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INTERTIDAL ZONATION OF MACROINFAUNA ON A DISSIPATIVE, SANDY BEACH AT DE PANNE (BELGIUM) : A PILOT STUDY

by

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ABSTRACT. — To elucidate vertical (= from high to low water mark) macroinfaunal community patterns on little-studied Belgian dissipative sandy beaches, macroinfauna was sampled at eight stations along a seaward transect at De Panne. Mean sand particle size was 196 µm, and the beach slope was *ca.* 1 : 90. Nineteen species were collected (excluding non-quantitatively sampled species), nine of which were polychaetes and eight were crustaceans. Total macroinfaunal abundance per station ranged from 103 to 585 ind./m^2. Polychaetes and crustaceans were numerically dominant, comprising more than 98% of total numbers. Seaward spatial distributions of abundant species were interpreted to represent three biotic zones or macroinfaunal communities, as suggested by a kite diagram, TWINSPAN and CCA. These findings indicate that an environmental gradient of seaward variation in elevation above MLWS, sediment gravel fraction and sediment organic content largely determines the sandy beach community structure at De Panne.

INTRODUCTION

Although the distribution of macroinfauna (the fauna living actually buried in the sediment and retained by a 1 mm mesh sieve) on sandy beaches has been well-documented in many parts of the world (*e.g.*

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MORTON & 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 & GIANUCA, 1995) the macroinfauna inhabiting European and Belgian sandy beaches has been, respectively, poorly and not documented.

This project was initiated as a pilot study for a larger project investigating zonation and seasonal variation of the intertidal macroinfauna on a range of Belgian beaches, with the objective of investigating the most important factors, natural and anthropogenic, influencing macroinfaunal community structure.

Study area

A dissipative beach (a beach characterized by a low beach gradient, fine to very fine sediments and a surf zone with the presence of numerous spilling lines of breakers) fronting the 'Westhoek' dune reserve at De Panne, nearby the Belgian-French border (51°05′3″N-2°34″0″E) was selected as an example of a relatively undisturbed Belgian beach (Fig. 1). Although there are housing developments within the foredune zone, the relatively low density of buildings and the smaller

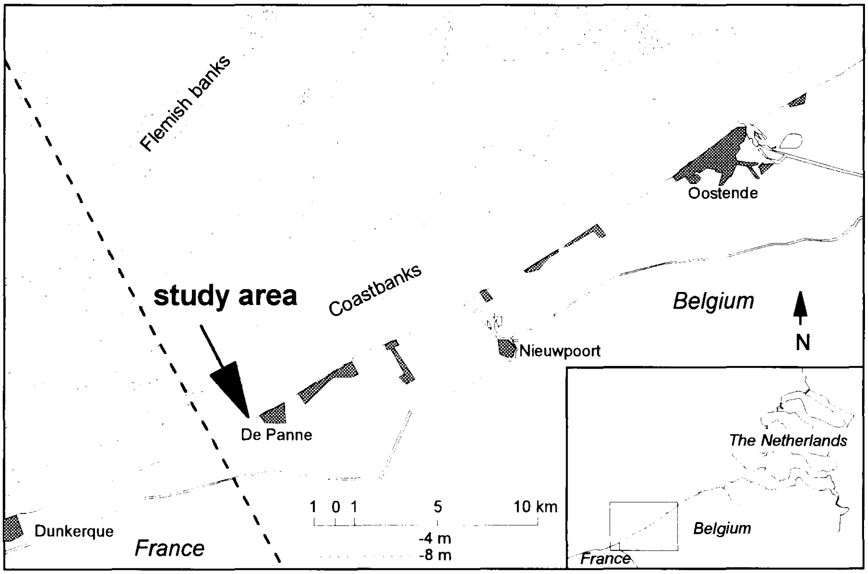

FIG. 1. — Map of the Belgian coastline, showing the position of the study area.

number of visitors to the beach (because of restricted access), contributes to reduced anthropogenic influences compared to other Belgian beaches.

The landward margin of the intertidal zone is interrupted by a concrete storm-water dyke, built to protect the coastal development from seawater inundation. Beyond the dyke is a low-lying dune area, stabilized by marram grass, *Ammophila arenaria*. The width of the intertidal zone is approximately 450 m, and the general slope of the beach is *ca.* 1 : 90 (LAHOUSSE, HAECON, pers. comm.), resulting in a dissipative beach. When sampling was done in summer 1995, wave height was small and the beach rated as 'sheltered' according to MCLACHLAN's (1980) universal exposure rating system. The beach has several shallow depressions parallel to the water's edge, in which water is retained on the outgoing tide.

MATERIAL AND METHODS

Sampling was undertaken on 23 August 1995, when high tide was scheduled for 11 : 40 am (4,57 m above mean low water spring, or MLWS), and low tide for 18 : 16 pm (1,05 m above MLWS). The distance from the dyke to the shore was divided into six approximately equal segments, with a sample station at each, and one station between the two closest to the seaward margin. Sampling began at high tide, and followed the receding water down the beach. The highest station (B1) was immediately in front of the storm-water dyke, and the lowest (B8) was 1,08 m above MLWS. Elevation above MLWS of each station was estimated with a dumpy level.

Five samples, each with a surface area of 0,1026 m^2 and a depth of *ca.* 0,1 m were taken at each of the eight stations. The sediment was sieved on the beach through a 1 mm mesh sieve and the residual was fixed in 8% buffered formaldehyde-seawater solution in the field, and stained with Bengal Rose. Additional cores, adjacent to the samples, were collected for analysis of sediment characteristics.

In the laboratory, the sediment collected for faunal analysis was decanted ten times to separate all fauna from the remaining sediment and the remaining sediment was examined to collect larger macroinfauna, such as bivalves, that were too heavy to be floated out by decantation. Fauna was extracted under a dissecting microscope. All macroinfauna was counted and identified to species level where possible. Fauna that was not sampled quantitatively (nematodes, copepods, Cnidaria and Ophiuroidea smaller than 1 mm) was included in the species list, but excluded from all analyses.

For all further analyses, faunal densities were extrapolated to number of individuals per m^2 (ind./m^2). To characterize vertical (from high to low water mark) community patterns, macroinfaunal data were subjected to 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). Macroinfaunal abundance data (ind./m^2) were normalized by means of a fourth root transformation (SOKAL & ROHLF, 1981 ; FIELD *et al.*, 1982) and further subjected to a Canonical Correspondance Analysis (CCA) (TER BRAAK, 1988), together with elevation above MLWS, and sand physical and chemical properties as environmental variables. A number of descriptors were linearly correlated, and were subsequently eliminated from the ordination.

Biomass (Ash-Free Dry Weight, or AFDW) estimates of the polychaete families Spionidae, Glyceridae, Capitellidae, and Phyllodocidae, and the crab *Portumnus latipes* were obtained by loss of mass on ignition ($500 \pm 50°C$ for 2 hours) of oven-dried samples (70°C for 48 hours). Biomass (AFDW) of all other fauna was calculated by regression analysis : the standard length of crustaceans, the maximum shell length of bivalves, and the width of the tenth segment of the polychaete family Nephtyidae were drawn at the highest possible magnification under a dissecting microscope. The sketches were digitized, and the calculated lengths subjected to regressions to estimate AFDW (GOVAERE, 1978 ; MEES, 1994 ; DEGRAER & VINCX, 1995).

The sediment was analyzed for physical and chemical properties. Sediment sub-samples were oven-dried at 105°C for 12 hours, and then ashed in a muffle furnace at $500 \pm 50°C$ for 2 hours 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. Sand particle size ($<$ 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.

General

Mean sand particle size (Fig. 2a) was between 180 and 217 μm (average 196 μm), and became progressively finer towards the subtidal zone. Carbonate (CO_3^{2-}) content (Fig. 2b) was between 2,8 and 25,0% (average 12,2%) of the sand mass, and generally increased downshore, although erratically. TOM (Fig. 2c) ranged from 0,4 to 1,0% (average 0,6%) of the sand mass, peaking at station B5 and decreasing land- and seawards. Gravel was only present at the stations B2 and B3, with a minimum of 1,5 and a maximum of 10,5% of the sand mass.

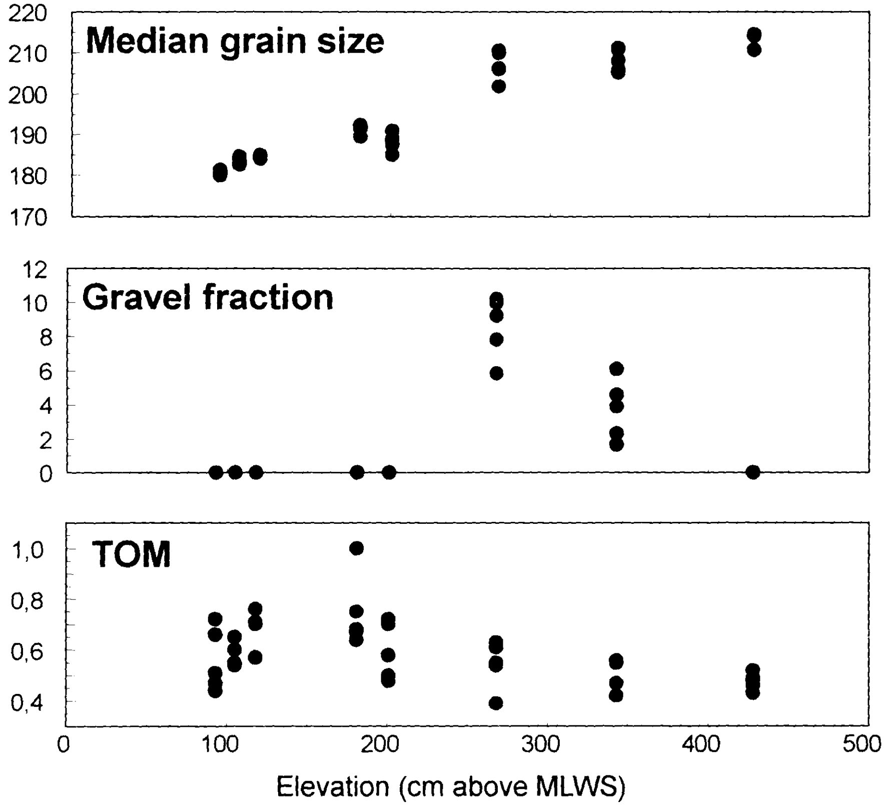

FIG. 2. — The vertical distribution over the intertidal zone of the median grain size in μm (Fig. 2a), gravel fraction in mass percentage (Fig. 2b) and TOM in mass percentage (Fig. 2c).

A total of 19 species was collected on the beach (excluding non-quantitatively sampled taxa), nine of which were polychaete worms and eight were crustaceans. Total macroinfaunal abundances ranged from 103 ind./m^2 at station B4 to 585 ind./m^2 at station B3. Polychaetes and crustaceans were numerically dominant in all samples, always comprising more than 98% of total macroinfaunal numbers. On the upper shore, *Bathyporeia* sp. formed 88% of total numbers, while polychaetes formed at least 70% of total numbers at all the other stations. Polychaete density ranged from 34 to 538 ind./m^2, with *Scolelepis squamata* and *Nephtys cirrosa* being the most abundant. Crustaceans reached a maximum of 339 ind./m^2, largely dominated by the amphipods of the genus *Bathyporeia* (maximum 293 ind./m^2), followed by far lower densities of the isopod *Eurydice pulchra* (maximum 30 ind./m^2).

Vertical density distribution

There were clear zonational changes in the distribution and abundance of the macroinfauna (Fig. 3).

Bathyporeia and *E. pulchra* were characteristic for the high intertidal zone, attaining a maximum density (respectively, 293 and 30 ind./m^2) at the most landward station (B1). *S. squamata* was virtually confined to the three uppermost stations and was most abundant at the second and third station, B2 and B3 (respectively, 36 and 13 ind./m^2).

The mid-intertidal stations (B4 and B5) did not support any species in great abundance.

Concerning the low intertidal stations, the predator *N. cirrosa* dominated the macroinfaunal numbers at the lower stations (B4-B8), being most numerous at B7 (134 ind./m^2). Though this species occurred throughout the whole intertidal zone except for the most landward station. Other species important at the lower beach stations were the mysid shrimp *Gastrosaccus spinifer* (maximum density of 28 ind./m^2) and small individuals of the crab *Portumnus latipes*. Spionid polychaetes of the genus *Spiophanes* occurred only at the stations B7 and B8.

Vertical biomass distribution

Total biomass (AFDW) peaked at station B3 at about 800 mgAFDW/m^2. The minimum total biomass (40 mgAFDW/m^2) was found at station B1. Generally, from high to low water, the total biomass increased from B1 to B3, decreased from B3 to B5 and then tended to increase slowly towards the subtidal zone.

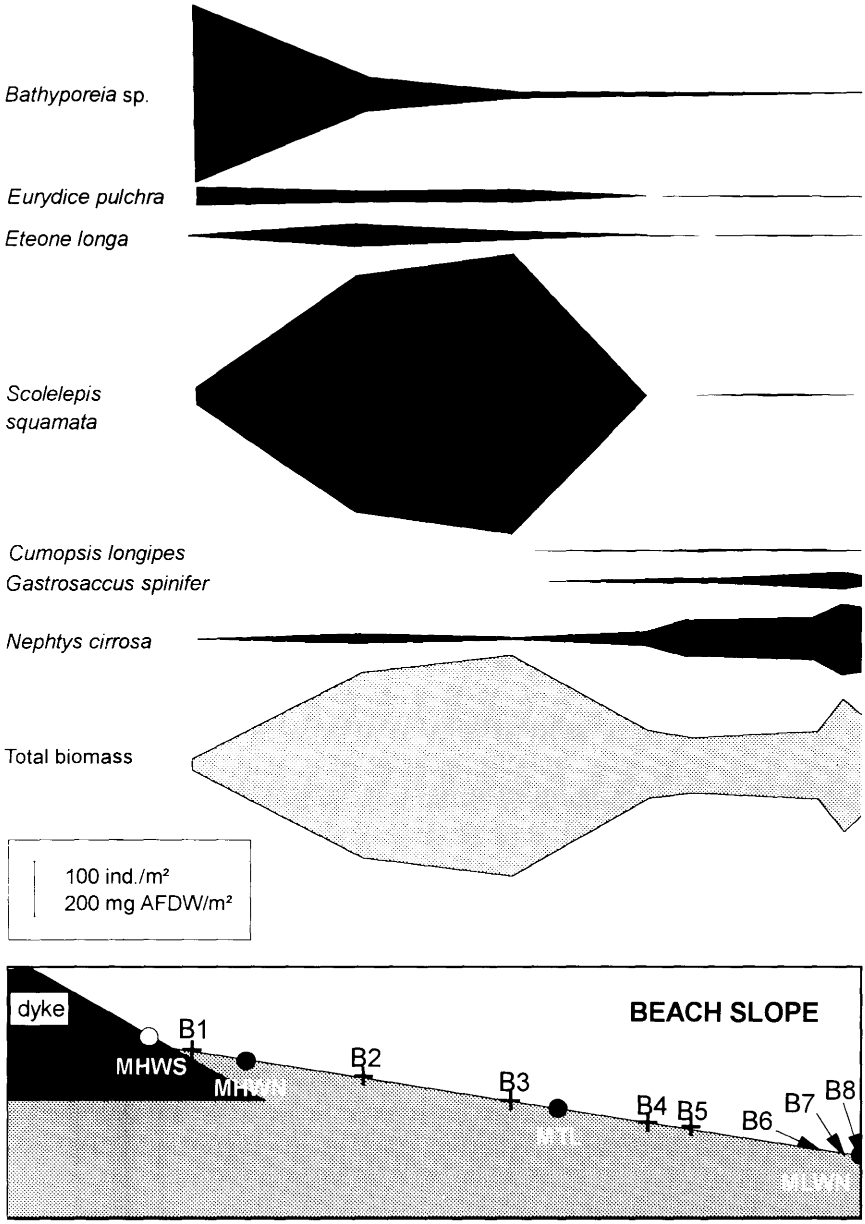

FIG. 3. — Kite diagram representing the intertidal distribution of the macroinfauna at De Panne beach : densities in black, biomass in grey. Distance between sample stations on the horizontal and vertical plane is proportional to elevation, with MHWS = mean high-water spring ; MHWN = mean high-water neap ; MTL = mean tidal level ; MLWN = mean low-water neap. The beach slope is presented schematically : without indication of bars and troughs occurring on the beach.

Communities

The graphical presentation of the two-way table (Table 1), with indication of the indicator species at each division, resulting out of TWINSPAN with the densities, is shown is Fig. 4. There was a high ecologically relevant splitting at the first division (eigenvalue 0,698) between the high-shore and low-shore stations. As suggested by the species distributions in the kite diagram (Fig. 3), *N. cirrosa* and *G. spinifer* were indicative for low-shore stations, while *E. pulchra*, *S. squamata* and *Bathyporeia* sp. were typical for stations closer to the

Table 1

Two-way table ordered and classified by TWINSPAN.

Species names are shown on the left ; samples at the top. The classification of the samples is indicated along the bottom margin. Values indicate a scale of abundance (1 : 1-10 ind./m^2 ; 2 : 11-20 ind./m^2 ; 3 : 21-60 ind./m^2 ; 4 : 61-150 ind./m^2 ; 5 : > 150 ind./m^2), with absence of species represented by the symbol '—'. TWINSPAN indicator species on the first level are indicated in bold.

Campaign	BBBBBBBBBBBBBBBBBBBBBBB	BBBBBBBBBBBBBBBBB
Station	66667784557788855574468	41114222223333311
Replica	23451232344512412533415	51341123451324525
Phyllodocidae	-1---------------------	-----------------
Cumopsis longipes	1-1------1-----1-1--1--	-----------------
Urothoe poseidonis	-------------1-3223----	--------1--------
Crangon crangon	----1---2------2-------	-----------------
Nephtys cirrosa	**44444443445545543343334**	**----31--22-12----**
Gastrosaccus spinifer	**1323211---11---2-11113-**	**1----------------**
Portumnus latipes	---11-132--2111-1-1311-	2------------1---
Spio filicornis	22--2-2-33131-23-3-33-3	-----231-211-----
Mytilus edulis spat	--------------------111	---1-------------
Eteone longa	-------------------1111	-----24333-1222--
Glycera capitata	-------------------1---	------1---11-21--
Scolelepis squamata	**---------------------3-**	**-----555555555534**
Oligochaeta	-----------------------	------13---------
Capitellidae	-----------------------	------11--------2
Eurydice pulchra	**--1---2----------------**	**-11--221-22133234**
Pygospio elegans	-----------------------	1----1-----------
Spionidae	-----------------------	--131------------
***Bathyporeia* sp.**	**------1--------1---12--**	**244534233423---55**
Haustorius arenarius	-----------------------	-2-------------1-
	00000000000000000000000	11111111111111111
	00000000000000000001111	00000111111111111
	0000000000000001111	01111000000000011
	000000011111111	0000000111

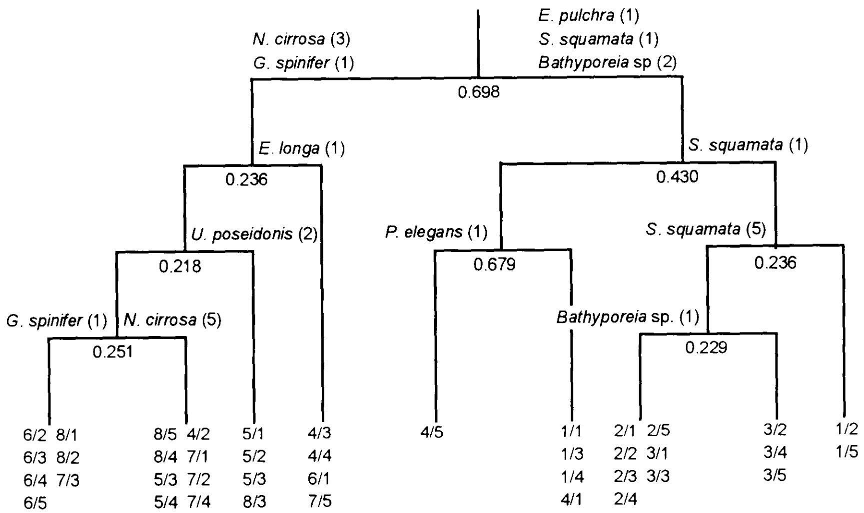

FIG. 4. — Two-way dendrogram resulting from the application of TWINSPAN on the macroinfaunal data collected at De Panne beach. Indicator species which demarcate samples to either side of the divisions are provided. Numbers in brackets represent categories of abundance defined by pseudospecies cut levels. The cut levels were 0, 10, 20, 60 and 150 ind./m^2. Numbers at the divisions are eigenvalues, an indication of the importance of the split. Codes at the bottom of the dendrogram represent sampling stations, with as an example 4/2 for station 4 replica 2.

driftline. Station B4 was split between the two main divisions, and possibly represents a transition zone.

CCA with the macroinfaunal data (densities) together with environmental variables supported previous trends in the clustering of similar stations (Fig. 5) : the analysis also divided the samples into an upper and a lower shore community, but with a trend in separating the upper shore community into two zones, of which the higher zone was dominated by *Bathyporeia* sp. and the lower by *S. squamata.* Indicator species, identified by TWINSPAN, were superimposed on the ordination. Since gravel was only recorded at station B2 and B3, this sediment property was strongly associated with these stations. Elevation above MLWS and TOM content of the sediment explained a high percentage of the spread on axis I, and it is likely that these attributes determine the distribution of species occurring on the high and low-shore respectively. Monte Carlo permutations showed that the first canonical axis (eigenvalue 0,59) was highly significant ($p < 0{,}01$) with the environmental variables.

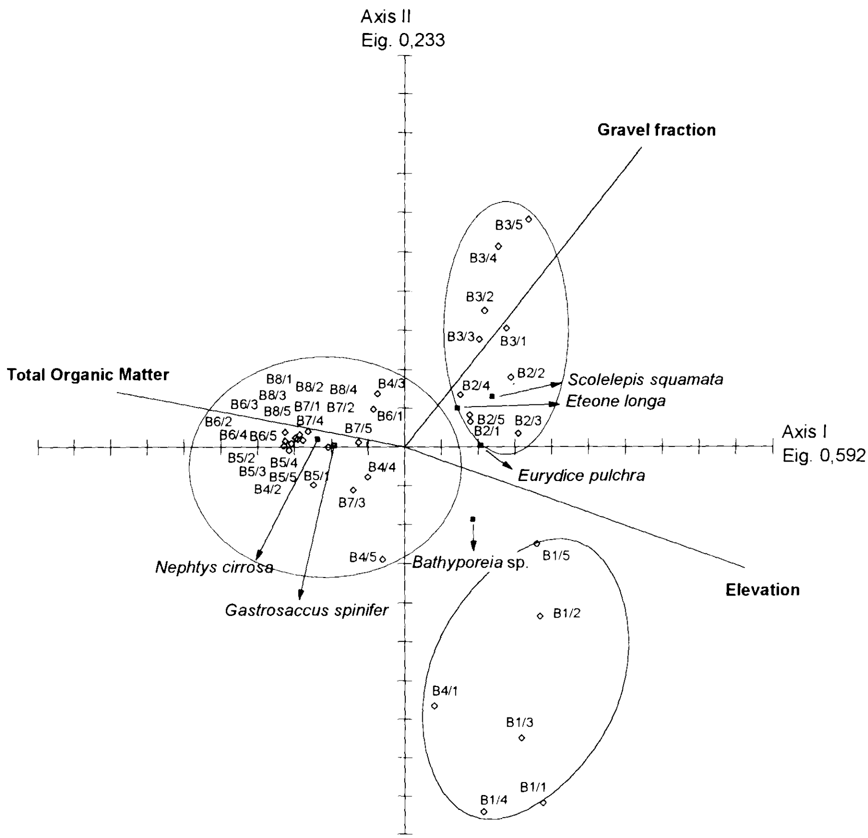

FIG. 5. — Canonical Correspondance Analysis of the macroinfaunal composition at De Panne beach. B1 is the most landward margin, and B8 is the station closest to the sea. B1/5 represents replicate 5 at station 1. Arrows indicate differential species identified with TWINSPAN analysis. Important, differentiating environmental variables are bold.

DISCUSSION

As this study was initiated as a pilot study for macroinfaunal research on Belgian beaches only one transect, which has been chosen to represent a typical Belgian beach, was sampled only once. This fact makes restrictions on the generalization of the results to all Belgian beaches, but nevertheless comparisons with other studies already give a first idea about similarities with intertidal zones world-wide.

On a European scale, macroinfaunal density and composition at De Panne beach were similar to that encountered by JUNOY & VIÉITEZ (1992) on exposed beaches near the mouth of an estuary in northwest

Spain (19-825 ind./m²), where polychaetes and crustaceans were the most dominant macroinfauna. There was a number of species in common, although the median grain size on the Spanish estuarine beaches was larger (300 µm compared to 196 µm at De Panne). At Norderney (on the German North Sea coast), *S. squamata*, *Bathyporeia* spp., *Haustorius arenarius*, *E. pulchra* and *Eteone longa* were among the ten most abundant species in the area between the high water mark and 1,5 m below the low water mark (DÖRJES, 1976). British sandy beaches vary in location from sheltered sea lochs to open coasts ; consequently there are major differences in faunal species composition and density (*e.g.* STEPHEN, 1929, 1930 ; SOUTHWARD, 1953). Although this makes comparisons with results of the present study difficult, most species collected at De Panne were also among the dominant species collected during early studies on British open beaches (*e.g.* STEPHEN, 1929 ; ELMHIRST, 1931 ; MCINTYRE & ELEFTHERIOU, 1968 ; WITHERS, 1977).

On a world-wide scale, crustaceans tend to be the most abundant macroinfauna on exposed (and tropical) beaches, while molluscs and polychaetes abound on sheltered beaches (*e.g.* MORGANS, 1967 ; MORTON & MILLER, 1968 ; WOOD, 1968 ; CROKER *et al.*, 1974 ; SEAPY & KITTING, 1978 ; DEXTER, 1983). At De Panne, crustaceans dominated only the most landward station (B1), while polychaetes dominated all the other stations. Crustaceans may have been impoverished because of the dyke, restricting the upper intertidal region. The reason for the paucity of molluscs is unclear, since there are extensive bivalve communities on the shallow subtidal sandbanks in the area (DEGRAER *et al.*, submitted).

Zonational patterns

The spionid polychaete *S. squamata* was the most abundant species at De Panne, reaching maximum abundance on the upper shore (431 and 505 ind./m² at the stations B2 and B3 respectively), and the most important in terms of biomass. *S. squamata* is important on sandy beaches in many parts of the world (*e.g.* DÖRJES, 1976 ; WITHERS, 1977 ; MCLACHLAN *et al.*, 1981 ; BALLY, 1983), although its position on the shore varies. At Norderney, *S. squamata* was the most abundant species, occurring with an average density of 160 ind./m² across the entire intertidal zone (DÖRJES, 1976). Furthermore, the polychaete was one of the numerically most abundant species on the middle to low shore on several sandy beaches in Wales (WITHERS, 1977), a sandy beach in Paraná State, Brazil (SOUZA & GIANUCA, 1995) and South Africa (MCLACHLAN *et al.*, 1981).

Maximum total biomass at De Panne was recorded at station B3 (1,5 g AFDW/m^2) as a result of the high numbers of *S. squamata*, while the average biomass over all eight stations was 0,4 g AFDW/m^2. Few biomass data are available for comparison with other intertidal areas. MCINTYRE & ELEFTHERIOU (1968) recorded an average biomass of 1,3 g DW/m^2 for infauna retained on a 0,5 mm sieve at Firemore Bay in Scotland, while WITHERS (1977) obtained mean values of between 0,3 and 13,8 g DW/m^2 for 16 beaches along the south-west coast of Wales. The average biomass for a sedimentary tidal flat in the northern Wadden Sea was calculated to be 65 g AFDW/m^2 (REISE *et al.*, 1994), which was dominated by species typical of sheltered areas, such as *Arenicola marina* and six species of molluscs (REISE *et al.*, 1994). Using the results of 105 published sandy beach surveys, BALLY (1981) calculated the average biomass on medium energy beaches to be 1,97 g DW/m^2, and three times that figure on low energy beaches. The low biomass on the beach of De Panne could be attributed to the paucity of molluscs, which taxon MCLACHLAN (1983) considered the most important in terms of biomass.

Communities

At De Panne, three faunal communities were identified on the basis of species distribution and abundance represented by the kite diagram.

The first community (B1), characterized by high densities of *Bathyporeia* sp. and the presence of *H. arenarius*, supported the lowest biomass of all the sampling stations. Usual high-shore species, notably talitrid amphipods (DAHL, 1952), were probably excluded by the presence of the dyke.

The second community (B2 and B3) was identified as that in which the polychaetes *S. squamata* and *E. longa* attained the highest densities. Other species collected in this community included *E. pulchra* and *Bathyporeia* sp., although at lower densities than in the first community.

The third community (B4 to B8) was characterized by the carnivorous polychaete *N. cirrosa*, which increased in abundance towards the lower stations. Other collected species included the crustaceans *Gastrosaccus spinifer*, *Portumnus latipes*, *Cumposis longipes*, *Urothoe poseidonis* and *Crangon crangon*.

The designation of these three communities was supported to some extent by the application of TWINSPAN. There was clearly an early division between high- and low-shore stations, and stations B4 to B8 (corresponding to community 3) were closely grouped together. By means of TWINSPAN, no separation between the first and the third community was detected. CCA produced similar groupings to those inferred from the kite diagrams. Station B1 (community 1) was isolated from all other stations, while stations B2 and B3 (community 2) were all placed in close proximity, and stations B4 to B8 were clustered tightly together (community 3).

Station B1 seemed to incorporate a first community (not recognized by TWINSPAN). However, this station may be influenced by the presence of the dyke, as B1 is situated only 1 meter from the dyke. The first community may thus be an atypical community, not representing a naturally existing community.

A number of zonation schemes for sandy beaches have been proposed, including DAHL's (1952) universal zonation based on the distribution of crustacean fauna, SALVAT's (1964) zonation according to the degree of moisture in the sand, and BROWN & McLACHLAN's (1990) scheme which incorporates features of both DAHL's and SALVAT's zonations, as well as the distribution of a range of macroinfauna (polychaetes, molluscs and crustaceans). All three schemes have been supported by examples of zonational patterns on beaches worldwide (*e.g.* WOOD, 1968 ; MORTON & MILLER, 1968 ; PHILIP, 1974 ; BALLY, 1983 ; McLACHLAN *et al.*, 1981 ; McLACHLAN, 1990 : JARAMILLO *et al.*, 1993 ; SOUZA & GIANUCA, 1995), and in several cases characteristic macroinfaunal species were superimposed onto Salvat's communities (*e.g.* BALLY, 1983 ; SOUZA & GIANUCA, 1995). At De Panne, community 1 and community 2 corresponded to DAHL's (1952) midlittoral and BROWN & McLACHLAN's (1990) littoral community. The uppermost community of all the schemes was probably excluded at De Panne because of the storm-water dyke constructed at about 17 cm vertically below the mean high water spring mark.

Amongst the factors considered to be of significance in the distribution and abundance of intertidal sandy beach macroinfauna, beach type, grain size, exposure to wave action, organic enrichment, water temperature, tidal level, and the swash climate have been recognized as being of major importance (SOUTHWARD, 1953 ; DEXTER, 1983 ; McLACHLAN, 1990 ; JUNOY & VIÉITEZ, 1992 ; McARDLE & McLACHLAN, 1992 ; GIBSON *et al.*, 1993 ; JARAMILLO & McLACHLAN, 1993). Of the environmental variables measured in this study, principally the gravel and TOM content of the sediment and the elevation above MLWS were influencing the macroinfaunal community structure.

In conclusion, this study revealed three communities clearly linked with the elevation above MLWS. From the dyke to the low water level, dominant species changed from *Bathyporeia* spp. over *S. squamata* and *E. pulchra* to *N. cirrosa*, all genera and species showing the same vertical distribution on many sandy beaches world-wide. The natural occurrence of the highest community, dominated by *Bathyporeia*, may be doubtful because of the nearby concrete dyke, which possibly influences the water currents and sedimentology at station B1.

As this study, being a pilot study, only refers to one transect from the high to the low water level, no general conclusions about the zonation of the macrobenthos on Belgian sandy beaches or even De Panne beach can be made. Further research should concentrate on a greater number of transects across the length of the beach of interest, at different seasons, before intertidal zonational patterns can be proposed.

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