CHAPTER 4

In situ study of the autecology of two closely related, co-occurring sandy beach amphipods

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Abstract

Population dynamics and zonation of the amphipods *Bathyporeia pilosa* and *B. sarsi*, co-occurring on some Belgian beaches, were studied through monthly sampling of eight cross-shore transects (October 2003-October 2004). Their biomass and production were assessed for the first time. Abundance and biomass of *B. pilosa* were ten times higher along western ultra-dissipative transects than along slightly more reflective, eastern transects. For *B. sarsi*, (less prominent) differences between the two westernmost transects (2-5x higher) and all others were observed, whereas P/B ratio was comparable for all. *Bathyporeia pilosa* could reach two times higher abundance and biomass and higher levels of production (max. *B. sarsi* = 7580 $mg*m^{-2}*y^{-1}$; max. *B. pilosa* = 16040 $mg*m^{-2}*y^{-1}$), while nearly absent along eastern transects. Continuous reproduction and recruitment with three relative peaks of the latter (February, July, October) were observed. Fecundity showed parallel temporal variation for both species, peaking in February and September-October. Interestingly, the July relative recruitment peak could not be explained by relative abundance of gravid females or fecundity, but is probably caused by adult mortality. Both species displayed comparable gonad production (*B. pilosa*: P_g = 0.73 mg/ind*year; *B. sarsi:* P_g = 0.71 mg/ind*year), but *B. pilosa* produced fewer yet larger embryos. Peak abundances were found at 436 ± 25 SD cm (*B. pilosa*) and 357 ± 40 SD cm (*B. sarsi*) above MLLWS, corresponding to a 40-62 m cross-shore distance between the peaks of both species. The occupied cross-shore range was larger for *B. sarsi* than for *B. pilosa* (35-54 m), for females than for males (15-23 m), and for adults than for juveniles of *B. pilosa* (5-8 m). Both species displayed many comparable life history features. Differences in abundance and biomass may be related to beach morphodynamics and zonation.

Keywords: sandy beaches, population dynamics, amphipods, zonation

Introduction

Bathyporeia pilosa and *B. sarsi* are common amphipod species of beaches of the eastern Atlantic, from Norway to France (Gulf of Biscay), with *B. sarsi* stretching even a little further south (until southern Portugal) (Marques and Bellan-Santini, 1991). *Bathyporeia pilosa* is found in the upper parts of the intertidal zone of sheltered beaches, between MHWS and mid-tide level (Fish and Preece, 1970a); in the retention zone and the upper parts of the resurgence zone, but not in the saturation zone (Salvat, 1962, 1964). It is absent from strongly exposed beaches (Vader, 1965), yet also encountered in subtidal areas, namely in estuarine and brackish conditions (Lindström, 1855; Dahl, 1944; Vader, 1966; Persson, 1982; Köhn and Gosselck, 1989). Slight morphological differences have been observed between intertidal and subtidal populations (d'Udekem d'Acoz, 2004), which may provoke doubt on the conspecifity of those populations. Along an open coastline, *Bathyporeia sarsi* is a strictly intertidal species (Toulmond, 1964; Vader, 1965), where it can be found between MHWN and MLWS (Toulmond, 1964). In some estuaries, however, the species has been found to live below the low water line (Vader, 1965, 1966; Degraer *et al.*, 2002). On Belgian beaches, *B. pilosa* is a species of 'drying sands' (around MHWN), while B. sarsi is said to occur somewhat below it (Degraer et al., 2003). Both species can be highly abundant; in Belgium they can frequently be found together on the same beaches, reaching abundances of up to 10.000 ind/m² (Degraer *et al.*, 2003). These high numbers of amphipods are of high functional importance as food source for wading birds (mainly Sanderling (*Calidris alba*)) and surf zone fish (Lasiak, 1983; Nicolaisen and Kanneworff, 1983; Gibson and Robb, 1996) like juvenile plaice (*Pleuronectes platessa*) (Beyst *et al.*, 2002a) and sand-eel species like *Ammodytes tobianus* (Persson, 1982). Both *Bathyporeia* species are said to feed solely on epipsammic food items and their mouthparts are considered to be specialised for that purpose (Nicolaisen and Kanneworff, 1969). Diatoms (and more specifically species of the genus *Coconeis*) comprise an important part of their diet (Nicolaisen and Kanneworff, 1969; Sundbäck and Persson, 1981).

While *Bathyporeia pilosa* is rather well studied (Vader, 1965, 1966; Nicolaisen and Kanneworff 1969, 1983; Fish and Preece, 1970a, 1970b; Preece, 1970, 1971a, 1971b; Fish, 1975; Khayrallah and Jones, 1980a, 1980b; Sundbäck and Persson, 1981; Persson, 1982; Mettam, 1989; Köhn and Sammour, 1990), far less is known on the ecology of *B. sarsi* (Vader, 1965, 1966; Nicolaisen and Kanneworff 1969, 1983; Bamber, 1993). Several studies have focused on both *B. pilosa* and a third species, *B. pelagica* (Fish and Preece, 1970a, 1970b; Preece, 1971a; Fish, 1975). To a certain degree, *Bathyporeia sarsi* might be regarded as intermediate between *B. pilosa* and *B. pelagica* concerning a number of ecological traits e.g. cross-shore distribution and substrate preferences (Vader, 1965, 1966). Only occasionally, their syntopic occurrence on beaches has been investigated (Vader, 1965, 1966; Nicolaisen and Kanneworff, 1969, 1983). Thus, a combined ecological study of *B. pilosa* and *B. sarsi* was conducted to investigate their life history, population dynamics and zonation patterns and to try to unravel elements of their interspecific ecological segregation in co-occurrence. The first published assessment of biomass and secondary production of these sandy beach key species is presented. Tests were conducted to identify significant spatial and temporal patterns within both species and to compare between them. Based on literature data, we *a priori* hypothesise *B. pilosa* to be the more stress tolerant species, due to life higher up on the beach. We expect interspecific differences in population dynamics characteristics to be related to these different environmental conditions.

Methods

SAMPLING

Along the Belgian shore, eight cross-shore transects were sampled monthly from October 2003 until October 2004, January 2004 excluded (Fig. 1). Sampling started each time at high tide and continued until the low tide level was reached, taking a sample every half hour just above the upper swash limit. In order to minimise differences in tidal range among sampling months, sampling dates related to a fixed point in the lunar spring tide-neap tide cycle. Each sample involved a 0.1026 m² rectangle being dug out to a depth of 20 cm and sieved over a sieve with a 1 mm mesh width. An additional sample was taken for analysis of sedimentology. Elevation of sampling stations and the entire beach profile were measured using a leveller and corroborated afterwards with the output of the M2 tidal reduction model (Coastal Division of the Agency of Maritime and Coastal Services).

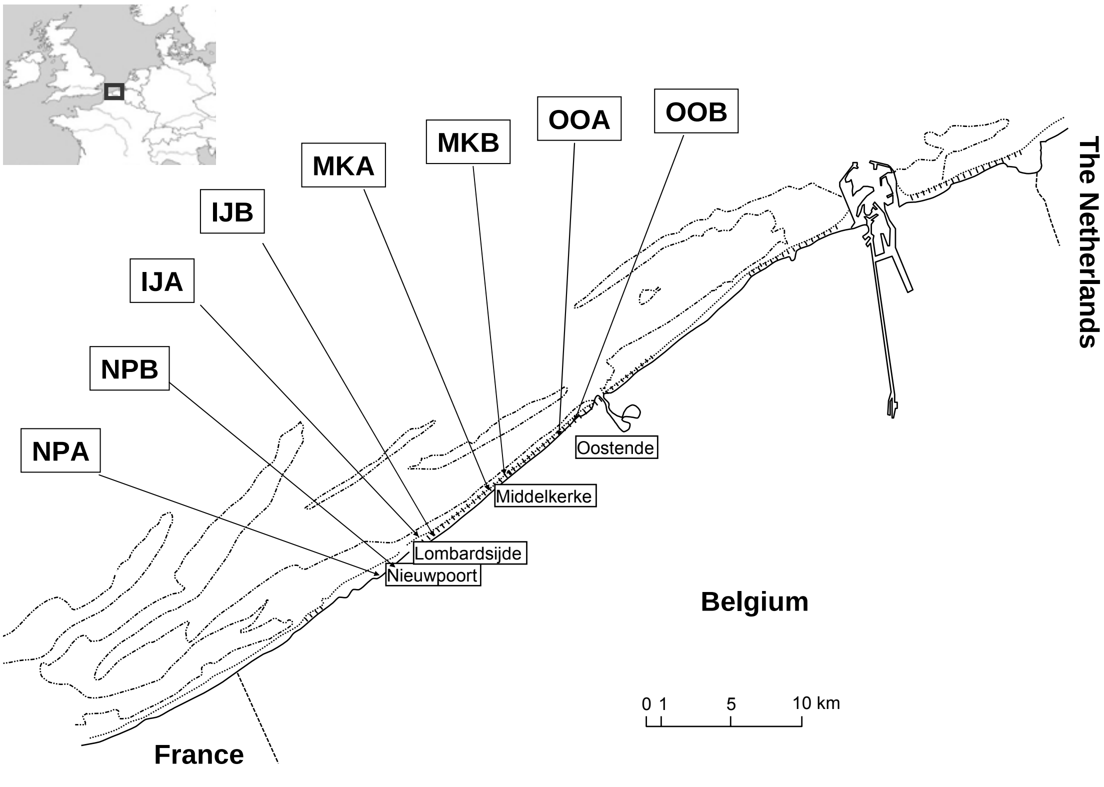

Figure 1. Location of sampled transects along the Belgian coast; NP = Nieuwpoort-Bad, IJZ = beach of Flemish nature reserve “Ijzermonding”, MK = Middelkerke-Bad, OO = Oostende-Bad; capitals A and B are to identify each of two transects within the same beach.

On two occasions, a part of the data was intentionally omitted from analysis. First, after the Oostende nourishment of June 2004, involving nourishment of the previously selected OOB transect, samples from the affected transect were not taken into consideration anymore. Furthermore, due to an unanticipated low elevation of high tide and high elevation of low tide, sampling in September 2004 covered a clearly smaller tidal range than during the other sampling months. This resulted in incomplete sampling of the populations of *B. pilosa*, and therefore this month was left out from further analysis of the data for that species.

LABORATORY PROCEDURES

Species identification was achieved with the key by d'Udekem d'Acoz (2004). To obtain a length-biomass regression, allowing calculation of biomass from measurement data, 100 undamaged specimens of both species and all sizes were randomly collected from March (50 ind.) and September (50 ind.) samples. Total body length was measured as in Persson (1982): from the basal segment of the first antenna or antennule (= pseudorostrum) to the end of the telson. Fish and Preece (1970a) and Mettam (1989) chose to measure body length until the spine of the fourth pleon segment. We believe measurement of the entire body to be preferable, even though this might somewhat limit comparability between studies. One hundred specimens of each species were dried (4h at 110°C) and dry weight was established. Subsequent combustion (2h at 550°C) delivered the specimens' ash weight and subtraction of both weights delivered ash-free dry weight (AFDW). After log transformation of the biomass data and having ensured that assumptions were met, linear regression analyses were executed. Thus, with the obtained equations (*B. pilosa*: $R^2 = 0.863$; $p < 0.01$; df = (1. 86); *B. sarsi*: $R^2 = 0.885$; $p < 0.01$; df (1. 97)) and measurement of body length of all collected specimens (10.588 individuals of *B. pilosa* and 3.275 of *B. sarsi*), AFDW was calculated. Three percent of the collected specimens (495 individuals) were damaged to a degree that they could not be identified up to species level. These specimens were omitted from the data.

Individuals were counted and identified as males, females and juveniles according to Watkin (1938). Stations delivering zero values (lower intertidal area) have been omitted to obtain values of abundance and biomass, relating to the occupied long-shore strip of the beach only. Embryos, if present within the female's marsupium or brood pouch, were counted to assess fecundity.

For *Bathyporeia pilosa*, zonation was studied based on the western transects (IJA, IJB, NPA and NPB) only because their numbers at the eastern transects (MKA, MKB, OOA en OOB) are very low.

DATA ANALYSIS

Count data were used for abundance-related analysis. Biomass calculation allowed calculation of secondary production, using the size frequency method (SFM: Hynes and Coleman, 1968): $E_{j\text{-}j+1} = (M_j + M_{j+1})^{0.5} * (N_j - N_{j+1})$; with M_j and M_{j+1} being mean biomass for respectively size class j and j+1 and N_j and N_{j+1} being the mean number of individuals in respectively class j and j+1. Elimination of the average cohort (as all cohorts are spread over the applied size classes and maximum life span is not taken into account yet) is given by: $E_{ac} = \Sigma (E_{j\text{-}j+1})$; with j = (1, 2, 3,...m). Production equals elimination of the entire population, taking life span (A_{max}) and number of size classes (m) into account: $E = E_{ac} * m/A_{max}$. Female gonad production, relating to gonadal products released between times t and t+1 was calculated with the formula for direct measurement: $P_{g.ind.t=>t-1} = \Sigma N_{egg} * M_{egg}$ (egg mass* ind^{-1} *time^{-1}). Cohort analysis (decomposition of size-frequency distributions into Gaussian components with Bhattacharya's method (Bhattacharya, 1967) and NORMSEP (Hasselblad, 1966; Tomlinson, 1971)) was conducted with FiSat II software (Gayanilo *et al.*, 1996). Due to the confusing output of the cohort analysis, no von Bertalanffy growth function was fit, nor was the instantaneous mortality rate calculated, but this had no further bearing on other estimates of population characteristics, except for a more indirect determination of the adult life span.

Due to its more descriptive rather than predictive capacity (Short, 1999), the beach index (BI) (McLachlan and Dorvlo, 2005) was preferred over the more conventional Dean's parameter and relative tidal range parameters for characterisation of morphodynamics: $BI = \log((-\log_2(\text{median grain size in } \mu m) + 1) * \text{tidal range}) / \text{slope}$. Given the spatial (intra-transect comparisons - zonation) and temporal (monthly sampling at the same exact transect locations) dependent nature of the data, statistical tests were chosen accordingly.

Results

Due to the strong interconnectivity of marine habitats, we consider the entire Belgian coastline to harbour a single population of both species. Therefore, transects can be regarded as samples of one population. This was confirmed by the fact that only differences in abundance, biomass, production and zonation, related to small-scale variation of the physical environment rather than to the geographical position of the transects, were observed; no spatial variation was observed in most of the population characteristics. In our analyses, no beach effect was evident (among-transect variation comparable to or even less than among-beach variation), thus transects could be used as independent replicates. Given the dependent nature of the data and the type of statistical tests used, spatial comparison (between transects) was, however, possible using sampling months as repeated observations on the same items.

PHYSICAL ENVIRONMENT

All sampled beaches are wide, macrotidal beaches with a sampled intertidal section ranging from about 170 to over 200 m in width and an average spring tide tidal range ranging more or less from 4.5 to 4.7 meter. Beach slope was weak (0.75-1.15°). Sediment analysis showed median grain size to range from 171 to 347 µm and the sediment to be well to moderately well sorted (SD of median grain size (µm) = 1.29-1.58). With a beach index (BI) of 2.7 to 3.0, the morphodynamic type of all four beaches is clearly dissipative, in concordance to Degraer *et al.* (2003). Western transects have, however, higher beach index values (BI = 2.95 ± 0.03 SD) than eastern ones (BI = 2.75 ± 0.03 SD) (Mann-Whitney U Test: Z = 2.12; p = 0.03), suggesting eastern transects to be a little less dissipative. Significant differences between transects were found in median grain size (Friedman Chi Square (N = 4, df = 6) = 22.39; p < 0.01). Western transects (IJA, IJB, NPA, NPB) exhibit lower median grain sizes, especially those from Nieuwpoort (NP; e.g. NPB: 192 ± 6 SD µm), whereas grain size on Middelkerke and Oostende beaches seems comparably larger (e.g. MKB: 268 ± 24 SD µm).

Minor quantities of fines (< 63 µm) were encountered in western transects (highest in NPB: 0.14 ± 1.00 SD % but at least 4x less in other western transects), but were usually completely absent from eastern transect sediment samples.

ABUNDANCE AND BIOMASS

While sampled transects were initially selected as morphodynamically similar, data analysis revealed some clear spatial variation regarding the abundance and biomass of the present *Bathyporeia* populations. Concerning *B. pilosa,* a sharp distinction can be made between western and eastern transects, with significantly higher abundance (Friedman Chi Square (N = 11, df = 6) = 51.74 p < 0.01) (Fig. 2) and biomass (Friedman Chi Square (N = 11, df = 6) = 41.63 p < 0.01)) on western ones. Whereas western abundance averages are all above 150 ind/m², eastern ones are lower than 10 ind/m². Biomass supports the same distinction, with biomass ranging from 3 ± 5 SD mg/m² for MKA to 714 ± 476 SD mg/m² for IJA.

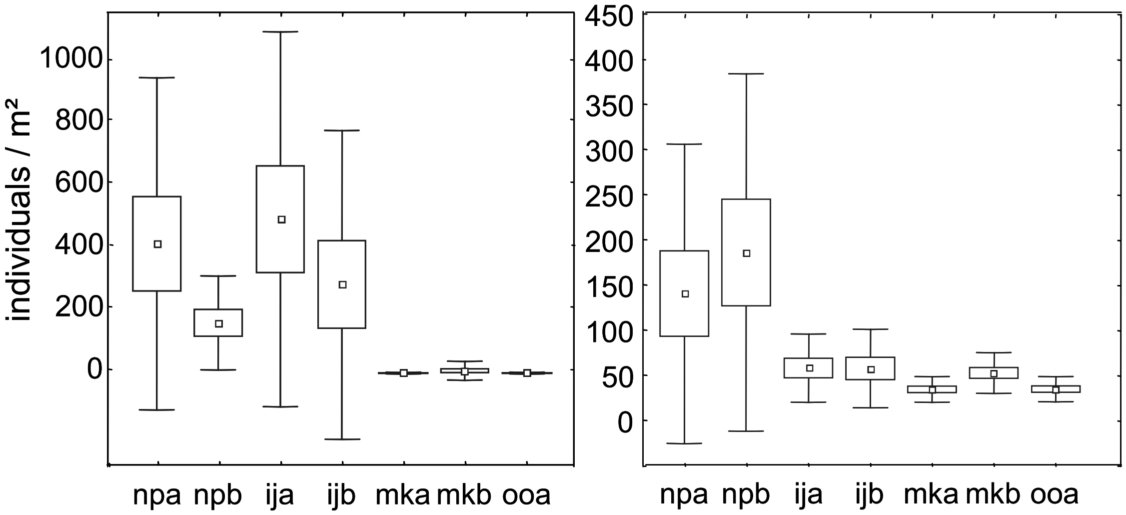

Figure 2. Spatial variation of abundance of *Bathyporeia pilosa* (left) and *B. sarsi* (right) (ind/m²). Box: SE; whisker: SD. Transects ordered from west (left) to east (right) in both graphs.

Also *B. sarsi* shows significant differences between transects regarding both abundance (Friedman Chi Square (N = 9, df = 6) = 35.48; p < 0.01) and biomass (Friedman Chi Square (N = 9, df = 6) = 25.19; p < 0.01), however, grouping those differently. In this species, only the Nieuwpoort transects have higher densities (averages of more than 125 ind/m²), while all other beaches maintain moderate densities of the species (averaging at 40 ind/m²). The difference between transects is clearly not as strong as with *B. pilosa* and all transects seem to maintain viable populations of *B. sarsi*. From a -rather trivial- comparison between the densities of both species, we can conclude that *B. pilosa* is significantly more abundant on the IJA, IJB and NPA (Wilcoxon Matched Pairs Test: respectively $Z = 2.82$ and $p < 0.01$; $Z = 2.43$ and $p = 0.02$; $Z = 2.51$; $p = 0.01$) transects, while *B. sarsi* is significantly more abundant than *B. pilosa* on MKA, MKB and OOA (Wilcoxon Matched Pairs Test: respectively $Z = 3.06$ and $p < 0.01$; $Z = 2.12$ and $p = 0.03$; $Z = 3.06$ and $p < 0.01$). Finally, both occur in comparable numbers on the NPB transect (Wilcoxon Matched Pairs Test: $Z = 0.40$ and $p < 0.69$).

Maximum observed densities were 8209 ind/m² for *B. pilosa* (NPA in July 2004) and 2205 ind/m² for *B. sarsi* (NPB in May 2004).

While no significant temporal variation was observed for *B. pilosa* (abundance: Friedman Chi Square ($N = 3$, $df = 10$) = 10.18 $p = 0.42$; biomass: Friedman Chi Square ($N = 3$, $df = 10$) = 8.08 $p = 0.21$), both numbers and biomass of *B. sarsi* peaked in spring and were lowest in autumn and winter (abundance: Friedman Chi Square ($N = 4$, $df = 11$) = 21.80 $p = 0.03$; biomass: Friedman Chi Square ($N = 4$, $df = 11$) = 11.87 $p < 0.01$).

Conclusively, significant differences in size between both species were found (Wilcoxon Matched Pairs Test: $Z = 2.90$ and $p < 0.01$), with *B. sarsi* (6.10 ± 0.68 SD mm) being about 10% larger than *B. pilosa* (5.45 ± 0.73 mm).

LIFE CYCLE, DEMOGRAPHY, REPRODUCTION AND RECRUITMENT

Cohort analysis for both species delivered confusing results, making it impossible to track down any age group through time and suggesting continuous reproduction. Therefore, we also prefer to refrain from any, undoubtedly confusing, graphic representation. A nine months maximal adult life span for both species could be deduced from partially traceable cohorts. Arrival of new, small *B. pilosa* individuals (i.e. recruitment) was e.g. observed in October, with an average length of 3.11 mm in 2003 and 3.86 in 2004. Another peak in recruitment was observed in February, with individuals of 4.08 mm of average length. Tracing individual cohort life history from month to month proved to be very difficult, if not pointless. This is due to continuous reproduction and recruitment and merging and re-splitting of groups of recruits of the same age. The February 2003 recruitment cohort can be traced somewhat more clearly than that of October 2003, growing from February until September-October, albeit with exception of collision in April 2004. Besides the juvenile cohort in February, a second cohort is present of 5.98 mm in average size. This cohort consists most likely of recruits of October 2003. They will give raise to peak recruitment in October 2004, after which most of them die.

In *B. sarsi*, as in *B. pilosa*, a new cohort appears in October (average size: 4.22 mm in 2003; 4.52 mm in 2004). Also another recruitment peak can be observed in February (average size: 4.39 mm).

Again, drawing temporal growth patterns for single cohorts was hardly possible. The cohort of October (2003) recruits collided with a group of larger and older individuals in December. Again, like with *B. pilosa*, the February recruits are a little easier to follow during the consecutive months, however, being inseparable from another cohort in June and August.

The number of gravid, egg-bearing females displayed two peaks for both species. A spring peak in April and an autumn one (September-October), separated by low values in winter (December) and summer (July) were observed (Fig. 3 - above). In *B. pilosa*, the spring adult cohort responsible for reproductive peak activity contained individuals of 5.98 mm on average; those of October 2004 were of 5.05 mm on average, while in October 2003 two non-juvenile cohorts seemed to be present (5.88 mm and 4.26 mm on average). A comparable pattern is observed for *B. sarsi*: from February onwards the number of gravid females grew, peaking in May, dropping to a July low and peaking again in autumn (October). Relative abundance apparently can differ strongly between years: 55% in October 2003 and only 29% in October 2004 for *B. sarsi* and 29% versus 11% in the same respective years for *B. pilosa* (Fig. 3 - above).

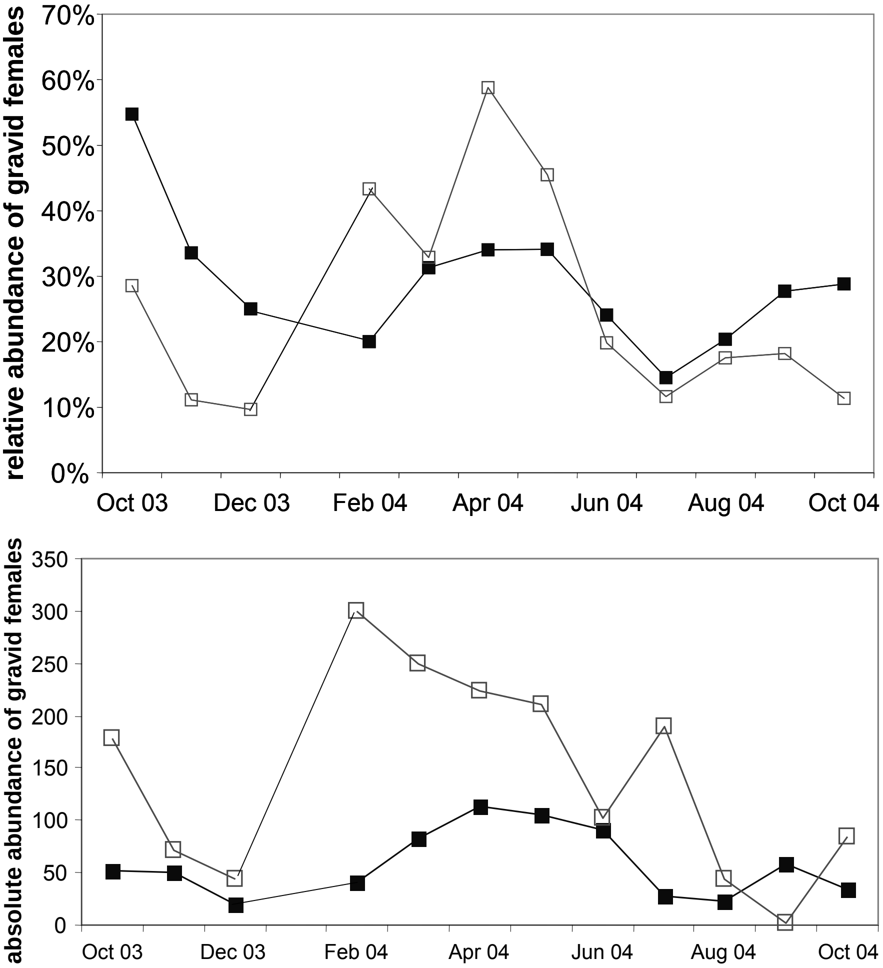

Figure 3. Temporal variation of relative (above) and absolute (below) number gravid females (percentage of gravid females on total of females); solid squares: *B. sarsi*; open squares: *B. pilosa*. Error bars omitted for graphic representation.

Fecundity patterns were clearer (Fig. 4). *Bathyporeia sarsi* females carried about 1.75 times as much eggs as *B. pilosa* (Wilcoxon Matched Pairs Test: Z = 5.07; p < 0.01), whereas the weight of an individual *B. pilosa* egg was about 1.8 times the weight of one belonging to *B. sarsi*. Thus, total carried egg mass was comparable for both species and this is confirmed by their gonad production values (*B. pilosa*: P_g = 0.73 mg/ind*year; *B. sarsi:* P_g = 0.71 mg/ind*year). Fecundity peaked for both species in February 2004 and was lowest in August 2004, the latter low coinciding with rather low numbers of gravid females for both species. Both species showed a -rather trivial albeit weak- correlation between female size and egg load (Spearman Rank Order Correlation: *B. pilosa*: SR = 0.35; p < 0.01; *B. sarsi*: SR = 0.33; p < 0.01).

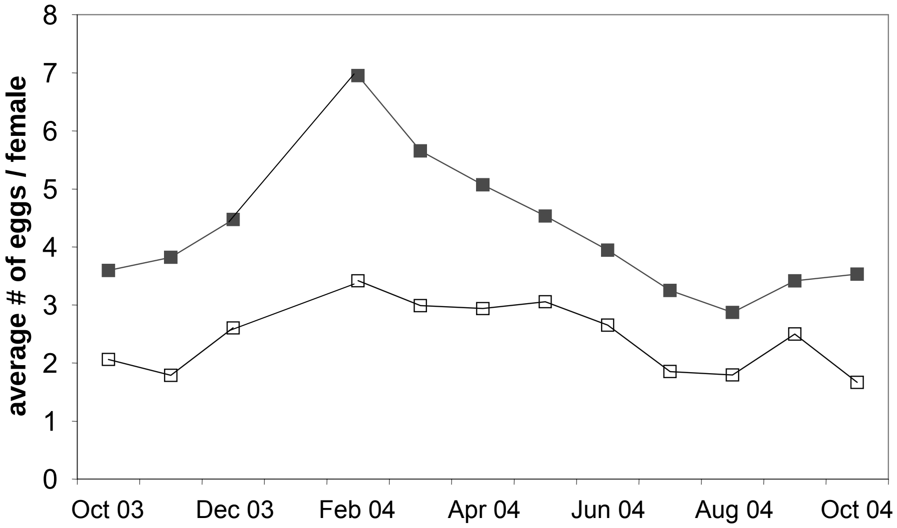

Figure 4. Temporal variation of fecundity (average number of eggs per female); solid squares: *B. sarsi*; open squares: *B. pilosa*. Error bars omitted for graphic representation.

Juvenile abundance, expected to result from the combined variation in both number of gravid females and fecundity, shows a February-March, a July and an October peak for both species (Fig. 5). Peaks are more pronounced in *B. pilosa*, indicating somewhat less continuous recruitment patterns.

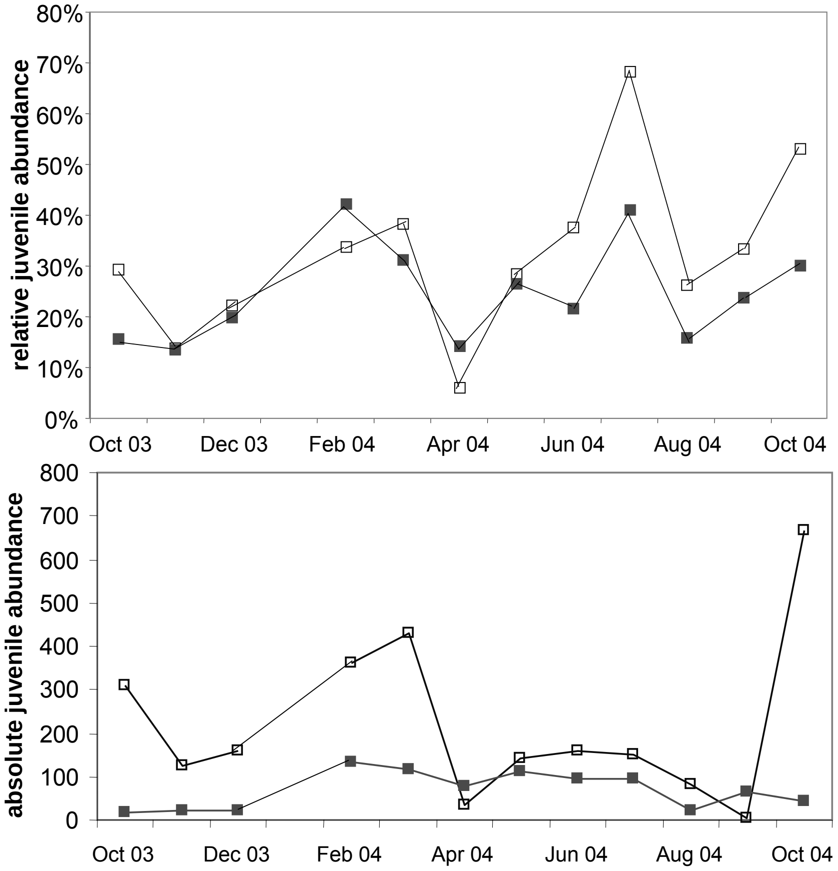

Figure 5. Temporal variation of relative (above) and absolute (below – total number) juvenile abundance; solid squares: *B. sarsi*; open squares: *B. pilosa.* Error bars omitted for graphic representation.

The sex ratio displayed a largely similar trend for both species, both showing about twice as much females as males from December 2003 until May 2004 (Fig. 6). From June 2004 onwards, a clear increase in female predominance is observed, up to ratios of 6 females per male. The only difference between both species is found at the start of the sampling period (October-November 2003), with *B. sarsi* displaying a ratio similar to that of summer months (up to 6x more females), while *B. pilosa* already had the typical winter-spring ratio (about 2x more females).

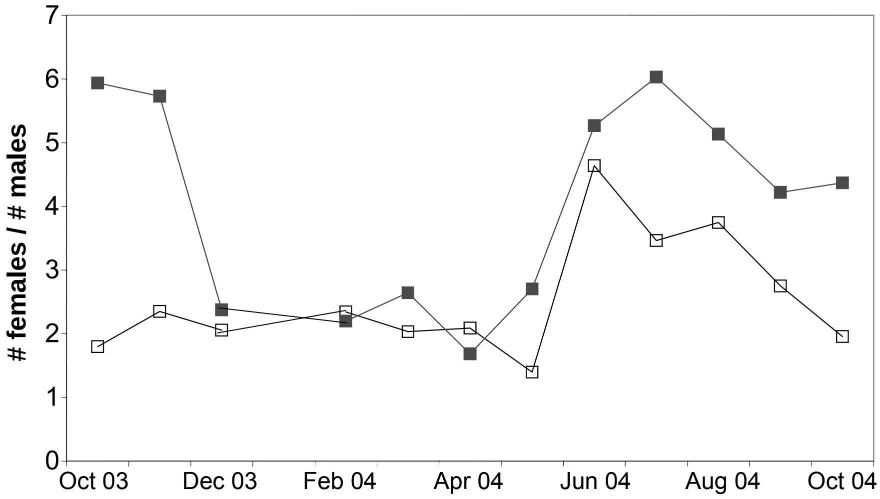

Figure 6. Sex ratio (# females / # males) over time; solid squares: *B. sarsi*; open squares: *B. pilosa.* Error bars omitted for graphic representation.

In conclusion, both species display continuous reproduction and recruitment, with two absolute peaks of the latter being visible in October and February. The third peak in July is most probably more relative (see Discussion).

MEAN ANNUAL BIOMASS, SECONDARY PRODUCTION AND P/B RATIO

For *B. pilosa*, mean annual biomass (MAB), secondary production and P/B ratio all reached clearly higher values along the western transects (Tab. 1).

Table 1. Mean annual biomass (MAB; mg AFDW/m²), secondary production (P - Size Frequency Method; mg * m^{-2} * y^{-1})) and P/B-ratio (P/B; y^{-1}); NP = Nieuwpoort; IJ = Ijzermonding; MK = Middelkerke; OO = Oostende

	NP			**IJ**			**MK**			**OO**		
	MAB	**P**	**P/B**	**MAB**	**P**	**P/B**	**MAB**	**P**	**P/B**	**MAB**	**P**	**P/B**
B. pilosa	2035	16040	7.88	1458	10165	6.97	9.13	28	3.08	3	1.84	0.59
B. sarsi	1005	7580	7.54	209	1245	5.95	496	3279	6.62	187	1260	6.74

P/B ratios varied more than tenfold with regard to sampling location. Also in *B. sarsi*, large differences in the MAB values can be recognised, yet somatic production seemed to vary to the same degree, resulting in rather comparable P/B ratio values for all beaches. Nevertheless, P/B ratios show high relative productivity of the Nieuwpoort transects for both *Bathyporeia* species.

CROSS-SHORE ZONATION

Figure 7 offers a schematic overview of the cross-shore distribution of the investigated species, introducing investigated variables.

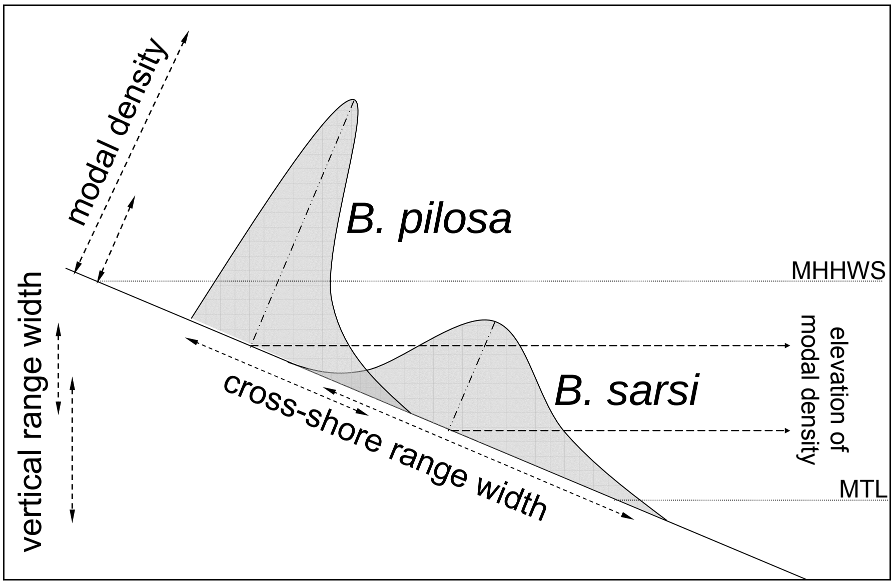

Figure 7. Schematic overview of cross-shore distribution of *Bathyporeia pilosa* and *B. sarsi* across the intertidal gradient. MHHWS = level of mean highest high water at spring tide; MTL = mid-tidal level.

First, elevation of the maximum density sample of each transect at each sampling month is considered. Secondly, we will address the width of the occupied vertical range.

Peak abundances of *B. pilosa* were found at 436 ± 25 SD cm above MLLWS, while those of *B. sarsi* were found at 357 ± 40 SD cm above MLLWS. *Bathyporeia pilosa* was found significantly higher on the beach than *B. sarsi* (Wilcoxon Matched Pairs Test: $Z = 4.11$, $p < 0.01$). This vertical difference of about 80 cm corresponds (depending on beach slope) to a 40 to 62 m cross-shore distance.

Significant differences in elevation of peak abundance were found as well between the four transects under consideration for *B. pilosa* (Friedman Chi Square ($N = 10$, $df = 3$) = 14.39; $p < 0.01$) (Fig. 8 - left).

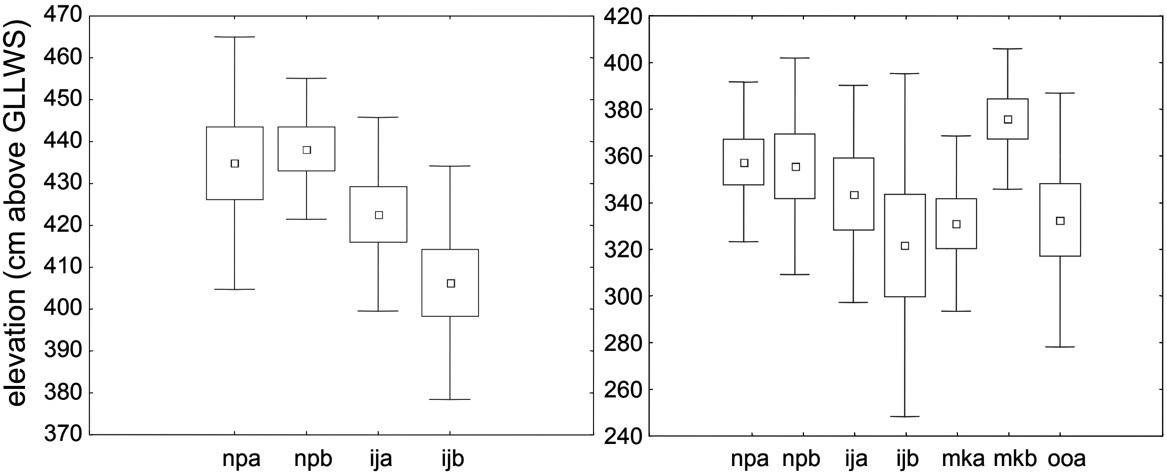

Figure 8. Spatial variation of elevation of peak abundance of *Bathyporeia pilosa* (left) and *B. sarsi* (right)(in cm). Box: SE; whisker: SD. Transects ordered from west (left) to east (right) in both graphs.

For *B. sarsi*, differences were significant at the 10% level (Friedman Chi Square (N = 8, df = 6) = 11.78; p = 0.07) (Fig. 8 - right), with, like in *B. pilosa*, a tendency of peak abundances being found higher up on the beach of Nieuwpoort than on that of the Ijzermonding and a remarkable 40 cm difference between both transects at Middelkerke.

Considering only western transects (npa, npb, ija and ijb), no significant variation over time was observed (Friedman Chi Square (N = 3, df = 10) = 14.01; p = 0.17) for *B. pilosa*. Yet, peak density elevation was highest from May to July and lowest from October to February. For *B. sarsi* there was significant variation over time (Friedman Chi Square (N = 4, df = 11) = 24.31; p = 0.01), with peak abundances being found higher up on the beach in summer, but interannual variation seems to be high too (comparing October 2003 and October 2004).

No differences in modal height were detected between juveniles and adults (Wilcoxon Matched Pairs Test: *B. pilosa*: Z = 1.069, p = 0.29; *B. sarsi* Z = 0.1825, p = 0.86) nor between females vs. males (Wilcoxon Matched Pairs Test: *B. pilosa*: Z = 0.700, p = 0.48; *B. sarsi* Z = 0.1778, p = 0.86) for either species, thus no evidence for intraspecific cross-shore segregation was found.

Comparing both species (while considering western transects only), it is clear that *B. sarsi* occupies a wider vertical range or zone than *B. pilosa* (Wilcoxon Matched Pairs Test: Z = 3.38, p < 0.001). This difference is of about 70 cm in vertical distance, corresponding with 35-54 m cross-shore.

Females of both species occupy a significantly wider zone than males (*B. pilosa*: Wilcoxon Matched Pairs test: Z = 2.52, p = 0.01; *B. sarsi*: Wilcoxon Matched Pairs Test: Z = 2.37, p = 0.02), and, strikingly, the female range is an equal 30 cm wider in vertical distance (15-23 m cross-shore) in both species. Adults of *B. pilosa*, occupied a somewhat wider zone than juveniles (Wilcoxon Matched Pairs test: Z = 2.02, p = 0.04) with a difference of 10 cm in vertical distance (5-8 m cross-shore). For *B. sarsi*, this was only significant at the 10% level (Wilcoxon Matched Pairs Test: Z = 1.85, p = 0.06), corresponding to about 20 cm vertical range difference (10-16 m cross-shore).

Comparing all transects for *B. sarsi*, vertical range width appeared to be significantly higher on western transects (Friedman Chi Square (N = 12, df = 6) = 30.02; p < 0.01) (Fig. 9 – left) and the widest range is occupied in April, while autumn and winter values are lower (Friedman Chi Square (N = 7, df = 11) = 20.06; p = 0.04) (Fig. 9 – right). For *B. pilosa*, it is most likely that the fact that only the western transects were available as replicates, disallowed observation of such differences (spatial: Friedman Chi Square (N = 11, df = 3) = 2.74, p = 0.43; temporal: Friedman Chi Square (N = 4, df = 10) = 4.76; p = 0.91).

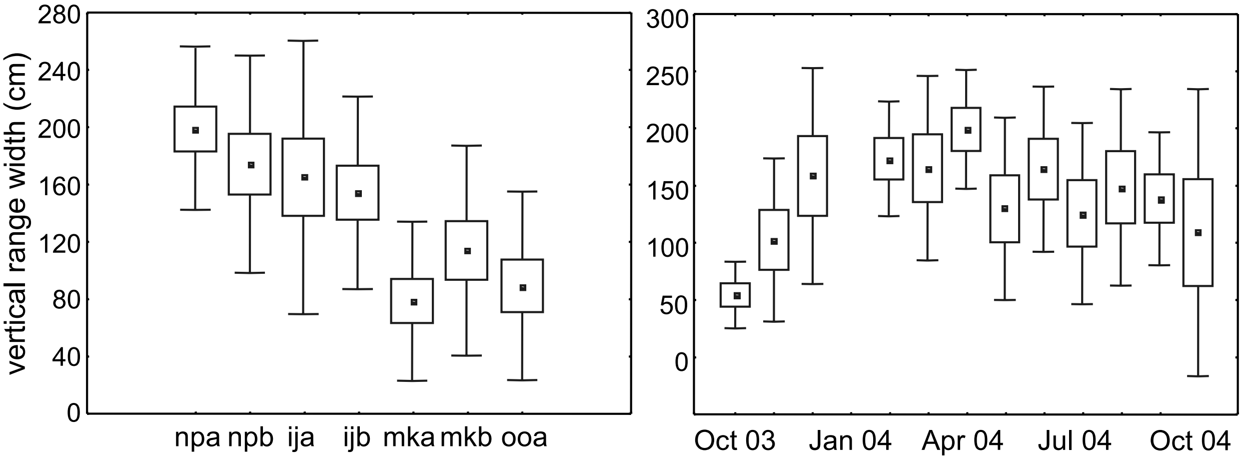

Figure 9. Spatial (left - transects ordered from west (left) to east (right)) and temporal variation (right) of width of vertical range *Bathyporeia sarsi* (cm). Box: SE; whisker: SD

MEDIAN GRAIN SIZE RELATED TO PEAK ABUNDANCE

Median grain size at stations of peak abundance along each transect were considered. Attempting reliable comparison of species, once more only western transects are considered. *Bathyporeia pilosa* just failed to show significant differences between those transects (Friedman Chi Square (N = 3, df = 3) = 7.40, p = 0.06), whereas significant differences for *B. sarsi* were found within those same transects (Friedman Chi Square (N = 3, df = 3) = 8.20, p = 0.04). No significant temporal fluctuation was observed for either species (all p > 0.05).

Discussion

ABUNDANCE AND BIOMASS

At transects where both species co-occurred in reasonable numbers (i.e. where also *B. pilosa* lives), densities of *B. sarsi* are clearly lower than those of *B. pilosa*. Burrowed in the sand at low tide, *B. pilosa* seems to display a patchy distribution (Khayrallah and Jones, 1980b; Persson, 1982; Nicolaisen and Kanneworff, 1983). Comparison of observed densities with those found by other authors (Vader, 1965, 1966; Salvat, 1967; Persson, 1982; Bamber, 1993), suggests that observed differences might be attributed to differences in habitat conditions, related to mainly tidal range, sediment characteristics and slope. In general, these findings have to be considered taking into account their temporal (only one year studied) and spatial (only 7 usable transects) constraints.

The presence of strong spatial abundance differences in *B. pilosa* and their absence in *B. sarsi*, might be attributed to small-scale differences in morphodynamics. The sampled eastern transects are somewhat less dissipative than the western ones (Degraer *et al*., 2003a), as corroborated by a steeper slope, coarser sediment. This might concur with well established links between species richness and morphodynamics (e.g. Defeo and McLachlan, 2005) but no such assessment is available from our data. Nicolaisen and Kanneworff (1969) stated that *B. sarsi* dominates on exposed shores, and *B. pilosa* on sheltered localities. In this study, *Bathyporeia sarsi* was found in comparable numbers along the different transects. Both species seem to reach their highest numbers on both transects at Nieuwpoort. The other transects, namely those at the Ijzermonding beach, might be less favourable, due to a somewhat steeper slope, coarser sediment and stronger changes in the beach profile throughout the year. *Bathyporeia sarsi* seems to be able to cope with the somewhat more reflective conditions at the eastern transects, in contrast to *B. pilosa*. Vader (1965) stated that *B. sarsi* prefers, or maybe better tolerates, somewhat coarser sands than *B. pilosa,* but both have been found in both finer and coarser sands. *Bathyporeia pilosa* has been described as preferring fine sands containing some fines (Vader, 1965, 1966). Concentrations of fines were clearly lower along eastern transects (always practically zero). Conditions might also differ on a small scale for both species, as they live at different heights on the beach.

In both species, biomass trends coincide with those in abundance, with a similar distinction between western and eastern transects. Yet, total biomass of *B. pilosa* at transect MKB is comparable with that at transect IJB, whereas MKB abundance was clearly lower than that of IJB. No significant differences between sampling months were observed, while November and December show somewhat higher values, implying higher food availability for predators in that period. These higher values might be due to the presence of a higher number of cohorts present: juveniles from the autumn recruitment peak, adults born in spring and survivors of the reproducing population of spring, with especially the two latter groups producing high biomass values. Given this interpretation, a similar pattern could be expected just before summer in May and June. Compared to July, this is indeed the case. In this month, biomass drops due to mortality of larger animals, i.e. parent animals of the earliest recruitment peak.

Remarkable in comparing both species is the contrast in abundance versus biomass patterns. At all western transects, *B. pilosa* abundance ranges from comparable to ten times larger than that of *B. sarsi*, whereas *B. sarsi* biomass has a relative importance that runs from five to ten times higher. Thus, predators of *Bathyporeia* are offered a choice between more abundant, smaller prey and somewhat larger, yet scarcer food items. Higher individual biomass of *B. sarsi* seems only related to their larger adult size, as biomass increment with growth seems comparable for both species and in fact even a little higher in *B. pilosa*.

No significant temporal variation in abundance was observed for *B. pilosa*, while it was present in *B. sarsi.* Significant higher densities of *B. sarsi*, as observed in spring and early summer, might be artefacts attributable to random aggregations, and sample size might have to be reconsidered in that respect. Yet, comparable variations in density have been observed for *B. pilosa* in the past (Persson, 1982; Nicolaisen and Kanneworff, 1983).

Fincham (1971) related low numbers in autumn and winter to mortality. Maranhão *et al*. (2001), investigating *Echinogammarus marinus*, showed water temperature and salinity to influence seasonal changes in abundance, with higher temperatures and salinity levels relating to lower densities. High temperatures might enhance desiccation of the animals during emersion periods, causing lower numbers in summer. However, in this Portuguese study winter temperatures may present less stress than they do in Belgium. High densities earlier in the year are attributable to a peak of successful reproduction in spring and rising temperatures after spring, creating favourable conditions for development and reproduction.

LIFE CYCLE, DEMOGRAPHY, REPRODUCTION AND RECRUITMENT

Confusing output of the cohort analysis made it hard to unravel *Bathyporeia* life history; cohorts are often inseparable due to continuous reproduction. This is not new to the research on these species (Fish and Preece, 1970a). Nevertheless, two relative peaks of reproduction, as indicated by the relative abundance of gravid females and to a large degree corroborated by trends in fecundity and juvenile abundance, were visible in this study. Peaks in the number of gravid females (April and September-October) are pretty much in concordance with earlier findings (Salvat, 1967; Fish and Preece, 1970a) and can be summarised as a (broader) spring peak and an autumn peak. Timing of these peaks may differ slightly between locations and probably among years. This may be due to small differences in microclimate and food availability. Lower reproductive activity in winter and summer is probably an indirect effect of elevated female mortality after reproduction, as hinted by drops in female abundance (see gravid females' abundance and sex ratio data). In contrast to Fish (1975), only a single peak of male abundance (in October for *B. pilosa*; in April in *B. sarsi*) was apparent, coinciding with the peak in gravid females' abundance, rather than preceding it. It is likely that our sampling frequency was too low to observe this precedence pattern.

Mettam (1989) also found sex ratio to be shifted towards female predominance, but observed a nearly equilibrium during the major reproduction peak. This is not the case in our Belgian populations, where male relative abundance peaks in May, being still 50% less than female abundance. From June until the end of summer, five to six times more females are observed. Mettam (1989) suggested this might be due to slower growth and shorter life span in males and difficulties in sexing juveniles. Watkin (1939) attributed these differences to sampling method, giving contrasting results between towing and digging results. Digging samples out, like we did, should however reflect the true population best.

As sex ratio, also fecundity (number of embryos per female) showed a highly comparable trend in both species, peaking in February and again -but less sharp- in autumn (September in *B. pilosa*; October in *B. sarsi*). The lower fecundity of *B. pilosa* shows less clear peaking, with a rather continuous period of higher fecundity from February to May and an additional peak in September. Peaking fecundity in spring was also found by Fish (1975), with lower values afterwards due to adult mortality. Maranhão *et al.* (2001) related lower fecundity to lower temperature and salinity drops due to rainfall. Lower fecundity in those conditions in the year should favour individual development. This could also be the case for Belgian *B. pilosa* in autumn and early winter, yet peak fecundity was observed as soon as February. This might be due to the mild winter of 2003-2004. The observed correlation between fecundity and female body size has been found for several amphipods before (Fish, 1975).

Differences in fecundity between *B. pilosa* and *B. sarsi* reveal a different reproduction strategy (cf. Maranhão *et al.*, 2001). *Bathyporeia pilosa* has fewer embryos of larger size and containing more yolk, giving each single embryo a higher chance of survival, as a response to its more stressful environment in the highest parts of the intertidal zone. The upper parts of the intertidal zone exhibit strong fluctuations in temperature, salinity and sediment water content. Gonad production showed energy costs for both strategies to be of the same magnitude.

Continuous recruitment occurs but is low in between recruitment peaks. Fish (1975) mentions hatchlings size of about 1.5 mm. Next to differences in measuring methodology, applied mesh width did not allow retention of animals of this size. This is likely to result in loss of data in cohort analysis and the study of age/size-based cross-shore segregation. Furthermore, monthly sampling might cause new recruitment to be observed not until after already over three weeks of growth. Yet, throughout all our data we never encountered such small animals, the smallest individual being 1.977 mm. Three peaks in recruitment, as apparent by the appearance of new cohorts in the cohort analysis and peaks in juvenile abundance, were observed (February-March, July and October). Remarkable is that the peaks of juvenile abundance only in part seem to coincide with those in abundance of gravid females: the July peak in juvenile abundance does not coincide with a peak in neither gravid female abundance nor fecundity. Yet, sex ratio does and perhaps higher proportional numbers of females in June-July may have compensated for lower fecundity and the lower abundance of gravid females. However, adult mortality, as observed by a drop in biomass in July samples, seems most likely to explain an artificial relative peak in juvenile abundance, and the shift in sex-ratio may be due to a (relatively) higher male mortality. A spring plus autumn recruitment peak scenario seems most likely and is confirmed by the fecundity data, absolute numbers of juveniles per month and the output of the cohort analysis, showing new cohorts appearing in February and October. Thus, a bivoltine life cycle was observed, with a broad spring peak of reproductive activity and recruitment and a second, concerning fecundity much smaller one in autumn, which may slightly vary in magnitude and timing from one location to another.

Some interesting temporal spring-autumn and year-year differences require further discussion. In *B. pilosa*, spring females are larger than autumn ones, formerly explained as a consequence of a longer period of growth (Fish and Preece, 1970a). Yet, individuals hatched in February have six to seven months to grow before they reproduce, as have the wintering ones, born in autumn. The spring reproduction peak is, however, rather wide and lasts in fact until May, giving late hatchlings little time to grow during summer and perhaps, thus, resulting in lower average adult size.

Juveniles from February are larger than those from October. Due to the lack of January data, no precise assessment of the time of hatching could be made and this could not be tested properly.

Gravid females of *B. pilosa* were much less abundant in October 2004 than in October 2003, while the opposite was observed for juveniles. Peak recruitment might have occurred just before the 2004 sampling, with hatchlings having already left the marsupial pouch to a higher degree, resulting in fewer gravid females and more juveniles in the samples. A higher sampling frequency may be useful in this respect. Higher average size of October 2004 juveniles compared to the ones from October 2003 has to be attributed to the power of the cohort analysis. In 2004, two small cohorts, as they were found in 2003, could not be separated, resulting in one cohort of intermediate average body size and larger than the smallest cohort from 2003. Thus, interannual variation in juvenile abundance seems to allow important differences in the result of the cohort analysis.

GROWTH AND MORTALITY

A growth function could not be defined, as the output of the cohort analysis provided confusing results.

The magnitude of adult cohort growth, observed in part from one month to the next, suggests quasi-linear growth in the investigated populations of *Bathyporeia pilosa*. In juvenile cohorts of the same species, continuous reproduction and recruitment, together with considerable juvenile mortality, seem to induce strong monthly oscillations in average cohort body length, disallowing assessment of growth for these younger animals. No evidence of the presence of a growth stop can be found. Growth assessment was, due to an even more erratic pattern in the cohort analysis, even harder in *Bathyporeia sarsi*, yet, again a linear growth pattern seemed present. There seems to be no indication of difference in growth rate between the species, as suggested by comparable slopes of the calculated regression equations (*B. pilosa*: 0.2687; *B. sarsi*: 0.2616). Yet, given their comparable life span and, as *B. sarsi* reaches larger adult size than *B. pilosa* and the former has smaller eggs with less yolk, to be expected to result in smaller hatchlings, *B. sarsi* might be thought to grow faster. This might be also facilitated by more benign conditions governing the habitat somewhat lower down on the beach, i.e. where *B. sarsi* reaches highest numbers. The available data, however, shows *B. sarsi* juveniles of February and October to be 1 mm larger on average than those of *B. pilosa.* This confusing phenomenon has to be considered in view of the snapshot nature of monthly sampling and it is possible that more frequent sampling, combined with sieving over a finer mesh, could corroborate our hypothesis of higher growth rate in *B. sarsi.*

Also mortality could not be quantified, as small month-to-month variations need not be due to mortality, but can be caused by incidental aggregations of individuals (Defeo and McLachlan, 2005). Disappearance of entire adult cohorts might, however, indicate mortality more truly. This seems to occur from June to July, when the disappearance of adults causes biomass to drop. The described bivoltine life cycle of the species, with 2 generations per year (as also found by Salvat, 1967; Fish and Preece, 1970a), explains two peaks in adult mortality, as observed in disappearance of adult cohorts in February and July. *Bathyporeia pilosa* is a highly tolerant species, resistant to different forms of environmental stress (Mettam, 1989), while *B. sarsi*'s stress tolerance can be assumed lower (Vader, 1965). Nicolaisen and Kanneworff (1983) mentioned a discrete episode of high mortality in a population from Denmark during the reproductive season, from May to September, most likely occurring in both juveniles and adults. Winter mortality until March and summer mortality at least seem to confirm the existence of two generations.

SECONDARY PRODUCTION

Considering P/B ratios per beach, *Bathyporeia pilosa* showed clear differences between beaches, with eastern beaches delivering ratios half those of western ones (see Tab. 1). To assess the value of the studied beaches for higher trophic levels, total macrobenthic biomass should be considered, besides other factors, e.g. levels of disturbance for wading birds as potential predators. In any case, the eastern beaches showed both low abundance and low P/B ratios for this species. Higher P/B ratios as found on the western beaches are comparable to those found by Maranhão *et al.* (2001) for *Echinogammarus marinus,* (from 4.14 to 6.56). In contrast, P/B ratios of *B.sarsi* were highly similar for all beaches. Thus, intertidal *B. pilosa* can, if present, provide a highly abundant food source for any predator able to manage itself in the upper parts of the intertidal zone. In second place, also *B. sarsi* is a fairly abundant food source, but it is more widespread across the shore and occupies a part of the intertidal zone that might be easier to reach for submerged predators. *Bathyporeia* P/B ratios are in general much higher than those of the syntopic polychaete *Scolelepis squamata* (reaching 2.40 / year) (Speybroeck *et al.,* 2007).

HABITAT (1) – CROSS-SHORE ZONATION

Bathyporeia pilosa was always found higher up on the beach than *B. sarsi*, in confirmation of earlier work (e.g. Salvat, 1962, 1964; Degraer *et al*., 2003a). Peak abundances of *B. pilosa* occurred always above 4 m above MLLWS, while modal density of *Bathyporeia sarsi* was found between 3 and 4 m above MLLWS. Our results demonstrate differences in the optimal elevation for both species, without strict separation of both: low numbers of both species can frequently be found together in a single sample, resulting in a bimodal combined *Bathyporeia* distribution. No intraspecific segregation based on sex or age was observed for either species, and neither did Nicolaisen and Kanneworff (1983).

Differences in the elevation of the modal density (along each transect) of *B. pilosa* were observed between the western transects. It is unclear whether the higher variability in beach morphology at the Ijzermonding beach might cause changes in microhabitat conditions, influencing the presence of *B. pilosa* and *B. sarsi*, as suggested for the former by Khayrallah and Jones (1980b).

Judging from the temporal variability in zonation pattern and elevation of modal density, no significant seasonal migration was observed for *B. pilosa*, while contrasting results have been obtained in the past (Salvat, 1967; Fish and Preece, 1970a; Persson, 1982). Most likely, habitat type can explain this, with Fish and Preece (1970a) investigating an estuarine population, while Persson (1982) worked at the Baltic Sea. Temperature, light intensity and length of day might trigger seasonal migration, somewhat complicating comparison between studies. Our intertidal sandy beach population seems to show a (poorly significant) more onshore presence from the end of summer until November, observed in the elevation of the modal density. Fish and Preece (1970a) found the same from April to October, but with animals being situated higher up on the beach in winter. Though generally confusing, differences in climate and hydrology might explain this. Stress by desiccation (mainly in summer) might be less immanent on Belgian beaches, whereas freezing in winter might urge animals to migrate to areas of longer submersion, buffered in temperature and less subjected to storms and heavy rainfall. Further, on beaches where runnels are present, highest numbers of *B. pilosa* but also *B. sarsi* have been observed within these runnels, retaining water throughout the tidal cycle (pers. obs.). This might possibly cause both seawards and landwards, or better 'runnelwards', migration in autumn.

On the other hand, *Bathyporeia sarsi* displayed a clear seawards shift of animals from January to March, comparable to findings of Nicolaisen and Kanneworff (1983) in the Baltic Sea and to what Persson (1982) described for *B. pilosa*. Again, animals were found higher up in summer.

The lack of intraspecific segregation of both species is in contrast to the size-segregation observed in the syntopic polychaete *Scolelepis squamata* (Speybroeck *et al.,* 2007).

HABITAT (2) – WIDTH OF THE OCCUPIED VERTICAL RANGE

Bathyporeia sarsi occupies a wider vertical, thus also cross-shore, range on the beach than *B. pilosa*. Due to lack of knowledge of the former species, explaining this is hard. Small spatial differences can be observed for *B. pilosa* between transects from Nieuwpoort and Ijzermonding. In *Bathyporeia sarsi*, more erratic, hard to explain variation through space and time could be observed and variation seemed to be due primarily to local fluctuations. Range width might be related to abundance, thus explaining a narrower range of *B. pilosa* at the Ijzermonding beach. Differences between eastern and western transects in *B. sarsi* might be due to established differences in median grain size and beach slope, causing harsher conditions on eastern transects and resulting in lower abundance and smaller vertical range width. No temporal variation was found, yet, in October 2004, the *B. pilosa* occupied zone is wider than that in October 2003, perhaps due to annual variation in temperature, wave energy, food supply and/or patchiness.

Interestingly, females occupied a wider range than males in both species, concurring Preece's (1970, 1971a) experimental results for *B. pilosa*, demonstrating higher stress tolerance of females towards extremes in temperature and salinity, even though Preece's results might have been hampered by shorter male life span. No experimental data on intraspecific variation of stress are available for *B. sarsi.* Furthermore, range width was higher in adults (being mainly females, as established earlier) than in juveniles. Combining sex and age analysis was not possible due to too small numbers remaining within each category.

Finally, it is striking that the species inhabiting the widest range (*B. sarsi*) shows the fewest evidence for intraspecific segregation within its occupied zone.

HABITAT (3) – MEDIAN GRAIN SIZE AT PEAK ABUNDANCE

Apparent differences between the two species in median grain size at stations of peak abundance were observed, as well as significant spatial differences in median grain size. All these cannot be considered independently from the differences in elevation of these abundances peaks. On one hand, a species living lower in the intertidal zone will of course live in a somewhat, finer sediment. On the other hand, both species occur lower on Ijzermonding transects than in Nieuwpoort transects. It is possible that they can live higher up in Nieuwpoort because of the finer sediment. Thus, intertidal zonation is related to both substrate characteristics and elevation.

Observed non-significant seasonal changes in grain size preference are most likely an indirect effect of seasonal migration, caused by climate and hydrology. Thus, elevation and median grain size are, once more, strongly related. To allow drawing relations between abundance and grain size, sampling of much more transects at specific elevations seems necessary. This fell, however, out of the scope of this study and an experimental approach, dealing with grain size preference of both species has been pursued (Speybroeck *et al.*, submitted). Available sands on the investigated beaches were largely situated well within mentioned ranges of tolerance for both species, although Vader (1965) stated *B. sarsi* to prefer somewhat coarser sands than *B. pilosa* and to be more tolerant regarding grain size. Still, differences in exposition as mentioned by Nicolaisen and Kanneworff (1969) seem more explanatory than strict grain size responses.

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