 sampling dates, unpubl. data, courtesy of C. Hill). The macrobenthos at this site has a wet weight biomass of about 100 gm⁻² shells included, and is dominated by the bivalve *Macoma balthica* (L.), but the deposit-feeding amphipods *Monoporeia affinis* (Lindström) and *Pontoporeia femorata* Kröyer are also common (about 2000 m⁻² before release of young in spring, 15 gm⁻² wet weight; C. Hill, unpubl.).

Water column and sediment samples. Settling matter was collected in a sediment trap (Larsson *et al.*, 1986) placed 20 m below surface, *c.* 200 m from the benthic sampling station. The sediment trap was retrieved at least once a month, the dry weight of settling matter was estimated (Blomqvist & Larsson, 1994), and its content of carbon and nitrogen was determined in a LECO CHN-900 elemental analyser following combustion at 950 °C. Primary production was measured on whole, unfiltered water using the ¹⁴C-method as described by Larsson and Hagström (1982), chlorophyll *a* was determined spectrophotometrically following acetone extraction, and diatom biomass was

determined using inverted microscope measurements, both according to Edler (1979).

Benthic samples. Eight replicate Kajak cores of 50 cm² (Blomqvist & Abrahamsson, 1985) were taken monthly from October 1988 to October 1989, except in November 1988. Each sediment core was sectioned into four layers: 0–2, 2–4, 4–6 and 6–8 cm. Three cores were used to estimate sediment organic content (by ashing) and C and N content, as for sediment trap material above (C. Hill, unpubl.), five were preserved in 4% formaldehyde solution and used for faunal analysis. Faunal samples were sieved through 500 and 40 µm mesh sieves, and the animals retained on the 500 µm sieve were counted as macrofauna. The 40 µm screenings were suspended in Ludox (colloidal silica polymer, density 1.15) in 2 l conical flasks. After settling for 1 h, the supernatant was decanted through a 40 µm mesh. The sediment was then re-suspended in Ludox and the process repeated once. Ólafsson and Elmgren (1991) found the average extraction efficiency of a very similar procedure to be 98% (range 97–99%) for nematodes, 87% (range 70–100%) for copepods, and 71% (range 58–84%) for other groups combined. As extraction efficiency for ostracods was often low, the sediment was re-sieved through a 100 µm sieve, fine enough to retain all instars of common ostracods, and all ostracods picked out. Foraminifera were not reliably extracted with the method used, and thus were excluded from study. The animals retained on the 40 µm screen, plus ostracods from the 100 µm screen, were enumerated in a Petri dish under a stereo microscope at 25–50× magnification, and identified to major taxon, or to species level for nematodes, harpacticoids and ostracods. Ostracods retained on 500 µm were counted as meiofauna and used in biomass estimates. Meiofauna counts from four cores (October 1988 and May 1989) revealed that more than 98% of animals were found in the top two layers (0–2 and 2–4 cm), hence deeper layers (4–6 and 6–8 cm) were not studied further. For the nematode species counts, the extracted sample was re-suspended in 500 ml of tap water, vigorously agitated, and five subsamples of 10 ml were taken with a syringe and pooled before processing. About 100 nematodes per core were transferred to anhydrous glycerine (Platt & Warwick, 1983) and mounted on slides for species identification under a high-power microscope. Nematodes were identified from all five replicate cores in January, May and August, from two cores in June and one core on other sampling dates, except October 1988. In the May samples, nematodes from the two top layers (0–2 and 2–4 cm) were

identified separately, but for other months, both layers were combined.

Biomass estimates

For the nematodes, the volumetric method of Andrassy (1956) was applied, using a dry/wet weight ratio of 0.23 (Ankar & Elmgren, 1976) and a density of 1.13 (Wieser, 1960). The average dry weight was calculated for juveniles, females, gravid females and males of each species, based on five individuals in each category when numbers permitted. For replicates where species composition and population structure were unknown, the biomass values were estimated using the population composition from other replicates from the same month. Apart from 3 months (October 1988, February and September 1989), all ostracods were measured for maximum length and width, biomass was estimated according to Feller and Warwick (1988), and dry/wet weight ratio and shell-free dry weight/dry weight ratio were estimated from Ankar and Elmgren (1976). For all other taxa including harpacticoids the weighted mean abundance/dry weight ratios from the Askö area (Ankar & Elmgren, 1976) were used for biomass calculations.

Statistics. For each taxon, differences in density between the months were investigated by means of one-way analyses of variance. Paired *a posteriori* comparisons of density estimates were carried out with the Tukey test using 95% confidence limits. Prior to the analysis of variance, all data were log₁₀(x+1) transformed and Cochran's C test was used to check the assumption of homoscedasticity. When conditions for the use of parametric tests were not fulfilled, the Kruskal–Wallis test was employed.

Results

Water column and sediment

Bottom water temperature ranged from 1.5 to 10 °C over the study year (Figure 1). In October 1988 there was a sudden increase in bottom temperature, as a storm homogenized the water column, followed by a gradual cooling to winter temperatures of around 2 °C. The 1988–89 winter was the warmest on record, and some phytoplankton and chlorophyll persisted in the water column all season, unlike normal winters. The onset of the spring bloom was the earliest recorded and occurred at c. 2.5 °C in the beginning of March, with a marked increase in chlorophyll *a* values, primary production and diatom biomass (Figure 1). By mid-April, inorganic nitrogen was

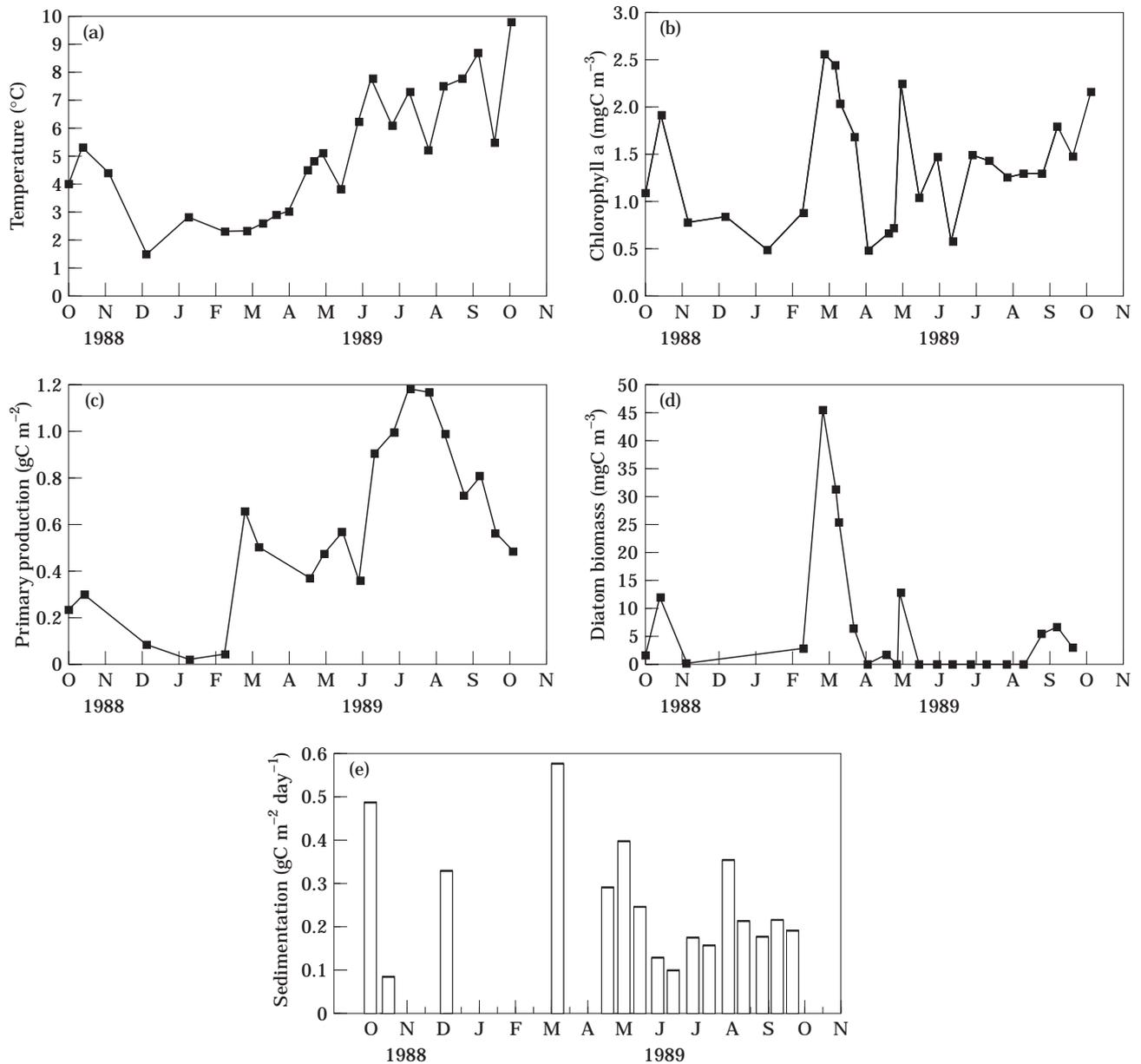


FIGURE 1. (a) Water-temperature ($^{\circ}\text{C}$) at 35 m, (b) chlorophyll *a* concentration, (c) primary production and (d) diatom biomass in the water column (0–20 m), and (e) the rate of sedimentation of organic carbon in a sediment trap placed 20 m below the water surface. Measurements over the study period were taken about 200 m from the benthic study site in the Askö area.

exhausted in the water column, and the spring bloom was over. The spring bloom was more prolonged, but less intense, than in normal years. The bottom water temperature increased slowly to about 5°C in late May, and gradually to 10°C in October 1989. Primary production in summer was unusually high, around $1\text{ gC m}^{-2}\text{ day}^{-1}$, but was not reflected in high chlorophyll *a* values (Figure 1). Sedimentation reached over $0.5\text{ gC m}^{-2}\text{ day}^{-1}$ during the 1989 spring bloom, compared to around

$0.2\text{ gC m}^{-2}\text{ day}^{-1}$ the following summer (Figure 1). The C/N ratio was relatively stable all year near 7–8, apart from a single high value (13) after a dinoflagellate bloom in May. Annual primary production was higher than the long-term average for the station in both years, with 183 gC m^{-2} in 1988 (highest recorded) and 162 gC m^{-2} in 1989. The variation between dates in sediment loss-on-ignition and C and N content was too large to reflect just a build-up of sedimenting material, and was probably influenced by

sediment patchiness, and thus could not be used to estimate organic matter input.

Meiobenthos

General composition. Nematodes were always the dominant major taxon, with an annual mean of 89% of the total abundance (range 67% in February to 91% in September), and harpacticoid copepods were almost always the second most common group (mean 5.6%, range 2% in September to 15% in February). Other groups of some importance were Turbellaria (mean 2.3%), Kinorhyncha (1.6%), Ostracoda (0.6%), *Macoma balthica* spat (0.5%), and larvae of *Halicryptus spinulosus* (von Siebold) (0.2%). Groups found infrequently in low numbers were Oligochaeta, Rotifera, Amphipoda, Halacaridae, Cyclopoida and Calanoida (0.1% or less). All groups, except nematodes, were found almost exclusively in the top 2 cm of the sediment.

Nematodes. Total numbers of nematodes differed significantly among dates (Table 1, Kruskal–Wallis, $P < 0.001$). Nematodes were least abundant in winter and spring, i.e. from October 1988 to April 1989 (mean 1900 ind. 10 cm^{-2}), and reached double this in May and June (Figure 2). Most nematodes were always found in the surface 2 cm of sediment, but substantial numbers were also found in the 2–4 cm layer, with the lowest average in December (190 ind. 10 cm^{-2}) and the highest in April (604 ind. 10 cm^{-2}) (Figure 2).

Altogether, 36 nematode species belonging to 17 families and 23 genera were found (Table 2). The five most abundant taxa, the small *Calomicrolaimus honestus*, *Leptolaimus elegans*, *L. papilliger*, and the larger *Paracanthochus* spp. and *Sabatieria pulchra* made up three quarters of individuals examined. Other common species found year round included *Microlaimus globiceps*, *Desmolaimus zeelandicus*, *Campylaimus gerlachi*, *Eleutherolaimus stenosoma* and *Axonolaimus spinosus*. A number of species had a sporadic temporal distribution pattern, and 10 species were only recorded once or twice.

Of the 10 most abundant nematodes, five differed significantly among January, May and August (Table 3). The two most abundant species, *C. honestus* and *L. elegans* were more abundant in May than in January and August, but the difference was not significant. *Leptolaimus papilliger*, *Paracanthochus* spp. and *M. globiceps* all differed significantly in numbers among months, with highest numbers in May, and the difference between January and May was statistically

significant for the first two species (Table 3). Two species, *Sabatieria pulchra* and *Monhystera* sp., were found in highest numbers in August (Table 3).

According to Wieser's (1953) feeding classification, almost half the species (17) were non-selective deposit feeders, but most individuals were epistrate feeders (57%), while predators and omnivores were rare (Figure 3). Comparing May and June, after the spring bloom, to December–March, before and during the bloom (Figure 4), there were significant increases in selective deposit feeders and epistrate feeders (both ANOVA, $P < 0.0001$) after the spring bloom, but no change in non-selective deposit feeders and predators/omnivores (ANOVA, $P > 0.05$).

As expected, the assemblage structure in May differed between the 0–2 and 2–4 cm layers. Most taxa were significantly more abundant in the surface layer, e.g. *C. honestus* (95% in top layer, Mann–Whitney U test, $P < 0.05$), *Paracanthochus* spp. (99% in top layer, ANOVA, $P < 0.001$), *L. elegans* (74% in top layer, ANOVA, $P < 0.05$), *L. papilliger* (77% in top layer, ANOVA, $P < 0.01$), *M. globiceps* (91% in top layer, Mann–Whitney U test, $P < 0.05$), while a few were more common in the lower layer, e.g. *D. zeelandicus* (80% in lower layer, ANOVA, $P < 0.05$) and *S. pulchra* (68% in lower layer, Mann–Whitney U -test, not significant). There was a shift from a domination by epistrate feeders in the top layer to a preponderance of deposit feeders in the deeper layer (Figure 5).

Harpacticoid copepods. The abundance of harpacticoid copepods (adults plus copepodites) was significantly different among months (Table 1, ANOVA, $P < 0.001$), being highest in winter, i.e. December–February (Figure 6), but with a peak also in May. There was also a significant difference in number of harpacticoid nauplii among months (Table 1, Kruskal–Wallis, $P < 0.001$). Nauplii were most abundant in December, prior to the peak of the adult and copepodite population in February, and in May–July (Figure 6).

The harpacticoid copepods belonged almost exclusively to two species, *Pseudobradia* sp. and *M. littorale* (Poppe). Occasionally, one or two individuals of other harpacticoid spp. (in the family Ameiridae) were recorded. *Pseudobradia* sp. was the most abundant species in almost all samples, and has previously been identified as *Halectinosoma abrau* (Kricagin) (Noodt, 1970; Sarvala, 1971; Ankar & Elmgren, 1976), but appears to be a species new to science (C. G. Moore & M. Clement, pers. comm.). The abundance of *Pseudobradia* sp. differed significantly among months (Table 1, one-way ANOVA, $P < 0.001$), being

TABLE 1. Summary statistics on major meiofaunal taxa/species time series data [$\log(x+1)$ transformed] from the field station

Taxon/Species	One-way ANOVA		Kruskal-Wallis P value	Tukey a posteriori test (min to max)
	F ratio	P value		
Nematoda	-	-	<0.0001	Heterogeneous variance
Harpacticoida	07.55	<0.0001	-	8909 8910 8810 8903 8908 8906 8904 8907 8905 8901 8812 8902
Pseudobryadia sp.	15.91	<0.0001	-	8909 8906 8910 8908 8810 8907 8903 8904 8905 8901 8812 8902
Ovigerous females	2.2	0.0303	-	8908 8909 8906 8907 8910 8903 8810 8904 8901 8902 8905 8812
Precopula	9.55	<0.0001	-	8906 8910 8909 8908 8907 8904 8903 8810 8905 8901 8812 8902
Microarthridion littorale	4.37	0.0002	-	8901 8906 8810 8903 8812 8902 8905 8904 8908 8910 8907 8909
Ovigerous females	4.31	0.0002	-	8909 8908 8910 8901 8902 8810 8906 8903 8812 8907 8905 8904
Nauplii	-	-	<0.0001	Heterogeneous variance
Turbellaria	-	-	<0.0001	Heterogeneous variance
Kinorhyncha	-	-	0.046	Heterogeneous variance
Ostracoda	-	-	0.0678	Heterogeneous variance
Paracyprideis fennica	-	-	0.02	Heterogeneous variance
Candona neglecta	5.01	0.0003	-	8910 8907 8908 8905 8901 8903 8906 8904 8812
Heterocyprideis sorbyana	4.89	0.0004	-	8907 8901 8908 8903 8904 8812 8905 8910 8906
Macoma balthica (spat)	15.6	<0.001	-	8904 8905 8910 8903 8906 8902 8812 8909 8901 8810 8908 8907
Halicryptus spinulosus	1.52	0.1563	-	

Values from dates (first two figures indicate year and the last two figures indicate month) with common underline are not significantly different at the 95% significance level.

TABLE 2. List of nematode species found at the field station, and their feeding type percentage of total individuals examined and frequency of occurrence

Family/species	Feeding type	% of total	% freq.
Phanodermatidae			
<i>Phanodermopsis</i> sp.	1A	<1	3
Oxystominidae			
<i>Halalaimus gracialis</i> De Man	1A	<1	6
<i>Halalaimus</i> sp.	1A	<1	48
<i>Adorus astridae</i> Jensen	1A	<1	3
Ocholaimidae			
<i>Adoncholaimus thalassophygas</i> (De Man)	2B	<1	3
Enchelidiidae			
<i>Eurystomina</i> sp.	2B	<1	3
Tripyloididae			
<i>Bathylaimus</i> sp.1	1B	<1	23
<i>Bathylaimus</i> sp.2	1B	<1	3
Chromadoridae			
<i>Dichromadora</i> sp.	2A	<1	10
<i>Chromadorita fennica</i> Jensen	2A	2	81
Cyatholaimidae			
<i>Paracanthochus caceus</i> (Bastian)	2A	<i>a</i>	<i>a</i>
<i>Paracanthochus</i> sp.1	2A	<i>a</i>	<i>a</i>
<i>Paracanthochus</i> sp.2	2A	<i>a</i>	<i>a</i>
<i>Paracanthochus</i> spp.	2A	9	90
Comesammatidae			
<i>Sabatieria pulchra</i> (Schneider)	1B	10	94
Microlaimidae			
<i>Calomicrolaimus honestus</i> (De Man)	2A	25	100
<i>Microlaimus globiceps</i> De Man	2A	4	94
Leptolaimidae			
<i>Leptolaimus elegans</i> (Stekhoven and De Coninck)	1A	17	100
<i>Leptolaimus papilliger</i> De Man	1A	12	100
Plectidae			
<i>Plectus</i> sp.	1B	1	65
Monhysteridae			
<i>Monhystera</i> sp.1	1B	<1	23
<i>Monhystera</i> sp.2	1B	<1	13
<i>Monhystera</i> sp.3	1B	4	74
<i>Monhystera</i> sp.4	1B	<1	19
<i>Monhystera</i> sp.5	1B	<1	6
Xyalidae			
<i>Daptonema</i> sp.1	1B	<1	32
<i>Daptonema</i> sp.2	1B	<1	3
<i>Daptonema</i> sp.3	1B	<1	3
<i>Paramonhystera</i> sp.1	1B	<1	19
<i>Paramonhystera</i> sp.2	1B	<1	16
Sphaerolaimidae			
<i>Sphaerolaimus</i> sp.	2B	<1	39
Linhomoeidae			
<i>Desmolaimus zeelandicus</i> De Man	1B	5	87
<i>Eleutherolaimus stenosoma</i> (De Man)	1B	2	74
Axonolaimidae			
<i>Axonolaimus spinosus</i> (Bütshli)	1B	1	68
Diplopeltidae			
<i>Campylaimus gerlachi</i> Timm	1A	1	74
<i>Southerniella</i> sp.	1A	<1	3

1A, Selective deposit feeders; 1B, non-selective deposit feeders; 2A, epistrate feeders; 2B, predators/omnivores based on Wieser (1953). Classification is based on Platt and Warwick (1983).

^aNot estimated for individual species.

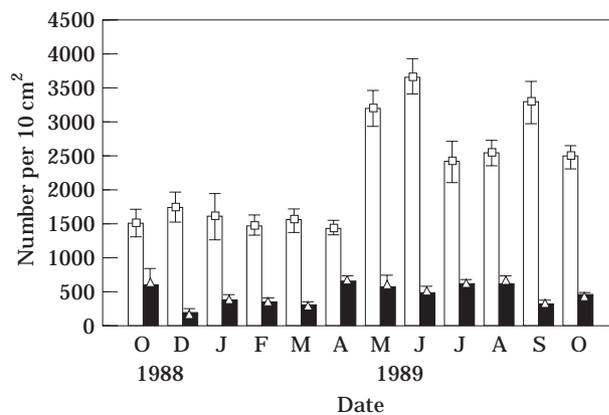


FIGURE 2. Average number of nematodes per 10 cm² ($n=5$) \pm 1 standard error in two depth layers for each sampling date. Open bars, 0–2 cm; solid bars, 2–4 cm.

significantly (Tukey test, $P<0.05$) higher in December–February than in June–October (Table 1, Figure 6). The February peak of over 500 ind. 10 cm⁻² was significantly higher than all other months, except December and January. After a low in March, the population increased to a second peak in May (Figure 6), with numbers significantly (Table 1) higher than in the next 5 months, apart from July. The precopula stage was more common in winter than in other months (Table 1, one-way ANOVA, $P<0.001$, Figure 6). The number of ovigerous females was relatively low all year, but with significantly higher numbers in May and December than in August and September (Table 1, one-way ANOVA, $P<0.05$, Figure 6).

There was a significant (Table 1, one-way ANOVA, $P<0.001$) difference in the numbers of *M. littorale* among months. On average, they were more abundant from July to October than in other months (Figure 6), though the difference was significant only for January (Table 1). There was a significant difference in the number of ovigerous females among months (Table 1, $P<0.001$), with peak numbers in April and May (Figure 6). Ovigerous females were recorded in all months except September, when the population peaked.

Ostracods. The total number of ostracods was not significantly different among months (Table 1, Kruskal–Wallis, $P>0.05$, Figure 7), but the three commonest ostracod species, which made up 99% of identified ostracods, all showed significant differences in numbers among months (Table 1, Figure 7). *Paracyprideis fennica* (Hirschmann) was found in lowest number in January, and peaked in June. *Candona neglecta* Sars was found in significantly lower

numbers in October compared to many months, while *Heterocyprideis sorbyana* (Jones) was most abundant in June, significantly more so than in January, July and August (Table 1, Figure 7). Other ostracods found occasionally were *Candona* cf. *candida*, *Cytheridea* cf. *punctillata*, *Cypria* cf. *ophthalmica* and *Leptocythere lacertosa* (Hirschmann).

Minor taxa. Numbers of Turbellaria, Kinorhyncha and *M. balthica* spat were all significantly different among months (Table 1). Turbellaria were least abundant in winter, and then gradually increased to a peak in June and July (Figure 8). Kinorhynchs had a less clear pattern, with maximum values in May and July (Figure 8). A few *M. balthica* spat were found in winter, none in April and May, followed by a significant peak in July and August (Table 1, Figure 8). The number of *Halicryptus* larvae was low all year (average 5 ind. 10 cm⁻², with no significant difference among months (Table 1, Figure 8).

Biomass

Major taxa. Total meiofaunal shell-free dry weight biomass was lowest in January, 0.9 mg 10cm⁻², and then increased monotonously to its maximum in July, 1.7 mg 10 cm⁻², and the July peak was significantly higher than all other months, except the preceding May and June (Table 4). As an annual average, ostracods contributed most to the biomass, 38%, while nematodes and harpacticoid copepods made up 24 and 15%, respectively. Ostracod biomass varied with no significant pattern, but the highest value was in June (Table 4). Nematode biomass almost doubled between the winter–spring period, before the end of the spring bloom (January–April), and late spring–summer (May–August) (Table 4), and the peak values in June–July were significantly higher than all winter–spring months, except May. Harpacticoid biomass was highest in February, like abundance, and lowest in June (Table 4).

Species and genera. Nematodes: The taxa contributing most biomass (Table 3) are relatively large, i.e. *S. pulchra*, *D. zeelandicus*, *Paracanthochus* spp., and *Chromadorita fennica*, with average ($n=15$) individual adult dry weights of 620, 340, 330 and 290 ng, respectively. The abundant but small species *L. elegans*, *C. honestus* and *L. papilliger* contributed relatively little biomass, with average ($n=15$) individual adult dry weights of 25, 24 and 18 ng, respectively. In May, 83% of nematode biomass was found in the top 2 cm, with *Paracanthochus* spp. accounting for

TABLE 3. Mean number per 10 cm² and standard error (SE) of the 10 most abundant nematode species from three different seasons, January (n=5), May (n=5) and August (n=5)

Species	January		May		August		One-way ANOVA		Kruskal-Wallis P value	Tukey a posteriori test
	Mean	SE	Mean	SE	Mean	SE	F ratio	P value		
<i>Calomicrolaimus honestus</i>	810 (17.5)	63 8%	1022 (26.8)	125 7%	860 (18.4)	61 6%	1.20	0.340		
<i>Leptolaimus elegans</i>	413 (9.1)	116 4%	733 (16.3)	171 5%	380 (7.9)	56 2%	2.37	0.140		
<i>Leptolaimus papilliger</i>	229 (4.1)	43 2%	473 (6.8)	52 2%	343 (5.8)	80 2%	4.15	0.045		May>January
<i>Paracanthochus</i> spp.	144 (24.0)	19 12%	592 (132.7)	76 37%	283 (111.0)	32 34%	30.33	<0.0001		May>January, August; August>January
<i>Sabatieria pulchra</i>	229 (65.6)	43 32%	126 (36.7)	23 10%	345 (75.9)	99 23%	4.22	0.044		August>May
<i>Microilaimus globiceps</i>	71 (1.8)	27 1%	225 (6.4)	34 2%	169 (5.0)	55 1%	Variance heterogeneous		0.04	
<i>Monhystera</i> sp.3	24 (0.02)	14 <1%	133 (0.2)	41 <1%	336 (0.3)	38 <1%	Variance heterogeneous		0.01	
<i>Desmolaimus zeelandicus</i>	81 (41.1)	8 20%	77 (24.4)	21 7%	107 (51.6)	23 15%	0.72	0.506		
<i>Eleutherolaimus stenosoma</i>	37 (2.8)	27 1%	61 (5.2)	28 1%	50 (2.6)	7 1%	Variance heterogeneous		0.76	
<i>Chromadorita fennica</i>	22 (11.3)	9 5%	43 (13.8)	13 4%	80 (30.7)	15 9%	1.80	0.211		

Mean dry weight (µg) and percentage of total biomass are given in brackets. The results from one-way ANOVA, Tukey a posteriori tests and Kruskal-Wallis tests are also presented.

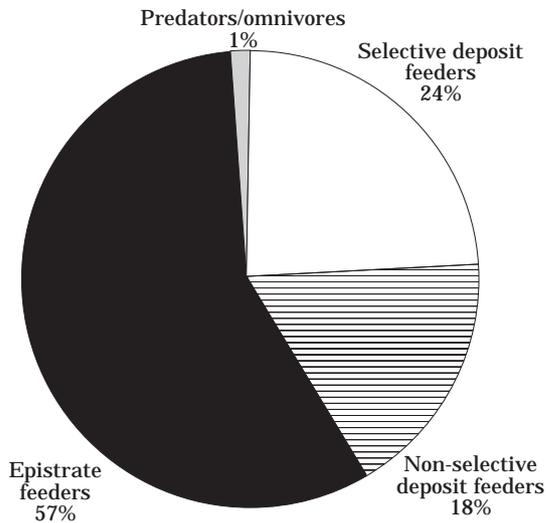


FIGURE 3. Percentage abundance of nematode-feeding groups (1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epistrate feeders; 2B, predators/omnivores) for all months pooled.

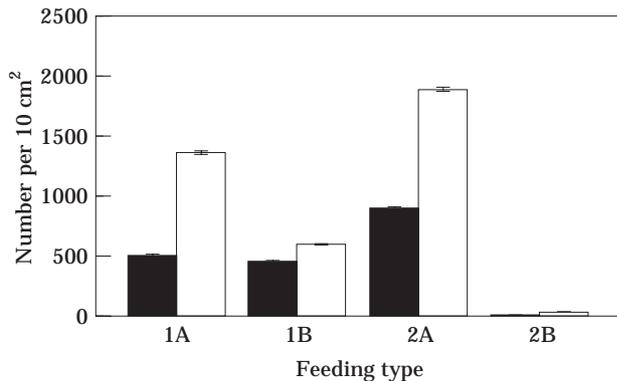


FIGURE 4. Average number per 10 cm² ($n=5$) \pm 1 standard error of nematodes of each feeding group (1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epistrate feeders; 2B, predators/omnivores) before (solid bars) and after (open bars) the spring bloom (December–April, $n=9$) and after (May–June, $n=7$).

almost half, while *S. pulchra* and *D. zeelandicus* constituted three quarters of the biomass in the 2–4 cm layer.

Harpacticoids: As an annual mean, *Pseudobrydia* sp. and *M. littorale* each contributed about half the harpacticoid biomass. From December to June, *Pseudobrydia* sp. contributed over half, while *M. littorale* dominated in July–October.

Ostracods: The relative importance of each species to the total ostracod biomass was similar for all months, *Candona neglecta* (59–78%), *Paracyprideis fennica* (21–38%), *Heterocyprideis sorbyana* (1–5%),

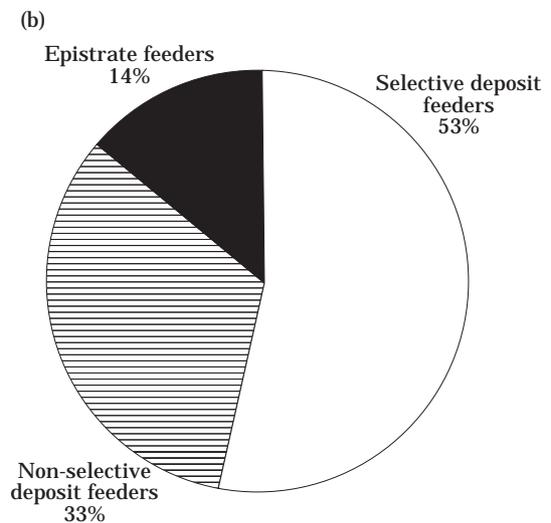
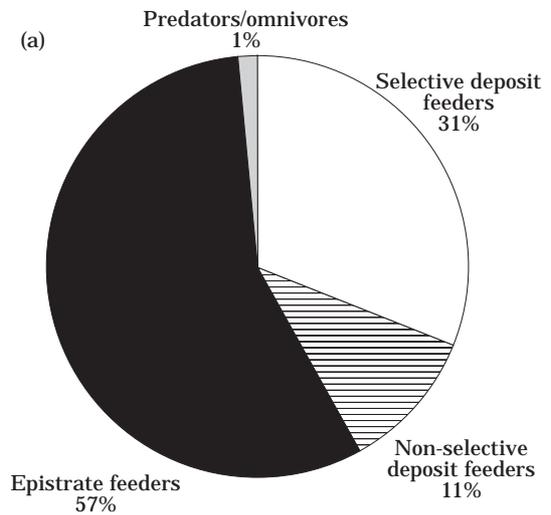


FIGURE 5. Percentage abundance of nematode-feeding groups (1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epistrate feeders; 2B, predators/omnivores) from two sediment depth layers in May 1989. (a) 0–2 cm, (b) 2–4 cm.

apart from October 1989, when *P. fennica* dominated (58%).

Discussion

A 1-year study of seasonal dynamics at a single station must not be overinterpreted, particularly when the study year had unique weather conditions. Still, comparison with the survey of the macro- and meio-benthos of the area by Ankar and Elmgren (1976) indicates that the study site is representative of its area and depth zone. The meiobenthos of the Askö area

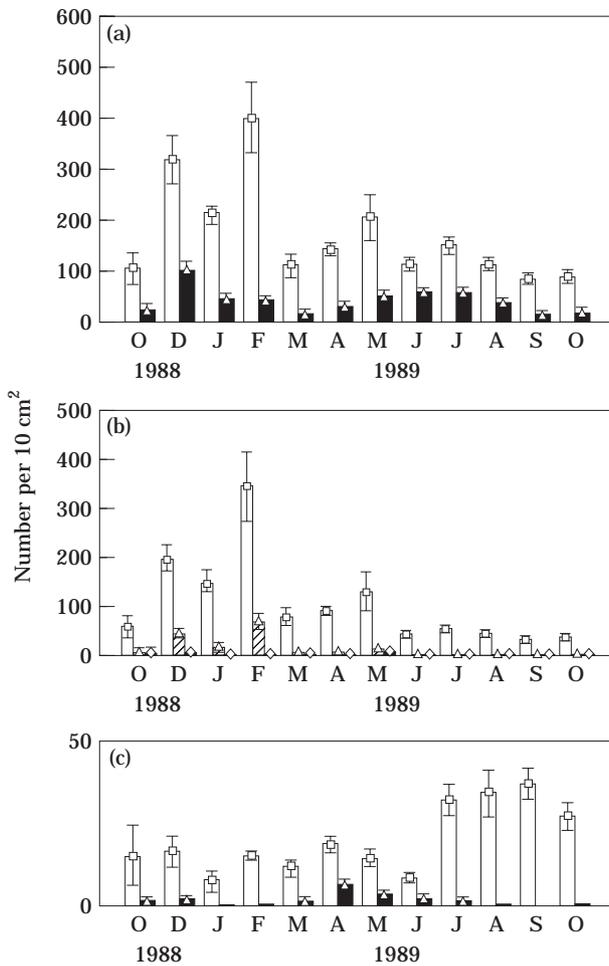


FIGURE 6. Average number of harpacticoid copepods per 10 cm² ($n=5$) \pm 1 standard error for each sampling date. Nauplii excluded for individual species. (a) Harpacticoida. Open bars, adults and copepodites; solid bars, nauplii. (b) *Pseudobradya* sp. Open bars, total; hatched bars, precouplula stage; solid bars, ovigerous females. (c) *Microarthridion littorale*. Open bars, total; solid bars, ovigerous females.

(Elmgren, 1976; Ólafsson & Elmgren, 1991) features species commonly found in brackish water environments (Heip *et al.*, 1985), and appears typical of the northern Baltic Sea, as the same dominant nematode and harpacticoid species are found also at the west coast of Finland (Sarvala, 1971; Keynäs & Keynäs, 1978), and in the Gulf of Riga (P. Pallo, pers. comm.). The effect of the mild winter and early spring bloom of 1989 was to diminish the difference between spring and summer inputs of phytodetritus. Thus, conclusions based on 1989 and stressing the importance of the spring bloom in benthic annual dynamics are likely to be conservative when applied to more normal years.

All the major meiobenthic groups displayed significant seasonal variability, either for total abundance,

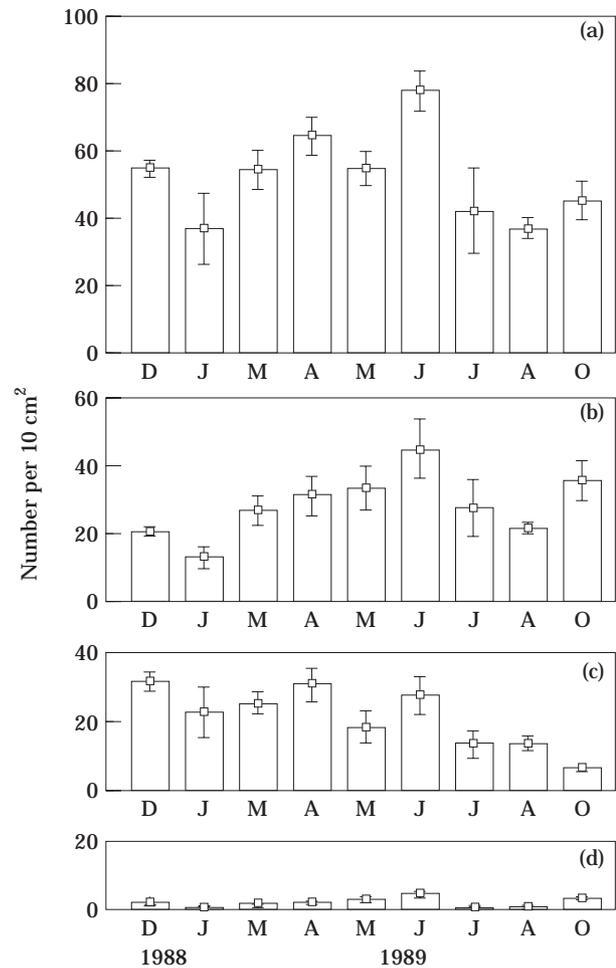


FIGURE 7. Average number of ostracods per 10 cm² ($n=5$) \pm 1 standard error for each sampling date. (a) Total ostracoda, (b) *Paracyprideis fennica*, (c) *Candona neglecta*, (d) *Heterocyprideis sorbyana*.

total biomass or in the abundance of some common species. In the Askö area, the spring bloom started uniquely early in 1989, at the beginning of March (Figure 1). Total number of nematodes showed a significant increase in abundance in May, 2 months after the onset of the spring bloom. It is unlikely that increasing water temperature is responsible for this pattern as the temperature at 35 m increased little from January to May, and did not peak until October (Figure 1). Furthermore, even though there was a peak in water temperature in October–November 1988, no increase in nematode numbers followed. At that time, primary production, chlorophyll *a*, diatom biomass and sedimentation were all lower than in the post-bloom period prior to the nematode increase in Spring 1989 (Figure 1). If nematodes were food limited, a time lag between the spring bloom sedimentation and peak abundance would be expected, but it

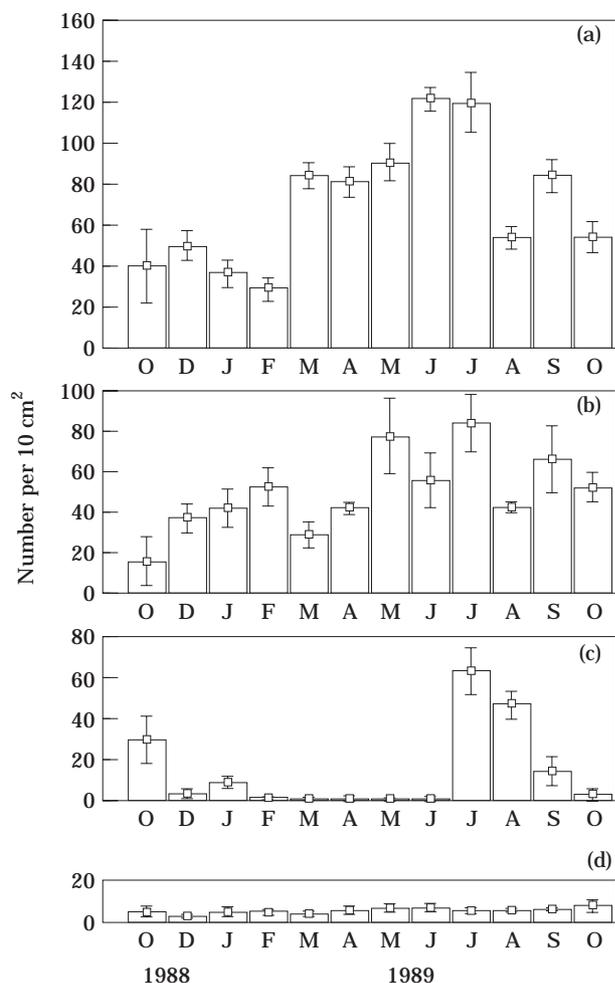


FIGURE 8. Average number per 10 cm² ($n=5$) ± 1 standard error of (a) Turbellaria, (b) Kinorhyncha, (c) *Macoma balthica* spat and (d) Priapulida for each sampling date.

is difficult to predict the length of such a lag, as few data exist on the effect of temperature on demographic characters of marine nematodes, and none on the effects of food availability (Heip *et al.*, 1985). During summer and early autumn, bottom water temperature continued its erratic rise (Figure 1), but meiobenthos declined, after reaching maximal abundance in June, and biomass in July. This is consistent with food being important in the earlier increase, since chlorophyll *a*, diatom biomass and sedimentation were all lower than during the spring bloom period (Figure 1). As in most field studies, the available evidence is circumstantial, stressing the need for experimental hypothesis testing concerning the causes of the observed patterns.

The major taxon responding most dramatically to the spring-bloom-derived phytodetritus input was the Nematoda, but an analysis at species level indicates

that both depth in the sediment and feeding mode influence the response of individual species to settling phytoplankton. Epistrate feeding nematodes that live close to the sediment surface may be expected to be the first to utilize settling phytoplankton. Rudnick (1989), who studied the assimilation of radio-labelled phytodetritus within the top 5 mm of sediment, proposed that meiobenthic animals reacted to deposition of phytodetritus in two ways, with surface feeders (top 2 mm, e.g. epibenthic harpacticoids, small nematodes) directly assimilating sedimented phytoplankton, and subsurface feeders (below 2 mm, e.g. larger nematodes, narrow harpacticoids) utilizing a more stable food resource, mainly composed of buried old organic matter (Rudnick, 1989). The present results support Rudnick's proposal in that nematodes in feeding groups known to live close to the sediment surface appeared to utilize the settling phytoplankton first, and increased most markedly in numbers. The present results show a clear increase in selective deposit feeders and epistrate feeders after the spring bloom. The increase in selective deposit feeders may be the result of increased numbers of bacteria and protozoa in the sediment following the spring bloom. While like Rudnick *et al.* (1985) and Rudnick (1989), the present authors found large nematodes dominating the deeper dwelling fauna, the present authors also found that the settling phytodetritus appears to have stimulated reproduction of the large-bodied diatom-feeding *Paracanthochus* spp. in the surface layer. The response of the nematode community to settling phytoplankton may, therefore, be better described in terms of relative importance of species belonging to the various feeding groups. A seasonal change in the relative abundance of nematode-feeding groups was noted by Tietjen (1969) in two estuaries in New England, where annual spring peaks in nematode densities were due to an increase in epigrowth feeders. Similarly, Hopper and Meyers (1967) found summer increases in epigrowth species in seagrass beds in Florida. Although seasonal variations of nematodes have been studied in subtidal areas of similar depth as in the current study (30–40 m), showing either significant increase during some part of the year (Soyer, 1971; Bovée & Soyer, 1974) or no significant changes at all (Fleeger *et al.*, 1989), the relative importance of different feeding groups has not often been assessed. However, Juario (1975) found no significant difference among months in the relative abundance of different feeding groups over a year at 35 m in the German Bight.

It is clear that the four, morphologically defined nematode feeding groups of Wieser (1953) can only approximate the true feeding behaviours of marine

TABLE 4. Average (n=5) dry weight (mg) per 10 cm², standard error (SE) and percentage of total dry weight for major taxa at Askö 1988-89

Taxon	1988												1989				Average	Sig. level	Tukey a posteriori test (min to max)
	Oct	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct							
Nematoda	mg	0.23	0.25	0.21	0.16	0.24	0.22	0.36	0.44	0.47	0.33	0.31	0.28	0.29	***	8902 8901 8904 8810 8903 8812 8910 8909 8908 8905 8906 8907			
	SE	0.05	0.03	0.03	0.01	0.02	0.01	0.05	0.06	0.05	0.03	0.03	0.01	0.03					
Ostracoda	%		21	23		21	18	27	26	27	26	27	24	**	8901 8907 8910 8905 8908 8812 8903 8904 8906				
	mg	0.52	0.34	0.34	0.07	0.55	0.58	0.39	0.77	0.39	0.43	^a 0.37	0.48	0.07					
Harpacticoida	SE	0.05	0.07	0.07	0.07	0.07	0.05	0.03	0.15	0.08	0.07	0.03	0.03	0.07					
	%	42	37			47	47	30	46	23	33	36	38	0.07					
Turbellaria	mg	0.13	0.28	0.19	0.41	0.13	0.18	0.25	0.09	0.20	0.17	0.20	0.16	0.20	***	8906 8810 8903 8910 8908 8904 8901 8909 8907 8905 8812 8902			
	SE	0.06	0.05	0.02	0.07	0.03	0.01	0.07	0.01	0.01	0.03	0.02	0.02	0.03					
Macoma spat	%	23	21			12	14	19	5	12	13	15	15	0.03					
	mg	0.09	0.11	0.08	0.07	0.19	0.18	0.20	0.28	0.27	0.12	0.19	0.12	0.16	***	8902 8901 8810 8812 8908 8910 8904 8909 8903 8905 8907 8906			
Other	SE	0.04	0.02	0.01	0.01	0.01	0.02	0.02	0.01	0.03	0.01	0.02	0.02	0.02					
	%	9	9			16	15	16	16	16	9	12	13	0.02					
Total	mg	0.08	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.17	0.12	0.04	0.01	0.04	***	8904 8905 8906 8903 8902 8910 8812 8901 8909 8810 8908 8907			
	SE	0.03	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.02	0.01	0.01					
Total	%	1	3			0	0	0	0	10	10	1	3	0.01					
	mg	0.06	0.06	0.06	0.06	0.04	0.08	0.11	0.11	0.21	0.12	0.10	0.10	0.09	**	8903 8812 8902 8901 8810 8904 8910 8909 8906 8905 8908 8907			
Total	SE	0.03	0.01	0.02	0.01	0.01	0.02	0.02	0.02	0.04	0.04	0.01	0.01	0.02					
	%	5	7			4	6	9	7	12	9	9	7	0.02					
Total	mg	1.24	0.91			1.16	1.24	1.31	1.69	1.71	1.29	1.04	1.29	1.29	***	8901 8910 8903 8812 8904 8908 8905 8906 8907			
	SE	0.12	0.08			0.10	0.04	0.05	0.12	0.10	0.09	0.06	0.08	0.08					

The results from one-way ANOVA and Tukey a posteriori test on time series data are presented.

Dates (first two figures indicate year and the last two figures indicate month) with common underline are not significantly different at the 95% significance level.

^aOstracods were not measured this month.

nematodes (e.g. Bouwman *et al.*, 1984; Jensen, 1987). Some species are borderline cases, e.g. *C. honestus*, with tiny teeth in a small buccal cavity, could be classified either as an epistrate feeder (2A) or as a selective deposit feeder (1A). There may be subgroups within feeding groups, e.g. within the selective deposit feeders (1a), one may find feeders on protozoa, bacteria, and even dissolved organic matter. Still, the different responses of nematodes belonging to these different feeding groups indicate that it is meaningful to use such a classification, and suggest that identification of nematodes at least to genus, and to feeding group, will allow more reliable evaluation of the response of nematode assemblages to environmental change.

A lack of response at major taxon level (see Fleeger *et al.*, 1989) may be misleading, if individual species within the taxon react differently to environmental change (Warwick *et al.*, 1988; Ólafsson, 1992), as illustrated by the two harpacticoid species in the present study. They displayed very different seasonal patterns of abundance, with *Pseudobrydya* sp. most abundant in winter and *M. littorale* most abundant in summer. In the Askö area, *M. littorale* seems to reproduce throughout the year, as in various other intertidal and subtidal areas (Coull & Vernberg, 1975; Fleeger, 1979; Palmer, 1980; Huys *et al.*, 1986). Many authors regard temperature as the main environmental control on the reproductive periodicity of harpacticoid copepods in the field (see Hicks & Coull, 1983 for review). However, the present results suggest that the spring bloom sedimentation triggered the increase in reproductive activity in *M. littorale*, leading to the peak in ovigerous females in April, as temperature remained low in the preceding month, while chlorophyll *a* concentration, diatom biomass and the rate of carbon sedimentation all had distinct peaks in March (Figure 1). Fleeger and Shirley (1990) found that the reproductive cycles in the dominant harpacticoid species in Auke Bay (Alaska) were related to the spring bloom sedimentation event, although densities of individual species were poorly related to sedimentation. It is more difficult to explain the pattern displayed by *Pseudobrydya* sp., i.e. a peak in the winter and low abundance in summer. A similar pattern occurs in the open Gulf of Bothnia, where this species is found in highest densities at the coldest time of the year, i.e. in the autumn (Widbom, pers. com.). Perhaps the simplest explanation is that this species is an arctic species, thus reproducing in cold water.

Other taxa showing possible influence from the spring bloom were: ostracods, with abundance and biomass at maximum in June; kinorhynchans, with highest abundance in May–June; and Turbellaria,

with a spring–summer maximum, where June–July were significantly higher than all autumn and winter months, except September (Figure 8). The summer peak in *M. balthica* spat was only to be expected from its normal life cycle, with settling in late June (cf. Ankar, 1980). The rapid disappearance of this peak is the first field confirmation of predictions from laboratory experiments, showing strong predation pressure on newly settled *M. balthica* spat from the deposit-feeding amphipod *Monoporeia affinis* (Elmgren *et al.*, 1986, as *Pontoporeia affinis*).

This analysis of the seasonal dynamics of Baltic meiobenthos indicates that the sedimentation of phytodetritus following the spring phytoplankton bloom is of great importance, not only for deposit-feeding Baltic macrobenthos, but also for some groups of the meiobenthos. Uitto and Sarvala (1991) have argued, based on energetic calculations, that the dominant deposit-feeding amphipods in the Baltic, *M. affinis* and *P. femorata*, cannot live predominantly on benthic micro-organisms, but must directly assimilate settled algal cells and phytodetritus derived from phytoplankton. The same seems likely for the groups of meiobenthos responding most rapidly to the spring bloom, based on the short lag time (1–2 months at 2–5 °C), and for nematodes based on the differential response of different feeding groups reported above. Since only some groups of the meiobenthos seem to respond directly to the sinking out of the spring bloom, this major carbon input is perhaps less crucial for meiobenthos as a whole than for deposit-feeding macrofauna. This agrees with field studies showing meiobenthos responding less dramatically than the macrobenthos to the north–south productivity gradient of the Baltic Sea (Elmgren, 1978; Elmgren *et al.*, 1986). In fact, some experimental studies have found relatively moderate responses in the meiobenthos assemblage as a whole to rather large manipulations of their food supply (Widbom & Elmgren, 1984; Austen & Warwick, 1995).

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