



# Surf Zone Hyperbenthos of Belgian Sandy Beaches: Seasonal Patterns

B. Beyst<sup>a,c</sup>, D. Buysse<sup>a</sup>, A. Dewicke<sup>a</sup> and J. Mees<sup>b</sup>



Vlaams Instituut voor de Zee  
 Flanders Marine Institute

<sup>a</sup>Marine Biology Section, Biology Department, Ghent University, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

<sup>b</sup>Flanders Marine Institute (VLIZ), Victoriaalaan 3, B-8400 Oostende, Belgium

Received 25 October 2000 and accepted in revised form 17 April 2001

Since surf zone hyperbenthos, although highly important in local food webs, has often been neglected and very little information is available, a survey of the Belgian sandy beaches was carried out from May 1996 until July 1997. Monthly samples were taken to give a complete record of hyperbenthic organisms occurring in the surf zone of Belgian sandy beaches and to evaluate the intensity by which this surf zone is used. In total 172 species were recorded. The number of species occurring in the surf zone is comparable to that of adjacent areas. As well as true hyperbenthic species, endobenthic and planktonic organisms were sampled. More than 75% of the average total sample composition consisted of mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei* (holohyperbenthos). Apart from several resident species, active and passive seasonal migration towards the surf zone by a number of species is suggested. A large number of sporadic species adds to the composition of surf zone hyperbenthos. Within the merohyperbenthos, postlarval decapods and fish were the dominant organisms. During the year three recruitment peaks were observed. Average densities per month exceeded 1500 ind. 100 m<sup>-2</sup>. Yearly biomass averages ranged from 300 to over 3000 mg ADW 100 m<sup>-2</sup>. Densities of the common species are slightly higher in the surf zone than in other habitats, emphasising the importance of the area. Besides a possible nursery function, the surf zone may also be used as a transient area between different habitats. Finally, the influence of several abiotic factors on the hyperbenthic assemblages was evaluated. The main structuring variables determining the occurrence of most of the organisms are water temperature and hydrodynamic factors such as wave height and turbidity. The influence of wave height seems to be two-fold: several good swimmers such as mysids and some fish species are suggested to be able to actively avoid severe wave conditions, whereas other, more planktonic organisms, are passively transported towards the area if wave height increases. © 2001 Academic Press

**Keywords:** surf zone; nursery; hyperbenthos; Mysidacea; ichthyoplankton; North Sea

## Introduction

A surf zone is defined here as the moving water envelope from the water up-rush on the shore to the most seaward breaker. The hyperbenthos is the association of small animals living in the water layer close to the sea bed (Mees & Jones, 1997). Studies on these small organisms within the surf zones are very scarce. While several taxonomic papers describe species collected on sandy beaches, few of them sampled the surf zone or include ecological notes (reviewed by McLachlan, 1983). Moreover, ecological studies rarely describe whole assemblages, they are mostly restricted to the ecology of one species (e.g. San Vicente & Sorbe, 1993a; Hanamura, 1999) or one taxonomic group (e.g. mysids: Wooldridge, 1983, 1989; fish larvae: Kinoshita, 1993; Harris & Cyrus, 1996). Research areas are very scattered; except for the Mediterranean (e.g. Moran, 1972; Macquart-

Moulin, 1977; San Vicente & Sorbe, 1999), the only surf zone studies in European waters are those in the United Kingdom (Colman & Segrove, 1955; Fincham, 1970), the Bay of Biscay (San Vicente & Sorbe, 1993a) and the Belgian coast (Lock *et al.*, 1999). With the exception of San Vicente and Sorbe (1993a), none of these report temporal data.

The hyperbenthos of the surf zone seems to be characterised by high biomass (McLachlan, 1983). For example, *Schistomysis parkeri* in the Bay of Biscay, was found to have an estimated annual production of 52.6 mg m<sup>-2</sup>, with a corresponding production/biomass ratio (P/B) of 9.7 (San Vicente & Sorbe, 1993a). Since most fish species occurring within the surf zone of sandy beaches show a high degree of opportunism in feeding, all feeding types may predate heavily on zooplankton and larger schooling crustaceans when they are locally abundant (McLachlan, 1983), as shown for several gobies (*Pomatoschistus* spp.), Nilsson's pipefish (*Syngnathus rostellatus*) and several juvenile flatfish species (Cattrijsse *et al.*, 1993;

<sup>c</sup>Corresponding author. E-mail: bregje.beyst@rug.ac.be

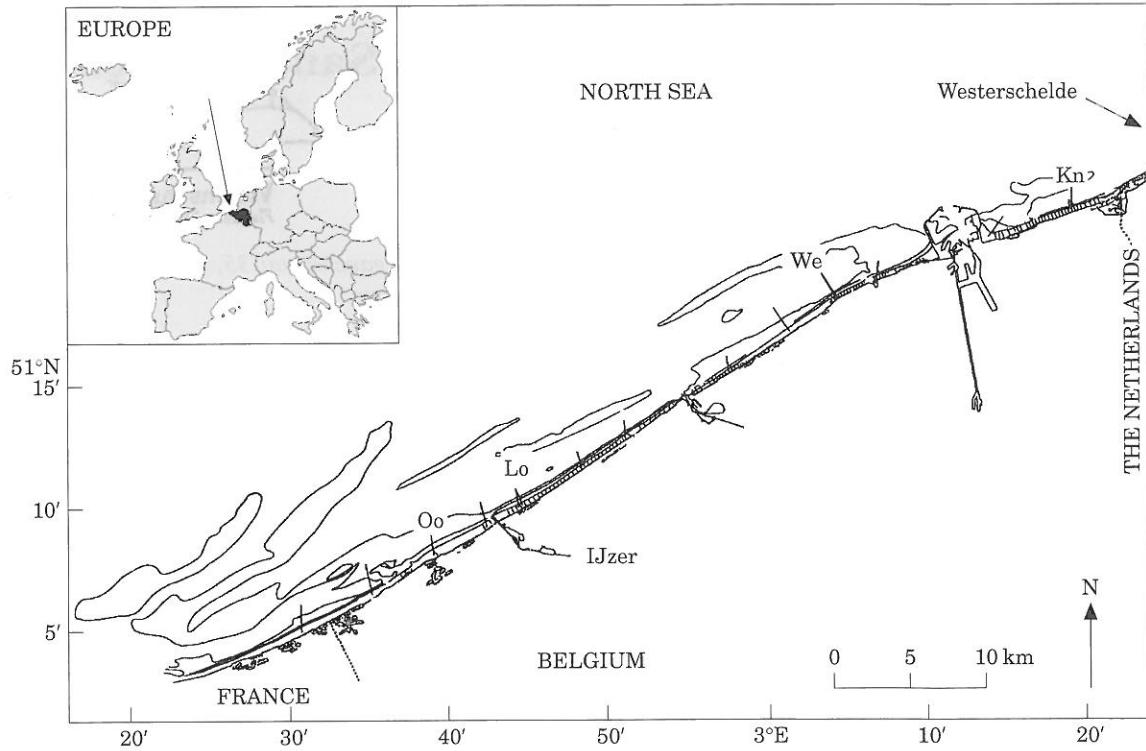


FIGURE 1. Study area with indication of sampling sites. (Oo=Oostduinkerke, Lo=Lombardsijde, We=Wenduine, Kn=Knokke). ..... border; dunes; groins.

Hamerlynck *et al.*, 1990, 1993, Hamerlynck & Hostens, 1993; Beyst *et al.*, 1999a). Hyperbenthic animals are therefore an important (and often neglected) link within the local food webs (McLachlan, 1983). Knowledge about the distribution patterns, densities and biomass of the hyperbenthos is of major importance in order to understand the functioning and natural variability of surf zone ecosystems.

In order to enhance knowledge of the European surf zone ecosystems, the purpose of this study is primarily to give a complete record of hyperbenthic organisms occurring in the surf zone of Belgian sandy beaches, secondly to evaluate the intensity by which this surf zone is used, by studying the temporal patterns within the assemblages and finally to identify what abiotic factors are responsible for structuring these hyperbenthic assemblages.

## Materials and methods

### Study area

The study area comprises the surf zone of four sandy beaches of the Belgian coast (Figure 1) in the most southern part of the North Sea. The Belgian coastline

is 67 km long and is characterised by built dykes which are interrupted by dune areas, and with groins on most of the beaches. In some parts these groins are less than 300 m apart, while elsewhere they are absent for several kilometres. Three major harbours (Zeebrugge, Oostende and Nieuwpoort) are situated in the eastern, middle and western part of the coast and a smaller harbour is present at Blankenberge. The mouth of the IJzer Estuary is situated in the western part, while just over the Belgian-Dutch border the large Westerschelde Estuary opens. A strong semi-diurnal tidal regime and a net tidal current running north-east parallel to the coastline are characteristic for the area. According to the morphodynamic classification scheme of Masselink and Short (1993) all beaches studied were low-tide bar/rip beaches (LTBR). These beaches are characterised by a relatively steep upper intertidal zone, but fronted by a low gradient mid-intertidal zone, possibly with swash bars, and then bar and rip morphology around low tide level. The main characteristics of each site are given by Table 1. In general, only the slope of the intertidal area is measured. Since the morphodynamic features may however change severely beneath the low water line and these changes are more likely to characterise the shallow surf zone habitat, slopes of the shallow

TABLE 1. Study site characteristics (D: low tide beach sediment size averaged over whole study period ( $\mu\text{m}$ ); MSR: mean spring tide range (m); SE: standard error; IT: intertidal; ST: first 300 m of shallow subtidal)

	D $\pm$ SE ( $\mu\text{m}$ )	MSR (m)	Beach width (m)	Slope IT	Slope ST	Groins	Bar/rip IT	Bar/rip ST
Oostduinkerke (Oo)	186 $\pm$ 1	4.92	390	1:128	1:210		+	+
Lombardsijde (Lo)	187 $\pm$ 1	4.78	180	1:55	1:108	+	+	+
Wenduine (We)	263 $\pm$ 5	4.45	195	1:49	1:62	+	+	+
Knokke (Kn)	344 $\pm$ 11	4.28	174	1:57	1:41	+	+	

subtidal (first 300 m after MLLWS, <8 m depth) are also reported.

### Sampling

Monthly samples were taken from May 1996 until July 1997. In July and November 1996, persistent bad weather conditions prevented sampling in all stations. This was also the case in January 1997 for Lombardsijde (Lo), in February 1997 for Wenduine (We) and Knokke (Kn) and in April 1997 for We. In Lo, one additional sample was taken in April and 1 in May 1997. All samples were taken with a hyperbenthic sledge at daytime neap tide and ebb. The sledge was especially designed for this study. The metal frame measured 100  $\times$  40 cm and it was equipped with two nets, one above the other. Both nets were 3 m long, and (at the mouth) 20 cm high, with a mesh size of 1  $\times$  1 mm. The sledge was pulled by two persons in the surf zone parallel to the coastline at a depth of approximately 1 m. One haul lasted approximately 20 (We and Kn) or 30 (Oo and Lo) minutes and covered a distance of 450–500 m. When groins were present, the sledge was lifted over the obstacle. Since the sledge remained in motion during this process, sampling efficiency was not affected. The catch was preserved in a 8% formalin solution.

### Environmental variables

Portable conductivity and oximeters (WTW) were used for measurements of water temperature and salinity and oxygen content, respectively. Turbidity was measured with a portable microprocessor turbidity meter (HANNA). For the analyses of pigments (chlorophyll *a* and *c* and fucoxanthine) and particulate organic carbon (POC), water samples were passed through Whatman GF/F filters. For the pigments, an immediate extraction with acetone (90%) was performed prior to chromatography, with a Gilson high-performance liquid chromatography chain using the method of Mantoura and Llewellyn (1983). For

POC an automatic CN-analyzer (Carlo Erba) was used. The concentrations of nitrate plus nitrite, phosphate, ammonia and silicate were measured through an automatic chain (SAN<sup>plus</sup> segmented flow analyzer, SKALAR). Median grain size was determined with a Coulter Counter LS particle size analyzer. For the measurement of organic matter within the sediment (OM), samples were dried at 110 °C for 2 h and subsequently burned at 540 °C for 2 h. Hydrodynamic variables (wave height, wind speed and direction) at the time of sampling were obtained from the Coastal Waterways Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community). Wave height is expressed as H33: the average of the 33% highest waves occurring during a period of 15 min. Wind speed is given as the average speed and wind direction as the scalar average of the measured directions, over a period of 10 min.

### Data treatment

In the laboratory, all hyperbenthic animals were identified and counted. Identification was not always possible to the lowest level. Several organisms were damaged, and the available identification keys were not always sufficient (e.g. in case of metamorphosing individuals such as some clupeids, or of confusing species descriptions such as for *Bathyporeia* species). In some cases the preservation method caused contraction of structures, prohibiting an accurate identification (e.g. *Bougainvillia* species). Different developmental stages of decapods (zoeae, megalopae, postlarvae and juveniles) were treated as separate 'species' since they have a different ecology, and a distinction was made between holo- and merohyperbenthos. Holohyperbenthos is defined as animals spending variable periods of their adult life in the hyperbenthos, whereas merohyperbenthos is applied to those that spend only part of their early life history in the hyperbenthos and recruit to the nekton, epibenthos or endobenthos (Hamerlynck & Mees, 1991). Total biomass was calculated for the samples

TABLE 2. Selected and excluded environmental variables together with an indication (\*) of their correlation (Spearman Rank correlation coefficient, only shown if  $P < 0.05$  and  $r > 0.5$ ), (IT: intertidal; ST: shallow subtidal)

Selected variables	Excluded variables											
	Water temperature ST	Oxygen content	Salinity	Wind direction	Current speed	POC	Organic matter	Oxidized nitrogen-N	Phosphate-P	Silicate	Chlorophyll c	Fucoxanthine
Water temperature IT		*	*	*	*	*	*	*	*	*	*	*
Chlorophyll <i>a</i>	*										*	*
Median grain size			*	*								
Turbidity												
Wave height		*										
Wind speed												
Ammonia-N						*	*	*	*			

of one station at the west (Oo) and one at the east coast (Kn). Assigned ashfree dry weight (ADW) values, independent of the animals' length, were used to estimate biomasses of cnidarians, ctenophores and small crustaceans. Of all other animals, total or standard lengths were measured and their ADW was estimated from length-ADW regressions. Assigned ADW values and length-ADW regressions were derived from Mees *et al.* (1994); Beyst *et al.* (1999a) and Dewicke and Mees (unpublished data). For this paper the contents of both nets were combined and treated as one sample. Densities and biomasses are expressed as number of individuals and mg ADW  $100 \text{ m}^{-2}$  respectively. Averages are reported  $\pm$  their standard error (SE). Since net efficiency is unknown, all density and biomass values are considered as minimum estimates (Mees & Hamerlynck, 1992). Diversity was calculated and expressed as Hill numbers of the order of 0, 1, 2 and  $+\infty$  (Hill, 1973). The indices differ in their tendency to include or ignore the relatively rarer species: the impact of dominance increases and the influence of species richness decreases with an increasing order of the diversity number.

Spatio-temporal patterns were examined with the following multivariate statistical techniques: Correspondence Analysis (CA), (Ter Braak, 1986, 1988), Two-Way INDicator SPecies ANalysis (TWINSPAN, Hill, 1979) and cluster analysis using group average sorting and the Bray-Curtis dissimilarity index (Bray & Curtis, 1957). Empty samples were excluded from the analyses. A fourth root transformation (Field *et al.*, 1982) was performed on the abundance data prior to the analyses. Differences between the obtained groups

of samples were assessed using the non-parametric Kruskal-Wallis Test. The influence of environmental factors on temporal variations in total density was examined using multiple stepwise regression analyses using an adjusted multiple coefficient of determination ( $R_{\text{adj}}^2$ ) as an index of fit (Sokal & Rohlf, 1981). If variables were significantly correlated (Spearman Rank correlations,  $P < 0.05$ ), only one of them was retained for further analyses. This selection was done after performing preliminary Canonical Correspondence Analyses (CCA) with forward selection, to determine which environmental variables in each group explained the greatest amount of variance in the hyperbenthic data (Hall & Smol, 1992). Since wind direction is a circular variable, it was transformed to a linear scale by using the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore (Clark *et al.*, 1996). Offshore winds at each site were allocated the greatest values (+1), onshore winds the lowest (-1), while winds with a cross-shore component from either direction received scores between +0.9 and -0.9. For wind speed and wave height values are expressed into arbitrary classes ranging from 0 to 4, with class 4 indicating values of 20 knots and 100 cm, respectively.

## Results

### *Environmental variables*

The selected and excluded environmental variables after evaluation of their correlation coefficients and forward selection, are given by Table 2. Median grain size differed substantially between the four stations (Table 1): while the two west coast stations (Oo and



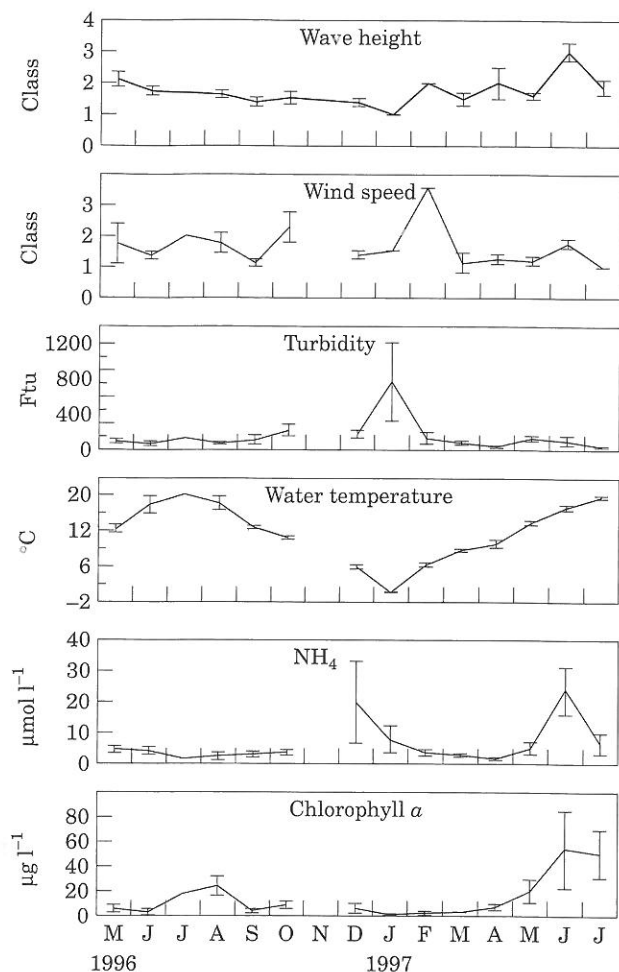


FIGURE 2. Monthly variation of the selected environmental variables (see text) (IT: intertidal).

Lo) were characterised by fine sediments (median grain size between 125 and 250  $\mu\text{m}$ ), the two east coast stations (We and Kn) consisted of medium sands (median grain size between 250 and 500  $\mu\text{m}$ ). The monthly variation of the other selected variables is shown in Figure 2. The winter of 1996–1997 was extremely cold. In January 1997 surf zone temperatures were below zero and ice covered the whole beach area. Of several variables maximum values were reported during winter (average of four stations): wind speed (15–20 knots), turbidity (770  $\pm$  440 ftu), and ammonia (29  $\pm$  19  $\mu\text{mol l}^{-1}$ ). The latter peak again during early summer of 1997 (34  $\pm$  11  $\mu\text{mol l}^{-1}$ ), together with wave height ( $\pm$  75 cm), surf zone water temperature (21.3  $\pm$  0.4  $^{\circ}\text{C}$ ) and chlorophyll *a* (54  $\pm$  31  $\mu\text{g l}^{-1}$ ).

#### Community composition

In total 172 functional taxa were found (Table 3): 104 were holo- and 68 were merohyperbenthic species,

all belonging to 17 higher taxonomical levels. More than 75% of the average total sample composition were mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei* (holohyperbenthos). Other common groups were early life stages of caridean shrimps, brachyuran crabs and fish, small cnidarians, isopods and amphipods (>1%). Of the merohyperbenthos, postlarval decapods such as the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon*, and postlarval fish such as gobies *Pomatoschistus* species (a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*) and clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*), were the dominant organisms.

Average total densities of the four stations per month exceeded 1500 ind. 100  $\text{m}^{-2}$ . Maxima were found in May 1997 (3430  $\pm$  1760 ind. 100  $\text{m}^{-2}$ ) [Figure 3(a)]. In January, several samples yielded no specimens. The average total density over all months (yearly average) of the holohyperbenthos was higher than that of the merohyperbenthos; 920  $\pm$  220 ind. 100  $\text{m}^{-2}$  compared to 110  $\pm$  40 ind. 100  $\text{m}^{-2}$ . Only in Kn yearly average total densities were lower than 1000 ind. 100  $\text{m}^{-2}$  (280  $\pm$  120 ind. 100  $\text{m}^{-2}$ ). Yearly averages of the total biomass were much higher at the west coast (Oo: 3020  $\pm$  1040 mg ADW 100  $\text{m}^{-2}$ ) than at the east coast (Kn: 340  $\pm$  80 mg ADW 100  $\text{m}^{-2}$ ) [Figure 3(b)]. In both stations maxima were recorded in spring (up to  $\pm$  15 000 mg ADW 100  $\text{m}^{-2}$  at Oo and  $\pm$  820 mg ADW 100  $\text{m}^{-2}$  at Kn) and a second, but lower peak, was reported in September. High biomass in spring was mainly due to mysids (Oo) and isopods (Kn), whereas the second peak could be attributed to fish. Finally, multivariate statistical techniques (TWINSPAN and CA), indicated that seasonal patterns dominated spatial patterns (not figured). The latter will therefore not be discussed further in this paper.

#### Seasonal occurrence: holohyperbenthos

To investigate the seasonal occurrence of the different species, a distinction was made between holo- and merohyperbenthic organisms. Table 4 gives the average monthly density for the holohyperbenthic species together with an indication of their resident status within the surf zone. Species were classified as 'residents' if they were present in the catches more or less throughout the year (Clark *et al.*, 1996). 'Migrants' are species which only occurred during certain periods in the surf zone or during the same month in the subsequent years. Other species were classified as 'sporadics'. Fifteen resident species were reported

TABLE 3. Taxa list with indication of stage and type

Taxon	Stage	Type	Taxon	Stage	Type	Taxon	Stage	Type	Taxon	Stage	Type
Cnidaria											
<i>Cnidaria species</i>											
<i>Sarsia tubulosa</i>											
<i>Phialidium hemisphaericum</i>											
<i>Phialella quadrata</i>											
<i>Margelopsis haeckeli</i>											
<i>Eutomina indicans</i>											
<i>Euchelota maculata</i>											
<i>Bougainvillia species</i>											
<i>Aequorea forskalea</i>											
Ctenophora											
<i>Beroe gracilis</i>											
<i>Pleurobrachia pileus</i>											
Polychaeta											
<i>Polychaeta species</i>											
<i>Sponidae species</i>											
Phyllozoa											
<i>Phyllozoa species</i>											
Polynoidae											
<i>Polynoidae species</i>											
<i>Eulalia pusillus</i>											
<i>Spio species</i>											
<i>Spiophanes bombyx</i>											
<i>Scolecopsis squamata</i>											
<i>Typosyllis species</i>											
<i>Lanice species</i>											
<i>Lanice conchilega</i>											
<i>Nephtys cirrosa</i>											
<i>Nereis species</i>											
<i>Polydora species</i>											
<i>Eteone species</i>											
<i>Ophelia rathkei</i>											
<i>Anatides species</i>											
Copepoda											
<i>Calanus helgolandicus</i>											
<i>Centropages hamatus</i>											
<i>Anomalocera patersoni</i>											
<i>Temora longicornis</i>											
<i>Euphausiacea</i>											
<i>Nyctiphanes couchi</i>											
Caridea											
<i>Crangon crangon</i>											
<i>Crangonidae species</i>											
<i>Hippolyte varians</i>											
<i>Philocheras trispinosus</i>											
<i>Palaemon cf. longirostris</i>											
<i>Palaemon species 1</i>											
<i>Palaemon species 2</i>											
<i>Palaemon species</i>											
Processidae											
<i>Anomura</i>											
<i>Pagurus bernhardus</i>											
<i>Pagurus bernhardus</i>											
<i>Diogenes pugilator</i>											
<i>Paguridae species</i>											
<i>Achaetus cranchii</i>											
<i>Achaetus cranchii</i>											
Majidae											
<i>Majidae species</i>											
<i>Porcellana platycheles</i>											
<i>Porcellana species</i>											
<i>Psidita longicornis</i>											
<i>Psidita species 1</i>											
Brachyura											
<i>Brachyura species</i>											
<i>Brachyura species</i>											
<i>Brachyura species</i>											
<i>Carcinus maenas</i>											
<i>Carcinus maenas</i>											
<i>Carcinus maenas</i>											
<i>Copys casvelaunus</i>											
<i>Liocarcinus holzatus</i>											
<i>Liocarcinus holzatus</i>											
<i>Liocarcinus holzatus</i>											
<i>Portunus latipes</i>											
<i>Portunus latipes</i>											
<i>Pilumnus hirtellus</i>											
Ebaltia											
<i>Ebaltia tuberosa</i>											
<i>Necora puber</i>											
Mysidacea											
<i>Anchitana agilis</i>											
<i>Gastrosaccus spinifer</i>											
<i>Mesopodopsis slabberi</i>											
<i>Neomysis integer</i>											
<i>Praunus flexuosus</i>											
<i>Schistomysis kerwilli</i>											
<i>Schistomysis spiritus</i>											
<i>Mysidopsis gibbosa</i>											
<i>Siriella clausii</i>											
<i>Siriella jaltensis</i>											
<i>Siriella armata</i>											
Mysidacea											
<i>Cumacea</i>											
<i>Gumopsis goodsi</i>											
<i>Diastylis bradyi</i>											
<i>Diastylis rathkei</i>											
<i>Diastylis laevis</i>											
Isopoda											
<i>Eurydice affinis</i>											
<i>Eurydice pulchra</i>											
<i>Idotea granulosa</i>											
<i>Idotea linearis</i>											
<i>Idotea pelagica</i>											
<i>Idotea baltica</i>											
<i>Idotea metallica</i>											
<i>Idotea emarginata</i>											
<i>Idotea species</i>											
<i>Jaera nordmanni</i>											
Pycnogonida											
<i>Nymphon rubrum</i>											
<i>Nymphon brevispinis</i>											
<i>Nymphon species</i>											
<i>Callipallene brevispinis</i>											
<i>Phoxichilidium tubulariae</i>											
Amphipoda											
<i>Paranibis typicus</i>											
<i>Caprella linearis</i>											
<i>Phiticea marina</i>											
<i>Amphipoda species</i>											
<i>Atylus falcatus</i>											
<i>Atylus swammerdami</i>											
<i>Bathyporeia sarsi</i>											
<i>Bathyporeia pilosa</i>											
<i>Bathyporeia species</i>											
<i>Calliopius larvisculus</i>											
<i>Corophium achenisicum</i>											
<i>Corophium insidiosum</i>											
<i>Corophium species</i>											
<i>Gammaridae species</i>											
<i>Gammarus crinicornis</i>											
<i>Gammarus insensibilis</i>											
<i>Gammarus locusta</i>											
<i>Gammarus zaddachi</i>											
<i>Hausiorius arenarius</i>											
<i>Ischyroceridae species</i>											
<i>Jassa falcata</i>											
<i>Jassa species</i>											
<i>Pontocrates altamarinus</i>											
<i>Pontocrates arenarius</i>											
<i>Stenothoe marina</i>											
<i>Urothoe poseidonis</i>											
<i>Urothoe marina</i>											
<i>Hyale nilsoni</i>											
<i>Melita species 1</i>											
<i>Melita palmata</i>											
<i>Melita dentata</i>											
<i>Melita hergensis</i>											
<i>Melita obtusata</i>											
<i>Melita species</i>											
<i>Orchomeene nana</i>											

(H: holohyperbenthic; M: merohyperbenthic; la: larva; pl: postlarva; juv: juvenile).

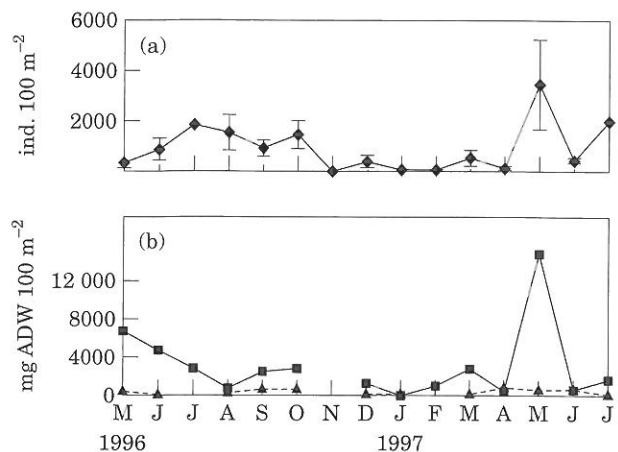


FIGURE 3. Average total hyperbenthic density ( $\pm$  SE) (a) and total biomass (b) per month. (■) Oo; (▲) Kn. — west (Oo); ---- east (Kn).

(Cnidaria species not taken into account since they were not identified to a lower taxonomical level); many of them were absent during January and February. Only 10 species could be classified as migrants. Most of them were present in the surf zone from May until June (July), only a few species occurred later in the year (e.g. *Euceilota maculata* from June to January) or appeared earlier (e.g. *Calanus helgolandicus* from October to May). For 13 other (possibly migratory) species the patterns were less obvious (indicated as S/M in Table 4) and densities were low (monthly densities  $\leq 5$  ind. 100 m<sup>-2</sup>). The remaining majority showed no clear occurrence patterns and therefore were classified as sporadic.

Figure 4 shows the seasonal appearance of the three most common species in more detail. For the clarity of the figures, the indication of a trend line was preferred above monthly averages. There was a clear seasonal pattern of abundance. *Schistomysis spiritus* reached its maximum abundance in May, *M. slabberi* in July–September, and finally *S. kervillei* in October–December. The first two species were virtually absent in the surf zone during the winter months, whereas the lowest densities of the latter were observed during spring and summer.

#### Seasonal occurrence: merohyperbenthos

Table 5 gives the seasonal occurrence of the merohyperbenthic species. Postlarvae and zoeae of the common shrimp and gobies occurred during most months, whereas a clear seasonal pattern could be observed for the other species. Multivariate analyses (only TWINSPAN depicted, Figure 5) revealed the presence of three major recruitment periods into the

surf zone. First, the summer-autumn samples were separated (TWIN1) and secondly a distinction was made between spring (TWIN2) and winter (TWIN3). Misclassified and borderline samples were excluded from further analyses (six in total).

Average total densities and number of species ( $N_0$ ) were significantly different between the TWIN groups (Kruskal–Wallis Test,  $P < 0.05$ ) [Figures 6(a and b)]. Total density was highest in spring ( $220 \pm 50$  ind. 100 m<sup>-2</sup>) and lowest during winter ( $20 \pm 6$  ind. 100 m<sup>-2</sup>). On average, more than 12 species per sample were found between spring and autumn (the total number of species caught during this period exceeded 40) compared to  $6 \pm 1$  species in the winter samples (total number 23). Also the relative species composition of the three TWIN groups differed substantially [Figure 6(c), depicted species that represented at least 5% of one of the groups], the evenness being lowest during spring. Densities of all these species (except zoeae of the common shrimp and postlarvae of clupeids) differed significantly between the three TWIN groups (Kruskal–Wallis Test,  $P < 0.05$ ).

Figures 7(a,b) (fish) & 7(c) (decapods) show the seasonal appearance of the most common species in more detail. Postlarvae of plaice *Pleuronectes platessa* appeared first in February–March [mean standard length (SL) of  $\pm 12$  mm], followed by postlarval flounder *Pleuronectes flesus* in April–May (mean SL  $\pm 7$  mm) and clupeid larvae in May–June (mean SL  $\pm 30$  mm) [Figure 7(a)]. Maximal densities of these three species were 7, 40 and 240 ind. 100 m<sup>-2</sup> respectively. Postlarval gobies became more abundant between June and August. Nilsson's pipefish *Syngnathus rostellatus* mainly occurred from August until October [Figure 7(b)]. The latter two species were found at maximal densities of 210 and 40 ind. 100 m<sup>-2</sup> and mean lengths of 13 and 79 mm SL respectively. Fish eggs were found commonly during March and April (maximum of 40 ind. 100 m<sup>-2</sup>). Zoeae of the common shrimp first appeared in March and were still very abundant in May, while postlarvae of the same species were abundant from May–July (maxima of 40 and 120 ind. 100 m<sup>-2</sup> respectively) [Figure 7(c)]. Megalopae of the shore crab reached their maximum densities in June (620 ind. 100 m<sup>-2</sup>).

#### Influencing factors

The influence of the environmental variables on the total density, the total density per taxonomic group and the individual densities of the three main species was examined using stepwise multiple regression

TABLE 5. Average merohyperbenthic density of the four stations per month (ind. 100 m<sup>-2</sup>), species sorted by seasonal occurrence

Taxon	Stage	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
<i>Crangon crangon</i>	pl	***	***	***	***	***	**	—	*	*	*	**	**	***	**	*
Crangonidae species	zoa	**	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Pomatoschistus</i> species	pl	***	***	***	***	***	*	—	*	*	*	*	*	*	*	***
<i>Ammodytes tobianus</i>	pl	*	*	*	*	*	*	—	*	*	*	*	*	*	*	*
<i>Ammodytes tobianus</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Anguilla anguilla</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Pleuronectes platessa</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Trisopterus minutus</i>	pl	**	*	*	*	*	*	—	—	**	**	**	**	*	*	*
Pisces species	eggs	**	*	*	*	*	*	—	—	**	**	**	**	*	*	*
<i>Hippolyte varians</i>	zoa	*	**	*	*	*	*	—	—	*	*	*	*	**	**	*
Brachyura species	juv	*	**	*	*	*	*	—	—	*	*	*	*	**	*	*
<i>Carcinus maenas</i>	juv	*	**	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Liocarcinus holsatus</i>	zoa	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
Opisthobranchia species	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
Bivalvia species	spat	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Ophiura</i> species	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Asterias rubens</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Clupea harengus</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
Clupeidae species	pl	***	**	**	*	*	*	—	*	**	**	**	**	**	*	*
<i>Pleuronectes flesus</i>	pl	**	**	**	*	*	*	—	—	**	**	**	**	**	*	*
<i>Solea solea</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Solea solea</i>	juv	*	*	*	**	*	**	—	—	*	*	*	*	*	*	*
<i>Syngnathus rostellatus</i>	juv	*	*	*	**	*	**	—	—	*	*	*	*	*	*	*
<i>Lamice</i> species	la	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Palaemon</i> species2	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Palaemon</i> species	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Pagurus bernhardus</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Pagurus bernhardus</i>	zoa	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
Paguridae species	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
Brachyura species	zoa	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Carcinus maenas</i>	pl	**	***	***	***	*	*	—	—	***	***	***	***	***	***	***
<i>Carcinus maenas</i>	zoa	**	**	**	**	*	*	—	—	**	**	**	**	**	**	**
<i>Corystes cassivelaunus</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Liocarcinus holsatus</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Liocarcinus holsatus</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Liocarcinus holsatus</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Necora puber</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Sepiola atlantica</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
Clupeidae species	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Myoxocephalus scorpius</i>	pl	*	*	*	*	*	*	—	*	*	*	*	*	*	*	*
<i>Pleuronectes platessa</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Buglossidium luteum</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Sprattus sprattus</i>	juv	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*
<i>Syngnathus rostellatus</i>	pl	*	*	*	*	*	*	—	—	*	*	*	*	*	*	*



TABLE 5. Continued

Taxon	Stage	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
<i>Dicentrarchus labrax</i>	pl	*	**	**	*										*	*
<i>Belone belone</i>	pl	*	*												*	*
<i>Agonus cataphractus</i>	juv	*				*	*									
<i>Hippolyte varians</i>	pl		*	*	*	*	*		*							
<i>Philocheilus trispinosus</i>	pl		*	*	*	*	*									
<i>Palaemon cf. longirostris</i>	pl		**	**	*	*	*								*	*
<i>Palaemon</i> species 1	pl		*	*	**	**	*								*	*
<i>Diogenes pugilator</i>	juv				*											*
<i>Diogenes pugilator</i>	pl		*	*	*											*
<i>Achaeus cranchii</i>	pl				*											
<i>Achaeus cranchii</i>	juv				*											
Majidae species	juv		*	*	*											*
<i>Porcellana platycheles</i>	pl		*	*	*											*
<i>Porcellana</i> species	pl		*	*	*											*
<i>Pisidia longicornis</i>	pl					*	*									*
<i>Pisidia</i> species 1	pl				*	*	*									*
<i>Brachyura</i> species	pl				*	*	*									*
<i>Portunus latipes</i>	juv		*	*	*	*	*									*
<i>Portunus latipes</i>	pl		*	*	*	*	*									*
<i>Pilumnus hirrellius</i>	pl		*	*	*	*	*									*
<i>Dicentrarchus labrax</i>	juv				*	*	*									*
<i>Ciliata mustela</i>	juv				*	*	*									*
Mugilidae species	pl				*	*	*		*							*
<i>Ebalia tuberosa</i>	pl				*	*	*					*			*	*
Pisces species	pl-juv				*	*	*					*			*	*

(—: no data; \*: <=5 ind. 100 m<sup>-2</sup>; \*\*: 5,1–20 ind. 100 m<sup>-2</sup>; \*\*\*: 20,1–100 ind. 100 m<sup>-2</sup>; \*\*\*\*: 100,1–500 ind. 100 m<sup>-2</sup>; \*\*\*\*\*: >500 ind. 100 m<sup>-2</sup>).

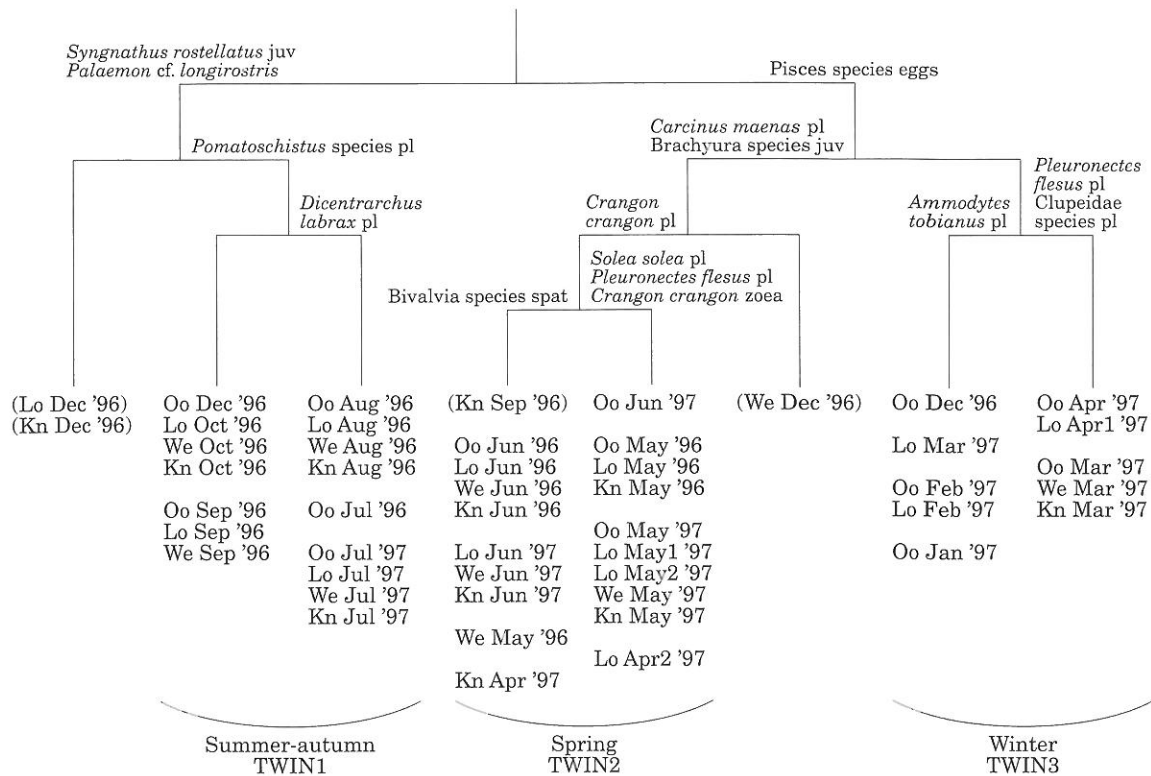


FIGURE 5. TWINSPAN dendrogram based on the presence/absence of the merohyperbenthic data (misclassified and borderline samples between brackets).

and Segrove (1955) reported much higher numbers during night catches, however these were more diverse than the day catches.

**Density & biomass.** In the North Sea, hyperbenthic studies have been restricted to the deeper subtidal area. Of these studies, yearly averages of both total density and biomass of the hyperbenthic community were given by Hamerlynck and Mees (1991) (Dutch Delta). Yearly averages of total density were also reported by Vallet and Dauvin (1999) for the western English Channel and Dewicke (unpublished data) for the shallow subtidal of the Belgian coast. Total densities were highest in the surf zone (present study), and only comparable to those of Dewicke (unpublished,  $>900$  ind.  $100\text{ m}^{-2}$ ). Also, total surf zone biomass was slightly higher than in the Dutch Delta (between 300–3000 and 200–1000 mg ADW  $100\text{ m}^{-2}$  respectively) (Hamerlynck & Mees, 1991). These results emphasise the importance of the shallow surf zone habitat at the Belgian coast for hyperbenthic animals.

Since a community approach has rarely been applied to hyperbenthic surf zone assemblages, there are very few other studies to compare with. Total hyperbenthic densities are of the same order of mag-

nitude as those found in most Mediterranean studies (San Vicente & Sorbe, 1993b, 1999; Munilla *et al.*, 1998). Much lower densities were found at a sandy beach of England (Colman & Segrove, 1955), the Atlantic (San Vicente & Sorbe, 1993b) and the Belgian coast (Lock *et al.*, 1999). The latter, however, was carried out during late autumn when densities were also low in the present study ( $420 \pm 210$  ind.  $100\text{ m}^{-2}$  in December). Next to sampling device, the differences in total densities between the different study areas might be linked to the degree of exposure: the Mediterranean beaches are the least exposed, the North Sea is semi-enclosed (Ducrottoy *et al.*, 2000) and can be considered as intermediate exposure. Moreover, the Belgian coast is characterised by an extensive sand bank system in front of the shore that might buffer wave action. Total hyperbenthic biomass is reported by Wooldridge (1983), but only per  $\text{m}^3$ .

#### Community composition: holohyperbenthos

**Resident status.** For the 15 resident species found in the surf zone, three different life styles can be observed. Most of them have a true hyperbenthic life style (e.g. most mysids, *Atylus swammerdami*), some

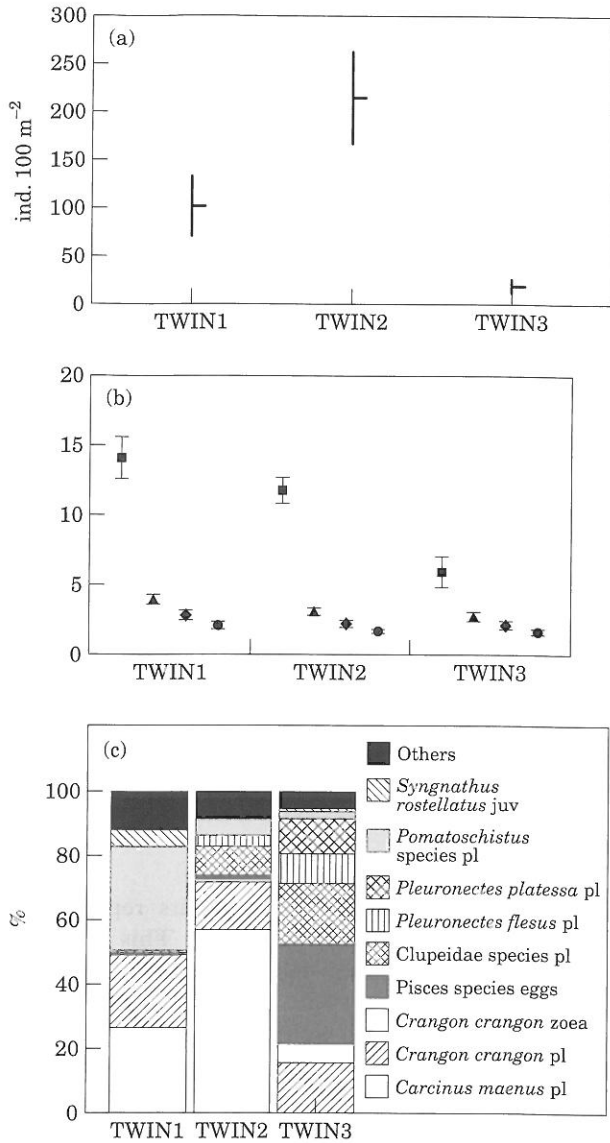


FIGURE 6. Average total density ( $\pm$  SE) (a), average Hill numbers ( $\pm$  SE) ( $\blacksquare$  N<sub>0</sub>;  $\blacktriangle$  N<sub>1</sub>;  $\blacklozenge$  N<sub>2</sub>;  $\bullet$  N<sub>inf</sub>) (b) and relative species composition (c) per TWIN group (mero-hyperbenthos).

are known to inhabit the underlying sand and make vertical excursions to the water column (e.g. *Eurydice pulchra*, *Bathyporeia* species) (Watkin, 1939, 1941; Colman & Segrove, 1955) and some are associated with drifting detritus (e.g. *Gammarus crinicornis*) (Jones & Naylor, 1967; Lincoln, 1979; Mauchline, 1980). Although indicated as residents, most of them were absent in January when temperatures dropped below 1 °C. Also during July and August when average temperatures were higher than 20 °C, several species were absent from the samples. Field and laboratory observations suggest that some mysids perform sea-

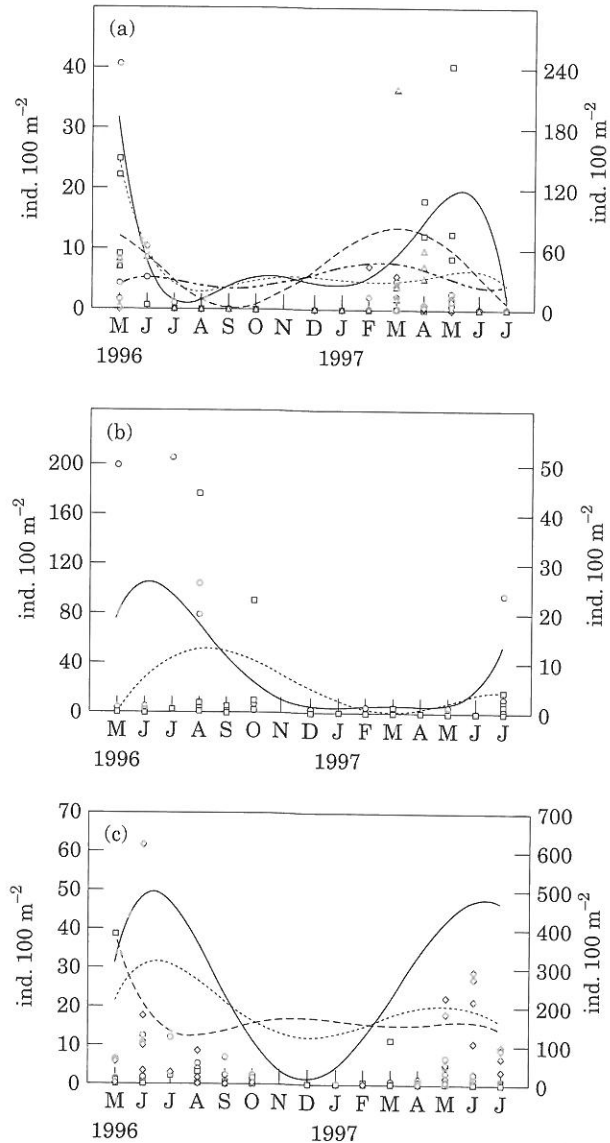


FIGURE 7. Seasonal occurrence of merohyperbenthos: (a) winter and spring recruitment of fish eggs and postlarvae ( $\square$  — Clupeidae species pl\*;  $\triangle$  — *Pleuronectes flesus* pl;  $\diamond$  — *Pleuronectes platessa* pl;  $\circ$  — fish eggs); (b) summer recruitment of postlarval fish ( $\circ$  — *Pomatoschistus* species pl\*;  $\square$  — *Syngnathus rostellatus* juv) and (c) zoeae and postlarval crustaceans ( $\circ$  — *Crangon crangon* pl;  $\square$  — *Crangon crangon* zoea;  $\diamond$  — *Carcinus maenas* pl\*) (\*: right axis) (scale on Y-axis is only for points, trend line is relative).

sonal migrations to avoid unfavourable temperatures (Tattersall & Tattersall, 1951; Hesthagen, 1973). Also endobenthic species show a decrease in density on the Belgian sandy beaches in winter (Degraer *et al.*, 1999). This decline is probably a result of population dynamics and/or shifts in the distribution up and down the beach (e.g. Jaramillo *et al.*, 1996).

TABLE 6. Results of the stepwise multiple regression analyses of the influence of seven selected variables on the halohyperbenthic total density, density per higher taxonomical group and individual density of the three dominant species. The adjusted  $R^2$  ( $R^2_{adj}$ ) is included for each combination of variables selected by the model

	Water temperature IT	Chlorophyll <i>a</i>	Median grain size	Turbidity	Wave height	Wind speed	Ammonia-N	$R^2_{adj}$
Total density	×				×			0.24
Cnidaria				×				0.27
Ctenophora			×					0.2
Polychaeta				×	×			0.17
Copepoda								—
Euphausiacea								—
Caridea								—
Mysidacea		×						0.11
Cumacea		×						0.11
Isopoda								—
Pycnogonida								—
Amphipoda		×						0.14
Chaetognatha						×		0.07
<i>Mesopodopsis slabberi</i>	×							0.13
<i>Schistomysis spiritus</i>		×						0.48
<i>Schistomysis kervillei</i>			×					0.07

Almost all species indicated as ‘migrants’ have a real planktonic (e.g. jellyfish, copepods), or endobenthic (e.g. most amphipods, polychaets) lifestyle. Planktonic organisms are likely passively transported toward the coast seasonally. Most of them occur in spring: e.g. the jellyfish *Margelopsis haeckeli* (June), which has not been recorded from the British coast but was found at the Belgian coast in June by Kramp (1930). Also *Eutonina indicans* and *Sarsia tubulosa*, were only caught in the surf zone between March and May. Other species are present at different times of the year: for example, *Eucheilota maculata* (June–January) and *Bougainvillia brittanica* (June–October). These results of seasonal occurrence are in general agreement with the current knowledge (Sanderson, 1930; Watson, 1930; Russel, 1953). Active migration may be plausible for species like the chaetognath *Sagitta elegans*. Of the endobenthic ‘migrants’, some species are mainly found during their breeding season. The polychaet *Eteone longa*, for example, leaves the sediment during this period (March–May) and is known to swim close to the water surface and eggs are deposited superficially on the sediment (Hartmann-Schröder, 1971). *Polydora ciliata* reproduces from April until September and is mainly found in the present study as a juvenile. In contrast, *Scolecopsis*

*squamata* was caught only outside its reproduction period (late spring, early summer). This species is known to swim during longer or shorter periods (Hartmann-Schröder, 1971).

Species that occurred sporadically may be common in deeper waters and accidentally caught in the surf zone or moved into the surf zone periodically (e.g. *Melita dentata*, Lincoln, 1979). Some of the sporadics are typical intertidal endobenthic organisms which only occur in low densities in the water column (e.g. *Cumopsis goodsiri*, *Eurydice affinis*, Jones & Naylor, 1967; Jones, 1976), some are true planktonic (e.g. *Anomalocera patersoni*, Mauchline, 1998) or associated with hydroids and/or algae (e.g. sea spiders, King, 1974, *Idotea metallica*, Naylor, 1957) and thus not likely to be caught with a hyperbenthic sledge in deeper waters. Organisms may be washed out of the nearby estuaries (e.g. *Gammarus zaddachi* is an estuarine species that prefers areas of very low salinity, Lincoln, 1979) or of the higher reaches of the beach (e.g. *Jaera nordmanni* is mainly found under stones in freshwater streams flowing down the shore, Naylor, 1972). Still, some species are restricted to the water column of shallow water or intertidal areas: *Idotea granulosa* (Naylor, 1955), *Corophium insidiosum*, *Corophium acherusicum* and *Hyale nilssoni* (Lincoln,

TABLE 7. Results of the stepwise multiple regression analyses of the influence of seven selected variables on the merohyperbenthic total density, density per higher taxonomical group and individual density of the nine dominant merohyperbenthic species. The adjusted  $R^2$  ( $R^2_{adj}$ ) is included for each combination of variables selected by the model

	Water temperature IT	Chlorophyll <i>a</i>	Median grain size	Turbidity	Wave height	Wind speed	Ammonia-N	$R^2_{adj}$
Total density	×							0.52
Polychaeta					×			0.11
Caridia	×							0.13
Anomura	×							0.07
Brachyura		×			×			0.32
Mollusca	×							0.09
Echinodermata								—
Pisces	×							0.07
<i>Pleuronectes flesus</i> pl								—
<i>Pleuronectes platessa</i> pl								—
<i>Pomatoschistus</i> species pl	×				×	×		0.34
<i>Syngnathus rostellatus</i> juv								—
Clupeidae species pl	×							0.08
Pisces eggs								—
<i>Crangon crangon</i> pl	×		×					0.3
<i>Crangon crangon</i> zoa	×							0.07
<i>Carcinus maenas</i> pl	×				×			0.36

1979). Most of all species found however, have a wide distribution area and can occur in the shallow surf zone as well as in the deeper subtidal region.

*Common species.* Of the most common species, *M. slabberi* is a very widely distributed mysid that is also dominant in the surf zone of sandy beaches in South Africa (Wooldridge, 1983). Of the other two mysids, only *S. spiritus* was reported in surf zone assemblages (Colman & Segrove, 1955). Although indicated as a brackish water species by Tattersall and Tattersall (1951), *M. slabberi* was much more abundant in the surf zone of the Belgian coast than in the adjacent estuarine areas (yearly averages of  $420 \pm 110$  ind.  $100 \text{ m}^{-2}$  in the surf and  $10 \pm 3$  ind.  $100 \text{ m}^{-2}$  in the Westerschelde Estuary, Mees *et al.*, 1993). Furthermore, in the adjacent shallow subtidal (5–10 m depth) it occurred mainly in winter but also in much lower densities (yearly average of  $20 \pm 8$  ind.  $100 \text{ m}^{-2}$ , Dewicke, unpublished data). These data and the absence of the species in the surf zone during the cold months, suggest migration towards deeper waters to avoid cold temperatures during winter. This migration pattern was also found by

Zatkutskiy (1970) and Van der Baan and Holthuis (1971) and is further confirmed by the selection of water temperature by multiple regression analysis as an important variable explaining variation in the monthly densities of this species. An offshore migration towards deeper water and/or migration into the estuary during winter is also suggested for both *Schistomysis* species, although other factors might be important (see further).

#### *Community composition: merohyperbenthos*

*Recruitment peaks and seasonal occurrence.* In general three recruitment peaks were observed in Belgian surf zones: winter, spring and summer. The winter is characterised by very low total densities and diversity, and by the presence of fish eggs. In spring total merohyperbenthic densities are highest and postlarvae of the shore crab dominate, while in summer the merohyperbenthos is dominated by postlarvae of gobies.

The surf zones of the Belgian coast seem to be used intensively by a number of (post)larval organisms. Postlarvae and zoeae of the common shrimp and



- Hamerlynck, O. & Mees, J. 1991 Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. *Oceanologica Acta* **11**, 205–212.
- Hamerlynck, O., Van De Vyver, P. & Janssen, C. R. 1990 The trophic position of *Pomatoschistus lozanoi* (Pisces: Gobiidae) in the Southern Bight. 'Trophic relationships in the marine environment'. *Proceedings 24th European Marine Biology Symposium*, Aberdeen University Press, Aberdeen, 183–190.
- Hamerlynck, O., Mees, J., Craeymeersch, J. A., Soetaert, K., Hostens, K., Cattrijsse, A. & Van Damme, P. A. 1993 The Westerschelde Estuary: two food webs and a nutrient rich desert. *Proceedings of the Belgian National Commission of Oceanology* 217–234.
- Hanamura, Y. 1999 Seasonal abundance and life cycle of *Archaeomysis articulata* (Crustacea: Mysidacea) on a sandy beach of western Hokkaido, Japan. *Journal of Natural History* **33**, 1811–1830.
- Harris, S. A. & Cyrus, D. P. 1996 Larval and juvenile fishes in the surf zone adjacent to the St Lucia Estuary Mouth, KwaZulu-Natal, South Africa. *Marine and Freshwater Research* **47**, 465–482.
- Hartmann-Schröder, G. 1971 Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Teil 58: Annelida—Borstenwürmer—Polychaeta. VEB Gustav Fischer Verlag Jena, Hamburg, 894 pp.
- Hesthagen, I. H. 1973 Diurnal and seasonal variation in the near-bottom fauna—the hyperbenthos—in one of the deeper channels of the Kieler Bucht (Western Baltic). *Kieler Meeresforschungen* **29**, 116–140.
- Hill, M. O. 1973 Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**, 427–432.
- Hill, M. O. 1979 TWINSPAN. A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York.
- Jaramillo, E., Stead, R., Quijon, P., Contreras, H. & Gonzalez, M. 1996 Temporal variability of the sand beach macroinfauna in south-central Chile. *Revista Chilena de Historia Natural* **69**, 641–653.
- Jones, N. S. 1976 *British cumaceans. Arthropoda: Crustacea*. Keys and notes for the identification of the species. Academic Press, London, 66 pp.
- Jones, D. A. & Naylor, E. 1967 The distribution of *Eurydice* (Crustacea: Isopoda) in British waters, including *E. affinis* new to Britain. *Journal of the Marine Biological Association of the United Kingdom* **47**, 373–382.
- King, P. E. 1974 *British sea spiders. Arthropoda: Pycnogonida*. Keys and notes for the identification of the species. Academic Press, London, 68 pp.
- Kinoshita, I. 1993 Ecological study on larvae and juveniles of sparine fishes occurring in surf zones of sandy beaches. *Bulletin of Marine Science and Fisheries, Kochi University* **13**, 21–99.
- Kramer, K. J. M., Brockmann, U. H. & Warwick, R. M. 1994 *Tidal estuaries*. Manual of sampling and analytical procedures. Published for the European Commission by A. A. Balkema, Rotterdam, 304 pp.
- Kramp, P. L. 1930 Hydromedusae collected in the south-western part of the North Sea and the eastern part of the Channel in 1903–14. *Mémoires Musée Royale Histoire Naturelle Belgique* **45**, 1–55.
- Lasenby, D. C. & Sherman, R. K. 1991 Design and evaluation of a bottom-closing net used to capture mysids and other supra-benthic fauna. *Canadian Journal of Zoology* **69**, 783–786.
- Lincoln, R. J. 1979 *British marine Amphipoda: Gammaridea*. British Museum (Natural History), London, 658 pp.
- Lock, K., Beyst, B. & Mees, J. 1999 Circadiel patterns in the tidal plankton of a sandy beach in Zeebrugge (Belgium). *Belgian Journal of Zoology* **129**, 339–352.
- Macquart-Moulin, C. 1977 Le contrôle de l'émergence et des nages nocturnes chez les Péricarides des plages de Méditerranée *Eurydice affinis* Hansen (Isopodan), *Gastrosaccus mediterraneus* Băcescu, *Gastrosaccus spinifer* (Goës) (Mysidacea). *Journal of Experimental Marine Biology and Ecology* **27**, 61–81.
- Mantoura, R. F. C. & Llewellyn, C. A. 1983 The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. *Analytica Chimica Acta* **151**, 297–314.
- Mauchline, J. 1980 *The biology of mysids and euphausiids*. Academic Press, London, 681 pp.
- Mauchline, J. 1998 *The biology of calanoid copepods*. Academic Press, London, 710 pp.
- Masselink, G. & Short, A. D. 1993 The effect of tide range on beach morphodynamics and morphology: a conceptual beach model. *Journal of Coastal Research* **9**, 785–800.
- McLachlan, A. 1983 Sandy beach ecology—A review. In *Sandy Beaches As Ecosystems* (McLachlan, A. & Erasmus, T., eds). Dr W. Junk Publishers, The Hague, 321–380.
- Mees, J. & Hamerlynck, O. 1992 Spatial community structure of the winter hyperbenthos of the Schelde Estuary, The Netherlands, and the adjacent coastal waters. *Netherlands Journal of Sea Research* **29** (4), 357–370.
- Mees, J. & Jones, M. B. 1997 The hyperbenthos. *Oceanography and Marine Biology: an Annual Review* **35**, 221–255.
- Mees, J., Abdulkarim, Z. & Hamerlynck, O. 1994 Life history, growth and production of *Neomysis integer* in the Westerschelde Estuary (SW Netherlands). *Marine Ecology Progress Series* **109**, 43–57.
- Mees, J., Cattrijsse, A. & Hamerlynck, O. 1993 Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands. *Cahiers de Biologie Marine* **34**, 165–186.
- Moran, S. 1972 Ecology and distribution of the sand-dwelling mysid crustacean *Gastrosaccus sanctus* (Van Beneden, 1861) along the Mediterranean sandy shore of Israel. *Crustaceana* (suppl.) **3**, 357–361.
- Munilla, T. & Corrales, M. J. 1995 Suprabenthos de la plage de Rosas (Gerona, Mediterranea occidental). *Orsis* **10**, 83–90.
- Munilla, T., Corrales, M. J. & San Vicente, C. 1998 Suprabenthic assemblages from Catalan beaches: zoological groups. *Orsis* **13**, 67–78.
- Naylor, E. 1955 The ecological distribution of British species of *Idotea* (Isopoda). *Journal of Animal Ecology* **24**, 270–281.
- Naylor, E. 1957 The occurrence of *Idotea metallica* Bosc. in British waters. *Journal of the Marine Biological Association of the United Kingdom* **36**, 599–602.
- Naylor, E. 1972 *British Marine Isopods*. Keys and notes for the identification of the species. Academic Press, London, 86 pp.
- Riley, J. D., Symonds, D. J., Woolner, L. 1981 On the factors influencing the distribution of O-group demersal fish in coastal waters. *Rapports et Procès-Verbaux des Réunions Conseil International Exploration de la Mer* **178**, 223–228.
- Romer, G. S. 1990 Surf zone fish community and species response to a wave energy gradient. *Journal of Fish Biology* **36**, 279–287.
- Ross, S. T. 1983 A review of the surf zone ichthyofauna in the Gulf of Mexico. In *Proceedings of the northern Gulf of Mexico estuaries and barrier islands research conference* (Shabica, S. V. & Cake, E. W. Jr., eds). U.S. Department of the Interior, Atlanta, 25–34.
- Ross, T. S., McMichael, R. H. Jr. & Ruple, D. L. 1987 Seasonal and diel variation in the standing crop of fishes and macro-invertebrates from a Gulf of Mexico surf zone. *Estuarine, Coastal and Shelf Science* **25**, 391–412.
- Russel, F. S. 1953 *The medusae of the British Isles*. University Press, Cambridge, 530 pp.
- Russel, F. S. 1976 *The eggs and planktonic stages of British marine fishes*. Academic Press, London, 524 pp.
- Sanderson, A. R. 1930 The coelenterate plankton of the Northumbrian coast during the year 1924. *Journal of the Marine Biology Association (N.S.)* **17**, 219–232.

- San Vicente, C. & Sorbe, J. C. 1993a Biologie du mysidacé suprabenthique *Schistomysis parkeri* Norman, 1892 dans la zone sud du Golfe de Gascogne (Plage d'Hendaye). *Crustaceana* 65, 222-252.
- San Vicente, C. & Sorbe, J. C. 1993b Estudio comparado del suprabenthos de una playa catalana y otra vasca: metodología y resultados preliminares. *Pub. Esp. Inst. Esp. Ocean.* 11, 299-304.
- San Vicente, C. & Sorbe, J. C. 1999 Spatio-temporal structure of the suprabenthic community from Creixell beach (western Mediterranean). *Acta Oecologica* 20, 377-389.
- Sokal, R. R. & Rohlf, F. J. 1981 *Biometry*. W.H. Freeman and Company, New York, 859 pp.
- Subiyanto, Hirata, I. & Senta, T. 1993 Larval settlement of the japanese flounder on sandy beaches of the Yatsushiro Sea, Japan. *Nippon Suisan Gakkaishi* 59, 1121-1128.
- Tattersall, W. M. & Tattersall, O. S. 1951 *The British Mysidacea*. Ray Society, London, 460 pp.
- Ter Braak, C. J. F. 1986 Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167-1179.
- Ter Braak, C. J. F. 1988 CANOCO—a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis (version 2.1). Agricultural Mat. Group. Ministry of Agriculture and Fisheries.
- Vallet, C. & Dauvin, J. C. 1999 Seasonal changes of macrozooplankton and benthic boundary layer macrofauna from the Bay of Sau-int-Brieuc (western English Channel). *Journal of Plankton Research* 21, 35-49.
- Van der Baan, S. M. & Holthuis, L. B. 1971 Seasonal occurrence of Mysidacea in the surface plankton of the Southern North Sea near the 'Texel' lightship. *Netherlands Journal of Sea Research* 5, 227-239.
- Watkin, E. E. 1939 The pelagic phase in the life-history of the amphipod genus *Bathyporeia*. *Journal of the Marine Biological Association of the United Kingdom* 23, 467-481.
- Watkin, E. E. 1941 Observations on the night tidal migrant Crustacea of Kames Bay. *Journal of the Marine Biological Association of the United Kingdom* 25, 81-96.
- Watson, H. G. 1930 The coelenterate plankton of the Northumbrian coast during the year 1925. *Journal of the Marine Biological Association of the United Kingdom* 17, 233-239.
- Wooldridge, T. 1983 Ecology of beach and surf zone mysid shrimps in the eastern Cape, South Africa. In *Sandy Beaches As Ecosystems* (McLachlan, A. & Erasmus, T., eds). Dr W. Junk Publishers, The Hague, 449-460.
- Wooldridge, T. 1989 The spatial and temporal distribution of mysid shrimps and phytoplankton accumulations in a high energy surf zone. *Vie Milieu* 39, 127-133.
- Zatkutskiy, V. P. 1970 Some biological features of mysids of the hyponeuston in the Black Sea and Sea of Azov. *Gidrobiologicheskii Zhurnal* 6, 17-22.

