Mariene Biologie
Instituut voor Dierkunde
Vakgroep morfologie, systematiek en ecologie

UNIVERSITEIT
GENT

MACROBENTHOS OF SHALLOW MARINE HABITATS (BELGIAN COAST) AND ITS USE IN COASTAL ZONE MANAGEMENT

HET MACROBENTHOS VAN ONDIEPE MARIENE HABITATS (DE BELGISCHE KUST) EN HET BELANG VOOR HET BEHEER VAN DE KUSTZONE

Steven Degraer

Academiejaar 1998 – 1999

Promotor: Prof. Dr. Magda Vincx
Co-promotor: Prof. Dr. Eckhart Kuijken
Prof. Dr. Patrick Meire

Proefschrift voorgelegd tot
het behalen van de titel van
Doctor in de Wetenschappen,
groep Biologie

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Faculteit Wetenschappen

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DANKWOORD

Naar het einde van deze studie – die nu toch al 5 ½ jaar in beslag neemt – toe, begin ik mij te realiseren dat (inclusief mijn opleiding in de Biologie) 33.9 % van mijn leven zich nu al heeft afgespeeld aan de Universiteit Gent. Eigenlijk is dat evenveel als de totale duur die ik op de kleuter- en lagere schoolbanken samen heb gespendeerd en dat leek me (toen) toch wel héél lang. Het is dan ook vrij logisch dat heel wat van mijn kennissen en vrienden rechtstreeks of onrechtstreeks iets met deze universiteit hebben te maken. In dit dankwoord (*nota bene* de enige bladzijde van dit werk die door velen gelezen zal worden) wil ik dan ook eventjes op een rijtje zetten wat vele van deze personen voor mij hebben betekend tijdens mijn 'universitaire carriere' – die trouwens hopelijk niet ophoudt bij de verdediging van dit doctoraat.

Eerst en vooral (en zo hoort het, lieve mensen!) wil ik mijn promotor, Prof. Dr. Magda Vincx, bedanken voor alles wat ze voor mij reeds heeft gedaan. Aangezien zij ook de begeleiding van mijn licentiaats thesis op haar heeft genomen, heb ik gedurende meer dan zes jaar van haar kennis kunnen profiteren (of is 'genieten' hier een beter woord?). Dankzij haar jarenlange ervaring in het wetenschappelijk onderzoek, eerst als diensthoofd van de Sectie Mariene Biologie en later van de groep Dierkunde, kreeg ik de ideale kans mijn zin voor het mariene wetenschappelijk onderzoek bij te scherpen. Verder, wil ik haar ook bedanken voor de vele congressen, workshops en cursussen die ik dankzij haar bereidwillige (financiële) medewerking heb kunnen bijwonen. Het waren stuk voor stuk interessante belevenissen! Ook eigen initiatieven, zoals het onderzoek naar het macrobenthos van de Vlaamse stranden, werden steeds door haar gesteund. Daarbovenop komt nog (en dat is misschien wel het aller belangrijkste) dat het, wat mij betreft, altijd aangenaam samenwerken is geweest, zo ook wat betreft de vele project-vergaderingen waaraan we samen deelnamen.
Tijdens deze studie heb ik Prof. Dr. Patrick Meire – co-promotor van dit werk – leren kennen als iemand die van heel veel zaken goed op de hoogte is. Dat dit rechtstreeks ten goede van dit werk kwam, hoeft hier eigenlijk zelfs niet vermeld te worden. Hij probeerde steeds tijd voor mij te maken als dat nodig was – alhoewel dit niet altijd makkelijk geweest moet zijn,

gezien zijn drukke agenda – en stond me bij met raad en daad. Vooral de vele discussies, die we samen hebben gevoerd, hebben zeker bijgedragen tot een (significante) verbetering van dit werk. Prof. Dr. Eckhart Kuijken – co-promotor van dit werk – wil ik vooral bedanken voor de onvoorwaardelijke steun die hij me gaf bij het prille begin van deze studie. Samen met Prof. Dr. Patrick Meire, voorzag hij me van allerhande literatuur over zeevogels en natuurbehoud, noodzakelijk voor de IWT beurs aanvragen. Verder zijn zijn opmerkingen over deze IWT aanvragen steeds van groot belang geweest.

Waardevolle commentaren op dit werk werden gegeven door Prof. Dr. Magda Vincx, Prof. Dr. Patrick Meire, Maaike Steyaert, Dr. Jan Mees, Dr. Jan Schrijvers, Alex Soares, en Dr. Ann De Ruyck.

Tijdens vier jaren van deze study (januari 1994 – december 1998) ontving ik een studiebeurs van het Vlaams Instituut ter bevordering van het Wetenschappelijk - Technologisch Onderzoek in de Industrie (IWT). Een gedeelte van deze studie werd gefinancierd door de Administratie Milieu, Natuur, Land- en Waterbeheer, afdeling Natuur (AMINAL) en de Afdeling Waterwegen en Kust (AWK). De firma SILT wordt bedankt voor het ter beschikking stellen van de OOSTENDE XI. Hierbij wil ik graag de goede samenwerking met de bemanning, George, Ivan, Jef, Johan, Lucas, and Patrick, onderstrepen en hen bedanken voor de bereidwillige medewerking bij het nemen van de stalen, de overuren, de soep en uiteraard ook de graanjenever, want soms was het toch wel een beetje frisjes.

This thesis would have been impossible without the help of Norma Arellano, who worked out part of the samples in the frame of her Master's thesis. 'Mijn' thesisstudenten, Liesbeth De Neve, Iris Mouton, Ciska Mortier, Johan Coenjaerts en Annemie Volckaert ben ik heel dankbaar voor de hulp bij het uitwerken van de vele stalen, maar ook voor de aangename en leerrijke babbels. *I also want to thank Bridget Elliott and Mary Bursey (University of Port Elizabeth, South Africa), who helped to start up the investigation of the macrobenthos of the sandy beaches.*

Op Johan Vandevelde, Vera Van Lancker en Annick Van Kenhove kon ik steeds rekenen bij het nemen van de stalen. Vrijwilligers, die uiteraard altijd welkom zijn geweest tijdens de staalname campagnes, waren Liesbeth Labarque, Koen Camelbeke, Dr. Olivier De Clerck, Edwin Ramboer, Ann Depoortere, Maaike Steyaert, Tjen, Alex Soares, Dr. Ann De Ruyck, An B., Liesbet D. en Liesbet M.

Alle medewerkers van de Sectie Mariene Biologie (Prof. Dr. Magda Vincx, Dr. Jan Schrijvers, Dr. Dré Catrijsse, Dr. Jan Mees, Dr. Ann Vanreusel, Dr. Tom Moens, Maaike Steyaert, Ann De Wicke, Nancy Fockedey, Bregje Beyst, Jan Vanaverbeke, Wendy Bonne, Marleen De Troch, Sandra Vanhove, Kris Hostens, Dirk Van Gansbeke, Myriam Beghyn, Danielle Schram, Annick Van Kenhove, Johan Vandevelde, Yves Israel *and all foreign students*) wil ik bedanken voor de verleende adviezen, het vele practische werk dat ik niet zelf heb uitgevoerd, en de vele babbels.

Verder stonden vele personen altijd klaar om mij met raad en daad bij te staan. Speciaal wil ik daarvoor bedanken: Jan Seys, Tom Ysebaert, Jeroen Van Waeyenberghe, Koen Devos en Prof. Dr. Maurice Hoffmann (Instituut voor Natuurbehoud), Johan Craeymeersch (Nederlands Instituut voor Oecologisch Onderzoek), Dr. Thierry Jacques, Ronny Schallier en Jan Haelters (Beheerseenheid Mathematisch Model Noordzee), ir. Jean-Louis Herrier (Administratie Milieu, Natuur, Land- en Waterbeheer), ir. Peter Dewolf, ir. Toon Verwaest en Bart Provoost (Afdeling Waterwegen en Kust), ir. Dirk Leroy en ir. Koen Mergaert (ECOLAS), Ed Ambrogio en Ralph Spagnolo (Environmental Protection Agency, USA), Dr. Ingrid Kröncke (Forschunginstitut Senckenberg, Deutschland) en Prof. Dr. John McDermott (Franklin and Marshall College, USA).

Alhoewel de bijdrage tot het tot stand komen van deze thesis misschien wel niet zo heel groot zal zijn geweest, wil ik toch mijn goede vrienden, Ludwig De Loose, Koen Camelbeke, Liesbeth Labarque, Ann Degrande, Olivier De Clerck, Heidi Mariën, Kris Rombouts, Kris Hostens, Els Vandeputte, Marc Libeer, Mieke Verbeke, Ruben Walleyn en Ann Bogaerts, bedanken voor de vele leuke momenten (en ik denk hierbij vooral aan de 'wintervakanties' en 'feestjes') die we samen hebben gehad.

Mijn lieve vriendin, Ann Depoortere, wil ik hierbij ook eens extra in de bloemetjes zetten Alhoewel ik er zeker van ben dat het niet altijd even gemakkelijk zal zijn geweest, heeft ze niet alleen reeds vele jaren samen met mij doorgebracht, maar zorgde ze er zelfs voor dat het altijd heel aangenaam thuiskomen was. Tijdens het finaliseren van deze thesis zorgde ze er verder voor dat ik al mijn aandacht aan 'mijn' werk kon besteden en kon ze (voorlopig) wel begrip opbrengen dat er niets aan ons 'huisje' veranderde. Ik zou ze nog voor heel veel willen bedanken... maar dat hang ik niet aan jullie neus. Wolfje, Flosjke, Pitoetje en Poesjkie waren altijd uitstekende stress-verlagende huisdieren. Ze bleven trouwens ook altijd luisteren!

Ook mijn ouders wil ik hier bedanken. Ze hebben me altijd ten volle in mijn keuzes gesteund, bleven in mij geloven en zijn dan ook een onmisbare steun voor mij geweest. Ook de ouders van Ann, Pol en Frieda, volgden met veel interesse mijn activiteiten.

Bedankt.

ABSTRACT

Several sandbank systems are found on the Belgian Continental Plate (BCP): (1) the Hinderbanks, (2) the Zeelandbanks, (3) the Flemish Banks, and (4) the Coastal Banks.

The Coastal Banks are composed of a combination of (1) a subtidal extension of the sandy beaches and (2) a series of shallow (< 8 m) sandbanks parallel to the coast. The latter can be subtidal as well as intertidal with mobile sandripples of different scales (De Moor, 1986; Ashley, 1990; Van Lancker, 1993). Within the area of the western Coastal Banks, two major geomorphological regions were distinguished (Figure 1). Within area 1, including the Stroombank and Balandbank, the sandbanks are oriented parallel to the coastline and separated from the beach by a gully, Kleine Rede. Their depth ranges from 3 to 8 m below mean low water spring (MLWS). The second area (area 2) comprises three sandbanks (Den Oever, Broersbank and Trapegeer) and a tidal trough (Potje), of which the depth ranges from about 0.5 to 8 m below MLWS. Being shallow and having a highly diverse topography, currents can change drastically within only tens of metres. This implies a large variety in sediments (Bastin, 1974; Buchanan, 1984; Houthuys, 1989), with median grain sizes from 160 to over 500 µm (Degraer *et al.*, in press a). Next to the Coastal banks, the shallow Belgian coast further includes the intertidal zone, fully composed of sandy beaches. From West to East, the slopes of these beaches generally increase and, consequently, a natural gradient from ultra-dissipative (UD) beaches in the West to low tide bar/rip (LTBR) beaches in the East is found. Due to the construction of the harbour walls of Zeebrugge, a disturbance of the natural morphodynamical gradient of beaches is demonstrated by the presence of ultra-dissipative beaches nearby Zeebrugge.

The western Belgian Coastal Banks are known for their great ecological importance. The area is designated as an area of international importance for waterfowl, according the Ramsar Convention (Kuijken, 1972), and fulfils all criteria of the EC Bird and Habitat Directives (Anonymous, 1979, 1992a). Furthermore, the Belgian government is studying the possibility to create two large marine protected areas (area 1: Stroombank and Balandbank; area 2: Potje, Trapegeer, Broersbank and part of Den Oever and Westdiep) within the area of the western Coastal Banks (Figure 1). The final designation of the protected areas will not

be considered before all concerned parties and interests have been consulted and a management plan has been set up.

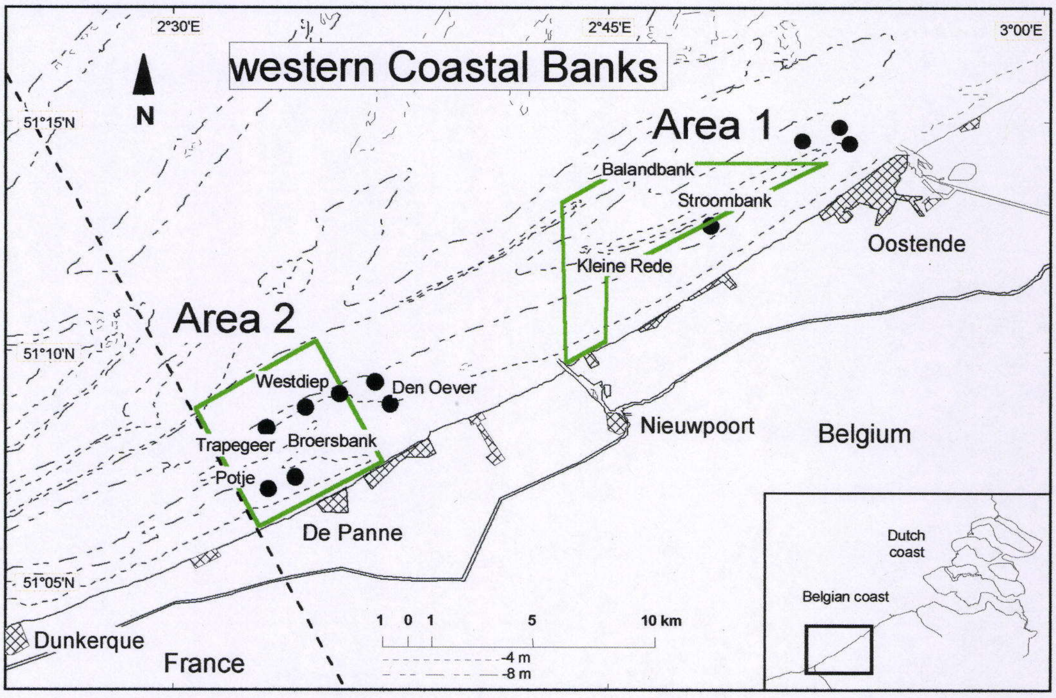


Figure 1. The geographical situation of the western Coastal Banks, with indication of the two major planned marine protected areas (green polygons: area 1 and area 2) and the spatial distribution of the *Lanice conchilega* community (●).

In order (1) to argue about the necessity of Belgian marine protected areas, (2) to select the marine protected areas, (3) to set up a management plan, and (4) to be able to evaluate the management plan, there is a strong need for scientific ecological information on the area. At present, except for the ornithological part (Maertens *et al.*, 1988, 1990; Devos, 1990; Offringa *et al.*, 1998), this information is largely lacking. The importance of the macrobenthos as the food resource for the common scoter (*Melanitta nigra*), being the most important seabird in the area (Maertens *et al.*, 1988, 1990; Devos, 1990), and the possible necessity of coastal defence works in the area, directly affecting the macrobenthos as bottom dwelling organisms, has led to the selection of the macrobenthos of shallow, Belgian marine habitats as the central study object.

As shallow marine habitats not only include the subtidal part down to a depth of 6 m, but also the intertidal zone up to the high water level (Reilly *et al.*, 1996), the macrobenthos of both the subtidal and intertidal Belgian coast (the western Coastal Banks and the sandy beaches, respectively) was studied, inclusive the Flemish beach nature reserve *Baai van Heist*. In first instance, the spatial distribution of the (subtidal and intertidal) macrobenthos in relation to the environment was investigated (Chapters 1, 5 and 6). Furthermore, the temporal variation, dynamics and stability of the subtidal macrobenthos (Chapters 2 and 3) and the spatial distribution and population dynamics of the bivalve *Spisula subtruncata* (Chapter 4) was studied.

To study the spatial distribution of the macrobenthos of the western Coastal Banks (Chapter 1), 39 macrobenthic samples, divided over two areas, were taken in October 1994. The two areas could not be clearly divided concerning their macrobenthic communities. TWINSPAN, Bray-Curtis Group-Averaging Cluster Analysis, and CCA revealed five coherent communities, linked with typical sedimentological factors: (1) the *Barnea candida* community in a very compact muddy sediment (median 14 µm), (2) a second community characterized by the presence of spat of *Mytilus edulis* (*'Mytilus edulis'* community), with a medium sandy sediment (median 456 µm), (3) the *Lanice conchilega* community inhabiting a fine sandy sediment (median 211 µm) (Figure 1), (4) the *Nephtys cirrosa-Echinocardium cordatum* community in a coarser fine sandy sediment (median 242 µm), and (5), closely related to the latter, the *N. cirrosa* community also occurring in a fine sandy sediment (median 224 µm). Only the *L. conchilega* community belongs to the diverse transition zone (Govaere *et al.*, 1980). The other four communities seem to be part of the heterogeneous, species-poor coastal zone associations. No open sea communities have been detected in the area. On the western Coastal Banks, only the *L. conchilega* community, because of the high numbers of *Abra alba, Tellina fabula*, and *Spisula subtruncata*, can be interesting as feeding grounds for the common scoter (*Melanitta nigra*). Comparison of the spatial distribution of the wintering common scoters and the *L. conchilega* community revealed no direct similarity. The factors possibly causing this dissimilarity were (1) the large mobility of the common scoter compared to the sessile macrobenthos or (2) the selection of 'sub-optimal' feeding grounds by the common scoter.

The macrobenthos of shallow coastal habitats is subject to a variety of physical and biological disturbances, varying in frequency and intensity, as well on a temporal and spatial scale. Consequently, the macrobenthic parameters (species composition, abundances, etc.) are continuously changing. To evaluate the ecological value of the *Lanice conchilega* community, knowledge on its temporal variation is indispensable. Furthermore, because of the possibility of recolonization by means of recruitment via the planktonic stages of many macrobenthic species, knowledge on the period of recruitment of the species allows to decrease the negative impact of the planned coastal defence works. The macrobenthic temporal variation and recruitment was studied in two stations over a 2.5 yr study period

(April '95 – October '97) (Chapter 2). From Spring till Summer '95, a general amelioration of the community's condition was attributed to the recruitment of, at least, the dominant species. Though the polychaete *Notomastus latericeus*, the bivalves *Abra alba* and *Tellina fabula*, and the gastropod *Hinia reticulata* showed no recruitment, recruitment of all other dominant species was detected. Recruitment of the polychaetes mainly occurred between April and August '95, while amphipode and bivalve recruitments were observed between July and October '95. An overwhelming recruitment of *Spisula subtruncata* with densities up to 150000 ind m^{-2}, taking place in August '95, possibly caused a general decrease of the number of species per sample (N_0) and the density of all dominant polychaete species in one or both stations after August '95. A new deterioration of the community between January and March '96, only observed in one station, was attributed to the drastic increase of the sediment's mud content of the station (from 5 to 30 %), negatively affecting the macrobenthos of the *L. conchilega* community usually found in a fine sandy sediment with low mud concentrations. In contrary to 1995, no successful recruitments were observed in 1996 nor 1997, illustrating the large year-to-year within the success of recruitment of the macrobenthos. It is thus extremely important to be aware of the natural variability or 'potentials' of a macrobenthic community in order to evaluate its ecological importance.

The macrobenthos of the western Coastal Banks thus show a large temporal variation, both within and between years. These benthic dynamics create a problem when setting up a management plan for benthic habitats: How many sampling campaigns, spread over how many years are necessary to draw the right conclusions? Therefore, one major question is to what level environmental managers can trust on a single sampling campaign, when trying to identify macrobenthos-rich area or communities, taking into account the macrobenthic dynamics. For this purpose, the macrobenthic species composition and density of 39 stations on the western Belgian Coastal Banks in October 1994 (Chapter 1) and 1997 are compared (Chapter 3). Though only minor changes within the physical characteristics of the 39 stations were detected, generally, a lower number of species and a lower density is found in 1997 in comparison with 1994. This deterioration is most obvious within the Polychaeta. Still, combining the closely related *Nephtys cirrosa – Echinocardium cordatum* and the *N. cirrosa* community to the *N. cirrosa* community *s.l.*, the same three macrobenthic communities, with similar macrobenthic species composition and densities, were found in 1994 and 1997: the *Lanice conchilega* community, the *N. cirrosa* community *s.l.*, and the '*Mytilus edulis*' community. On the community-level, especially the deterioration of the *L. conchilega* community, possibly partly caused by an extremely successful recruitment of the bivalve *Spisula subtruncata*, was clear. 84% of the stations is designated to the same community in 1997 as in 1994, indicating a quite stable spatial distribution of the macrobenthic communities. Furthermore, it is demonstrated that the relation between the stations' physical characteristics, especially the median grain size and the percentages of silt and coarse sand, and the occurrence of the macrobenthic communities on the western Belgian Coastal Banks can be used to predict the spatial distribution of the communities with an accuracy of 83%, only having information on the physical environment. Monitoring of the macrobenthos in the frame of coastal zone management should thus concentrate on the spatial distribution of the macrobenthic 'potentials' of the area, by the identification of (1) the spatial distribution of the macrobenthic communities, (2) the communities' environmental 'needs', and (3) the communities' 'potentials' by means of long-term monitoring of some selected stations within each community.

Within the communities of the western Coastal banks bivalves are fulfilling an important ecological role, not at least being the major food resource of the common scoter (*Melanitta nigra*), thousands of which are wintering on the western Coastal Banks. Next to this ecological importance, one of these bivalves, *Spisula subtruncata*, occurs in fishable stocks in the area and shellfisheries become interested in the commercial harvesting of these stocks. In order to provide information for a sustainable management of the *S. subtruncata* stocks on the western Coastal Banks, Chapter 4 aimed at (1) the description *S. subtruncata*'s spatial distribution and population dynamics and (2) understanding the implications for future *Spisula*-fishery in the area. The spatial distribution of *S. subtruncata* was studied in 1994 and 1997 in 40 stations in two areas of the western Coastal Banks. The population dynamics were investigated by monthly sampling of two stations between April 1995 and April 1996 and a seasonal sampling between April 1996 and April 1998. *Spisula subtruncata* had a patchy distribution in the deeper (6 m), fine sandy (200 ± 20 µm) sediments of the *Lanice conchilega* community, mainly found in the most western part of the Coastal Banks. In August '95, an overwhelming and successful recruitment was observed in this area. Local densities were as high as 150000 ind m^{-2}. Minor, non-successful recruitments were detected in August '96 and August '97. Growth could be described by a seasonally oscillating version of the von Bertalanffy growth function: a growth stop was observed from late Autumn till early Spring. Probably because of differences in environmental conditions, the growth parameters K and L_∞ differed slightly between the two stations (0.7 and 32 – 33 mm for one stations and 0.9 and 31 – 32 mm for the other station. A combination of length and individual biomass increment shows: (1) a faster length increment of smaller individuals during the second growing period (catching-up phenomenon), (2) a constant length combined with a decreasing individual biomass during the suboptimal winter periods (except for the first one, when the individual biomass slightly increased), (3) a positive relation between the individual biomass decrease and the seawater temperature during the winter periods, and (4) a strong increase of the individual biomass in early Spring (April '97 and April '98) because of gametogenesis, followed by a decrease because of spawning (August '97). The total production of the cohort '95 in the tidal gully (Potje) during the study period is estimated at about 1500 g AFDW m^{-2}. Shellfishery on the ecologically important western Coastal Banks should not be considered since: (1) the food resource for the common scoter will decrease and will possibly lead to the disappearance of the seaducks in the area, (2) the ecologically most diverse and rich macrobenthic *Lanice conchilega* community will be destructed, and (3) the economical rendability of *Spisula*-fishery is doubtful, because of the highly variable recruitment along the Belgian coastline.

As already mentioned, the Belgian shallow marine habitat is not only composed of the shallow subtidal zone, but also includes the intertidal zone. To study the detailed 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 (Chapter 5). 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* community *s.l.*, 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.

As the species composition, densities, biomass and zonation patterns of the macrobenthos of sandy beaches is influenced by the morphodynamics and morphology of the beaches, the macrobenthos of the Belgian coast was further investigated along a small-scale morphodynamic gradient (Chapter 6). From the mean high water spring level (MHWS) to the mean low water spring level (MLWS), eight Belgian beaches have been investigated along a single transect, perpendicular to the water line. At each transect, ten to 14 stations were sampled, each with two replicates. Taking into account the dimensionless fall velocity (Ω) and the relative tidal range (RTR), the beaches were ordered along the gradient from the ultra-dissipative beach type (UD) to the low tide bar/rip beach type (LTBR). The beach state index (BSI) varied between 1.8 and 4.2. Generally, the beach profiles were related with the beaches' morphodynamic state. At all beaches, the distribution of the macrobenthic characteristics were mainly determined by the height on the beach. In total 35 macrobenthic species, mainly polychaetes and crustaceans, were encountered, varying between 19 and 23 species per beach. The beaches' species composition was quite similar, with *Scolelepis squamata* being abundant at all eight beaches. Still, some remarkable differences, largely explained by the beach morphodynamics and the consequent hydrodynamics, were found. At macrobenthos-rich UD beaches, the highest macrobenthic densities and biomass were found on the upper beach, while at the macrobenthos-poor LTBR beaches, the highest densities and biomass were situated in the middle beach zone. Species, typically occurring on the upper UD beaches, such as *Bathyporeia sarsi*, *S. squamata*, and *Psammodrilus balanoglossoides*, were restricted to the sub-optimal middle beach zone at LTBR beaches. Only *Bathyporeia pilosa* could be found on the upper beach of UD and LTBR beaches, but was clearly more abundant on UD beaches. The robust polychaete *Ophelia rathkei* and the interstitial polychaete *Hesionides arenaria* were exclusively found in the upper beach zone of LTBR beaches. A summarizing zonation scheme, representing the typical species' distributions of the Belgian UD and LTBR beaches, is presented (Chapter 6, figure 10).

The western Belgian Coastal Banks and their adjacent beaches are harbouring an abundant and diverse macrobenthic fauna. Its ecological importance is demonstrated by the number of birds (e.g. common scoter in the subtidal zone and sanderling in the intertidal zone) and fish (e.g. cod in the subtidal zone and juvenile plaice in the intertidal zone) using the macrobenthos as their major food resource. Furthermore, the area is characterized by a unique geomorphology, as defined by the EC Habitat Directive, and an international *importance for waterfowl, e.g. common scoter, as acknowledged by the Ramsar Convention. The protection of the Belgian shallow marine habitat, or at least part of it, including the intertidal and subtidal zone, is thus certainly indispensable. As marine protected areas can be safeguarded against anthropogenic influences, such as (shell)fisheries and sand extraction, the macrobenthos and other ecosystem components are protected from many unnatural disturbances and a natural development of the ecosystem can be expected. Such natural ecosystems help to preserve the biodiversity of shallow marine habitats, not only in the marine protected area itself, but also in adjacent habitats by increasing the recolonization possibilities of disturbed areas. Considering the common scoter, being the most important seabird in the area, the protection of areas as wintering place for the seaduck is important. As tranquility zones, e.g. marine protected areas, can be safeguarded against anthropogenic influences, such as shellfisheries and sand extraction, the establishment of these areas, rich in bivalves, will have a positive influence on and may even attract the common scoter. Even if the marine protected area is not visited by a large number of common scoters every year, the area can act as a refuge in times of food shortage or disturbance.*

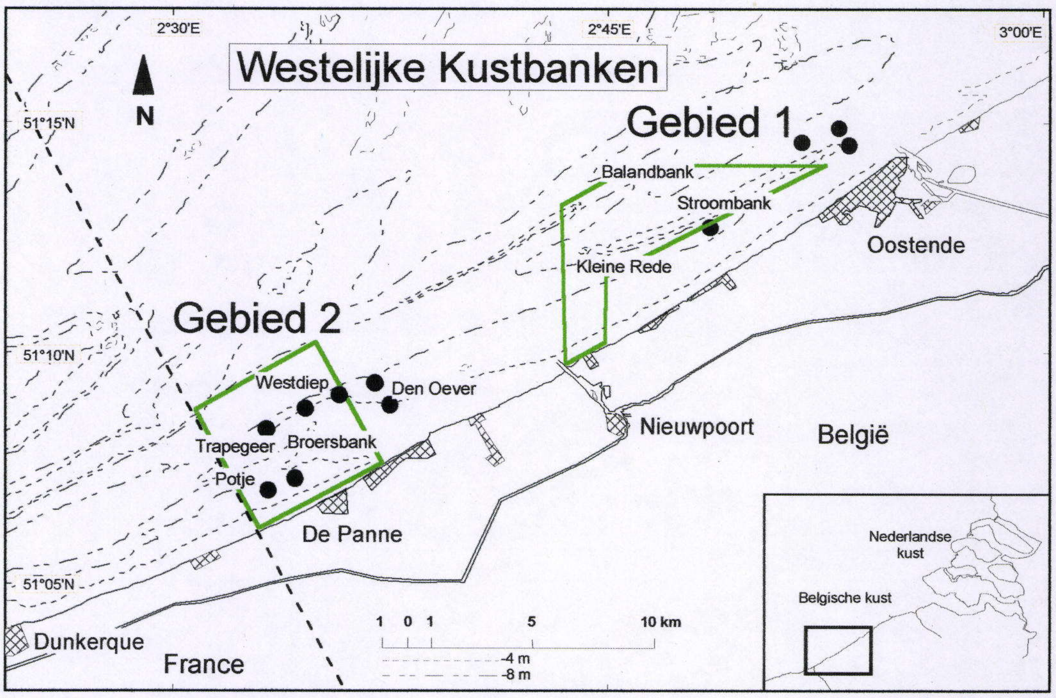
SAMENVATTING

Verschillende zandbanksystemen zijn aanwezig op het Belgisch Continentaal Plat (BCP): (1) de Hinderbanken, (2) de Zeelandbanken, (3) de Vlaamse Banken en (4) de Kustbanken.

De Kustbanken bestaan uit een combinatie van (1) een subtidale extensie van de zandstranden en (2) een reeks ondiepe (< 8 m) zandbanken, parallel met de kustlijn geöriënteerd. Deze laatste kunnen zich zowel subtidaal als intertidaal bevinden en bezitten mobiele zandgolven van verschillende grootte (De Moor, 1986; Ashley, 1990; Van Lancker, 1993). Binnen het gebied van de westelijke Kustbanken kunnen twee grote geomorfologische eenheden onderscheiden worden (Figuur 1). Parallel aan de kustlijn geöriënteerde zandbanken (Stroom- en Balandbank), van het strand gescheiden door een geul, de Kleine Rede, worden aangetroffen in gebied 1. Hun diepte varieert van 3 tot 8 meter onder de gemiddelde laagwater lijn bij springtij (GLWS). Het tweede gebied (gebied 2) omvat drie zandbanken (Den Oever, Broersbank en Trapegeer) en een geul (Potje), waarvan de diepte schommelt tussen ongeveer 0.5 en 8 m onder GLWS. Omwille van het ondiepe karakter en de diverse topografie van beide gebieden, kan op een korte afstand een sterk verschillende stroomsnelheid worden aangetroffen. Deze variatie in stroomsnelheid impliceert een grote variatie in de sedimentologie (Bastin, 1974; Buchanan, 1984; Houthuys, 1989), met mediane korrelgroottes van 160 tot meer dan 500 µm (Degraer *et al.*, in press a). Naast de Kustbanken, omvat de Belgische ondiepe kustzone verder ook de intergetijdenzone, die volledig uit zandstranden bestaat. Een algemene stijging van de strandhelling van west naar oost kan worden waargenomen. Bijgevolg bestaat er een natuurlijke gradiënt van 'ultra-dissipative' (UD) stranden in het westen naar 'low tide bar/rip' (LTBR) stranden in het oosten. Als gevolg van de aanleg van de strekdammen van de haven van Zeebrugge wordt deze natuurlijke morfologische gradiënt verstoord, zoals kan worden aangetoond met de aanwezigheid van UD stranden in de omgeving van Zeebrugge.

De westelijke Belgische Kustbanken zijn gekend voor hun groot ecologisch belang. De zone is reeds toegekend aan de gebieden met een internationaal belang voor watervogels, zoals bepaald door de Ramsar Convention (Kuijken, 1972). Verder voldoet het gebied ook aan alle

criteria zoals opgesteld door de EG Vogel- en Habitatrichtlijn (Anoniem, 1979, 1992a). Momenteel bestudeert de Belgische overheid de mogelijkheid om twee grote mariene natuurgebieden binnen de westelijk Kustbanken (gebied1: Stroom- en Balandbank; gebied2: Potje, Trapegeer, Broersbank en een deel van Den Oever en Westdiep) te erkennen (Figuur 1). De definitieve afbakening van de beschermde mariene gebieden zal niet plaats grijpen voordat alle belangengroepen en geïnteresseerde partijen geconsulteerd werden en een beheersplan is opgesteld.



Figuur 1. De geografische situering van de westelijke Kustbanken, met aanduiding van de twee geplande mariene beschermde gebieden (groene veelhoeken: gebied 1 en gebied 2) en de ruimtelijke verspreiding van de *Lanice conchilega* gemeenschap (●).

Teneinde (1) het belang van Belgische mariene natuurgebieden te bediscussiëren, (2) deze natuurgebieden te selecteren, (3) een beheersplan op te stellen en (4) dit beheersplan te evalueren, is er een grote noodzaak aan wetenschappelijke ecologische informatie van het gebied. Behalve wat betreft de ornithologische component (Maertens *et al.*, 1988, 1990; Devos, 1990; Offringa *et al.*, 1998), ontbreekt deze informatie grotendeels op dit ogenblik. Het belang van het macrobenthos als de voedselbron voor de Zwarte zee-eend (*Melanitta nigra*), de belangrijkste zeevogel in het gebied (Maertens *et al.*, 1988, 1990; Devos, 1990), en de mogelijke noodzaak van kustverdedigingswerken in het gebied, die rechtstreekse gevolgen voor het macrobenthos als bodem bewonende organismen zullen hebben, leidden ertoe het macrobenthos van ondiepe, Belgische mariene habitats als centraal studieobject te selecteren.

Aangezien ondiepe mariene habitats niet enkel het subtidaal deel, tot een diepte van 6 m, omvatten, maar ook de intergetijdenzone tot de hoogwaterlijn (Reilly *et al.*, 1996), werd het macrobenthos van de subtidale en intertidale Belgische kust (respectievelijk, de westelijke Kustbanken en de zandstranden, inclusief het Vlaams natuurreservaat *Baai van Heist*) bestudeerd. In eerste instantie werd de ruimtelijke verspreiding van het (subtidale en intertidale) macrobenthos in relatie tot de fysische omgeving onderzocht (Hoofdstukken 1, 5 en 6). Verder werd ook nog de temporele variatie, dynamiek en stabiliteit van het subtidale macrobenthos (Hoofdstukken 2 en 3) en de ruimtelijke verspreiding en populatie dynamica van de Tweekleppige *Spisula subtruncata* (Hoofdstuk 4) bestudeerd.

Om de ruimtelijke verspreiding van het macrobenthos van de westelijke Kustbanken te onderzoeken, werden 39 stations, verdeeld over de twee gebieden, in oktober 1994 naar hun macrobenthos bemonsterd (Hoofdstuk 1). De twee gebieden konden niet onderscheiden worden wat betreft hun macrobenthische gemeenschappen. TWINSPAN, Bray-Curtis Group-Averaging Cluster Analysis en CCA onderscheidden vijf gemeenschappen, elk gelinkt met een typische fysische omgeving: (1) de *Barnea candida* gemeenschap in een compacte kleibodem (mediane korrelgrootte: 14 µm), (2) een tweede gemeenschap gekarakteriseerd door de aanwezigheid van juvenielen van *Mytilus edulis* (de '*M. edulis*' gemeenschap), in een mediumzandig sediment (mediane korrelgrootte: 456 µm), (3) de *Lanice conchilega* gemeenschap, gevonden in een fijnzandige bodem (mediane korrelgrootte: 211 µm) (Figuur 1), (4) the *Nephtys cirrosa – Echinocardium cordatum* gemeenschap in een iets grover fijnzandig sediment (mediane korrelgrootte: 242 µm) en (5) de, met de laatste gemeenschap sterk verwante, *N. cirrosa* gemeenschap, alsook aangetroffen in een fijnzandig sediment (mediane korrelgrootte: 224 µm). Enkel de *L. conchilega* gemeenschap behoort tot de rijke transitie zone (Govaere *et al.*, 1980). De overige vier gemeenschappen maken deel uit van de heterogene, soorten-arme kustzone gemeenschappen. Geen gemeenschappen van de open zee zone werden gevonden in het gebied. Enkel de *L. conchilega* gemeenschap, met hoge aantallen bivalven als *Abra alba*, *Tellina fabula* en *Spisula subtruncata*, kan dienen als voedselbron voor de Zwarte zee-eend (*Melanitta nigra*). Een vergelijking tussen de ruimtelijke verspreiding van de overwinterende Zwarte zee-eenden en de *L. conchilega* gemeenschap vertoonde echter geen duidelijke gelijkenissen. Mogelijke verklaringen hiervoor zijn: (1) de hoge mobiliteit van de Zwarte zee-eenden in vergelijking met de hoofdzakelijk sessiele macrobenthische organismen en/of (2) de selectie van 'sub-optimale' voedingsgronden door de Zwarte zee-eend.

Het macrobenthos van ondiepe kusthabitats is onderworpen aan tal van fysische en biologische verstoringen, variërend in frequentie en intensiteit, op zowel een temporele als een ruimtelijke schaal. Als gevolg daarvan, variëren de macrobenthische parameters (soorten samenstelling, densiteiten, etc.) continu. Om de ecologische waarde van de *Lanice conchilega* gemeenschap te kunnen evalueren is kennis van de temporele variatie binnen de gemeenschap dus onmisbaar. Daarenboven laat de kennis van de recruteringsperiode van de verschillende soorten toe de negatieve invloed van de geplande kustverdedigingswerken te beperken. Als de werken worden uitgevoerd vóór de belangrijkste recruteringsperiode kan namelijk een herkolonisatie via de planktonische larven van vele macrobenthische soorten in het verstoorde gebied worden verwacht. De temporele variatie en recrutering in de *L. conchilega* gemeenschap is bestudeerd in twee stations tijdens een 2,5 jaar durende studie (april '95 – oktober '97) (Hoofdstuk 2). Gedurende de lente en zomer '95 kon de algemene stijging van de conditie van de gemeenschap worden verklaard door de recrutering van vele dominante soorten. Alhoewel de Borstelworm *Notomastus latericeus*, de Tweekleppigen *Abra alba* en *Tellina fabula* en de Buikpotige *Hinia reticulata* geen recrutering hadden, werd een recrutering van alle andere dominante soorten gedetecteerd. De Borstelwormen recruteerden voornamelijk tussen april en augustus '95, terwijl de recrutering van de Vlokreeften en Tweekleppigen voornamelijk tussen juli en oktober '95 gebeurde. Een overweldigende recrutering van *Spisula subtruncata*, met densiteiten tot 150000 ind m^{-2}, vond plaats in augustus '95. Mogelijks veroorzaakte deze recrutering de algemene verlaging van het aantal soorten per staal (N_0) en de densiteit van alle dominante Borstelwormen in één of beide stations na augustus '95. Een stijging van het modder gehalte in de bodem van één station (van 5 % naar 30 %) wordt verantwoordelijk geacht voor een nieuwe verarming van de gemeenschap in dit stations tussen januari en maart '96. Een verhoging van het moddergehalte heeft een negatief effect op het macrobenthos van de *L. conchilega* gemeenschap die *normaliter* in een fijnzandig sediment met een lage concentratie modder wordt aangetroffen. In tegenstelling tot 1995 werden in 1996, noch 1997 geen succesvolle recruteringen waargenomen. Dit illustreert de grote variatie in het succes van recrutering van het macrobenthos tussen de verschillende jaren. Bijgevolg is het zeer belangrijk de natuurlijke variabiliteit of 'potenties' van een macrobenthische gemeenschap te onderkennen bij de evaluatie van het ecologisch belang.

Het macrobenthos van de westelijke Kustbanken vertoont dus een grote temporele variatie binnen één jaar en tussen verschillende jaren. Deze benthische dynamiek creëert een probleem bij het opstellen van een beheersplan voor benthische habitats: Hoeveel staalname campagnes, gespreid over hoeveel jaren, zijn noodzakelijk om de juiste conclusies omtrent het macrobenthos te kunnen trekken? Eén van de belangrijke vragen is daarom tot op welk niveau een beheerscommissie, bij het opstellen van het beheersplan, op een éénmalige staalname kan vertrouwen. Daarom werden de soortensamenstelling en de densiteit van oktober ’94 (Hoofdstuk 1) vergeleken met deze van oktober ’97 (Hoofdstuk 3). Alhoewel slechts kleine fysische verschillen binnen de 39 stations werden waargenomen, werd, in vergelijking met 1994, een algemeen lager aantal soorten en densiteit gevonden in 1997. Deze verarming was het duidelijkst bij de Borstelwormen. Na samenvoeging van de *Nephtys cirrosa – Echinocardium cordatum* en *N. cirrosa* gemeenschap tot de *N. cirrosa* gemeenschap *s.l.*, werden dezelfde drie macrobenthische zandbank gemeenschappen, met een gelijkaardige soortensamenstelling en densiteit, gevonden in 1997 als in 1994: the *Lanice conchilega* gemeenschap, de *N. cirrosa* gemeenschap *s.l.* en de ‘*Mytilus edulis*‘ gemeenschap. Op het vlak van de gemeenschappen was vooral de verarming van de *L. conchilega* gemeenschap duidelijk. Deze verarming werd mogelijks gedeeltelijk veroorzaakt door de overweldigende recrutering van *Spisula subtruncata* in augustus ’95. Aangezien 84 % van de stations tot dezelfde gemeenschap in 1997 als in 1994 werd toegekend, kan de ruimtelijke verspreiding van de gemeenschappen als vrij stabiel worden aanzien. Bovendien is aangetoond dat de relatie tussen het macrobenthos en de fysische omgeving, voornamelijk de mediane korrelgrootte en de percentages leem en grof zand, gebruikt kan worden om de ruimtelijke verspreiding van de gemeenschappen in een gebied met gekende fysische parameters met een accuraatheid van 83 % te voorspellen. Monitoring van het macrobenthos in het kader van een kustzonebeheer kan zich dus concentreren op de ruimtelijke verspreiding van de macrobenthische ‘potenties’ van het gebied. Dit kan worden gedaan door (1) de ruimtelijke verspreiding van de macrobenthische gemeenschappen te onderzoeken, (2) de specifieke fysische ‘noden’ van iedere gemeenschap te bepalen en (3) de ‘potenties’ van deze gemeenschappen te bepalen door middel van lange termijn monitoring van enkele geselecteerde stations binnenin iedere gemeenschap.

Binnen het ecosysteem van de westelijke Kustbanken vervullen de Tweekleppigen een belangrijke rol, niet in het minst als belangrijkste voedselbron voor de Zwarte zee-eend (*Melanitta nigra*) waarvan er duizenden in het gebied overwinteren. Naast dit ecologisch belang, komt één van die Tweekleppigen, *Spisula subtruncata*, in het gebied in bevisbare stocks voor en de schelpdiervisserij toonde reeds zijn interesse in het bevissen van deze soort. Om de informatie, nodig voor een duurzaam beheer van de *S. subtruncata* stocks op de westelijke Kustbanken, te bekomen, heeft hoofdstuk 4 tot doel (1) de ruimtelijke verspreiding en populatie dynamica van *S. subtruncata* en (2) de implicaties van een mogelijke schelpdiervisserij in het gebied te beschrijven. De ruimtelijke verspreiding van *S.*

subtruncata werd in 40 stations, verspreid over de twee gebieden, in 1994 en 1997 bestudeerd. De populatie dynamica werd onderzocht door middel van maandelijkse staalnames van twee stations tussen april ’95 en april ’96 en seizoenale staalnames tussen april ’96 en april ’98. *Spisula subtruncata* vertoonde een ongelijke verspreiding in de dieper gelegen (6 m), fijnzandige (200 ± 20 µm) sedimenten van de *L. conchilega* gemeenschap. In augustus ’95 werd een overweldigende recrutering, met densiteiten tot 150000 ind m^{-2}, waargenomen. Kleinere en niet-succesvolle recruteringen werden gevonden in augustus ’96 en augustus ’97. De groei werd beschreven met een seizoenaal oscillerende versie van de von Bertalanffy groei vergelijking. Een groei-stop werd waargenomen vanaf de late herfst tot de vroege lente. Waarschijnlijk omwille van milieu verschillen verschilden de groei parameters, K en L_∞, licht tussen beide stations (0.7 en 32 – 3 mm voor een station en 0.9 en 31 – 32 mm voor het andere station). Een combinatie van toename in lengte en individueel gewicht toonde aan dat (1) kleinere individuen een snellere groei tijdens de tweede groei periode vertoonden, (2) de lengte constant bleef terwijl het individuele gewicht daalde tijdens de (sub-optimale) winterperioden (behalve tijdens de eerste winterperiode wanneer het individuele gewicht zwak bleef stijgen), (3) er een positieve relatie bestaat tussen het individuele gewichtsverlies en de zeewater temperatuur tijdens de winters en (4) de sterke individuele gewichtstoename in de vroege lente (april ’97 en april ’98), gevolgd door een gewichtsafname (augustus ’97), veroorzaakt wordt door, respectievelijk, gametogenesis en spawning. De totale productie van de cohorte ’95 in de geul, Potje, gedurende de volledige studie periode werd geschat op 1500 g AFDW m^{-2}. Schelpdiervisserij op de ecologisch belangrijke Kustbanken moet worden uitgesloten omdat (1) de hoeveelheid voedsel voor de Zwarte zee-eend zal dalen met als mogelijk gevolg het verdwijnen van de zee-eend in het gebied, (2) deze een nefast effect op de ecologisch belangrijke L. conchilega gemeenschap zal hebben en (3) de economische rendabiliteit van de *Spisula*-visserij twijfelachtig is omwille van de zeer variabele recrutering van *S. subtruncata* langs de Belgische kust.

Zoals reeds vermeld omvatten de ondiepe Belgische mariene habitats niet alleen de ondiepe subtidale zone, maar ook de intergetijdenzone. Om een gedetailleerde kennis van de gemeenschapsstructuur en intertidale zonatie van het macrobenthos van een ultra-dissipatief strand te bekomen, werd het macrobenthos van het strand van De Panne bestudeerd (Hoofdstuk 5). Zes transecten, loodrecht op de waterlijn, werden elk op vijf stations (2 replicaten) bemonsterd in september 1995 (zomer) en maart 1996 (winter). Om het macrobenthos van zoveel mogelijk verschillende hoogtes op het strand te bemonsteren, werden de 30 stations verdeeld langs het continuum tussen de hoog- en de laagwaterlijn.

Negenendertig soorten werden aangetroffen in densiteiten van maximaal 5500 ind m^{-2} in de zomer en 1400 ind m^{-2} in de winter. De Borstelwormen, *Scolelepis squamata*, *Spio filicornis* en *Nephtys cirrosa*, de Zeepissebed *Eurydice pulchra* en de Vlokreeft *Bathyporeia* spp. hadden de hoogste densiteiten. Door middel van de soortensamenstelling, specifieke densiteiten en biomassa werden twee soorten associaties gedefinieerd: (1) een relatief soorten-arme, hoog intertidale soorten associatie, gedomineerd door *S. squamata* en met een gemiddelde densiteit van 1413 ind m^{-2} en biomassa van 808 mg AFDW m^{-2} (zomer) en (2) een relatief soorten-rijke, laag intertidale soorten associatie, gedomineerd door *N. cirrosa* en met een lagere gemiddelde densiteit (104 ind m^{-2}) en biomassa (162 mg AFDW m^{-2}) tijdens de zomer.Tijdens beide seizoenen was de hoog intertidale soorten associatie in zijn verspreiding beperkt tot de zone tussen de gemiddelde getijhoogte en de gemiddelde hoogwaterlijn bij springtij (GHWS), terwijl de laag intertidale soorten associatie altijd beneden de gemiddelde getijhoogte werd aangetroffen. Deze laatste toonde veel gelijkenissen met de subtidale N. cirrosa gemeenschap s.l. (Hoofdstuk 4) en bevestigt aldus de relatie tussen het laag intertidale en het subtidale macrobenthos. De vergelijking tussen de zomer en de winter toonde een sterke daling in de densiteiten en biomassa binnen de hoog intertidale soorten associatie tijdens de winterperiode. De continuïteit binnen het laag intertidale habitat met de subtidale zone liet subtidale organismen toe de laag intertidale zone te herkoloniseren na een verarming van de populaties.

Aangezien de soortensamenstelling, densiteit, biomassa en zonatiepatronen van het macrobenthos van zandstranden wordt beïnvloed door de morfodynamiek en morfologie van het strand, werd het macrobenthos van de Belgische kust verder nog langs een morfodynamisch kleinschalige gradiënt onderzocht (Hoofdstuk 6). Daartoe werden acht Belgische stranden bestudeerd aan de hand van één transect per strand, loodrecht op de waterlijn en gelegen tussen de gemiddelde hoog- en laagwaterlijn bij springtij. Per transect werden 10 tot 14 stations, elk met 2 replicaten, bemonsterd. Aan de hand van de dimensieloze valsnelheid (Ω) en het relatieve getij verschil (RTR) werden de stranden langs het continuum van 'ultra-dissipative' (UD) naar 'low tide bar/rip' (LTBR) stranden geördend. De 'beach state index' (BSI) schommelde tussen 1,8 en 4,2. Algemeen waren de strandprofielen gecorreleerd met de morfodynamiek van de stranden. De ruimtelijke verspreiding van het macrobenthos was op ieder strand voornamelijk bepaald door de hoogte. In totaal werden 35 macrobenthische soorten gevonden, hoofdzakelijk Borstelwormen en Kreeftachtigen en schommelend tussen 19 en 23 soorten per strand. De soortensamenstelling van de acht stranden vertoonde heel wat gelijkenissen, met hoge densiteiten van *Scolelepis squamata* op alle stranden. Toch werden enkele opmerkelijke verschillen, hoofdzakelijk gerelateerd aan de morfodynamiek van de stranden, waargenomen. De hoogste densiteiten en biomassa werden bovenaan het strand aangetroffen op UD stranden, terwijl deze op LTBR stranden ongeveer in het midden van het strand werden gevonden. Enkele soorten die typisch op het hoog strand van UD stranden worden gevonden, zoals *Bathyporeia sarsi*, *S. squamata* en *Psammodrilus balanoglossoides*, werden op LTBR stranden in hun verspreiding beperkt tot het sub-optimale midden strand. Enkel Bathyporeia pilosa werd op het hoog strand van UD en LTBR stranden waargenomen, maar was duidelijk in hogere densiteiten aanwezig op de UD stranden. De robuuste Borstelworm *Ophelia rathkei* en de interstitieel levende Borstelworm *Hesionides arenaria* werden exclusief op het hoog strand van LTBR stranden gevonden. De typische verspreiding van het macrobenthos op UD en LTBR stranden in België werd weergegeven in een samenvattend schema (Hoofdstuk 6, Figuur 10)

De westelijke Belgische Kustbanken en de aangrenzende stranden bevatten een abundante en diverse macrobenthische fauna, waarvan het ecologisch belang aangetoond wordt door de vogels (zoals de Zwarte zee-eend in het subtidaal en de Drieteenstrandloper in het intertidaal) en vissen (zoals Kabeljauw in het subtidaal en juveniele Schol in het intertidaal) die zich met het macrobenthos voeden. Het gebied wordt verder gekarakteriseerd door een unieke geomorfologie, zoals bepaald door de EG Habitatrichtlijn, en een internationaal belangrijk watervogelbestand, zoals erkend door de Ramsar Conventie. Het is dus zeker noodzakelijk het ondiepe Belgische mariene milieu, of toch ten minste een deel daarvan, te beschermen. Aangezien mariene natuurgebieden van menselijke (negatieve) invloeden, zoals schelpdiervisserij en zandwinning, kunnen vrijwaard worden, kan het macrobenthos, net zoals de andere ecosysteem componenten, beschermd worden van tal van onnatuurlijke verstoringen. Zodoende kan een natuurlijke ontwikkeling van het ecosysteem worden verwacht. Dergelijke natuurlijke ecosystemen helpen bij het bewaren van de biodiversiteit van het ondiepe mariene milieu en dit niet enkel binnen het beschermde gebied, maar ook in de aangrenzende habitats door middel van de verhoogde mogelijkheid tot herkolonisatie. Wat betreft de Zwarte zee-eend – de belangrijkste zeevogel in het gebied – is de bescherming van overwinteringsplaatsen belangrijk. Als rustgebieden kunnen mariene beschermde milieus zelfs Zwarte zee-eenden aantrekken. Zelfs al wordt het gebied niet ieder jaar door grote aantallen zee-eenden bezocht, toch kan een dergelijk rustgebied functioneren als een schuilplaats en voedingsgrond tijdens perioden van voedselschaarste.

GENERAL INTRODUCTION

The shallow marine habitat extends from the high water level down to 6 m below the low water level (Reilly *et al.*, 1996, 1st Annual Marine and Estuarine Shallow Water Science and Management Conference, Atlantic City, NJ, USA, March 1994). Worldwide, these habitats have in common to be very important, not only on the socio – economical level, as the place of major anthropogenic interaction with the marine environment (fisheries, tourism, waste water discharge, etc.), but also ecologically, as very diverse and productive ecosystems (Reilly *et al.*, 1996). Different shallow marine habitats can be distinguished, of which the difference between rocky and soft-sediment shores is most obvious. Partly because of the conspicuous presence of a rich fauna and flora, the ecological and sceneric value of rocky shores has met a lot of public comprehension and a number of rocky shore habitats have received the status of marine protected area (MPA). Except for mud flats and salt marshes, the ecological value of soft-sediment shores, with a less striking biological richness, has largely been ignored in the past and lots of these habitats are often undervalued in the public opinion (major topic of the 2nd Annual Marine and Estuarine Shallow Water Science and Management Conference, Atlantic City, NJ, USA, December 1995). Based on the combination of the desinterested public opinion and limited scientific knowledge on the biology of the soft-sediment shallow marine habitat, the idea existed that anything, in favour of the comfort of mankind, could be done without doing any ecological harm. In Belgium, this can be illustrated by means of, for instance, the offshore extension of the harbour of Zeebrugge since the late 70's, the presence of concrete dykes (destroying the natural beach – dune transition at many places along the Belgian coast) and groins, and, last but not least, the continuous beach profiling and suppletions of many Belgian beaches (Anonymous, 1995 b; De Wolf, 1996; De Wolf *et al.*, 1997). Furthermore, an intensive fishery takes place in the nearshore environment (personal communication, MUMM) and millions of tourists are spending their holidays along the Belgian coast, increasing the ecological stress for the maritime and shallow marine habitat.

In contrast to the lack of interest for the shallow marine habitat, the ecological consciousness for Belgian dune areas already leaded to the creation of several protected dune areas and fossil sand planes, e.g. *De Westhoek*, *Ter Yde*, *Ijzermonding and Zwin*. Furthermore, the 'Duinendecreet' (*Decree for the Dunes*) (B.S. 30/8/1993), followed by two implementing orders (B.S. 17/9/93 and B.S. 30/11/94), provided the legal framework for the protection of Belgian dune areas.

In the shallow marine habitat, the ornithological value of the offshore sandbanks became known during the late 60's (e.g. Bulteel and Van der Vloet, 1969). Since 1992, the Institute of Nature Conservation is studying the distribution of seabirds in Belgian coastal waters, in cooperation with the World Wildlife Fund (WWF) and, later, the Management Unit of the North Sea Mathematical Models (MUMM). In succession of the 'Impulse Programme in Marine Sciences, a large strategic research project 'Sustainable Management North Sea', funded by OSTC (Belgian government), combines studies of the numerous components of the shallow marine ecosystem (meiobenthos, macrobenthos, epibenthos, hyperbenthos, plankton, birds and marine mammals) since 1997. The project aims at the description and evaluation of the sandbank ecosystem and the interactions between the different components in order to provide scientific ecological information to be used for the sustainable management of marine (sandbank) resources.

The recognition of the ecological importance of the Belgian shallow marine habitat already led to the addition of parts of the marine coastal zone (roughly Coastal Banks between the Belgian – French border and Oostende) to the lists of proposed Belgian Ramsar areas (Kuijken, 1972) and the proposal to include it under the Natura 2000 network areas, in execution of the EC Habitat Directive (MUMM, January 1996: proposal by the federal administration of 'Trapegeer – Stroombank' as a Site of Community Importance (SCI); Natura 2000 network). Although the Coastal Banks further fulfil all criteria of the EC Bird Directive, an attempt to include the area in the final list of the EC Bird Directive areas failed. At this moment, the interest in marine nature conservation is thus increasing and a first translation is made by the protection of the beaches, *Baai van Heist* en the beach bordering the former military base of Lombardsijde, both including the intertidal zone. Considering the subtidal zone, the Belgian government worked out the framework law for the protection of the marine environment (framework law of 20/01/1999), among other things allowing to create marine nature reserves. So far, nine sites are considered: two larger and one smaller areas, in combination with the near environment of six ship wrecks. The two larger ones are situated nearby the Belgian – French border (including Potje, Broersbank, Trapegeer, and part of Den Oever and Westdiep) and between Nieuwpoort and Oostende (including Stroombank and Balandbank) (Figure 1).

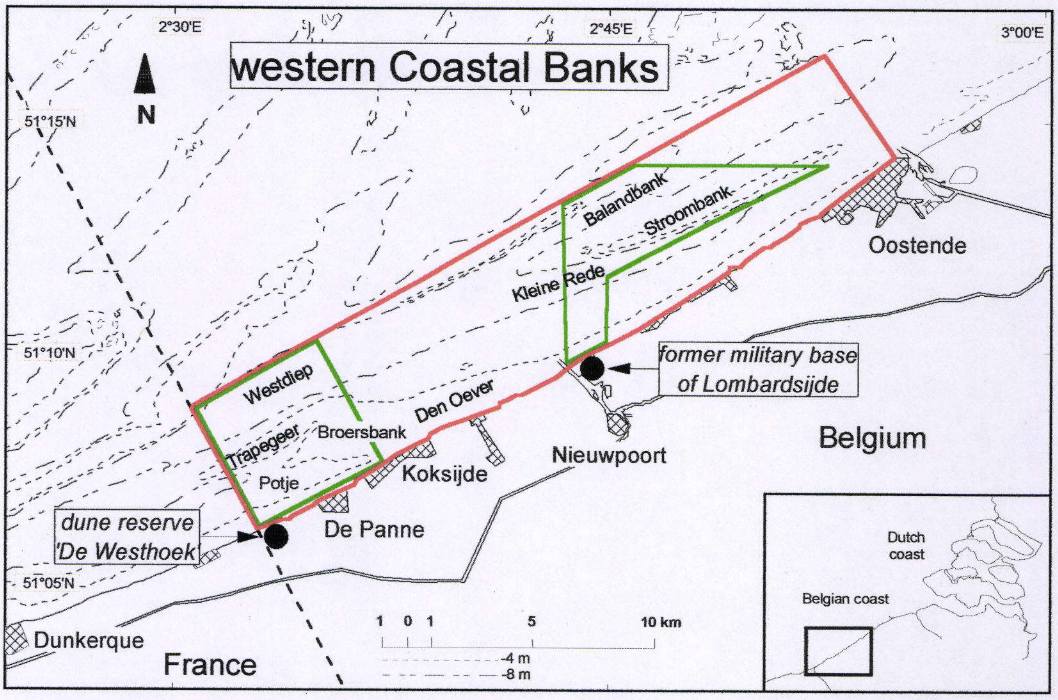


Figure 1. The geographical situation of the western Belgian Coastal Banks, with indication of the proposed Special Protection Area (SPA) (red polygon) and the two major proposed Sites of Community Importance (SCI) (green polygons), as part of the Natura 2000 areas (MUMM, January 1996: proposal by the federal administration of 'Trapegeer – Stroombank' as SCI; Natura 2000 network).

Except for the shipwrecks, the considered marine protected areas are directly connected with the intertidal zone, e.g. the beach reserves *Baai van Heist* and the beach bordering the former military base of Lombardsijde, and extended dune reserves, e.g. *De Westhoek* and the fomer military base of Lombardsijde, pointing towards an integrated approach of nature conservation in the Belgian coastal zone. Unfortunately, other users of the marine resources (especially fisheries and nautical sports) are not yet convinced of the necessity of marine protected areas and, so far, these groups caused a delay in the definite protection of the areas. Consequently, implementing orders for the definitive designation of marine nature reserves are still unavailable. Furthermore, at this moment, there is still a lack on information on the biology of the areas in order to argue, on a scientifical base, about the advantages and disadvantages of marine protected areas. As stated by Prof. Dr. E. Kuijken (Director of the Institute of Nature Conservation) during the workshop 'Natuur voor de Toekomst, een wetenschappelijke onderbouwing' (*Nature for the Future, a scientific foundation*) (Brussel, 22 November 1996), the scientific world is obliged to provide objective information for the fundaments of the sustainable management of natural resources, e.g. marine natural resources. Data on the spatial distribution and temporal variation of the seabirds and -mammals are gathered by the Institute of Nature Conservation (IN) and the Royal Belgian Institute for Natural Sciences (RBINS), but information on any other component of the Belgian marine coastal zone (e.g. Coastal Banks) ecosystem is largely lacking. Considering the seabirds, the Coastal Banks are predominantly important as a wintering place for the common scoter (*Melanitta nigra*) (Maertens *et al.*, 1988, 1990; Devos, 1990, Offringa *et al.*, 1998). Because of the presence of these, internationally important, numbers of wintering seaducks, information on the reason of the scoters' presence in the area was necessary. As scoters are known to feed on bivalves, as part of the macrobenthos, knowledge on the macrobenthos of the Coastal Banks was necessary in first instance. Furthermore, as coastal defence works, directly influencing the macrobenthos, as bottom dwelling organisms, seemed to be inevitable in the subtidal zone nearby the Belgian – French border, an ecological correction of the course of the works in such an ecologically significant area was certainly necessary. It were these planned coastal defence works, which formed the start of this study, investigating the macrobenthos of the Belgian shallow marine habitat.

Firstly, the spatial distribution of the macrobenthos on the Coastal Banks needed to be studied (Chapter 1). Except for one study of the macrobenthos of a small part of the western Coastal Banks (Van Steen, 1978), so far, nothing was known about the macrobenthos of the area. By means of this part of the study, a first view on the macrobenthic component of the ecosystem was obtained. On the other hand, based on the knowledge of the macrobenthic spatial distribution, the ecological importance and vulnerability of the different communities could be evaluated. This was necessary in order to diminish the environmental impact of the planned coastal defence works. As macrobenthic communities are known to show large temporal variations, both within and between years (Beukema, 1974; Bonsdorff and Österman, 1985; Arntz and Rumohr, 1986; Dauvin and Ibanez, 1986; Dörjes *et al.*, 1986; Essink and Beukema, 1986; Ibanez and Dauvin, 1988; Dauvin, 1990, 1991; Anderlini and Wear, 1992; Feller et al., 1992; Beukema *et al.*, 1993; Meire *et al.*, 1994; Seys *et al.*, 1994; Turner *et al.*, 1995; Essink *et al.*, 1998; Herman *et al.*, in press), the temporal variation of the species composition and densities of the ecologically most important macrobenthic community was studied (Chapter 2). Knowledge on the temporal variation is necessary to enable one to objectively evaluate the effects of anthropogenic influences, e.g. coastal defence works, versus the natural dynamics of the macrobenthos. Because of this natural variability of the macrobenthos, constantly changing the communities' species composition and abundances, doubts arose about the consistency of the spatial distribution of the macrobenthos of the Coastal Banks. Therefore, the stability and dynamics of all macrobenthic communities of the Coastal Banks were studied by repeating the study of the spatial distribution (see Chapter 1) three years later (Chapter 3). The spatial distribution and population dynamics of the most abundant bivalve of the Coastal Banks, *Spisula subtruncata*, is studied in Chapter 4. Possibly this species is the most important food item for the common scoter (Leopold, 1993, 1995). On the other hand, *Spisula*-fishery in the southern North Sea is currently expanding (Leopold, 1993; Kock, 1995; Kristensen, 1996; Vanhee *et al.*, 1998) and, although *S. subtruncata* fishery does not occur in Belgium, harvestable stocks of the bivalve are present in the area of the Coastal Banks. Unfortunately – at least from an ecological point of view – competition between the shellfisheries and the common scoters has already been observed in the Netherlands (Leopold, 1993). In order to evaluate the ecological impact of *Spisula*-fishery on the western Coastal Banks, knowledge on the life history, population dynamics and production of the species is necessary.

As all these data can be used for the selection and management of planned marine protected areas, possibly including subtidal and intertidal zones, knowledge on the ecology of the intertidal zone is also necessary. Therefore, the last two chapters are dealing with the macrobenthos of the Belgian intertidal zone. In first instance, the community structure and intertidal zonation of the macrobenthos of the beach of De Panne, directly adjacent to one of the large (possible) marine protected areas, was studied in detail (Chapter 5). A comparison between a summer and a winter sampling campaign already revealed a preliminary view on the temporal variation of the intertidal macrobenthos. As different beach types occur along the Belgian coast, the zonation of the intertidal macrobenthos is also studied in relation to the morphodynamical state of Belgian beaches (Chapter 6).

CHAPTER 1

THE MACROBENTHOS OF AN IMPORTANT WINTERING AREA OF THE COMMON SCOTER (*MELANITTA NIGRA*)

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Journal of the Marine Biological Association of the U.K., **79**:243-251

ACKNOWLEDGEMENTS

The research was financed by project BNO/NO/Wh.94.12 of Flemish administration responsible for environment, nature, land and water management, department Nature (AMINAL) and a specialization scholarship of the Flemish Institute for the Promotion of Scientific – Technological Research in Industry (IWT, Flemish government). Johan Van De Velde, Wim Bert, Myriam Beghyn, Dirk Van Gansbeke and the crew of the OOSTENDE XI, George, Ivan, Jef, Johan, Lucas, and Patrick (SILT) are acknowledged for their help in collecting and processing the data.

ABSTRACT

In October 1994, 39 macrobenthic samples, divided over two areas, were taken on the western Belgian Coastal Banks. The two areas could not be clearly divided concerning their macrobenthic communities. TWINSPAN, Bray-Curtis Group-Averaging Cluster Analysis, and CCA revealed five coherent communities, linked with typical sedimentological factors: (1) the *Barnea candida* community in a very compact muddy sediment (median 14 µm), (2) a second community characterized by the presence of spat of *Mytilus edulis*, with a medium sandy sediment (median 456 µm), (3) the *Lanice conchilega* community inhabiting a fine sandy sediment (median 211 µm), (4) the *Nephtys cirrosa-Echinocardium cordatum* community in a coarser fine sandy sediment (median 242 µm), and (5), closely related to the latter, the *N. cirrosa* community also occurring in a fine sandy sediment (median 224 µm). Only the *L. conchilega* community belongs to the diverse transition zone. The other four communities seem to be part of the heterogeneous, species-poor coastal zone associations. No open sea communities have been detected in the area.

On the western Coastal Banks, only the *L. conchilega* community, because of the high numbers of *Abra alba, Tellina fabula*, and *Spisula subtruncata*, can be interesting as feeding grounds for the common scoter (*Melanitta nigra* (Aves: Mergini)). Comparison of the spatial distribution of the wintering common scoters and the *L. conchilega* community revealed no direct similarity. The factors possibly causing this dissimilarity have been discussed.

INTRODUCTION

On the Belgian Continental Platform, several sandbank systems occur: (1) the Hinderbanks, about 35 – 60 km offshore, (2) the Zeelandbanks, some 15 – 30 km offshore, (3) the Flemish Banks, about 10 – 30 km offshore of the western Belgian coast, and (4) the Coastal Banks, parallel to the coastline and typical for the coastal zone between Oostende and De Panne.

These Coastal Banks are composed of a combination of (1) a subtidal extension of the sandy beaches and (2) a series of shallow (< 8 m) sandbanks parallel to the coast. The latter can be subtidal as well as intertidal with mobile sandripples of different scales (De Moor, 1986; Ashley, 1990; Van Lancker, 1993). The sandbanks may be separated by swales. Being shallow and having a highly variable and diverse topography, currents can change drastically within only tens of meters because of the compression of the water column (Van Veen, 1936). This implies a large variety of sediments (Bastin, 1974; Buchanan, 1984; Houthuys, 1989), with patchy distribution over the area. Regarding this very heterogeneous topography and the ensuring very diverse, patchy sediment texture, the macrobenthic communities, due to the close relation between the benthos and the sediments, will also be patchy distributed. So far, the benthos along the western Belgian coast has been poorly studied (Govaere, 1978; Govaere *et al.*, 1980; Van Steen, 1978; Van Assche and Lowagie, 1991).

The area of the western Belgian Coastal Banks is an important wintering area for the common scoters (*Melanitta nigra*) (Maertens *et al.*, 1988, 1990), reflecting its ecological importance. The seaducks, whose diet consists of macrobenthos, mainly bivalves (Madsen, 1954; Glutz von Blotzheim and Bauer, 1980; Nilsson, 1972; Cramp and Simmons, 1977; Van Steen, 1978; Meissner and Bräger, 1990; Durinck *et al.*, 1993), winter mainly on the Coastal Banks in front of Oostende (Stroombank and Balandbank) and/or in front of De Panne-Koksijde (Potje, Broersbank and Den Oever) (Maertens *et al.*, 1988, 1990). The RAMSAR convention (Kuijken, 1972; Skov *et al.*, 1994, 1995) has therefore put the area of the western Coastal Banks under an international preservation convention. The western Belgian Coastal Banks were also put in the list of Belgian areas for the EC Bird Directive 79/4099/EEC (Van Vessem and Kuijken, 1986) and EC Habitat Directive 92/43/EEC (Anonymous, 1992a). The area was skipped for the EC Bird Directive, but is still under consideration for the EC Habitat Directive.

Ecological information on the food resource of the common scoter will provide additional information: (1) on the potential distribution of the seaducks and (2) on food resource itself, the macrobenthos, as a component of the sandbank ecosystem. At this moment it is not clear to what extent the feeding grounds of the seaducks are linked with their wintering distribution.

In this paper the structural characteristics of the macrobenthic communities along the western Belgian coast will be investigated in relation to the granulometric characteristics of the sediments and will be correlated with the spatial distribution of the wintering common scoters. This knowledge should be of importance to the management of the coast. Indeed, large scale dredging on the sandbanks is planned within the framework of coastal defence. This could affect scoter populations in a very negative way, not at least by damaging their food supply.

MATERIALS AND METHODS

SAMPLING SITE

The sampling area (Figure 1) covers the Stroombank and Balandbank, separated from the beach by a deep trench (area 1), and Potje, Broersbank and part of Den Oever, directly adjacent to the beach (area 2). These are the most important wintering places for the common scoter.

In October 1994, 39 macrobenthic samples were taken. In area 1, 20 stations cover the different geomorphological formations: the southern and northern flanks (4 respectively 6 stations), and the top of the sandbanks (10 stations). As area 2 is geomorphologically more differentiated, the 19 stations were placed in a grid covering the whole area.

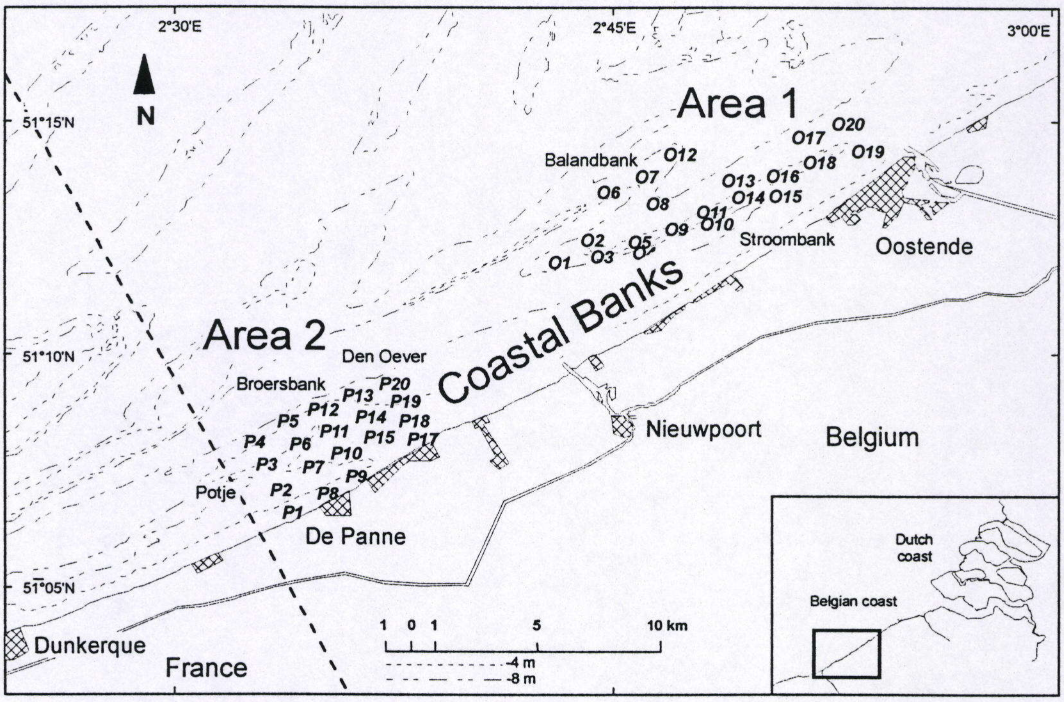

Figure 1. Geographical view on the western Coastal Banks, divided in area 1 and area 2; with indication of the 39 sampling sites.

SAMPLING METHOD

Samples were taken with a Van Veen grab (sampling surface area: 0.12 m^2) and sieved on board over a 1 mm sieve before fixation. The residual was preserved in a buffered 8% formaldehyde solution. Samples were decanted, stained with Bengal rose and the residuals were sorted under stereomicroscope. All the individuals were identified up to species level, except the oligochaetes.

ENVIRONMENTAL PARAMETERS

Water depth was recorded while sampling and standardized to mean low water spring (MLWS). The grain size analysis of a subsample was measured with a Coulter particle size analyser.

DATA ANALYSIS

To identify groups of similar stations, the density data were subjected to a Two-Way INdicator SPecies Analysis (TWINSPAN), with cutlevels: 0, 9, and 40 ind m^{-2}, a TWINSPAN on the presence/absence data (Hill, 1979) and, after fourth root transformation, to a Bray-Curtis group-average Cluster Analysis (van Tongeren, 1987) and a Canonical Correspondence Analysis (CCA) (Ter Braak, 1988).

The station groupings, resulting from the multivariate analyses, analysis were characterized by their typical species composition, diversity indices (Hill numbers: N_0, N_1 and N_{inf} and Shannon-Wiener diversity index, H') (Hill, 1973; Shannon and Weaver, 1949) and the measured environmental variables.

Statistical differences for biotic and abiotic variables between groups were analyzed by the Kruskal-Wallis test ($p < 0.05$). Significant differences were further analyzed by *a posteriori* multiple comparisons (Conover, 1971).

RESULTS

The number of species per station varied between three and 29 species, with a mode of four species (Figure 2A). About 47 % of the 71 identified species belongs to the Polychaeta, 20 % to the Bivalvia, 14 % to the Amphipoda, 6 % to the Decapoda, and another 11% are belonging to the remaining taxa (Figure 2B). The total density varied between 58 and 8350 ind m^{-2} with a mode of 100 – 200 ind m^{-2}; 18 of the 37 stations had densities from 100 – 400 ind m^{-2} (Figure 2C).

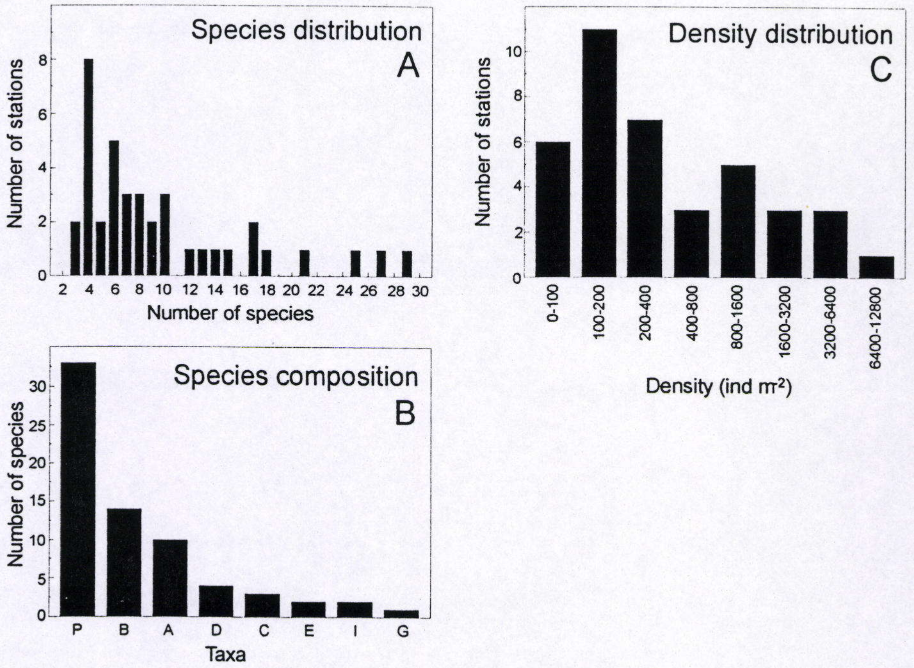

Figure 2. (A) Species distribution, (B) species composition (P, Polychaeta; B, Bivalvia; A, Amphipoda; D, Decapoda; C, Cumacea; E, Echinodermata; I, Isopoda; G, Gastropoda), and (C) density distribution of the 39 stations.

MULTIVARIATE ANALYSES

In the different multivariate analyses, the same stations were always grouped together, except for O13, O18 and P15 (Figure 3). Station O13 was placed in group 2 in three of the four analyses. The stations O18 and P15 showed no preferences for a group and were kept out of further analyses.

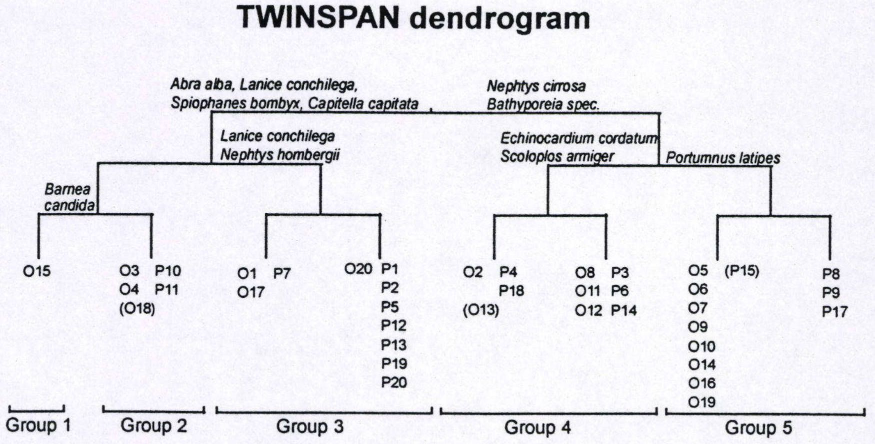

Figure 3. Presentation of the graphical result of one multivariate technique: TWINSPAN dendrogram of the presence/absence data; with indication of the five groups and their indicator species.

SPECIES COMPOSITION

The ten most dominant species differ between the five groups as do their relative importance within groups (Table 1). In group 1, only *Barnea candida* (Linnaeus, 1758) occurs in quite high densities. The second group is dominated by *Microphthalmus similis* (Bobretzky, 1870) and spat of *Mytilus edulis* (Linnaeus, 1758). *Magelona papillicornis* (F. Müller, 1858), *Eumida sanguinea* (Oersted, 1843), *Lanice conchilega* (Pallas, 1766), *Abra alba* (S. Wood, 1802), and *Tellina fabula* (Gronovius, 1781) are well represented in group 3. Group 4 has high densities of *M. papillicornis* and *Nephtys cirrosa* (Ehlers, 1868). Group 5 also has *M. papillicornis* and *N. cirrosa* as most dominant species.

Group 1			Group 2			Group 3		
Species	$N.m^{-2}$	%	Species	$N.m^{-2}$	%	Species	$N.m^{-2}$	%
B. candida	117	100	*M. similis*	237	60	*M. papillicornis*	1392	64
Ensis sp.	33	100	spat *M. edulis*	118	100	*E. sanguinea*	344	82
N. longissima	25	100	*N. cirrosa*	28	100	*L. conchilega*	228	64
N. succinea	25	100	*H. augeneri*	20	60	*A. alba*	139	91
G. capitata	25	100	Oligochaeta	15	20	*T. fabula*	104	64
Oligochaeta	17	100	*Ensis* sp.	10	40	*P. typicus*	69	64
E. longa	17	100	*S. armiger*	7	60	*Ensis* sp.	62	82
U. deltaura	8	100	*G. capitata*	7	40	*N. hombergii*	61	82
Bivalvia indet.	8	100	*S. subtruncata*	7	40	*S. subtruncata*	48	55
A. Mucosa	8	100	*O. limacina*	3	20	*C. capitata*	41	73

Group 4			Group 5		
Species	$N.m^{-2}$	%	Species	$N.m^{-2}$	%
M. papillicornis	72	77	*M. papillicornis*	125	75
N. cirrosa	70	100	*N. cirrosa*	93	100
E. cordatum	21	77	*Ensis* sp.	21	17
Bathyporeia sp.	16	66	*D. vittatus*	11	25
S. armiger	7	55	*Bathyporeia* sp.	7	50
P. altamarinus	6	55	*N. hombergii*	7	33
P. batei	5	22	*P. latipes*	7	42
D. bradyi	5	33	*U. poseidonis*	4	25
Ensis sp.	4	33	*E. sanguinea*	4	8
U. poseidonis	4	33	*D. bradyi*	2	25

Table 1. The ten most abundant species per group with indication of the density ($N.m^{-2}$) and the percentage of occurrence in the stations of the different groups (%).

The abundances of the indicator species of the TWINSPAN, presence/absence and absolute densities, were compared statistically in between groups (Table 2). Group 1 cannot be compared statistically with the other groups (N = 1), but the presence of *B. candida*, which occurs only in group 1 is likely to be typical for that kind of environment. Group 2 is put apart by the abundance of juvenile specimens of *M. edulis*. Group 3 differs from the other groups by the abundance of *A. alba* and *L. conchilega*. *Nephtys cirrosa* and *Echinocardium cordatum* (Pennant, 1777) are typical for group 4, and group 5 cannot be separated statistically by any TWINSPAN indicator, but possesses the highest number of *N. cirrosa*.

	Group 1	Group 2	Group 3	Group 4	Group 5	H	p
Barnea candida	117	0	0	0	0	---	---
Mytilus edulis spat	0	118	5	0	0	28.682	<0,0001
Abra alba	0	2	139	0	0	27.861	<0,0001
Lanice conchilega	0	0	228	0	0	25.813	<0,0001
Nephtys cirrosa	0	28	25	70	93	14.365	0,0025
Echinocardium cordatum	0	0	2	21	0	18.968	0,0003

Table 2. Densities (ind m^{-2}) of the differentiating species, with indication of the test statistic (H) of the Kruskal-Wallis test together with the p-level for differences between group 2, 3, 4, and 5.

Thirteen species of bivalves were found in the whole area: *Abra alba*, *Barnea candida*, *Donax vittatus*, *Ensis* sp., *Macoma balthica*, *Mactra corallina*, *Montacuta ferruginosa*, *Mytilus edulis*, *Spisula subtruncata*, *S. solida*, *Tellina fabula*, *T. tenuis*, and *Venerupis pullastra*. Group 1 is characterized by *B. candida* and *Ensis* spp. Group 2 has only high densities of *M. edulis* spat. *Abra alba, T. fabula, Spisula subtruncata, Ensis* spp., and *Montacuta ferruginosa* are reaching high densities in group 3. Group 4 does not have a typical bivalve species and no bivalve species has a density higher than 5 ind m^{-2}. Group 5 is also poor concerning bivalves, but *Donax vittatus* and *Ensis* spp. are found in low numbers. *Tellina tenuis, Macoma balthica, Spisula solida, Mactra corallina*, and *Venerupis pullastra* are only occurring in low densities (maximal 11 ind m^{-2}).

	Group 1	Group 2	Group 3	Group 4	Group 5
Exclusieve species	3	3	23	4	1
Total number of species	10	21	54	24	15
N_0	10	8	18	8	5
N_1	6.8	5.0	6.8	5.2	3.2
N_2	4.9	4.2	4.4	4.0	2.5
N_{inf}	2.6	2.7	2.3	2.6	1.7
H'	1.9	1.6	1.7	1.6	1.1

Table 3. The number of exclusive species per group; the total number of species per group and different diversity indices of the five groups: (1) Hill numbers (N_0, N_1, N_2 and $N_{inf,}$) and (2) Shannon-Wiener diversity index (H').

DIVERSITY

Table 3 is indicating different diversity indices. Each group is characterized by some exclusive species. Group 3 has 23 exclusive species in a total of 54 species. On a total of only ten species found, group 1 has 3 exclusive ones. N_0, which gives the group average of the number of species per station, indicates a very high number for group 3 (18 spp.). The other groups are having a N_0 varying from five (group 5) to ten (group 1). Taking into account the rest of the Hill numbers, group 1 is the most diverse group, followed by group 3.

ENVIRONMENTAL VARIABLES AND GEOGRAPHICAL DISTRIBUTION

As group 1 is composed of only one station, statistical comparisons with other groups is impossible. However, the relatively great depth (8.2 m), low median grain size (14 µm), and high volume percentage of silt (63 %), differentiate group 1 from the other groups.

	Group 1	Group 2	Group 3	Group 4	Group 5	p-level
Depth	8,2	4,8	5,7	4,8	3,8	0,3698
Median	14	456	211	242	224	0,0005
MM-ratio	1,2	1,0	0,9	1,0	1,0	0,0393
% Mud	18	0	1	0	0	0,0004
% Silt	63	0	3	0	0	0,0004
% Very fine sand	8	1	4	1	3	0,0007
% Fine sand	6	9	65	57	63	0,0019
% Medium sand	4	54	22	43	33	0,0063
% Coarse sand	1	36	5	1	1	0,0010
% Gravel	0	11	0	0	0	<0,0001
Area 1 : Area 2	1:0	3:2	3:8	4:5	8:3	—

Table 4. Average value of the measured environmental variables per group, with indication of the p-level of the Kruskal-Wallis test for differences between group 2, 3, 4, and 5, and the geographical distribution of the number of stations of the five groups over area1 and area2. Depth = meter under MLWS; median = median grain size (µm); MM-ratio = sediment mean/median ratio; different sediment fractions in volume percentages; percentage gravel in mass percentage.

Statistical differences between the other four groups (Table 4) were found for: median grain size, volume percentage clay (<4 µm), silt (4 – 63 µm), very fine sand (63 – 125 µm), medium sand (250 – 500 µm) and coarse sand (500 – 1000 µm), and mass percentage of gravel (>1000 µm). Depth, mean-median ratio, and volume percentage fine sand (125 – 250 µm) showed no differences. Most of the stations in group 3 (eight stations) occur in area 2, with only three stations in area 1. In all the other groups, there are more stations in area 1 (groups 1 and 5) or about the same number of stations in the two areas (groups 2 and 4). The results of the Kruskal-Wallis *a posteriori* tests on the differentiating environmental variables between the groups 2, 3, 4, and 5 are given in Table 5. In summary, group 1 has a typical very fine sediment, group 2 is characterized by a medium sandy sediment, group 3 by fine sandy sediments, and, the very similar, groups 4 and 5 by slightly coarser fine sandy sediments.

	Group 2	Group 3	Group 4	Group 5
Group 2	---			
Group 3	1234567	---		
Group 4	167	12345	---	
Group 5	14567	234	no differences	---

Table 5. Environmental variables indicating statistical differences between groups with an a-posteriori test after a negative Kruskal-Wallis test; 1, median grain size; 2, mud; 3, silt; 4, very fine sand; 5, medium sand; 6, coarse sand; and 7, gravel content of the sediment.

DISCUSSION

MACROBENTHIC COMMUNITIES

Govaere *et al.* (1980) described three macrobenthic communities occurring in the Southern Bight of the North Sea: (1) a very diverse open sea community, (2) a rather diverse transition zone community, where the following species are numerically dominant: *Lanice conchilega, Nephtys cirrosa, Spiophanes bombyx, Magelona papillicornis, Pectinaria koreni* (Malmgren, 1865), *Anaitides mucosa* (Oersted, 1843), *Tellina fabula, Eumida sanguinea*, and *Ophelia limacina* (Rathke, 1843), and (3) a species-poor, heterogeneous coastal zone community, dominated by *P. koreni, Macoma balthica, Nephtys hombergii* (Savigny, 1818), and *Abra alba*.

The presented study here, in the shallow subtidal part of the western Belgian coast, detected five macrobenthic communities, all characterized by a series of typical species and specific values of some environmental factors. As this study only results from an autumn campaign, differences with the communities described in Govaere *et al.* (1980), resulting from several campaigns, spread over several years, are expected (McIntyre *et al.*, 1982).

As *B. candida* (besides *Ensis* spp. the only bivalve species in group 1) is exclusively found in group 1, this group can be defined as the *B. candida* community. This rather diverse community occurs in a muddy (median grain size: 14 µm), deeper lying (8.2 m) sediment, containing high numbers of *B. candida* (117 ind m^{-2}). The species composition of this community does not resemble any of the three communities described in Govaere *et al.* (1980). However, due to the heterogeneous character of the coastal zone, with a typical deposition of fine sediments and a low number of species, the *B. candida* community possibly belongs to the coastal zone community complex. The very fine sediments, in contradiction to the generally high dynamic sandbanks with a consequently coarser sediment, and the depth indicate that this community is part of the communities occurring in the trenches in between, rather than on, the sandbanks. As this study aimed to sample the communities of the sandbanks, only one station belonging to the *B. candida* community has been encountered.

Group 2 could be differentiated by means of the presence of juvenile *Mytilus edulis*: the '*M. edulis*' community. This community is situated on top of the Broersbank (area 2) and along the top of the Stroombank (area 1). The very coarse sediments, with an average median grain size of 456 µm, imply high hydrodynamic forces. The community is characterized by a low diversity. Except for the juvenile *M. edulis* specimens, no other bivalves occurred in high densities. Due to the low diversity and low number of species, this community could also be part of the coastal zone community complex. Because of the absence of adult specimens of *M. edulis*, this bivalve may not be a typical species over all the seasons. The juvenile specimens can attach to the coarse sediment particles, but when they grow the chance of being washed out increases, as adult *M. edulis* attach firmly to hard substrata.

A fine sandy sediment (median 211 µm) with typically high densities of *A. alba* and *L. conchilega* and a very high diversity are characteristic elements for group 3, defined as the *L. conchilega* community. This community contains the highest densities of bivalves. The *L. conchilega* community coincides very well with the transition zone community (Govaere *et al.*, 1980). In fact the transition zone reaches the coast in front of De Panne and the *L. conchilega* community, in this study, is typical for the sandbank area at this place: eight of the 11 stations of the association are situated in area 2, only three transition zone stations can be found in area 1.

The groups 4 and 5, which are very similar, are occurring in a slightly coarse fine sandy sediment (median grain size: respectively 242 and 224 µm), with both a quite low diversity and low numbers of bivalves. *Echinocardium cordatum* and *Nephtys cirrosa* are reaching high densities, respectively 21 and 70 ind m^{-2}, and are characteristic for group 4: the *N. cirrosa-E. cordatum* community. The fifth group contains only high numbers of *N. cirrosa* (93 ind m^{-2}) and can thus be defined as the *N. cirrosa* community. These two communities both have a low diversity and can also be considered as a type of the coastal zone community complex.

Some studies on the macrobenthos of the nearby, but deeper lying, Flemish and Zeeland Banks have been carried out (Rappé, 1978; Meheus, 1981; De Rijcke, 1982; Vanosmael *et al.*, 1982). Generally these sandbanks have a typical open sea community, with affinities to the transition zone. The communities are relatively species-poor in comparison to the surrounding areas (Rappé, 1978) and no relation between the most abundant species of these Flemish and Zeeland Banks on the one hand and these of the Coastal Banks (this study) on the other hand could be detected (Table 6). The lack of high densities of bivalves is also in contrast with the Coastal Bank communities or at least with the *L. conchilega* community. Craeymeersch *et al.* (1990a) described for the Voordelta area (the Netherlands), a shallow, sandy, subtidal marine area, five communities, related with typical abiotic parameters, of which the sedimentology seemed to be the most important (Craeymeersch *et al.*, 1990b). Generally, the macrobenthos of the Voordelta area has higher densities (500-15000 ind m^{-2}) and higher number of species (55-120 spp.) in comparison with the five communities of this study. Yet, a clear similarity between the median grain size of the richest communities of Craeymeersch *et al.* (1990a), namely 180 – 220 µm, and the median grain size of the rich *L. conchilega* community (average 211 µm) can be noticed. Biologically seen, among the most abundant species are also *S. bombyx, L. conchilega, A. alba, Spio filicornis,* and *Mysella bidentata*. *Spisula subtruncata* occurs in high densities, but the lack of high densities of this bivalve species in the *L. conchilega* community is discussed below.

Zeelandbanks	Flemish Banks
Spisula elliptica	*Ophelia borealis*
Nephtys cirrosa	*Hesionura augeneri*
Ophelia borealis	Oligochaeta
Nephtys longosetosa	*Bathyporeia elegans*
Nephtys caeca	*Nephtys cirrosa*
Scolelepis bonnieri	*Spio filicornis*
Bathyporeia guillamsoniana	*Eteone longa*
Thia scutellata	*Bathyporeia guillamsoniana*
Eteone longa	*Nephtys hombergii*

Table 8. The most abundant macrobenthic species of other sandbank ecosystems on the B.C.P. The species list of the Zeelandbanks is based on the species lists of samples from the Thornton Bank and Gootebank; the list of the Flemish banks is based on samples from the Oostdijck, Buiten Ratel and Kwintebank (Meheus, 1981).

Van Steen (1978) surveyed area 2, with special attention to the bivalves. As only a selective part of the western Coastal Banks, mainly Potje, was sampled, the sediment analyses all resulted in a fine sandy sediment (median grain size: 170 – 240 µm). Yet, the high densities of *A. alba*, *T. fabula*, and *L. conchilega*, show a clear relationship with the *L. conchilega* community described here.

Sandbank systems are abiotically extremely diverse and a depth difference of 0.5 m in a shallow area affects the hydrodynamics very much. Consequently, extremely diverse hydrodynamics are expected. Because of the linkage between hydrodynamics and sedimentology (Gullentops *et al.*, 1977; Buchanan, 1984), even within some tens of metres completely different types of sediment can be encountered, each with their own typical macrobenthic community. However, as the 39 stations (without the exceptional *B. candida* community) are only divided into four consistent communities, it is unlikely that a new community will be found when taking more samples in the same area.

Since the dynamics of the benthic system are a reflection of the distribution of residual and tidal currents and the load of suspended materials, the basic composition and distribution of the respective communities and their spatial distribution will remain stable (within the natural variability due to erratic recruitment and mortality) as long as the currents and the amount of suspended material carried will not change drastically (Govaere *et al.*, 1980). A comparison of the geomorphology and sedimentology of area 2 between 1973 (Bastin, 1974) and 1994 (this study) reveals no substantial differences. This implies no drastic changes in hydrodynamic regime and, consequently, an over years rather constant spatial variation of the macrobenthic communities, even for a very high dynamic region such as the western Coastal Banks. No reasons could be found to presume a different situation in area 1.

FOOD AVAILABILITY FOR THE COMMON SCOTER

In total 13 bivalve species are found in this study. Yet, for the common scoter, not all bivalves in any density are a potential food resource: (1) the bivalves have to occur in a fairly high density, so the scoter is likely to find a bivalve specimen while diving, (2) the bivalve specimens cannot be too big for swallowing or too small, which make it energetically unfavourable diving for, and (3) may not be digging to deep, which make it unlikely to be found (Leopold, 1995; Leopold *et al.*, 1995). Of the 13 species, only *D. vittatus, A. alba, T. fabula, T. tenuis, M. balthica*, *S. subtruncata,* and *B. candida* are likely to be eaten by the wintering common scoters. Thus, the common scoters are expected to feed on the *L. conchilega* community, with fairly high densities of *A. alba, T. fabula*, and *S. subtruncata*, and to a lesser extent on the *B. candida* community. Although, morphologically seen, *B. candida* is a potential food resource for the common scoter, the bivalve lives in a very compact muddy sediment (clay) and it is doubtful the common scoter could find these bivalves.

While studying the bivalves in area just east of area 2, Van Assche and Lowagie (1991) encountered a community with very high densities of *S. subtruncata* (up to over 500 ind m^{-2}), *M. balthica* (up to 500 ind m^{-2}), *T. fabula*, and *A. alba*. This community would probably also act as a very important food resource for seaducks, but this community has not been detected in this study. Possibly, due to their irregular recruitment, the bivalve populations disappeared by: (1) natural mortality, (2) maybe predation by the common scoters, and (3) the lack of recruitment in the area for several years. Concerning *S. subtruncata*, the high number of individuals found in February 1991 (Van Assche and Lowagie, 1991) were probably all recruits from 1989 or earlier (personal observation from maximal shell length) and the present study reveals few individuals which were at least recruited in 1993, but the low densities are giving the idea that recruitment has taken place even earlier. Maybe, between 1990 and 1994, there has been even no recruitment at all, which could explain the extreme low densities of *S. subtruncata* in comparison with 1991. Unfortunately, between 1990 and 1994 no more macrobenthic samples have been taken in the area to prove this idea.

The expected similarity between the spatial distribution of the macrobenthos (Nilsson, 1972), more specifically the *L. conchilega* community, and the wintering scoters (Table 7), as discussed above, cannot be detected. Most of the scoters are staying in area 1, whereas the highest densities of bivalves (*L. conchilega* community) are mostly found in area 2. Obviously there exist some problems when linking both spatial distributions. A first problem is the difference in scales used. The macrobenthic species are, in comparison to the ducks, very sessile: one sampling campaign for the macrobenthos reveals already a detailed pattern, which normally is quite stable in time. As seaducks are a lot more mobile, for instance by flying and drifting (Winter, 1993) their spatial distribution can change significantly, even within some hours. Consequently, four seaduck counts during one winter half year do not necessarily show a detailed, temporal stable spatial pattern. It gives an idea about the total number in a large area, rather than their distribution over the area. This fact implies problems linking both distributions. Secondly, groups of the seaduck can be found on places where it is too deep to dive for food (pers. comm. H. Offringa) and research, trying to link the spatial distribution of the common scoter with the macrobenthos in the Netherlands, revealed an excess of *Spisula* banks: not all *Spisula* banks found possess constantly a group of common scoters feeding on them (Leopold, 1995). These two facts create the idea that the common scoter does not always have to select the best feeding grounds. Sometimes 'sub-optimal' or even 'bad' feeding places can be preferred. This can also be concluded from the presence of the scoters during winter 1994-1995 in area 1. What exactly or what combination of factors is determining the ducks' spatial distribution is not known at this moment. Possibly a combination of food availability and the lack of disturbance, by fishing activities for instance (Leopold and Land, 1996), determines their spatial distribution.

	13.11.94	31.12.94	12.02.95	04.03.95
Area1	52	1187	1366	184
Area 2	67	72	165	0
Total	343	1294	1585	188

Table 9. The distribution of the common scoter at the Belgian coast during winter 1995-1995, with distinction between area 1 and area 2 (H. Offringa, unpublished data).

Still the protection of areas as wintering place for the common scoter is important. As tranquillity zones, e.g. marine protected areas, can be safeguarded against anthropogenic influences, such as shellfish fisheries and sand extraction, the establishment of these areas, rich in bivalves, will have a positive influence on and may even attract the common scoter. Even if the tranquillity zone is not visited by the common scoter every year, the area can act as a refuge in times of food shortage or disturbance.

The monitoring of the macrobenthos in these areas allows estimates of potential productivity of renewable resources and is thus a major component in determining sustainable levels of use, for instance in the case the shellfish fisheries (Agardy, 1994).

CHAPTER 2

TEMPORAL CHANGES WITHIN THE *LANICE CONCHILEGA* COMMUNITY (NORTH SEA, BELGIAN COAST)

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paper in preparation

ACKNOWLEDGEMENTS

This research was funded by the Flemish administration responsible for environment, nature, land and water management, department Nature (AMINAL; AN/1995/nr.3) and the Administration of Waterways and Coast (AWK, Flemish Government; Onderhandse overeenkomst dd. 24.07.1997). The first author received a grant from the Institute to Encourage Scientifical-Technological Research in the Industry (IWT, Flemish Government). Furthermore, the authors want to thank Johan Van de Velde, Vera Van Lancker, Annick Van Kenhove, Myriam Beghyn, Danielle Schram and Dirk Van Gansbeke for their help in the field and the lab.

ABSTRACT

The macrobenthos of shallow coastal habitats is subject to a variety of physical and biological disturbances, varying in frequency and intensity, as well on a temporal and spatial scale. Consequently, the macrobenthic parameters (species composition, abundances, etc.) are continuously changing. To evaluate the ecological value of the *Lanice conchilega* community, knowledge on its temporal variation is indispensable. Furthermore, because of the possibility of recolonization by means of recruitment via the planktonic stages of many macrobenthic species, knowledge on the period of recruitment of the species allows to decrease the negative impact of the planned coastal defence works. The macrobenthic temporal variation and recruitment was studied in two stations over a 2.5 yr study period (April '95 – October '97). From Spring till Summer '95, a general amelioration of the community's condition was attributed to the recruitment of, at least, the dominant species. Though the polychaete *Notomastus latericeus*, the bivalves *Abra alba* and *Tellina fabula*, and the gastropod *Hinia reticulata* showed no recruitment, recruitment of all other dominant species was detected. Recruitment of the polychaetes mainly occurred between April and August '95, while amphipode and bivalve recruitments were observed between July and October '95. An overwhelming recruitment of *Spisula subtruncata* with densities up to 150000 ind m^{-2}, taking place in August '95, possibly caused a general decrease of the number of species per sample (N_0) and the density of all dominant polychaete species in one or both stations after August '95. A new deterioration of the community between January and March '96, only observed in one station, was attributed to the drastic increase of the sediment's mud content of the station (from 5 to 30 %), negatively affecting the macrobenthos of the *L. conchilega* community usually found in a fine sandy sediment with low mud concentrations. In contrary to 1995, no successful recruitments were observed in 1996 nor 1997, illustrating the large year-to-year within the success of recruitment of the macrobenthos. It is thus extremely important to be aware of the natural variability or 'potentials' of a macrobenthic community in order to evaluate its ecological importance.

INTRODUCTION

The macrobenthic communities of shallow coastal waters are subject to a variety of physical and biological disturbances which vary in frequency and intensity, as well on a temporal and spatial scale (Turner *et al.*, 1995). Consequently, the communities' parameters (species composition, dominant species, abundances, etc.) are continuously changing (Arntz and Rumohr, 1986; Dörjes *et al.*, 1986). In temperate regions, these changes are primarily influenced by the seasonality (Bonsdorff and Österman, 1985; Dörjes *et al.*, 1986; Ibanez and Dauvin, 1988; Anderlini and Wear, 1992; Seys *et al.*, 1994), altering the sea water temperature, light intensity, and, consequently, the primary production within the water column (Moll, 1998). Due to this seasonality, a strong response within the time of recruitment, mortality and production of macrobenthic populations is a well-known phenomenon (Beukema, 1974; Arntz and Rumohr, 1986; Herman *et al.*, in press).

In contrary to the yearly repeating cycle of (physical) seasonality, the shallow coastal water macrobenthos shows a large year-to-year variation (Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema *et al.*, 1993; Turner *et al.*, 1995). Weather conditions are greatly influencing the success of recruitment, mortality and production of the composing macrobenthic species (Dörjes *et al.*, 1986; Meire *et al.*, 1994) and are thus constantly altering the density, biomass and, consequently, the biological interactions of the composing species of a macrobenthic community. As the biological interactions, on their turn will also influence the community's parameters (Dörjes *et al.*, 1986; Meire *et al.*, 1994; Herman *et al.*, in press), by, e.g., predation, competition for food and space, and inhibition of recruitment, highly variable macrobenthic community parameters are expected, even in the natural, undisturbed situation. The natural variation within the macrobenthic communities should help to explain issues fundamental to ecology, but also for the conservation and management of marine benthic habitats (Turner *et al.*, 1995).

Because of beach erosion along the western Belgian coast, coastal defence works on the western Coastal Banks may be necessary. To diminish the ecological damage to the Coastal Banks, an area of international importance for waterfowl (Kuijken, 1972), e.g. the common scoter (*Melanitta nigra*) (Maertens *et al.*, 1988; Devos, 1990; Maertens *et al.*, 1990) a study of the macrobenthos in the area, to be directly affected by the works, has been set up. Next to the study of the spatial distribution of the macrobenthic communities (Chapters 1 and 3) and the population dynamics of the bivalve *Spisula subtruncata* (Chapter 4), the project also concentrates on the temporal variation of the *Lanice conchilega* community, the ecologically most important and diverse macrobenthic community of the western Coastal Banks. Furthermore, because of the possibility of recolonization by means of recruitment via the planktonic life stages of many macrobenthic species (Dauvin, 1990; Feller *et al.*, 1992), knowledge on the period of recruitment of the community's species allows to decrease the negative impact of the coastal defence works. If damage to the *L. conchilega* community occurs before the period of major recruitment, a fairly quick recovery of the community can be expected (Arntz and Rumohr, 1986). The study thus aims at (1) the description of the temporal variation within the community over a 2.5 yr period and (2) the identification of the periods of recruitment of the dominant species.

MATERIALS AND METHODS

STUDY AREA

The western Coastal Banks are a geomorphogically diverse shallow marine habitat, extending from the Belgian – French border eastwards to Oostende and from the mean low water level to a depth of about 8 m (Figure 1). The two areas investigated include a complex of sandbanks separated from the beach by a gully (area 1) an a subtidal extension of the beach, with sandbanks and tidal gullies (area 2). The sediments are composed of fine to coarse sand (Chapter 3). The mean wave height in the area is 0.5 m with a maximum of 3.5 m (Anonymous, 1998). During the sampling period the average monthly temperature of the seawater ranged from 0.5 to 21°C, with the lowest temperatures in January – February gradually increasing till August (unpublished data, Coastal Waterways Division).

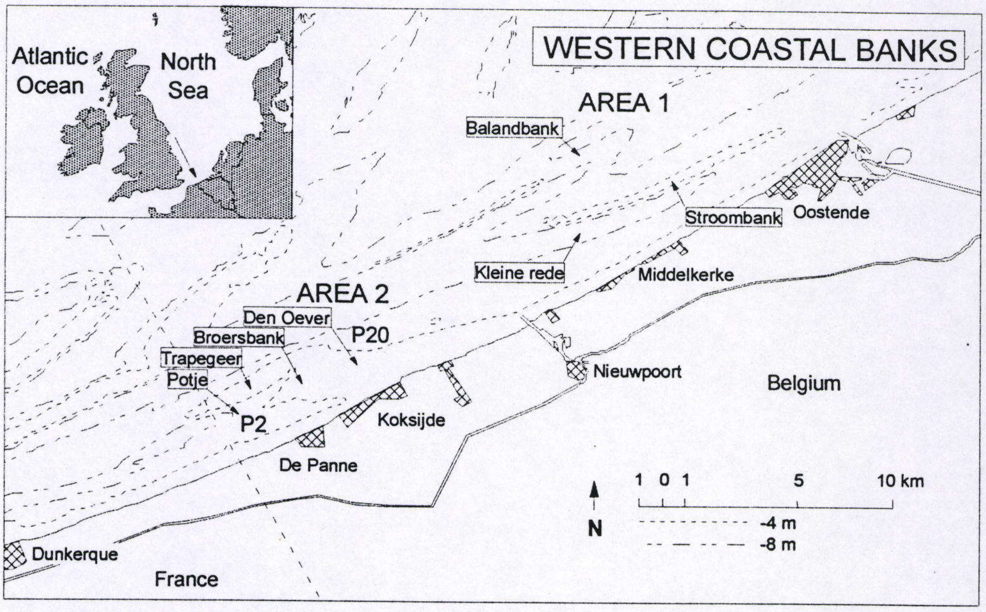

Figure 1. Geographical presentation of the western Coastal Banks, including area 1 and area 2, with indication of the two sampling sites (P2 and P20) for the study of the temporal variation within the *Lanice conchilega* community.

SAMPLING

Two stations (P2 and P20) were selected to study the temporal variation of the *Lanice conchilega* community on the western Coastal Banks (Figure 1). At each station, five Van Veen grabs (sampling surface area: 0.1026 m^2) were taken on 16 occasions: monthly between April '95 and April '96 and seasonally from April '96 till October '97. After fixation, with an 8 % formaldehyde – seawater solution, the samples were washed over two sieves with a 0.5- and 1 mm mesh size. The same samples were used to investigate the population dynamics of *Spisula subtruncata* within the *L. conchilega* community (Chapter 4). The residuals were preserved in an 8 % formaldehyde – seawater solution and stained with Bengal rose. From each macrobenthic sample, a subsample for sediment analysis was gathered.

DATA ANALYSIS

After the identification of all macrobenthic organisms up to the species level, the abundances were standardized to the number of individuals per square meter (ind m^{-2}). To investigate the gradual changes within the macrobenthos of the two stations during the sampling period, the dataset is subjected to a classification technique, Two-Way INdicator SPecies ANalysis (TWINSPAN) (Hill, 1979) and, after fourth root transformation of the densities, to an ordination technique, Correspondence Analysis (CA) (Ter Braak, 1988). The relation between two variables is studied by means of the non-parametric Spearman rank correlation (Conover, 1971).

RESULTS

PHYSICAL ENVIRONMENT

The fine sandy sediment of station P2 had a relatively constant median grain size of about 215 µm; the median grain size of station P20 showed a clear decrease between December '95 and March '96 (Figure 2). This major decrease in P20 coincided with an increase of the mud concentration of the sediment, with 5 % till December '95, up to 30 % in March '96, to decrease again to about 5 % after March '96. The mud concentration in P2 was never higher than 6 %.

MACROBENTHOS: GENERAL

In August '95, an the overwhelming recruitment of *Spisula subtruncata* occurred, with an average density up to 50000 (P20) and 150000 ind m^{-2} (P20) (Chapter 4). In order to understand the pattern of other macrobenthic temporal variation, macrobenthic density is given without incorporation of *S. subtruncata*, recruited in August '95 (Figure 3). The 'macrobenthic' density peaked between June and August '95, with densities up to about 5000 ind m^{-2} in both stations. After August '95, the density steeply decreased to reach a density of 1000 ind m^{-2} in January '96. After January '96, the density never exceeded 1000 ind m^{-2} and no clear density peaks were found.

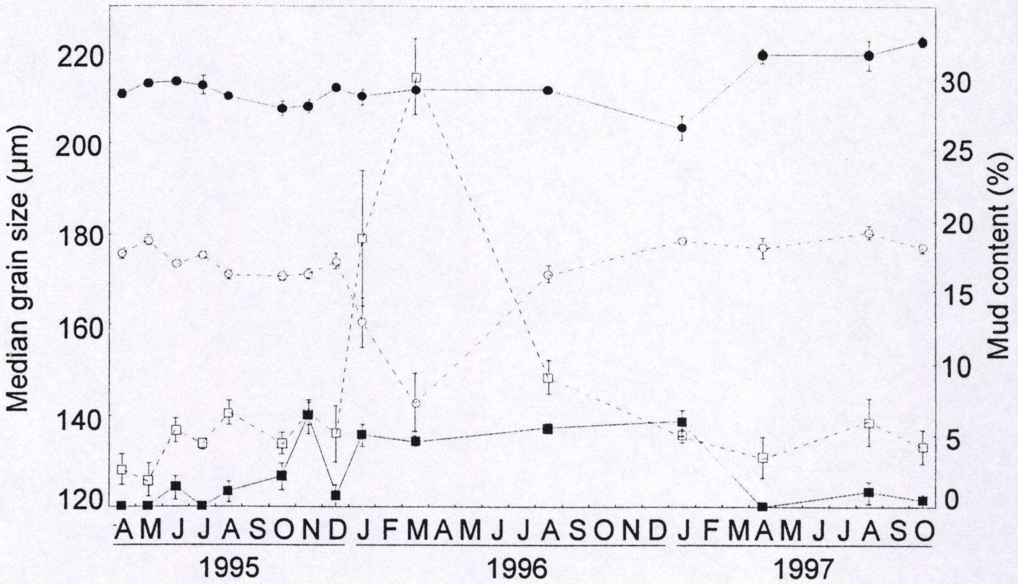

Figure 2. The temporal variation of the median grain size (P2, ●; P20, ○) and the mud content (0 – 63 µm) (P2, ■; P20, □) within both sampling sites, with indication of the standard error.

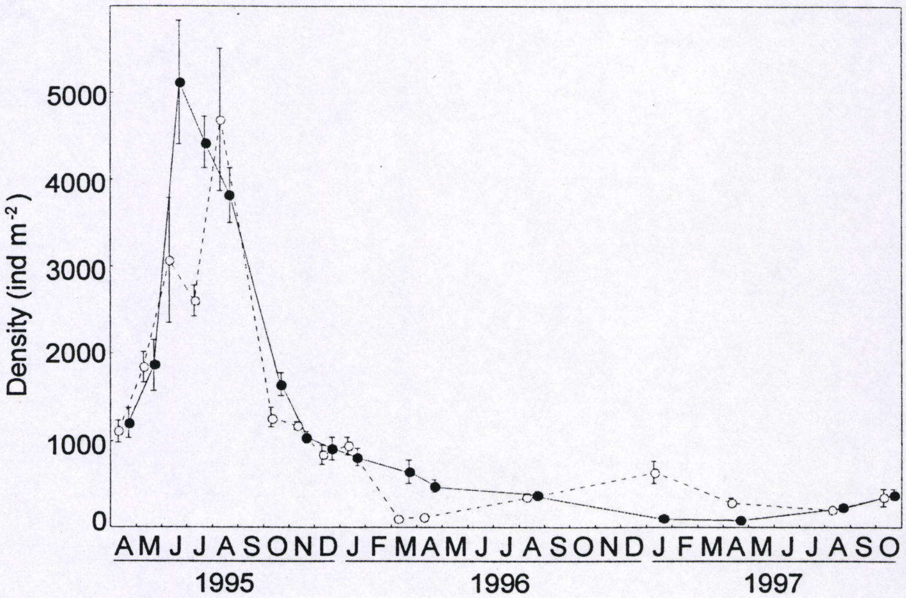

Figure 3. The temporal variation of the macrobenthic density (± standard error), with exclusion of the bivalve *Spisula subtruncata*, within both sampling sites: P2, ●; P20, ○.

Between April and August '95, the number of species per sample (N_0) increased from 20 to 32 and 38 species, in P2 and P20, respectively (Figure 4). After August' 95, N_0 of both stations decreased to less than 15 species from March '96 on. Except for April '96 (P20), N_0 continued to decrease till April '97 (P2: 6 spp.; P20: 3 spp.), after which N_0 increased again to 12 – 13 species. The Shannon-Wiener diversity index (H') was maximal between April and July '95 (P2: 2.2; P20: 2.6). A steep decrease of H' (to about 0.3) in both stations occurred between July and August '95. Whereas in P2, H' fluctuated between 0.2 and 1 from August '95 on, H' of P20 increased again after January '96 to a level of about 1.8.

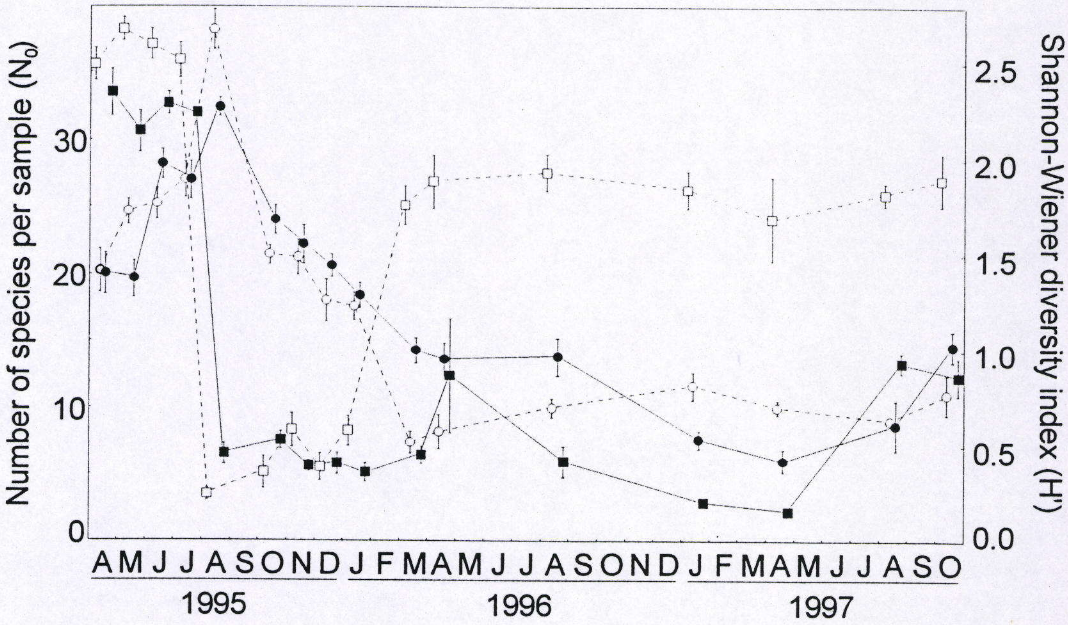

Figure 4. The temporal variation of the number of species per sample (N_0) and the Shannon-Wiener diversity index (H') (± standard error) within both sampling sites: N_0: P2, ●; P20, ○. H': P2, ■; P20, □.

RECRUITMENT

The temporal variation of the macrobenthic density, the number of species per sample (N_0), and the Shannon-Wiener diversity index (H'), changed most during the first year of the study. Therefore, the next part of the results will focus on the sampling period April '95 – April '96 by the investigation of the temporal variation of the abundances of the most dominant species, since after April '96 densities became too low.

Considering the most abundant polychaete species (Figure 5), an increase of the species' densities within the 0.5 mm fraction is found between April (*Nephtys hombergii*) and July (*Spio filicornis*). Except for *Spiophanes bombyx*, all species were about absent in the 0.5 mm fraction between October and April. No individuals of *Notomastus latericeus* were found in the 0.5 mm fraction. Except for *S. filicornis*, an increasing density within the 1 mm fraction, in one or both of the stations (P2 and P20), occurred together with or just after the appearance of small individuals (0.5 mm fraction). In the case of *Lanice conchilega*, where a discrimination between juvenile (smaller than 1 cm) and adult individuals is made within the

1 mm fraction, a drastically increasing density within the 0.5 mm fraction and juvenile individuals coincides in May, while an increase of the adults' density is found in June, and this in both stations.

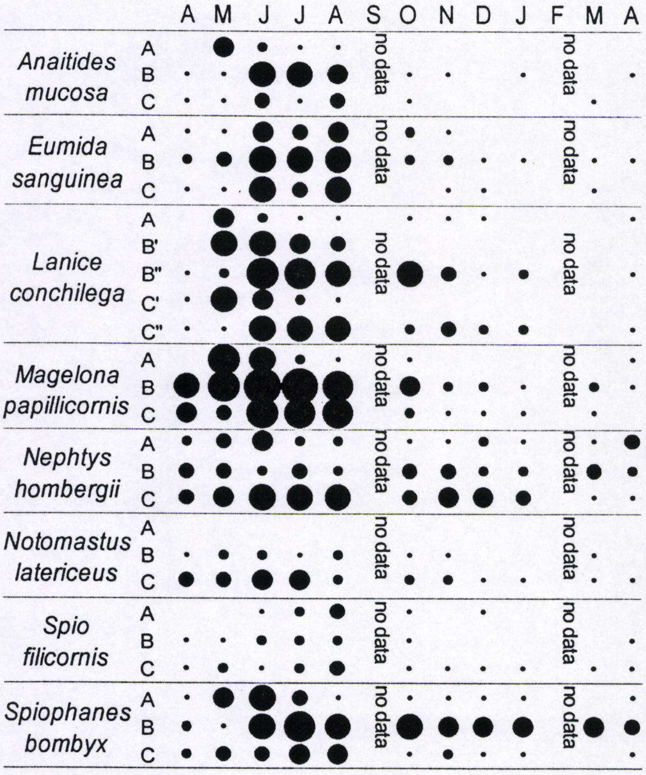

Figure 5. The temporal variation of the density of the eight most dominant polychaetes, within the 0.5 mm fraction of station P2 (A) and the 1 mm fraction of the stations P2 (B) and P20 (C).· , 1 – 20 ind m^{-2}; •, 21 – 50 ind m^{-2}; ●, 51 – 100 ind m^{-2};●, 101 – 200 ind m^{-2}; ●, 201 – 500 ind m^{-2}; ⬤, 501 – 1000 ind m^{-2}; ⬤, > 1000 ind m^{-2}.

Considering the dominant amphipods and molluscs (Figure 6), an increasing density within the 0.5 mm fraction, coinciding with or followed by an increasing density within the 1 mm fraction, is observed for both amphipods, *Pariambus typicus* and *Urothoe poseidonis* and for only one bivalve, *Ensis* sp. and this in July – August. All other molluscs were not encountered in the 0.5 mm fraction. Still, an increase of the density of the bivalve *Spisula subtruncata* (August) and the gastropod *Hinia reticulata* (October) within the 1 mm fraction is observed. In contrary to *S. subtruncata*, all individuals of *H. reticulata* had a height of at least 0.5 cm, most of them being larger than 1 cm.

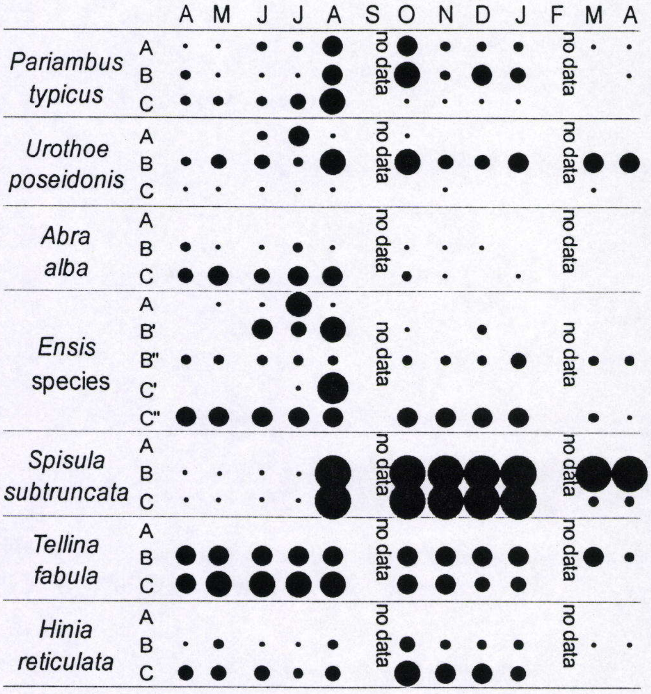

Figure 6. The temporal variation of the density of the seven most dominant amphipodes and gastropodes, within the 0.5 mm fraction of station P2 (A) and the 1 mm fraction of the stations P2 (B) and P20 (C).· , 1 – 20 ind m^{-2}; •, 21 – 50 ind m^{-2}; ●, 51 – 100 ind m^{-2}; ●, 101 – 200 ind m^{-2}; ●, 201 – 500 ind m^{-2}; ●, 501 – 1000 ind m^{-2}; ●, > 1000 ind m^{-2}.

Unlike the polychaetes *Eumida sanguinea*, *Lanice conchilega*, *Magelona papillicornis*, and *Spio filicornis*, the amphipod *Pariambus typicus*, and the bivalves *Spisula subtruncata* and *Tellina fabula*, other species were unevenly distributed over both stations (Figures 5 and 6). The polychaetes *Anaitides mucosa* and *Spiophanes bombyx*, and the amphipod *Urothoe poseidonis* showed a clear preference for station P2. Station P20 accounted for the highest densities of the polychaetes *Nephtys hombergii* and *Notomastus latericeus* and the molluscs *Abra alba*, *Ensis* sp., and *Hinia reticulata*. Furthermore, except for *S. bombyx* in P2 and *N. hombergii* in both stations, all polychaete species showed a drastic density decrease within the 1 mm fraction in both stations after August. A drastic density decrease of the amphipods and molluscs (1 mm fraction) was observed after August (*P. typicus* and *A. alba*) and after January (*Ensis* sp., *S. subtruncata*, *T. fabula* and *H. reticulata*) in P20, while in P2, only the density of *P. typicus* steeply decreased after January

TEMPORAL COMMUNITY CHANGES

By means of multivariate techniques (TWINSPAN and CA), the macrobenthic temporal variation within both stations during the whole sampling campaign is investigated. For station P2, the TWINSPAN revealed a clear temporal pattern with a major distinction (first level) between April '95 – March '96 (group 1) and April '96 – October '97 (group 2). On the second level, a distinction between April – August '95 (group 1A) and October '95 – March '96 (group 1B) and between April '96 – April '97 (group 2A) and August – October '97 (group 2B) is made. Station P20 grossly followed the same pattern: (1) April '95 – January '96 (group 1) and March '96 – October '97 (group 2) (first level) and (2) May – August '95 (group 1A), April '95 together with October '95 – January '96 (group 1B), March – April '96 (group 2A), and August '96 – October '97 (group 2B). 94 % (P2) and 96 % (P20) of the replicates of each month were grouped together, indicating that all replicates are representative for their respective month. In both stations, especially group 1 has a number of indicator species, while group 2 is characterized by the absence of indicator species (Table 1).

Station P2

Group 1A	Group 1B	Group 2A	Group 2B
Magelona papillicornis *Tellina fabula* *Notomastus latericeus*		---	
Magelona papillicornis	*Spisula subtruncata*	*Urothoe poseidonis*	*Spio filicornis* *Eumida sanguinea*

Station P20

Group 1A	Group 1B	Group 2A	Group 2B
Tellina fabula		---	
Lanice conchilega (juv.) *Notomastus latericeus* *Anaitides mucosa* *Abra alba* *Magelona papillicornis*	---	Oligochaeta	*Nephtys hombergii* *Spio filicornis* *Nephtys* sp. (juv.)

Table 1. Overview of the indicator species of all groups, retrieved by TWINSPAN analyses of both stations.

The ordination figure of the CA (Figure 7) clearly separates both stations and no overlap between the two stations is observed. Within both stations, a gradual transition from April '95 till April '96 along the second axis (Eigenvalue: 0.198) is found. A first relatively important change along the second ordination axis is found between July and August '95 (① and ④). Furthermore, a major change along the first ordination axis (Eigenvalue: 0.232), being very drastic in P20, occurred between April and August '96 (② and ⑤). In P2, from August '96 on, a gradual transition till October '97 along the second axis is detected (③). After August '96, a movement towards the original macrobenthic situation is found in P20 (⑥). A negative correlation (Spearman rank correlation: $p < 0.000001$) between the first axis and the number of species per sample (N_0) and the macrobenthic density is found. The standard error on the replicates ordination scores increased from April '95 till October '97.

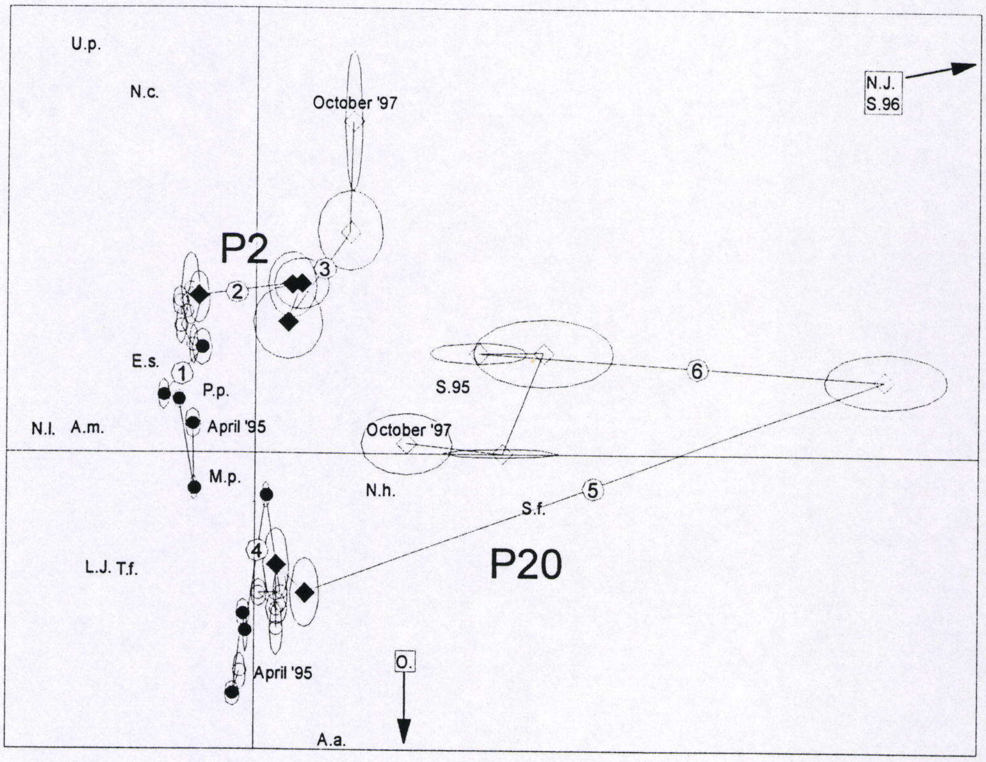

Figure 7. Correspondence Analysis (CA) plot (X-axis: first CA axis and Y-axis: second CA axis), including all samples of both sampling sites (P2 and P20). The temporal changes per sampling site (from April '95 till October '97) are represented by the centroids of all samples of each month ± standard error ellips. The TWINSPAN groups for both stations are: P2: ●, April ' – August '95; O, October '95 – March '96; ♦, April '96 – April '97; ◊, August '97 – October '97 and P20: ●, May '95 – August '95; O, April '95 and October '95 – January '96; ♦, March '96 – April '96; ◊, August '96 – October 97. The situation of the TWINSPAN indicator species: A.a., *Abra alba*; A.m., *Anaitides mucosa*; E.s., *Eumida sanguinea*; M.p., *Magelona papillicornis*; L.J., juvenile *Lanice conchilega*; N.c., *Nephtys cirrosa*; N.h., *Nephtys hombergii*; N.J., juvenile *Nephtys* spp.; N.I., *Notomastus latericeus*; O., Oligochaeta; P.p., *Polydora pulchra*; S.95, *Spisula subtruncata*, cohort '95 (Chapter 4); S.96, *Spisula subtruncata*, cohort '96 (Chapter 4); S.f., *Spio filicornis*; T.f., *Tellina fabula*; U.p., *Urothoe poseidonis*.

Most of the TWINSPAN indicator species are situated on the negative side of the first ordination axis, together with the first 11 sampling months (April '95 – April '96) of both stations. A distinction between both stations is made by means of *Urothoe poseidonis* and *Nephtys cirrosa* in P2, while *Abra alba* and Oligochaeta are typically found in P20. The major change between April and August '96 in P20 is explained by the appearance of juvenile *Nephtys* sp. and *Spisula subtruncata*, cohort '96.

DISCUSSION

As the macrobenthos of the two investigated stations belongs to the *Lanice conchilega* community in 1994 and 1997, typically occurring in area 2 of the western Coastal Banks (Chapter 3), only minor temporal changes within the macrobenthos were expected. Yet, in contrary to the expected stability of the stations' macrobenthos, temporal changes were obvious during this study. Considering the temporal variation of the macrobenthic density and the number of species per sample and the similarities between samples, depicted by TWINSPAN and CA, a large year-to-year variability of the community's parameters is observed, as already demonstrated for a variety of macrobenthic communities in temperate regions (Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema *et al.*, 1993; Turner *et al.*, 1995). Two different periods can be distincted within the 2.5 yr study period: (1) April '95 till April '96 and (2) April '96 till October '97.

During the first period an increase of the density and N_0 from April '95 till August '95 (Spring and Summer), followed by a decrease of both variables till April '96 (Autumn and Winter), was found. This general amelioration of the community's condition can be attributed to the recruitment of, at least, most of the dominant species. As a recruitment is indicated by the appearance of a large number of small, juvenile individuals, recruitments can be traced by means of an investigation of the temporal variation of the species' densities (increasing at a recruitment) and by the appearance of the species in the 0.5 mm fraction (small individuals) (Feller *et al.*, 1992). Considering the dominant species of the *L. conchilega* community, recruitment took place from April till August, with specifical recruitment peaks. Although the polychaetes' recruitments generally took place between April and August (as demonstrated by the density increase within the 0.5 and 1 mm fraction), four recuitment patterns of polychaete species could be recognized. A first type (*N. latericeus*) showed no recruitment in 1995. A prolonged recruitment, from April till August (second type) was typical for *N. hombergii.* The recruitment of *Anaitides mucosa*, *L. conchilega*, *Magelona papillicornis*, and *S. bombyx* took place in May – June (third type), while the fourth type showed a recruitment mainly in June – August (*Eumida sanguinea* and *S. filicornis*). Considering the period of recruitment of the amphipods and the molluscs, four types were discriminated. No recruitment is detected for *Abra alba*, *Tellina fabula*, and *H. reticulata* (see below) (type 1). A recruitment took place in July for *U. poseidonis* and *Ensis* sp. (type 2). A huge recruitment of *S. subtruncata* took place in August (type 3). *Pariambus typicus* showed a recruitment in August – October (type 4). A period of recruitment of the macrobenthos, starting in early Spring and ending at the end of the Summer or early Autumn, has already been demonstrated in other marine ecosystems (Dörjes *et al.*, 1986; Ibanez and Dauvin, 1988;

Dauvin, 1990) and is believed to be caused by an increased influx of organic matter to the sediment, due to an increased primary and secondary production within the plankton (Bonsdorff and Österman, 1985). Yet, even though the macrobenthic environmental conditions (e.g. temperature, sediment organic matter content, planktonic production and hydrodynamics) ameliorate from early Spring on (Dauvin, 1990), the settlement of planktonic larvae does not occur at the same time for the different species (Feller *et al.*, 1992).

A major distinction, considering the period of recruitment, is obvious between the Polychaeta, of which recuitment took place between April and August, and the Amphipoda and Bivalvia, recruting between July and October. Furthermore, while all polychaetes and amphipods had a recruitment in 1995, a recruitment of the bivalves was only observed for *Spisula subtruncata* and *Ensis* sp. The highly variable recruitment of *Spisula subtruncata* , being extremely succesful in August '95, has already been described for the western Coastal Banks (Chapter 4). As a consequence of the dominant presence of *S. subtruncata* in August '95, a steep decrease of the Shannon-Wiener diversity index (H'), in contrary to the high N_0, can be observed. Possibly because of drastically changing biological interactions due to the presence of large numbers of recruits of *S. subtruncata*, covering the sediment with a 1 cm thick layer (personal observation), this event may be responsible for the general decrease of N_0 and the density of all dominant polychaete species in one or both stations after August '95. Indeed, large recruitment events can induce biological alterations in the habitat, which may lead to changes in the overall community structure (Turner *et al.*, 1995). Because of the large post-settlement mortality of *S. subtruncata* between August and October, increasing the quantity of decomposing organisms, scavengers, as *Hinia reticulata*, may have been attracted to the increasing food resource. The consequent active immigration of *H. reticulata* in both stations may explain its increasing density of (large) individuals. Between January and March '96, another remarkable decrease of N_0 and macrobenthic density is found in P20. This new deterioration of the community coincided with a drastic increase of the sediment's mud concentration (from 5 to 30 %), only observed in P20. A temporary increase of the sediment's mud concentration can be expected in wintertime, when higher hydrodynamical forces (e.g. winter storms) increase the suspended mud concentration in the water column and settlement of the fine material during hydrodynamically calm periods is possible (unpublished materials, Van Lancker). The increase of the fine materials in the sediment of P20 then negatively affects the macrobenthos of the *L. conchilega* community, usually occurring in a fine sandy sediment with low mud concentrations (Degraer *et al.*, in press a). Because the filter feeding bivalve, *Spisula subtruncata*, cannot survive in an environment with high mud concentrations (Shackley and Collins, 1984, Chapter 4), the drastic decrease of its density (from over 1000 to less than 50 ind m^{-2}) and, consequently, an increase of H' can be explained. Furthermore, in March '96, a high number of recently died and dying *Ensis* sp. were found on top of the sediment. Probably because of the high biomass of decomposing bivalves (*S. subtruncata* and *Ensis* sp.), the oxygen level in the sediment decreased and an almost completely anoxic sediment with a strong rotting smell, was found in P20 in March '96 (personal observation). After March '96, the sediment's mud concentration slowly returned to its original level of about 5 %, but, in contrary to the 7 – 8 cm thick oxygenated top-layer of the sediment before January '96, the oxygenated level was never more than 2 cm after March '96. The condition of the *L. conchilega* community in P20 started to ameliorate again after April '96, but never reached the original condition of the first year of the study period. In P2, where the mud concentrations were never higher than about 6 %, high densities of *S. subtruncata* (> 1000 ind m^{-2}) were present till October '97. Possibly, because of the continuing competition, the condition of the *L. conchilega* community in P2, continued to deteriorate gradually till April '97: no drastic changes were observed between October '95 and April '97. After April '97, a gradually increasing N_0 and macrobenthic density, indicating a slow recovery of the original *L. conchilega* community in P2, was observed.

The second period (April '96 till October '97) is characterized by a generally low macrobenthic density, with only a low number of species in both stations. Furthermore, a number of species typically found during the first period (P2: *Magelona papillicornis* and *Notomastus latericeus*; both stations: *Tellina fabula*) were absent during this second period. Because of this generally poor macrobenthic condition, a greater chance of finding a large variability within the macrobenthos of the five replicate samples of each month exists. This explains the larger standard error of the samples' average ordination score (CA) for each months of the second period.

During the second period, no obvious macrobenthic density increases were found, indicating a possible absence of successful recruitments of the species. Yet, during the periods of expected recruitment, being April '96 – August '96 and April '97 – August '97, no samples are available. Recruitment of some species, recruting in Spring (mainly polychaetes), may thus have been taken place, but, if so, these recruitments have not been successful as no obvious density increase was noticed in August '96, nor August '97. In contrary to 1995, no successful recruitments could thus be observed in 1996, nor 1997. Many authors already reported on a large year-to-year variability within the success of recruitment of macrobenthic species (Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema *et al.*, 1993; Turner *et al.*, 1995), causing longer-term (e.g. more than one year) fluctuations of the populations. The population of *L. conchilega* in Liverpool Bay, for instance, is found to perform a cycle of six to seven years (Rees and Walker, 1983).

In P20, an increase of the density of juvenile *Nephtys* and *S. subtruncata* is found in August '96, causing its aberrant situation within the CA plot. Although recruitment of *S. subtruncata* is found in August '96, their density was much lower than in August '95 and no surviving individuals were detected after April '97 (Chapter 4).

Conclusion: seasonal fluctuations of the macrobenthic community's parameters are caused mainly by the settlement and post-settlement mortality of the composing species. Yet, the success of recruitment of different species differs from year to year and during some years significant recruitment (and post-settlement survival) can be absent as well. Although a large variability within the macrobenthos of the stations P2 and P20 between April '94 and October '97 is demonstrated, the macrobenthos of both stations still belonged to the *L. conchilega* community in October '97 (Chapter 3). As the detection of community stability does not require that a community remain unchanged, but rather that the observed change in structure is not larger than can normally be expected to occur given the natural temporal and spatial variability of the populations (Turner et al., 1995), the species composition and density is thus still typical for the *L. conchilega* community, even with the observed variability. However, even though the macrobenthos of both stations is part of the same community, not all species are evenly distributed over both stations: the different species are found in different absolute and relative abundances in both stations (no overlap in CA plot!). As demonstrated by Meire *et al.* (1994), many different combinations of dominant species are possible within each major habitat and which species actually do occur is probably mainly determined by differences in recruitment and subsequent biological interactions. The year-to-year variability in rates and, possibly, periods of recruitment (combining settlement and consequent survival) of the composing species of the *L. conchilega* community (as demonstrated above) may thus be responsible for the differing community parameters of both stations. It is thus extremely important to be aware of the natural variability or 'potentials' of a macrobenthic community in order to evaluate its ecological importance.

CHAPTER 3

MACROBENTHIC COMMUNITY CHANGES: DYNAMICS VERSUS STABILITY AND THEIR IMPORTANCE IN COASTAL ZONE MANAGEMENT

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ACKNOWLEDGEMENTS

The research costs of this study are financed by the Coastal Waterways Division (AWK, contract of 24.07.1997). This first author was funded by the Flemish Institute for the Promotion of Scientific – Technological Research in Industry (IWT). Valuable comments on the manuscript were given by Jan Mees. The authors want to thank Johan Van De Velde, Vera Van Lancker, Annick Van Kenhove, Myriam Beghyn, Danielle Schram, Dirk Van Gansbeke, and the crew of the OOSTENDE XI (SILT) for their assistance in the field and/or the lab.

ABSTRACT

Benthic communities are known to be subjected to temporal variations, caused by the variability in recruitment, survival and production of the composing species. These benthic dynamics create a problem when setting up a management plan for benthic habitats: How many sampling campaigns, spread over how many years are necessary to draw the right conclusions? Therefore, the major question through this paper is to what level environmental managers can trust on a single sampling campaign, when trying to identify macrobenthos-rich area or communities, taking into account the macrobenthic dynamics. For this purpose, the macrobenthic species composition and density of 39 stations on the western Belgian Coastal Banks in October 1994 (Degraer *et al.*, in press a) and 1997 (this study) are compared.

Though only minor changes within the physical characteristics of the 39 stations were detected, generally, a lower number of species and a lower density is found in 1997 in comparison with 1994. This deterioration is most obvious within the Polychaeta. Still, the same three macrobenthic communities were found in 1994 and 1997: the *Lanice conchilega* community, the *Nephtys cirrosa* community *s.l.*, and the *'Mytilus edulis'* community. On the community-level, especially the deterioration of the *L. conchilega* community, possibly partly caused by an extremely successful recruitment of the bivalve *Spisula subtruncata*, was clear. 84% of the stations is designated to the same community in 1997 as in 1994, indicating a quite stable spatial distribution of the macrobenthic communities. Furthermore, it is demonstrated that the relation between the stations' physical characteristics, especially the median grain size and the percentages of silt and coarse sand, and the occurrence of the macrobenthic communities on the western Belgian Coastal Banks can be used to predict the spatial distribution of the communities with an accuracy of 83%, only having information on the physical environment. Monitoring of the macrobenthos in the frame of coastal zone management should thus concentrate on the spatial distribution of the macrobenthic 'potentials' of the area, by the identification of (1) the spatial distribution of the macrobenthic communities, (2) the communities' environmental 'needs', and (3) the communities' 'potentials' by means of long-term monitoring of some selected stations within each community.

INTRODUCTION

Because of the increasing awareness of the need for an ecologically fundamented coastal zone management, an environmental assessment of the ecological impact of coastal defence works, become inevitable. As coastal defence works will directly influence the benthic communities, ecological information of the benthos, e.g. macrobenthos, is necessary. In first instance, this requires a decent knowledge of the species composition, abundances, ecological importance and spatial distribution of the different communities present. As the abiotic, physico-chemical environment of the species is subject to short-term (e.g. seasonality) and long-term changes (e.g. climate changes), a large variability in recruitment, survival and production of the benthic species is expected (Beukema, 1974; Bonsdorff and Österman, 1985; Arntz and Rumohr, 1986; Dörjes *et al.*, 1986; Ibanez and Dauvin, 1988; Anderlini and Wear, 1992; Seys *et al.*, 1994; Herman *et al.*, in press). Furthermore, benthic organisms are influenced by biological inter- and intraspecific interactions, such as competition and predation, and this not only within the benthos but also with other components of the ecosystem (Shackley and Collins, 1984; Dörjes *et al.*, 1986; Meire *et al.*, 1994; Herman *et al.*, in press). Because of this environmental and biological variability, benthic communities are known to show large variability, even in a natural, undisturbed environment, both within and between years (Beukema, 1974; Bonsdorff and Österman, 1985; Arntz and Rumohr, 1986; Dauvin and Ibanez, 1986; Dörjes *et al.*, 1986; Essink and Beukema, 1986; Ibanez and Dauvin, 1988; Dauvin, 1990, 1991; Anderlini and Wear, 1992; Feller et al., 1992; Beukema *et al.*, 1993; Meire *et al.*, 1994; Seys *et al.*, 1994; Turner *et al.*, 1995; Essink *et al.*, 1998; Herman *et al.*, in press). It is thus doubtful whether the communities' species composition, abundances and spatial distribution can be described relying on a single sampling campaign.

As, in first instance, coastal zone management will aim at the protection of the ecologically most important communities (Agardy, 1994; Nilsson, 1998), the benthic dynamics create a problem when trying to set up a management plan for a certain area: How many sampling campaigns, spread over how many years, are necessary in order to be able to value the ecological importance of the communities?, a question very hard to answer and probably different for each situation. Even if there was an answer, there is still the question whether there is enough time and resources to perform the research. On the other hand, managers do not always need to know the detailed species composition and abundances of a community, together with respective densities and biomass. A comparison of the community's ecological value with surrounding communities may give enough information to take the 'right' measures. Most species, if not all, are restricted to a specific habitat which is characterized by typical physico-chemical and biological parameters (Meire *et al.*, 1994; Degraer *et al.*, in press a). If a suitable habitat exists, the species has the possibility of colonizing the habitat, but may be absent because of 'colonizing problems', due to changes in the physico-chemical and/or biological environment (Meire *et al.*, 1994). The knowledge of the physico-chemical environment and its specific ecological potentials, may thus provide enough information for a decent coastal zone management.

Based on a single sampling campaign (October 1994), four macrobenthic communities were described and linked with physical characteristics, in the hydrodynamically and geomorphologically highly diverse region of the western Belgian Coastal Banks (Degraer *et al.*, in press a): (1) the *'Mytilus edulis'* community, (2) the *Lanice conchilega* community, (3) the *Nephtys cirrosa-Echinocardium cordatum* community and (4) the *N. cirrosa* community, the latter two communities being very similar in species composition and species' densities. Especially the grain size distribution of the sediment seemed to be important in structuring the communities. In order to check whether this one investigation gave a representative view on the macrobenthos of the area, the sampling of the macrobenthos was repeated during study (October 1997).

This paper describes the differences (dynamics) and similarities (stability) between the October 1994 and October 1997 campaign. It also discusses to what level conclusions out of one investigation can be used in management.

MATERIALS AND METHODS

DATA GATHERING

The 39 stations, sampled in 1997, were situated at the same places as the samples of Degraer *et al.* (in press a) (Figure 1). Sampling and data processing was exactly the same as described by Degraer *et al.* (in press a): at each station one sample was taken with a Van Veen grab (surface area: 0.1026 m²), the samples were sieved fresh trough a sieve with a mesh-size of 1 mm, and fixated and preserved in an 8 % buffered formaldehyde-seawater solution.

The sediment particle size analysis was done with a COULTER LS. The sediment fractions clay (0-4 µm), silt (4-63 µm), very fine sand (63-125 µm), fine sand (125-250 µm), medium sand (250-500 µm), and coarse sand (500-1000 µm) (Buchanan, 1984) are expressed as volume percentages, while mass percentage is used for the gravel fraction (>1000 µm).

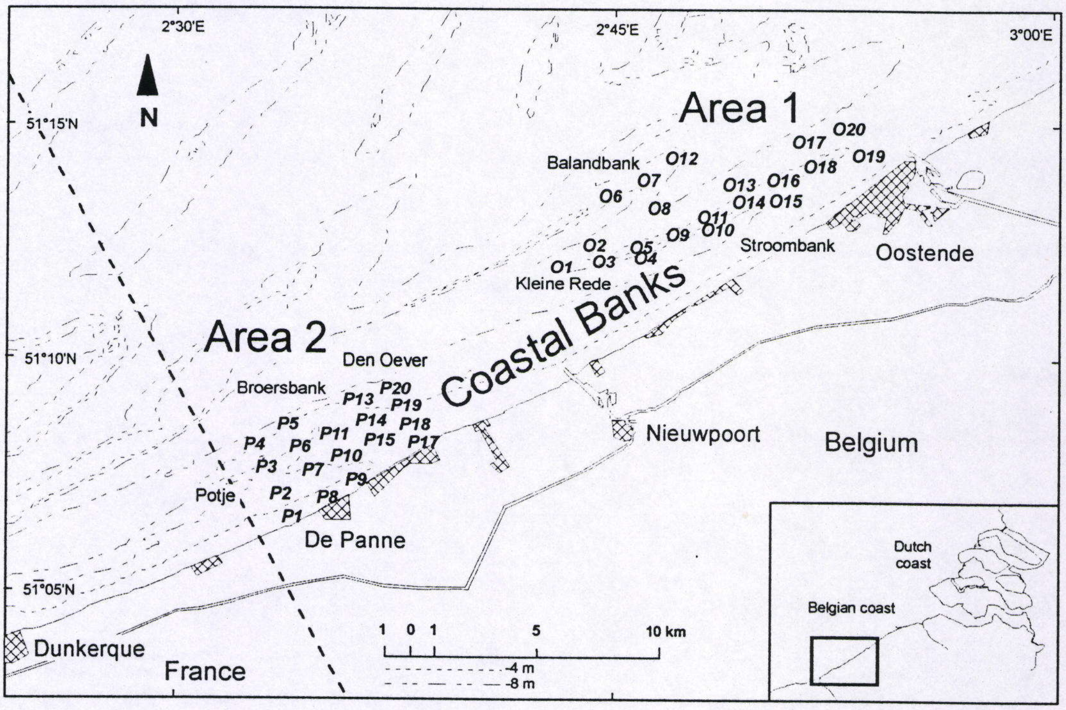

Figure 1. Geographical view on the western Coastal Banks, divided in area 1 and area 2; with indication of the 39 sampling sites.

DATA ANALYSIS

Wilcoxon matched pairs signed-ranks test

Dynamics and stability in the area can be described by differences or similarities between the two samples (pair) of each of the 39 stations in the two different years. As the two samples within each of the 39 pairs are related to each other (same station) and the measurements (diversity, density and physical parameters) are in an ordinal scale within and between pairs, the non-parametrical Wilcoxon matched pairs signed-ranks test is used to detect general trends of dynamics (differences) or stability (similarities) between the two sampling campaigns (Conover, 1971).

Discriminant analysis

Based on a discriminant analysis, three classification functions (one per community), including the discriminating physical variables, are retrieved. These functions may be used to 'predict' the designation of new samples (sampling campaign of October 1997) to one of the three communities. Next to this predictive function, the classification functions also give information on the stability of the physical properties of the 39 stations: if a new sample (campaign October 1997) is designated to the same community as in 1994, a similar combination of physical parameters, important for the species' distribution, was present in 1994 and 1997 and, thus, stability of the physical environment is assumed.

Multivariate techniques

In order to detect macrobenthic communities in 1997 and to search for relations between these communities and the communities detected in October 1994 (Degraer *et al.*, in press a), three multivariate techniques were used: a Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979), on the absolute density data (with the cutlevels 0, 10, 20, 40, 80, and 150 ind m^{-2}) and a Canonical Correspondence Analysis, CCA (Ter Braak, 1988), and a group averaging Clusteranalysis, with Bray-Curtis similarities (van Tongeren, 1987), after fourth-root transformation of the density data.

RESULTS

PHYSICAL CHARACTERISTICS, SPECIES COMPOSITION AND DENSITY OF 1994 VERSUS 1997

Of all environmental variables measured (depth, median grain size, mean-median ratio, and the percentages of clay, silt, very fine sand, fine sand, medium sand, coarse sand and gravel) only median grain size (Wilcoxon test: $N = 38$; $Z = 3.524$; $p = 0.0004$) and the percentage of fine sand ($Z = 2.610$; $p = 0.0090$), and medium sand ($Z = 4.358$; $p < 0.0001$) changed significantly (Wilcoxon test: $p = 0.0004$, $p = 0.009$, $p < 0.0001$, and $p = 0.04$ respectively). These differences all pointed towards a slightly coarser sediment in 1997: on average the median grain size per station increased with 8.83 µm (SE: 7.68 µm). Consequently, as most of the sediment is restricted to the fine and medium sand fraction, these fractions slightly decrease per station (-2.73 % ± SE: 1.58 %) and increase per station (5.12 % ± SE: 0.88 %) respectively.

A total of 60 macrobenthic species was found in 1994, 39 in 1997. This decrease can be attributed to the disappearance of 26 spp. and the appearance of only 6 spp. A general loss in the number of species per taxon, with a maximum within the Polychaeta, was observed (Figure 2). Still, both sampling campaigns had 33 species in common. A general decrease of the total number of species per station could be observed (Wilcoxon test: $N = 38$; $Z = 3.477$; $p = 0.0005$). A decrease of species per station was found in 27 stations, while in 11 stations the number of species was similar or increased.

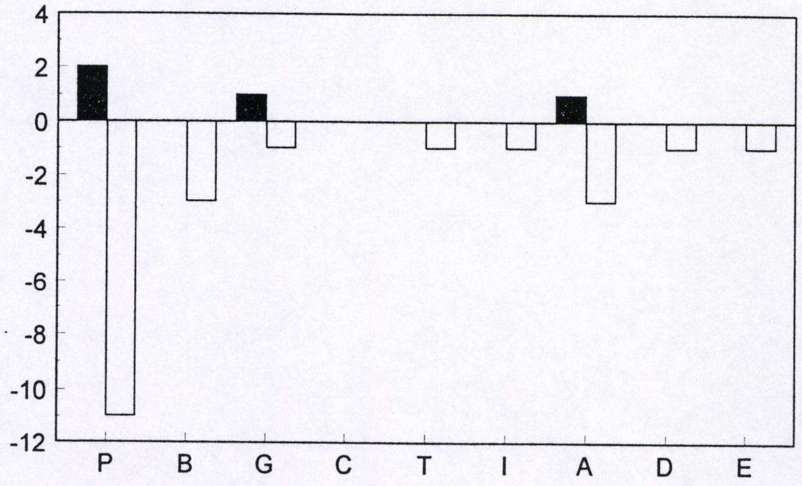

Figure 2. The gain and loss of the number of species per taxon between 1994 and 1997. P, Polychaeta; B, Bivalvia; G, Gastropoda; C, Cumacea; T, Tanaidacea; I, Isopoda; A, Amphipoda; D, Decapoda; E, Echinodermata.

Though less clear (non-significant) than the number of species, a general decrease of the macrobenthic density per station exists (Wilcoxon test: N = 38; Z = 1.835; p = 0.0666). The average macrobenthic density of 1032 ind m^{-2} decreased with 62 % from 1994 to 392 ind m^{-2} in 1997. This decrease is almost completely due to the Polychaeta (Wilcoxon test: N = 38; Z = 3.386: p = 0.0007) (Figure 3). The only other taxa of any importance, the Bivalvia (Wilcoxon test: N = 38; Z = 1.849; p = 0.0644) and the Amphipoda (Wilcoxon test: N = 38; Z = 2.113; p = 0.0431), had similar or higher average densities in 1997. In total 20 stations are having a lower, 13 are having a higher and 5 are having the same density in 1997.

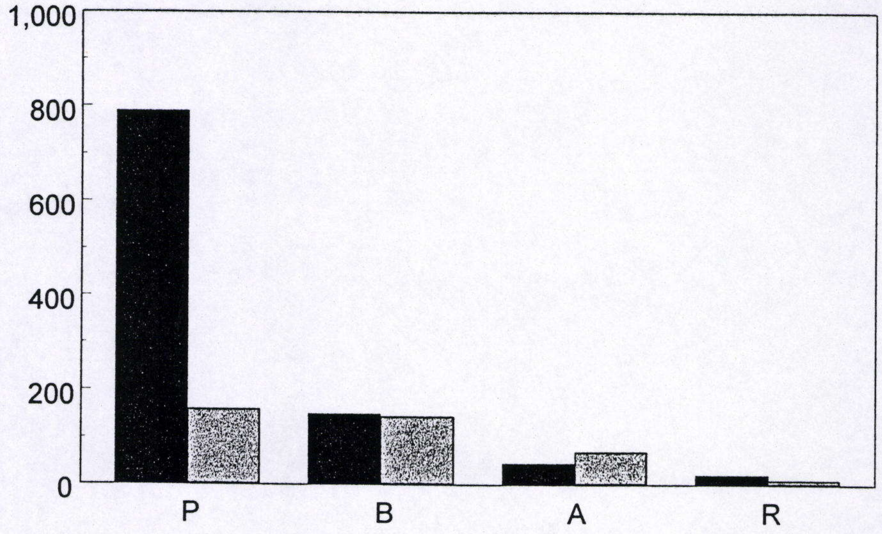

Figure 3. The differences of the densities of the three most abundant taxa and other taxa between 1994 and 1997. P, Polychaeta; B, Bivalvia; A, Amphipoda; R, rest.

MACROBENTHIC COMMUNITIES IN 1997: BIOLOGICAL CLASSIFICATION

By means of TWINSPAN, both on the absolute densities and presence/absence data, cluster analysis and CA - three groups of stations, with similar species composition and densities, were detected in 1997 (Table 1). Because of their unstable behaviour during the multivariate analyses, four stations (O1, O6, P4, and P19) could not be designated uniformely to one of the three groups. These four stations constantly switched between BIO 1 and BIO 2 and were rejected for further analyses. Considering the remaining 35 stations, at least 95 % of the stations were designated correctly to their respective group in the four multivariate analyses. These 35 stations were regarded as 'biologically classifiable'.

High densities (more than 20 ind m^{-2}) of *Spisula subtruncata* and *Nephtys hombergii* and the presence of *Tellina fabula*, *Spiophanes bombyx* and *Diastylis bradyi* are indicative for BIO 1 (TWINSPAN on the absolute densities and presence/absence). The presence of *Bathyporeia* sp. is typical for BIO 2, while *Hesionura augeneri* is the only TWINSPAN indicator species for BIO 3.

Groups	Composing stations
BIO 1	O15, O17, O19, O20 and P2, P5, P13, P20
BIO 2	O2, O4, O5, O7, O8, O9, O10, O11, O12, O13, O14, O16, O18 and P1, P3, P6, P7, P8, P9, P14, P15, P16, P17, P18
BIO 3	O3 and P10, P11

Table 1. The station composition of the three groups, differentiated by means of four multivariate techniques: TWINSPAN, both on absolute densities and presence/absence data, clusteranalysis and CCA.

BIO 1 clearly had the highest diversity and the highest macrobenthic density (Table 2). The lowest diversity and density were found in BIO 3. BIO 2 had intermediate values of diversity and macrobenthic density.

	BIO 1	BIO 2	BIO 3
Total number of species	30	24	7
N_0	10 ± 2	6 ± < 1	4 ± 1
N_1	5.7 ± 0.9	3.8 ± 0.3	0.9 ± 0.5
N_{inf}	3.0 ± 0.5	2.2 ± 0.2	1.9 ± 0.1
H'	1.6 ± 0.2	1.3 ± 0.1	1.0 ± 0.2
Macrobenthic density	1001 ± 452	246 ± 30	177 ± 52

Table 2. The average diversity indices: total number of species, number of species per station (N_0), the Hill-numbers N_1 and N_{inf}, and the Shannon-Wiener diversity index (H'), together with the average macrobenthic density (ind m^{-2}). All values ± the standard error.

The bivalve *Spisula subtruncata* and the polychaetes *Lanice conchilega* and *Nephtys hombergii* have over 50 ind m^{-2} in BIO 1 (Table 3.). BIO 2 has high densities of the amphipodes *Bathyporeia* sp. and the polychaetes *Nephtys cirrosa, Magelona papillicornis* and *Nephtys hombergii*, with more than 10 ind m^{-2}. The most abundant species of BIO 3 are the polychaetes *Ophelia limacina*, *Spio filicornis*, *Scoloplos armiger*, *Hesionura augeneri* and *Glycera capitata*, with more than 10 ind m^{-2}. Without taking into account *Spisula subtruncata*, which is found in each group, each pair of groups has at most two dominant species in common.

BIO 1		BIO 2		BIO 3	
Species	Density	Species	Density	Species	Density
Spisula subtruncata	549	*Bathyporeia* sp.	99	*Ophelia limacina*	42
Lanice conchilega	139	*Nephtys cirrosa*	40	*Spio filicornis*	26
Nephtys hombergii	73	*Magelona papillicornis*	32	*Scoloplos armiger*	16
Cirratulidae	33	*Nephtys hombergii*	14	*Hesionura augeneri*	13
Abra alba	33	*Scoloplos armiger*	9	*Glycera capitata*	13
Diastylis bradyi	23	*Urothoe poseidonis*	7	*Spisula subtruncata*	3
Mysella bidentata	23	*Urothoe brevicornis*	7	*Bathyporeia* sp.	3
Juvenile *Nephtys*	16	*Spisula subtruncata*	5		
Spiophanes bombyx	12	Juvenile *Nephtys*	4		
Eumida sanguinea	10	*Ensis* sp.	3		

Table 3. The list of the (ten) most dominant species of the three groups with indication of the average density (ind m^{-2}).

	BIO 1	BIO 2	BIO 3
Depth	7.0 ± 0.4	4.0 ± 0.5	3.0 ± 1.5
Median grain size	201 ± 10	253 ± 11	434 ± 15
MM-ratio	0.93 ± 0.03	1.00 ± 0.00	0.99 ± 0.01
Clay content	0.57 ± 0.24	0.01 ± 0.01	0.05 ± 0.03
Silt content	4.46 ± 2.68	0.09 ± 0.05	0.14 ± 0.07
Very fine sand content	5.70 ± 1.97	2.22 ± 0.61	0.47 ± 0.25
Fine sand content	63.96 ± 4.45	51.11 ± 4.36	7.64 ± 0.18
Medium sand content	24.40 ± 3.57	42.65 ± 3.91	55.36 ± 5.06
Coarse sand content	0.92 ± 0.40	3.92 ± 1.69	36.34 ± 4.63
Gravel content	0.00 ± 0.00	2.48 ± 1.60	24.15 ± 15.61

Table 4. The values of the different environmental variables of the three groups. Depth, m below MLWS; Median grain size (µm); MM-ratio, mean – median ratio; volume percentages of clay, silt, very fine sand, fine sand, medium sand, coarse sand and mass percentage of gravel. All values ± the standard error.

BIO 1 is characterized by deeper lying stations (7 m), with a fine sandy sediment (median grain size: 201 µm), a rather high percentage of silt (4%) and the absence of gravel (Table 4). In contrast, BIO 3 comprized shallow (3 m) stations, with a coarse sediment (median grain size: 434 µm), a low percentage of silt (0.1%) and a high percentage of gravel (24%).

BIO 2 is composed of stations with an intermediate depth (4 m) and grain size distribution (median grain size: 253 µm; 0.1% silt; 2% gravel).

DISCRIMINANT ANALYSIS AND CLASSIFICATION FUNCTIONS: ENVIRONMENTAL CLASSIFICATION

Retrieving the classification functions

In order to determine which physical variables discriminate between the four sandbank communities, detected in October 1994 and defined by Degraer *et al.* (in press a), a new approach is followed in this paper. By means of a discriminant analysis, taking into account the communities' physical variables, only three (and not four) communities could be discriminated: the *Nephtys cirrosa* community and the *N. cirrosa-Echinocardium cordatum* community (Degraer *et al.*, in press a) could not be separated. Therefore, both communities were lumped to the *Nephtys cirrosa* community *s.l.* The *'Mytilus edulis'* (ENV 1), the *Lanice conchilega* communities (ENV 2), and the *Nephtys cirrosa* community *s.l.* (ENV 3) could be distinguished significantly (Chi square test: $p < 0.001$) (Figure 4).

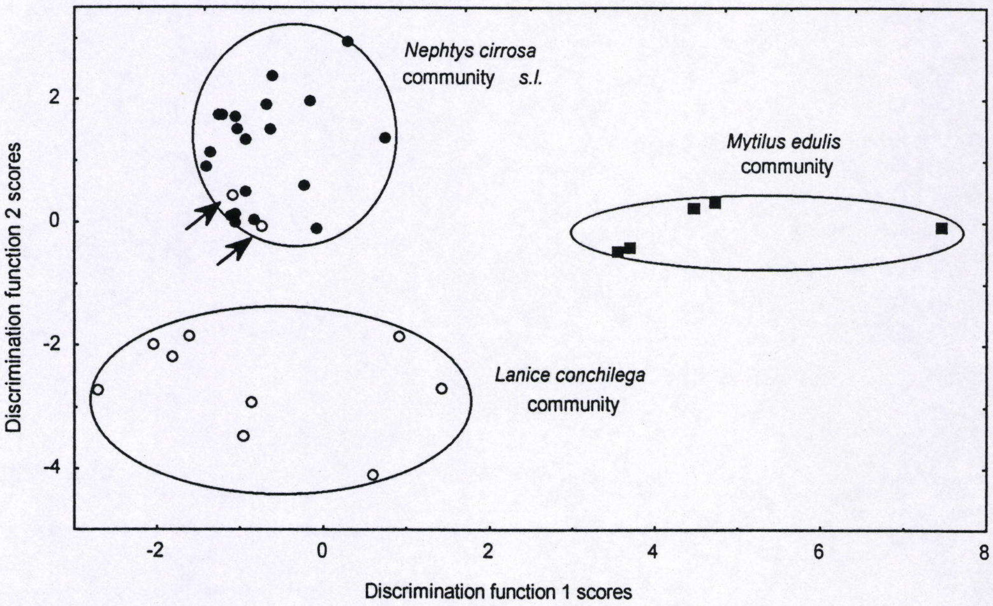

Figure 4. Graphical presentation of the differences between the three communities by means of their canonical scores of the two discrimination functions. Each point represents a station, sampled in October 1994, designated to one of the three communities by Degraer *et al.* (in press a). The two arrows are pointing at the by the classification functions misclassified stations, P2 and P5.

The two discrimination functions take into account, in decreasing order of importance, the percentage of coarse sand and silt, the median grain size, the percentage of clay and fine sand, the depth and the percentage of medium sand as biologically important, discriminating environmental variables.

The coefficients and constant of the three classification functions, to be used when designating new observations to one of the three groups (communities), are given in Table 5. Only 2 stations of ENV 2 (P2 and P5) are identified as being misclassified by the *post hoc* predictions as already suggested by Figure 4. The *a posteriori* accuracy of the classification functions was 94 %: on a total of 36 stations the derived classification functions are placing 34 stations in the same community as defined by Degraer *et al.* (in press a).

	ENV 1	ENV 2	ENV 3
Coarse sand (CS)	-0.5147	-0.4208	-1.1245
Silt (SI)	4.2937	10.7117	5.1821
Median grain size (ME)	0.3392	0.2990	0.3360
Clay (CL)	-7.1601	-18.4768	-9.2059
Fine sand (FS)	0.8641	0.9411	0.8108
Depth (DE)	2.4331	2.7155	2.0932
Constant (c)	-79.7823	-76.0591	-67.5674

Table 5. The classification functions, derived by the discriminant analysis, are given $S_i = w_{iCS}*CS + w_{iSI}*SI + w_{iME}*ME + w_{iCL}*CL + w_{iFS}*FS + w_{iDE}*DE + c_i$ with S_i = total score for community $_i$, w_{iCS} = weight of the variable coarse sand (CS) for the community $_i$, etc. and c_i = constant of community $_i$, as given by the table. The new observations are designated to the community with the highest total score.

Environmental classification of the samples of 1997

When using the environmental parameters of the 39 stations sampled in 1997 as 'new observations' in the classification functions, the stations are designated to one of the three groups (Table 6), of which ENV 3 counts most of the stations.

Group	Composing stations
ENV 1	O1, O3, O4 and P7, P10, P11, P15
ENV 2	O15, O19, O20 and P5, P20
ENV 3	O2, O5, O6, O7, O8, O9, O10, O11, O12, O13, O14, O16, O17, O18 and P1, P2, P3, P4, P6, P8, P9, P13, P14, P16, P17, P18, P19

Table 6. The distribution of the 39 stations, sampled in 1997, over the three groups as predicted by the classification functions.

26 of the 35 stations (74 %), designated to a sandbank community by Degraer *et al.* (in press a) and sampled again in 1997, were classified in the same group as in 1994. This means that the 'biologically important' environmental variables changed significantly in only nine stations (O1, O13, O17, O19, P1, P2, P7, P13 and P19).

COMPARISON BETWEEN THE 'BIOLOGICAL' AND 'ENVIRONMENTAL' CLASSIFICATION

Five of the eight stations, biologically classified in BIO 1, were placed in ENV 2 by the classification functions (Table 7). The classification functions designated 21 of the 24 'BIO 2' stations in ENV 3. All three 'BIO 3' stations were classified in ENV 1. The classification functions only place six stations (17 %), three of BIO 1 (O17, P2 and P13) and three of BIO 2 (O4, P7 and P15), in another community as the majority of their group.

		'Environmental' classification		
		ENV 1	ENV 2	ENV 3
'Biological' classification	BIO 1	0	5	3
	BIO 2	3	0	21
	BIO 3	3	0	0

Table 7. The distribution of the 35 'biologically' classified stations (groups) over the 'environmentally' defined groups.

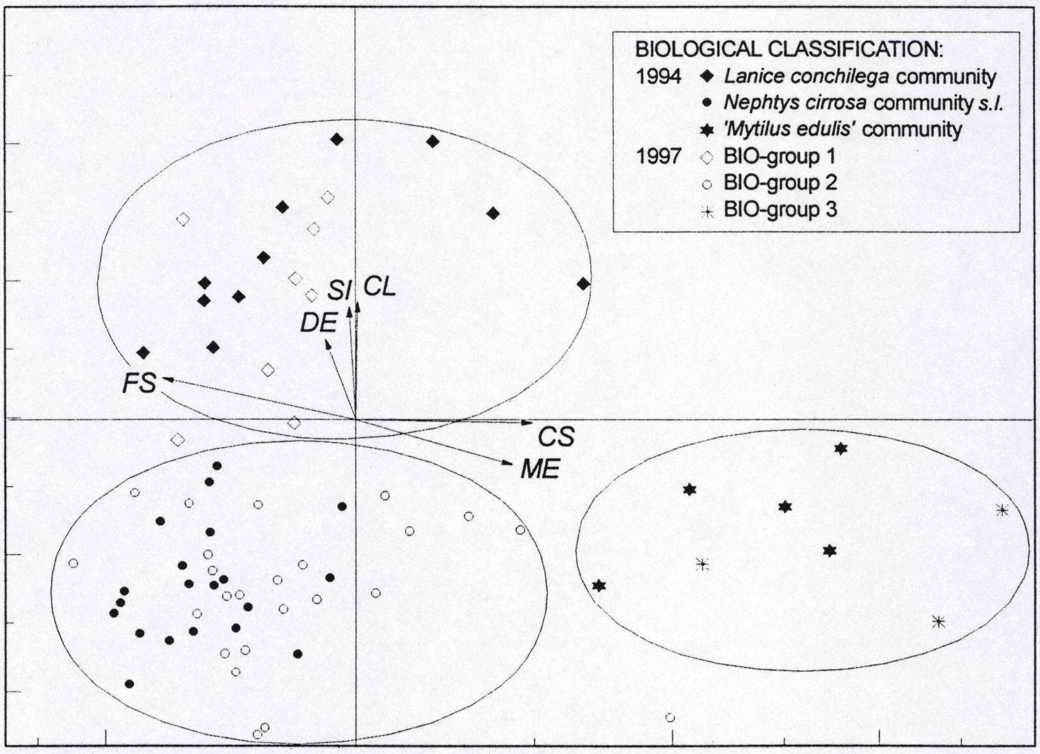

Figure 5. Graphical presentation of the first two axes of the Canonical Correspondence Analysis on the classified stations of 1994 and 1997, together with their typical environmental variables. Physical variables: DE, depth; ME, median grain size; CL, clay content; SI, silt content; FS, fine sand content; CS, coarse sand content.

RELATION BETWEEN THE COMMUNITIES OF 1994 AND THE BIOLOGICALLY DEFINED GROUPS OF 1997

The CCA with the biologically classifiable stations of 1994 and 1997 together showed a clear similarity between the ordination of the three biologically defined groups of 1997 (BIO1, BIO 2 and BIO 3) and the macrobenthic communities of 1994 (Figure 5). The stations of the *Lanice conchilega* community are placed together with these of BIO 1, the *'Mytilus edulis'* community with BIO 3 and the *Nephtys cirrosa* community *s.l.* with BIO 2. Indeed, a lot of similarity between the *L. conchilega* community and BIO 1 is found: (1) they have five of their ten most dominant species in common, (2) they both have the highest diversity and density, (3) they are situated in a deep, fine sandy sediment with silt, and (4) the polychaete *L. conchilega* and the bivalve *Abra alba*, most typical for the *L. conchilega* community, are dominantly present in BIO 1 (Table 8). The *N. cirrosa* community *s.l.* and BIO 2 (1) have (at least) six dominant species in common, (2) have a rather low diversity and density, (3) are situated in a fine sandy sediment without clay or silt and (4) both have a high density of *N. cirrosa*. Finally, the '*M. edulis*' community and BIO 3 have (1) five dominant species in common, (2) a low diversity and density, and (3) they are both occurring in a rather shallow (respectively 4.8 and 3.0 m below MLWS), medium sandy sediment (median grain size respectively, 456 and 434 µm) without clay or silt.

	Lanice conchilega community		*Nephtys cirrosa* community *s.l.*		*'Mytilus edulis'* community	
	1994	1997	1994	1997	1994	1997
1	54	30	15 – 24	24	21	7
2	18	10	5 – 8	6	8	4
3	1.7	1.6	1.1 – 1.6	1.3	1.6	1.0
4	2500	1001	250 – 300	246	450	117
5						
6	6	7	4 – 5	4	5	3
7	211	201	224 – 242	253	456	434
8	3	5	0 – 0	0	0	0
9	5	1	1 – 1	4	36	36

Table 8. Comparison of the three communities between 1994 and 1997. 1, total number of species; 2, N_0 (species); 3, H'; 4, macrobenthic density (ind m^{-2}); 5, number of the ten most dominant species in common (species); 6, depth (m below MLWS); 7, median grain size (µm); 8, silt content (%); 9, coarse sand content (%). The two values for the *Nephtys cirrosa* community *s.l.* in 1994 are derived from the *N. cirrosa* and the *N. cirrosa* – *Echinocardium cordatum* community of 1994 (Degraer *et al.*, in press a).

DISCUSSION

The major question in this paper is to what level environmental managers can trust on a single sampling campaign when trying to identify and protect macrobenthos-rich areas or communities, taking into account the dynamics of the macrobenthos. Translated to this study: 'Are the same macrobenthic communities, encountered in 1994, still present in 1997? And, if so, what are the major differences within each community and is their spatial distribution stable in time?'

ARE THE COMMUNITIES OF 1994 STILL PRESENT IN 1997?

One of the principle properties of marine benthic communities in high latitudes is their continuous change, as reflected in all population or community parameters at any time (Arntz and Rumohr, 1986). As already shown by many studies (Beukema, 1974; Bonsdorff and Österman, 1985; Arntz and Rumohr, 1986; Dauvin and Ibanez, 1986; Dörjes *et al.*, 1986; Essink and Beukema, 1986; Ibanez and Dauvin, 1988; Dauvin, 1990, 1991; Anderlini and Wear, 1992; Feller *et al.*, 1992; Beukema *et al.*, 1993; Meire *et al.*, 1994; Seys *et al.*, 1994; Turner *et al.*, 1995; Essink *et al.*, 1998; Herman *et al.*, in press), temporal variations, both within and between years, are indeed inherent for the benthos in temperate regions. Benthic communities are thus characterized by variability (dynamics), rather than by stability. Though, the detection of community stability does not require that a community remain unchanged, but rather that a community maintains a distinctly different species composition and abundance respective to other communities (Turner *et al.*, 1995). Because of the number of similarities (species composition, abundances and diversity) between each 'biologically defined' group of 1997 (BIO 1, BIO 2, and BIO 3) and one of the communities of 1994 (Figure 5 and Table 8), the same communities, as found in 1994 (Degraer *et al.*, in press a), were thus present in 1997.

STABILITY AND DYNAMICS OF THE MACROBENTHIC COMMUNITIES

The obvious similarity between 1994 and 1997 does not mean that the macrobenthos of the western Coastal Banks remained unchanged between 1994 and 1997. Quite a lot of variation is observed. This temporal variation or dynamics of the macrobenthos shows a patchy distribution over the western Coastal Banks: depending on the stations under consideration different levels of a decreasing or, eventually, increasing density and diversity between 1994 and 1997 are observed. Especially the polychaetes are having less species and a lower density in 1997. Designating the stations to one of the three macrobenthic

communities, these changes turn out to be community-dependent, as illustrated by Table 8: major changes were observed in the *Lanice conchilega* and the *'Mytilus edulis'* community, whereas only minor changes were detected in the *Nephtys cirrosa* community *s.l.*
Obviously, different macrobenthic communities show different temporal dynamics. Because each community is composed of a specific combination of species, the temporal variation of the complex biological interactions, due to the coexistence of these species, will differ from one community to another (Bonsdorff and Österman, 1985). A successful recruitment and survival of one species, for instance, will only take place in the community where this species belongs to and not in any other community. This recruitment may trigger a chain reaction of changing biological interactions (competition, predation, etc.), causing major shifts in the species composition and density of the community: formerly abundant species may become rare or even disappear and less abundant or even new species may become dominant (Meire *et al.*, 1994; Turner *et al.*, 1995).

In this study, major community-dependent temporal changes, possibly due to recruitment, are illustrated by the dynamics of the *L. conchilega* community, described as the richest and most important macrobenthic community of the western Coastal Banks (Degraer *et al.*, in press a). In August 1995, an extremely successful recruitment of the bivalve *Spisula subtruncata* took place in the *L. conchilega* community. Juvenile bivalves, with densities up to 250000 ind m^{-2}, formed a thick layer (up to 2 cm) on top of the sediment at least from August till October 1995 (Chapter 4). As indicated by the presence of *S. subtruncata* in the list of the ten most dominant species of each community, this recruitment presumably took place over a large part of the western Coastal Banks, but a fair survival of *S. subtruncata* is only observed in the *L. conchilega* community, with an average of 549 ind m^{-2} in October 1997, all of which belonged to the cohort '95 (Chapter 4). In comparison, at the same time in the two other communities *S. subtruncata* only has an average density of maximally 5 ind m^{-2}. Possibly because of the competition of *S. subtruncata* with the other species present, a major deterioration of the community, with a decrease of the total number of species (from 54 to 30 species), diversity (N_0: from 18 to 10 species; H': from 1.7 to 1.6) and the macrobenthic density (from about 2700 to 1001 ind m^{-2}), can be observed between 1994 and 1997 (Chapter 4). The community still has the highest densities and diversity in 1997, but the difference with the *Nephtys cirrosa* community *s.l.* is smaller in comparison with 1994. Lacking the overwhelming success of *S. subtruncata* and, most likely, any other macrobenthic species, no spectacular changes between 1994 and 1997 occurred in this *N.*

cirrosa community *s.l.*: a comparable total number of species (15 – 24 species), diversity (N_0: 5 – 8 species; H': 1.1 – 1.6) and macrobenthic density (150 – 250 ind m^{-2}) is found. In comparison with the *L. conchilega* only minor differences within the *N. cirrosa* community *s.l.* took place between 1994 and 1997.

Another decrease in total number of species (from 21 to 7 species), diversity (N_0: from 8 to 4 species; H': from 1.7 to 1.0) and density (from about 400 to 117 ind m^{-2}) is found in the *'Mytilus edulis'* community. The deterioration of this community cannot be explained by a recruitment or any other perceptible event between 1994 and 1997. The typical small, interstitial polychaetes, living in the interstitial spaces between sand grains, are known to prefer coarser sediments, with more interstitial spaces, as present in the *'M. edulis'* community (Vanosmael *et al.*, 1982). Unfortunately, the used sieving method (sieving before fixation with a 1 mm mesh-sieve) allows these small polychaetes to escape actively out of the sample, causing a general underestimation of the density of interstitial polychaetes. Some samples may even lack the interstitial polychaetes although they were present in the sediment. The large difference in density within the *'M. edulis'* community between 1994 and 1997 may be partly due to the uncontrolled underestimation of these abundant interstitial polychaetes. Because the decrease of the number of encountered species cannot be explained by this underestimation, other unknown events will have influenced the community between 1994 and 1997 as well. Furthermore, as already suggested by Degraer *et al.* (in press a) and because of the absence of *M. edulis* in BIO 3, this bivalve species cannot be used as the typical indicator species for this community. The rather abundant presence of interstitial polychaetes (*Microphthalmus similis* and *Hesionura augeneri* in 1994 and *H. augeneri* in 1997) seems to be a better characteristic species.

GEOGRAPHICAL STABILITY OF THE MACROBENTHIC COMMUNITIES

The western Belgian Coastal Banks are known as a geomorphologically very diverse area. Consequently, a highly diverse hydrodynamical regime, causing a high sedimentological diversity, exists (Degraer *et al.*, in press a). Because macrobenthic communities are restricted to a specific physical environment, of which sedimentology is very important, the spatial distribution of the communities coincide with these of the sedimentology (Shackley and Collins, 1984; Meire *et al.*, 1994; Degraer *et al.*, in press a). As long as the sedimentology does not change no shifts between communities are expected (Govaere *et al.*, 1980). In this study 84 % of the stations, classified in 1994 and 1997, is designated to the same community in 1997 as they were in 1994. The spatial distribution of the macrobenthic communities has to be considered as being quite stable. The community shift of the remaining 16% (5 stations: O4, O13, O19, P1 and P7) may be due to changes within the sedimentology of the stations. In the case of the stations O13, O19 and P1, for instance, these stations are designated to the same community by the biological and environmental classification. Or, in comparison with 1994 another sediment with its respective macrobenthic community is encountered in 1997. These shifts within the sedimentology and, consequently, the community of the stations can be explained by the dynamics within the sedimentology of the area of the western Coastal Banks or by positioning errors of the ship in the sedimentologically diverse area (Bastin, 1974). In the case of the two other stations (O4 and P7), the biological and environmental classification designate the stations to two different communities. This may be explained by errors when using the non-perfect classification functions, with an *a posteriori* accuracy of 94 %. There is still a chance of 6 % that a station is classified in the wrong community by means of its physical characteristics. Another reason might be the difficulties encountered when creating a biological classification of the stations. Macrobenthic communities cannot be regarded as isolated entities, but rather as entities connected with each other by means of transition zones (Mills, 1969). This continuum of communities is illustrated by the CCA plot (Figure 5), where the three macrobenthic communities are clearly connected. Within a transition zone of two communities a combination of species of both communities can be encountered. As these species occur in suboptimal conditions, generally low densities can be found (Degraer *et al.*, in press b).

THE MACROBENTHIC COMMUNITIES AND THEIR PHYSICAL ENVIRONMENT

The relation between the macrobenthos and their physical environment has often been demonstrated (e.g. Shackley and Collins, 1984; Ismail, 1990). Unfortunately, only few studies deal with the possible mathematical relation between the environment and the macrobenthos or try to model the macrobenthos based on the physical environment. The three macrobenthic communities of the western Coastal Banks in 1994 were all restricted to a very specific physical environment (Degraer *et al.*, in press a). Especially the median grain size and the percentage silt and coarse sand were linked with the distribution of the macrobenthic communities (Figure 6). The *'Mytilus edulis'* community was typically found in sediments with a median grain size and a coarse sand content of at least 360 µm and 16 %, respectively, in absence of silt. The *Lanice conchilega* community and the *Nephtys* *cirrosa* community *s.l.* are both found in fine sandy sediments with a median grain size between 150 and 350 µm and a low coarse sand content (maximum 18 %). Yet, in contrast to the *N. cirrosa* community s.l., the *L. conchilega* community prefers relative high silt contents (except for one exceptional observation of 23 %, normally between 0 and 8 %).

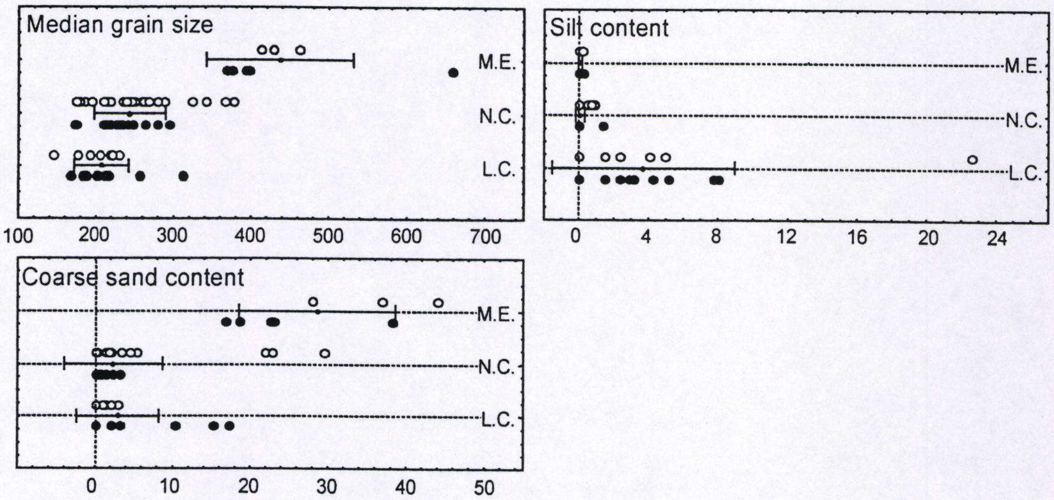

Figure 6. The distribution of the three macrobenthic communities (M.E., *'Mytilus edulis'* community; N.C., *Nephtys cirrosa* community *s.l.*; L.C., *Lanice conchilega* community) in 1994 (●) and 1997 (○) over the three most differentiating environmental variables: the median grain size (µm) and the silt content (%) and the coarse sand content (%). The whiskers are indicating the average value over the two years with the standard deviation.

The discriminant analysis also selected these three sedimentological characteristics as being most differentiating between the communities. Together with the depth and the percentage of clay and fine sand, three classification functions were set up (Table 5). The stations of the *'M. edulis'* community differed from the others by a high median grain size and the presence of coarse sand, while deep lying stations with a rather high percentage of clay, silt and fine sand are typical for the *L. conchilega* community. The intermediate fine sandy *N. cirrosa* community *s.l.* lacks clay, silt and coarse sand. Only two stations, P2 and P5, were identified as being misclassified (*a posteriori* accuracy: 94 %), because they lacked the presence of clay and silt, although they belonged to the *L. conchilega* community, with high numbers of *Spisula subtruncata* (1754 ind m^{-2}), *L. conchilega* (107 ind m^{-2}), and *Eumida sanguinea* (68 ind m^{-2}) in station P2 and high numbers of *S. subtruncata* (2300 ind m^{-2}), *L. conchilega* (673 ind m^{-2}), *Abra alba* (234 ind m^{-2}), *N. hombergii* (136 ind m^{-2}), and juvenile *Nephtys* (78 ind m^{-2}) in station P5.

To test whether these classification functions can be used to predict the existence of a macrobenthic community in a known physical environment (= *a priori* accuracy), the classifications were used to classify the samples of 1997. The 'environmental' classification coincided very well with the 'biological' classification (Table 7). Knowing that BIO 1 and ENV 2 have to be regarded as a synonym for the *L. conchilega* community, BIO 2 and ENV 3 for the *N. cirrosa* community *s.l.* and BIO 3 and ENV 1 for the *'M. edulis'* community, as demonstrated before, an *a priori* accuracy of 83% is found. By means of the classification functions the existence of one of the three macrobenthic community can thus be predicted correctly in 83 % of the cases, only having information about the depth and sedimentology of the environment.

Even though these particular functions are proved to be useful on the western Belgian Coastal Banks, they cannot be generalized for the whole North Sea, even not the whole Belgian Continental Shelf. The baseline for the deduction of the functions is the knowledge of the existing communities. All communities of a certain region, together with their preferential physical environment, have to be known to be able to set up the 'region specific' classification functions.

IMPORTANCE FOR COASTAL ZONE MANAGEMENT

Designating an ecological value to a macrobenthic community, based on the results out of a single sampling campaign, can lead to an underestimation of the community's importance, as demonstrated for the *Lanice conchilega* community. Two sampling campaigns already give some more information on the 'potentials' of the community, but in order to know all possible dynamics of a community long-term studies are necessary (Arntz and Rumohr, 1986; Turner *et al.*, 1995).

Though, quite a lot of stability can be observed in the three macrobenthic communities between 1994 and 1997. Next to the similar composition of the ten most dominant species of the respective communities, they are all restricted to a very specific, physical environment. Knowledge of the dynamics and the environmental 'needs' of all communities of the area under consideration may provide information on the ecological 'potentials' of a particular place with known physical environment. The possibility to predict the existence of a macrobenthic community only knowing the physical characteristics of a certain environment, would be an extremely powerful tool in coastal zone management. Detailed information on the physical environment is often available, certainly on the Belgian Continental Shelf and, if not, the information can easily be gathered on a low-cost base.

Furthermore, instead of putting a lot of effort, time and money in working out time-series of lots of macrobenthic samples, randomly spread over the area under consideration, monitoring of the macrobenthos should concentrate on the spatial distribution of the macrobenthic ‘potentials’. This can be done by the identification of (1) the spatial distribution of the macrobenthic communities actually present, (2) the communities’ environmental ‘needs’, and, finally, (3) the communities’ ‘potentials’ by means of long-term monitoring of some selected stations within each community. Following this strategy, a fast evaluation of measures, taken in the frame of the management plan for an area, is possible.

CHAPTER 4

SPATIAL DISTRIBUTION AND POPULATION DYNAMICS OF *SPISULA SUBTRUNCATA* IN A SHALLOW MARINE HABITAT

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paper in preparation

ACKNOWLEDGEMENTS

This study is financed by the Flemish administration responsible for environment, nature, land and water management, department Nature (AMINAL, contracts BNO/NO/Wh.94.12 and AN/1995/nr.3) and the Coastal Waterways Division (AWK, contract of 24.07.1997) of the Flemish Government. The first author was financed by the Flemisch Institute for the Promotion of the Scientific – Technological Research in Industry (IWT). Valuable comments on the manuscript are retrieved from Jan Mees. The authors want to thank Johan Van de Velde, Annick Van Kenhove, Myriam Beghyn, Vera Van Lancker and Froukje Clinck for their assistance in the field and the laboratory.

ABSTRACT

Bivalves are important in shallow marine habitats, not at least being the major food resource of the common scoter (*Melanitta nigra*), thousands of which are wintering on the western Coastal Banks, near the Belgian – French border. Next to this ecological importance, one of these bivalves, *Spisula subtruncata*, occurs in fishable stocks in the area and shellfisheries become interested in the commercial harvesting of these stocks. In order to provide information for a sustainable management of the *S. subtruncata* stocks on the western Coastal Banks, this study aimed at (1) the description *S. subtruncata*'s spatial distribution and population dynamics and (2) understanding the implications for future *Spisula*-fishery in the area. The spatial distribution of *S. subtruncata* was studied in 1994 and 1997 in 40 stations in two areas of the western Coastal Banks. The population dynamics were investigated by monthly sampling of two stations between April 1995 and April 1996 and a seasonal sampling between April 1996 and April 1998.

Spisula subtruncata had a patchy distribution in the deeper (6 m), fine sandy (200 ± 20 μm) sediments of the *Lanice conchilega* community, mainly found in the most western part of the Coastal Banks. In July '95, an overwhelming and successful recruitment was observed in this area. Local densities were as high as 150000 ind m^{-2}. Minor, non-successful recruitments were detected in August '96 and August '97. Growth could be described by a seasonally oscillating version of the von Bertalanffy growth function: a growth stop was observed from late autumn till early spring. Probably because of differences in environmental conditions, the growth parameters K and L_∞ differed slightly between the two stations (0.7 and 32 – 33 mm for one stations and 0.9 and 31 – 32 mm for the other station. A combination of length and individual biomass increment shows: (1) a faster length increment of smaller individuals during the second growing period (catching-up phenomenon), (2) a constant length combined with a decreasing individual biomass during the suboptimal winter periods (except for the first one, when the individual biomass slightly increased), (3) a positive relation between the individual biomass decrease and the seawater temperature during the winter periods, and (4) a strong increase of the individual biomass in early spring (April '97 and April '98) because of gametogenesis, followed by a decrease because of spawning (August '97). The total production of the cohort '95 in the tidal gully (Potje) during the study period is estimated at about 1500 g AFDW m^{-2}.

Shellfishery on the ecologically important western Coastal Banks should not be considered since: (1) the food resource for the common scoter will decrease and will possibly lead to the disappearance of the seaducks in the area, (2) the ecologically most diverse and rich macrobenthic *Lanice conchilega* community will be destructed, and (3) the economical

rendability of *Spisula*-fishery is doubtful, because of the highly variable recruitment along the Belgian coastline.

INTRODUCTION

Bivalves are an ecologically important component of the macrobenthos of coastal marine ecosystems. Although their densities are generally low in comparison to other taxa (e.g. polychaetes) their biomass generally constitutes a large proportion of total macrobenthic biomass (Van Steen, 1978; Brey *et al.*, 1990). This high bivalve biomass is a food resource by a variety of demersal fish species (Rainer, 1985; Brey *et al.*, 1990) and by diving seaducks, e.g. the common scoter (*Melanitta nigra*) (Cramp and Simmons, 1977; Meissner and Bräger, 1990; Meire, 1993).

Because of the large number of wintering common scoters on the Belgian western Coastal Banks (Maertens *et al.*, 1988, 1990; Devos, 1990), this area is designated as an 'area of international importance for waterfowl', according to the Ramsar convention (Kuijken, 1972). Furthermore, the western Coastal Banks fulfill the criteria of the EC Bird Directive, although the area is not in the final list of the Belgian EC Bird Directive areas. The presence of the scoters can partly be explained by the undisturbed character of the western Coastal Banks (Degraer *et al.*, in press a), but food availability, mainly bivalves (Cramp and Simmons, 1977; Meissner and Bräger, 1990; Meire, 1993), plays an important role as well (Kirchoff, 1981). The relation between the spatial distribution of the common scoter and the presence of extensive bivalve beds, especially *Spisula subtruncata*, has already been demonstrated (Van Assche and Lowagie, 1991; Leopold *et al.*, 1995).

Since the early nineties, fishermen are interested in the commercial exploitation of *S. subtruncata* stocks and large amounts of the bivalve have already been harvested in the Netherlands, north of the area of investigation. Due to the competition between the *S. subtruncata* fishery and the common scoter, major shifts in the spatial distribution and a decrease of the density of the common scoter are observed (Leopold *et al.*, 1995). At this moment, *S. subtruncata* fishery does not occur in the Belgian coastal waters, but preliminary research to the possibility of harvesting *S. subtruncata* in Belgium already revealed the presence of a fishable standing stock of the bivalve in the area of the western Coastal Banks (Vanhee *et al.*, 1998). The conflicting situation, between the ecological and socio-economical interests in *S. subtruncata*, stresses the need for knowledge on the life history, population dynamics and production of *S. subtruncata*. Although necessary in order to set up a sustainable harvesting management strategy for *S. subtruncata*, this information is largely lacking at this moment. So far, only Davis (1923, 1925) provided some information on the life history and population dynamics of *S. subtruncata* on the Doggerbank.

The aims of this study are: (1) to describe the spatial distribution, population dynamics and production of *S. subtruncata* on the western Coastal Banks during a 2.5 yr study period and (2) to use this newly gathered information in the frame of the sustainable management of *S. subtruncata* in the area.

MATERIALS AND METHODS

STUDY AREA

The western Belgian Coastal Banks extend from the Belgian – French border in the West to Oostende in the East and from the low water line to about 8 m depth (Figure 1). Between Koksijde and Middelkerke, the banks are just a subtidal extension of the beach, whereas the areas 1 and 2 comprise a large range of geomorphological features. The Stroom- and Balandbank (area 1) are linear sandbanks, oriented parallel to the coastline and separated from the beach by a gully, the Kleine Rede. Their depth ranges from 3 to 8 m below mean low water spring level (MLWS). Area 2 comprises three sandbanks (Den Oever, Broersbank and Trapegeer) and a tidal gully (Potje), of which the depth ranges from about 0.5 to 8 m below MLWS. Due to this geomorphogically and, consequently, hydrodynamically diverse character of the area, a large variety of sediments (median grain size from over 500 to 160 μm) are present (Degraer *et al.*, in press a).

SAMPLING

To investigate the spatial distribution and habitat preferences of *Spisula subtruncata* on the western Belgian Coastal Banks, 40 and 39 stations were sampled in October 1994 and October 1997, respectively (Figure 1). At each station, one sample was taken with a Van Veen grab (sampling surface area: 0.1026 m^2) The samples were washed over a sieve, with a 1 mm mesh size, before fixation, and then fixated and preserved in an 8% formaldehyde-seawater solution.

To study the population dynamics of *S. subtruncata*, two of the 40 stations, P2 and P20, were selected because of the high numbers of bivalves observed in October 1994. At each station, five Van Veen grabs were taken on 17 occasions: monthly, between April 1995 and April 1996, and seasonally, between April 1996 and April 1998. After fixation, the samples were sieved through a 0.5 mm and 1 mm sieve and preserved in an 8% formaldehyde-seawater solution. Yet, no individuals of *S. subtruncata* were found in the 0.5 mm fraction.

From each sample, a subsample for sediment analysis was taken with a 1.5 cm diameter core.

LABORATORY PROCEDURES

All individuals of *Spisula* were sorted and identified to species level. Only two species of the genus, *Spisula subtruncata* and *Spisula solida*, were found, of which *S. solida* only occurred in small numbers (< 20 ind m^{-2}) in three stations sampled in 1994. *Spisula solida* was not detected in the stations P2 nor P20. The number of *S. subtruncata* was counted. To study the population dynamics of *S. subtruncata*, 150 to 400 individuals from the stations P2 and P20 were randomly selected for biometrical analyses. Length, width and height were measured with a drawing mirror and dissecting microscope of individuals shorter than 1 cm and by means of a vernier caliper (precision: 0.01 mm) for individuals longer than 1 cm. At station P2, the individual biomass (ash-free dry weight, AFDW) of 30 to 50 individuals was measured by loss of mass on ignition (500°C ± 50 °C for 2 h) of whole oven-dried individuals (70°C for 48 h), giving a good estimate of the individual biomass (Palmerini and Bianchi, 1994). Because all individuals were preserved in a formaldehyde-seawater solution, a decrease of the AFDW, stabilizing after about 3 months, is expected (Brey, 1986). In order to diminish the differences in individual biomass estimates between different sampling months, at least three months were left between fixation and determination of the AFDW. Yet, an underestimation of the individual biomass and, consequently, also standing stock and production, is expected.

The reproductive condition of *S. subtruncata* was studied by dissecting 20 individuals of station P2 for all months from April '96 till April '98. Because of the use of Bengal rose (darkening the gonads), gametogenesis could only clearly be detected when the gonads covered at least half of the visceral mass. In all other situations, the gonadal development could not be assessed with certainty. The subjective rating of gonadal development into five classes from fully to non-developed gonads (Caddy, 1967), could not be used and a discrimination of the individuals' reproductive condition was only made into two classes: (1) well-developed, with more than half of the visceral mass covered by the gonads and (2) poorly or non-developed, with the gonads covering less than half of the visceral mass or being undetectable.

The grain size distribution of sediment sample is analyzed with a laser COULTER LS. The seawater temperature during the sampling period is provided by the Division of Waterways and Coast of the Flemish Government.

DATA ANALYSIS

The biometric relations (length, width, height, individual biomass) are studied by regression analysis. The statistical significance of density differences between two consecutive sampling months are analyzed by means of the non-parametric Mann-Whitney U-test.

The length increment is described by the von Bertalanffy growth function (VBGF) with incorporation of winter growth stop. The mathematical equation is given by:

$$L_t = L_\infty \left\{ 1 - e^{-K(t-t_0) + \frac{CK}{2\pi}\sin[2\pi(t-t_s)]} \right\}$$

with	L_t	the predicted length at age t
	L_∞	the asymptotic length
	K	the growth constant
	t_0	the (theoretic) age at zero length
	C	determining the amplitude of the seasonal growth oscillation
	t_s	the starting point of the oscillation

The values of the five parameters (L_∞, K, t_0, C, and t_s) were estimated by means of non-linear estimation, with the least squares method, as provided by the statistical software package STATISTICA 5.1 (StatSoft, 1996). The cohort '95 could easily be distinguished from other cohorts by means of monthly length-frequency distributions, as other cohorts were only present in very low numbers. The input data points, in order to retrieve the VBGF, are the average lengths of the cohort '95 of each sampled month. Next to the estimation of the parameters' averages, STATISTICA 5.1 also provides the standard error and the level of significance of each estimate.

The values of K and L_∞ were also estimated using the Ford-Walford method in which age – length data are rearranged as length at a specific time L_t and length at a succeeding time L_{t+dt} data pairs. If the time differences between the consecutive length measurements is constant, the intercept and slope of the linear regression (y = ax + b) of the data pairs can be used for the estimation of K and L_∞, by $K = -1/dt \ln(a)$ and $L_\infty = b / (1 - a)$. In order to fulfill the requirement of constant time differences between two consecutive length measurements, age – length data were only used from all August and January samples (five data pairs).

Production is estimated with the growth and removal summation methods (Crisp, 1984). The growth summation method estimates the production as the increment of biomass from one sampling month to the next for the whole sampling period. The removal summation method sums the loss in weight between consecutive sampling months during the whole sampling period.

RESULTS

SPATIAL DISTRIBUTION

With maximum densities of up to 5000 ind m^{-2}, *Spisula subtruncata* was abundant on the western Belgian Coastal Banks (Figure 1). The species occurred in 25 and 41 % of the stations in October 1994 and October 1997, respectively. A clear preference for area 2 was observed: it was present in 35 % (1994) and 58 % (1997) of the stations in area 2 as compared to 15 and 20 % in area 1. Densities in area 2 were generally higher than in area 1. Overall, the density of *S. subtruncata* in 1997 was higher than in 1994.

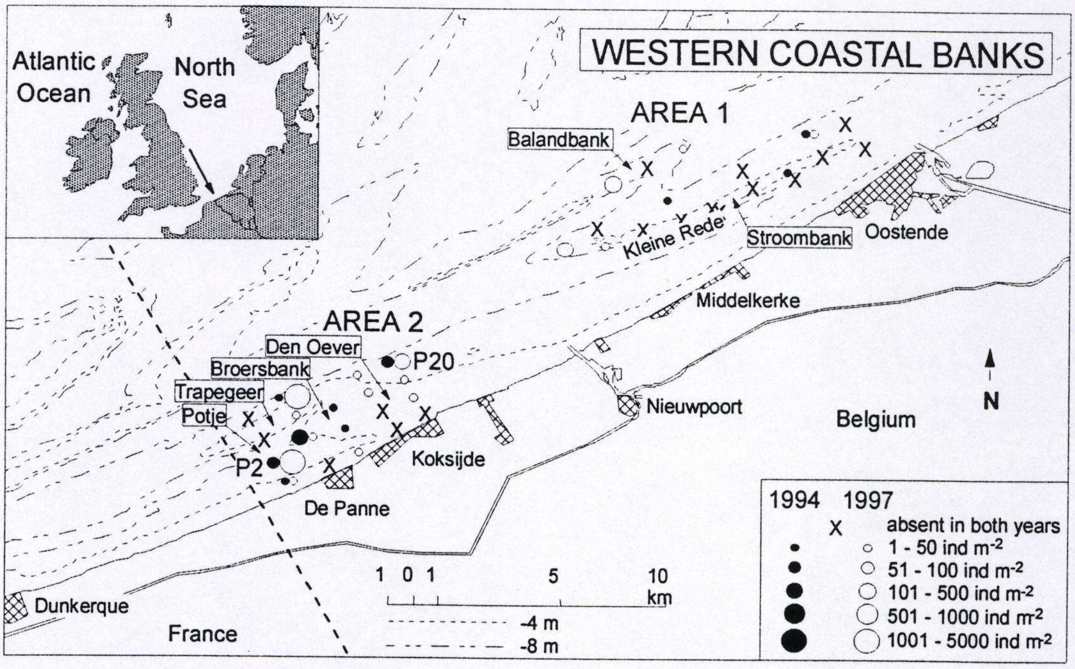


Figure 1. The geographical situation of the study area and the spatial distribution of *Spisula subtruncata* over the western Belgian Coastal Banks in 1994 and 1997, with indication of the two areas under consideration.

Spisula subtruncata was mainly found in the *Lanice conchilega* community (Table 1), where it occurred with an average density of 48 and 549 ind m^{-2} in 1994 and 1997, respectively. Whereas *S. subtruncata* is found in less than 40 % of the stations of the two other macrobenthic Coastal Bank communities, it was present in at least 55 % of the stations of the *L. conchilega* community in 1994 and 1997.

	1994			1997		
	Density	Occ.	n°	Density	Occ.	n°
Lanice conchilega community	48 ± 29	55	6	549 ± 328	63	5
Nephtys cirrosa community	<1 ± <1	10	2	5 ± 2	29	7
'*Mytilus edulis*' community	7 ± 4	40	2	3 ± 3	33	1

Table 1. The distribution of *Spisula subtruncata* over the three macrobenthic Coastal Bank communities in 1994 and 1997, as defined in chapter 3, with the average density ± standard error (ind m^{-2}), together with the percentage of occurrence (Occ.) in the stations of the three communities (%) and the number of stations with *S. subtruncata* (n°).

During the whole sampling period, the variance of the density of *S. subtruncata* was always much higher than the mean. Thus, the spatial dispersion of *S. subtruncata* was contagious (Elliott, 1977).

DENSITY FLUCTUATIONS

All individuals of *Spisula subtruncata* were retained on a 1 mm sieve; no individuals were found in the 0.5 mm fraction. Between April and July 1995, the maximal density of *Spisula subtruncata* in the stations P2 and P20 was 20 ind m^{-2} (Figure 2). In August '95, the species became very abundant in both stations, with densities up to 150000 ind m^{-2}. Between August '95 and January '96, the density decreased to about 10000 ind m^{-2} in both stations. After January '96, the density of *S. subtruncata* in P20 continued to decrease and never exceeded some hundreds of ind m^{-2}, while in P2 the density also continued to decrease, but was never lower than about 1000 ind m^{-2}.

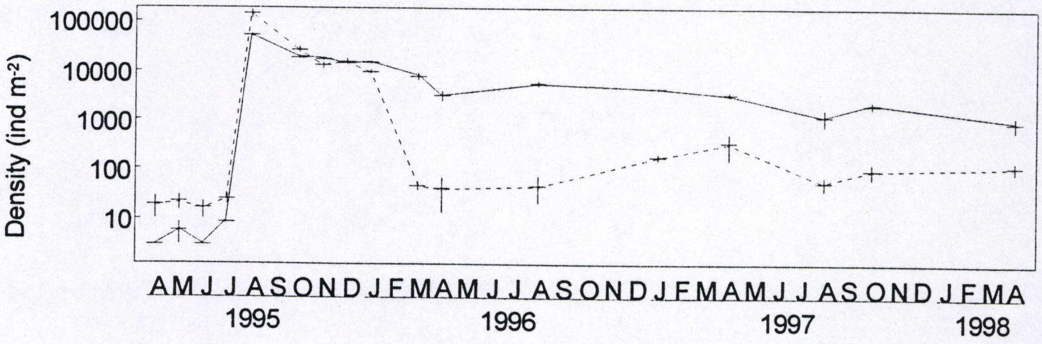


Figure 2. The temporal variation of the density (ind m^{-2}) of *Spisula subtruncata* in the stations P2 (solid line) and P20 (dashed line), with indication of the standard error (vertical lines)

BIOMETRICS

The relation between length and biomass of *Spisula* subtruncata during the study period is presented per month and for all months together in Table 2. Except for August '96 and October '97, when regressions were non significant, highly significant ($p < 0.0001$) regressions were found. The same applies for regressions between length and height and width (p always < 0.0001).

	N	a		b	
		Mean	S.E.	Mean	S.E.
Aug '95	23	2.93	0.49	-5.19	0.90
Oct '95	48	3.10	0.20	-5.54	0.49
Nov '95	20	3.72	0.43	-7.07	1.07
Dec '95	20	2.59	0.44	-4.29	1.09
Jan '96	47	3.00	0.18	-5.23	0.45
Mar '96	30	2.44	0.21	-3.58	0.53
Apr '96	17	2.95	0.42	-4.39	1.11
Aug '96	49	-0.03	0.73	4.69	2.20
Jan '97	49	2.38	0.29	-2.72	0.87
Apr '97	49	3.73	0.70	-5.86	2.23
Aug '97	46	5.18	0.78	-11.25	2.55
Oct '97	50	1.73	1.12	0.94	3.72
Apr '98	49	2.34	0.26	-2.01	0.86
All months	508	4.36	0.05	-8.43	0.16
Length – Height	439	0.73	< 0.01	-0.76	0.11
Length – Width	415	0.49	0.01	-1.14	0.12
Height – Width	415	0.67	0.01	-0.66	0.10

Table 2. The parameters (a and b) of the correlation : ln(biomass) = a * ln(length) + b), as defined for each sampling date and for all months together and the parameters of the biometric correlations between length, height, and width (Height or Width = a * Length + b) for all months together. S.E., standard error; N, number of observations.

During most of the sampling period *S. subtruncata* had a 'normal' shape (Figure 3). From August '96 till August '97, some aberrant shapes, with a clear ventral indentation, occurred next to the 'normal' forms. Except for January '97, a generally increasing percentage of aberrant forms with increasing density was detected (Figure 4). This trend was especially obvious in August '96 and April '97, whereas in January '97 the general trend was disturbed by the high percentage of aberrant forms (80 %) at the lowest density (3300 ind m^{-2}). No data are available for August '97. After August '97, no clear aberrant forms were detected anymore.

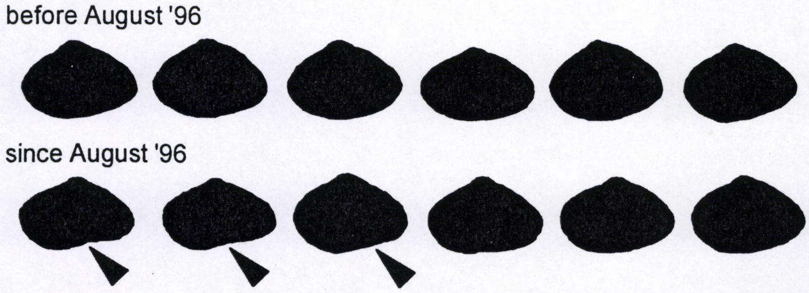


Figure 3. The variability in outline of *Spisula subtruncata* before August '96 and from August '96 on. The arrows are pointing to the ventral indentation.

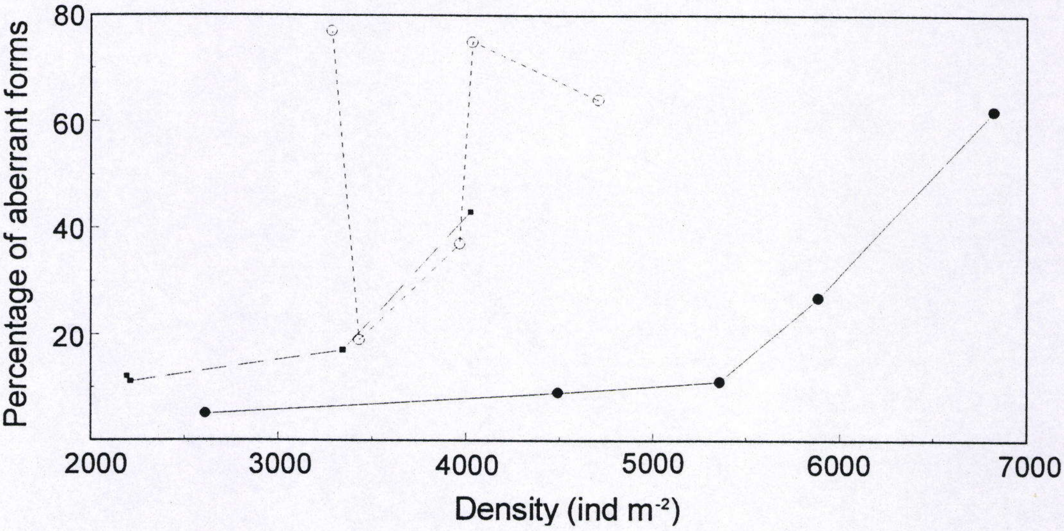


Figure 4. The relation between the density and the percentage of aberrant forms of *Spisula subtruncata* in station P2. ●, August '96; ○, January '97; ■, April '97.

GROWTH

Between April and July '95, a low number of larger individuals of *S. subtruncata* (17 – 33 mm) were found in both stations (Figure 5). Such large individuals were present till January '96 in station P20. The length-frequency distributions show the appearance of a high number of small individuals (P2: 3 – 10 mm; P20: 2 – 6 mm) in August '95. These double their length by October '95. Between October '95 and March '96, individuals, belonging to this cohort, were still present in large numbers, but they ceased growing. After March '96, the cohort could still be detected in high densities in station P2, while their density decreased steeply in station P20, their density steeply decreased. Still, in both stations, periods of growth (March '96 – January '97 and April '97 – October '97) alternated with periods of more or less zero growth (August '96 – January '97 and October '97 – April '98). In both stations, the length-frequency distribution of the cohort, appearing in August '95, remained unimodal during the whole study period. Furthermore, the appearance of small individuals of *S. subtruncata* (3 – 6 mm) was also found in station P20 in August '96 and in August '97. On both occasions, their density remained low and they growed till April of the next year. The small individuals of August '96 were not detected again in 1997.

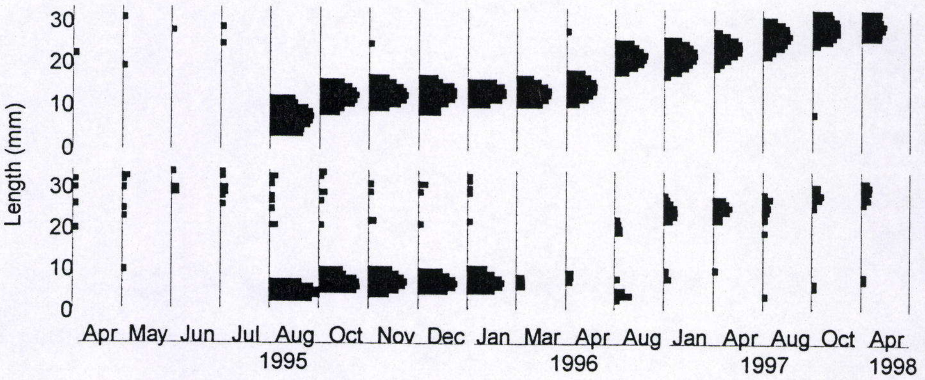
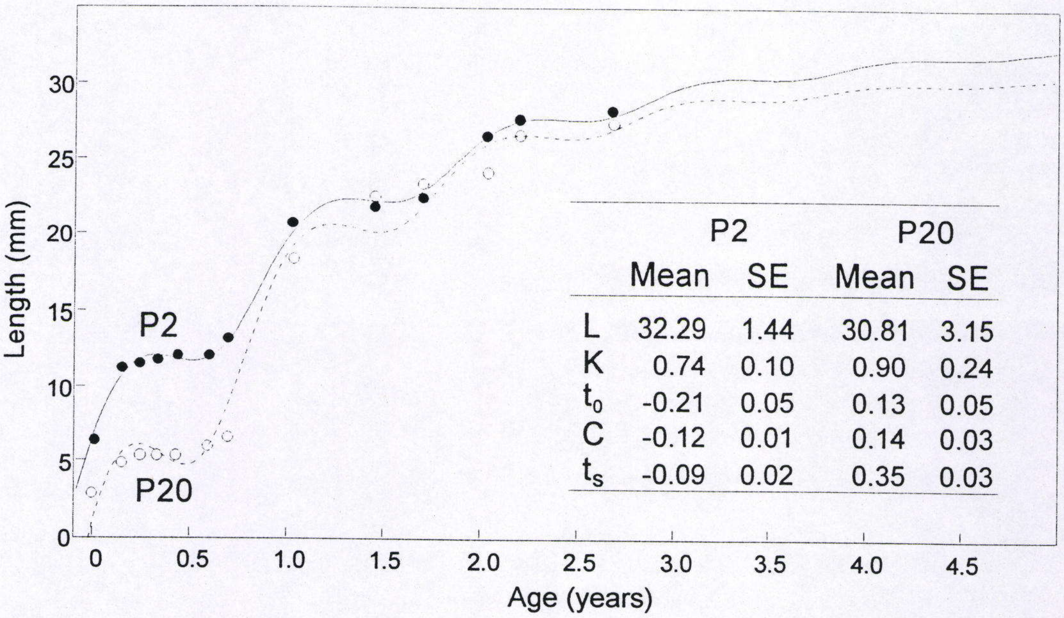


Figure 5. The length – frequency distributions of the stations P2 and P20 during all sampling months. X-axis (logarithmic): density (ind m^{-2}) with a maximum of 74000 ind m^{-2}; Y-axis (linear): length of *Spisula subtruncata* (mm).

Not taking into account the larger individuals present in both stations till August '95 and probably belonging to several cohorts, one cohort, appearing in August '95 (cohort '95), was detected in station P2. In station P20, three cohorts were distinguished: cohort '95, '96, and '97, first detected in August '95, August '96, and 'August '97, respectively. The growth curves of all cohorts showed a general pattern of periods of growth alternated with periods of growth stop. As the most succesful cohort was cohort '95, the parameters of the von Bertalanffy growth function (VBGF) were estimated for this cohort only (Figure 6).

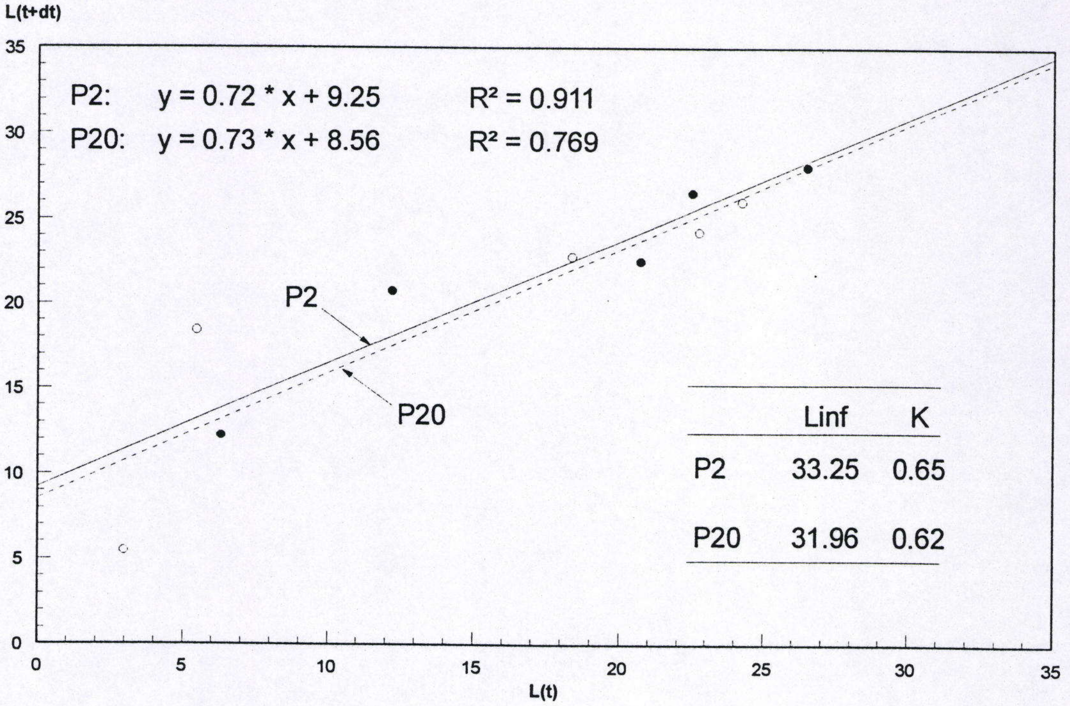
The VBGF of station P2 coincides very well with the observed data points: 99.7 % of the variance in the data points is explained by the VBGF. Furthermore, the standard errors on the estimated growth parameters were all very small ($p < 0.002$). In station P20, the VBGF coincided less clearly with the data points, especially during the second year, when the VBGF was generally below the observed data points. In P20, the VBGF predicts a clear decreasing length during the winter periods. Even though the standard errors of the estimated VBGF parameters are higher than in station P2 ($p < 0.0283$), 98.08 % of the variance is explained by the VBGF. According to the VBGF, L_∞ is higher in P2 (32.29 mm) than in P20 (30.81 mm), while K is higher in P20 (0.90) than in P2 (0.74).

Estimates of K and L_∞ by means of the Ford-Walford method (Figure 7), yielded comparable values for both stations (L_∞: 33.25 and 31.96 mm; K: 0.65 and 0.62, in P2 and P20, respectively).



	P2		P20	
	Mean	SE	Mean	SE
L	32.29	1.44	30.81	3.15
K	0.74	0.10	0.90	0.24
t_0	-0.21	0.05	0.13	0.05
C	-0.12	0.01	0.14	0.03
t_s	-0.09	0.02	0.35	0.03

Figure 6. The graphical presentation of the von Bertalanffy growth function, together with the estimates of the five parameters of the function (L_∞, K, t_0, C, and t_s) and the standard error (SE). P2, • and solid line; P20, ○ and dashed line.



P2: $y = 0.72 * x + 9.25$ $R^2 = 0.911$

P20: $y = 0.73 * x + 8.56$ $R^2 = 0.769$

	Linf	K
P2	33.25	0.65
P20	31.96	0.62

Figure 7. The graphical presentation of the Ford-Walford method for the estimation of L_∞ and K, with L_∞ = intercept / (1 – slope) and K = (-1 / dt) * ln(slope).

PRODUCTION

In August '95, the individual weight of cohort '95 individuals in station P2 ranged from 0.1 to 2.1 mg (mean: 0.5 mg ind^{-1}) (Figure 8). During their first winter (October '95 – January '96) the average individual weight was 9 mg ind^{-1}, slightly increasing over winter. Between January and August '96, the individual weight steeply increased to more than 100 mg ind^{-1}. During the second winter period, it decreased slightly to about 90 mg ind^{-1} (January '97). After the second winter period, individual weight increments were detected between January and April '97 (90 to 400 mg ind^{-1}) and between August and October '97 (250 to 900 mg ind^{-1}). Individual weight losses were observed between April and August '97 (400 to 250 mg ind^{-1}) and between October '97 and April '98 (= third winter period) (900 to 250 mg ind^{-1}).

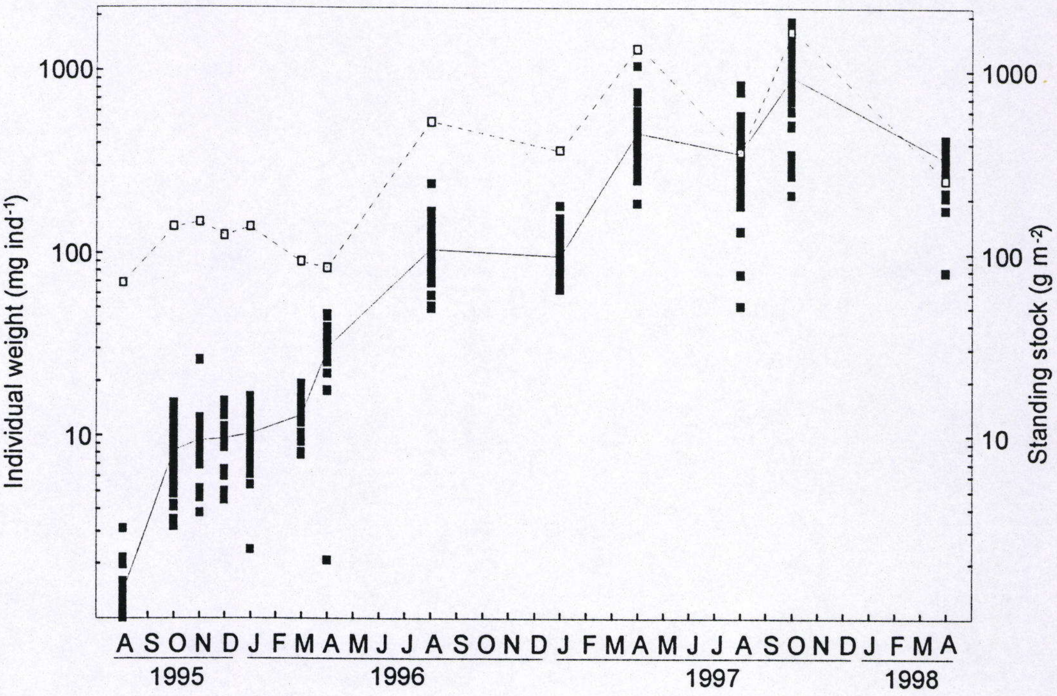


Figure 8. The temporal variation of the individual weight (mg AFDW ind^{-1}) and the standing stock (g AFDW m^{-2}) of the cohort '95 of *Spisula subtruncata* in station P2.

The standing stock of the cohort '95 in station P2 generally followed the same pattern as the individual weight, with a minimum of 65 g m^{-2} (August '95) and a maximum of 1500 g m^{-2} (October '97) (Figure 8). The main difference with the individual weight was found during the first winter: the standing stock decreased (150 to 80 g m^{-2}), while the individual weight increased slightly.

The gonadal development of *S. subtruncata* was studied from April '96 till April '98. A clear peak in the reproductive condition was found in April '97 and in April '98, with the gonads covering at least half of the visceral mass. Though it was difficult to discriminate between the gonadal and visceral mass, all other months revealed non-developed or only slightly developed gonads.

Except for the negative production between December '95 and January '96 according to the removal summation method, a positive production was assessed by both methods between August '95 and April '96 (Table 3). During this period, the total production was estimated at 366 (growth summation method) and 354 g m^{-2} (removal summation method). About half of this production was found between August and October '95. After April '96, both methods yielded different production estimates with a maximum of 1214 g m^{-2} between January and April '97 (growth summation method) and a minimum of –765 g m^{-2} between October '97 and April '98 (growth summation method). The two production estimates (growth and removal summation methods) of the cohort '95 in station P2 yielded similar results of 1657 and 1473 g m^{-2} during the study period (979 d).

The daily mean weight specific growth rate was maximal between August and October '95 (0.033 mg mg^{-1} d^{-1}). High values (minimal 0.017 mg mg^{-1} d^{-1}) were also found during the periods March – April '96, January – April '97, and August – October '97. During the first winter period, low, but positive daily mean weight specific growth rates were observed (maximal 0.004 mg mg^{-1} d^{-1}). Negative values (down to -0.006 mg mg^{-1} d^{-1}) were found during the second and third winter period (August '96 – January '97 and October '97 – April '98) and between April and August '97.

DISCUSSION

SPATIAL DISTRIBUTION AND RECRUITMENT

The bivalve, *Spisula subtruncata* is known to be an abundant species in shallow coastal waters of the Southern North Sea (Van Urk, 1959; Tebble, 1966). In this study, the bivalve is found to be abundant and widespread on the western Coastal Banks. Within this area, *S. subtruncata* is not distributed uniformely: its highest densities were found in the macrobenthos-rich *Lanice conchilega* community. This community occurs in the, relative to other Coastal Bank zones, deeper lying (about 6 m), fine sandy sediments (median grain size: 200 ± 20 µm), mainly of the gully, Potje (P2), and the northern flank of a sandbank, Den Oever (P20), both situated in area 2 (Degraer *et al.*, in press a). Still, *S. subtruncata*

Sampling date	Period	N° of days	Individual weight	Density	Average I.W.	Average Density	Increment I.W.	Decrement Density	Production G.S.	Production R.S.	$\overline{C}_w$
August '95	---		1.4	50117							
October '95	1	54	8.1	16848	4.8	33483	6.8	33269	224	158	0.033
November '95	2	36	9.3	15749	8.7	16299	1.1	1099	20	10	0.004
December '95	3	30	9.5	13006	9.4	14378	0.3	2743	3	26	0.001
January '96	4	38	10.1	13702	9.8	13354	0.6	-696	8	-7	0.002
March '96	5	58	12.8	6925	11.5	10314	2.7	6777	28	78	0.004
April '96	6	37	29.9	2770	21.4	4848	17.1	4155	83	89	0.023
August '96	7	124	104.0	5035	67.0	3903	74.1	-2265	289	-152	0.010
January '97	8	154	94.8	3885	99.4	4460	-9.2	1150	-41	114	-0.001
April '97	9	90	449.8	2955	272.3	3420	355.0	930	1214	253	0.017
August '97	10	126	347.1	1033	398.5	1994	-102.7	1922	-205	766	-0.002
October '97	11	57	909.2	1807	628.2	1420	562.1	-774	798	-486	0.017
April '98	12	175	320.6	791	615.0	1299	-588.6	1016	-765	625	-0.006
TOTAL	---	979	---	---	---	---	---	---	1657	1473	

Table 3. Calculation of the production of the cohort '95 of *Spisula subtruncata* in station P2, according to the growth summation and the removal summation method (Crisp, 1984) and the daily mean weight specific growth rate (Winberg 1971), with: N° of days: the number of days between two consequent sampling dates or during one period; Individual Weight in mg ind^{-1}; Density in ind m^{-2}; Average I.W. and Density: the average individual weight and density; Increment I.W.: the individual weight increment, in mg ind^{-1} period^{-1}; Increment Density: in ind period^{-1}; Production G.S. and R.S.: production estimates, in g m^{-2}, according to the growth summation method, $P = \Sigma$ (Average Density$_i$ * Increment I.W.$_i$) and the removal summation method, $P = \Sigma$ (Average I.W.$_i$ * Increment Density$_i$); $\overline{C}_w$: daily mean weight specific growth rate, in mg mg^{-1} d^{-1}, $\overline{C}_w$ = (ln(individual weight$_2$) – ln(Individual Weight$_1$)) * N° of days^{-1}.

was absent in a rather large proportion (37 %) of the stations of the *L. conchilega* community. Together with the contagious small scale spatial distribution, these facts support the idea of a patchy distribution of the bivalve, even within the optimal habitat, and the existence of *Spisula* banks (Davis, 1923; Van Assche and Lowagie, 1991; Meire, 1993).

Especially within area 2, an increase in occurrence and density of *S. subtruncata* is detected between 1994 and 1997: an overwhelming recruitment, with densities up to 150000 ind m^{-2}, has been taking place during July '95 (first detected at 10 August 1995). The recruitment not only took place in the stations P2 (Potje) and P20 (Den Oever), but probably over a large range of the western Coastal Banks and certainly of area 2, where the small individuals formed a dense mat of about 1 cm on top of the sediment in at least two more stations (personal observation). One of these two other stations was situated in the *Nephtys cirrosa* community, occurring in shallower (about 4 m), coarser (median grain size: about 250 µm) sediments (Chapter 3). This, together with the higher densities and occurrence of *S. subtruncata* in the *N. cirrosa* community in 1997, compared to 1994, suggests that the recruitment also occurred in suboptimal environments. Yet, a succesful recruitment, followed by fair survival of the individuals, was only noticed in the *L. conchilega* community. As post-settlement mortality often operates as a density regulation of soft-sediment invertebrates (Olafsson *et al.*, 1994), it probably explains the steep density decrease between August and October '95 in both stations. In October '95, both stations had a similar density of 15000 - 20000 ind m^{-2}. Due to this mortality of *S. subtruncata*, small (at maximum 1 cm), dead and dying individuals of *S. subtruncata* formed large banks at the high water line of the beach of De Panne, situated in area 2, in September '95 (personal observation).

Furthermore, after January '96, a drastic decrease in density (to less than 100 ind m^{-2}) occurs in station P20, while the density in P2 was never below 1000 ind m^{-2}. This high mortality of *S. subtruncata* coincided with an increase of the sediment's mud concentration: till December '95 a mud concentration of maximal 5 % was found, while this concentration started to increase from January '96 on to reach up to 30 % in March '96. This sedimentological change was not detected in P2, where the mud concentration was never higher than 6 %. This sedimentological change may be responsible for the high mortality of *S. subtruncata* in P20 between January and March '96. High mortality of *Spisula*, related to mud deposition, has also been demonstrated in Swansea Bay (U.K.) (Shackley and Collins, 1984)

Next to the succesful recruitment, detected in August '95 in both stations, two other recruitments were detected in August '96 (cohort '96) and August '97 (cohort '97) in P20 (Den Oever). The appearance of the three cohorts all point towards a period of recruitment in July – August. This coincides with the recruitment of many other bivalve species in temperate regions, as *Abra alba* (Rainer, 1985). On the Doggerbank, recruitment of *S. subtruncata* was also assessed to take place between June and the beginning of August, followed by a mean date of settlement not many weeks or even days later (Davis, 1923, 1925). The recruitments revealed a low number of individuals and were found till at least April of the following year. In the case of cohort '96, the few surviving individuals possibly survived for a longer period, but they could not be discriminated from the cohort '95 by means of the length-frequency distributions since August '97. A successful recruitment of the cohort '96 and the cohort '97, increasing the occurrence and density of the bivalve, is thus doubtful and certainly minor to the cohort '95. The highly variable recruitment, common in many benthic organisms with planktonic life stages (Fogarty *et al.*, 1991), is responsible for the high temporal variability within the spatial distribution and density of *S. subtruncata*. On the western Coastal Banks, the bivalve was only present in low densities in 1977 (Van Steen, 1978), whereas high densities (more than 1000 ind m^{-2}) were found in 1991 in the eastern part of area 2 (Van Assche and Lowagie, 1991), where *S. subtruncata* was almost absent during this study.

GROWTH AND PRODUCTION

Like *Macoma balthica* (Bachelet, 1980) and *Scrobicularia plana* (Bachelet, 1981), the growth curve (length increment) of *S. subtruncata*, comprizing periods of growth (early spring till early autumn) interrupted by periods of growth cessations (late autumn and winter), can be described by the von Bertalanffy growth function (VBGF) with incorporation of a winterpoint, explaining 99.7 % of the total variance within the data of P2 and 98 % in P20. The growth constant (K), estimated at 0.74 and 0.90 (VBGF) and 0.65 and 0.62 (Ford-Walford method) in P2 and P20, respectively, is generally high respective to many populations of other bivalves, with K-values generally below 0.5 and maximum 0.9 (Bachelet, 1980; Urban and Campos, 1994; Walker and Heffernan, 1994; Kock, 1995; Ramón *et al.*, 1995). L_∞, the length of an individual of maximal age, was estimated at 32.3 and 30.8 mm (VBGF) and 33.3 and 32.0 mm (Ford-Walford method) in P2 and P20, respectively, while the longest individual of this study measured 33.14 mm. The comparable estimation of L_∞ by means of the three methods confirms the reliability of L_∞. Yet, a slightly lower L_∞ is expected for individuals inhabiting the sediments of P20. Though relatively small, the different K and L_∞ values may be caused by the differences in the habitat of P2 and P20, as already shown for *M. balthica* (Bachelet, 1982; Harvey *et al.*, 1993).

Yet, growth is a combined length and individual biomass increment. Shortly after the recruitment of cohort '95 (August '95), an obvious difference in length between P2 (6 mm) and P20 (3 mm) is detected. This difference in length may be the result of (1) a higher density of recruits in P20, causing an increased competition for food and space, (2) a later settlement of the planktonic larvae out of the water column, decreasing the duration of the growing period, and/or (3) environmental differences between the two stations, favouring growth of the individuals in P2. Only the higher density in P20 could be detected, but the two other may play a role as well. Davis (1923), who found two separable (length-frequency distributions) length classes of recently settled individuals of *Spisula subtruncata* on the Doggerbank, stated: "*...This appears to indicate a double spawning season, not necessarily the result of two spawnings of the same adult group, but more probably the result of two adult groups maturing at different seasons...*". The differential maturation and spawning of two adult groups, will create a time lag between the presence and settlement of planktonic larvae of the two groups. If this explains the difference in length of recently settled individuals of *S. subtruncata* between P2 and P20, the populations in both stations are probably originating from two different adult populations or patches of *S. subtruncata*. Taking into account the prevailing residual currents along the Belgian coastline, causing a northeastern flow of the water masses, including planktonic organisms (e.g. larvae of *S. subtruncata*), these adult populations should be found southwest of the study area (northern France). Distances of several tens of kilometers between the geographical position of the adult population and the place of settlement of juvenile *S. subtruncata* are already described for the Doggerbank (Davis, 1923)

Till October '95, the newly settled recruits had a short growing period, during which their length almost doubled (P2: 11 mm; P20: 5 mm) and the individual biomass (Ash-Free Dry Weight, AFDW) in P2 increased from 0.5 to 8 mg. An average length of *S. subtruncata* of 5 – 6 mm on the Doggerbank (October 1922) has already been demonstrated by Davis (1923). A similar fast length and biomass increment during the first growing period has already been demonstrated for the bivalve *Macoma balthica* (Ankar, 1980; Bachelet, 1980).

As expected, a length increment could hardly be noticed during the winter conditions (October '95 till March '96). Yet, during this first winter period the individual biomass steadily, though slowly, continued to increase. During the second growing season (March '96 till

August '96) the length and biomass increased to about 22 mm (both stations) and 100 mg ind^{-1} (P2). This implies a faster length increment of the individuals of P20, starting at a lower length in March '96. This differential growth of *S. subtruncata* during the second growing season, also observed by Davis (1923), may be explained by the 'catching up phenomenon', describing a faster growth of individuals starting at a smaller size (Lammens, 1967; Bachelet, 1980). Because the VBGF is based on a single, and thus constant in time, growth constant (K), the faster length increment of *S. subtruncata* in P20 during this second growing period, in comparison with other growing periods, explains the underestimation of the length of the individuals at the end of the growing period. During the second and third winter period, *S. subtruncata* had a relatively constant length of about 22 – 24 and 27 – 28 mm, respectively, in both stations. In P2, the individual biomass twice decreased from 100 to 90 mg ind^{-1} and from 900 to 300 mg ind^{-1}. Because the growth of different bivalves show a positive correlation with the seawater temperature and the chlorophyll a-content of the watercolumn (Ankar, 1980), suboptimal growing conditions are expected during these winter periods, with low temperatures and chlorophyl a-content along the Belgian coast (Moll, 1998). The most obvious biomass decrease during the third winter (decreasing 65 %), may be related with the relatively high seawater temperatures during the winter 1997 – 1998 (minimum 4 C°), when bivalves need to spend more energy at their basic metabolism than at lower temperatures (winter 1996 – 1997: minimum – 0.5°C, with 1.5 months below 4 °C) (Zwarts, 1991). Yet, an age-dependent increase of basic metabolism rates may play an important role as well.

Finally, during the third growing period, the length steadily increased to about 27 – 28 mm in both stations, whereas the individual biomass is fluctuating. The steep increase in biomass between January and April '97 (from 90 to 450 mg ind^{-1}) in combination with an only minor length increment, may be attributed to gametogenesis (gonadal production). Just like many other bivalve species in temperate regions, the gametogenesis takes place in Spring (well developed gonads in April '97 and April '98), when food availability increases (Bachelet, 1980; Nakaoka and Matsui, 1994). A spectacular individual biomass increase, partly as a consequence of the gametogenesis, is also observed in other bivalve species (Bachelet, 1982; Zwarts, 1991). Between April and August '97, the less spectacular drop in the individual biomass (from 450 to 350 mg ind^{-1}) in combination with a new length increment (from about 22 to 25 mm), may be explained by the release of the gametes and new somatic production, respectively, drastically decreasing and slightly increasing the individual biomass (Bachelet, 1980). After August '97, the increment in individual biomass, from 350 to 900 mg ind^{-1}, probably points towards an increased somatic production in order to survive the next starving period, their third winter period. Combining the somatic and gonadal growth, the cohort '95 of *S. subtruncata* had a net production of about 1.5 kg AFDW m^{-2} over a 2.5 yr period in station P2 or an average yearly production of the cohort '95 of 600 g AFDW. This is very high in comparison with many other studies on the production of bivalves, where a yearly production, expressed in g AFDW m^{-2} yr^{-1}, of maximum 156 found (Table 4).

Species	Site	Yearly production (g m^{-2} yr^{-1})	Biomass type	Source
Arctica islandica	Western Baltic Sea	15	AFDW	Brey *et al.*, 1990
Corbicula fluminea	Georgia, USA (freshwater)	9 – 23 (max.)	SFDW	Stites *et al.*, 1995
Macoma balthica	Southwestern France	0.71 – 3.24	AFDW	Bachelet, 1982
Macoma balthica	Northern Baltic Sea	62.8	SFDW	Ankar, 1980
Mytilus edulis	Southwestern Netherlands	156	AFDW	Craeymeersch *et al.*, 1986
Scrobicularia plana	Southwestern France	0.62 – 25.21	AFDW	Bachelet, 1982

Table 4. Yearly production estimates of a variety of bivalves, with biomass type: AFDW, Ash-free Dry Weight and SFDW, Shell-free Dry Weight.

IMPLICATIONS OF SHELLFISHERY ON THE WESTERN COASTAL BANKS

Spisula subtruncata is known to be an important food resource for the common scoter (*Melanitta nigra*) (Leopold *et al.*, 1995). Within its wintering area, the common scoter prefers shallow coastal waters, with a lack of disturbance and a fair density of bivalves (Kirchoff, 1981), being its major food resource (Cramp and Simmons, 1977; Meissner and Bräger, 1990). The western Coastal Banks, being too shallow for commercial shipping and having high densities of bivalves, as *S. subtruncata*, are fulfilling all demands of the seaducks and, consequently, thousands the common scoter were staying in the area during some winter periods (Maertens *et al.*, 1988, 1990; Devos, 1990; Offringa *et al.*, 1998). As the fishery of *S. subtruncata* will evidently lead to a decrease in the standing stock of the bivalve in the area, the food resources for the common scoter may not be fulfilling the seaduck's demands anymore and can lead to the disappearance of the common scoter in the area, as already demonstrated in the Netherlands (Leopold, 1993; Leopold *et al.*, 1995). Furthermore, though being the most abundant bivalve in all macrobenthic communities of the western Coastal Banks, certainly in 1997, *Spisula subtruncata* is only found in high densities in the *Lanice conchilega* community. This ecologically, highly important community is only encountered in the deeper parts of area 1, as the tidal gully, Potje, and the northern flank of Den Oever and a few spots of area 2 (Degraer *et al.*, in press a). In comparison with the shallow parts of the western Coastal Banks, these relatively deeper areas create a hydrodynamically more benign situation for the macrobenthos, strongly increasing the density and diversity of the macrobenthos. Shellfishery in the most important areas (*L. conchilega* community), can lead to an impoverishment (density, biomass and diversity) of the macrobenthos (Craeymeersch, 1997).

Finally, because the occurrence of fishable stocks of *Spisula subtruncata* (86000 ton) is concentrated in small areas, mainly situated in area 2 (Potje and northern flank of Den Oever and Trapegeer) (Vanhee *et al.*, 1998), this stock can be depleted within a short period of time. In Belgium, where no shellfishery occurs at this moment, first of all large investments within the shellfishery are necessary to harvest the bivalve. On the other hand, as the relatively small stock of *S. subtruncata* may be depleted quickly and no other fishable stocks of this species are present along the Belgian coastline (only 65 km!), the investments will only render for one season. After the depletion of the stocks, the natural recovery of the stocks may take several years, as demonstrated by highly variable recruitment of *S. subtruncata*. It is thus doubtful whether the Belgian *Spisula*-fishery can render over a longer period of time.

CHAPTER 5

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

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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

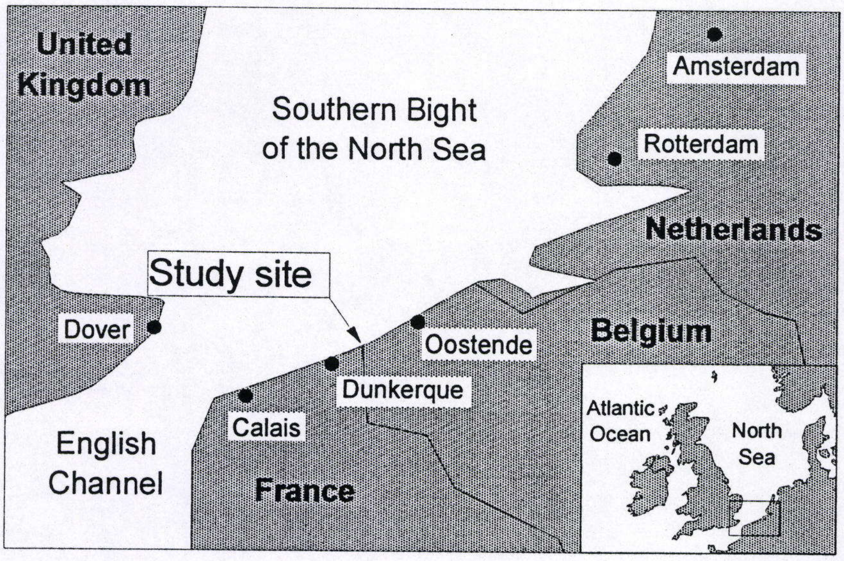

Figure 1. Geographical disposition of the study area.

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.

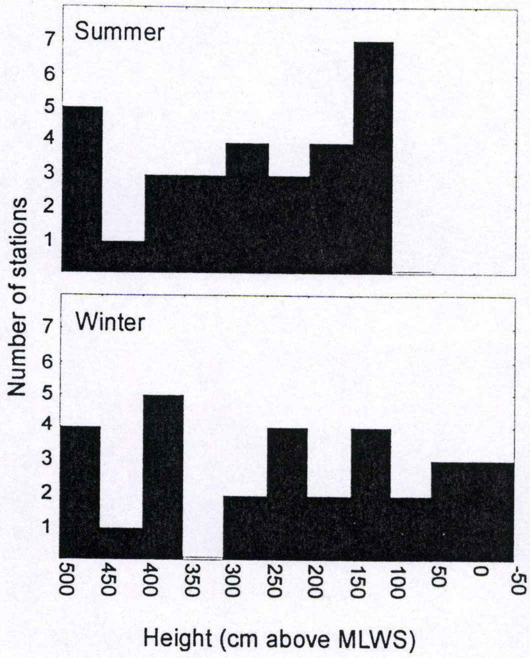

Figure 2. The distribution of the 30 stations along the intertidal continuum during the summer and winter sampling campaign.

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).

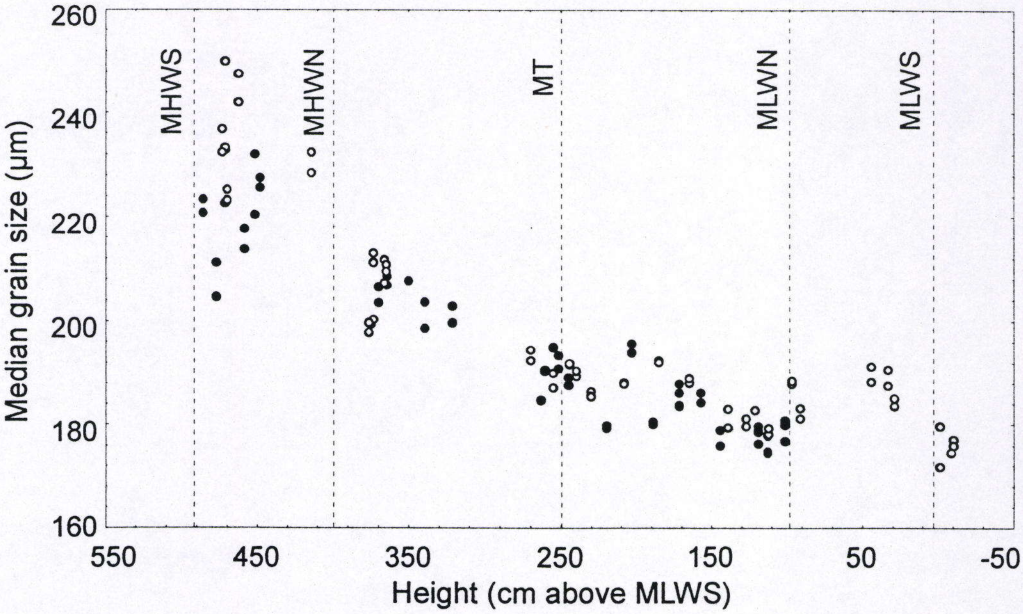

Figure 3. The intertidal distribution (height in cm above MLWS) of the median grain size (µm). ● : summer; ○ : winter.

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.

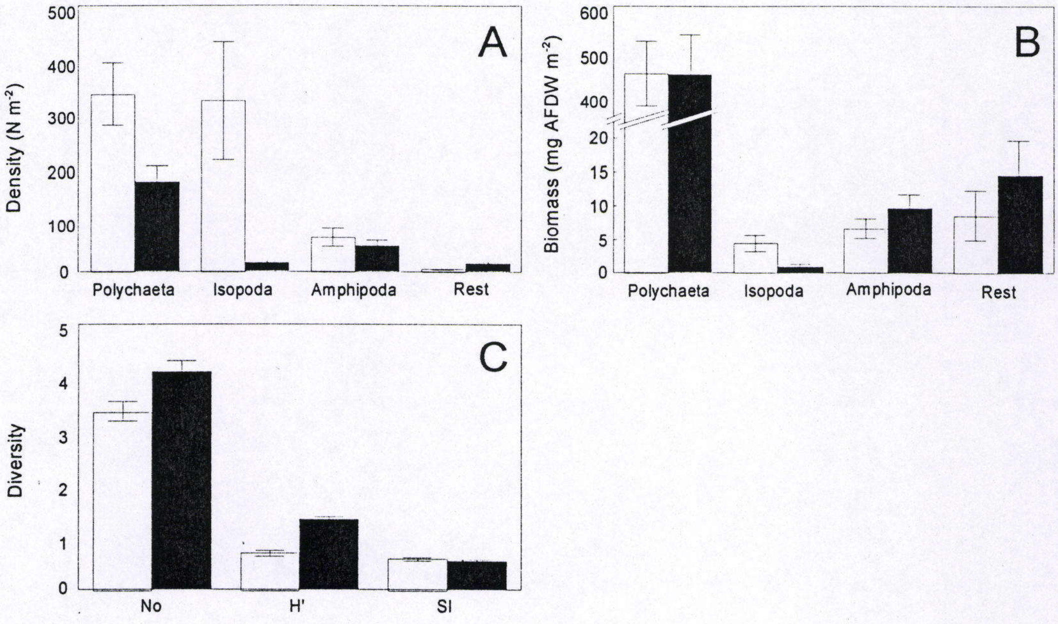

Figure 4. The distribution over the different taxa of A. the density (N m^{-2} ± standard error, SE) and B. the biomass (mg AFDW m^{-2} ± SE). C. Diversity indices (number of species per sample, N_0 and Shannon-Wiener diversity index, H', both ± SE) and eveness index (Simpson dominance index, SI, ± SE).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

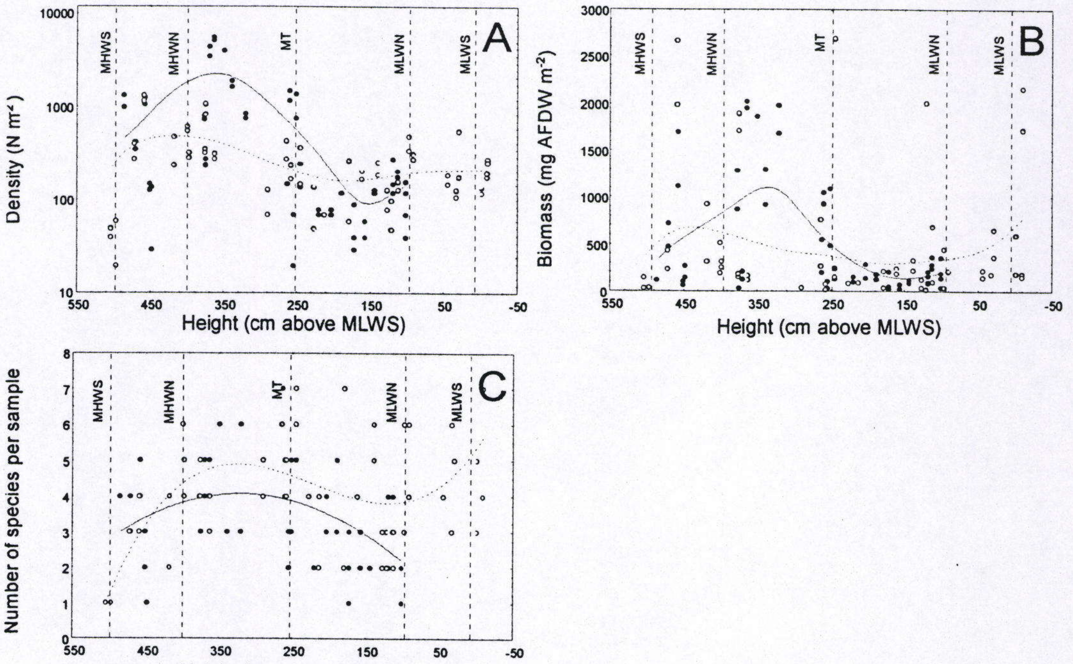

Figure 5. The intertidal distribution (cm above MLWS) of the macrobenthic density (N m^{-2}), macrobenthic biomass (mg AFDW m^{-2}) and number of species per sample. ● : summer; ○ : winter; density presented on a logarithmic scale.

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).

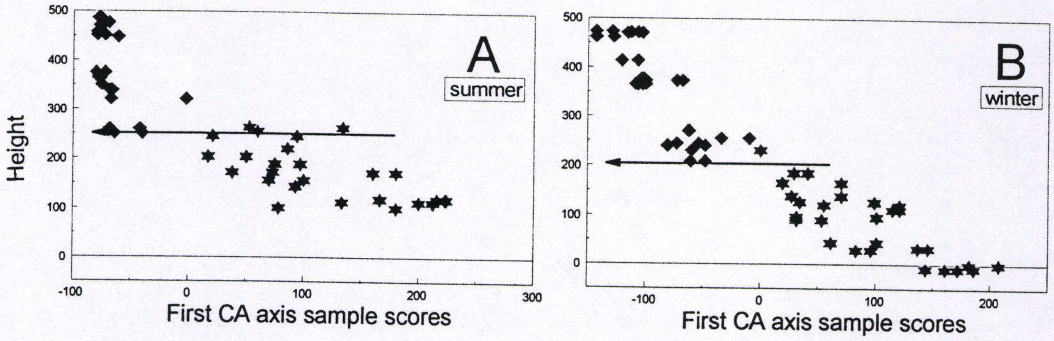

Figure 6. The continuous relation between the CA sample scores of the first axis and the height on the beach (cm above MLWS); with indication of the two species associations (★: species association 1 & ◆: species association 2) and the distinctive height between both (arrow). The sample scores on the 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.

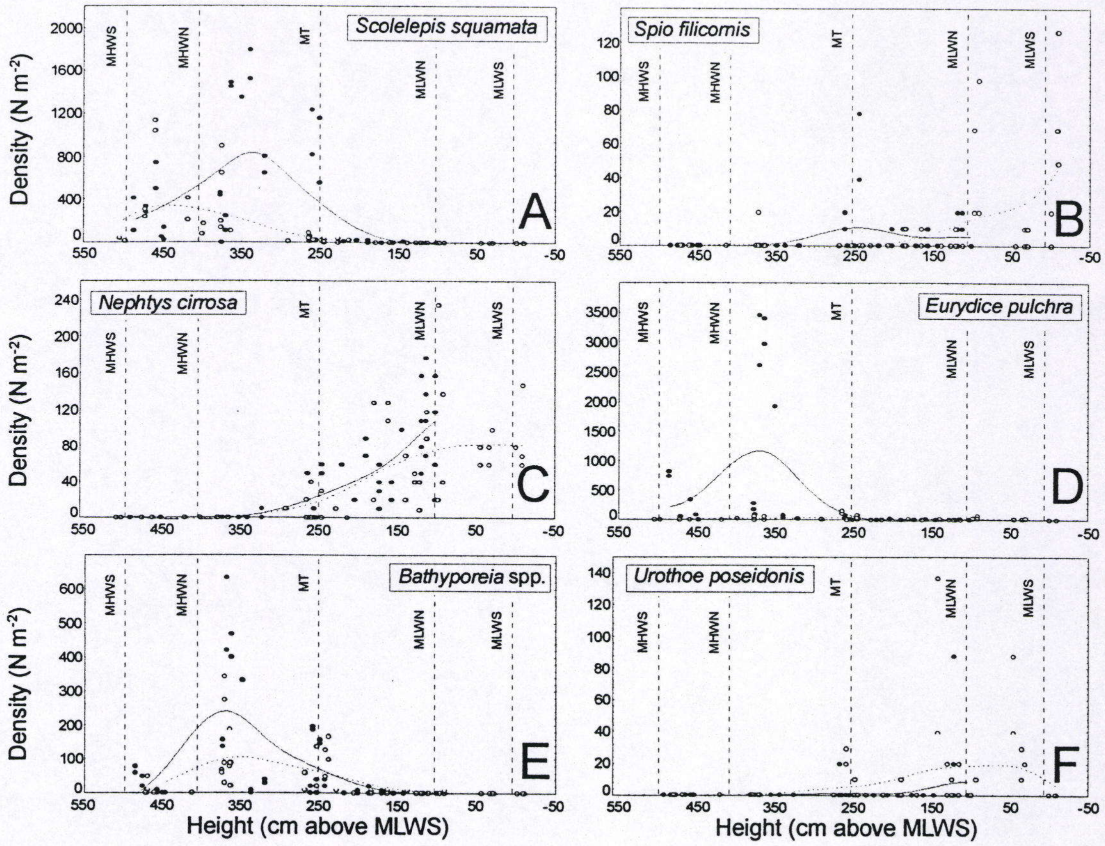

Figure 7. The intertidal density (N m^{-2}) distribution of the 3 most dominant species of each species association and per sampling campaign: A. *Scolelepis squamata*; B. *Spio filicornis*; C. *Nephtys cirrosa*; D. *Eurydice pulchra*; E. *Bathyporeia* spp.; F. *Urothoe poseidonis*. ● : summer; ○ : winter.

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.

CHAPTER 6

MACROBENTHIC ZONATION PATTERNS ALONG A MORPHODYNAMICAL CONTINUUM OF MACROTIDAL, LOW TIDE BAR/RIP AND ULTRA-DISSIPATIVE BEACHES

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ACKNOWLEDGEMENTS

The first author was financed by the Flemisch Institute for the Promotion of the Scientific – Technological Research in Industry (IWT). Valuable comments on the manuscript are retrieved from Patrick Meire and Jan Mees. The authors want to thank Johan Van de Velde, Annick Van Kenhove, Myriam Beghyn, Danielle Schram, Ann Depoortere, Koen Camelbeke, Liesbeth Labarque, Maaike Steyaert, Liesbet M., Liesbet D., and An B. for their assistance in the field and the laboratory.

ABSTRACT

The species composition, densities, biomass and zonation patterns of the macrobenthos of sandy beaches is influenced by the morphodynamics and morphology of the beaches to a great extent. To investigate the macrobenthos along a small-scale morphodynamic gradient, from the mean high water spring level (MHWS) to the mean low water spring level (MLWS), eight Belgian beaches have been investigated along a single transect, perpendicular to the water line. At each transect, ten to 14 stations were sampled, each with two replicates. Taking into account the dimensionless fall velocity (Ω) and the relative tidal range (RTR), the beaches were ordered along the gradient from the ultra-dissipative beach type (UD) to the low tide bar/rip beach type (LTBR). The beach state index (BSI) varied between 1.8 and 4.2. Generally, the beach profiles were related with the beaches' morphodynamic state.

At all beaches, the distribution of the macrobenthic characteristics were mainly determined by the height on the beach. In total 35 macrobenthic species, mainly polychaetes and crustaceans, were encountered, varying between 19 and 23 species per beach. The beaches' species composition was quite similar, with *Scolelepis squamata* being abundant at all eight beaches. Still, some remarkable differences, largely explained by the beach morphodynamics and the consequent hydrodynamics, were found. At macrobenthos-rich UD beaches, the highest macrobenthic densities and biomass were found on the upper beach, while at the macrobenthos-poor LTBR beaches, the highest densities and biomass were situated in the middle beach zone. Species, typically occurring on the upper UD beaches, such as *Bathyporeia sarsi*, *S. squamata*, and *Psammodrilus balanoglossoides*, were restricted to the sub-optimal middle beach zone at LTBR beaches. Only *Bathyporeia pilosa* could be found on the upper beach of UD and LTBR beaches, but was clearly more abundant on UD beaches. The robust polychaete *Ophelia rathkei* and the interstitial polychaete *Hesionides arenaria* were exclusively found in the upper beach zone of LTBR beaches. A summarizing zonation scheme, representing the typical species' distributions of the Belgian UD and LTBR beaches, is presented.

INTRODUCTION

The zonation of macrobenthic organisms on sandy beaches is a worldwide, well-known phenomenon: in the intertidal zone, species are occurring in very specific height zones on the beach (McLachlan and Jaramillo, 1995). Attempts to apply universal zonation schemes (Dahl, 1952; Salvat, 1964) often fail, partly due to temporal variations within the zonation patterns (Haynes and Quinn, 1995), but certainly also due to morphodynamic differences between beaches (McLachlan and Jaramillo, 1995).

Originally, the morphodynamic differences were described by differences in waves and sediment characteristics between beaches by means of the dimensionless fall velocity, Ω (Dean, 1973): beaches were classified along the continuum from reflective (Ω < 1), over intermediate (1 < Ω < 6), to dissipative (Ω > 6) beaches (Wright and Short, 1984). Still, the influence of the tidal range on the beach morphodynamics cannot be neglected (Wright *et al.*, 1987). Nowadays, beach morphodynamics can be described by the beach state index (BSI) (McLachlan *et al.*, 1993) and the 2-dimensional beach model of Masselink and Short (1993), both taking into account the wave regime, the sediment characteristics and the tidal range of the beaches under consideration. Short (1996) slightly modified the 2-dimensional beach model and distincted six beach types (Figure 1).

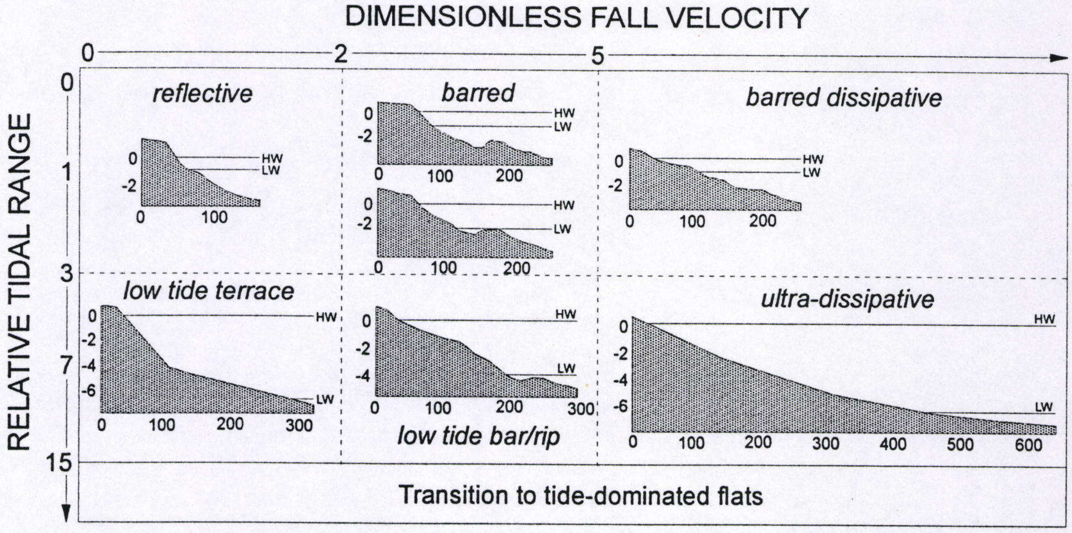

Figure 1. Schematical presentation of beach types, based on the dimensionless fall velocity (Ω) and the relative tidal range (RTR) (modified from Masselink and Short, 1993; Short, 1996). HW, high water level; LW, low water level.

Within the 2-dimensional beach model (Masselink and Short, 1993; Short, 1996), the macrobenthic number of species and density are known to increase with increasing relative tidal range (RTR) and dimensionless fall velocity (Ω): from the reflective to the ultra-dissipative beach type (e.g. McLachlan *et al.*, 1996; Borzone *et al.*, 1996).

So far, the macrobenthos of Belgian beaches is only surveyed at the macrotidal, ultra-dissipative beach of De Panne (Elliott *et al.*, 1997; Degraer *et al.*, in press b). For a detailed description of the macrobenthic community structure and zonation patterns, one is referred to Degraer *et al.* (in press b).

To investigate the influences of Ω and RTR on the macrobenthos within the small-scale morphodynamic gradient along the Belgian coastline, this study investigates the macrobenthos of eight macrotidal Belgian beaches.

MATERIALS AND METHODS

STUDY SITE

The Belgian coastline (65 km) is situated between 2°33'24"E - 51°05'42"N and 3°20'24"E - 51°22'00"N. All beaches have a semi-diurnal, macrotidal regime, with a spring tidal range of 4.5 – 5 m and a neap tidal range of 3.7 – 3.9 m. The tidal range slightly decreases from West to East. The average height and period of the waves just in front of the western Belgian coastline in 1997 were about 0.5 m and 3 s, respectively, while 3.5 m and 7 s were the maximum measured wave height and period (Anonymous, 1998). The beaches are completely composed of fine to medium sands (Degraer, unpublished results). A natural gradient of slightly increasing beach slopes, causing a decrease in beach width, exists from West to East (Depuydt, 1972). This gradient is disturbed by the construction of the harbour walls of Zeebrugge, increasing the sedimentation in their near environment by tempering the tidal currents and, consequently, increasing the width of the beaches. The tidal currents are West – East oriented during flood and East – West during ebb.

Strong tidal currents on the beaches are responsible for beach erosion on several sites along the Belgian coastline. To prevent beach erosion and inundation of the hinterland, a large part of the coastline is subjected to coastal defence works: groins, up to a length of 500 m, are numerous especially Eastwards of Nieuwpoort, while concrete dykes are found along about the whole coastline. Natural beach–dune transitions, with a length of more than 1 km, can only be found in 4 sites (total: about 9 km). A large number of tourists visit Belgian beaches, especially during summer. Most of them are concentrated near the numerous cities. One beach, 'Baai van Heist', situated just East of the harbour of Zeebrugge at Heist, is designated as a nature reserve since October 1997 (Anonymous, 1997).

To study the macrobenthos of Belgian beaches, eight sampling sites, spread over the whole coastline, were selected. From West to East, the sampling sites are: De Panne (DP), Schipgatduinen (SG), St.-Laureins (SL), Raversijde (RA), Vosseslag (VS), Fonteintjes (FO), Heist (HE) and Zwin (ZW) (Figure 2). These sites have little disturbance from recreation compared to other sites. Except for SG and VS, some important anthropogenic influences were found on the beaches (Table 1).

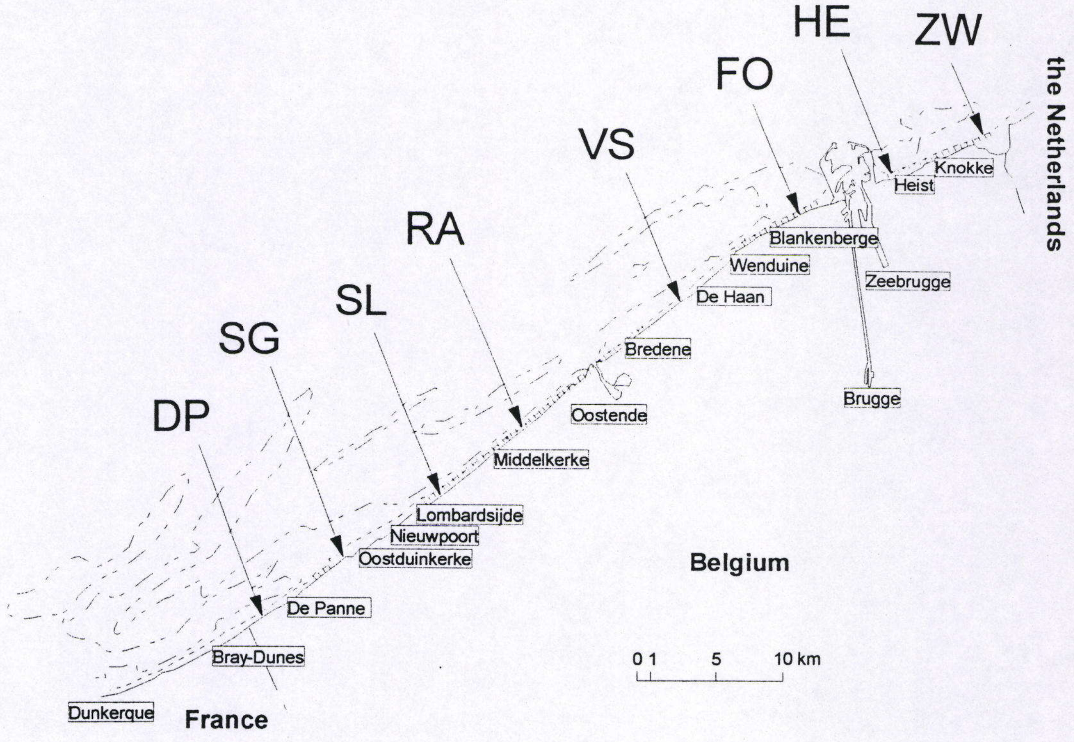

Figure 2. Geographical situation of the eight sampling sites along the Belgian coast. DP, De Panne; SG, Schigatduinen; SL, Sint-Laureins; RA, Raversijde; VS, Vosseslag; FO, Fonteintjes; HE, Heist; ZW, Zwin.

Beach	Dyke	Groins	Remarks
DP	T1	No	Fronting 'De Westhoek' nature reserve (dunes)
SG	---	No	Fronting large dune area
SL	T1	Yes	Fronting small dune area
RA	T2	Yes	
VS	---	No	Fronting small dune area
FO	T1	Yes	Fronting 'Fonteintjes' nature reserve (dunes)
HE	T1	No	'Baai van Heist' nature reserve (beach)
ZW	T1	Yes	Fronting large dune area

Table 1. General characterization of the eight beaches: Presence of a concrete dyke, with ---, dyke absent; T1, dyke above MHWS and T2, concrete dyke below MHWS; Presence/absence of groynes; Special remarks.

SAMPLING

The sampling (one beach per day) took place between 8 and 17 September 1997. At each beach, ten to 14 stations (two replicates) were sampled along a single transect, running from about MHWS to MLWS. A total of 178 samples were collected. Sampling always started at high tide and followed the receding water down the beach, ending at low tide. Samples were taken by excavating a frame (surface area, 0.1026 m²) to a depth of 0.15 m. The samples were immediately sieved through a sieve, with a 1 mm-mesh size and fixed and preserved in an 8% formaldehyde-seawater solution. At each station, one core (diameter, 1.5 cm) for sediment analysis was collected.

LABORATORY WORK

In the laboratory, the sieved samples for faunal analysis were elutriated ten times to collect the macrobenthos. Afterwards, the remaining material was examined to collect the larger macrobenthic organisms that were to 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 the number of individuals per m² (ind 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 h) of oven-dried samples (70°C for 48 h). The biomass of all other macrobenthic organisms 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 ashed at 500 ± 50°C for 2 h to determine the percentage of Total Organic Matter (TOM) by loss on ignition. The percentage of shell fragments was determined by means of the volume of the remaining sediment, consisting of shell fragments for about 100 % (Degraer, unpublished data), versus the total excavated volume of sediment. The grain size distribution of all sediment particles between 2 and 850 µm was determined with a laser COULTER LS.

MATHEMATICAL ANALYSES

The morphodynamic state of the beaches is given by the dimensionless fall velocity ($\Omega = H_b/w_sT$), the relative tidal range ($RTR = MSR/H_b$), and the beach state index ($BSI = \log_{10}\Omega * MSR$), where H_b is the modal breaker height in m, T is the modal wave period in s, MSR is the mean spring range in m, and w_s is the sediment fall velocity in m s^{-1}, obtained from Gibbs *et al.* (1971) (Masselink and Short, 1993; McLachlan *et al.*, 1993).

Macrobenthic abundances are used to calculate the diversity as the number of species per sample (N_0) (Hill, 1973). In order to investigate the mutual similarities and dissimilarities between all stations of the eight beaches, the density data (fourth root transformed) were subjected to a Canonical Correspondence Analysis (CCA) (Ter Braak, 1988). The polynomial functions, showing the general zonation trend of the macrobenthic density and the densities of the most abundant species, were retrieved by means of a distance-weighted least squares smoothing procedure of the data points as calculated by the program STATISTICA 5.1 (StatSoft, 1996). The correlations between the environmental variables were analyzed by means of the non-parametric Spearman rank correlation coefficient (Siegel, 1952; Conover, 1971).

RESULTS

ENVIRONMENT

Based on their profiles, the eight beaches (Figure 3) could be separated into two groups. A first group, including DP, SL, RA, FO, and HE, are showing a straight profile with a slope varying between 0.7° and 1.2°.

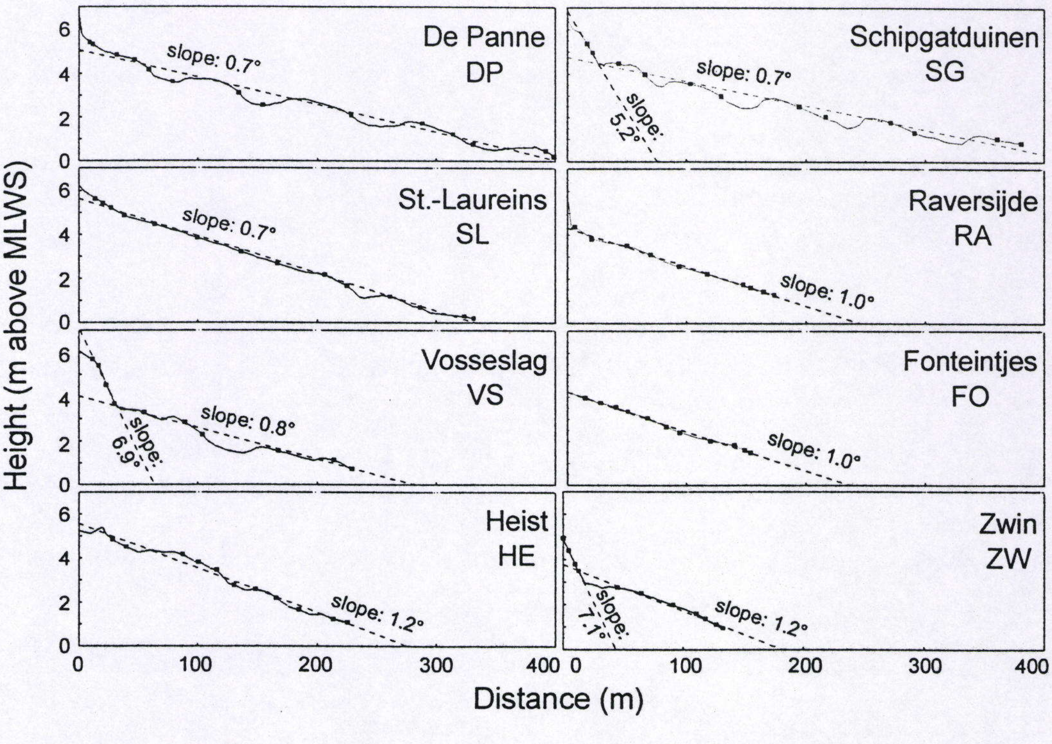

Figure 3. The beach profiles of the eight sampling sites, with indication of (1) the sampling stations (▪) and (2) the overall beach slope (DP, SL, RA, FO, and HE) or the beach slopes of the lower and upper beach (SG, VS, and ZW).

The profiles of the second group (VS and ZW) are having a break in their slope between 3 and 4 m above MLWS, separating the beach into an upper and a lower beach. The slope of the lower beach was situated between 0.7° and 1.2°, while the upper beach slope was found between 6.9° and 7.1°. SG had a large lower beach (slope: 0.7°) and a small upper beach (slope: 5.2°). An alternation of ridges and runnels was present on DP, SG, VS, and HE, while all other beaches had a quite featureless profile.

During the sampling campaign, the salinity of the coastal water was between 35.1 and 31.9 PSU, generally decreasing Eastwards; temperature varied between 15.6 and 18.6°C, generally increasing Eastwards. The average median grain size for each beach varied between 199 and 352 µm (Table 2). A general trend of increasing average median grain sizes from the western towards the eastern beaches, only disturbed by SG and VS, was found. The minimum and maximum median grain sizes were 177 and 525 µm. The percentage TOM varied between 0.4 and 1.9 %, averaging between 0.5 and 0.8 % per beach. Except for VS and ZW, the percentage of shell fragments varied between 1 and 16 %, averaging between 1 and 5 % per beach. VS and ZW had an average of 11 and 15 % of shell fragments and a maximum of 49 and 61 %, respectively. The relative tidal range (RTR) varied only little between 8.5 and 10, while the dimensionless fall velocity (Ω) and the beach state index (BSI) were spread over a larger range: 2.6 – 7.0 and 1.8 – 4.2, respectively.

	Median grain size		TOM		Shell fragments		Ω	RTR	BSI
	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean			
DP	177-235	199	0.5-0.8	0.6	1-10	4	6.8	10	4.2
SG	183-464	247	0.6-1.2	0.7	1-16	3	4.3	9.8	3.1
SL	182-246	209	0.6-1.0	0.8	1-12	5	7.0	9.5	4.0
RA	195-225	211	0.4-0.8	0.6	1-7	3	6.8	9.2	3.8
VS	235-539	352	0.5-1.9	0.7	1-49	11	3.1	9.0	2.2
FO	225-265	241	0.4-0.7	0.5	1-3	1	5.5	8.8	3.3
HE	227-275	255	0.4-1.0	0.6	1-9	2	6.2	8.7	3.4
ZW	249-525	325	0.5-1.2	0.7	1-61	15	2.6	8.5	1.8

Table 2. Median grain size, µm; Total Organic Matter (TOM), mass %; Shell fragments, volume %. Dean's parameter or dimensionless fall velocity: Ω (dimensionless); Relative Tidal Range: RTR (dimensionless); Beach State Index: BSI (dimensionless).

According to the morphodynamical classification scheme of Masselink and Short (1993), DP, SL, RA, FO, and HE are placed within the ultra-dissipative beach type (UD beaches), while SG, VS, and ZW are situated in the low tide bar/rip beach type (LTBR beaches) (Figure 4). The two most extreme beaches, regarding the dimensionless fall velocity, were SL for the UD beaches and ZW for the LTBR beaches.

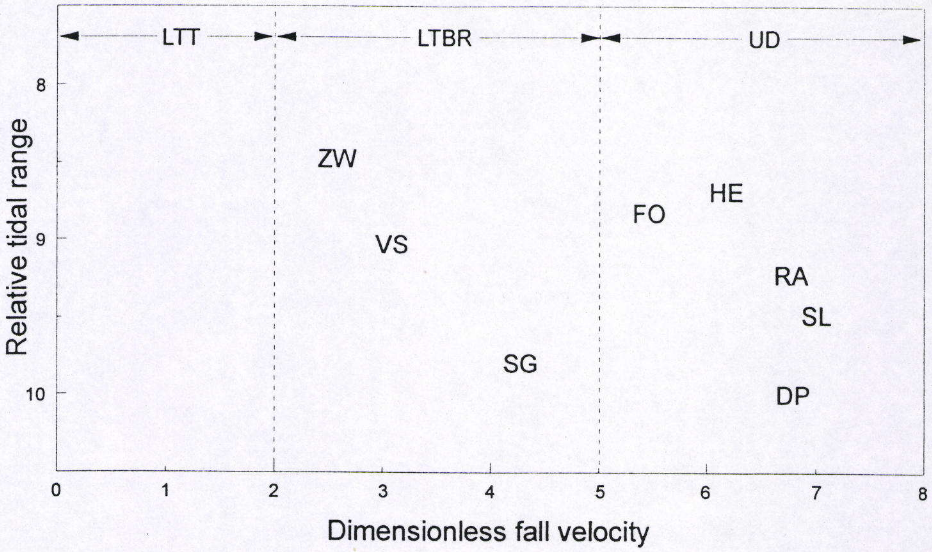

Figure 4. The situation of the eight sampling sites within the morphodynamic classification scheme of Masselink and Short (1993), based on the dimensionless fall velocity (Ω) and the relative tidal range (RTR)

MACROBENTHOS

In total 35 macrobenthic species were encountered: 17 crustaceans, 16 polychaetes and 2 bivalves. The overall average macrobenthic density and biomass were 897 ind m^{-2} and 62 mg AFDW m^{-2}, respectively. The total number of species per beach ranged from 19 to 23 species, evenly divided over the polychaetes and the crustaceans (Table 3). The macrobenthic density (289 – 1841 ind m^{-2}) and the biomass (24 – 122 mg AFDW m^{-2}) were generally dominated by the polychaetes. Combing the five most dominant species of each beach, a total of only 13 species is found. *Scolelepis squamata* was dominant in all beaches, while *Bathyporeia sarsi*, *B. pilosa*, *Eurydice pulchra*, and *Capitella capitata* were abundant in at least five of the eight beaches.

		DP	SG	SL	RA
N° of spp.	All species	19	20	23	19
	Polychaeta	9	8	11	11
	Crustacea	9	12	11	8
Density	All species	1841	289	829	1295
	Polychaeta	177	177	592	674
	Crustacea	1664	112	237	621
Biomass	All species	85	62	68	122
	Polychaeta	61	60	62	107
	Crustacea	19	2	3	15
5 most dominant species		*B. pilosa* *E. pulchra* *S. squamata* *C. capitata* *B. sarsi*	*S. squamata* *E. pulchra* *B. pilosa* *C. capitata* *B. sarsi*	*C. capitata* *S. squamata* *E. longa* *E. pulchra* *B. pilosa*	*B. sarsi* *S. squamata* *E. longa* *P. elegans* *E. pulchra*

		VS	FO	HE	ZW
N° of spp.	All species	19	19	21	19
	Polychaeta	7	7	10	12
	Crustacea	11	11	10	7
Density	All species	377	435	1369	395
	Polychaeta	216	229	972	341
	Crustacea	160	205	390	54
Biomass	All species	27	51	47	24
	Polychaeta	13	40	35	23
	Crustcea	3	4	7	1
5 most dominant species		*S. squamata* *B. pelagica* *H. arenarius* *B. pilosa* *C. capitata*	*B. sarsi* *S. squamata* *P. balanoglossoides* *E. pulchra* *B. pilosa*	*S. filicornis* *C. capitata* *B. sarsi* *S. squamata* *P. elegans*	*S. squamata* *H. arenaria* *P. balanoglossoides* *O. rathkei* *B. sarsi*

Table 3. General macrobenthic characteristics of the eight beaches

The minimum and maximum number of species per station were 0 (SL and ZW) and 15 (HE) species. Generally, an increasing number of species from the mean high water spring level (MHWS) to the mean low water spring level (MLWS) was found (Figure 5). A minimum number of species was found in the highest stations of each beach. In the extreme situation of the UD beaches (SL), the number of species increased from MHWS to 2.2 m above MLWS, then steeply decreased to 1.7 m above MLWS, and finally increased again towards MLWS. Other UD beaches and SG showed the same, though more erratical, trend. The number of species of the LTBR beaches, except SG, slightly increased between MHWS and 3 to 3.5 m above MLWS, then steeply increased to about 1.5 m above MLWS, then steeply decreased to 1 and 1.5 m above MLWS, and finally increased again towards MLWS.

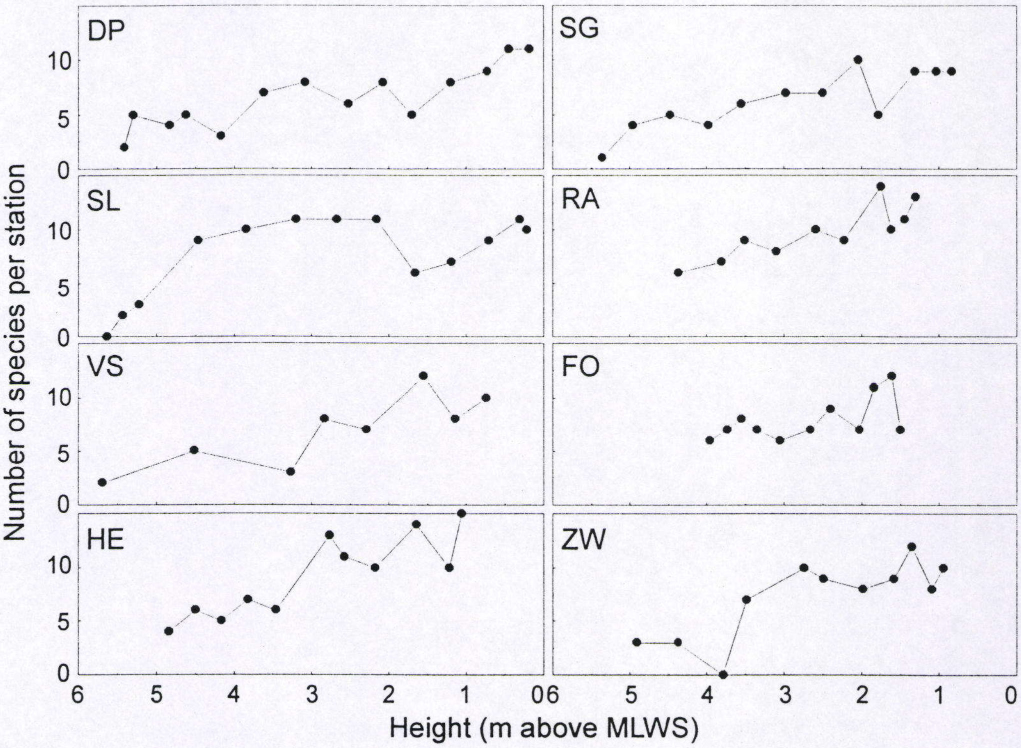

Figure 5. The distribution of the number of species per station over the intertidal zone of the eight sampling sites.

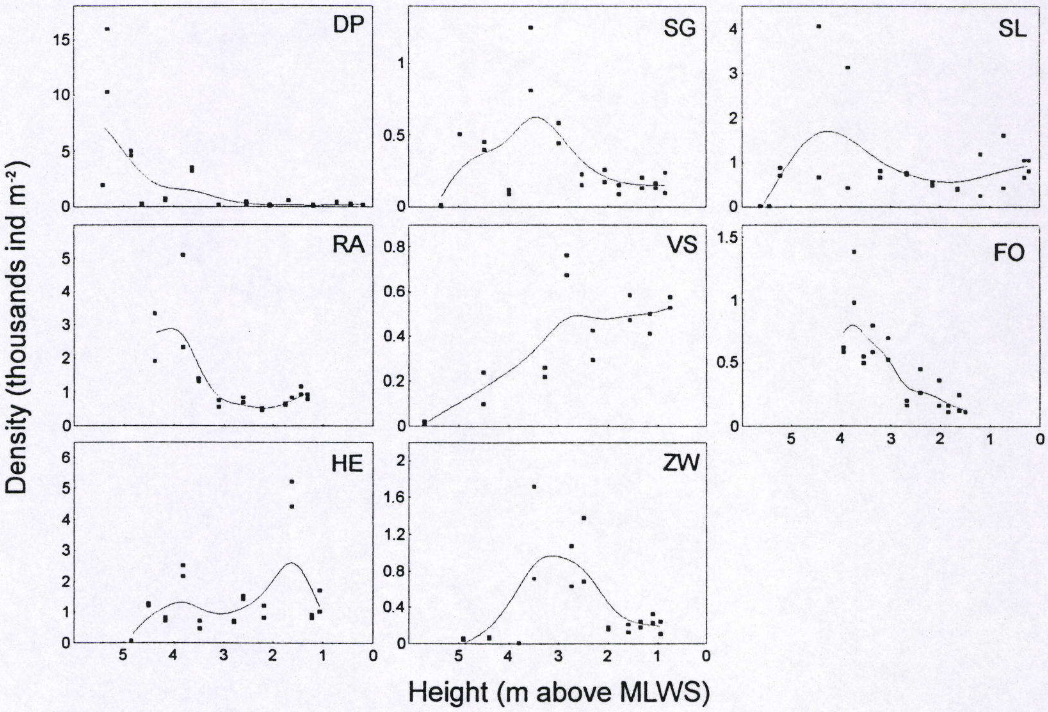

Figure 6. The distribution over the intertidal zone of the macrobenthic density of the eight sampling sites.

The densities of the UD beaches (except HE) and SG were at their maximum (1400 to 16000 ind m^{-2}) between 3.5 and 5 m above MLWS and decreased to a minimum at MHWS and 1.5 and 2.5 m above MLWS (Figure 6). At DP, SL, and RA, the densities slightly increase between 1.5 - 2.5 m above MLWS towards MLWS. Two density peaks, one at 4 m and another at 1.5 m above MLWS (2500 and 5000 ind m^{-2} respectively) were found in HE. The highest densities of the LTBR beaches (800 to 1700 ind m^{-2}), were situated between 2.5 and 3.5 m above MLWS and steeply decreased towards MHWS. At SG and ZW, the density also decreased towards MLWS, while, at VS, the density tended to increase towards MLWS.

The description of the detailed zonation patterns is based on the distributions of the main biological characteristics and the species of the two most extreme UD and LTBR beaches (SL and ZW, respectively) (Table 4). Dividing the intertidal zone into height zones, each of 1 m height, in SL and ZW, respectively, six and five height zones were sampled: in ZW, no samples were taken above 5 m above MLWS.

The average density over all height zones was 995 ind m^{-2} in SL and 443 ind m^{-2} in ZW. The maximum density of SL (2453 ind m^{-2}) was found in zone 4, while in ZW zone 4 had the lowest density (43 ind m^{-2}) and its maximum density was found in zone 2 (933 ind m^{-2}). The average biomass per height zone showed somewhat the same pattern as the average density, with (1) the lowest biomass in zone 4 of ZW (<1 mg AFDW m^{-2}), (2) the highest biomass of ZW in zone 2 (84 mg AFDW m^{-2}), and the highest density of SL in zone 3 and 4 (150 and 173 mg AFDW m^{-2}, respectively). In both beaches the number of species per sample (N_0) increased from the highest zone to zone 2, then decreased in zone 1 to increase again in SL and to further decrease in ZW in zone 0. In contrary to ZW, SL had a relatively high average N_0 over all height zones (5 versus 7 spp.). In SL, a N_0 of 8 species was already found in zone 4, while a N_0 of 8 species in ZW was only found in zone 2. In both beaches the maximum N_0 was found in zone 2. A total of 23 species was found in SL, while only 19 species were encountered in ZW. The lowest total number of species (3 spp.) was found in the highest zone of both beaches, while the highest total number of species (15 spp.) occurred in zone 0 for SL and in zone 1 for ZW. In accordance to N_0, a higher total number of species as found in the zones 4 – 2.

			Typical ultra-dissipative beach: St.-Laureins							Typical low-tide terrace beach: Zwin					
General			5	4	3	2	1	0	0-5	4	3	2	1	0	0-4
Sampled area (m²)			0.6	0.2	0.4	0.4	0.4	0.6	2.6	0.4	0.3	0.4	0.8	0.2	2.1
Average density (ind m^{-2})			263	2453	1252	629	548	925	995	49	806	933	200	175	433
Average biomass (mg AFDW m^{-2})			2	150	173	74	32	59	82	<1	3	84	17	10	23
Average N_0			1.2	8.0	8.3	8.8	5.5	8.3	6.7	2.3	3.3	7.8	7.0	6.5	5.4
Total number of species			3	9	12	14	8	15	23	3	7	11	15	10	19
Species	Taxon	Occurrence	5	4	3	2	1	0	ind.	4	3	2	1	0	Ind.
Eurydice naylori	I	SL	**	***					5						-
Bathyporeia pilosa	A	SL	**	***	*	*			176						-
Eurydice pulchra	I	both	**	***	**				186			***	*		10
Calanoidea	Co	ZW							-	***		*	*		9
Polydora sp.	P	both		***					26	***	**				3
Hesionides arenaria	P	ZW							-		***				171
Ophelia rathkei	P	ZW							-		***	***	*		124
Psammodrilus balanoglossoides	P	both		***	**	*		*	36		*	***	*	*	166
Pygospio elegans	P	both		*	**	**			20			***	**		11
Portumnus latipes	D	SL			***	***			2						-
Gastrosaccus spinifer	M	SL			**	***			4						-
Arenicola marina	P	SL			***	***			7						-
Scolelepis squamata	P	both		***	**	*	*	*	571		*	***	*	*	172
Bathyporeia sarsi	A	both		***	*	**	*	*	91		*	***	**	*	43
Paraonis fulgens	P	ZW							-				***		1
Eteone longa	P	both		*	**	**	**	**	217			**	*	***	23
Capitella capitata	P	both			*	**	**	***	635				***		21
Harpacticoidea	Co	both			*	***	**	**	94	***	*	**	*	*	50
Cumopsis goodsiri	Cu	SL				*	***	**	63						-
Spio filicornis	P	both				*	*	***	52			*	**	***	37
Haustorius arenarius	A	ZW							-			***		***	2
Spiophanes bombyx	P	SL				**		***	4						-
Nephtys cirrosa	P	both					**	***	7				***		2
Pontocrates arenarius	A	ZW							-				***	***	2
Nephtys hombergii	P	both						***	5				*	***	3
Urothoe poseidonis	A	SL						***	8						-
Crangon crangon	D	SL						***	1						-
Pontocrates altamarinus	A	SL						***	1						-
Macoma balthica	B	SL						***	1						-
Bathyporeia pelagica	A	ZW							-					***	1

Table 4. Detailed zonation patterns of the two most extreme beaches considering the dimensionless fall velocity (Ω): SL (= typical UD beach) and ZW (= typical sub-LTT beach). Zones: 5, > 5 m; 4, 4-5 m; 3, 3-4 m; 2, 2-3 m; 1, 1-2 m; 0, 0-1 m above MLWS. Taxon: P, Polychaeta; Co, Copepoda; Cu, Cumacea; I, Isopoda; A, Amphipoda; M, Mysidacea; D, Decapoda; B, Bivalvia. *, 1-20 %; **, 21-40 %; ***, >40 % of the total density over the whole beach. Ind., total number of individuals encounteres on the whole beach.

Thirty species occurred in at least one of the two beaches. These species were divided over the Crustacea (15 spp.), the Polychaeta (14 spp.) and the Bivalvia (1 sp.). 40% of the species (12 spp.) were found in both beaches, 37% is exclusively found in SL, and 23% is only encountered in ZW. Only the polychaete *Scolelepis squamata* was found in large numbers in both beaches (SL, 571 ind; ZW, 172 ind). Other species, encountered with more than 100 individuals, were the polychaetes, *Capitella capitata* and *Eteone longa*, and the isopods, *Eurydice pulchra* and *Bathyporeia pilosa*, in SL and the polychaetes, *Hesionides arenaria*, *Psammodrilus balanoglossoides*, and *Ophelia rathkei*, in ZW.

Clear groupings of species per height zone were not detected: most species were encountered over a specifical range of height zones, each with their own optimal height. A continuum of species' shifts over the full intertidal zone was present on both beaches. Considering the most abundant species of both stations, at SL, the optimal height of *E. pulchra*, *B. pilosa*, *P. balanoglossoides*, and *S. squamata* was found in zone 4, while the optimal height for *E. longa* and *C. capitata* was found in zone 0-3 and 0, respectively. At ZW, a lower optimal height for *E. pulchra*, *P. balanoglossoides*, and *S. squamata* was found (zone 2). *Eteone longa* was also occurred lower on the beach (zone 0), while zone 1 was the optimal height zone of *C. capitata*. Higher on the beach, zone 3 comprized the highest densities of *H. arenaria* and *O. rathkei*. Low densities of Urothoe poseidonis (SL), Crangon crangon (SL), Pontocrates altamarinus (SL), Macoma balthica (SL), and Bathyporeia pelagica (ZW) were exclusively found in zone 0.

GRADIENT ANALYSIS: CCA

The first axis of the CCA (eigenvalue: 0.43), comprizing all samples taken on the eight beaches, is negatively correlated with the height of the stations (Figure 7). This correlation is very clear for the UD beach (SL) and less clear for the LTBR beach (ZW). Within this height gradient no distinct groups of stations could be detected: the stations form a continuum from the upper part of the beaches towards the lower part of the beaches.

The second axis (eigenvalue: 0.15) is faintly correlated with the percentage of very fine sand (125 – 250 µm) and the median grain size. Obviously, a differentiation between the eight beaches shows up along the second axis, with the samples of DP, SG, SL, and RA having the highest values and the samples of VS and ZW having the lowest values. The samples of FO and HE are situated in between (Figure 8).

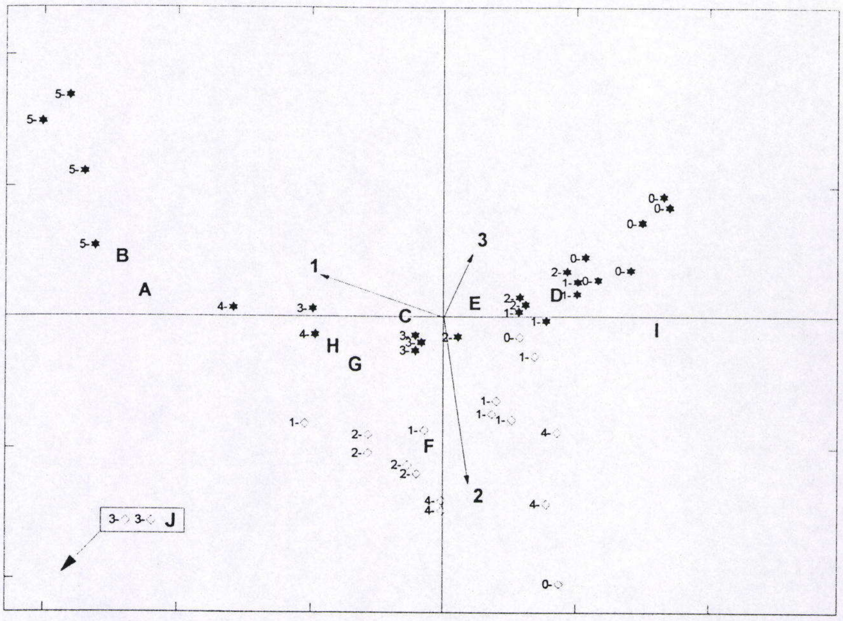

Figure 7. Situation of the samples of the typical UD beach (SL) and the typical LTBR beach (ZW), based on the Canonical Correspondence Analysis (CCA) including the samples of the eight sampling sites. ★ , SL; ◇ , ZW and 0, 0 – 1 m; 1, 1 – 2 m; 2, 2 – 3 m; 3, 3 – 4 m; 4, 4 – 5 m; 5, 5 – 6 m above MLWS. 1, height; 2, median grain size; 3, very fine sand content. A, *Eurydice pulchra*; B, *Bathyporeia pilosa*; C, *B. sarsi*; D, *Capitella capitata*; E, *Eteone longa*; F, *Ophelia rathkei*; G, *Psammodrilus balanoglossoides*; H, *Scolelepis squamata*; I, *Spio filicornis*; J, *Hesionura augeneri*.

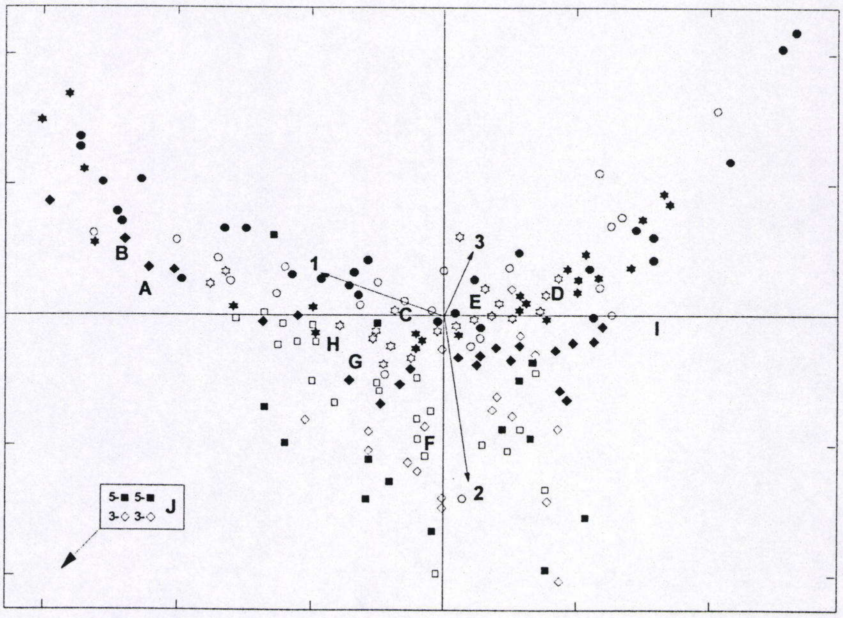

Figure 8. Situation of the samples of all beaches, based on the Canonical Correspondence Analysis (CCA) including the samples of the eight sampling sites. ● , DP; ★, SL; O, SG; ☆, RA; ■, VS; □, FO; ◆, HE; ◇, ZW and 0, 0 – 1 m; 1, 1 – 2 m; 2, 2 – 3 m; 3, 3 – 4 m; 4, 4 – 5 m; 5, 5 – 6 m above MLWS. 1, height; 2, median grain size; 3, very fine sand content. A, *Eurydice pulchra*; B, *Bathyporeia pilosa*; C, *B. sarsi*; D, *Capitella capitata*; E, *Eteone longa*; F, *Ophelia rathkei*; G, *Psammodrilus balanoglossoides*; H, *Scolelepis squamata*; I, *Spio filicornis*; J, *Hesionura augeneri*.

Their exists a significant relation (Spearman rank correlation, $r > 0.80$; $p < 0.02$) between the average ordination scores of the samples of each beach, along the second axis of the CCA, and the dimensionless fall velocity (Ω), the relative tidal range (RTR) and the beach state index (BSI) (Figure 9). The relation with Ω and BSI is only disturbed by SG, having a lower Ω and BSI than expected form its average CCA-axis 2 score. The relation with the relative tidal range (RTR) is only disturbed by FO and HE, having a lower RTR than expected from their position along the second CCA-axis.

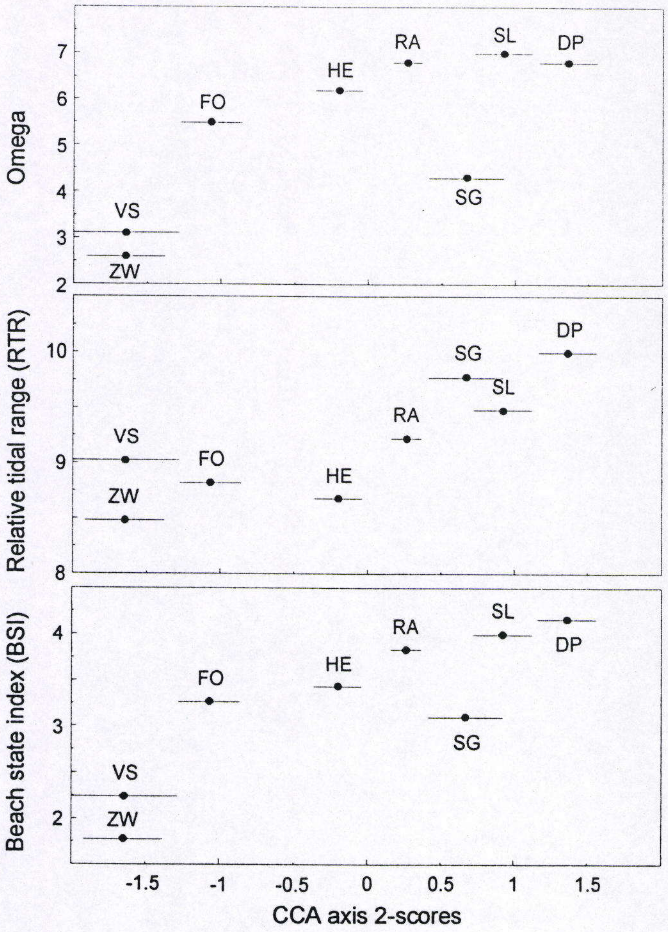

Figure 9. The relation between the average ordination scores of the samples of the eight sampling sites along the second CCA axis and the dimensionless fall velocity (Ω), the relative tidal range (RTR), and the beach state index (BSI) ± standard error.

DISCUSSION

The morphodynamic differences between the sampled beaches along the Belgian coast are small in comparison with other types of beaches (Masselink and Short, 1993). Certainly considering the relative tidal range (RTR), only a slight decrease is observed from West to

East. The major differences in morphodynamics and morphology of the beaches are indicated by the dimensionless fall velocity (Ω) and the beach state index (BSI) and visualized in the profiles of the beaches. Although, two beach types are distincted by means of Ω: the ultra-dissipative or UD beaches (DP, SL, RA, FO, and HE) and the low tide bar/rip or LTBR beaches (SG, VS, and ZW) (Short, 1996), the beaches are ordered gradually between UD and LTBR. The disturbance in the gradual transition (West to East) from UD to LTBR beaches, by FO and HE, can be explained by the presence of the harbour walls of Zeebrugge. These constructions are altering the natural tidal currents and wave regime, possibly influencing the beach morphodynamics and morphology. The beach profiles of FO and HE are also suggesting the unnatural morphology of the beaches, in comparison with the surrounding, relatively undisturbed beaches, VS and ZW.

As expected from the small morphodynamic and morphological differences, the general macrobenthic characteristics of the eight beaches have a lot of similarities (1) a similar number of species, increasing from the mean high water spring level (MHWS) to the mean low water spring level (MLWS), (2) the highest macrobenthic densities between MHWS and 2.5 m above MLWS, (3) the dominance of polychaetes and crustaceans, in terms of number of species, density, and biomass, (4) *Scolelepis squamata* as one of the five most dominant species, (5) the dominance of *Bathyporeia sarsi*, *B. pilosa*, *Eurydice pulchra*, and *Capitella capitata* in most of the beaches.
The total number of species per beach, ranging between 19 and 23 species and generally increasing towards MLWS, is similar to many other studies (e.g. Jaramillo *et al.*, 1993; James and Fairweather, 1996). The lower number of species in comparison with the 39 species, found on the beach of De Panne (39 spp.) (Degraer *et al.*, in press b), can be explained by the presence of samples below MLWS, including typical subtidal species, in the latter study (Degraer *et al.*, in press b). The macrobenthic densities are generally high, but are showing a common zonation pattern, with high densities in the upper intertidal zone. The dominance of polychaetes and crustaceans is common on most of the sandy beaches worldwide (e.g. McLachlan and Jaramillo, 1995) and has already been described for Belgian beaches as well (Elliott *et al.*, 1996; Degraer *et al.*, in press b). *Bathyporeia* spp. and *E. pulchra* are found to be abundant on many European beaches (e.g. Eleftheriou and McIntyre, 1976; Dexter, 1988; Bamber, 1993; Degraer *et al.*, in press b), while *S. squamata* is an abundant species on many Atlantic beaches (e.g. Brasilia: Souza and Gianuca, 1995; Europe: Eleftheriou and McIntyre, 1976; USA: McDermott, 1987; Rakocinski *et al.*, 1993).

Although the morphodynamic differences between the eight beaches are small in comparison with other sandy beaches (Masselink and Short, 1993), the profiles of the beaches show some clear differences. The two most extreme situations are the flat and featureless beach (SL) and the beach type with a distinction between the steeper upper intertidal and the flat lower intertidal zone (ZW). These two extremes are placed within the UD and LTBR beach type (Short, 1996).

The differences within the beach profiles are not only a visualization of the morphodynamic variation, but are directly influencing the hydrodynamical regime during the tidal cycle. On beaches with a flat slope, as the UD beach type (DP, SL, RA, FO, and HE), the swash zone is separated from the breaker zone by means of a wide (> 10 m) surf zone. This situation is also found in the lower part of the LTBR beach type (VS and ZW), where the beaches have a flat slope. On the steeper, upper part of the LTBR beaches, the breaker zone is situated directly in front of the swash zone, in absence of a surf zone. The surf zone creates a hydrodynamically benign situation, by dissipating the wave energy, while in absence of a surf zone the wave energy is directly reflected on the beach face (Masselink and Short, 1993). The high hydrodynamical forces on the upper beach of LTBR beaches, is directly responsible for the high median grain size and percentage of shell fragments, present at SG, VS, and ZW. The presence of a surf zone is thus favouring the more fragile macrobenthic organisms, such as tube-building polychaetes. The profile of SG, with a steep, but small upper beach and a flat, large lower beach, indicates towards a hybrid situation between the UD and the LTBR beach type.

Although the macrobenthos of the eight beaches show a lot of similarities, as described above, some remarkable differences between the two morphodynamically most extreme beaches, (SL for the UD beaches and ZW for the LTBR beaches) are found: (1) a lower average density and biomass in ZW, (2) the lower position of the macrobenthos-rich (density, biomass, number of species) zone in ZW, and (3) the occurrence of beach type-typical species, with *Capitella capitata*, *Eteone longa*, *Eurydice pulchra*, and *Bathyporeia pilosa*, in SL and *Hesionides arenaria*, *Psammodrilus balanoglossoides*, and *Ophelia rathkei*, in ZW. Especially the macrobenthos-rich situation of the UD beach type, SL, also demonstrated by the zonation patterns of the number of species and the density of other UD beaches (DP, RA, FO, and HE), is indicating the more benign environment of the UD beach type, with the richest zone just below MHWS. In contrary to the steeper, upper LTBR beaches (VS and ZW), the flat, lower part of the beaches allows the macrobenthos to reach a relatively high number of species, density and biomass, but still lower than the UD beaches.

The summarizing zonation scheme (Figure 10) is not aiming at the presentation of the detailed zonation patterns of all species, possibly encountered on the Belgian beaches. It rather presents the modal zonation patterns of the abundant species on the two Belgian beach types. As the Belgian beaches can be ordered along the morphodynamic gradient from typical UD to typical LTBR beaches, there exists a gradual transition between the two zonation schemes. Both types of beaches have a number of abundant species in common: the amphipods *Bathyporeia pilosa* and *B. sarsi* and the polychaetes *Scolelepis squamata*, *Psammodrilus balanoglossoides*, *Capitella capitata*, and *Spio filicornis*. At the UD beaches, three zones can be distincted: (1) an upper beach zone, with the optima of *Eurydice pulchra*, *B. pilosa*, *S. squamata*, *B. sarsi*, and *P. balanoglossoides* between 3.5 and 5 m

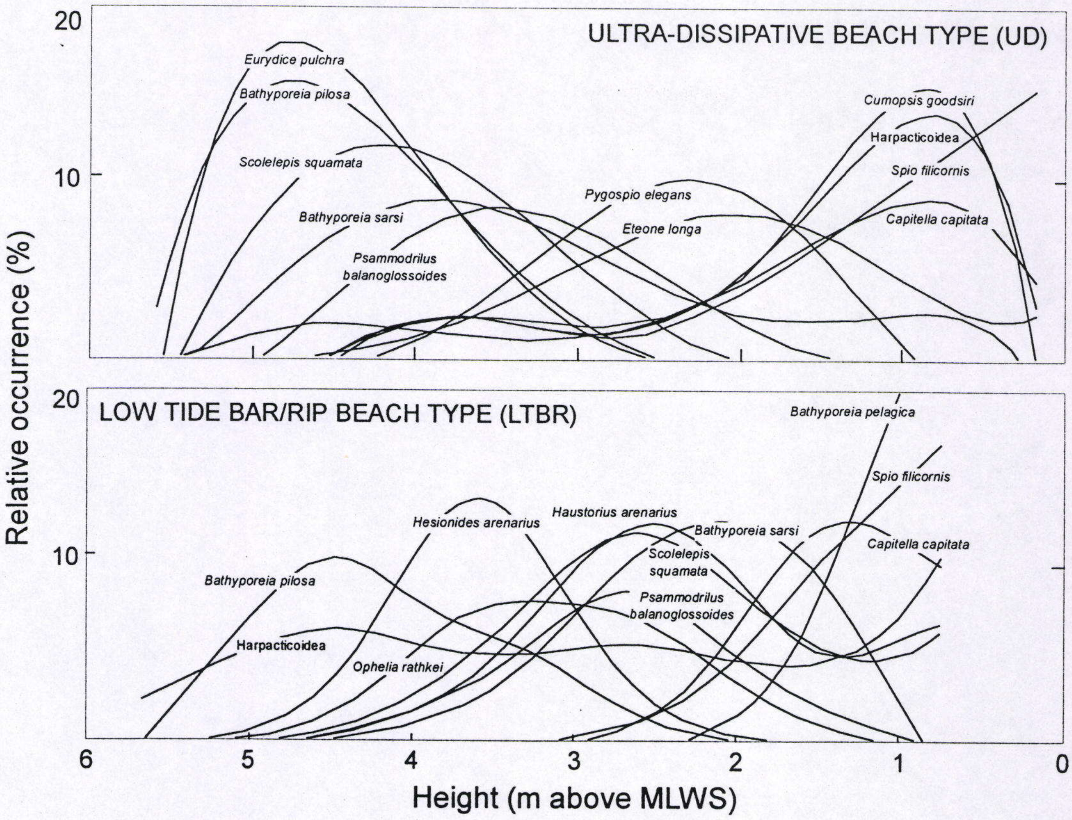

Figure 10. Summarizing zonation scheme of the macrobenthos on the UD and the LTBR beach type in Belgium, with indication of the relative occurrence of the abundant species of each beach type. In order to present the zonation schemes of typical UD and LTBR beaches, the beach SG, situated in the middle of the morphodynamic gradient, is not used to set up the summarizing zonation schemes.

above MLWS, (2) a mid beach zone, with the optima of *Pygospio elegans* and *Eteone longa* between 2 and 2.5 m above MLWS, and (3) a lower beach zone, with the optima of *Cumopsis goodsiri*, harpacticoid copepods, *S. filicornis*, and *C. capitata* below 1 m above MLWS. Obviously, a distinction between the upper and middle beach zone on Belgian UD beaches is not always possible. When studying the beach of De Panne, Degraer *et al.* (in press b) only distinguished between two zones: a high intertidal zone, dominated by *S. squamata*, and a low intertidal zone, dominated by *Nephtys cirrosa*. The low intertidal species association corresponds with the lower beach zone in this study, while the high intertidal species association is a combination of the upper and middle beach zone of this study. In this study, *N. cirrosa* is also restricted to the lower beach, but the polychaete is not abundant on any beach studied. Seasonal differences in the species' densities and distributions on sandy beaches, often related with yearly cycles of recruitment, are known to influence the zonation patterns (Haynes and Quinn, 1995). A combination of these seasonal changes and long-term changes within the macrobenthos, possibly caused by dramatic events, such as high summer temperatures or storms (Bamber, 1993), may be responsible for the observed differences of the zonation patterns and the decrease of the density of *N. cirrosa*.

At the LTBR beaches, the zonation pattern is less clear than at the UD beaches: all species are found at a specific place in the intertidal zone, but groupings of species are far less evident. The upper beach of the UD and LTBR beaches only have *B. pilosa* in common, but at the LTBR, some species, uniquely found on these LTBR beaches, as *Hesionides arenaria* and *Ophelia rathkei*, are found at the upper beach. Just like *Ophelia limacina* inhabits dynamical, coarse sediments in the shallow subtidal Belgian coast (Degraer *et al.* in press a), the robust polychaete, *O. rathkei*, is able to survive in an environment with high hydrodynamical forces, as the steep beaches (Hartmann-Schröder, 1971). The interstitial polychaete, *H. arenaria*, is known to inhabit the interstitial spaces of the coarse sediments of beaches (Hartmann-Schröder, 1971). Consequently, both species are found at the steep upper beaches of LTBR beaches, composed of coarse sediments. The optima of typical upper beach species of the UD beaches, as *B. sarsi*, *S. squamata*, and *P. balanoglossoides*, are found much lower on the LTBR beaches, where they are found together with *E. longa*. Obviously, the physical environment of the upper beach does not allow these species to survive in their optimal environment and their specifical occurrence is restricted to the middle beach. Except for *P. balanoglossoides*, they are also encountered in much lower numbers, indicating their occurrence in a sub-optimal environment.

The presence of typical subtidal species in the lower beach is demonstrated by the distribution of *S. filicornis* and *C. capitata* in both beach types, with at least a part of their vertical distribution is located in the subtidal zone (Figure 9) and suggested by the presence of *Nephtys hombergii*, *Urothoe poseidonis*, *Crangon crangon*, *Pontocrates altamarinus*, and *Macoma balthica* at the lowest heights of SL. All seven species are known to be abundant in the shallow subtidal environment of the western Belgian coast (Degraer *et al.,* in press a). The relation between subtidal and low intertidal species association is already demonstrated on several beaches worldwide (McIntyre and Eleftheriou, 1968; Souza and Gianuca, 1995; Borzone, 1996; Degraer *et al.*, in press b)

In conclusion it can be stated that, although a lot of affinities between the macrobenthic characteristics of the different beaches are found, some remarkable differences are detected, as discussed above. Generally, these differences can be explained by the morphodynamic state of the beaches. One of the most obvious differences is the general richer macrobenthos of the UD beaches, with a relatively high number of species, density and biomass on the upper beach. Species, typically found on the upper UD beaches, are restricted to the middle beach zone of the LTBR beaches. Still, the upper LTBR beach zone comprises some unique species, not encountered on UD beaches.

GENERAL CONCLUSIONS WITH SPECIAL ATTENTION TO THE MANAGEMENT OF THE BELGIAN SHALLOW MARINE HABITAT

The western Belgian Coastal Banks are known for their great ecological importance. The area is designated as an area of international importance for waterfowl, according the Ramsar Convention (Kuijken, 1972), fulfils the criteria of the EC Bird Directive (Anonymous, 1979), and is proposed to the European Commission to include it under the Natura 2000 network, in execution of the EC Habitat Directive (MUMM, January 1996: proposal by the federal administration of 'Trapegeer – Stroombank as SCI; Natura 2000 network). Furthermore, the Belgian government is studying the possibility of creating marine protected areas. Two larger possible marine protected areas are situated on the western Coastal Banks: area 1, including Stroombank and Balandbank and area 2, including Potje, Trapegeer, Broersbank and part of Den Oever and Westdiep (Figure 1). Although its ecological value is acknowledged, the economic importance of the area is also emphasized. The final designation of the protected areas will not be considered before all concerned parties and interests have been consulted and a management plan has been set up.

In order (1) to provide supporting information about the necessity of Belgian marine protected areas, (2) to help select the marine protected areas, (3) to help set up a management plan, and (4) to be able to evaluate *a posteriori* the effectiveness of this management plan, there is a strong need for scientific ecological information on the area. Untill now, except for the ornithological part (Maertens *et al.*, 1988, 1990; Devos, 1990; Offringa *et al.*, 1998), this information is largely lacking. The importance of the macrobenthos as the food resource for the common scoter (*Melanitta nigra*), being the most important seabird in the area (Maertens *et al.*, 1988, 1990; Devos, 1990), and the possible necessity of coastal defence works in the area, directly affecting the macrobenthos as bottom dwelling organisms, has led to the selection of the macrobenthos of shallow, Belgian marine habitats as the central object of this study.

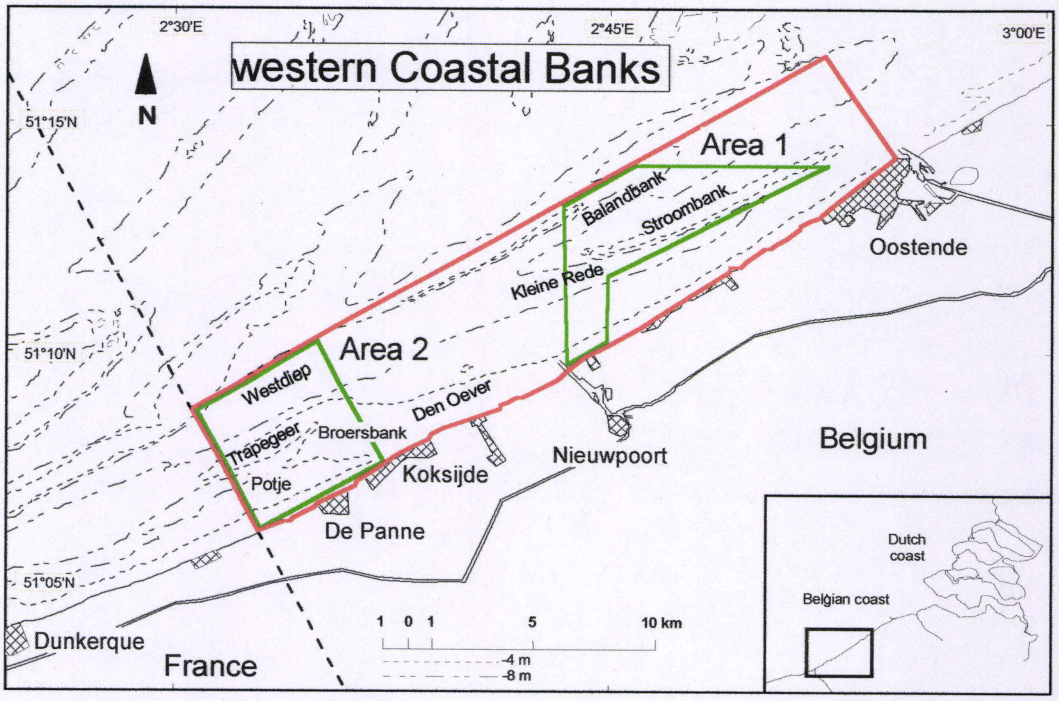

Figure 1. The geographical situation of the western Belgian Coastal Banks, with indication of (1) the proposed Special Protection Area (SPA) (red polygon), (2) the two major proposed Sites of Community Importance (SCI) (green polygons: areas 1 and 2), as part of the Natura 2000 areas (MUMM, January 1996: proposal by the federal administration of 'Trapegeer – Stroombank' as SCI; Natura 2000 network), and (3) the spatial distribution of the *Lanice conchilega* community (●).

During a 3.5 year study, aiming at the ecological correction of the course of planned coastal defence works in area 2 (Figure 1), the macrobenthos of the western Coastal Banks was investigated (Chapters 1 to 4). The whole study, supported by the Flemish Institute for the Promotion of Scientific – Technological Research in Industry (IWT), the Flemish administration responsible for environment, nature, land and water management (AMINAL; BNO/NO/1994 and AN/1995/nr.3: Degraer *et al.*, 1995, 1997) and the Coastal Waterways Division (Onderhandse overeenkomst dd. 24.07.1997: Degraer *et al.*, 1998), was divided into four topics. In order to evaluate and detect macrobenthos-rich and, thus, vulnerable sites on the western Coastal Banks (topic 1), the spatial distribution of the macrobenthic communities was studied within the areas 1 and 2 (Figure 1). Secondly, by means of the study of the temporal variation of the macrobenthos, information about the vulnerable periods (= periods of recruitment) and the 'potentials' (= the ecological importance, including the temporal variation) of a macrobenthos-rich community was gathered (topic 2). In order to retrieve a confirmation about the spatial distribution of the vulnerable sites (topic 1), the stability and dynamics of the spatial distribution of all macrobenthic communities was investigated (topic 3). Finally, because of the importance of the bivalve *Spisula subtruncata* as a food resource for the common scoter and the threat of *Spisula*-fisheries on the western Coastal Banks, the species' spatial distribution, population dynamics and production were studied (topic 4).

As shallow marine habitats not only include the subtidal part down to a depth of 6 m, but also the intertidal zone up to the high water level (Reilly *et al.*, 1996), the macrobenthos of both the subtidal and intertidal Belgian coast (the western Coastal Banks and the sandy beaches, respectively) was studied, including the Flemish beach nature reserve *Baai van Heist*.

However, within the scope of this work, not all aspects of the ecology of the macrobenthos could be covered: (1) the temporal variation has been studied within only one subtidal community, (2) long-term changes remain largely unstudied, (3) except for *S. subtruncata*, the population dynamics of other possible food items for the common scoter, e.g. the abundant bivalves *Abra alba* and *Tellina fabula*, is still unknown, (4) little information on the biological interactions within the communities (e.g. competition, predation, etc.) is available, etc. Furthermore, no data on other components of the Coastal Banks ecosystem, e.g. meiobenthos, hyperbenthos, epibenthos, phyto- and zooplankton, and pelagic fish, are available yet. Still, by means of this study of the macrobenthos of the Coastal Banks and adjacent sandy beaches, some first remarks on the conservation of the Belgian shallow marine habitat can be formulated.

THE NEED FOR MARINE PROTECTED AREAS

Next to several activities possibly disturbing the seabirds, fish and/or marine mammals in the area of the western Coastal Banks, e.g. nautical sports, angling, target practicing from the military base of Lombardsijde, and the presence of mazes, the only threat for the natural development of the macrobenthos at this moment is the intensive fishery for sole (*Solea solea*) in the Potje in Spring (MUMM, personal communication). Although there is hardly any conclusive scientific evidence that beamtrawl fishing is altering the benthic ecology, there are many signals that fisheries have something to do with observed changes and impoverishments within the benthos (Lindeboom, 1995). However, even though an intensive beamtrawl fishery exists, a rich macrobenthic fauna (*Lanice conchilega* community) can still be found in the Potje. One could thus conclude that fishery for sole in the Potje has no negative impact on the macrobenthos. Yet, even though the macrobenthos of the Potje is rich, no information on the macrobenthos of the Potje, if beamtrawl fishing would be absent, is available, because there exist no reference area (= comparable habitat without fishery) to compare with. In order to study the impact of anthropogenic influences, e.g. fishery, on the benthos there is a strong need for such reference areas. The establishment of a marine protected area, where several anthropogenic activities may be limited or prohibited, may thus provide the practical means to study the effects of these activities (Lindeboom, 1995). Furthermore, by means of these protected areas, the conservation and rehabilitation of the natural diversity of the (part of) the ecologically valuable western Coastal Banks would be possible. Yet, it is clear that in the marine environment, where horizontal connections with other habitats are extremely important (e.g. planktonic larvae of the macrobenthos, migrating fishes, seabirds and marine mammals, etc.), a single marine protected area has only limited reasons for existence. For instance, if *Spisula subtruncata* would be absent in the environment of the Potje, the future existence of the bivalve in the Potje is doubtful because of the lack of recruitment. Next to the need for the establishment of marine protected areas, there is thus a strong need for integrated coastal area management where one of the primary goals is the sustainable use of the coastal biodiversity, not only in the marine protected areas, but also outside these areas (Gray, 1997).

REVALUATION OF THE INTERTIDAL ZONE

So far, sandy beaches are undervalued by the public opinion: many still consider sandy beaches as 'biological deserts', in order to biologically justify the malification of beaches for coastal protection works and tourism developments. Knowledge of the ecology of sandy beaches is thus certainly indispensable. In order to revaluate the ecological importance of the Belgian beaches, the macrobenthos of the intertidal zone, as part of the shallow marine habitat, was investigated (Chapters 5 and 6).

THE MACROBENTHOS OF THE INTERTIDAL ZONE

Because the subtidal and intertidal zone are not strictly separated from each other and, in fact, the intertidal zone is a gradual transition from the marine to the terrestrial environment, both zones are ecologically closely related. A number of species of the subtidal communities (e.g. the polychaetes *Nephtys cirrosa*, *Spio filicornis*, and *Capitella capitata*) can thus be found in the intertidal zone. These typical subtidal species occur in sub-optimal conditions, as they are not constantly submersed. Consequently, they are generally found in lower densities than in the subtidal zone. From the low water upwards the beach, their densities decrease and none of the subtidal species is found above the mean tidal level. Above the mean tidal level, a typical high intertidal species association, combining species adapted to less than 2 x 6 hours of submersion per day, is encountered. Generally, this species association is composed of a combination of a low number of macrobenthic species, typically found in the high intertidal zone (e.g. the isopod *Eurydice pulchra*; the amphipods, *Bathyporeia pilosa* and *B. sarsi*; the polychaetes *Scolelepis squamata* and *Psammodrilus balanoglossoides*). Contrary to the low number of species, the macrobenthic density of the high intertidal zone is much higher than at most other sites of the subtidal or intertidal western Coastal Banks. This is certainly true for the ultra-dissipative beaches, characterized by a gentle slope and situated mainly along the western Belgian coast. Along the eastern Belgian coast, a number of low tide bar/rip (LTBR) beaches, characterized by a gently sloping lower beach and a steeply sloping upper beach, occur. Because of the hydrodynamically harsh conditions of the upper part of LTBR beaches, where the waves are breaking directly on the beach face, only few species are found in low densities. Still, some of these species are uniquely found in these coarse sediments (e.g. the polychaetes *Ophelia rathkei* and *Hesionides arenaria*).

ECOLOGICAL IMPORTANCE OF THE INTERTIDAL MACROBENTHOS

The macrobenthic fauna of Belgian sandy beaches is an important food resource for many shorebirds and fishes (Witherby *et al.*, 1947; Thijssen *et al.*, 1974), which underscores the ecological importance of Belgian beaches. Indeed, at low tide, a rich avifauna consisting of waders, such as sanderling (*Calidris alba*), is feeding on Belgian sandy beaches (Devos *et al.*, 1996), whereas at high tide, a rich marine fauna, e.g. smaller fish as juvenile plaice (*Pleuronectes platessa*) feeds in the intertidal zone (Beyst, unpublished information).

Because of its importance, the rich macrobenthic fauna of sandy beaches has to be acknowledged. It has already been taken into account in the development of the management plan for the Flemish nature reserve, Baai van Heist (Cosijns *et al.*, 1999). Furthermore, as beach suppletions are commonly performed in Belgium, it is advized to take into account the ecological value of the intertidal zone. Several measures can be taken in order to diminish the damage of beach suppletions to the ecosystem. One of these measures is the selection of the sediment's grain size distribution. So far, the sediments to be used for beach suppletions were selected only on the base of the sustainability of the works and the economical aspects. As the sedimentology is one of the major factors determining the distribution of the macrobenthos, the sediments to be used for the beach suppletions should be similar to the original intertidal sediments. If so, a recovery of the original macrobenthos of the intertidal zone may be expected.

MONITORING OF THE BENTHIC HABITAT

Considering the geomorphology of the Belgian shallow marine habitat, several entities were distinguished: the upper beach, the lower beach, the foreshore, the gullies and troughs, and the sandbanks (Figure 2). Within each of these major habitats a different community or combination of communities can be encountered. In the intertidal zone, the spatial distribution of the macrobenthos is determined mainly by the height on the beach and the morphodynamical state of the beach (Chapters 5 and 6), whereas the sedimentology and the depth are the main determining factors in the subtidal zone (Chapters 1 and 3).

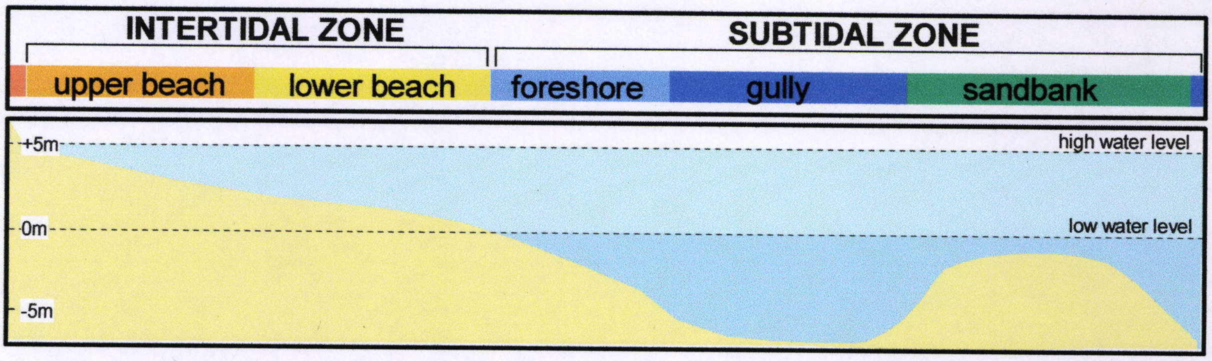

Figure 2. Schematical presentation of the Belgian shallow water habitat.

Information on the environmental needs of the macrobenthic communities can be used to predict the spatial distribution of different macrobenthic communities, only knowing the physical characteristics of the region and is an extremely powerful tool in coastal zone management (Chapter 3).

However, the macrobenthic communities are known to show a large variability, both within and between years (Chapters 2 and 5). The large temporal variability of the macrobenthos thus creates a problem when setting up a management plan for the western Coastal Banks. One of the questions is to what level scientists can rely on a single sampling campaign when trying to identify macrobenthos-rich areas or communities, knowing that benthic communities are characterized by variability (dynamics), rather than by stability. The dynamics and stability within the spatial distribution of the macrobenthic communities is one part of this possible variability. Yet, as 84 % of the stations, sampled on the western Coastal Banks, harboured the same macrobenthic community in 1997 as in 1994 (Chapter 3), the stability within the spatial distribution of the three western Coastal Bank communities was demonstrated. This was explained by the relative stability of the sedimentology on the western Coastal Banks and the fact that as long as the sedimentology does not change no shifts between communities are expected (Govaere *et al*., 1980). So far, this spatial stability is not evidenced for the intertidal species associations, but the relative consistency between the distribution of the abundant intertidal species point towards a spatial stability within the intertidal zone.

A second part of the dynamics and stability of macrobenthic communities considers the changes within the species composition and specific densities of the different communities. In 1996 and 1997, this temporal variability within the *L. conchilega* community was evidenced by a general decreasing macrobenthic diversity and specific densities, caused by an overwhelming recruitment of *Spisula subtruncata* and an increasing mud content in the sediment. The recruitment of *S. subtruncata* probably triggered a chain reaction of altering biological interactions and subsequently caused shifts in the community's species composition and density. The increase of the fine material in the sediment negatively affected the macrobenthos of the *L. conchilega* community, which usually occurrs in a fine sandy sediment with low mud contents (Chapter 2).

It is thus extremely important to be aware of the natural variability within a macrobenthic community in order to evaluate its ecological importance. By means of long-term investigations of the macrobenthos, the temporal variation of the species composition and density of the different communities can be defined. The 'potentials' of a community can be defined as all different combinations of the species composition and densities within the habitat of the community, which is probably determined by differences in recruitment and subsequent biological interactions, as demonstrated by Meire *et al.*, 1994. The ecological importance of the communities or habitats can know be evaluated by means of the knowledge of their respective 'potentials'.

The combination of the knowledge of the environmental needs and the 'potentials' of the different communities allows scientists to monitor the benthic habitat. Instead of putting a lot of effort, time, and money in working out time-series of lots of macrobenthic samples, randomly spread over the area under consideration, monitoring of the macrobenthos should concentrate on the spatial distribution of the macrobenthic 'potentials'. This can be done by the identification of (1) the spatial distribution of the macrobenthic communities actually present, (2) the communities' environmental needs, and, finally, (3) the communities 'potentials' by means of long-term investigations of the macrobenthos of some selected stations within each community. Following this strategy, a fast evaluation of measures, taken in the frame of the coastal zone management plan, is possible.

FUTURE THREATS FOR THE MACROBENTHOS OF THE WESTERN COASTAL BANKS

COASTAL DEFENCE WORKS

Correction of the course of coastal defence works

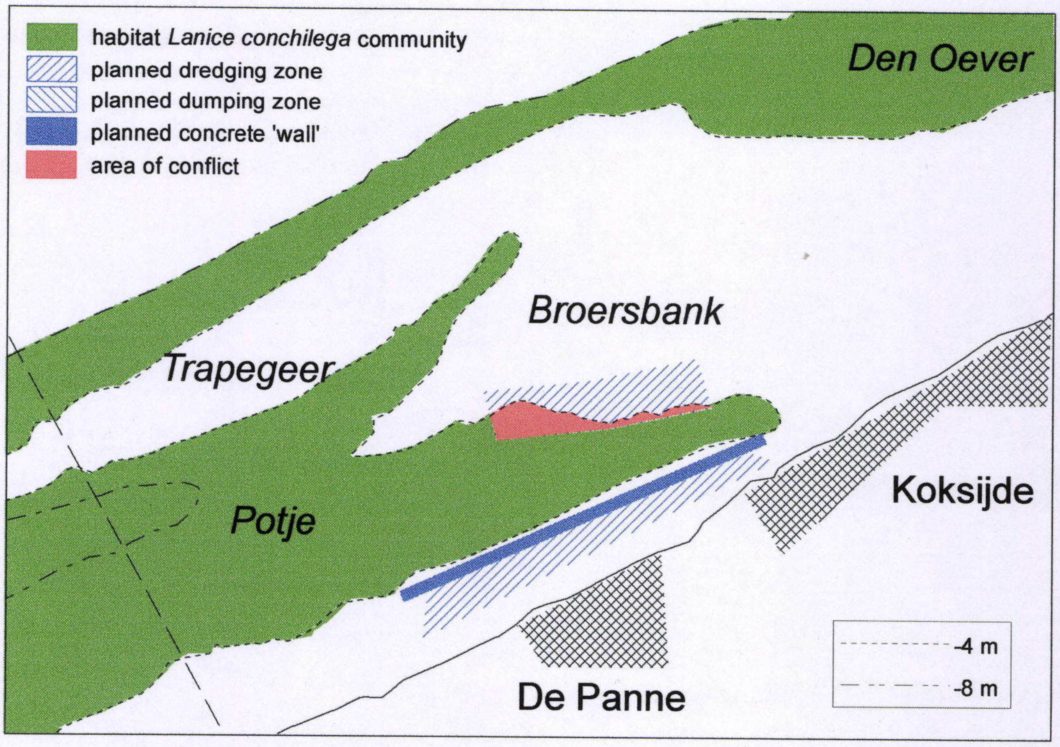

Figure 3. Schematical presentation of the planned coastal defence works in the area of the western Coastal Banks.

The information about the spatial distribution and temporal variation of the macrobenthos of the western Coastal Banks already allows to correct the course of the planned coastal defence works. By means of several meetings, with AMINAL, the Coastal Waterways Division, HAECON, the Management Unit of the North Sea Mathematical Models, and the Marine Biology Section of the University of Gent, the different alternatives for an effective coastal defence have been discussed. Although it has to be stressed that all alternatives will cause a disturbance of the ecosystem, the proposal minimizing the ecological stress was selected. This proposal includes a dredging zone along the southern flank of the Broersbank and a dumping zone on the foreshore nearby the southern tidal branch of the Potje (Figure 3). Furthermore, in order to stabilize the dumped sediment a subtidal, concrete 'wall' would be constructed. This method would not only decrease the direct beach erosion, by means of a consolidation of the foreshore, but would also remove the cause of the erosion, by redirecting the flood dominated currents towards the open sea. Because of the rich macrobenthic fauna in the Potje (*L. conchilega* community, with high densities of *Spisula subtruncata*) and the rare, shallow water habitat of the Broersbank (Chapters 1 and 3), the extension of the dredging zone was restricted in western and eastern direction, respectively. The subsequent loss in sediment volume would be compensated by an extension of the dredging zone in northern direction. The restriction of the dredging zone would result in a minimalization of the direct negative effects on the macrobenthos and geomorphology of the planned works: the area of conflict is relatively small.

Negative impacts of coastal defence works on the macrobenthos

Although the *L. conchilega* community would be safeguarded against major negative influences, the macrobenthos of other communities would be directly damaged by the dredging and dumping activities. As each community should be regarded as an unique piece of the ecosystem of the Coastal Banks, a deterioration of the ecosystem might be expected. In order to allow a quick recovery of the macrobenthos in the disturbed area, the coastal defences works should take place preferably before the period of major recruitment (= before April for the *L. conchilega* community) (Chapter 2). However, a successful recruitment is not to be expected each year for all species. In contrast to 1995, no successful recruitments were observed in 1996, nor 1997 (Chapter 2). An immediate recovery of the macrobenthos within the disturbed area can thus not be confirmed with certainty.

Indirect impacts of the planned coastal defence works on the benthic habitat are much more difficult to predict. One of these indirect effects is the increased concentration of suspended (fine) material in the water during the works. In areas where settlement of fine material may be expected because of a lower speed of the currents, e.g. Potje, the suspended, fine material may settle down and cover the original sediment. The impact of this increasing concentration of the fine sediment fraction on the macrobenthic fauna of the Potje depends on the quantity and the rates of sedimentation. A fast sedimentation of large quantities of fine materials may have a lethal impact on the benthic fauna, as demonstrated by the drastic deterioration of the *L. conchilega* community after an increasing mud fraction in December '95 – March '96 (Chapters 2 and 4). Secondly, a redirection of the tidal currents within the southern branch of the Potje will undoubtedly alter the hydrodynamical regime in the area. These changing currents may cause sedimentological and geomorphological alterations within the area of the western Coastal Banks. As demonstrated by the very specific habitat needs of the macrobenthos (Chapters 1 and 3), changes within the sedimentology and geomorphology within the area may lead to an altering spatial distribution of the macrobenthic communities.

It is clear that the accepted alternative for the coastal defence works includes a compromise between the socio-economical and ecological interests. The proposal excludes a major part of the direct negative effects. The indirect impact of the coastal defence works on the macrobenthos, which are difficult to assess, could not be excluded. Even though all measures, to minimize the stress on the benthic habitat on a spatial and temporal scale, are taken into account when performing the coastal defence works, damage to an ecosystem of international importance, such as the western Coastal Banks, will certainly be inflicted. The necessity of the proposed coastal defence works must thus certainly been thought over.

SPISULA-FISHERIES ON THE WESTERN COASTAL BANKS

Because a fishable standing stock of *Spisula subtruncata*, mainly found in the *Lanice conchilega* community, is present in the Belgian shallow marine habitat (Vanhee *et al.*, 1998), the feasability and sustainability of *Spisula*-fisheries creates a new problem for the protection of the western Coastal Banks. The conflicting situation, between the ecological and socio-economical interests in *S. subtruncata*, stresses the need for knowledge on the spatial distribution, population dynamics and production of the bivalve. The fishery of *S. subtruncata* would evidently lead to a decrease in the standing stock of the bivalve on the western Coastal banks and, consequently, the food resources for the common scoter may not be fulfilling the seaduck's demands anymore, possibly leading to the disappearance of the common scoter in the area (Leopold, 1993; Leopold *et al.*, 1995). After depletion of the *Spisula*-stocks, the natural recovery may take several years, as demonstrated by the highly variable recruitment of *S. subtruncata* (Chapter 4). Furthermore, as *S. subtruncata* mainly occurs in the *L. conchilega* community, shellfisheries would lead to an impoverishment of the macrobenthos in this ecologically important community (Chapter 4). Shellfisheries in the area of the western Coastal Banks will be incompatible with the aims of a marine protected area.

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