Structural biodiversity of benthic copepod communities on two subtidal sandbanks

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1 Introduction

Off the Belgian coast in the Southern Bight of the North Sea a remarkable complex of large offshore sandbanks, separated by swales, structures the sea bottom. The linear sandbanks are maintained by tidal forces (Stride, 1982; De Moor, 1989; De Moor & Lanckneus, 1993). Four sets of sandbanks can be discerned: the Coastal Banks, the Flemish Banks, the Zeeland Banks and the Hinder Banks. To the west of Oostende the Flemish Banks stretch between the 6- and the 12-nautical-mile zone. The Flemish Banks are unique from an ecological point of view and harbour a rich fauna (Seys *et al.*, 1993; Maes & Cliquet, 1997; Dewicke, 2001; Cattrijsse & Vincx, 2001). The southern Flemish Banks yield a variety of macrobenthic communities (Van Hoey *et al.*, submitted). The rich *Abra alba-Mysella bidentata* community occurs in the gullies and is of exceptional ecological importance serving as an important food resource for scoters and demersal fish (Degraer *et al.*, 1999). The Flemish Banks harbour a most diverse hyperbenthic community, characterized by planktonic species (Vincx *et al.*, 2002). Zoea stages of nearly all decapod species were typically found at the Flemish Banks and most anomurans and certain fish species preferentially occurred in this area (Dewicke, 2001). The Flemish Banks are also important for fish larvae in their transport from offshore waters towards suitable nursery grounds in the Belgian coastal area (Vincx *et al.*, 2002). The area is a key-site for wintering Little Gull, Red-throated Diver, Razorbill and Guillemot (Seys *et al.*, 1993, 1999; Maes *et al.*, 2000; Vincx *et al.*, 2002) and acts as a feeding ground for Sandwich Tern during the breeding season (Seys *et al.*, 1999; Vincx *et al.*, 2002). The richness of the sandbanks is related to the topographic variability of the area (Gullentops *et al.*, 1977). Because of the linkage between hydrodynamics and sedimentology (Gullentops *et al.*, 1977; Buchanan, 1984), even within some tens of metres, completely different types of sediment are encountered, each with their own typical benthic community (Degraer *et al.*, 1999). A large variety of benthic communities can thus be expected.

Sandbanks are also challenging environments for benthic organisms. The occurrence of preferentially planktonic species in the hyperbenthos indicates that scarce food supply and strong currents in this offshore area are less favourable for bottom-dependent animals compared to onshore waters (Vincx *et al.*, 2002). The flanks and tops of sandbanks are characterized by quickly migrating small and large dunes. Consequently, benthic organisms are constantly buried under progressing sandbodies, implying an extremely unfavourable benthic environment (Gullentops *et al.*, 1977). By contrast less dynamic environmental conditions prevail in the deeper zones, the base of the banks and the gullies in between (Trentesaux *et al.*, 1994), which form a much more stable and favourable habitat. Indeed, Van Hoey *et al.* (submitted) found that the macrobenthos on top of the banks was very poor, while a dense and rich community was encountered in the gullies. The area hence comprises a high variety of poor as well as rich communities. Vanaverbeke *et al.* (2000) proved that the meiobenthos on the sandbanks was less dense than in the deeper gullies. An analysis of nematode diversity, however, showed the opposite trend, reflecting that nematodes are able to occupy a large variety of microhabitats on the dynamic sandbanks (Vanaverbeke *et al.*, 2002). The fauna of sandbanks is not only subject to naturally induced physical forces, but also to intensive human-induced stress, caused by several user groups of the marine environment (Maes *et al.*, 2000). The Flemish Banks area is the most important sand extraction zone and it borders the main shipping route towards Zeebrugge. Six telephone cables cross the Flemish sandbanks and military exercises are conducted at four of the five Flemish sandbanks. The gullies are not only heavily impacted by Belgian fishermen, in the zone between 3 and 12 nautical miles also Dutch fishermen are allowed to catch all species of fish and French fishermen are allowed to catch herring (Maes *et al.*, 2000).

To allow a sustainable management of the marine resources, it is very important to examine to what extent the fauna can cope with disturbances. Human impacts may disturb the established equilibrium and may result in an impoverishment of these areas. Moreover, the Coastal Banks and the Flemish Banks are of special interest for nature management because they constitute a continuous zone of various coastal biotopes. In this respect, special attention is paid to these areas to designate marine protected areas (Maes & Cliquet, 1997). In order to take measures for the protection of the marine environment, knowledge on the spatial distribution of the different faunal groups and the natural values of the Belgian maritime waters is required. In this chapter the structural biodiversity of the harpacticoid fauna on two Flemish Banks will be presented, in order to provide the necessary background knowledge for the impact assessment in further chapters. It concerns a study of density, diversity and community structure on the Kwintebank and the Middelkerkebank, in relation to sediment characteristics and depth.

2 Material & Methods

2.1 Description of the study area

The Kwintebank and the Middelkerkebank belong to the Flemish Banks, a group of subtidal sandbanks situated at 10 to 30 km off the Belgian coast (Fig.I.1.a). These sandbanks are SW-NE directed and display a transverse asymmetry with a steeper western slope as a result of the strong impact of the flood stream. Flanks and summit of the banks are covered with various types of bedforms, especially at their northern edges, where the energy of waves and currents is higher (Lanckneus *et al.*, 1994). The banks are separated by swales that dip to the northeast and generally do not reach 30 m below low water level at spring tide. The study area is characterized by a macro tidal regime, the tidal range approaching 5 m during spring tides (Stolk, 1993). The tides north of the Flemish Banks area are symmetric. The Flemish Banks and the inshore waters are flood dominated (Lanckneus *et al.*, 1994). Tidal currents are slightly oblique with regard to the bank elongation and their velocity may exceed 1 m/s during spring tides (Stolk, 1993). At times, the very strong tidal currents resuspend the whole upper layer of the sediment and create a stressed, high-energy environment, subject to extreme physical disturbance (Willems *et al.*, 1982a). Numerous authors [Caston & Stride, 1970; Caston, 1972; McCave, 1979; Caston, 1981; Kenyon *et al.*, 1981; McCave & Langhorne, 1982; Stride, 1982, Venn & D'Olier, 1983; Howarth & Huthnance, 1984; De Moor, 1985; De Moor & Lanckneus, 1988] pointed out that in the inter-bank swales, the near-bottom currents are parallel to the channels' long axis, and that they are gradually deflected towards the sandbanks' crests when approaching these crests. A local flood dominance of the near-bottom currents is observed on the northwestern flanks of the sandbanks, whereas the ebb currents are dominant on the opposite slopes (De Moor, 1985, 1986). The currents in the swales are ebb-dominated (Dewicke, 2001).

The Kwintebank (Fig.I.1.b) is the central sandbank of the five Flemish Banks. It is an elongated linear subtidal sandbank of about 25 km long, 3 km wide and rising about 10 m in the north up to 20 m in the south above the surrounding seafloor. The mean water depth varies between 6 m in the central part to over 20 m in the northern and southern edges. (Lanckneus *et al.*, 1992a) The longitudinal profile shows a kink in the centre of the sandbank. The local tidal current patterns give rise to different macro-morphological units. The northern half as well as the southern tip are characterized by sandwaves, which are absent from the centre to the southern tip of the sandbank (Fig.I.1.b). In the north the sandwaves have a mean wavelength of 210 m and a mean height of 4 m with a maximum of 8 m high. The length of an individual sandwave can reach 2.9 km. The sandwaves at the southern tip of the sandbank are approximately only 1 to 2 m high. (De Moor & Lanckneus, 1994) The two swales adjacent to the Kwintebank are known as the Kwinte, to the northwest, and the Negenvaam to the southeast. The latter is situated in between the Kwintebank and the Middelkerkebank and is 2 to 3 km wide and 12 to 20 m deep (Lanckneus *et al.*, 1994).

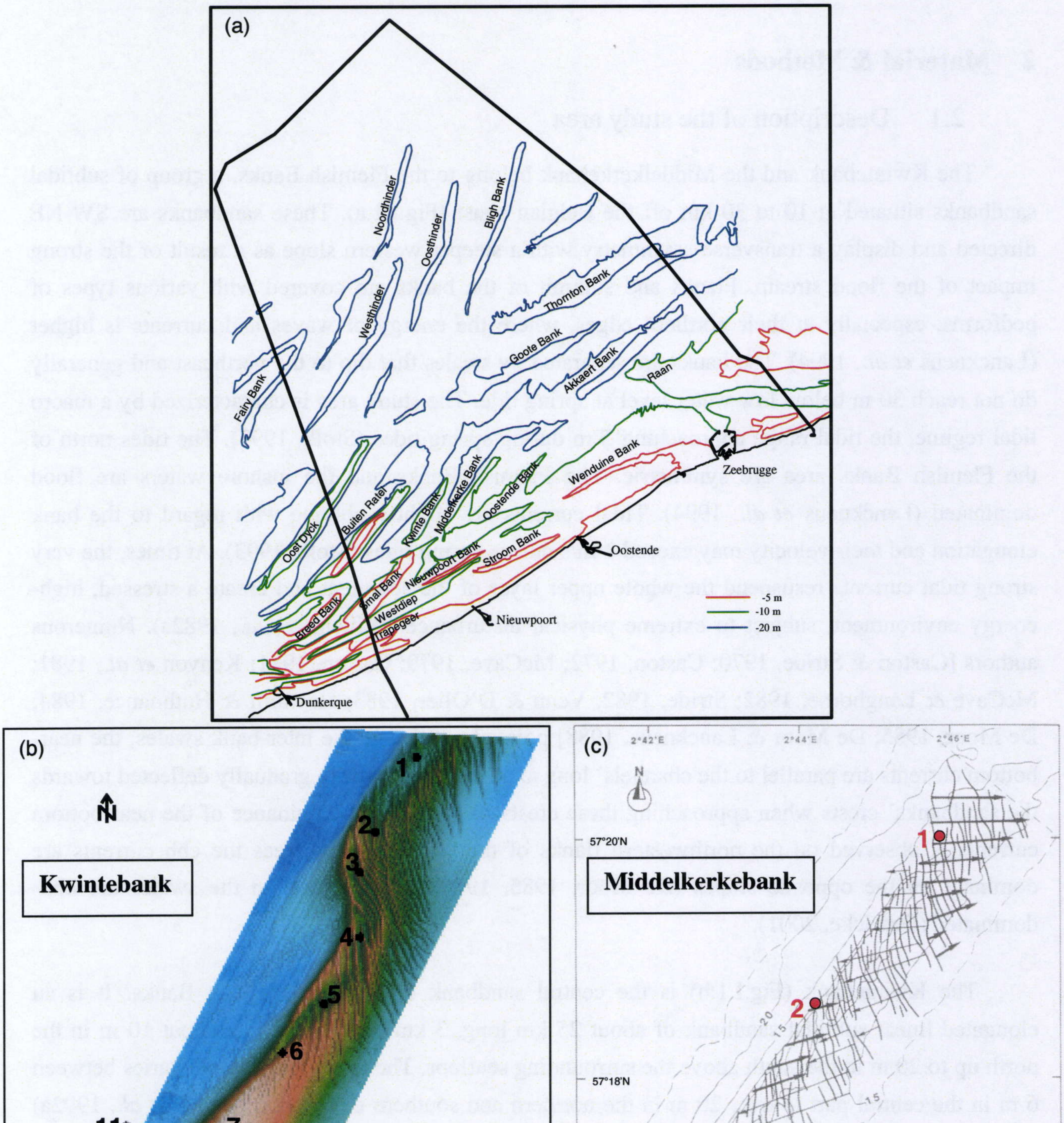

Fig.I.1: The subtidal sandbanks of the Belgian Continental Shelf (a: after Cattrijsse & Vincx, 2001) with detailed maps of the Kwintebank (b: multibeam image 2000 Fund For Sand Extraction) and Middelkerkebank (c: Side-scan sonar image with bathymetric registrations from May 1990 after Lanckneus *et al.*, 1994)

The Middelkerkebank (Fig.I.1.c) has a length of 12 km, a mean width of 1.5 km and a height above the sea floor varying between 8 m in the northeast and 15 m in the southwest. Depth varies between 4 m in the southwest and 20 m in the northeast. The southern edge of the bank is relatively wide while the northern tip tends to be rather narrow. The northern part of the bank is characterized by large to very large sandwaves, which occur on the bank summit. They have a constant orientation, a height ranging from 0.5 to 5 m, a wavelength from 75 to 150 m and in most cases an asymmetrical profile. The slopes of both lee and stoss flanks are very low. The southern part of the bank has a flatter morphology and forms a plateau with the western end of the Oostendebank. In the central part the Middelkerkebank is split up into two parts by a deeper section reaching –13 m. Small and medium dune fields occur on the entire bank and in the adjacent swales. The swale at the northwestern side is known as the Negenvaam, the southeastern side of the bank borders the Uitdiep. The Uitdiep swale has a width of 1 to 3 km and a depth of 12 to 20 m. (Lanckneus *et al.*, 1994)

2.2 Sampling and processing

Quantitative bottom samples were taken with a modified 0.017 m² Reineck boxcorer (Farris & Crezee, 1976). In total 12 stations along the Kwintebank were sampled on 28 January 1997, ten at regular distances along the top of the sandbank, corresponding with the stations sampled by Willems *et al.* (1982b), and one at each side in the gully near the middle of the bank (Fig.I.1.b). At the Middelkerkebank, only five stations were sampled on top of the bank and two additional samples were taken in each adjacent gully on 6 October 1997 (Fig.I.1.c).

Per station three replicate boxcores were taken. Per boxcore two subsamples were taken with a 10.35 cm² perspex coring tube in the centre of the boxcore in order to eliminate any edge-effects. Each replicate for meiofauna was fixed with a warm neutral formalin (70°C) tap-water solution to a final concentration of 4 %. The other subsamples were dried immediately at 60°C for granulometric analysis.

In the lab, meiofauna samples were washed by decantation (repeated 10 times) through a 0.038 mm-sieve, excluding macrofauna by means of a 1-mm sieve. Subsequently, the organisms were extracted from the sediment using a density gradient centrifugation–flotation technique (Bowen *et al.*, 1972; de Jonge & Bouwman, 1977) using LUDOX HS 40% (TM®) colloidal silica gel (specific density 1.18) (Heip *et al.*, 1985). After staining with Rose Bengal, all copepods were picked out, counted and identified to species level under a microscope with a 100 X oil immersion lens. One or more specimens were mounted in glycerol on glass slides in non-permanent toto preparates. The coverslip is supported on both sides or on one side, by fragments of broken coverslip, allowing the specimens to be re-orientated by manipulation of the top coverslip. Copepodite stages were counted as a single group and identified to species level where possible. Nauplii were disregarded, their identification being too difficult. Identification was based on the descriptions given in Lang (1948, 1965), Wells (1967), Bodin (1997 and references therein) and more recent papers. Four different ecotypes were discerned: epibenthic species, endobenthic species, interstitial species and phytal - free-swimming species (Hicks & Coull, 1983).

Sediment analysis was performed using a Coulter LS100 Particle Size Analyser (measuring range: 0.4 – 850 µm). Sediment fractions up to 1000 µm are expressed as volume percentages, while the fractions between 1000-2000 µm and >2000 µm are mass percentages. Sediment fractions are defined according to the Wenthworth scale (Buchanan, 1984). Median grain size is calculated from the sand fraction 0.4 – 850 µm. Water depth measurements were standardized to Mean Low Water Spring (MLWS) using the M2 reduction model (AWK).

2.3 Statistics

Hill's numbers (Hill, 1973) were used to calculate diversity. The importance of rare species decreases with increasing order of diversity index.

N_0 = number of species

N_1 = exponential Shannon index = $\exp(H') = \exp\left(-\sum_{i=1}^{n} p_i \ln p_i\right)$

with $p_i = \frac{N_i}{N}$ = relative abundance of the i^{th} species

N_2 = reciprocal of Simpon's index (Simpson, 1949) = $\frac{1}{D} = \frac{1}{\sum_{i=1}^{n} p_i^2}$

N_∞ = reciprocal of the proportional abundance of the commonest species (reciprocal of the Berger-Parker index (Berger & Parker, 1970))

In order to compare densities and diversity indices among Kwintebank and Middelkerkebank stations, ANOVA's were performed on untransformed or log (x+1) transformed data if needed to meet the assumptions for ANOVA. For non-parametric data Kruskall-Wallis ANOVA by Ranks was preferred. Overall significant differences were pairwise compared using the planned comparison option in ANOVA for parametric data or following Conover (1971) for non-parametric data. Product-moment correlations or Spearman Rank Order Correlations were used to unravel relationships between granulometric characteristics and densities or diversity indices. All univariate analyses (ANOVA, Kruskall-Wallis ANOVA by Ranks, Product-moment correlations and Spearman Rank Order Correlations) were performed with STATISTICA™ software (Microsoft, StatSoft, Inc., 2000).

The harpacticoid community structure was analyzed by means of multivariate classification and ordination techniques. A classification clustering (Cluster Analysis) based on the Bray-Curtis similarity index and Group Average Sorting (Clifford & Stephenson, 1975) and a TWINSPAN (TWo-way INdicator SPecies Analysis) classification technique (Hill, 1979a) were applied to the absolute replicate abundances of all copepod species. The program TWINDEND (Gauch & Whittaker, 1981) was used to decide which TWINSPAN groups were worth retaining. The results of both classification techniques were compared with the program CLASSTAT (Moss, 1985).

A Detrended Correspondence Analysis (DCA, Hill 1979b) on fourth root transformed data was chosen as indirect gradient analysis. A Canonical Correspondence Analysis (CCA, Hill, 1974) was applied to describe the structure of the harpacticoid communities in relation to granulometric characteristics and depth. The environmental variables retained in the CCA were selected by forward selection using Monte Carlo Permutation Tests (number of unrestricted permutations set to 999). The ordination analyses were performed with CANOCO for Windows (ter Braak & Smilauer, 1998).

3 Results

3.1 Kwintebank

3.1.1 Depth

Depth measurements (Fig.I.2) were compared with depth profiles obtained with multibeam soundings of the Kwintebank, providing a valuable and more comprehensive picture of the morphology of the sandbank (Fig.I.3). The deepest station on the bank was station 1 at 18 m depth. In the northern part of the sandbank, characterized by sandwaves, depth fluctuated around 15 m. Station 5, however, was situated at greater depth (17 m) in a depression, clearly distinguished on the multibeam picture. Station 6 was situated at the transition between the northern deeper area and the southern more elevated area. The southern flat plateau was in average 8 m more elevated than the northern part. The most elevated station was station 8 at 7 m depth. Depth differed 4 m between the two gully stations, the Kwinte gully station 11 being situated at 24 m depth and the Negenvaam gully station 12 at 20 m.

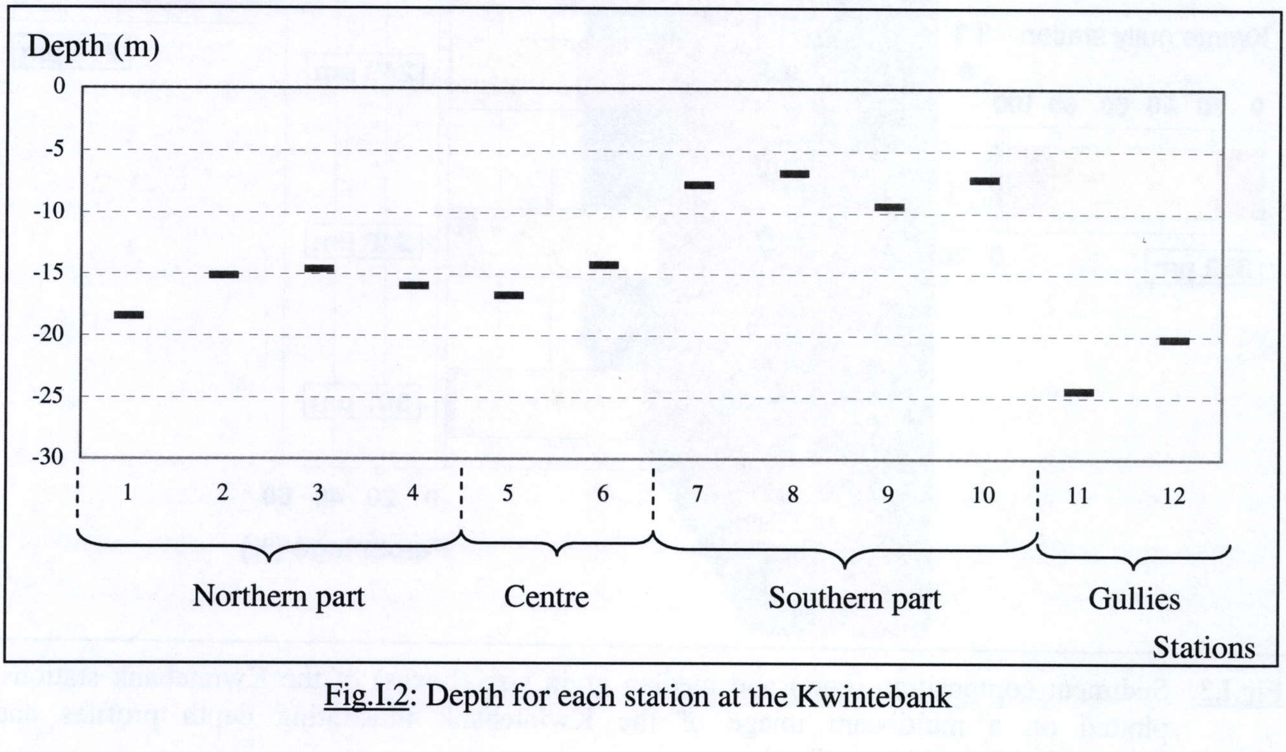

Fig.I.2: Depth for each station at the Kwintebank

3.1.2 Sediment characteristics

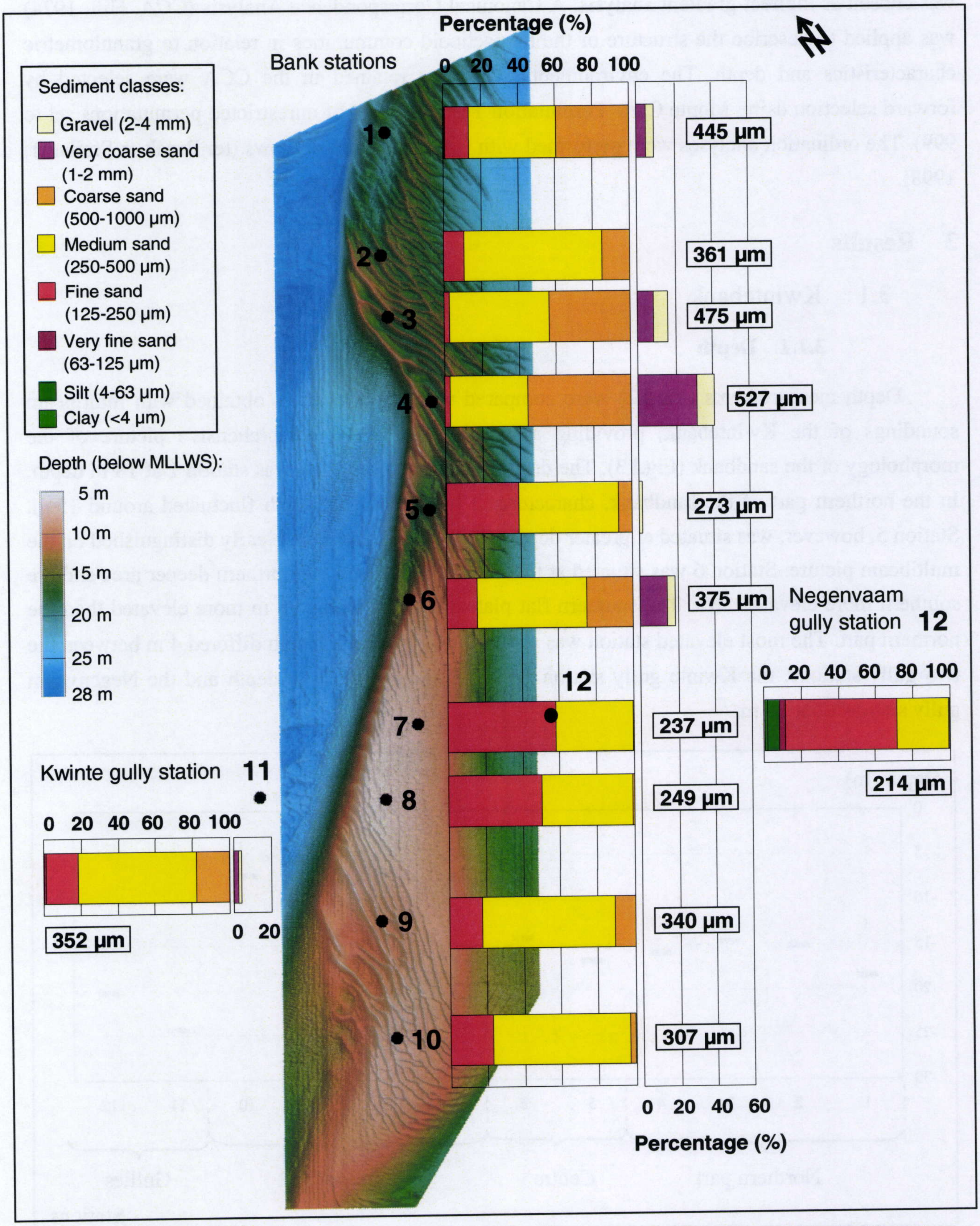

Fig.I.3: Sediment composition (bars) and median grain size (boxes) of the Kwintebank stations, plotted on a multibeam image of the Kwintebank illustrating depth profiles and geomorphology of the sandbank.

Medium sand dominated in all but three stations along the Kwintebank. Station 4 in the northern part contained mainly coarse sand and two stations (7 and 8) in the southern part contained mainly fine sand. The sediment of station 12 in the Negenvaam gully also consisted of fine sand and was much finer than at station 11 in the Kwinte gully.

A large amount of medium sand was present all over the sandbank, ranging from 40 % to 75 %. In the northern part coarse and very coarse sands and gravel contributed considerably to the sediment composition, up to 55 %, 33 % and 8 % respectively, while fine sands were important in the southern part (17 % - 58 %). Only at the Negenvaam gully station silt and clay made up a substantial part of the sediment (6 % and 2 % respectively).

Generally a linear gradient can be distinguished from coarse sands in the northern area with sandwaves to fine sands on the southern flat plateau. The linear gradient however is discontinuous. The coarsest station (4) was situated just north of the centre of the sandbank. In the centre the contribution of fine sand increased at station 5 (39 %) while it was less important at station 6 (16 %), situated just to the south of station 5. Coarse sand, very coarse sand and gravel were barely found at station 5 (6.4 %, 0.8 % and 0.4 % respectively) while the sediment of station 6 contained much coarse (24 %) and very coarse sand (15 %). Station 7 and 8, which are located in the most elevated and flat part of the sandbank, contained most fine sand (58 % and 51 % respectively). The small sandwaves to the south of this area were characterized by predominantly medium sands.

3.1.3 Harpacticoid density and diversity

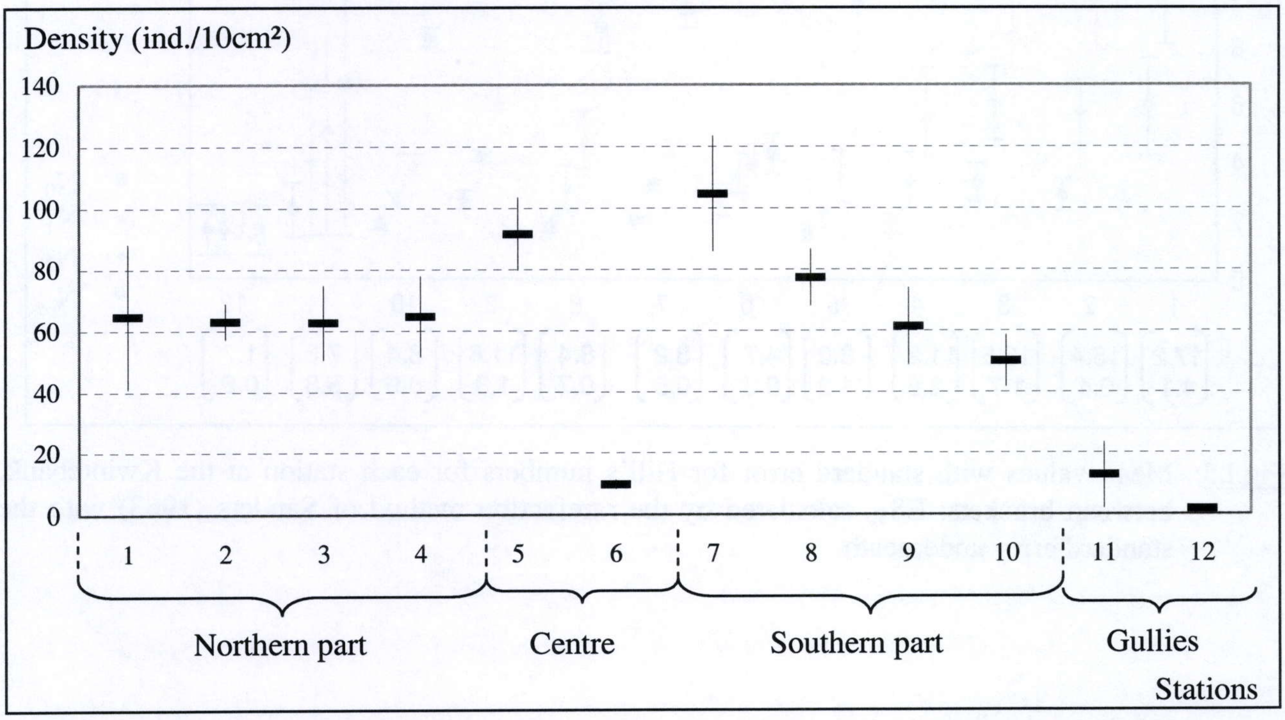

Fig.I.4: Mean total density with standard error for each station at the Kwintebank

In total 80 copepod species were found on the Kwintebank, of which 75 harpacticoids, belonging to 36 genera and divided over 11 families (Addendum I.1). Five species were cyclopoid copepods. 37.5 % of the harpacticoid species were new to science. At stations 1 to 4 (in the northern part of the Kwintebank) mean densities were comparable and counted 63 to 65 ind./10 cm² (Fig.I.4). Mean density was highest at station 7 (105 ind./10 cm²) and decreased to the south of the bank. Density at station 7 differed significantly from the northern part (stations 1-4) and from the southern extremity (stations 9-10) of the bank. An extreme low mean density was recorded in the centre of the sandbank for station 6 (10 ind./10 cm²) and in the gully stations, significantly differing from all the other bank stations. Densities did not show any correlation with sediment characteristics.

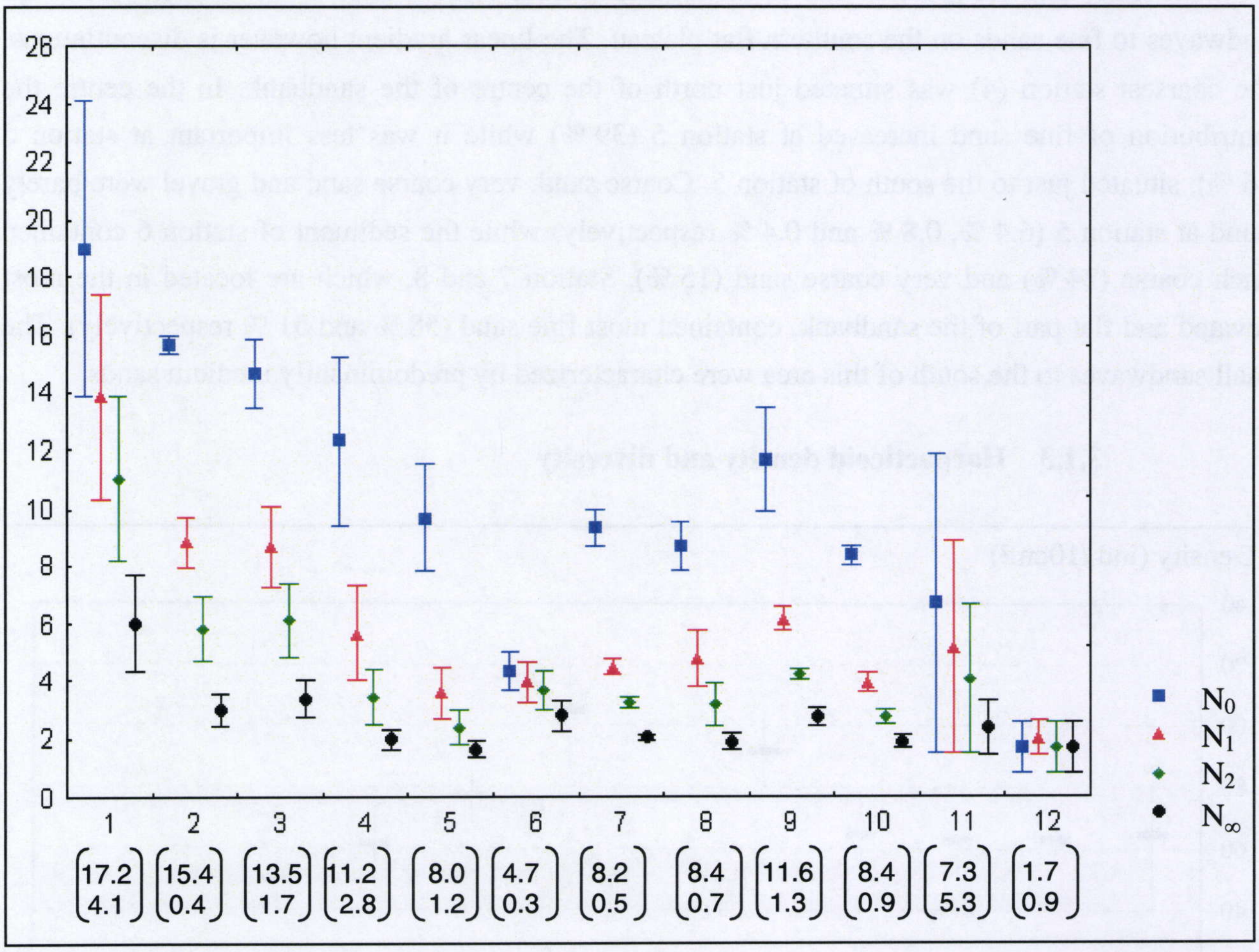

Fig.I.5: Mean values with standard error for Hill's numbers for each station at the Kwintebank, between brackets: ES_{50} calculated by the rarefaction method of Sanders (1968) with the standard error underneath

Diversity was highest at the northern tip (station 1) and decreased linearly to the south of the sandbank (Fig.I.5). The lowest species richness (N_0) was recorded at station 6. N_0 at station 6 was significantly lower than at stations 1, 2, 3 and 4. N_0 , N_1 and N_2 were positively correlated with median grain size ($p < 0.05$). N_1 was negatively correlated with fine sand and clay and silt content ($p < 0.05$) and N_2 negatively with fine sand ($p < 0.05$).

3.1.4 Ecotype distribution

97 % of all harpacticoids on the Kwintebank (total density) were interstitial copepods, 1 % were epibenthic and 2 % endobenthic. The proportion of the different ecotypes was very similar for all bank stations, the interstitial species accounting for 95 % up to 99 %. The relative abundance of epibenthic species was higher (25 %) at the fine sand gully station 12 and the endobenthic species were relatively more important (14 %) at the coarser gully station 11.

Table I.1 summarizes the significant (Kruskall-Wallis ANOVA, $p < 0.05$) correlations between the different sediment classes and epibenthic, endobenthic and interstitial species:

	Median grain size	Clay	Silt	Fine sand	Coarse sand
Epibenthic species				+	
Endobenthic species	+				+
Interstitial species		-	-		

3.1.5 Harpacticoid communities

Based on multivariate techniques (TWINSPAN, Cluster Analysis and CA) four copepod communities were distinguished on the Kwintebank in 1997:

Community I (KI): Northern bank stations 1 and 2
Community II (KII): Northern bank stations 3 and 4
Community III (KIII): Central station 5 and southern bank stations 7, 8, 9 and 10
Community IV (KIV): Central bank station 6 and gully stations 11 and 12

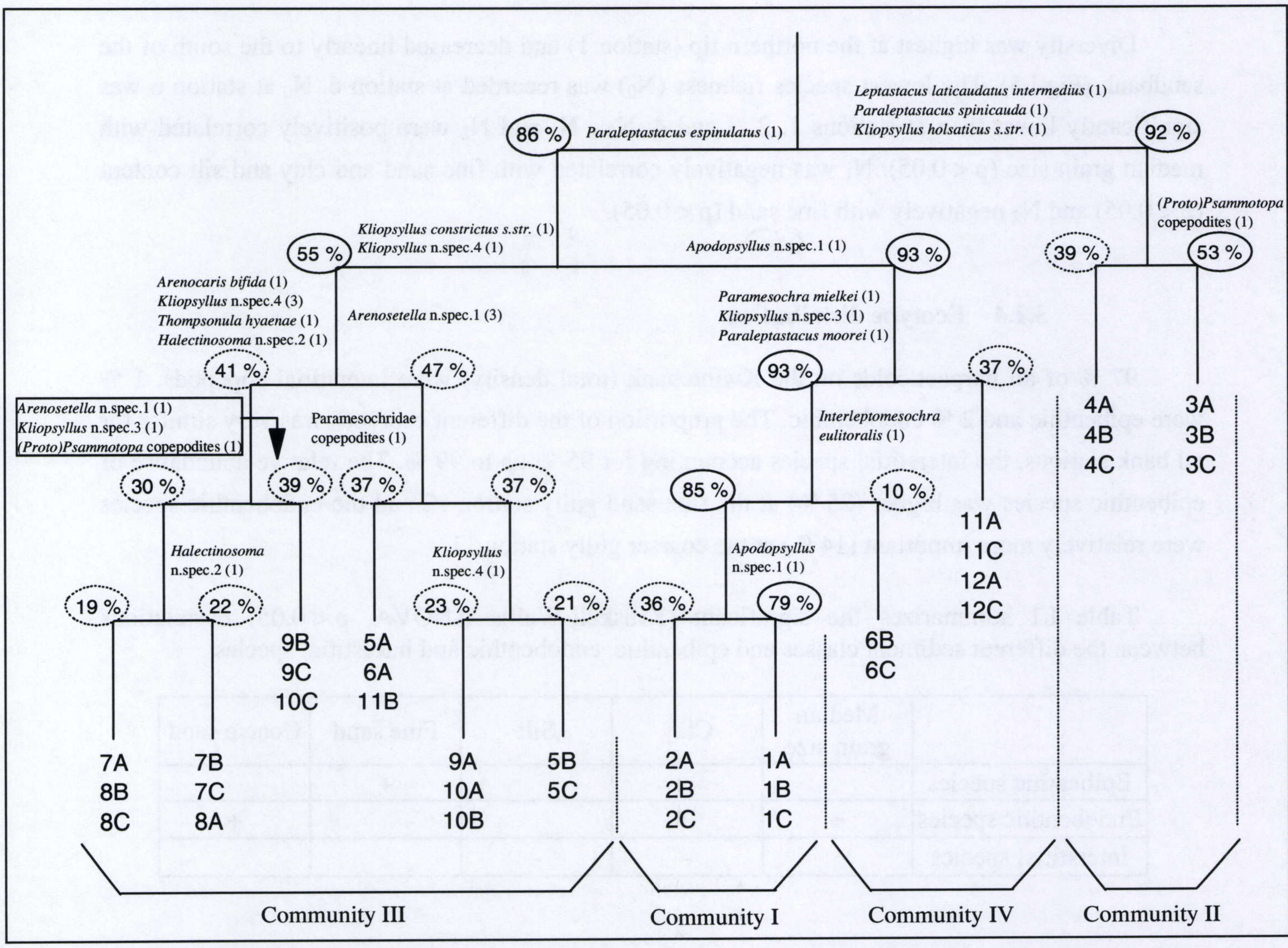

Fig.I.6: TWINSPAN diagram of the replicates of the Kwintebank based on absolute species abundances (cutlevels 0, 1, 4, 70). The percentages given are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). Only the percentages exceeding 50 % indicate that the concerned division can still be subdivided. The percentages within dotted circles indicate that further divisions have to be disregarded.

In Fig.I.6 the TWINSPAN diagram of the replicate samples of the Kwintebank is illustrated. The within-group variance between the replicates of station 1 was high. Nevertheless, this station was considered to make up one group with station 2. Although it had a very low density, sample 6A was more similar to the stations belonging to community III than the other replicates of station 6. Five out of the ten specimens of 6A were *Paraleptastacus espinulatus* and three specimens *Kliopsyllus constrictus s.str.*, two species characteristic of community III, while these species were not present in the other replicates of station 6. In further analyses, excluding stations 3 and 4, similarities between station 6 and the gully stations were more obvious. Therefore, station 6 and the gully stations were considered to form one group as indicated by the Cluster Analysis (Fig.I.7). Stations 3 and 4 joined in one group but the relatively low similarity between these two stations had to be taken into account as well. The similarity between the divisive and the agglomerative (Fig.I.7) classification technique was 87 % so the results of the classifications were consistent. The output of the ordination analysis (Fig.I.8) was similar to the results of the classification analyses.

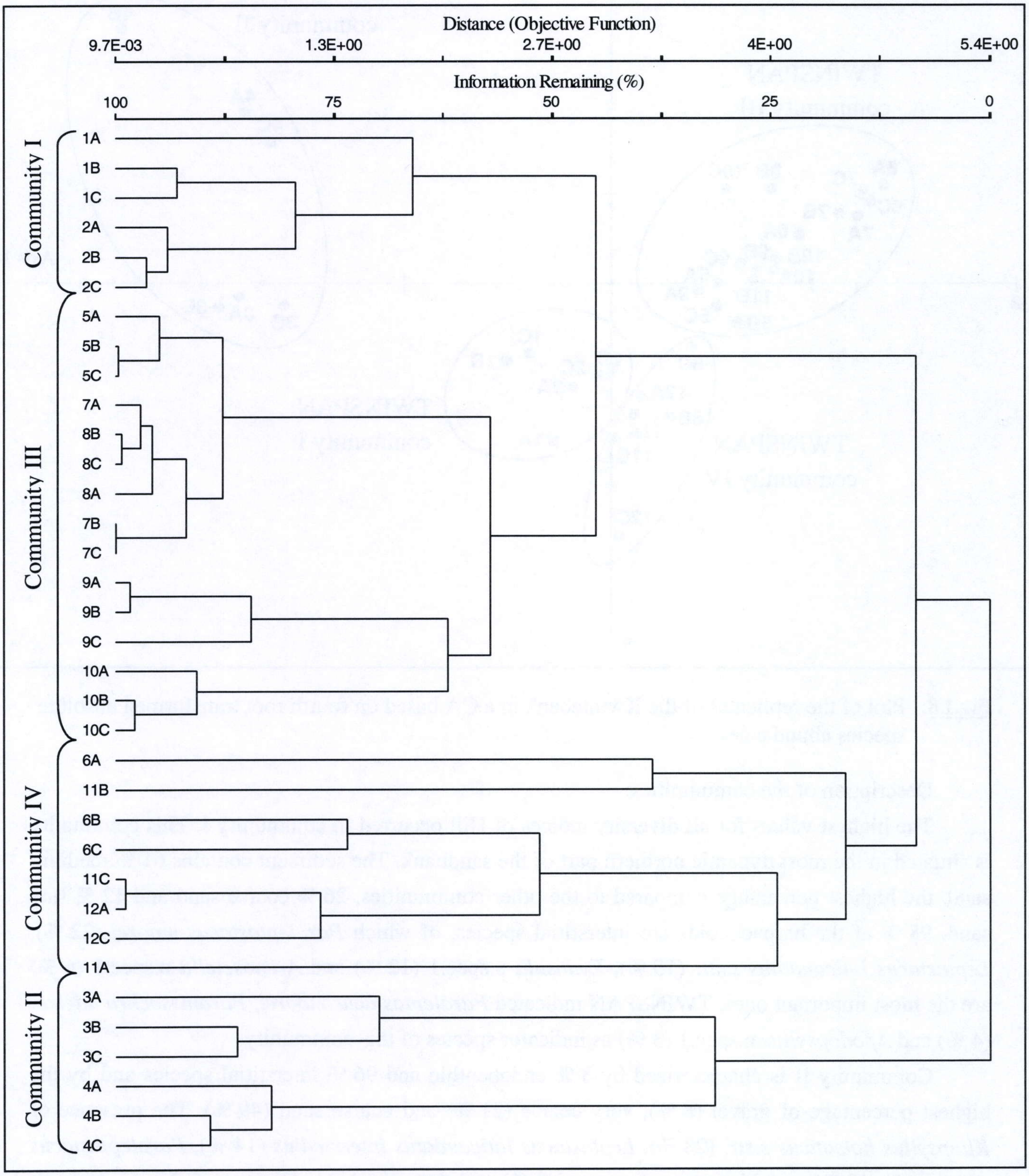

Fig.I.7: Cluster analysis of the replicates of the Kwintebank based on absolute species abundances, using the Bray-Curtis similarity index and Group Average Sorting

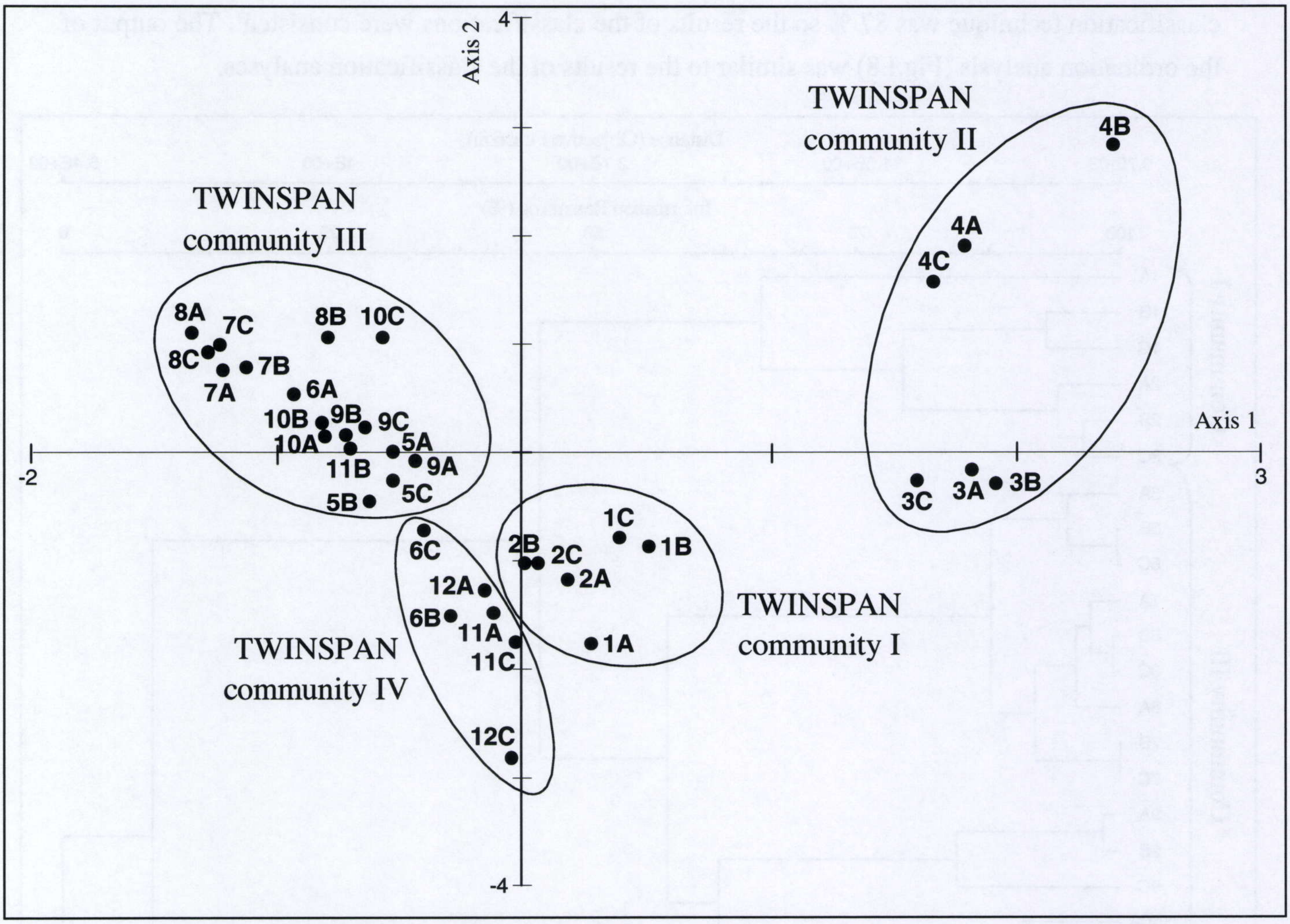

Fig.I.8: Plot of the replicates of the Kwintebank in a CA based on fourth root transformed absolute species abundances

Description of the communities:

The highest values for all diversity indices of Hill occurred in community I. This community is situated in the most dynamic northern part of the sandbank. The sediment contains 61 % medium sand, the highest percentage compared to the other communities, 26 % coarse sand and 12 % fine sand. 98 % of the harpacticoids are interstitial species, of which *Paraleptastacus moorei* (22 %), *Leptastacus laticaudatus s.str.* (15 %), *Evansula* n.spec.1 (12 %) and *Arenosetella* n.spec.1 (6 %) are the most important ones. TWINSPAN indicated *Paraleptastacus moorei, Paramesochra mielkei* (4 %) and *Apodopsyllus* n.spec.1 (3 %) as indicator species of this community.

Community II is characterized by 3 % endobenthic and 96 % interstitial species and by the highest percentage of gravel (8 %), very coarse (21 %) and coarse sand (49 %). The presence of *Kliopsyllus holsaticus s.str.* (28 %), *Leptastacus laticaudatus intermedius* (14 %), *Paraleptastacus spinicauda* (10 %) and *Metacyclopina* spec. (9 %) and the remarkable absence of *Paraleptastacus espinulatus* are the decisive factors to distinguish this community from the other bank stations.

Community III is found in sediment with the highest percentage of fine sand (38 %). This community harbours less species than the communities in the northern part ($p < 0.05$ for community I and $p < 0.001$ for community II). A high dominance of a few species (*Paraleptastacus espinulatus* (35 %), *Kliopsyllus constrictus s.str.* (17 %), *Leptastacus laticaudatus s.str.* (16 %) and *Kliopsyllus* n.spec.4 (13 %)) characterizes this community.

Community IV consists of the gully stations and station 6 and has the lowest mean density (8 ind./10 cm²) as well as the lowest values for all Hill diversity numbers. *Apodopsyllus* n.spec.1 (21 %), *Leptastacus laticaudatus s.str.* (15 %), *Arenosetella* n.spec.1 (10 %) and *Paraleptastacus espinulatus* (9 %) are the four most important species. The contribution of epi- and endobenthic species is somewhat higher (7 % for both), while 85 % of the copepods consists of interstitial species.

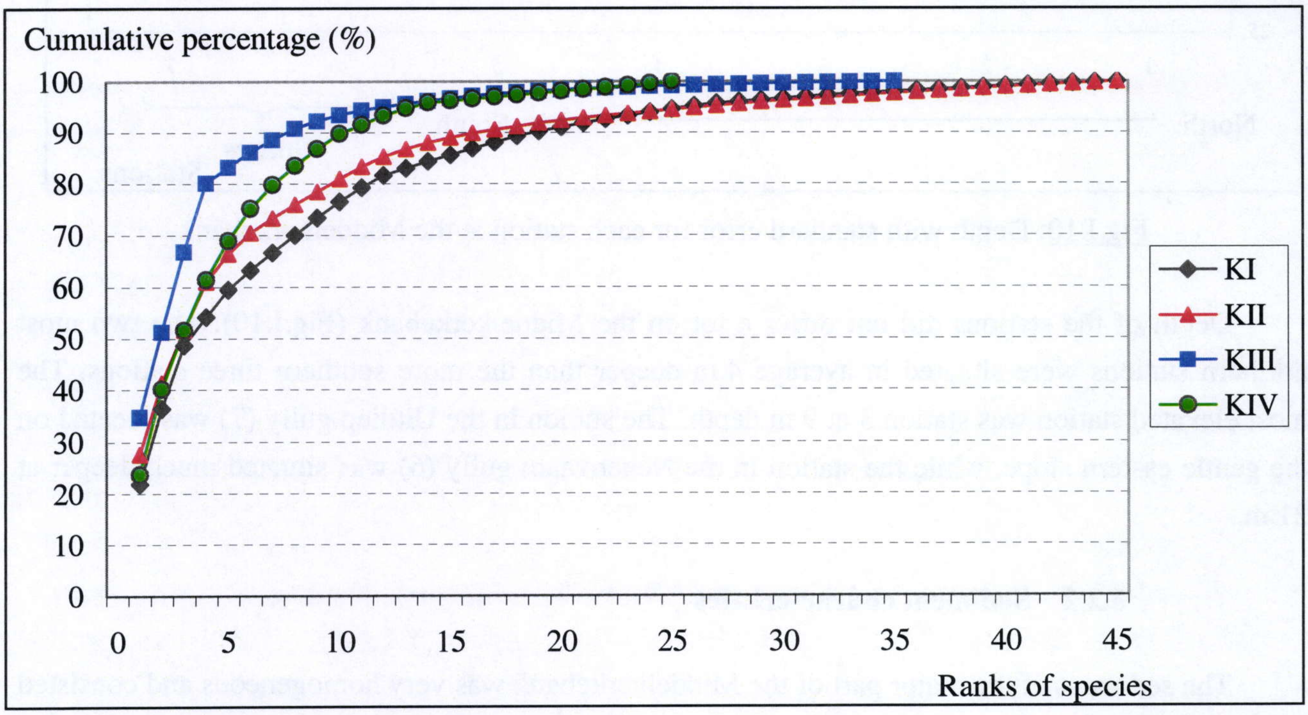

Fig.I.9: k-dominance curves of the communities at the Kwintebank

k-Dominance curves distinguished between communities I and II and communities III and IV (Fig.I.9). The contribution of the most important species was somewhat higher in community II than in community I while the species richness and the evenness were very similar. Species richness was higher in community III than in community IV but the contribution of the most important species was much higher in the former.

3.2 Middelkerkebank

3.2.1 Depth

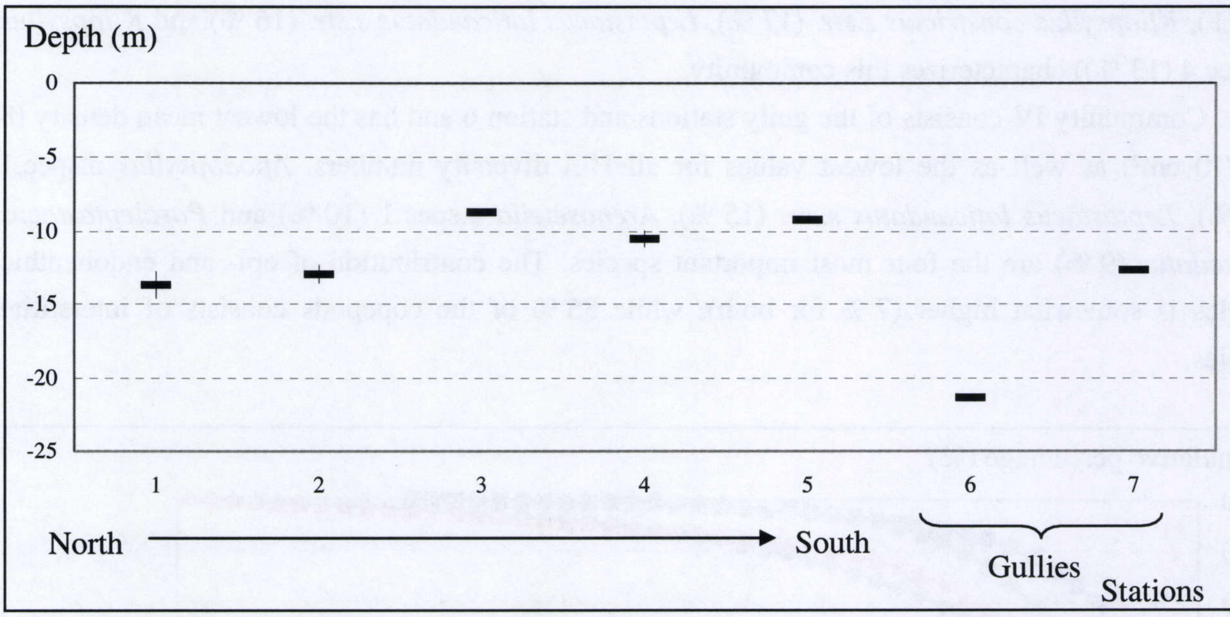

Fig.I.10: Depth with standard error for each station at the Middelkerkebank

Depth of the stations did not differ a lot on the Middelkerkebank (Fig.I.10). The two most northern stations were situated in average 4 m deeper than the more southern three stations. The most elevated station was station 3 at 9 m depth. The station in the Uitdiep gully (7) was located on the gentle eastern slope, while the station in the Negenvaam gully (6) was situated much deeper at 21 m.

3.2.2 Sediment characteristics

The sediment of the major part of the Middelkerkebank was very homogeneous and consisted mainly of medium sand for all stations, except for the most southern station 5 and the Negenvaam gully station 6. Medium sand predominated at four of the five bank stations, ranging from 37 % to 63 %. The coarse sand content was very similar for these four stations (20 % - 33 %), as well as the very coarse sand (6 % - 12 %) and gravel content (2 % - 7 %). The latter two sediment classes increased slightly from the most northern station towards the south. Very coarse sand reached its maximum percentage at station 3, gravel at station 4. From north to south a linear increase of fine sands was observed, corresponding with a decreasing amount of medium sand and a linearly decreasing median grain size. Station 5 differed a lot from the other stations on the sandbank. At this topographically flat southern end coarse sand, very coarse sand and gravel were absent. Fine sands predominated with 63 %, the remaining part consisted of medium sand only.

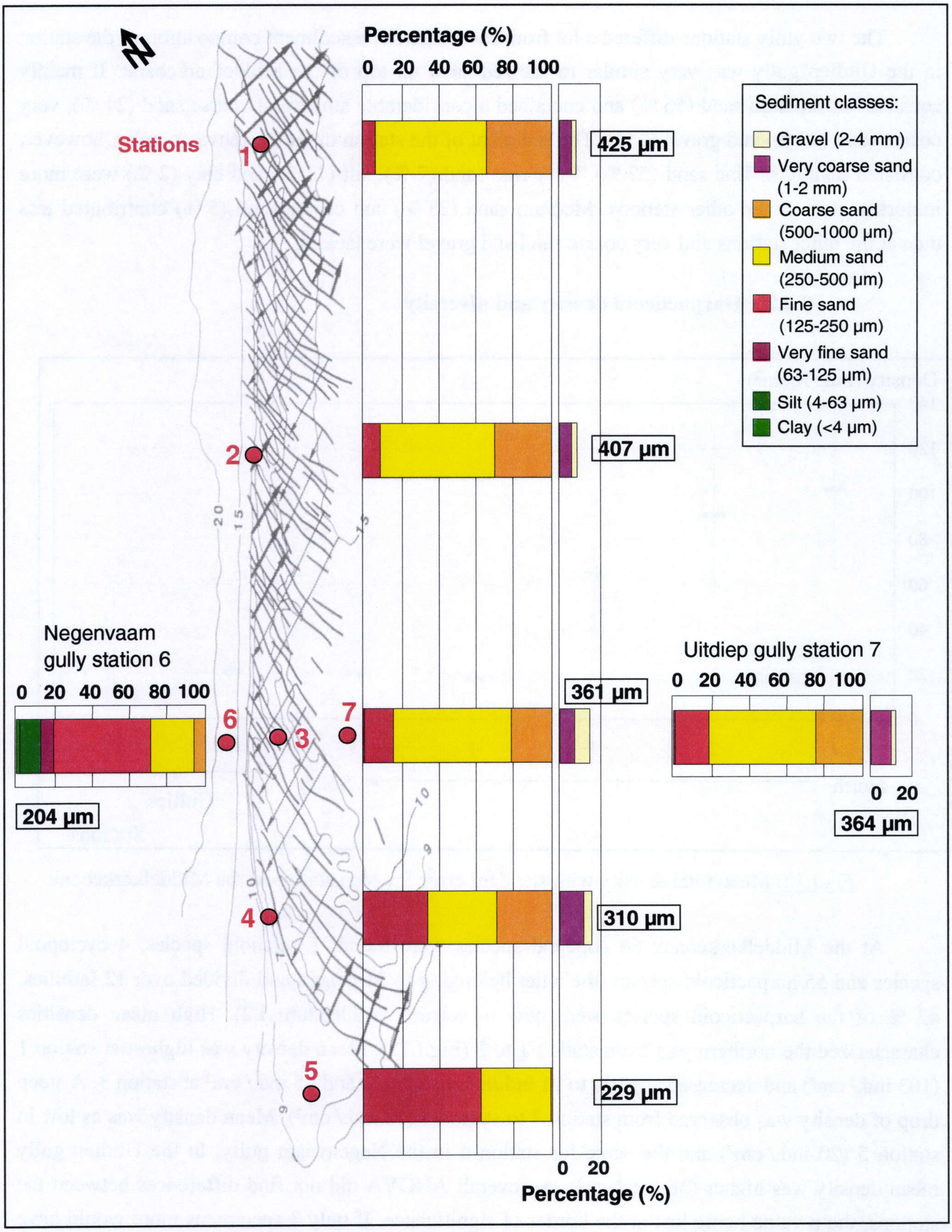

Fig.I.11: Sediment composition (bars) and median grain size (boxes) of the Middelkerkebank stations, which are plotted on a side-scan sonar image with bathymetric registrations (isobaths 9-10-15-20) taken in May 1990 (Lanckneus *et al.*, 1994). The picture also illustrates the geomorphology of the sandbank (flood dominated sandwaves (crest lines crossed by bold arrows) and ebb dominated sandwaves (crossed by regular arrows)

The two gully stations differed a lot from each other. The sediment composition of the station in the Uitdiep gully was very similar to the sediment on top of the Middelkerkebank. It mainly consisted of medium sand (56 %) and contained a considerable amount of coarse sand (24 %), very coarse sand (10 %) and gravel (2 %). The sediment of the station in the Negenvaam gully, however, consisted mainly of fine sand (52 %). Very fine sand (7 %), silt (11 %) and clay (2 %) were more important than at the other stations. Medium sand (23 %) and coarse sand (5 %) contributed less than at the other stations and very coarse sand and gravel were lacking.

3.2.3 Harpacticoid density and diversity

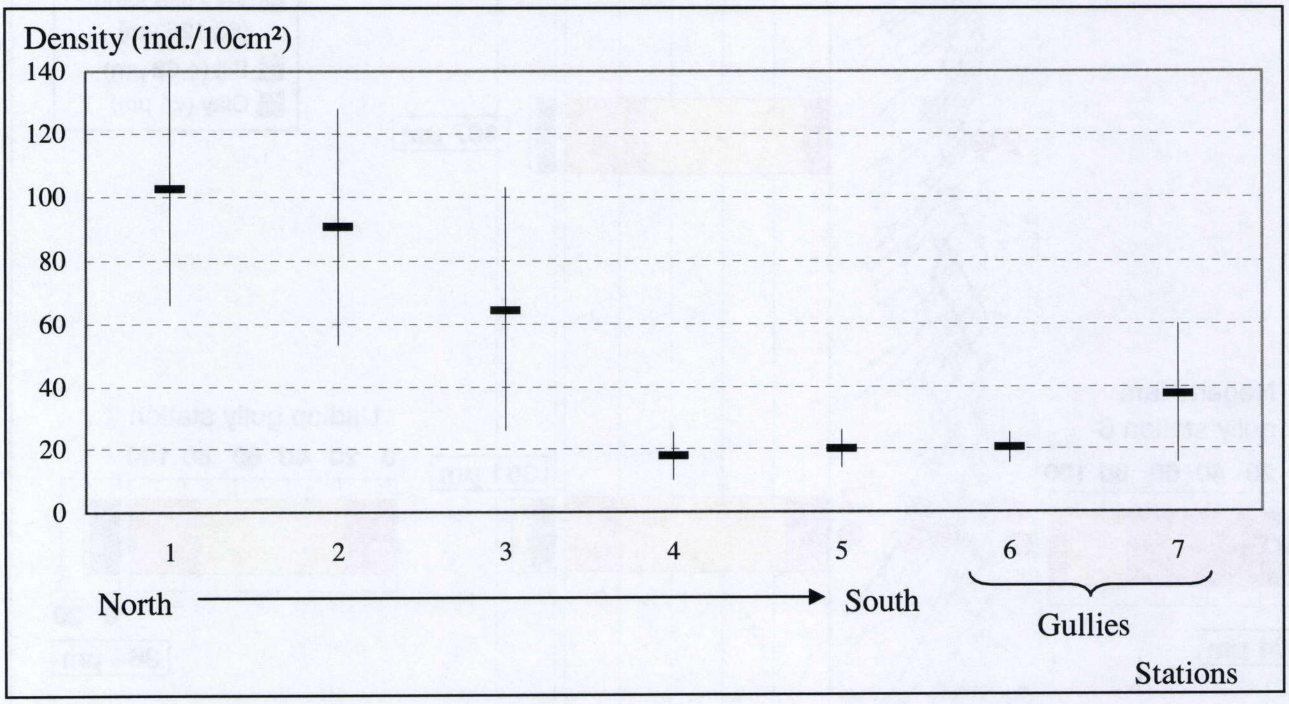

Fig.I.12: Mean total density with standard error for each station at the Middelkerkebank

At the Middelkerkebank 60 copepod species were found: 1 calanoid species, 4 cyclopoid species and 55 harpacticoid species, the latter belonging to 31 genera and divided over 12 families. 42 % of the harpacticoid species were new to science (Addendum I.2). High mean densities characterized the northern part from station 1 to 3 (Fig.I.12). Mean density was highest at station 1 (103 ind./ cm^2) and decreased slightly to 91 ind./m^2 at station 2 and 65 ind./ cm^2 at station 3. A steep drop of density was observed from station 3 to station 4 (18 ind./ cm^2). Mean density was as low in station 5 (20 ind./ cm^2) and the same for station 6 in the Negenvaam gully. In the Uitdiep gully mean density was higher (38 ind./ cm^2). An overall ANOVA did not find differences between the stations, the p value being just at the border of significance. If only 3 specimens more would have been found in the northern stations, the difference would have been significant. The power of the ANOVA was calculated as 78 %. Hence, the probability of committing a type II error by disregarding the observed differences between the northern and the more southern stations is 22 %.

Moreover, sampling error can imply such a small difference but the higher variance in the northern area in comparison with the southern part has to be taken into account as well. Density was positively correlated with medium sand content and negatively correlated with fine and very fine sand contents ($p < 0.05$).

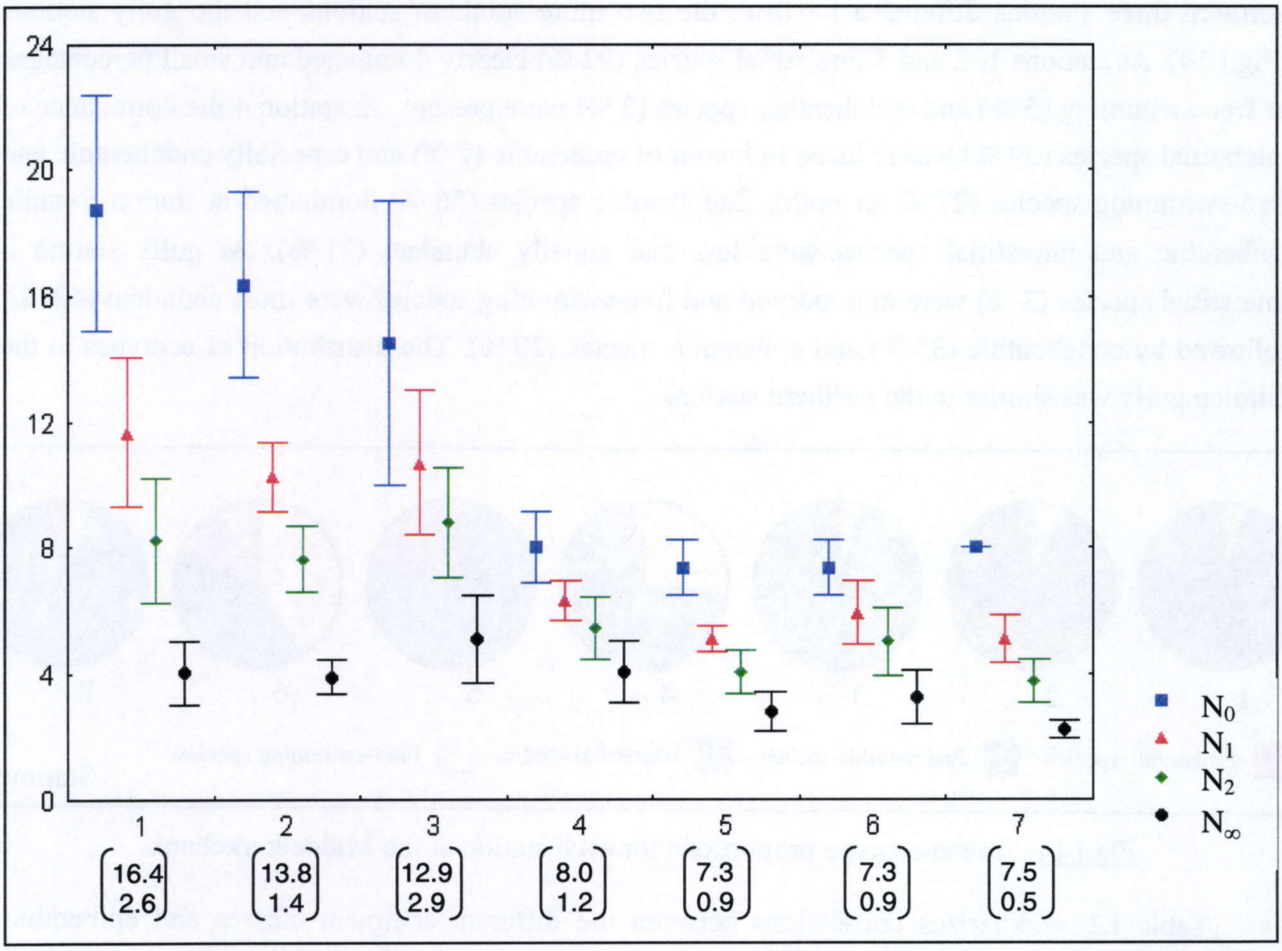

Fig.I.13: Mean values with standard error for Hill's numbers for each station at the Middelkerkebank, between brackets: ES_{50} calculated by the rarefaction method of Sanders (1968) with the standard error underneath

The decline in density corresponded with a steep decline in diversity (Fig.I.13). Consequently density and Hill numbers N_0 and N_1 were strongly correlated. The values for the two most southern stations were as low as for both gully stations. N_0 and N_1 were significantly higher in the northern stations 1, 2 and 3. The value for N_2 at the stations 1, 2 and 3 was significantly higher than the value at the most southern station 5 and the Uitdiep gully station 7. N_0 was negatively correlated with very fine and fine sand ($p < 0.05$ and $p < 0.0001$ respectively) and positively correlated with medium and coarse sand ($p < 0.05$ for both). N_1 was negatively correlated with fine sand ($p < 0.05$).

3.2.4 Ecotype distribution

87 % of all copepods on the Middelkerkebank were interstitial, 4 % were epibenthic, 9 % endobenthic and 7 % free-swimming species. From north to south along the sandbank, interstitial species became less important, while the gully stations differed clearly from each other. The northern three stations differed a lot from the two more southern stations and the gully stations (Fig.I.14). At stations 1, 2 and 3 interstitial species (92 %) clearly dominated and small percentages of free-swimming (5 %) and endobenthic species (2 %) were present. At station 4 the dominance of interstitial species (39 %) was reduced in favour of epibenthic (7 %) and especially endobenthic and free-swimming species (27 % for both). Endobenthic species (56 %) dominated at station 5 while epibenthic and interstitial species were less and equally abundant (21 %). At gully station 6 interstitial species (3 %) were unimportant and free-swimming species were most abundant (42 %), followed by endobenthic (35 %) and epibenthic species (20 %). The distribution of ecotypes in the Uitdiep gully was similar to the northern stations.

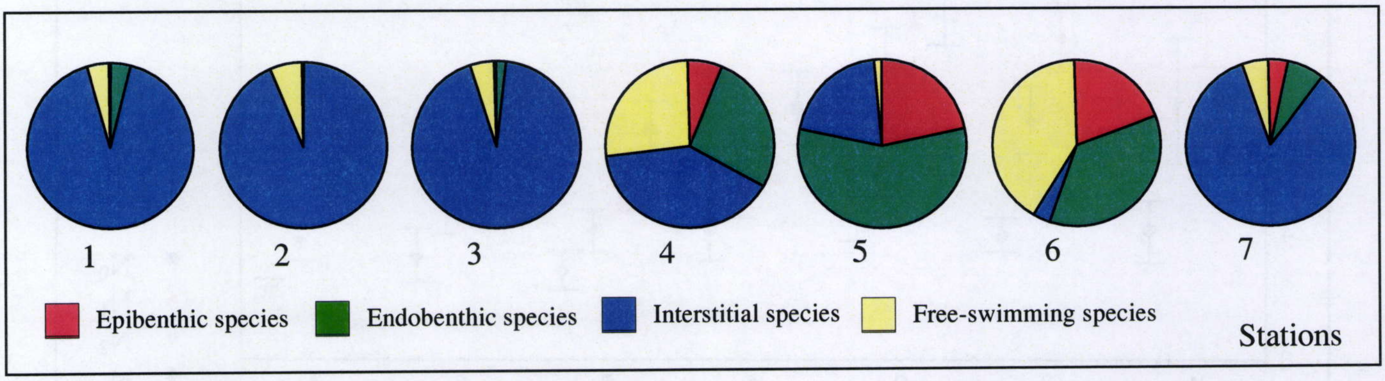

Fig.I.14: Mean ecotype proportions for each station at the Middelkerkebank

Table I.2 summarizes correlations between the different sediment classes and epibenthic, endobenthic and interstitial species:

	Very fine sand	Fine sand	Medium sand	Coarse sand
Epibenthic species	+ (★)	+ (★★★)	- (★)	- (★)
Endobenthic species		+ (★★★★)	- (★)	- (★)
Interstitial species	- (★)	- (★★★)	+ (★★★★)	+ (★)
★ = $p < 0.05$; ★★ = $p < 0.01$; ★★★ = $p < 0.001$; ★★★★ = $p < 0.0001$				

3.2.5 Harpacticoid communities

Two copepod communities and an intermediate species association between these two communities were distinguished on the Middelkerkebank in 1997:

Community I (MI):	Northern bank stations 1, 2 and 3
Intermediate species association (MISA):	Uitdiep gully station 7
Community II (MII):	Southern bank stations 4 and 5 and Negenvaam gully station 6

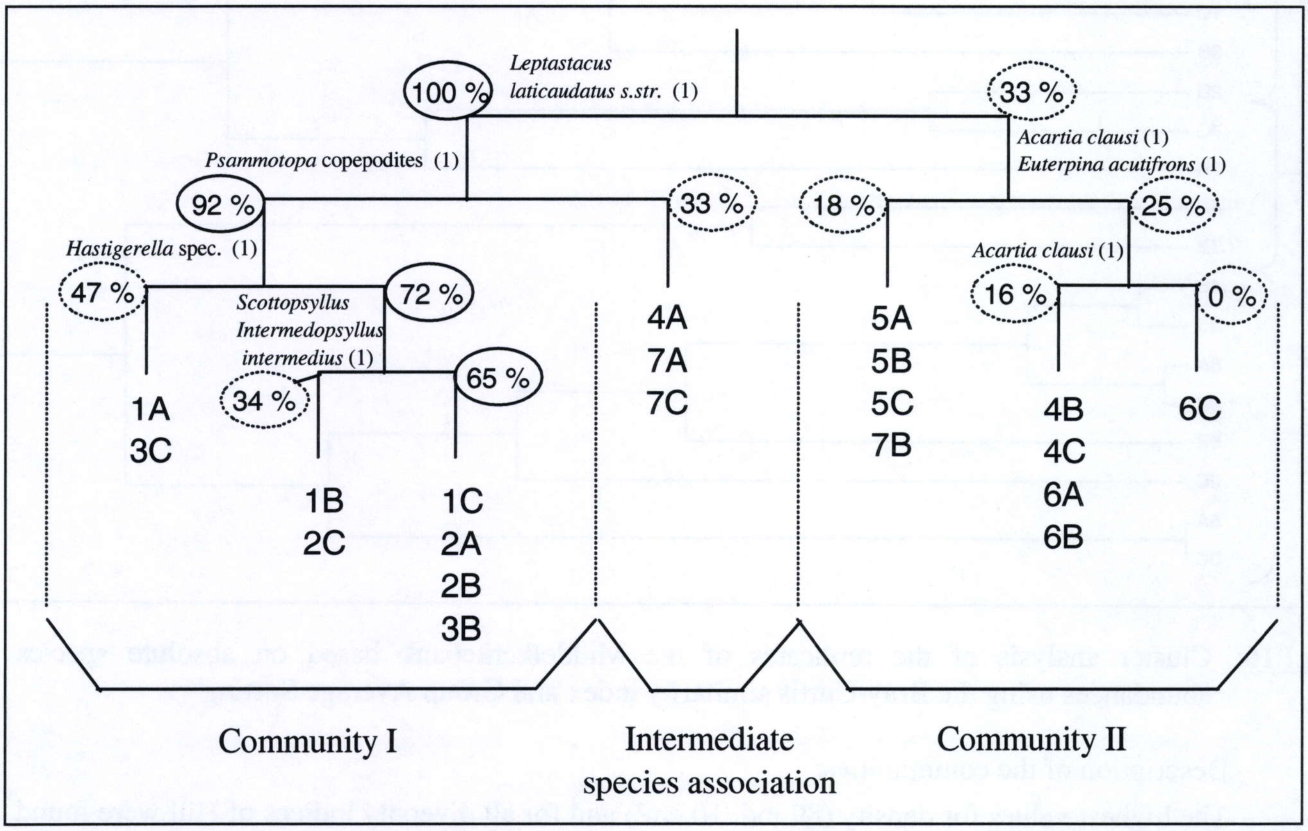

Fig.I.15: TWINSPAN diagram of the replicates based on absolute species abundances (cutlevels 0, 2, 5, 55). The percentages given are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). The percentages within full circles exceed 50 % and indicate that the concerned group can still be split up. The percentages within dotted circles indicate that further divisions should be disregarded.

The northern stations 1, 2 and 3 could easily be distinguished from the other stations (Fig.I.15). The replicates of these stations, however, were divided over different divisions so they are considered as one group. Stations 4, 5 and 6 formed one group as well. The within group variance was too low in relation to the total variance to retain further divisions. Station 7 had characteristics of both communities and was considered as an intermediate species association. The same pattern was illustrated by cluster (Fig.I.16) and ordination analyses. The similarity between the divisive and the agglomerative classification technique was 75 %, defining the classifications as consistent.

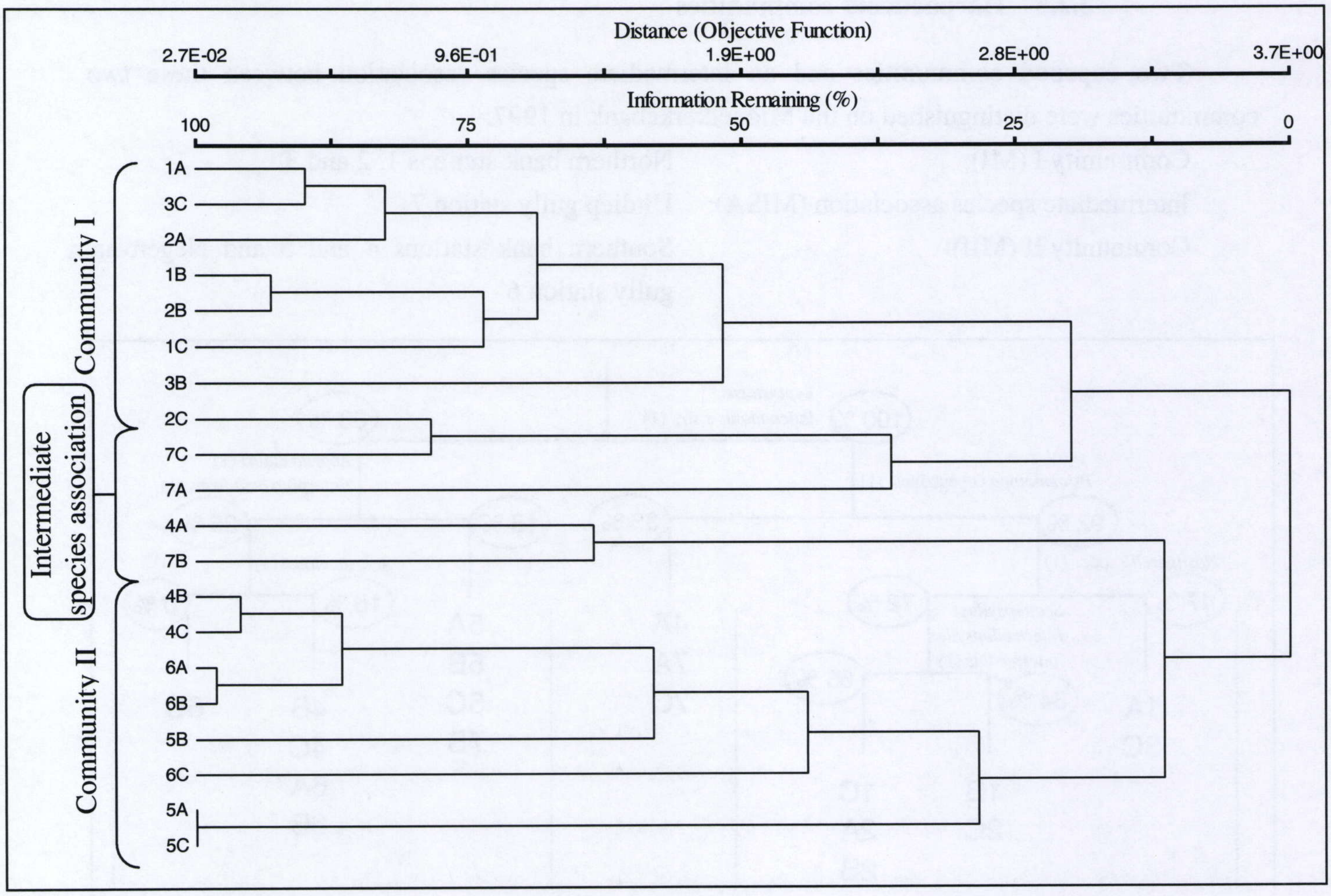

Fig.I.16: Cluster analysis of the replicates of the Middelkerkebank based on absolute species abundances using the Bray-Curtis similarity index and Group Average Sorting

Description of the communities:

The highest values for density (89 ind./10 cm²) and for all diversity indices of Hill were found in community I. This community is situated in the most dynamic northern part of the sandbank. The sediment contains the highest percentages of medium sand (61 %), coarse sand (27 %) and gravel (4 %), as well as 7 % very coarse sand and the lowest value for fine sand (11 %). 92 % of the harpacticoids are interstitial species, of which *Evansula* n.spec.3 (13 %), *Leptastacus laticaudatus s.str.* (11 %), *Psammotopa* copepodites (9 %), *Paraleptastacus* n.spec.1 (8 %) and *Arenosetella* n.spec. 1 (7 %) are the most important ones. TWINSPAN selected *Leptastacus laticaudatus s.str.* and *Psammotopa* copepodites as indicators of this community.

Community II was found in sediments with the highest percentage of fine sand (50 %), very fine sand (3 %), silt (4 %) and clay (1 %) and the lowest amount of gravel (1 %), very coarse sand (4 %), coarse sand (11 %) and medium sand (32 %). This community was characterized by 16 % endobenthic, 39 % endobenthic, 21 % interstitial species and 23 % of free-swimming species. The presence of *Acartia clausi* (4 %) and *Euterpina acutifrons* (5 %) distinguished this community from the other bank stations. *Halectinosoma* n.spec.2 (23 %), *Oithona robusta* (12 %), *Canuella perplexa*

(10 %), *Pseudobradya beduina* (10 %) and *Enhydrosoma propinquum* (7 %) were the most abundant species. Mean density (19 ind./10 cm²) was much lower than in community I ($p < 0.001$), as diversity ($p < 0.0001$ for N_0, $p < 0.001$ for N_1, $p < 0.01$ for N_2).

The contribution of epi- and endobenthic species in the intermediate species association was a bit higher (4 % and 7 % respectively) than in community I but much lower than in community II. 84 % of the copepods consisted of interstitial species. Mean density (38 ind./10 cm²) was higher and mean species richness (8) was similar to the values recorded in community II. Species dominance was much more expressed than in the two other communities (Fig.I.17). This was already clear from the contributions of the most important species: *Paraleptastacus espinulatus* (39 %), *Apodopsyllus* n.spec.1 (19 %), *Leptastacus laticaudatus s.str.* (9 %), *Arenosetella* n.spec.1 (5 %), which are all interstitial species and *Halectinosoma* n.spec.2 (5 %), an endobenthic species.

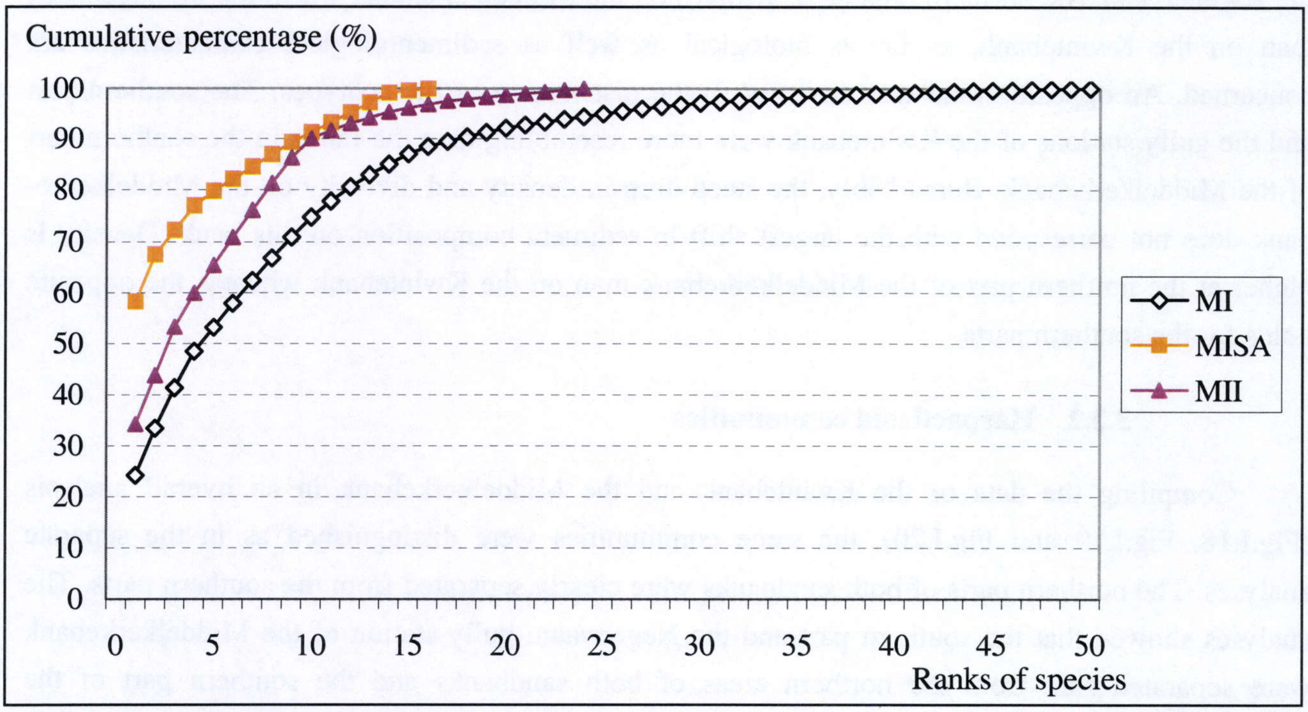

Fig.I.17: k-dominance curves of the communities at the Middelkerkebank

Fig.I.17 illustrates the increasing contribution of the most dominant species and the decreasing species richness comparing community I (MI) with community II (MII) and the intermediate species association (MISA). The latter is characterized by the smallest number of species and a very high dominance of the most important species, confirming the distinct differences between this association and the two other communities.

3.3 Comparison between Kwintebank and Middelkerkebank

3.3.1 Harpacticoid density and diversity

34 out of 104 species were found on both the Kwintebank and the Middelkerkebank. Especially the epibenthic and free-swimming species were completely different between the sandbanks, only one out of the ten epibenthic species was found on both sandbanks and one out of nine of the free-swimming species. One third of the endobenthic species occurred on both sandbanks and 40 % of the interstitial species. The gradients in densities and Hill's numbers between the northern and the southern part of both sandbanks were sharper on the Middelkerkebank than on the Kwintebank. The gradient along the sandbank from coarse sediments in the north to fine sediments in the south was smoother on the Middelkerkebank and showed more heterogeneity on the Kwintebank. The northern area of sandwaves on the Middelkerkebank was more homogeneous than on the Kwintebank, as far as biological as well as sedimentological characteristics are concerned. An opposite trend was observed in the distribution of the ecotypes. The southern part and the gully stations of the Kwintebank were more resembling than the fauna in the southern part of the Middelkerkebank. Remarkably, the steep drop in density and diversity on the Middelkerkebank does not correspond with the largest shift in sediment composition on this bank. Density is higher at the northern part of the Middelkerkebank than on the Kwintebank whereas the opposite holds for the southern parts.

3.3.2 Harpacticoid communities

Compiling the data of the Kwintebank and the Middelkerkebank in an overall analysis (Fig.I.18, Fig.I.19 and Fig.I.20), the same communities were distinguished as in the separate analyses. The northern parts of both sandbanks were clearly separated from the southern parts. The analyses showed that the southern part and the Negenvaam gully station of the Middelkerkebank were separated first from the northern areas of both sandbanks and the southern part of the Kwintebank, illustrating the special characteristics of the area. The replicates of Middelkerkebank station 7, defined as an intermediate species association earlier, were spread among different groups in the different analyses. In the TWINSPAN for instance one replicate showed high similarity with the northern part of the Middelkerkebank, a second one with the southern part of the Middelkerkebank and a third one with the southern part of the Kwintebank. This classification differed slightly between the different analyses. Again, this station was retained as an intermediate species association. In the TWINSPAN and the DCA analysis, one replicate of Kwintebank station 12, situated in the Negenvaam gully, showed similarities with station 6 of the Middelkerkebank, situated in the Negenvaam gully as well, due to the high relative abundance of *Enhydrosoma propinquum*. The results of the divisive and the agglomerative classification techniques attained 79 % similarity.

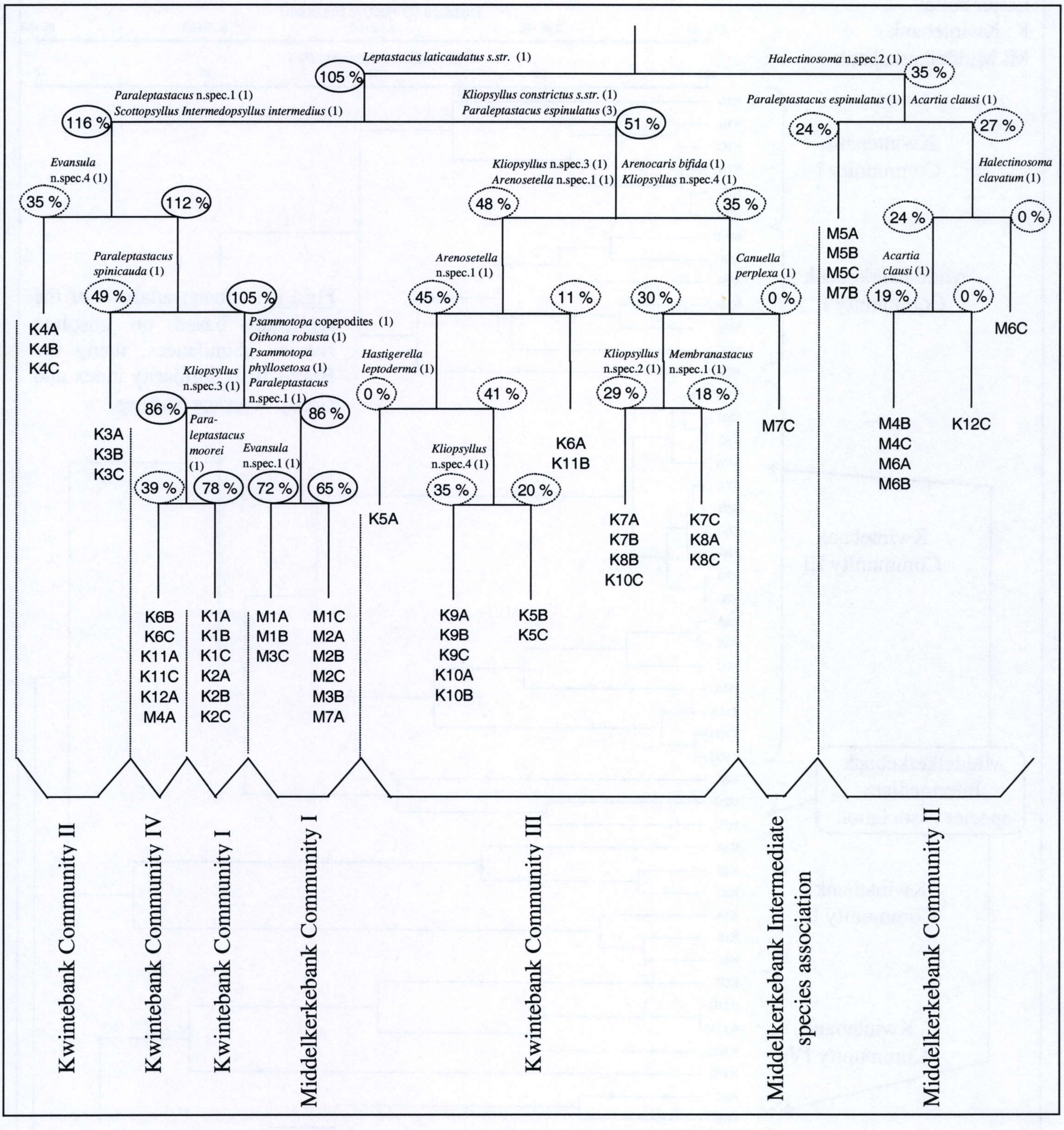

Fig.I.18: TWINSPAN diagram of the replicates based on absolute species abundances (cutlevels 0, 1, 4, 70). The percentages given are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). The percentages within full circles exceed 50 % and indicate that the concerned group can still be split up. The percentages within dotted circles indicate that further divisions should be disregarded. Letter code K stands for Kwintebank, M for Middelkerkebank.

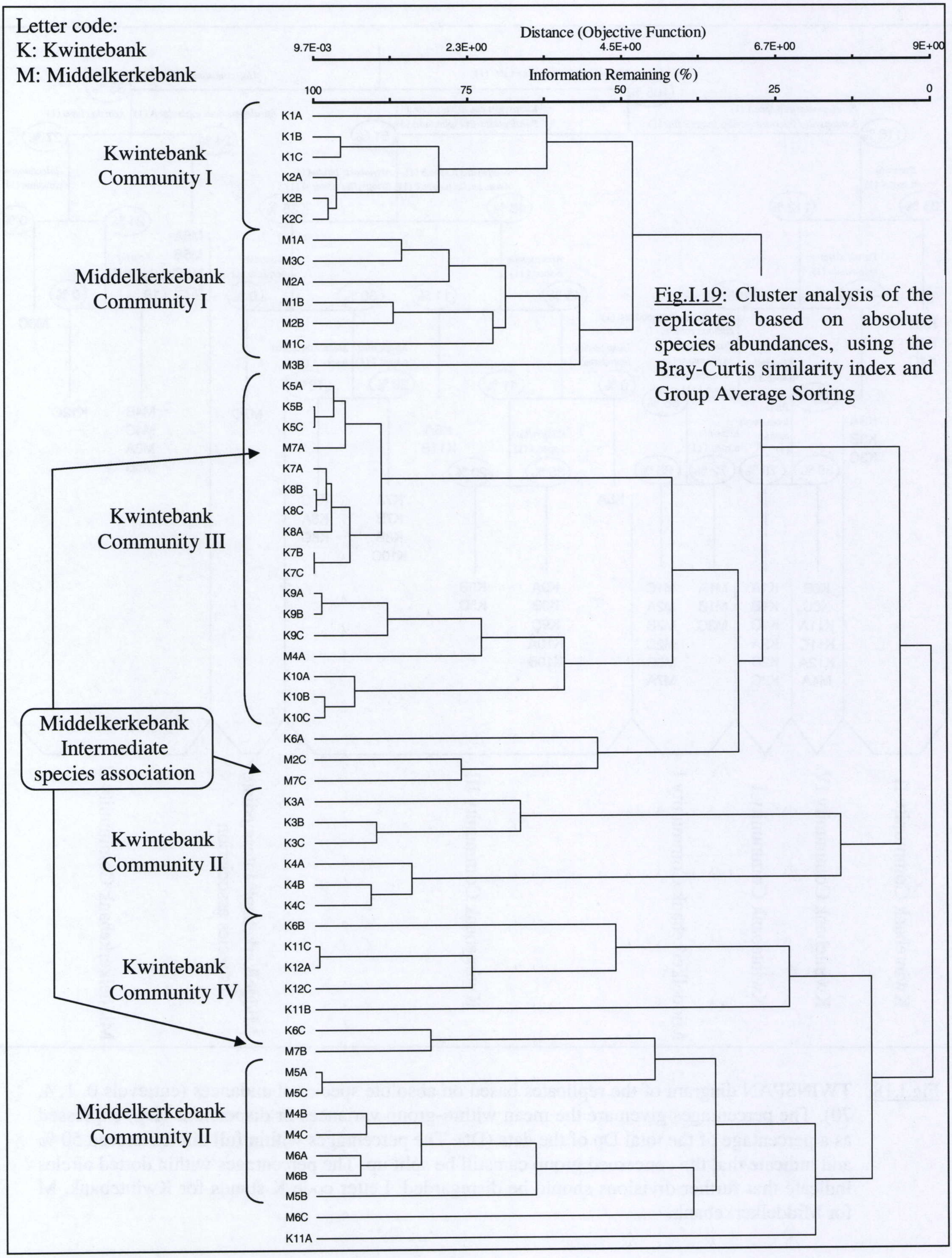

Fig.I.19: Cluster analysis of the replicates based on absolute species abundances, using the Bray-Curtis similarity index and Group Average Sorting

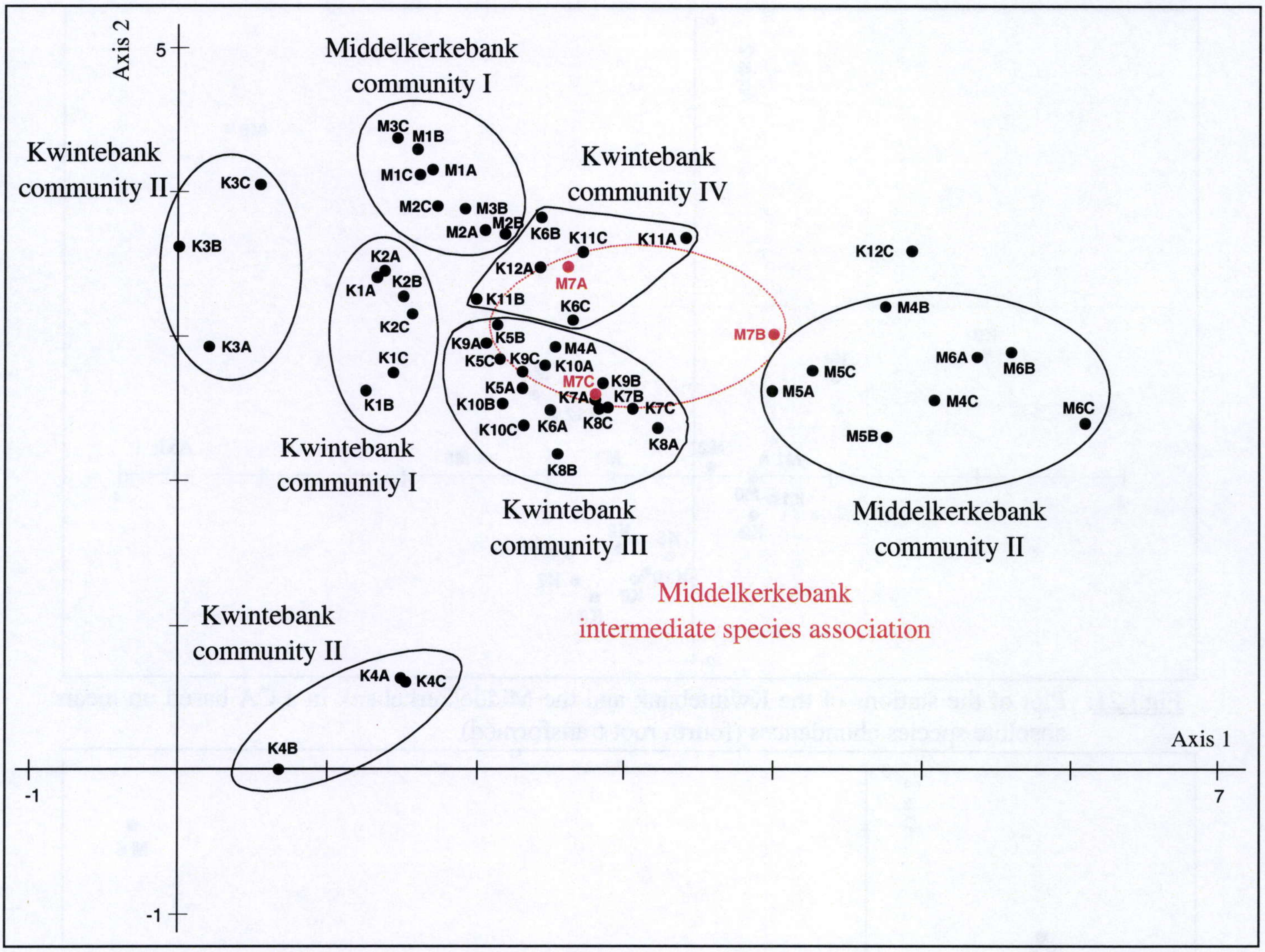

Fig.I.20: Plot of the replicates of the Kwintebank and the Middelkerkebank in a DCA based on fourth root transformed absolute species abundances

Fig.I.22 shows that the first axis of the CCA, of length 5.86 SD and explaining 49 % of the variation, is interpreted as a granulometric gradient from coarse to very fine sands mainly along the Middelkerkebank. The second axis, of length 4.31 SD (eigenvalue 0.43), represents a gradient in depth and coarse sand mainly along the Kwintebank. The plot of the stations in the CCA does not completely match the plot of the stations of the CA (Fig.I.21), indicating that not all important environmental variables were included in the constrained analysis. Especially for stations K1, K4, K6, K11 and M5 important shifts along the axes of the CCA relative to the axes of the CA were observed, reflecting that relative differences in species composition are not caused by similar relative differences in sediment characteristics or depth. In the CCA of the Middelkerkebank stations only, granulometric characteristics could even not significantly explain the variation along the axes.

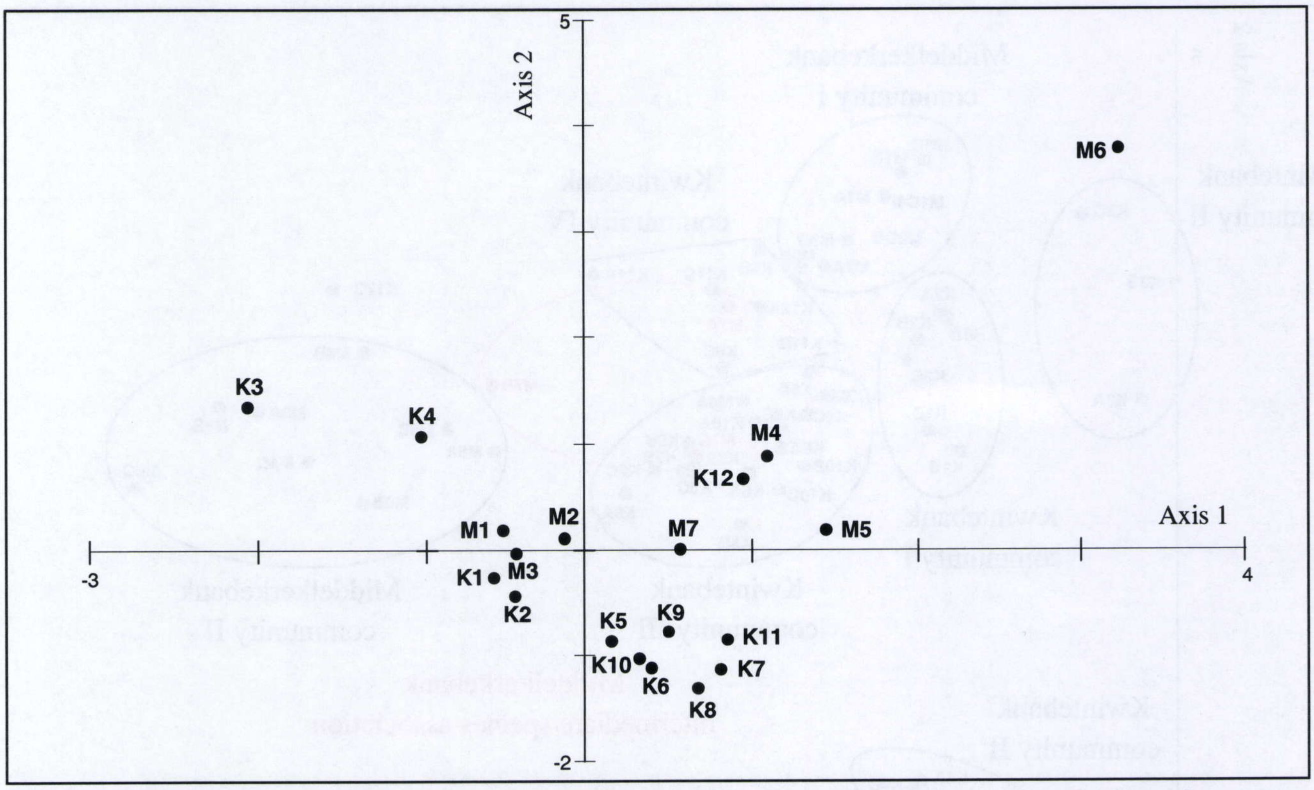

Fig.I.21: Plot of the stations of the Kwintebank and the Middelkerkebank in a CA based on mean absolute species abundances (fourth root transformed)

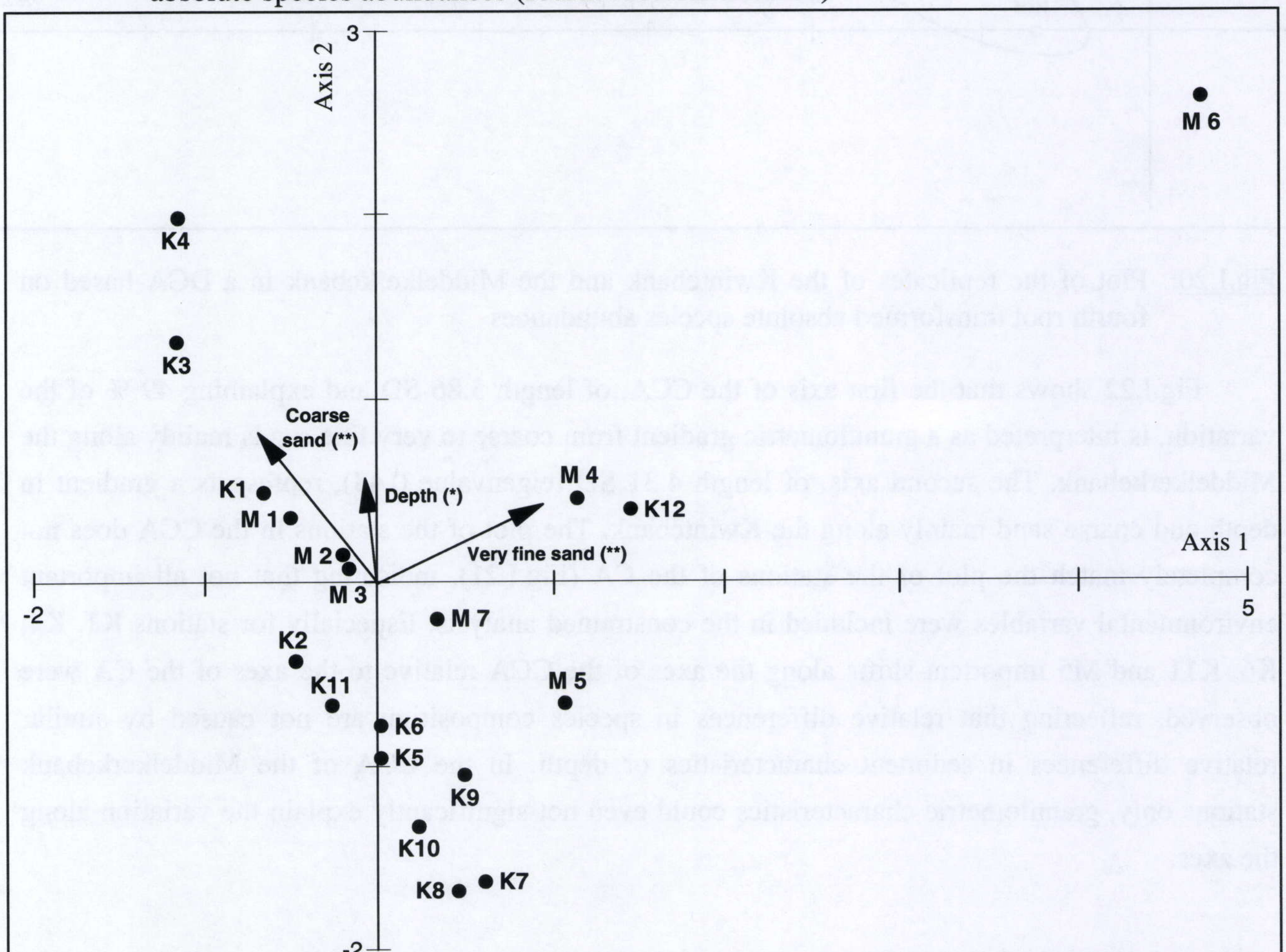

Fig.I.22: Plot of the stations of the Kwintebank and the Middelkerkebank in a CCA with environmental variables which were selected by Monte Carlo Permutation tests as statistically significant (* $p < 0.05$, ** $p < 0.01$).

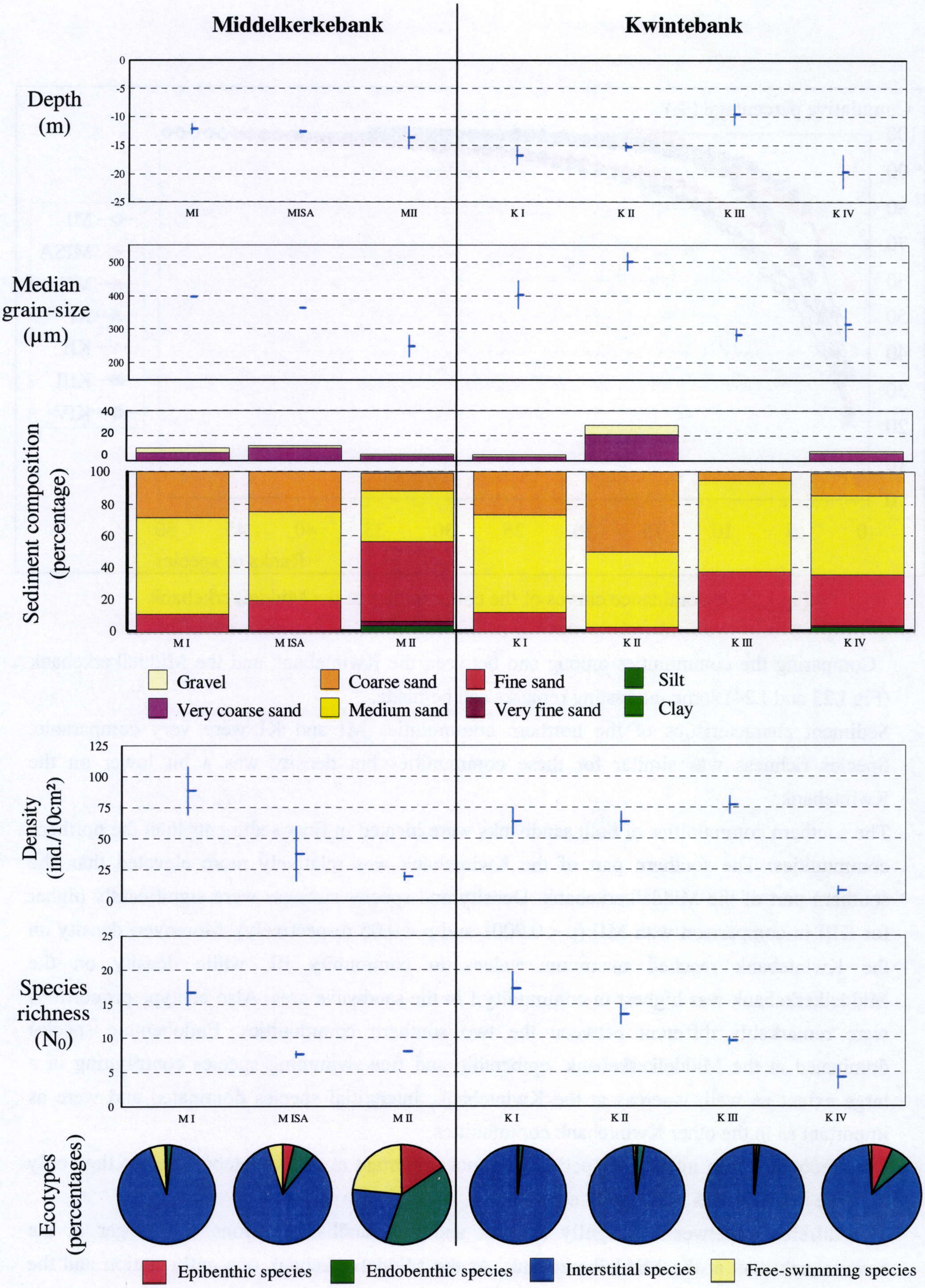

Fig.I.23: Abiotic variables (depth (a), median grain-size (b) and sediment composition (c)) and biotic variables (density (d), species richness (e) and ecotype proportion (f)) of the different communities at the Middelkerkebank and the Kwintebank

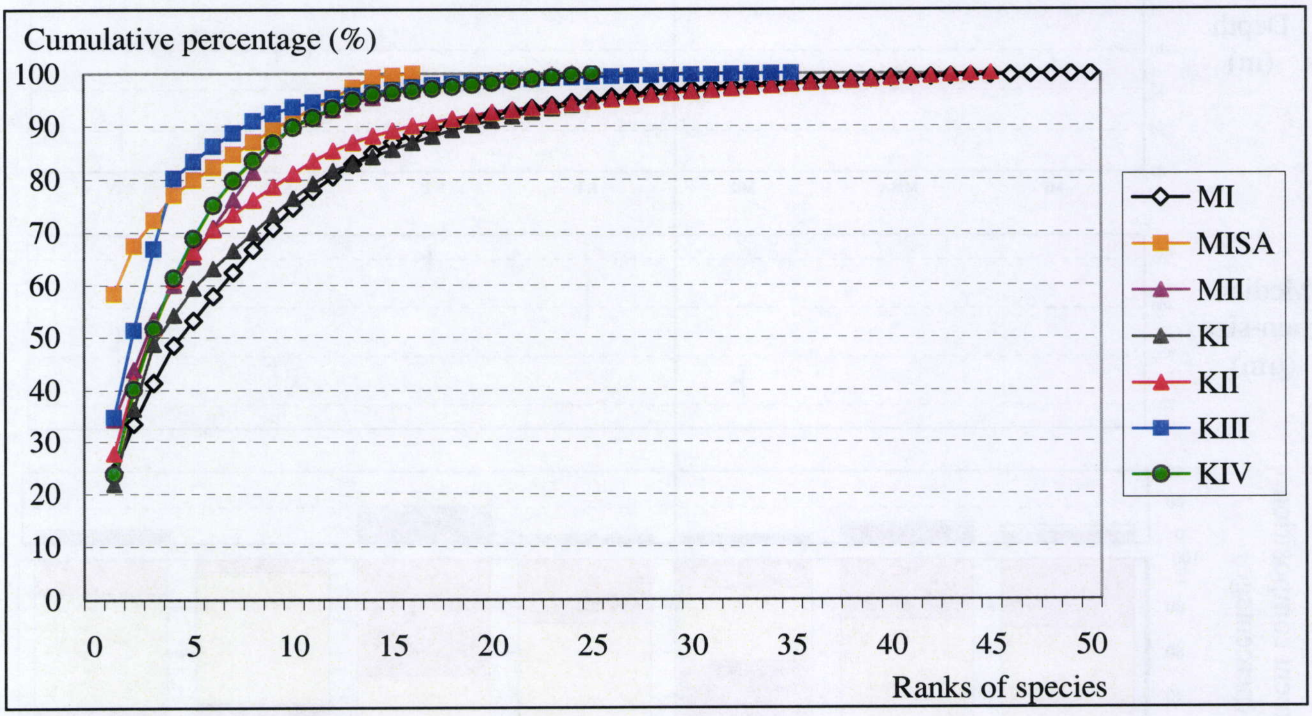

Fig.I.24: k-dominance curves of the communities at the Middelkerkebank

Comparing the communities among and between the Kwintebank and the Middelkerkebank (Fig.I.23 and I.24) some interesting remarks can be made.

- Sediment characteristics of the northern communities MI and KI were very comparable. Species richness was similar for these communities but density was a bit lower on the Kwintebank.
- The southern communities of both sandbanks were located in finer sediments than the northern communities. The southern part of the Kwintebank was relatively more elevated than the southern part of the Middelkerkebank. Density and species richness were significantly higher for KIII in comparison with MII ($p < 0.0001$ and $p < 0.05$ respectively). Moreover, density on the Kwintebank reached maximum values in community III, while density on the Middelkerkebank was highest in community I in the sandwave area. Also ecotype proportions were remarkably different between the two southern communities. Endobenthic species dominated at the Middelkerkebank, epibenthic and free-swimming species contributing in a large extent as well, whereas at the Kwintebank, interstitial species dominated and were as important as in the other Kwintebank communities.
- Other ecotypes than interstitial species were not important at the Kwintebank, since they only occur in low densities in the gully community.
- The difference between the gully stations and the sandbank stations was larger at the Kwintebank than at the Middelkerkebank. At the Middelkerkebank one gully station and the southern part of the bank harboured one community, while a second gully station formed an intermediate species association. At the Kwintebank the gully stations were clearly different

from the bank stations. Community KIV was situated at greater depth but the sediment characteristics were comparable with these of MII. The relative importance of fine sands was however higher for MII. Density and species richness were significantly lower in KIV in comparison with MII ($p < 0.05$ and $p < 0.01$ respectively).

- Community I on the Middelkerkebank did not differ in depth and sediment characteristics from the intermediate species association, though density and diversity were significantly ($p < 0.05$) lower and endo- and epibenthic species were more abundant in the intermediate species association.
- Kwintebank community II occurred approximately at the same depth as KI but sediment composition was much coarser, resulting in a higher median grain size. Density was the same in these both communities but species richness was lower in community II.

4 Discussion

4.1 Density

4.1.1 Comparison with earlier studies on the Belgian Continental Shelf

Copepod densities at the Kwintebank and the Middelkerkebank were very similar (2-105 and 18-103 respectively) but low in comparison with previous studies (Table I.3). The harpacticoid fauna of the Kwintebank has been studied in the late seventies (1978) and mid eighties (1985) (Claeys, 1979; Willems *et al.*, 1982b and Chen, 1987). The authors Govaere *et al.* (1980), Vincx & Herman (1989) and Huys *et al.* (1992) summarized general considerations of harpacticoid distribution at a larger scale on the Belgian Continental Shelf or in the North Sea. Claeys (1979) and Willems *et al.* (1982b) extensively surveyed the Kwintebank. Willems *et al.* (1982b) observed that copepod densities were consistent with those found in similar offshore and subtidal biotopes (McIntyre & Murison, 1973; Moore, 1979d). The values of 1997 are not consistent anymore with these similar subtidal biotopes. The density values in 1997 are comparable with those of the Vlakte van de Raan (Huys *et al.*, 1986a), situated at a similar distance from the coast near the polluted Westerschelde estuary (Herman *et al.*, 1985; Vincx & Herman, 1989).

In order to compare the densities of end January of the Kwintebank with the densities of October on the Middelkerkebank and with earlier studies (Claeys, 1979), seasonal variation has to be taken into account. At the Thornton bank, the Noordhinder and the Bligh Bank higher harpacticoid densities were recorded in October than in February (Vanaverbeke *et al.*, 2000). Higher densities in October may be related to higher temperatures (Hicks & Coull, 1983) and may result from primary production in the water column during summer, leading to higher food input (Vanaverbeke *et al.*, 2000). The lower density values in February may also be attributed to the fact that the winter is the most stormy period of the year. Animals may be swept away during the storm events because winter storms can be responsible for an important dispersion of sand and are able to decrease the bank top volume up to 70 % (Lanckneus *et al.*, 1994). Yet, on the Gootebank harpacticoid densities were higher in February in comparison with October (Vanaverbeke *et al.*, 2000). The maximum decrease in harpacticoid density between October and February was 50 %. A threefold decrease in the mean density over the sandbank indicates that, besides bad weather conditions, lower temperatures and reduced food availability during winter, other environmental factors may also be responsible for this decrease. A more detailed comparison of the densities recorded at the Kwintebank will be given in Chapter III.

Flemish Banks	Density (ind./10 cm²) minimum and maximum per station	N_0	N_1	Sampling area	Sampling period
Claeys, 1979	34-577	4-18 [(1)]		Kwintebank	September 1978
Willems *et al.*, 1982b	25-342	5-37 [(2)]		Kwintebank	September 1978
Chen, 1987	120-267	9-25	6.16-14.90	Kwintebank	May 1985
Vincx & Herman, 1989	20-70 [(3)]			Coastal area + Kwintebank	1977-1984
Huys *et al.*, 1992	24-651 (mean: 178)	mean: 29 ± 5	5-29 (mean: 22.8 ± 3.3)	Southern Bight of the North Sea	April-May 1986
Present study	2-105	2-19	2-14	Kwintebank + Middelkerkebank	January 1997/ October 1997

(1) Underestimated since Ectinosomatidae and Ameiridae were not taken into account
(2) Overestimated since the total number of species present in the replicates is listed instead of the mean species richness
(3) These values are not minimum and maximum mean densities per station but mean values for the eastern and the western part of the study area.

Table I.3: Densities and Hill's numbers N_0 and N_1 for the harpacticoid fauna of the Flemish Banks

Belgian and Dutch Continental Shelf	Density (ind./10 cm²) minimum and maximum per station or mean per station	N_0	N_1	Sampling area	Sampling period
			Coastal area		
Govaere *et al.*, 1980		0.89	1.15	Belgian and Dutch coastal area	1971-1975
Heip *et al.*, 1984	1.6-45.1	7-10		Belgian coastal area	1972-1980
Herman, 1989	1-835 Winter: 1-127 September: 3-255 October: 1-287	1-15	1-8.15	Belgian coastal area	June 1977-December 1984
Herman *et al.*, 1985		5.13 0.7-8.3		Belgian coastal area	June 1977-September 1979

Belgian and Dutch Continental Shelf	Density (ind./10 cm²) minimum and maximum per station or mean per station	N_0	N_1	Sampling area	Sampling period
	Transition zone				
Govaere *et al.*, 1980		8.9	3.94	Transition zone on Belgian and Dutch Continental Shelf	1971-1975
Huys *et al.*, 1986a	8-110.5 January: 22-40 February: 16 September: 78 October: 33	4-20 (20 cm²)		Vlakte van de Raan	January 1983-January 1984
Heip *et al.*, 1990	upto 1400			Dutch Delta region [(1)]	
	Open Sea area				
Govaere *et al.*, 1980		13.7	6.63	Open Sea area Belgian and Dutch Continental Shelf	1971-1975
Chen, 1987	50	12	6.58	Gully Hinderbanks	March-June 1985
Vandenberghe, 1987	44-260			Gullies Hinderbanks	March 1985
Chen, 1987	207	33	18.95	Open sea Belgian Continental Shelf	March-June 1985
Heip *et al.*, 1983		13.7	6.49	Southern North Sea, Dutch Continental Shelf	
	<u>Remarks</u>: 113 µm median grain size, 12.7 % silt, at 46 m				
Chen, 1987	63	1	1	Southern North Sea, Dutch Continental Shelf	March-June 1985
	<u>Remarks</u>: 165 µm median grain size, 78.41 % silt				
Herman, 1989	10-263	5.7-23	4.18-13.6	Southern North Sea, Dutch Continental Shelf	
Huys *et al.*, 1984	7.5-536 116	2-22		TiO²-waste dumping site	June 1984
Herman, 1989	5-206	2-22	1.65-14.9	TiO²-waste dumping site	

(1) Dutch Delta region in front of Lake Grevelingen and the Eastern Scheldt is also characterized by deep channels and shallow sandbanks (Heip *et al.*, 1990)

<u>Table I.4</u>: Densities and Hill's numbers N_0 and N_1 of the harpacticoid fauna of the Belgian and Dutch Continental Shelfs; geographical division according to Govaere *et al.*, 1980

4.1.2 Comparison with sandy intertidal and subtidal biotopes

Minimum and maximum and mean harpacticoid densities are generally higher in different sandy marine sediments all over the world (Table I.5) than on the Kwintebank and the Middelkerkebank. Mean values in shallow-water ecosystems (< 100 m) are typically in the 100's/10cm² (Hicks & Coull, 1983). Mean values at the Kwintebank (55 ind./10 cm²) and the Middelkerkebank (51 ind./10 cm²) are considerably lower than these estimates. Some of the studies listed in tables I.4 and I.5 contain information on temporal variability. The density values in January or October in several studies were always higher than the values in the present study, except for the Vlakte van de Raan (Huys *et al.*, 1986a). Thus as studied so far, the Flemish Banks system is for harpacticoids among the most stressed sandy environments at comparable depth in the world.

Sandy soft bottoms

Subtidal	Density minimum and maximum per station or mean per station	N_0	Sampling area/ Sampling period	Depth	Sediment class/ Grain size
Guille & Soyer, 1968	**78** cores to 7 cm depth		Banyuls-sur-mer, France	15-16 m	Fine sand 170 µm
Soyer, 1971	**118-258** cores to 7 cm depth		Banyuls-sur-mer, France	5-10 m	Fine sand
McIntyre & Murison, 1973	**40-1588** cores to 25 cm depth	**14** cores to 16 cm depth	Firemore, Scotland / July 1963-'72	Shallow subtidal 1-7 m	Fine sand 162-208 µm
Soyer & Bovée, 1974	**19-22**		Kerguelen, Indian-Southern Ocean Baie Morbihan Est/ March 1974	4-21 m	Fine sand
	259		Fjord Karl Luyken	7 m	Fine sand
Bovée & Soyer, 1975	**27**		Kerguelen Islands		Fine sand
Bovée & Soyer, 1977	**424**		Kerguelen, Indian-Southern Ocean Summer Fjord Karl Luyken	1 m	Fine sand
	97			3 m	Fine sand
	25-38		Baie Morbihan Est	4-21 m	Fine sand

Sandy soft bottoms					
Subtidal	Density minimum and maximum per station or mean per station	N_0	Sampling area/ Sampling period	Depth	Sediment class/ Grain size
Coull & Fleeger, 1977	**20-670** October: 60-120 September: 90-540 January: 35-150 February: 30-100	**6-16** October: 11-14 September: 10-13 January: 9-14 February: 9-12	South Carolina, U.S.A. January 1973-November 1975	shallow subtidal	Fine to medium sand 190-350 µm
Itô, 1978	**14-302** September: 151 October: 214		Jokkaido, Japan June-November 1977	25 m	Fine sand 180 µm without gravel
Moore, 1979a	**3-353**		Isle of Man, U.K		sand
	47-102	**6-7** (ES_{50})	Isle of Man, U.K August and December 1973	0-1.3 m	Shallow fine sand
Moore, 1979d	**77-88**	**9-20** (ES_{50})	Isle of Man, U.K January '77, March '78 and December '76	6.2-19.2 m	Offshore fine sand
	151-503	**33** (ES_{50})	August '77 and May '78	37.3-37.9 m	Medium sand
Arlt, 1983	**3-96**	**1-7**	BRACKISH Baltic Sea	13-20 m	Fine sand
	3-376	**1-9**		13-35 m	Coarse sand
Renaud-Mornant *et al.*, 1971	**14-97**		Polynesia		Coarse sands
Soyer, 1971	**10-181** cores to 7 cm depth		Banyuls-sur-mer, France	± 5-40 m	Coarse and very coarse sand
McLachlan *et al.*, 1977	**2-211**		South Africa Shelf		sand
Tenore *et al.*, 1978	**10-129**		Southeast U.S. Shelf		sand
Coull *et al.*, 1982	**5-710**		Southeast U.S. Shelf		sand

(ES_{50}) Species richness calculated by the rarefaction method of Sanders (1968)

Table I.5: Densities and species richness (N_0 or ES_{50}) of the harpacticoid fauna of sandy soft bottoms. Values for muddy sand and mud or deep-sea were not taken into account. Sample core depths different from 10 cm are specified.

Beaches	Density minimum-maximum per station or mean per station	N_0	Area	Sediment class/ Grain size	Period
McIntyre, 1968	**10-12.5**		India	Fine sand	February 1966
McIntyre & Murison, 1973	**6** (spring)- **1850** (autumn) Autumn:18-1850 cores to 32 cm depth	**11** cores to 16 cm depth	Firemore, Scotland	Fine sand 210-270 µm	1963-1972
Moore, 1979b		**2-13** (ES_{50}) cores to 15 cm depth	Isle of Man, Irish Sea, U.K.	Largely fine to medium sand	August 1973
Ansari and Ingole, 1983	**102-888**		Andaman Islands, India	Fine-medium sand	February 1983
Bodin & Jackson, 1989	**6.1-935.7** (means)	**5-28**	France	Fine to medium sand 122-355 µm	1979-1984
	6.1-368.4	**3-18**	Ireland		
Gheskiere *et al.*, 2002	**1-40** (means)		De Panne, Belgium	Fine to medium sand	Augustus 2000
Harris, 1972a	**65-588** 122.2 (mean annual density) cores to 50 cm depth		Cornwall, England	Medium sand	May 1968 to May 1970
Hulings, 1974	**5-669** January: 159-421 February: 203-315 September: 120-503		Libanon	Medium sand	November 1970-September 1971
Gray & Rieger, 1971	**3-179**	**2-3**		Medium sand	August 1969
Schmidt, 1978	**106-246**		Galapagos	Medium to very coarse sand	January 1973
Schmidt, 1972	**4-337**		Germany	Coarse to very coarse sand	June 1986
Olafsson, 1991	**2-354** cores to 5 cm depth		Iceland	Very coarse sand- gravel 651-2949µm	Summer 1983
Ax & Ax, 1970	**68-250** September: 68	**4**	Germany, Estuary, beach BRACKISH	Medium to very coarse sand	August-September 1968
Martinez, 1975	**1-16**		New York, U.S.A.		
McLachlan, 1977	**72-3387**		South Africa	sand	

(ES_{50}) Species richness calculated by the rarefaction method of Sanders (1968)

4.1.3 Onshore-offshore gradient

A review on meiobenthic research at the Belgian Continental Shelf showed that mean meiobenthos densities at the Kwintebank were much lower than in the surrounding regions on the Belgian Continental Shelf (Cattrijsse & Vincx, 2001). The values of the surrounding regions, however, originated from the near coastal area and gully stations only. Information on other sandbanks was not available yet, so a comparison between the Kwintebank and similar bank habitats was not possible at that time. Willems *et al.* (1982b) mentioned that nematode densities on the Kwintebank were low in comparison with what was found by Govaere *et al.* (1980) but Willems erroneously compared nematode densities with total meiofauna densities of Govaere *et al.* (1980). Moreover, Govaere *et al.* (1980) did not sample sandbanks. Vanosmael (1977) recorded very low macrofaunal densities and biomass on the Kwintebank and Buiten Ratel in comparison with mean values found by Govaere (1978) (Claeys, 1979). Again, sandbanks were compared with the gullies in between. Vanaverbeke *et al.* (2000) studied meiofauna of different sandbank systems on the Belgian Continental Shelf and confirmed that meiobenthos and nematode densities were low at the Kwintebank. More specifically, meiobenthic densities were low at all sandbank tops in comparison with the channels in between. This difference was explained by the high hydrodynamic stress on top of sandbanks, reducing meiobenthic densities and rendering the settlement of food particles for the benthos more difficult. Nematode densities were comparably low at all sandbank tops. For harpacticoids, however, low values were only recorded at the Flemish Banks. Densities at the Oostendebank ranged between 1-15 ind./10 cm² and were even lower than at the Kwintebank and Middelkerkebank. Harpacticoid densities of sandbank systems further offshore were always higher and comparable with other subtidal sandy biotopes and beaches (Vanaverbeke *et al.*, 2000 versus table I.5).

The lower harpacticoid densities at the Flemish Banks in comparison with sandbank systems more offshore may be related to hydrodynamical stress. The current velocity in the coastal area peaks at 6 m/s (Van Damme & Heip, 1977), while it measures 1 m/s in the Flemish Banks area (Stolk, 1993). The effects of these tidal currents and the impact of waves and storm-induced currents are important at the top of sandbanks (Houthuys *et al.*, 1994) and decrease with depth (Trentesaux *et al.*, 1994). The impact of these hydrodynamic forces on the top of sandbanks will be higher on the Flemish Banks than on sandbanks at greater depths. During strong gales significant wave height reaches 4 m and in extreme conditions may be higher than 5 m (Houthuys, 1993). Considering the elevation of the highest parts of the Flemish Banks, waves may break on top of the bank during severe storms (Trentesaux *et al.*, 1994), whereas this is less the case for the sandbanks more offshore. Since disturbance by currents and agitation of superficial bottom layers have been shown to considerably affect harpacticoids (Giere, 1993; Thistle & Levin, 1998; Thistle *et al.*, 1999), the gradient in hydrodynamic stress may explain the linearly increasing onshore-offshore trend in harpacticoid density on the sandbanks. Hulings & Gray (1976) even assumed that physical factors of wave, tide and current action dominate in controlling meiofauna abundance patterns.

According to this explanation, higher densities are expected in the northern part of the Kwintebank than in the northern part of the Middelkerkebank. But the northern part of the Kwintebank does not harbour more harpacticoids than the northern part of the Middelkerkebank, despite the similar sediment characteristics and the larger depth. In contrast, the southern part of the Kwintebank rises approximately 3 m higher than the southern part of the Middelkerkebank but contains about 4 times more harpacticoids. Environmental variables that may explain these differences will be extensively discussed when comparing the harpacticoid communities on both sandbanks (see 4.3).

4.1.4 Comparison between sandbank tops and gullies

Trentesaux *et al.* (1994) assumed that there is a lower influence of currents and wave action in the channels and consequently less dynamic environmental conditions prevail, implying a more stable and more favourable biotope for benthic life. Indeed, in the channels meiofauna and in particular nematode densities were much higher (Govaere *et al.*, 1980; Vanaverbeke *et al.*, 2001). This was not the case for harpacticoid densities. The lowest values were all recorded in the gullies. Extremely low values (0-3 ind./10cm²) were encountered in the Negenvaam gully. The Negenvaam is rather shallow (12 to 20 m deep) and is characterized by a gentle western slope towards the Kwintebank and a steeper eastern slope towards the northern part of the Middelkerkebank. At both Negenvaam stations fine sediments predominated and silt and clay load was much higher than on the sandbanks. Trentesaux *et al.* (1994) demonstrated that oxygen content was largely low in the Negenvaam sediments. Reduced oxygen tension may cause greatly decreased harpacticoid densities because harpacticoids are typically the most sensitive meiobenthic taxon to decreased oxygen tension (Hicks & Coull, 1983).

The characteristics of the Negenvaam differed from the Uitdiep and the Kwinte gully stations. The coarser sediments of these stations were similar to some bank stations but contained reduced harpacticoid densities as well. Additionally, the Kwinte and the Uitdiep gully stations showed a higher density variation than in the Negenvaam gully. The gullies are definitely not alike and harpacticoid densities are low in silty as well as sandy gully stations.

In gully stations very high harpacticoid densities are recorded as well. The maximum harpacticoid density at the Kwintebank (457 ind./10 cm²) found by Vanaverbeke *et al.* (2000) did not originate from the Kwintebank but from a gully station near the Buiten Ratel. High values (101 and 120 ind./10 cm²) were also found in the channel north of the Kwintebank (Vanaverbeke, unpubl. data). Thus, harpacticoids show a very patchy distribution in the gullies. These measures cast doubt on the statement that gullies are a stable benthic environment.

Tidal currents, waves and storms act upon the sandbanks but gullies may be subject to hydrodynamic stress of near-bottom currents (Ramster, 1965). The fine sands and the clay and silt load, encountered in the Negenvaam, indicate that current stress must be low there. But this cannot be generalized for all gullies. Gullentops *et al.* (1977) pointed out that extensive gravel fields are present in the channels between the sandbanks, indicating that hydrodynamic stress may be high too. Such gravel patches outcrop in the Kwinte gully (Tytgat, 1989; Lanckneus, 1989). They can be covered with a layer of sand or sometimes the spaces in between the gravel are filled with silt (Houbolt, 1968; Davies, 1980; McCave & Langhorne, 1982; Trentesaux *et al.*, 1994), but this is not always the case since also pure gravel is found (Gullentops *et al.*, 1977). Moreover, near the northern top of the Buiten Ratel gravel is even transported as a result of extremely strong near-bottom currents. Tytgat (1989) pointed out that local higher concentrations of gravel in the channels can be connected with a deepening by locally more intensive erosion. This erosion causes a blow out of the sediments. Besides the gravel and sand patches, pure clay layers are encountered in the gullies as well. This clay originates from Tertiary outcrops (Trentesaux *et al.*, 1999) and they are extremely sensitive to desaggregation (Tytgat, 1989). Strong currents and severe storms erode these clay deposits, as well as sand and gravel layers in the gullies. Clay, silt and sand are then deposited during fair-weather conditions at other locations. Suspended clay and silt can be carried over long distances as it is not deposited but only temporarily and periodically decanted (Gullentops *et al.*, 1977). Sand being swept away from sandbank tops during storm events, end up in the gullies and are transported upslope towards the sandbank top again by means of sand dunes piling up toward the crest of the sandbank (De Moor *et al.*, 1989). Consequently, gullies are the main pathways for sediment transport.

Different kinds of sediment are present in the gullies, their presence is related to the intensity of near-bottom currents and these sediments are transported with irregularly different intensities, inducing a temporal and spatial patchiness of different kinds of sediments in the gullies. This information allows assuming that gullies should also be regarded dynamic, at least at an intermittent basis; on sandbank tops however, processes act more continuously. How these dynamics are related to harpacticoid densities is not clear. It is obvious that nematodes and macrofauna can develop very easily while harpacticoids encounter more problems to be successful in the gully environment.

Natural disturbances will be definitely involved but it is also important to mention that human disturbances increased remarkably since the seventies, which was not taken into account in this study. Fishing pressure is high in the gullies between the sandbanks and these disturbances may induce severe pressure on harpacticoid communities as well.

Another aspect may be that predation by predatory polychaetes, shrimps, mysids and small fishes (Hicks & Coull, 1983; Gee & Warwick, 1984; Gee, 1987; Van Damme *et al.*, 1984) may differ between banks and gullies. The gullies are much richer in macrobenthos and demersal fishes than the sandbank tops (Van Hoey *et al.*, submitted; Dewicke, pers. comm.; Cattrijsse, pers. comm.; Cattrijsse & Vincx, unpubl. data). Below a depth of 16 m, 76 % of the boxcores in the Negenvaam deposits showed facies bioturbated mainly by macrobenthos (Trentesaux *et al.*, 1994). In the centre of the Negenvaam and Kwinte gully an *Abra alba-Mysella bidentata* community was found, which shifted to a *Nephtys cirrosa-Abra alba-Mysella bidentata* transitional species association at shallower depths towards the Kwintebank. A *Nephthys cirrosa* community was found on the slopes and the summit of the bank (Rekecki, 2002). Filter and detritus feeders predominate the *Abra alba-*

Mysella bidentata community (Erdey, 2000). Therefore, higher predation pressure by polychaetes in the gullies than on the sandbank is unlikely. Predation by small fishes and mysids is more probable. Mysids were significantly more abundant in the swales than on the sandbank crests (Dewicke, 2001). A huge amount of fish larvae may migrate through the gullies as the Flemish Banks are regarded as playing a key role in the supply of fish larvae from offshore waters towards more sheltered onshore nursery areas (Vincx *et al.*, 2002). Sole larvae caught in that area consume large numbers of copepods (Dewicke, pers. observ.) and *Pomatoschistus minutus* larvae up to a length of 25-30 mm feed only on copepods (Redant, 1977), but mainly calanoid copepods.

The importance of the harpacticoid copepods and meiofauna in general in food chains is not well understood and has been a matter of discussion. Several authors consider the role of meiofauna as a food source for higher trophic levels as negligible while others consider the meiofauna as an important link in the complex food web leading to macrofauna and fish (see Alheit & Scheibel, 1982 for references). Hicks & Coull (1983) suggested that harpacticoids are the major meiofaunal organisms as food for higher trophic levels, primarily fish. They represent a discrete meal, regularly occupy habitats (surface of mud or sand) where they are readily visible to sight-feeders and are relatively easy to catch (if you're a fish !). Coull & Bell (1979) assumed that predation on meiofauna was significant in muddy or detrital substrata, and not significant in sandy systems. Hicks & Coull (1983) however suggested that epibenthic and phytal copepods of sandy substrata may still be important food items for predatory fishes. Alheit & Scheibel (1982) found that harpacticoids represent an essential food source for the juveniles of several demersal fish species. Juveniles up to 3 cm length of one species fed exclusively on harpacticoids. Meiobenthic harpacticoids may be an important component of food chains leading to higher trophic levels but Alheit & Scheibel (1982) also concluded that the feeding pressure exerted by the fish on the harpacticoid populations is negligible.

4.2 Diversity

Unlike density, diversity at the sandbank tops was relatively high. Diversity in the northern part of the Kwintebank and the Middelkerkebank was comparable with other shallow subtidal sandy biotopes (Table I.5: Coull & Fleeger, 1977; Moore, 1979d; McIntyre & Murison, 1973; Huys *et al.*, 1986a), higher than the values from beaches (Gray & Rieger, 1971; Moore, 1979d) and than the Belgian coastal area (Heip *et al.*, 1984; Herman *et al.*, 1985; Herman, 1989) and lower than in sands at greater depth (Moore, 1979d; Chen, 1987; Huys *et al.*, 1992). The harpacticoid diversity increases from exposed littoral habitats over shallow to deeper sublittoral habitats. This suggests a correlation with a decrease in hydrodynamical stress (Hartzband & Hummon, 1974). Higher diversity can also be found at a sheltered beach (Bodin & Jackson, 1989) and much lower diversity offshore in muddy sediments in the brackish Baltic Sea (Arlt, 1983). Diversity at the southern parts of the sandbanks was significantly lower than at the northern parts and similar to the diversity values at beaches (McIntyre & Murison, 1973; Moore, 1979b).

Based on harpacticoid associations, Govaere *et al.* (1980) distinguished three zones for the Southern Bight: a coastal zone characterized by an extremely low number of species, all large epibenthic and endobenthic forms; a transition zone where both epibenthic and interstitial harpacticoids occur and a species rich open sea area where large epibenthic or endobenthic species are nearly absent. Govaere *et al.* (1980) interpreted the harpacticoid assemblages of Claeys (1979) at the Kwintebank as a transitional type of fauna and predicted that it probably occurred over the entire area of the banks. Vincx *et al.* (1990) and Vincx (1990), for nematode communities, and Willems *et al.* (1982b) for harpacticoid communities, however, considered the Kwintebank as a separate unit on the Belgian Continental Shelf because of the high diversity of the characteristic meiofauna, comparable with the open sea communities. The prevailing clean coarse sands in both the open sea area and at the Kwintebank explained the high diversity. The comparison between the Kwintebank and the Middelkerkebank revealed that highly diverse harpacticoid communities are not exceptional, they do not only occur on the Kwintebank but on other sandbanks as well. The resemblence between different sandbanks was also illustrated for macrofauna. A comparison between the Kwintebank and the Buiten Ratel showed that macrobenthos density, diversity, biomass and species composition were quite similar on the two sandbanks, both in October and in March (Heip *et al.*, 1979). For macrobenthos the uniformity of sandbanks concerned a similar species poverty instead of a similar species richness for harpacticoids and nematodes. The considerations of Govaere *et al.* (1980) do not apply to sandbanks but only to the surrounding gullies.

Sandbanks and gullies in between are two different entities, as was already put forward by Rappé (1978) for macrobenthos. On the sandbanks a very diverse sandwave inhabiting fauna and a less diverse fauna in flattened areas can be distinguished. The Flemish Banks are to be considered as islands of coarser and mostly well-sorted sediments, characterized by a fauna typical of the open sea area and superimposed on a seabed with partly finer grained and silty sediments. These gullies harbour a harpacticoid fauna that can be described as a transition zone community. Vanaverbeke *et al.* (2002) also emphasized marked differences of nematode diversity between the sandbank crests and gullies in the Flemish Banks area.

Higher nematode diversities were found on sandbanks more offshore in comparison with the Flemish Banks. Even higher diversities were found in the open sea area (Vanaverbeke *et al.*, 2001). The values of the open sea area were also higher than previously recorded by Vincx (1990) in the same area. So an increasing nematode diversity exists with distance from the coast (Vanaverbeke *et al.*, 2002). This trend still has to be checked for harpacticoids, as data on harpacticoid diversities more offshore on the Belgian Continental Shelf are too scarce. So far, species richness recorded more offshore was comparable with the values at the Kwintebank.

In the seventies diversity increased from the north towards the centre of the sandbank (Willems *et al.*, 1982b), whereas in the present study exactly the opposite is found. The number of species was positively correlated with median grain size in Willems *et al.* (unpubl. report), so a reversed gradient in grain size is expected to explain the opposite trend in species richness. Apart from station 5, the median grain size in this study increased from the northern top towards the centre and remarkably species richness was still correlated with median grain size. This correlation results from the large differences in diversity between the coarse and the fine sediments. Diversity among coarse stations or among fine stations is not correlated with median grain size, indicating that sediment characteristics are not important in accounting for variation in species richness in the northern part proper. The reversed diversity gradient in the northern part (stations 1-4) between the seventies and the nineties must probably be due to other environmental changes and will be discussed in Chapter III.

4.3 Harpacticoid communities

Clearly different harpacticoid communities occurred on both sandbanks. Community differences within the sandbanks were larger than between the sandbanks and largely reflected the sedimentological diversity of the sandbanks. This was also observed for meiofauna taxa distribution of several sandbank systems on the Belgian Continental Shelf (Vanaverbeke *et al.*, 2000). The station groups, based on meiofauna taxa densities, did not coincide with the geographical position of the sandbanks systems either but reflected differences in sediment structure, even within sandbanks. In the present study two main trends could be distinguished: a north-south gradient on the sandbanks and a gradient from the sandbank top towards the gullies. Both trends are related to a decreasing grain size trend.

4.3.1 North-south gradient

4.3.1.1 Gradient in sediment characteristics

The Kwintebank and the Middelkerkebank are both characterized by an extensive sandwave area in the northern part, changing into a flat plateau towards the south. These morphological characteristics correspond to a decreasing median grain size from the north to the south. Observed sediment characteristics at the Middelkerkebank and the Kwintebank corresponded very well to the general ones described earlier for the Flemish Banks (Lanckneus, 1989). The relationship between morphology and grain size parameters is created by the decreasing gradient of near-bottom current velocity from north to south. In the swales, the strong NE-oriented flood stream runs parallel to the sandbank's long axis near the more elevated southern parts of the sandbanks. In the deeper northern parts of the sandbanks the currents are dispersed and deflected towards the sandbank's crests (De Moor, 1985; De Moor & Lanckneus, 1988), shaping the sandwaves and hampering the accumulation of fine material. In this way a high-energy environment is created, while hydrodynamic and bedform interactions differ in the flat southern parts.

The two distinct parts of the sandbanks are inhabited with clearly different harpacticoid communities. In the CCA very fine sand and coarse sand content were found to be the significant environmental variables explaining most of the variation. Sediment structure strongly determines the structure of benthic communities as has been demonstrated by many authors (Sanders, 1968, 1969; Sanders & Hessler, 1969; Coull, 1972, 1985; Giere, 1993). The two most northern communities at the Kwintebank and Middelkerkebank are very similar, occurring in similar coarser deposits and characterized by a high species richness of predominantly interstitial species. On both sandbanks diversity was negatively correlated with fine sand. The northern community at the Middelkerkebank covers three quarters of the bank, while the corresponding most northern community of the Kwintebank only comprises the upper fifth of the sandbank. The dissimilarity between the latter community on the Kwintebank and the adjacent community to the south, both situated in the sandwave area, was more pronounced than between the north and the south or between the sandbank top and the gullies of the Kwintebank. Yet, differences in sediment characteristics were clearly more pronounced between the north and the south than within the sandwave area. Another remark is that higher densities were recorded in the southern part of the Kwintebank than in the northern part. Generally speaking, densities would be higher in coarser deposits than in finer sediments (Ax & Ax, 1970; Williams, 1972; Moore, 1979a; Hicks & Coull, 1983). Densities at the Middelkerkebank were clearly higher in the coarser northern part than in the southern part. On the Kwintebank the opposite was observed. Densities in the fine sands of the southern part of the Middelkerkebank are very low, as low as in the gullies along the Middelkerkebank. At this sandbank density was negatively correlated with fine sand content and positively with medium sand, which was not the case at the Kwintebank. At the Kwintebank density was even highest at the station with the highest fine sand content.

At the Middelkerkebank ecotype proportions correlated most significantly with fine sand content. Interstitial species became less important and were gradually replaced by endo- and epibenthic species with increasing fine sand content from north to south. Although the dominance of interstitial forms in the coarser deposits may prove that the substrate influences faunal composition, contrasting observations were made on the Kwintebank. On this sandbank no transition was recorded between different ecotypes, although in the southern most elevated part of the Kwintebank well-sorted and predominantly fine sands prevailed. Still, they were almost exclusively inhabited by interstitial species. Completely different communities inhabit the southern parts of both sandbanks, although no differences are expected because sediment characteristics are nearly the same.

4.3.1.2 Gradient in physical stress

Trentesaux *et al.* (1994) postulated that the morphology of the southern top of the Middelkerkebank does not correspond to a normal bank profile. The southern part of the bank is not well pronounced and forms a plateau with the western end of the Oostendebank. In this topographically flattened area with gentle slopes towards the deeper areas, the grain size values show little variations and sediment composition is comparable with the gullies surrounding the area. Maximum current speeds, near the bottom as well as near the surface, are significantly lower here compared with the northern end (Lanckneus *et al.*, 1994). The orientation of the currents was similar to the orientation in the Negenvaam swale and differed from the current direction at the sandbank top. Depth in the south is about the same as more to the north of the sandbank and cannot be responsible of these hydrodynamic and bank profile differences. Irrespective of depth, hydrodynamic forces differ at the southern top of the Middelkerkebank, creating an environment similar to the surrounding shallow areas of the gullies. Consequently, a community occurs which covers the southern top as well as the surrounding areas in the swales.

These characteristics may also explain the differences between the southern parts of the Kwintebank and the Middelkerkebank, since the Kwintebank still follows a linear bank profile in the south. On the southern edge of the Kwintebank sandwaves still occur while they are absent in the most elevated part. Current strength and direction at this elevated part of the Kwintebank are probably the same as at the southern edge with sandwaves. Peak current direction can be derived from the strike and asymmetry from megaripples (McCave & Langhorne, 1982; Lanckneus *et al.*, 1992b) and the few megaripples in the most elevated part are oriented in the same way as at the southern edge. The absence of sandwaves in this elevated southern part is not related to a decline in near-bottom current strength but probably to a locally insufficient sand supply (De Moor & Lanckneus, 1988). Sandwaves are formed in medium sand and are nearly absent in fine sand (Van Lancker & Jacobs, 2000). During flood and ebb residual sediment transport medium sand is deposited first, in the northern part as well as at the southern edge of the Kwintebank, the remaining fine sands are deposited at the most elevated southern part, rendering the sediment unfit for sandwave shaping. The near-bottom currents may be somewhat lower allowing the settlement of fine sands but it's very likely that hydrodynamic stress in the elevated area of the Kwintebank is more severe than at the more sheltered southern top of the Middelkerkebank (Van Lancker, pers. comm.). Data on near-bottom current velocities at the southern part of the Kwintebank are however not available to prove this hypothesis. As near-bottom hydrodynamics in this area are probably stronger than in the southern part of the Middelkerkebank big endobenthic species are outcompeted by interstitial species. Strong bottom flows are known to reduce the proportion of surface-living epi- and endobenthic species in favour of interstitial species (Thistle *et al.*, 1999). The influence of wave action and storms may also contribute to more harsh hydrodynamic conditions at the southern part of the Kwintebank as it is more elevated than the southern top of the Middelkerkebank.

4.3.1.3 Gradient in trophic diversity

The enhanced physical stress at the southern part of the Kwintebank may cause a problem for the endobenthic species through food shortage, since growth of epibenthic diatoms may be impossible in this area. Reactions to different interstitial water characteristics or different water circulation may also be important, since these factors may be of greater significance for the animals than the grain size proper (Jansson, 1967). The shift between interstitial dominance in the sandwave area and endo-epibenthic dominance in the calmer flattened southern top of the Middelkerkebank confirms that the mesobenthic assemblage, consisting of small, interstitially living grazers, is typical of pure, coarser sands. The absence of detritus or epibenthic diatoms and the high turbulence exclude the presence of epibenthic copepods. The endo-epibenthic assemblage consisting of large burrowing or epibenthic detritus-feeders is characteristic of low energy zones. (Van Damme *et al.*, 1984) Comparable gradients from an interstitial association in the coarser sands of the high energy swash-zone towards a fine sand association of non-interstitial forms at the more sheltered shallow subtidal flats are observed at sandy beaches (Moore, 1979b; Mielke, 1975; Noodt, 1957).

Van Damme *et al.* (1984) stated that the two distinct assemblages never co-occur because the two habitat types are incompatible, at least in the Westerschelde. This hypothesis had arisen because mixed sediments were not encountered in the Westerschelde, only pure coarser sands in very turbulent conditions with an interstitial assemblage or very fine sands (< 200 µm) where exclusively epi- and endobenthic species occurred. In these fine sediments the interstitial spaces are too small to allow for interstitial life (Moore, 1979d). In fine to medium sands interstitial forms (mesopsammon) as well as epibenthic forms (epipsammon) co-occur (Hicks & Coull, 1983), as long as turbulence is not too high for epi- and endobenthic species. In the fine sands with median grain size of 229 µm at the southern part of the Middelkerkebank (station 5) interstitial and epibenthic species contribute in a great extent to the predominantly endobenthic species assemblage. Endobenthic and free-living species were as important as interstitial species at station 4 with a median grain size of 310 µm. This station also belonged to the southern community and is located at the transition between the sandwave area and the flattened southern top of the Middelkerkebank. Sediment characteristics show more similarities with the sandwave area than with the southern top, especially because of the high percentage of coarse sand and gravel. The proportion of fine sand, medium and coarse sand content was similar. In this poorly sorted sediment interstitial species were less abundant, since they require clean well-sorted sands (Huys *et al.*, 1992). Endobenthic life is probably protected from strong currents because the area is located at the lee side of the southwestern bank flank with respect to the ebb-currents, which dominate in this specific area (Lanckneus *et al.*, 1994). In these sediments and under these hydrodynamic conditions different feeding types can coexist.

Marcotte (1986) predicted that more copepod species may co-occur in sediments with a median particle diameter of 200 µm than in sediments with larger or smaller particle diameters, because the former contain more interstitial space. Gray (1974) assumed that the 'structural complexity' of these usually poorly sorted sediments cause them to contain 'more potential niches' and thus to hold more diverse communities. At station 5 at the Middelkerkebank trophic diversity is indeed high, but diversity is rather low. Species and trophic diversity is somewhat higher at the coarser station 4. Marcotte (1986) meant that the co-occurring of sand particles with sheared and pitted surface would attract a more diverse community, but the bacterial diversity may be more important than grain surface variability proper. According to Giere (1993) sand grains with diameters > 300 µm have more plain surfaces than do smaller particles; they also have a different bacterial cover. Meadows & Anderson (1968) illustrated that large sandgrains (400 µm) contained a variety of microbial colonies, while small irregular sandgrains (200 µm) lacked microbial colonies and were covered by many large diatoms, which serve as food for endo- and epibenthic species. The bacterial diversification in coarser sands explains the higher diversity of interstitial species in the sandwave areas at the Middelkerkebank as well as at the Kwintebank, of which the mean grain size definitely exceeds 300 µm.

4.3.1.4 Differences with previous studies

In the Kwintebank study of Willems *et al.* (1982b) the clustering of two station groups reflected the existence of a coarse sand and a fine sand association at the Kwintebank, just as the present study showed at the Middelkerkebank. In the nineties, the Kwintebank harbours more distinct communities and is divided in different smaller parts. Remarkable differences between the communities defined in 1978 and 1997 include the subdivision of the coarser northern part into two communities, the fine sand community in the centre and the very poor station just to the south of the centre in 1997.

In the seventies the clean sands of the northern part of the Kwintebank were characterized by the dominance of Cylindropsyllidae, Paramesochridae, Ectinosomatidae and Ameiridae. Tetragonicipitidae, typical of very coarse sands and gravel, were also encountered though only once (Willems *et al.*, 1982b). In the present study the characteristic endobenthic ectinosomatid and ameirid species are less abundant. Vanosmael *et al.* (1982) showed that up to 7 % organic matter was trapped in sediments rich in gravel in the northern part of the Kwintebank, which may have attracted a lot of epi- and endobenthic species. Median grain sizes at different stations varied considerably between the seventies and the nineties, including a much higher maximum median grain size in the seventies. In the nineties station 5 in the centre of the Kwintebank is defined as a relatively fine sand station harbouring a harpacticoid community typical of the southern part of the Kwintebank. In the seventies this station clustered within the northern stations group because of the presence of coarse sands at that time (Willems *et al.*, 1982b). The changed sediment composition induced a shift from a rich northern bank community, characteristic of the sandwave area, to a species poor southern bank community, typical of finer sands. Such abrupt sediment changes are never recorded in monitoring surveys of sandwave and sandbank areas (Lanckneus *et al.*, 1992a; De Moor & Lanckneus, 1994; Vernemmen, 2001), unless they were the result of human induced perturbations such as intensive fishing or dredging activities or dumping of dredge spoil (Desprez, 2000; van Dalfsen *et al.*, 2000; Sarda *et al.*, 2000). Human disturbances may have seriously affected the Kwintebank because this sandbank is intensively exploited to provide sand for the building industry, contrary to the adjacent Middelkerkebank, which is not subject to aggregate extraction.

Remarkable changes are also recorded at station 6. This station clustered within the southern stations group in the seventies (Willems *et al.*, 1982b) while it shows a high similarity to the poor gully stations in the nineties. In the nineties the diversity gradient from high in the north to low in the south on the Kwintebank is interrupted at this station. Surprisingly the lowest density and species richness were recorded at station 6 in 1997, although higher values were expected due to the considerable amount of coarse sands (Coull, 1985). In 1997 sediment characteristics at station 6 are very similar to these at station 1, the richest station at the Kwintebank. But in the multivariate analysis the species composition of station 6 shows more affinities to the gully inhabiting community, differing a lot from the community in the northern tip of the sandbank. The highest species richness was recorded at station 1 and density was high. Some similarities were detected between station 1, the gully stations and station 6, such as the presence of *Apodopsyllus* n.spec.1. Station 1 is the deepest station on the sandbank and may be related to the gully stations in this way. Its depth (18 m) is intermediate between the gully stations 11 and 12 at 24 m and 20 m respectively and station 6, which is located at 14 m depth. The reason for the similarity between station 6 and the gully stations is hence not clear. The similarity between stations 1 and 6 was higher in the seventies (Willems *et al.*, 1982b). The very low density and diversity in the centre indicates unfavourable conditions for harpacticoids, although sediment composition was clearly appropriate. Station 6 is situated at the border of the bank summit, where potentially stronger near-bottom currents occur. Some stations at the Middelkerkebank were also situated at the border of the sandbank top and did not show any differences with stations located more on the summit of the bank.

Without a more detailed study of the biological and sedimentological proportional differences at the different stations between the seventies and the nineties it's not possible to define the extent of the changes and to decide whether these faunistic changes are related to seasonal fluctuations and hence reduced food availability, to sediment changes proper or to other environmental factors such as the intensive sand extractions. It's also difficult to accurately compare sediment characteristics at this point because granulometric characteristics in the seventies were defined in a different way than in the present study. A detailed and accurate comparison will be made in Chapter III, in which also sand extraction intensity will be taken into account.

4.3.2 Bank-gully differences

From the Kwintebank as well as from the Middelkerkebank top towards the Negenvaam gully stations a gradient is observed from well-sorted medium sands towards poorly sorted fine sands. This gradient in grain size corresponded with a decrease in harpacticoid density, diversity and interstitial forms. Moore (1979c) pointed out that an increase in the silt-clay content of the sediments from 4 to 10 % leads to the loss of the interstitial forms due to occlusion of the pore spaces. The silt-clay content of the Negenvaam gully station along the Middelkerkebank came to 8 %. This sediment was indeed very poor in interstitial copepods (only 3 %). But the silt and clay content was not the most important sediment characteristic. In the CCA very fine sand was selected as the significant environmental variable explaining the variation along the first axis, which separated the Negenvaam gully stations and the southern part of the Middelkerkebank from the other parts of the sandbanks. Most significant correlations were found between ecotype proportions and fine sand content, relations with clay and silt could not be found at the Middelkerkebank. Vanaverbeke *et al.* 2002 explained that the lower nematode diversity in the fine-grained sediments of the gullies was associated with low oxygen content or oxygen depletion, which also negatively affects harpacticoids to a great extent (Hicks & Coull, 1983). Measurements of oxygen content are not available in the present study but strong evidence for oxygen depletion exists as Trentesaux *et al.* (1994) found a matrix of black reduced sands in the Negenvaam gully. The differences between both Negenvaam samples may be attributed to seasonal fluctuations.

Oxygen shortage may affect harpacticoids in the sheltered and fine-grained deposits in the Negenvaam gully but other conditions are present in the Uitdiep and the Kwinte gully sediments. Apart from lower coarse sand content, the granulometric characteristics of the Kwinte gully station are similar to those of the richest station at the Kwintebank. Such small differences in sediment composition cannot explain the huge differences in density and diversity. At the Uitdiep gully station sediment characteristics and depth were comparable with the sandwave area at the sandbank top, though sandwaves were lacking on this gentle southeastern slope. Interstitial species predominated but density and diversity were also much reduced. It's very doubtful that the sediments at the slope would be less oxygenated than sediments in the sandwave area with the same granulometric characteristics. Presence or absence of sandwaves or herewith-related factors may influence harpacticoid density and diversity. The interaction between the topography and the tidal currents in a sandwave area may generate special hydrodynamic characteristics resulting in a more favourable turbulence or pore water flow and enhanced or more diverse food availability. It's also possible that, due to enhanced turbulence in sandwave areas, the small-scale disturbances reduce the competitive ability of specific species, which would have become dominant in a more homogeneous habitat. Increased dominance was also observed in the well-drained fine sands of the southern part of the Kwintebank and the Middelkerkebank, where sandwaves were also lacking.

The reduced density at the Kwinte gully station compared to the Uitdiep station may be attributed to seasonal differences, although the greater depth of the Kwinte gully station may induce environmental differences as well. A high variability among replicates at the Uitdiep and Kwinte stations indicated that patches with higher densities and diversity are nevertheless present in the gullies. A developing interstitial community in the gullies may be suffocated by a temporarily occlusion of the pore spaces as a result of deposition of silt and clay. Despite the strong dominant ebb current in the gullies, velocities diminish during a tidal cycle enabling sedimentation of particular matter (Dewicke, 2001). Endo- and epibenthic species colonizing these silty sand patches may be washed away when currents increase again. Such dynamics may explain the absence of a well developed interstitial as well as of a surface-living community. The dynamics in the gullies, predation and fishing pressure were illustrated while discussing the density gradient between sandbank tops and gullies.

5 Conclusions

At the Flemish Banks system sandbank tops are different from the swales in between from a sedimentologic and biologic point of view. Sandbank tops are largely characterized by higher harpacticoid densities and higher diversities than the gullies. Apart from sediment characteristics, still poorly determined factors such as reduced pore water flow resulting in oxygen stress in fine grained gully sediments, the absence of sandwaves in coarser deposits but also hydrodynamic stress and deposition of different kinds of sediment, predation and fishing pressure may be responsible for the distinct differences between sandbank tops and gullies.

On the sandbanks two distinct parts can be distinguished: the northern sandwave area is inhabited by a typical interstitial community with a high density and diversity while the finer grained southern parts are much poorer. The northern sandwave areas at the Kwintebank and the Middelkerkebank were quite similar whereas the southern topographically flat areas of the two sandbanks yielded totally different communities. Remarkably the Kwintebank showed a more patchy community distribution than the Middelkerkebank. It's not clear yet if this subdivision is related to purely natural granulometric variability or if extraction activities may have induced changes relative to the seventies, as the fine sand assemblage in the centre points to an 'unnatural' feature of sandwave areas. Sediment characteristics are related to harpacticoid density and diversity gradients along the sandbanks but could not explain the differences between the southern parts of the sandbanks. Near-bottom current dynamics seem to be as important as sediment characteristics in accounting for community variation. Strong tidal currents, wave action or storm events may generate these strong near-bottom current velocities. Also the topography of the seabed and the herewith-related interactions between tidal currents and sediment surface influences community structure significantly, irrespective of grain size or depth.

The conclusion to be drawn from these results is that biological community composition is not controlled by one or a combination of simple granulometric properties of the sediments. It is considered more likely that biological community composition is controlled by an array of environmental variables, many of them reflecting an interaction between particle mobility at the sediment-water interface and complex associations of chemical and biological factors. Clean coarse sands, well-sorted fine sands as well as mixed deposits under different hydrodynamic conditions with their respective harpacticoid communities create a heterogeneous environment, with highest diversity in the most dynamic parts at the sandbank top. In comparison with subtidal sandy habitats world-wide the relatively low densities and relatively high diversity indicate that the Flemish banks system is quite a stressed but rich environment.