

Incorporation and burial of carbon from settling cyanobacterial blooms by deposit-feeding macrofauna

Abstract—Summer blooms of filamentous, nitrogen-fixing cyanobacteria are typical of the Baltic Sea, and recent findings indicate that cyanobacteria may be an important food source for the benthos below the euphotic zone. In a 2-week laboratory experiment, we measured incorporation of cyanobacterial carbon by the deposit-feeding amphipod *Monoporeia affinis* when exposed to ^{14}C -radiolabeled, natural blooms of cyanobacteria dominated by either the toxic *Nodularia spumigena* or nontoxic *Aphanizomenon* sp. Carbon from both cyanobacterial blooms was used, with greater incorporation from *Aphanizomenon*-dominated bloom material than from *N. spumigena*, indicating that the latter is less suitable as food. However, neither cyanobacterium supported significant amphipod growth. Also, less cyanobacterial carbon was mixed down in the sediment in the *N. spumigena* treatment, indicating lower bioturbation activity in this treatment. Long-term effects on feeding and survival remain to be studied, especially for the toxic *N. spumigena*.

Benthic communities below the euphotic zone are largely fueled by settling organic matter from phytoplankton blooms. In the Baltic Sea, the spring bloom of diatoms is considered to be the most important input of high-quality organic matter to the subthermocline soft-bottom community (Elmgren 1978). However, recurring summer blooms of nitrogen-fixing, toxic cyanobacteria have probably increased in frequency, magnitude, and duration in recent decades (Poutanen and Nikkilä 2001). The settling of the two dominant cyanobacterial species, *Aphanizomenon* sp. and *Nodularia spumigena*, to the sediment was earlier considered negligible (Sellner 1997). Later, high settling fluxes of *Aphanizomenon* sp. have been reported (Tallberg and Heiskanen 1998), and recently Gustafsson et al. (2004) showed that sediment trap collections may underestimate true rates of summer sedimentation several-fold in the Baltic Sea. Other evidence of substantial input of nitrogen-fixing cyanobacteria to sediments includes the presence in sediments of the cyanobacterial pigment zeaxanthin and the cyanotoxin nodularin (Bianchi et al. 2000; Mazur-Marzec et al. 2007) as well as isotopic signatures in meiofauna and sediment that resemble the signatures of cyanobacteria (Limén and Ólafsson 2002; Voss et al. 2005). There is thus a need to clarify whether cyanobacterial inputs can be used as food by the benthos.

Cyanobacteria have long been considered poor food for invertebrates as a result of their toxin content, low nutritional value, and morphology. In the Baltic Sea, *N. spumigena* always produces the hepatotoxin nodularin (Laamanen et al. 2001), while *Aphanizomenon* sp. is considered nontoxic (Sivonen et al. 1989). Blooms of *N. spumigena* have caused mortality in domestic animals (Edler et al. 1985), and the effects of cyanobacterial blooms on pelagic organisms and the potential of nodularin to

bioaccumulate have been extensively studied (Karjalainen et al. 2007). Experimental studies have demonstrated negative effects of *N. spumigena* on ingestion, reproduction, and survival of copepods and mysids (Engström et al. 2000, 2001). Cyanobacteria seem to have a low content of long-chain polyunsaturated fatty acids, which are important for egg production in invertebrates (DeMott and Müller-Navarra 1997), and may therefore be nutritionally inadequate, even if they are not toxic. However, small additions of a cyanobacterium to a diatom diet led to a higher rate of zooplankton egg production than was observed based on a pure diatom diet (Schmidt and Jonasdóttir 1997). Decaying cyanobacterial filaments are reported to be more suitable as food for zooplankton (Meyer-Harms et al. 1999), perhaps because they are associated with a rich community of bacteria, flagellates, and ciliates that could provide a variety of food types (Engström-Öst et al. 2002).

A cyanobacterial input might affect deposit-feeding fauna either positively, by providing food when the spring bloom input to the sediment is exhausted, or negatively (e.g., by being toxic). The macrobenthic soft-bottom community in the northern Baltic proper is often dominated by the amphipod *Monoporeia affinis* (Ankar and Elmgren 1976), which feeds preferentially on freshly deposited phytodetritus (van de Bund et al. 2001) and is important food for several fish species (Aneer 1975). In this study, we exposed *M. affinis* to ^{14}C -radiolabeled, natural blooms of cyanobacteria dominated by either *N. spumigena* or *Aphanizomenon* sp. in a 2-week experiment. Our main questions were as follows: (1) Does exposure to settled blooms of either toxic *N. spumigena* or nontoxic *Aphanizomenon* sp. reduce survival of *M. affinis*? (2) Does *M. affinis* incorporate carbon from these cyanobacterial species? (3) Are there differences between blooms in rates of carbon incorporation or burial?

Cyanobacterial sampling and labeling—Naturally occurring cyanobacterial blooms were collected with a plankton net (mesh size 90 μm) in the southern Stockholm archipelago. The bloom dominated by *Aphanizomenon* sp. was collected in Himmerfjärden bay (59°04'N, 17°41'E) on 05 July 2005, and the *N. spumigena* bloom was collected the next day in the open Baltic Sea (58°35'N, 18°14'E). After collection, the bloom samples were placed in black funnels illuminated from the bottom to remove zooplankton, which concentrated at the bottom, while cyanobacteria floated to the top. The cyanobacteria were then incubated in the laboratory at 18°C in constant light (45 $\mu\text{mol ms}^{-1}$) with nutrients (f/2 medium) and were labeled by adding a total of 3.4×10^7 Bq of ^{14}C - NaHCO_3 , (DKI; specific activity: 200×10^7 Bq mmol^{-1}) in 2-liter Erlenmeyer flasks. *N. spumigena* was harvested after 6 d and the *Aphanizomenon*-dominated sample after 7 d of incubation; both were concentrated by sieving through 40- μm sieve and were rinsed with filtered,

brackish water (salinity, 6) to remove nonincorporated radioactivity. Subsamples were taken both for carbon–nitrogen–phosphorus (CNP) measurements and for qualitative species determination at 50 \times magnification. The concentrated cyanobacterial batches were kept frozen at -20°C . After thawing slowly at 2°C , the filaments appeared intact when checked under the microscope.

Sampling of sediment and amphipods—Sediment and amphipods were collected with an epibenthic sled at 27-m depth ($58^{\circ}49'\text{N}$, $17^{\circ}31'\text{E}$) on 23 June 2005, before the cyanobacterial summer bloom, and were stored in the dark with aerated brackish seawater for 3 weeks at 5°C . Before the start of the experiment, the sediment was sieved through 0.5 mm and added to thirty 1-liter plastic jars to a depth of 3 cm (200 mL, 81% water), resulting in a 78.5 cm² sediment surface. Samples of sediment were stored for analyses of CNP content. Filtered brackish seawater (0.45 liters) was then carefully added to the microcosms and aerated without disturbing the sediment surface. Before adding cyanobacteria, 20 actively swimming adult *M. affinis* individuals were placed in each microcosm, resulting in a density of 2546 individuals m⁻², a density that has been commonly recorded in the area (Ankar and Elmgren 1976). Initial amphipods were analyzed for dry weight and CNP content.

Experiment start and termination—The experiment had three treatments of 10 replicates each: (1) *N. spumigena* bloom; (2) *Aphanizomenon*-dominated bloom; and (3) no addition of cyanobacteria (control). We added similar amounts of cyanobacterial material (dry weight), namely 1.95 g C m⁻² of *N. spumigena* or 1.37 g C m⁻² of *Aphanizomenon*-dominated material. These quantities are within the reported literature range for sedimentation rates of cyanobacterial blooms (Tallberg and Heiskanen 1998). The cyanobacterial concentrates were mixed with 1.94 g wet wt of the sieved sediment before addition to facilitate settling on the sediment surface and were carefully spread on the surface of the microcosms with a Pasteur pipette. The cyanobacteria were allowed to settle for 12 h, after which each microcosm was reconnected to the air system. The experiment was run from 17 July to 01 August 2005 at the Askö Laboratory ($58^{\circ}49'\text{N}$, $17^{\circ}38'\text{E}$) on the Swedish East Coast, northwestern Baltic Proper, in conditions of natural light (faint green, 16:8 light:dark cycle), salinity (6.4), and temperature (5°C).

Immediately before terminating the experiment we sampled 5 mL of water from all replicates in order to measure radioactivity. After siphoning off the remaining water, sediment cores (diameter 1.5 cm, depth 2.5 cm) were taken from five replicates per treatment using a cut-off syringe; cores were immediately frozen at -20°C . Sediment from all replicates was sieved, and the amphipods were counted and placed in filtered brackish water for 24 h to empty their guts. The animals were then rinsed in distilled water and dried at 60°C .

Chemical analyses and radioactivity measurements—Samples for measurement of ¹⁴C and CNP content in

cyanobacteria were taken by pipetting 400 μL of the suspensions onto pre-dried GFF-filters, which were dried to constant weight at 60°C before analyses. Content of C and N was analyzed with a Leco-CHN analyzer with ethylenediaminetetraacetic acid as standard; P content was measured according to the method of Larsson et al. (2001). Final radioactivity of the cyanobacteria was determined in a liquid scintillation counter (1214 Rackbeta, LKB Wallac) after solubilization in 1 mL Soluene and addition of 10 mL Hionic-Fluor (Perkin Elmer). Samples were counted for 10 min using automatic quench compensation and background elimination. Dried, weighed, individual amphipods were solubilized in 1 mL of Soluene-350 in a sonicator-bath for 1 h and were then left overnight in darkness to reduce chemiluminescence. After addition of 10 mL Hionic-Fluor, radioactivity was measured as described above. Radioactivity in 5-mL water samples was measured by adding 5 mL of Ultima Gold XR (Perkin Elmer) before counting. The sediment cores were sliced frozen in 0.5-cm layers from 0 to 2.5 cm in depth. Each layer was homogenized and dried at 60°C . Samples of ~ 15 mg from each layer were vortexed and sonicated with 1 mL water. After addition of 10 mL Ultima Gold XR, radioactivity was measured as described above.

Data analyses—An average radioactivity value for 10 individuals from each replicate and for five subsamples of sediment per replicate sediment layer was used in statistical tests. Radioactivity in individual amphipods was corrected for background radioactivity and recalculated to carbon incorporation in micrograms. Data related to amphipod survival and individual weight were analyzed with ANOVA and incorporation of carbon with a *t*-test, after testing for homogeneity of variance with Cochran's *C*-test. The measured radioactivity (per mg dry wt) in each 0.5-cm-thick sediment layer was multiplied by the total dry weight of that layer, and the total radioactivity in the sediment of each experimental unit was calculated as the sum of the activities in the five layers (0–2.5 cm). Sediment profiles are thus based on the percentage of the total activity in the sediment at each 0.5-cm depth interval. The proportion of recovered radioactivity in sediment mixed down below the surface layer was tested with the nonparametric Mann–Whitney *U*-test. All statistical tests were performed in Statistica 8 (Statsoft).

Cyanobacteria composition and radiolabeling—The *Nodularia* sample consisted of $\sim 100\%$ healthy, intact *N. spumigena* filaments. The *Aphanizomenon* sample was dominated by *Aphanizomenon* sp., but *Anabaena* spp. contributed about 25% to the biomass, with other present species, such as *N. spumigena*, *Scenedesmus*, *Aphanocapsa*, *Oscillatoria*, and *Botryococcus* of negligible importance ($<5\%$). The CNP contents of cyanobacteria, amphipods, and initial sediment used in the experiment are given in Table 1. The cyanobacteria had C:N ratios that measured below the Redfield ratio (C₁₀₆:N₁₆:P₁; Redfield et al. 1963), but *N. spumigena* had N:P and C:P ratios that clearly measured above the Redfield ratio. The *N.*

Table 1. Carbon–nitrogen–phosphorus (CNP) content and molar ratios of *Aphanizomenon*-dominated material, *Nodularia spumigena*, and of initial sediment and animals used in the experiment.*

	<i>Aphanizomenon</i>	<i>Nodularia</i>	Initial sediment	Initial <i>Monoporeia affinis</i>
C%±SD (n)	42.1±3.9(5)	45.3±2.6(5)	4.3±0.2(3)	43.7±2.7(5)
N%±SD (n)	9.1±1.3(5)	9.8±0.7(5)	0.6±0.0(3)	7.3±0.7(5)
P%±SD (n)	1.3±0.1(3)	0.6±0.0(3)	0.2±0.0(3)	0.9±0.2(5)
C:N:P (mol: mol)	84:17:1	186:35:1	79:9:1	109:18:1

* SD, standard deviation.

spumigena bloom material was hepatotoxic in a mouse bioassay test (R. Mattsson, National Veterinary Institute, Uppsala, Sweden). Final radioactivity was $13.7 \pm 0.7 \text{ Bq} \times \mu\text{g C}^{-1}$ for the *Aphanizomenon*-dominated material and $10.4 \pm 0.4 \text{ Bq} \times \mu\text{g C}^{-1}$ for *N. spumigena*, as calculated from C% of dry weight from each species (Table 1). The total amount of radioactivity added to each replicate was $14.8 \times 10^4 \text{ Bq}$ (*Aphanizomenon*-dominated material) and $16.0 \times 10^4 \text{ Bq}$ (*N. spumigena*).

Amphipod survival and incorporation of cyanobacterial C—Amphipod survival was about 75%, which is normal for this species and experimental duration, without significant differences between treatments (ANOVA; $F_{2,27} = 0.57$, $p = 0.58$). Individual mass did not change significantly during the experiment, and no significant differences between treatments were found (ANOVA; $F_{2,27} = 0.09$, $p = 0.91$). All amphipods given labeled cyanobacteria had higher radioactivity than the controls, namely 250 ± 98 (*Aphanizomenon*-treatment) and 115 ± 60 (*Nodularia*-treatment) $\text{Bq} \times \text{mg dry wt}^{-1}$ after deduction of a background of 1 Bq. No correlation between mass-corrected incorporation of radioactivity and amphipod weight was seen in any treatment. *M. affinis* incorporated significantly more carbon $\mu\text{g} \times (\text{mg dry wt})^{-1}$ from *Aphanizomenon*-dominated material than did *N. spumigena* (Fig. 1; $t = 2.41$, $\text{df} = 18$, $p = 0.027$). When analyzed as carbon incorporated per individual, the result was even more significant (Fig. 1; $t = 3.33$, $\text{df} = 18$, $p = 0.004$).

Burial of cyanobacteria and ^{14}C recovery—The highest radioactivity was found in the top 0.5-cm layer for both treatments (*Aphanizomenon* treatment; $2.9 \pm 1.1 \text{ Bq} \times \text{mg dry wt}^{-1}$; *Nodularia* treatment; $4.1 \pm 2.7 \text{ Bq} \times \text{mg dry wt}^{-1}$), but the *Aphanizomenon*-dominated bloom material was buried significantly deeper in the sediment than was *N. spumigena*, since about 44% of the recovered radioactivity was found below 1 cm, compared to 28% in the *Nodularia* treatment (Fig. 2; Mann–Whitney U -test, $Z = 2.40$, $p = 0.016$). Radioactivity in water was $0.7 \pm 0.2 \text{ Bq} \times \text{mL}^{-1}$ (*Aphanizomenon* treatment) and $1.2 \pm 0.2 \text{ Bq} \times \text{mL}^{-1}$ (*Nodularia* treatment) ($n = 9$). Total recovery of added radioactivity in the *Aphanizomenon* and *Nodularia* treatments was, respectively, 4% and 2% in animals, 0.2% and 0.4% in water, and, on average, 28% (maximum 55%) in sediment for both species. This experiment did not use CO_2 traps, but in a similar experiment, about 35% of the added radioactivity was respired, and total recovery, including the respired fraction, was 80% (van de Bund et al. 2001).

Discussion—This is the first experimental study to demonstrate that Baltic deposit-feeding macrofauna can utilize carbon from settling cyanobacterial blooms. The method of incubating natural bloom material for short-term isotope labeling in the laboratory worked well, giving a strong isotopic signal that could be traced in the amphipods. In addition to representing the field situation better than does the use of pure laboratory cultures, incubation of natural blooms is simple and cost-effective compared to growing large quantities of phytoplankton. The high replication of this study, which was necessary due to large variation in individual amphipod carbon incorporation, demanded a total amount of cyanobacteria of about 1200 mg dry wt. There was no difference in survival between treatments, indicating that settling cyanobacterial blooms have no immediate negative effects on the survival of *M. affinis*. Cyanobacteria play a central role in the Baltic pelagic system during summer (Larsson et al. 2001), and it is possible that the settling cyanobacterial blooms may provide additional food for the benthos at a critical time of the year, when the spring bloom input to the sediment has been exhausted and amphipod growth ceases (Cederwall 1979). The amount of cyanobacterial carbon incorporated by *M. affinis* corresponds to about 10% of the metabolism during the experiment, as calculated by energy equivalents from *M.*

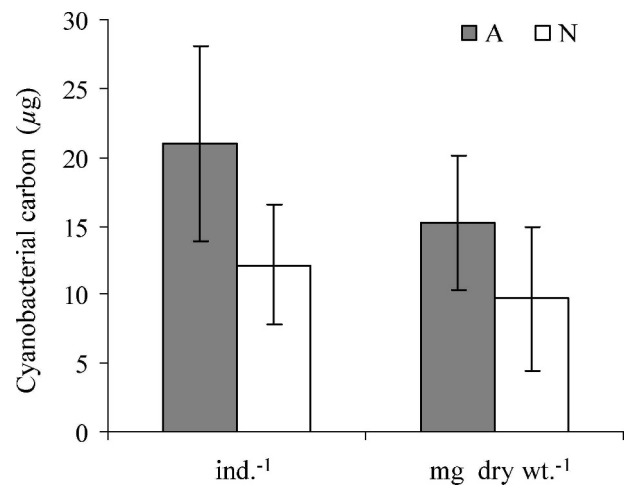


Fig. 1. *Monoporeia affinis*: incorporation of cyanobacterial carbon (μg) per individual and per mg dry wt amphipod. A = *Aphanizomenon*-dominated material; N = *Nodularia spumigena*. Values are mean \pm standard deviation ($n = 10$). Incorporation of carbon was significantly higher from A than from N (both per individual, $p < 0.01$, and per mg dry wt, $p < 0.05$).

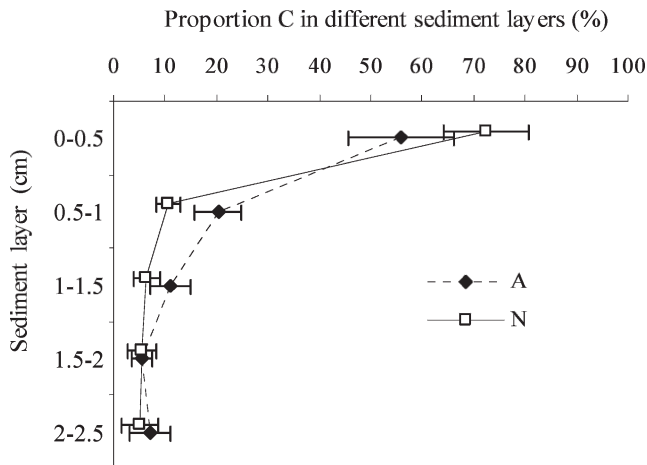


Fig. 2. Burial of cyanobacterial carbon (C) in the two treatments. A = *Aphanizomenon*-dominated material; N = *Nodularia spumigena*. The diagram shows % of total sediment radioactivity for each layer, calculated as mean \pm standard deviation for all replicates in each treatment ($n = 5$).

affinis respiration data in summer (Cederwall 1979), but this did not result in increased amphipod biomass. In similar experiments with diatoms, incorporation was several-fold higher, and amphipods showed rapid growth (van de Bund et al. 2001; Byrén et al. 2002). Low carbon uptake has been found in several studies of zooplankton grazing on various filamentous cyanobacterial species (de Bernardi and Giussani 1990), including *N. spumigena* (Engström et al. 2000). Coping with toxins might involve a metabolic cost, which could lead to decreased growth. Kozłowski-Suzuki et al. (2003) found a decrease in gross growth efficiency with an increase in nodularin concentration in copepods, and Lehtonen et al. (2003) found that *N. spumigena* affected the physiological condition of a soft-bottom clam. *Aphanizomenon* sp. is not toxic in the Baltic Sea (Sivonen et al. 1989), but the *Anabaena* spp. present in the *Aphanizomenon*-dominated material are known to produce microcystin (Halinen et al. 2007).

The lower incorporation of carbon from *N. spumigena* indicates that it is less adequate as food than the *Aphanizomenon*-dominated material. These results are in agreement with earlier studies on mysid shrimps (Engström et al. 2001). The amphipods not only incorporated less carbon from *N. spumigena*, but they also mixed down into the sediment less, indicating a lower bioturbation activity than in the *Aphanizomenon* treatment. Bioturbation activity can be a sensitive indicator of contaminant effects (e.g., polychaetes exposed to toxins stop reworking the sediment) (Fernandes et al. 2006). Decreased bioturbation by *M. affinis* could influence mineralization rates and reduce the availability of freshly deposited organic matter to sub-surface-feeding organisms (Tuominen et al. 1999; van de Bund et al. 2001).

As cyanobacterial blooms have existed in the Baltic for the last 7000 yr (Bianchi et al. 2000), the low incorporation values of *N. spumigena* by *M. affinis* might reflect an evolutionarily developed avoidance behavior. Another explanation of the higher incorporation of the *Aphanizomenon*-dominated material could be that it contained

several phytoplankton species (i.e., *Anabaena* spp.), unlike the *N. spumigena* bloom. Differences in nutritional status (Table 1), palatability, and morphology between *N. spumigena* and *Aphanizomenon* sp. filaments could also affect amphipod ingestion rate or absorption efficiency. However, this study deals with the short-term effects of settling cyanobacterial blooms, and it is possible that incorporation of carbon from aged cyanobacterial matter, including *N. spumigena*, is higher once sediment microorganisms and meiofauna have conditioned the food source (Tenore et al. 1977). Another positive effect of ageing could be toxin degradation, although Mazur-Marzec et al. (2007) found high concentrations of nodularin in surface sediments several months after a bloom.

In conclusion, our results demonstrate that cyanobacterial carbon is incorporated by *M. affinis*, although less so when the bloom material is dominated by *N. spumigena* rather than *Aphanizomenon* sp. Further studies are needed to evaluate the importance of cyanobacterial blooms for benthic production, with special emphasis on the long-term effects of toxic *N. spumigena* on growth rate, reproduction, trophic transfer of cyanotoxins, and organic matter mineralization by the benthos.

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