
CHAPTER 3

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

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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 through 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).

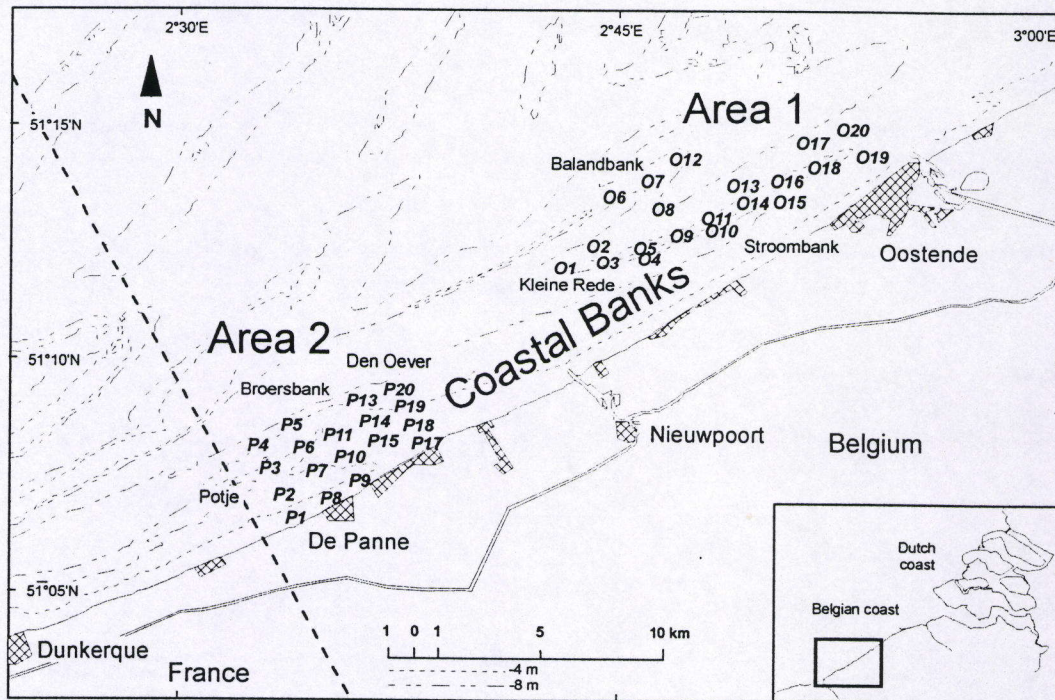


Figure 1. Geographical view on the western Coastal Banks, divided in area 1 and area 2; with indication of the 39 sampling sites.

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 ($-2.73\% \pm \text{SE: } 1.58\%$) and increase per station ($5.12\% \pm \text{SE: } 0.88\%$) 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.

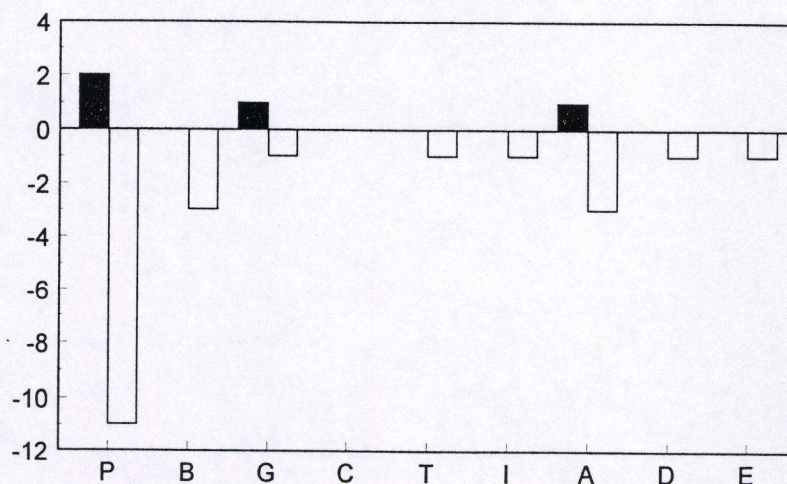


Figure 2. The gain and loss of the number of species per taxon between 1994 and 1997. P, Polychaeta; B, Bivalvia; G, Gastropoda; C, Cumacea; T, Tanaidacea; I, Isopoda; A, Amphipoda; D, Decapoda; E, Echinodermata.

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.

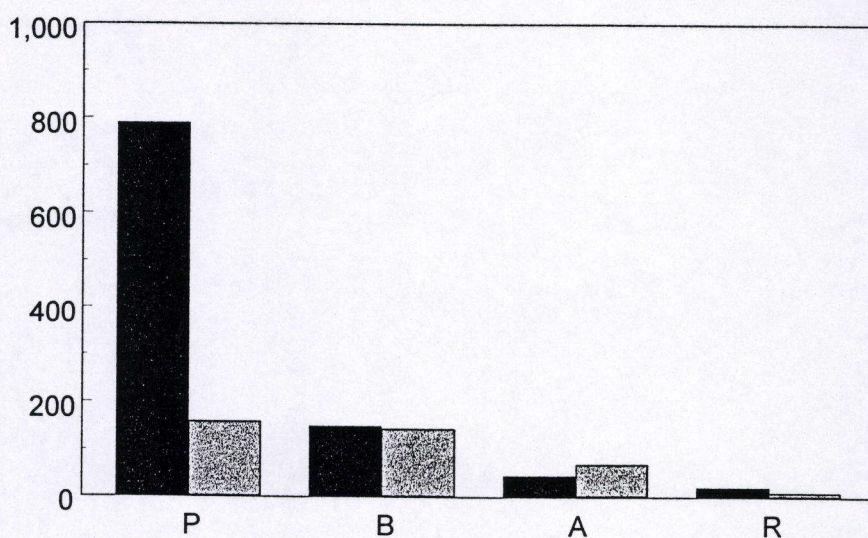


Figure 3. The differences of the densities of the three most abundant taxa and other taxa between 1994 and 1997. P, Polychaeta; B, Bivalvia; A, Amphipoda; R, rest.

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 uniformly 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 (N₀), the Hill-numbers N₁ 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
<i>Spisula subtruncata</i>	549	<i>Bathyporeia</i> sp.	99	<i>Ophelia limacina</i>	42
<i>Lanice conchilega</i>	139	<i>Nephtys cirrosa</i>	40	<i>Spio filicornis</i>	26
<i>Nephtys hombergii</i>	73	<i>Magelona papillicornis</i>	32	<i>Scoloplos armiger</i>	16
Cirratulidae	33	<i>Nephtys hombergii</i>	14	<i>Hesionura augeneri</i>	13
<i>Abra alba</i>	33	<i>Scoloplos armiger</i>	9	<i>Glycera capitata</i>	13
<i>Diastylis bradyi</i>	23	<i>Urothoe poseidonis</i>	7	<i>Spisula subtruncata</i>	3
<i>Mysella bidentata</i>	23	<i>Urothoe brevicornis</i>	7	<i>Bathyporeia</i> sp.	3
Juvenile <i>Nephtys</i>	16	<i>Spisula subtruncata</i>	5		
<i>Spiophanes bombyx</i>	12	Juvenile <i>Nephtys</i>	4		
<i>Eumida sanguinea</i>	10	<i>Ensis</i> 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 comprised 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).

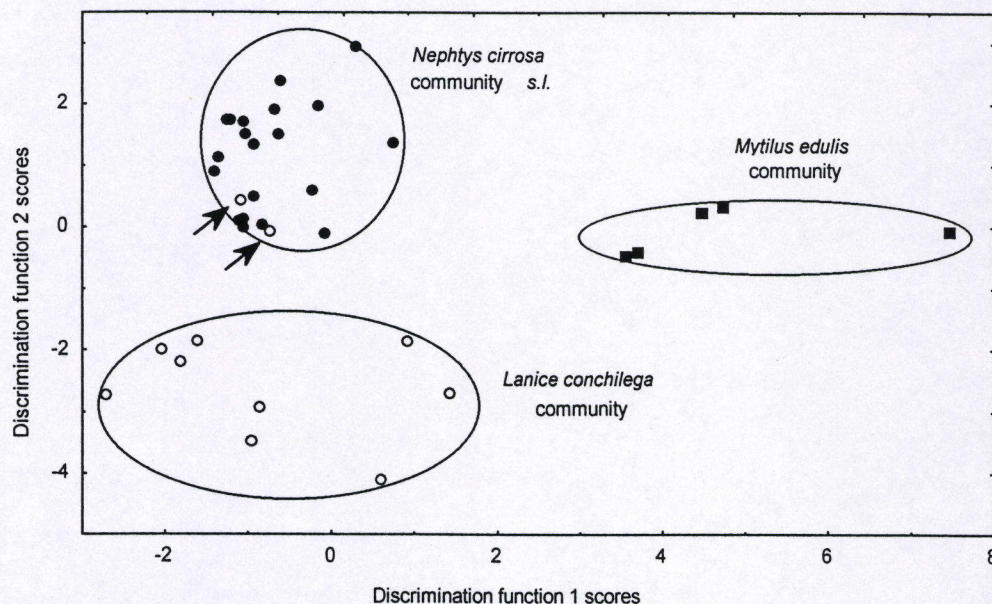


Figure 4. Graphical presentation of the differences between the three communities by means of their canonical scores of the two discrimination functions. Each point represents a station, sampled in October 1994, designated to one of the three communities by Degraer *et al.* (in press a). The two arrows 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 $S_i = w_{iCS} \cdot CS + w_{iSI} \cdot SI + w_{iME} \cdot ME + w_{iCL} \cdot CL + w_{iFS} \cdot FS + w_{iDE} \cdot DE + c_i$ 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.

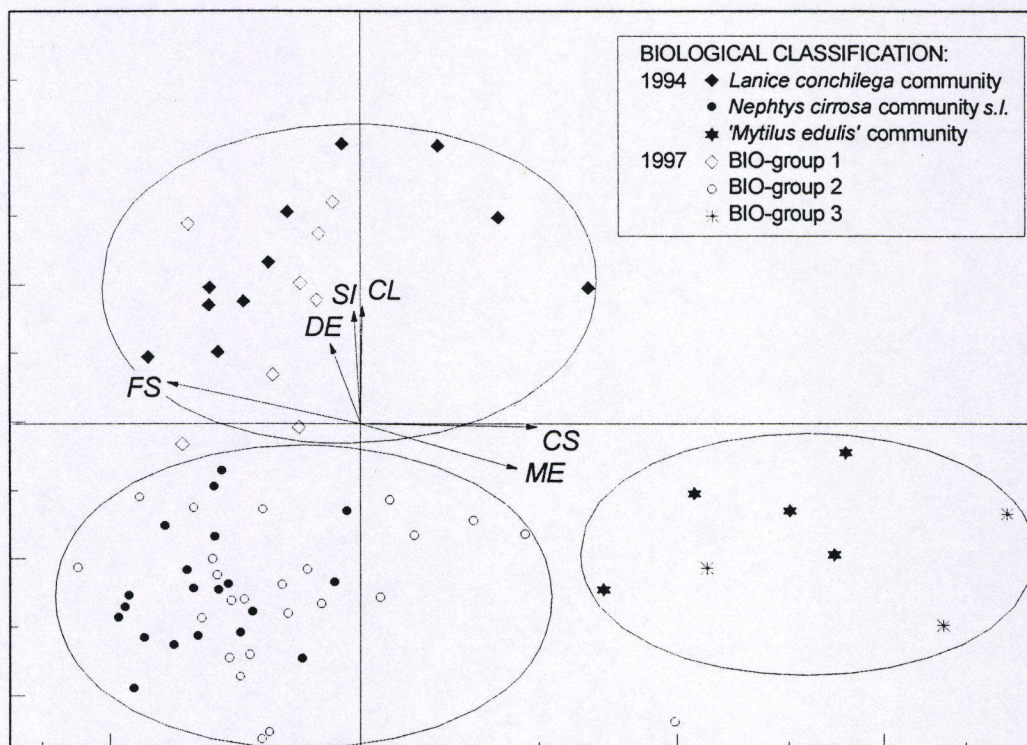


Figure 5. Graphical presentation of the first two axes of the Canonical Correspondence Analysis on the classified stations of 1994 and 1997, together with their typical environmental variables. Physical variables: DE, depth; ME, median grain size; CL, clay content; SI, silt content; FS, fine sand content;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

	<i>Lanice conchilega</i> community		<i>Nephtys cirrosa</i> community <i>s.l.</i>		' <i>Mytilus edulis</i> ' 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 %).

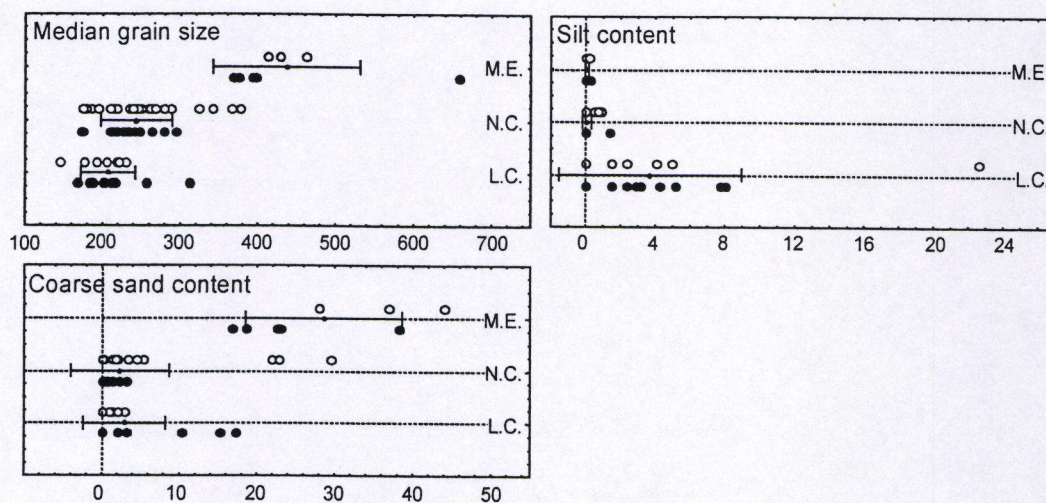


Figure 6. The distribution of the three macrobenthic communities (M.E., '*Mytilus edulis*' community; N.C., *Nephtys cirrosa* community *s.l.*; L.C., *Lanice conchilega* community) in 1994 (●) and 1997 (○) over the three most differentiating environmental variables: the median grain size (μm) and the 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.