

H. Limén · E. Ólafsson

Ostracod species-specific utilisation of sediment detritus and newly settled cyanobacteria, *Aphanizomenon* sp., in the Baltic Sea: evidence from stable carbon isotopes

Received: 24 July 2001 / Accepted: 22 October 2001 / Published online: 21 November 2001
© Springer-Verlag 2001

Abstract The three meiobenthic ostracod species *Candona neglecta*, *Paracyprideis fennica* and *Heterocyprideis sorbyana* are commonly encountered in the deep (20–40 m) soft bottoms of the Baltic proper, and may contribute more to the total meiobenthic biomass than any other group. Experimental data indicate substantial differences in their utilisation of settling phytodetritus, with *C. neglecta* able to exploit newly settled organic material to a larger extent than *P. fennica* and *H. sorbyana*. Ostracod species composition, as well as ostracod and sediment carbon isotope contents, were studied in the field from an area with local differences in potential food resources. The study was performed during the late period of summer blooms of the cyanobacteria *Aphanizomenon* sp. Results showed that when all samples were taken together, adult *C. neglecta* (–22.4‰) was significantly more depleted in $\delta^{13}\text{C}$ than adult *P. fennica* (–21.0‰) and *H. sorbyana* (–20.3‰), indicating differences in food selection among the species. The flocculent sediment layer had, in all instances, lighter carbon ratios than did the lower layers. This trend was mirrored in most cases in the slight enrichment in *C. neglecta* compared to generally greater enrichment in the other two species. Carbon signatures of *C. neglecta* also varied significantly between stations, indicating that this species fed on different resources depending on location. Juvenile *C. neglecta* were far more depleted in $\delta^{13}\text{C}$ than adults and reflected the carbon signature of the cyanobacteria *Aphanizomenon* sp. The latter is known to be

the most $\delta^{13}\text{C}$ -depleted phytoplankton member in the area.

Introduction

Three meiobenthic ostracod species are commonly encountered in muddy areas of deep (20–40 m) soft bottoms in the Baltic proper. Even though they are generally found in low numbers, i.e. about 1% of the total meiofauna abundance, they may contribute more to the total meiobenthic biomass than any other group (Ólafsson and Elmgren 1997). The largest species, *Candona neglecta*, is of freshwater origin, has two generations per year in Swedish lakes (Alm 1915) and is able to reach adulthood within 4 months in the Gulf of Bothnian (Savolainen and Valtonen 1983). The other two species, *Paracyprideis fennica* and *Heterocyprideis sorbyana*, of brackish and marine origin respectively, are more slow growing and seem to have a life cycle of at least 2 years (Ankar and Elmgren 1976). Ólafsson et al. (1999) showed that the uptake of radio-labelled diatoms by *C. neglecta* was by far the highest amongst examined meiobenthic species, and that *C. neglecta* took up 10 to 100 times more of the phytodetritus than *P. fennica* and *H. sorbyana*. Modig et al. (2000) did not find evidence of interspecific competition for settling phytodetritus among ostracod species, but suggested that differences in food resources better explained the species-specific uptake of newly settled diatoms. It is plausible that *C. neglecta* lives in the top millimetres, feeding on relatively new organic material in the sediment, while the other two may live a few millimetres below, feeding on older organic material.

In the Baltic Sea, blooms of the filamentous cyanobacteria *Aphanizomenon* sp. often dominate the phytoplankton assemblages in late summer (e.g. Olli and Heiskanen 1999). Cyanobacteria can control their vertical position in the water column by means of gas vacuoles (Walsby 1987), and therefore sedimentation of

Communicated by L. Hagerman, Helsingør

H. Limén (✉) · E. Ólafsson
Department of Zoology,
University of Stockholm,
10691 Stockholm, Sweden

Present address: H. Limén
GLIER, University of Windsor, Windsor,
Ontario, N9B 3P4, Canada,
e-mail: helenelimen@hotmail.com
Tel.: +1-519-2533000 ext. 2734

cyanobacteria has been regarded as minimal (e.g. Sellner et al. 1994). There appears to be a lack of substantial copepod herbivory in *Aphanizomenon* blooms, leading Sellner et al. (1996) to conclude that the often huge production is recycled in the water column, possibly through the cladoceran *Bosmina longispina maritima* or more likely through the microbial loop of bacteria–heterotrophic flagellates and their consumers. However, there is now clear evidence for sedimentation of *Aphanizomenon* sp. (Fallon and Brock 1980; Heiskanen and Kononen 1994), and, recently, Tallberg and Heiskanen (1998) noted that there was a substantial deposition of *Aphanizomenon* sp. in sediment traps in the Gulf of Finland. Clarification on whether such settlement is incorporated in the benthic food web is still lacking.

Stable carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotopic ratios of secondary producers can provide valuable information about the sources of their food. Animals often have $\delta^{13}\text{C}$ values similar to their food resource or are slightly enriched by about 1‰ (Peterson and Fry 1987). Isotopic measurements, made on the body tissue, reflect the accumulation of food over long time periods. Stable isotope analyses have been widely used in benthic food-web studies, but few include measurements of meiofauna (Schwinghamer et al. 1983; Spies and DesMarais 1983; Gearing et al. 1984; Siemstad and Wissmar 1985; Couch 1989; Riera et al. 1996), and to our knowledge no data on isotope measurements of ostracods are available.

The aim of the present study was to investigate if there was a significant difference in the stable carbon isotope values in the very top sediment layer compared to deeper down and if this would be mirrored in the tissue of the three ostracod species. We expected that the stable carbon isotope ratios of *C. neglecta* would differ from those of *P. fennica* and *H. sorbyana*, being more similar to the top layer than deeper layers. We chose to sample in an area with a relatively strong horizontal gradient in organic enrichment, as we expected different food regimes along such a gradient. We expected that *C. neglecta* would be favoured at the most-enriched areas because of higher phytoplankton production, its rapid uptake of newly settled material, short generation time and tolerance of low oxygen conditions. We also chose to sample during the late summer blooms of the cyanobacteria *Aphanizomenon* sp. to assess if it is transferred into the benthic food web. *Aphanizomenon* sp. has been found to be most depleted in $\delta^{13}\text{C}$ of all phytoplankton organisms accounted for in the water column, during this time of the year, in the Baltic proper (Rolff 2000).

Materials and methods

Study site and analysis preparation

The bay of Himmerfjärden in the northern Baltic proper (58°55'00–58°65'00N; 17°40'00–17°50'00W) is composed of a number of basins separated by shallow sounds. It is non-tidal and covers a surface area of ca. 175 km². The area is eutrophicated, with a gradient of organic material peaking near the vicinity of a sewage plant located

at the head of the bay. A total of five stations were chosen along the gradient at water depths between 24 and 36 m (Fig. 1).

Eight Kajak cores (50 cm² surface area) were taken at each station, five for ostracods and three for sediment analyses, in the beginning of August 2000. The first 3 cm were sectioned from cores taken for animal analysis. Cores for sediment analyses were sectioned into two layers, 0–2 mm and 2–10 mm. The first 2 mm, the flocculent layer of the sediment, was carefully siphoned from the sediment surface and kept separately from the rest of the first centimetre.

The sediment for ostracod analyses was sieved (200 µm), and retained ostracods were picked out, counted and identified. A number of individuals (15–25) of the same species and similar sizes were pooled to obtain a sufficient biomass for isotope analyses. Animals were placed in glass vials containing 6 psu MilliQ water and immediately frozen (–20°C). Prior to analyses, the samples were thawed and transferred to tin capsules containing 1 M HCl, to remove inorganic carbon, and then dried at 60°C for 24 h.

Samples for sediment analyses were homogenised, and about 10 ml was transferred to a glass vial and dried at 60°C for 24 h. The dried sediment was finely ground in a mortar, 10–15 mg put into tin capsules containing 1 M HCl and then dried at 60°C for 24 h. High densities of *C. neglecta* at stations 1 and 5 allowed separate analyses for juveniles and adults. Juveniles of the two other species were not sufficiently abundant for separate analyses. Stable carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) were measured using a solids/liquids preparation module (Europa Scientific, ANCA-NT system) coupled to an isotope quota mass spectrometer (Europa 20-20) as described by Ohlsson and Wallmark (1999).

Statistics

Differences in isotopic signatures were investigated by means of analysis of variance (ANOVA). Prior to the ANOVA, all data were log-transformed and tested for homoscedasticity by Cochran's C-test. Regression analyses were conducted to examine the relationship between sediment $\delta^{13}\text{C}$ and distance from the sewage plant.

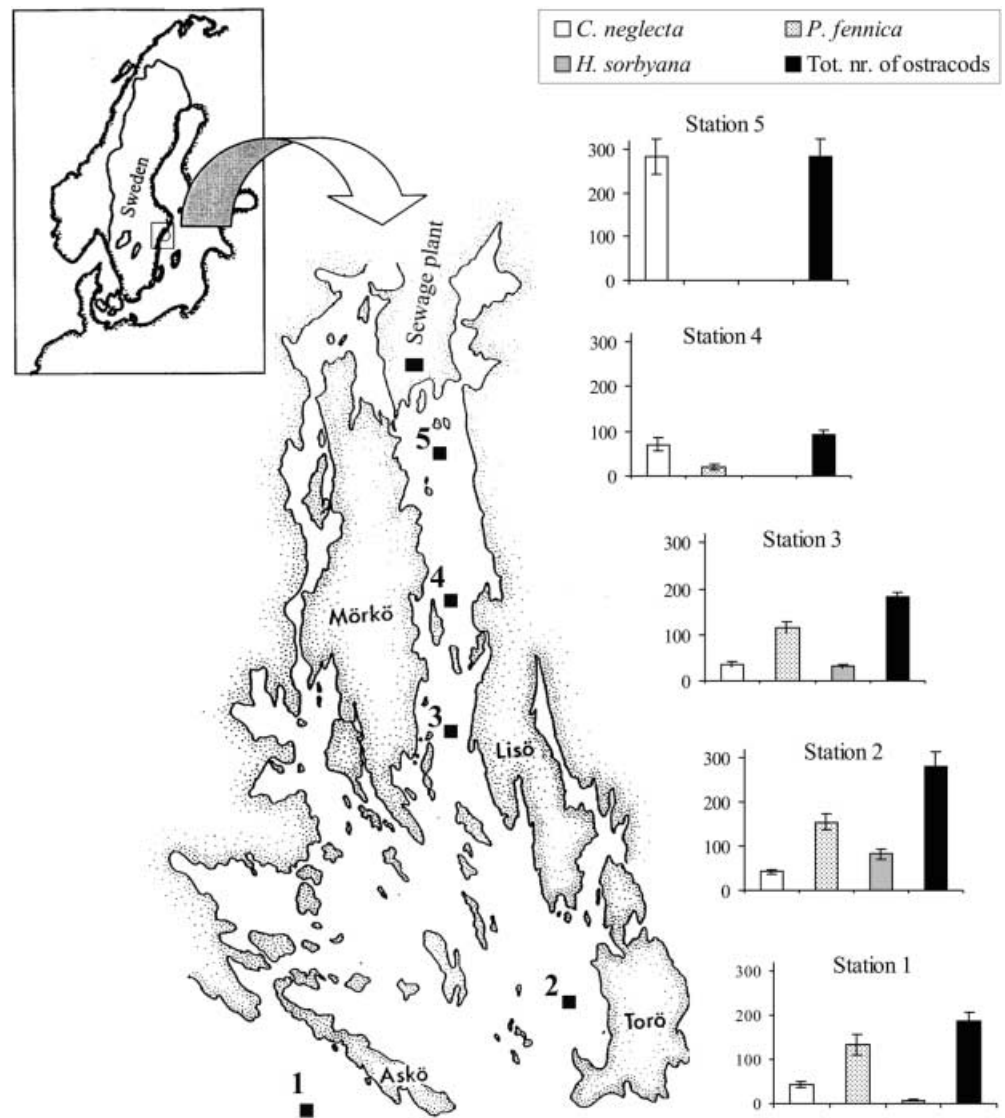
Results

Ostracods

The ostracod species composition varied among the stations. All three species were present at stations 1–3, in the outer part of the bay; here *Paracyprideis fennica* was the dominant species. At the two inner stations, *Candona neglecta* dominated and was the only species present at station 5, close to the sewage plant (Fig. 1).

When all samples were taken together, the $\delta^{13}\text{C}$ values were significantly lighter in adult *C. neglecta*, on average –22.4‰, compared with adult *P. fennica* and *Heterocyprideis sorbyana*, measuring on average –21.0‰ and –20.3‰, respectively (ANOVA, $P < 0.001$). However the station and ontogenetic stage largely influenced the isotopic carbon values in *C. neglecta*, which ranged from –28.1‰ to –20.9‰. Juvenile *C. neglecta* were much lower in $\delta^{13}\text{C}$ than adults at both stations 1 and 5 (Fig. 2). Adult *C. neglecta* were more enriched in $\delta^{13}\text{C}$ at station 4 compared with both stations 1 and 5 (ANOVA, $P < 0.003$) and most depleted at station 5 compared with stations 2, 3 and 4 (ANOVA, $P < 0.003$). *H. sorbyana* became more enriched in $\delta^{13}\text{C}$ at station 2 (ANOVA, $P < 0.05$), while *P. fennica* had similar carbon isotopic values at all stations (ANOVA, $P > 0.05$; Fig. 2).

Fig. 1 Map of Himmerfjärden. Numbers refer to sampling stations. At each station the ostracod assemblage structure is illustrated showing the average number of each species, total numbers of ostracods and standard error ($N=4$)



Sediment

Highly significant differences in $\delta^{13}\text{C}$ values of the sediment were found between stations and between sediment layers, with no significant interactions between the factors (two-way ANOVA, $P < 0.001$). The $\delta^{13}\text{C}$ values in the top 2 mm sediment layer changed along the gradient and became lighter in the inner part of the bay ($R^2 = 0.69$, $P < 0.001$; Fig. 3). The values ranged from -21.6‰ at station 1 to -24.8‰ at station 5 (Table 1).

Discussion

The ostracod species composition was relatively similar at the outer stations, but there was a clear shift to the dominance of *Candona neglecta* toward the sewage plant, with *C. neglecta* being the only species present in the vicinity of the sewage plant. Several factors may

influence the species composition in the bay. Close to the sewage plant the abundance of common phytoplankton species is larger than for the stations in the outer parts of the bay (Hajdu et al. 1997). Large amounts of settled phytoplankton at the bottom are likely to reduce oxygen levels associated with the breakdown of the phytodetritus. At the innermost station visual observations indicated the presence of sulphide in the sediment; beyond a thin (a couple of millimetres thick), light-brown layer, the sediment was black and smelled of sulphide, indicating anoxic conditions. *C. neglecta* has proven to be tolerant to long periods of hypoxia and sulphide exposure (Modig and Ólafsson 1998). *Heterocyprideis sorbyana*, despite also displaying tolerance to extended periods of low oxygen concentrations and sulphide exposure (Modig and Ólafsson 1998), was nevertheless absent at the two inner stations, indicating that factors other than oxygen and sulphide concentrations affect the species composition. Spatial differences in species

Fig. 2 Average carbon isotope values in the 0–2 mm and 2–10 mm sediment layers ($N=3$) and in each ostracod species ($N=5$): *Candona neglecta* (*C. neg.*), *C. neglecta* juveniles (*C. neg. juv.*), *Paracyprideis fennica* (*P. fen*) and *Heterocyprideis sorbyana* (*H. sorb*) at each station. Error bars: standard error

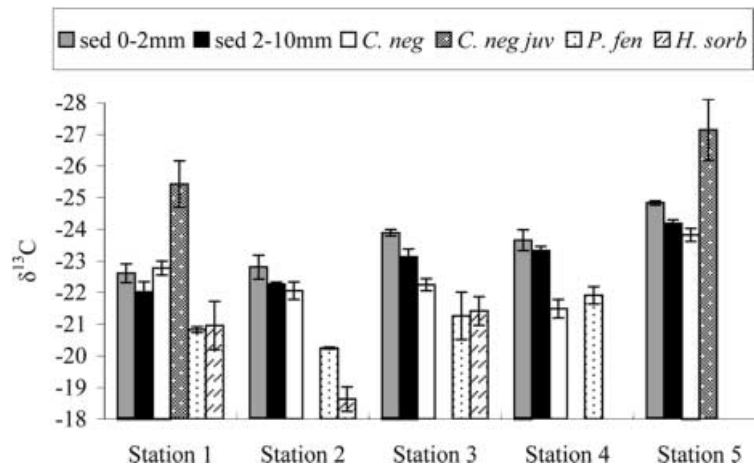
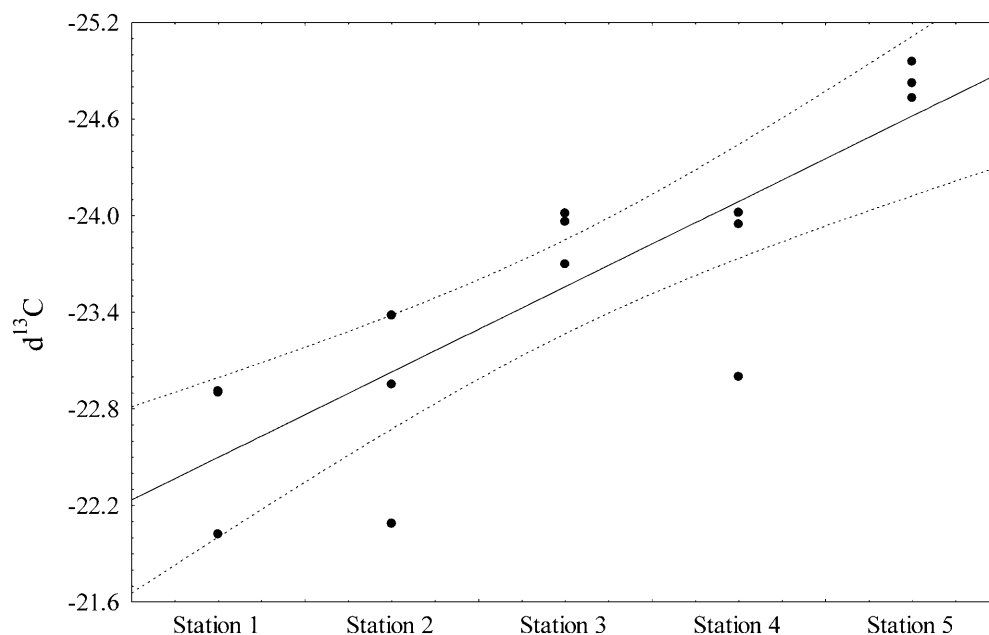


Fig. 3 Stable carbon isotopic values in the 0–2 mm sediment layer at all stations ($R^2=0.69$, $P<0.001$), with 95% confidence limits



composition might also originate from differences in the colonisation strategy: *C. neglecta* has several opportunistic characteristics including an ability to quickly exploit newly settled organic material (Ólafsson et al. 1999; Modig et al. 2000) and to complete its life cycle on a relatively short time scale. At the head of the bay, where the phytoplankton production is higher than in the outer parts (Hajdu et al. 1997), *C. neglecta* was clearly favoured. Assuming that *C. neglecta* occurs higher in the sediment than the other two species, *C. neglecta* should be more easily re-suspended and transported with the water currents to earlier azoic areas. The fact that mainly *C. neglecta* juveniles (99%) were found at station 5 might indicate that the conditions trigger its reproduction.

From the results it was clear that *C. neglecta* had a lighter isotopic carbon ratio than the other two species. This indicates that these three species are not utilising the same food resources in the field, a finding that is

Table 1 Results of the $\delta^{13}C$ values in the 0–2 mm and 2–10 mm sediment layers. Average values and standard error (SE) are presented ($N=3$)

Station	Sediment: 0–2 mm		Sediment: 2–10 mm	
	Avg. $\delta^{13}C$	SE	Avg. $\delta^{13}C$	SE
1	-22.6	0.30	-22.0	0.32
2	-22.8	0.38	-22.3	0.07
3	-23.9	0.10	-23.1	0.24
4	-23.7	0.33	-23.3	0.14
5	-24.8	0.06	-24.2	0.11

consistent with earlier laboratory studies (Ólafsson et al. 1999; Modig et al. 2000). *C. neglecta* also displayed significant differences in carbon signatures among stations, indicating that the species fed on different resources depending on where they were found. Such local differences have been recorded for several other brackish

Table 2 Average values (\pm SE in parentheses) of $\delta^{13}\text{C}$ in cyanobacteria (*Aphanizomenon* sp.) and seston (phytoplankton $< 10\ \mu\text{m}$) measured in late July 1999 (L. Hansson, unpublished data)

	Station 2	Station 3	Station 4	Station 5
<i>Aphanizomenon</i> sp.	-25.8 (0.05)	-26.8 (0.16)	-27.3 (0.56)	-27.7 (0.26)
N	4	4	3	4
Seston	-24.0 (0.14)	-25.2 (0.04)	-25.4 (0.03)	-23.5 (0.10)
N	3	3	3	3

water species, such as the amphipod *Monoporeia affinis* in the Baltic Sea (Rolff 1998). Spatial variations in the $\delta^{13}\text{C}$ of *C. neglecta* may reflect differences across the bay in the settlement of phytoplankton species of which *C. neglecta* subsequently ingests. It may, however, reflect that there is some choice of organic matter as there was for instance no enrichment of *C. neglecta* at station 1 and relatively high enrichment at station 4. Similarly, at station 2, *H. sorbyana* was more enriched than one would expect if they fed indiscriminately on the sediment organic matter. Obviously, the sediment particular matter (SPM) is composed of several components, which are likely to differ in carbon isotopic ratios, and therefore our signal may not represent the actual feeding source as it is an average value of all the SPM components. Ostracods are also able to feed on protozoans and meiobenthic animals (Liperovskaya 1948), which would result in a more enriched carbon isotopic ratio than if they were feeding on primary producers alone.

The flocculent sediment layer always had lighter carbon ratios than the sediment below, and in most cases this was mirrored in a slight enrichment in *C. neglecta*, while the other two species were generally more enriched. It is conceivable that *C. neglecta* is more or less confined to the upper 2 or 3 mm and feeds on the flocculent layer, while the other two species have a slightly deeper vertical distribution and hence are feeding on an older, isotopically more enriched carbon source. We have tried in vain to assess their vertical distribution on a millimetre scale by various procedures. These studies have been hampered by the fact that the first millimetre of the sediment is flocculent, and therefore difficult to slice on a scale satisfying our objectives. The results clearly indicate a niche differentiation by the three ostracod species. To establish the importance of specific phytoplankton species for the ostracods, analyses of gut pigments can, for example, be used.

The carbon isotopic ratio was much lighter in *C. neglecta* juveniles compared with adults. Studies performed in the bay in July 1999 (L. Hansson, personal communication) showed that the carbon isotopic signal of the pelagic cyanobacteria, *Aphanizomenon* sp. was on average -27.7 in the vicinity of the sewage plant and became more enriched in the outer parts of the bay measuring -25.8 (Table 2). In the present study, the average $\delta^{13}\text{C}$ value of *C. neglecta* juveniles was -27.1 at the head of the bay and -25.4 in the outer part of the bay, which strongly indicates that they feed on cyanobacteria. Animals often have $\delta^{13}\text{C}$ values similar to their food resource or are slightly enriched by about 1‰ (Peterson and Fry 1987). The seston (phytoplankton and

detritus) in the water column was clearly too enriched in carbon isotopic composition to be a plausible food source to juvenile *C. neglecta*. In the study area diatoms constitute the largest biomass of the phytoplankton in spring; during summer they are only a small fraction while cyanobacteria become more important (Hajdu et al. 1997). An extensive seasonal study on the planktonic food web in the outer part of the bay showed that $\delta^{13}\text{C}$ values for cyanobacteria were far more depleted than those of other phytoplankton species in late summer (Rolff 2000). As the phytoplankton settles it might change in carbon isotopic composition. However, Gearing et al. (1984) showed that there was little isotopic change in planktonic carbon as it decomposed to detritus. The carbon isotopic value in *C. neglecta* adults ranged between -22.8 and -23.8 . These values indicate that *C. neglecta* does not solely ingest cyanobacteria during its life span. Rolff (2000) showed that the $\delta^{13}\text{C}$ values of phytoplankton undergo large seasonal variations according to a bimodal pattern, with enriched values during spring and autumn blooms. *C. neglecta* has been demonstrated to exploit newly settled diatoms (Ólafsson et al. 1999; Modig et al. 2000) and most likely use a wide range of settled material, with different carbon isotopic compositions during the year. Benthic cyanobacteria can either be avoided (O'Neil and Roman 1994; Buffan-Dubau and Carman 2000) or ingested by meiobenthic species (Grant et al. 1983; Buffan-Dubau et al. 1996). Whether pelagic cyanobacteria contribute significantly to sub-tidal benthic food webs has not been elucidated yet. It has been shown that *Aphanizomenon* sp. settles to the bottom (Fallon and Brock 1980; Heiskanen and Kononen 1994) and that it may even be a large part of settled material (Tallberg and Heiskanen 1998). This is the first study that shows evidence of incorporation of such material into the benthic food web.

Acknowledgements We thank the staff at the Askö laboratory for assistance in the field and its director B. Ganning for providing laboratory facilities. Many thanks to L. Hansson and U. Larsson for access to unpublished data and to H. Wallmark who performed isotopic measurements. We also want to thank M. Skov and C. Rolff who made valuable remarks on the manuscript. This study was financially supported by SMF (Stockholm Marine Research Centre) and Åke Stordals Minne fund.

References

- Alm G (1915) Monographie der Schwedischen Süßwasser-Ostracoden nebst systematischen Besprechungen der Tribus Podocopa. Zool Bidr Upps 4:1–247

- Ankar S, Elmgren R (1976) The benthic macro- and meiofauna of the Askö-Landsort area (northern Baltic proper). A stratified random sampling survey. Contrib Askö Lab, Univ Stockholm 11:1–115
- Buffan-Dubau E, Carman KR (2000) Diel feeding behaviour of meiofauna and their relationships with microalgal resources. *Limnol Oceanogr* 45:381–395
- Buffan-Dubau E, de Wit R, Castel J (1996) Feeding selectivity of the harpacticoid copepod *Canuella perplexa* in benthic muddy environments demonstrated by HPLC analyses of chlorin and carotenoid pigments. *Mar Ecol Prog Ser* 137:71–82
- Couch CA (1989) Carbon and nitrogen stable isotopes of meiobenthos and their food resources. *Estuar Coast Shelf Sci* 28:433–441
- Fallon RD, Brock TD (1980) Decomposition of blue-green algae (cyanobacterial) blooms in Lake Mendota, Wisconsin. *Appl Environ Microbiol* 37:820–830
- Gearing JN, Gearing PJ, Rudnick DT, Requejo AG, Hutchins MJ (1984) Isotopic variability of organic carbon in a phytoplankton-based temperate estuary. *Geochim Cosmochim Acta* 48:1089–1098
- Grant IF, Egan EA, Alexander M (1983) Measurement of rates of grazing of the ostracod *Cyprinotus carolinensis* on blue-green algae. *Hydrobiologia* 106:199–208
- Hajdu S, Larsson U, Skärnlund K (1997) Växtplankton. In: Elmgren R, Larsson U (eds) *Himmerfjärden, Förändringar i ett näringsbelastat kustekosystem i Östersjön*. Naturvårdsverket Report, pp 1–197
- Heiskanen A-S, Kononen K (1994) Sedimentation of vernal and late summer phytoplankton communities in the coastal Baltic Sea. *Arch Hydrobiol* 131:175–198
- Liperovskaya ES (1948) On the feeding of freshwater ostracods. Translated by Freshwater Biological Association, NS no. 1, Far Sawrey Amleside, Cumbria, U.K. Originally published in *Russian, in Zool Zh* 27:125–136
- Modig H, Ólafsson E (1998) Responses of Baltic benthic invertebrates to hypoxic events. *J Exp Mar Biol Ecol* 229:133–148
- Modig H, van de Bund WJ, Ólafsson E (2000) Uptake of phytodetritus by three ostracod species from the Baltic Sea: effects of amphipod disturbance and ostracod density. *Mar Ecol Prog Ser* 202:125–134
- Ohlsson KEA, Wallmark PH (1999) Novel calibration with correction for drift and non-linear response for continuous flow isotope ratio mass spectrometry applied to the determination of $\delta^{15}\text{N}$, total nitrogen, $\delta^{13}\text{C}$ and total carbon in biological material. *Analyst, Lond* 124:571–577
- Ólafsson E, Elmgren R (1997) Seasonal dynamics of sublittoral meiobenthos in relation to phytoplankton sedimentation in the Baltic Sea. *Estuar Coast Shelf Sci* 45:149–164
- Ólafsson E, Modig H, van de Bund WJ (1999) Species specific uptake of radio-labelled phytodetritus by benthic meiofauna from the Baltic Sea. *Mar Ecol Prog Ser* 177:63–72
- Olli K, Heiskanen A-S (1999) Seasonal stages of phytoplankton community structure and sinking loss in the Gulf of Riga. *J Mar Syst* 23:165–184
- O'Neil JM, Roman MR (1994) Ingestion of the cyanobacterium *Trichodesmium* spp. by pelagic harpacticoid copepods *Macrosetella*, *Miracia* and *Oculosetella*. *Hydrobiologia* 292/293:235–240
- Peterson B, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Riera R, Richard P, Grémare A, Blanchard G (1996) Food source of intertidal nematodes in the Bay of Marennes-Oléron (France), as determined by dual stable isotope analysis. *Mar Ecol Prog Ser* 142:303–309
- Rolf C (1998) Stable isotope studies of contaminant and material transport in Baltic pelagic food-webs. PhD thesis, University of Stockholm, Stockholm, Sweden. ISBN 91-87272-62-8
- Rolf C (2000) Seasonal variation in delta 13-C and delta 15-N of size-fractionated plankton organisms at a coastal station in the northern Baltic proper. *Mar Ecol Prog Ser* 203:47–65
- Savolainen I, Valtonen T (1983) Ostracods of the north-eastern Bothnian Bay and population dynamics of the principal species. *Aquilo Ser Zool* 22:69–76
- Schwinghamer P, Tan FC, Gordon DC Jr (1983) Stable carbon isotope studies on the Pecks Cove mudflat ecosystem in the Cumberland Basin, Bay of Fundy. *Can J Fish Aquat Sci* 40:262–272
- Sellner KG, Olson MM, Kononen K (1994) Copepod grazing in a summer cyanobacteria bloom in the Gulf of Finland. *Hydrobiologia* 292/293:249–254
- Sellner KG, Olson MM, Olli K (1996) Copepod interactions with toxic and non-toxic cyanobacteria from the Gulf of Finland. *Phycologia* 35[Suppl 6]:177–182
- Siemenstad CA, Wissmar RC (1985) $\delta^{13}\text{C}$ evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. *Mar Ecol Prog Ser* 22:141–152
- Spies RB, DesMarais DJ (1983) Natural isotope study of trophic enrichment of marine benthic communities by petroleum seepage. *Mar Biol* 73:67–71
- Tallberg P, Heiskanen A-S (1998) Species-specific phytoplankton sedimentation in relation to primary production along an in-shore-offshore gradient in the Baltic Sea. *J Plankton Res* 20:2053–2070
- Walsby AE (1987) Mechanisms of buoyancy regulation by cyanobacteria in the Baltic Sea. *Eur J Phycol* 20:87–94