



Encounter competition partly explains the segregation of the sandy beach amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi*. A mesocosm experiment

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ABSTRACT

Biotic interactions such as competition and predation are known to play an important role in structuring communities. In this study, the intra- and interspecific competition between two congeneric sandy beach amphipods *Bathyporeia pilosa* and *B. sarsi* was examined by means of a two-way factorial mesocosm experiment. The amount of natural food resources as well as population densities of *B. pilosa* and *B. sarsi* were manipulated in order to investigate whether firstly, the species compete for food, and secondly, whether crowding effects, such as damaging encounter competition, are present within and between both *Bathyporeia* species. The absence of food negatively influenced survival and recruitment and enhanced aggressive behavior in the *B. sarsi* population, while there was no influence of the absence of food in the *B. pilosa* population. In the field, *B. pilosa* is occurring high in the intertidal where food supply is low, while *B. sarsi* is occurring in the mid-intertidal where food supply is higher. Hence, *B. pilosa* is more adapted to low food conditions than *B. sarsi*. Although an increased intraspecific density stimulated encounter competition within the *B. sarsi* population, no evidence of interspecific competition was found in this study. This first report on encounter competition for the deposit-feeding amphipod *Bathyporeia sarsi* suggests that zonation patterns of the two amphipods may be the result of the combined influence of species-specific physiological restrictions and biotic interactions within the *B. sarsi* population, indicating that on dissipative beaches, biotic interactions may be more common than generally considered.

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1. Introduction

Sandy beaches are harsh environments that are strongly stressed by winds and waves (McArdle & McLachlan, 1991, 1992; McLachlan, 1983). Consequently, the distribution and zonation of infaunal sandy beach organisms have been typically related to beach morphodynamical factors such as slope, wave energy, tidal range and sediment characteristics (Defeo & McLachlan, 2005; McLachlan, 1996; McLachlan & Jaramillo, 1995). Moreover, food supply has been shown to be even more important for structuring communities on sandy beaches (Dugan et al., 2003; Lastra et al., 2006; Rodil et al., 2012). Studies on sandy beach food web dynamics indicate that beside allochthonous wrack material (Dugan et al., 2003; Ince et al., 2007; Lastra et al., 2008), also primary production in the water column (Lastra et al., 2006) and on dissipative beaches even *in situ* primary production (Bergamino et al., 2011; Schlacher & Hartwig, 2012) are supporting the beach food web and are structuring meio- and macrofaunal communities. Yet, biological interactions, in particular competition, are considered of minor importance in structuring benthos zonation patterns (McLachlan, 1983, 1996, 2001; McLachlan et al., 1993). This is in contrast to rocky shore ecosystems where biotic

interactions often play an additional role to the dominant structuring influence of the physical environment. For example Ragnarsson & Raffaelli (1999) and Benedetti-Cecchi (2001) showed that species interactions significantly influenced community structure and species densities in this habitat. Consequently, it is currently stated that biotic interactions are instrumental to habitat selection, niche segregation and niche overlap of benthic organisms on rocky shores (e.g. Iken et al., 2001; Liess & Hillebrand, 2004; McPeck, 1996; Schluter, 2001). Dugan et al. (2004) and McLachlan & Dorvlo (2005) have recently postulated that biotic interactions do play a role in structuring the distribution of macrofaunal communities on sandy beaches as well, especially on more benign dissipative beaches (Defeo & McLachlan, 2005; McLachlan & Dorvlo, 2005). Empirical evidence about this structuring role of biotic interactions on sandy beach macrobenthos distribution is however scarce (but see Croker & Hatfield, 1980; Defeo et al., 1997; Dugan et al., 2004) and to our knowledge only one of these studies has focused on congeneric species so far. Defeo et al. (1997) demonstrated that congeneric isopods (*Excirrolana*) changed their sediment preference in syntopic conditions.

The congeneric amphipods, *Bathyporeia pilosa* and *Bathyporeia sarsi*, show a segregated zonation pattern on intertidal sandy beaches with only a restricted overlap along the Northwest European coast: i.e. *Bathyporeia pilosa* inhabits a narrow zone between MHWS and mid-tide level (Fish & Preece, 1970), while *Bathyporeia sarsi* inhabits

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a broader zone in the mid-intertidal, between MHW and MLWS (Nicolaisen & Kanneworff, 1983; Toulmond, 1964). On Belgian beaches, peak abundances of *B. pilosa* were found at 436 ± 25 SD cm above MLWS, while those of *B. sarsi* were found at 357 ± 40 SD cm above MLWS, corresponding (depending on beach slope) to a 40–62 m cross-shore distance (Speybroeck et al., 2008). It remains however unclear why these two closely related and morphologically highly similar species perform this cross-shore spatial segregation. The mouthparts of *B. pilosa* and *B. sarsi* are very similar and their feeding strategy is very alike (Nicolaisen & Kanneworff, 1969). Based on their similar feeding behavior we hypothesize that competition for food may govern the cross-shore spatial segregation of both congeneric species across sandy beaches.

Here we report on a mesocosm experiment where both natural food resources; i.e. diatoms, and population densities of *B. pilosa* and *B. sarsi* were manipulated in order to investigate whether firstly, the species compete for food, and secondly, whether crowding effects, such as damaging encounter competition (Schoener, 1983) are present within and between both *Bathyporeia* species. This information should allow understanding of whether biotic interactions, such as competition for food and encounter competition, contribute to the cross-shore spatial segregation of both *Bathyporeia* species.

2. Materials and methods

2.1. Experimental design

A two-way factorial experiment was designed in order to investigate competitive interactions between and within the amphipods *B. pilosa* and *B. sarsi*. Both amphipod species were mixed together in seven different density combinations, crossed with three dissimilar food levels: no food, ambient food conditions and double the amount of ambient food available. As natural population densities of *B. pilosa* and *B. sarsi* are unequal and can differ substantially between beaches, experimental densities had to be chosen carefully. Too low densities would underestimate competition effects, while too high densities on the other hand would overestimate the effects. Therefore, two different total densities were used, each one reflecting existing field densities of *B. pilosa* or *B. sarsi*. The first density ($20 \text{ ind.treatment}^{-1} = 3000 \text{ ind. m}^{-2}$) was observed in natural *B. sarsi* populations, while the second density ($40 \text{ ind.treatment}^{-1} = 6000 \text{ ind. m}^{-2}$) was observed in natural *B. pilosa* populations (Speybroeck et al., 2008).

The experimental set-up consists of four sub-units: (1) intraspecific effects within the *B. pilosa* population; (2) intraspecific effects within the *B. sarsi* population; (3) interspecific effects of *B. sarsi* on *B. pilosa* and (4) interspecific effects of *B. pilosa* on *B. sarsi* (Table 1). If competition for food exists within and between amphipod populations we would expect less survival and less recruitment at high amphipod densities in the treatments with less food. If encounter competition is a dominant biotic interaction within and between both amphipod populations we would expect higher interaction rates at higher densities and lower food conditions.

2.2. Collection of study organisms and experimental conditions

Adults of *B. pilosa* and *B. sarsi* were collected from two sandy beaches along the Belgian coast: *Bathyporeia pilosa* was collected on the high-intertidal beach in Ostend ($2^{\circ}55'43''$ E $51^{\circ}14'17''$ N), while *B. sarsi* was collected at the mid-intertidal in De Panne ($2^{\circ}33'24''$ E $51^{\circ}05'42''$ N). Study organisms were kept in the lab for 24 h before initiation of the experiment which allowed adaptation to laboratory conditions and removal of accidentally injured organisms during processing. Sediment was collected in the mid-intertidal beach zone of De Panne and subsequently sieved over a 0.5 mm sieve and decanted to remove all benthos and detritus. Sediment composition did not differ among both sites where organisms were collected (Two

Table 1

Experimental design to test for intraspecific effects within and interspecific effects between *Bathyporeia pilosa* and *Bathyporeia sarsi* at three different food levels. five replicates implied 105 treatments in total.

Treatment	Density <i>B. pilosa</i>	Density <i>B. sarsi</i>	Total density	Food level
1	20	0	20	no food
2	20	0	20	ambient food
3	20	0	20	enhanced
4	40	0	40	no food
5	40	0	40	ambient food
6	40	0	40	enhanced
7	0	20	20	no food
8	0	20	20	ambient food
9	0	20	20	enhanced
10	0	40	40	no food
11	0	40	40	ambient food
12	0	40	40	enhanced
13	10	10	20	no food
14	10	10	20	ambient food
15	10	10	20	enhanced
16	10	30	40	no food
17	10	30	40	ambient food
18	10	30	40	enhanced
19	30	10	40	no food
20	30	10	40	ambient food
21	30	10	40	enhanced

Sample Wilcoxon test: $W = 12$; $p = 0.34$), indicating that the obtained results and posed conclusions regarding governing factors of field distribution are not compromised by the sediment used. Decantation did not remove the epipsammon attached to the sand grains but only the epipelon and the detritus from the interstitial spaces between the sand grains (cf. Baird & Wetzel, 1968; Moss & Round, 1967). Sediment for the treatments without food was heated for 4 h (540°C) to eliminate all organic matter. Enhanced food supply treatments were achieved by stimulation of epipsammic microphytobenthos growth during incubation for 14 days with f2 culture medium (Guillard, 1975) in a climate-controlled room at 19°C prior to the experiment. At the start of the experiment, the chlorophyll a contents were $0 \mu\text{g g}^{-1}$, $0.78 \pm 0.05 \text{ SD } \mu\text{g g}^{-1}$ and $1.64 \pm 0.14 \text{ SD } \mu\text{g g}^{-1}$, respectively for the treatments with no food, ambient food and enhanced food supply. Natural sea water was filtered over a $45 \mu\text{m}$ filter.

PVC cylinders ($\varnothing 8 \text{ cm}$, 30 cm height) were filled for one third with the collected sediment and placed in an aquarium ($120 \text{ cm} \times 120 \text{ cm} \times 40 \text{ cm}$). Two rows of little permeable holes (covered with $250 \mu\text{m}$ gauze), one under and one above the sediment-water interface, allowed refreshment of seawater in the cylinders during each tidal cycle, keeping the sediment and organisms inside, while the sea water could flow in and out of the cylinders. Circulation pumps and timers were used to imitate the tidal cycle, enabling conditions as similar as possible to the field situation, which ensured a good survival of the test organisms. A total of 105 cylinders were used to permit 21 treatments (7 density treatments \times 3 food levels) in 5 replicate aquaria each, arranged in a randomized block design. Each replicate aquarium had its own independent maintenance system and its own sea water tank of 120 l where water was pumped in and out according to the tidal cycle. The experiment was carried out in a temperature-controlled room at 19°C with a 11:13-h dark/light regime, i.e. the natural dark/light regime during late summer at the beach where the study organisms were retrieved. The experiment was started at high tide on the 3th of September 2009 and was terminated 3 weeks later, at low tide on the 24th of September 2009. The amphipods that were alive at the end of the experiment were extracted from the sediment, counted and preserved in a 70% ethanol solution. Additionally, a sediment sample of 2 ml was collected from each of the 105 cylinders to analyze the final food concentration.

Table 2
Permanova results on intraspecific effects in the *Bathyporeia pilosa*-population.

Survival	df	SS	Pseudo-F	p
Density	1	33.333	1.70E+02	0.901
Food	2	382.92	0.97922	0.3907
density × food	2	362.92	0.92808	0.415
Res	24	4692.5		
Total	29	5441.7		

Recruitment	df	SS	Pseudo-F	p
Density	1	541.88	21.876	0.1579
Food	2	992.92	20.042	0.1566
Density × food	2	71.25	0.14382	0.8724
Res	24	5945		
Total	29	7551		

Injury free	df	SS	Pseudo-F	p
Density	1	130.21	0.79365	0.3797
Food	2	593.75	18.095	0.181
Density × food	2	165.42	0.50413	0.6063
Res	24	3937.5		
Total	29	4826.9		

2.3. Data analysis

The following population characteristics of *B. pilosa* and *B. sarsi* were determined for each treatment: (i) survival, (ii) recruitment and (iii) the amount of injury free organisms.

- Survival was expressed as the ratio between the number of adult organisms alive at the end of the experiment and the number of organisms added at the start of the experiment. Average body size of adult amphipods was 5.4 ± 0.6 SD mm and 6.1 ± 0.7 SD mm for *B. pilosa* and *B. sarsi* respectively.
- Recruitment was calculated likewise for the number of recruits alive at the end of the experiment, so this ratio actually reflects the average recruitment per individual. The recruits were small juvenile amphipods that freshly hatched during the experiment (average size juvenile *B. pilosa*: 3.0 ± 0.05 SD mm; juvenile *B. sarsi*: 4.0 ± 0.08 SD mm).
- Encounter competition was assessed by calculation of the ratio between the number of organisms without injuries at the end of the experiment and the number of organisms added at the start of the experiment. Injuries were only taken into account when black scar tissue was present on the wound, amphipods having wounds without scar tissue were assumed to have been damaged during sample processing at the end of the experiment (Halcrow, 1988; Halcrow & Smith, 1986; Sheader, 1998). Amphipods with regenerated body parts were likewise not considered to be wounded during the experiment, taken into account that regeneration time is longer than the experimental time, i.e. 11 weeks (Wilhelm et al., 2003).

Statistical analyses were performed by using PRIMER v6 (Primer-E Ltd, UK) in conjunction with PERMANOVA add-on software (Anderson et al., 2008; Clarke & Gorley, 2006) and the statistical package R (version 2.10.1, R Foundation for Statistical Computing).

For each of the four sub-units, a two-factor design was performed in PERMANOVA (Permutational multivariate analysis of variance (Anderson, 2001)) to separate the effects of density and food and test for an interaction, using Euclidian distance dissimilarities. PERMANOVA allows to perform univariate ANOVAs with *p*-values obtained by permutation (Anderson & Millar, 2004), thus avoiding the assumption of normality. Homogeneity of dispersion was tested with PERMDISP, using distances among centroids in order to check whether obtained results could be attributed to the factors examined. Factors were considered significant at $p < 0.05$ in all analyses. The PERMDISP-test was never significant for the analysis of *B. pilosa*, indicating equally dispersed distances to centroids, hence a difference due to location.

However, for *B. sarsi*, the PERMDISP-test was significant for some factors. If both PERMDISP and PERMANOVA tests are significant, dispersion effects occur but the presence of location effects is uncertain (Anderson et al., 2008). Therefore, prudence is advised when interpreting these results and the relative sizes of the within and between-group resemblances deserve further attention (Anderson et al., 2008).

In case of significant single factor effects, pair-wise tests within each factor were carried out to distinguish what treatments differed exactly. Because of the restricted number of possible permutations in pair-wise tests, *p*-values were obtained from Monte Carlo samplings (Anderson & Robinson, 2003).

3. Results

3.1. *Bathyporeia pilosa*: intraspecific competition

Survival, recruitment and the ratio of injury free *B. pilosa* organisms varied between 6.7% and 85.0%, 0.0% and 100.0%, and 10.0% to 100.0% respectively. However, none of the population characteristics differed significantly among density and food levels (Table 2 and Fig. 1).

3.2. *Bathyporeia sarsi*: intraspecific competition

Survival, recruitment and the ratio of injury free *B. sarsi* organisms did not differ significantly among density levels (density: $p > 0.05$; Table 3). However, all population characteristics varied significantly among food levels ($p < 0.05$; Table 3). In sediments without food the survival was on average 15.5 ± 4.7 SE %, while survival was 40.0 ± 8.5 SE % and 40.5 ± 4.2 SE % in the sediments with ambient food supply and enhanced food supply, respectively. The recruitment showed a similar pattern with no recruitment in the treatments without food, 13.8 ± 4.2 SE % of

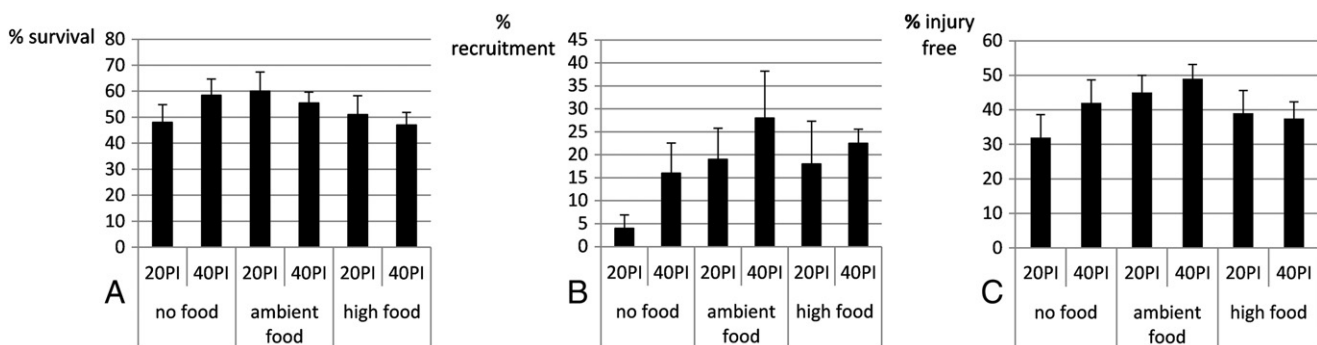


Fig. 1. Survival (A), recruitment (B) and injury free (C) ratio (%; mean \pm SE) of *Bathyporeia pilosa*. 20PI: low-density treatment of *Bathyporeia pilosa*, 40PI: high-density treatment of *Bathyporeia pilosa*.

Table 3
Permanova results on intraspecific effects in the *Bathyporeia sarsi*-population.

Survival	df	SS	Pseudo-F	p
Density	1	676.88	35.703	0.0713
Food	2	3721.2	98.143	0.0014
Density × food	2	16.25	4.29E + 02	0.9632
Res	24	4550		
Total	29	8964.4		
<i>Recruitment</i>				
Density	1	163.33	18.127	0.1933
Food	2	1137.9	63.145	0.006
Density × food	2	182.92	1.015	0.375
Res	24	2162.5		
Total	29	3646.7		
<i>Injury free</i>				
Density	1	676.88	35.703	0.0694
Food	2	3721.2	98.143	0.0017
Density × food	2	16.25	4.29E + 02	0.9555
Res	24	4550		
Total	29	8964.4		

recruitment in the treatments with ambient food and 12.3 ± 6.2 SE % of recruitment in the treatments with enhanced food.

Although not significant at the 0.05 level, aggressive attacks (leading to injuries or even mortality) increased with density (injury free: $p=0.069$ and survival: $p=0.071$; Table 3), independent of the amount of food available. The amount of injury free organisms was lowest in sediments which contained high densities and no food (Fig. 2).

3.3. *Bathyporeia pilosa*: interspecific effects of *B. sarsi*

Survival, recruitment and the ratio of injury free *B. pilosa* organisms did not differ significantly among levels of *B. sarsi* density or food ($p > 0.1$; Table 4 and Fig. 3).

3.4. *Bathyporeia sarsi*: interspecific effects of *B. pilosa*

Survival, recruitment and the ratio of injury free *B. sarsi* organisms did not differ significantly among *B. pilosa* density levels (density: $p > 0.1$; Table 5). However, all population characteristics varied significantly among food levels (food: $p < 0.05$; Table 5). In sediments without food the survival was on average 25.0 ± 7.06 SE %. In the sediments with ambient food supply average survival rates were 39.0 ± 8.75 SE % whereas in the sediments with enhanced food supply survival increased even up to 41.0 ± 7.86 SE %. The ratio of injury free organisms showed a similar pattern with the lowest ratio in the no food treatments (20.0 ± 5.83 SE %), 32.0 ± 8.26 SE % of injury-free organisms in the ambient food

treatments and the highest ratio of injury-free organisms (39.0 ± 6.84 SE %) in the enhanced food treatments (Fig. 4).

4. Discussion

Relatively few experiments have been designed to directly infer whether resources of any sort are ever limiting to soft-sediment species or whether competition for limited resources is a structuring factor for soft-sediment communities (although see Levinton & Lopez, 1977; Peterson, 1977; Peterson & Andre, 1980; Woodin, 1974). However, competitive interactions among individuals cannot be fully understood without manipulations of the resources that are subject to competition. Generally, competition rate is known to be higher when food is scarce (Dolman, 1995; Kotrschal et al., 1993; Moody & Ruxton, 1996; Steinwascher, 1978). During this experiment, it was observed that some animals seemed to attack others while swimming in the water column. Detailed analyses of the surviving organisms confirmed these attacks by showing remarkable injuries on several amphipods. Generally, amphipods are known to perform aggressive attacks, both intra- and interspecific (Dick et al., 1995; van der Velde et al., 2009). However, aggression is mostly acknowledged for predator species like *Gammarus*, where cannibalism and intraguild predation is well-described (Dick & Platvoet, 2000; Dick et al., 1999; Polis et al., 1989). For the deposit feeding amphipod *Bathyporeia*, aggressive behavior has never been observed yet. As *Bathyporeia* normally feeds by scraping organic material and diatoms from sand grains (Nicolaisen & Kannevorff, 1969), its mouth parts are not designed to attack other species. Nevertheless, the observed injuries during the experiment clearly confirm the presence of encounter competition (Schoener, 1983) in the non-predaceous amphipods *B. pilosa* and *B. sarsi*. Black scar tissue was covering the injured parts of the wounded amphipods and in several cases the start of regeneration of the lost appendage was observed. In crustaceans, wounds are known to be sealed rapidly by blood clotting and the damaged area is subsequently hardened by tanning (Halcrow, 1988; Halcrow & Smith, 1986). Depending on the extent of the damage, appendages or body parts can be regenerated over several moults (Hopkins, 2001; Skinner, 1985; Wilhelm et al., 2003). Although wounds resulting from encounter competition might thus not be directly lethal, wound healing and regeneration of lost limbs requires a reasonable energy investment decreasing overall organism fitness, enhancing its vulnerability to diseases and to subsequent attacks, and hence affect the outcome of competition (Wilhelm et al., 2003).

In this study, no intraspecific interaction among *B. pilosa* individuals was demonstrated, nor was there a distinct indication of damaging interference. Although wounded animals were occasionally observed in the allopatric treatments of *B. pilosa*, we did not notice a significant negative effect of higher density on the survival, the recruitment and the ratio of injury free organisms. Consequently, we conclude that intraspecific attacks might have occurred, but that the intensity was obviously

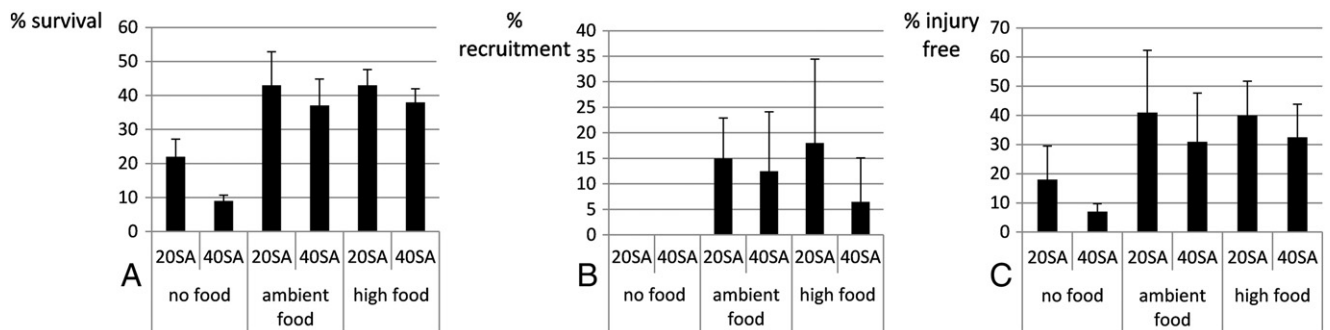


Fig. 2. Survival (A), recruitment (B) and injury free (C) ratio (%; mean ± SE) of *Bathyporeia sarsi*. 20SA: low-density treatment of *Bathyporeia sarsi*, 40SA: high-density treatment of *Bathyporeia sarsi*.

Table 4
Permanova results on interspecific effects on the *Bathyporeia pilosa*-population.

Survival	df	SS	Pseudo-F	p
Density	3	1341.3	11.575	0.3337
Food	2	110.83	0.14347	0.8669
Density × food	6	1932.5	0.83387	0.5494
Res	48	18,540		
Total	59	21,925		
<i>Recruitment</i>				
Density	3	1521.2	0.94561	0.4345
Food	2	965.83	0.90054	0.4203
Density × food	6	3537.5	10.995	0.3718
Res	48	25,740		
Total	59	31,765		
<i>Injury free</i>				
Density	3	293.33	0.28053	0.841
Food	2	395.83	0.56784	0.5737
Density × food	6	1374.2	0.6571	0.689
Res	48	16,730		
Total	59	18,793		

Table 5
Permanova results on interspecific effects on the *Bathyporeia sarsi*-population.

Survival	df	SS	Pseudo-F	p
Density	1	563.33	20.994	0.1662
Food	2	6806.7	12.683	0.0004
Density × food	2	526.67	0.98137	0.3862
Res	24	6440		
Total	29	14,337		
<i>Recruitment</i>				
Density	1	83.333	0.37313	0.5355
Food	2	2286.7	51.194	0.0147
Density × food	2	886.67	19.851	0.1588
Res	24	5360		
Total	29	8616.7		
<i>Injury free</i>				
Density	1	213.33	0.84211	0.3614
Food	2	5180	10.224	0.0011
Density × food	2	126.67	0.25	0.7811
Res	24	6080		
Total	29	11,600		

too low to induce distinct effects on the population of *B. pilosa* and that this mechanism is thus most likely not a governing ecological interaction at the natural population densities of *B. pilosa* that were investigated in this experiment. This corroborates [Wenngren & Ólafsson \(2002\)](#) who empirically demonstrated that crowding effects such as damaging interference were not important at common field densities of *Monoporeia affinis*, an amphipod which like *Bathyporeia* belongs to the family of Pontoporeiidae. Similarly, we did not find a significant effect of *B. sarsi* density on *B. sarsi* population characteristics, although survival, recruitment and amount of injury free organisms were always higher at the lowest density level. The results of this study show that under mesocosm conditions, *B. sarsi* population characteristics are mediated by food availability. Survival, recruitment and the amount of injury free organisms were significantly diminished in sediments without food. Consequently, one would expect an increase of these characteristics from ambient to high food conditions. The amphipods did however not benefit from the high food conditions in this experiment suggesting that they were already satisfied by the ambient food conditions. The tested population characteristics did not significantly differ among density levels at the 95% confidence level but the higher survival and the enhanced occurrence of injury free *B. sarsi* individuals in the low density treatments at all three food levels suggest that aggressive attacks might be enhanced at higher densities of this species ($p = 0.07$ for survival, $p = 0.07$ for injury-free ratio). In the treatments without food this pattern was best illustrated as the ratio of injury free organisms was 18.0 ± 12.0 SE % in the low density and 7.0 ± 2.7 SE % in the high density treatments.

Analysis of the sympatric treatment x food combinations did not reveal clear indications of the occurrence of interspecific competitive interactions. Moreover, sympatric species combinations further emphasized the dependence of *B. sarsi* on food to attain good fitness, characterized by high survival, recruitment and low rates of intraspecific attacks.

Extrapolation of experimental mesocosm results to natural systems should be considered with caution. However, the chosen experimental densities and conditions were carefully determined to mimic the field situation as good as possible. In addition to the available knowledge on species distribution and physiology, the obtained information deduced from this study should enable a better assessment of the processes structuring benthic communities on sandy beaches.

[Speybroeck et al. \(2008\)](#) described spatially segregated populations of both amphipods along the Belgian coast with densities of *B. sarsi* being two to even four times lower than *B. pilosa*-densities. The enhanced intraspecific attacks found under experimental low-food and high-density conditions for *B. sarsi*, are likely to occur in the field when food is scarce and amphipod densities high, resulting in a lower fitness under these conditions. Since the only resident primary producers on sandy beaches are epipsammic diatoms, the general food supply on beaches is limited (0 to $50 \text{ gC} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) ([McLachlan & Brown, 2006](#)). However, surf zone diatoms may also occur and locally enhance the food supply in the mid-intertidal zone ([McLachlan & Brown, 2006](#)) that *B. sarsi* inhabits. *B. sarsi* is known to be less tolerant for starvation compared to *B. pilosa*, since the physiology of *B. pilosa* can stand a substantial amount of desiccation, deprivation and other

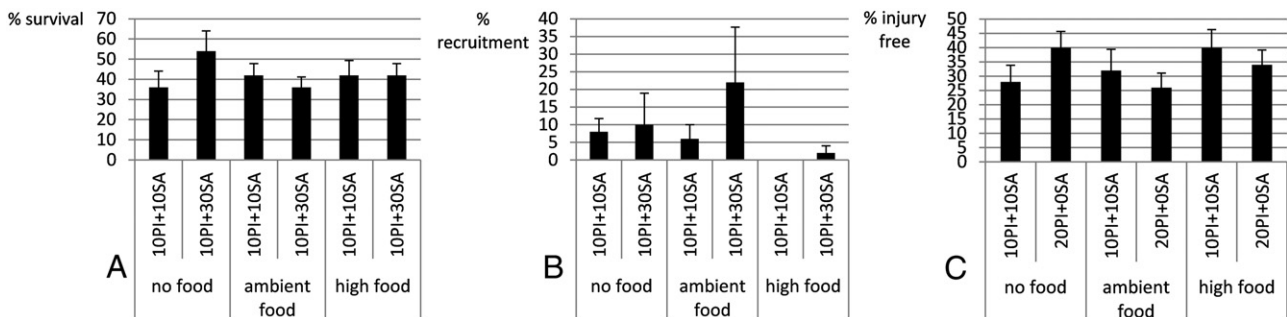


Fig. 3. Survival (A), recruitment (B) and injury free (C) ratio (%; mean \pm SE) of *Bathyporeia pilosa*. 10P+10SA: treatment with 10 individuals of *Bathyporeia pilosa* and 10 individuals of *Bathyporeia sarsi*, 30P+10SA: treatment with 30 individuals of *Bathyporeia pilosa* and 10 individuals of *Bathyporeia sarsi*.

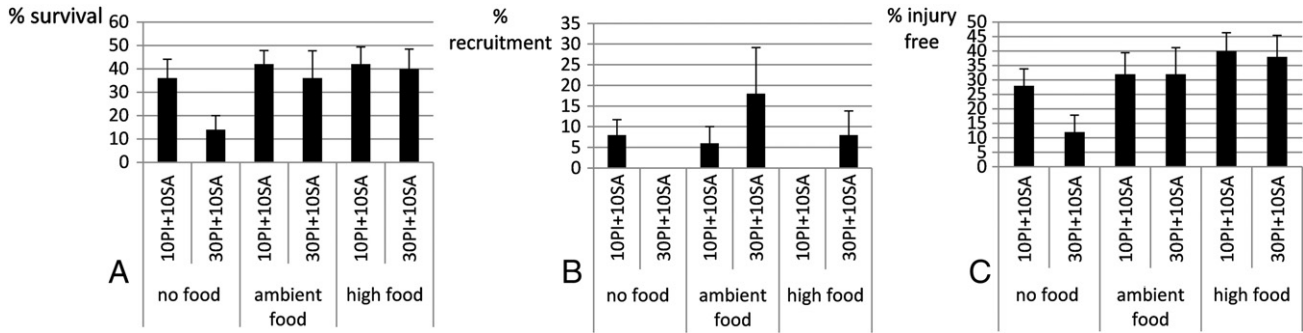


Fig. 4. Survival (A), recruitment (B) and injury free (C) ratio (%; mean ± SE) of *Bathyporeia sarsi*. 10PI + 10SA: treatment with 10 individuals of *Bathyporeia pilosa* and 10 individuals of *Bathyporeia sarsi*, 10PI + 30SA: treatment with 10 individuals of *Bathyporeia pilosa* and 30 individuals of *Bathyporeia sarsi*.

stress (Preece, 1971). Therefore, unlike *B. sarsi*, *B. pilosa* is well adapted to the harsh environmental and food conditions high in the intertidal. Our observations of enhanced encounter competition in *B. sarsi*, especially under lowered food conditions, suggest that intraspecific competition contributes to this species' upper distribution limit and peak density in the mid-intertidal zone. No indications of competition effects on *B. pilosa* populations were detected. We therefore suggest that the high abundance in the high intertidal zone of this species is independent from *B. sarsi* occurrence lower on the beach and primarily relates to lower predation pressure by epi- and hyperbenthic organisms in the high intertidal zone.

5. Conclusions

This is the first study that indicates the presence of encounter competition in the deposit-feeding amphipod *Bathyporeia*. In the *B. sarsi* population, intraspecific encounter competition increased at lower food levels and higher densities, while intraspecific competition was not shown in the *B. pilosa* population. The occurrence of interspecific competition among both congeneric species could not be demonstrated. In general, this study shows that biotic interactions may have a more structuring role on benthic communities from dissipative sandy beaches than generally considered.

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