Vol. 212: 107–115, 2001 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published March 8

Effects of the coexisting Baltic amphipods *Monoporeia affinis* and *Pontoporeia femorata* on the fate of a simulated spring diatom bloom

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ABSTRACT: A laboratory experiment was performed to quantify the fate of diatom phytodetritus and how this is affected by the presence of benthic amphipods. A Baltic Sea spring bloom sedimentation event was simulated by adding ^{14}C-labeled diatoms (*Skeletonema costatum*) to microcosms with varying densities of the amphipods *Monoporeia affinis* and *Pontoporeia femorata*, as well as to microcosms without amphipods, where the sediment was disturbed mechanically. After 1 mo of incubation, 51 to 77% of the added diatom carbon was still in the sediment; 2 mo later 49 to 66% remained. The effect of amphipods on the fate of the phytodetritus differed between species. At near-field density, *M. affinis* incorporated 6 to 11% of the added ^{14}C, *P. femorata* only 1.2%. The results indicate that burrowing slows mineralization, presumably by mixing organic material to anoxic depths in the sediment. The effect of *P. femorata* on mineralization could not be distinguished from the effect of mechanical stirring. *M. affinis* feeding and respiration resulted in a significant increase in mineralization; at low densities this compensated for the mixing effect, at high densities *M. affinis* feeding resulted in enhanced net mineralization.

KEY WORDS: Pelagic-benthic coupling · Amphipods · Deposit feeding · Mineralization

INTRODUCTION

The growth and population dynamics of profundal benthic organisms are often closely related to sedimentation of spring bloom phytodetritus. The importance of this form of pelagic-benthic coupling has been demonstrated in many marine, freshwater and brackish systems (Graf 1987, Rudnick 1989, Pfannkuche et al. 1992, Noji et al. 1993, Goedkoop & Johnson 1996, Soetaert et al. 1996, Ólafsson & Elmgren 1997, Lehtonen & Andersin 1998). Both benthic animals (Lopez & Levinton 1987) and bacteria (Graf 1987) can readily assimilate diatom phytodetritus at high efficiencies. One would therefore expect that organic matter would be consumed very rapidly after sedimentation; however, there is ample evidence that this is not the case. In a comprehensive field study quantifying the fate of spring bloom diatom deposition in a eutrophic lake, Goedkoop & Johnson (1996) estimated that bacteria, meiofauna and macrofauna together assimilated only 26% of the deposited diatom carbon, leaving 74% unaccounted for. Similarly, the results of laboratory microcosm studies using ^{14}C-labelled phytodetritus show that up to 87% of the added phytodetritus remains in the sediment as particulate organic matter even after several weeks or even months incubation (Andersen & Kristensen 1992, Kristensen et al. 1995, Andersen 1996, Gullberg et al. 1997). It has been hypothesised that degradation is slowed down by the burial of sedimented organic matter by the activity of benthic animals (van Duyl et al. 1992, van de Bund et al. 1994, Blair et al. 1996, Gullberg et al. 1997) or by

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temporary hypoxia following sedimentation events (Heiskanen & Leppänen 1995, Kristensen et al. 1995, Andersen 1996). In contrast, a laboratory study of the loss of phytoplankton pigments from a simulated sedimentation of Baltic spring bloom material found that the presence of the amphipod *Monoporeia affinis* speeded up degradation (Bianchi et al. 2000).

In this paper we present a laboratory experiment demonstrating the quantitative importance of macrobenthic animals in determining the fate of a pulse of diatom phytodetritus. We compared species-specific effects of 2 Baltic amphipod species with mechanically disturbed sediments, in order to separate direct effects of the animals (feeding) from indirect effects (burial of organic matter).

The sediment and animals we used in our experiments were collected from the northern part of the Baltic Sea, where benthic communities are relatively species-poor, with only a few macrofauna species and 30 to 50 meiofauna species (Elmgren 1978, 1984, Ólafsson & Elmgren 1997). Spring bloom phytodetritus provides a very substantial part of the annual organic matter input to these sediments (Elmgren 1978). Its fate is a key factor in the carbon budget of the Baltic Sea; it has been estimated that 32% of the estimated yearly primary production reaches the sediments (Elmgren 1984). After the brief spring diatom bloom, as much as three-quarters of its primary production may reach the sediment (Lignell et al. 1993). As a result of increasing eutrophication, large areas below the halocline of the Baltic Proper have become permanently anoxic with laminated sediments (Andersin et al. 1978). Also in shallower coastal areas benthic hypoxia frequently occurs after spring bloom sedimentation (U. Larsson pers. comm.).

In our experiments, we used the amphipods *Monoporeia affinis* (Lindström) and *Pontoporeia femorata* (Kröyer), which co-occur in the Baltic Proper, where salinity conditions are appropriate, dominating the benthic biomass and production. Many aspects of the ecology of these amphipods have been studied, including food and feeding activity (Hill & Elmgren 1987, Lopez & Elmgren 1989, Hill et al. 1992, Johnson & Wiederholm 1992, Goedkoop & Johnson 1994, Lehtonen 1994), predation (Abrams et al. 1990, Sparrevik & Leonardsson 1995), interactions between year classes (Hill 1992), and interactions with meiobenthos (Ólafsson & Elmgren 1991, Modig et al. 2000). *M. affinis* and *P. femorata* are morphologically similar, but there are important ecological differences between the 2 species. *M. affinis* is of freshwater origin, is very active, has a high feeding rate and accumulates lipids following spring bloom sedimentation. *P. femorata* is a marine species with a lower feeding rate and a smaller seasonal variation in its lipid reserves (Hill et al. 1992, Lehtonen 1996). It can therefore be expected that these 2 amphipod species will respond differently to phytodetritus pulses. We expect that *M. affinis* will more effectively enhance the mineralization of spring bloom material than *P. femorata*, because of its higher feeding rate (direct effect) and more intensive mixing of the surface sediment later (indirect effect).

METHODS

Field sampling. Sediment and animals were collected in early spring 1996 from a depth of 30 to 40 m near the Askö field station, in the north-western Baltic Proper (58° 49′ N, 17° 38′ E). At this location *Monoporeia affinis* and *Pontoporeia femorata* co-occur at high densities (Elmgren 1978).

Surface sediment (ca 0 to 2 cm) was collected using an epibenthic sled (Blomqvist & Lundgren 1996) in early April, just after ice-out and several weeks before the onset of the spring diatom bloom. The sediment was sieved (0.5 mm mesh) to remove ambient macrofauna. The sediment was stored in the dark at 4°C in an aquarium containing aerated brackish water for ca 6 wk until the start of the experiment. Amphipods *Pontoporeia femorata* and *Monoporeia affinis* were collected at the same site using an epibenthic sled and a 0.5 mm sieve in late April, a few days before the start of the spring bloom. Only 1-yr-old individuals of both species were used. Animals were stored in the dark at 4°C in aquaria with sieved sediment and aerated brackish water for ca 3 wk before the start of the experiment.

Preparation of labelled diatoms. The diatom *Skeletonema costatum* Greville was cultured in artificial seawater (salinity 15‰; Kester et al. 1967), with 25% reduced $NaHCO_3$, with added nutrients (f/2 plus Si; Guillard 1975) at 15°C in 500 ml Erlenmeyer flasks. The diatoms were labelled by adding 0.34 mCi $NaH^{14}CO_3$ (Amersham; specific activity 54.0 mCi $mmol^{-1}$) to each culture flask 4 d after starting the culture. After 7 more days of incubation, the labelled algae were harvested in a separatory funnel. The labelled algae were washed 3 times by resuspension in clean brackish water followed by re-settling. The final radioactivity was 0.62 mCi g^{-1} diatom dry mass.

Microcosm setup (Fig. 1). Stoppered 750 ml Erlenmeyer flasks with a bottom surface area of 78.5 cm^2, completely filled with water, were used as microcosms. Each microcosm was connected to a 1500 ml water reservoir, from which water was recirculated to the microcosms using peristaltic pumps. The residence time in the microcosms was 7.8 h. A preliminary experiment using dyed inflowing water showed that at this pumping rate the water was mixed homoge-

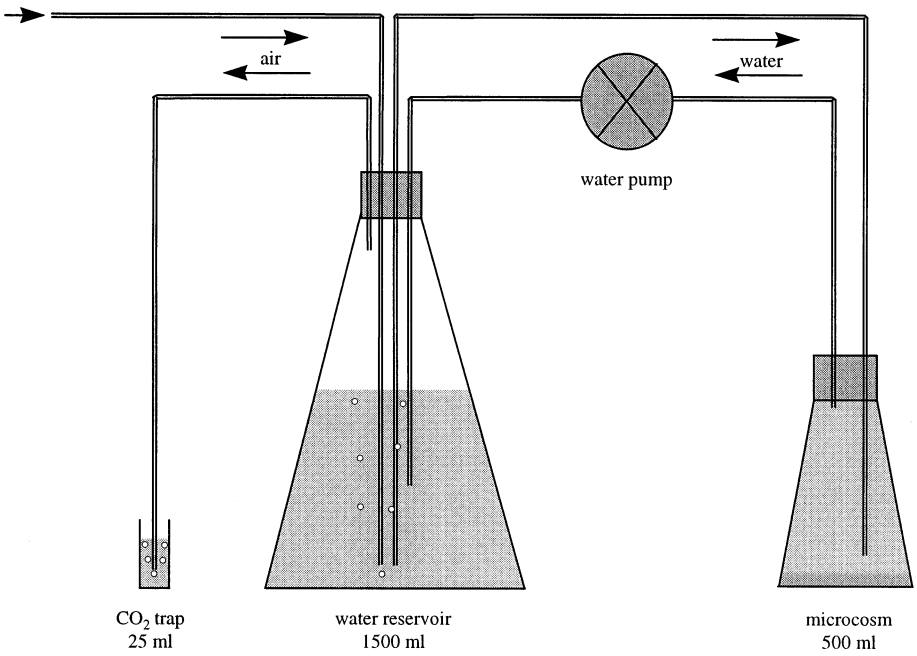

Fig. 1. Schematic of 1 of the 54 identical experimental units

neously. The water reservoirs were continuously aerated throughout the experiment; the oxygen supply to the microcosms was entirely from the inflowing aerated water, and this kept the microcosms close to saturation. Outgoing air was washed in tubes filled with 25 ml CarboSorb E (Packard) to retain CO_2.

Experimental treatments. Treatments (Table 1) included controls with sieved sediment only (S), formaldehyde-killed blinds (F), sediment with *Monoporeia affinis* at densities of 640, 1280 and 2560 ind. m^{-2} (M, M10 and M20), sediment with *Pontoporeia femorata* at a density of 640 ind. m^{-2} (P), sediment with both amphipods at densities of 640 ind. m^{-2} each (MP) and mechanically disturbed sediment without amphipods (ST). In the latter, the sediment was disturbed 3 times a week by repeated brief (<0.5 s) switching on of a stirring magnet (length 2.5 cm), which was buried in the sediment. This resuspended the surface sediment to a few centimetres above the sediment-water interface. Amphipod densities used in the experiment were in the range typically found in the sampling area (Elmgren 1978). Microcosms were incubated at 4°C in the dark for 1 mo. Additional microcosms of the S and M treatments were incubated for 2 more months (SL and ML).

Originally, our experimental design consisted of 54 microcosms. However, during the first days of the experiment 1 of the 4 peristaltic pumps broke down, resulting in temporary hypoxia and consequent amphipod mortality in 15 microcosms. The reported results are from the 39 unaffected microcosms only; as a result, the division of replicates over the treatments is

Table 1. *Monoporeia affinis* and *Pontoporeia femorata.* Overview of experimental treatments. Numbers of replicates as used in data analysis; treatments M10 and M20 were pooled into MH (see text)

	Treatment	No. of replicates	
		1 mo incubation	3 mo incubation
Sieved sediment	S, SL	5 (S)	4 (SL)
M. affinis: 5 ind. microcosm^{-1}	M, ML	6 (M)	4 (ML)
M. affinis: 10 ind. microcosm^{-1}	M10 → MH	2	–
M. affinis: 20 ind. microcosm^{-1}	M20 → MH	2	–
P. femorata: 5 ind. microcosm^{-1}	P	4	–
M. affinis + *P. femorata*: 5 + 5 ind. microcosm^{-1}	MP	6	–
Disturbed sieved sediment	ST	4	–
Formaldehyde-killed sieved blinds	F	2	–

unbalanced (Table 1). The 2 treatments with high *Monoporeia affinis* densities (M10 and M20) were particularly affected. Since their results were quite similar, these 2 were pooled into 1 treatment (MH) for statistical analysis to ensure sufficient replicates.

Start of the experiment. The microcosms were incubated in the dark at a constant temperature of 4°C. Three weeks before addition of labelled algae, 75 g sediment (wet mass) was added to each microcosm, forming a layer of ca 1.5 cm. Microcosms and water reservoirs were filled with brackish seawater (salinity 7‰) and the sediment was allowed to settle for 24 h before the pumps were switched on. Four days later amphipods were added, and stirring of the sediment in the ST treatment started. In the blinds (F), formaldehyde was added to the water reservoirs 2 d before addition of labelled diatoms, to a final concentration of 4%.

Using a Pasteur pipette, 3 ml of diatom suspension containing 28.8 mg diatom dry mass with a total activity of 2.8×10^7 DPM was added to each microcosm, evenly distributing the algae over the sediment surface. The added diatom biomass (3.7 g dry mass m^{-2}) corresponds to a few days of sedimentation during a typical spring bloom in the field (Blomqvist & Larsson 1994). The CO_2 traps were connected immediately after addition of the diatoms.

Community respiration measurements. Radioactivity in the CO_2 traps was measured after 7, 9, 23 and 29 d (all microcosms), as well as after 2 and 3 mo (SL and ML treatments) by taking a 1 ml subsample from the traps, adding 10 ml scintillation liquid (PermaFluor E+, Packard), and counting in a liquid scintillation counter (see below). The CO_2 traps were replaced after each sampling. At the same instances, two 1 ml water samples were taken from each water reservoir. To 1 of these samples 1 ml CarboSorb was added to fix CO_2, to the other 1 ml 1 N HCl was added to release CO_2. Water samples were counted in 10 ml Hionic-Fluor (Packard). Dissolved $^{14}CO_2$ in the water was calculated from the activity in samples with fixed and released CO_2. Total released $^{14}CO_2$ was calculated from activity in the traps and dissolved $^{14}CO_2$.

End of the experiment. When the experiment was terminated after 1 or 3 mo, the water was carefully removed from the microcosms; the sediment was sieved using a 0.5 mm mesh; and dead and live animals were counted, rinsed in distilled water, and frozen individually in 1 ml Eppendorf vials. Sediment radioactivity was measured by solubilizing a freeze-dried sample of the homogenised sediment overnight at 50°C in 80% Soluene-350 (Packard), adding 10 ml Hionic-Fluor (Packard) and counting using a liquid scintillation counter (see below). Amphipods were freeze-dried and individually weighed on an electrobalance. To measure radioactivity in individual amphipods, they were solubilized overnight at 50°C in 80% Soluene-350 (Packard); 5 ml Hionic-Fluor (Packard) was added to each sample. All radioactivity samples were counted with a LKB scintillation counter using a standard ^{14}C counting program.

We checked the variability of replicate samples within individual microcosms for all radioactivity measurements (sediment, water, CO_2 traps and animals) before performing the experiment; this variability was always below ca 10%, in most cases considerably lower. For practical reasons we therefore analysed unreplicated samples.

Data analysis. To reduce variation caused by differences in the amount of radioactivity added to each microcosm, the radioactivity measured as $^{14}CO_2$, amphipod ^{14}C, $DO^{14}C$ and sediment ^{14}C in each microcosm was expressed as a fraction of the total radioactivity measured in that microcosm. To minimize handling of radioactive material, the algae were added in a small volume from a highly concentrated suspension. The reported statistical analyses are based on these fractionated data.

Data were transformed using the arcsine (percentage data) or $\log_{10}$ (other data) transformations; homogeneity of the variances was checked using Cochran's *C*-test. Data were analysed using analysis of variance (ANOVA) and Tukey's test for unequal sample size for *a posteriori* comparison of means.

RESULTS

Budget for recovered ^{14}C

On average, 80% of the added diatom ^{14}C was recovered in the measured fractions (sediment ^{14}C, $^{14}CO_2$, $DO^{14}C$ and amphipod ^{14}C; Table 2a,b). There was no significant treatment effect (1-way ANOVA, $p = 0.19$) on total recovery of added radioactivity for either incubation period.

In the 2 formalin blinds the average recovery of the added radioactivity was 83%. Of the recovered material in the blinds, 1.5% was measured as $^{14}CO_2$, 6.5% as $DO^{14}C$, and the remaining 92.0% as sediment ^{14}C.

After 1 mo, 51 to 77% of the recovered radioactivity was measured as sediment ^{14}C (Table 2a). There was a significant treatment effect (1-way ANOVA, $p < 0.002$); sediment radioactivity was lower in the treatment with *Monoporeia affinis* at high density (MH) than in all other treatments ($p < 0.05$), while differences between the other treatments were not significant ($p > 0.05$). Radioactivity in the $^{14}CO_2$ and $DO^{14}C$ fractions did not differ between treatments (1-way ANOVA, $p > 0.05$). The amount of radioactivity accumulated in amphipod bio-

Table 2. *Monoporeia affinis* and *Pontoporeia femorata*. ^{14}C budget of microcosms after (a) 1 mo and (b) 3 mo incubation with labeled phytodetritus; standard errors in parentheses. Letter codes show homogeneous groups (Tukey test for unequal n, $p < 0.05$) between treatments. (c) Effect of presence/absence of *Monoporeia affinis* and incubation time on the ^{14}C budget of microcosms with labeled phytodetritus; analysis by 2-way ANOVA. ns: not significant; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

(a) ^{14}C budget after 1 mo

Treatment		Total measured ^{14}C (10^7 dpm) (=100%)	% of total measured ^{14}C				
			$^{14}CO_2$	DO^{14}C	*M. affinis*	*P. femorata*	Sediment
S		2.2 (0.2)	29 (8)	8 (4)	–	–	63 (9)b
M		2.2 (0.3)	24 (7)	5 (2)	6 (3)a	–	65 (10)b
MH		2.5 (0.1)	31 (8)	7 (0)	11 (2)b	–	51 (9)a
P		2.1 (0.2)	16 (5)	5 (1)	–	1.2 (0.2)a	77 (5)b
MP		2.2 (0.3)	23 (4)	6 (1)	4 (1)a	0.2 (0.1)b	67 (5)b
ST		2.0 (0.3)	19 (10)	5 (1)	–	–	77 (10)b
ANOVA results	df:	5,23	5,23	5,23	2,13	1,8	5,23
	p:	0.14 ns	0.07 ns	0.36 ns	0.001**	0.000***	0.002**

(b) ^{14}C budget after 3 mo

Treatment	Total measured ^{14}C (10^7 dpm)	% of total measured ^{14}C			
		$^{14}CO_2$	DO^{14}C	*M. affinis*	Sediment
SL	2.2 (0.4)	30 (5)	5 (4)	–	66 (8)
ML	2.0 (0.2)	41 (9)	7 (1)	3 (2)	49 (7)

(c) Effect of *M. affinis* and incubation time

		Total measured ^{14}C	% ^{14}C as $^{14}CO_2$	% ^{14}C in DO^{14}C	% ^{14}C in *M. affinis*	% ^{14}C in sediment
	df:	1,15	1,15	1,15	1,8	1,15
(1) *M. affinis*		0.43 ns	0.72 ns	0.83 ns	–	0.07 ns
(2) Incubation		0.48 ns	0.03*	0.55 ns	0.21 ns	0.08 ns
Interaction 1 × 2		0.42 ns	0.07 ns	0.09 ns	–	0.03*

mass ranged from 1 to 11%. *M. affinis* incorporated 4 to 11% of total measured ^{14}C, with significant differences between the 3 treatments where it was present (1-way ANOVA, $p < 0.001$). More label was incorporated in *M. affinis* at high density (MH) than at low density in presence (MP) and absence (M) of *Pontoporeia femorata* ($p < 0.01$). The presence of *P. femorata* had no significant effect on *M. affinis* label uptake ($p > 0.05$).

Much less radioactivity was measured in *Pontoporeia femorata* than in *Monoporeia affinis* (Table 2a). When incubated alone (P), *P. femorata* incorporated 1.2% of the total measured ^{14}C; in presence of *M. affinis* (MP) incorporation was only 0.2%. This difference was highly significant (*t*-test, $p < 0.001$) and is the combined effect of an increased mortality (see Fig. 2) and a decrease in the radioactivity per individual amphipod (see Fig. 4).

After 3 mo, the recovery of the added radioactivity (Table 2b) was about the same as after 1 mo. A 2-way ANOVA with presence/absence of *Monoporeia affinis* and incubation time as independent variables was used to analyse the data from the treatments S, SL, M and ML (Table 2c). Effects on total measured ^{14}C, DO^{14}C and ^{14}C in *M affinis* were not significant. Total released $^{14}CO_2$ was significantly higher after 3 mo than after 1 mo ($p < 0.05$). There was a significant interaction effect ($p < 0.05$) between incubation time and the presence of *M. affinis* on ^{14}C remaining in the sediment. In the treatments with added *M. affinis*, less ^{14}C remained in the sediment after 3 mo than after 1 mo, while without amphipods similar amounts were measured in both cases.

^{14}C in CO_2 traps

Table 3a summarises the rates of $^{14}CO_2$ release during the experiment. The data for the periods 0–7, 7–9, 9–23 and 23–29 d were analysed using a 2-way repeated-measures ANOVA (Table 3b); significant effects were found for treatment ($p < 0.05$), incubation time ($p < 0.0001$) and the interaction between these factors ($p < 0.001$). The rate of $^{14}CO_2$ release decreased significantly over time (Table 3a).

Table 3. *Monoporeia affinis* and *Pontoporeia femorata*. (a) $^{14}CO_2$ production (% of total measured $^{14}Cd^{-1}$) in microcosms with labeled phytodetritus throughout the experiment; standard errors in parentheses. (b) Effect of treatment and incubation time on $^{14}CO_2$ production rates (2-way repeated-measures ANOVA, t = 7, 9, 23 and 29 d). $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

(a) $^{14}CO_2$ production

Treatment	$^{14}CO_2$ production rates					
	t = 7	t = 9	t = 23	t = 29	t = 59	t = 95
S	1.0 (0.5)	0.5 (0.2)	1.1 (0.4)	0.9 (0.2)	0.3 (0.2)	0.0 (0.0)
M	1.1 (0.3)	0.8 (0.2)	0.8 (0.23)	0.5 (0.3)	0.6 (0.4)	−0.0 (0.1)
MH	1.6 (0.3)	1.2 (0.2)	1.1 (0.4)	0.5 (0.3)	–	–
P	1.0 (0.8)	0.4 (0.2)	0.4 (0.4)	0.1 (0.2)	–	–
MP	1.2 (0.3)	1.0 (0.3)	0.8 (0.2)	0.4 (0.2)	–	–
ST	0.5 (0.2)	0.6 (0.4)	0.9 (0.5)	0.3 (0.4)	–	–

(b) Effect of treatment and incubation time

Effect	df	p
(1) Treatment	5, 23	0.03*
(2) Incubation time	3, 69	0.000***
Interaction 1 × 2	15, 69	0.001**

Effects on amphipods

There was a significant treatment effect on amphipod mortality after 1 mo of incubation (Fig. 2; 1-way ANOVA, $p < 0.001$). *Monoporeia affinis* mortality was always less than 10%, without significant differences among treatments ($p > 0.05$). *Pontoporeia femorata* mortality was 15% when incubated alone, but 57% when incubated together with *M. affinis*; the latter value was significantly higher than all other mortalities ($p < 0.05$). Observations of the appearance of dead amphipods on the sediment surface showed that mortality occurred almost exclusively during the first week of the experiment, just after addition of the diatoms to the microcosms.

Individual amphipod biomasses (Fig. 3) differed significantly between species (1-way ANOVA, $p < 0.05$), with *Pontoporeia femorata* being heavier than *Monoporeia affinis* ($p < 0.05$). There was no significant treatment effect on biomass for either species ($p > 0.05$). Intra- and interspecific differences were found for the amount of radioactivity measured per individual amphipod (Fig. 4; 1-way ANOVA, $p < 0.001$). *P. femorata* incorporated consistently less than *M. affinis* ($p < 0.01$). When incubated alone, *P. femorata* incorporated more ^{14}C than when incubated with *M. affinis* ($p < 0.05$).

Monoporeia affinis mortality after 3 mo incubation (Table 4) was higher than after 1 mo (Mann-Whitney *U*-test, $p < 0.001$; a non-parametric test was used be-

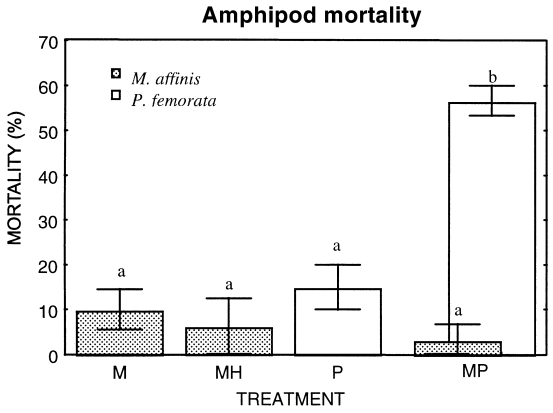

Fig. 2. *Monoporeia affinis* and *Pontoporeia femorata*. Amphipod mortality after 1 mo of incubation. Letter codes show significant differences (Tukey test for unequal n, $p < 0.05$) between treatments

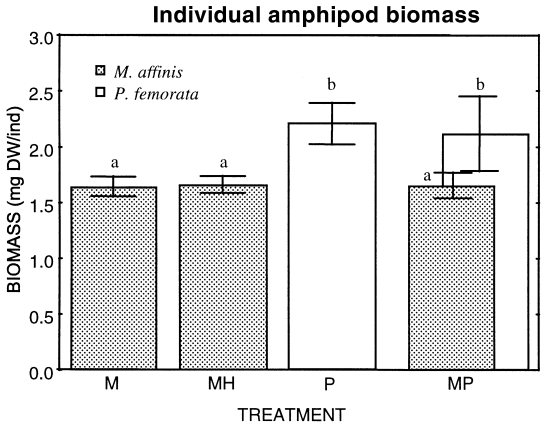

Fig. 3. *Monoporeia affinis* and *Pontoporeia femorata*. Amphipod individual biomass after 1 mo of incubation. Letter codes show significant differences (Tukey test for unequal n, $p < 0.05$) between treatments

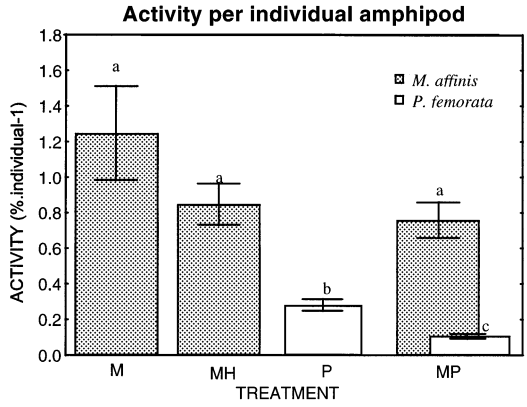

Fig. 4. *Monoporeia affinis* and *Pontoporeia femorata*. Incorporated ^{14}C in amphipods after 1 mo incubation (as percentage of total recovered ^{14}C). Letter codes show homogeneous groups (Tukey test for unequal n, $p < 0.05$)

cause the variance in 1 of the treatments was 0). There were no significant differences in individual *M. affinis* dry mass and radioactivity per individual (*t*-test, $p > 0.05$) between incubation times.

DISCUSSION

Slightly over 80% of the radioactivity added in the experiment could be accounted for; this was the case for all treatments, including the formalin blinds. Where the remaining near 20% went is not clear; possibly it was absorbed to the walls of the microcosms, water reservoirs and/or tubing. Another possibility is that part of the radioactivity was washed out of the microcosms as particulate material and sedimented in the water reservoirs.

From the carbon budgets it is clear that most of the added phytodetritus was neither released as $^{14}CO_2$ nor taken up by amphipods during the 3 mo experiment, but remained in the sediment. This result is in agreement with many laboratory studies with a variety of experimental setups (Andersen & Kristensen 1992, Hansen & Blackburn 1992, Fitzgerald & Gardner 1993, Webb & Montagna 1993, Andersen 1996, Gullberg et al. 1997, Ólafsson et al. 1999). It is likely that most of this material is utilised on longer time scales. Graf (1987) found that after addition of fresh phytodetritus most of the heat production in the sediment was from old organic material already present in the sediment. In a mesocosm experiment, Rudnick (1989) showed that there are 2 distinct meiofauna groups utilising fresh and old detrital food sources, respectively; Ólafsson & Elmgren (1997) came to the same conclusion from a field study quantifying seasonal dynamics of the meiofauna in the Baltic Sea. The mineralization of the more refractory organic material occurs probably on a time scale much longer than the duration of the average microcosm experiment, years rather than months. In contrast, compounds that are relatively easily degraded, such as chlorophyll *a* in spring bloom material, can be totally broken down in less than 2 mo in the presence of the amphipod *Monoporeia affinis* under conditions similar to those of our study (Bianchi et al 2000).

Stirring, resulting in the burial of diatom material, appears to inhibit phytodetritus mineralization, while the feeding activity of *Monoporeia affinis* seems to enhance it. At low *M. affinis* densities, these inhibiting and enhancing effects appear more or less balanced, while at higher densities the enhancement of mineralization by *M. affinis* feeding is more important, as also found by Bianchi et al. (2000). The effect of *Pontoporeia femorata* on carbon mineralization in our experiment appears to be mostly abiotic: a burial of freshly sedimented material resulting in slower mineralization.

Monoporeia affinis took up more of the labelled phytodetritus than *Pontoporeia femorata*. The smaller size of *M. affinis* would tend to increase its relative metabolic rate, but the difference in uptake in radioactive material was far greater than can be explained by the small difference in mean mass between the 2 species. This difference is consistent with the higher feeding (Lopez & Elmgren 1989) and respiration rates (Cederwall 1979, Lehtonen 1995) of *M. affinis*, and with its more opportunistic utilisation of available food resources, as reflected by seasonal patterns of lipid storage related to sedimentation events in the field

Table 4. *Monoporeia affinis*. Mortality, individual dry mass, and radioactivity per individual after 1 and 3 mo incubation with labeled phytodetritus (treatments M and ML) with test results; standard errors in parentheses. ns: not significant; ***$p < 0.001$

Treatment	Incubation (mo)	Mortality (%)	Biomass (mg dw ind.$^{-1}$)	^{14}C (% of total ind.$^{-1}$)
M	1	10 (1.8)	1.6 (0.04)	1.2 (0.11)
ML	3	20 (0.0)	1.4 (0.06)	0.8 (0.14)
t-test p		–	0.20 ns	0.15 ns
Mann-Whitney test p		0.000***	–	–

(Hill et al. 1992, Lehtonen 1996). Most individuals of both species had full guts upon termination of the experiment, indicating that they were feeding. When incubated alone at equal density, *M. affinis* incorporated almost 5-fold more label than *P. femorata*. This is in good agreement with reported differences in feeding rates between the 2 species; Lopez & Elmgren (1989) estimated that *P. femorata* and *M. affinis* have gut turnover times of ca 2.6 and 0.9 h, respectively. The gut volume of *M. affinis* of a size similar to those used in our experiment was estimated to be 0.25 mm^3 (Elmgren et al. 1986). If we assume the gut volume of *P. femorata* is the same, and that both species feed exclusively from the top centimetre of the sediment, each amphipod could in 1 mo only have ingested 0.08% (*P. femorata*) and 0.25% (*M. affinis*) of the sediment available to them in our 78.5 cm^2 microcosms. If feeding would be non-selective with an assimilation efficiency of 40% (Lopez & Elmgren 1989), and the labelled food was uniformly mixed into the sediment, the 5 *P. femorata* could have taken up maximally 0.15% and the 20 *M. affinis* maximally 2% of the added radioactivity. However, their maximum label uptake was over 5 times higher (Fig. 4), indicating that 1 or more of the assumptions were not valid. Initially, the added phytodetritus was clearly not uniformly mixed into the sediment, allowing the amphipods to feed selectively on a thin surface layer of high food quality, for which assimilation efficiency may be higher than 40%. Our finding that label uptake by *P. femorata* was significantly reduced in sympatry with *M. affinis* (Fig. 4) may be the result of interactive spatial niche segregation of the 2 species, as mentioned above. This may have caused *P. femorata* to burrow deeper into the sediment, from where it had little access to the high-quality food at the sediment surface.

The high *Pontoporeia femorata* mortality in the presence of *Monoporeia affinis* during the first days of the experiment may have been caused by unfavourable oxygen conditions and/or sulphide toxicity. Following sedimentation events, brief periods of oxygen deficiency and increased sulphate reduction rates in surface sediments have been demonstrated (Graf 1987, Hansen & Blackburn 1992, Moeslund et al. 1994). Oxygen penetration following addition of diatom phytodetritus in a similar experiment with the same microcosm setup as the one used in our experiment was not more than 2 mm, even though the oxygen concentration remained high in the overlying water (W.J.v.d.B. unpubl. results). The observed difference in mortality between *M. affinis* and *P. femorata* is consistent with the known behavioural and physiological differences between these species. In sympatry *M. affinis* and *P. femorata* segregate spatially, with the latter species burrowing deeper into the sediment (Hill & Elmgren 1987), thereby exposing itself to more unfavourable oxygen conditions. Furthermore, *P. femorata* is more sensitive to oxygen stress than *M. affinis* (Johansson 1997). *M. affinis* thus appears to be better equipped to deal with brief periods of oxygen deficiency than *P. femorata*. In the restricted sediment depth of our experiments, *P. femorata* was not able to fully escape interactions with *M. affinis* by burrowing, which may have caused intense escape activity that interacted with oxygen stress to increase mortality.

The results of these microcosm experiments cannot be directly extrapolated to the field situation. Our 'phytodetritus' input consisted of fresh material from 1 species of diatoms, the sediment depth in the microcosms was less than 2 cm, and the experimental setup eliminates lateral transport and reduces resuspension of sediment, 2 processes likely to be very important in the field (Blomqvist & Larsson 1994). However, the results presented clearly demonstrate the close relation between phytodetritus sedimentation events, macroinvertebrate feeding and mixing activity.

Acknowledgements. Many thanks to Nils Walberg for building the microcosm setup, to Jan-Erik Hägerroth for assistance in the field, and to Lars-Åke Gisselsson for providing the algae. Willem Goedkoop and Lars Byrén gave helpful comments on the manuscript. This research was supported by a Marie Curie postdoctoral fellowship to W.J.v.d.B. and NFR grants to R.E.

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Editorial responsibility: Kenneth Tenore (Contributing Editor), Solomons, Maryland, USA

Submitted: August 21, 2000; Accepted: December 6, 2000
Proofs received from author(s): February 21, 2001