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Species specific uptake of radio-labelled phytodetritus by benthic meiofauna from the Baltic Sea

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ABSTRACT: The diatom *Skeletonema costatum* is one of the dominant phytoplankton species during spring in the northern Baltic Sea. We followed the uptake of radio-labelled *S. costatum* by all major meiofauna species in a laboratory experiment. The uptake of labelled diatom carbon varied greatly among major meiobenthic taxa and among species belonging to the same class or phylum. Both total uptake and uptake per unit biomass were by far highest in the ostracod *Candona neglecta* accounting for 46% of the total meiofauna uptake. The total uptake of ^{14}C was significantly different among all 3 common ostracod species, *Candona neglecta* taking 10 and 100 times more than *Paracyprideis fennica* and *Heterocyprideis sorbyana* respectively. Nematodes accounted for over 40% of the total uptake of ^{14}C in the microcosms, of which 84% was taken up by large nematode species such as *Paracanthonchus* spp. Nematodes with similar buccal cavities and of similar size showed surprisingly large differences in the uptake of the radio-labelled material. There seems to be quite strong selection both for and against the diatom among epistrate feeders as well as among so-called non-selective deposit feeders. Only a small portion of the total meiofauna population was found below 1 cm in the sediment; this was composed almost solely of nematodes. These nematodes assimilated as much ^{14}C per unit biomass as the surface ones did, which contradicts the hypothesis claiming that meiobenthic animals react in 2 ways to phytoplankton sedimentation, with surface feeders directly assimilating sedimented phytoplankton, while subsurface feeders experience a more stable food supply and rely only indirectly on sedimented phytoplankton.

KEY WORDS: Pelagic-benthic coupling · Food-web · Meiofauna · ^{14}C radio label

INTRODUCTION

Sedimentation of organic material from phytoplankton blooms often represents a considerable amount of annual benthic organic inputs (see Graf 1992 for a review). Only a few studies have addressed the importance of plankton blooms for meiobenthos. The results are contradictory, with several studies indicating no or only a slight response of meiofauna taxa to sedimented plankton material (e.g. Fleeger et al. 1989, Fleeger & Shirley 1990, Gooday et al. 1996, Webb 1996), while others indicate a tight link between spring bloom sedimentation and increase in the abundance or biomass of the meiofauna (e.g Goedkoop & Johnson 1996, Ólafsson & Elmgren 1997). Radziejewska et al. (1996) found that major meiofauna taxa significantly correlated with sediment pigments in an area of low primary production, while under conditions of abundant pelagic production no such relationship was evident.

Meiofauna are known to utilise food resources that are produced in the pelagic zone, either directly by feeding on sedimented algal cells, or indirectly by feeding on decomposing organic matter with associated bacteria (for reviews see: Hicks & Coull 1983, Heip et al. 1985, 1995). The diverse morphology of the mouth-parts of meiobenthic species has prompted researchers to classify these animals into various trophic groups. Wieser (1953), for instance, divided nematodes into 4 feeding categories depending on the armature of the buccal cavity, i.e. species with unarmed buccal cavities were considered as deposit feeders, either selective (small cavities) or non-selective (large cavities), and species with armed buccal cavities were considered as epistrate feeders or omni-

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vores/predators. Several authors have criticised this classification and made modifications by adding to and/or altering these 4 groups (Alongi & Tietjen 1980, Romeyn & Bouwman 1983, Schiemer 1984, Jensen 1987, Moens & Vincx 1997).

It appears that many meiofauna species feed selectively, which may give rise to interspecific food preferences (e.g. Van den Berghe & Bergmans 1981, Moens et al. 1996, Pace & Carman 1996). Diatoms are usually the major component of the phytoplankton spring blooms reaching the bottom. Radioactive tracer techniques have been used in many experiments dealing with diatom grazing rates of meiobenthos. Label has either been added directly into experimental units (i.e. sediment or water-column; Daro 1978, Montagna 1984, Rudnick 1989, Widbom & Frithsen 1995) or by prelabelling diatom cultures and then adding to experimental units (Decho 1986, Decho & Fleeger 1988, Pace & Carman 1996). Prelabelled material is particularly useful in testing food selectivity, but might give inaccurate estimates of overall grazing rates in the field (Moens & Vincx 1996). However, there are also several problems associated with the use of direct addition of radioactive label ($NaH^{14}CO_3$) for estimating selectivity and grazing rates of meiofauna, including absorption into surface tissues of grazers, ingestion of free label, homogenous label distribution, etc. (e.g. Montagna 1983, 1984, Carman et al. 1989, Carman 1990). Nonetheless the above-mentioned studies indicate species-specific uptake of diatoms among harpacticoid copepods (Decho 1986, Decho & Fleeger 1988, Pace & Carman 1996) and taxon-specific uptake by several major meiofaunal taxa (Montagna 1984, Rudnick 1989, Widbom & Frithsen 1995). Further, Austen & Warwick (1995) noted a decrease in diatom-feeding nematodes when diatoms were not offered as food for 16 wk, and Montagna et al. (1995) noted different responses among the major meiofauna taxa when diatoms were added to sediments.

During spring, in the cold waters of the northern Baltic Sea, the development of phytoplankton assemblages does not appear to be controlled by grazers, but rather by nutrient concentrations (Lignell et al. 1993). This results in a major build up of phytoplankton biomass, until availability of nitrogen and phosphorus becomes low, after which a large part of the bloom settles out (Kuparinen et al. 1984, Smetacek et al. 1984, Lignell et al. 1993). Although experimental evidence is lacking, the settling spring bloom material is probably a driving force for the benthic communities in the northern Baltic Sea, as it contributes the bulk of primary settling organic matter (i.e. not resuspended old material) on a yearly basis (Blomqvist & Larsson 1994).

In a field study at a 37 m deep station in the northwestern Baltic proper, Ólafsson & Elmgren (1997) found that both meiofauna biomass and abundance increased rapidly following the spring bloom, although this was both taxon and species specific. For example, almost twice as many nematodes, the most abundant metazoans, were found after, compared to before, the spring bloom. The common epistrate feeders *Paracanthonchus* spp. increased about 4-fold after the spring bloom, while the most abundant species, *Calomicrolaimus honestus* and *Leptolaimus elegans*, showed no significant seasonal variations. Furthermore, the highest numbers of the common deep-dwelling nematode, *Sabatieria pulchra* were found in autumn. The authors concluded that their results supported Rudnick's (1989) hypothesis that meiobenthic animals react in 2 ways to phytoplankton sedimentation, with surface feeders directly assimilating sedimented phytoplankton, while subsurface feeders experience a more stable food supply and rely only indirectly on sedimented phytoplankton.

Here we report on the first laboratory study in which the uptake of ^{14}C labelled diatoms by all major meiofauna species in a given area has been followed in intact cores. We chose to work with the diatom *Skeletonema costatum* as it is a dominant phytoplankton species in large areas of the Baltic Sea (e.g. Kononen et al. 1992), forms the major part of the settling spring bloom biomass (Heiskanen & Kononen 1994), and is easily cultured and labelled in the laboratory.

In this paper we specifically address the following questions: (1) Is there an interspecific difference in the assimilation of *Skeletonema costatum* among the major meiofaunal species? We expected that species within a given taxon (Ostracoda, Harpacticoida, etc.) would take up dissimilar amounts of this diatom. (2) Is there an inter- or intraspecific difference in the assimilation of *S. costatum* between the surface and the deeper living fauna? We expected relatively higher uptake by the surface living individuals. (3) Is there a difference in the uptake of *S. costatum* among the various nematode trophic groups? We expected that diatom feeders (*Paracanthonchus* spp. and *Chromadorita fennica*) would assimilate more than deposit feeders (*Sabatieria pulchra*) or predators (*Sphaerolaimus* sp.).

MATERIAL AND METHODS

Prior to the onset of the spring bloom, 6 Kajak cores (50 cm^2) were collected (21 March 1996) near the Askö Laboratory, in the northwestern Baltic proper (58°49'N, 17°38'E). The cores were retrieved from a 37 m deep muddy location, the same as in Ólafsson & Elmgren (1997), and stored in a thermoconstant room (4°C) in the dark. During storage individual cores were aerated

using an airstone. The cores were left for approximately 3 wk for the meiofauna to acclimatise; 2 wk before adding the diatoms the microcosms were completely filled with water, with no air phase, and connected to a 1500 ml water reservoir (Fig. 1). The water from the reservoirs was recirculated into the cores using peristaltic pumps; the residence time in the microcosms was 7.8 h. A preliminary experiment showed that the water in the cores was homogeneously mixed at this pumping rate. The water reservoirs were aerated; the outgoing air was washed in tubes filled with 25 ml Carbo-Sorb E (Packard) to retain outgoing CO_2.

The diatom *Skeletonema costatum* was cultured at 15°C in artificial seawater (Kester et al. 1967) at a salinity of 15‰, with added nutrients (*f*/2 plus Si; Guillard 1975) and 25% reduced $NaHCO_3$. Cultures were shaken manually once every 2 d. Algae were labelled by adding 0.34 mCi $NaH^{14}CO_3$ (Amersham; specific activity 54.0 mCi $mmol^{-1}$) to each culture flask 4 d after starting the culture. After an additional 7 d of incubation, the labelled algae were harvested by allowing them to settle for 5 h at 4°C in the dark in a separatory funnel. The labelled algae were washed by re-suspending them in clean medium and allowing them to settle again; this procedure was repeated twice. The final radioactivity in the diatoms was 0.38 mCi g dry wt^{-1}; this was measured by solubilizing dried algae overnight at 50°C in 80% Soluene-350 tissue solubilizer (Packard), adding 5 ml scintillation cocktail (Hionic-Fluor, Packard) and counting on a liquid scintillation counter (see below).

Two months after sampling cores (22 May), 3 ml diatom suspension containing 46.8 mg dry wt and a total activity of 2.8×10^7 DPM (disintegrations per minute) was added with a Pasteur pipette to each core, evenly distributing the algae over the whole sediment surface. Immediately after addition of the diatoms the CO_2 traps were connected. Radioactivity in the CO_2 traps was measured after 7 d, 9 d and 1 mo by taking a 1 ml sub-sample from the traps, adding 10 ml scintillation liquid (PermaFluor E+, Packard), and counting in a liquid scintillation counter (see below). The CO_2 traps were then filled with fresh CarboSorb. At the same time, two 1 ml water samples were taken from each water reservoir. To one of these samples 1 ml Carbo-Sorb was added to fix CO_2, to the other 1 ml of 1 N HCl to release CO_2. Water samples were counted in 10 ml Hionic-Fluor (Packard). Dissolved $^{14}CO_2$ in the water was calculated from the activity in samples with fixed and released CO_2; total released $^{14}CO_2$ was calculated from activity in the traps and dissolved $^{14}CO_2$.

On 18 June the experiment was terminated, 1 mo after the addition of algae. Each core was sectioned into 2 layers, 0 to 1 cm and 1 to 4 cm, and small sub-

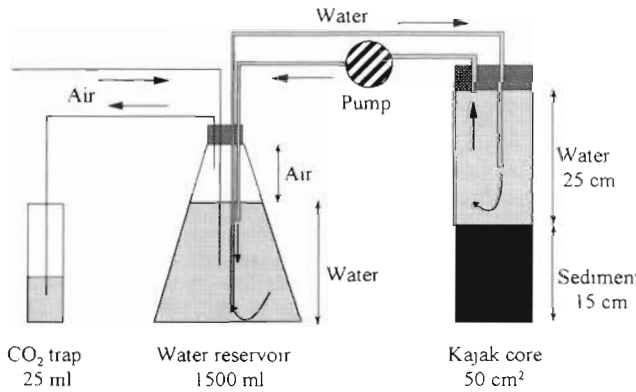

Fig. 1. Schematic illustration of the experimental set-up

samples (ca 3 g wet wt) were taken from both layers for radioactivity measurements in the sediment (see below). The rest of the sediment was then passed through 500 and 40 µm sieves, and the 40 µm screenings fixed in 4% formaldehyde solution for meiofaunal analysis. The meiofauna was extracted from the sediment using Ludox colloidal silica at a specific gravity of 1.15 (Ólafsson & Elmgren 1997). As extraction efficiency for ostracods is often low (Ólafsson & Elmgren 1997), the sediment was re-sieved (200 µm mesh), and all ostracods picked out. Animals retained on 40 µm sieves were enumerated, washed twice in distilled water by transferring them between watch-glasses and then placed in scintillation vials. Species or taxa were analysed separately for each Kajak core when the amount of radioactivity per group (at least 3 µg C) was sufficient; those taxa found at low biomasses were pooled until they reached at least 3 µg C. To facilitate collection of the larger nematode species, the meiofauna extracts were passed through 200 and 40 µm sieves. Prior to gathering the larger nematodes, species were enumerated under a 50× stereo microscope and in some cases under higher magnification. Biomass was estimated from a size-weight relationship (see Ólafsson & Elmgren 1997). Each nematode was classified as: adult male, adult female, gravid female or juvenile; the biomass was then estimated separately for each of these categories.

Sediment radioactivity was measured by solubilizing a small freeze-dried sample overnight at 50°C in 80% Soluene-350 (Packard), adding 10 ml Hionic-Fluor (Packard) and counting using a liquid scintillation counter (see below). Meiofauna samples were dried at 60°C overnight, and solubilized overnight at 50°C in 80% Soluene-350 (Packard); 5 ml Hionic-Fluor (Packard) was added to each sample. All radioactivity samples were counted with a LKB scintillation counter using a standard ^{14}C counting program. Quenching was corrected for each sample by measuring a quench-

ing parameter (SQP[E]) using an external standard, and calculating counting efficiency from a calibration curve obtained from quenched standard samples.

Abiotic uptake of label by ostracods was assessed in 2 formaldehyde-treated microcosms (750 ml Erlenmeyer flasks of 78.5 cm^2 bottom area, 1 cm deep sediment layer, connected to 1500 ml water reservoir, water recirculated) where meiofauna was killed prior to adding labelled algae. This uptake was compared with uptake in 6 microcosms without formalin. Both treatments ran for 1 mo.

Differences in assimilation among the various species/taxa were investigated by means of 1-way analyses of variance (ANOVA). Paired *a posteriori* comparisons were carried out with the Tukey test using 95% confidence limits. Prior to the ANOVA, all data were $\log_{10}(x+1)$ transformed and Cochran's *C*-test used to check the assumption of homoscedasticity.

Table 1. Average number per core, percentage, average individual size, percentage of total biomass, average, maximum and minimum specific organic carbon activity (DPM mgC^{-1}) and total ^{14}C uptake per core for the major meiofaunal groups and species. *Not estimated

Taxon/species	Depth	Abundance		Ind. size	Total biomass	DPM μgC^{-1}				Total uptake $core^{-1}$	
	(cm)	Avg.	%	(µgC)	(%)	Avg	Max	Min	n	DPM	%
Nematoda											
Sabatieria pulchra	0–1	421	7	0.32	21	5	17	2	6	674	8
Paracanthonchus spp.	0–1	329	5	0.16	8	22	40	7	6	1165	14
Axonolaimus spinosus	0–1	121	2	0.09	2	22	34	7	5	237	3
Eleutherolaimus stenosoma	0–1	104	2	0.04	1	0	–	–	1	0	0
Sphaerolaimus sp.	0–1	116	2	0.40	8	2	3	0.3	2	80	1
Chromadorita fennica	0–1	87	1	0.08	1	0	–	–	1	0	0
Desmolaimus zeelandicus	0–1	42	1	0.15	1	2	–	–	1	13	0.2
Other nematodes (<200 µm)											
Leptolaimus papilliger	0–1	1005	17	0.01							
Microlaimus globiceps	0–1	764	13	0.01							
Calomicrolaimus honestus	0–1	721	12	0.01							
Dichromadora sp.	0–1	612	10	0.05							
Leptolaimus elegans	0–1	480	8	0.01	13	7	9	4	6	562	7
Halalaimus sp.	0–1	87	1	0.03							
Daptonema sp.	0–1	44	1	0.01							
Monhystera sp.	0–1	44	1	0.01							
Campylaimus gerlachi	0–1	22	0.4	0.01							
Sabatieria pulchra	1–4	371	6	0.33	20	4	9	1	6	460	5
Paracanthonchus spp.	1–4	14	0.2	0.16	0	27	–	–	1	62	1
Sphaerolaimus sp.	1–4	10	0.2	0.28	0	1	–	–	1	3	0.03
Chromadorita fennica	1–4	7	0.1	0.17	0	0	–	–	1	0	0
Nematoda (<200 µm)	1–4	478	8	0.01	1	50	67	34	2	256	3
Nematoda total	0–4	5899	97		76					**3512**	**41**
Ostracoda											
Candona neglecta	0–1	16	0.3	1.7	4	147	460	25	6	3947	46
Heterocyprideis sorbyana	0–1	6	0.1	2.6	3	2	8	0.0	6	33	0.4
Paracyprideis fennica	0–1	20	0.3	2.8	9	6	18	1	6	336	4
Leptocythere lacertosa	0–1	0.2	0.0	0.6	0	43	–	–	1	5	0.1
Ostracoda total		42	1		16					**4321**	**50**
Harpacticoida											
Pseudobradya sp.	0–1	64	1	0.3	3	21	36	11	6	412	5
Microarthridion littorale	0–1	6	0.1	1.4	1	4	4	4	1	31	0.4
Harpacticoida total		70	1.2		4.5					**443**	**5**
Other groups											
Kinorhyncha	0–1	37	1	0.3	2	1	3	0.4	6	15	0.2
Macoma balthica (spat)	0–1	3	0.0	1.2	1	67	122	37	5	247	3
Oligochaeta	0–1	0.5	0.0	10.4	1	0.3	0.3	0.3	1	1	0.0
Priapulida	0–1	0.5	0.0	*	–	–	–	–	1	1	0.0
Turbellaria	0–1	9	0.1	*	–	–	–	–	3	52	1
Other groups total		50	0.8		–					**316**	**4**

RESULTS

Composition

Total number of meiobenthic animals in the cores was on average 1212 ind. $10\,cm^{-2}$. Apart from the nematodes, all groups were primarily confined to the 0 to 1 cm sediment layer. Nematodes were the dominant major taxon comprising on average 97% of the total abundance (Table 1). Most of these occurred in the 0 to 1 cm layer (83%) where small nematodes, *Leptolaimus papilliger*, *L. elegans*, *Microlaimus globiceps* and *Calomicrolaimus honestus*, dominated. Of the larger nematodes *Sabatieria pulchra* occurred in similar numbers in both sediment layers, while other species were more abundant in the upper layer (Table 1). Harpacticoid copepods and ostracods were found in low numbers or on average 14 and 8 ind. $10\,cm^{-2}$, respectively. Nematodes, ostracods and harpacticoids comprised 76, 16 and 4% of the total biomass, respectively. The large nematode species contributed more than 60% of the total meiofauna biomass. In terms of biomass, *S. pulchra* was by far the most important meiofauna species, contributing over 40% of the total meiofauna biomass. Other groups were found in low numbers and contributed less than 5% to the total biomass.

^{14}C uptake

We accounted for 80% of the total label added, of which 34% was released as $^{14}CO_2$ (half of this was released in the first 7 d), 1% was found as dissolved organic carbon, 55% remained in the sediment (52% from 0 to 1 cm, 3% from 1 to 4 cm) and only 0.04% was stored in meiofauna tissue.

The uptake of labelled diatom carbon varied greatly among major meiobenthic taxa and among species belonging to the same class or phylum (Table 1). Both total uptake and uptake per unit biomass were by far the highest in the ostracod *Candona neglecta*, accounting for 46% of the total meiofauna uptake. The radioactivity was much lower in other ostracods, apart from a single individual of *Leptocythere lacertosa* in which the radioactivity was relatively high (Table 1). There was a highly significant difference among the non-nematode species (ANOVA, $p < 0.001$, Fig. 2) in both total uptake and the specific organic carbon activity (SOCA: DPM μgC^{-1}). The total uptake of ^{14}C was significantly different among all 3 common ostracod species, *Candona neglecta* taking up 10 and 100 times more than *Paracyprideis fennica* and *Heterocyprideis sorbyana*, respectively (Tukey test, $p < 0.01$). Although the bivalve *Macoma balthica* took up in total about 10 times less ^{14}C than *C. neglecta*, the specific activity was not significantly different among these species (Tukey test, $p > 0.05$). The harpacticoid *Pseudobradya* sp. showed a higher SOCA than did the 2 ostracod species *Paracyprideis fennica* and *Heterocyprideis sorbyana*, but lower than *M. balthica* and *C. neglecta* (Tukey test, $p < 0.05$, Fig. 2).

Nematodes accounted for over 40% of the total meiofaunal uptake of ^{14}C in the cores, of which 84% was taken up by the large nematode species (Table 1). There was a significant difference in total ^{14}C among the nematode species (ANOVA, $p < 0.05$, Fig. 2). *Paracanthonchus* spp. took up on average more ^{14}C than other species though this was only significant in comparison with *Axonolaimus spinosus* (Tukey test, $p < 0.01$, Fig. 3). The SOCA was variable among species. In 2 species, *Chromadorita fennica*, and *Eleutherolaimus stenosoma*, there was no measurable uptake of radioactivity (Table 1). *A. spinosus* and *Paracanthonchus* spp. from the upper layer reached about a 4 times higher SOCA (ANOVA, $p < 0.001$, Tukey-test, Fig. 3) than did *Sabatieria pulchra* (in either 0 to 1 or 1 to 4 cm depth layer). *S. pulchra* showed similar SOCA in both layers, and total uptake was not significantly

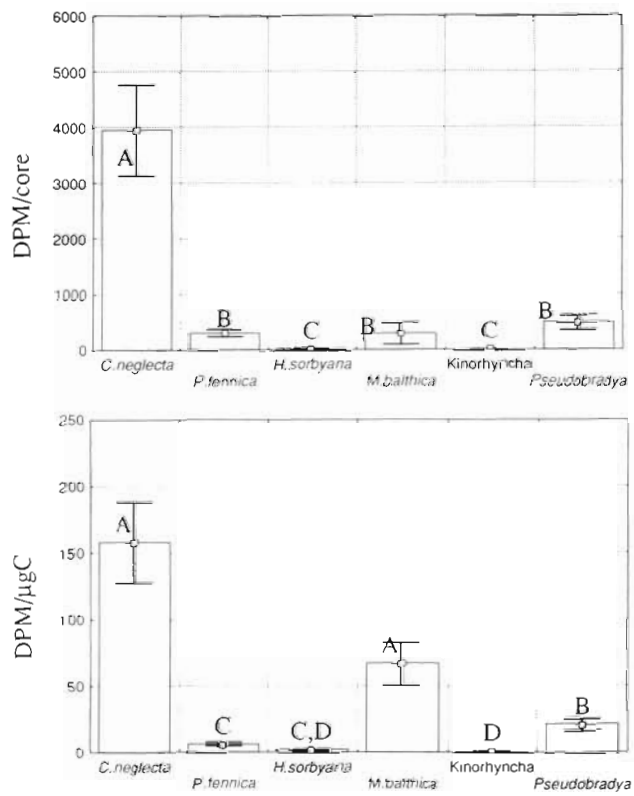

Fig. 2. Average (n = 6, for all but *Macoma balthica* [n = 5]) ^{14}C uptake for the major non-nematode species/taxa in the 0 to 1 cm layer in the mesocosms. Common letter codes indicate no significant difference (Tukey test). (DPM: disintegrations per minute)

different between the 2 layers (ANOVA, $p > 0.05$, Tukey-test, Fig 3). The few *Parcanthonchus* spp. found in the deeper layer had very similar SOCA as the surface population. Even though SOCA was about 2 times higher on average in the smaller nematodes in the deeper layer compared to the top layer this was not significant (Mann-Whitney *U*-test, $p > 0.05$).

DISCUSSION

This study clearly demonstrates that there are major interspecific differences in the assimilation of labelled material among the meiofauna species from the Baltic Sea. These differences occurred within all the major taxonomic groups in our experiment. The ostracod *Candona neglecta* accounted for almost half of the total meiofauna assimilation of the labelled material although it accounted for only 4% of the total meiofaunal biomass. This species is widely distributed throughout Europe, N Africa and Britain (Henderson 1990), and is abundant in the Baltic proper (Ólafsson & Elmgren 1997). Little is known about its feeding habits,

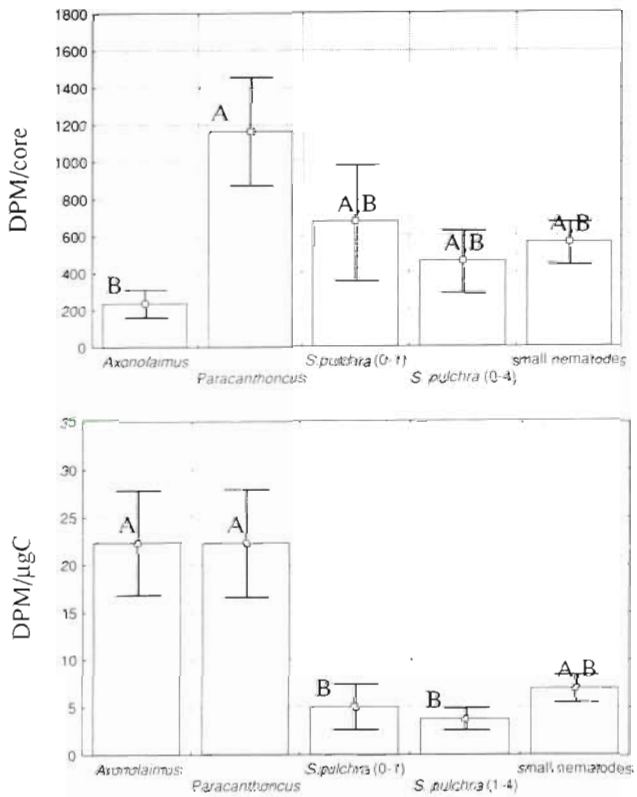

Fig. 3. Average (n = 6, for all but *Axonolaimus spinosus* [n = 5]) ^{14}C uptake for the major nematode species in the mesocosms. Only *Sabatieria pulchra* is presented from the 1 to 4 cm layer. Common letter codes indicate no significant difference (Tukey test)

but ostracods in general eat a wide spectrum of both dead and living material, with diatoms representing a particularly common type of food (Athersuch et al. 1989, Henderson 1990). This study indicates that diatoms are a major food resource for *C. neglecta* after the settling of phytodetritus during spring.

The ostracods comprise the largest individuals of all the meiofauna taxa in the northern Baltic proper, and often contribute more than other taxa to the total biomass, they are more or less confined to the top 1 cm sediment layer (Ólafsson & Elmgren 1991, 1997) and seem to be efficient feeders on detrital matter (laboratory observations). In 2 previous studies relatively high SOCA has been reported in ostracods (Rudnick 1989, Widbom & Frithsen 1995). Therefore it was not surprising to note that these animals as a group were so efficient in assimilating the labelled material. However, the interspecific variation in the uptake of labelled material was not expected. There could be several reasons for this, one being little vertical separation. Such fine scale vertical stratification of meiofauna species has been found for both nematodes and harpacticoids, several species of which show clear segregation within the top 1 cm (Joint et al. 1982, Warwick & Gee 1984, Fleeger et al. 1995). If *Candona neglecta* lives in the top millimeters of the sediment and the other 2 common ostracod species a few millimeters below, microhabitat location would obviously help to explain the interspecific difference we found. We have no data to support this speculation, however, and the study of other forms of resource partitioning may provide a better explanation for our results, e.g. food selection.

The few *Macoma balthica* spat in the microcosms also had high SOCA, comparable to *Candona neglecta*. In muddy substrates *M. balthica* is a deposit feeder, gathering food particles on the sediment surface (Hulscher 1973) and utilising detritus, microflora and microfauna as food (Newell 1965, Fenchel 1972, Tunnicliffe & Risk 1977). Adults and juveniles seem to feed on similar sources, as intraspecific competition over food resources has been demonstrated in the laboratory (Bonsdorff et al. 1986, Ólafsson 1989). Our results therefore substantiate that these juveniles are feeding on surface material. The low SOCA of the kinorhynchs is in accordance with Rudnick (1989) and Widbom & Frithsen (1995).

As a group the nematodes took up almost as much ^{14}C as the ostracods, but uptake was highly variable among species. *Paracanthonchus* spp. and *Axonolaimus spinosus* had much higher carbon-specific activity in their bodies than other nematodes. This was expected in the case of *Paracanthonchus* spp. as these nematodes showed a very clear increase in abundance after the settling of spring bloom material in a field study from the same site, i.e. Askö area (Ólafsson &

Elmgren 1997). Further, the structure of their buccal cavity (Fig. 4) places them in a group of nematodes that have been classified as epistrate feeders (Wieser 1953). These primarily feed on diatoms (Heip et al. 1985), either by cracking or piercing the cells with a large dorsal tooth, before sucking up the contents (e.g. Nehring 1992, Moens & Vincx 1997). Another common relatively large epistrate feeder in the Askö area, *Chromadorita fennica*, was expected to utilise the diatoms as well, but clearly did not in our experiment. It is about half the size of *Paracanthoncus* spp. (Fig. 4) and perhaps too small to handle the *Skeletonema costatum* cells. We believe that this nematode selects some other phytal species which may be more easily eaten. For instance Jensen (1982) described how a species of the same genus, *Chromadorita tenuis*, brings one end of the pennate diatom *Nitzschia* sp. into the buccal cavity and then breaks it open, after which it sucks out the contents. We do not consider it likely that this species was scraping significant amounts of bacteria or other micro-organisms from the sediment grains, as some epistrate feeders do (e.g. Moens & Vincx 1997), because no radioactivity was recorded at all in *C. fennica*. In contrast small nematodes, which are unable to eat diatoms, accumulated considerable radioactivity which must have originated from the uptake of radioactive micro-organisms or dissolved organic matter. The relatively high radioactivity in *A. spinosus* was not expected, as this species has no teeth in its buccal cavity (Fig. 4) and, therefore, is obviously not adapted to piercing or cracking diatoms. Moreover, though this species is quite common in the Baltic proper, it is usually found in low abundance and did not display significant variation among seasons ($p > 0.05$, Fig. 5) (data from Ólafsson & Elmgren 1997). It has a rather large buccal cavity and, hence, belongs to the non-selective deposit feeders (Wieser 1953) like other common nematodes from the Baltic proper, e.g. *Sabatieria pulchra*, *Eleutherolaimus stenosoma* and *Desmolaimus zeelandicus* (Fig. 4), all of which had much lower radioactivity in their bodies. Nonetheless diatoms are an important food resource for several representatives of deposit feeders (Moens & Vincx 1997), which ingest diatoms entirely and digest them as they pass through the intestine (Nehring 1992). However *A. spinosus* might also have been feeding on micro-organisms as well as dissolved organic matter. So among the so-called non-selective deposit feeders, there appears to be selection both for (in *A. spinosus*) and against (in *E. stenosoma)* certain food items in the Baltic Sea. Thus, classification of nematodes in feeding categories based on the morphology of the buccal cavity alone is not altogether reliable. Empirical data show that there is considerable variation within each feeding category (e.g. Jensen 1987, Moens & Vincx 1997), and it seems to us that much more data are needed on the feeding habits of individual nematode species before an ecologically valid grouping of nematodes into feeding categories can be attempted.

We hypothesized that animals in the top 1 cm layer should display higher SOCA levels than the deeper living animals. This assumption was not borne out by the results, which contradicts Rudnick's (1989) hypothesis. He postulated that meiobenthic animals react in 2 ways to phytoplankton sedimentation, with surface feeders directly assimilating sedimented phytoplankton, while subsurface feeders experience a more stable food supply and rely only indirectly on sedimented phytoplankton. The nematode *Sabatieria pulchra* was found in similar numbers in both sediment layers, with

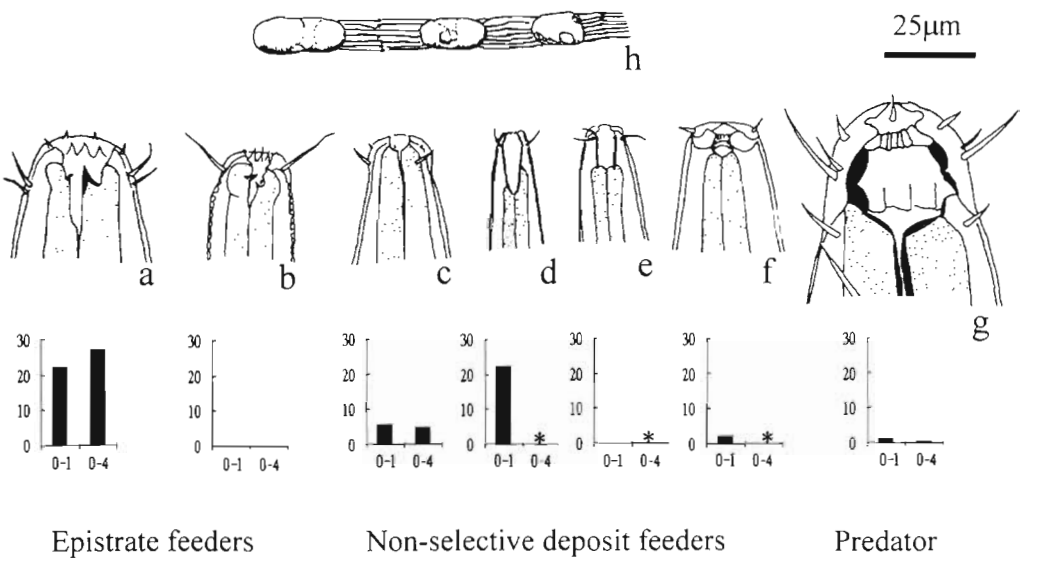

Fig. 4. The buccal cavity of the 7 most common large (retained on 200 µm sieve) nematodes in the Kajak cores. (a) *Paracanthonchus* spp., (b) *Chromadorita fennica*, (c) *Sabatieria pulchra*, (d) *Axonolaimus spinosus*, (e) *Eleutherolaimus stenosoma*, (f) *Desmolaimus zeelandicus*, (g) *Sphaerolaimus* sp. The diatom *Skeletonema costatum* (h) is drawn to scale. Bar diagrams display the average DPM μgC^{-1} for each of the species in the 2 depth layers. *Not estimated

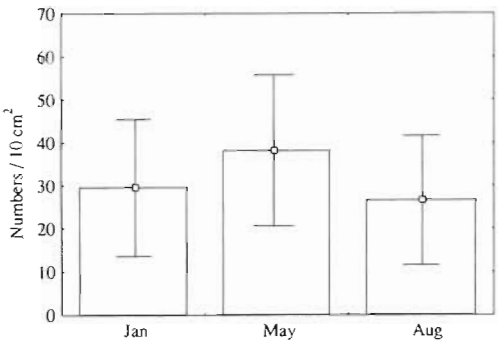

Fig. 5. *Axonolaimus spinosus*. Average numbers (±SE; n = 5) of the nematode from 3 different seasons: January, May and August 1989 from the field station at Askö

no significant difference between layers in the SOCA levels determined in tissues. This species is typically found at depths near the redox potential discontinuity (RPD) layer and has shown tolerance to long periods of oxygen deficiency (Wieser & Kanwisher 1961, Jensen 1981, 1983, Warwick & Gee 1984, Ólafsson 1992, Hendelberg & Jensen 1993, Modig & Ólafsson 1998). We have noted in the laboratory that freshly fixed individuals placed in brackish water regurgitate considerable amounts of ciliates (Ólafsson & Dragas pers. obs.). We therefore suspect that the diatoms were partly broken down by micro-organisms and that the label entered these nematodes via the microbial community, possibly by feeding on ciliates. One can envisage a similar scenario for the small nematodes, which, due to their small buccal cavities, must feed upon micro-organisms or dissolved organic matter. Though we did not identify the small nematodes from the deeper layer it is likely that these were mainly *Leptolaimus elegans* and *L. papilliger*, as these tend to dominate deeper layers in the field (Ólafsson & Elmgren 1991) and show high tolerance toward oxygen deficiency in the laboratory (Modig & Ólafsson 1998). Both are best described as microvores (sensu Moens & Vincx 1997), with minute mouth openings (1 to 2 µm), unable to capture objects larger than bacteria (Romeyn & Bouwman 1983). The radioactive material, 3% of the total measured in the sediment, may have reached the deeper layers by various different processes, such as meiofaunal burial (e.g. Webb & Montagna 1993), migration of micro- and meiofaunal organisms or by passive transport of dissolved organic carbon.

The lack of a significant difference between surface and deeper living nematodes may also be explained by vertical migration in the sediment during the course of the experiment. It is plausible that some of the nematodes isolated from the deeper layers spent some time feeding in the surface layer. However, we have no data to substantiate such migration for the species in question.

A passive 'uptake' of label by the meiofauna is always possible via absorption and adsorption of the radioactive material. Also, uptake of dissolved organic matter by epibiotic bacteria associated with meiofauna can vary dramatically among species (Carman 1994, Carman & Dobbs 1997). However we do not believe that this was important in the present experiment because of the following. (1) In experimental units, where meiofauna were killed with formalin prior to adding the radioactive material, the SOCA was similar among ostracod species and was a small fraction of the SOCA found in experimental units where meiofauna were not killed with formalin (Table 2). (2) In closely related species SOCA was often found to be very different. (3) The sediment in the 1 to 4 cm layers had about 17 times lower radioactivity than in the 0 to 1 cm layers, but the assimilated label and SOCA in nematodes was not higher in the upper layer.

Even though more than 50% of the added diatom carbon was still in the sediment and only 0.04% was stored in the tissues of meiobenthic animals after 1 mo, the sedimentation of *Skeletonema costatum* could be of major significance for the meiobenthic community. Clearly meiofauna processed much more than 0.04% of the labelled diatoms when taking into consideration meiofaunal respiration, multiple gut passage times and meiofaunal mortality over the 1 mo experiment. Further a considerable part of the label may be lost due to fixation in formaldehyde (Moens & Vincx 1996). Even 3 mo after settling, a large proportion of the diatoms may still be present in the sediment (van de Bund et al. unpubl.), which is in agreement with many laboratory studies from other areas (e.g. Andersen & Kristensen 1992, Fitzgerald & Gardner 1993, Gullberg et al. 1997). This material may thus fuel the benthic communities at relatively constant rates over longer periods, especially the microvores. This appears to be the case for several dominant nematode species in the Askö area, where a slight increase in numbers after the spring bloom and then a gradual decrease during the rest of the year have been noted (Ólafsson & Elmgren 1997).

Table 2. Average specific organic carbon activity for (SOCA) 3 common ostracod species in formalin-treated microcosms (n = 2) and in microcosms not treated with formalin (n = 5)

Species	With formalin DPM µgC^{-1}	Without formalin DPM µgC^{-1}
Paracyprideis fennica	2.24	28
Heterocyprideis sorbyana	1.40	10
Candona neglecta	3.75	643

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