

# Intraspecific food competition in the deposit-feeding benthic amphipod *Monoporeia affinis*—a laboratory study

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**ABSTRACT:** Field studies in the Baltic Sea indicate that the growth rate of the deposit-feeding benthic amphipod *Monoporeia affinis* (Lindström), which is found in densities of up to  $\approx 25\,000$  ind.  $m^{-2}$ , is negatively density-dependent. We tested the density-dependence of growth in *M. affinis* under controlled laboratory conditions, using sediment of high organic content (loss on ignition 10.9%) and a wide density range of 2 amphipod year-classes (juveniles, 1150 to 38 000 ind.  $m^{-2}$ , 1 yr old subadults, 580 to 18 000 ind.  $m^{-2}$ ). Growth was strongly negatively density-dependent for both juveniles and subadults. We then used sediment of low organic content (loss on ignition 3.7%) to test whether the density-dependence of growth was due to a direct crowding effect at high density, or mainly due to food limitation. Using an intermediate amphipod density (2800 ind.  $m^{-2}$ ) expected to give clear growth depression, we added baker's yeast as supplementary food at 6 levels corresponding to an input of 0 (control) to 147 g C  $m^{-2}$  over an 8 wk period. The 3 highest yeast additions resulted in black, reduced sediment and elevated amphipod mortality in some replicates, but where the sediment did not become reduced, food additions enhanced growth significantly, demonstrating that growth depression at high density was primarily due to food limitation and not to crowding as such.

**KEY WORDS:** Baltic Sea · Deposit-feeder · Macrobenthos · Food limitation · Intraspecific competition · *Monoporeia affinis*

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## INTRODUCTION

It is often taken more or less for granted that the biomass of benthic macrofauna that can be supported on a given area of subtidal soft sediment is limited primarily by the amount of food available (e.g. Pearson & Rosenberg 1987, Josefson 1998). This idea is consistent with the large-scale distribution of soft-bottom benthos, such as the decrease in biomass with increasing depth and consequently lower availability of organic matter from the continental shelf, down the continental slope, to abyssal depths (Rowe 1971, Thiel 1983). Obvious exceptions occur, such as macrotidal continental shelves and exposed shallow sandy bottoms, where

regular or intermittent turbulence, strong enough to sweep away, bury or kill animals, is a limiting factor (e.g. Rees et al. 1977). In some shallow areas, predation limits macrobenthic biomass (Blegvad 1928, Virnstein 1977, Reise 1985). The initial response of macrobenthos to organic enrichment is often an increase in biomass, until excessive oxygen consumption leads to anoxia and eventual elimination of the macrobenthos (Pearson & Rosenberg 1978). This also supports the idea of benthic food limitation as the norm and other limiting factors as being rather the exception (Pearson & Rosenberg 1987).

If the biomass of the whole macrobenthic community is food-limited, then some populations of deposit-feeding animal populations must also be food-limited. If other deposit-feeding populations are limited by predation, by abiotic factors, or by interference competi-

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tion, then the food resources they leave unused should increase the biomass of the food-limited populations. Levinton (1972) suggested that competition for food should be more common in deposit-feeders than in suspension-feeders, yet there are few experimental demonstrations of food limitation in benthic deposit-feeders. The few experimental demonstrations of competition in marine deposit-feeding populations reported in reviews by Connell (1983), Schoener (1983) and Branch (1984) concerned animals that feed primarily on benthic microalgae, and either did not demonstrate the competitive mechanism or indicated that interference competition was involved. Careful laboratory studies have demonstrated food limitation in the opportunistic polychaete *Capitella capitata* (Chesney & Tenore 1985, Tenore & Chesney 1985). Kamermans et al. (1992) reported density-dependent growth in a deposit-feeding bivalve population in an outdoor flow-through basin, and concluded that the cause was intraspecific competition for sedimentary food. Even when field data clearly show individual growth rates to decrease as population density increases, experimental evidence is needed to demonstrate if this is due to food limitation or is a crowding effect, because of intraspecific interference competition in a dense population (e.g. Miralto et al. 1996, Wheatcroft et al. 1998).

In the Baltic Sea, where tides are negligible, benthic biomass increases steeply from the oligotrophic northernmost end to the much more productive southwestern end (Elmgren 1978). Food is thought to regulate individual growth rate and thus population biomass in the most abundant deposit-feeder in the Baltic Sea, the amphipod *Monoporeia affinis* (Lindström) (syn. *Pontoporeia affinis*; see Bousfield 1989). Its individual growth rate peaks after the sinking spring diatom bloom has enriched the sediment with high-quality organic matter (Cederwall 1977, Elmgren 1978, Lehtonen & Andersin 1998). Sarvala (1986) and Leonardsson (1994) noted a negative density-dependence of growth in Baltic Sea populations of *M. affinis*, and Johnson (1987) reported similar results for a Swedish lake population. In lakes with good feeding conditions, its growth is rapid and its life cycle shortened from the normal 2 yr to 1 yr (Wiederholm 1973, Johnson 1987). Temperature also seems to affect the length of its life cycle, since 1 yr life cycles are common in the warmer, shallower areas, even where deeper populations have life cycles of 2 or 3 yr (Segerstråle 1950, Ankar & Elmgren 1976). Uitto & Sarvala (1991) argued that *M. affinis* derives most of its energy from sediment organic matter, not from micro-organisms or meiofauna, and that field populations are likely to be strictly food-limited. Studies of the annual dynamics of lipid reserves in *M. affinis* support this interpretation (Hill et al. 1992,

Lehtonen & Andersin 1998). Field evidence thus suggests that food limitation, and consequent intraspecific competition for food, regulates the dense *M. affinis* populations that are common in the Baltic Sea. Yet it is hard from field data to rule out the influence of a possible natural growth periodicity or of direct crowding effects, rather than food limitation, as explanations for the patterns described. We here report laboratory experiments that test the hypotheses that: (1) growth of *M. affinis* is negatively density-dependent; (2) the reduced growth at high population density is due to food limitation.

## MATERIALS AND METHODS

**Study area.** Experiments were carried out in 1982 at the Askö Laboratory, NW Baltic proper (58°49'N, 17°38'E). In this brackish-water area (salinity = 6 to 7.5), *Monoporeia affinis* (Lindström) is an important species in the macrobenthos below a depth of about 20 m. It alone contributed almost half the abundance (on average 1640 ind. m<sup>-2</sup>), and a quarter of the shell-free dry biomass of macrobenthos in the 9 to 50 m depth zone in 1971 (Ankar & Elmgren 1976), and 8 to 16% of the shell-free dry biomass in 1982 to 1994 (Cederwall 1999). The situation is similar over large areas of the Baltic Sea (Rumohr et al. 1996). Further north, *M. affinis* forms dense and almost monospecific communities over large areas (Hessle 1924, Ankar 1977, Elmgren et al. 1984, Sparrevik & Leonardsson 1999). Elmgren et al. (1984) found average densities in the Bothnian Sea of 1900 ind. m<sup>-2</sup> (plus 4000 juveniles m<sup>-2</sup> in the meiofauna fraction), and numbers as high as 23 400 ind. m<sup>-2</sup> in the Gulf of Bothnia (Leonardsson et al. 1988) and 27 600 ind. m<sup>-2</sup> in the Gulf of Finland (Sarvala 1986) have been recorded.

**Experimental system.** Small experimental jars (vol. = 2 l, sediment area = 104 cm<sup>2</sup>; see Fig. 1 in Elmgren et al. 1986) were supplied with seawater pumped from 16 m depth at a flow rate of 0.9 ± 0.1 l h<sup>-1</sup> (mean ± SEM) and filtered through a 90 µm plankton net. The experimental water temperature was 6 ± 2°C (n = 31) and the salinity 6.7 ± 0.1 (n = 5) compared to field values of 4 ± 1°C and 7.2 ± 0.1 at 30 m depth during the same period (n = 9 in both cases; Larsson & Johansson 1984). A dim green light simulated roughly the ambient light at 30 m depth, with natural day-length regulated automatically by an outdoor photocell.

Sediments were collected with a van Veen grab from sites with *Monoporeia affinis*, sieved through a 300 µm sieve to remove macrofauna and homogenised. Water content was determined after drying overnight at 105°C, and loss on ignition (LOI) after 2 h at 500°C. Amphipods were collected with a dredge at 30 to 50 m

depth, gently sieved out with cold seawater, and quickly sorted into batches of 25 (juvenile and subadult density-dependence experiments) or 5 (subadult food-limitation experiment), keeping temperature low at all times. Before the experiments, juveniles were kept for  $\leq 3$  d and subadults for  $\leq 16$  d (food-limitation experiment  $\leq 2$  d) in natural sediment in the same room and conditions as during the experiments. Each jar received 560 ml of sediment slurry, giving a sediment depth of  $\sim 6$  cm after settling. After 12 to 24 h, amphipods were added in haphazardly selected batches. Batches preserved at once in 10% formalin buffered with hexamethylenetetramine gave estimates of initial amphipod length and dry mass (60°C, after several months in formalin). Jars were placed randomly in the experiment room to minimise differences in light, temperature, and flow among treatments. The water leaving 8 jars per experiment was led to an additional, empty 3 l jar, to estimate the loss of sediments with the outflow during the experiment. At the end of the experiments the content of these outflow jars was filtered through Whatman GF/F filters (nominal pore size 0.8  $\mu\text{m}$ ) and analysed for sediment wet mass and amphipod presence.

At the end of the experiments, amphipods were recovered by sieving through a 1 mm net, followed by a 0.5 mm net in the experiment with juveniles, and were preserved as above. Length from the tip of the

rostrum to the end of the last urosome segment was measured on straightened-out amphipods under a stereo microscope. Dry mass, including gut content, was measured to the nearest 0.01 mg. In each jar, a sediment core of 25 mm inner diameter was taken to 2 cm depth and analysed for LOI.

**Experimental design. Tests of density-dependence of growth rates:** The sediment was collected on March 29, before the spring phytoplankton bloom, from a 30 m-deep inshore station. It had high water content ( $80 \pm 5\%$ ;  $n = 2$ ) and LOI ( $10.9 \pm 0.3\%$ ;  $n = 2$ ) after sieving. Juvenile treatments had from 12 to 400 *Monoporeia affinis* young-of-the-year  $\text{jar}^{-1}$ , corresponding to a density of about 1150 to 38 000 ind.  $\text{m}^{-2}$  (details in Table 1). Handling large numbers of small juveniles takes time. The experiment with juveniles was therefore started over several days, with 1 (March 30, 31, April 1, 5) or 2 (April 2) replicates per treatment each day, and ended over 2 d (June 2: 100, 200 and 400 ind.  $\text{jar}^{-1}$  treatments; June 3: 12, 25 and 50 ind.  $\text{jar}^{-1}$  treatments). Subadult treatments had from 6 to 200 1 yr old *M. affinis*  $\text{jar}^{-1}$  and ran from 14 April to 9 June (details in Table 2). Outflow jars were connected to juvenile 12, 100 and 400 ind.  $\text{jar}^{-1}$  treatments and to subadult 6, 50 and 100 ind.  $\text{jar}^{-1}$  treatments.

**Test of food limitation of subadult growth rate:** This experiment ran from April 7 to June 8, using sediment collected on March 29 from a 45 m-deep offshore sta-

Table 1. *Monoporeia affinis* and *Pontoporeia femorata*. Test of density-dependence of growth rate in juveniles (mean  $\pm$  SEM). Initial numbers estimated from preserved batches, except for the 12 ind.  $\text{jar}^{-1}$  treatment, to which amphipods were added individually, excluding all *P. femorata*. Initial length: all amphipods =  $1.52 \pm 0.06$  mm. *M. affinis* =  $1.42 \pm 0.01$  mm; *P. femorata* =  $1.67 \pm 0.03$  mm. Initial individual amphipod dry mass =  $0.010 \pm 0.001$  mg. Average experiment duration was 62 d. n: number of replicates,  $\Delta$ : changes in length and mass

	Treatment (intended no. of ind. $\text{jar}^{-1}$ )					
	12	25	50	100	200	400
<b>All amphipods</b>						
Initial number of ind. $\text{jar}^{-1}$	12	24.8 $\pm$ 0.3	49.5 $\pm$ 0.6	99 $\pm$ 1	198 $\pm$ 3	396 $\pm$ 5
Initial number of ind. $\text{m}^{-2}$	1150	2375	4750	9500	19 000	38 000
Final number of ind. $\text{jar}^{-1}$	7 $\pm$ 1	19 $\pm$ 1	35 $\pm$ 3	65 $\pm$ 8	149 $\pm$ 6	109 $\pm$ 38
% survival	58 $\pm$ 8	73 $\pm$ 6	73 $\pm$ 7	67 $\pm$ 8	78 $\pm$ 2	26 $\pm$ 11
Final ind. dry mass (mg)	0.20 $\pm$ 0.01	0.22 $\pm$ 0.02	0.14 $\pm$ 0.01	0.11 $\pm$ 0.01	0.06 $\pm$ 0.01	0.05 $\pm$ 0.01
$\Delta$ individual dry mass (mg)	0.19	0.21	0.13	0.10	0.05	0.04
$\Delta$ final dry biomass (mg)	1.3	3.9	4.4	5.6	5.5	0.4
<b><i>Monoporeia affinis</i></b>						
Initial number of ind. $\text{jar}^{-1}$	12	24 $\pm$ 1	47 $\pm$ 2	94 $\pm$ 3	188 $\pm$ 6	376 $\pm$ 12
Final number of ind. $\text{jar}^{-1}$	7.2 $\pm$ 0.9	19 $\pm$ 1	32 $\pm$ 3	62 $\pm$ 7	143 $\pm$ 5	107 $\pm$ 38
Final length (mm)	3.9 $\pm$ 0.1	3.9 $\pm$ 0.1	3.6 $\pm$ 0.1	3.2 $\pm$ 0.1	2.8 $\pm$ 0.1	2.7 $\pm$ 0.1
$\Delta$ length (mm)	2.5 $\pm$ 0.1	2.5 $\pm$ 0.1	2.2 $\pm$ 0.1	1.8 $\pm$ 0.1	1.4 $\pm$ 0.1	1.3 $\pm$ 0.1
<b><i>Pontoporeia femorata</i></b>						
Initial number of ind. $\text{jar}^{-1}$	0	1.2 $\pm$ 0.8	2.5 $\pm$ 1.6	5 $\pm$ 3	10 $\pm$ 6	20 $\pm$ 13
Final number of ind. $\text{jar}^{-1}$	0	0	2.8 $\pm$ 1.2	4 $\pm$ 2	6 $\pm$ 2	2 $\pm$ 1
Final length (mm)	–	–	2.6 $\pm$ 0.1	2.4 $\pm$ 0.1	2.3 $\pm$ 0.1	2.3 $\pm$ 0.2
$\Delta$ length (mm)	–	–	0.9 $\pm$ 0.1	0.6 $\pm$ 0.1	0.7 $\pm$ 0.1	0.6 $\pm$ 0.1
n	6	6	6	6	6	6

Table 2. *Monoporeia affinis*. Test of density-dependence of subadult growth rate (mean  $\pm$  SEM); initial amphipod length =  $6.0 \pm 0.1$  mm; initial individual amphipod dry mass =  $0.51 \pm 0.05$  mg. Experiment duration was 57 d. (n): number of replicates;  $\Delta$ : changes in length and mass

	Treatment (intended no. of ind. jar <sup>-1</sup> )					
	6	12	25	50	100	200
Initial number of ind. jar <sup>-1</sup>	6	12	24 $\pm$ 1	47 $\pm$ 2	94 $\pm$ 3	189 $\pm$ 6
Initial number of ind. m <sup>-2</sup>	580	1150	2300	4500	9000	18000
Final number of ind. jar <sup>-1</sup>	4.8 $\pm$ 0.4	9.2 $\pm$ 0.5	21 $\pm$ 1	38 $\pm$ 1	78 $\pm$ 4	157 $\pm$ 7
% survival	80	77	91	81	83	83
Final length (mm)	7.3 $\pm$ 0.2	7.1 $\pm$ 0.1	7.0 $\pm$ 0.1	6.7 $\pm$ 0.1	6.5 $\pm$ 0.1	6.4 $\pm$ 0.1
$\Delta$ length (mm)	1.3 $\pm$ 0.2	1.1 $\pm$ 0.1	1.0 $\pm$ 0.1	0.7 $\pm$ 0.1	0.5 $\pm$ 0.1	0.4 $\pm$ 0.1
Final ind. dry mass (mg)	1.40 $\pm$ 0.09	1.06 $\pm$ 0.07	1.02 $\pm$ 0.05	0.78 $\pm$ 0.03	0.77 $\pm$ 0.06	0.72 $\pm$ 0.02
$\Delta$ total dry biomass (mg)	3.7	3.6	9.2	5.7	12	17
n	5	5	5	5	5	5

Table 3. *Monoporeia affinis*. Test of food limitation of subadult growth rate (mean  $\pm$  SEM). Initial abundance =  $29.5 \pm 0.4$  ind. jar<sup>-1</sup> or 2800 ind. m<sup>-2</sup>; initial length =  $6.6 \pm 0.1$  mm; initial dry mass =  $0.94 \pm 0.11$  mg. Experiment duration was 62 d. (n): number of replicates;  $\Delta$ : changes in length and mass

	Treatment (yeast dose, 2 $\times$ per week [g])					
	0	0.05	0.1	0.2	0.4	0.8
$\Sigma$ yeast added (g C m <sup>-2</sup> )	0	9.2	18	37	74	147
Final number of ind. jar <sup>-1</sup>	24 $\pm$ 1	25 $\pm$ 1	23 $\pm$ 1	19 $\pm$ 4	17 $\pm$ 5	10 $\pm$ 4
% survival	80 $\pm$ 3	83 $\pm$ 3	77 $\pm$ 3	64 $\pm$ 13	57 $\pm$ 16	34 $\pm$ 12
Final length (mm)	7.0 $\pm$ 0.1	7.3 $\pm$ 0.1	7.5 $\pm$ 0.1	7.5 $\pm$ 0.1	7.3 $\pm$ 0.1	7.7 $\pm$ 0.2
$\Delta$ length (mm)	0.4 $\pm$ 0.1	0.7 $\pm$ 0.1	0.9 $\pm$ 0.1	0.9 $\pm$ 0.1	0.8 $\pm$ 0.1	1.2 $\pm$ 0.2
Final ind. dry mass (mg <sup>d</sup> )	1.0 $\pm$ 0.1	1.4 $\pm$ 0.1	1.4 $\pm$ 0.1	1.8 $\pm$ 0.1	1.2 $\pm$ 0.1	1.7 $\pm$ 0.1
$\Delta$ ind. dry mass (mg)	0.1	0.5	0.5	0.9	0.3	0.8
$\Delta$ total dry biomass (mg)	-3.7	7.3	4.5	6.5	-7.3	-10.7
n	6	6	6	6 <sup>a</sup>	6 <sup>b</sup>	6 <sup>c</sup>

<sup>a</sup>n = 5 for length, n = 4 for mass; <sup>b</sup>n = 5 for length and mass; <sup>c</sup>n = 4 for length and mass; <sup>d</sup>a few individuals missing part of body were excluded from weighing

tion. After sieving, this clay-like sediment had a low water content ( $55 \pm 1\%$ ; n = 4) and LOI (3.7%; n = 1), indicating low organic content and nutritive value. The *Monoporeia affinis* density used corresponded to about 2800 ind. m<sup>-2</sup> (details in Table 3). Starting on April 14, baker's yeast was added to the jars twice a week as supplementary food, in doses of 0 (control), 0.05, 0.1, 0.2, 0.4 and 0.8 g wet mass. A single yeast lot was divided into doses and deep-frozen until used. It had a water content of  $74 \pm 1\%$  (n = 6), and a dry content of  $46 \pm 1\%$  C (n = 5),  $7.9 \pm 0.2\%$  N (n = 6) and  $1.4 \pm 0.1\%$  P (n = 3). Each dose was suspended in 10 ml filtered seawater and injected near the bottom of the jar with a syringe, with the water flow turned off for 2 h after the addition to let the yeast settle. Each jar received 16 yeast additions, corresponding totally to 0 (control), 9, 18, 37, 74 and 147 g C m<sup>-2</sup>. Outflow jars were connected to jars receiving 0, 0.1 and 0.8 g yeast additions.

**Statistical treatment.** Statistical analyses were performed using 'Statistica '99' Edition, Statsoft Inc., Tulsa, OK, USA. Variance of homogeneity was tested

with Cochran's or Bartlett's tests. Heterogeneous variances were removed through data transformation, as noted in individual cases below. Percentage values were arcsine-transformed before testing. When an analysis of variance was significant ( $p < 0.05$ ), multiple comparisons were made using the Tukey HSD test or the Tukey HSD test for unequal n.

## RESULTS

### Test of density-dependence of juvenile growth rate

The 400 ind. jar<sup>-1</sup> treatment was excluded from all analyses (except outflow jars), since many amphipods were found in the outflow jars at termination, indicating failure of the plankton net. The water in the 400 ind. jar<sup>-1</sup> treatment was turbid, and swimming amphipods were seen all day, even though they normally swim only at night (Cederwall 1979, Lindström 1991).

Because of the difficulty of assigning small amphipods to species without harming them, some *Pontoporeia femorata* were inadvertently used in the experiment (except the 12 ind. jar<sup>-1</sup> treatment, see Table 1). The fraction of *P. femorata* was ~5% initially (estimated from preserved batches), and 4% among the survivors, with no significant variation among the treatments (data arcsine-transformed, ANOVA,  $F_{2,15} = 0.14$ ,  $p = 0.87$ ).

There were no significant differences in sediment LOI among treatments at the end of the experiment, (data arcsine-transformed, ANOVA,  $F_{3,16} = 0.18$ ,  $p = 0.91$ ). Sediment accumulation in outflow jars was small (~0.01% of initial sediment in experimental jar), and did not differ significantly among treatments (ANOVA,  $F_{2,4} = 0.60$ ,  $p = 0.59$ ).

Mean amphipod survival was 58 to 78%, with no significant difference among the treatments, either for total amphipods (data arcsine-transformed, ANOVA,  $F_{4,25} = 1.08$ ,  $p = 0.39$ ) or for the individual species (ANOVA; *Monoporeia affinis*: data arcsine-transformed,  $F_{4,25} = 1.24$ ,  $p = 0.32$ ; *Pontoporeia femorata*: data arcsine-transformed,  $F_{2,15} = 0.14$ ,  $p = 0.87$ ). Individual length increased in all treatments (Fig. 1) for both species (surviving *P. femorata* were found only in treatments with  $\geq 50$  amphipods) and for pooled amphipods (ANOVA: *M. affinis*, data log-transformed,  $F_{5,30} = 363$ ,  $p < 0.001$ , Tukey's test,  $p < 0.05$ ; *P. femorata*,  $F_{4,15} = 13.52$ ,  $p < 0.001$ , Tukey's test for unequal  $n$ ,  $p < 0.05$ ; pooled:  $F_{5,30} = 123$ ,  $p < 0.001$ , Tukey's test,  $p < 0.05$ ).

Mean individual mass gain was measured on pooled amphipods, and was significant during the experiment for all treatments (log-transformed values, ANOVA,  $F_{5,26} = 97.4$ ,  $p < 0.001$ ; Tukey's test for unequal  $n$ ,  $p < 0.05$ ). Final individual mass was greatest in the 12 and 25 ind. jar<sup>-1</sup> treatments, and declined at higher densities, being negatively correlated to initial density ( $r = -0.79$ ,  $n = 30$ ). Total population mass gain peaked in the 100 ind. jar<sup>-1</sup> treatment. Growth in length was greatest in the 12 and 25 ind. jar<sup>-1</sup> treatments for *Monoporeia affinis*, and in the 50 ind. jar<sup>-1</sup> treatment for *Pontoporeia femorata* (absent in the 12 and 25 ind. jar<sup>-1</sup> treatments), and was negatively correlated to initial density (all amphipods,  $r = -0.89$ ,  $n = 30$ ). Individual *M. affinis* juveniles grew better than *P. femorata* juveniles at all densities, and ended up longer, even though they started out shorter.

#### Test of density-dependence of subadult growth rate

Since this experiment had <1% *Pontoporeia femorata*, this species can be ignored. There were no significant differences in sediment LOI among treatments at

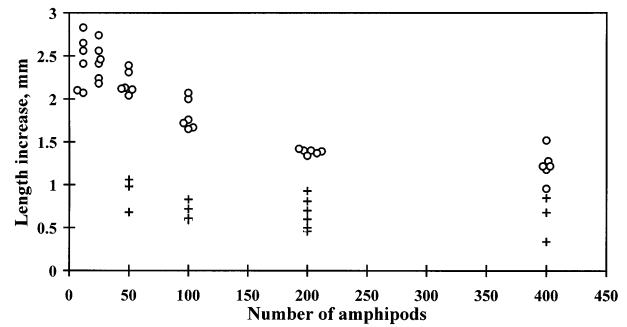


Fig. 1. *Monoporeia affinis* (○), and *Pontoporeia femorata* (+). Test of density-dependence of juvenile growth rate: increase in length of juveniles over 62 d as a function of initial amphipod density. To allow all data points to be seen, some overlapping points have been slightly displaced along x-axis

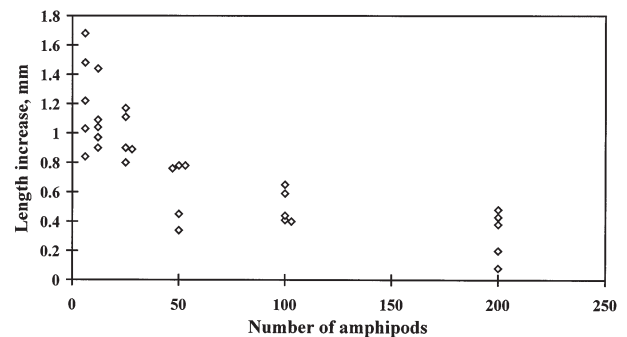


Fig. 2. *Monoporeia affinis*. Test of density-dependence of subadult growth rate. Increase in length of subadult amphipods over 57 d as a function of initial amphipod density. To allow all data points to be seen, some overlapping points have been slightly displaced along x-axis

the end of the experiment (data arcsine-transformed, ANOVA,  $F_{3,6} = 3.15$ ,  $p = 0.11$ ). Little sediment accumulated in the outflow jars for the 6 ind. jar<sup>-1</sup> treatment (~0.01% of initial sediment in experimental jar), significantly more in the 50 and 200 ind. jar<sup>-1</sup> treatments (ANOVA,  $F_{3,6} = 339$ ,  $p < 0.001$ ; Tukey's test for unequal  $n$ ,  $p < 0.05$ ) (~0.1 and 0.5% of initial sediment, respectively).

Mean amphipod survival was 77 to 91%, with no significant difference among treatments (data arcsine-transformed, ANOVA,  $F_{5,24} = 1.03$ ,  $p = 0.42$ ). Individual amphipod length increased significantly in all but the 200 ind. jar<sup>-1</sup> treatment (Fig. 2, ANOVA,  $F_{6,28} = 21.0$ ,  $p < 0.001$ ; Tukey's test,  $p < 0.05$ ), but always proportionally less than for juveniles at the same density. Individual amphipod mass increased significantly in the 3 lowest densities (ANOVA,  $F_{6,27} = 23.7$ ,  $p < 0.001$ , Tukey's test for unequal  $n$ ,  $p < 0.05$ ). Both final length ( $r = -0.78$ ;  $n = 30$ ) and final mass ( $r = -0.64$ ,  $n = 29$ ) were negatively correlated with initial density.

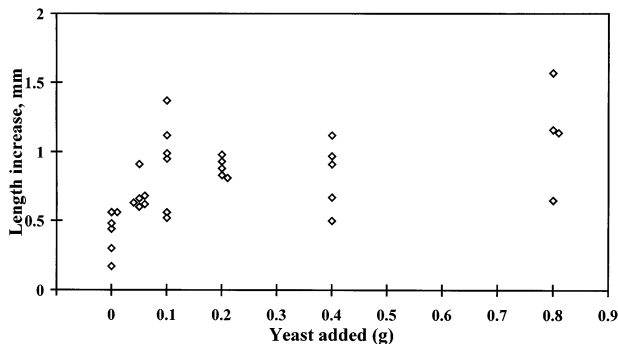


Fig. 3. *Monoporeia affinis*. Test of food limitation of subadult growth rate. Increase in length of subadult amphipods over 62 d as a function of amount of baker's yeast added. To allow all data points to be seen, some overlapping points have been slightly displaced along x-axis

#### Test of food limitation of subadult growth rate

No *Pontoporeia femorata* were found in this experiment. There were no significant differences in sediment LOI among treatments at termination (data arcsine-transformed, ANOVA,  $F_{3,4} = 6.42$ ,  $p = 0.052$ ). Sediment accumulation in outflow jars was small (~0.05% of initial sediment in experimental jar) and did not differ significantly among the treatments (ANOVA,  $F_{3,6} = 2.12$ ,  $p = 0.20$ ).

Mean amphipod survival was 34 to 83% (Table 3), and significantly lower at additions of 0.8 g yeast than in the control and the 2 lowest levels of addition (ANOVA,  $F_{5,30} = 3.46$ ,  $p = 0.014$ ; Tukey's test,  $p < 0.05$ ). Most jars with 0.8 g additions and some with 0.4 and 0.2 g additions developed black, reduced patches on the sediment surface, and had high amphipod mortalities. When such jars were excluded, no significant difference in survival among treatments remained (ANOVA,  $F_{4,21} = 2.13$ ,  $p = 0.11$ ), and mean survival was 77 to 89%.

Amphipod length and mass both increased significantly during the experiment in all treatments (Fig. 3) except the controls (length: log-transformed data, ANOVA,  $F_{6,29} = 12.0$ ,  $p < 0.001$ ; Tukey's test for unequal  $n$ ,  $p < 0.05$ ; individual mass:  $F_{6,28} = 11.4$ ,  $p < 0.001$ ; Tukey's test for unequal  $n$ ,  $p < 0.05$ ). Growth was positively correlated with the amount of yeast added (length: log-transformed data,  $r = 0.54$ ,  $n = 32$ ; mass:  $r = 0.45$ ,  $n = 31$ ).

## DISCUSSION

#### Tests of density-dependence of growth rates

The experiments confirmed a strong density-dependence for growth, but not for survival, in both juvenile

and subadult *Monoporeia affinis*. The span of growth rates in the experiment covered that of field populations of the same age in Cederwall's (1977) study, but was somewhat lower at equivalent population densities, especially when the presence of 3 age classes in the field is considered. Hill (1992) showed experimentally that juvenile growth rate in *M. affinis* is density-dependent and is reduced in the presence of 1 yr old subadults. Hill also found that mortality increased in the high-density treatments after 3 mo, and that this mortality slowed the body-mass loss of survivors, presumably since the dead individuals served as food. Goedkoop & Johnson (1994) reported that growth of juvenile *M. affinis* was strongly density-dependent in freshwater also, but found no effect on survival after 43 d.

The experiment on juvenile growth inadvertently included some individuals of the similar amphipod *Pontoporeia femorata*. They were too few in number ( $\leq 5\%$ ) to be likely to have influenced the results for *Monoporeia affinis*, but the interspecific negative effect of *M. affinis* on the growth of *P. femorata* was significant. As in the field (Cederwall 1977), we found that juvenile growth was slower in *P. femorata* than in *M. affinis*. This is not surprising, given the lower rates of ingestion (Lopez & Elmgren 1989) and metabolism (Cederwall 1979) of *P. femorata*. The experimental salinity was, however, near the lower salinity limit for *P. femorata*, as judged from its field distribution (Seegerstråle 1950, Järvekülg 1973). In the Askö area, *P. femorata* is normally found below ~30 m depth, at a salinity about 0.5 higher than in our experiment, where its slow growth may have been partly an effect of low salinity.

Apparent mortality was high in the 400 ind. jar<sup>-1</sup> treatment of the juvenile growth experiment, but outflow jars showed that much of this was in fact an artefact, as juveniles had escaped through the 90  $\mu\text{m}$  net. Outflow jars for other treatments showed no escape through the net. The daytime swimming and constantly turbid water in the 400 ind. jar<sup>-1</sup> treatment suggested that amphipods were trying to escape, seemingly in direct response to the high density of conspecifics rather than in response to lower food quality, since the initial food quality was the same in all treatments. Ambrose (1986) likewise interpreted density-dependent emigration by a deposit-feeding amphipod as arising from avoidance of competing individuals. Donner et al. (1987) reported field observations of increased swimming by *Monoporeia affinis* as feeding conditions deteriorated in late summer, suggesting that food shortage can also cause emigration from the sediment. *M. affinis* has been reported to swim away from unfavourable conditions, such as the presence of toxic contaminants (Lindström & Lindström 1980), low

oxygen (Johansson 1997) and predator presence (Ejdung 1998, Sparrevik & Leonardsson 1999).

Amphipod mortality during the experiment was mostly 9 to 27%, but reached over 40% in some treatments. At most, this added ~25 mg of organic matter to sediment already containing 15 to 25 g of organic matter, a small addition to the total organic carbon store available to the amphipods. The highest individual amphipod biomass gains were not found in the treatments with the highest mortality. The highest total amphipod biomass gain (final minus initial biomass) was only ~18 mg dry mass (subadult growth rate, 200 ind. jar<sup>-1</sup> treatment), indicating utilisation of only a minute part of the total sediment store of organic material. This suggests that most of the organic matter in the sediment was of low quality (cf. Levinton & Stewart 1988), and that organic matter from dead amphipods may have improved the quality of food for the survivors, as assumed by Hill (1992). Since the percent mortality rate did not differ between treatments, the high-density treatments received most of this inadvertent enrichment of the sediment, without which differences in individual growth rate between high- and low-density treatments would probably have been somewhat greater.

#### Test of food limitation of subadult growth rate

The use of baker's yeast as supplementary food can be criticised, since it is not a natural food item for these amphipods and it is not known whether they possess the enzymes to break it down. Baker's yeast has, however, been found to constitute an excellent food in other crustacean growth experiments, in which it was selected as a readily available non-toxic micro-organism that lacked a hard, protective cell wall (Coutteau et al. 1992). Since our intention was to study if supplementary food could reduce or eliminate the density-dependence of growth in *Monoporeia affinis*, it was not necessary for the added food to be of the very highest quality. Our results prove that yeast can be assimilated by the amphipods, either directly or after initial processing by sediment microbiota.

The test of food limitation of growth rate showed clearly that supplemental feeding could counteract the negative effect of a relatively high density of subadults. This experiment used sediment of low organic content, and daily growth in length in the control was as low as for 200 ind. jar<sup>-1</sup> in the subadult density-dependence experiment, which used sediment of higher organic content. By adding 0.2 g of yeast twice a week, a higher growth rate, falling between those obtained for 25 and 50 ind. jar<sup>-1</sup> in the subadult density-dependence experiment, was achieved. Still

higher yeast additions caused reduced sediments and greatly increased mortality, making it difficult to evaluate changes in growth, since mortality may have been size-selective. We do not know why only some replicates receiving high yeast additions developed reduced sediments, but suspect the cause may be related to small initial differences in water flow, settling of yeast and amphipod activity among individual jars. Even the lowest addition added about as much organic matter (9 g C m<sup>-2</sup>) as would be expected from a normal spring bloom. Larsson et al. (1986) reported sedimentation of 4.9 g C m<sup>-2</sup> during a spring bloom event near the Askö Laboratory, while Graf et al. (1982) recorded 11.5 g C m<sup>-2</sup> over 4 wk of a spring bloom in Kiel Bight, SW Baltic Sea. The higher yeast additions correspond more to local accumulations of detritus, which can be very patchy in the field.

#### Conclusions

Individual growth rate decreased with increasing amphipod density for juvenile and subadult *Monoporeia affinis* as well as for juvenile *Pontoporeia femorata*, confirming interpretations of field growth data that indicate that food limitation is common for Baltic Sea deposit-feeding benthic amphipods of the species *M. affinis* and *P. femorata*. This was true even though the greater number of amphipods dying at higher density added more organic matter to the sediment in those treatments. Our results thus confirm the density-dependence of growth in *M. affinis*, inferred from field experiments and shown for juveniles in the laboratory by Hill (1992) and Goedkoop & Johnson (1994), and extend the results to subadults and to interspecific effects on juveniles of the co-occurring amphipod *P. femorata*.

Crowding can have dramatic negative effects on growth, even in the presence of abundant food (Miralto et al. 1996, Wheatcroft et al. 1998). Our results for *Monoporeia affinis* show that supplemental feeding can largely eliminate the growth reduction at high density. Hence, shortage of food explains most of the negative density-dependence of individual growth noted in field studies, even if some contribution from crowding cannot be ruled out, particularly between year-classes, which we did not test for (cf. Hill 1992). We can thus conclude that the most abundant species of deposit-feeding macrofauna in the Baltic Sea is primarily limited by food, not by interspecific interference effects.

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