



**Long term trends in
the macrobenthos of the
Belgian Continental Shelf**

**SUSTAINABLE
MANAGEMENT OF
THE NORTH SEA**



LONG-TERM TRENDS OF THE MACROBENTHOS OF THE BELGIAN CONTINENTAL SHELF

MACROBEL

Programme
“Sustainable management of the North Sea” – SPSD I
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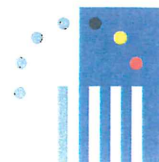
Final report

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Introductory note

This report presents the final results of the MACROBEL project, which aims to deliver a substantial contribution to the knowledge of the long-term variability in the biodiversity and density patterns of the macrobenthos of the Belgian Continental Shelf (further abbreviated as BCS) and the relationship with anthropogenic activities.

The scientific work mainly consisted of compiling biological data about the macrobenthos gathered by different institutes during the periods 1976-1986 and 1994-2001 scattered over the BCS for the first part of this study, and during the period 1979-1997 at 5 specific stations for the second part. The project was a collaborative venture between three partners: Marine Biology Section of Ghent University (SMB), Sea Fisheries Department (DvZ) and Flanders marine Institute (VLIZ). SMB was coordinator; both SMB and DvZ were responsible for delivering the data and the quality-control of the data; VLIZ developed the MACROBEL web-interface, based on an existing relational Access database MACRODAT. The MACROBEL database is linked to other databases hosted at VLIZ and is coupled to a Geographical Information System (GIS), wherefrom spatial distribution maps may be generated for the macrobenthos species and communities on the BCS.

We wish to acknowledge all people who assisted in the three decennia of sampling and the compilation of the macrobenthic data. Also, we would like to thank the Belgian Federal Science Policy Office who supported MACROBEL and for their trust in the project.

The MACROBEL partners

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Abstract

Within the MACROBEL project a large dataset, based on old and newly processed data from 1475 samples, has been compiled concerning the macrobenthos of the Belgian Continental Shelf (BCS). The study is divided in two parts and synthesizes the spatial and long-term variability in biodiversity and density of the macrobenthic communities of this small North Sea area. Besides this report, the project will be disseminated by means of an interactive website <http://www.vliz.be/vmdcdata/MACROBEL>. This long-term series will be updated on a regularly basis in the future. As an extension of this study, the distribution of ca. 50 macrobenthos species on the BCS will be presented in an atlas '*Beknopte Atlas van de Mariene Bodemdieren van België*'.

By means of multivariate statistical techniques, four Type I and seven transitional Type II species assemblages were identified for the BCS. The *Abra alba*-*Mysella bidentata* and *Macoma balthica* assemblages are typically found in fine sand sediments with medium to high mud contents near the coast, with a high diversity and sometimes high densities. The *Nephtys cirrosa* assemblage is distributed nearly all over the BCS in well-sorted mobile sands with low diversity and density. The *Ophelia limacina*-*Glycera capitata* assemblage is typically found offshore in medium to coarse sand sediments with low mud content. Similar macrobenthic communities were found in both periods (1976-'86 and 1994-2001), although higher average values for both species composition and density were recorded for the latter period. Changes in sediment type, drifting and invasion of exotic species, and habitat disturbance due to pollution can explain the loss and gain of 5 species on the BCS. However, most dissimilarities were mainly due to differences in sampling methodology rather than to long-term biological variations. Five main variables introduced bias in the spatial and long-term analysis of the macrobenthos data: (1) location of the sampling stations and sampling effort per area; (2) sampling frequency or time interval; (3) sieve mesh size; (4) size of the Van Veen grab; and (5) fixation of the animals prior of after sieving. Conversion factors calculated by means of intercomparison and experimental studies might improve the analysis of non-uniform long-term series.

Secondly, hardly any long-term patterns in terms of diversity, density or biomass were found for most macrobenthos species at five subtidal stations on the BCS. The densities were rather low during most of the sampled period (1979-'97) with some higher peaks in certain years or seasons, and the biomass peaks not necessarily coinciding with the peaks in density. The success of recruitment and production, which leads to year-to-year variation in macrobenthic communities, is controlled by both physical and biological conditions. Changes in temperature, sediment composition, wind and currents can affect the temporal distribution and abundance of the larval, juvenile and/or adult macrobenthic life stages, seasonally as well as on a long-term scale. Annually recruiting species generally increase in numbers and biomass in summer and autumn, followed by considerable winter mortalities. Large fluctuations in species density and biomass on a longer time-scale can have an effect on biological interactions such as predation and competition for food and space. An extensive discussion on the impact of anthropogenic activities is beyond the scope of this study. Although the monitoring sampling strategy, which is based on two campaigns per year organized independently of the dumping frequency, may be inadequate for sound decision-making, it is concluded that the dumping of dredged material has no clear long-term effect on the macrobenthos communities of the BCS.

1 Introduction

The Belgian maritime zones of the North Sea cover a surface area of 3600 km², approximately 0.5 % of the total North Sea. This relatively small area is characterized by the presence of several elongated sandbank formations, unique for the whole North Sea, which provide a high variability in geomorphology, hydrodynamics and sediment (De Moor, 1986a). This leads to a high natural diversity in marine habitats and the associated benthic fauna (Degraer, 1999). Also, important socio-economic activities (e.g. shipping, fisheries, sand and gravel extraction, dredging and dumping operations) take place on the BCS. The combination of the high ecological and high socio-economic values of the BCS leads in many ways to conflict situations.

Macrobenthic organisms are useful to investigate the ecological effects of both natural and anthropogenic influences on marine ecosystems, because of their relative immobility and their direct link with the adjacent environment (Holtmann et al., 1996; Pearson, 1997). Seasonal (Beukema, 1974; Bonsdorf & Österman, 1985; Arntz & Rumohr, 1986; Dörjes et al., 1986; Ibanez & Dauvin, 1988; Moll, 1998) and year-to-year variability (Gray et al., 1980; Arntz & Rumohr, 1986; Dörjes et al., 1986; Essink & Beukema, 1986; Austen et al., 1991; Beukema et al., 1993; Meire et al., 1994; Turner et al., 1995) are important natural parameters that influence the presence of the macrobenthic fauna of shallow and temperate coastal waters. But the macrobenthic diversity is also influenced by anthropogenic activities. The direct or indirect impact of sand exploitation and dumping of dredge materials (extraction/covering up of habitats; changes in sediment composition) can have repercussions on the present macrobenthos fauna.

For a sustainable management of marine resources (cf. OSPAR convention - North Sea Task Force, 1993) the following information is needed: (1) the geographic distribution of the marine fauna, (2) the structure of the communities, (3) their relation with the local physical and chemical environment, (4) the natural ecological variability and (5) the nature, magnitude and the effect of the anthropogenic influences on the ecosystem. Therefore, long-term data series are needed. This study tries to compile most available macrobenthos data from the BCS dating back from the late seventies.

The general aim of the MACROBEL project is to deliver a substantial contribution to the knowledge of the long-term variability in biodiversity and density patterns of the macrobenthos of the Belgian Continental Shelf (BCS) and its relation to anthropogenic activities.

More specifically, an interactive web-interface based on the unique database MACROBEL will be created, where spatial and temporal data of the macrobenthos from the BCS are combined with a description, ecology and recent taxonomy of most species. Also, a distribution atlas of 50 macrobenthos species on the BCS for the periods 1976-1986 and 1994-2001 will be made. The basis for the website and the atlas are given in the first part of this study. Secondly, the causal relationships between a selection of anthropogenic activities and the macrobenthos of the BCS will be evaluated, with an emphasis on the possible effects of the dumping of dredged material on the macrobenthic community. This will be based on data from 5 selected stations sampled between 1979 and 1997.

2 Material & Methods

2.1 Study area

The study area covers the Belgian part in the Southern Bight of the North Sea (3600 km²). This is divided into two zones: (1) the Belgian territorial zone extending 12 nautical miles from the coastline (low-water line along the coast), and (2) the Belgian Exclusive Economic zone (= Belgian Continental Shelf or BCS *s.s.*) extending about 47 nautical miles from the coastline and adjacent to the territorial waters (Maes et al., 2000). However for the purpose of this study the BCS is considered as the whole Belgian part of the North Sea, including both maritime zones.

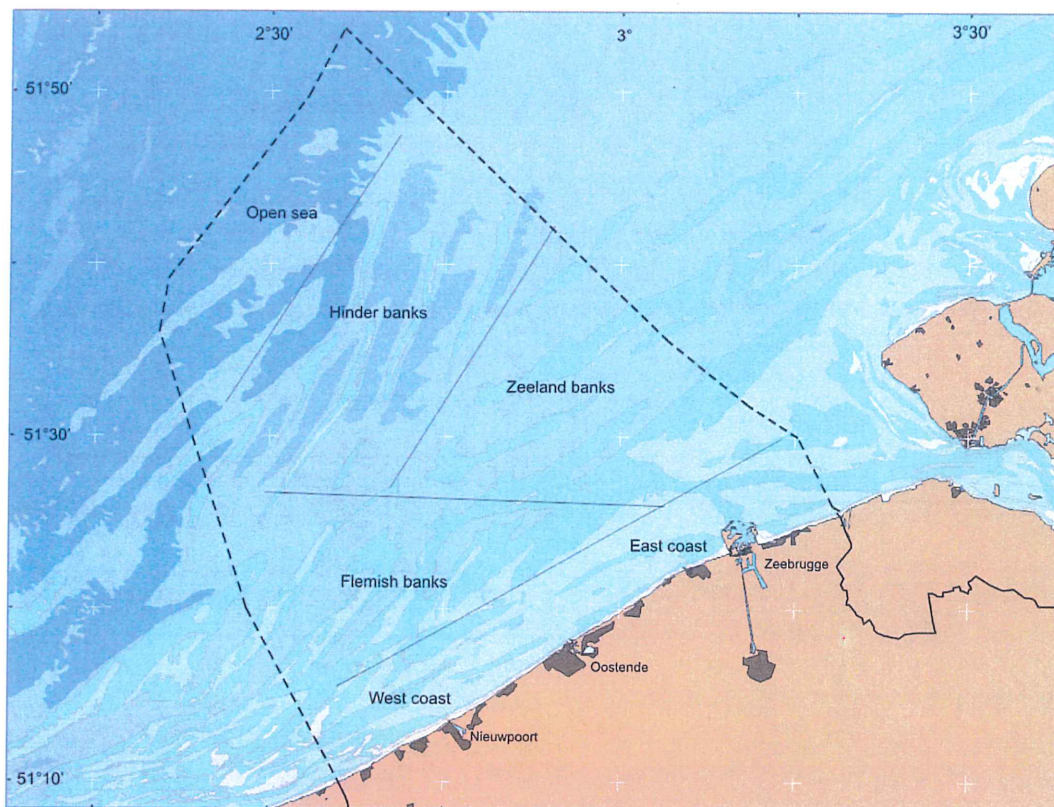


Figure 1. Location of the sand bank formations on the Belgian Continental Shelf (BCS, dotted line).

The BCS is characterized by several sandbank formations (Figure 1): (1) Coastal banks, parallel to the coastline, (2) Flemish Banks, about 10-30 km offshore the western Belgian coast, (3) Zeeland Banks, some 15-30 km offshore the eastern Belgian coast, and (4) Hinderbanks, about 35-60 km offshore (Degraer et al., 1999). The average depth of the BCS is -20 metres.

2.2 Data origin

2.2.1 Spatial and long-term variation

The MACROBEL project is meant as a compilation study of the available macrobenthos data from the Belgian Continental Shelf. For this study macrobenthos is considered as all organisms living in the sea-bottom which are retained on a sieve with a mesh size of 1 mm.

Table 1. Summary of literature wherefrom macrobenthos data of the BCS were retrieved

Author/year	Title	Type
Vanosmael, C. (1977)	Studie van het macrobenthos ter hoogte van de monding van de Westerschelde en de Belgische kust	Licentiate thesis
Van Steen, E. (1978)	Het macrobenthos van een overwinteringsgebied van <i>Melanitta nigra</i> (Linné, 1758) voor de Belgische kust	Licentiate thesis
Rappé, G. (1978)	Studie van het macrobenthos van de zandbanken Kwinte Bank en Buiten Ratel	Licentiate thesis
Vanosmael et al. (1979)	De invloed van zandwinning op de bodemfauna voor de Belgische kust	Report
Kerckhof, F. (1980)	Studie van het macrobenthos ter hoogte van de Belgische kust	Licentiate thesis
Meheus, L. (1981)	Vergelijkende studie van het makrobenthos van enkele zandbanken in de zuidelijke bocht van de Noordzee	Licentiate thesis
De Rycke, R. (1982)	Macrofauna en interstitiële anneliden van vijf zandbanken in de Belgische kustwateren	Licentiate thesis
Waeterschoot, H. (1984)	Macrobenthos van de Kwintebank (1979-1980). Studie in het kader van de zand- en grindexploitatie voor de Belgische kust	Licentiate thesis
Brendonck, L. (1985)	Studie van het macrobenthos van een ondiep station in de Noordzee	Licentiate thesis
Coenjaerts, J. (1997)	Het macrobenthos van de Vlaamse banken en de omliggende zandbankecosystemen	Licentiate thesis
Phillips, F. (1998)	Het macrobenthos van de Vlaamse banken: temporele variabiliteit.	Licentiate thesis
Degraer, S. (1999)	Macrobenthos of shallow marine habitats (Belgian Coast) and its use in coastal zone management	PhD thesis
Van Hoey, G. (2000)	Benthisch-pelagische koppeling: structurele en functionele respons van het macrobenthos van twee stations in de Noordzee	Licentiate thesis
Erdey, M. (2000)	Macrobenthic trophic structure and species interaction within a future marine protected area (Belgian Coastal Banks)	Licentiate thesis
Deneudt, K. (2000)	Habitatspreferenties van het macrobenthos op de Westelijke kustbanken	Licentiate thesis
Taverniers, K. (2000)	Het macrobenthos van subtidale zandbanken op het Belgische Continentaal Plat	Licentiate thesis
Gheerardyn, H. (2002)	Aanzet tot het opstellen van de macrobenthische waarderingskaart van het Belgisch Continentaal Plat	Licentiate thesis
Glorie, S. (2002)	Macrobenthos van Hinderbanken: Gemeenschapsanalyse en gevoeligheidsstudie in geval van scheepvaartaccidenten met zware olie-ontreiniging	Licentiate thesis

During the periods 1977-1986 and 1994-2001 both SMB and DvZ collected thousands of macrobenthos samples, covering the whole BCS. Macrobenthos data for the period 1977-1986 have been partially processed and analysed (Govaere et al., 1980; Vanosmael et al., 1982; Willems et al., 1982). Macrobenthos data for the period 1994-2000 have been used in several recent projects (Degraer et al., 1999; Van Hoey et al., 2004; OSTC/DWTC project 'Structurele en functionele diversiteit van Noordzee ecosystemen', contract number MN/02/40). Actually, the data set (period 1994-2000) used by Van Hoey et al. (2004) was re-analysed with additional subtidal macrobenthos data from the periods 1976-'86 and 2001. As such, the subtidal macrobenthos samples/data that were available at SMB for the period 1977-2001 together with the accompanying meta-data and environmental data (water depth, median grain size and mud content) were compiled (Table 1). This information was then integrated in the existing database MACRODAT (a relational MS-Access database combining taxonomy, geography, biotic and abiotic data created by T. Deprez at SMB).

The compiled data so far mainly covered the western coast and some nearby sandbank complexes. However, several old samples from both the Marine Biology Section of Ghent University (SMB) and the Sea Fisheries Department (DvZ) from other areas (e.g. east coast, open sea) were, although many times sampled, never analysed. A selection of 312 samples from the period 1976-'86 (104 stations, 3 replicates) gathered by SMB and DvZ were newly analysed and together with their environmental parameters also incorporated in the MACRODAT database. An overview of all sampling locations used in the present study is given in Figure 2. A combination of both old and newly analysed macrobenthos data may give an overall view of the spatial distribution of the macrobenthos for the periods 1977-1986 and 1994-2001.

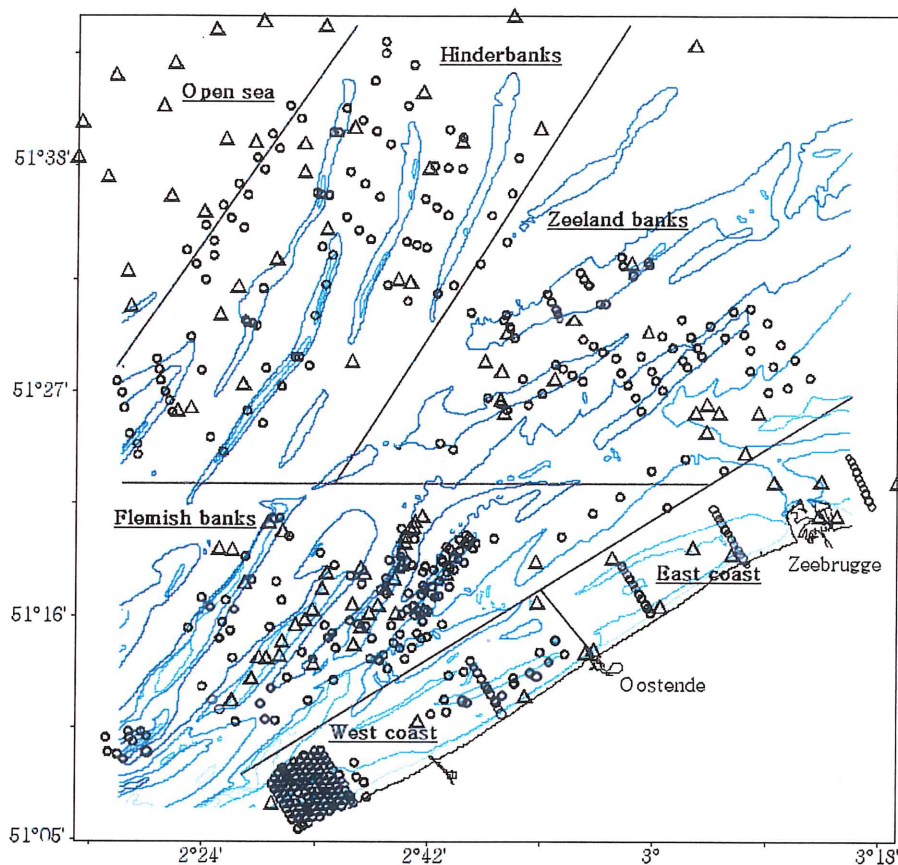


Figure 2. Spatial distribution of the sampling locations during '76-'86 (triangles) and '94-'01 (circles)

2.2.2 Detailed long-term variation

A more detailed analysis of the long-term distribution patterns in macrobenthos densities and biomasses is presented in the second part of this study. Although many data have been compiled and analysed by DVZ in the framework of several impact studies since 1979, the number of stations used for this detailed analysis has been limited to 5 (Figure 3, Table 2), which are related to the biological monitoring of four dumping sites in the coastal areas of the BCS. The data for the period 1979-'97 were retrieved from Wittoeck & Hillewaert (1999).

Data for station 120 have been separately analysed in a Master of Science thesis (Pelgrims, 2003). For the purpose of this study the data from both studies were compiled and re-analysed.

Besides information on the spatial and temporal distribution of the macrobenthos of the BCS, this project also provides information on the possible impact of different anthropogenic activities on the macrobenthos communities.

Table 2. Positions of the dumping sites on the BCS

Dumping site	Geographical position	Period of use
Oostende °	51°17.22' NB 02°56.73' OL	1954-until now
Zeebrugge Oost (1)	51°22.60' NB 03°15.57' OL	1980 - 1985
Zeebrugge Oost	51°22.50' NB 03°16.00' OL	1985 - until now
S1 (1)	51°26.00' NB 03°06.00' OL	1966 - 1970
S1 (2)	51°26.00' NB 03°05.00' OL	1970 - 1980
S1 (3)	51°26.00' NB 03°04.00' OL	1981 - 1984
S1	51°26.80' NB 03°03.00' OL	1984 - until now
S2	51°26.00' NB 03°08.50' OL	1984 - until now

° Comparable to the changed positions for other dumping sites, Loswal Oostende has shifted to a more westerly position since 1954.

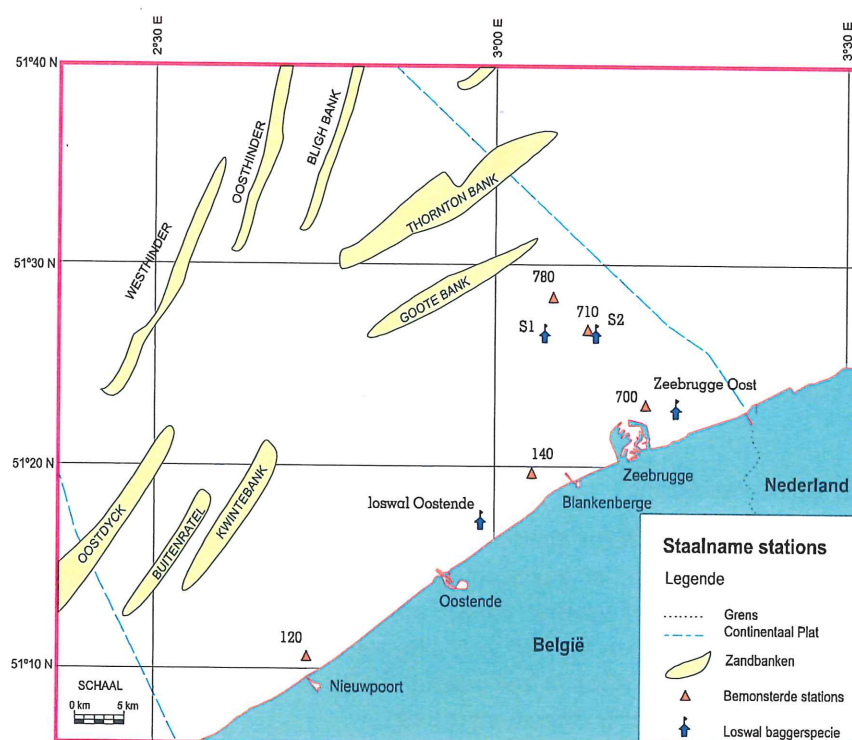


Figure 3. Location of the four dumping sites (S1, S2, Zeebrugge Oost and Oostende) and the positions of the sampling sites.

2.3 Data acquisition

During 1976-1983 different vessels from the Royal Navy (type MSI or MSC) were used for sampling: "Mechelen", "Spa" and "Kortrijk". After 1984 most offshore sampling was done on board the oceanographic research vessel A962 "Belgica" (BMM-MUMM). During the late nineties several ships were used for near shore sampling (Ter Streep and Oostende XI). From 2000 the coastal areas were sampled with R.V. "Zeeleeuw", a former pilot boat belonging to AWZ that was transformed into a multifunctional research vessel.

All macrobenthos and sediment samples were taken with a Van Veen Grab of approximately 50 kg (Figure 4). The grab has a sampling surface of 0.10 m², but for some studies another Van Veen was used with a sampling surface of 0.12 m² (see Table 4 and Table 5).

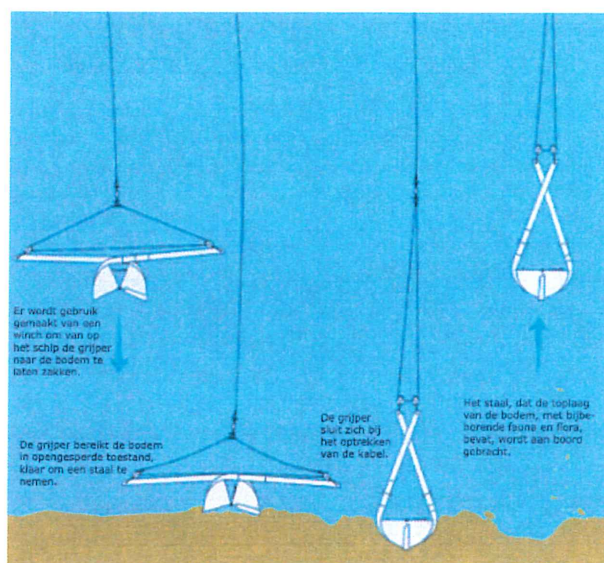


Figure 4. The functioning of a Van Veen grab

2.3.1 Sediment

For the sediment characterization a small sample is taken from the Van Veen grab using a plastic tube or core. Approximately 25 g of homogenized substrate was further analysed using either a number of sieves with different mesh sizes or by means of a Coulter LS 100 (see Table 4 and Table 5). During the period 1976-'86 a tower of at least 7 sieves was used to analyse the sand fraction according to Buchanan (1984). The wet-sieved fraction <63 µm was used as a measure for mud content.

From 1994 onwards the fraction >850 µm was first separated by means of a sieve and expressed as weighed percentage. Then a Coulter counter was used to measure the different sediment fractions in the range 2 - 850 µm as volume percentages following the Wentworth scale (Buchanan, 1984, Table 3).

Table 3. Sediment characterisation after Wentworth (in Buchanan 1984)

Fractions	Grain size (µm)
Clay	< 4
Silt	4 - 63
Very fine sand	63 - 125
Fine sand	125 - 250
Medium sand	250 - 500
Coarse sand	500 - 1000
Very coarse sand	1000 - 2000
Gravel	> 2000

2.3.2 Macrobenthos

For the separation of the biota from the sediment, the rest (or the entire content) of the Van Veen grab is emptied over a 1 mm sieve (although in some studies a sieve with a smaller mesh-size was used) and rinsed until only the coarse sediment and the macrobenthos organisms remain.

A Van Veen grab enables fast sampling, but also has some disadvantages:

- The Van Veen grab efficiently samples the endofauna living in the sediment, but fast moving organisms (e.g. some Brachyura, Mysida) can easily escape from the closing grab. Hence, the number of mobile species that is found in the samples may be underestimated.
- The maximum penetration depth in the sediment of the Van Veen grab is about 15 cm. This limited depth range biases the sampling of bigger and deeper burrowing macrobenthos species such as *Ensis* sp., *Lanice conchilega*, *Venerupis senegalensis*
- On harder substrates (e.g. very fine sands and gravel) the penetration is sometimes limited to the upper centimetres of the sediment. However, to ensure the catch efficiency the penetration depth of the grab should be at least 5 cm, which corresponds with a minimum sediment volume of 5 l as was assumed in former studies
- The separation of the biota from the sediment by means of sieving (with or without the use of a gutter) incorporates a potential loss of organisms through the sieve pores, which is also dependent on whether the fixation of the organisms in formalin has occurred before or after sieving.

Table 4. Sampling methodology period 1976-1986 (the samples in the study of Wittoeck (2001) were gathered during the period 1976-'86 but analysed in 2001).

Scientist	Van Veen (m ²)	Fixed before sieving	Replica	Sieve mesh size (µm)	Gutter	Sediment # sieves
Vanosmael, C. (1977)	0.1	Yes	3	870		19
Van Steen, E. (1978)	0.1	Yes	3	870	Yes	17
Rappé, G. (1978)	0.1	Yes	3	870		17-18-19
Kerckhof, F. (1980)	0.1	Yes	3-2	870		15
Meheus, L. (1981)	0.1	Yes	3	250	Yes	9
De Rycke, R. (1982)	0.1	Yes	3	870	Yes	9
Vanosmael, C. (1982)	0.1	Yes	3	250		
Waeterschoot, H. (1984)	0.1	Yes	3	870	Yes	8
Brendonck, L. (1985)	0.1	Yes	3	870	Yes	15
Wittoeck, J. (2001)	0.1	Yes	1-3	1000		
DvZ	0.12	Yes	1-10	1000	Yes	7

Table 5. Sampling methodology period 1994-2001.

Scientist	Van Veen (m ²)	Fixed before sieving	Replica	Sieve mesh size (µm)	Gutter	Sediment # sieves
Coenjaerts, J. (1997)	0.1	no	1	1000	no	Coulter
Phillips, F. (1998)	0.12	no	1	1000	no	Coulter
Degraer, S. (1999)	0.1/0.12	no	1	1000	no	Coulter
Taverniers, K. (2000)	0.12	no	1	1000	no	Coulter
Deneudt, K. (2000)	0.1	no	1	1000	no	Coulter
Erdey, M. (2000)	0.1	no	1	1000	no	Coulter
Van Hoey, G. (2000)	0.1/0.12	no	5	1000	no	Coulter
Gheerardyn, H. (2002)	0.1	yes	1	1000	no	Coulter
Glorie, S. (2002)	0.1	yes	1	1000	no	Coulter
Schallier, R. Wittoeck, J. (2002)	0.1	yes	1	1000	no	Coulter

For the coarse sediment samples, the residues were decanted (10 times) on a 1 mm sieve in order to separate the present fauna from the sediment. With this technique the residue of coarse sediment and fauna is poured into a measuring cup (5 litres) and is brought into suspension with a strong jet of water. During this process the smaller and lighter organisms will go into suspension, whereas the heavier sediment and organisms remain on the bottom. Then the water with the organisms is poured over a 1 mm sieve. All retained animals are stored in a 4-8 % neutral formalin solution and stained with Bengal-Rose or eosin (if not done earlier) to colour all organic material,

which makes sorting of the animals easier. After decantation the residue is checked for bigger and heavier organisms (e.g. Mollusca, Actiniaria). Decantation is not applied to fine sediment samples (< 1000 µm) as all sediment is directly rinsed through the 1 mm sieve leaving only the fauna on the sieve.

2.3.3 Identification

All macrobenthic organisms are counted and identified, if possible to species level (Table 6). The main species belong to the taxonomic groups of bristle worms (Annelida), bivalves and gastropods (Mollusca), echinoderms (Echinodermata) and amphipods (Arthropoda).

Some other animal groups cannot be identified down to species level:

- Nematoda, Nemertinea, Sipunculida, Turbellaria, Oligochaeta and Copepoda are never identified to a lower taxonomical level
- The identification of some taxa is still unclear due to uncertainties in taxonomy. Within the Polychaeta the species *Phyllodoce maculata* and *Phyllodoce mucosa* are difficult to separate from one another and were therefore lumped. The identification keys refer to differences in dorsal and ventral cirri, which in many cases were broken off. According to Fiege et al. (2000) all *Magelona mirabilis* individuals were altered to the species name *M. johnstoni*. In the case of *Spio spp.* there are some recent developments that clarify the differences between the species (pers. comm. Künitzer). However to avoid large discrepancies between both old and new datasets in the present study they were lumped on genus level.

Table 6. Overview of the used identification manuals.

group	reference
General	Hayward P.J. & J.S. Ryland (1996). <i>General Handbook of the Marine Fauna of North-West Europe</i> .
Polychaeta	Hartmann-Schröder (1996). <i>Die Tierwelt Deutschlands: Annelida, Borstenwürmer, Polychaeta, Teil 58</i> . Fauvel P. (1923). <i>Faune de France 5. Polychètes errantes</i> Fauchald K. (1977). <i>The polychaete worms - definitions and keys to the orders, families and genera</i>
Amphipoda	Lincoln R.J. (1979). <i>British Marine Amphipoda: Gammaridea</i> .
Cumacea	Jones N.S. (1976). <i>British Cumaceans</i> .
Brachyura	Adema J.P.H.M. (1991). <i>Krabben van Nederland en België</i> .
Pycnogonida	King P.E. (1974). <i>British Seaspiders</i> .
Isopoda	Naylor E. (1972). <i>British Marine Isopods</i> .
Bivalvia	Tebble N. (1966) and (1976). <i>British Bivalve Seashells</i> . de Bruyne R.H. (1994). <i>Schelpen van de Nederlandse kust</i> .
Caridea	Smaldon G. (1979). <i>British coastal shrimps and prawns (Caridea)</i> .

The revised species list finally contained 272 different 'species' or taxa. To calculate the density of the species, the counted numbers of individuals per sample are converted to number of individuals per square meter (ind/m²). Only the anterior parts of the organisms were counted, in order not to overestimate densities.

For the second part of the study regarding the detailed long-term analysis both density and biomass were recorded at species or higher taxonomic level. Before weighing all fixated specimens were thoroughly rinsed in water. The Ash-Free Dry Weight (AFDW) of the macrobenthos species was calculated by converting the blotted wet weight (WW, weighed to the nearest 0.1 mg) according to Rumohr et al. (1987) and Ricciardi & Bourget (1998).

2.4 Data analysis

2.4.1 Univariate analyses

The non-parametric Spearman R test was used for the correlation analyses. One-way ANOVA – Analysis of Variance - testing differences in means (for groups or variables) for statistical significance was used for comparisons among the average densities and number of species of the two separate data sets ('76-'86 and '94-'01) based on fourth root-transformed data. In case the ANOVA assumptions were not fulfilled a Mann-Whitney U test, a non-parametric alternative to the t-test for independent samples, was performed as alternative for the one-way ANOVA.

2.4.2 Multivariate analyses

Before applying the multivariate techniques several data reductions were performed. The criteria used to omit species from the final datasets were: (1) species that were not sampled quantitatively (e.g. hyperbenthos, epibenthos), (2) rare taxa (frequency of occurrence < 2%), (3) species or taxa that were lumped into a higher taxonomic level (genus or even family), because of inconsistent identification throughout the different studies.

For the spatial and long-term analyses density data from the 2 periods separately (1976-86 and 1994-2001) and from the combined dataset were used. Average densities for the 5 selected stations separately were used in the multivariate analyses concerning the detailed long-term variation of the macrobenthos.

TWINSpan (Two Way INdicator SPecies ANalysis) (Hill, 1979) was based on non-transformed data sets. Cut levels (Table 7) were chosen in such a way as to obtain an even distribution of the number of values over the consecutive cut levels, except the first (containing all zero values) and the last 2 cut levels which contain an equal number of values (half of the other cut levels). For every 'dataset' a second TWINSpan was performed based on the presence/absence of species.

Table 7. Cutlevels and number of species used in the analyses for the different 'datasets'

Dataset	Cutlevels (ind./m²)	#
period 1976-'86	0, 9.75, 40 & 95	87
Period 1994-2001	0, 9.75, 25, 70 & 160	78
combined dataset	0, 10, 30, 100 & 220	81
station 120	0, 3.4, 10, 27, 73 & 155	60
station 140	0, 4, 10, 40 & 100	31
station 700	0, 4, 14, 70 & 250	38
station 710	0, 3.5, 10, 30 & 65	46
station 780	0, 3.5, 12, 37 & 106	53

Also, group-averaging cluster analyses based on the Bray-Curtis similarity (Clifford and Stephenson, 1975) and DCA (Detrended Correspondence Analysis) (Hill and Gauch, 1980) or CA (Correspondence analysis) were performed. For the latter analyses the dataset was fourth root transformed.

All results (except for stations 120, 140, 700, 710 and 780) were compared in order to typify groups of biological similar samples. For each group a set of indicator species was calculated through Indicator Species Analysis (Indval) and the statistical significance of the groups was tested

by a Monte Carlo Test (Dufrêne & Legendre, 1997). The resulting sample groups were characterised by means of their species composition, abundance and physical habitat (D50 median grain size, mud content and bathymetry).

PRIMER (Plymouth Routines In Multivariate Ecological Research) v5 (Clarke & Gorley, 2001) was used to run two basic routines: ANOSIM (Analysis Of SIMilarity) and SIMPER (SIMilarity PERcentages), respectively to test for statistically significant differences between the groups of samples that resulted from the TWINSpan analysis of the combined data set ('76-'86 & '94-'01) and identifying the species primarily contributing to the discrimination between the different sample clusters.

2.5 Dissemination

2.5.1 MACROBEL website and interface

The original MACRODAT database (which also contains data from intertidal macrobenthos studies) was developed as an MS-Access file at SMB. Separate tables were created for cruises, samples, and replicates and distribution records within samples. Also each taxonomic rank was represented by a separate table. This version of the database was used for data input.

For the current project, the MACRODAT database was translated into an MS-SQL Server database at VLIZ and renamed into MACROBEL. A separate table implementing taxonomic names and hierarchy was added, linked with the species table that was used in SMB. This made it possible to use more sophisticated taxonomic browse and search mechanisms in the web interface.

All taxonomic names in the database were thoroughly checked against the VLIZ species register APHIA. This synchrony makes it possible to extract taxon information, such as synonymy and vernacular names from APHIA and present it through the MACROBEL interface. Pictures are stored in the Integrated Marine Information System (IMIS2), the information management tool from VLIZ, and are dynamically retrieved for display in the MACROBEL interface.

The website and the web interface (the database menu and pages) are developed in PHP (Hypertext Processor) scripting language, and are running on an Apache web server. The PHP scripts parse the user requests, dynamically retrieve data from the MS SQL database, and pass the information on to the Apache web server, either as textual information, or as graphics in Scalable Vector Graphics (SVG) format.

The web interface allows for sophisticated search and browse operations. Searches for taxonomic names can be 'exact' or 'fuzzy', taking into account spelling mistakes. Hits on taxonomic names can be restricted to a taxon at any level above genus. It is possible to query all distribution records of a taxon, including all dependent ('child') taxa or synonyms. Distribution hits can be restricted in time or position, either by specifying two coordinate pairs, or by graphically indicating the area of interest on the map. Various types of output can be selected: tables, graphs or maps. Individual stations can be clicked in the map, resulting in more detailed information on that station. Being SVG, all maps can be zoomed and panned.

The use of SVG in this context is rather novel and required some extra functions to be developed (like geographical projections and showing of a scale bar). The methodology used in MACROBEL seems to satisfy a genuine need and makes SVG a good solution to apply in other biogeographic web applications: it allows the construction of powerful geographical web-interfaces; SVG can easily be generated directly from PHP; the processing demands at either the client or server side are very small; it is open standard software and viewers are available as freeware.

The MACROBEL website and web interface is currently hosted by VLIZ (Flanders Marine Institute) (<http://www.vliz.be/vmdcdata/MACROBEL>). The aim of MACROBEL is to provide people with a tool to gather information (spatial & temporal; description, ecology; taxonomy) about the macrobenthos

on the BCS. This unique dataset will regularly be updated with newly available data. This will enable other people to monitor possible changes in the macrobenthic communities over the entire BCS.

2.5.2 Symposia

The MACROBEL project and the MACROBEL web-interface have been presented at two symposia:

- Wittoeck J., Degraer S., Hillewaert H., Declerck R. and Vincx M. 2002. Long-term trends of the macrobenthos of the Belgian Continental Shelf (BCS). The Colour of Ocean Data (COD) symposium, Brussels, Belgium, 25-27 November (Poster).
- Wittoeck J., Degraer S., Vanden Berghe E., Mees J., Hillewaert H., Declerck R. and Vincx M. 2003. Long-term trends of the macrobenthos of the Belgian Continental Shelf (BCS). 38th EMBS congress, Aveiro, Portugal, 8-12 September (Poster).

2.5.3 Macrobenthos distribution atlas

The concept of the atlas '*Beknopte Atlas van de Mariene Bodemdieren van België*' is twofold: (1) describing the occurrence and distribution patterns of a selection of macrobenthos species (>50) which were found in the sediments of the BCS during the periods '76-'86 versus '94-'01 and (2) characterizing their physical habitat based on present and former sediment characteristics.

Of course the usefulness of the atlas is limited in time and in space. Most of the sampling sites were sampled only once throughout the whole period. Still, by combining most of the available macrobenthos data from SMB and DvZ, the spatial coverage of the whole BCS is largely met. However, the distribution maps (generated from the MACROBEL interface) of the different macrobenthos species can only be seen as a snapshot of a constantly changing habitat. This implies that the maps, which aim to present variation in space and time, may be distorted by year to year variation. Inevitably the atlas is limited to the BCS which is determined by its political borders. From a biogeographical or ecological point of view such borders do not make much sense.

The selection of the macrobenthos species included in the Atlas was based on four major criteria:

- Frequency, i.e. the species occurring in more than 10 % of all stations sampled on the BCS during one or both sampled periods
- abundance or quantitative data
- possible indicator species for a macrobenthos assemblage or a sediment type according to Degraer (1999) and Van Hoey et al. (2004)
- the public interest for a number of species, like the polychaete *Arenicola marina*; the bivalves *Mya truncata*, *Cerastoderma edule*, *Petricola pholadiformis* and *Venerupis senegalensis*; the echinoderms *Echinocyamus pusillus* and *Ophiura ophiura*. Species like *Ensis directus*, *Barnea candida*, *Mytilus edulis*, *Crepidula fornicata* and *Asterias rubens* were not selected because of insufficient data for one or both sampling periods.

The distribution atlas gives information on 60 macrobenthos taxa in terms of habitat preferences, spatial distribution and temporal variation between the periods '76-'86 and '94-'01. The latter is visualised by means of two maps based on the average densities (# ind/m²) of the species over the BCS during both periods. Each species is accompanied by a short morphological description and a photograph. All taxonomic names in the atlas were thoroughly checked against the VLIZ species register APHIA. To insure the reliability and the interpretation of the sediment plots, a threshold of minimum three observations was used. The plotted values show the ratios of the number of observations of a particular species in relation to the total observations over the whole BCS with respect to median grain size and silt concentration. A draft version for one species (*Lanice conchilega*) is given in Figure 5.



Picture © Declaer, M.

Lanice conchilega (Pallas, 1766)

Synonym: *Nereis conchilega* Pallas, 1766

Volksnamen: schelpkokenworm (Nl),
Zandkokenworm (Nl), Sand mason (En)
Muschelsammerlin (D)

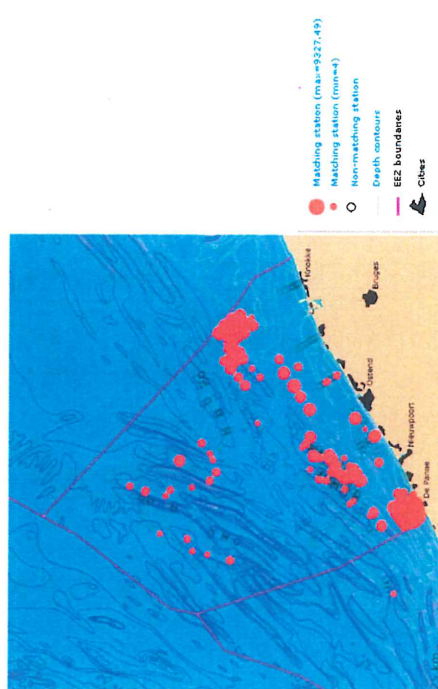
Beschrijving: Kokerbewonende borstelworm, waarvan het lichaam is opgebouwd uit 2 delen. Een gezwollen borststuk met gereduceerde kop en speciaal gevormde segmenten en een achtereinde naar achteren versmaald met gereduceerde aanhangsels. Lengte tot 300 mm. Koker samengesteld uit middelgrote tot grote zandkorrels met een karakteristieke waaiervorm aan de top.

Habitat preferentie: *Lanice conchilega* wordt hoofdzakelijk aangetroffen in fijn zandige substraten. Tijdens de periode '94-'01 worden er tevens hoge abundenties opgemeten in medium, zandige sedimenttypes. Het percentage silt dat telkens aanwezig is varieert tussen 0 en 30 %.

Verspreiding: *L. conchilega* komt in beide periodes vrij algemeen voor op het BCP (26 % met gemiddelde densiteiten van 95 ind./m²). Hoge concentraties van de soort worden voornamelijk gevonden langsheen de westkust en de Vlaamse banken (periode '76-'86 en '94-'01) en ter hoogte van de Zeeland banken (periode '94-'01). Lokaal worden er soms zeer hoge dichtheden opgemeten (Vlaakte van de Raan tot 9300 ind/m² in '94-'01).



Verspreidingsdichtheden (ind./m²) van *L. conchilega* (Pallas, 1766) in de periode 1976-1986



Verspreidingsdichtheden (ind./m²) van *L. conchilega* (Pallas, 1766) in de periode 1994-2001

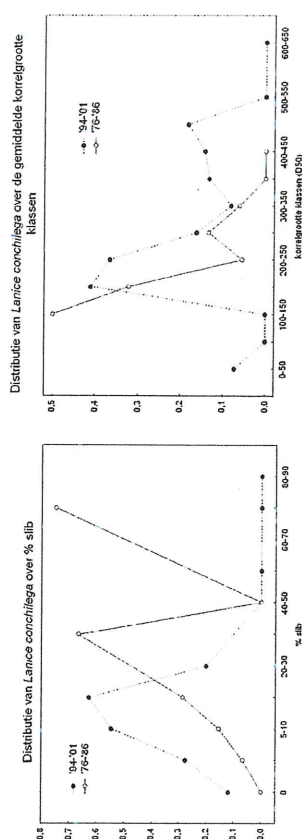


Figure 5. Draft page of one of the selected species (*Lanice conchilega*) from the macrobenthos distribution atlas.

Results

2.6 Spatial and long-term variation

2.6.1 Overall description of the macrobenthic infauna of the BCS

During both sampling periods (1976-'86 and 1994-2001) a total of 272 species (see Annex 1) – of which 242 specific macrobenthic infauna species - were collected in 775 sampling stations (or 1475 Van Veen grabs, if replicates are considered as separate samples) scattered over the BCS.

Polychaetes were the most diverse taxon with 109 species comprising 45 % of the total number of species, followed by crustaceans (82 species) and molluscs (40 species) covering resp. 34 and 17 %. Only 8 species of echinoderms and 3 species from other taxa comprised respectively 3 and 1 % of the overall number of species. The number of species per sample/replicate (N0) ranged from 1 to 51 species per sample with an average of 11 species per sample (Figure 6).

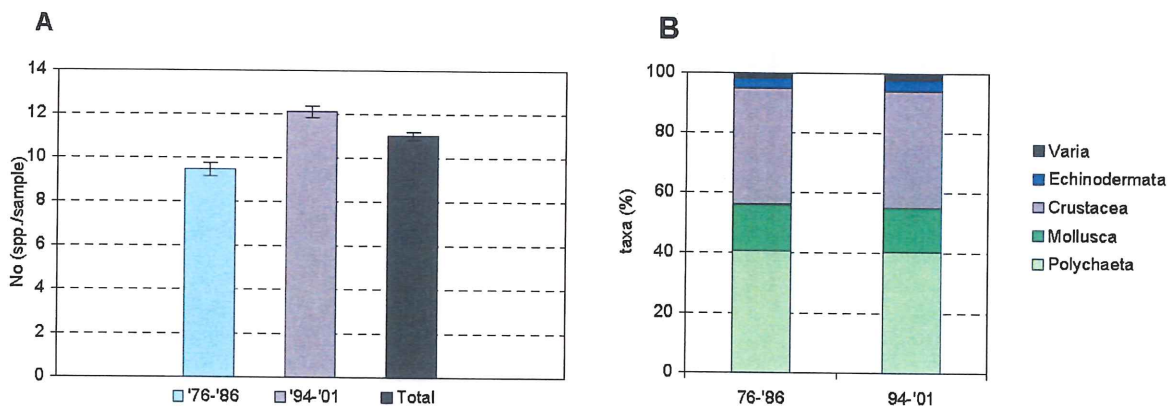


Figure 6. Average number of macrobenthic species per sample (\pm standard error) (left) and relative species composition (right) for the periods 1976-'86 and 1994-2001

During '94-'01 the average number of species per sample was significantly higher (one-way ANOVA: $p < 0.001$) than in the period '76-'86. The relative composition of the macrobenthic communities showed no major changes or differences between both periods (Figure 6).

Table 8. Species that disappeared/appeared during the periods '94-'01 and '76-'86.

	Loss	Gain
Polychaeta	<i>Goniadella bobrezkii</i> <i>Pectinaria belgica</i>	<i>Nephtys assimilis</i> <i>Pomatoceros triqueter</i>
Mollusca	<i>Phaxas pellucidus</i>	<i>Nassarius reticulatus</i>
Crustacea	<i>Corophium arenarium</i> <i>Iphinoe trispinosa</i>	<i>Diogenes pugilator</i>
Echinodermata	-	<i>Acrocnida brachiata</i>

The majority of the macrobenthic species were found in both sampling periods. However, considering criteria such as sampling methodology, undersampling of habitats, possible identification errors or new insights in taxonomy, the rareness of species (< 2% frequency) and eliminating all non-

macrobenthos species (e.g. accidentally caught pelagic species, epibenthic species), 5 species did not occur in the '94-'01 data set (Table 8). Likewise, 5 species that were found in the period '94-'01 were not found during the period '76-'86.

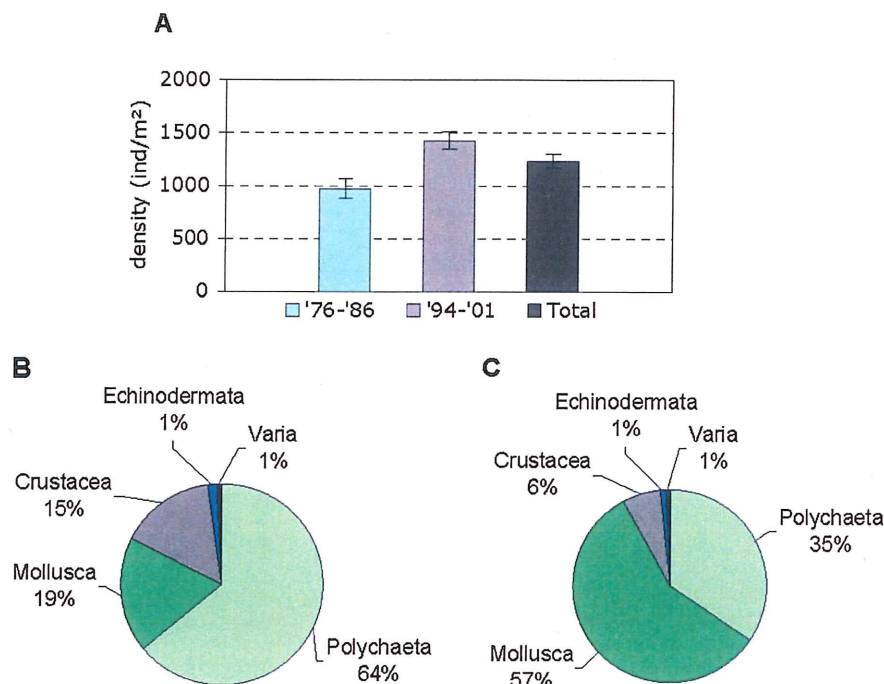


Figure 7. Average macrobenthos density per sample (A) and relative abundance of the common taxa during the periods '76-'86 (B) and '94-'01 (C)

Total average densities varied between 3 and 2.6 10^5 ind/m² with an average of 1240 ind/m² (Figure 7). Molluscs and polychaetes showed highest average densities (respectively 57 and 35 %). Crustaceans comprised only 6 % of the total average density, whilst echinoderms and other taxa filled up the remaining gap (1 % each). Comparable with species richness, the average densities were significantly higher during the period '94-'01 (Mann-Whitney U: $p < 0.0001$). During '76-'86 polychaetes and crustaceans were more abundant than during the following period. The opposite trend was observed for molluscs.

The species richness was highly correlated (Spearman rank: $p < 0.05$) with median grain size and mud content. A higher species richness (>15) was observed in fine to medium sandy sediments (median grain size <300 μm) with a mud concentration varying between 5 and 10 %. Coarser substrates, either with or without a low mud fraction, yielded samples with a low number of species and lower densities. Higher densities mostly corresponded with higher species richness (Spearman rank: $R^2 = 0.77$; $p > 0.05$).

The western coastal area of the BCS, characterised by its large variety in habitats (shallow sand banks, swales, typical hydrodynamics, etc.) showed highest abundances and species richness. A high diversity was locally found on parts of the Flemish and Zeeland Banks. Settlement of young bivalve species, such as *Spisula subtruncata*, *Abra alba* and *Mysella bidentata* or sampling in a patch of *Lanice conchilega*, *Magelona johnstoni* or *Spiophanes bombyx* are the main reasons for the very high densities found in some samples.

2.6.2 Spatial community structure

Multivariate analyses

Based on different multivariate analyses (TWINSPAN, Cluster analysis) of the combined dataset ('76-'86 and '94-'01) 11 groups could be distinguished, each composed of samples with similar species compositions (Figure 8).

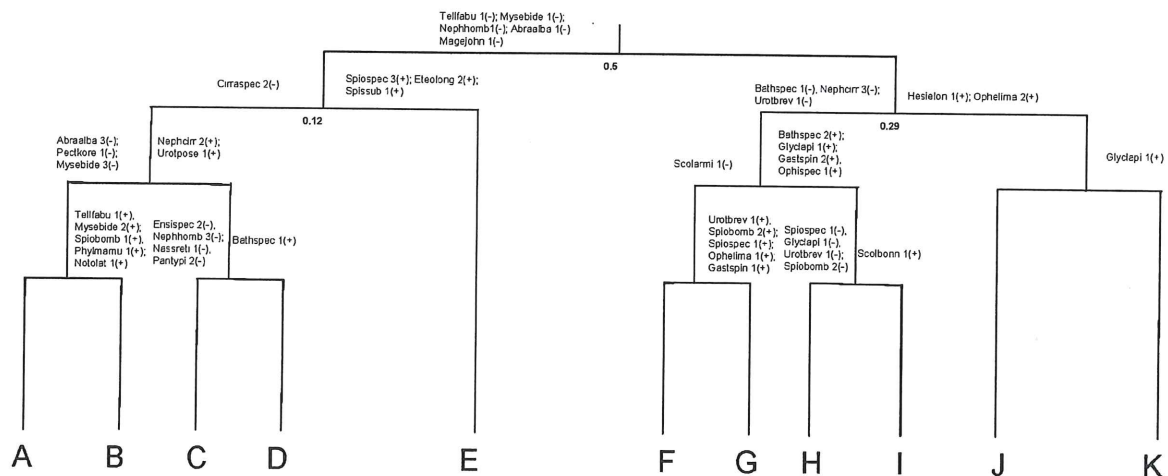


Figure 8. Dendrogram representing the TWINSPAN classification based on macrofauna abundance (combined dataset '76-'86 and '94-'01; >2% freq, n=1468 samples)

In a first division two clusters (A-E and F-K) were separated, which could be related to differences in median grain size and mud content (Table 9). Indicator species for group A-E were *Tellina fabula*, *Mysella bidentata*, *Nephtys hombergii*, *Abra alba* and *Magelona johnstoni*.

A second division separated A-D from cluster E. The latter samples were characterised by medium sand sediments with a mud concentration <5 %. This type of sediment is typical for a densely populated and diverse macrobenthic community (average density > 4500 ind/m²; on average 16 species per sample), mainly dominated by polychaetes (*Magelona johnstoni*, *Lanice conchilega*, *Spiophanes bombyx* and *Spio spp*). Significant indicator species were *Spio spp*, *Lanice conchilega* and *Magelona johnstoni*. This community was mainly found in the coastal areas and towards the adjacent deeper sandbanks (Flemish and Zeeland Banks) at an average depth of 13 m below MLWS.

Cluster A-D showed the highest average density and number of species, varying between 1680 and 8390 ind/m² and 11 and 23 spp/sample. All samples were taken at an average depth of 11 m below MLWS. The samples within these clusters were located around the coastal near shore sandbanks. The samples in the B-D cluster were characterised by fine sand sediments with an average mud concentration between 5 and 10 %. The most commonly found species were *Mysella bidentata*, *Tellina fabula*, *Lanice conchilega*, *Magelona johnstoni* and *Abra alba*. Cluster A grouped all stations sampled in very fine to fine sand sediment with an average mud content of 39 % at an average depth of 8 m below MLWS. The densities and the number of species were rather low in these samples (resp. 730 ind/m² and 6 spp/sample). Significant indicator species were *Cirratulidae spp* and *Diastylis rathkei*. This species assemblage was mainly found in the eastern part of the Belgian coast.

At the second level, clusters J and K were separated from the cluster F-I. Samples from the clusters J and K were taken from similar physical habitats (average grain size: 400 µm, mud content <1 %) and characterized by the presence of two predominant polychaetes *Hesionura elongata* and *Ophelia limacina*. The further division of cluster J from K was based on the absence of the interstitial poly-

chaete *Polygordius spp* and the overall lacking of *Glycera capitata* in J. The latter species was a significant indicator species for cluster K.

The F-I cluster grouped a variety of stations that were associated with clean medium sand with hardly any mud content. The depth ranged from 12 to 24 m below MLWS. Important species were *Nephtys cirrosa*, *Bathyporeia spp* and *Urothoe brevicornis*. The average number of species per sample was 7 and the densities ranged from 370 to 1460 ind/m². The geographical distribution of the macrobenthos communities within the F-I cluster ranged from the coastal areas towards the deeper sandbank formations (Hinder Banks) and even further towards the open sea.

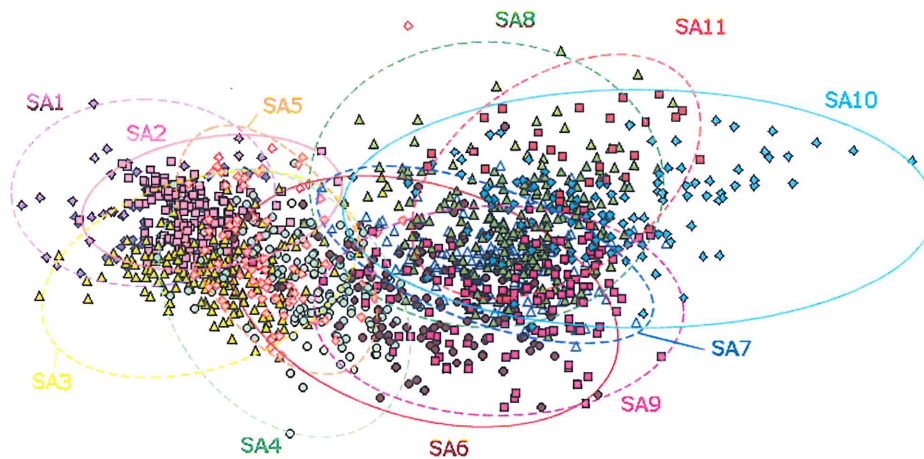


Figure 9. DCA plot of the combined dataset ('76-'86 and '94-'01) along the first 2 axes. The discrimination between the SA's was based on TWINSpan, Cluster and DCA.

The clusters that were found in the TWINSpan/Cluster analyses (A-K, further referred to as SA1-SA11) largely overlapped when projected on the plot of the DCA analysis (Figure 9). The samples rather seemed to be grouped along a habitat related gradient. Although no direct correlation could be made with the environment due to insufficient data for period '76-'86, the first axis (eigenvalue 0.49) and second axis (eigenvalue 0.19) were most likely correlated with median grain size and mud content.

Characterisation of the species assemblages

Based on their biotic and abiotic characteristics (Table 9) the sample clusters (A-K) generated from the multivariate analyses (TWINSpan and DCA) partly resembled the two types of species assemblages as described in Van Hoey et al. (2004). In that study a distinction was made between Type I and Type II species assemblages. The Type I assemblages represent three macrobenthos communities: the subtidal *Abra alba*-*Myrella bidentata* community, the *Nephtys cirrosa* community and the *Ophelia limacina*-*Glycera capitata* community. In this study a fourth Type I species assemblage was added: the *Macoma balthica* community. Several Type II assemblages were considered as intermediate communities between the different Type I assemblages.

Table 9. Some characteristics of the species assemblages: sediment type (fine or medium sand), medium grain size (μm), mud content (%), sampling depth (m), number of species (N_0), average density for total and top 10 species (ind/m^2), IndVal values for indicator species, and species association typology.

	SA1	SA2	SA3	SA4	SA5	SA6
samples ratio (%) '76-'86 vs '94-'01	10/3	8/14	3/17	11/9	3/7	7/12
Sediment type	FS	FS	FS	FS	MS	MS
median grain size (μm)	128	220	210	242	253	294
% mud	39	10	8	7	4	0
depth (m)	8	13	11	10	13	12
No Species	6	23	14	11	16	6
Average dens (ind/m^2)	729	8590	3066	1678	4547	418
Density top 10 (ind/m^2)						
Indicator species (from IndVal)	<i>Cirratulidae</i> spp. 290 <i>Spisula subaruncata</i> 143 <i>Polydora</i> spp. 83 <i>Abra alba</i> 81 <i>Pectanaria koreni</i> 51 <i>Myrella bidentata</i> 33 <i>Nephtys hombergii</i> 27 <i>Macoma balthica</i> 13 <i>Lanice conchilega</i> 12 <i>Spiophanes bombyx</i> 9	<i>Abra alba</i> 571 <i>Myrella bidentata</i> 510 <i>Panambus typicus</i> 326 <i>Spiophanes bombyx</i> 270 <i>Scoloplos armiger</i> 265 <i>Lanice conchilega</i> 237 <i>Tellina fabula</i> 166 <i>Eumida sanguinea</i> 161 <i>Magelona johnstoni</i> 160 <i>Cirratulidae</i> spp. 138	<i>Magelona johnstoni</i> 334 <i>Spiophanes bombyx</i> 202 <i>Lanice conchilega</i> 97 <i>Tellina fabula</i> 93 <i>Nephtys hombergii</i> 57 <i>Ensis</i> spp. 44 <i>Eumida sanguinea</i> 44 <i>Nephtys cirrosa</i> 44 <i>Urothoe poseidonis</i> 43 <i>Myrella bidentata</i> 36	<i>Magelona johnstoni</i> 318 <i>Spiophanes bombyx</i> 101 <i>Nephtys cirrosa</i> 71 <i>Tellina fabula</i> 50 <i>Lanice conchilega</i> 45 <i>Bathyporeia</i> spp. 40 <i>Scoloplos armiger</i> 38 <i>Myrella bidentata</i> 28 <i>Cirratulidae</i> spp. 27 <i>Urothoe poseidonis</i> 23	<i>Magelona johnstoni</i> 1060 <i>Lanice conchilega</i> 772 <i>Spiophanes bombyx</i> 586 <i>Spio</i> spp. 432 <i>Scoloplos armiger</i> 285 <i>Eumida sanguinea</i> 196 <i>Tellina fabula</i> 146 <i>Phyllodoce inamui</i> * 119 <i>Myrella bidentata</i> 91 <i>Erisis</i> spp. 72	<i>Nephtys cirrosa</i> 56 <i>Microphthalmus sirinillis</i> 34 <i>Bathyporeia</i> spp. 21 <i>Scoloplos armiger</i> 20 <i>Spiophanes bombyx</i> 12 <i>Magelona johnstoni</i> 11 <i>Urothoe poseidonis</i> 7 <i>Urothoe brevicornis</i> 6 <i>Echinocardium cordatum</i> 4 <i>Hesionura elongata</i> 4
species association	Type I SA <i>Macoma balthica</i> community	Type I SA <i>A. alba</i> - <i>M. bidentata</i> community	Type II SA	Type II SA	Type II SA	Type I SA <i>N. cirrosa</i> community
samples ratio (%) '76-'86 vs '94-'01	4/13	14/15	15/5	22/3	3/2	
Sediment type	MS	MS	MS	MS	MS	
median grain size (μm)	342	381	283	388	421	
% mud	1	0	0	1	1	
depth (m)	13	24	12	15	13	
No Species	8	9	6	6	7	
Average dens (ind/m^2)	641	1462	366	950	197	
Density top 10 (ind/m^2)						
Indicator species (from IndVal)	<i>Spiophanes bombyx</i> 57 <i>Scoloplos armiger</i> 55 <i>Nephtys cirrosa</i> 54 <i>Urothoe brevicornis</i> 47 <i>Ophelia limacina</i> 42 <i>Spio</i> spp. 15 <i>Bathyporeia</i> spp. 12 <i>Gastrosaccus spinifer</i> 8 <i>Mytilus edulis</i> 6 <i>Hesionura elongata</i> 3	<i>Spiophanes bombyx</i> 88 <i>Bathyporeia</i> spp. 72 <i>Gastrosaccus spinifer</i> 66 <i>Nephtys cirrosa</i> 44 <i>Scoloplos armiger</i> 42 <i>Urothoe brevicornis</i> 36 <i>Ophiura</i> spp. 29 <i>Spio</i> spp. 15 <i>Lanice conchilega</i> 14 <i>Ophelia limacina</i> 13	<i>Bathyporeia</i> spp. 93 <i>Nephtys cirrosa</i> 60 <i>Ophiura</i> spp. 16 <i>Scolecipus bormieri</i> 13 <i>Gastrosaccus spinifer</i> 10 <i>Magelona johnstoni</i> 7 <i>Spiophanes bombyx</i> 6 <i>Tanaidus</i> spp. 6 <i>Ophelia limacina</i> 5 <i>Hesionura elongata</i> 5	<i>Hesionura elongata</i> 412 <i>Ophelia limacina</i> 111 <i>Nephtys cirrosa</i> 25 <i>Gastrosaccus spinifer</i> 10 <i>Scoloplos armiger</i> 8 <i>Eteone longa</i> 7 <i>Spisula solida</i> 5 <i>Bathyporeia</i> spp. 4 <i>Spisula elliptica</i> 3 <i>Spiophanes bombyx</i> 3	<i>Polygordius</i> spp. 232 <i>Hesionura elongata</i> 65 <i>Ophelia limacina</i> 46 <i>Glycera capitata</i> 37 <i>Bathyporeia</i> spp. 32 <i>Aonides paucibranchiata</i> 11 <i>Branchiostoma lanceolatum</i> 9 <i>Nephtys cirrosa</i> 8 <i>Gastrosaccus spinifer</i> 7 <i>Nektomastus latericus</i> 7	<i>Glycera capitata</i> 60 <i>Aonides paucibranchiata</i> 18 <i>Branchiostoma lanceolatum</i> 17
species association	Type II SA	Type II SA	Type I SA <i>O. limacina</i> - <i>G. capitata</i> community	Type II SA	Type II SA	

(1) Although the species assemblage SA1 (cluster A) was closely related to the *Abra alba*-*Mysella bidentata* community, it was assigned as a *Macoma balthica* Type I SA, as it corresponded to the *Macoma balthica* community as described by Budd (2002). The biotope of this species assemblage was characterised by near-shore shallow (average 8 m below MLWS) muddy sands (median grain size 130 μm , mud content 40 %). Typical species were *Macoma balthica* and *Abra alba*. *Pectinaria koreni* and *Donax vittatus* may also be significant components, although not necessarily all present simultaneously.

(2) The *Abra alba*-*Mysella bidentata* community was identified in cluster B (SA2). The physical habitat was characterised by fine sandy sediments (median grain size 220 μm) with medium mud contents (10 %), at an average depth of 13 m below MLWS. The assemblage was characterised by high species richness (23 spp/sample) and high average macrobenthic densities (8400 ind/m²). Two bivalves *Abra alba* and *Mysella bidentata* reached high densities (respectively 570 and 510 ind/m²) followed by the amphipod *Pariambus typicus* (330 ind/m²) and several polychaetes with an average abundance >200 ind/m² (*Spiophanes bombyx*, *Scoloplos armiger* and *Lanice conchilega*). According to the Monte-Carlo permutation test ($p < 0.05$), seven species were indicative for SA2 (indicator value >40).

(3) Species assemblage SA6 (Cluster F) resembled best the *Nephtys cirrosa* community. Samples in SA6 consisted of well-sorted medium sandy sediments with low mud contents (<1 %) located at an average depth of 12 m below MLWS. The species richness was low (6 spp/sample) as well as the overall densities (420 ind/m²). Besides the polychaete *Nephtys cirrosa* (60 ind/m²) as indicator species, three other species reached high abundances: *Microphthalmus similis* (30 ind/m²), *Bathyporeia spp* and *Scoloplos armiger* (each 20 ind/m²).

(4) SA10 showed the typical characteristics of the *Ophelia limacina*-*Glycera capitata* community. The samples taken within this community were taken at an average depth of 15 m below MLWS, and were characterised by medium sandy sediments (median grain size 390 μm) with almost no mud (<1 %). Except for the interstitial polychaete *Hesionura elongata* (410 ind/m²) and *Ophelia limacina* (110 ind/m²), which were significantly indicative for this species assemblage, all species had an average abundance <30 ind/m². The species richness was low (7 spp/sample).

(5) The seven transition assemblages represent a gradual shift between the above described Type I species assemblages. Based on an ANOSIM (global R 0.59), they all differ from one another. Nevertheless, the pairwise R values (Table 10) indicated that some species assemblages were either closely related or clearly different.

Table 10. Results of the ANOSIM pairwise test comparisons (R values) between all SA's of the combined data set ('76-'86 and '94-'01). R>0.75: well separated; R>0.5: overlapping; R<0.25: hardly separable.

	SA1	SA2	SA3	SA4	SA5	SA6	SA7	SA8	SA9	SA10	SA11
SA1		0.713									
SA2			0.615	0.605	0.523	0.841	0.904	0.875	0.866	0.874	0.807
SA3				0.545	0.515	0.870	0.918	0.833	0.945	0.930	0.976
SA4					0.237	0.232	0.704	0.771	0.725	0.815	0.870
SA5							0.286	0.472	0.439	0.436	0.688
SA6							0.715	0.800	0.701	0.822	0.819
SA7								0.278	0.305	0.223	0.562
SA8									0.148	0.524	0.548
SA9										0.181	0.471
SA10											0.471
SA11											
										0.551	0.737
											0.409

The transitional species assemblages SA3, SA4 and SA5 can be situated between the Type I SA of *A. alba*-*M. bidentata* (SA2) and *N. cirrosa* (SA6) along a habitat related gradient (increase in median grain size and decrease in mud content). Statistically all three SA's were closely related to each other (ANOSIM, global R 0.59) with 6 dominant taxa in common. The three SA's also had 6

dominant taxa in common with SA2. Despite this overlap they were still defined as clearly different species groups. Towards SA6 only SA4 showed clear signs of an overlap (ANOSIM, global R 0.59), with 6 common dominant taxa. SA3 and SA5 only had 4 and 3 taxa in common with SA6, respectively. For species assemblages SA4 a lower average density and species richness was calculated (1680 ind/m², 11 spp/sample) than for SA3 (3070 ind/m², 14 spp/sample) or SA5 (4550 ind/m², 16 spp/sample).

Between the Type I SA's 6 (*N. cirrosa*) and 10 (*O. limacina*-*G. capitata*) three transitional assemblages could be distinguished (SA7, SA8 and SA9), which were all closely related to each other (ANOSIM, global R 0.59). The number of dominant taxa in common with SA6 decreased from 6 to 4, and with SA10 from 7 to 6. The physical habitat was characterised by medium sand with a very low mud fraction (< 1%). The average depth was around 12 m below MLWS, except in SA8 (24 m).

Also species assemblage SA11 was comparable with Type I SA10 (ANOSIM, global R 0.59) with 5 dominant taxa in common and a similar habitat type.

Differences between both periods

For each species assemblage a ratio in number of samples was calculated, referring to the different periods '76-'86 (in total 433 samples) and '94-'01 (in total 1036 samples) (Figure 10, Table 9). Most samples are more or less evenly distributed over all SA's in both periods, except that more samples belonged to SA9 and SA10 for the period '76-'86 and more samples grouped in SA2 and SA3 for the period '94-'01. These differences can be explained by discrepancies in sampling methodology and sampling effort per habitat. For example, the mesh size used for sieving during '76-'86 (870 µm) favoured the capture of smaller interstitial polychaetes like *Hesionura elongata* and *Polygordius spp* (cf. SA9 and SA10). During both periods a limited area of the BCS was studied, namely a number of sandbanks like the Kwintebank in '76-'86 or the western part of the Belgian coast in '94-'01, which increases the chance of sampling within a certain species assemblage.

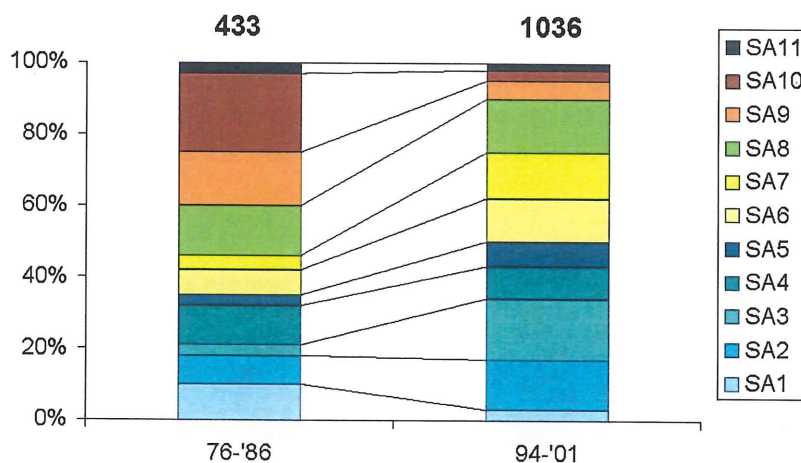


Figure 10. Distribution of the samples over the TWINSpan generated species assemblages (SA1-SA11) for both periods.

To find (dis)similarities between both periods each of the transitional species assemblages (Type II) were assigned to the most closely related Type I SA as described above. Based on an ANOSIM analysis, significant differences ($p < 0.001$) were found between the three Type I SA's in both periods. A SIMPER analysis showed clear dissimilarities between all SA's, but the *A. alba*-*M. bidentata*

communities of both periods were more similar than respectively the *N. cirrosa* or *O. limacina*-*G. capitata* communities of both periods (Table 11).

Table 11. Average dissimilarities between the Type I SA's of both sampled periods, based on a SIMPER analysis (see text for abbreviations).

	Type I SA	Period '76-'86		
		AA-MB	NC	OL-GC
'94-'01	AA-MB	58	88	94
	NC	92	75	85
	OL-GC	96	91	78

Table 12. ANOSIM pairwise comparisons between the Type I SA's of both sampled periods.

Type I SA	R value
<i>A. alba</i> - <i>M. bidentata</i>	0.246
<i>N. cirrosa</i>	0.435
<i>O. limacina</i> - <i>G. capitata</i>	0.305

Table 13. Species that contributed most to the dissimilarities between Type I SA's

<i>A. alba</i> - <i>M. bidentata</i> SA	<i>N. cirrosa</i> SA	<i>O. Limacina</i> - <i>G. capitata</i> SA
<i>Spiophanes bombyx</i> (6 %)	<i>Nephtys cirrosa</i> (14 %)	<i>Hesionura elongata</i> (14 %)
<i>Lanice conchilega</i> (5 %)	<i>Bathyporeia</i> spp (11 %)	<i>Ophelia limacina</i> (10 %)
<i>Mysella bidentata</i> (5 %)	<i>Scoloplos armiger</i> (8 %)	<i>Nephtys cirrosa</i> (7 %)
<i>Pariambus typicus</i> (4 %)		<i>Glycera capitata</i> (6 %)

Also, the pairwise R values showed a larger overlap between the *A. alba*-*M. bidentata* communities of both sampling periods Table 12. The species that were found at consistent high abundances in most samples, and thus contributed most to the above dissimilarities between the different Type I SA's in the SIMPER analysis, are given in Table 13.

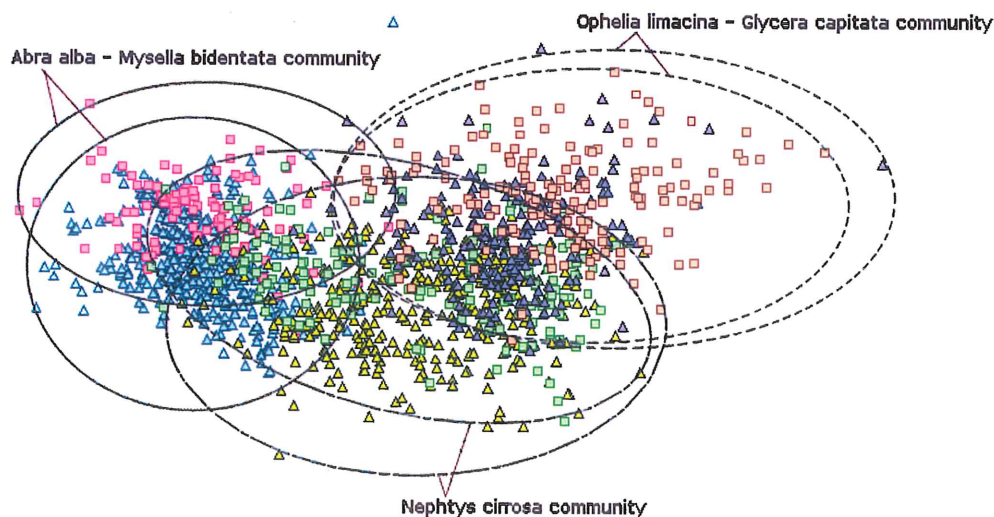


Figure 11. DCA plot of the combined data set ('76-'86: squares & '94-'01: triangles) along the first 2 axes, where all type II assemblages were assigned to a type I assemblage.

The DCA plot of the combined data set showed distinct overlaps between all Type I species assemblages of both sampled periods (Figure 11). In '94-'01, the *Macoma balthica* community was hardly separable by DCA from the *Abra alba*-*Mysella bidentata* community (Figure 12).

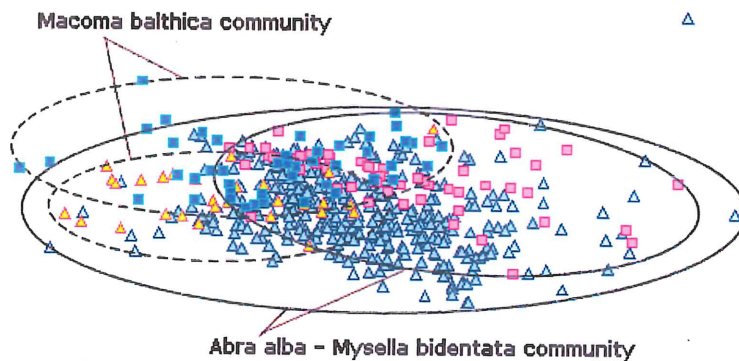


Figure 12. Part of DCA plot to show the resemblance of the *M. balthica* community to the *A. alba*-*M. bidentata* community ('76-'86: squares & '94-'01: triangles).

Spatial distribution of the Type I SA's

The distribution of the Type I SA *Abra alba*-*Mysella bidentata* community (SA2) together with its associated Type II SA's (SA3, SA4 and SA5) was mostly confined to the 12 nmile zone of the BCS (13). The distribution of this community was quite similar when comparing both sampling periods. However, the *A. alba*-*M. bidentata* community largely disappeared from the gullies in between the Flemish Banks, and was found more often in the neighbourhood of the Zeeland Banks during the period '94-'01.

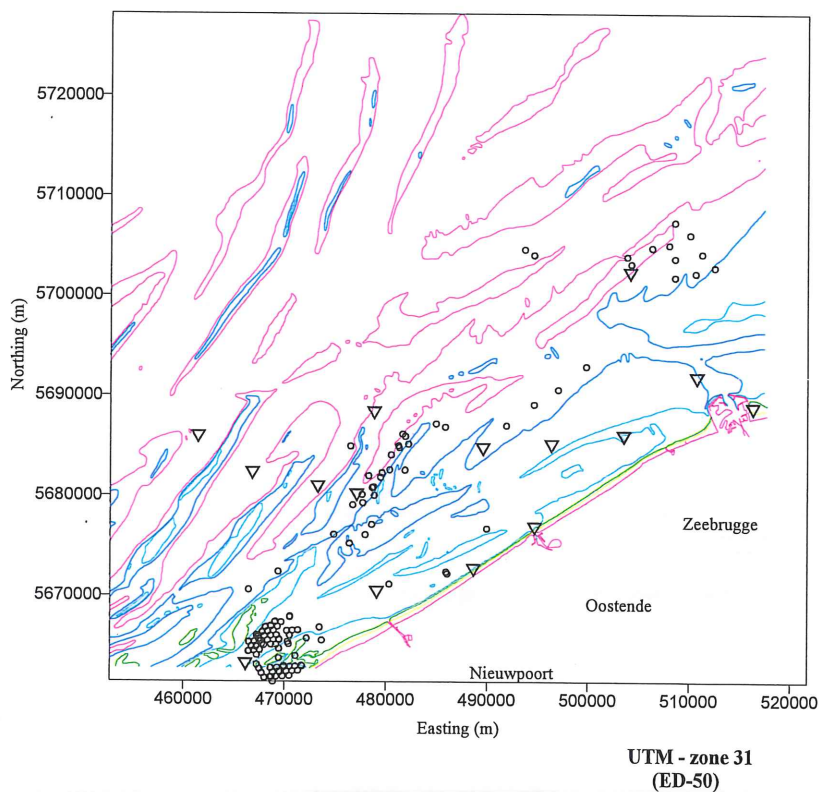


Figure 13. Spatial distribution of the *Abra alba*-*Mysella bidentata* species assemblages over the BCS (period '76-'86: triangles; period '94-'01: circles)

The *Macoma balthica* community (SA1) was strictly associated with the near shore coastal areas. Its distribution was patchy and more limited to the eastern part of the Flemish coast in the period '94-'01 (Figure 14).

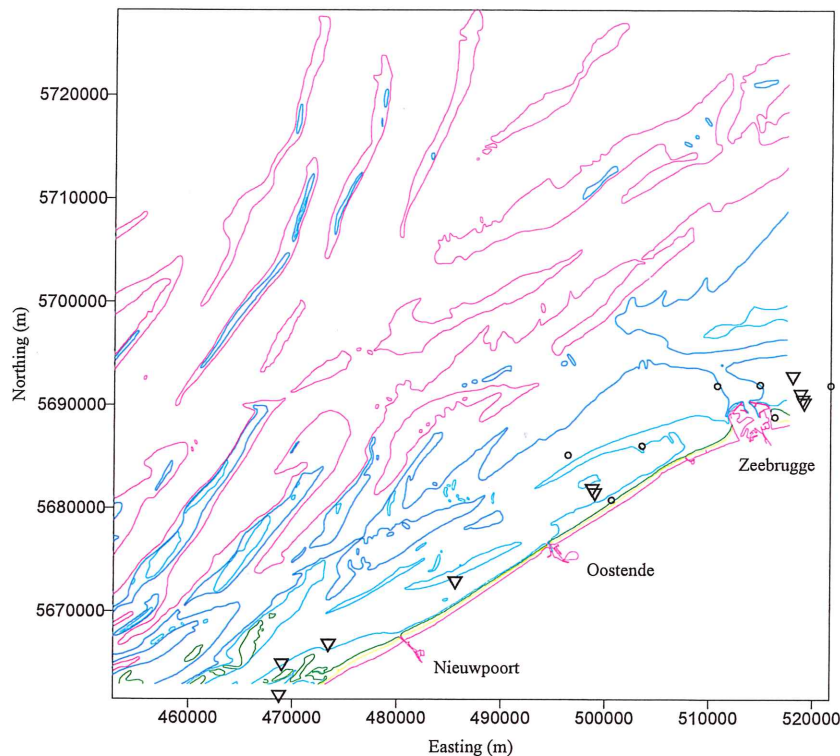


Figure 14. Spatial distribution of the *Macoma balthica* species assemblages over the BCS (period '76-'86: triangles; period '94-'01: circles)

The *Nephtys cirrosa* community (SA6) and its associated Type II SA's (SA7, SA8 and SA9) covered nearly the whole BCS in both periods. This community was not only found on the different sandbank formations (Flemish, Zeeland and Hinderbanks), but also in the gullies between the sand banks (Figure 15).

The *Ophelia limacina*-*Glycera capitata* community (SA10) and its associated Type II SA (SA11) were found in the more offshore part of the BCS (Hinderbanks and open sea) during both sampling periods (Figure 16). During the period '76-'86 this community was also frequently encountered on the Flemish Banks, while during '94-'01 the *O. limacina*-*G. capitata* community was sometimes found near the western coast of the BCS.

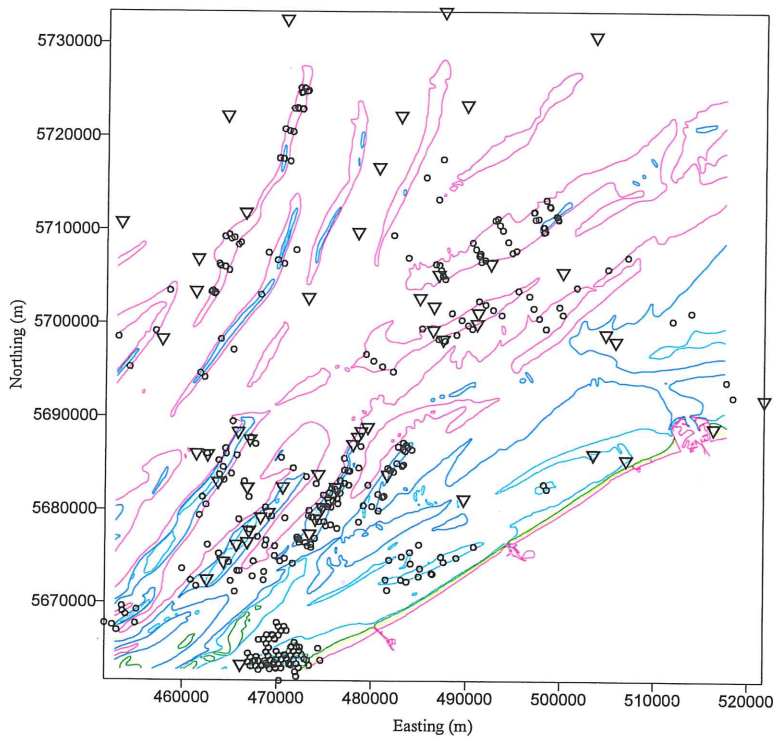


Figure 15. Spatial distribution of the *Nephtys cirrosa* species assemblages over the BCS (period '76-'86: triangles; period '94-'01: circles)

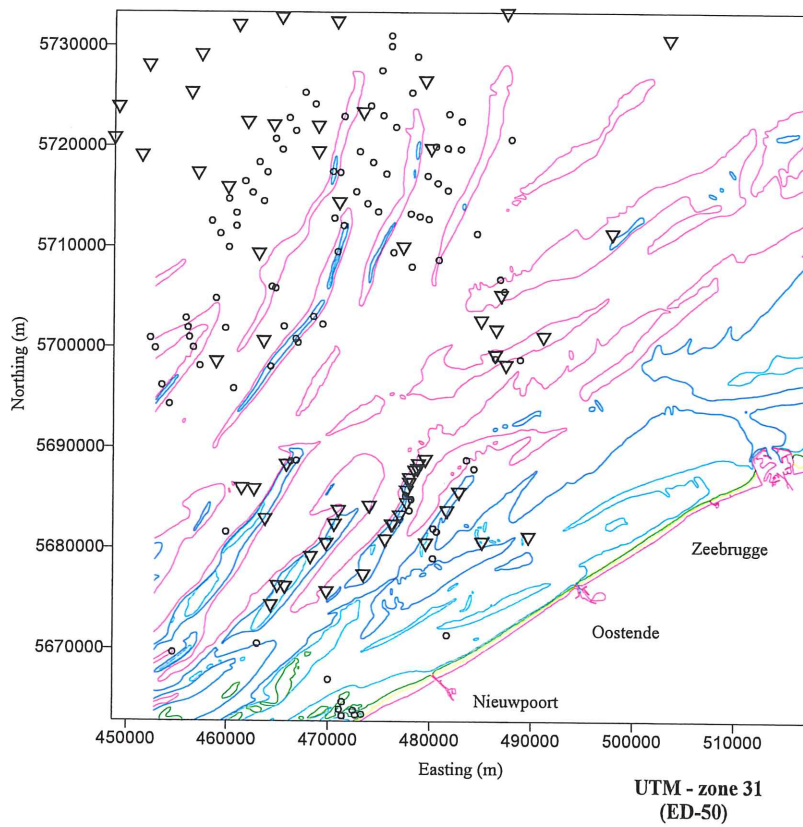


Figure 16. Spatial distribution of the *Ophelia limacina*-*Glycera capitata* species assemblages over the BCS (period '76-'86: triangles; period '94-'01: circles)

2.7 Detailed long-term variation

A more detailed analysis of the long-term variation in the macrobenthos is given for 5 subtidal sampling sites on the BCS, based on sediment type and a number of macrobenthos parameters, like diversity, density and biomass.

2.7.1 Station 140

Sediment

The modal median grain size at station 140 over the entire time series was 110 μm , fluctuating between 33 and 254 μm (Figure 17). The median grain size was more or less stable during the 90's (on average 160 μm). During the 80's the median grain size was much lower in most years (ca. 50 μm), but reached higher peaks on many occasions, comparable with the nineties. In general, the average mud content (fraction <63 μm) was high during the 80's (>55 %) in comparison with the 90's (on average 16 %).

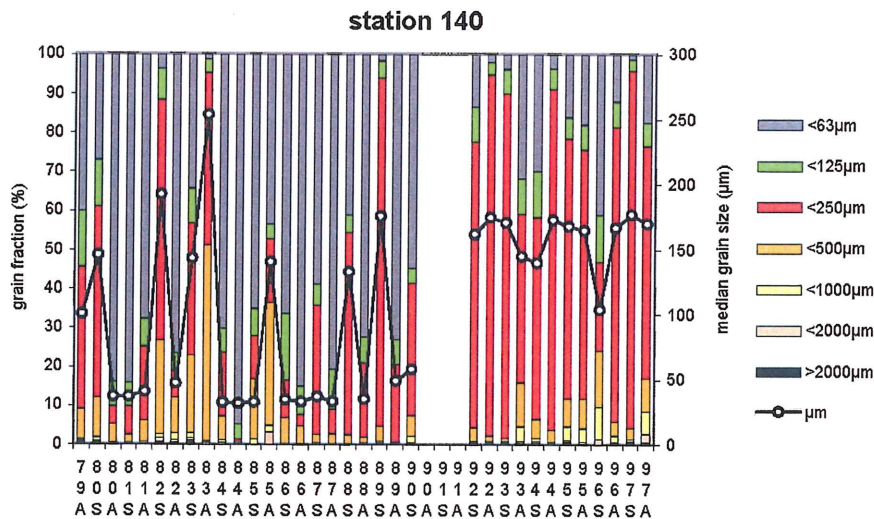


Figure 17. Time series of the grain fractions and median grain size over the period 1979-'97 (A= autumn, S= spring sampling campaign) for station 140.

Macrobenthos

The most abundant taxa for station 140 were Annelida which constituted >50 % of the macrobenthic community, followed by Bivalvia and Crustacea. The remaining species belonged to the Anthozoa (Figure 18). The average density varied between 10 (spring 1980, 80S) and 1260 ind/m² (autumn 1983, 83A) (Figure 19). Generally, the biomass was low (average of 25 g AFDW/m²) ranging from 0.05 (88A) to 355 g AFDW/m² (95S). Only two high peaks in biomass (in 94A and 95S) were noticed, due to the presence of the bivalves *Spisula subtruncata* and *Macoma balthica*.

The diversity (No) never reached high values (average 8 spp/sample) ranging from 1 (in 81S) to 17 spp/sample (in 94S and 94A). There were no clear trends in total density, biomass or diversity. However, there were significant correlations between the total density and diversity and the fluctuating changes in sediment composition (median grain size) during both periods (respectively $p=0.02$, $R=0.41$ for density and $p=0.007$, $R=0.47$ for diversity).

The most abundant species found at station 140 were the polychaetes *Chaetozone setosa*, *Nephtys spp* and *Spio spp*, and the bivalves *Abra alba*, *Spisula subtruncata* and *Macoma balthica*. The latter species was mainly present during the first half of the nineties (Figure 20).

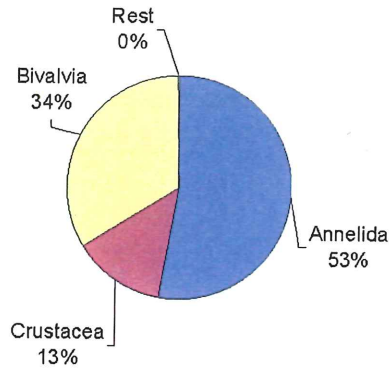


Figure 18. Relative abundance of the higher taxonomic classes at station 140.

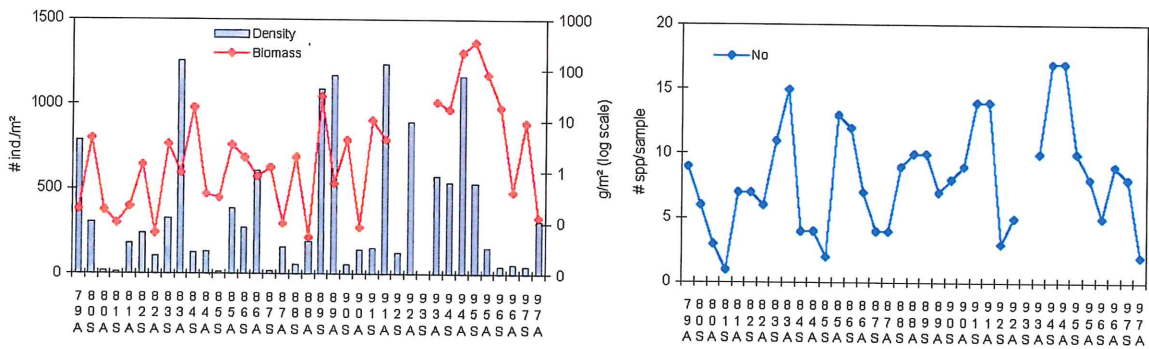


Figure 19. Time series of the overall density, biomass and diversity at station 140.

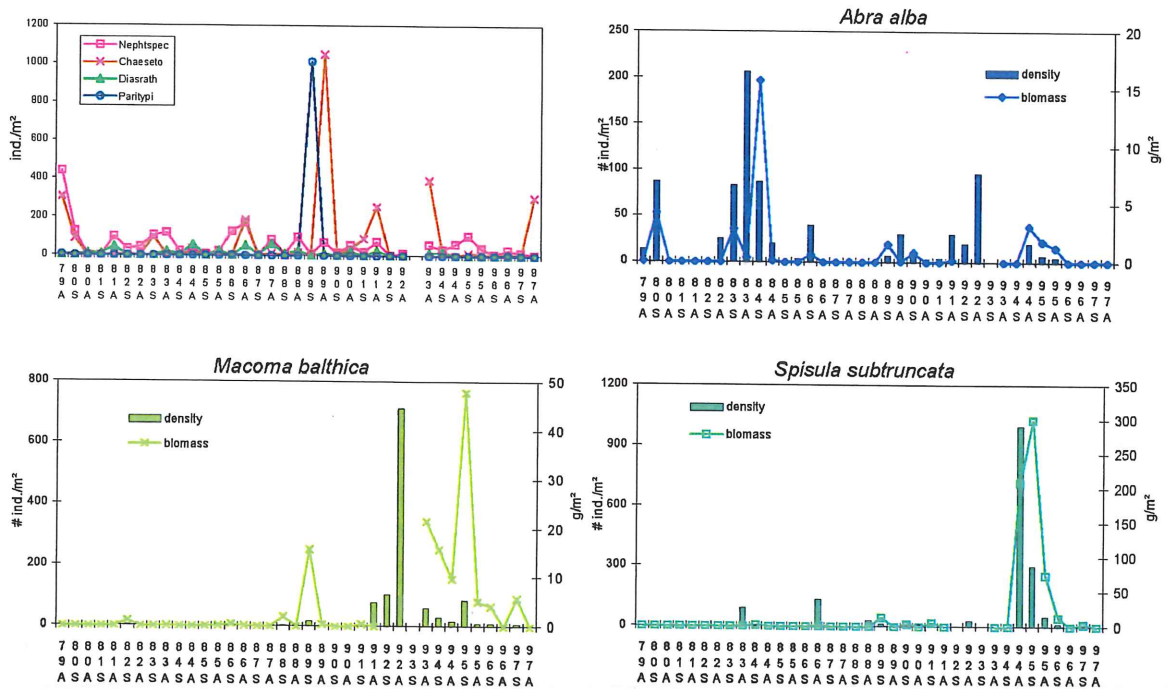


Figure 20. Time series of some important species in terms of density and biomass at station 140.

The cumacean *Diastylis rathkei* was the most frequently sampled crustacean at station 140 throughout the whole period with higher densities in autumn. Also, *Nephtys spp.* were found at higher densities in autumn every year. For *Abra alba* and *Chaetozone setosa* higher densities were noted in a 2 to 4 year cycle. Onetime peaks were found for the crustacean *Pariambus typicus* with 1000 ind/m² in 89S and for the bivalve *Ensis spp.* with 750 ind/m² in 91A.

There were hardly any patterns seen in terms of biomass, and the peaks did not necessarily coincide with the peaks in density. The bivalve *Spisula subtruncata* was responsible for the two peaks in total biomass in 94A and 95S (210 and 300 g AFDW/m², respectively). In 94A just settling juvenile species (1000 ind/m²) dominated the samples, whereas in 95S mature specimens were more abundant (300 ind/m²).

2.7.2 Station 700

Sediment

The average median grain size at station 700 over the consecutive samplings was 80 µm, ranging from 33 to 478 µm (Figure 21). Apart from a few higher values in 87A, 88S, 94S, 95S and 95A, the median grain size averaged around 50 µm. The sediments were characterised by high mud concentrations (on average 61 %).

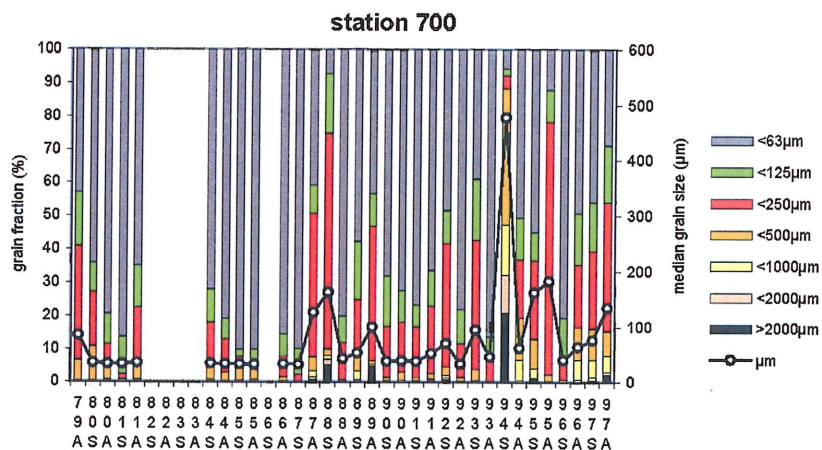


Figure 21. Time series of the grain fractions and median grain size over the period 1979-'97 (A= autumn, S= spring sampling campaign) for station 700.

Macrobenthos

At station 700 average densities ranged from 20 to 46000 ind/m² (respectively in 96S and 88A). Annelida were the most abundant taxa, constituting almost 70 % of the macrobenthic community, followed by Bivalvia, Crustacea and some Anthozoa (22).

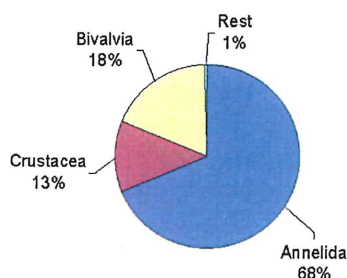


Figure 22. Relative abundance of the higher taxonomic classes at station 700.

The diversity (No) ranged from 2 (in 96S) to 30 (in 88A) with on average 14 spp/sample (Figure 23). The overall patterns in total density, total biomass and diversity showed cyclic upward-downward trends. No significant correlations were found between these biotic changes and the measured abiotic parameters.

Species that were almost always found at station 700 but with varying densities were the bivalves *Petricola pholadiformis* and *Abra alba*, the polychaetes *Nereis spp* and *Polydora spp* and the crustacean *Corophium spp*. All above mentioned species, except *Abra alba* appeared at higher densities during the 80's than during the nineties (Figure 24). Juvenile bivalves (*Abra alba*, *Ensis spp* and *Petricola pholadiformis*) and mud loving polychaetes (*Capitella spp*, *Heteromastus filiformis*, *Pygospio elegans* and *Nephtys hombergii*) and crustaceans (*Corophium spp*) were more abundant during the periods with higher mud concentrations. The presence of *Abra alba* during the nineties was mainly related with changes in the sediment (less mud, higher median grain size). When the median grain size decreased again, high numbers of mobile, predatory polychaetes (*Nereis spp*, *Eumida sanguinea* and *Phyllodoce spp*) appeared at station 700. Although some species (e.g. *Polydora spp.* and *Corophium spp*) were sometimes found in high abundances, their share in the overall biomass was always small in comparison with larger polychaetes or bivalves.

2.7.3 Station 710

Sediment

The average median grain size at station 710 over the consecutive sampling years was 210 µm, fluctuating between 173 and 317 µm (Figure 25). This station was characterised by sandy sediments with a dominance of the fine sand fraction, although during the mid 80's the medium sand fraction was more dominant (average median grain size 250 µm compared to 185 µm in the other years). The mud content was low (on average 2 %) during the whole sampling period.

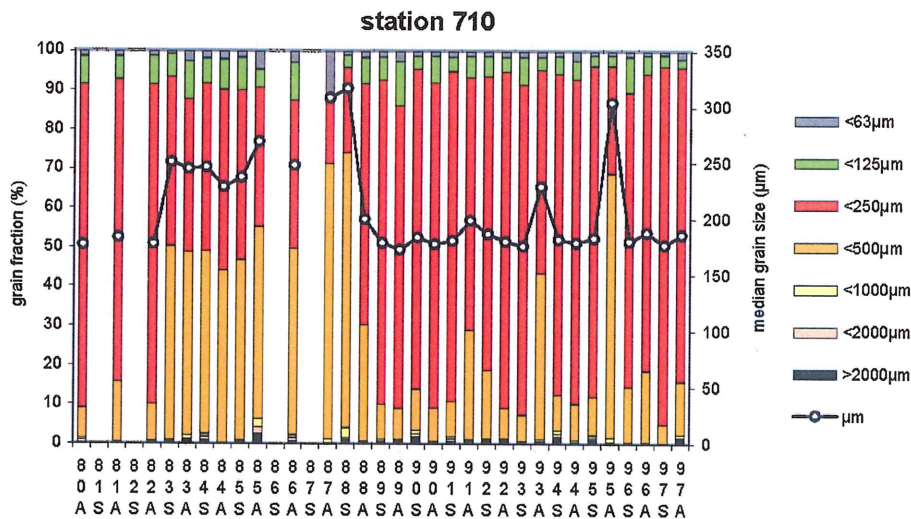


Figure 25. Time series of the grain fractions and median grain size over the period 1979-'97 (A= autumn, S= spring sampling campaign) for station 710.

Macrobenthos

The average densities at station 710 varied between 10 (92A) and 3920 ind/m² (94A). Annelida were the dominant taxa (>70 %) followed by Bivalvia and Crustacea (Figure 26). The rest fraction contained Anthozoa, Gastropoda and some Echinodermata species.

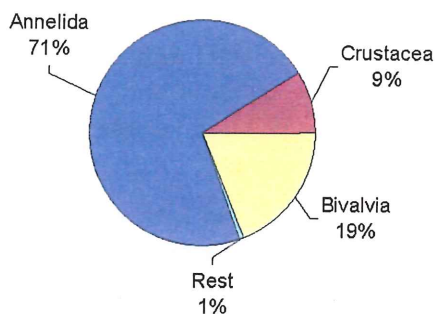


Figure 26. Relative abundance of the higher taxonomic classes at station 710.

Three peaks in abundance were observed in 81A, 88A, 94A, dominated by the polychaetes *Spio spp.*, *Spiophanes bombyx*, *Magelona johnstoni*, *Nephtys spp.* and *Lanice conchilega* (Figure 27). In most years the total density was <1000 ind/m². The diversity (No) more or less followed the same trend as total density with respectively 26, 25 and 19 spp/sample in 81A, 88A and 94A. The average diversity over the consecutive sampling periods was 17 spp/sample. The average biomass at station 710 was 50 g AFDW/m², ranging from <1 (84A) to 310 g AFDW/m² (97A). The biomass pattern showed strong fluctuations throughout the 80's and early 90's, but was more stable during the mid 90's with on average 150 g AFDW/m².

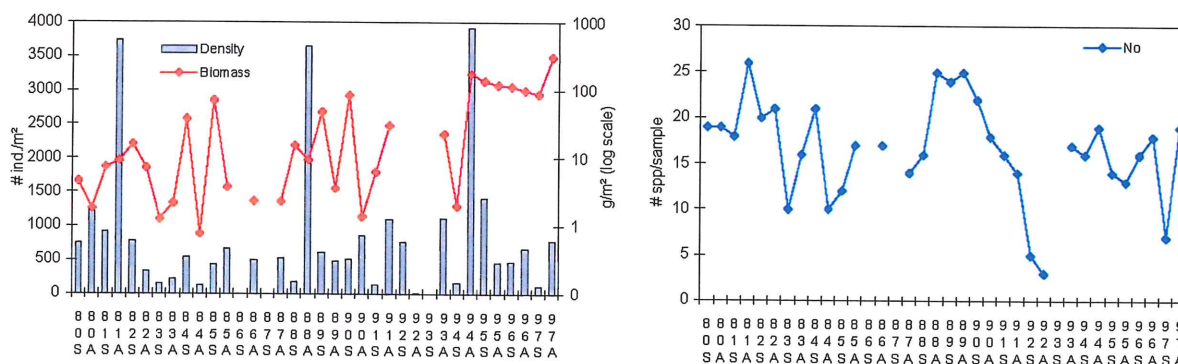


Figure 27. Time series of the overall density, biomass and diversity at station 710.

The species that were frequently found at station 710 throughout the sampled periods with varying densities were: *Nephtys spp.*, *Spiophanes bombyx* and *Spisula subtruncata*. The polychaetes *Nephtys spp* and *Scoloplos armiger* played an important role within the macrobenthos community of station 710 as they were constantly present at considerable densities (on average 70 and 30 ind/m², respectively) at this station (Figure 28). The higher biomass values of *Nephtys spp* were nearly all measured in early spring. *Magelona johnstoni* occurred at higher densities during the early 80's, but in 94A this species completely dominated the macrobenthos community (3170 ind/m² and 9 g AFDW/m²). The spionid polychaetes *Spio spp* and *Spiophanes bombyx* were also constantly present throughout the entire time series, and in three occasions they dominated the macrobenthos communities (81A, 88A and 93A).

Also, the crustaceans *Bathyporeia spp* and *Urothoe poseidonis* were frequently sampled at station 710, with higher densities during the 80's, although the peaks never occurred during the same period. This could suggest that both species are in competition of one another. Higher abundances of both species coincided with lower median grain sizes. The bivalve species *Abra alba*, *Spisula subtruncata* and *Tellina fabula* were frequently present during the whole time series, but never reached high densities. *Spisula subtruncata* showed a more or less 10 year cycle with lower densities during the beginning and end of the 80's and 90's, and peak densities during the mid 80's and 90's. For

Tellina fabula densities were higher (up to 190 ind/m²) during the 80's. In contrast, *Ensis spp.* were not recorded at station 710 before the 90's. The latter species showed a peak density of 1000 ind/m² in 91A and a peak biomass of 310 g AFDW/m² in 97A.

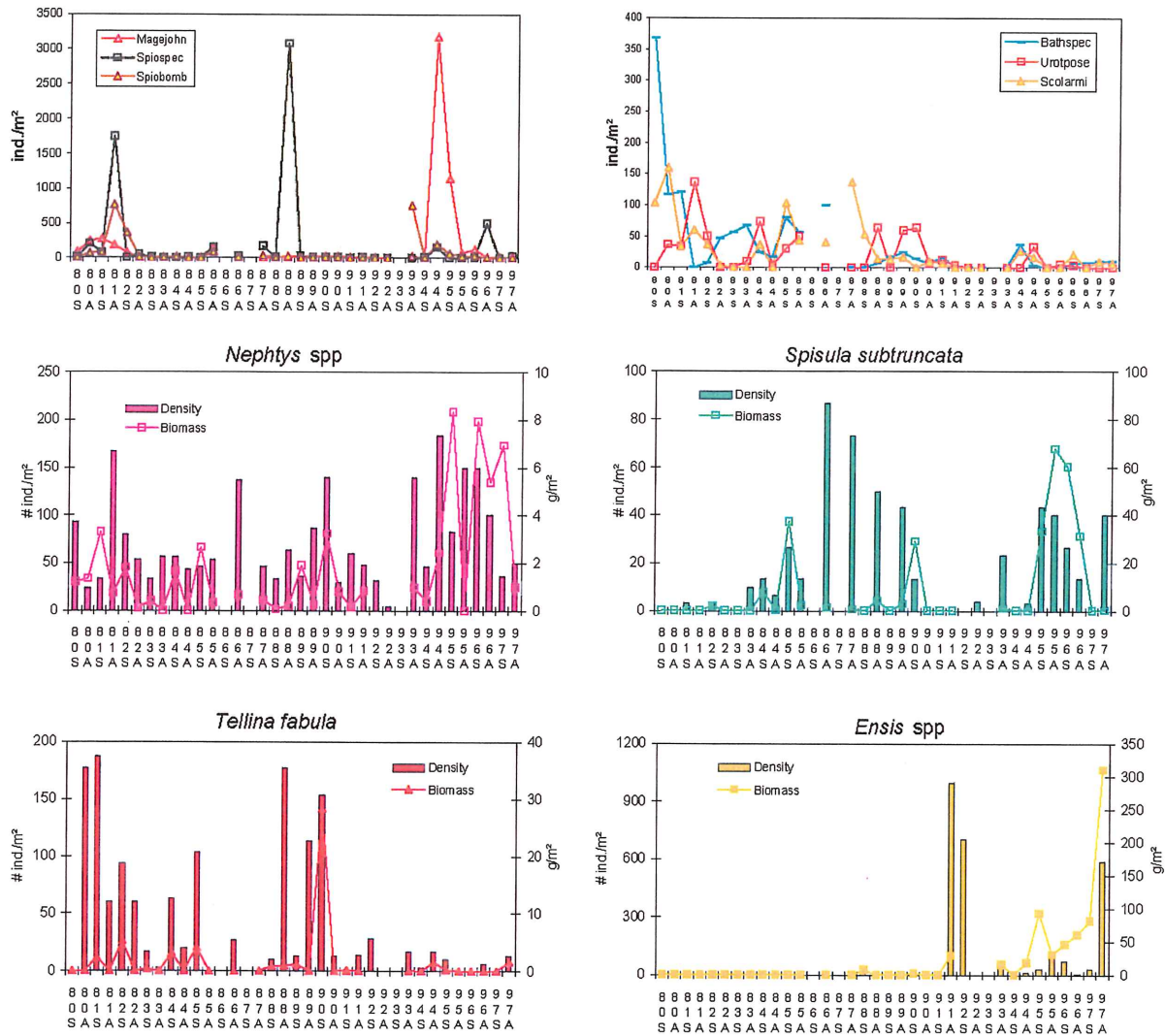


Figure 28. Time series of some important species in terms of density and biomass at station 710.

2.7.4 Station 780

Sediment

The average median grain size at station 780 over the consecutive samplings was 140 µm, fluctuating between 45 and 355 µm (Figure 29). During the early 80's the sediment was dominated by very fine substrates and the median grain size fluctuated around an average of 80 µm. During the late 80's and the 90's the sediment was more stable and fine sand (on average 170 µm) became the most important fraction.

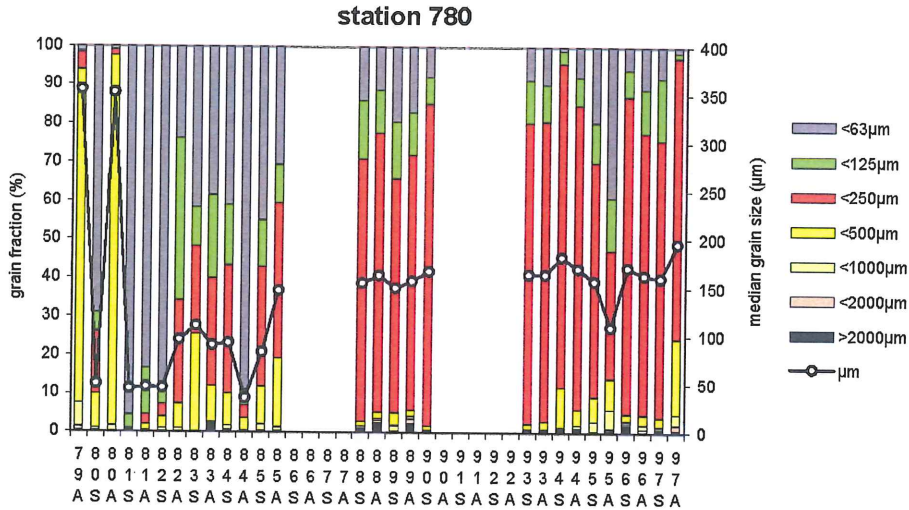


Figure 29. Time series of the grain fractions and median grain size over the period 1979-'97 (A= autumn, S= spring sampling campaign) for station 780.

Macrobenthos

At station 780 the average density ranged from 190 (94S) to 3900 ind/m² (89S). More than half of the taxa found at station 780 were Bivalvia and >30 % Annelida, followed by Crustacea, Echinodermata, Anthozoa and Gastropoda (Figure 30). The total densities largely fluctuated, with higher abundances (on average 3130 ind/m²) in 85A, 89S, 90A, 91A and 96S (Figure 31). Also, the total biomass fluctuated around an average of 220 g AFDW/m² with 4 higher peaks (on average 800 g AFDW/m²) at 90S, 91S, 94A and 95A. The average diversity (No) at station 780 over the entire time series was 21 spp/sample. A higher diversity was always noted for the autumn sampling campaigns, with three peaks >30 spp/sample in 85A, 88A and 94A. The observed patterns in total density, biomass and diversity were mainly related to seasonal fluctuations.

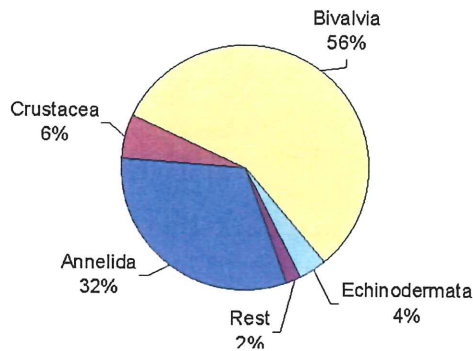


Figure 30. Relative abundance of the higher taxonomic classes at station 780.

The most common species in terms of abundance and frequency were the bivalves *Abra alba*, *Mysella bidentata* and *Spisula subtruncata*; the polychaetes *Nephtys hombergii* and *Scoloplos armiger*; the crustacean *Pariambus typicus*; and the echinoderms *Ophiura spp.* The density and biomass pattern of all above mentioned species largely fluctuated with peaks and dips throughout the sampled period (Figure 32). In contrast to the other bivalve species, the density and biomass of *Abra alba* remained much lower during the mid-nineties. The higher densities for *Mysella bidentata* coincided with lower densities for *Spisula subtruncata* and vice versa.

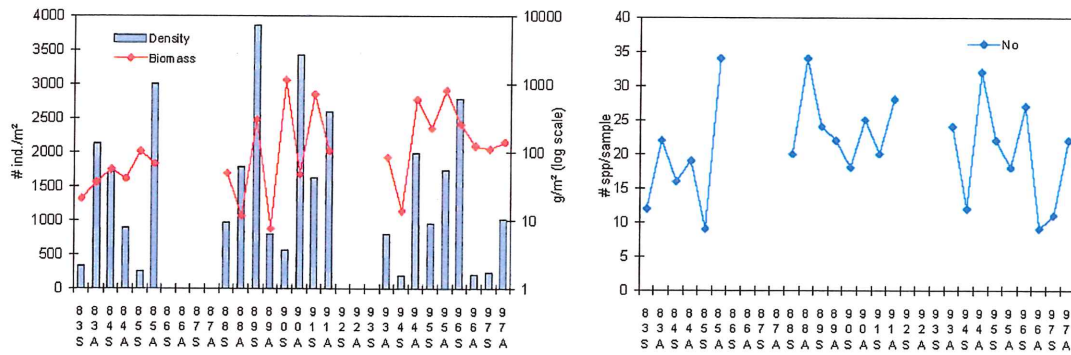


Figure 31. Time series of the overall density, biomass and diversity at station 780.

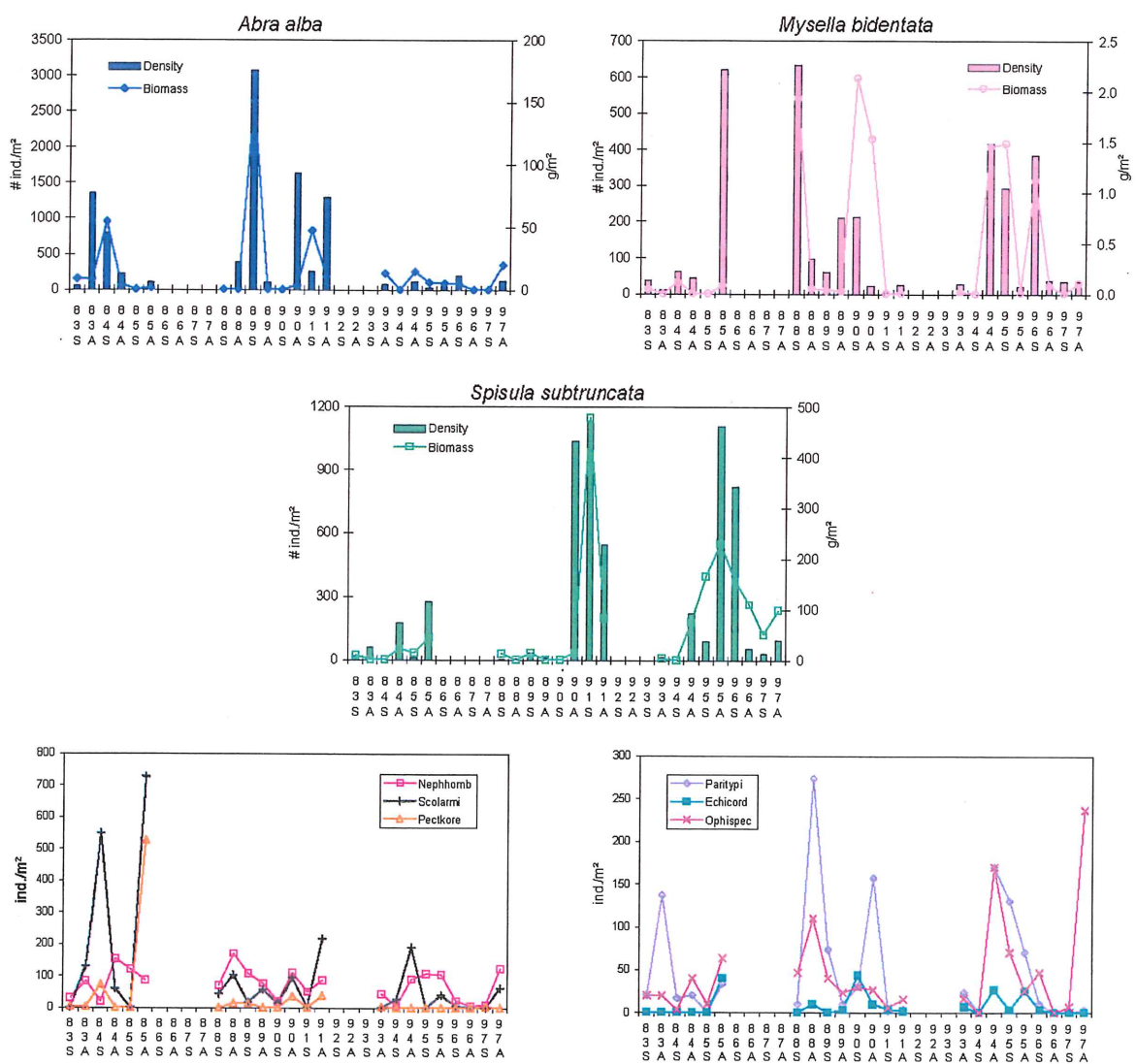


Figure 32. Time series of some important species in terms of density and biomass at station 780.

The density pattern for *Nephtys hombergii* was quite similar to that of *Scoloplos armiger*, except for the peaks in 84A and 85S (550 and 730 ind/m² respectively). Also, *Pectinaria koreni* was hardly found during the mid-nineties. The only common crustacean *Paritypi* also showed fluctuating densities, with higher density peaks more or less correlated with a little higher median grain

size. The common presence of echinoderms, sometimes in high numbers, was typical for station 780. *Echinocardium cordatum* was frequently sampled throughout the entire time series but always in low abundance. *Ophiura spp* showed peak densities during several autumn periods. Strong decreases in density, diversity (No) and biomass were recorded for several periods, where the common taxa were found at either low or high abundances during the same period.

2.7.5 Station 120

Sediment

The average median grain size at station 120 over the entire time series was 200 μm , fluctuating between 115 and 286 μm , with the highest values noticed during the period 1981 to 1985 (Figure 33). The mud concentration varied between 2 and 10 %. Spring 1996 could be considered as an outlier with mud concentrations of 40 % and median grain size of 115 μm .

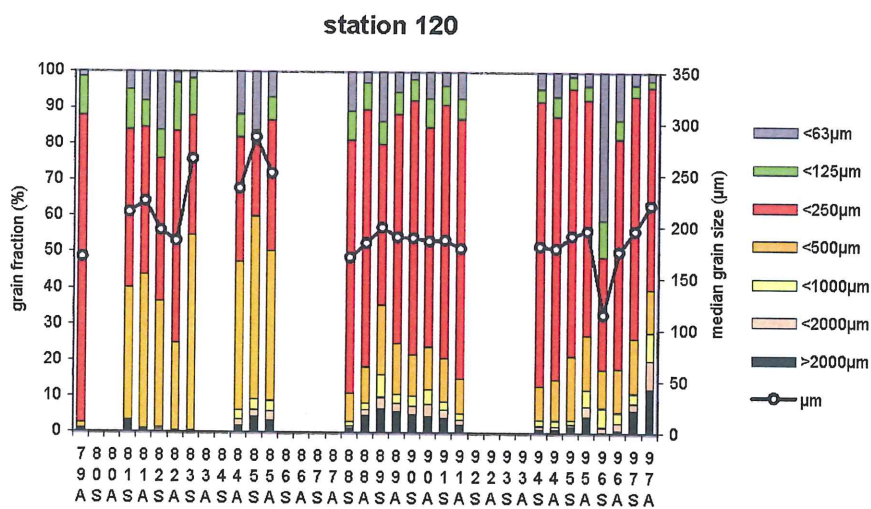


Figure 33. Time series of the grain fractions and median grain size over the period 1979-'97 (A= autumn, S= spring sampling campaign) for station 120.

Macrobenthos

The average total densities at station 120 varied between 220 (85S) and 5000 ind/m² (83A). The most abundant taxa were Annelida (>50 %), followed by Bivalvia and Crustacea (Figure 34). Echinodermata, Gastropoda, Anthozoa and Pycnogonida filled the remaining gap. In general, higher densities in autumn were followed by lower values in early spring (except for 90S). Highest total densities (on average 3870 ind/m²) were recorded in 83A, 94A, 95A and 97A (Figure 35).

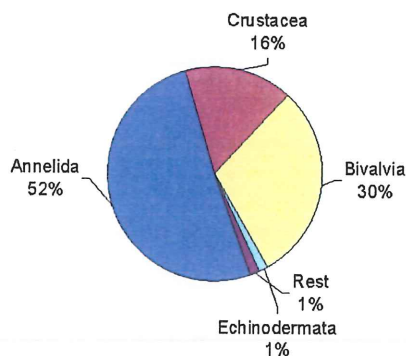


Figure 34. Relative abundance of the higher taxonomic classes at station 120.

The diversity (No) followed an almost identical pattern as the total density. The average diversity (No) at station 120 during the sampled periods was 26 spp/sample, ranging from 8 (83S) to 48 spp/sample (83A). The total biomass varied from 2 (81A) to 1550 g AFDW/m² (97A), with an average of 220 g AFDW/m². During the 80's the biomass followed an opposite pattern compared to density with higher biomass values in spring. During the mid-nineties seasonal patterns in biomass were less pronounced, with higher peaks in autumn and overall higher values (on average 650 g AFDW/m²) than the previous period (on average 80 g AFDW/m²).

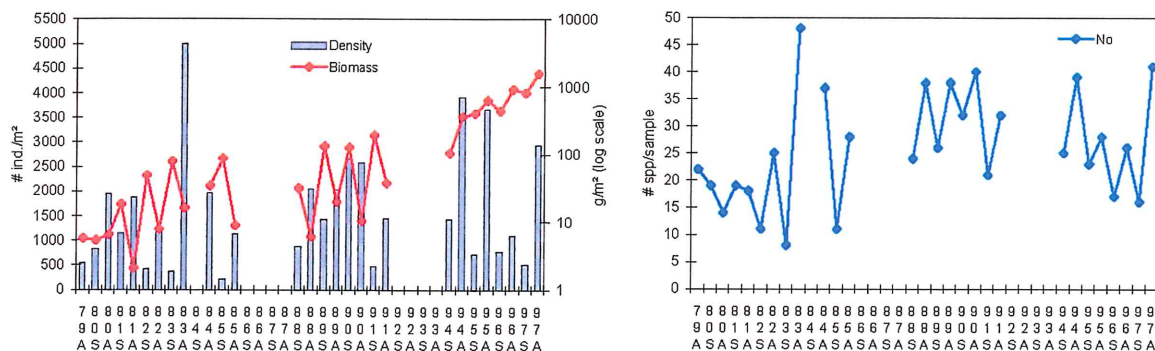


Figure 35. Time series of the overall density, biomass and diversity at station 120.

Species that were frequently found at station 120, sometimes at high densities were the bivalves *Abra alba*, *Tellina fabula*, *Mysella bidentata*, *Spisula subtruncata* and *Ensis spp*; the polychaetes *Chaetozone setosa*, *Eumida sanguinea*, *Lanice conchilega*, *Nephtys spp*, *Scoloplos armiger*, *Pectinaria koreni*, *Phyllodoce spp*, and *Spiophanes bombyx*; and the crustaceans *Pariambus typicus*, *Microtopotus maculatus* and *Abludomelita obtusata*.

Abra alba was almost always present at station 120, but with large fluctuations in density and biomass and with peak densities in autumn '83 and '90 (660 ind/m²). Also, a few biomass peaks were noted for *Abra alba*, although these peaks were not necessarily followed by higher recruitment the following year (Figure 36). Both *Tellina fabula* and *Mysella bidentata* reached higher values during the early 80's at station 120, while they were present at low numbers during the rest of the sampled periods. On the contrary, *Ensis spp*. and *Spisula subtruncata* were mainly found during the 90's, with the latter species limited to the second half of the nineties. *Spisula subtruncata* dominated the macrobenthic community after a massive recruitment in summer '95 (data not shown here). The density pattern for *Tellina fabula* and *Spisula subtruncata* was comparable to the pattern found at station 710. Also, the density peaks were followed by biomass peaks in the consecutive years.

Several polychaete species showed one or more peaks, while during the rest of the sampled period they were present only at low densities. In the beginning of the 80's *Pectinaria koreni* dominated the macrobenthic community at station 120, with a peak density of 1610 ind/m² in 80A followed by a peak biomass of 9 g AFDW/m² in 81S. After 1983, *Lanice conchilega* became the most frequently sampled polychaete species, with largely fluctuating densities. The biomass peaks for *Lanice conchilega* were always noted in the same season as the density peaks. Almost the same pattern was found for *Eumida sanguinea*, a species that dominated several times the macrobenthic community at station 120. At the beginning of the 90's *Spiophanes bombyx* and *Nephtys spp* were dominant with maxima of 350 and 480 ind/m² respectively in 90A. The latter species was always present in higher abundances. During the mid-nineties *Magelona johnstoni* and the opportunistic species *Chaetozone setosa* were dominantly present.

For three crustaceans *Pariambus typicus*, *Abludomelita obtusata* and *Microprotopus maculatus* higher densities were noted since 1983. The density pattern of all three species revealed similar seasonal oscillations.

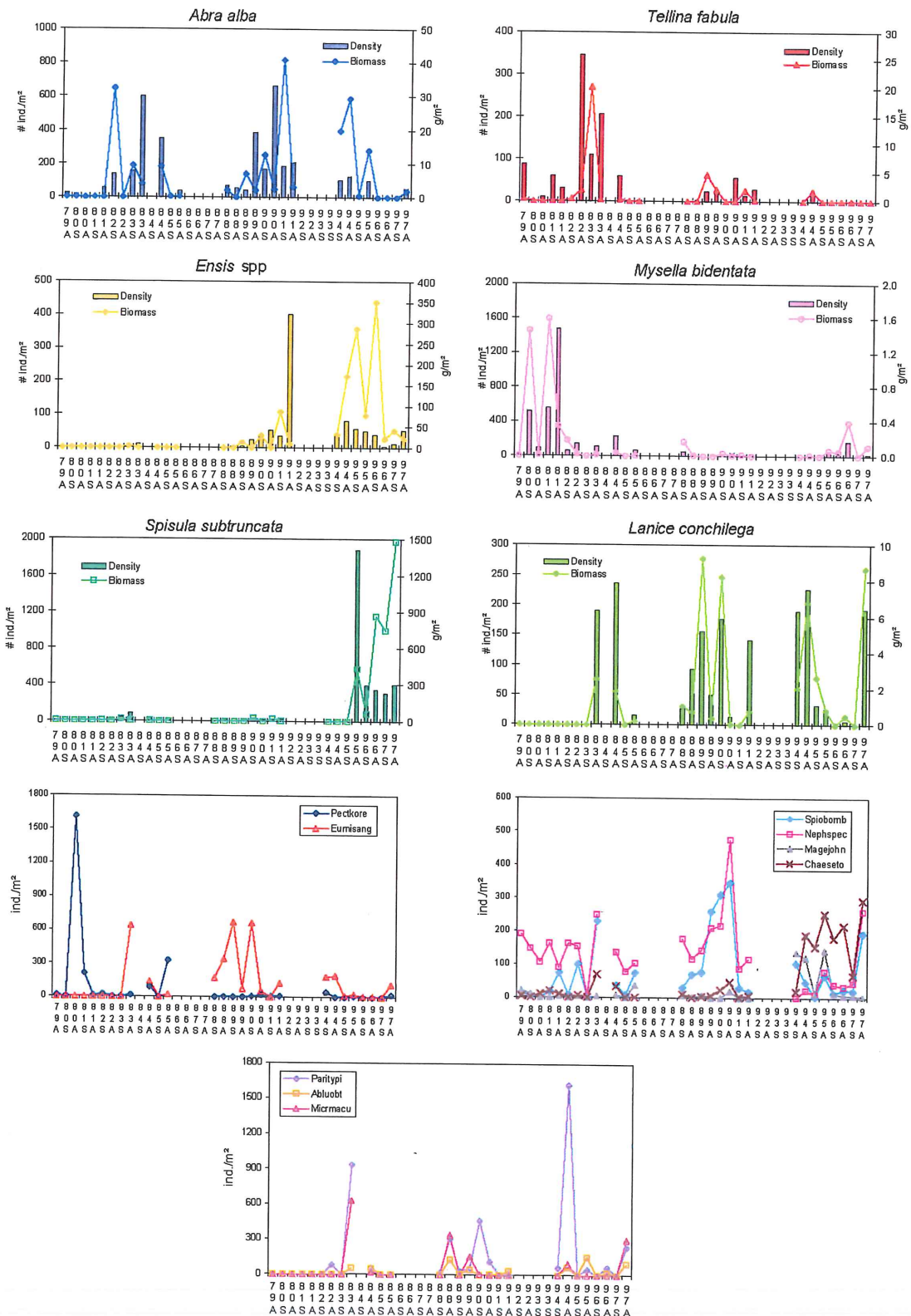


Figure 36. Time series of some important species in terms of density and biomass at station 120.

2.8 Impact of anthropogenic activities on macrobenthos

2.8.1 Sand and gravel extraction

The extraction of sand and gravel started in 1979 in two specific zones of the BCS: Thorntonbank and Gootebank as parts of extraction zone 1, and Kwintebank, Buiten Ratel and Oost Dyck as parts of zone 2. From 1979 to 1986 private companies extracted ca. $0.5 \cdot 10^6 \text{ m}^3$ yearly, which was mainly used for building, beach nourishment and land reclamation (e.g. port of Zeebrugge). From 1987 onwards (data available until 2002) the extracted amount more than doubled with a peak of $3.9 \cdot 10^6 \text{ m}^3$ in 1997 (Rzonzef, 1993) (Figure 37).

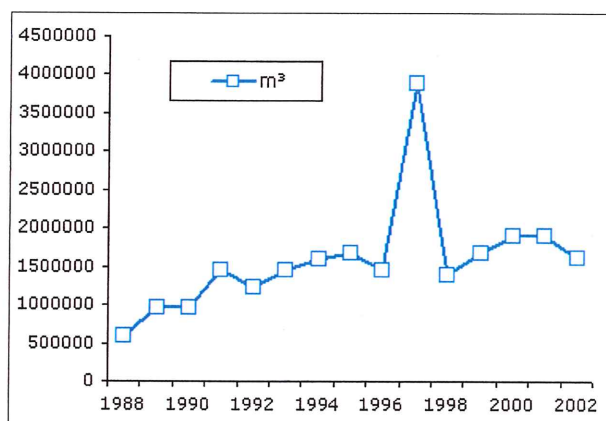


Figure 37. Total volume of sand extracted between 1988 and 2002 on the BCS.

The ecological impact of sand and gravel extraction on the marine environment is monitored by DvZ (Sea Fisheries Department) and MUMM (Management Unit of the Mathematical Model of the North Sea). Kenny & Rees (1996) and Desprez (2000) concluded that sand extraction activities have an impact on macrobenthic communities. The extraction processes may affect the benthic species through removal, smothering, and damage caused by the dredge head (Phua et al., 2004). As benthos is considered the main food source for demersal fish, it is expected that destroying the benthos will have an impact on the present fish stocks. On the other hand, the extracted and discarded biota can be seen as an easy food source for scavengers. However, the only biological changes in macrobenthic density and diversity that were found in the ongoing monitoring studies by DvZ were related to seasonal fluctuations rather than to sand extraction (Maertens, 1981a,b; Maertens, 1988; Maertens, 1990; Anon. 1997b; Moulart et al. 2005).

2.8.2 Dredging

During the period 1979-1991 about $30 \cdot 10^6 \text{ m}^3$ dry material was dredged yearly for the maintenance and deepening of the sea ports (Zeebrugge, Oostende, Nieuwpoort and Blankenberge) and their sea approaches (Scheur West and Oost, Pas van het Zand) (Anon, 1993). Most of the dredged material is dumped back in the sea at licensed dumping sites (Oostende, Zeebrugge Oost, S1 and S2). Physical processes involved in dredging and dumping are: (re)suspension, secondary deposit, loss and transport by currents (Essink, 1996) (Figure 38).

The ecological impact of dredge dumping is monitored by DVZ since 1979. No negative effects on the macrobenthos and epibenthos communities could be detected in the surroundings of the different dumping sites of the Belgian Continental Shelf (Hostens et al., 2005). Also, several chemical

and biochemical indicators that are monitored did not show any relation with the dredge dumping (Cooreman et al., 2001).

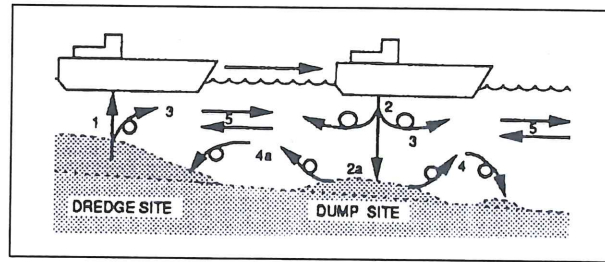


Figure 38. Physical processes during dredging (1) and dumping (2): suspension (3), resuspension and secondary deposition (4), loss (4a) and transport by currents (5)

2.8.3 Fisheries

The coastal and Flemish Banks are rich fishing grounds and intensively fished by means of beam trawls. In general, the coastal zone is mainly fished by small shrimp trawlers, whereas the bigger flatfish trawlers operate near the Flemish Banks. The penetration of the beam trawl in the bottom varies from 1 to 8 cm. Depending on the local circumstances, the pathways left by the beam trawls will disappear. In areas with fine sandy sediments which are exposed to tidal currents the marks disappear in a period of 37 hours, but on muddy sediments in sheltered areas it may take 18 months. The negative effect on the benthos community mainly depends on the size of the animals: fragile or superficial living species show high mortalities (>50 %), while the mortality is low for robust or deeply burrowing species (Anon, 1998).

2.8.4 Former industrial waste sites

Between 1960 and 1990 industrial waste (titanium dioxide, thiocarbamate and aniline) was legally dumped in an area near the Hinderbanks. No clear impacts on the structural diversity of the macrobenthic communities could be measured (Maertens 1984, 1987, 1989). Also, for the meiofauna communities within dumping area of the Dutch Continental Shelf no significant changes could be shown (Smol et al., 1989, 1990 & 1991).

2.8.5 Military exercises

Besides military exercises at sea conducted by the Belgian navy and NATO partners, there are military shooting exercises on land in the direction of the sea at Nieuwpoort-Lombardsijde. These activities are no direct threat to the marine benthos communities.

3 Discussion

3.1 Methodological considerations

Variations in sampling methodology may lead in many ways to different species compositions. Four main variables can introduce bias in the processing of macrobenthic samples: the location of the sampling stations, the size of the sampling gear, the moment of fixation of the animals, and the sieve mesh size.

During most of the '94-'01 campaigns the macrobenthos was gathered by only one Van Veen grab per station, from which a sub-sample was taken for sediment analysis. In the period '76-'86, several Van Veen 'replicates' for the macrobenthos and one separate sediment sample were taken per station. Depending on the weather and current conditions, the distance between the 'replicates' can amount from 10 to a few hundred metres, leading to a possible risk of sampling different sediment types or even different macrobenthic communities. Therefore, all 'replicates' were considered as separate samples in the present study.

With a smaller Van Veen grab (0.1 against 0.12 m²) less sediment can be extracted which can lead to a possible underestimation of the local diversity. The same holds if the animals are sieved 'alive' over a 1 mm sieve, prior to fixation in formaline. A recent study by Moulart (2003) confirmed that small polychaetes (*Nephtys cirrosa*, *Nephtys* juv., *Eteone longa*, *Hesionura elongata*, *Polygordius appendiculatus*, *Spiophanes bombyx*, *Spio filicornis*, *Eumida sanguinea*, *Glycera capitata*, *Pisione remota*, *Magelona johnstoni* and *Sphaerosyllis hystrix*) and even amphipods (*Bathyporeia* spp and *Pontocrates arenarius*) can escape through a 1 mm sieve, either actively or passively.

Finally and probably the most important source of bias, different sieve mesh sizes largely affect the final species composition. Mare (1942) defined macrofauna as organisms larger than 1 mm, a definition adopted by most scientists. However, Holme & McIntyre (1971) recommended a lower size limit of 0.5 mm, as part of the macrofauna is not being examined and many small (interstitial) species and juveniles are under-represented or excluded (Reish, 1959; Govaere, 1978; Hartley, 1982). By excluding the smaller and less frequently sampled species the common species will be overestimated, which might obscure the separation of the different macrobenthic communities (Govaere, 1978). Of course, the choice of the mesh size is a cost effective compromise between ease of sorting and accuracy of results. In general, a 1 mm mesh is appropriate for pollution monitoring studies, while studies with a more frequent sampling scheme are advised to use a 0.5 mm mesh size (Hartley, 1982). This would increase the potential for detailed inter-study comparisons and thus facilitate the demonstration of widespread faunal changes at the species or community level.

3.2 Spatial and long-term variation

As the macrobenthos data from the extensive Gilson collection from 1898-1939, which is stored at the Royal Belgian Institute of Natural Sciences (RBINS/KBIN), were not yet available, the spatial and long-term comparison of the macrobenthos was limited to the periods 1976-'86 and 1994-2001, based upon data from the Marine Biology Section at Ghent University and from the Sea Fisheries Department.

3.2.1 Spatial variation

Many authors have described and quantified macrobenthic soft-bottom communities. Petersen (1914) was the first one to draw attention to the recurring associations of soft-bottom animals, characterised by the dominant species in terms of numbers and/or biomass. Alternative classifications, but equally based on sediment and depth characteristics, have been put forward and followed by different authors (Jones, 1950, Kingston and Rachor, 1982; Duineveld et al., 1991; Künitzer et al., 1992; Heip and Craeymeersch, 1995; Degraer et al., 1999; Van Hoey et al., 2004).

In the present study the identification of the different communities or species assemblages was based on Morin (1999), by means of (1) their position along a habitat gradient outlined by habitat boundaries; (2) dominance of indicator species; and (3) the result of several multivariate analyses (all species assemblages were positioned along the first axis of the DCA, which was strongly correlated with median grain size and mud content). A distinction in Type I and Type II species assemblages has been made according to Van Hoey et al. (2004). Based on the difference in habitat and species composition, three so-called Type I species assemblages were identified for the BCS: the *Abra alba*-*Mysella bidentata* community (SA2), the *Nephtys cirrosa* community (SA5), and the *Ophelia limacina*-*Glycera capitata* community (SA10). A fourth Type I species assemblage was identified according to Budd (2002) as a *Macoma balthica* community.

Seven transitional Type II assemblages were identified, although each of them was more or less comparable to one of the Type I SA's. Of course, due to some arbitrary criteria (e.g. exclusion of species based on rareness) some transitions between related species assemblages could be considered variable. This is mostly observed between the *Nephtys cirrosa* community and the *Ophelia limacina*-*Glycera capitata* community. Also, the spatial distribution maps of the different species assemblages should merely be used as a guide in detecting them. Dependent on the habitat type one species assemblage can flourish better than the other, but as there are no real barriers a natural overlap between the species assemblages is evident.

Abra alba-*Mysella bidentata* species assemblage

The *Abra alba*-*Mysella bidentata* community has been described by several authors for the northern and southern areas bordering the BCS (Souplet & Dewarumez, 1980; Kingston & Rachor, 1982; Künitzer et al., 1992; Olivier et al., 1996; Holtmann et al., 1996, Desroy et al., 2002). This species assemblage is characterised as a species rich community with sometimes high abundances. Its distribution on the BCS was mostly confined to the 12 nmile zone in both periods.

The average density (5080 ind/m²), diversity (33 spp/sample) and species composition of the *A. alba* community along the neighbouring Northern French coast were comparable to the BCS, but the total number of species increased further to the south from 150 species at Gravelines (Côte d' Opale) to 400 species at Pierre Noire (Baie de Morlaix) (Fromentin et al., 1997b; Desroy et al., 2002). Towards the north along the Dutch coast, the *A. alba* community was characterised by a lower average density (2560 ind/m²) and a lower diversity (14 spp/sample) (Holtmann et al., 1996).

Nephtys cirrosa species assemblage

The *N. cirrosa* community as described in Van Hoey et al. (2004) has also been referred to as the 'Boreal offshore sand association' (Jones, 1950) or Venus community (Petersen, 1914). The distribution of the *N. cirrosa* community ranged from the coastal area to the most offshore areas of the BCS, but mainly concentrated on clean medium sand sediments on top of the Flemish Banks (Kwintebank and Buitenratel). This species assemblage plays a central role on the BCS, with a low diversity and low average density (respectively 6 spp/sample and 420 ind/m²). This is typical for

well-sorted mobile sands, which are characterised by mobile polychaetes (e.g. *N. cirrosa*) and amphipods (*Bathyporeia* spp) (Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996; Van Hoey et al., 2004). The fact that *N. cirrosa* was found in several other SA's at relatively high abundances confirmed the large niche width of this eurytopic species (Rainer, 1991).

Ophelia limacina–*Glycera capitata* species assemblage

The *Ophelia limacina*–*Glycera capitata* assemblage is typically found in medium sand sediments with low mud contents (Degraer, 1999; Van Hoey et al., 2004). The SA was characterised by species like *Hesionura elongata*, *Ophelia limacina*, *Nephtys cirrosa*, and *Glycera capitata*, comparable with Van Hoey et al. (2004). Other indicator species that were not found in the latter study are *Gastrosaccus spinifer* and *Polygordius* spp.

Macoma balthica species assemblage

The *Macoma balthica* community was closely related to the *A. alba*–*M. bidentata* community. A clear separation was not observed but the habitat characteristics (very high mud contents) and the occurrence of some specific species (e.g. *Macoma balthica*, *Pectinaria koreni*) within the *M. balthica* community were enough to separate them from the *A. alba*–*M. bidentata* cluster. In recent years, the distribution of the *M. balthica* species assemblage was limited to the eastern part of the Belgian coast.

3.2.2 Comparison between both periods

In general, it can be concluded that although similar macrobenthic communities were found in both periods (taking into account the differences in sampling methodology), significantly higher numbers of species per sample and higher densities were recorded during the period 1994-2001.

Loss and gain of species

As already mentioned, the number of species per sample during the period 1994-2001 was significantly higher than during the period 1976-'86. However, several species were not recorded in one of the two periods. Taken into account criteria such as sampling methodology, undersampling of habitats, possible identification errors, new insights in taxonomy, species rareness, and after eliminating all non-macrobenthos species, five frequently sampled species in 1976-'86 were missing in the '94-'01 data set, and vice versa.

Possible explanations concerning the loss and gain of macrobenthic species on the BCS are related to sediment type, drifting and invasion of exotic species, and habitat disturbance due to pollution. It is known and confirmed by this study that species richness is correlated with sediment grain size and mud concentration (Van Hoey et al., 2004). For example, the absence of *Pectinaria belgica* in '94-'01 is probably related to the fact that its preferred habitat (*i.e.* fine sandy sediments with >10 % mud content) was almost not sampled during that period.

The dispersal by larvae is usually considered as the main process which determines the spatial distribution of marine invertebrates with a benthoplanktonic life cycle (Olafsson et al., 1994). However, some polychaetes and molluscs are able to drift in the water column (Butman, 1987). Two species that were present in low numbers in the western part of the BCS in different periods, namely *Phaxas pellucidus* and *Acrocorda brachiata* are known to use this type of dispersion (Olivier et al., 1996). Invasive species that can adapt to the North Sea climate often remain permanently in the system. Some species, like slipper limpet *Crepidula fornicata*, which was imported at the end of

the 19th century, or American jack-knife clam *Ensis directus*, which was observed in 1987 for the first time on the BCS, develop so strong that they negatively impact the native benthic fauna.

Finally, the species composition and the density of the macrobenthos may change in response to pollutant stress, as not all species are equally sensitive to pollution (Hartley, 1982). Evidence of macrofauna changes in relation to increased eutrophication in the coastal parts of the North Sea has been given by Rachor (1990). However, habitat disturbance due to organic enrichment and contamination by toxic substances of the sediment (Pearson & Rosenberg, 1978; Gray, 1981; Hartley 1982) are beyond the scope of this study.

Changes in density

In general, similar Type I SA's were found in both periods ('76-'86 and '94-'01) in terms of species composition. Nevertheless, several dissimilarities were noted, mainly due to differences in sampling methodology rather than to long-term biological variations.

The dissimilarity within the *Ophelia limacina*-*Glycera capitata* community of both sampled periods was mainly caused by a small interstitial polychaete *Hesionura elongata*. As already argued before this was due to the smaller sieve mesh size used in the period 1976-'86.

The higher average density per sample for the period 1994-2001 over the whole BCS was related to the fact that most of the samples in this period were taken in the *A. alba*-*M. bidentata* species assemblage, in contrast to the period 1976-'86 where the samples were more evenly distributed over the different species assemblages. Moreover, twice as many samples were analysed for the period '94-'01. The concentration of samples within a small area (mainly around the West coastal banks) with a higher density and diversity, surely contributed to the higher average density over the whole BCS for the period '94-'01.

Also, the difference in sampling frequency (*i.e.* seasonality) was not taken into account: for the period '76-'86 most samples were taken in (late) autumn, in contrast to the period '94-'01 where different months and seasons were sampled. This explains why the recruitment and settlement of young bivalves (e.g. *Abra alba* or *Spisula subtruncata*) in sometimes high densities was only observed in the latter period.

The central position of the *N. cirrosa* species assemblage within the macrobenthic communities of the BCS (Van Hoey et al., 2004) was largely confirmed for both sampling periods. The fact that this community was more found on than between the sandbanks during the period 1994-2001, is probably related to the sampling strategy rather than to local changes in sediment composition due to hydrodynamic changes.

3.3 Detailed long-term variation

The success of recruitment and production, and hence mortality and the year-to-year variation in macrobenthic communities are controlled by both physical and biological conditions. Extreme weather conditions (Dörjes et al., 1986; Meire et al., 1994; Fromentin et al., 1997a), currents (De-warumez et al., 1986), and sediment type (Rees et al., 1975; Shackley & Collins, 1984; Holtmann et al., 1996; Degraer et al., 1999) play significant roles in the abundance of macrobenthos species. As long as the main habitat characteristics do not change drastically, the basic composition and distribution of the benthos communities remain 'stable' for longer time periods (Govaere et al., 1980; Turner et al., 1995; Degraer et al., 1999).

3.3.1 Weather and hydrodynamic conditions

In temperate regions short-term seasonal changes in the environment (mainly temperature) are very important in the temporal structuring of the macrobenthos species assemblages (Beukema, 1974; Arntz & Rumohr, 1986; Dauvin & Ibanez, 1986; Ibanez & Dauvin, 1988; Beukema et al., 1993; Seys et al., 1994; Degraer et al., 1999). Species with an annual recruitment mostly increase in numbers and biomass in summer and autumn, followed by considerable winter mortalities (Gray, 1981). For example, at station 120 both abundance and diversity patterns showed seasonal fluctuations, with low densities and species richness in early spring and higher values in autumn.

However not every species recruits every year and the amplitude of this seasonal pattern can fluctuate strongly over the years. This phenomenon was observed for several bivalve species. According to Fromentin et al. (1997a), temperature changes have an important long-term effect on the distribution and abundance of species, especially in northern Europe where the temperature largely fluctuates. Very cold winters may be disastrous for several macrobenthic species. For example, the density pattern of *Abra alba* showed strong fluctuations during the beginning and end of the 80's at 3 stations. *A. alba* is considered as an indicator species because of its short life expectancy of 1 to 2 years (Holtmann et al., 1996) and its capacity to quickly colonise a habitat (Fromentin et al., 1997a).

It has been shown that frequent changes in wind and current direction affected the larval transport between the English Channel and the southern part of the North Sea (Fromentin et al., 1997a). This explained the mass recruitment of several dominant macrobenthic species in the Gravelines area (France) (Duwarumez et al., 1986; Konstantinos et al., 2001). Strong NE-winds together with strong currents can carry large numbers of larvae towards the Belgian coast. This secondary recruitment during the autumn period might explain some of the density peaks noted at station 120.

3.3.2 Sediment type and dredge dumping

The physical environment around the stations where dredged material is dumped might change, although <40 % of the dumped material stays behind on the dumping sites (IHE-BMM, 1990). However, the sediment on the dumping sites is almost clean sand, as the fine silt fraction is mostly suspended and spread around according to the local wind and current pattern (IHE-BMM, 1994).

Several authors concluded that changes in the local macrobenthic communities only occurred immediately after the dumping of dredged material (Anon, 1997a; Essink, 1996; Daan et al., 1998). Possible effects of dredge dumping are: (1) interference in primary production due to changes in light conditions; (2) physical burying of the benthos; and (3) ecotoxicological effects (Essink, 1996).

Consecutive dumpings might be followed by a gradual increase of short-living opportunistic species, as they can adapt quickly to sudden disturbances due to their high growing and turn-over rates (Levings, 1982; Rumohr, 1996). In case all dumped material is suspended (or after dumping has ceased) less opportunistic long-living species may be found (again) in the area (Mazijn, 1988; Harvey, 1998).

The present detailed long-term study is based on a sampling strategy with spring and autumn campaigns organized independently of the dumping frequency. This makes it difficult to measure the impact of sediment dumping on the local fauna. Similar conclusions were drawn from studies on the Dutch Continental Shelf (Anon, 1997a) and in other areas (Underwood, 1993). Still, it is concluded that dredge dumping has no clear long-term effect on the macrobenthos communities of the BCS.

3.3.3 Biological interactions

Large fluctuations in species density and biomass can have an effect on biological interactions such as predation and competition for food and space (Meire et al., 1994; Turner et al., 1995). For example, in the summer of 1995 an overwhelming recruitment of *Spisula subtruncata* took place with a maximum recorded density of $1.5 \cdot 10^5$ ind/m² in the vicinity of station 120 (Degraer, 1999). These juvenile *S. subtruncata* out-competed the other species for space, food and oxygen as they covered the sediment with a 1 cm thick layer of animals. Consequently, the diversity and density of most other species decreased considerably during the following months, leading to clear changes in the community structure (Degraer, 1999). This was reflected in the present study, where several pre-dating polychaetes (*Phyllodoce* spp, *Nephtys hombergii*, *Nereis* spp) were found at higher densities at station 120 during that period. Also scavengers like *Hinia reticulata* and *Ophiura ophiura* were attracted to the growing food source. On the other hand, *S. subtruncata* was absent in >30 % of the *A. alba*-*M. bidentata* community around station 120. This supports the idea of the patchy distribution of most bivalves, even in an optimal habitat (Meire et al., 1994).

Another example is given by means of the tube building polychaete *Lanice conchilega*. This species is an important key species in the *A. alba*-*M. bidentata* species assemblage and its presence affects in many ways the abundance and diversity of the entire macrobenthos community. First of all, the tube aggregations have a marked, but short-lived effect on the benthic community (Zühlke, 2001). Species like *Harmothoe* spp, *Eumida sanguinea*, *Gammarus* spp and *Microtopopus maculatus* are clearly associated with these *Lanice* tubes (Dauvin et al., 2000; Zühlke, 2001). Secondly, they facilitate the oxygen supply in the sediment around the tubes. Finally, the tube aggregations provide a settlement surface for other larval and post-larval benthic organisms (Qian et al., 1999), and they can serve as a refuge from predation (Crowder & Cooper, 1982). *Lanice conchilega* was first recorded in autumn 1983 at station 120. Three amphipods *Microtopopus maculatus*, *Pariambus typicus* and *Abludomelita obtusata* were closely associated with *L. conchilega*, as they were found in higher densities when *L. conchilega* was present in considerable densities.

4 Conclusions and Recommendations

The first part of the MACROBEL project describes the spatial and long-term distribution patterns of the macrobenthos on the Belgian Continental Shelf (BCS), by means of multivariate analyses and variation in density and species composition. Next to this report, the results, based on spatially scattered data from the periods 1976-'86 and 1994-2001, are disseminated by means of an interactive website hosted at VLIZ (<http://www.vliz.be/vmdcdata/MACROBEL>) and (as an extension of this project) in a distribution atlas considering approximately 50 interesting macrobenthos species.

Recommendation 1. New data are continuously gathered and processed through various projects at several institutes. An update of the long-term series on a regularly basis will improve the value of the dataset.

Based on the differences in habitat and species composition, four so-called Type I species assemblages were identified for the BCS: the *Abra alba*-*Mysella bidentata*, *Nephtys cirrosa*, *Ophelia limacina*-*Glycera capitata*, and *Macoma balthica* communities. Seven transitional Type II assemblages were identified, which could largely be associated with one of the Type I SA's. The *Abra alba*-*Mysella bidentata* and *Macoma balthica* assemblages are typically found in fine sand sediments with medium (or high for the *M. balthica* SA) mud contents, and largely confined to the 12 nautical mile zone, with a high diversity and sometimes high densities. The *Nephtys cirrosa* assemblage plays a central role on the BCS, found nearly all over the BCS, with low diversity and density which is typical for well-sorted mobile sands. The *Ophelia limacina*-*Glycera capitata* assemblage is typically found in medium to coarse sand sediments with low mud content, mainly in the more offshore part of the BCS and on the Flemish banks.

Based on several subjective reduction criteria, it was concluded that 5 macrobenthos species were newly recorded in the period 1994-2001, while 5 other species were not recorded anymore during that period. Possible explanations concerning the loss and gain of macrobenthic species on the BCS are related to sediment type, drifting and invasion of exotic species, and habitat disturbance due to pollution. Still, it can be concluded that although similar macrobenthic communities were found in both periods (1976-'86 and 1994-2001), most dissimilarities were mainly due to differences in sampling methodology rather than to long-term biological variations. It was shown that both species composition and density were seriously influenced (with higher average values for the latter period), which inevitably had implications on the structure of the forthcoming species assemblages. Five main variables introduced bias in the spatial and long-term analysis of the macrobenthos data: (1) location of the sampling stations and sampling effort per area; (2) sampling frequency or time interval; (3) sieve mesh size; (4) size of the Van Veen grab; and (5) fixation of the animals prior of after sieving.

Recommendation 2. Of course most data are gathered in different project with specific aims and objectives, which complicates comparisons between different datasets. Therefore there is an urgent need for intercomparison and experimental studies on small and newly gathered datasets to calculate conversion factors (cf. the study on the effect of fixation prior or after sieving). These will surely help to improve the comparison of long-term series.

Recommendation 3. In view of latter conclusions we strongly recommend to formulate a standardised protocol for macrobenthos sampling in the future to eliminate the bias introduced by the five variables described above.

In the second part of the MACROBEL project, a more detailed analysis of the long-term variation in the macrobenthos is given for 5 selected subtidal sampling sites on the BCS for the period 1979-'97, based on sediment type and a number of macrobenthos parameters like diversity, density and biomass. The possible effect of a selection of anthropogenic activities on the macrobenthos is briefly touched upon, with an emphasis on dumping of dredged material on the BCS.

Recommendation 4. Data exist (or can be processed) for several other sampling stations scattered over the BCS. These will be thoroughly analysed in a PhD study by I. Moulart.

The densities for most species were rather low during most of the sampled period with some higher peaks in certain years or seasons. In many cases there were hardly any patterns in terms of diversity, density or biomass, and the biomass peaks did not necessarily coincide with the peaks in density. It can be stated that the success of recruitment and production, and hence mortality and the year-to-year variation in macrobenthic communities are controlled by both physical and biological conditions. Changes in temperature, sediment composition, wind and current direction and strength, all have an effect on the temporal (both seasonal and long-term) distribution and abundance of macrobenthos species, either on the larval, juvenile or adult life stages.

Species with an annual recruitment pattern generally increase in numbers and biomass in summer and autumn, followed by considerable winter mortalities. However, large fluctuations in species density and biomass can have an effect on biological interactions such as predation and competition for food and space. Examples are given for (1) *Spisula subtruncata* with peak densities in 1995 at station 120 and subsequent higher densities of several predators and scavengers; and (2) the association of several crustaceans with tube aggregations of *Lanice conchilega*.

At present, it is difficult to measure the impact of sediment dumping on the local macrofauna, as this study is based on a sampling strategy with spring and autumn campaigns which are organized independently of the dumping frequency. Still, it is concluded that dredge dumping has no clear long-term effect on the macrobenthos communities of the BCS. An extensive discussion on other anthropogenic effects falls beyond the scope of this study.

Recommendation 5. Several studies showed that anthropogenic impacts on the macrobenthos are only measurable during a short period after the disturbance. To improve the decision-making that arises from anthropogenic impact studies, detailed sampling strategies should be followed, although in practice it is very difficult to implement such schemes.

5 Summary

The Belgian Continental Shelf (BCS) is characterized by a high diversity in marine habitats and a high diversity in the associated macrobenthic fauna. Therefore, the knowledge of the spatial and long-term variability in the distribution of the **macrobenthos** may contribute to a sustainable management of marine resources.

Within the MACROBEL project a large dataset (based on old and newly processed data) has been compiled concerning the macrobenthos of the BCS. The results can be seen as a first synthesis of the long-term variability in biodiversity and density patterns in the macrobenthic communities of a relatively small area of the North Sea. Macrobenthos data from the Marine Biology Section (Ghent University) and the Sea Fisheries Department were used, covering the periods 1976-'86 and 1994-2001 for the spatial and long-term variation (part 1), and the period 1979-1997 for the detailed long-term variation, including anthropogenic impact (part 2).

Next to this report, the project will be disseminated by means of an **interactive website**, and a macrobenthos species atlas as extension of the present study. The web-interface will be hosted at Flanders Marine Institute (VLIZ), and can be found at the following URL-address: <http://www.vliz.be/vmdcdata/MACROBEL>. The data used in the first part of the present study are coupled to a Geographical Information System (GIS), wherefrom spatial distribution maps may be generated for all macrobenthos species found during the sampled periods on the BCS. The long-term series will be updated on a regularly basis, as new data are still gathered and processed through various projects at several institutes. The **atlas 'Beknopte Atlas van de Mariene Bodemdieren van België'** will give an overview of the distribution of *ca.* 50 macrobenthos species on the BCS for the periods 1976-1986 and 1994-2001.

The **first part** of the MACROBEL project describes the **spatial and long-term distribution patterns** of the macrobenthos on the Belgian Continental Shelf by means of multivariate analyses and variation in density and species composition. During both sampling periods (1976-'86 and 1994-2001) a total of 242 macrobenthic infauna species were collected in 1475 Van Veen grabs scattered over the BCS. Polychaetes were the most diverse taxon with almost half of the species, followed by crustaceans and molluscs. Several other taxa comprised less than 5 % of the total species richness. Higher numbers of species were observed in sediments composed of fine to medium sand (median grain size <300 μm) with a little mud. Total average densities varied between 3 and $2.6 \cdot 10^5$ ind/m² (on average 1240 ind/m²). Molluscs and polychaetes together constituted more than 80 % of the macrobenthos density in both periods. Higher densities mostly corresponded with higher species richness. Highest values were recorded near the western coast of the BCS, a relatively small area characterised by a large variety in habitats.

Based on the differences in habitat and species composition, **four so-called Type I species assemblages** were identified for the BCS: the *Abra alba*-*Mysella bidentata*, *Nephtys cirrosa*, *Ophelia limacina*-*Glycera capitata*, and *Macoma balthica* communities. Seven transitional Type II assemblages were identified, which could largely be associated with one of the Type I SA's. The *Abra alba*-*Mysella bidentata* assemblage is typically found in fine sand sediments with medium mud contents, and largely confined to the 12 nautical mile zone. High diversity values and sometimes high densities were recorded for this species assemblage. The *Macoma balthica* assemblage was hardly separable from the *A. alba*-*M. bidentata* assemblage, but was characterised by higher mud contents and some typical species. The *Nephtys cirrosa* assemblage plays a central role on the BCS, scattered all over the BCS. The low diversity and density values in this species assemblage are typical

for well-sorted mobile sands with the sediment fraction $<63 \mu\text{m}$ almost zero. The *Ophelia limacina*-*Glycera capitata* assemblage is typically found in medium to coarse sand sediments with low mud content. This species assemblage is mainly recorded in the more offshore part of the BCS and on the Flemish banks.

Higher average numbers of species per sample and higher average densities were recorded during the period 1994-2001. Although the ANOSIM and SIMPER analyses showed significant differences between the three Type I species assemblages, distinct overlaps between all Type I SA's (and their associated Type II SA's) were found in the DCA analysis when comparing both sampled periods. Based on several subjective reduction criteria, it was concluded that 5 macrobenthos species were newly recorded in the period 1994-2001, while 5 other species were not recorded anymore during that period. Possible explanations concerning the loss and gain of macrobenthic species on the BCS are related to sediment type, drifting and invasion of exotic species, and habitat disturbance due to pollution.

Still, most dissimilarities that were noted are mainly due to **differences in sampling methodology** rather than to long-term biological variations. It was shown that both species composition and density were seriously influenced, which inevitably had implications on the structure of the forthcoming species assemblages. Five main variables introduced bias in the spatial and long-term analysis of the macrobenthos data: (1) location of the sampling stations and sampling effort per area; (2) sampling frequency or time interval; (3) sieve mesh size; (4) size of the Van Veen grab; and (5) fixation of the animals prior of after sieving. During the period 1976-'86 the positioning of the replicates was mostly not exact, while during 1994-2001 twice as many samples were analysed, of which many were taken in the macrobenthos rich *Abra alba*-*Mysella bidentata* species assemblage. Also, the inclusion of monthly samples during the latter period (in contrast to 1976-'86) made it possible to cover the recruitment peaks for a number of bivalve and polychaete species. Several small (interstitial) species were retained on a sieve with smaller mesh sizes during the earlier period, while a number of species can escape through the meshes when sieved prior to fixation as was done during most of the latter period. Therefore, there is an urgent need for experimental comparison studies to calculate conversion factors, which will improve the comparison of long-term data series.

In the **second part** of the MACROBEL project, a more **detailed analysis of the long-term variation** in the macrobenthos is given for 5 selected subtidal sampling sites on the BCS for the period 1979-'97, based on sediment type and a number of macrobenthos parameters like diversity, density and biomass. The possible effect of a selection of anthropogenic activities on the macrobenthos is briefly touched upon, with an emphasis on dumping of dredged material on the BCS.

Polychaetes dominated the macrofauna assemblage in terms of density at four stations (between 50 and 70 %), followed by bivalves (between 20 and 30 %), crustaceans (around 10 %), and a number of uncommon taxa (<1 %). Only at station 780, bivalves were more abundant than polychaetes, and echinoderms were recorded at higher densities. Except for station 700, important species were the polychaetes *Nephtys spp.* and *Spio spp.*; the bivalves *Abra alba*, *Spisula subtruncata* and *Ensis spp.*; and the amphipod *Pariambus typicus*. Several other species reached higher densities and biomasses in one or more stations.

At **station 140**, the median grain size was higher during the nineties (160 vs. 50 μm), while during the eighties a higher mud content (>50 %) was recorded. Diversity was rather low and ranged between 1 and 17 spp/sample. Two biomass peaks were noted, due to the massive recruitment of the bivalves *Spisula subtruncata* and *Macoma balthica* in 1994 and 1995.

Station 700 was characterized by muddy sediments (median grain size 50 μm and >60 % mud concentration) throughout the studied period. The overall diversity (between 2 and 30 spp/sample)

was higher than at station 140. Both average densities and species composition at station 700 clearly deviated from the other four stations. Several peak densities were recorded mainly attributed to the polychaete *Polydora spp.* Also, several other mud-loving species (e.g. *Corophium spp.*) were found at station 700. Higher biomasses were measured in 87S, 89S and 94A, due to the presence of three bivalve species *Petricola pholadiformis*, *Barnea candida* and *Abra alba*.

For the whole sampling period the sediment at **station 710** was typical fine to medium sand (average median grain size 220 μm) with low mud contents. The average diversity over the consecutive sampling periods was 17 spp/sample. Three peaks in abundance were observed in autumn (81A, 88A and 94A) each dominated by one or more polychaete species, i.e. *Scoloplos armiger*, *Magelona johnstoni*, *Nephtys spp.*, *Spio spp* and *Spiophanes bombyx*. The amphipods *Bathyporeia spp* and *Urothoe poseidonis* were the main crustaceans at station 710, but they never peaked simultaneously.

At **station 780**, the sediment changed from very fine sand and mud (average median grain size 80 μm) in the early 80's to fine sand (170 μm) in the mid-eighties – early-nineties. Diversity ranged between 9 and 35 spp/sample. Next to the common species, the bivalve *Mysella bidentata* and the polychaetes *Scoloplos armiger* and *Pectinaria koreni* were sometimes abundant. The common presence of echinoderms, sometimes in high numbers (mainly *Echinocardium cordatum* and *Ophiura spp.*) was typical for station 780. Strong decreases in density, diversity and biomass were recorded for several periods at this station, where the common taxa were found at either low or high abundances during the same period.

Station 120 was characterized by stable sediments with an average median grain size of 200 μm and mud concentration around 5 %, which was comparable with station 710. Highest macrobenthos diversity values were recorded at this station (on average 21 and a maximum of 48 spp/sample). Next to the common species, the bivalve species *Tellina fabula* and *Mysella bidentata* reached higher density values during the early 80's, while *Ensis spp.* and *Spisula subtruncata* were mainly found during the 90's at station 120. The average biomass increased from 1979 towards 1997. Over the studied period, several polychaete species consecutively dominated the macrobenthos at station 120, i.e. *Pectinaria koreni*, *Lanice conchilega*, *Eumida sanguinea*, *Spiophanes bombyx*, *Nephtys spp.*, *Magelona johnstoni* and *Chaetozone setosa*.

Overall, **large fluctuations** in diversity and density were noted for most macrobenthos species, either seasonally or over a longer time period. In many cases there were hardly any patterns in terms of density or biomass, and the biomass peaks did not necessarily coincide with the peaks in density. It can be stated that the success of recruitment and production, and hence mortality and the year-to-year variation in macrobenthic communities are controlled by both **physical and biological conditions**. Changes in temperature, sediment composition, wind and current direction and strength, all have an effect on the temporal (both seasonal and long-term) distribution and abundance of macrobenthos species, either on the larval, juvenile or adult life stages.

Species with an annual recruitment pattern generally increase in numbers and biomass in summer and autumn, followed by considerable winter mortalities. For a number of species a 2 (*Abra alba*), 4 (*Chaetozone setosa*) or even 10 (*Spisula subtruncata*) year cycle could be described, with high peaks in one year in one or more stations followed by a decrease and lower values during several consecutive years. These large fluctuations in species density and biomass can have an effect on biological interactions such as predation and competition for food and space. Examples are given for (1) *Spisula subtruncata* with peak densities in 1995 at station 120 and subsequent higher densities of several predators and scavengers; and (2) the association of several crustaceans with tube aggregations of *Lanice conchilega*.

An extensive discussion on the **impact of anthropogenic activities** on the macrobenthos, like sand extraction, industrial waste dumping or fisheries, falls beyond the scope of this study. Only the effect of **dredge dumping** is briefly touched upon. Several studies showed that anthropogenic ef-

fects are only measurable during a short period after the disturbance. For the present study, it was difficult to measure the impact of sediment dumping on the local macrofauna. The sampling strategy was based on spring and autumn campaigns which are organized independently of the dumping frequency, and no real 'pristine' base-line study exists for the studied areas. Still, it is concluded that dredge dumping has no clear long-term effect on the macrobenthos communities of the BCS.

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Annex 1. Macrobenthos species list of the BCS.

Higher taxon	Species name	Presence/Absence			Frequency (count)		
		Atlas	1976-'86	1994-2001	1976-'86	1994-2001	Totaal
Cnidaria	<i>Actinaria species</i>		x	x	28	153	181
Nemertea	<i>Nemertina species</i>		x	x	38	46	84
Annelida							
Polychaeta	<i>Ampharete acutifrons</i>		x		1	0	2
	<i>Ampharete baltica</i>			x	0	1	1
	<i>Aonides oxycephala</i>			x	0	34	34
	<i>Aonides paucibranchiata</i>	☉	x	x	21	27	48
	<i>Aphelochaeta filiformis</i>			x	0	1	1
	<i>Aphelochaeta marioni</i>		x	x	14	12	26
	<i>Aphrodita aculeata</i>			x	0	1	1
	<i>Arenicola marina</i>	☉	x	x	3	2	5
	<i>Aricidea minuta</i>		x	x	1	2	3
	<i>Autolytus edwardsi</i>		x		1	0	1
	<i>Autolytus prolifer</i>		x	x	7	5	12
	<i>Capitella capitata</i>	☉	x	x	31	128	159
	<i>Capitella minima</i>		x		1	0	1
	<i>Caulerliella killariensis</i>		x	x	11	1	12
	<i>Caulerliella serrata</i>		x		1	0	1
	<i>Chaetozone setosa</i>		x	x	27	6	33
	<i>Eteone flava</i>		x	x	8	16	24
	<i>Eteone longa</i>	☉	x	x	48	105	153
	<i>Eulalia viridis</i>			x	0	1	1
	<i>Eumida bahusiensis</i>			x	0	16	16
	<i>Eumida sanguinea</i>	☉	x	x	32	120	152
	<i>Eunereis longissima</i>	☉	x	x	8	89	97
	<i>Eusyllis blomstrandii</i>		x		1	0	1
	<i>Euzonus flabelligerus</i>		x	x	1	2	3
	<i>Exogone hebes</i>		x		7	0	7
	<i>Gattyana cirrhosa</i>		x	x	1	6	7
	<i>Glycera alba</i>	☉	x	x	2	92	94
	<i>Glycera capitata</i>	☉	x	x	36	84	120
	<i>Glycera tridactyla</i>		x	x	1	32	33
	<i>Goniadella bobrezkii</i>		x		12	0	12
	<i>Harmothoe impar</i>			x	0	1	1
	<i>Harmothoe spinifera</i>			x	0	2	2
	<i>Hesionura elongata</i>	☉	x	x	51	47	98
	<i>Heteromastus filiformis</i>	☉	x	x	17	39	56
	<i>Hypereteone foliosa</i>			x	0	15	15
	<i>Lanice conchilega</i>	☉	x	x	36	164	200
	<i>Lepidonotus squamatus</i>		x		1	0	1
	<i>Lumbrineris fragilis</i>			x	0	2	2
	<i>Lumbrineris latreilli</i>		x	x	2	4	6
	<i>Macrochaeta helgolandica</i>		x		2	0	2
	<i>Magelona filiformis</i>			x	0	3	3
	<i>Magelona johnstoni</i>	☉	x	x	33	240	273
	<i>Malacoceros fuliginosus</i>			x	0	1	1
	<i>Malacoceros vulgaris</i>		x		1	0	1
	<i>Malmgrenia castanea</i>			x	0	4	4
	<i>Malmgrenia glabra</i>		x	x	6	13	19
	<i>Malmgrenia jungmani</i>		x	x	1	2	3
	<i>Microphthalmus listensis</i>		x		3	0	3
	<i>Microphthalmus similis</i>		x	x	9	30	39
	<i>Nephtys assimilis</i>			x	0	25	25
	<i>Nephtys caeca</i>		x	x	20	6	26
	<i>Nephtys cirrosa</i>	☉	x	x	77	531	608
	<i>Nephtys longosetosa</i>	☉	x	x	34	80	114
	<i>Nephtys hombergii</i>	☉	x	x	29	237	266
	<i>Nereis succinea</i>		x		2	0	2
	<i>Nicomache species</i>		x		3	0	3
	<i>Notomastus latericeus</i>	☉	x	x	30	136	166
	<i>Ophelia limacina</i>	☉	x	x	75	185	260
	<i>Ophiodromus flexuosus</i>			x	0	5	5
	<i>Opisthodonta pterochaeta</i>			x	0	2	2
	<i>Orbinia sertulata</i>		x	x	5	2	7
	<i>Owenia fusiformis</i>	☉	x	x	10	95	105
	<i>Paraonis fulgens</i>		x	x	5	19	24

	<i>Parougia eliasoni</i>	x		1	0	1
	<i>Pectinaria belgica</i>	x		12	0	12
	<i>Pectinaria koreni</i>	⊖ x	x	30	106	136
	<i>Pholoe minuta</i>	⊖ x	x	17	53	70
	<i>Pholoe pallida</i>		x	0	1	1
	<i>Phyllodoce groenlandica</i>	x	x	9	19	28
	<i>Phyllodoce laminosa</i>		x	0	1	1
	<i>Phyllodoce lineata</i>	x		2	0	2
	<i>Phyllodoce mucosa/maculata</i>	⊖ x	x	32	177	209
	<i>Phyllodoce rosea</i>	x	x	8	6	14
	<i>Pisione remota</i>	x	x	7	14	21
	<i>Podarkeopsis helgolandica</i>	x	x	1	17	18
	<i>Poecilochaetus serpens</i>	⊖ x	x	14	72	86
	<i>Polycirrus medusa</i>	x	x	13	5	18
	<i>Polydora ciliata</i>	x		1	0	1
	<i>Polydora cornuta</i>	x		5	0	5
	<i>Polygordius appendiculatus</i>	x	x	13	8	21
	<i>Pomatoceros triquetter</i>		x	0	26	26
	<i>Protodorvillea kefersteini</i>	x	x	8	14	22
	<i>Protodriloides chaetifer</i>	x		6	0	6
	<i>Protodrilus species</i>	x		7	0	7
	<i>Pseudopolydora antennata</i>	x	x	1	1	2
	<i>Pseudopolydora paucibranchiata</i>		x	0	2	2
	<i>Pseudopolydora pulchra</i>	x	x	7	11	18
	<i>Pygospio elegans</i>	x	x	4	7	11
	<i>Sabellaria spinulosa</i>	x	x	1	1	2
	<i>Saccocirrus papillocercus</i>	x		2	0	2
	<i>Scalibregma inflatum</i>	x	x	1	5	6
	<i>Scolecopsis bonnieri</i>	⊖ x	x	41	89	130
	<i>Scolecopsis foliosa</i>		x	0	3	3
	<i>Scolecopsis squamata</i>	x	x	1	10	11
	<i>Scoloplos armiger</i>	⊖ x	x	81	342	423
	<i>Sigalion mathildae</i>	⊖ x	x	3	52	55
	<i>Sphaerosyllis hystrix</i>	x	x	1	1	2
	<i>Spio gonioccephala</i>		x	0	36	36
	<i>Spio martinensis</i>		x	0	10	10
	<i>Spio filicornis</i>	⊖ x	x	12	200	212
	<i>Spiophanes bombyx</i>	⊖ x	x	70	383	453
	<i>Spiophanes kröyeri</i>		x	0	1	1
	<i>Sthenelais boa</i>	⊖ x	x	9	94	103
	<i>Streblospio benedicti</i>		x	0	1	1
	<i>Streptosyllis arenae</i>	x		2	0	2
	<i>Streptosyllis websteri</i>	x	x	3	1	4
	<i>Syllis gracilis</i>	x	x	6	3	9
	<i>Travisia forbesii</i>	x	x	4	14	18
	<i>Typosyllis armillaris</i>	x	x	3	11	14
Pycnogonida	<i>Anoplodactylus petiolatus</i>	x	x	10	4	14
	<i>Nymphon brevistroste</i>	x	x	1	1	2
	<i>Pycnogonum littorale</i>	x		2	0	2
Crustacea						
Cirripedia	<i>Elminius modestus</i>	x		1	0	1
Leptostraca	<i>Nebalia bipes</i>	x		2	0	2
Cumacea	<i>Bodotria arenosa</i>	x	x	2	16	18
	<i>Bodotria pulchella</i>	x		2	0	2
	<i>Bodotria scorpoides</i>	x	x	8	17	25
	<i>Cumopsis goodsiri</i>	x		1	0	1
	<i>Diastylis bradyi</i>	⊖ x	x	11	103	114
	<i>Diastylis laevis</i>		x	0	1	1
	<i>Diastylis lucifera</i>	x		1	0	1
	<i>Diastylis rathkei</i>	⊖ x	x	19	11	30
	<i>Diastylis rugosa</i>		x	0	1	1
	<i>Iphinoe trispinosa</i>	x		7	0	7
	<i>Pseudocuma longicornis-gilsoni</i>	x	x	27	24	51
	<i>Pseudocuma similis</i>	x	x	1	7	8
Tanaidacea	<i>Pseudoparatanaeis batei</i>	x	x	1	13	14
	<i>Tanaissus liljeborgi</i>	x	x	18	4	22

Mysida	<i>Gastrosaccus sanctus</i>		X		1	0	1
	<i>Gastrosaccus spinifer</i>	☹	X	X	63	181	244
	<i>Leptomysis gracilis</i>			X	0	1	1
	<i>Mesopodopsis slabberi</i>			X	0	4	4
	<i>Praunus inermis</i>			X	0	1	1
	<i>Schistomysis kervillei</i>		X	X	3	5	8
	<i>Schistomysis spirtus</i>		X	X	5	16	21
Isopoda	<i>Eurydice pulchra</i>		X	X	1	1	2
	<i>Eurydice spinigera</i>		X	X	3	3	6
	<i>Idotea linearis</i>		X	X	1	1	2
	<i>Idotea metallica</i>			X	0	1	1
	<i>Ione thoracica</i>			X	0	1	1
Amphipoda	<i>Abludomelita obtusata</i>	☹	X	X	14	80	94
	<i>Ampelisca brevicornis</i>	☹	X	X	7	58	65
	<i>Ampelisca tenuicornis</i>		X		1	0	1
	<i>Amphilochus neapolitanus</i>		X	X	1	11	12
	<i>Aora typica</i>		X		3	0	3
	<i>Atylus falcatus</i>	☹	X	X	23	53	76
	<i>Atylus swammerdami</i>	☹	X	X	15	47	62
	<i>Atylus vedlomensis</i>			X	0	2	2
	<i>Bathyporeia elegans</i>	☹	X	X	31	146	177
	<i>Bathyporeia gracilis</i>			X	0	1	1
	<i>Bathyporeia guilliamsoniana</i>	☹	X	X	54	158	212
	<i>Bathyporeia pelagica</i>		X	X	7	29	36
	<i>Bathyporeia pilosa</i>		X		1	0	1
	<i>Bathyporeia sarsi</i>			X	0	2	2
	<i>Callopius laeviusculus</i>			X	0	4	4
	<i>Cheirocratus sundevallii</i>		X		1	0	1
	<i>Corophium acherusicum</i>		X	X	1	4	5
	<i>Corophium arenarium</i>		X		5	0	5
	<i>Corophium sextonae</i>			X	0	1	1
	<i>Corophium volutator</i>		X	X	3	1	4
	<i>Ericthonius brasiliensis</i>		X		1	0	1
	<i>Hippomedon denticulatus</i>		X	X	4	1	5
	<i>Iphimedia minuta</i>			X	0	1	1
	<i>Jassa falcata</i>		X		1	0	1
	<i>Jassa marmorata</i>			X	0	1	1
	<i>Jassa pusilla</i>			X	0	1	1
	<i>Leucothoe incisa</i>	☹	X	X	5	76	81
	<i>Leucothoe liljeborgii</i>		X		1	0	1
	<i>Maerella tenuimana</i>			X	0	1	1
	<i>Megaluropus agilis</i>		X		10	12	22
	<i>Melita dentata</i>			X	0	1	1
	<i>Melita palmata</i>		X		1	0	1
	<i>Microprotopus maculatus</i>		X	X	10	35	45
	<i>Monoculodes carinatus</i>		X	X	1	1	2
	<i>Orchomene nanus</i>		X	X	2	5	7
	<i>Pariambus typicus</i>	☹	X	X	22	108	130
	<i>Perioculodes longimanus</i>		X	X	3	23	26
	<i>Phoxocephalus holbolli</i>		X		1	0	1
	<i>Phtisica marina</i>		X	X	1	13	14
	<i>Pontocrates altamarinus</i>	☹	X	X	26	66	92
	<i>Pontocrates arenarius</i>		X	X	1	10	11
	<i>Stenothoe marina</i>		X	X	9	17	26
	<i>Stenula rubrovittata</i>		X		1	0	1
	<i>Synchelidium haplocheles</i>			X	0	1	1
	<i>Synchelidium maculatum</i>			X	0	4	4
	<i>Unciola planipes</i>		X		2	0	2
	<i>Urothoe brevicornis</i>	☹	X	X	21	178	199
<i>Urothoe elegans</i>			X	0	14	14	
<i>Urothoe marina</i>		X	X	1	1	2	
<i>Urothoe poseidonis</i>	☹	X	X	17	133	150	
<i>Urothoe pulchella</i>			X	0	6	6	
Caridea	<i>Crangon crangon</i>	☹	X	X	14	27	41
	<i>Hippolyte varians</i>		X	X	1	3	4
	<i>Palaemon elegans</i>			X	0	1	1
	<i>Philocheras trispinosus</i>		X	X	1	13	14

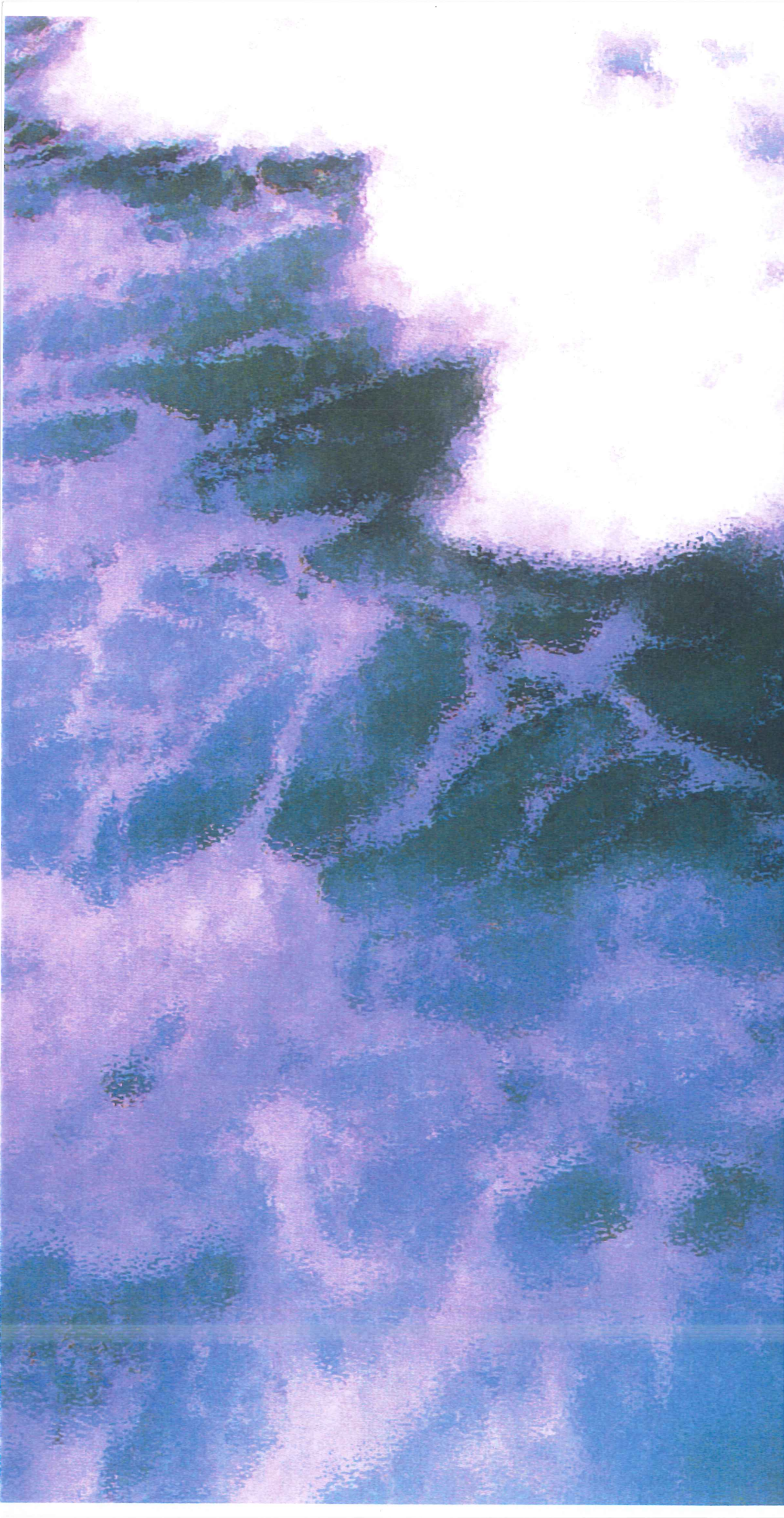
	<i>Processa novelli holthuisi</i>	x		7	0	7	
	<i>Processa modica</i>		x	0	9	9	
	<i>Thoralus cranchii</i>		x	0	1	1	
Anomura	<i>Callianassa subterranea</i>		x	0	1	1	
	<i>Callianassa tyrrhena</i>		x	0	7	7	
	<i>Diogenes pugillator</i>		x	0	27	27	
	<i>Galathea intermedia</i>	x		1	0	1	
	<i>Pagurus bernhardus</i>	x	x	3	12	15	
	<i>Pisidia longicornis</i>	x	x	1	6	7	
Brachyura	<i>Achaeus cranchii</i>	x		1	0	1	
	<i>Atelecyclus rotundatus</i>	x		1	0	1	
	<i>Corystes cassiveiaunus</i>		x	0	2	2	
	<i>Ebalia species</i>	x		6	0	6	
	<i>Liocarcinus arcuatus</i>	x	x	6	20	26	
	<i>Liocarcinus holsatus</i>	x	x	13	46	59	
	<i>Liocarcinus depurator</i>	x		1	0	1	
	<i>Liocarcinus pusillus</i>	x	x	2	14	16	
	<i>Macropodia rostrata</i>	x	x	4	3	7	
	<i>Pilumnus hirtellus</i>		x	0	1	1	
	<i>Pinnotheres pisum</i>	x	x	5	2	7	
	<i>Portunus latipes</i>	x	x	2	21	23	
	<i>Thia scutellata</i>	⊕ x	x	17	52	69	
	<i>Upogebia deltaura</i>	x	x	2	2	4	
	<i>Upogebia pusilla</i>	x		1	0	1	
	Mollusca						
	Bivalvia	<i>Abra alba</i>	⊕ x	x	39	190	229
<i>Abra prismatica</i>			x	1	4	5	
<i>Aequipecten opercularis</i>			x	0	2	2	
<i>Astarte elliptica</i>			x	0	1	1	
<i>Barnea candida</i>			x	2	1	3	
<i>Cerastoderma edule</i>		⊕ x		3	0	3	
<i>Chlamys varians</i>		x		1	0	1	
<i>Donax vittatus</i>		⊕ x	x	9	65	74	
<i>Dosinia exoleta</i>		x		1	0	1	
<i>Ensis arcuatus</i>		x	x	3	34	37	
<i>Ensis directus</i>			x	0	6	6	
<i>Goodallia triangularis</i>		x		4	0	4	
<i>Macoma balthica</i>		⊕ x	x	13	64	77	
<i>Mactra corallina</i>		x		3	0	3	
<i>Modiolus modiolus</i>		x	x	22	1	23	
<i>Modiolus phaseolinus</i>		x		4	0	4	
<i>Montacuta ferruginosa</i>		⊕ x	x	11	88	99	
<i>Mya truncata</i>		⊕ x	x	1	13	14	
<i>Mysella bidentata</i>		⊕ x	x	49	182	231	
<i>Mytilus edulis</i>		x	x	7	61	68	
<i>Petricola pholadiformis</i>		⊕ x	x	6	13	19	
<i>Phaxas pellucidus</i>		x		9	0	9	
<i>Sphenia binghami</i>		x	x	6	16	22	
<i>Spisula elliptica</i>		x	x	28	23	51	
<i>Spisula solida</i>		⊕ x	x	32	13	45	
<i>Spisula subtruncata</i>		⊕ x	x	35	164	199	
<i>Striarca lactea</i>			x	0	1	1	
<i>Tellina fabula</i>		⊕ x	x	36	176	212	
<i>Tellina pygmaeus</i>		x	x	22	43	65	
<i>Tellina tenuis</i>		⊕ x	x	14	45	59	
<i>Thracia papyracea</i>		x		1	0	1	
<i>Venerupis senegalensis</i>		⊕ x	x	10	62	72	
Gastropoda		<i>Caecum glabrum</i>	x	x	1	1	2
		<i>Coryphella verrucosa</i>	x		1	0	1
	<i>Crepidula fornicata</i>	x	x	4	39	43	
	<i>Epitonium clathrus</i>		x	0	5	5	
	<i>Nassarius reticulatus</i>		x	0	72	72	
	<i>Polinices poliana</i>		x	0	2	2	
<i>Polinices pulchellus</i>	x	x	14	32	46		
Chaetognatha	<i>Chaetognatha species</i>	x	x	9	15	24	

Echinodermata							
Asteroidea	<i>Asterias rubens</i>		x	x	2	10	12
Echinoidea	<i>Echinocardium cordatum</i>	⊕	x	x	20	190	210
	<i>Echinocyamus pusillus</i>	⊕	x	x	18	50	68
	<i>Psammechinus miliaris</i>		x	x	2	1	3
Ophiuroidea	<i>Acrocnida brachiata</i>			x	0	14	14
	<i>Amphipholis squamata</i>		x		1	0	1
	<i>Amphiura filiformis</i>			x	0	3	3
	<i>Ophiura albida</i>	⊕	x	x	24	89	113
	<i>Ophiura ophiura</i>	⊕	x	x	14	61	75
Chordata	<i>Branchiostoma lanceolatum</i>	⊕	x	x	29	12	41
	Total # species		Atlas	'76-'86	'94-'01	# stations	
	271		62	206	210	129	646 775

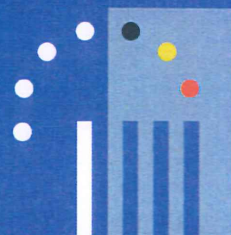
Remark 1: **Genera that have not (always) been identified further to the species level:**
 Autolytus, Harmathoe; Nereis, Nephtys, Spio, Polydora, Protodrilus, Cirratulidae, Capitellidae, Nicomache, Archannelida, Pseudocuma, Gammarus, Corophium, Bathyporeia, Hippolyte, Callinassa, Eballa, Bivalvia, Ensis, Gastropoda, Chaetognatha, Ophiura, Amphiura, Nemertina, Acllnaria.

Remark 2: **Taxa that were sampled but not considered as macrobenthos:**
 Nematoda, Turbellaria, Oligochaeta, Hydrozoa, Scyphozoa, Ostracoda, Copepoda, Polyplacophora, Opisthobranchia, Pisce:





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