

Effects of bioturbation by three macrozoobenthic species and predation by necto-benthic mysids on cladoceran benthic eggs

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ABSTRACT: The effects of bioturbation and predation by the amphipod *Monoporeia affinis*, the bivalve *Macoma balthica* and the polychaetes *Marenzelleria* spp. were studied on the number, vertical distribution and hatching of benthic eggs (ephippia) of the cladoceran *Bosmina longispina maritima*. It was hypothesised that the 3 functionally different macrobenthic species affect *Bosmina* ephippia to different degrees. In addition, it was hypothesised that macrofaunal bioturbation either inhibits or enhances predation by the necto-benthic mysid *Mysis mixta* on cladoceran benthic eggs. *M. affinis* and *M. balthica* caused a 48 and 23 % decrease in the total number of *Bosmina* ephippia, respectively, indicating egg predation. In addition, *M. balthica* extended the distribution of eggs into deeper sediment layers. Both *M. affinis* and *M. balthica* suppressed the daily hatching rate of *Bosmina*, and the effect of the bivalves (reduction 92 %) was stronger than that of the amphipods (34 to 78 %). None of the benthic species promoted the predation of mysids on *Bosmina* eggs. Instead, both *M. affinis* and *M. balthica* reduced the number of ephippia in the sediment surface (by 79 and 43 %, respectively), implying that these species decrease the ability of mysids to feed on cladoceran benthic eggs. *M. balthica* was the most harmful species for the recruitment of *Bosmina*, whereas the nonindigenous *Marenzelleria* spp. did not affect ephippia.

KEY WORDS: *Bosmina* ephippia · Bioturbation · Macrofauna · Mysids · Recruitment

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INTRODUCTION

The production of dormant eggs is an important means for zooplankton to escape unfavourable conditions, e.g. decreasing temperature and deteriorating food conditions (Marcus & Boero 1998). High numbers of zooplankton resting stages have been recovered in marine (Onbé 1985), brackish (Viitasalo & Katajisto 1994) and limnetic sediments (De Stasio 1989). Various benthic processes affect the viability and recruitment of dormant eggs from bottom sediments to plankton (Marcus & Boero 1998), which, in turn, may be crucial for the success of subsequent generations (De Stasio 1989).

Translocation of zooplankton eggs in the sediment is a critical factor since eggs may hatch only when close to the sediment-water interface, presumably mainly due to the supply of dissolved oxygen (Uye et al. 1979,

Kankaala 1983). High sedimentation rates typical of the northern Baltic Sea ($>10 \text{ g m}^{-2} \text{ d}^{-1}$; Heiskanen & Tallberg 1999) cause a rapid burial of settling particles. Moreover, soft-bottom macrofauna actively rework their habitat, changing the physical structure, layering and oxygen content of the sediment (Rhoads 1974). Certain deposit-feeding polychaete species transport copepod eggs upwards (Marcus & Schmidt-Gengenbach 1986), whereas the amphipod *Monoporeia affinis* (hereafter *Monoporeia*) has been considered to bury eggs in Baltic sediments (Albertsson & Leonardsson 2000). In addition to vertical movements, predation may also play a role, as benthic deposit-feeders may ingest dinoflagellate cysts (Persson & Rosenberg 2003), copepod eggs (Parker et al. 1996) and ephippia (benthic eggs shielded by a transparent membrane) of daphnid cladocerans (Cáceres & Hairston 1998). Moreover, Albertsson & Leonardsson (2001) observed a neg-

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ative effect of *Monoporeia* on the hatching of the brackish water cladoceran *Bosmina longispina maritima* (hereafter *Bosmina*) and suggested that it resulted from predation by the amphipods. However, the mechanism underlying this observation remains unclear.

Besides infauna, epifaunal predators may affect the sediment surface properties. The necto-benthic mysid *Mysis mixta* is mainly a zooplanktivore (Viherluoto et al. 2000), but spends a large proportion of its life in the vicinity of the sea floor. To date, however, information on the overall impact of pelagic mysids on benthic habitats is limited (Albertsson 2004, Roast et al. 2004). Recently, *M. mixta* was found to eat *Bosmina* ephippia distributed on the sediment surface (Viitasalo & Viitasalo 2004). In contrast, mysids appeared incapable of feeding on ephippia that were mixed within the sediment, suggesting that the vertical distribution of sedimented ephippia is crucial not only for the recruitment of cladocerans but also for the rate of epibenthic predation by mysids (Viitasalo & Viitasalo 2004).

The effects of bioturbation on the movement of sediment particles have been investigated intensively during the few last years. Nevertheless, few data exist on the impact of various benthic taxa on zooplankton propagules and even less on cladoceran resting eggs, which are relatively large (e.g. *Bosmina* ephippia: ~400 µm). The objective of the present study was to reveal how 3 functionally different zoobenthic species—the mobile surface deposit-feeding *Monoporeia*, the semi-mobile suspension- and deposit-feeding bivalve *Macoma balthica* (hereafter *Macoma*) and the non-indigenous deep-burrowing polychaetes *Marenzelleria* spp. (hereafter *Marenzelleria*)—affect the vertical distribution, abundance and recruitment of *Bosmina* ephippia in the sediment. In addition, the aim was to define the effect of bioturbation on the ability of mysids to reach *Bosmina* benthic stages. It was hypothesised that due to their different feeding and burrowing modes, the 3 benthic species have different impacts on *Bosmina* ephippia.

Two separate experiments were conducted, one examining the effects of benthic animals and mysids on the vertical distribution and abundance of *Bosmina* ephippia (bioturbation experiment, BE) and another examining the effect of *Monoporeia* and *Macoma* on the recruitment of *Bosmina* (hatching experiment, HE). Experiments were done during 2003 and 2004 at the Tvärminne Zoological Station (University of Helsinki), southwestern coast of Finland.

MATERIALS AND METHODS

Natural history of the experimental species. During the last few decades, soft-bottom macrofaunal commu-

nities of the northern Baltic Sea have experienced broad-scale changes, driven by eutrophication and changes in the deep-water salinity (Laine et al. 1997). *Monoporeia*, previously a numerical dominant of benthic communities over large areas, has drastically decreased, while *Macoma* has gradually increased in importance in many coastal habitats and may form almost monospecific communities (Perus & Bonsdorff 2004). Furthermore, polychaetes from the genus *Marenzelleria* have spread rapidly since their introduction to the Baltic Sea in the 1980s (Bastrop & Blank 2006). The densities range from less than 100 up to 10 000 ind. m⁻² for *Monoporeia*, to 2000 ind. m⁻² for *Macoma* and to 5000 ind. m⁻² for *Marenzelleria* (Cederwall et al. 1999, Kangas et al. 2001, Zettler et al. 2002).

Field collections. Zoobenthos, mysids and muddy surface sediment (15% loss on ignition of dry weight after 2 h at 550°C) with *Bosmina* ephippia were collected from soft-bottom areas in the Gulf of Finland (59° N, 23° E) and in the Bothnian Sea (61° N, 20° E) from depths of 35 to 100 m. An Ockelmann benthic sledge (mouth opening 12 × 30 cm, net length 52 cm, mesh size 150 µm) was used to collect surface layers of the sediment (approximately the upper 5 cm) containing high densities of *Bosmina* eggs. The sediment was kept in cool boxes to retain the prevailing temperature (~5°C) until it was transported to the laboratory for processing. *Macoma* was collected with a bottom trawl (length 7 m, width 4 m, mesh size 10 mm) and *Mysis mixta* with an epibenthic sledge (mouth opening 41 × 23 cm, net length 115 cm, 1 l cod end). *Monoporeia* and *Marenzelleria* were taken with a van Veen grab. Sediment was put into 90 l buckets filled with seawater, and the fragile amphipods and polychaetes were gently picked up under water by small sieves. In the field, all animals were immediately transferred into cool boxes with seawater from below the thermocline (5 to 10°C), and for macrofauna, some sediment from the grab was added.

In the laboratory, animals were transferred to 30–50 l aquaria (macrofauna with some sediment from the collection site) with continuously flowing seawater (5 to 6 PSU, 5 to 10°C) and with gentle aeration until initiating the experiments. Amphipods and mysids were always handled in dim light to protect their sensitive eyes.

Bioturbation experiment (BE). The experimental units in BE consisted of plexiglass cylinders (height 20 cm, diameter 14 cm) equipped with a movable bottom. The sediment was sieved through a series of 500, 200 and 100 µm meshes to remove macrofauna and *Bosmina* ephippia (~400 µm) from smaller material. The 100 to 500 µm fraction was put aside and kept at 5°C until collection of *Bosmina* eggs. The <100 µm

fraction was homogenised by stirring, measured out to the experimental cores, 1.2 l in each, producing a final sediment thickness of ~6 cm, and allowed to settle for 8 d at 5°C. The cores were immersed in 90 l basins, 6 cores in each, carefully filled with seawater. The water (5 to 6 PSU) was pumped from 7 to 8 m depth from a nearby archipelago area and was not likely to contain cladoceran benthic eggs, which do not remain suspended in water but sink to the bottom upon their release. The inflowing water was checked under a dissecting microscope, and no *Bosmina* ephippia were found. The water was allowed to flow through the basins, and aeration was added to each basin. During the incubation, the temperature (measured 3 times wk^{-1}) was $8.2 \pm 0.9^\circ\text{C}$ (mean \pm SD), the flow rate (measured once weekly) was $370 \pm 80 \text{ ml min}^{-1}$ (mean \pm SD) and the oxygen concentration (measured once weekly with a VWR D0200 Portable Dissolved Oxygen and Temperature Instrument) was $11.1 \pm 0.3 \text{ mg l}^{-1}$ (mean \pm SD). To prevent the escape of the amphipods, polychaetes and mysids, all cores were capped with a steel net with 0.5 mm mesh size.

To separate *Bosmina* eggs from the 100 to 500 μm sediment fraction, it was poured on a 100 μm sieve, washed with sugar-water solution (0.5 kg of sugar in 0.5 l of water) into centrifuge tubes and centrifuged for 3 min at $906 \times g$. After centrifuging, ephippia remained floating in the supernatant and were easy to collect with a pipette. This 'sugar flotation method' does not harm cladoceran benthic stages (Onbé 1978). Ephippia ($n = 120$) were pipetted into each core and distributed evenly onto the sediment. After 1 h, 160 ml of sediment ($<100 \mu\text{m}$) were added to each core to bury the eggs under a 0.5 to 1 cm thick sediment layer, approximating an average annual accumulation rate in the study area (Viitasalo & Katajisto 1994, Heiskanen & Tallberg 1999), and the sediment was allowed to settle overnight. Hatching of ephippia introduced to a depth of 0.5 to 1 cm should be inhibited (cf. Kankaala 1983); hence, eggs were not expected to hatch in the initial conditions.

Seven treatments ($n = 5$) were carried out: controls without animals, 3 treatments with only macrofauna—*Monoporeia* (treatment notation: Mo), *Macoma* (Ma) and *Marenzelleria* (Mz)—and 3 treatments combining macrofauna with mysids (Mo + My, Ma + My and Mz + My). The animal densities and sizes are defined in Table 1.

The 5 replicates of the 7 treatments were distributed each in a different basin, and within a basin the experi-

mental units were randomly assigned to the different treatments. Macrofauna were introduced to the cores and left to rework the sediment in darkness for 22 d. In the treatments with *Mysis mixta*, 1 mysid was added to each core on Day 22 for 3 d. At the end of the incubations, the average thickness of the light brown oxidised layer was visually estimated and measured with a ruler. In addition, the maximum mixing depth by the animals was estimated on the basis of visible extensions of animal burrows or paths. The water above the sediment was carefully siphoned off and checked for ephippia. The upper 1 cm of the sediment was cut into two 0.5 cm slices and the rest into 1 cm slices. The slicing apparatus consisted of a piston attached to a stand and a separate cutting plate (following the principle of Hakala 1971). A core was attached to the piston, which pushed the sediment upwards. During the sectioning, the sediment sank slightly due to some loss of water. As a result, the deepest layer acquired was the 3 to 4 cm stratum.

Each slice was washed onto a 100 μm mesh and the number of ephippia was counted under a dissecting microscope. The condition of the animals was defined on the basis of their motion (*Macoma*) or swimming behaviour (*Monoporeia* and *Marenzelleria*). The survival of *Macoma* was 97%, while the other species were in good health. Animals were preserved in 5% buffered formalin and measured for length. The number of recovered ephippia in the control cores was 100.6 ± 3.1 (mean \pm SE). The predation rates of mysids on ephippia (ephippia d^{-1}) were determined by subtracting the number of recovered ephippia in the treatments with mysids to the average recovery of ephippia in the corresponding treatments with only infauna.

Sediment oxygen profiles. In the BE, the effect of the activities of macrofauna on the oxygen penetration depth in the sediment was investigated by measuring oxygen profiles with a Clark-type microelectrode

Table 1. Body sizes (mean \pm SD) and densities (ind. core^{-1} and ind. m^{-2}) of macrofauna and mysids used in the bioturbation and hatching experiments. *Marenzelleria*, *Monoporeia* and *Mysis mixta* were measured from the front of the head to the tip of the last setiger (*Marenzelleria*) or telson (*Monoporeia* and *M. mixta*). *Macoma* was measured across the maximum shell width

Experiment	Species	Size	n (mm)	Density core^{-1} m^{-2}	
Bioturbation (BE)	<i>Monoporeia</i>	6.0 ± 0.6	267	30	1950
	<i>Macoma</i>	17.2 ± 1.1	117	12	780
	<i>Marenzelleria</i>	30.0 ± 4.4	20	3	190
	<i>Mysis mixta</i>	17.4 ± 1.5	15	1	65
Hatching (HE)	<i>Monoporeia</i>	7.0 ± 0.8	112	20	1960
		7.0 ± 0.8	112	50	4900
	<i>Macoma</i>	16.9 ± 1.3	96	8	780

(Unisense OX100). A micromanipulator was used to introduce the sensor (outer tip diameter 90 to 110 μm) vertically in the sediment at 0.5 mm intervals. The sensor current was measured by a high-sensitivity picoammeter (Unisense PA2000) and converted to O_2 partial pressure values. The penetration depth of dissolved oxygen was estimated from the oxygen tension curves according to Glud et al. (2003). Three to 4 replicate profiles were measured in 3 replicate cores of each treatment (no measurements in the treatments with mysids), yielding a total of 9 to 10 profiles per treatment.

Hatching experiment (HE). The sediment used for the HE was sieved through 0.5 mm mesh to remove macrofauna (but not ephippia) and stirred to homogenise the distribution of cladoceran eggs. Two replicate samples of 50 ml of the homogenised sediment were taken to determine the initial density of *Bosmina* ephippia. Ephippia were separated from sediment as in the BE (Onbé's sugar flotation method) and preserved in 70% ethanol for examination and counting under a dissecting microscope.

Experimental plexiglass cores (height 20 cm, diameter 11.4 cm) were filled with 600 ml of homogenised sediment and ~1.4 l of 10 μm filtered seawater (FSW), until the water surface reached ~2 cm from the top margin of the core. Sediment was allowed to settle for 32 h. The average final sediment depth was 3.7 cm at the end of the experiment. Gentle aeration through a thin needle was added right below the water surface to keep the oxygen content sufficiently high (>80%) but to avoid disturbance at the sediment surface. In addition to the amphipod and bivalve densities used in the BE, a higher amphipod density of 50 ind. core⁻¹ was used ($n = 4$; Table 1). As in the BE, control cores ($n = 4$) without macrofauna were included and treated in the same manner as cores with animals. Treatments were randomly distributed among the experimental units.

Cores were incubated in darkness in a temperature-controlled room (3°C) for 21 d ('cold period'). Subsequently, the temperature was raised to 13°C for 5 d ('warm period'). At 2 to 4 d intervals, the water in each core was carefully siphoned off and replaced with new water. The water collected was poured on a 50 μm sieve to collect hatched cladocerans. Water was removed 8 times during the cold period and once during the warm period. The samples were preserved in 5% buffered formalin. Prior to siphoning, the oxygen concentration in the water ($11.7 \pm 0.3 \text{ mg l}^{-1}$) was measured at ~6 cm depth in the water (YSI Model 95 Handheld Dissolved Oxygen and Temperature System). All hatched individuals were counted under a dissecting microscope. A 200 μm sieve capped with paper was lowered right above the sediment surface, ensuring a steady and slow water flow through the margins of the

sieve and minimising sediment resuspension. At the end of the experiments, water was siphoned off, sediment was thoroughly mixed and a sediment sample of 40 ml was taken with a syringe from 3 replicate cores to define the final cladoceran egg density. Benthic animals were checked for condition and measured for length as in the BE.

To determine the vertical distribution of eggs in the 0.5 mm sieved sediment after settling (the procedure used in the HE), an additional depth distribution control was included. Sieved and stirred sediment (800 ml) was added to 3 plexiglass cores (height 20 cm, diameter 14 cm) with a movable bottom. The cores were filled with FSW and sediment was allowed to settle in darkness (5°C). No macrofauna was added to the cores. After 36 d, the sediment was sliced into four 0.5 cm (the upper 2 cm) and one 1 cm sections down to 3 cm (other details as in the BE). A sediment sample of 40 ml was taken with a syringe from each slice. The average density of *Bosmina* ephippia was $790 \pm 70 \text{ core}^{-1}$ (mean \pm SE), corresponding to $5.1 \times 10^4 \text{ ephippia m}^{-2}$. Vertically, the density ranged from 1.3 to 1.9 ephippia cm^{-3} , but the depth distribution was rather even throughout the layers, i.e. concentration of eggs at a certain depth was not observed (the difference in the egg density across the 5 depth strata in a 1-way F -test: $F_{4,10} = 1.63$, $p = 0.24$).

Statistical tests. For normally distributed and homoscedastic data, a parametric t -test or single- or 2-factor analysis of variance (ANOVA; F -test) was used to test the differences between 2 or more groups, respectively. Square-root and logarithmic transformations were used to fulfil the parametric assumptions. Otherwise, a nonparametric procedure (Mann-Whitney U -test) was applied. Multiple comparisons were made using a Tukey HSD post hoc test. All statistical analyses were done with SPSS 11.5 software.

RESULTS

Sediment reworking by three benthic species (BE)

Bioturbation patterns. In the BE, distinctive sediment reworking patterns were observed among the 3 macrofaunal species. The mixing effect of *Monoporeia* was confined to the upper 1 to 2 cm, whereas *Macoma* extended the mixed zone down to ~5 cm. Faecal pellets of the amphipods (diameter ~200 μm) were mainly found in the sediment samples from the 2 uppermost strata (0 to 0.5 and 0.5 to 1 cm), while bivalve pellets (diameter ~300 μm) were recorded in the layers down to 3 cm depth. A 0.5 cm thick stratum could contain several 10 000 pellets. In the cores with *Marenzelleria*, pellets (diameter ~100 μm) were much less abundant

but burrows were observed vertically all through the sediment. The topmost sediment layers were oxidised down to 1.7 to 2.7 cm depth; *Macoma* and mysids significantly deepened the light brown layer (Tables 2 & 3).

Oxygen properties. The average depth of O₂ penetration ranged from 2.2 mm in Mz and control to 3.2 mm in Mo, and the average O₂ concentrations at the sediment–water interface ranged from 1.6 ml O₂ l⁻¹ in Ma and control to 2.0 ml O₂ l⁻¹ in Mo (Table 2). The differences between the treatments were not statistically significant (Table 3).

Depth distribution and abundance of ephippia. In the BE, the 3 macrofaunal species had different effects on the distribution of *Bosmina* benthic eggs (Table 4, Fig. 1). In the treatment with *Marenzelleria*, the distribution of ephippia was almost identical to the control cores, indicating that the activities of polychaetes did not translocate ephippia vertically. In contrast, *Macoma* significantly extended the distribution of ephippia into deeper layers, whereas *Monoporeia* caused a decrease in the number of eggs in the uppermost 0.5 cm stratum (Tables 4 & 5, Fig. 1). Both *Monoporeia* and *Macoma* decreased the total number of ephippia by 48 and 22%, respectively, and the effect of *Monoporeia* was stronger than that of *Macoma* (Table 4).

Table 2. Bioturbation experiment. Depth of the light brown (mixed) sediment layer (n = 5) and the O₂ penetration depth (n = 3) and concentration (n = 3) at the sediment-water interface (mean ± SE). Mo: *Monoporeia*, Ma: *Macoma*, Mz: *Marenzelleria*, My: mysid

Treatment	Light brown layer (cm)		O ₂ penetration (mm)	O ₂ concentration (ml l ⁻¹)
	No mysids	Mysids	No mysids	No mysids
Control	1.9 ± 0.1		2.2 ± 0	1.6 ± 0.3
Mo/Mo + My	2.1 ± <0.1	2.2 ± <0.1	3.2 ± 0.4	2.0 ± 0.3
Ma/Ma + My	2.3 ± 0.2	2.7 ± 0.1	2.7 ± 0.7	1.6 ± 0.3
Mz/Mz + My	1.7 ± 0.2	1.8 ± 0.1	2.2 ± 0.1	1.7 ± 0.2

Table 3. Bioturbation experiment. Effects of macrofauna and mysids on various sediment parameters. ANOVA notations: 1-f = single-factor, 2-f = 2-factor. Significant values in **bold** (p < 0.05). C: control. See Table 2 for other abbreviations

Parameter	ANOVA	Factor	Between subject	Tukey HSD
Oxidised layer	2-f	Macrofauna	$F_{3,25} = 15.7, p < \mathbf{0.001}$	C-Ma: 0.001 Mo-Ma: 0.016 Mo-Mz: 0.007 Ma-Mz: <0.001
		Mysid	$F_{1,25} = 4.6, p = \mathbf{0.042}$	
		Interaction	$F_{2,25} = 0.8, p = 0.46$	
O ₂ penetration	1-f	Macrofauna	$F_{3,8} = 1.4, p = 0.32$	
O ₂ concentration	1-f	Macrofauna	$F_{3,8} = 0.5, p = 0.72$	

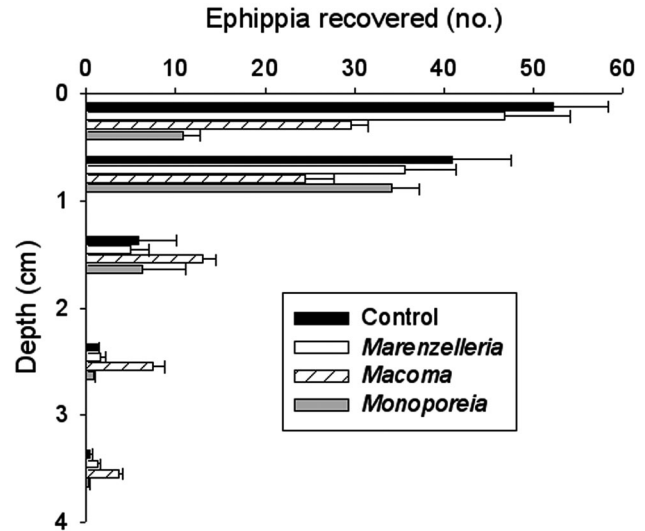


Fig. 1. *Bosmina longispina maritima*. Bioturbation experiment. Recovered cladoceran ephippia (no.) in each depth stratum in treatments without mysids (mean ± SE)

Epibenthic predation (BE)

When *Mysis mixta* was added to the *Monoporeia* cores, the total recovery of ephippia declined slightly (from 52 to 44%) but not significantly (Tables 4 & 5).

The calculated average predation rate of the mysids was 2.7 ± 2.1 ephippia d⁻¹ (Mo + My compared to Mo). In the cores with *Macoma* or *Marenzelleria*, mysids caused no additional loss of ephippia (Tables 4 & 5), indicating that benthic fauna did not bring ephippia within reach of the mysids. A few marginally significant differences, however, were found: Mysids appeared to increase *Bosmina* ephippia in the deepest sediment layer, suggesting additional burial, and the interaction term in the 2 to 3 cm layer and in the total recovery of ephippia indicated that the effect of macrofauna on cladoceran benthic eggs was affected by the presence of mysids (Table 4).

Effects of macrofauna on hatching (HE)

In the HE, the average initial total density of *Bosmina* ephippia in the sediment was 3640 ephippia core⁻¹, corresponding to 3.6×10^5 ephippia m⁻² (Table 6). This is within the range

of the field densities in the study area (Viitasalo & Katajisto 1994). At the end of the experiment, the densities ranged from 2820 to 3060 ephippia core⁻¹ among the treatments, but these differences were not significant ($F_{3,8} = 1.3$, $p = 0.35$); differences between the ini-

tial and final conditions were also not significant (control: $t = 2.1$, $df = 3$, $p = 0.12$; Mo: $U = 0.0$, $df = 3$, $p = 0.08$; Mo high: $t = 2.8$, $df = 3$, $p = 0.07$; Ma: $t = 1.9$, $df = 3$, $p = 0.15$). Almost no hatching occurred during the cold period (Days 0 to 21). After 21 d, hatching was promoted by the raised temperature (13°C for 5 d), and the average total number of hatched individuals per core ranged from 1 in Ma to 13 in the control (Table 6). Macrofauna significantly decreased *Bosmina* hatching rates ($F_{3,12} = 8.4$, $p = 0.003$); the reduction from the control cores was significant with *Macoma* (Tukey HSD, $p = 0.004$) and *Monoporeia* at the higher density (Tukey HSD, $p = 0.012$). *Macoma* caused the strongest decline, while the effect of *Monoporeia* was intensified at the higher amphipod density (although this increase was not significant; Mo vs. Mo high, Tukey HSD, $p = 0.20$).

Table 4. Bioturbation experiment. Effects of macrofauna and mysids (2-factor F -test) on *Bosmina* ephippia in different depth strata and on the total number of ephippia recovered. Significant values in **bold** ($p < 0.05$). See Tables 2 & 3 for abbreviations

Depth (cm)	Factor	Between-subject	Tukey HSD
0–0.5	Macrofauna	$F_{3,28} = 33.9$, $p < \mathbf{0.001}$	C-Mo: <0.001 C-Ma: 0.015 Mo-Ma: <0.001 Mo-Mz: <0.001 Ma-Mz: 0.010
	Mysid	$F_{1,28} = 1.7$, $p = 0.20$	
	Interaction	$F_{2,28} = 1.1$, $p = 0.35$	
0.5–1	Macrofauna	$F_{3,28} = 3.2$, $p = \mathbf{0.039}$	
	Mysid	$F_{1,28} < 0.1$, $p = 0.93$	
	Interaction	$F_{2,28} = 2.0$, $p = 0.16$	
1–2	Macrofauna	$F_{3,28} = 5.7$, $p = \mathbf{0.004}$	C-Ma: 0.008 Mo-Ma: 0.024 Mz-Ma: 0.006
	Mysid	$F_{1,28} = 1.5$, $p = 0.23$	
	Interaction	$F_{2,28} = 2.3$, $p = 0.12$	
2–3	Macrofauna	$F_{3,28} = 45.9$, $p < \mathbf{0.001}$	C-Ma: <0.001 Mo-Ma: <0.001 Mz-Ma: <0.001
	Mysid	$F_{1,28} < 0.1$, $p = 0.99$	
	Interaction	$F_{2,28} = 3.4$, $p = \mathbf{0.049}$	
3–4	Macrofauna	$F_{3,28} = 12.8$, $p < \mathbf{0.001}$	C-Ma: <0.001 Mo-Ma: <0.001 Mz-Ma: 0.006
	Mysid	$F_{1,28} = 4.0$, $p = 0.054$	
	Interaction	$F_{2,28} = 0.1$, $p = 0.89$	
Sum	Macrofauna	$F_{3,28} = 52.2$, $p < \mathbf{0.001}$	C-Mo: <0.001 C-Ma: 0.020 Mo-Ma: <0.001 Mo-Mz: <0.001 Ma-Mz: 0.045
	Mysid	$F_{1,28} = 2.0$, $p = 0.17$	
	Interaction	$F_{2,28} = 3.3$, $p = 0.051$	

DISCUSSION

Many of the earlier studies investigating the effects of zoobenthos on resting stages of planktonic organisms have concentrated on vertical translocation of copepod eggs in the sediment by deposit-feeders (Marcus & Schmidt-Gengenbach 1986, Albertsson & Leonardsson 2000, 2001) or resistance of eggs to macrofaunal consumption (e.g. Marcus 1984). Predatory regulation of zooplankton and phytoplankton benthic propagules by macrofauna is relatively less studied (Parker et al. 1996, Cáceres & Hairston 1998, Persson & Rosenberg 2003). Furthermore, the impact of benthic fauna on zooplankton hatching has been widely discussed but rarely documented (Abertsson & Leonardsson 2001, Ståhl-Delbanco & Hansson 2002). Especially cladoceran benthic eggs have received little attention. To my knowledge,

Table 5. *Bosmina longispina maritima*. Bioturbation experiment. Number of cladoceran ephippia recovered in each depth stratum (mean \pm SE, $n = 5$)

Depth (cm)	Control	<i>Monoporeia</i>		<i>Macoma</i>		<i>Marenzelleria</i>	
		No mysids	Mysids	No mysids	Mysids	No mysids	Mysids
0–0.5	52 \pm 6	11 \pm 2	7 \pm 3	29 \pm 2	24 \pm 2	47 \pm 7	51 \pm 8
0.5–1	41 \pm 6	34 \pm 3	24 \pm 2	24 \pm 3	29 \pm 6	35 \pm 6	45 \pm 5
1–2	6 \pm 4	6 \pm 5	12 \pm 5	13 \pm 1	19 \pm 1	5 \pm 2	3 \pm 1
2–3	1 \pm 0	1 \pm 0	<1 \pm 0	7 \pm 1	12 \pm 2	2 \pm 1	1 \pm 0
3–4	<1 \pm 0	<1 \pm 0	1 \pm 0	4 \pm 1	6 \pm 2	1 \pm 0	2 \pm 1
Total	101 \pm 3	52 \pm 3	44 \pm 6	78 \pm 5	89 \pm 2	90 \pm 6	102 \pm 4

Table 6. *Bosmina longispina maritima*. Hatching experiment. Egg densities and the number of hatched cladocerans during the cold (21 d) and warm (5 d) periods (mean \pm SE). Eph.: ephippia; Mo high: amphipod density = 4900 ind. m⁻². See Table 2 for other abbreviations

Treatment	Egg density (eph. core ⁻¹)	n	Hatched (ind. core ⁻¹)	
			3°C	13°C
Initial	3640 \pm 260	2		
Control	3060 \pm 150	3	0.3 \pm 0.3	12.5 \pm 1.7
Mo	3260 \pm 30	3	0	8.3 \pm 2.4
Mo high	2820 \pm 180	3	0	2.8 \pm 2.1
Ma	2830 \pm 290	3	0.3 \pm 0.3	1.0 \pm 0.6

this is the first study to document the combined effect of translocation and predation of cladoceran ephippia by polychaetes, bivalves and amphipods.

Effects of zoobenthos on ephippia in sediment

Patterns of particle mixing, investigated with inert tracer introduced at the sediment surface, provide general insight into the impact of benthic infauna on sediment structure (e.g. François et al. 1997, 2002). In a study by Bradshaw et al. (2006), both *Monoporeia* and *Macoma* were classified as biodiffusers, which mix particles up and down within the few upper centimetres of the sediment. The average mixing depth of *Monoporeia* (8000 ind. m⁻²) was as high as 6 cm, and the calculated particle mixing rate (D_b) was double that of *Macoma* (1000 ind. m⁻²; Bradshaw et al. 2006). This is surprising given the practically non-existent downward transport of cladoceran eggs demonstrated in my study. While *Monoporeia* did not affect the distribution of ephippia in the deeper layers, it decreased their abundance in the sediment surface, resulting in a 48% reduction in the total number of eggs.

Monoporeia mainly inhabits and feeds on the top layers of the sediment (Lopez & Elmgren 1989). It is not able to ingest particles >60 μ m whole (Ankar 1977), although it may consume relatively large prey items, for example newly settled postlarval stages of *Macoma*, by crushing them (Elmgren et al. 1986). The size of *Bosmina* ephippia corresponds to the size of postlarval *Macoma* (~400 μ m; Elmgren et al. 1986), and thus would need to be crushed if ingested.

Bradshaw et al. (2006) found that *Macoma* buried tracer particles down to 4 cm depth, but its overall effect on particle profiles during the 3 wk experiment was relatively weak. Due to the non-conservative nature of ephippia, it is not possible to calculate the theoretical particle transport rates with them, but, on the basis of the egg distribution curves (Fig. 1), the vertical mixing of these large-sized resting stages by

Macoma was clearly much more effective than that caused by *Monoporeia*. Thus, the particle transport patterns demonstrated with various tracers may not be directly applied for viable objects with large and asymmetric dimensions such as cladoceran eggs.

Macoma generally occupies the uppermost 5 cm of the sediment, primarily feeding on deposited matter at the sediment surface (Lin & Hines 1994) and may consume particles of up to 300 μ m (Gilbert 1977). The mechanism of egg translocation by *Macoma* is not obvious, but it is reasonable that the burrowing of this relatively large species mixes the sediment down to several centimetres depth, resulting in a more even depth distribution of eggs. Descriptive observations revealed that all ephippia buried by *Macoma* appeared intact, implying that they are not damaged by translocation by this species. *Macoma* also decreased the total number of cladoceran eggs by 23%, indicating that some eggs were ingested. The presence of macrofauna may, however, evoke mechanisms other than consumption causing losses in the egg pool. Hence, detailed ingestion studies will be needed to determine the magnitude of zoobenthos predatory regulation on *Bosmina* ephippia.

Head-down positioned polychaetes may reintroduce copepod eggs (Marcus & Schmidt-Gengenbach 1986) and dinoflagellate cysts (Giangrande et al. 2002) to the sediment-water interface. On the other hand, other polychaete species such as the gallery-forming *Nereis diversicolor* transport tracer particles into deeper layers (François et al. 2002). To my knowledge, there are no data on the general particle mixing by *Marenzelleria*, but on the basis of its feeding and burrowing mode it resembles gallery-forming species in that it collects food mainly at surface sediments (Dauer et al. 1981) but burrows down to a depth of 35 cm (Zettler et al. 2002). Although burrows extending several centimetres in sediment might function as funnels for cladoceran eggs, in the current study, no effects of this polychaete were found on *Bosmina* ephippia, i.e. *Marenzelleria* seems unable either to feed on or transport particles of the size of cladoceran eggs.

Sexual reproduction in *Bosmina* mainly occurs in August to September (Purasjoki 1958, Kankaala 1983). The ephippia produced are not capable of hatching before termination of the diapause, probably lasting for 1 to 6 mo, and hatching generally starts in the following spring (Purasjoki 1958, Kankaala 1983). In this study, *Monoporeia* and *Macoma* decreased ephippia in the 0.5 cm thick sediment surface layer by 79 and 43%, respectively, in ~3 wk. Given the duration that *Bosmina* ephippia need to spend in the sea floor before they start to hatch, such faunal-mediated decline in the egg density is remarkable.

Effects of zoobenthos on *Bosmina* recruitment

Albertsson & Leonardsson (2001) found that *Monoporeia* inhibited the hatching of *Bosmina* and suggested that amphipods crushed ephippia or newly hatched cladocerans. In this study, *Bosmina* started to emerge during the 5 d period of raised temperature at the end of the HE. Due to the brief duration of the warm incubation, the overall hatching remained at a relatively low level. Compared to the control (13 hatched ind. core⁻¹), *Monoporeia* caused a 34 to 78% decline (8 to 3 ind. core⁻¹) in the total hatching, while the reduction caused by *Macoma* was >90% (1 ind. core⁻¹). On the basis of the BE, the mechanism underlying these figures appears to differ between the 2 species: *Monoporeia* probably feeds on ephippia, whereas *Macoma* seems to have a combined effect of egg burial and predation (Fig. 2).

Apart from mechanical transport or damage, changes in the sediment chemistry may affect the fate and recruitment of planktonic propagules. Bioturbation by the isopod *Asellus aquaticus* and the chironomid *Chironomus plumosus* was shown to promote the germination of various phytoplankton taxa, most likely due to increased nutrient concentrations, whereas the hatching of cladocerans and copepods was not affected (Ståhl-Delbanco & Hansson 2002). The presence of dissolved oxygen, generally limited to the upper few millimetres of the sediment (Revsbech et al. 1980), is a predominant factor controlling the hatching of zooplankton benthic eggs (Lutz et al. 1994, Katajisto 2004), contrary to phytoplankton cysts. The threshold

oxygen concentration inhibiting the hatching of copepod eggs in sediments ranges between 0.10 and 0.20 ml l⁻¹ (Lutz et al. 1994, Katajisto 2004), but corresponding data on cladoceran eggs are not available. In the BE, there were no significant differences in O₂ concentrations (1.6 to 2.0 ml l⁻¹, depending on the treatment) at the sediment surface or in the penetration depth of O₂ in sediment, which, in all treatments, was restricted to the upper 0.3 cm. Thus, the effect of the slight increase in the O₂ values caused by the amphipods was outweighed by the predatory effect, and may be ignored when interpreting differences in the hatching success of *Bosmina*.

Considering the abundance and vertical distribution of ephippia in the 2 experiments, the HE (3.6 × 10⁵ eggs m⁻², evenly distributed) mimicked natural conditions better than the BE (7800 eggs m⁻², at 0.5 to 1 cm). Burial of ephippia under 0.5 to 1 cm of sediment in the BE, simulating a rapid sediment accumulation of the northern Baltic waters (Viitasalo & Katajisto 1994, Heiskanen & Tallberg 1999), possibly made them more available for *Monoporeia* (feeding on the top few centimetres) than for *Macoma* (collecting food mainly at the surface). In the BE, the amphipod density (1950 ind. m⁻²) that strongly decreased ephippia in the sediment surface (from 0 to 0.5 cm) did not cause as large a decline in hatching in the HE. In contrast, *Macoma* had a dramatic effect on the hatching rate of *Bosmina*, indicating that at natural egg abundances distributed throughout the sediment the bivalves limit *Bosmina* recruitment more efficiently than the amphipods (Fig. 2). Zooplankton benthic eggs survive well in anoxic conditions (Katajisto 2004), and in the study area, viable *Bosmina* ephippia were found in 8 to 10 yr old sediment layers (Viitasalo & Katajisto 1994). Thus, in the field, the situation becomes more complicated; burial per se is not harmful to the eggs while predation is, i.e. buried eggs may still hatch at some future time if reintroduced to the sediment-water interface.

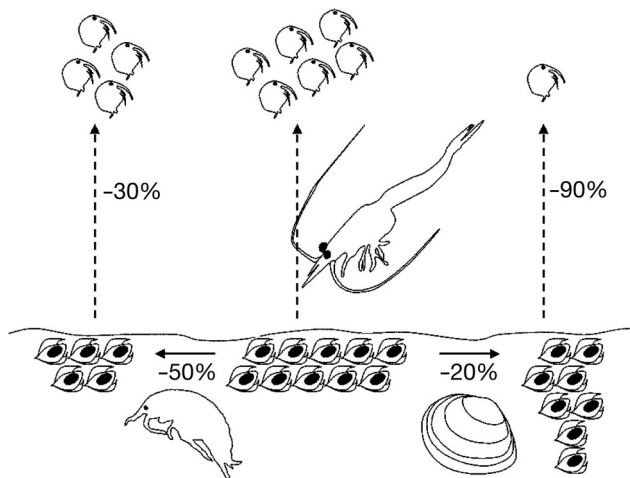


Fig. 2. *Bosmina longispina maritima*. Effects of *Macoma* (780 ind m⁻²) and *Monoporeia* (1950 ind. m⁻²) on the total abundance, vertical distribution and hatching of *Bosmina* ephippia. Solid arrows: reduction in the total number of ephippia caused by macrofauna (bioturbation experiment). Hatched arrows: reduction in the hatching of *Bosmina* (hatching experiment). The mysid is added for illustration

Epibenthic predation by mysids

As cladoceran eggs sink to the sea bottom, the rates of the sedimentation of organic matter, resuspension and bioturbation will determine how rapidly the eggs are buried under the sediment. According to Viitasalo & Viitasalo (2004) *Mysis mixta* is unable to feed on ephippia buried in sediment; hence, it was suggested that bioturbation by macrofauna may essentially affect the predation by epibenthic mysids on their non-motile benthic prey. Consequently, one aim of this study was to test whether macrofauna could, by means of particle mixing, redistribute ephippia, buried under a sediment layer of 0.5 to 1 cm, within the reach of the mysids.

The feeding period of 72 h in the BE should have been enough to reveal any predatory effect since mysids may eat up to 61 cladoceran eggs ind.⁻¹ in only 12 h (Viitasalo & Viitasalo 2004). However, except for the statistically insignificant additional decrease in ephippia (<3 d⁻¹) in the treatment combining *Monoporeia* with mysids, no such effect was observed, i.e. macrofauna did not facilitate mysid predation on *Bosmina* ephippia. From these results, it can also be indirectly deduced that, since both *Macoma* and *Monoporeia* reduce the number of ephippia close to the sediment surface, they decrease the availability of *Bosmina* eggs as food for these benthic-pelagic predators.

Mysis mixta probably has no major effects on *Monoporeia* (Albertsson 2004), but epibenthic predators may affect the burrowing and feeding behaviour of *Macoma* (e.g. Bonsdorff et al. 1995). Despite the short period (3 d) of co-occurrence in this study, mysids seemed to increase the bivalve- and amphipod-mediated egg burial and thereby affect the eventual fate of ephippia in the sediment.

Long-term implications

To estimate how the shift in the Baltic Sea benthic communities might affect the dynamics of *Bosmina* benthic eggs, we need to consider the historical trends in the zoobenthic populations as well as the different impacts the 3 benthic species have on *Bosmina*. Based on the findings of this study, the species most detrimental to *Bosmina* is *Macoma*, followed by *Monoporeia*; *Marenzelleria* is the least detrimental. Accordingly, the rapid spread of the polychaetes with a simultaneous crash of the amphipods, as demonstrated in the Åland archipelago (Perus & Bonsdorff 2004) and the Gulf of Riga (Cederwall et al. 1999), should be favourable for *Bosmina*. In the study area, on the other hand, the recent change from moderate *Monoporeia* abundances (1000 to 6000 ind. m⁻² during the 1970s and 1980s; A. Laine pers. comm.) to dense *Macoma* beds (from nonexistent in the 1970s and 1980s to ~1000 ind. m⁻² in the 2000s; A. Laine pers. comm.) should affect *Bosmina* dynamics negatively. Notably, the expansion of the bivalve populations in the northern Baltic Sea has occurred in relatively shallow archipelago waters (Perus & Bonsdorff 2004), which are the most important zones for *Bosmina* recruitment (Purasjoki 1958).

The dynamics of the 3 benthic species are linked together by a series of negative interactions: *Monoporeia* preys on the settling spat of *Macoma* (Elmgren et al. 1986), *Macoma* reduces the survival of *Marenzelleria* (Kotta et al. 2001), and sediments inhabited by

Marenzelleria are avoided by *Monoporeia* (Neideman et al. 2003), which is also competitively inferior to *Marenzelleria* (Kotta et al. 2001). In addition to environmental change and intraspecific fluctuations, such interactions presumably play a role in the succession of the soft bottom communities. Considering the success of *Bosmina* recruitment, it may be concluded that it is crucial whether areas previously occupied by amphipods eventually become colonised by bivalves or polychaetes.

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LITERATURE CITED

- Albertsson J (2004) Trophic interactions involving mysid shrimps (Mysidacea) in the near-bottom habitat in the Baltic Sea. *Aquatic Ecol* 38:457–469
- Albertsson J, Leonardsson K (2000) Impact of a burrowing deposit-feeder, *Monoporeia affinis*, on viable zooplankton resting eggs in the northern Baltic Sea. *Mar Biol* 136: 611–619
- Albertsson J, Leonardsson K (2001) Deposit-feeding amphipods (*Monoporeia affinis*) reduce the recruitment of copepod nauplii from benthic resting eggs in the northern Baltic Sea. *Mar Biol* 138:793–801
- Ankar (1977) The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna. Contributions from the Askö Laboratory, University of Stockholm, No. 19
- Bastrop R, Blank M (2006) Multiple invasions—a polychaete genus enters the Baltic Sea. *Biol Invasions* 8:1195–1200
- Bonsdorff E, Norkko A, Sandberg E (1995) Structuring zoobenthos: the importance of predation, siphon cropping and physical disturbance. *J Exp Mar Biol Ecol* 192: 125–144
- Bradshaw C, Kumblad L, Fagrell A (2006) The use of tracers to evaluate the importance of bioturbation in remobilising contaminants in Baltic sediments. *Estuar Coast Shelf Sci* 66:123–134
- Cáceres CE, Hairston NG Jr (1998) Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. *Ergeb Limnol* 52:163–174
- Cederwall H, Jermakovs V, Lagzdins G (1999) Long-term changes in the soft-bottom macrofauna of the Gulf of Riga. *ICES J Mar Sci* 56 (Suppl.):41–48
- Dauer DM, Maybury CA, Ewing RM (1981) Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J Exp Mar Biol Ecol* 54:21–38
- De Stasio BT Jr (1989) The seed bank of a freshwater crustacean: copepodology for the plant ecologist. *Ecology* 70: 1377–1389

- Elmgren R, Ankar S, Marteleur B, Ejdung G (1986) Adult interference with postlarvae in soft sediments: the *Pontoporeia-Macoma* example. *Ecology* 67:827–836
- François F, Poggiale JC, Durbec JP, Stora G (1997) A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheor* 45: 295–319
- François F, Gerino M, Stora G, Durbec JP, Poggiale JC (2002) Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modeling and application with the polychaete *Nereis diversicolor*. *Mar Ecol Prog Ser* 229:127–136
- Giangrande A, Montresor M, Cavallo A, Licciano M (2002) Influence of *Naineris laevigata* (Polychaeta: Orbiniidae) on vertical grain size distribution, and dinoflagellate resting stages in the sediment. *J Sea Res* 47:97–108
- Gilbert MA (1977) The behaviour and functional morphology of deposit feeding in *Macoma balthica* (Linne, 1758), in New England. *J Molluscan Stud* 43:18–27
- Glud RN, Gundersen JK, Roye H, Joergensen BB (2003) Seasonal dynamics of benthic O₂ uptake in a semienclosed bay: importance of diffusion and faunal activity. *Limnol Oceanogr* 48:1265–1276
- Hakala (1971) A new model of the Kajak bottom sampler, and other improvements in the zoobenthos sampling technique. *Ann Zool Fenn* 8:422–426
- Heiskanen AS, Tallberg P (1999) Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. 393:127–140
- Kangas P, Byholm L, Stigzelius J (2001) Changes in zoobenthic communities. In: Kauppila P, Bäck S (eds) The state of Finnish coastal waters in the 1990s. The Finnish Environment. Edita, Helsinki, p 79–88
- Kankaala P (1983) Resting eggs, seasonal dynamics, and production of *Bosmina longispina maritima* (P. E. Müller) (Cladocera) in the northern Baltic proper. *J Plankton Res* 5:53–69
- Katajisto T (2004) Effects of anoxia and hypoxia on the dormancy and survival of subitaneous eggs of *Acartia bifilosa* (Copepoda: Calanoida). *Mar Biol* 145:751–757
- Kotta J, Orav H, Sandberg-Kilpi E (2001) Ecological consequence of the introduction of the polychaete *Marenzelleria cf. viridis* into a shallow-water biotope of the northern Baltic Sea. *J Sea Res* 46:273–280
- Laine A, Sandler H, Andersin AB, Stigzelius J (1997) Long-term changes of macrozoobenthos in the Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. *J Sea Res* 38:135–159
- Lin J, Hines AH (1994) Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, *Macoma balthica*. *Oikos* 69:28–36
- Lopez G, Elmgren R (1989) Feeding depths and organic absorption for the deposit-feeding benthic amphipods *Pontoporeia affinis* and *Pontoporeia femorata*. *Limnol Oceanogr* 34:982–991
- Lutz RV, Marcus NH, Chanton JP (1994) Hatching and viability of copepod eggs at two stages of embryological development: anoxic/hypoxic effect. *Mar Biol* 119:199–204
- Marcus NH (1984) Recruitment of copepod nauplii into the plankton: importance of diapausing eggs and benthic processes. *Mar Ecol Prog Ser* 15:47–54
- Marcus NH, Boero F (1998) Minireview: the importance of benthic-pelagic coupling and the forgotten role of the life cycles in coastal aquatic systems. *Limnol Oceanogr* 43: 763–768
- Marcus NH, Schmidt-Gengenbach J (1986) Recruitment of individuals into the plankton: the importance of bioturbation. *Limnol Oceanogr* 31:206–210
- Neideman R, Wenngren J, Ólafsson E (2003) Competition between the introduced polychaete *Marenzelleria* sp. and the native amphipod *Monoporeia affinis* in Baltic soft bottoms. *Mar Ecol Prog Ser* 264:49–55
- Onbé T (1978) Sugar flotation method for sorting the resting eggs of marine cladocerans and copepods from seabottom sediment. *Bull Jpn Soc Sci Fish* 44:1411
- Onbé T (1985) Seasonal fluctuations in the abundance of populations of marine cladocerans and their eggs in the Sea of Japan. *Mar Biol* 87:83–88
- Parker BR, Wilhelm FM, Schindler DW (1996) Recovery of *Hesperodiaptomus arcticus* populations from diapausing eggs following elimination by stocked salmonids. *Can J Zool* 74:1292–1297
- Persson A, Rosenberg R (2003) Impact of grazing and bioturbation of marine benthic deposit feeders on dinoflagellate cysts. *Harmful Algae* 2:43–50
- Perus J, Bonsdorff E (2004) Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. *J Sea Res* 52:45–56
- Purasjoki KJ (1958) Zur Biologie der Brackwasserkladozere *Bosmina coregoni maritima* (P. E. Müller). *Ann Zool Soc Zool-Bot Fenn 'Vanamo'* 19:1–117
- Revsbech NP, Sorensen J, Blackburn TH (1980) Distribution of oxygen in marine sediments measured with microelectrodes. *Limnol Oceanogr* 25:403–411
- Rhoads DC (1974) Organism-sediment relations on the muddy sea floor. *Oceanogr Mar Biol Annu Rev* 12:263–300
- Roast SD, Widdows J, Pope N, Jones MB (2004) Sediment-biota interactions: mysid feeding activity enhances water turbidity and sediment erodability. *Mar Ecol Prog Ser* 281:145–154
- Ståhl-Delbanco A, Hansson LA (2002). Effects of bioturbation on recruitment of algal cells from the 'seed bank' of lake sediment. *Limnol Oceanogr* 47:1836–1843
- Uye S, Kasahara S, Onbé T (1979) Calanoid eggs in seabottom muds. IV. Effects of some environmental factors on the hatching of resting eggs. *Mar Biol* 51:151–156
- Viherluoto M, Kuosa H, Flinkman J, Viitasalo M (2000) Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. *Mar Biol* 136:553–559
- Viitasalo M, Katajisto T (1994) Mesozooplankton resting eggs: identification and vertical distribution in laminated and mixed sediments. *Mar Biol* 120:455–466
- Viitasalo S, Viitasalo M (2004) Predation by mysid shrimps *Mysis mixta* and *M. relicta* on benthic eggs of *Bosmina longispina maritima* (Cladocera) in the northern Baltic Sea. *Mar Ecol Prog Ser* 281:155–163
- Zettler ML, Daynus D, Kotta J, Bick A (2002) History and success of an invasion into the Baltic Sea: the polychaete *Marenzelleria cf. viridis*, development and strategies. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive aquatic species of Europe: distribution, impacts and management. Kluwer Academic Publishers, Dordrecht, p 66–75