

LIMNOLOGY AND OCEANOGRAPHY

November 2007

Volume 52

Number 6

Limnol. Oceanogr., 52(6), 2007, 2325–2339
© 2007, by the American Society of Limnology and Oceanography, Inc.

Bioturbation changes the patterns of benthic emergence in zooplankton

Satu Viitasalo

Tvärminne Zoological Station, University of Helsinki, FI-10900 Hanko, Finland; Finnish Institute of Marine Research, P.O. Box 2, FI-00561 Helsinki, Finland

Tarja Katajisto and Markku Viitasalo

Finnish Institute of Marine Research, P.O. Box 2, FI-00561 Helsinki, Finland

Abstract

We investigated the effects of two functionally different deposit feeders, the amphipod *Monoporeia affinis* and the bivalve *Macoma balthica*, on the benthic emergence of copepods (*Acartia* spp., *Eurytemora affinis*, *Temora longicornis*), cladocerans (*Bosmina longispina maritima*, *Daphnia* spp.), and rotifers (*Synchaeta* spp., *Keratella* spp., *Notholca* spp.) in the northern Baltic Sea. We performed 3.5-week laboratory experiments in June–July and in September–October using surface sediment containing zooplankton eggs and various combinations of amphipod and bivalve densities. Both zoobenthic species increased egg mortality rates in *Synchaeta* spp. and in calanoids. Each amphipod consumed a maximum of one *Synchaeta* spp. egg and 31 calanoid eggs per day, while the bivalves consumed six *Synchaeta* and 143 calanoid eggs per day. Monthly consumption throughout the community matches or even exceeds the field densities of eggs. In summer, *M. affinis* decreased the daily emergence rate of *Synchaeta* spp. by 31–53% and of *M. balthica* by 57%. The effect on calanoids was less severe: the emergence rate of *Acartia* spp. and *E. affinis* was significantly suppressed only by *M. balthica* (the reduction was 48% and 28% in *Acartia* spp. and in *E. affinis*, respectively). *T. longicornis* was the only species that benefited from macrofauna: together the two zoobenthic species resulted in a 2.7-fold increase in the emergence of this calanoid. Bioturbation significantly influences the benthic emergence of zooplankton, with effects varying among species, and may thus affect the dynamics of pelagic populations.

Bioturbation by macrofauna is a major component modifying the chemistry and physical structure of benthic habitats (Rhoads 1974). Macrozoobenthos feed on the deposited matter, burrow into and mix the sediment layers, transport sediment particles upwards or downwards (Marcus and Schmidt-Gengenbach 1986; Kearns et al. 1996; François et al. 1997), and increase resuspension (Rhoads and Young 1970). They also alter the rate and pathways of organic matter mineralization and solute

(e.g., oxygen) exchange between sediment and water and enhance the growth and function of other compartments of the benthic biota (e.g., the microbial [Mermillod-Blondin et al. 2004] and meiofaunal communities [Fenchel 1996]).

Beyond truly benthic species, marine sediments provide a temporal refuge for a variety of planktonic organisms. Accumulation of the dormant stages of plankton in the seafloor not only buffers against unfavorable periods or catastrophic events but also substantially extends the generation time and modifies the outcome of selection in plankton communities (Ellner and Hairston 1994). Emergence from the seafloor is strongly species-specific and often seasonally restricted, but it may essentially contribute to pelagic populations, as demonstrated for copepods (De Stasio 1990; Katajisto et al. 1998; Hairston et al. 2000) and cladocerans (Kankaala 1983; Onbé 1985; Cáceres 1998). Investment in a benthic egg or seed bank is not, however, a risk-free strategy: feeding and burrowing of zoobenthos may strongly influence the dormant life stages of plankton (e.g., Albertsson and Leonardsson 2001; Giangrande et al. 2002; Viitasalo 2007).

Acknowledgments

We are grateful to S. Saesmaa and K. Kivi for their help in analyzing the plankton samples and to T. Sjölund, S. Londesborough, E. Sandberg-Kilpi, and M. Lindström for help in the field and in the laboratory. J. Rapo designed and manufactured the sediment-slicing device. Tvärminne Zoological Station is acknowledged for use of laboratory facilities. We thank M. Lehtiniemi, J. Norkko, and two reviewers for important and helpful comments on the manuscript.

The study was funded by the Onni Talas and Walter and André de Nottbeck Foundations and by the Finnish Institute of Marine Research.

Zooplankton eggs in sediment deposits may hatch only when they are close to the sediment surface (Uye et al. 1979). As a result, faunal-mediated egg burial inhibits benthic emergence (Albertsson and Leonardsson 2001; Viitasalo 2007), whereas upward transport may promote it (Kearns et al. 1996; Marcus and Schmidt-Gengenbach 1986). In addition to translocation, predation on benthic resting stages can be potentially intense (Albertsson and Leonardsson 2001; Persson and Rosenberg 2003; Viitasalo 2007), although the importance of such regulation is not well known.

Few studies have addressed the success of zooplankton emergence in the presence of macrofauna. The deposit-feeding amphipod *Monoporeia affinis* Lindström (hereafter *Monoporeia*) decreases hatching of the copepod *Eurytemora affinis* in the Baltic Sea (Albertsson and Leonardsson 2001), and both *Monoporeia* and the deposit- and suspension-feeding bivalve *Macoma balthica* (L.) (hereafter *Macoma*) inhibit hatching of the cladoceran *Bosmina longispina maritima* (Viitasalo 2007). However, since there are large differences in resistance of the benthic eggs of different zooplankton taxa to various stresses (reviews by Gilbert [1974]; Marcus [1996]; Gyllström and Hansson [2004]), results for single species cannot be extrapolated to other species or areas. To determine the extent to which benthic organisms affect the emergence of zooplankton from the sediment, community-wide studies are needed. Thus far, such studies are lacking.

The Baltic Sea is a particularly appealing location for the purpose of this study, since the soft sediment macrozoobenthos of this brackish sea is characterized by an exceptionally low number of species, *Monoporeia* and *Macoma* belonging to the few abundant ones (Laine et al. 1997). A remarkable change, however, in the relative proportion of these two species has occurred during recent decades: *Monoporeia*, which was the dominant species during most of the 20th century, rapidly declined in the 1980s and 1990s and was subsequently replaced by *Macoma*. Currently *Macoma* accounts for much of the total biomass in the Gulf of Finland, while *Monoporeia* is found in greater abundances only in the Gulf of Bothnia (Laine et al. 2007). *Monoporeia* mainly occupies and mixes the top few centimeters of the sediment (Lopez and Elmgren 1989) and performs active burrowing and nocturnal swimming behavior. It feeds on the deposited matter and may crush particles up to 400 μm in size with its mouthparts (Elmgren et al. 1986). In contrast, *Macoma* is a semimobile species that burrows down to 5 cm or deeper (Lin and Hines 1994) and feeds either on the sediment surface, by sucking in the deposited matter with its inhalant siphon, or on suspensions. Thus, *Macoma* probably mixes the sediment layers mainly by deposition of feces below the sediment surface (Reise 1983). However, burrowing may also play a role, given that *Macoma* adjusts its depth in the sediment, depending on the food conditions and the presence of epibenthic predators (Lin and Hines 1994). The shift in relative abundance of these species presumably causes major changes in the structure and chemistry of the surface sediments and, hence, the living conditions of benthic eggs in the northern Baltic Sea.

The occurrence of mesozooplankton in the northern Baltic Sea shows strong seasonal patterns (Viitasalo et al. 1995). The two most abundant calanoid copepods, *Acartia bifilosa* and *Eurytemora affinis*, are present in plankton throughout the year, albeit in low numbers in winter, whereas benthic resting eggs form the only quantitatively important means of overwintering in cladocerans and rotifers, which practically disappear from the water column in late autumn (Viitasalo et al. 1995). The Baltic populations of *A. bifilosa* rely solely on the production of subitaneous eggs (Katajisto 2003), capable of hatching whenever conditions are favorable. The benthic eggs of *E. affinis* and all rotifers and cladocerans, in turn, are of the diapause type (i.e., they must complete a refractory phase before the development may be resumed; Kankaala 1983; Katajisto 2006).

In favorable conditions, rotifers and cladocerans produce instantly hatching parthenogenetic eggs that are not subject to the benthic environment, whereas the subitaneous eggs of copepods may or may not sink to the seabed prior to hatching. *A. bifilosa* lays and releases eggs solitarily in the water, most of which probably reach the bottom (Katajisto et al. 1998). Females in *E. affinis*, in turn, carry subitaneous eggs with them until hatching, and only diapause eggs, produced later in the season, sink to the seabed.

This study aims to elucidate the effects of *Macoma* and *Monoporeia*, each possessing different functional traits, on the emergence of zooplankton benthic eggs. In studying the present-day interactions between these two macrofaunal species and zooplankton, we aimed to establish how historic changes in the benthic communities may have influenced zooplankton emergence from the sediment. We hypothesized that *Monoporeia* and *Macoma* have different effects on zooplankton and that the various zooplankton taxa show different responses to macrofaunal disturbances. Since the responses may also vary on a seasonal scale because of internal physiological changes in the eggs (Katajisto 2006), we performed similar experiments during early summer (June–July), when the eggs were assumed to be actively hatching, and in autumn (September–October). We performed 3.5-week laboratory hatching experiments using natural surface sediment containing zooplankton eggs and various combinations of these two benthic species.

Materials and methods

Field collections—*Macoma* and surface sediment containing zooplankton benthic eggs were collected at 35-m depths in an archipelago area (59°45.58'N, 23°15.23'E) on the southwest coast of Finland. *Monoporeia* were collected from 80–100-m-deep open sea areas (61°03.01'N, 20°15.82'E and 61°05.01'N, 20°35.79'E) in the Gulf of Bothnia. The salinity at the collection sites ranges between 5 and 6. An Ockelmann benthic sledge (mouth opening 12 \times 30 cm, net length 52 cm, mesh size 150 μm) was used to collect the surface layers of the sediment (approximately the upper 5 cm). Cool water from above the bottom (4–5°C) was added to the sediment buckets to retain the ambient temperature, and the buckets were immediately

Table 1. Treatments and the animal densities and sizes (mean \pm standard deviation [SD]) in the two experiments. Exp., Experiment; Mo, *Monoporeia affinis*; Ma, *Macoma balthica*; ind., individuals.

Exp.	Treatment code	Density ind. core ⁻¹ (ind. m ⁻²)			Size (mm) (No. of measurements)	
		<i>Monoporeia</i>	<i>Macoma</i>	<i>n</i>	<i>Monoporeia</i>	<i>Macoma</i>
1 (summer)	Control	0 (0)	0 (0)	4	—	—
	Mo20	20 (1,960)	0 (0)	4	7.0 \pm 0.8 (112)	—
	Mo50	50 (4,900)	0 (0)	4	7.0 \pm 0.8 (112)	—
	Ma8	0 (0)	8 (780)	4	—	17.0 \pm 1.3 (96)
	Ma8+Mo20	20 (1,960)	8 (780)	4	7.0 \pm 0.8 (112)	17.0 \pm 1.3 (96)
	Ma8+Mo50	50 (4,900)	8 (780)	2/4*	7.0 \pm 0.8 (112)	17.0 \pm 1.3 (96)
2 (autumn)	Control	0 (0)	0 (0)	4	—	—
	Mo20	20 (1,960)	0 (0)	4	4.5 \pm 0.4 (440)	—
	Mo50	50 (4,900)	0 (0)	4	4.5 \pm 0.4 (440)	—
	Ma8	0 (0)	8 (780)	4	—	17.4 \pm 1.3 (96)
	Ma8+Mo20	20 (1,960)	8 (780)	4	4.5 \pm 0.4 (440)	17.4 \pm 1.3 (96)
	Ma8+Mo50	50 (4,900)	8 (780)	2/4*	4.5 \pm 0.4 (440)	17.4 \pm 1.3 (96)

* For all but cladocerans, $n = 2$ as a result of improper sample preparation (see text).

transported to a temperature-controlled room. The sediment was rich in organic matter, as indicated by $\sim 15\%$ loss on ignition of dry weight (after 2 h at 550°C).

To obtain *Macoma* and *Monoporeia*, sediment was taken with a bottom trawl (length 7 m, width 4 m, mesh size 10 mm) and a van Veen grab, respectively. The sediment was put into 90-liter buckets filled with seawater, and the amphipods that were swimming in the water were carefully picked up under the water with small sieves. The animals were immediately placed in cool boxes with seawater from below the thermocline ($\sim 5^\circ\text{C}$) and some sediment from the grab and were transferred to the laboratory within 3 d.

In the laboratory, the animals were transferred to 30–50-liter aquaria with some sediment from the collection site and with continuously flowing seawater and light aeration, where they were housed until the experiments were initiated, within 15 d. The amphipods were always handled in dim light to protect their sensitive eyes.

Hatching experiments—To investigate the seasonal variation in response of zooplankton emergence rates to macrofauna, two experiments were carried out: Experiment 1 (Exp. 1) in summer (12 June–08 July) and Experiment 2 (Exp. 2) in autumn (11 September–07 October) of 2003.

The sediment was sieved through a 500- μm mesh to remove macrofauna, stirred with a ladle to homogenize the distribution of zooplankton eggs, and transferred to a cold room at 4°C. The homogenized sediment was put into Plexiglas cores (height 20 cm, diameter 11.4 cm), 600 mL in each, and ~ 1.4 liters of 10- μm -filtered seawater (FSW) was added, until the water surface rose to ~ 2 cm from the top of the core. The sediment was allowed to settle for 32 h. At the end of the experiment the mean sediment depth was 3.7 cm (Exp. 1) and 4.3 cm (Exp. 2). Light aeration through a thin needle was added immediately below the water surface to keep the oxygen saturation level sufficiently high ($>80\%$) but, at the same time, to avoid disturbance at the sediment surface. Six treatments ($n = 4$) were included: control cores without macrofauna, *Monoporeia* at densities of 1,960 and 4,900 individuals (ind.)

m^{-2} , *Macoma* at 870 ind. m^{-2} , and two treatments with the species combined (Table 1). The amphipods in Exp. 1 were ~ 7 mm in length, belonging to the 2+ year-class (Laakkonen 2002), whereas in Exp. 2 the 1+ year-class (~ 4 mm) was used. The densities were chosen to correspond with the lower (*Monoporeia* lower) and higher (*Macoma* and *Monoporeia* higher) end of the field densities (Kangas et al. 2001; Laine et al. 2007). The experimental cores were assigned randomly to the different treatments; the control cores were treated in a manner similar to that of the cores with macrofauna.

The cores were incubated in darkness at ambient temperature (3°C in Exp. 1 and 4°C in Exp. 2) and salinity (5–6) conditions for 21 d (the cold period). Subsequently, the temperature was raised to 13°C (both experiments) for 5 d (the warm period). Temperature is an important factor controlling the rate of egg development in zooplankton (Katajisto 2006), and, thus, the temperature increase was implemented to provoke emergence, especially in species in which embryonic development typically requires >2 weeks at temperatures of 3–4°C (e.g., cladocerans [Kankaala and Wulff 1981]). At the 35-m-deep study site, such warming of the waters down to the bottom is not unusual (Katajisto et al. 1998). At 2–4-d intervals the water in each core was carefully siphoned off and poured through a 50- μm sieve to collect the emerged zooplankton. A water layer of about 5 mm was left above the sediment, however. Prior to siphoning, the oxygen concentration in the water (10.9 ± 1.5 mg L⁻¹ in Exp. 1 and 10.6 ± 1.2 mg L⁻¹ in Exp. 2) was measured (YSI Model 95 Handheld Dissolved Oxygen and Temperature System, YSI). The water samples containing the zooplankton hatchlings were preserved in 5% buffered formalin.

Immediately after collecting the zooplankton samples, new water (10 μm FSW) was carefully siphoned into the cores. A 200- μm sieve capped with paper was lowered immediately above the sediment surface, ensuring a steady and slow water flow through the margins of the sieve and minimizing sediment resuspension. The water was changed eight times during the cold period and once during the

warm period. At the end, the condition of the macrofauna was defined, based on swimming behavior (*Monoporeia*) or locomotion (*Macoma*). The animals were counted and measured for length (Table 1).

The densities of zooplankton resting eggs in the sediment were determined both before (E_{start}) and after (E_{end}) the incubations. Two (Exp. 1) or four (Exp. 2) replicate samples with 40–50 mL of the homogenized sediment were taken with a syringe to determine E_{start} . At the end of the experiments, the water was siphoned off, the sediment thoroughly mixed, and a 40-mL sample taken with a syringe from three replicate cores from each treatment to define E_{end} . To separate the eggs from the sediment, the sediment was poured through a 50- μm sieve, washed with a sugar-water solution (1 kg of sugar in 1 liter of water) in centrifuge tubes, and centrifuged for 3 min at $906 \times g$ (the 'sugar flotation method,' developed by Onbé [1978]). After centrifugation, the eggs in the supernatant were poured through a 50- μm sieve, rinsed with FSW, and preserved in 70% ethanol for examination and counting under a dissecting microscope.

All emerged calanoid copepods, rotifers, and cladocerans were identified and counted under a Leica Wild MZ 8 dissecting microscope at $\times 50$ – 100 magnification (Leica Microsystems GmbH). Since the hatchlings were a maximum of 4 d old, not all organisms (e.g., *Acartia* spp. and *Synchaeta* spp.) could be identified to the species level. The water samples also contained nauplii and adults of cyclopoids and harpacticoids, but they are not included in the present results.

Unfortunately, as a result of the accidental use of a 100- μm sieve, two replicate hatching series in the treatment combining the bivalves with the higher amphipod density (Ma8+Mo50) in both experiments were lost during preparation of the samples for microscopy. Thus, $n = 2$ in this treatment for all calanoid and rotifer species. Since newly hatched cladocerans ($\sim 300 \mu\text{m}$; cf. Kankaala 1983) are larger and remain on a 100- μm sieve, all four replicates were included.

To define the effects of macrofauna on the emergence of *Acartia* spp., *E. affinis*, and *Synchaeta* spp., which hatched in high numbers throughout the incubations, the mean slope of daily emergence rates ($\text{ind. core}^{-1} \text{d}^{-1}$) for each of the three taxa was calculated from the period of highest daily increase, representing a dynamic phase of the experiment. Thus, the period of slow emergence at the beginning and the period of saturation at the end were excluded.

To examine the vertical distribution of eggs in the sediment after settling, an additional depth distribution experiment was carried out. The sediment was sieved and stirred as in the hatching experiments and was added to three Plexiglas cores (height 20 cm, diameter 14 cm) with a movable bottom, 800 mL in each. The cores were filled with FSW and the sediment was allowed to settle in darkness (5°C). No macrofauna were added to the cores. After 36 d, the upper 2-cm layer was cut into 0.5-cm slices and the rest of the core into 1-cm slices. The slicing apparatus comprised a movable piston attached to a stand and a separate cutting plate (the same principle as in Hakala [1971]). The slices were pushed onto plates, and

a 40-mL sample was taken with a syringe from each slice and processed in a manner similar to that of the egg density samples in the hatching experiments.

Behavioral filming—To determine whether *Macoma* can suspension-feed on copepod nauplii or rotifers in the water column, we filmed bivalves in a small aquarium with washed fine-grained sand on the bottom. To obtain newly hatched nauplii and rotifers, some of the sediment collected for the experiments was kept in a bucket, filled with FSW, and aerated (6 – 7°C). The bivalves were starved for 28 h before adding a dense batch of nauplii and rotifers from the culture. Filming (~ 3 h) was performed at 6°C using an infrared-sensitive camera (Mintron MTV-1802CD, Mintron Enterprise) with a 105-mm Nikon macro objective (Nikon Corp.). The magnification enabled viewing of the behavior and escape reactions of the copepod nauplii and rotifers in the siphon flow of the bivalves.

Statistical analyses—For normally distributed and homoscedastic data, a two-way analysis of variance (F -test) was used to test the effect of *Monoporeia* (with three levels, including the 0-level) and *Macoma* (with two levels, including the 0-level) on the slopes (the rate of emergence) calculated for *Acartia* spp., *E. affinis*, and *Synchaeta* spp. In addition, for all taxa, a two-way F -test was used to test the effect of macrofauna on the total cumulative emergence at the end. A one-way F -test was used to test the differences in egg densities between the depth strata in the depth distribution experiment. Logarithmic, square-root, or arcsine (for proportional data) transformations were used to fulfill the parametric assumptions of the F -tests. A nonparametric Kruskal–Wallis H -test was applied in case these premises were not met. The differences in total emergence in each taxon between Exp. 1 and Exp. 2 in the absence of macrofauna were tested using a Mann–Whitney U -test. Multiple comparisons were made using a Tukey Honestly Significantly Different post hoc test. All statistical analyses were done with SPSS 14.0 software.

Results

Initial egg pool in the sediment—Calanoid eggs were the most numerous benthic eggs in the egg density samples, the initial densities ranging from $109 \pm 22 \text{ cm}^{-3}$ ($4.1 \times 10^6 \text{ m}^{-2}$) in Exp. 1 (summer) to $225 \pm 5 \text{ cm}^{-3}$ ($9.7 \times 10^6 \text{ m}^{-2}$) in Exp. 2 (autumn). These values correspond to the higher end of the abundances recorded in the northern Baltic surface sediments (Katajisto et al. 1998). In addition to the calanoid eggs, those of the cladocerans *B. longispina maritima* ($9.6 \pm 0.7 \text{ cm}^{-3}$ in Exp. 1 and $4.3 \pm 0.5 \text{ cm}^{-3}$ in Exp. 2), *Daphnia* spp. ($1.2 \pm 0.2 \text{ cm}^{-3}$ and $1.7 \pm 0.1 \text{ cm}^{-3}$), *Pleopsis polyphemoides* ($1.2 \pm 0.0 \text{ cm}^{-3}$ and $1.4 \pm 0.3 \text{ cm}^{-3}$), *Evadne nordmanni* (0.7 cm^{-3} and $0.9 \pm 0.1 \text{ cm}^{-3}$), and *Cercopagis pengoi* ($0.3 \pm 0.1 \text{ cm}^{-3}$ and $0.4 \pm 0.1 \text{ cm}^{-3}$) and eggs of the rotifers *Synchaeta* spp. (4.7 cm^{-3} and $2.3 \pm 0.4 \text{ cm}^{-3}$) were identified. These figures are in the range of the field densities (Viitasalo and Katajisto 1994), although the values for *Synchaeta* spp. were somewhat higher than those reported by Viitasalo and

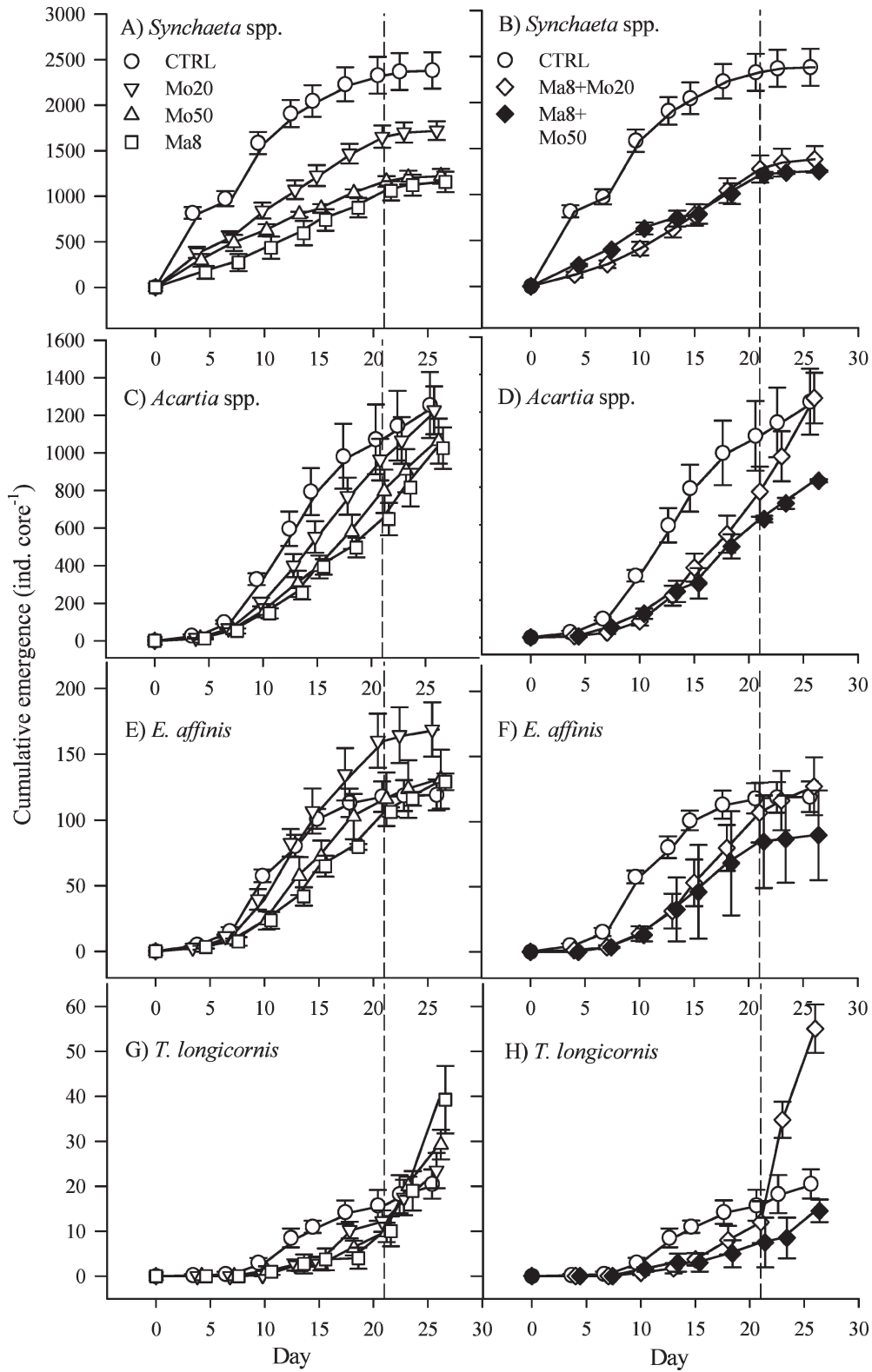


Fig. 1. Experiment 1 (summer). Cumulative emergence of (A, B) *Synchaeta* spp., (C, D) *Acartia* spp., (E, F) *Eurytemora affinis*, and (G, H) *Temora longicornis* (mean \pm standard error [SE]). The single-species and two-species treatments are presented in panels A, C, E, and G and panels B, D, F, and H, respectively. The symbols at each sampling have been slightly shifted horizontally for clarity. Note the different scales on the y-axis. The dashed line indicates the temperature rise from 3°C to 13°C. For the treatment codes, see Table 1.

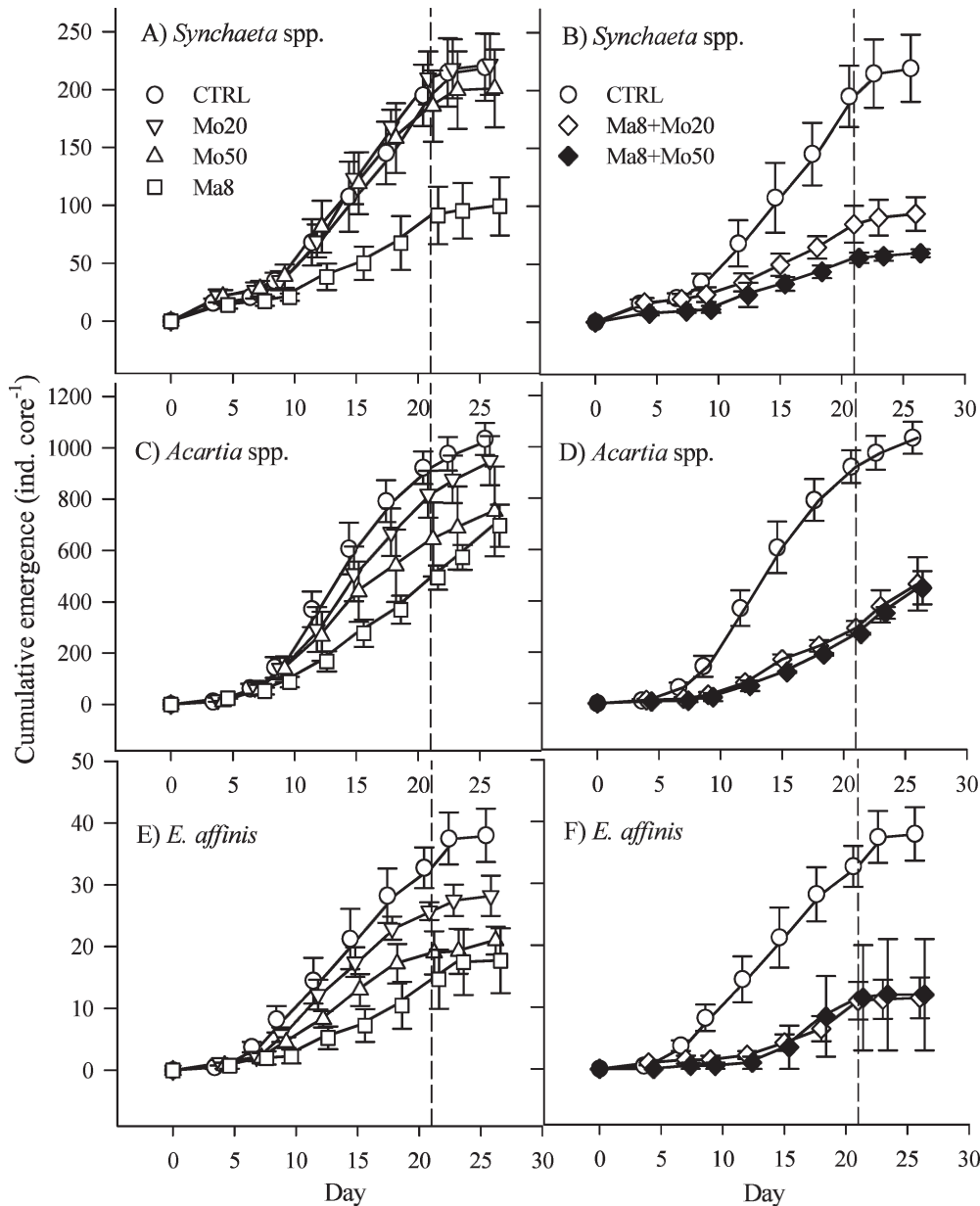


Fig. 2. Experiment 2 (autumn). Cumulative emergence of *Acartia* spp., *Eurytemora affinis*, and *Synchaeta* spp. (mean \pm standard error [SE]). Other details as in Fig. 1. Note the different scales on the y-axis. For the treatment codes, see Table 1.

Katajisto (1994). As a result of difficulties in egg identification, only one (*Synchaeta* spp. and *E. nordmanni*) or two (others) replicate E_{start} values were obtained in Exp. 1, and, thus, they should be considered indicative.

In the depth distribution experiment, the density of eggs (cm^{-3}) in each sediment stratum for calanoids, *B. longispina maritima*, *Daphnia* spp., *P. polyphemoides*, *E. nordmanni*, and *Synchaeta* spp. was determined. The uppermost stratum contained fewer eggs of *Synchaeta* spp. than the deeper strata (7.8 eggs cm^{-3} compared with 8.8–13.5 eggs cm^{-3} ; one-way F -test: $F_{4,10} = 4.7$, $p < 0.05$), while for all the other species, the eggs were uniformly distributed throughout the sediment (one-way F -test: $F_{4,10} = 0.2$ – 2.7 , $p > 0.05$).

Zooplankton emergence—In both experiments, the three most numerous taxa in the water samples were the rotifers *Synchaeta* spp. (mainly *Synchaeta baltica* and *Synchaeta monopus*) and the copepods *Acartia* spp. (*Acartia bifilosa* and *Acartia tonsa*) and *E. affinis* (Figs. 1, 2). In *Synchaeta* spp., the total emergence during the 26-d incubation averaged $>2,300$ ind. $core^{-1}$ (in the controls, in Exp. 1). A third copepod, *Temora longicornis*, emerged throughout the experiment in summer but only occasionally in Exp. 2. The cladocerans *B. longispina maritima* and *Daphnia* spp. and the rotifers *Keratella quadrata*, *Keratella cochlearis*, *Keratella cruciformis*, *Notholca acuminata*, and *Notholca* spp. were scarce in both experiments (Fig. 3). Co-occurrence of planktonic species originating from both freshwa-

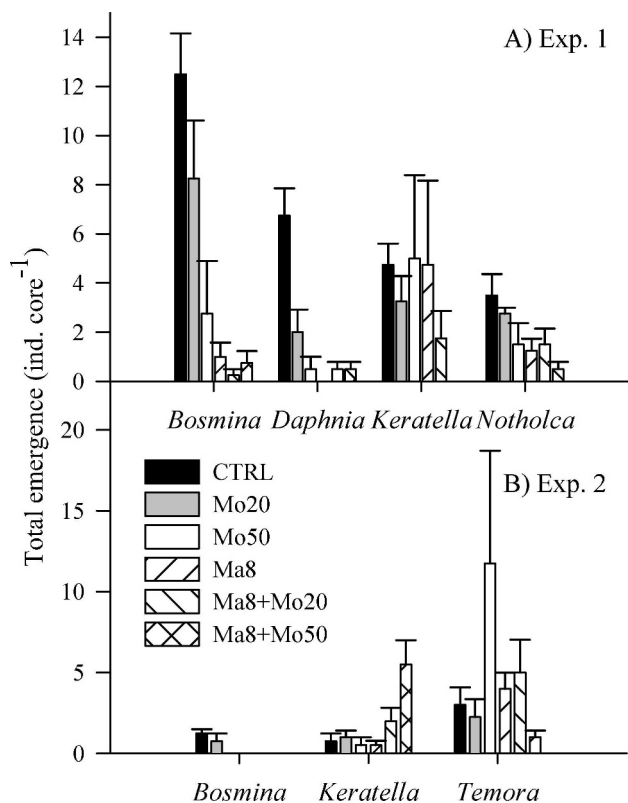


Fig. 3. Total emergence (mean \pm standard error [SE]) of *Bosmina longispina maritima*, *Daphnia* spp., *Keratella* spp., *Notholca* spp., and *Temora longicornis* in (A) Experiment 1 (summer) and (B) Experiment 2 (autumn). For the treatment codes, see Table 1.

ter and marine environments is a typical feature of Baltic fauna (cf. Viitasalo et al. 1995). Despite occurring in the sediment samples as resting eggs, hatched specimens of *E. nordmanni*, *P. polyphemoides*, and *C. pengoi* were not observed.

For all but *Acartia* spp. ($U = 6.0, p > 0.05$), the total number of hatched individuals in the controls was considerably higher in Exp. 1 than in Exp. 2 ($U = 0.0, p$

< 0.05 for *E. affinis*, *Synchaeta* spp., *T. longicornis*, *B. longispina maritima*, and *Keratella* spp.), despite similar temperature conditions (3°C in Exp. 1 and 4°C in Exp. 2).

Cumulative emergence curves (ind. core⁻¹) are shown for the taxa present throughout the experiments (Figs. 1, 2). *T. longicornis*, although less abundant, was also frequently present during the cold period in Exp. 1 and is included in Fig. 1. For the other taxa, observed to a large extent only during the warm period, only the total emergence is presented (Fig. 3). The emergence curves of *Synchaeta* spp., *Acartia* spp., and *E. affinis* appeared sigmoidal in shape: there was a 7–9-d period of low emergence rates, followed by a phase of higher and relatively steady emergence. After 15–21 d, the rates slowed down again, particularly in the controls, indicating that eggs became depleted in the sediment surface. The mean daily rates (ind. core⁻¹ d⁻¹) calculated in the steady phase are specified in Table 2. In Exp. 1, the rates in the control correspond to 11,400 ind. m⁻² d⁻¹ (*Synchaeta* spp.), 8,010 ind. m⁻² d⁻¹ (*Acartia* spp.), and 1,040 ind. m⁻² d⁻¹ (*E. affinis*). In Exp. 2 the rates were lower: 1,310; 6,350; and 210 ind. m⁻² d⁻¹ in *Synchaeta* spp., *Acartia* spp., and *E. affinis*, respectively.

Effects of macrofauna—In general, both *Macoma* and *Monoporeia* suppressed the emergence rates of zooplankton in both experiments (Figs. 1, 2; Tables 2–4). *Macoma* had a strong negative effect on *Synchaeta* spp. in both experiments (Tables 2, 3): the reduction in emergence rates was 57% (Exp. 1) and 56% (Exp. 2; Table 2). In addition, on film *Macoma* caught swimming rotifers from the water column. *Monoporeia* decreased the rate of emergence in Exp. 1 (the reduction was 31% and 53% in Mo20 and Mo50, respectively; for the treatment codes, see Table 1) but had no effect in Exp. 2 (Tables 2, 3). In Exp. 1, the summed (additive) effect of *Monoporeia* and *Macoma* in the single-species treatments was stronger than that observed in the two-species treatments (i.e., the effect of either species was stronger under monospecific conditions than in co-occurrence; Table 3).

The other rotifer taxa were two to three orders of magnitude less abundant than *Synchaeta* spp. Despite the low number of hatchlings, *Macoma* weakened the total

Table 2. Slopes (individuals [ind.] core⁻¹ d⁻¹) calculated from the daily emergence rates of *Synchaeta* spp., *Acartia* spp., and *Eurytemora affinis* (mean \pm standard error [SE]). The numbers in parentheses denote the dates (i.e., the time period), from which the slopes are calculated. Treatment codes as in Table 1. Exp., Experiment.

Exp.	Treatment	<i>Synchaeta</i> spp.	<i>Acartia</i> spp.	<i>Eurytemora affinis</i>
1 (summer)	Control	116 \pm 10 (0–18)	82 \pm 15 (7–18)	11 \pm 1 (7–15)
	Mo20	80 \pm 5 (0–18)	65 \pm 9 (7–18)	12 \pm 2 (7–15)
	Mo50	55 \pm 2 (0–18)	47 \pm 7 (7–18)	8 \pm 1 (7–15)
	Ma8	50 \pm 5 (0–18)	42 \pm 4 (7–18)	8 \pm 1 (7–15)
	Ma8+Mo20	60 \pm 8 (0–18)	50 \pm 9 (7–18)	7 \pm 2 (7–15)
	Ma8+Mo50	54 \pm 7 (0–18)	38 \pm 6 (7–18)	5 \pm 5 (7–15)
2 (autumn)	Control	13 \pm 2 (9–21)	65 \pm 4 (9–21)	2.1 \pm 0.3 (7–23)
	Mo20	15 \pm 2 (9–21)	57 \pm 5 (9–21)	1.5 \pm 0.2 (7–23)
	Mo50	12 \pm 2 (9–21)	42 \pm 8 (9–21)	1.0 \pm 0.2 (7–23)
	Ma8	6 \pm 2 (9–21)	34 \pm 3 (9–21)	0.9 \pm 0.3 (7–23)
	Ma8+Mo20	5 \pm 1 (9–21)	22 \pm 2 (9–21)	0.5 \pm 0.2 (7–23)
	Ma8+Mo50	4 \pm <1 (9–21)	21 \pm 1 (9–21)	0.7 \pm 0.5 (7–23)

Table 3. Test statistics for the effects of macrofauna on the emergence rates (slopes) of the three most abundant taxa, as defined in Table 2. Factors: Mo, *Monoporeia affinis* (three levels); Ma, *Macoma balthica* (two levels). The significance levels given are $p > 0.05$ (ns), $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). *Monoporeia* levels that significantly differed ($\alpha = 0.05$) from each other in Tukey post hoc comparisons are specified in the footnotes. Exp., Experiment.

Taxon	Factor	Exp. 1 (summer)		Exp. 2 (autumn)	
<i>Synchaeta</i> spp.	Mo	$F_{2,16}=5.6$	*†	$F_{2,16}=0.6$	ns
	Ma	$F_{1,16}=24.6$	***	$F_{1,16}=38.9$	***
	Mo×Ma	$F_{2,16}=9.2$	**	$F_{2,16}=0.2$	ns
<i>Acartia</i> spp.	Mo	$F_{2,16}=1.9$	ns	$F_{2,16}=4.0$	*
	Ma	$F_{1,16}=6.9$	*	$F_{1,16}=17.2$	**
	Mo×Ma	$F_{2,16}=0.8$	ns	$F_{2,16}=1.2$	ns
<i>Eurytemora affinis</i>	Mo	$F_{2,16}=1.1$	ns	$F_{2,16}=5.6$	*†
	Ma	$F_{1,16}=5.4$	*	$F_{1,16}=45.2$	***
	Mo×Ma	$F_{2,16}=0.3$	ns	$F_{2,16}=0.7$	ns

† Control versus Mo50.

emergence of *Keratella* spp. in Exp. 1, while in Exp. 2, interaction between *Monoporeia* and *Macoma* caused an increase in this rotifer taxon (Fig. 3; Table 4). *Notholca* spp. (present only in Exp. 1) were not significantly affected by zoobenthos (Fig. 3; Table 4).

Both zoobenthic species suppressed the total emergence of *B. longispina maritima* (during both seasons) and *Daphnia* spp. (only present in Exp. 1) (probably *Daphnia cucullata*, cf. Viitasalo 1992), *Macoma* more severely than *Monoporeia* (Fig. 3; Table 4). Interaction occurred: as in the case of *Synchaeta* spp., the reduction in emergence of *B. longispina maritima* relative to the control, caused by

a single benthic species, was as strong as that observed in the two-species treatments (i.e., the effect was nonadditive).

The presence of *Macoma* significantly suppressed the rate of emergence of the two most abundant copepod taxa, *Acartia* spp. and *E. affinis*, in both experiments (Tables 2, 3), although the cumulative emergence in the macrofaunal treatments attained the level of the control toward the end of Exp. 1 (Fig. 1; Tables 3, 4). The reduction caused by *Macoma* in the emergence rates was 48% in *Acartia* spp. (both experiments) and 28% (Exp. 1) and 56% (Exp. 2) in *E. affinis*. In the treatments with *Monoporeia*, the two calanoid species also showed slower emergence relative to

Table 4. Test statistics for the effects of macrofauna on the total emergence of the various zooplankton taxa at the end of the experiments (Exp.). The significance levels given are $p > 0.05$ (ns), $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Note that for *Temora longicornis* (Exp. 2), *Bosmina longispina maritima* (Exp. 2), *Daphnia* spp., and *Notholca* spp., a nonparametric Kruskal–Wallis H -test (one-way, $df = 5$ for all) was applied.

Taxon	Factor	Exp. 1 (summer)		Exp. 2 (autumn)	
<i>Synchaeta</i> spp.	Mo	$F_{2,16}=6.1$	*†	$F_{2,16}=1.2$	ns
	Ma	$F_{1,16}=20.0$	***	$F_{1,16}=42.6$	***
	Mo×Ma	$F_{2,16}=10.5$	**	$F_{2,16}=0.4$	ns
<i>Acartia</i> spp.	Mo	$F_{2,16}=2.2$	ns	$F_{2,16}=2.8$	ns
	Ma	$F_{1,16}=1.4$	ns	$F_{1,16}=13.9$	**
	Mo×Ma	$F_{2,16}=0.6$	ns	$F_{2,16}=0.7$	ns
<i>Eurytemora affinis</i>	Mo	$F_{2,16}=1.8$	ns	$F_{2,16}=3.7$	*
	Ma	$F_{1,16}=2.3$	ns	$F_{1,16}=18.7$	**
	Mo×Ma	$F_{2,16}=1.2$	ns	$F_{2,16}=0.8$	ns
<i>Temora longicornis</i>	Mo	$F_{2,16}=5.5$	*		
	Ma	$F_{1,16}=6.3$	*		
	Mo×Ma	$F_{2,16}=11.0$	**	$H=6.7$	ns
<i>Bosmina longispina maritima</i>	Mo	$F_{2,18}=5.5$	*		
	Ma	$F_{1,18}=38.8$	***		
	Mo×Ma	$F_{2,18}=5.2$	*	$H=17.2$	**†
<i>Daphnia</i> spp.		$H=14.7$	*§	—	
<i>Keratella</i> spp.	Mo	$F_{2,16}=2.0$	ns	$F_{2,16}=2.7$	ns
	Ma	$F_{1,16}=5.5$	*	$F_{1,16}=6.7$	***
	Mo×Ma	$F_{2,16}=0.5$	ns	$F_{2,16}=4.2$	***
<i>Notholca</i> spp.		$H=8.4$	ns	—	

† Control versus Mo50.

‡ Control versus Mo50, Ma8, Ma8+Mo20, and Ma8+Mo50.

§ Control versus all others.

the control (Figs. 1, 2): the reduction in *Acartia* spp. was 21–42% (Exp. 1) and 13–35% (Exp. 2) and in *E. affinis* it was 0–26% (Exp. 1) and 27–51% (Exp. 2). However, the effect was significant only in Exp. 2 (Table 3).

T. longicornis emerged in low numbers in the control throughout Exp. 1, and the macrofauna appeared to decrease the emergence (Fig. 1G). However, both benthic species significantly promoted emergence during the warm period, and the effect was nonadditive; a strong positive interaction was observed (Fig. 1G; Table 3). The increase in emergence of *T. longicornis*, relative to the control, caused by *Monoporeia* (at the lower density) and *Macoma*, when occurring together, was larger (the difference in total emergence between the control and Ma8+Mo20 was 35 ind.; for the treatment codes, see Table 1) than the summed increase in the single-species treatments (22 ind.). Instead, at the higher amphipod density, the two-species treatment decreased the number of hatchlings. In Exp. 2, *T. longicornis* was scarce and showed no response to the presence of macrofauna (Table 4).

The film demonstrated that all attempts by *Macoma* to catch swimming copepod nauplii from the water failed.

Egg pool analysis—By comparing the emergence rates and changes in the benthic egg pool in the course of the experiments, we may estimate which factors control the rate of benthic emergence (i.e., the degree of egg depletion and the role of promotion or inhibition caused by bioturbation or predation).

The dynamics in the benthic egg pool may be expressed as the amount of eggs at the beginning (E_{start}), amount of eggs at the end (E_{end}), and hatched eggs (H). In addition, egg mortality, due either to microbial degradation or to macrofauna, is represented by a loss term, M, thus:

$$E_{\text{end}} = E_{\text{start}} - H - M \quad (1)$$

The calculations were performed for calanoids (as one group) and for *Synchaeta* spp. In the absence of new egg production it must be that $E_{\text{start}} \geq E_{\text{end}} + H$ for each replicate core. This inequality did not hold, however, indicating an underestimation of E_{start} . Thus, we need to assume that

$$E_{\text{start}} = (E_{\text{end}} + H)_{\text{max}} \quad (2)$$

where $(E_{\text{end}} + H)_{\text{max}}$ is calculated from the replicate giving the highest value for this sum. For *Synchaeta* spp., the E_{start} values given by Eq. 2 are 3,952 eggs core⁻¹ in Exp. 1 and 1,480 eggs core⁻¹ in Exp. 2, compared with the original values of 1,771 (Exp. 1) and 1,038 eggs core⁻¹ (Exp. 2). Similarly, Eq. 2 gives 70,935 (Exp. 1) and 103,044 eggs core⁻¹ (Exp. 2) for copepods, instead of 41,598 (Exp. 1) and 99,358 eggs core⁻¹ (Exp. 2). These estimates were used, although they may have resulted in underestimation of the true level of E_{start} .

In copepods, the proportion of hatched eggs was minor (<1–2% of all eggs) during both seasons (Table 5), despite the relatively high total emergence of >1,000 nauplii core⁻¹. In Exp. 1, the vast majority of eggs were recovered (i.e., remained unhatched) in the controls, but this pro-

Table 5. Proportions of *Synchaeta* spp. and calanoid eggs that were hatched (H), unhatched (U), and lost (L) during the incubations ($n = 3$ for all but Ma8+Mo50, in which $n = 2$), as derived from Eq. 1, in which E_{start} is estimated using Eq. 2 (see text). Treatment codes as in Table 1. Exp., Experiment.

Exp.	Taxon	Treatment	Proportions (%) of eggs				
			H	U	L		
1 (summer)	<i>Synchaeta</i> spp.	Control	62±7	20±6	17±12		
		Mo20	45±3	28±6	27±5		
		Mo50	32±2	14±1	54±1		
		Ma8	31±3	19±6	51±7		
		Ma8+Mo20	34±5	12±3	54±2		
		Ma8+Mo50	32±<1	13±2	56±3		
	Calanoida	Control	2±<1	89±7	9±7		
		Mo20	2±<1	66±10	32±9		
		Mo50	2±<1	48±8	51±9		
		Ma8	2±<1	47±5	51±5		
		Ma8+Mo20	2±<1	48±15	50±15		
		Ma8+Mo50	1±<1	46±10	53±10		
		2 (autumn)	<i>Synchaeta</i> spp.	Control	13±3	32±3	55±5
				Mo20	14±2	45±12	42±10
Mo50	13±3			52±9	35±10		
Ma8	6±2			52±22	41±22		
Ma8+Mo20	7±1			58±18	35±19		
Ma8+Mo50	4±<1			43±11	53±11		
Calanoida	Control		1±<1	65±17	34±17		
	Mo20		1±<1	63±10	36±10		
	Mo50		1±<1	76±11	23±11		
	Ma8		1±<1	76±6	23±6		
	Ma8+Mo20		1±<1	55±22	44±22		
	Ma8+Mo50		<1 ± <1	67±3	32±3		

portion declined in the macrofaunal treatments. The loss term M was 9% in the controls but rose above 50% in Mo50, Ma8, Ma8+Mo20, and Ma8+Mo50 (for the treatment codes, see Table 1); *Macoma* increased it significantly ($F_{1,10} = 6.9$, $p < 0.05$), indicating predation. In Exp. 2, M was >20% in all treatments and showed no clear trend (*Monoporeia*: $F_{2,10} = 0.5$, $p > 0.05$; *Macoma*: $F_{1,10} < 0.1$, $p > 0.05$). In Exp. 2, however, *Macoma* decreased the proportion of hatched eggs ($F_{1,10} = 12.2$, $p < 0.01$).

For *Synchaeta* spp., the total of 2,463 hatched rotifers core⁻¹ in the controls accounted for 62% of all eggs in Exp. 1 (Table 5). The macrofauna decreased the proportion of hatched eggs in both experiments (Exp. 1: $H = 11.4$, $p < 0.05$, $df = 5$; Exp. 2: *Macoma*: $F_{1,10} = 12.9$, $p < 0.01$). In Exp. 2, the proportion of hatched eggs was much lower (6–19%). As in the case of copepods, the macrofauna increased the level of M in Exp. 1 ($H = 11.5$, $p < 0.05$, $df = 5$), while no such effect was observed in Exp. 2 (*Monoporeia*: $F_{2,10} = 0.3$, $p > 0.05$; *Macoma*: $F_{1,10} = 0.1$, $p > 0.05$).

The theoretical daily and monthly egg consumption rates per animal and per experimental community were calculated by subtracting the number of lost eggs in the controls from those in the macrofaunal treatments (Table 6). The rates were higher in calanoids than in *Synchaeta* spp., and consumption by *Macoma* was higher than that by *Monoporeia*, although the rates declined in the two-species treatments.

Table 6. Experiment 1 (summer). Theoretical egg consumption rates (mean \pm standard error [SE]) of *Synchaeta* spp. and of calanoids. The third and fifth columns show the average monthly consumption by the experimental community. Treatment codes as in Table 1.

Treatment	<i>Synchaeta</i> spp.		Calanoida	
	Eggs animal ⁻¹ d ⁻¹	Eggs month ⁻¹	Eggs animal ⁻¹ d ⁻¹	Eggs month ⁻¹
Mo20	0.8 \pm 0.4	0.4 \times 10 ⁵	31.3 \pm 12.9	1.8 \times 10 ⁶
Mo50	1.1 \pm <0.1	1.6 \times 10 ⁵	22.6 \pm 4.6	3.3 \times 10 ⁶
Ma8	6.3 \pm 1.3	1.5 \times 10 ⁵	142.7 \pm 15.8	3.4 \times 10 ⁶
Ma8+Mo20	2.0 \pm 0.1	1.7 \times 10 ⁵	39.3 \pm 14.9	3.2 \times 10 ⁶
Ma8+Mo50	1.0 \pm 0.1	1.7 \times 10 ⁵	20.3 \pm 4.9	3.5 \times 10 ⁶

Zooplankton assemblages—Three taxa, *Synchaeta* spp., *Acartia* spp., and *E. affinis*, together comprised 97.9–99.2% of all emerged taxa in Exp. 1 and 98.6–99.7% in Exp. 2 (Fig. 4). In Exp. 1, the residual 1–2% were *T. longicornis*, *B. longispina maritima*, *Daphnia* spp., *Keratella* spp., and *Notholca* spp. In Exp. 2, the proportion of these less numerous taxa was very limited, contributing to only 0.3–1.4% of the total emergence (Fig. 4).

In Exp. 1, *Macoma* decreased the dominance of *Synchaeta* spp., by increasing the proportion of *Acartia* spp. (Fig. 4A; Table 7). The interaction terms for *Synchaeta* spp., *Acartia* spp., and *E. affinis* indicate that the effect of the two zoobenthic species on the assemblage composition was nonadditive (Table 7). In Exp. 2, *Synchaeta* spp. were much less numerous, but *Acartia* spp. were present in numbers almost similar to those in Exp. 1 (Fig. 4B). Although the macrofauna did not cause a severe shift in the assemblage, *Macoma* decreased the proportion of *Synchaeta* spp. (Fig. 4B; Table 7).

The macrofauna drastically altered the relative abundances of the less abundant taxa in Exp. 1 from a more diverse assemblage toward one mainly consisting of *T. longicornis*; meanwhile, the relative abundance of *B. longispina maritima* and *Daphnia* spp. declined (Fig. 5A; Table 7). In Exp. 2, the numbers remained low and the changes were less evident. However, *B. longispina maritima* showed a trend toward decrease with the macrofauna, similar to that observed in Exp. 1 (Fig. 5B; Table 7).

Discussion

The role of bioturbation and benthic predation in the success of zooplankton benthic emergence has been debated in several studies (e.g., De Stasio 1989; Cáceres 1998; Marcus and Boero 1998). Experimental documentation of the effects of macrofauna on the recruitment of resting eggs to plankton are few, however (Albertsson and Leonardsson 2001; Ståhl-Delbanco and Hansson 2002; Viitasalo 2007). Here we present evidence that two surface deposit feeders, *Monoporeia affinis* and *Macoma balthica*, alter the patterns of zooplankton emergence in a way that reflects their species-specific traits and that depends on the zooplankton taxon and the season.

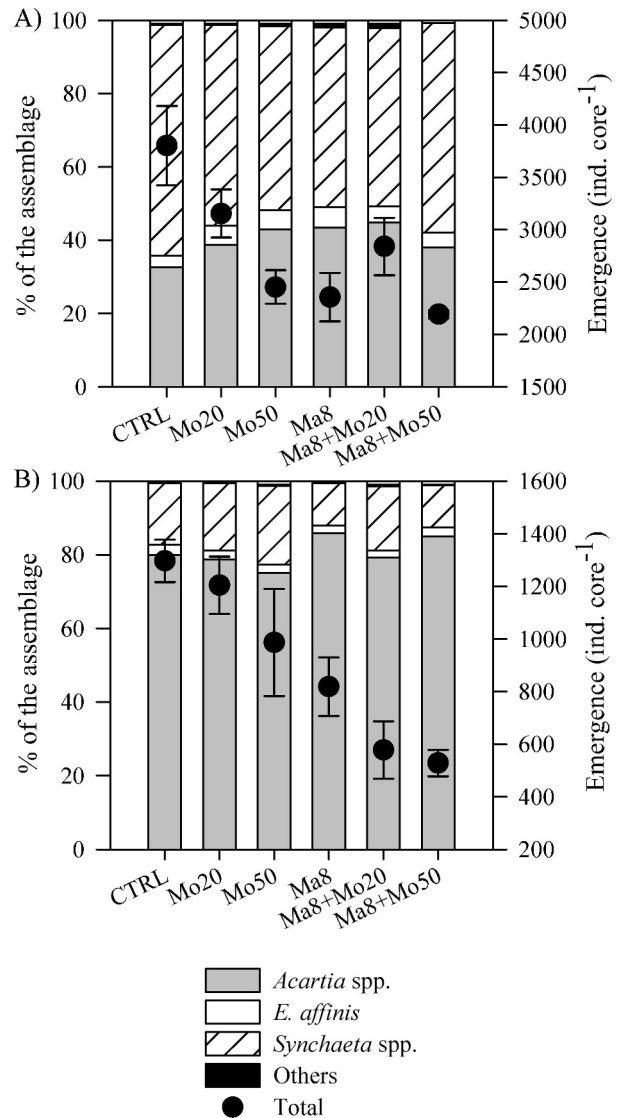


Fig. 4. Total emergence and composition of the emerged zooplankton assemblage as relative abundances at the end of (A) Experiment 1 (summer) and (B) Experiment 2 (autumn).

Patterns of zooplankton emergence—In the summer experiment (Exp. 1), the emergence rates of copepods and *Synchaeta* spp., when presented as maximum daily emergence per unit area, were high relative to the corresponding size of the pelagic populations (Viitasalo et al. 1995). In *Acartia* spp., the daily benthic input yielded densities similar to the size of the standing stock (nauplii stages I and II) observed in the study area (Katajisto et al. 1998). The sediment used in this study contained eggs of different ages. Egg viability decreases with time, but an important difference between ‘new’ and ‘old’ eggs is related to the diapause character: only postrefractory eggs may hatch. Most of the diapause eggs in Exp. 1 (summer) originated from the preceding season and had completed their diapause, while in Exp. 2 (autumn), some of the eggs supposedly were recently laid and were still in the phase of

Table 7. Test statistics for the effects of macrofauna on the relative abundance of the various zooplankton taxa at the end of the experiments (Exp.). The significance levels given are $p > 0.05$ (ns), $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Note that for *Acartia* spp. (Exp. 2), *Eurytemora affinis* (Exp. 2), *Temora longicornis* (Exp. 2), *Bosmina longispina maritima*, *Daphnia* spp., *Keratella* spp., and *Notholca* spp., a nonparametric Kruskal–Wallis H -test (one-way, $df = 5$ for all) was applied.

Taxon	Factor	Exp. 1 (summer)		Exp. 2 (autumn)	
<i>Synchaeta</i> spp.	Mo	$F_{2,16}=1.9$	ns	$F_{2,16}=1.4$	ns
	Ma	$F_{1,16}=5.0$	*	$F_{1,16}=7.3$	*
	Mo×Ma	$F_{2,16}=8.9$	**	$F_{2,16}=1.6$	*
<i>Acartia</i> spp.	Mo	$F_{2,16}=1.7$	ns		
	Ma	$F_{1,16}=4.8$	*		
	Mo×Ma	$F_{2,16}=5.9$	*		
<i>E. affinis</i>	Mo	$F_{2,16}=0.4$	ns	$H=8.6$	ns
	Ma	$F_{1,16}=0.1$	ns		
	Mo×Ma	$F_{2,16}=7.1$	**		
<i>T. longicornis</i>	Mo	$F_{2,16}=3.7$	*	$H=3.9$	ns
	Ma	$F_{1,16}=20.8$	***		
	Mo×Ma	$F_{2,16}=16.8$	***		
<i>B. longispina maritima</i>		$H=13.9$	*†	$H=14.9$	*‡
<i>Daphnia</i> spp.		$H=13.7$	*§	—	—
<i>Keratella</i> spp.		$H=6.9$	ns	$H=9.3$	ns
<i>Notholca</i> spp.		$H=2.7$	ns	—	—

† Control versus Mo50, Ma8, Ma8+Mo20, and Ma8+Mo50; Mo20 versus Ma8 and Ma8+Mo20.
 ‡ Control versus Mo20, Ma8, Ma8+Mo20, and Ma8+Mo50.
 § Control versus all others.

arrested development. Consequently, emergence in species producing diapause eggs was higher in Exp. 1 than in Exp. 2. *E. affinis*, however, does not produce diapause eggs until October (Katajisto 2006); hence, the lower emergence of *E. affinis* in Exp. 2 was probably due to a lower egg density in the sediment. Meanwhile, emergence of the subitaneous egg-producing *Acartia* spp. showed only slight seasonal variation.

Calculations of the proportions of hatched, unhatched, or lost eggs revealed some fundamental differences between the strategies of calanoids and rotifers (*Synchaeta* spp.). The proportion of unhatched eggs was large in calanoids during both seasons but was much smaller in *Synchaeta*

spp. It should be noted that only those eggs at the sediment surface may hatch, while E_{end} expressed the total egg pool over the entire sediment core. Assuming an even depth distribution of eggs in the control at the end of the experiments (cf. the depth distribution experiment), 14% (in Exp. 1) and 12% (in Exp. 2) of the calanoid eggs were within the topmost 5 mm. Applying this estimate for the hatching experiment ($E_{end} = 62,800$ in Exp. 1 and 66,500 in Exp. 2), the number of unhatched eggs in the uppermost 5 mm (E_{top}) was 8,792 and 7,980 in Exp. 1 and Exp. 2, respectively. Thus, only 12% and 11% of the eggs within the 0–5-mm layer in the control ($H/[H + E_{top}]$, $H = 1,455$ in Exp. 1 and $H = 1,045$ in Exp. 2).

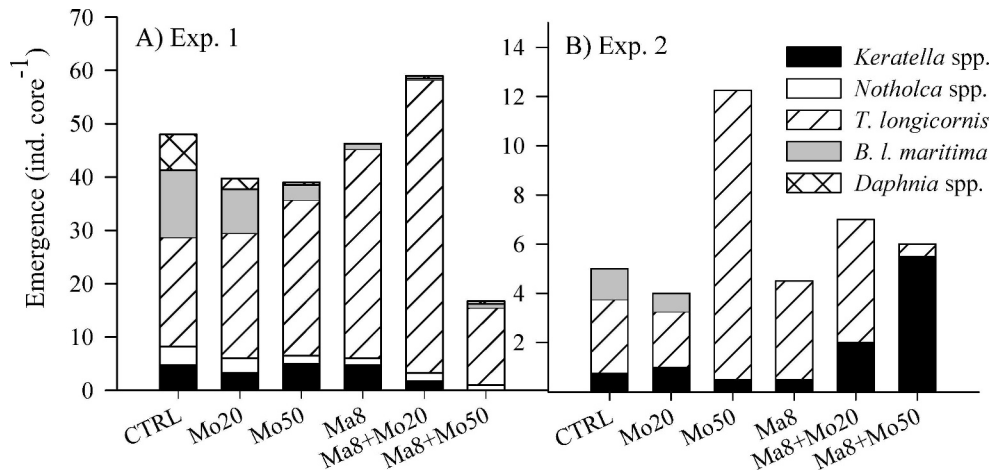


Fig. 5. The less abundant taxa (comprising ‘others’ in Fig. 4) at the end of (A) Experiment 1 (summer) and (B) Experiment 2 (autumn).

With similar assumptions, the egg pool dynamics observed in *Synchaeta* spp. appear strikingly different: 96% of the available eggs in the top 5 mm hatched in Exp. 1 and 78% hatched in Exp. 2. The calculations indicate that the egg pool of *Synchaeta* spp. may become severely depleted in the course of the summer, while the benthic emergence in calanoids covers a much smaller proportion of eggs, enabling the existence of a large egg bank. Katajisto et al. (1998), however, showed that calanoid eggs hatch throughout the year, and the field densities of benthic eggs within the top 2 cm of sediment may decline to as low as $\sim 10^4$ eggs m^{-2} in early spring, before new eggs begin to accumulate in the seafloor.

Effects of macrofauna—In the absence of a compensating production of new eggs, the egg pool in the sediment surface gradually becomes depleted, and hatching ceases. This determines the level of total emergence in the control cores. In contrast, predation or permanent egg burial by the macrofauna yields a lowered emergence, whereas continuous sediment mixing may transport eggs up and down in a more or less random pattern (François et al. 1997). This evens out any layering of eggs and should slow down the hatching rate but, on the other hand, may counteract egg depletion, enhancing the total emergence. Increased resuspension and improved oxygen conditions should also promote hatching (Hairston and Kearns 2002). It is, however, possible that the eggs hatch successfully but that the hatchlings are subsequently eaten or buried before escaping from the sediment.

Assuming that the lost rotifer and calanoid eggs were eaten by macrofauna, the egg consumption rates in Exp. 1 were high relative to the in situ egg densities. When expressed as monthly consumption by the zoobenthic community, the values match or even exceed the field densities given by Viitasalo and Katajisto (1994) and Katajisto et al. (1998), implying that, at least in the absence of significant new egg production, benthic fauna may severely suppress the size of the benthic egg bank. On the other hand, species such as *Macoma*, feeding mainly at the sediment surface, may exert even stronger predation pressure on newly sedimented eggs. Such regulation has been proposed by several authors (e.g., Cáceres 1998; Cáceres and Hairston 1998). The 'inactive temporary meiobenthos' may form an important food source for deposit feeders, as suggested by Pati et al. (1999).

The increased egg mortality together with the lowered number of hatchlings in the macrofaunal treatments indicate that predation controlled the emergence of *Synchaeta* spp. In addition, the film demonstrated that *Macoma* is able to suspension-feed on rotifers, which strengthens its negative effect on these taxa.

In contrast to rotifers, emerged copepod nauplii can escape bivalve predation, as revealed by the film. Prior to emergence, however, predation may be intense: the egg pool analysis indicated that $>50\%$ of calanoid eggs in Exp. 1 were consumed by the benthic fauna. *Macoma* slowed down the emergence rates of *Acartia* spp. and *E. affinis* in both experiments, although the emergence curves in the control and in the macrofaunal cores overlapped at the end of Exp.

1. This indicates that sediment mixing may counteract the negative effects of predation or egg destruction.

Despite suppressing the size of the benthic egg pool, *Monoporeia* did not significantly inhibit the emergence of copepods in Exp. 1. This apparently contrasts with the study by Albertsson and Leonardsson (2001), in which *Monoporeia* reduced the number of *E. affinis* hatchlings. Albertsson and Leonardsson (2001), however, collected plankton samples only once, at the end of the 40-d incubation period (of which 37 d were spent at 2–3°C, followed by 3 d at 13°C), which makes it difficult to determine the differences in the emergence rates.

A striking exception to the general trend of decreasing emergence success was *T. longicornis*, the emergence of which significantly increased in Exp. 1 in the presence of benthic fauna and which attained the highest numbers in the treatments combining the bivalves with the lower amphipod density (Ma8+Mo20). However, at the higher *Monoporeia* density (Ma8+Mo50), the emergence remained low, indicating that increased predation by the amphipods defeats the positive effects of bioturbation. The reproductive strategy of the pelagic populations of *T. longicornis* is similar to that of *Acartia* spp. in that it spawns subitaneous eggs freely in the water, allowing them to sink to the seabed (Tang et al. 1998). This is the first time the existence of *T. longicornis* eggs has been documented in Baltic sediments, although their type of dormancy remains unknown (Katajisto 2006). In other sea areas, *T. longicornis* produces both diapause and subitaneous eggs (Castellani and Lucas 2003). The mechanism causing the positive effect in this study is not evident but may be related to increased resuspension and oxygen supply. If the eggs of *T. longicornis* are of the diapause type, shielded by thick and tough outer coverings (Castellani and Lucas 2003), they may be better protected against benthic predators than eggs of the other taxa.

In the cladocerans *B. longispina maritima* and *Daphnia* spp., both zoobenthic species suppressed the total emergence, the bivalves more efficiently than the amphipods. The benthic eggs (ephippia) of *Daphnia* spp. are nearly identical in size to those of *B. longispina maritima*, but they appear more robust (Viitasalo pers. obs.). It is not clear whether they are similarly affected by macrofauna (i.e., fed upon by *Monoporeia* and buried and consumed by *Macoma*) (Viitasalo 2007).

A seasonal change was observed in the response of zooplankton to macrofauna (e.g., *Monoporeia* significantly decreased the emergence of *Synchaeta* spp. in Exp. 1 but did not affect this taxon in Exp. 2). In contrast, *Monoporeia* did not affect the emergence of copepods in Exp. 1 but lowered it significantly in Exp. 2. The different age groups of *Monoporeia* used in the two experiments (year-class 2+ in Exp. 1 and year-class 1+ in Exp. 2) may explain part of the seasonal effects observed in *Synchaeta* spp., the eggs of which appeared tolerant to the 1+ year-class *Monoporeia*. In general, the rates of growth and consumption of benthic fauna are higher in early summer than in late autumn (Ankar 1980; Lehtonen and Andersin 1998). Indeed, analysis of the egg pool dynamics indicates that predation on rotifer and calanoid eggs was negligible in Exp. 2. A

strengthened influence of the amphipods on copepods in Exp. 2 is hence due to some factor other than predation. It is plausible that the seasonal variability may result from physiological changes in both macrofauna and zooplankton eggs.

The role of functional traits—In eight out of 14 species–taxon combinations, *Macoma* had a stronger negative effect on zooplankton emergence than *Monoporeia*, reflecting their functional differences: sediment mixing by *Monoporeia* is confined to a thinner layer than that by *Macoma* (Viitasalo 2007). Vigorous sediment resuspension by *Monoporeia* (Viitasalo pers. obs.) may enhance the hatching of eggs in the sediment surface. Mixing by *Macoma*, in turn, predominantly causes egg burial and thereby mostly harmful effects. On the other hand, predation by *Monoporeia* may be more intense than that by *Macoma* (Viitasalo 2007), at least on eggs located below the sediment surface. The suppressing effect of *Monoporeia* was strongest on *Synchaeta* spp. and on cladocerans, indicating that eggs of these taxa are particularly subject to predation by amphipods.

Eggs are not uniformly distributed in the sediment under natural conditions (Viitasalo and Katajisto 1994). During seasons of intense egg production, resulting in high egg densities near the sediment surface, the effect of surface deposit feeders may be more pronounced than in our experiments. In addition to physical effects, bioturbation greatly changes the sediment chemistry (e.g., Mermillod-Blondin et al. 2004). Fluctuations in solutes other than dissolved oxygen, however, have not been reported to affect the hatching of zooplankton benthic eggs (Gyllström and Hansson 2004).

Interaction between *Monoporeia* and *Macoma* significantly changed the overall outcome of bioturbation in the summer experiment. The negative influence of the two species, when occurring together, was always less severe than expected based on the summed effect of the single-species treatments, while in the extreme case of *T. longicornis* (which was the only species clearly benefiting from macrofauna), a strong positive effect was observed. Nonadditive effects of functionally different zoobenthic species have been established in studies investigating solute fluxes and physical reworking of sediments (e.g., Mermillod-Blondin et al. 2005). It is plausible that such effects may result from inhibition or interference between benthic species. However, the exceptional response of *T. longicornis* demonstrates that more elaborate interactions may occur, stressing the importance of the multispecies approach in ecological studies.

Population dynamics—Contribution of the benthic input to the structure and abundance of pelagic populations varies remarkably among species and systems. In most cases, it is most pronounced at the onset of a favorable season, when it determines the timing of the annual population reappearance to plankton in species that are periodically absent, and may be important in determining the initial size of the planktonic population (Cáceres 1998; Hairston et al. 2000; Gilbert and Schröder 2004).

Coupling of the life stages in plankton and benthos is tight in *A. bifilosa* populations in the Baltic Sea (Katajisto et al. 1998). The first pelagic annual peak of *Acartia* spp. occurs during the spring phytoplankton bloom in April and May and is probably caused by recruits from benthic eggs (Katajisto et al. 1998). The early pelagic increase in *A. bifilosa* not only enables utilization of the spring phytoplankton bloom but also prevents benthic eggs from being buried by sedimenting algae (cf. Katajisto et al. 1998), which is responsible for the largest annual pelagic input of organic matter to the seafloor (Lignell et al. 1993). Any factor slowing down the hatching rate of benthic eggs suppresses population growth, and, therefore, the effect of macrofauna on *Acartia* spp. probably is mostly negative.

In species in which only diapause eggs sink to the seabed, benthic emergence, in turn, is probably most important at the beginning of the first annual population peak. *E. affinis*, *S. monopus*, *S. baltica*, and *K. quadrata* usually peak in June, and *T. longicornis* and *B. longispina maritima* typically attain their maxima later in summer (in July–August; Viitasalo et al. 1995), in other words, after sedimentation of the spring bloom. Shortage of postre-fractory eggs at the sediment surface may occur in the absence of continuous sediment mixing, and, hence, bioturbation may be a positive factor if it makes buried eggs more liable to hatch. This applies especially to *E. affinis* and *T. longicornis*, whereas in rotifers and cladocerans, the inhibitory effects, presumably caused by predation (both *Monoporeia* and *Macoma*) and burial (*Macoma*), probably overrun any benefits.

In conclusion, copepods were less severely affected than rotifers and cladocerans, while *Acartia* spp., producing subitaneous eggs, appeared to suffer more from macrofauna than the other copepod taxa. This may reflect species- and egg type-specific differences in the vulnerability of eggs to benthic predation. For example, eggs of rotifers and cladocerans may be more vulnerable than eggs of copepods, while in copepods, subitaneous eggs are probably more susceptible than diapause eggs (Marcus 1996).

The differences in functional traits between *Macoma* and *Monoporeia* were reflected in the patterns of zooplankton emergence: The total number of hatchlings as well as the composition of the emerged zooplankton assemblage changed, depending on the zoobenthic species present. A nearly total disappearance of *Monoporeia*, followed by establishment of dense *Macoma* beds, occurs commonly in the coastal soft sediment communities of the northern Baltic Sea (Kangas et al. 2001; Laine et al. 2007). Based on the results, we suggest that that this trend may have caused an absolute decrease in the benthic emergence of all taxa studied, except *T. longicornis*. In the emerging assemblage, in turn, our data predict a relative increase in *Acartia* spp. and *T. longicornis* and a decline in the proportion of *Synchaeta* spp. and *B. longispina maritima*.

Long-term monitoring data on zooplankton abundances (years 1979–2005), measured on a single date in August, show a decrease in the populations of *B. longispina maritima* from the early 1990s onward in the Gulf of Finland (Flinkman et al. 2007), consistent with our results. The three copepod taxa in the present study do not show

a long-term trend, although the populations of both *E. affinis* and *Acartia* spp. in the Gulf have decreased since 2000 (Flinkman et al. 2007). These declines may be associated with the concurrent spread of *Macoma*. However, direct comparison of the development of planktonic and benthic populations is not straightforward, given their high range of temporal and spatial variability. Also, simultaneous fluctuations in the hydrography and deep-water oxygen conditions (e.g., Laine et al. 2007) complicate the conclusions.

Nevertheless, this study demonstrates that bioturbation significantly influences the viability and hatching rates of zooplankton benthic eggs in the Baltic Sea. In other marine ecosystems, where benthic communities are composed of species with a greater variability of functional traits (including, for example, deep-burrowing taxa), bioturbation may have an even greater influence on the success of zooplankton emergence. Large-scale changes in the species composition of macrozoobenthos have been recorded in coastal ecosystems worldwide (Diaz and Rosenberg 1995). We suggest that such shifts will also influence the patterns of benthic emergence in zooplankton.

References

- ALBERTSSON, J., AND K. LEONARDSSON. 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, S. 1980. Growth and production of *Macoma balthica* (L.) in a Northern Baltic soft bottom. *Ophelia* (suppl.) **1**: 31–48.
- CÁCERES, C. E. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* **79**: 1699–1710.
- , AND N. G. HAIRSTON, JR. 1998. Benthic-pelagic coupling in planktonic crustaceans: The role of the benthos. *Ergeb. Limnol.* **52**: 163–174.
- CASTELLANI, C., AND I. A. N. LUCAS. 2003. Seasonal variation in egg morphology and hatching success in the calanoid copepods *Temora longicornis*, *Acartia clausi* and *Centropages hamatus*. *J. Plankton Res.* **25**: 527–537.
- DE STASIO, B. T., JR. 1989. The seed bank of a freshwater crustacean: Copepodology for the plant ecologist. *Ecology* **70**: 1377–1389.
- . 1990. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnol. Oceanogr.* **35**: 1079–1090.
- DIÁZ, R. J., AND R. ROSENBERG. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Ann. Rev.* **33**: 245–303.
- ELLNER, S., AND N. G. HAIRSTON JR. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* **143**: 403–417.
- ELMGREN, R., S. ANKAR, B. MARTELEUR, AND G. EJDUNG. 1986. Adult interference with postlarvae in soft sediments: The Pontoporeia-Macoma example. *Ecology* **67**: 827–836.
- FENCHEL, T. 1996. Worm burrows and oxic microniches in marine sediments. 2. Distribution patterns of ciliated Protozoa. *Mar. Biol.* **127**: 297–301.
- FLINKMAN, J., J.-P. PÄÄKKÖNEN, S. SAESMAA, AND J.-E. BRUUN. 2007. Zooplankton time series in the Baltic Sea—life in a vice of bottom-up and top-down forces, p. 73–86. *In* R. Olsson [ed.], FIMR monitoring of the Baltic Sea environment—annual report 2006. Meri-Report Series of the Finnish Institute of Marine Research.
- FRANÇOIS, F., J.-C. POGGIALE, J.-P. DURBEC, AND G. STORA. 1997. A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheor.* **45**: 295–319.
- GIANGRANDE, A., M. MONTRESOR, A. CAVALLO, AND M. LICCIANO. 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, J. J. 1974. Dormancy in rotifers. *Trans. Am. Microsc. Soc.* **93**: 490–513.
- , AND T. SCHRÖDER. 2004. Rotifers from diapausing, fertilized eggs: Unique features and emergence. *Limnol. Oceanogr.* **49**: 1341–1354.
- GYLLSTRÖM, M., AND L.-A. HANSSON. 2004. Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquat. Sci.* **66**: 274–295.
- HAIRSTON, N. G., JR., A.-M. HANSEN, AND W. R. SCHAFFNER. 2000. The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. *Freshw. Biol.* **45**: 133–145.
- , AND C. M. KEARNS. 2002. Temporal dispersal: Ecological and evolutionary aspects of zooplankton egg banks and the role of sediment mixing. *Integr. Comp. Biol.* **42**: 481–491.
- HAKALA, I. 1971. A new model of the Kajak bottom sampler, and other improvements in the zoobenthos sampling technique. *Ann. Zool. Fenn.* **8**: 422–426.
- KANGAS, P., L. BYHOLM, AND J. STIGZELIUS. 2001. Changes in zoobenthic communities, p. 79–88. *In* P. Kauppila and S. Bäck [eds.], The state of Finnish coastal waters in the 1990s. The Finnish Environment.
- 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.
- , AND F. WULFF. 1981. Experimental studies on temperature-dependent embryonic and postembryonic developmental rates of *Bosmina longispina maritima* (Cladocera) in the Baltic. *Oikos* **36**: 137–146.
- KATAJISTO, T. 2003. Development of *Acartia bifilosa* (Copepoda: Calanoida) eggs in the northern Baltic Sea with special reference to dormancy. *J. Plankton Res.* **25**: 357–364.
- . 2006. Benthic resting eggs in the life cycles of calanoid copepods in the northern Baltic Sea. Ph.D. thesis, Univ. of Helsinki.
- , M. VIITASALO, AND M. KOSKI. 1998. Seasonal occurrence and hatching of calanoid eggs in the sediments of the northern Baltic Sea. *Mar. Ecol. Prog. Ser.* **163**: 133–143.
- KEARNS, C. M., N. G. HAIRSTON, AND D. H. KESLER. 1996. Particle transport by benthic invertebrates: Its role in egg bank dynamics. *Hydrobiologia* **332**: 63–70.
- LAACKONEN, T. 2002. Valkokatkan (*Monoporeia affinis*) populaatiodynamiikan säätely Pohjanlahdella. M.Sc. thesis [in Finnish]. Univ. of Helsinki.
- LAINE, A. O., A.-B. ANDERSIN, S. LEINIÖ, AND A. F. ZUUR. 2007. Stratification-induced hypoxia as a structuring factor of macrozoobenthos in the open Gulf of Finland (Baltic Sea). *J. Sea Res.* **57**: 65–77.
- , H. SANDLER, A.-B. ANDERSIN, AND J. STIGZELIUS. 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.

- LEHTONEN, K., AND A.-B. ANDERSIN. 1998. Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. *Mar. Ecol. Prog. Ser.* **168**: 71–85.
- LIGNELL, R., A.-S. HEISKANEN, H. KUOSA, K. GUNDERSEN, P. KUUPPO-LEINIKKI, R. PAJUNIEMI, AND A. UITTO. 1993. Fate of a phytoplankton spring bloom: Sedimentation and carbon flow in the planktonic food web in the northern Baltic. *Mar. Ecol. Prog. Ser.* **94**: 239–252.
- LIN, J., AND A. H. HINES. 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., AND R. ELMGREN. 1989. Feeding depths and organic absorption for the deposit-feeding benthic amphipods *Pontoporeia affinis* and *Pontoporeia femorata*. *Limnol. Oceanogr.* **34**: 982–991.
- MARCUS, N. H. 1996. Ecological and evolutionary significance of the resting eggs in marine copepods: Past, present, and future studies. *Hydrobiologia* **320**: 141–152.
- , AND F. BOERO. 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.
- , AND J. SCHMIDT-GENGENBACH. 1986. Recruitment of individuals into the plankton: The importance of bioturbation. *Limnol. Oceanogr.* **31**: 206–210.
- MERMILLOD-BLONDIN, F., F. FRANÇOIS-CARCAILLET, AND R. ROSENBERG. 2005. Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: An experimental study. *J. Exp. Mar. Biol. Ecol.* **315**: 187–209.
- , R. ROSENBERG, F. FRANÇOIS-CARCAILLET, K. NORLING, AND L. MAUCLAIRE. 2004. Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. *Aquat. Mar. Ecol.* **36**: 271–284.
- ONBÉ, T. 1978. Sugar flotation method for sorting the resting eggs of marine cladocerans and copepods from sea-bottom sediment. *Bull. Jpn. Soc. Sci. Fish.* **44**: 1411.
- . 1985. Seasonal fluctuations in the abundance of populations of marine cladocerans and their eggs in the Sea of Japan. *Mar. Biol.* **87**: 83–88.
- PATI, A. C., G. BELMONTE, V. U. CECCHERELLI, AND F. BOERO. 1999. The inactive temporary component: An unexplored fraction of meiobenthos. *Mar. Biol.* **134**: 419–427.
- PERSSON, A., AND R. ROSENBERG. 2003. Impact of grazing and bioturbation of marine benthic deposit feeders on dinoflagellate cysts. *Harmful Algae* **2**: 43–50.
- REISE, K. 1983. Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. *Mar. Ecol. Prog. Ser.* **12**: 229–236.
- RHOADS, D. C. 1974. Organism-sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Ann. Rev.* **12**: 263–300.
- , AND D. K. YOUNG. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* **28**: 150–178.
- STÄHL-DELBANCO, A., AND L.-A. HANSSON. 2002. Effects of bioturbation on recruitment of algal cells from the “seed bank” of lake sediment. *Limnol. Oceanogr.* **47**: 1836–1843.
- TANG, K. W., H. G. DAM, AND L. R. FEINBERG. 1998. The relative importance of egg production rate, hatching success, hatching duration and egg sinking in population recruitment of two species of marine copepods. *J. Plankton Res.* **20**: 1971–1987.
- UYE, S., S. KASAHARA, AND T. ONBÉ. 1979. Calanoid eggs in sea-bottom muds. IV. Effects of some environmental factors on the hatching of resting eggs. *Mar. Biol.* **51**: 151–156.
- VIITASALO, M. 1992. Mesozooplankton of the Gulf of Finland and northern Baltic Proper. *Ophelia* **35**: 147–168.
- , AND T. KATAJISTO. 1994. Mesozooplankton resting eggs: Identification and vertical distribution in laminated and mixed sediments. *Mar. Biol.* **120**: 455–466.
- , I. VUORINEN, AND S. SAESMAA. 1995. Mesozooplankton dynamics in the northern Baltic Sea: Implications of variations in hydrography and climate. *J. Plankton Res.* **17**: 1857–1878.
- VIITASALO, S. 2007. Effects of bioturbation by three macrozoobenthic species and predation by necto-benthic mysids on cladoceran benthic eggs. *Mar. Ecol. Prog. Ser.* **336**: 131–140.

Received: 11 January 2007

Accepted: 13 July 2007

Amended: 2 August 2007