

## Settling blooms of filamentous cyanobacteria as food for meiofauna assemblages

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### Abstract

Summer blooms of filamentous nitrogen-fixing cyanobacteria in the Baltic Sea are normally dominated by *Aphanizomenon* sp. and the toxin-producing *Nodularia spumigena*. In a 2-week laboratory experiment, we followed the uptake by representative benthic meiofauna species of  $^{14}\text{C}$ -labeled organic carbon from blooms, each dominated by one of these cyanobacteria. Natural bloom material was collected and labeled by incubation with  $\text{NaH}^{14}\text{CO}_3$ . Uptake of cyanobacterial carbon was recorded for the major meiofauna taxa living in the first-centimeter layer, namely ostracods, harpacticoids, and nematodes. The uptake rates were within the range found for diatoms in other studies, indicating that cyanobacteria may be an important food resource for the meiobenthos. The uptake of cyanobacterial carbon varied significantly among species, even within the same class. The ostracod *Candona neglecta* showed the highest uptake values, whereas two other ostracod species took up very little of the label. There was no significant difference in utilization of carbon from *Aphanizomenon* sp. and *N. spumigena* and no reduction in the abundance of the meiofaunal taxa analyzed compared to unexposed controls, indicating that Baltic meiofaunal assemblages in general experience no mortality when exposed to settled cyanobacteria, even the hepatotoxic *N. spumigena*.

The study of food webs and the trophic relationships that characterize them are essential for understanding an ecosystem. Marine soft-bottom sediments constitute the second largest ecosystem on Earth and are mainly found below the photic zone. Benthic communities inhabiting these sediments must feed primarily on allochthonous organic matter derived from settling and seasonal phytoplankton blooms (Elmgren 1978; Graf 1992; Ólafsson and Elmgren 1997). This energy supply to the benthic community and the processes that decompose the settled organic matter are among the fundamental factors shaping the benthic ecosystem.

Meiofauna play an important role in the benthic food web through the breakdown of organic material and nutrient regeneration (Coull 1999) as a result of their feeding on sedimented algal cells and their associated bacteria (Hicks and Coull 1983; Heip et al. 1995; Ólafsson et al. 1999). However, the meiobenthic food web dynamics and its response times to phytoplankton bloom sedimentation are not fully understood. Several studies show evidence of important interspecific differences in how meiobenthos react to inputs of settling blooms (Rudnick 1989; Ólafsson and Elmgren 1997; Ólafsson et al. 1999). These studies have yielded conflicting conclusions with regard to whether interspecific time lags between phytoplankton sedimentation and meiofauna production exist

and with regard to whether or not they are due to utilization of different fractions of organic matter (Rudnick 1989) or to differences in sediment mixing rates (Moens et al. 2002).

In the Baltic Sea, the spring bloom has been considered the most important bloom event, providing most of the annual new production and input to the benthos (Elmgren 1978). However, some literature suggests that cyanobacterial summer blooms, generally dominated by the species *Aphanizomenon* sp. and *Nodularia spumigena*, may play a more important role in the Baltic food web than previously thought. Cyanobacteria-dominated summer blooms were until recently thought to be to a large extent disintegrated and mineralized by bacteria and heterotrophic flagellates in the microbial loop (Sellner 1997). Nevertheless, a number of studies in the Baltic have provided evidence of sedimentation of significant quantities of organic matter derived from blooms dominated by *Aphanizomenon* sp. (Heiskanen and Kononen 1994; Tallberg and Heiskanen 1998), and Gustafsson et al. (2004) showed that sediment trap collections may significantly underestimate the sedimentation rates of summer blooms of cyanobacteria. The presence in sediments of cyanobacterial pigments (Bianchi et al. 2000, 2002) and of the toxin nodularin, produced by *N. spumigena* (Mazur-Marzec et al. 2007) in considerable quantities, together with the light nitrogen isotopic composition of sediments of the central Baltic proper (Bianchi et al. 2000; Voss et al. 2005) also indicate a considerable input of organic matter derived from cyanobacteria to the benthic ecosystems of the Baltic. Hence, there is a need to clarify how such inputs are incorporated in the benthic food web. Although benthic ostracods have been suggested to be able to utilize newly settled blooms of *Aphanizomenon* sp. (Limén and Ólafsson 2002), there is still a lack of understanding of how and to what extent these organic matter inputs are processed by the benthic meiofauna community.

*N. spumigena* produces the hepatotoxin nodularin, a toxin closely related to the microcystins that can cause toxic

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effects in vertebrates at low levels of exposure (Sivonen and Jones 1999). Although the effects of feeding on *N. spumigena* and consequent exposure to nodularin have been documented for the zooplankton community (Engström et al. 2000; Engström-Öst et al. 2002) and to a lesser extent in some benthic fish and bivalves (Lehtonen et al. 2003; Sipilä et al. 2006), their effects on benthic meiofauna are unknown, and meiofaunal feeding on *N. spumigena* has not yet been studied. On the other hand, even though it can produce neurotoxins in freshwater environments, *Aphanizomenon* sp. is not known to be toxic in the Baltic Sea (Sivonen et al. 1989; Stal et al. 2003).

In this paper we follow the uptake by the major meiofaunal taxa in the Baltic Sea of radiolabeled organic carbon from the two most common cyanobacteria in the Baltic Sea, *N. spumigena* and *Aphanizomenon* sp., in intact sediment cores incubated in the laboratory. We specifically address the following questions: First, can exposure to and assimilation of organic matter from the toxic cyanobacterium *N. spumigena* increase mortality in meiofauna assemblages? Second, do common meiofaunal species feed on simulated blooms of *N. spumigena* and *Aphanizomenon* sp.? Third, are there interspecific differences in the assimilation of the cyanobacterial summer blooms among the major meiofaunal taxa?

## Methods

**Collection and labeling of cyanobacteria**—A natural cyanobacterial bloom dominated by *Aphanizomenon* sp. was sampled in Himmerfjärden bay in the Baltic proper on 05 July 2005 (Fig. 1). The next day an extensive natural bloom dominated by *N. spumigena* was sampled in the open Baltic proper, near the Landsort deep (Fig. 1). After collection with a 90- $\mu\text{m}$  mesh plankton net, the cyanobacteria were repeatedly separated from the zooplankton in a light funnel (a black funnel lighted from below). After 1 h most zooplankton was found at the bottom of the funnel and the buoyant cyanobacteria at the top. The cyanobacteria were then incubated at 18°C with added nutrients (modified f/2 medium) for labeling with a total of  $3.4 \times 10^{-7}$  Bq of  $\text{NaH}^{14}\text{CO}_3$  (DKI: specific activity  $1.9 \times 10^{-9}$  Bq  $\text{nmol}^{-1}$ ). *N. spumigena* was harvested after 6 d and *Aphanizomenon* sp. after 7 d of incubation. The cyanobacteria were sieved through 90- $\mu\text{m}$  and 40- $\mu\text{m}$  sieves and rinsed with approximately 1 liter of brackish water ( $6 \text{ g L}^{-1}$ ) to remove nonincorporated radioactivity. The radioactivity present in this rinsing water was measured after the addition of 5 mL of Ultima Gold XR. Only 0.06% of the radioactivity incorporated in the cyanobacteria was found in the rinsing water, indicating that very little nonincorporated radioactivity was present in the interstitial water between the cyanobacterial filaments after the rinsing. Samples of the cyanobacteria were dried for 24 h at 60°C and analyzed for carbon:nitrogen (C:N) ratio, phosphorus (P) content, and radioactivity uptake by pipetting 400  $\mu\text{L}$  of the solutions onto pre-dried GFF filters. C and N content was analyzed with a Leco-CHN analyzer with ethylenediaminetetraacetic acid as standard. P content was determined according to the method of Larsson et al.

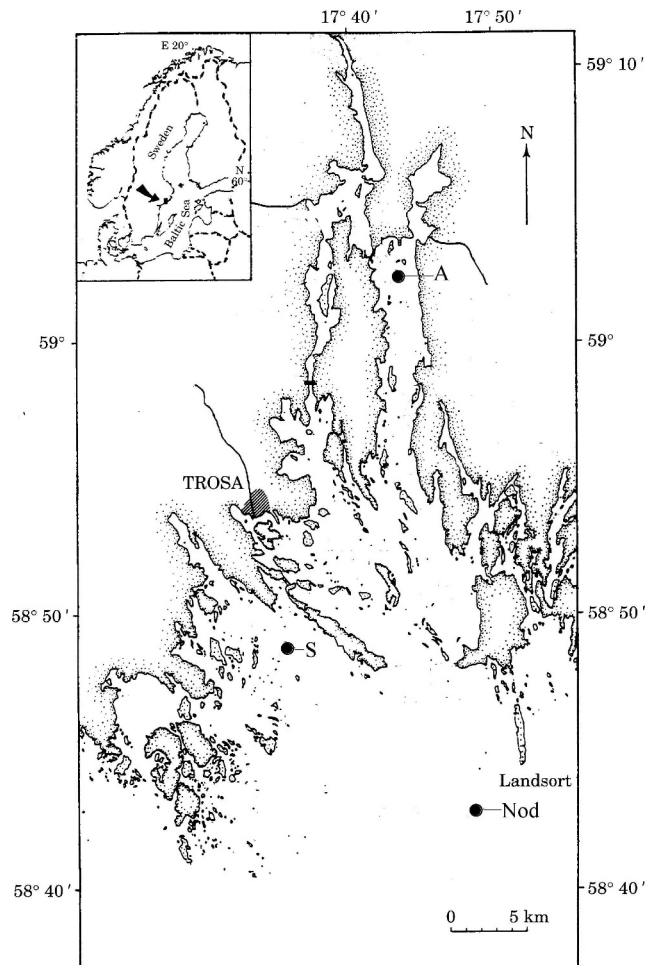


Fig. 1. Map of the Baltic Sea, with stations (A, Nod, and S) for sampling in the northern Baltic proper (A = *Aphanizomenon* sp.; Nod = sampling station for *Nodularia spumigena*, and S = sediment cores).

(2001). Radioactivity was measured in a liquid scintillation counter (LKB Wallac) after the addition of a scintillation cocktail (Ultima Gold, Packard). The final radioactivity of the suspensions was  $10.4 \pm 0.37$  Bq  $\text{mg dry wt}^{-1}$  for *N. spumigena* and  $13.7 \pm 0.73$  Bq  $\text{mg dry wt}^{-1}$  for *Aphanizomenon* sp. Additional samples of the cyanobacterial suspension were preserved in Lugol's solution for taxonomic identification under a microscope at 10 $\times$  and 50 $\times$  magnification. After sieving and rinsing, the concentrated cyanobacterial suspensions were frozen at  $-20^\circ\text{C}$  until the start of the experiment.

**Collection of natural Kajak cores and addition of cyanobacteria**—We collected 20 sediment cores with a surface area of 50  $\text{cm}^2$  using a Kajak corer (Blomqvist and Abrahamsson 1985) at a 27-m-deep site in Hällsviken in the Baltic proper (Fig. 1). The cores were kept aerated for 2 weeks at 5°C under a faint green light (obtained with a green filter involving a normal lamp) with a light intensity lower than  $1 \mu\text{E cm}^{-2}$  (measured with a Cognis photometer) in 16:8 light:dark cycle until the start of the experiment.

The experiment had three treatments: First, cores with added bloom material dominated by *N. spumigena* (*Nodularia* treatment); second, cores with the addition of bloom material dominated by *Aphanizomenon* sp. (*Aphanizomenon* treatment); and third, cores without the addition of cyanobacteria (controls). Five extra cores were used to estimate initial meiofaunal densities at the start of the experiment (initials).

Before addition to the cores, the cyanobacterial bloom material was mixed with 1.94 g wet weight of sediment sieved with a 500- $\mu\text{m}$  sieve from the station at which the Kajak cores were collected in order to facilitate its settling on the sediment surface. After homogenization, we added bloom material corresponding to 1.37 g C m<sup>-2</sup> for the *Aphanizomenon* and 1.97 g C m<sup>-2</sup> for the *Nodularia* treatment, which is within the range reported in the literature for sedimenting cyanobacterial blooms (Tallberg and Heiskanen 1998). The cyanobacteria were spread evenly over the surface of each core with a Pasteur pipette and left to settle for 12 h, after which each microcosm was covered with parafilm and the aeration restarted. The same weight of sieved sediment was added to the control and initial cores. Immediately after the addition of the bloom material to the cores, the cores for estimating initial meiofaunal densities were sectioned into two layers (0–1 cm and 1–4 cm) and preserved in 4% formalin.

*Termination of experiment and sample processing*—After 2 weeks the experiment was terminated and each core was sectioned with a modified device (Blomqvist and Abrahamsson 1987) into 0–1-cm and 1–4-cm layers and preserved in 4% formalin. Sediment subsamples from both layers and 5-mL water samples from the middle of each replicate's water column were taken for radioactivity measurements. The sliced sediment was sieved through 500- $\mu\text{m}$  and 40- $\mu\text{m}$  sieves. The meiofauna was extracted from the 40- $\mu\text{m}$  sediment fraction using Ludox colloidal silica at a specific gravity of 1.15 (Ólafsson et al. 1999); this procedure was repeated three times. The remaining sediment was again sieved through a 160- $\mu\text{m}$  sieve and checked for ostracods under a 50 $\times$  binocular stereomicroscope, since low extraction efficiency has been reported for this faunal group (Ólafsson et al. 1999). Extracted meiofauna were sorted, counted, and identified to major taxa or to species level for harpacticoids, ostracods, and some nematode taxa under a 50 $\times$  binocular stereomicroscope; meiofauna were then washed in distilled water. Ostracods retained on the 500- $\mu\text{m}$  sieve were also counted as meiofauna.

Individuals of three ostracod species (*Candona neglecta*, *Heterocyprideis sorbyana*, and *Paracyprideis fennica*), two harpacticoid species (*Pseudobryadia artica* and *Microarthridion littorale*), and four nematode taxa (*Paracanthocheilus* spp., *Sabatieria pulchra*, *Desmolaimus* spp., and *Axonolaimus spinosus*) were picked out for <sup>14</sup>C uptake analysis. When possible, sufficient numbers of each of these taxa to collect around 20  $\mu\text{g}$  dry weight of biomass were placed on a pre-dried 0.2- $\mu\text{m}$  filter with a drop of distilled water. These filters were dried for 24 h at 60°C, weighed, and placed in a scintillation vial. To facilitate collection of large

nematodes the meiofauna extracts were passed through a 160- $\mu\text{m}$  sieve and retained nematodes were picked out under a 50 $\times$  stereomicroscope for scintillation analyses. Additionally, for nematode species counts, the extracted sample was resuspended in 2 liters of tap water, vigorously agitated, and four subsamples of 50 mL each were taken with a syringe and pooled before processing (Ólafsson and Elmgren 1997). About 200 nematodes per core were transferred to anhydrous glycerine (Platt and Warwick 1983) and mounted on slides for species identification under a high-power microscope.

Sediment radioactivity was measured in both layers and in the 5-mL water samples (five replicates per treatment in all measurements) by adding Ultima Gold XR. Filters with picked meiofauna were solubilized for 24 h at room temperature in 80% Soluene 350 (Packard), after which 5 mL of Hionic Fluor (Packard) was added to each sample. Radioactivity was counted using a liquid scintillation counter, and all measurements were corrected for background radioactivity.

*Statistical analysis*—Differences in assimilation of both cyanobacterial species among the different meiofaunal taxa were investigated with two-way ANOVA. Prior to the analysis of variance the uptake data were double square-rooted-transformed, and a Bartlett's test was used to check the assumption of homoscedasticity. Paired a posteriori comparisons were carried out with the Unequal *N* HSD test using 95% confidence limits.

Since meiofaunal abundance data did not deviate from the assumption of homoscedasticity, differences in meiofaunal abundances between the different treatments were tested untransformed with one-way ANOVA. Paired a posteriori comparisons were carried out with the Tukey HSD test using 95% confidence limits.

## Results

*Composition of cyanobacterial blooms*—The *N. spumigena* bloom was composed of almost 100% healthy, intact *N. spumigena* filaments. Although *Anabaena* sp. contributed almost 25% of the total biomass of the *Aphanizomenon* bloom, the rest was almost entirely *Aphanizomenon* sp., with other taxa, such as *Scenedesmus* sp., *Aphanocapsa* sp., *Oscillatoria* sp., and *Botryococcus* sp., of negligible importance.

Both cyanobacteria had relatively low C:N ratios but varied in N:P and C:P ratios (Table 1). The *N. spumigena* sample was hepatotoxic in a mouse bioassay test carried out by R. Mattsson (National Veterinary Institute, Uppsala, Sweden). The *Aphanizomenon* sample was not tested.

*Composition of the initial meiofaunal community in the sediment layers*—The abundance of the major meiobenthic groups estimated from the initial cores ( $n = 5$ ) was on average  $(1.9 \pm 0.1) \times 10^6$  individuals (ind.) m<sup>-2</sup>. As expected, nematodes were the dominant major taxon, comprising on average  $92\% \pm 2\%$  of the total abundance. Harpacticoid copepods were the second most common

Table 1. Carbon–nitrogen–phosphorus (CNP) content, molar ratios, and radioactivity of *Aphanizomenon* sp. and *Nodularia spumigena* suspensions used in this experiment. Values represent average  $\pm$  standard deviation (SD) (No. of replicates).

	<i>Aphanizomenon</i> sp.	<i>Nodularia spumigena</i>
C% $\pm$ SD (n)	42 $\pm$ 4(5)	45 $\pm$ 3(5)
N% $\pm$ SD (n)	9.1 $\pm$ 1.3(5)	9.8 $\pm$ 0.7(5)
P% $\pm$ SD (n)	1.3 $\pm$ 0.1(3)	0.62 $\pm$ 0.01(3)
C:N (mol mol <sup>-1</sup> )	5.1	5.3
C:P (mol mol <sup>-1</sup> )	84	186
N:P (mol mol <sup>-1</sup> )	17	35
Radioactivity (Bq mg dry wt <sup>-1</sup> )	13.7 $\pm$ 0.7(3)	10.4 $\pm$ 0.4(3)
Toxicity	No data	Present

group (average 4.8%  $\pm$  0.9%) and ostracods the third most abundant taxon (average 1.7%  $\pm$  0.4%). Other groups of some importance were Turbellaria and Kinorhyncha (average 0.6%  $\pm$  0.3% and 0.5%  $\pm$  0.1%, respectively).

Nematodes apart, all other analyzed taxa were most abundant in the surface layer (0–1 cm) of all four treatments. The nematode genus *Paracanthonus* comprised more than 60% of the large nematodes in the surface layer.

The deeper layer was totally dominated by nematodes, with groups other than nematodes contributing less than 1% of total abundance. The community of large nematodes was in general dominated by four taxa: *Paracanthonus* spp., *Sabatieria pulchra*, *Desmolaimus* spp., and *Axonolaimus spinosus*, which together made up about 77% of the total meiofauna abundance in this layer.

The meiofaunal community composition of the sediment used in this experiment is representative of the study area in that its abundance and distribution characteristics are within the ranges found in previous studies performed in the same area (Ankar and Elmgren 1976; Ólafsson and Elmgren 1997).

*Abundance of meiofauna taxa in the different treatments*—Only two significant differences in abundance between the treatments were recorded for species analyzed in the surface sediment layer. The abundance of the large individuals of the nematode *Paracanthonus* spp. was significantly lower in the *Nodularia* treatment (Fig. 2a) than in the *Aphanizomenon* treatment ( $F_{3,15} = 4.4$ ,  $p = 0.032$ ) and was nearly significantly lower than in the controls ( $F_{3,15} = 4.4$ ,  $p = 0.051$ ). The numbers of the ostracod *P. fennica* were significantly lower in the initials (Fig. 2b) than in the controls and *Aphanizomenon* and *Nodularia* treatments ( $F_{3,16} = 4.15$ ,  $p = 0.018$ , 0.026, and 0.018, respectively). Since this species has been reported to have a life cycle of 2 yr (Ankar and Elmgren 1976), it is not likely that reproduction occurred during the duration of the experiment, thereby altering this species abundance during the study. The most likely explanation for this difference between the numbers of *P. fennica* among the initials and the three experimental treatments is, thus, a chance event attributable to spatial heterogeneity at the sampling site.

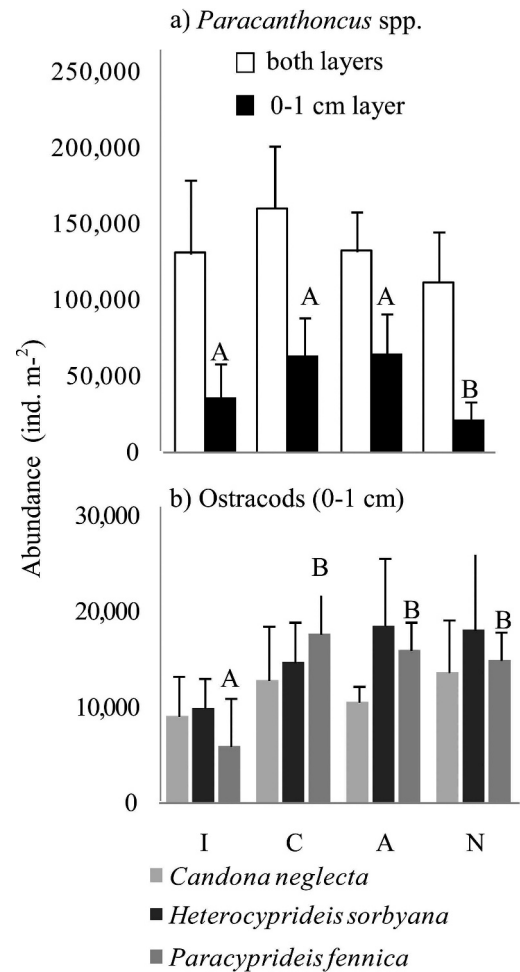


Fig. 2. Average numbers of individuals per replicate ( $n = 5$ ) of the nematode *Paracanthonus* spp. and of ostracods in the sediment layers analyzed (0–1 and 1–4 cm): (a) large individuals of *Paracanthonus* spp. in both layers (empty bars) and in the 0–1 cm layer (full bars); (b) ostracods (0–1 cm). X-axis indicates the treatments; I = initials; C = control; A = *Aphanizomenon* sp.; N = *Nodularia spumigena*. Bars show standard deviation; different letters indicate significant differences (ANOVA) in the 0–1 cm layer. The abundance of large individuals of the nematode *Paracanthonus* spp. in treatment N was significantly lower than in C and A (a). The abundance of *Paracyprideis fennica* in I were significantly lower than in C, A, and N (b). No other significant differences were found.

There were no significant differences in abundance in the 1–4 cm sediment layer among the treatments for any of the meiofaunal taxa studied (data not shown).

*Cyanobacterial carbon distribution*—At the end of the experiment the surface sediment layer contained 24%  $\pm$  3% and 27%  $\pm$  4% of the added radioactivity for the *Aphanizomenon* and *Nodularia* treatments, respectively, considerably more than was found in the deeper layer (0.8%  $\pm$  0.3% and 0.7%  $\pm$  0.5% for the *Aphanizomenon* and *Nodularia* treatments, respectively). In the water column we found only 0.7%  $\pm$  0.2% of the carbon in the *Aphanizomenon* treatment and 0.3%  $\pm$  0.2% in the

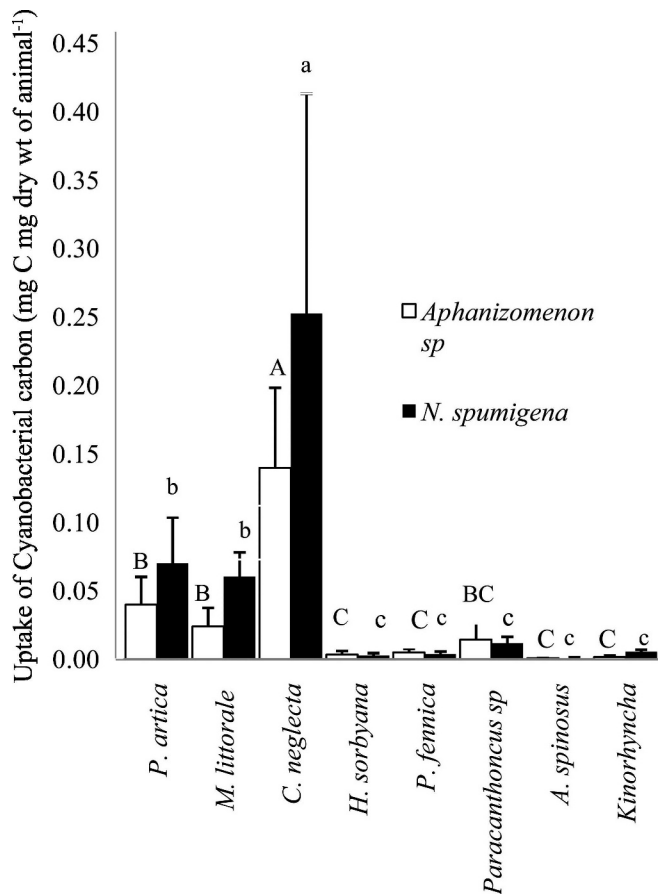


Fig. 3. Average  $^{14}\text{C}$  uptake from both cyanobacterial blooms by the major meiofaunal taxa in the surface layer (0–1 cm) ( $n = 5$ , except  $n = 3$  for *Axonolaimus spinosus* and Kinorhyncha). Uptake values given as mg C of cyanobacteria per mg dry wt of animal. Full bars show uptake for *Nodularia spumigena*; empty bars uptake for *Aphanizomenon* sp. Error bars give standard deviation; different letters indicate significant differences (ANOVA); capital letters show test results for the *Aphanizomenon* treatment, lowercase letters for the *Nodularia* treatment.

*Nodularia* treatment. Around  $0.3\% \pm 0.2\%$  and  $0.3\% \pm 0.1\%$  were found in meiofauna tissues, while  $1.4\% \pm 0.5\%$  and  $1.1\% \pm 0.7\%$  were incorporated in macrofauna individuals for the *Aphanizomenon* and *Nodularia* treatments, respectively. This experiment did not use  $\text{CO}_2$  traps, but in similar radiolabeling experiments with diatoms, about 35% of the radioactivity was released by respiration in 1 month (Ólafsson et al. 1999; Van De Bund et al. 2001).

**Uptake of cyanobacterial carbon by meiofauna**—For both blooms, uptake of cyanobacterial carbon was recorded for a number of different meiofauna species in the surface layer. The uptake was highly variable among the major Baltic meiofaunal taxa, even among species of the same class (Fig. 3). The carbon uptake values were significantly higher for the ostracod *C. neglecta* than for any other species analyzed for both cyanobacteria blooms, with values up to 100 times higher than for the other two ostracod species, *H. sorbyana* and *P. fennica* ( $F_{1,8} = 65.8$ ,  $p = 0.000174$ ).

The harpacticoids *P. artica* and *M. littorale* also showed considerable carbon uptake from both cyanobacterial blooms, with no significant differences between species. The uptake of carbon of cyanobacterial origin by both harpacticoids was significantly higher than for *Paracanthonus* spp. in the *Nodularia* treatment ( $F_{1,8} = 65.8$ ,  $p = 0.0006$  and  $p = 0.002$  for *P. artica* and *M. littorale*, respectively), but not in the *Aphanizomenon* treatment.

Of the nematode species studied, only *Paracanthonus* spp. and *A. spinosus* had sufficient biomass in the surface layer for uptake analysis. Only *Paracanthonus* spp. registered a measurable uptake (Fig. 3). Kinorhyncha as a group had low uptake values, in agreement with the results of other studies (Rudnick 1989; Widbom and Frithsen 1995), in which this meiofaunal taxon showed little uptake of freshly deposited phytodetritus.

In the subsurface layer, four nematode taxa (*Paracanthonus* spp., *S. pulchra*, *Desmolaimus* spp., and *A. spinosus*) were available in sufficient numbers for uptake analysis. Again, uptake from either cyanobacterial species was measurable in only *Paracanthonus* spp., at rates similar to those found for this taxon in the surface layer ( $F_{1,8} = 6.4$ ,  $p = 0.667$  and  $p = 0.993$  for *Aphanizomenon* and *Nodularia*, respectively).

## Discussion

**Effects of feeding on the toxin-producing *N. spumigena***—We found no significant effects on the abundances of any of the meiofaunal taxa studied after exposure to cyanobacteria in the sediment, not even for those species that readily assimilated carbon from the toxin-producer *N. spumigena*. Furthermore, there was no indication of greater carbon uptake from *Aphanizomenon* sp. for any meiofauna taxon. In fact, there was a slight but nonsignificant tendency for higher carbon uptake from *N. spumigena* in all the meiofauna taxa analyzed, except the nematode *Paracanthonus* spp. Although *Aphanizomenon* sp. in the Baltic Sea is considered to be nontoxic (Sivonen et al. 1989; Stal et al. 2003), we cannot completely rule out the presence of toxins in this treatment since the *Aphanizomenon* bloom material also contained some *Anabaena* spp., a genus that has recently been found to produce microcystins in the Baltic Sea (Halinen et al. 2007).

Considering the uptake of carbon from both cyanobacterial blooms by some meiofaunal species in our study and the evidence that cyanobacterial blooms have existed in the Baltic for the past 7000 yr (Bianchi et al. 2000), it is plausible that physiological tolerance to nodularin and other secondary metabolites produced by cyanobacteria has evolved in some meiofauna taxa, as it has in some aquatic crustacean groups (Demott and Moxter 1991). Nevertheless, the nematode abundance data show significantly fewer large individuals of *Paracanthonus* spp., the only nematode that showed an uptake of cyanobacterial carbon, in the surface layer of the *Nodularia* treatment than in the controls and the *Aphanizomenon* treatments (Fig. 2a). Together with the data that show no statistically significant differences in the total abundance of this nematode when both layers are combined (Fig. 2a), this

indicates that large individuals of this species may have moved down in the sediment to avoid exposure to *N. spumigena* or its toxins. However, mortality associated with feeding on *N. spumigena* cannot be ruled out as an explanation of the difference among treatments in vertical distribution of this nematode.

*Interspecific differences in uptake and the meiobenthic food web*—The results of this study demonstrate that a number of meiofaunal species can readily assimilate freshly deposited carbon from cyanobacterial blooms, whether they are dominated by *Aphanizomenon* sp. or *N. spumigena*. Large differences in cyanobacterial carbon uptake rates among species were found, even within the same taxonomic class, which is consistent with the results of other studies of the uptake of phytodetritus by meiofauna (Widbom and Frithsen 1995; Ólafsson et al. 1999; Moens et al. 2002). The high variability in uptake of carbon of cyanobacterial origin is particularly evident when comparing the three ostracod species common in the sediment. Ostracods have generally been considered efficient feeders on freshly deposited detritus (Rudnick 1989; Ólafsson et al. 1999; Modig et al. 2000) and are able to graze on some cyanobacteria species (Grant et al. 1983; Limén and Ólafsson 2002). However, while *C. neglecta* was by far the most efficient of all the meiofauna taxa analyzed in assimilating labeled material, *H. sorbyana* and *P. fennica* showed up to hundred-fold lower uptake rates than did *C. neglecta*, clearly indicating a niche differentiation among these three species (Fig. 3). Evidence of this niche differentiation has been observed in other studies performed in the Baltic proper with regard to uptake of freshly deposited diatoms (Ólafsson et al. 1999) and carbon stable isotope signals after an *Aphanizomenon* sp. bloom (Limén and Ólafsson 2002). These earlier studies proposed that this niche differentiation can be explained by vertical stratification in the first centimeter of the sediment and/or resource partitioning among these three species with regard to carbon pathways, with *C. neglecta* relying more on freshly deposited phytodetritus, while *H. sorbyana* and *P. fennica* mainly consume older, more refractory material (Ólafsson et al. 1999; Modig et al. 2000). *C. neglecta* has been thought to have a relatively short life cycle when compared to *H. sorbyana* and *P. fennica* (Ankar and Elmgren 1976). Shorter generation times necessitate greater investment in energy for growth and reproduction and might require the utilization of fresh organic matter of higher quality to sustain these energy requirements. Conversely, with longer and slower life cycles, *H. sorbyana* and *P. fennica* can rely on older and more refractory organic carbon and may thus benefit from lower competition levels (Modig et al. 2000). Interestingly, the interspecific differences in carbon uptake from cyanobacterial origin found in our study follow a pattern very similar to that found for a simulated spring bloom by Ólafsson et al. (1999), indicating that the ostracod niche differentiation is not seasonal and occurs with the settling of both spring and summer blooms in the Baltic Sea.

The only nematode taxon that recorded significant uptake of carbon of cyanobacterial origin was *Para-*

*canthonchus* spp. (Fig. 3). Ólafsson et al. (1999) hypothesized that the uptake of freshly deposited carbon depends on the large dorsal tooth in the buccal cavity of *Paracanthochus* spp. that enables them to pierce phytoplankton cells and suck out the contents, and the same mechanism may allow them to assimilate fresh carbon from cyanobacterial blooms. The other three nematodes investigated, *A. spinosus*, *S. pulchra*, and *Desmolaimus* sp., lack teeth and have a relatively large buccal cavity, characteristics that led Wieser (1953) to classify them as nonselective deposit feeders. Thus, anatomic differences in the buccal cavity may explain the differences in uptake among the nematodes we analyzed.

A valuable conclusion that can be drawn from this and other studies, such as that of Ólafsson et al. (1999), is that although it is time consuming, a detailed taxonomic analysis is necessary to correctly identify and interpret feeding patterns within meiofauna assemblages. This is well illustrated by the interspecific differences in uptake among the three ostracods, showing that an analysis at the class level would misrepresent the uptake rate of ostracods. The final values would depend on the proportions of individuals of the different species that are picked for analysis.

The surface layer uptake data from both cyanobacterial species supports Rudnick's (1989) hypothesis that there are two distinct meiofaunal groups within the first centimeter of sediment in terms of reaction to freshly deposited detritus. A similar species-specific difference in utilization of fresh carbon sources has also been established in the Baltic proper for the brackish water amphipods *Monoporeia affinis* and *Pontoporeia femorata* (Byrén et al. 2006). Experimental data using methodology similar to that of Byrén et al. (2006) could help clarify meiofaunal carbon sources.

*Cyanobacteria as food source for the meiobenthos*—Some of the radioactivity taken up by the meiofauna could be derived not from direct ingestion of cyanobacterial bloom material but rather from feeding on sediment microbes that have taken up labeled carbon from decomposing or leaking cyanobacterial cells. However, if this microbial pathway was a significant factor in our experiment, one would expect to find uptake of label also in nonselective deposit-feeding nematodes, such as *A. spinosus*, *Desmolaimus* spp., and *S. pulchra*. Thus, even though we cannot rule out some contribution from microbes to the labeling of meiofauna, interspecific differences in nematode uptake of radioactive carbon indicate that ingestion of cyanobacterial material is the main source of label in our experiment.

The uptake of a simulated diatom spring bloom by a similar meiobenthic community from the same area was studied at similar temperature and salinity by Ólafsson et al. (1999). Although the duration of their study was twice that of ours (4 weeks), it is still of interest to compare results (Table 2). The uptake rates of carbon from cyanobacteria and diatoms by species like *C. neglecta*, *P. artica*, and *M. littorale* were similar for cyanobacteria with half of the exposure time, indicating that cyanobacteria are potentially valuable as food for these species. On the other hand, the nematodes *Paracanthochus* spp. and, especially, *A. spinosus* showed a higher uptake of diatoms. Comparison of our results with those of the longer study of

Table 2. Uptake of carbon (C) by some meiofauna taxa from settled blooms of the cyanobacteria *Aphanizomenon* sp. and *Nodularia spumigena* and of diatoms calculated as mg C mg dry wt<sup>-1</sup> of animal (mean  $\pm$  standard deviation [SD]). Uptake values for diatoms are calculated from data reported by Ólafsson et al. (1999), for which SD values were not available.

Meiofaunal species or taxon	<i>Aphanizomenon</i> sp.	<i>N. spumigena</i>	Diatoms
<i>Pseudobradia artica</i>	40 $\pm$ 21	70 $\pm$ 33.5	35
<i>Microarthridion littorale</i>	24 $\pm$ 14	60 $\pm$ 18	6.6
<i>Candona neglecta</i>	140 $\pm$ 60	250 $\pm$ 160	245
<i>Heterocyprideis sorbyana</i>	3.3 $\pm$ 2.6	2.6 $\pm$ 1.8	3.3
<i>Paracyprideis fennica</i>	4.8 $\pm$ 2.9	3.7 $\pm$ 1.9	10.0
<i>Paracanthochus</i> spp.	14 $\pm$ 16	12 $\pm$ 5	45
<i>Axonolaimus spinosus</i>	0.5 $\pm$ 0.02	0.6 $\pm$ 0.8	37
<i>Kinorhyncha</i>	1.6 $\pm$ 0.9	5.5 $\pm$ 1.3	1.7

Ólafsson et al. (1999) shows that meiofauna taxa that reacted quickly to freshly deposited phytodetritus showed similar uptake of carbon from cyanobacteria and diatoms (Table 2). Conversely, meiofauna taxa that did not assimilate freshly deposited diatom carbon also did not use cyanobacteria as food.

This similarity in carbon uptake values from diatoms and cyanobacteria is somewhat surprising, since traits such as toxicity, poor nutritional quality, a low content of long-chain polyunsaturated fatty acids (Ahlgren et al. 1992), and a difficult-to-handle morphology have been shown to restrict the capacity of zooplankton grazers to exploit cyanobacteria as a food source (Demott and Moxter 1991; Schmidt and Jonasdóttir 1997). Nevertheless, several experimental studies have shown that crustaceans are able to survive and grow on Baltic cyanobacteria (Engström et al. 2000; Koski et al. 2002). Meiofauna as well as other benthic fauna living below the photic zone are highly dependent on the inputs of organic matter from the photic zone (Ólafsson and Elmgren 1997) and are probably food limited for most of the year (Rudnick 1989). Therefore, the settling of summer blooms of cyanobacteria may provide these sediments with a much-needed food source at a critical time, when the availability of fresh organic matter is low, after the spring bloom input to the sediments has been exhausted. Although poor in unsaturated fatty acids, cyanobacteria have a high amino acid content and may contain other elements that are important for the diet of grazers (Ahlgren et al. 1992). Small additions of cyanobacteria to a Baltic zooplankton diet have been shown to significantly increase zooplankton production (Schmidt and Jonasdóttir 1997). Demott and Moxter (1991) suggested that discrimination by herbivores against low-quality foods like cyanobacteria will decrease when optimal food is sparse. Thus, at least for animals with relatively short life cycles and high energy requirements, such as harpacticoid copepods and possibly *C. neglecta*, organic matter from cyanobacteria seems to be a useful and even important summer food. However, it is possible that these cyanobacterial blooms alone do not have the nutritional quality needed to sustain a high benthic production, as peaks of abundances of the species analyzed in this study were found to be connected to the inputs of detritus from the spring blooms (Ólafsson and Elmgren 1997).

In conclusion, our results show no negative effects on meiofaunal survival from exposure to phytodetritus from

summer cyanobacterial blooms, even from toxic *N. spumigena*. This may indicate that some meiofauna groups have evolved mechanisms to deal with the cyanotoxins produced by *N. spumigena*, via increased tolerance or possibly avoidance. Indeed, some meiofaunal groups use settling blooms of *Aphanizomenon* sp. and *N. spumigena* as food, with similar carbon uptake rates to those reported for the spring bloom of diatoms. The large differences in uptake of cyanobacterial carbon found among meiofaunal taxa support Rudnick's (1989) hypothesis that two separate benthic food webs, based on carbon sources of different ages, coexist within the first centimeter of the sediment.

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