CHAPTER 5

COMMUNITY STRUCTURE AND INTERTIDAL ZONATION OF THE MACROBENTHOS ON A MACROTIDAL, ULTRA-DISSIPATIVE SANDY BEACH: SUMMER – WINTER COMPARISON

Steven Degraer, Iris Mouton, Liesbeth De Neve and Magda Vincx

University of Gent, Department of Biology, Marine Biology Section
K.L. Ledeganckstraat 35, B-9000, Gent, Belgium

Estuaries, **22**(3B):742-752

ACKNOWLEDGEMENTS

The first author is funded by the Flemish Institute for the Promotion of Scientific-Technogical Research in Industry (IWT). The research costs were supported by Marine Biology Section of the University of Ghent. The Coastal Waterways Division (AWK) provided information on the physical environment of the beach of De Panne. The authors are grateful to Soares, A., A. De Ruyck and Meire P. for their valuable critical remarks on the manuscript. Several individuals assisted in the field and laboratory, including Van De Velde J., M. Beghyn, D. Van Gansbeke, D. Schram, A. Van Kenhove. Thanks to comments provided by two anonymous referees, the paper has significantly been improved.

ABSTRACT

To study community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative beach, the macrobenthos of the beach of De Panne (Belgium) was investigated. Six transects perpendicular to the waterline were sampled each with 5 stations in September 1995 (summer) and March 1996 (winter). To sample the macrobenthos at different levels of elevation, the 30 stations were distributed across the continuum from mean high water spring to mean low water spring. Thirty nine species were found to comprise total densities up to 5500 individuals m^{-2} in summer and 1400 individuals m^{-2} in winter. The highest densities were found in the spionid polychaetes, *Scolelepis squamata* and *Spio filicornis*, the nephtyid polychaete, *Nephtys cirrosa*, the cirolanid isopod, *Eurydice pulchra*, and the haustorid amphipods, *Bathyporeia* spp. By means of species composition, specific densities and biomass two species associations were defined: (1) a relatively species-poor, high intertidal species association, dominated by *S. squamata* and with an average density of 1413 individuals m^{-2} and biomass of 808 mg AFDW m^{-2} (summer) and (2) a relatively species-rich, low intertidal species association, dominated by *N. cirrosa* and with a lower average density (104 individuals m^{-2}) and biomass (162 mg AFDW m^{-2}) in summer. For both seasons, the high intertidal species association was restricted in its intertidal distribution between the mean tidal and the mean high-water spring level, whereas the low intertidal species association was found from the mean tidal level on downwards the beach. The latter showed good affinities with the subtidal *N. cirrosa* species association, occurring just offshore of De Panne beach, confirming the existence of a relationship between the low intertidal and subtidal macrobenthic species associations. Summer – winter comparison revealed a strong decrease in densities and biomass in the high intertidal zone during winter. Habitat continuity of the low intertidal zone with the subtidal allows subtidal organisms to repopulate the low intertidal zone after depletion of the populations.

INTRODUCTION

Although the distribution of macrobenthos on sandy beaches has been well-documented in many parts of the world (e.g., Morton and Miller, 1968; Trevallion *et al.*, 1970; McLachlan *et al.*, 1981; Dexter, 1983; Straughan, 1983; Ismail, 1990; McLachlan, 1990; Jaramillo *et al.*, 1993; Rakocinski *et al.*, 1993; Souza and Gianuca, 1995), the macrobenthos inhabiting European and particularly Belgian sandy beaches has been poorly studied (Elliott *et al.*, 1996). Moreover, many still consider sandy beaches as 'biological deserts', in order to biologically justify the malification of beaches for coastal protection works and tourism developments. However, in winter along the 65 km long Belgian coastline, a rich avifauna consisting of waders, such as Sanderling (*Calidris alba*), utilize food resources of beaches (Devos *et al.,* 1996). At high tide a rich marine fauna enters the intertidal zone (e.g., smaller fish as juvenile Plaice (*Pleuronectes platessa*) (Beyst unpublished information). The food of these birds and fishes consists mainly of the macrobenthos inhabiting the intertidal zone (e.g., Witherby *et al.,* 1947; Thijssen *et al.,* 1974), which underscores the ecological importance of Belgian sandy beaches.

As expected for a macrotidal, ultra-dissipative beach, such as the beach of De Panne (Jaramillo *et al.,* 1993), Elliott *et al.* (1996) found indications of the presence of a rich intertidal macrobenthic fauna with a maximum density of 600 individuals m^{-2} just above the mean tidal level, decreasing up- and downwards the beach to a minimum of 100 individuals m^{-2}. As the pilot study by Elliott *et al.* (1996) was based on only one transect and one sampling date, a larger benthic survey is necessary to obtain a more comprehensive view on the zonation of the macrobenthos of this macrotidal, ultra-dissipative beach.

The objective of this study was to describe community structure and the pattern of intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative beach, in summer and winter.

MATERIAL AND METHODS

STUDY AREA

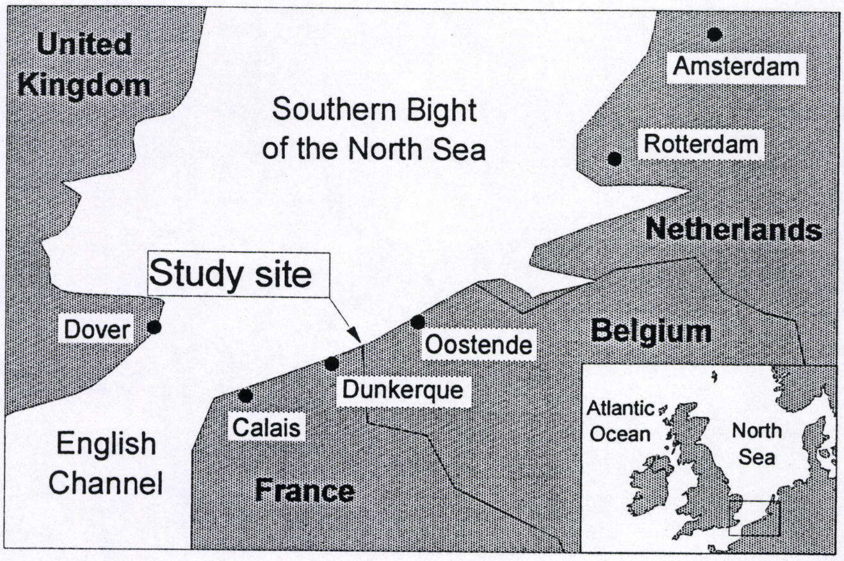

Figure 1. Geographical disposition of the study area.

A 4 km long beach fronting the 'Westhoek' dune reserve at De Panne (Belgium) - Bray-Dunes (France) (51°05'12"N-51°07'00"N - 2°31'06"E-2°34'00"E) was selected for this study (Figure 1). The beach habitat is located in a cold-temperate region: air temperatures were found between 10 to 25°C in September 1996 and between 5 and 13 °C in March 1997; seawater temperature was 18°C in September 1996 and 8°C in March 1997. During winter 1996-1997, the minimum air temperature was -15°C, whereas the minimum seawater temperature was 2°C (Coastal Waterways Division, unpublished information).

The width of the intertidal zone is approximately 450 m, increasing in width towards the French section. Mean spring and neap tide range are 5 and 3 m, respectively, modal breaker height is 0.5 m and modal wave period is 3 s (Coastal Waterways Division, unpublished information).The general slope of the beach is ca. 1:90 (Lahousse, unpublished information), decreasing towards the French section. Sediments are composed of fine sands (median grain size < 250 µm). The beach has several shallow troughs and bars, parallel to the water's edge with an average period of several tens of metres, in which water is retained on the outgoing tide.

Although there are some housing developments and a camp site within a small section of the foredune zone, the relatively small number of visitors to the beach (because of restricted access) and the lack of groins make this site a relatively unimpacted beach site compared to other Belgian beaches. At one transect, situated within the Belgian section of the beach, the landward margin of the intertidal zone is interrupted by a small concrete storm-water dyke between the mean high-water neap (MHWN) and MHWS level. At the three other 'Belgian' transects this storm-water dyke is located above the MHWS level. The French section, encomprizing two transects, has a natural beach-dune transition.

SAMPLING STRATEGY

On the beach, 6 horizontally equally spaced transects, perpendicular to the waterline, were sampled each with 5 stations divided between the MHWS and MLWN level in September 1995 (summer) and mean low-water spring (MLWS) in March 1996 (winter). To sample the macrobenthos at different heights on the beach, the 30 stations were distributed across the continuum from mean high water spring to mean low water spring level (Figure 2). In summer, all stations were located between 500 and 100 cm above MLWS, whereas in winter, samples were taken between 500 and -50 cm above MLWS. The use of six transects allowed generalization of the results for the whole beach, which cannot be adequately represented by just one transect (Haynes and Quinn, 1995). Per station 2 replicate samples were taken.

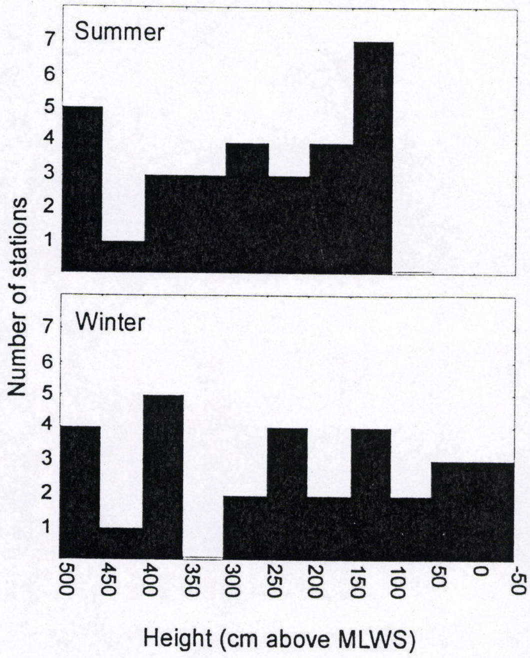

Figure 2. The distribution of the 30 stations along the intertidal continuum during the summer and winter sampling campaign.

Following Elliott *et al.* (1996) samples were taken by excavating sediment enclosed by a frame, with a surface area of 0.1026 m², to a depth of ca. 0.15 m. Organisms were retained on a 1 mm sieve, fixed and preserved in an 8 % formaldehyde-seawater solution. An additional core, with a diameter of 3.6 cm (penetration depth of 0.15 cm), was collected with each macrofauna sample for the analysis of sediment characteristics. Height above MLWS at each sampling site was determined from data provided by the Coastal Waterways Division.

The employed sampling technique is a method frequently used in the study of intertidal macrofauna. However, different surface areas, excavating depths, number of stations and number of replicates are used, depending on the beach type (e.g., McIntyre and Eleftheriou, 1968; McDermott, 1987; McLachlan, 1990; Jaramillo *et al.*, 1993; Haynes and Quinn, 1995; Souza and Gianuca, 1995). The pilot study of Elliott *et al.* (1996) revealed that the densities of the dominant species of the beach in De Panne were high enough that a sampling surface of about 0.1 m², with 2 replicates per station, and an excavation depth of 15 cm would satisfactorally represent the macrobenthic zonation of Belgian beaches. Although the deeper living lugworm *Arenicola marina* occurred in the study area, mainly in the troughs and towards the lower beach, this species was not sampled quantitatively by this sampling technique and was thus not included in subsequent analyses.

Finally, as the percentage of species expected for a beach increases with an increase in total sampling area, the total sampling area needs to be large enough to attain a representative sample of the macrobenthos of the beach. For the dissipative beaches, with a high diversity (Jaramillo and McLachlan, 1993), a sampling area of at least 4 m² is advized (Jaramillo *et al.*, 1995). The total sampling area in this study was 6 m² in both seasons and should thus be sufficient enough to collect more than 95 % of the total number of species present on the beach.

The beach of De Panne consists of a series of bars and troughs, each with different habitat characteristics, e.g., the retention of water in the troughs which might harbour subtidal fauna (Dörjes, 1976). As all samples were taken on top of the bars, this study excluded the macrobenthos of the troughs. In addition, to avoid bias due to tidal vertical migration of hyperbenthic organisms, samples were always taken on exposed sediments, just above the waterline. Thus, sampling always started at high tide and followed the receding water down the beach, ending at the low tidal level.

LABORATORY METHODS

In the laboratory, the sediment collected for faunal analysis was elutriated ten times to separate most of the fauna from the remaining material. The remaining material was then examined to collect the larger macrobenthic fauna, such as bivalves, that were too heavy to be floated out by elutriation.

Macrobenthic organisms were removed using a dissecting microscope, identified to species level, where possible, and counted. Faunal densities were extrapolated to number of individuals per m² (N m^{-2}). Biomass (Ash-Free Dry Weight, or AFDW) estimates of all polychaetes, except for the Nephtyidae, and crabs were obtained by loss of mass on ignition (500 ± 50°C for 2 hours) of oven-dried samples (70°C for 48 h). The biomass of all other fauna was calculated by regression analysis (Govaere, 1978; Mees, 1994; Degraer and Vincx, 1995).

Sediment samples were oven-dried at 105°C for 12 h, and then ashed at 500 ± 50°C for 2 h to determine Total Organic Matter (TOM) by loss of mass on ignition. The gravel fraction (mainly shell fragments) was that proportion by mass of sediment with a grain size larger than 850 µm. The grain size distribution of the particles smaller than 850 µm was determined with a COULTER LS. The percentage by mass of sand CO_3^{2-} content was determined by measuring the volume of CO_2 released from oven-dried sand upon addition of 25 % HCl.

MATHEMATICAL ANALYSES

The morphodynamic state of the beach is given by Dean's parameter ($\Omega = H_b/w_s T$) and the relative tidal range ($RTR = MSR/H_b$), where H_b is the modal breaker height in m, w_s is the sediment fall velocity in m s^{-1}, T is the modal wave periode in s and MSR is the mean spring tide range in m (Masselink and Short, 1993). Sediment fall velocity is estimated from the median grain size (Anonymous, 1995 a).

Macrobenthic abundances (N m^{-2}) were used to calculate the diversity as the number of species per sample (N_0) (Hill, 1973), the Shannon-Wiener diversity index (H') (Shannon and Weaver, 1949) and the Simpson dominance index (SI), each with the use of logarithms to the base 10.

To investigate the vertical (from high to low water) distribution patterns (zonation), the macrobenthic density data were subjected to three multivariate techniques (1) TWINSPAN (Two-Way INdicator SPecies ANalysis), a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes (Hill, 1979); and, after the density was normalized by means of a fourth root transformation (Sokal and Rohlf, 1981; Field *et al.,* 1982), the data were further subjected to (2) a (Canonical) Correspondance Analysis (CA and CCA) (Ter Braak, 1988), together with elevation and sand physical and chemical properties as environmental variables and (3) Cluster Analysis with the Bray-Curtis similarity index and the use of group averaging (Clifford and Stephenson, 1975).

The polynomial functions, showing the general zonation trend of the total abundances, the biomass, the number of species per station and the densities of *Scolelepis squamata*, *Spio filicornis*, *Nephtys cirrosa*, *Eurydice pulchra*, *Bathyporeia* spp. and *Urothoe poseidonis*, were retrieved by means of a distance-weighted least squares smoothing procedure of the data points as calculated by the program STATISTICA. The correlations between the environmental variables were analyzed by means of the nonparametric Spearman rank correlation coefficient (Siegel, 1952; Conover, 1971).

RESULTS

PHYSICAL ENVIRONMENT

All intertidal sediments at De Panne beach (between -10 and 500 cm above MLWS) consisted of fine, well-sorted sands. A general trend of increasing median grain sizes (from 170 to 250 µm) with increasing height on the beach was found in both summer and winter (Figure 3), and no obvious differences in the sedimentology of summer and winter could be detected. However, between 4 and 5 m height a slighty coarser sediment appeared in winter.

The percentage of CO_3^{2-} in the sediment varied between 7 % and 32 % and averaged about 16 %. The TOM was found to be low between 0.42 % and 1.4 %, with an average of 0.63 %. For both seasons height on the beach was related ($p < 0.001$) with modal grain size, sorting and skewness. The percentages of CO_3^{2-} and TOM were correlated with the height on the beach during one season only (CO_3^{2-}: $p < 0.003$, winter; TOM: $p < 0.001$, summer). With an average median grain size of 221 µm (summer) and 230 µm (winter) of the uppermost beach stations, H_b of 0.5 m and T of 3 s, Dean's parameter (Ω) was estimated at 6.9 in summer and 6.6 in winter. For both seasons, the estimated relative tidal range (RTR) was 10. Thus, the beach type can be considered as being ultra-dissipative (Masselink and Short, 1993).

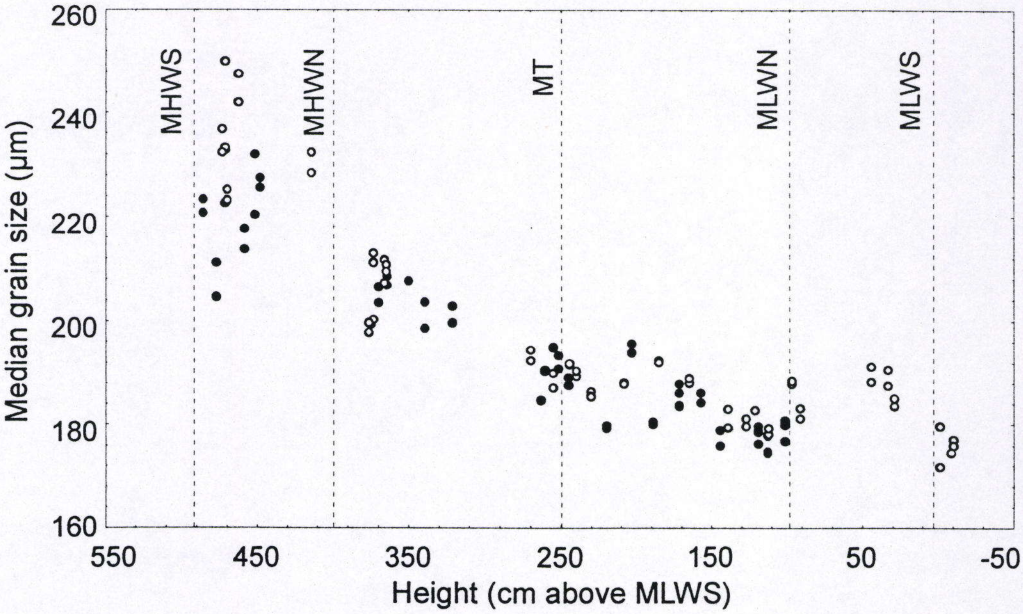

Figure 3. The intertidal distribution (height in cm above MLWS) of the median grain size (µm). ● : summer; ○ : winter.

MACROBENTHOS: GENERAL

On the beach of De Panne - Bray-Dunes, a total of 39 macrobenthic species were found (28 in summer and 32 in winter), 15 of which were polychaetes, 7 amphipods, and 6 bivalves. Polychaetes generally exhibited the highest densities and biomass (Figs. 4A and 4B). Isopods (summer) and amphipods (both seasons) were numerically abundant, while all other taxa, namely ostracods, copepods, cumaceans, mysids, decapods and bivalves, were represented by low densities and biomass. The average number of species per sample (N_0) (3 - 4) was similar in summer and winter (Figure 4C). The average Shannon-Wiener diversity index (H') was 0.7 (summer) and 1.3 (winter), whereas the average Simpson dominance index (SI) was 0.5 and 0.6, in winter and summer, respectively.

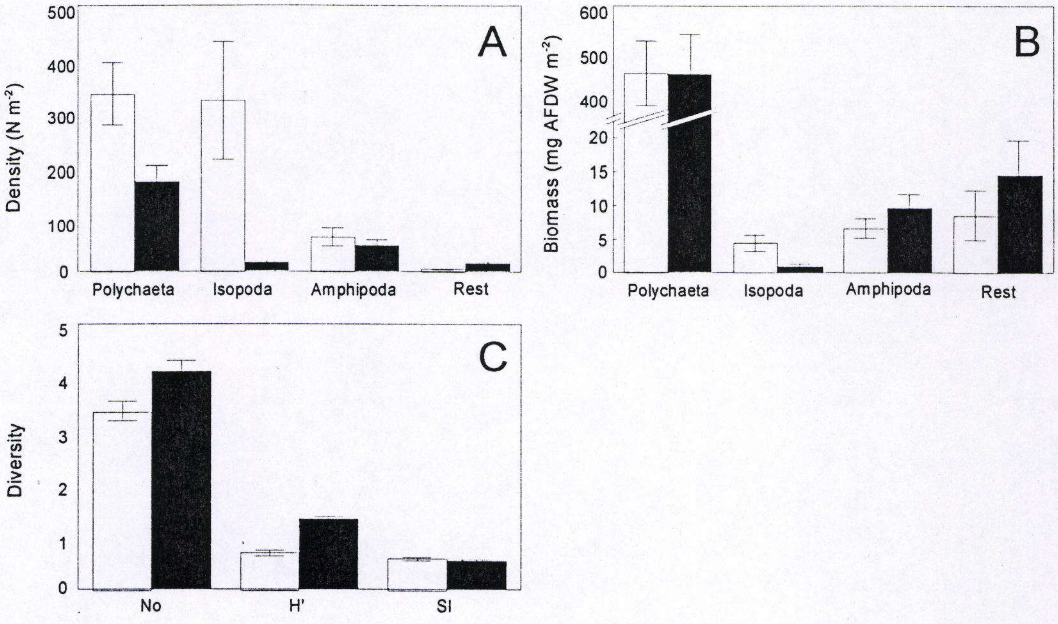

Figure 4. The distribution over the different taxa of A. the density (N m^{-2} ± standard error, SE) and B. the biomass (mg AFDW m^{-2} ± SE). C. Diversity indices (number of species per sample, N_0 and Shannon-Wiener diversity index, H', both ± SE) and eveness index (Simpson dominance index, SI, ± SE). Summer: white bars; winter: black bars.

Of 39 species only 5 were present at high densities (at least 25 specimens over all the samples in both seasons), namely the spionid polychaetes *Scolelepis squamata* and *Spio filicornis*, the nephtyid polychaete *Nephtys cirrosa*, the cirolanid isopod *Eurydice pulchra*, and the haustorid amphipods *Bathyporeia* spp. In summer, *S. squamata* and *E. pulchra*, each accounted for 30 % of the average macrobenthic density of 725 individuals m^{-2} (Table 1) over the full intertidal gradient. In winter, generally lower numbers were found, with an average macrobenthic density of 250 individuals m^{-2}, dominated by *S. squamata* (30 %). In summer, spionid polychaetes accounted for 80 % of a macrobenthic biomass of 470 mg AFDW m^{-2}, while in winter this percentage was lower but still 45 % of 473 mg AFDW m^{-2}. The only other species with a considerable biomass, *N. cirrosa*, represented about 15 % of the macrobenthic biomass in both seasons.

	Density ($N.m^{-2} \pm SE$)		Biomass (mg $AFDW.m^{-2} \pm SE$)	
	summer	winter	Summer	winter
*Scolelepis squamata*_(P)	287 ± 62	107 ± 31	377 ± 78	212 ± 67
Spio filicornis (P)	4 ± 2	10 ± 3		
Nephtys cirrosa (P)	37 ± 6	38 ± 6	61 ± 11	74 ± 14
Eurydice pulchra (I)	301 ± 107	15 ± 3	4 ± 1	0.9 ± 0.3
Bathyporeia spp. (A)	63 ± 17	34 ± 9	6 ± 1	4 ± 1
All species	725 ± 162	250 ± 33	470 ± 76	473 ± 88

Table 1. Average densities and biomass (± standard error, SE) of all species found with at least 25 specimens in both sampling periods. P, Polychaeta; I, Isopoda; A, Amphipoda.

ZONATION PATTERNS

In summer, the maximum macrobenthic density (5500 ind m^{-2}) was located at MT level and showed a sharp decline to MHWS and MLWN levels, to increase towards the MLWS level (Figure 5A). In winter, the maximum density (1400 m^{-2}) was found at about MHWN, and decreased towards the MHWS and MT levels.

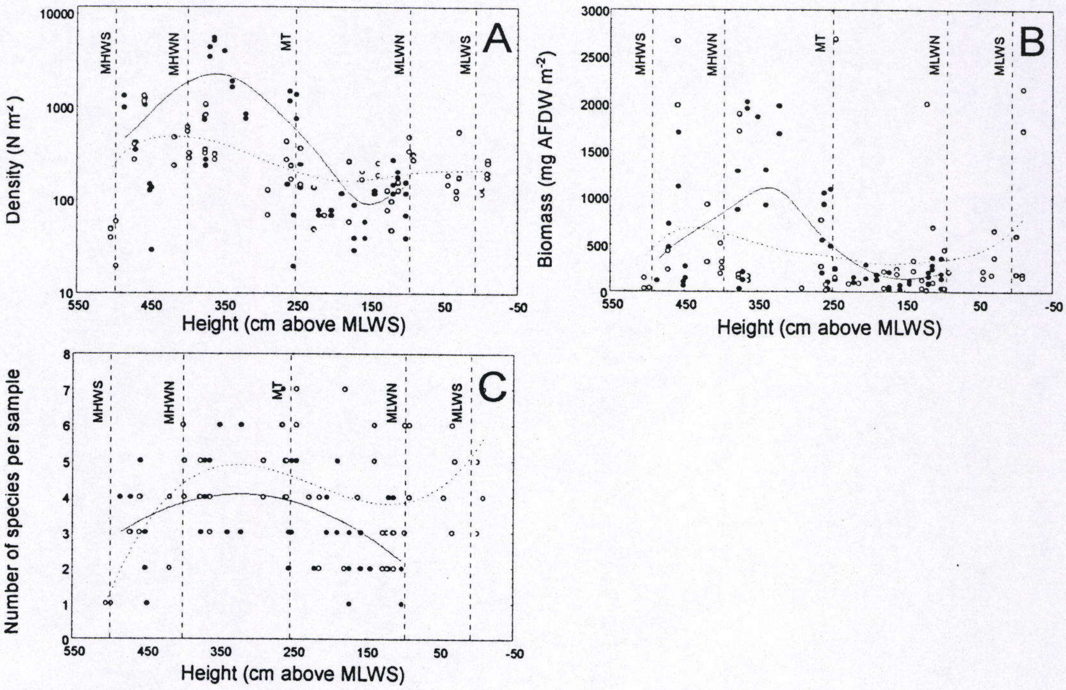

Figure 5. The intertidal distribution (cm above MLWS) of the macrobenthic density (N m^{-2}), macrobenthic biomass (mg AFDW m^{-2}) and number of species per sample. ● : summer; ○ : winter; density presented on a logarithmic scale.

The minimum density was located at MHWS, followed by MLWN levels. From the MLWN level on downwards the beach the macrobenthic density increased slightly. The macrobenthic biomass followed almost exactly the same trend as the macrobenthic density with a maximum of about 2000 mg AFDW m^{-2} in both seasons around MHWN or MT (Figure 5B). The number of species per sample was highly variable, but reached its maximum (7 species for both seasons) at the MT level (Figure 5C).

Multivariate analyses (TWINSPAN, (C)CA and Cluster Analysis) conducted, revealed two biological groups (species associations), differentiated by means of their intertidal distribution: a high intertidal and a low intertidal species association. The vertical border between the low and high intertidal species associations was situated at approximately 250 cm above MLWS in summer (Figure 6A), whereas in winter it was approximately 200 cm above MLWS (Figure 6B).

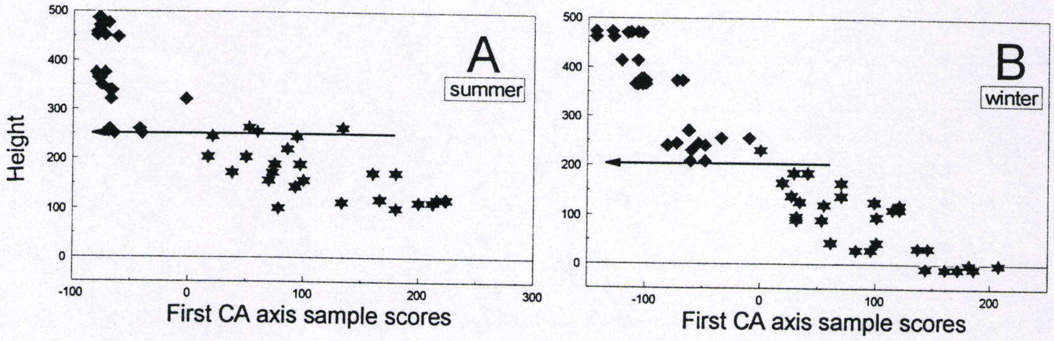

Figure 6. The continuous relation between the CA sample scores of the first axis and the height on the beach (cm above MLWS); with indication of the two species associations (★: species association 1 & ◆: species association 2) and the distinctive height between both (arrow). The sample scores on the first CA axis explained 31.1% of a total percentage of variance within the species data of 66.1% explained by the first 4 axes in summer and 18.9% of a total of 44.4% in winter.

In both seasons, macrobenthic density and biomass were highest in the high intertidal species association, with an average up to 1413 individuals m^{-2} and 808 mg AFDW m^{-2} (Table 2), while in the low intertidal species association averages of at most 162 individuals m^{-2} and 407 mg AFDW m^{-2} were measured. For N_0 (3-4 species) no differences between species associations nor periods were detected, whereas, for both seasons, the total number of species per species association was higher in the low intertidal species association, with a maximum of 22 species in March. Out of the top 5 species per species association, the 3 most abundant species remained the same over time with only minor shift in dominance. These species were *Nephtys cirrosa*, *Spio filicornis* and *Urothoe poseidonis* for the low intertidal species association and *Scolelepis squamata*, *Eurydice pulchra* and *Bathyporeia* spp. for the high intertidal species association. *Spio filicornis*, *N. cirrosa* and *U. poseidonis* were generally found from about the MT level on downwards the beach, increasing in density towards the subtidal (only in winter for *S. filicornis*) (Figs. 7B, 7C and 7F). In summer, *S. squamata*, *E. pulchra*, and *Bathyporeia* spp. occurred between the MT and MHWS levels, with a general maximal density just below MHWN (Figs. 7A, 7D and 7E). In winter, the highest densities of *S. squamata* were located between the MHWN and the MHWS level and *E. pulchra* was distributed throughout the intertidal zone.

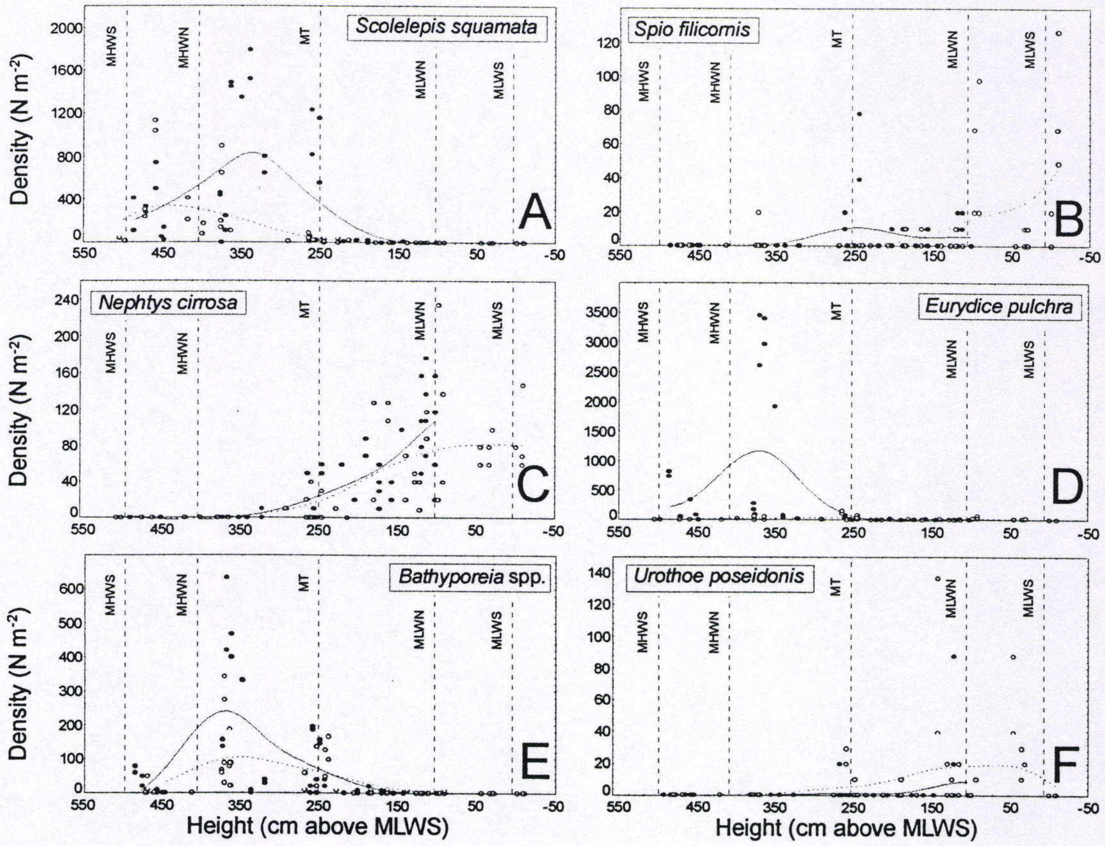

Figure 7. The intertidal density (N m^{-2}) distribution of the 3 most dominant species of each species association and per sampling campaign: A. *Scolelepis squamata*; B. *Spio filicornis*; C. *Nephtys cirrosa*; D. *Eurydice pulchra*; E. *Bathyporeia* spp.; F. *Urothoe poseidonis*. ● : summer; ○ : winter.

DISCUSSION

SPECIES COMPOSITION AND ABUNDANCE

The worldwide dominance of polychaetes, crustaceans and bivalves on sandy beaches (e.g., Dexter, 1983; McLachlan, 1983; Junoy and Viéitez, 1992) is obvious on the ultra-dissipative beach of De Panne: (1) polychaetes dominate in terms of density (*Scolelepis squamata*), biomass (*S. squamata* and *Nephtys cirrosa*) and number of species, (2) crustaceans are numerically abundant (*Eurydice pulchra*) and are relatively speciose (e.g., amphipods: 7 species), and (3) although bivalves are represented in low numbers, 6 bivalve species were encountered.

The polychaetes *S. squamata*, *Spio filicornis*, *N. cirrosa*, the isopod *E. pulchra*, and the amphipods *Bathyporeia* spp., are found abundant on various European beaches (e.g., Stephen, 1929; Elmhirst, 1931; McIntyre and Eleftheriou, 1968; Dörjes, 1976; Junoy and Viéitez, 1992). Moreover, *Scolelepis squamata* is found to be abundant on several beaches outside Europe (e.g., Brazilia: Souza and Gianuca, 1995; Florida: Rakocinski *et al.,* 1993; New Jersey: McDermott, 1987).

As expected from the general trend of an increasing number of species from the reflective towards the dissipative beach type (Jaramillo and McLachlan, 1993), more species (39 species) were found on the ultra-dissipative beach of De Panne in comparison with many other studies (e.g., 14 species: Jaramillo *et al.,* 1993; 35 species: Souza and Gianuca, 1995; 15 species: James and Fairweather, 1996). If all habitats of the beach of De Panne (subterrestrial fringe, above MHWS, and intertidal troughs) would have been taken into account it is likely to find even more species.

As most studies do not provide information on average densities or biomass or use other standardizations (expressed per m shoreline), comparison with other studies is very difficult. Yet, it appears that the average density (summer: 725 individuals m^{-2}; winter: 250 individuals m^{-2}) is high (Haynes and Quinn, 1995; Souza and Gianuca, 1995), as expected for an ultra-dissipative beach (Jaramillo *et al.,* 1993; McLachlan and Jaramillo, 1995; McLachlan *et al.,* 1996).

MACROBENTHIC ZONATION

In this study, two major restrictions on the zonation pattern have to be taken into account: (1) the absence of samples in the subterrestrial fringe (just above MHWS) (Dahl, 1952) and (2) the absence of samples in the troughs of the intertidal zone. Both zones may harbour other macrobenthic organisms, representing new species associations, which could not be detected in this study. The description of the zonation is still preliminary and should be interpreted with caution. Yet, the existence of at least two intertidal species associations is demonstrated: (1) between the MHWS and MT level (Dahl's (1952) midlittoral zone) a species association, dominated by *Scolelepis squamata* and, in summer, also *Eurydice pulchra*, occurs and (2) between the MT and MLWS level (Dahl's (1952) sublittoral fringe) the species association is dominated by *Nephtys cirrosa*. At about MT level an overlap of the two species associations exists. The high intertidal species association has a low number of species (summer: 10 species; winter: 16 species), occurring at high densities (summer: 1413 individuals m^{-2}; winter: 332 ind m^{-2}), whereas the low intertidal species association is composed of more species (summer: 13 species; winter: 22 species), but at lower densities (summer 104 ind m^{-2}; winter: 162 ind m^{-2}). The biomass followed the same trend as the density, with the highest values (maximum 808 mg AFDW m^{-2}) in the high intertidal zone. A general increase of the number of species, together with a general decrease of the densities, from the high intertidal towards the low intertidal, is a typical characteristic for many sandy beaches worldwide (e.g., Souza and Gianuca, 1995).

A detailled review of the macrobenthic zonation on sandy beaches is given by McLachlan and Jaramillo (1995): concerning the strictly intertidal zone (between MHWS and MLWS), generally 2 macrobenthic zones can be distinguished and the low intertidal zone tends to split into 2 macrobenthic zones on dissipative beaches. In their pilot study, Elliott *et al.* (1996) reported the existence of three species associations between MHWS and MLWS on the beach of De Panne: (1) an uppermost species association, dominated by *Bathyporeia* spp., (2) a high intertidal one, dominated by *S. squamata* and (3) a low intertidal zone, dominated by *N. cirrosa*. Though, the natural existence of the uppermost species association, dominated by *Bathyporeia* spp., is doubtful because of the presence of a storm-water dyke between MHWS and MHWN. In this study, where at all but the first transect the uppermost intertidal was not restricted by a storm-water dyke, *Bathyporeia* spp. and *S. squamata* were found between 200 and 500 cm above MLWS, with the population optimum of *Bathyporeia* spp. (370 cm above MLWS) only little higher than the optimum height for *S. squamata* (350 cm above MLWS). The expected division of the low intertidal species association on a macrotidal, ultra-dissipative beach (McLachlan and Jaramillo, 1995; Souza and Gianuca, 1995; Borzone *et al.*, 1996; McLachlan *et al.*, 1996) was not apparent in this study. Yet, as already stated, the troughs on the beach, which were not taken into account in this study, may harbour other species associations, which cannot be detected in this study.

The vertical distributions of several species of the low intertidal species association (e.g., *N. cirrosa* and *Spio filicornis*) are restricted to the zone from the MT level downwards the beach and these species seem to reach their optimum at or below MLWS. Comparing the five most dominant species of this low intertidal species association with the dominant species of the subtidal *N. cirrosa* species association, as described by Degraer *et al.* (in press a), *N. cirrosa* is always represented in high numbers and four species, the polychaetes *N. cirrosa* and *Magelona papillicornis* and the amphipods *Urothoe poseidonis* and *Bathyporeia* spp., are abundant in both species associations. Only three of the dominant species of the subtidal *N. cirrosa* community (*Ensis* spp., *Eumida sanguinea* and *Diastylis bradyi*) were absent in the intertidal zone. Except for *U. poseidonis*, the most dominant species occurred with lower densities in the low intertidal zone in comparison with the subtidal zone. Furthermore, in comparison with the subtidal macrobenthos (Degraer *et al.,* in press a: more than 70 species), the intertidal zone only comprises thirty nine species. Although temporal variations have to be considered, these findings suggest that the low intertidal species association, in fact, is an intertidal extension of the subtidal *N. cirrosa* species association. The relation between intertidal and subtidal macrobenthic species associations has also been demonstrated by other authors (e.g., McIntyre and Eleftheriou, 1968; Souza and Gianuca, 1995; Borzone *et al.,* 1996). The stress of longer exposure time, positively correlated with the height on the beach, creates a suboptimal situation for the originally subtidal populations and causes a decrease in density, biomass and number of species higher on the beach. At about the MT level (2 times 6 h exposed d^{-1}) no subtidal organism is likely to survive. Since samples were taken at lower levels on the beach in winter and, thus, into the optimal habitat for these low intertidal species, it explains (1) the higher average density and biomass of the low intertidal species association in winter in comparison to summer and (2) the higher number of species found in winter (22 species) in the low intertidal zone, in comparison to summer (13 species), with new, typically subtidal species as the polychaetes *Sigalion mathildae*, *Spiophanes bombyx*, *Anaitides mucosa*, *M. papillicornis* and *Harmothoe* sp. and the bivalve *Tellina tenuis* (Degraer *et al.,* in press a) in winter. Critical evaluation of the intertidal distribution of the samples, when comparing low intertidal species association characteristics with other studies, is thus advized.

SUMMER – WINTER COMPARISON

Temporal changes within the macrobenthos of sandy beaches may be related to changes in density and biomass of different species, caused by recruitment, mortality and production (e.g., Ismail, 1990; Bamber, 1993; Santos, 1994; Souza and Gianuca, 1995; Jaramillo *et al.,* 1996). As the temporal variation in this study only resulted out of one summer (September 1996) and one winter campaign (March 1997), the observed temporal variation cannot uniquely be attributed to seasonality.

Whereas the macrobenthic density and biomass of the low intertidal species association remained more or less constant during the sampling period, a decrease between summer and winter was obvious for the high intertidal species association. The drastic decrease of the density and biomass in the high intertidal zone may be explained by the heavy storms, slightly coarsening the sediment in the uppermost stations, and the freezing temperatures, covering the high intertidal zone with ice (personal observation), preceding the winter sampling campaign. In the low intertidal zone, no storm impact on the sedimentology was observed and because of the more frequent submersing of the low intertidal zone, temperatures on and in the sandy sediments were buffered by the more temperate water (minimum 2°C). On the other hand, even with high mortality rates during winter, the low intertidal species association can retain similar densities and biomass due to a possible continuous influx of animals from the subtidal into the low intertidal zone. The high intertidal species association lacks this habitat continuity with a source of immigrants: strong disturbances may thus deplete the populations.

It can be concluded that the macrobenthos of the macrotidal, ultra-dissipative sandy beach of De Panne shows a lot of similarity with other beaches worldwide. Yet, even though not all beach habitats have been taken into account, the number of species, recorded in this study, exceeds the number of species found on most other beaches. Two species associations, correlated with elevation, were detected. Conversely to the high intertidal species association, the low intertidal species association has to be regarded as an intertidal extension of a typically subtidal species association. Summer – winter comparison revealed a decrease in density and biomass within the high intertidal species association.