Faculteit Wetenschappen
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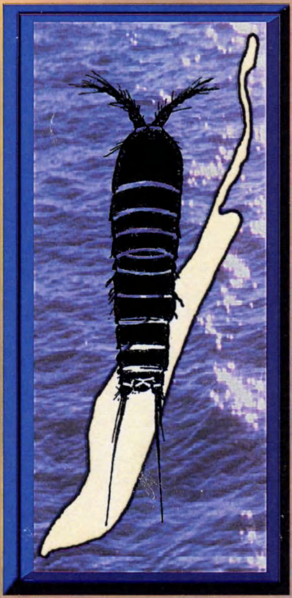
Benthic copepod communities in relation to natural and anthropogenic influences in the North Sea

Benthische copepodengemeenschappen in relatie tot natuurlijke en anthropogene invloeden in de Noordzee



Wendy Bonne

Promotor: Prof. Dr. M. Vincx

Proefschrift ingediend tot het
behalen van de graad van Doctor
in de Wetenschappen (Biologie)

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Universiteit Gent
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Sediments, sand extraction and phytoplankton blooms

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Sedimenten, zandontginning en de phytoplankton bloei

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"If we knew what it was we were doing, it would not be called research, would it?"
- Albert Einstein

"Or maybe it would ? "
- Wendy Bonne

And for all that's not clear yet in harpacticoid community analysis,
let's just look at them and say they're beautiful !

"It would be possible to describe everything scientifically, but it would make no sense; it would be without meaning, as if you described a Beethoven symphony as a variation of wave pressure."
Albert Einstein

Slicing ....
How it should not be
(Notice the core upside down !)

and fixing.... samples.

And let's get a bit emotional too ....

The Kwintebank
Steeply rising above the seabed
One day I will sink to the bottom
Touching you
And hold you in my arms
Riding on the waves of sand
Piling up toward the crest of the bank
Then being blown away
To settle in the gully
Again

Wendy Bonne
07/02/2003

The lab by night
The comfort of a song
The wet smell
Of grass and trees
Through the window
Fresh and chilly
You, thought in my mind, awake
Empty streets leading me blindly to my bed
The lab, I love you
I will always love you

Wendy Bonne
09/09/2002

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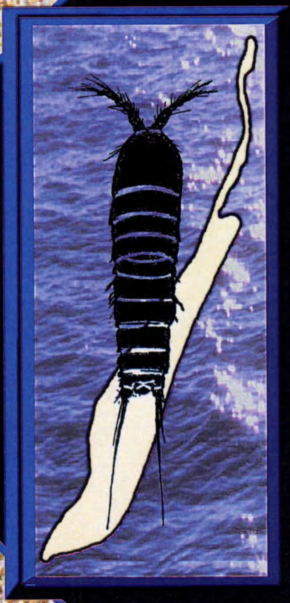
Dankwoord



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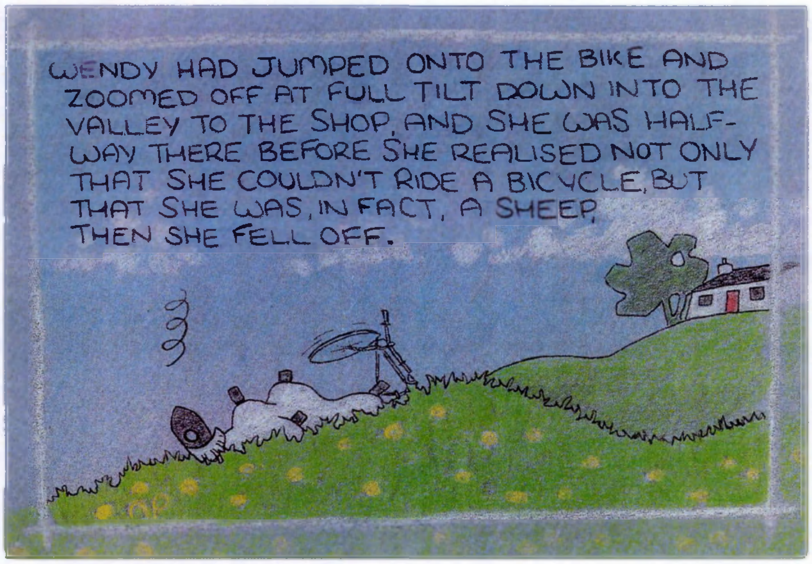

I remember a card a friend has sent me from England, being surprised that he knew me that much because sometimes I really felt like that sheep. Trapped in my enthusiasm to want to reach something but actually not really knowing if I would be able to do that and refusing to think that it might be impossible what I wanted.

Now I know that, in my world, sheep can ride bicycles!

But I would never have been able to reach that shop in such a short time (only 4,5 years) if the following people would not have helped to keep my balance from time to time and would not have shown me how to climb some hills.

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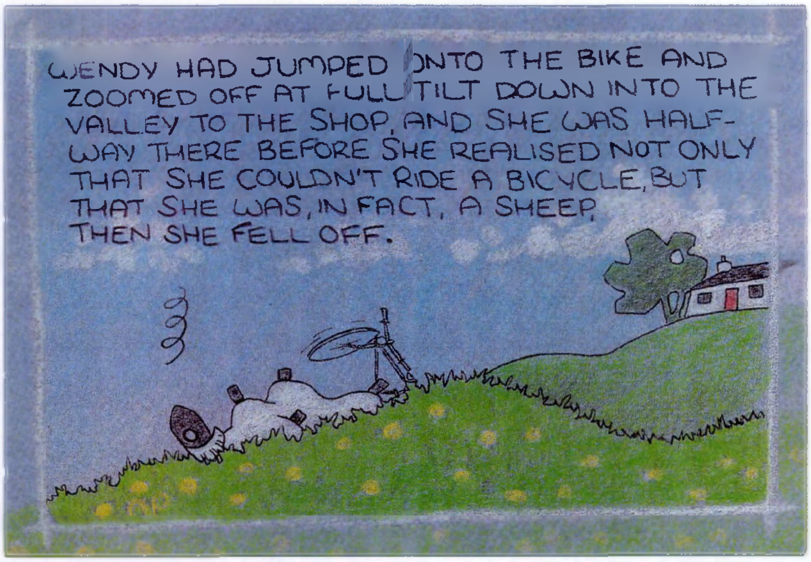
Dankwoord



Ik herinner me een kaartje dat een vriend me gestuurd heeft vanuit Engeland, verwonderd dat hij me zo goed kende want vaak voelde ik me zoals dat schaap. Gevangen in mijn enthousiasme om iets te bereiken maar eigenlijk niet wetend of ik in staat zou zijn om dat te doen en weigerend te denken dat het misschien onmogelijk was wat ik wilde.

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Summary

Samenvatting

Summary

The Belgian Continental Shelf is situated in the Southern Bight of the North Sea and consists of a number of sandbank systems separated by gullies. Benthic copepod (= harpacticoid) communities were investigated, focusing on the Flemish Banks system and the Gootebank, belonging to the Zeeland Banks.

1 Chapter I – Natural influences

Sediments

Low harpacticoid density and high diversity characterized the Flemish Banks. Sandbank tops differed from the gullies from a sedimentological and biological point of view. Harpacticoid densities and diversities were higher on sandbank tops than in the gullies.

In general, two distinct parts are distinguished on the Flemish Banks. The northern landscape of the sandbanks is characterized by big sand waves of coarser sands while the southern parts consist of a flat plateau of finer sands. These morphological characteristics and granulometric gradient result from the local tidal current patterns. The northern sandwave area was inhabited by a typical interstitial community with a high density and diversity while the finer grained southern parts were much poorer. The sandwave areas at the Kwintebank and the Middelkerkebank were similar whereas the topographically flat areas of both sandbanks yielded totally different communities. A dense community of interstitial species was found in the finer sediments of the Kwintebank, whereas endobenthic species predominated in the finer sands in the south of the Middelkerkebank, though in low abundance. Remarkably the Kwintebank showed a more patchy community distribution than the Middelkerkebank.

Sediment characteristics were 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.

The conclusion 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. 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.

2 Chapter II – Natural and anthropogenic influences

Spring phytoplankton blooms

Eutrophication in the North Sea is characterized by a shift from moderate early spring diatom growth to a *Phaeocystis* dominated phytoplankton community. Deposition of phytoplankton derived organic matter on the bottom was observed in the beginning of the diatom bloom and at the end of the *Phaeocystis* bloom. Over the whole period a minimum of about 60 % harpacticoids was present in the upper 5 cm of the sediment, with a mean of 75 %.

During the spring phytoplankton bloom there were clear temporal changes in the harpacticoid community with high diversity in April and high density and dominance in June. The high diversity in April during the diatom bloom may be attributed to the presence of subordinate species or specialist feeders. After *Phaeocystis* deposition opportunists predominated. Changes in community structure and density followed the same pattern on the Kwintebank and the Gootebank while diversity behaved differently. At the Kwintebank the organic matter is probably mixed through the upper layers of the sediment and reworked continuously. A great part of the deposited matter is resuspended during flood and hence not assimilated in a great extent by the infauna. The fraction of the deposited matter that is consumed by the harpacticoids continuously increases density and species richness. Yet, the *Phaeocystis* derived material increased the dominance in the community.

At the Gootebank the deposited organic matter is not reworked as intensively, resulting in a more stable food supply to the benthos. More harpacticoid species were present in the upper centimetres of the sediment in comparison with the Kwintebank, being concentrated in the upper 2 cm after *Phaeocystis* deposition. The dense interstitial fauna in the upper sediment layers reflects that deposited *Phaeocystis* derived organic matter is effectively assimilated and incorporated in the sediment through the microbial food web. Vertical migration of harpacticoids took place after the bloom reached the sediment surface in May, animals from deeper sediment layers attracted by the fresh food supply. In June and July particle and pore-water transport provided food particles at greater depth. A significant structuring effect is thus recorded in the interstitial community, which relies indirectly on sedimented phytoplankton, and not in the directly assimilating epibenthic harpacticoids, although these copepods are regarded as very mobile and may colonize food patches very quickly. Diversity increased remarkably during the diatom bloom, whereas the community was completely dominated by the most successful opportunistic interstitial species, *Apodopsyllus* n.spec.1, which exploits the detrital/bacterial food sources after *Phaeocystis* deposition. *Apodopsyllus* n.spec.1 may be the harpacticoid counterpart of the macrobenthic *Capitella capitata* and *Polydora* species.

Increased reproductive effort in May and June indicate that the reproductive cycles of most of the dominant harpacticoid species were related to the spring bloom sedimentation event. While not denying the role of temperature, the results suggest that breeding periodicity is also strongly related to food resource availability as a result of phytoplankton deposition. For some species migratory behaviour and reproductive activity were interrelated, whereas the total distribution of life history stages per depth layer did not reveal any changes in the vertical distribution over time.

3 Chapter III – Anthropogenic influences
Sand extraction

On the Kwintebank, sand is very intensively extracted for the building industry. More than 95 % of the sand extraction on the Belgian Continental Shelf occurs on the Kwintebank, being concentrated at the northwestern top and in the centre of the bank.

Harpacticoid community analysis distinguished only two parts on the Kwintebank in the seventies: a high variable northern part and a southern part with a high similarity. This pattern was more complicated in the nineties as indirect impacts of sand extraction were visible. In the nineties the Kwintebank was split up in four communities. Analogies were found in the occurrence of erosion and extraction areas and the distribution of harpacticoid communities. The northern top of the sandbank is very intensively exploited and subject to strong erosion, resulting in the formation of a depression. In this part a separate harpacticoid community has evolved from 1978 to 1997. Density and species richness, however, were still remarkably high in the nineties. The copepods of the dynamic area of sandwaves may be more resilient to extraction activities in terms of density and species richness than in the central part of the sandbank.

The centre of the sandbank is also very intensively exploited. A geomorphological survey indicated the presence of a distinct depression in this central area, which was not observed in the seventies. Due to sand extraction depth increased, sand waves were flattened and a depression was formed. In this depression changes in sediment characteristics from coarse sands in the seventies to fine sands in the nineties induced a shift from a species rich northern bank community to a species poor southern bank community with a high dominance of a few species. The altered sediment composition may be the result of a local accretion of fine sediments, as a consequence of overflow and changed current patterns in the depression. A station with a very low density and diversity, similar to the poor gully stations, was located near the southern border of the depression, although the sediment composition of this station was comparable to the richer bank stations. The sediment near this border coarsened, probably due to erosion, induced by sand extraction and enhanced by the strong currents.

The community in between the northern top and the central area still showed resemblance with the species assemblage defined for the northern part in the seventies. This community occurred in a less intensively exploited zone and a non-exploited zone, corresponding respectively with a zone of weak erosion and a zone of accumulation of sediment.

The southern part of the bank was characterized by low sand extraction intensity and no changes in the top volume of the bank except for one zone with weak erosion. The community structure of the southern part was still comparable after 20 years and hence stable in time.

A significantly higher density of juveniles was found in the intensively exploited areas and may be an indication of a direct impact of sand extraction. The abundance of big epi- and endobenthic species decreased and species composition altered in favour of very small interstitial species, which reproduce more frequently and are able to hide deeper into the sediment. Specific species correlate with disturbance intensity but the distribution and ecology of these species need to be studied more into detail in order to define them with certainty as indicator species for disturbance.

This study revealed that natural conditions define which harpacticoid species and communities occur but sand extraction can influence species composition both in a direct and an indirect way. Sand extraction on the Kwintebank is very patchy and much too intensive in the centre. The northern part and especially the centre of the Kwintebank can be defined as strongly impacted areas, while the harpacticoid community structure of the southern part of the bank is stable in time. The extension of the present depression in the centre of the sandbank due to sand extraction can become quite problematic if these human-induced physical disturbances may cause a continuing erosion and impoverishment.

4 Chapter IV – Anthropogenic influences

Sand extraction

Macrobenthic community analysis on the Kwintebank distinguished between a bank community, covering the whole sandbank from north to south, a slope community and a gully community. The community on the sandbank was characterized by low density and diversity, which is typical for mobile sands. Differences within the bank community reflected slight year-to-year variability but differences between areas of different levels of sand extraction intensity were not detected in the nineties.

The comparison of intensively exploited areas between the seventies and the nineties revealed that the *Spisula* species disappeared and the abundance of *Ophelia limacina* clearly decreased, which may be attributed to sand extraction activities. The potential impact of sand extraction on the macrobenthos of the Kwintebank was however not confirmed by clear changes in other biological characteristics, since density and diversity did not change. Only seasonal fluctuations were observed.

Increasing sand extraction intensity from the late seventies onwards did not result in an increase of the biotic coefficient. Moreover, the biotic coefficient did not differ between the stations, characterized by different sand extraction intensity. The biotic coefficient of a sporadically exploited station was even higher than at intensively exploited stations in 2001.

The investigation at community level, density and diversity measurements and the ecological groups used in the biotic coefficient were not sufficient to detect differences between impacted and non-impacted sites. The species composition of some areas changed and has become similar to the surrounding area, hampering the distinction between extracted and non-extracted sites at a fixed moment in time. In order to be able to use a biotic coefficient to measure dredging impacts in clean sands, a suggestion may be to modify the classification of the ecological groups used for the biotic coefficient, focusing on differences between the (interstitial) polychaetes and amphipods prevailing in these habitats or to examine the percentages of juveniles or biomasses.

5 Conclusions

5.1 Natural influences

5.1.1 Sediments

- Although sandbanks look like a homogeneous desert of sand with huge dunes and covered with sand ripples, they are very complex entities. Sediment characteristics cannot always explain the occurrence of clearly different harpacticoid communities. Natural disturbances such as different current bottom velocities, wave action and cycles of tidal mixing are supposed to be as important. The tight relation between sediment composition and hydrodynamics probably has to be refined. The potential interrelation between the topography of the sandbanks (sandwave *vs.* flattened areas) and other environmental characteristics implies still unrevealed secrets.

5.1.2 Diatom bloom

- Settling diatoms during the diatom bloom increase diversity in the harpacticoid community, probably favouring subordinate species or specialist feeders. Density however does not rise.

5.2 Anthropogenic influences

5.2.1 Eutrophication

- Deposition of *Phaeocystis* detritus has a structuring impact on the harpacticoid community, mainly favouring interstitial species and increasing productivity and species dominance within the community.
- *Phaeocystis* colonies sedimentation does not significantly influence the importance of the directly assimilating epibenthic or endobenthic species in the community but triggers a response of opportunistic species through the detrital/bacterial food web.
- Eutrophication may cause an increase in species richness in specific areas, an impoverishment in others, dependent on the amount of organic matter incorporated in the sediment, which is assumed to be dependent on tidal mixing.

5.2.2 Sand extraction

- Harpacticoids seem to be useful monitoring tools displaying a spatial variation at an appropriate scale (one sandbank) to detect community changes that are related to small-scale changes induced by sand extraction.
- Species richness and density measurements, however, were not appropriate to assess extraction effects at each impacted area in a simple way but species composition offered a more sensitive means of assessing environmental characteristics.

- Community changes are more difficult to detect if dealing with a faunal group consisting of a poor community of very mobile species, as is the case for the macrofauna on the Kwintebank. Differences between the macrobenthos of areas of different levels of human disturbance on the Kwintebank are not detected yet, because of potential homogenisation by the extractions, the poverty and wide niche width of the community and the extent to which the community is adapted to high levels of sediment disturbance in these dynamic systems. However, the poverty of samples so far is definitely an additional problem and comparisons with the macrofauna of similar undisturbed areas should be made.

5.3 Impact assessment

- Tidal mixing on the Kwintebank probably decreases potential negative effects of organic enrichment.
- The fauna on the Kwintebank is adapted to the prevailing dynamic conditions and hence more resilient to sand extraction activities.
- A threshold value does however exist in respect to sand extraction and care should be taken not to exceed the recovery capacity of the naturally present communities.
- Harpacticoid responses to environmental changes can clearly be detected because harpacticoid communities of clear sands on sandbanks are very rich, containing a lot of species differing in fitness and competitive abilities. In predominantly sandy sediments especially interstitial harpacticoids have a high value as ecological indicators. A slight community shift can be assessed by changes in the dominant species, because of the tight zonated occurrence of the indicator species.
- An increase of juveniles and interstitial species may reflect stressful conditions due to frequent disturbances, as a result of natural dynamics as well as a result of human-induced stress.
- The importance of harpacticoids in marine benthic community analysis and impact assessment cannot continue to be overlooked.
- An efficient monitoring should be maintained including the investigation of spatial and temporal variability.

Samenvatting

Het Belgisch Continentaal Plat situeert zich in de Zuidelijke Bocht van de Noordzee en bestaat uit een aantal zandbanken gescheiden door geulen. Dit onderzoek handelt over de benthische copepodengemeenschapen (= harpacticoidengemeenschappen) van de Vlaamse Banken en de Gootebank, die tot de Zeeland Banken behoort.

1 Hoofdstuk I – Natuurlijke invloeden

Sedimenten

De Vlaamse Banken werden gekarakteriseerd door lage harpacticoidendensiteiten en een hoge diversiteit. Een duidelijk onderscheid kon gemaakt worden tussen de zandbanktoppen en de geulen, zowel op sedimentologisch als op biologisch vlak. De densiteit en diversiteit aan harpacticoiden waren hoger op de zandbanktoppen dan in de geulen.

Op de Vlaamse Banken kunnen in het algemeen twee delen onderscheiden worden. In het noordelijk gedeelte bevinden zich grote zandgolven bestaande uit grovere sedimenten, terwijl het zuidelijk gedeelte een vlak plateau vormt en fijner sediment bevat. Deze morfologische en granulometrische gradiënt zijn een gevolg van de lokale patronen van de getijdestroom. In het noordelijke zandgolvengebied kwam een typische interstitiële gemeenschap voor met een hoge densiteit en diversiteit, terwijl het zuidelijk gedeelte veel armer was. De gemeenschappen van de zandgolfgebieden op de Kwintebank en de Middelkerkebank waren gelijkaardig terwijl de topografisch vlakke gebieden van beide zandbanken een totaal verschillende gemeenschap herbergden. Een abundante gemeenschap van interstitiële soorten kwam voor in de fijnere sedimenten van de Kwintebank terwijl endobenthische soorten domineerden in het zuiden van de Middelkerkebank maar wel in lage aantallen. Opmerkelijk was dat de Kwintebank opgesplitst was in meer verschillende gemeenschappen dan de Middelkerkebank.

De densiteits- en diversiteitsgradiënt van de harpacticoiden over de zandbanken was gerelateerd aan de sedimentkarakteristieken maar sedimentkarakteristieken konden de verschillen tussen de zuidelijke gedeelten van de zandbanken niet verklaren. De dynamiek van stromingen boven de bodem blijken even belangrijk te zijn als sedimentkarakteristieken om verschillen tussen gemeenschappen te veroorzaken. Sterke getijdestromingen, golfwerking en stormen kunnen deze sterke stromingen boven de bodem genereren.

De conclusie die uit deze resultaten kan getrokken worden is dat de samenstelling van biologische gemeenschappen niet bepaald wordt door één of door een samenstelling van granulometrische eigenschappen van het sediment. Het is meer waarschijnlijk dat de samenstelling van de gemeenschap bepaald wordt door een reeks van omgevingsvariabelen, waarvan een aantal een interactie aanduiden tussen de mobiliteit van de partikels in het raakvlak tussen sediment en waterkolom en complexe associaties van chemische en biologische factoren. Grove zanden, goed gesorteerde fijne zanden zowel als gemengde afzettingen onder verschillende hydrodynamische omstandigheden worden gekenmerkt door verschillende harpacticoidengemeenschappen en creëren een heterogeen gebied, met de hoogste diversiteit in de meest dynamische zandbanktoppen. In vergelijking met subtidale zandige gebieden wereldwijd zijn de densiteiten van harpacticoiden op de Vlaamse Banken relatief laag en de diversiteit relatief hoog, waardoor ze als een stressrijke maar diverse omgeving kunnen beschouwd worden.

2 Hoofdstuk II – Natuurlijke en anthropogene invloeden

De phytoplankton lentebloei

De eutrofiëring van de Noordzee wordt gekenmerkt door een overgang van een matige diatomeeëngroei in de vroege lente naar een *Phaeocystis* gedomineerde phytoplanktongemeenschap. Op de bodem werd een depositie van organisch materiaal, afkomstig van phytoplankton, waargenomen in het begin van de diatomeeënbloei en op het einde van de *Phaeocystis* bloei. Over de ganse periode bevond gemiddeld 75 % van de harpacticoiden zich in de bovenste 5 cm van het sediment, met een minimum van ongeveer 60 %.

Tijdens de phytoplankton lentebloei werden duidelijke temporele veranderingen waargenomen in de harpacticoidengemeenschap, met een hoge diversiteit in april en een hoge soortendominantie in juni. De hoge diversiteit in april tijdens de diatomeeënbloei kan te wijten zijn aan de aanwezigheid van 'ondergeschikte' soorten of voedselspecialisten. Na depositie van *Phaeocystis* kolonies domineerden opportunisten. Veranderingen in de gemeenschapsstruktuur en densiteit volgden hetzelfde patroon op de Kwintebank als op de Gootebank, terwijl de trend in diversiteit duidelijk verschilde. Op de Kwintebank wordt het organisch materiaal in de bovenste lagen van het sediment waarschijnlijk door getijdewerking gemengd en continu herwerkt. Een grote hoeveelheid van het afgezette materiaal wordt tijdens vloed in resuspensie gebracht en wordt daardoor niet in grote mate door de infauna geassimileerd. De fractie van het afgezette materiaal dat door de harpacticoiden wordt opgenomen veroorzaakt een continue stijging in densiteit en soortenrijkdom. De depositie van detritus afkomstig van *Phaeocystis* verhoogde evenwel de soortendominantie in de gemeenschap.

Op de Gootebank wordt het afgezette organische materiaal niet zo intensief herwerkt, wat een stabielere voedseltoevoer voor het benthos als gevolg heeft. Er waren meer soorten harpacticoiden aanwezig in de bovenste centimeters van het sediment in verglijking met de Kwintebank. Na de *Phaeocystis* depositie waren ze geconcentreerd in de bovenste 2 cm. De abundante interstitiële fauna in de bovenste centimeters weerspiegelt dat het afgezette organische materiaal van *Phaeocystis* effectief wordt geassimileerd en geïncorporeerd in het sediment doorheen het microbiële voedselweb. Verticale migratie van harpacticoiden nam plaats nadat de bloei het sediment bereikte in mei, aangezien organismen van diepere lagen door de verse voedseltoevoer werden aangetrokken. In juni en juli werden voedselpartikels door partikel- en poriënwatertransport beschikbaar op grotere diepte. Een significant structurerend effect werd dus gevonden in de interstitiële gemeenschap, die indirect afhankelijk is van gesedimenteerd phytoplankton en niet in de epibenthische harpacticoiden, die detritus direct assimileren. Deze zijn nochtans zeer mobiel en kunnen plekken aangerijkt met voedsel zeer vlug koloniseren. De diversiteit steeg opmerkelijk tijdens de diatomeeënbloei, terwijl de gemeenschap na *Phaeocystis* depositie volledig gedomineerd was door één enkele interstitiële soort, *Apodopsyllus* n. spec.1. Dit was de meest succesvolle opportunistische soort, die de dan voorhanden detritus- en bacteriënrijke voedselbronnen het meest efficiënt benutte. *Apodopsyllus* n. spec.1 kan als een harpacticoide tegenhanger van de macrobenthische *Capitella capitata* en *Polydora* soorten beschouwd worden.

Een verhoogde reproductie in mei en juni toonde aan dat de reproductiecycli van de meeste dominante harpacticoiden gerelateerd zijn aan de sedimentatie van de lentebloei. De invloed van temperatuur evenwel niet ontkennend, suggereren deze resultaten dat de voortplanting ook in sterk verband staat met de voedselbeschikbaarheid als gevolg van de phytoplankton sedimentatie. Voor sommige soorten stonden verticale migratie in het sediment en reproductieve activiteit met elkaar in verband, terwijl de verticale verdeling van adulten en juvenielen van alle soorten samen geen verandering vertoonde in de tijd.

3 Hoofdstuk III – Anthropogene invloeden Zandontginning

Op de Kwintebank wordt zeer intensief zand ontgonnen voor de bouwnijverheid. Meer dan 95 % van de zandontginning op het Belgisch Continentaal Plat gebeurt op de Kwintebank, geconcentreerd in het noordwestelijk en het centraal gedeelte van de bank.

De gemeenschapsanalyze van de harpacticoidendata van de jaren zeventig toonde aan dat er toen twee verschillende delen konden onderscheiden worden op de Kwintebank: een noordelijk gedeelte met een hoge variabiliteit in het voorkomen van harpacticoiden en een zuidelijke gemeenschap met een hoge similariteit. Dit patroon was ingewikkelder in de jaren negentig aangezien indirecte invloeden van de zandontginning zichtbaar waren. In de jaren negentig kwamen vier verschillende gemeenschappen voor op de Kwintebank. Er werden overeenkomsten gevonden tussen het voorkomen van erosiegebieden, gebieden met een bepaalde zandontginningsintensiteit en het voorkomen van bepaalde harpacticoide gemeenschappen.

De noordelijke top van de zandbank wordt zeer intensief ontgonnen en is onderhevig aan sterke erosie, wat de vorming van een depressie heeft teweeggebracht. In dit gedeelte heeft er zich een aparte harpacticoidengemeenschap afgesplitst sinds 1978. Densiteit en diversiteit was nochtans opmerkelijk hoog in de jaren negentig. De copepoden van dit dynamisch gebied kunnen mogelijks meer weerstand bieden aan de ontginningsactiviteiten dan de copepoden in het centrale gedeelte van de zandbank, tenminste wat de densiteit en diversiteit betreft.

Het centrum van de zandbank wordt ook zeer intensief ontgonnen. Een geomorfologische studie heeft het ontstaan van een depressie aangetoond in ditzelfde gebied, die in de jaren zeventig nog niet bestond. Door de zandontginning is de diepte toegenomen, werden de zandgolven afgevlakt en is er een depressie ontstaan. Een verfijning van het sediment in 1997 t.o.v. 1978 in de depressie induceerde een verschuiving van een soortenrijke gemeenschap, karakteristiek voor het grofzandig gebied in het noorden, naar een soortenarme gemeenschap, karakteristiek voor het fijnzandig milieu in het zuiden. Deze laatste gemeenschap werd gekenmerkt door een dominantie van een klein aantal soorten. De gewijzigde sedimentsamenstelling kan het gevolg zijn van een lokale accumulatie van fijn materiaal als gevolg van de overvloei van de fijne fractie van de zandontginningsschepen of van gewijzigde stromingspatronen in de depressie. Aan de rand van de depressie lag ook een gebied met een zeer lage densiteit en diversiteit, alhoewel de sedimenteigenschappen van dit station vergelijkbaar waren met andere rijkere bankstations. Het sediment in dit gebied werd grover, waarschijnlijk als een gevolg van erosie, geïnduceerd door de zandontginning en versterkt door de sterke stromingen.

De gemeenschap tussen de noordelijke top van de bank en het centraal gedeelte vertoonde nog gelijkenissen met de gemeenschap van het noordelijke gedeelte in de jaren zeventig. Deze gemeenschap bevond zich in een minder intensief ontgonnen zone en een niet ontgonnen zone, overeenkomend met een zone van zwakke erosie en een zone van sedimentaccumulatie respectievelijk.

Het zuidelijk gedeelte van de bank wordt gekarakteriseerd door een lage zandontginningsintensiteit en geen veranderingen in het topvolume van de bank, behalve in een gebied met zwakke erosie. De harpacticoide gemeenschapsstructuur van het zuidelijk gedeelte van de bank was na 20 jaar nog steeds vergelijkbaar en dus stabiel in de tijd.

Een toename van het aantal juvenielen in de meest ontgonnen gebieden kan een direct gevolg zijn van de zandontginning. Het aantal grote epi- en endobenthische soorten nam af terwijl de soortensamenstelling veranderde in het voordeel van de kleine interstitiële soorten, die zich vlugger voortplanten en in staat zijn om zich dieper in het sediment terug te trekken. Bepaalde soorten correleerden met de verstoringsintensiteit maar de verspreiding en de ecologie van deze soorten dient meer in detail bestudeerd te worden om hen met zekerheid als indicatoren voor verstoring te kunnen aanduiden.

Deze studie heeft aangetoond dat natuurlijke omstandigheden (sedimentkarakteristieken en stromingspatronen) bepalen welke harpacticoide soorten en gemeenschappen voorkomen maar dat zandontginning de soortensamenstelling kan beïnvloeden, zowel op een directe als op een indirecte manier. De zandontginningsintensiteit op de Kwintebank verschilt sterk van gebied tot gebied en is veel te intens in het centrum. Het meest noordelijke gedeelte en vooral het centrum van de Kwintebank kunnen gedefinieerd worden als sterk verstoorde gebieden, terwijl de harpacticoide gemeenschapsstructuur van het zuidelijk gedeelte van de bank stabiel is in de tijd. De uitbreiding van de huidige depressie in het centrum van de zandbank door zandontginning kan problematisch worden als deze menselijke fysische verstoringen een verdere erosie en verarming zullen veroorzaken.

4 Hoofdstuk IV – Anthropogene invloeden

Zandontginning

De gemeenschapsanalyze van het macrobenthos op de Kwintebank onderscheidde drie gemeenschappen: een bankgemeenschap, de volledige zandbank omvattend van het noorden tot het zuiden, een gemeenschap karakteristiek voor de helling van de zandbank en een geulgemeenschap. De gemeenschap van de zandbanktop was gekenmerkt door een lage densiteit en diversiteit, wat typisch is voor mobiele sedimenten. Verschillen binnen deze bankgemeenschap weerspiegelden enkel jaarlijkse variatie maar konden geen verschillen aanduiden tussen de gebieden met een verschillende zandontginningsintensiteit in de jaren negentig.

De vergelijking van de intensief ontgonnen gebieden tussen de jaren zeventig en de jaren negentig toonde aan dat de *Spisula* soorten verdwenen en dat de abundantie van *Ophelia limacina* duidelijk afnam, wat aan de zandontginningsactiviteiten kan te wijten zijn. De mogelijke invloed van de zandontginning werd echter niet bevestigd door duidelijke veranderingen in andere biologische kenmerken, aangezien de densiteit en de diversiteit niet veranderde. Er werden enkel seizoenale fluctuaties waargenomen.

Een toenemende zandontginningsintensiteit sinds de jaren zeventig veroorzaakte geen stijging in de biotische coëfficiënt, die ook niet verschilde tussen de stations met een verschillende zandontginningsintensiteit. De biotische coëfficiënt was zelfs hoger voor een sporadisch ontgonnen station dan voor de intensief ontgonnen stations in 2001.

De analyze op gemeenschapsniveau, de densiteits- en diversiteitswaarden en de afbakening van de ecologische groepen die in de biotische coëfficiënt gebruikt wordt, zijn niet voldoende om verschillen te ontdekken tussen verstoorde en niet verstoorde gebieden. Een aantal gebieden die vroeger andere soorten bevatten zijn gelijkaardig geworden aan de omliggende gebieden. Dit verhindert de mogelijkheid om een onderscheid te kunnen maken tussen ontgonnen en niet ontgonnen gebieden op een bepaald moment in de tijd. Om een geschikte biotische coëfficiënt te vinden om ontginningseffecten in zuivere mobiele zanden te kunnen aanduiden, wordt gesuggereerd om de indeling van de ecologische groepen voor de biotische coëfficiënt aan te passen, gebaseerd op verschillen tussen de (interstitiële) polychaeten of amphipoden die in dit habitat voorkomen of door het percentage juvenielen of biomassa's te bestuderen.

5 Conclusies

5.1 Natuurlijke invloeden

5.1.1 Sedimenten

- Alhoewel zandbanken een homogene woestijn van zand lijken, met grote zandduinen en bedekt met zandribbels, zijn het zeer complexe systemen. Sedimentkarakteristieken kunnen niet altijd het voorkomen van duidelijk verschillende harpacticoidengemeenschappen verklaren. Er wordt verondersteld dat natuurlijke verstoringen zoals verschillende stromingssterkten boven de bodem, golfwerking en tidale cycli van resuspensie van het sediment even belangrijk zijn. De sterke relatie tussen sedimentsamenstelling en hydrodynamiek moet waarschijnlijk meer genuanceerd worden. Het mogelijke verband tussen de topografie van de zandbanken (zandgolf- *vs.* vlakke gebieden) en andere omgevingskarakteristieken bevat nog ononthulde geheimen.

5.1.2 Diatomeeënbloei

- Diatomeeën die naar de bodem zinken tijdens de diatomeeënbloei verhogen de diversiteit van de harpacticoidengemeenschap. Waarschijnlijk worden 'ondergeschikte' soorten of voedings-specialisten bevoordeeld. De densiteit van de gemeenschap verhoogt echter niet.

5.2 Anthropogene invloeden

5.2.1 Eutrofiëring

- Depositie van *Phaeocystis* detritus heeft een structurerend effect op de harpacticoiden-gemeenschap. Vooral interstitiële soorten worden bevoordeeld en de productiviteit en de dominantie van bepaalde soorten stijgen.
- Sedimentatie van *Phaeocystis* kolonies beïnvloedt het belang van de epibenthische en endobenthische soorten in de gemeenschap niet significant. Deze soorten assimileren het detritus op een directe manier. De sedimentatie veroorzaakt daarentegen een respons van opportunistische soorten die deel uitmaken van een voedselweb dat gebaseerd is op de bacteriële afbraak van detritus.
- Eutrofiëring kan een stijging in de soortenrijkdom veroorzaken in bepaalde gebieden, een verarming in andere. Dit is afhankelijk van de hoeveelheid organisch material dat in het sediment geïncorporeerd wordt, wat waarschijnlijk beïnvloed wordt door tidale resuspensie en redepositie.

5.2.2 Zandontginning

- Harpacticoiden zijn geschikte organismen voor monitoring doeleinden omdat ze een ruimtelijke variatie vertonen op een schaal (één zandbank) die geschikt is om gemeenschapsveranderingen te ontdekken die in verband staan met veranderingen als een gevolg van zandontginning.

- De gegevens over soortenrijkdom en densiteit waren echter niet geschikt om in elk verstoord gebied gemakkelijk een effect te kunnen aanduiden. De soortensamenstelling daarentegen was gevoeliger aan veranderingen in de omgeving en bood een gemakkelijkere manier om deze veranderingen op te sporen.
- Gemeenschapsveranderingen zijn moeilijker waar te nemen bij een fauna die uit een arme gemeenschap bestaat van voornamelijk opportunistische soorten, zoals het geval is voor de macrofauna op de Kwintebank. Verschillen tussen het macrobenthos van gebieden met een verschillende graad van menselijke verstoring werden nog niet gevonden op de Kwintebank. Dit was mogelijks te wijten aan de homogenisatie ten gevolge van de ontginningen, de soortenarmoede en de wijde nichebreedte van de gemeenschap en de mate waarin de gemeenschap is aangepast aan sterke verstoringen van het sediment in deze dynamische systemen. Het ontoereikend aantal stalen is zeker een bijkomstig probleem en vergelijkingen met onverstoorde gebieden zouden moeten gemaakt worden.

5.3 Effectenbepaling

- Vermenging van het sediment en resuspensie van organisch materiaal door getijdewerking op de Kwintebank verminderen de mogelijke negatieve effecten van organische aanrijking.
- De fauna van de Kwintebank is aangepast aan de heersende dynamische omstandigheden en kan daardoor meer weerstand bieden aan de zandontginningsactiviteiten.
- Er bestaat echter een drempel voor die weerbaarheid tegen de zandontginning. Er moet op gelet worden om het recuperatievermogen van de natuurlijk aanwezige gemeenschappen niet te overschrijden.
- De respons van harpacticoiden op veranderingen in de omgeving kan duidelijk waargenomen worden omdat deze organismen een grote soortenrijkdom vertonen. De talrijke soorten verschillen in weerbaarheid en competitievermogen. In voornamelijk zandige sedimenten zijn vooral interstitiële harpacticoiden waardevol als ecologische indicatoren. Een geringe verschuiving in de gemeenschap kan vastgesteld worden aan de hand van veranderingen in de dominante soorten omdat deze indicatorsoorten een nauwe zonatie vertonen.
- Een toename van juvenielen en interstitiële soorten weerspiegelt mogelijks stressrijke omstandigheden omwille van frequente verstoringen, zowel als gevolg van natuurlijke dynamiek als van menselijk geïnduceerde stress.
- Het belang van harpacticoiden in mariene gemeenschapsanalyses en het vaststellen van verstoringsinvloeden kan niet genegeerd blijven.
- Een efficiënte monitoring zou moeten uitgevoerd worden, dat gedetailleerd onderzoek omvat naar de ruimtelijke en temporele variabiliteit.

Introduction

Introduction

1 Framework

Marine conservation is less developed than that of the terrestrial environment. The main three reasons are that the populations and communities are not normally visible; our knowledge of them is limited and no ongoing benthic monitoring was maintained (Suchanek, 1994). Major changes are however taking place in monitoring and approaching the control of marine pollution in the North Sea compared to a decade earlier. The international context is evolving constantly and is now oriented to 'protect' the marine environment. Research projects co-funded by the European Union or co-ordinated by ICES, or conducted by individual nations, continue to add significantly to the understanding of the North Sea. (Ducrotoy *et al.*, 2000) But the public response to the needs for marine biodiversity conservation is very limited compared with terrestrial habitat conservation. The list of threats on the marine environment is however very long. The threats on coastal systems include habitat loss, global climate change, fishing, sand extraction, oil and gas exploitation, pollution (including direct and indirect effects of inorganic and organic chemicals, eutrophication and related problems such as pathogenic bacteria and algal toxins), shipping, effluents of nuclear power stations, wind turbines, mariculture, species introductions, water-shed alteration and physical alterations of coasts, tourism, marine litter, military activities, atmospheric pathways and the fact that humans have little perception of the oceans and their marine life (Gray, 1997; Ducrotoy *et al.*, 2000).

Belgium is the smallest North Sea country with the shortest coastline (67 km) but a lot of user groups of the marine environment are concentrated on the Belgian Continental Shelf, comprising an area of only 3500 km² (Cattrijsse & Vincx, 2001; Maes *et al.*, 2000). The awareness of the Belgian authorities of the potential impact of anthropogenic stress on the marine environment dated from 1970, when the first national co-ordinated marine research programme 'Sea' was launched (e.g. Nihoul & De Coninck, 1977; Nihoul & Gullentops, 1977; Nihoul & Ronday, 1976). This project already had an interdisciplinary character and aimed to study the impact of natural and anthropogenic processes on the marine environment. After the end of the project marine research initiatives were scattered among different institutes and universities. In 1997 the Belgian Federal Office for Scientific, Technical and Cultural Affairs (OSTC) financed a second national research initiative, the 'Sustainable Management of the North Sea' research programme. The project 'Structural and Functional Biodiversity of North Sea Ecosystems: Species and their Habitats as Indicators for a Sustainable Development of the Belgian Continental Shelf' investigated the factors that determine and influence the biodiversity of the benthic fauna of subtidal sandbanks in order to find ecological indicators for monitoring purposes and to indicate vulnerable and threatened habitats (Vincx *et al.*, 2002). The project aimed at supporting a solid scientific background allowing a long-term policy for the use of the resources of the North Sea, by giving an overview of epibenthos, hyperbenthos, macrobenthos and meiobenthos on the Belgian Continental Shelf. Meiofauna and nematode results of this project are published in Vanaverbeke *et al.* (2000, 2002, 2003); hyperbenthos results in Dewicke *et al.* (2003) and macrobenthos results in Van Hoey *et al.* (submitted). The final report of the project also gives an overview of the bird countings and the results on the parasites of fish (Vincx *et al.*, 2002). In this thesis the results of the harpacticoid fauna related to this project will be presented. The investigated anthropogenic influences are sand extraction and eutrophication (*Phaeocystis* bloom).

2 Harpacticoids

The order Harpacticoida is one of ten orders of the subclass Copepoda which, along with six other subclasses (Boxshall & Huys, 1989) make up the class Maxillopoda, one of the classes of the lower Crustacea (Bowman & Abele, 1982). Harpacticoids can be seen as the diminutive of crabs and shrimps. At the moment, the order contains well over 3000 species belonging to 460 genera contained in 50 families. Marine harpacticoids are primarily bottom-living copepods, although a few are exclusively planktonic, and are most abundant in soft sediments and on macro-algae. They are small, predominantly less than 1 mm long, belonging to the meiofauna (38µm-1mm), and are usually the second most abundant group of animals (after nematodes) in benthic meiofaunal communities. (Huys *et al.*, 1996)

In the North Sea, copepod density and diversity are highest in the Southern Bight due to the presence of many interstitial species; about 1500 species are thought to occur. They show very distinct assemblages according to water depth and sediment type (Huys *et al.*, 1992). By contrast nematodes, the dominant meiofaunal taxon overall, are least abundant in the sandy sediments of the Southern Bight, increase to a maximum around 53°30N, and slowly decrease again towards the north (Huys *et al.*, 1992). The following studies, containing information on harpacticoid fauna, were conducted on the Belgian Continental Shelf: Claeys (1979), Govaere *et al.* (1980), Willems *et al.* (1982a,b), Heip *et al.* (1983, 1984, 1990), Herman *et al.* (1985), Chen (1987), Vandenberghe (1987), Herman (1989), Vincx & Herman (1989), Huys *et al.* (1986a, 1992) and Huys (1995). Most studies were conducted in the near coastal area and on the Kwintebank. In the beginning of the nineties, ecological research on harpacticoid copepods on the Belgian Continental Shelf ceased and the last ten years no additional information was gathered anymore.

Remane (1933) already assumed that meiofauna includes more stenotopic species than macrofauna and that meiofauna communities are more suitable to characterize subtidal sandy habitats. Meiofauna and in particular harpacticoid copepods react quickly on changes in the environment, making them suitable for ecological monitoring (Heip, 1980; van Damme *et al.*, 1984; Vincx & Heip, 1987; Moore & Bett, 1989). Recently Schratzberger *et al.* (2000) concluded that the inclusion of meiofauna in applied monitoring programmes offers the potential for improving the resolution of the spatial extent of anthropogenic impacts over that achievable from macrofauna investigations alone.

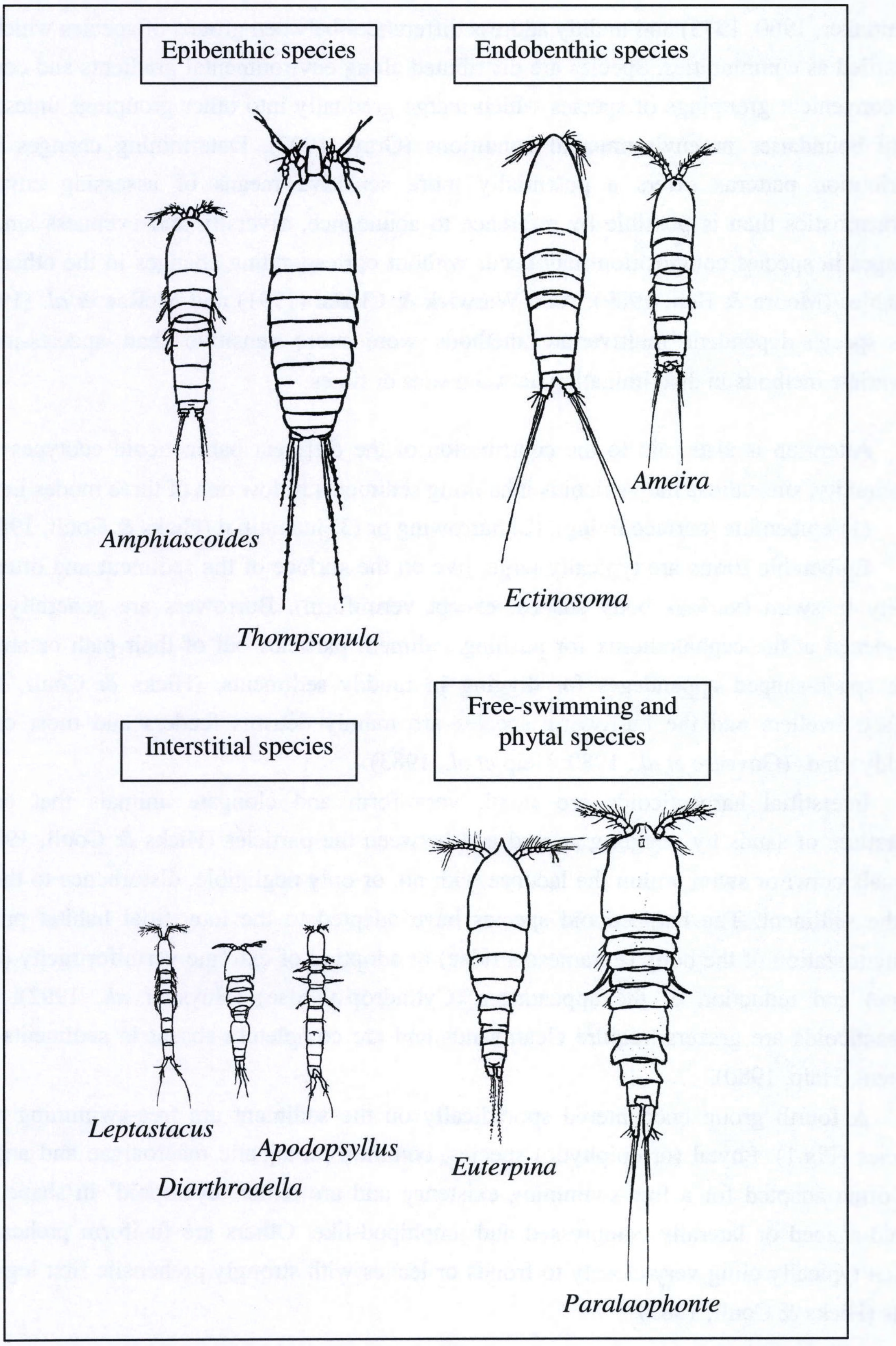


Fig.1: Different ecotypes of harpacticoids, illustrated by means of some typical genera

The analyses conducted in this thesis focus on density and between-habitat diversity (Whittaker, 1960, 1975) and mainly address differences between groups of species which could be classified as communities. Species are distributed along environmental gradients and communities are convenient groupings of species which merge gradually into other groupings unless there are sharp boundaries in environmental conditions (Gray, 1997). Determining changes in species distribution patterns offers a potentially more sensitive means of assessing environmental characteristics than is possible by reference to abundance, diversity and evenness since marked changes in species composition may occur without corresponding changes in the other measured variables (Moore & Bett, 1989). Also Warwick & Clarke (1991) and McRae *et al.* (1998) found that species-dependent multivariate methods were more sensitive than species-independent univariate methods in discriminating between sites or times.

Attention is also paid to the contribution of the different harpacticoid ecotypes within the community, since those harpacticoids inhabiting sediments follow one of three modes i.e.:

(1) epibenthic (surface living), (2) burrowing or (3) interstitial (Hicks & Coull, 1983).(Fig.1)

Epibenthic forms are typically large, live on the surface of the sediment and often have the ability to swim (various body shapes, except vermiform). Burrowers are generally large and broadened at the cephalothorax for pushing sediment particles out of their path or are equipped with spade-shaped appendages for digging in muddy sediments. (Hicks & Coull, 1983) The surface-dwellers and the burrowing species are mainly detritus feeders and most common in muddy sands (Govaere *et al.*, 1980; Heip *et al.*, 1983)

Interstitial harpacticoids are small, vermiform and elongate animals that occupy the interstices of sands by wiggling around and between the particles (Hicks & Coull, 1983). These animals crawl or swim within the lacunae with no, or only negligible, disturbance to the structure of the sediment. The harpacticoid species have adapted to the interstitial habitat primarily by miniaturization of the body (Paramesochridae) or adoption of extreme vermiformicity (cylindrical shape) and reduction of the appendages (Cylindropsyllidae) (Huys *et al.*, 1992). Interstitial harpacticoids are grazers, require clean sands and are completely absent in sediments with mud content (Heip, 1980).

A fourth group encountered sporadically on the sediment are free-swimming and phytal species (Fig.1). Phytal (or epiphytic) species, common on aquatic macroalgae and angiosperms, are often adapted for a free-swimming existence and are either ‘cyclopoid’ in shape, flattened, shield-shaped or laterally compressed and amphipod-like. Others are fusiform prehensile forms which typically cling very closely to fronds or leaves with strongly prehensile first legs or mouth parts (Hicks & Coull, 1983).

3 Belgian Continental Shelf

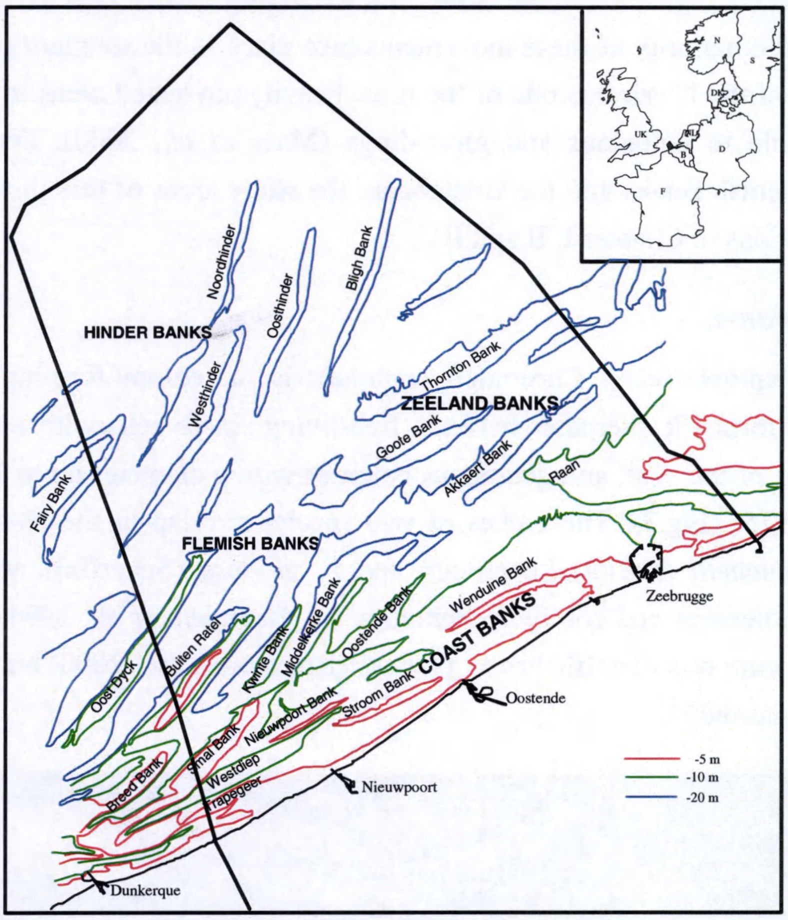


Fig.2: Different sandbank systems on the Belgian Continental Shelf

The Belgian Continental Shelf (Fig.2) is the most southwestern part of the Southern Bight of the North Sea and is bordered by the Dover Strait and the Central North Sea. The North Atlantic drift and the freshwater supply of the rivers Schelde and Yzer characterize the watermasses. Strong semi-diurnal tides and a net tidal current, running north-east parallel to the coast, keep the water column well mixed. (Cattrijsse & Vincx, 2001) Despite its small surface, the Belgian part of the North Sea comprises very valuable habitats (Maes & Cliquet, 1997). Geologically, this area consists of a number of more or less mobile sandbank systems separated by gullies. Sand banks and ridges occur in many coastal and shelf seas where there is abundant sand and where the currents are strong enough to move sediment (Dyer & Huntley, 1999). The subtidal sandbank area extends from Zeeland as far as Calais. A similar area is only known from the southeast of England. Differences in orientation and position allow grouping the sandbanks into several systems (De Moor, 1985). The coast banks are nearshore and run parallel to it. The Flemish Banks have a more SW-NE direction, the Hinder Banks lie further seawards and have a more or less S-N direction, the West Zeeland ridges lie most eastwards and run in a more W-E direction. A detailed description of the sandbank system can be found in Bastin (1974).

The banks consist of Holocene marine sands covering cores of older deposits (De Moor, 1984). Nearshore coastal sandbanks dissipate energy from incoming waves and are very effective in protecting the coast (Carter & Balsillie, 1983) but the shallowness of the crests may induce problems for coastal navigation (Trentesaux *et al.*, 1994). Every year more than 420 000 routebound ship movements are registered in the North Sea, excluding fishery vessels, navy vessels and recreational vessels. The majority of these movements take place in the southern part of the North Sea, making this part of the North Sea one of the most heavily navigated areas in the world. This area is very susceptible to collisions and groundings (Maes *et al.*, 2000). For more detailed information on the Flemish Banks and the Gootebank, the study areas of this thesis, the reader is referred to the descriptions in Chapter I, II and III.

4 *Phaeocystis* blooms

Phaeocystis (Haptophyceae, Chromophycophyta) is a colony-forming nanoflagellate occurring in different forms. It alternates between free-living single cells with a cell diameter of 6 µm, present for most of the year, and gelatinous colonies with a diameter up to 20 mm in spring (Gieskes & Kraay, 1975) (Fig.3). The niches of two species overlap in the North Sea (Rick & Aletsee, 1989): *P. pouchetii* (Hariot) Lagerheim and *P. globosa* (Scherffel), which apparently differ in temperature tolerance and colony morphology (*cf.* Baumann *et al.*, 1994). In the Belgian coastal waters *Phaeocystis* was identified as *P. globosa* (Rousseau *et al.*, 2000) but will be referred to as *Phaeocystis* in this study.

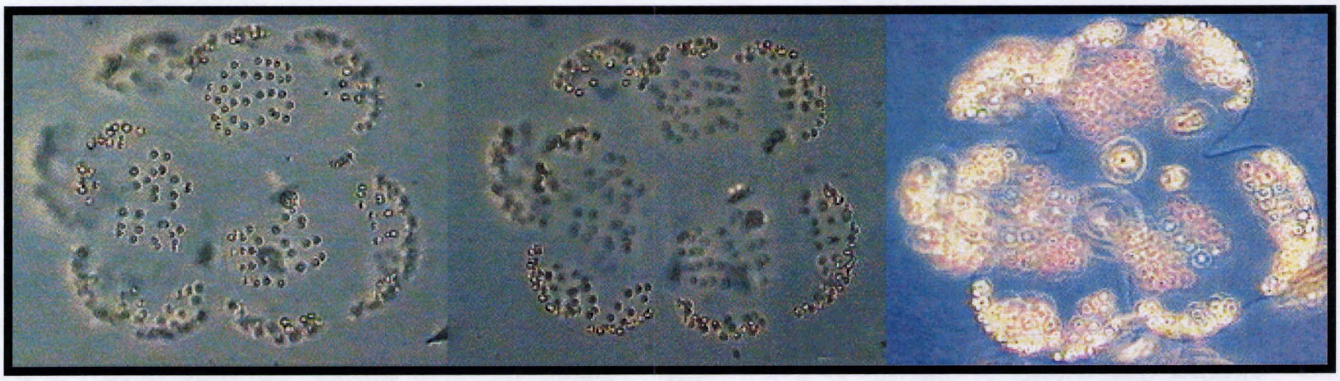


Fig.3: *Phaeocystis cf. pouchetii* (Hariot) Lagerheim 1893
Source: Göteborg University, Department of Marine Ecology, Marine Botany,
http://www.marbot.gu.se/sss/others/Phaeocystis_pouchetii.htm

In spring a dense bloom of the colony forming alga *Phaeocystis* is common in the coastal waters of the North Sea. In naturally enriched, non-eutrophicated, coastal systems nutrient sources are well balanced in terms of N:P:Si, favouring the growth of diatoms (Fig.4) (Brzezinski, 1985), which are efficiently controlled by grazers (Claustre *et al.*, 1994). The nutrient environment of phytoplankton in human-eutrophicated coastal areas is strongly modified by anthropogenic sources of nutrients from continental origin, accumulated during winter. The Southern Bight of the North Sea has a large excess of NO_3 over P and Si (Rousseau, 2000). When Si gets depleted during the spring diatom bloom, there is still enough N and P for *Phaeocystis* to grow (Joint & Pomroy, 1993). During the last few decades, dense blooms of *Phaeocystis* have increased in North European waters, especially in the southern part of the North Sea. This increase in abundance of *Phaeocystis* is related to increased input of nutrients to this area (Lancelot *et al.*, 1987, 1994).

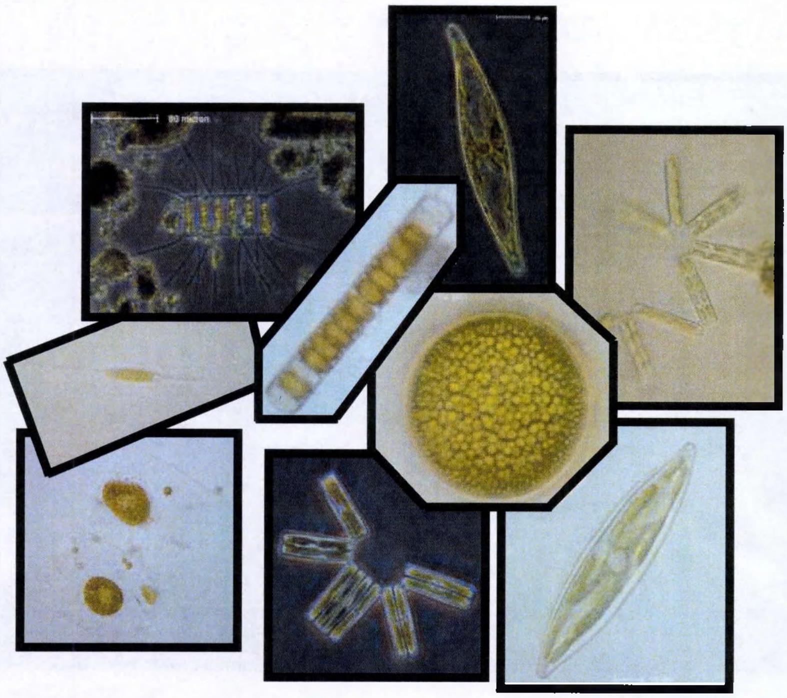


Fig.4: Diatoms occurring in the North Sea, source: Roscoff phytoplankton species http://www.sb-roscoff.fr/Phyto/Phyto_gallery/Phyto_gallery.htm

Weisse *et al.* (1994) summarized the negative effects of *Phaeocystis* as follows:

(1) growth inhibition of bacteria and certain algae (Sieburth, 1959, 1960, 1961, 1964; Smayda, 1973),

(2) clogging of mussel gills and copepod mouth parts leading to decreased effective feeding by these organisms (Kopp, 1978; Pieters *et al.*, 1980; Meixner, 1981),

(3) oxygen deficiency caused by the respiration of living *Phaeocystis* cells and by bacterial degradation of sedimented material (Kopp, 1978).

(4) Commercially, the clogging of fishing nets leading to reduced catches has been a problem since the beginning of the previous century (Hardy, 1926).

(5) Hardy (1926) identified an inverse relationship between *Phaeocystis* and herring catches. Savage (1932) reported that in the southern North Sea, *Phaeocystis* blooms "acted as a very effective barrier to the migration of herring".

(6) The beaches are often covered with transient foam layers of *Phaeocystis*-derived material (e.g. Dunne *et al.*, 1984; Lancelot *et al.*, 1987) (Fig.5).

(7) Indirect effects such as starvation are possible. Smaller herbivores might not find enough food during a *Phaeocystis* bloom, if large colonies are predominant and single cells are scarce (Martens, 1981).

(8) Studies have also shown that *Phaeocystis* may play an important role in ocean climate control by the emission of dimethylsulfide to the atmosphere (Liss *et al.*, 1994). This volatile compound has an impact on marine cloud formation and climate regulation (Charlson *et al.*, 1987).

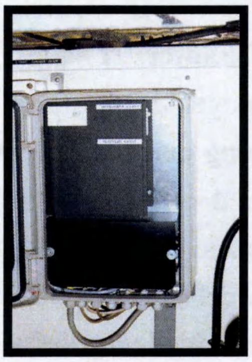
Fig.5: Foam from decomposing *Phaeocystis* colonies at the Belgian (a) and Dutch beaches (b); (a) Photograph: VLIZ/ M. Decleer; (b) Source: Waddenzee.nl: *Phaeocystis* http://www.waddenzee.nl/dutch/navigatie/fr_index.html?/dutch/ecomare/NED0147.HTM

Weisse *et al.* (1994) also pointed to the nutritive value of *Phaeocystis.* Both colonies and solitary cells of *Phaeocystis* are ingested by a wide array of marine vertebrates. Grazers include protozoa, bivalves, amphipods, euphausiids and many copepod species. Common fish species such as mackerel (*Scomber scomber*) and flounder (*Pleuronectus* flesus) have also been reported to feed upon *Phaeocystis*. By switching their food preference towards heterotrophic food, copepods may benefit from enhanced protozoan biomass during *Phaeocystis* blooms. Vast amounts of detritus in the form of decaying colonies (probably coated with bacteria and colonized by microheterotrophs) appear in the water-column during the decline phase of *Phaeocystis* blooms.

5 Sand extraction

Sand and gravel exploitation in Belgian maritime areas is regulated by the Law of 13 June 1969 Concerning the Continental Shelf. Exploration and exploitation of the continental shelf require a concession, granted by the federal government. Further rules and requirements for concessions are laid down in two royal decrees. (Maes *et al.*, 2000) Concessions are granted by the Federal Ministry of Economic Affairs, which also controls the activities themselves (Fund For Sand Extraction). To provide more information on the exact location of the extractions, an automatic registration system is used on the ships since 1996 (the so-called black-box). The black-box data are stored by MUMM Oostende, who checks on any violations. In Belgium marine sand extraction activities started in 1976 and increased fivefold between 1979 and 1999. 95 % of the sand exploited in the Belgian waters originates from the Kwintebank. This intense mining activity makes the Kwintebank a valuable but also a potentially threatened area. The impact of dredging activities mainly relates to the physical removal of substratum and associated organisms from the sea bed along the path of the dredge head, and partly on the impact of subsequent deposition of material rejected by screening and overspill from the hopper (Newell *et al.*, 1998). More detailed information about the concession zones, the extraction techniques and the impact assessment is given in Chapter III.

Photographs:
MUMM
Oostende



Black-box

6 Outline

Harpacticoid copepods are studied in order to define the different harpacticoid communities of well-selected areas on the Belgian Continental Shelf (North Sea) and to investigate which factors influence the structural and functional biodiversity of those communities. This research will contribute to answer the question to which extent harpacticoids can be used for monitoring purposes and whether indicator harpacticoid species or communities for anthropogenic disturbances can be defined. For this purpose, all harpacticoids were identified down to species level as species information greatly increases the value of pollution assessment. As so far the amount of data was limited. This project will reveal some useful results regarding this concept, since the data about the structural and functional biodiversity of harpacticoid copepods are related to two major anthropogenic influences on the Belgian Continental Shelf: eutrophication resulting in the extensive *Phaeocystis* spring bloom and sand extraction. Also the advantage of monitoring harpacticoids in this kind of habitats compared with macrofauna will be discussed.

Density, diversity and community structure of harpacticoid copepods are investigated on two Flemish Banks, the Middelkerkebank and the Kwintebank, and on the Gootebank, one of the Zeeland Banks. The Kwintebank is selected as an investigation area because of the availability of scientific background information. Since 1978 the Kwintebank has been the subject of several benthic research projects, making it possible to compare the present day community analyses with the situation in the seventies (Willems *et al.*, 1982b; Vincx, 1990; Vincx *et al.*, 1990). The Kwintebank is very important as a sand extraction area, contrary to the adjacent Middelkerkebank, which is situated outside the concession zone. The Middelkerkebank has comparable granulometric and geomorphological characteristics and is therefore selected as a reference area (Degrendele *et al.*, 2002).

In **Chapter I** the spatial distribution of different harpacticoid communities on the Middelkerkebank and the Kwintebank will be presented, in order to provide the necessary background knowledge for the impact assessment in further chapters. This study thus focuses on the natural influences. It concerns a study of the density and structural biodiversity in relation to sediment characteristics and depth. Two main gradients will be discussed: the north-south gradient along the sandbanks and the differences between sandbank tops and gullies.

Chapter II aims at describing the structuring impact of interplay of natural and anthropogenic influences, since the spring diatom bloom is a naturally occurring event but the increasing extent of the *Phaeocystis* spring bloom is mainly the result of human eutrophication. Temporal changes in harpacticoid density, diversity and community structure in relation to the diatom and *Phaeocystis* spring bloom have been examined. The investigated response is part of the bentho-pelagic coupling: organisms in the water column can be an energy source for benthic organisms and vice versa. Also temporal fluctuations in the vertical distribution of harpacticoids in the sediment have been studied. Special attention has been paid to the different response of epi- and endobenthic and interstitial species in order to describe the influence of organic enrichment on the functional biodiversity of harpacticoid communities. Temporal and vertical distribution patterns of the different life history stages were examined to reveal a potential interrelation between migratory behaviour and reproductive activity as a result of organic enrichment. Finally, differences are discussed between the response of the harpacticoid community on the Kwintebank and on the Gootebank.

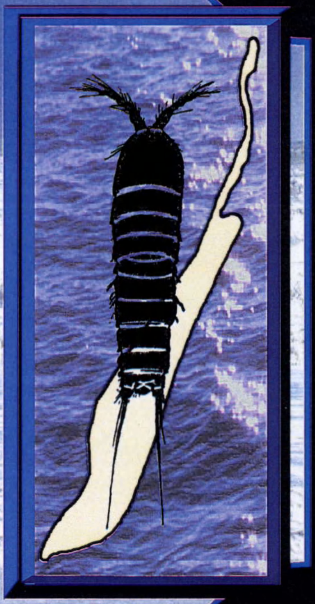
Chapter III and chapter IV focus on anthropogenic influences, more specifically sand extraction. In chapter III the harpacticoid data of the Kwintebank of the nineties were compared with information of sand extraction intensity and erosion. The results of the nineties were also compared with sediment characteristics and copepod species distribution data collected in the seventies prior to intensive sand extraction.

In **Chapter IV** the available data on the macrobenthos of the Kwintebank are analyzed in order to detect differences in macrobenthic density, diversity and community structure related to sand extraction, on a temporal as well as a spatial scale. In order to investigate the changes of macrobenthic species belonging to different ecological groups more accurately, the biotic coefficient was calculated according to Borja *et al.* (2000). This continuous index allows detecting changes in macrobenthic species with different sensitivity to a pollution gradient, giving a different weight to species with a different sensitivity.

Chapter I

Structural biodiversity of benthic copepod communities on two subtidal sandbanks

Structurele biodiversiteit van benthische copepodengemeenschappen op twee subtidale zandbanken



Structural biodiversity of benthic copepod communities on two subtidal sandbanks

Wendy Bonne & Magda Vincx

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).

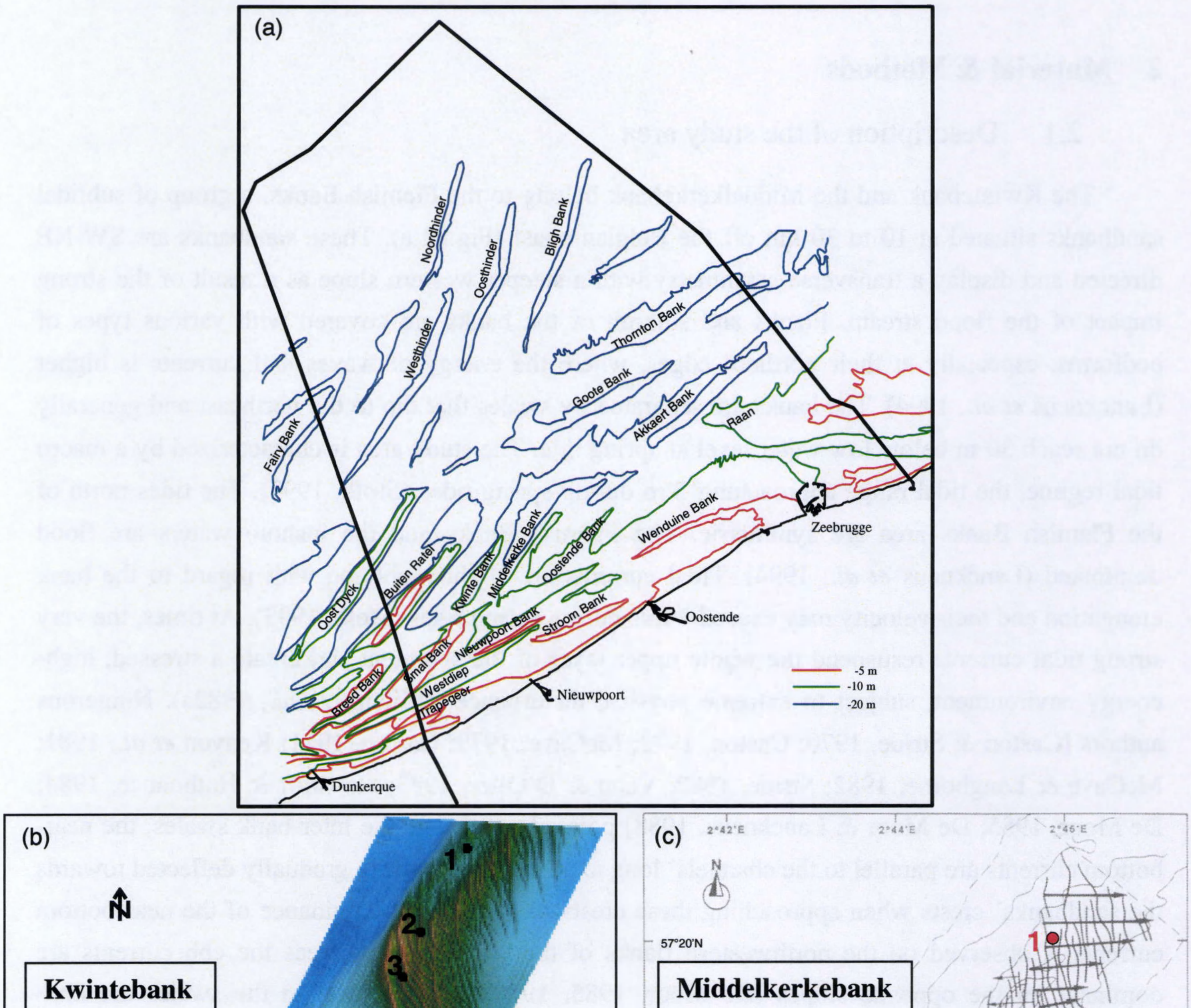


Fig.I.1: The subtidal sandbanks of the Belgian Continental Shelf (a: after Cattrijsse & Vincx, 2001) with detailed maps of the Kwintebank (b: multibeam image 2000 Fund For Sand Extraction) and Middelkerkebank (c: Side-scan sonar image with bathymetric registrations from May 1990 after Lanckneus *et al.*,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

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

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

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

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.

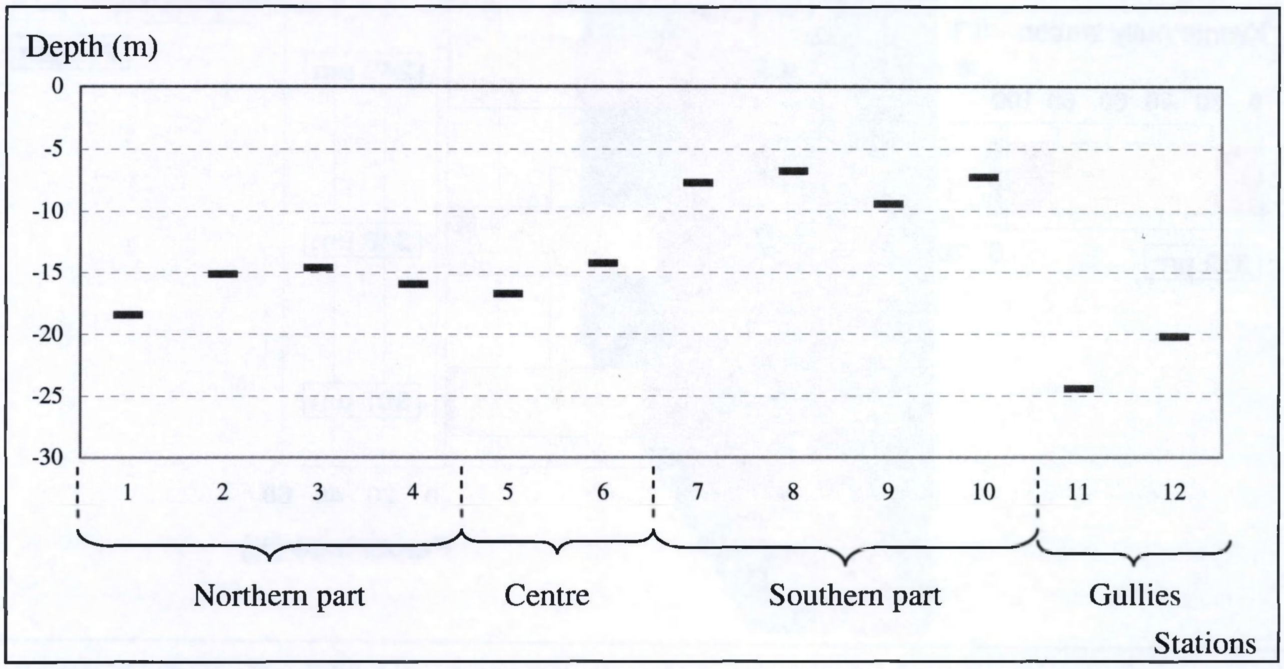


Fig.I.2: Depth for each station at the Kwintebank

3.1.2 Sediment characteristics

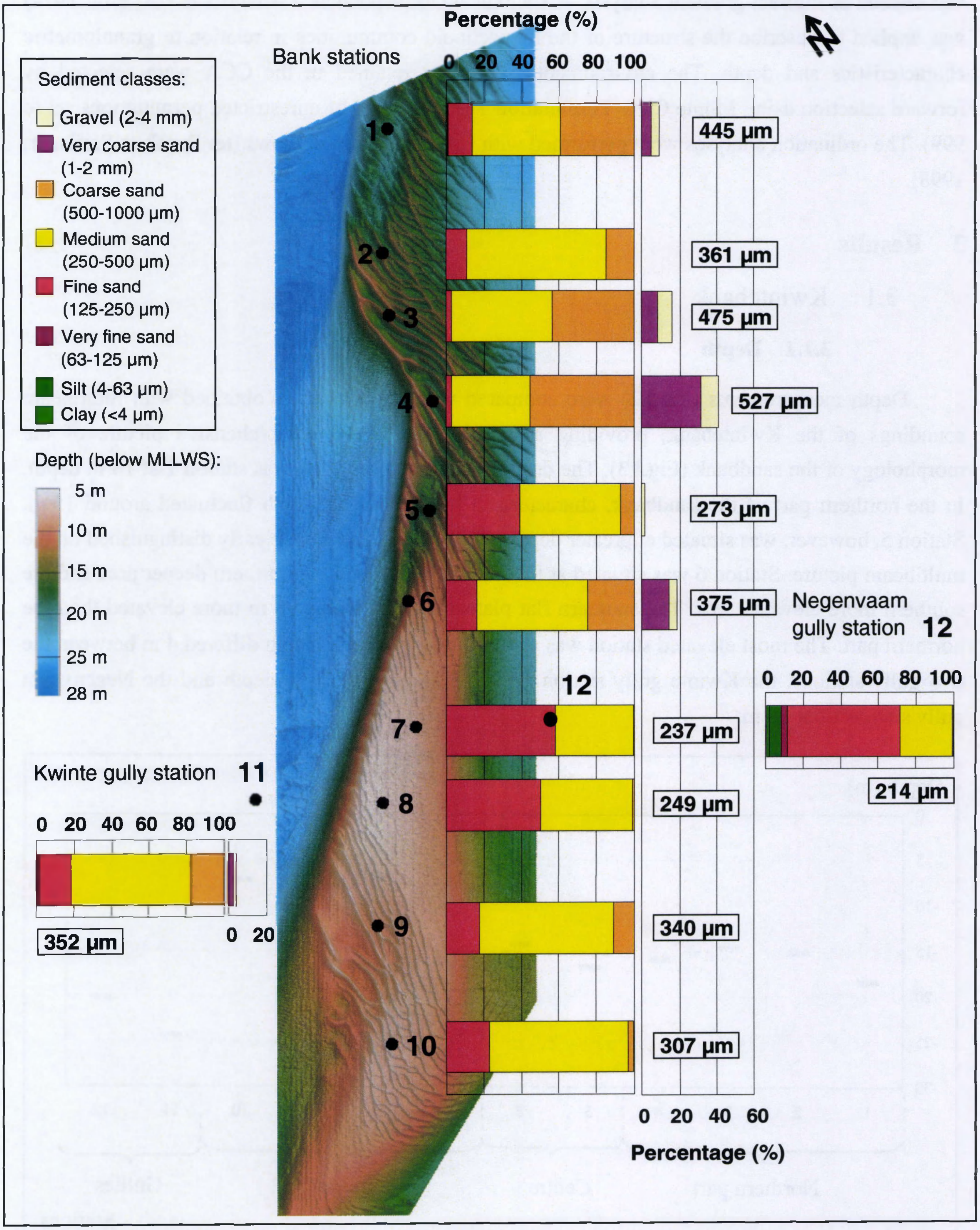


Fig.I.3: Sediment composition (bars) and median grain size (boxes) of the Kwintebank stations, plotted on a multibeam image of the Kwintebank illustrating depth profiles and geomorphology of the sandbank.

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

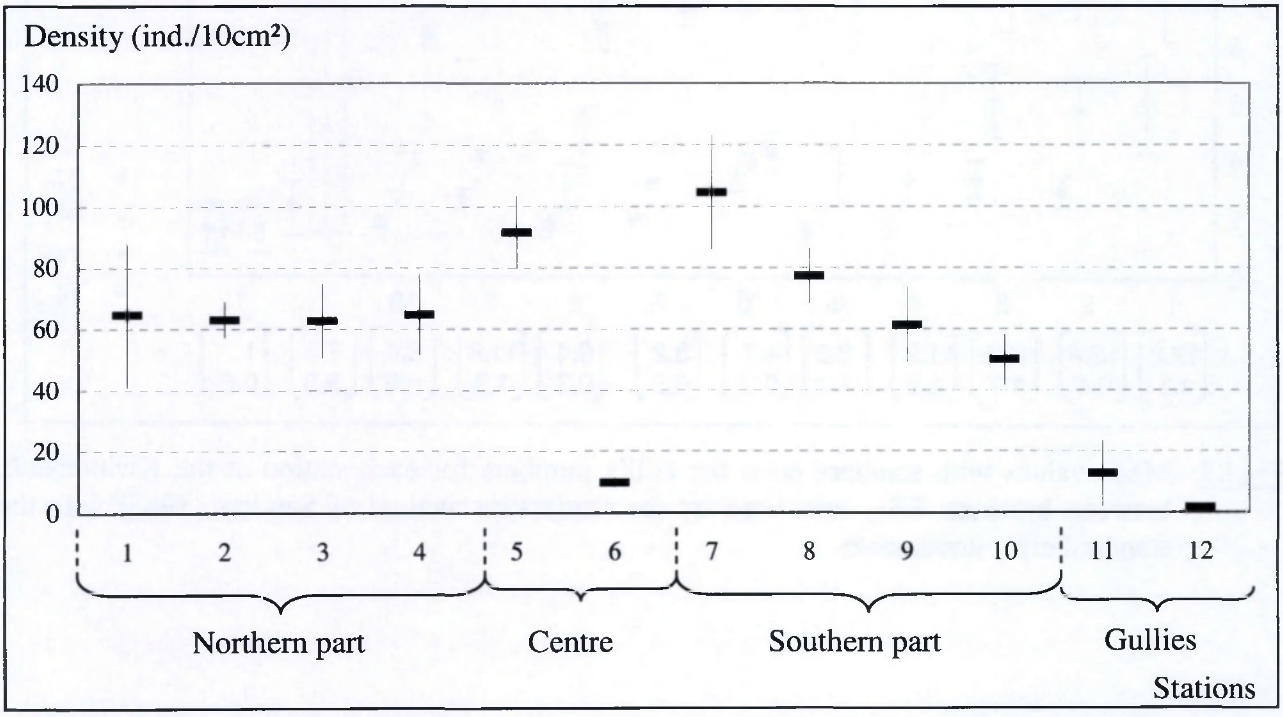


Fig.I.4: Mean total density with standard error for each station at the Kwintebank

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.

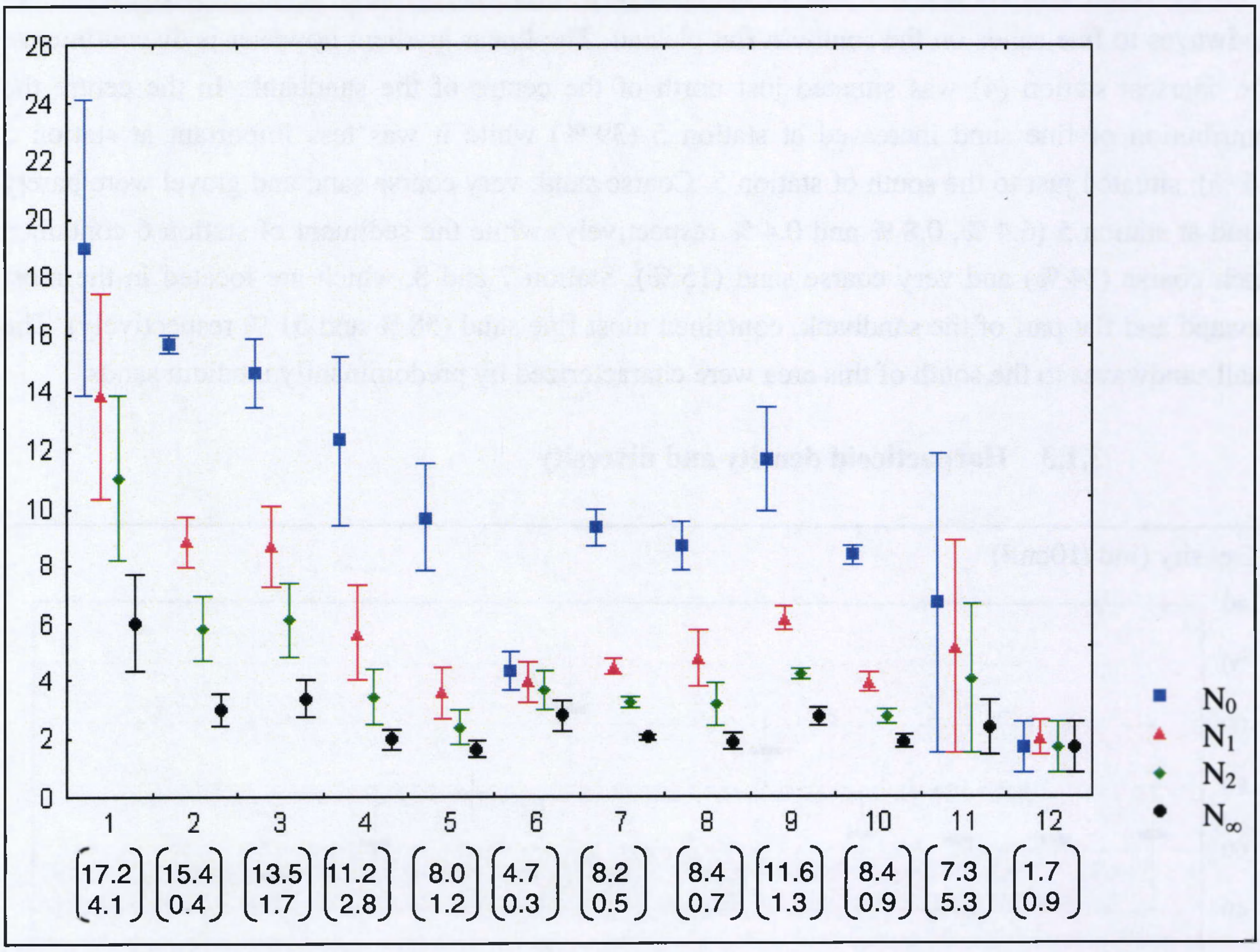


Fig.I.5: Mean values with standard error for Hill's numbers for each station at the Kwintebank, between brackets: ES$_{50}$ calculated by the rarefaction method of Sanders (1968) with the standard error underneath

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

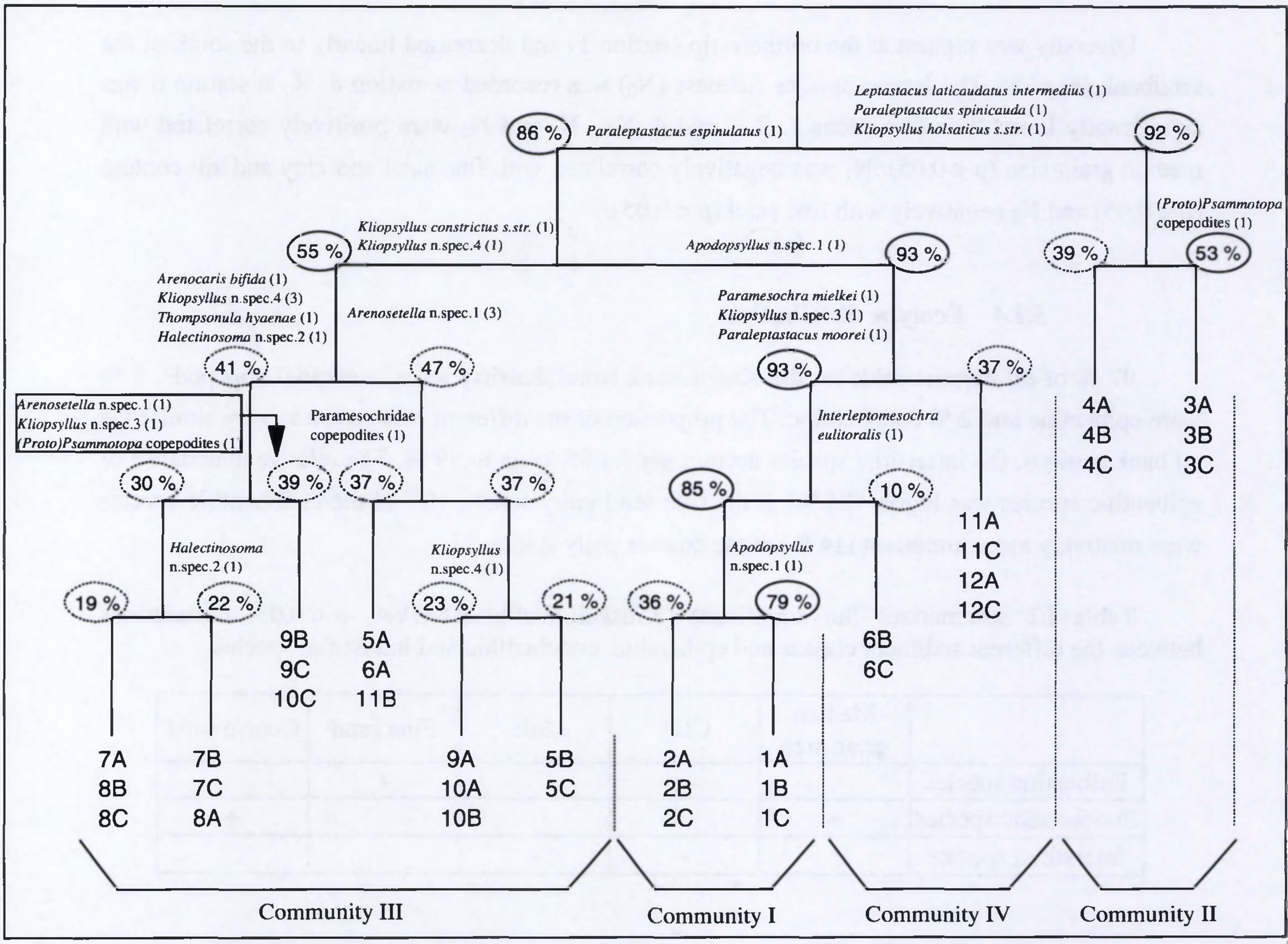


Fig.I.6: TWINSPAN diagram of the replicates of the Kwintebank based on absolute species abundances (cutlevels 0, 1, 4, 70). The percentages given are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). Only the percentages exceeding 50 % indicate 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.

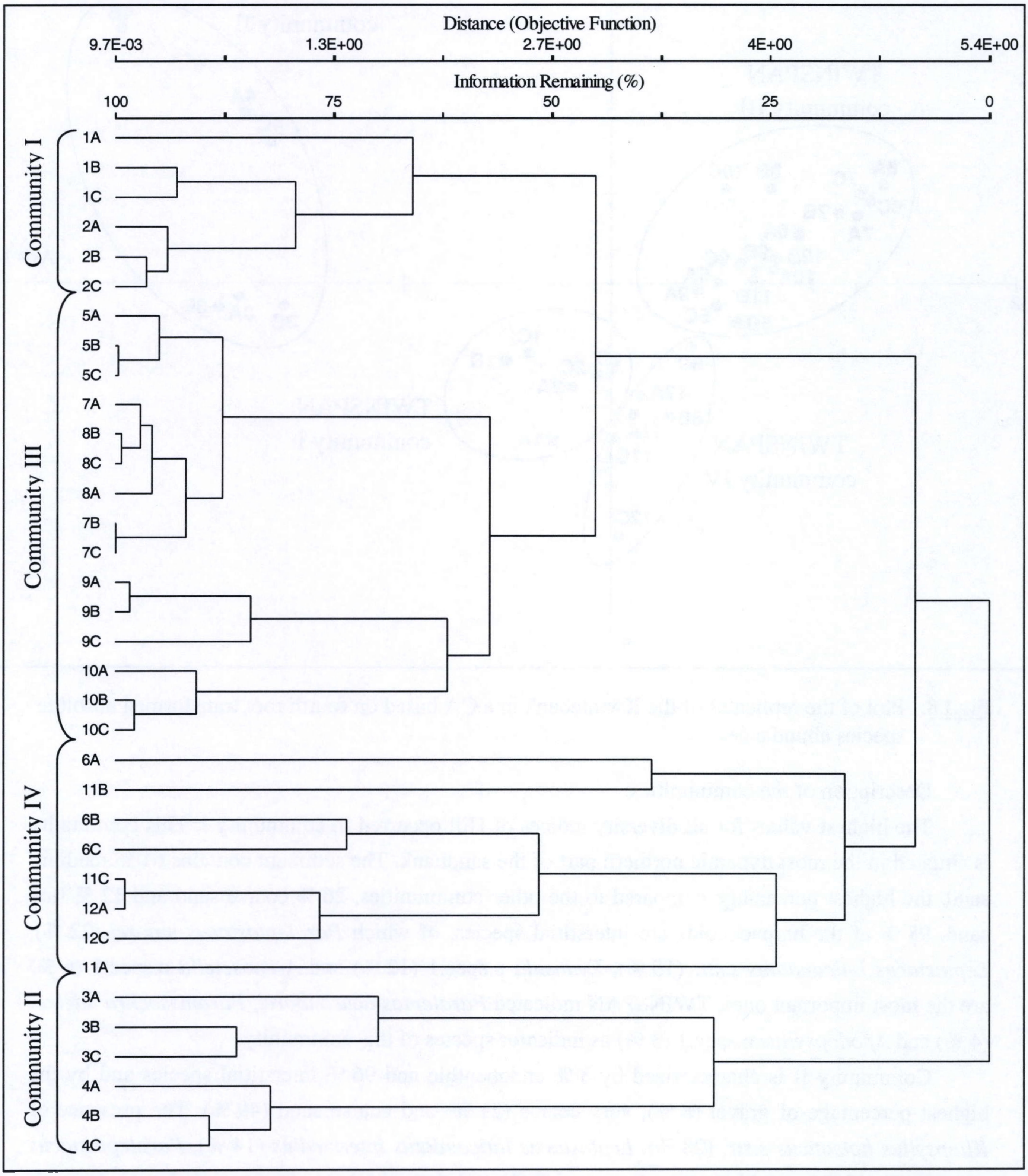


Fig.I.7: Cluster analysis of the replicates of the Kwintebank based on absolute species abundances, using the Bray-Curtis similarity index and Group Average Sorting

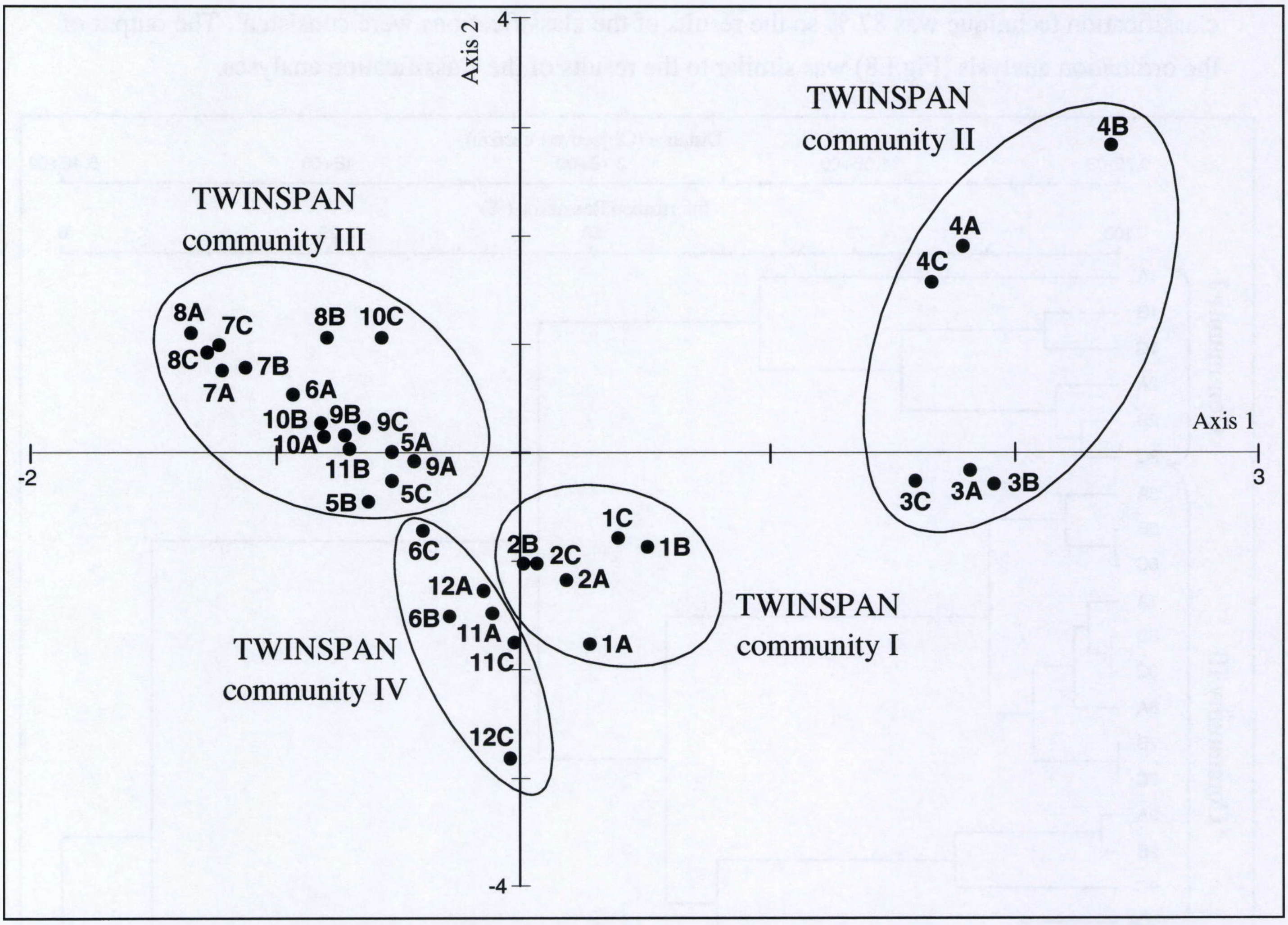


Fig.I.8: Plot of the replicates of the Kwintebank in a CA based on fourth root transformed absolute species abundances

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.

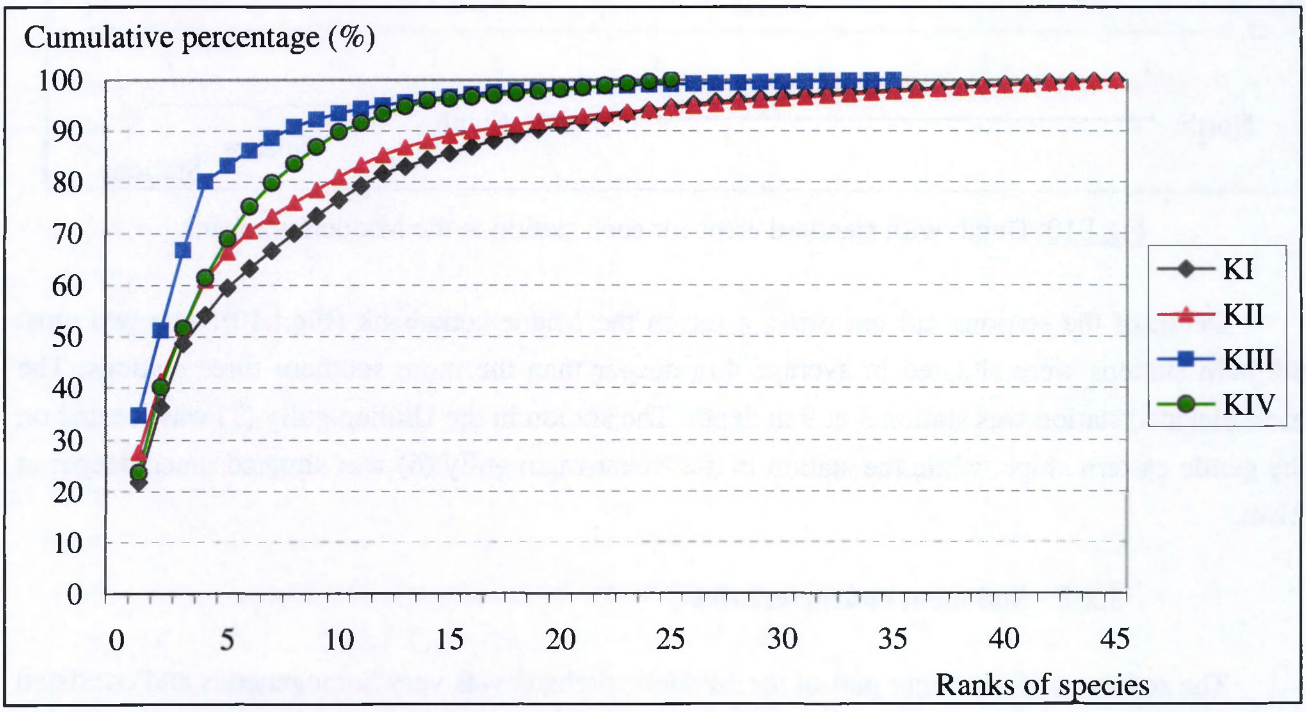


Fig.I.9: k-dominance curves of the communities at the Kwintebank

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

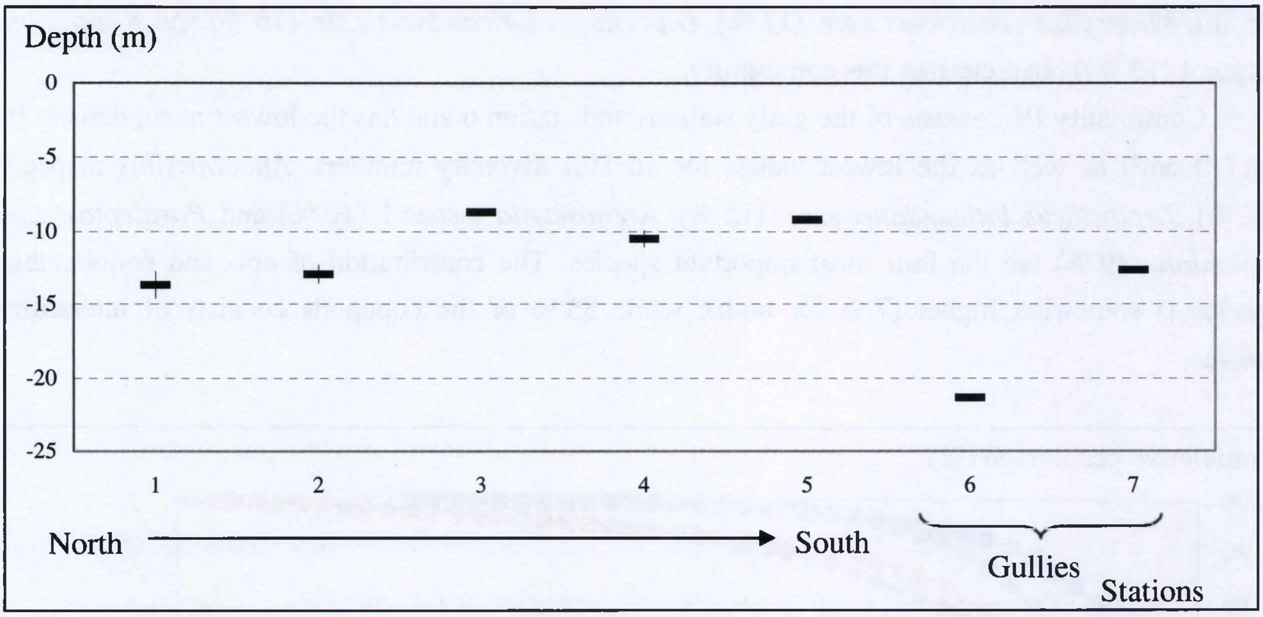


Fig.I.10: Depth with standard error for each station at the Middelkerkebank

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.

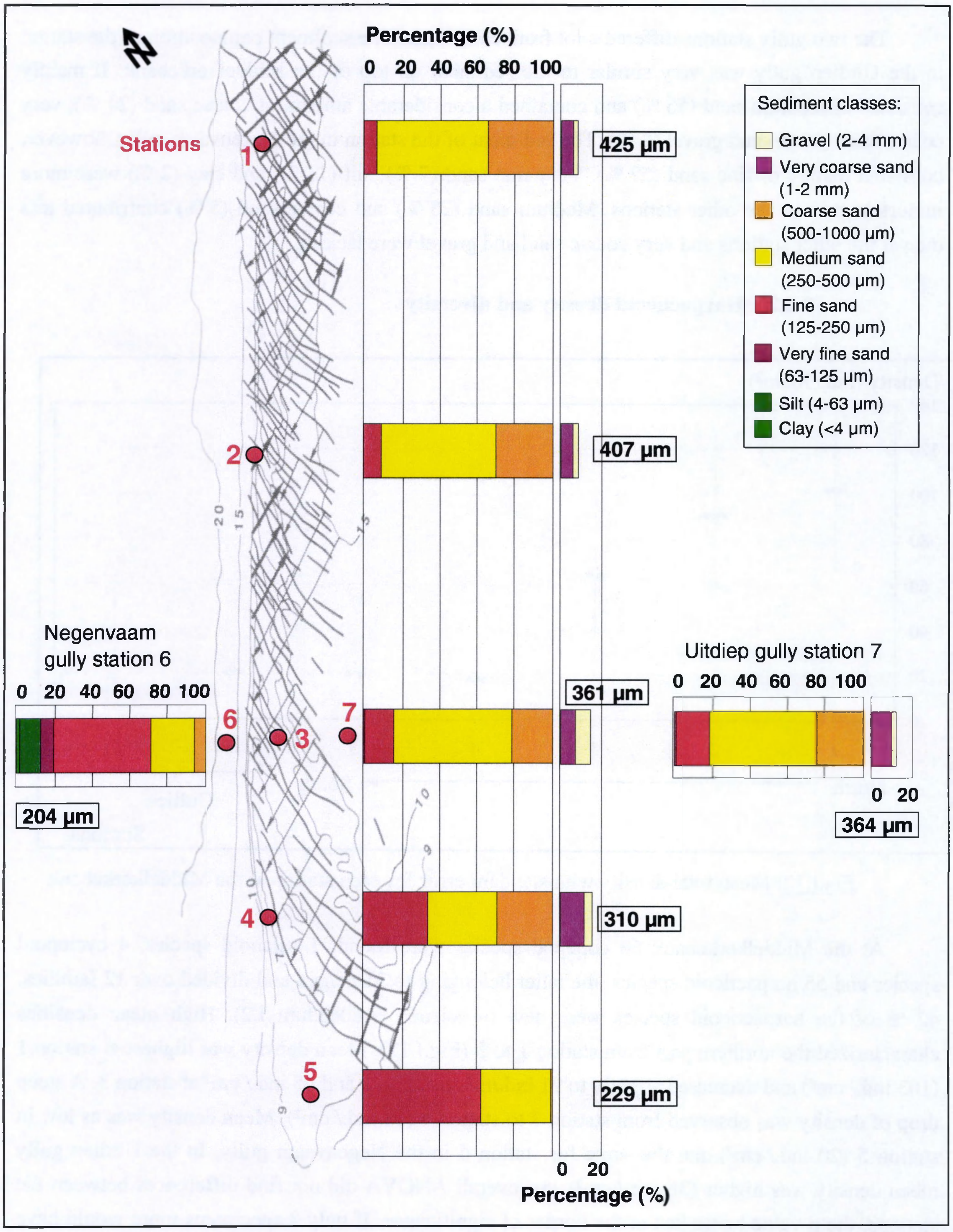


Fig.I.11: Sediment composition (bars) and median grain size (boxes) of the Middelkerkebank stations, which are plotted on a side-scan sonar image with bathymetric registrations (isobaths 9-10-15-20) taken in May 1990 (Lanckneus *et al.*, 1994). The picture also illustrates the geomorphology of the sandbank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

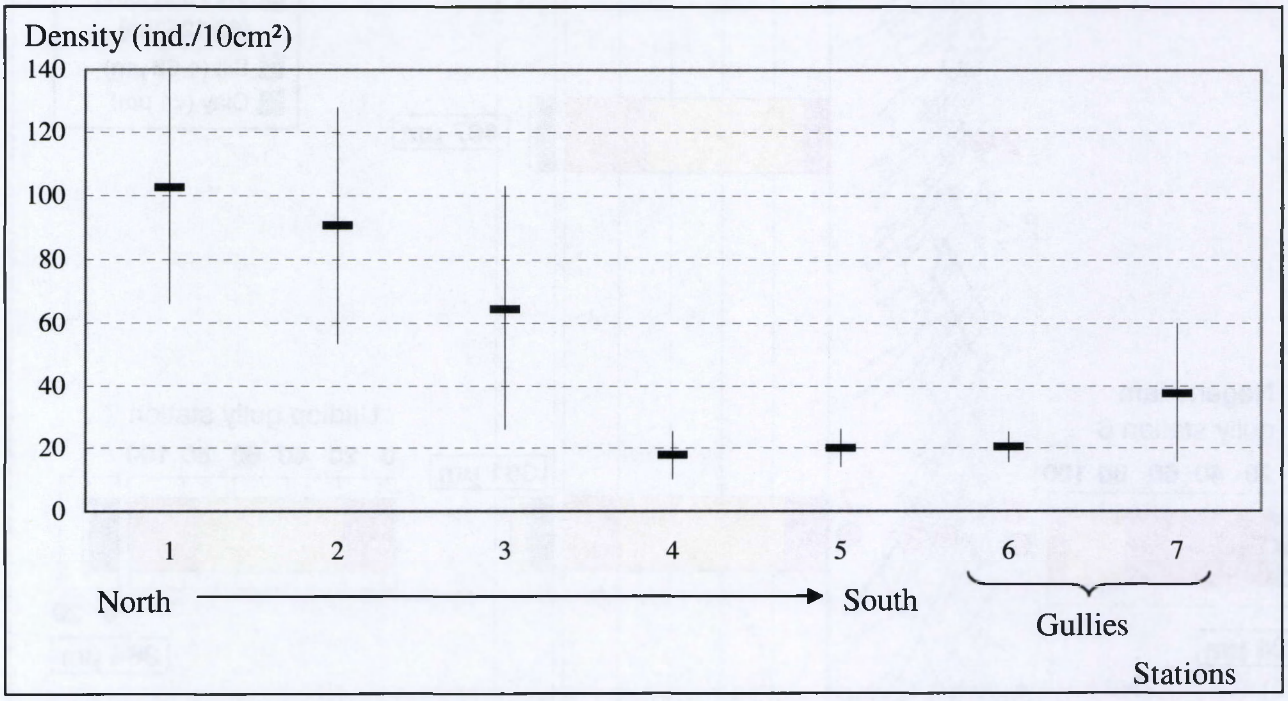


Fig.I.12: Mean total density with standard error for each station at the Middelkerkebank

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./ cm²) and decreased slightly to 91 ind./m² at station 2 and 65 ind./ cm² at station 3. A steep drop of density was observed from station 3 to station 4 (18 ind./ cm²). Mean density was as low in station 5 (20 ind./ cm²) and the same for station 6 in the Negenvaam gully. In the Uitdiep gully mean density was higher (38 ind./ cm²). 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 ($p < 0.05$).

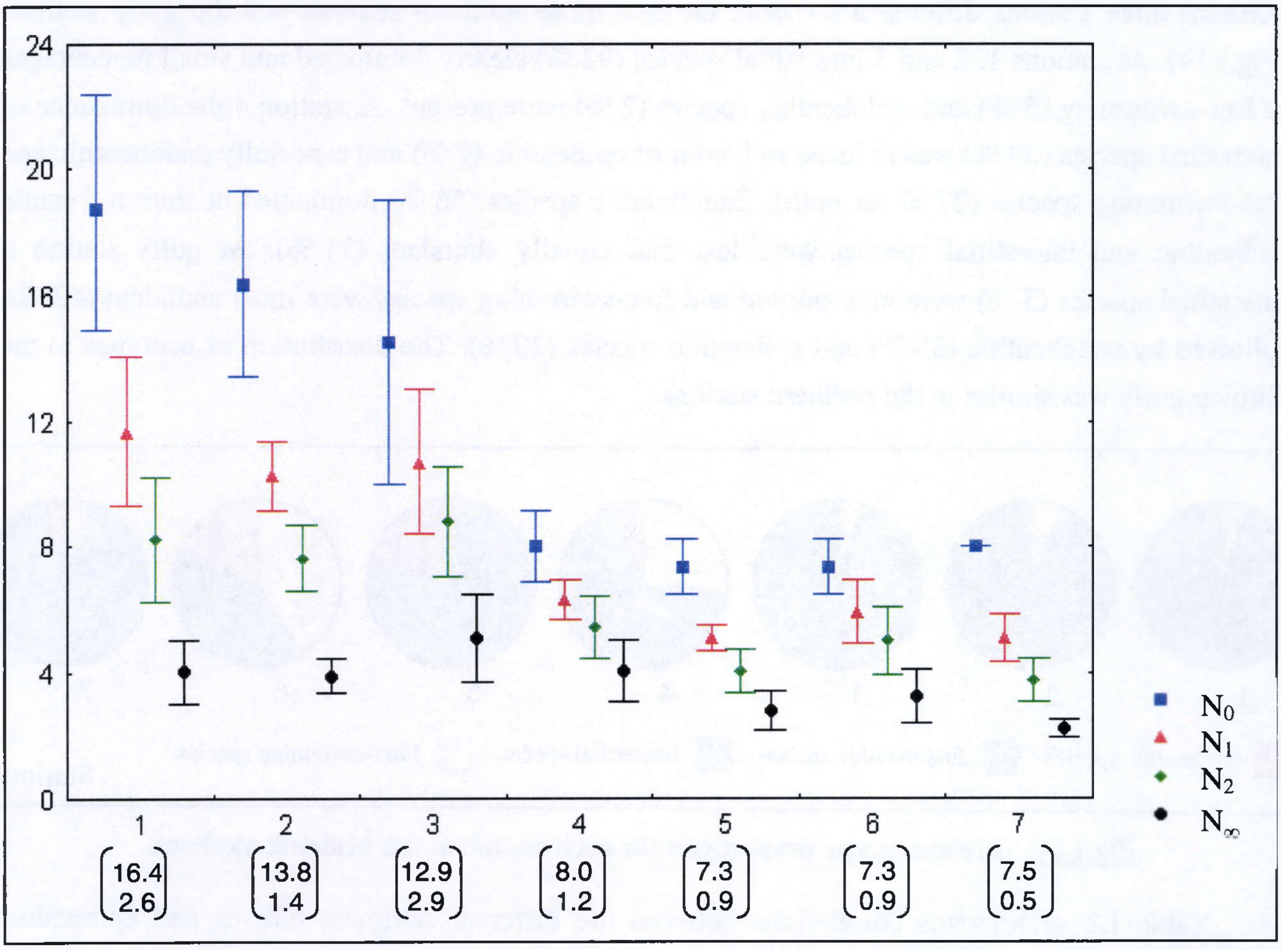


Fig.I.13: Mean values with standard error for Hill's numbers for each station at the Middelkerkebank, between brackets: ES_{50} calculated by the rarefaction method of Sanders (1968) with the standard error underneath

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.

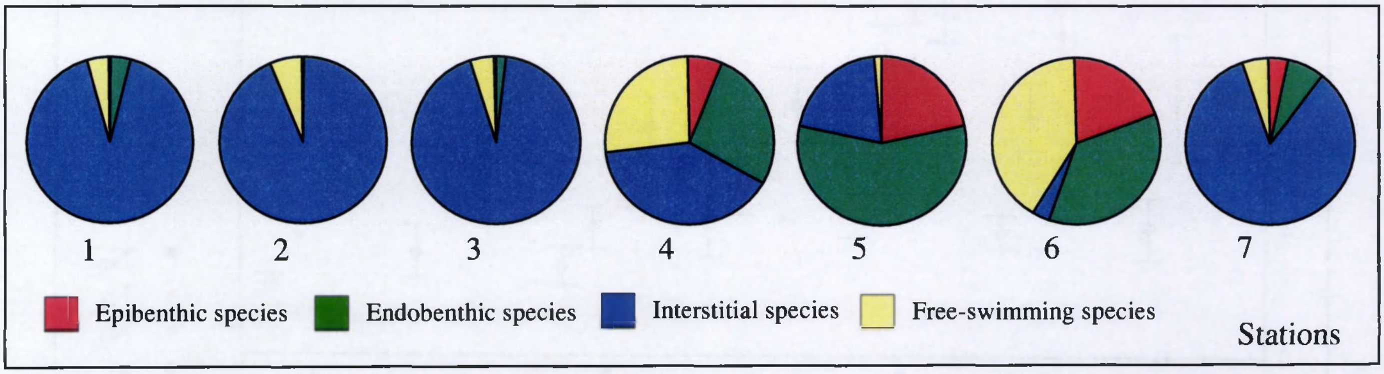


Fig.I.14: Mean ecotype proportions for each station at the Middelkerkebank

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

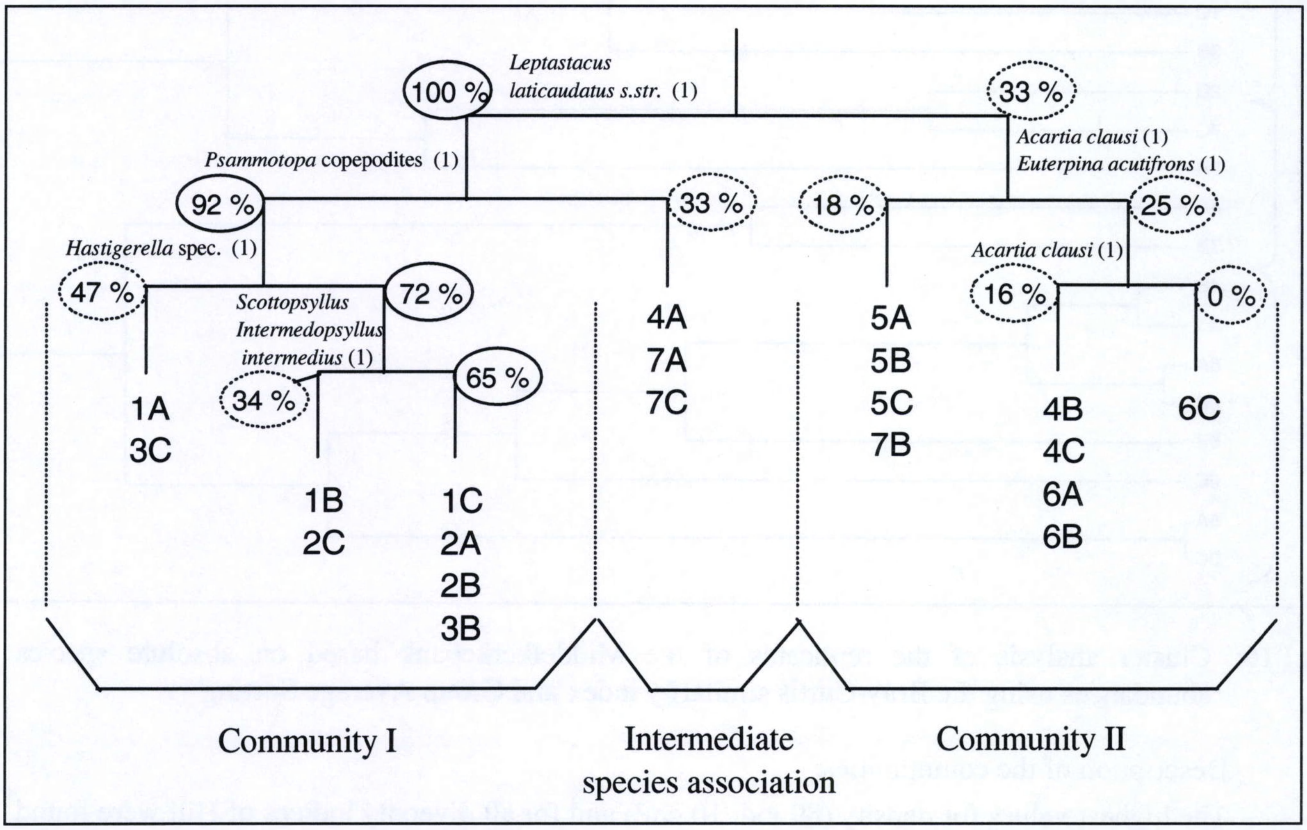


Fig.I.15: TWINSPAN diagram of the replicates based on absolute species abundances (cutlevels 0, 2, 5, 55). The percentages given are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). The percentages within full circles exceed 50 % and indicate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

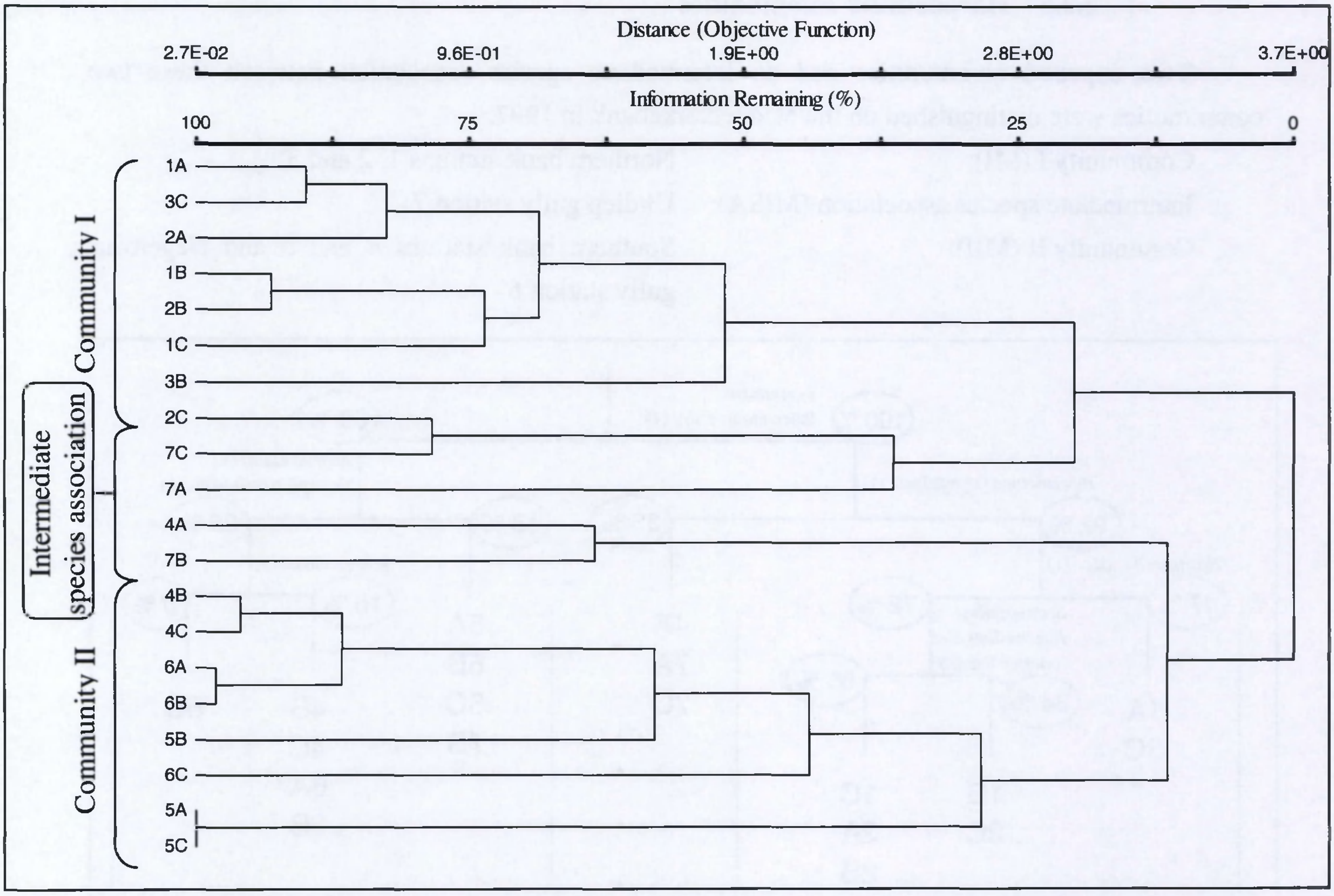


Fig.I.16: Cluster analysis of the replicates of the Middelkerkebank based on absolute species abundances using the Bray-Curtis similarity index and Group Average Sorting

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.

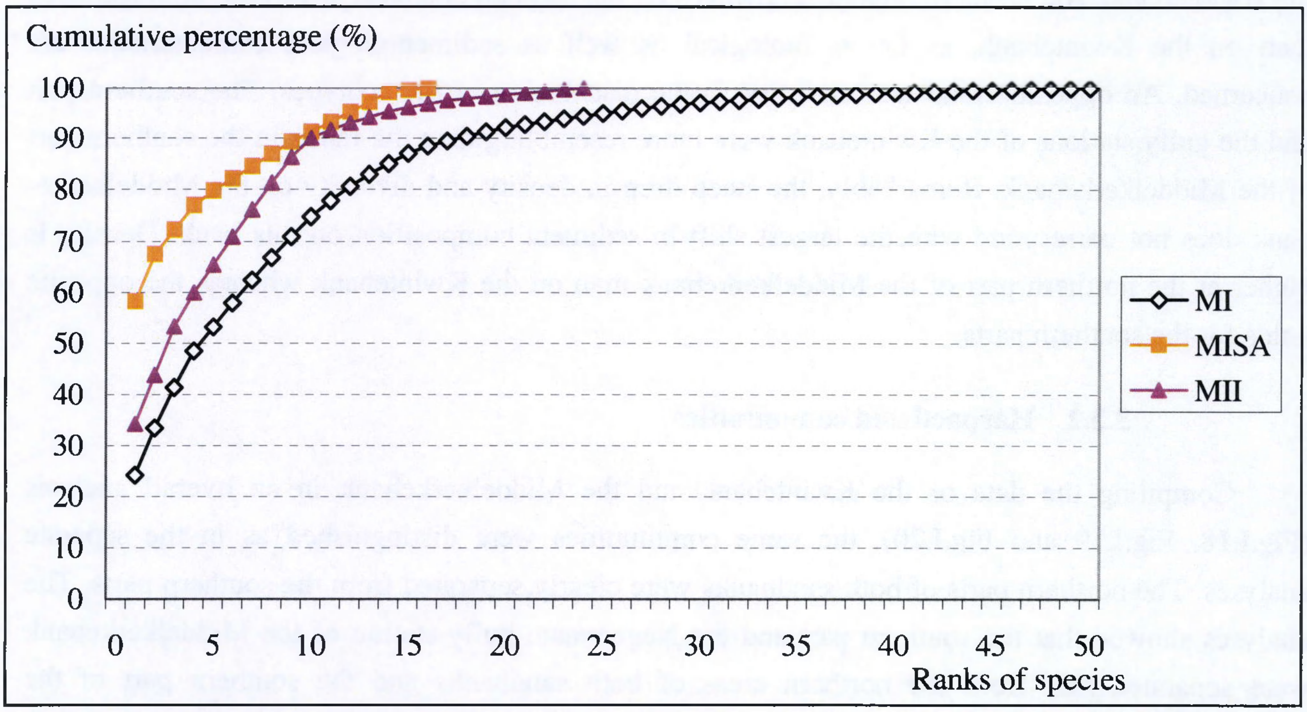


Fig.I.17: k-dominance curves of the communities at the Middelkerkebank

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.

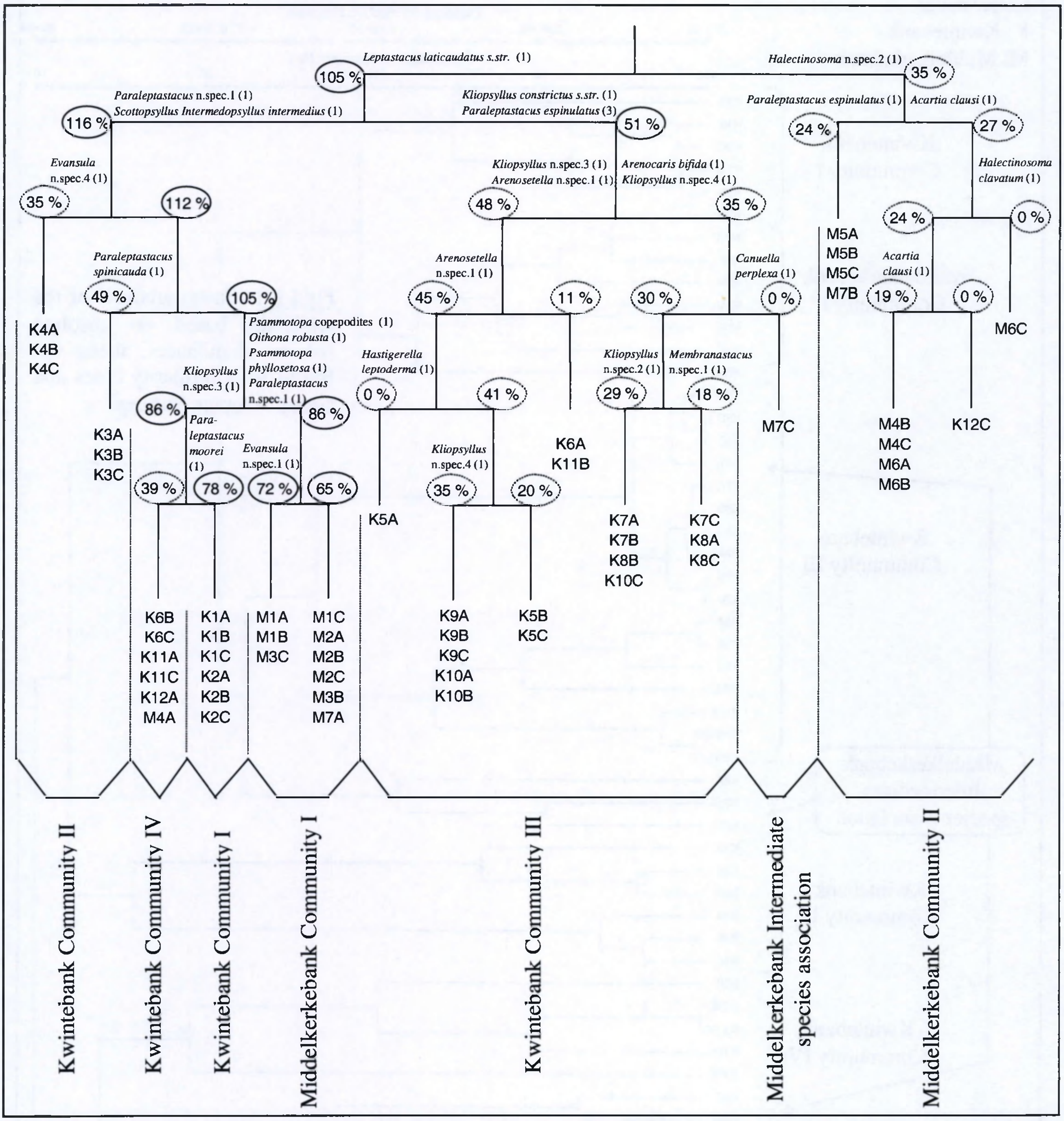


Fig.I.18: TWINSPAN diagram of the replicates based on absolute species abundances (cutlevels 0, 1, 4, 70). The percentages given are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). The percentages within full circles exceed 50 % and indicate 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.

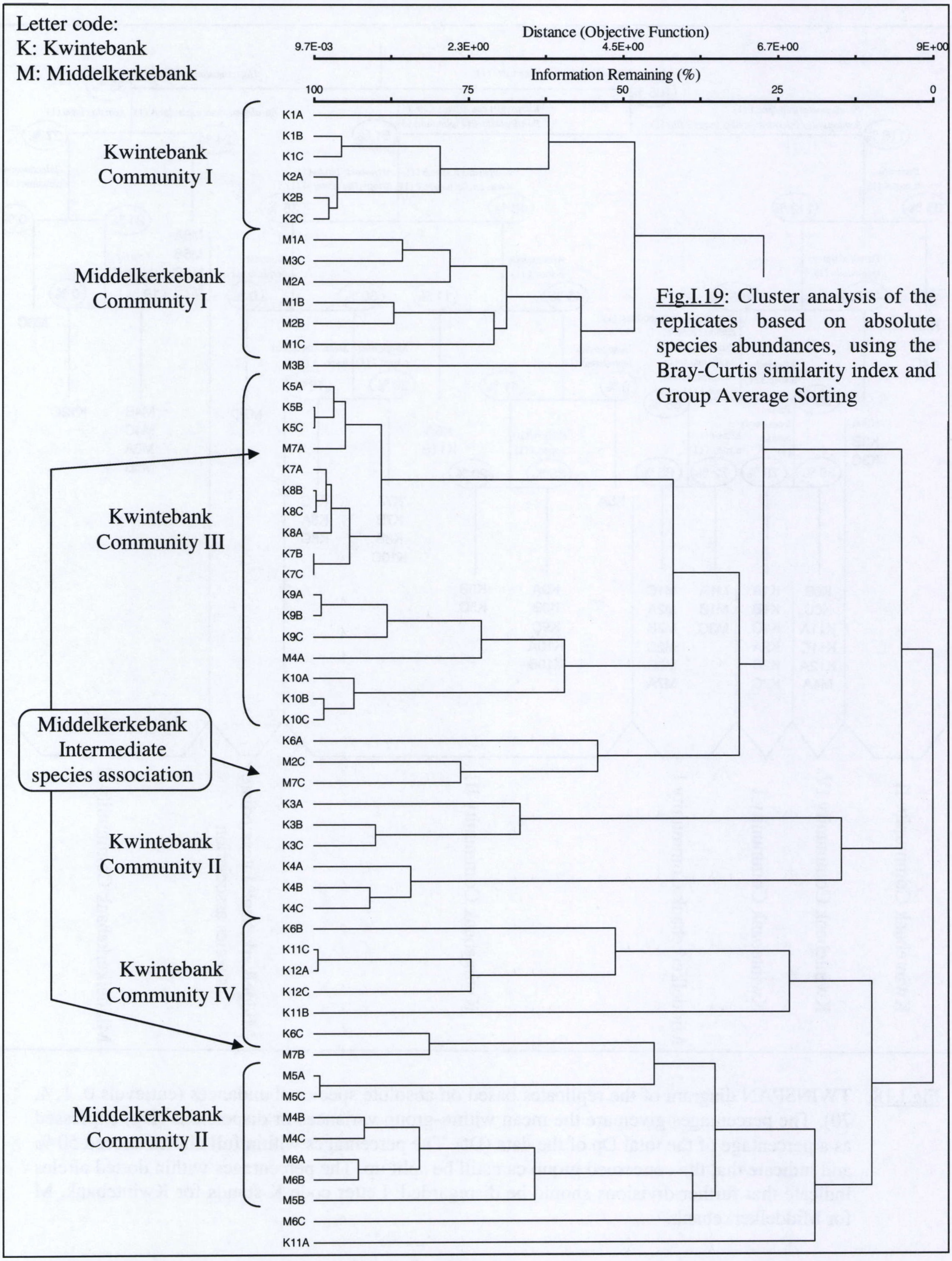


Fig.I.19: Cluster analysis of the replicates based on absolute species abundances, using the Bray-Curtis similarity index and Group Average Sorting

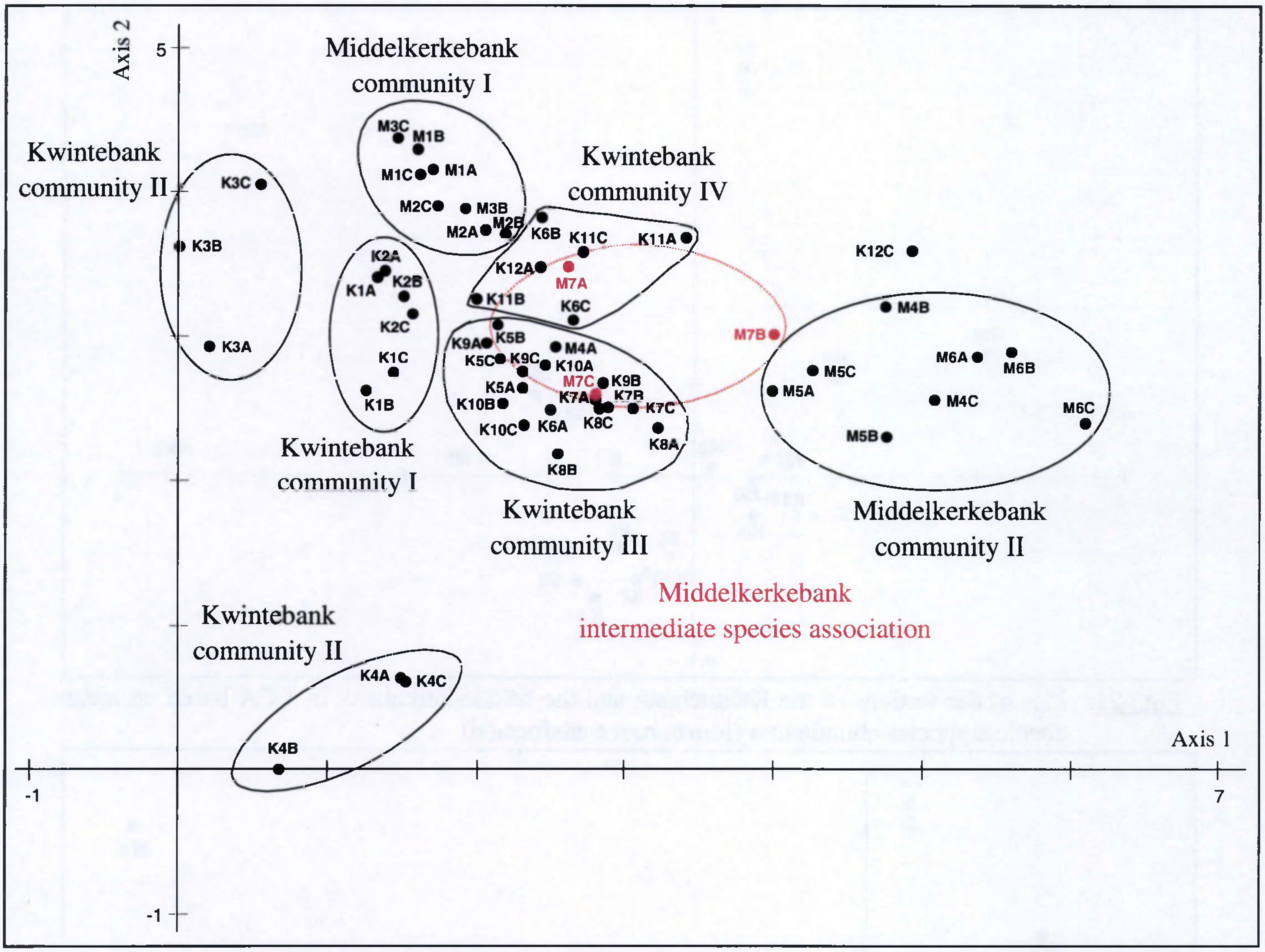


Fig.I.20: Plot of the replicates of the Kwintebank and the Middelkerkebank in a DCA based on fourth root transformed absolute species abundances

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.

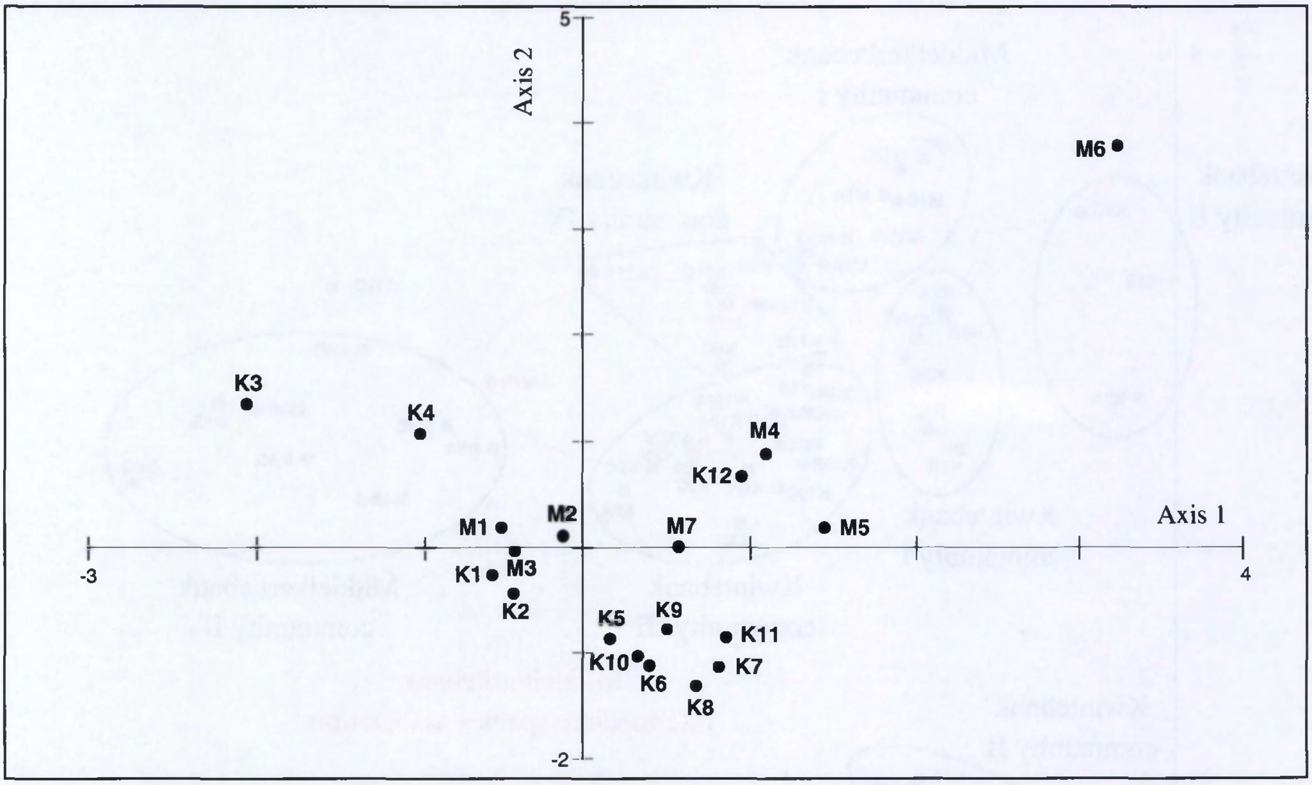


Fig.I.21: Plot of the stations of the Kwintebank and the Middelkerkebank in a CA based on mean absolute species abundances (fourth root transformed)

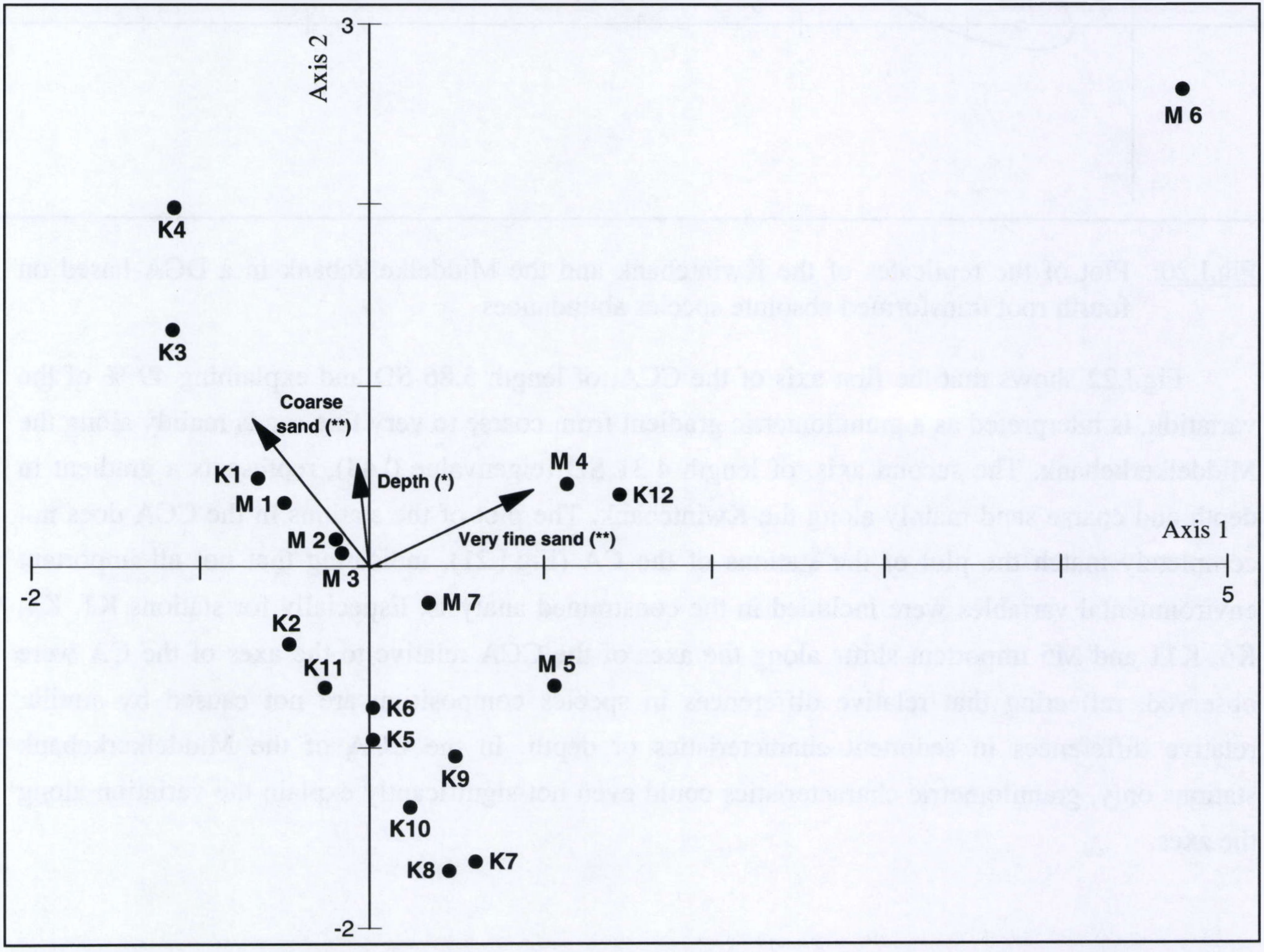


Fig.I.22: Plot of the stations of the Kwintebank and the Middelkerkebank in a CCA with environmental variables which were selected by Monte Carlo Permutation tests as statistically significant (* $p < 0.05$, ** $p < 0.01$).

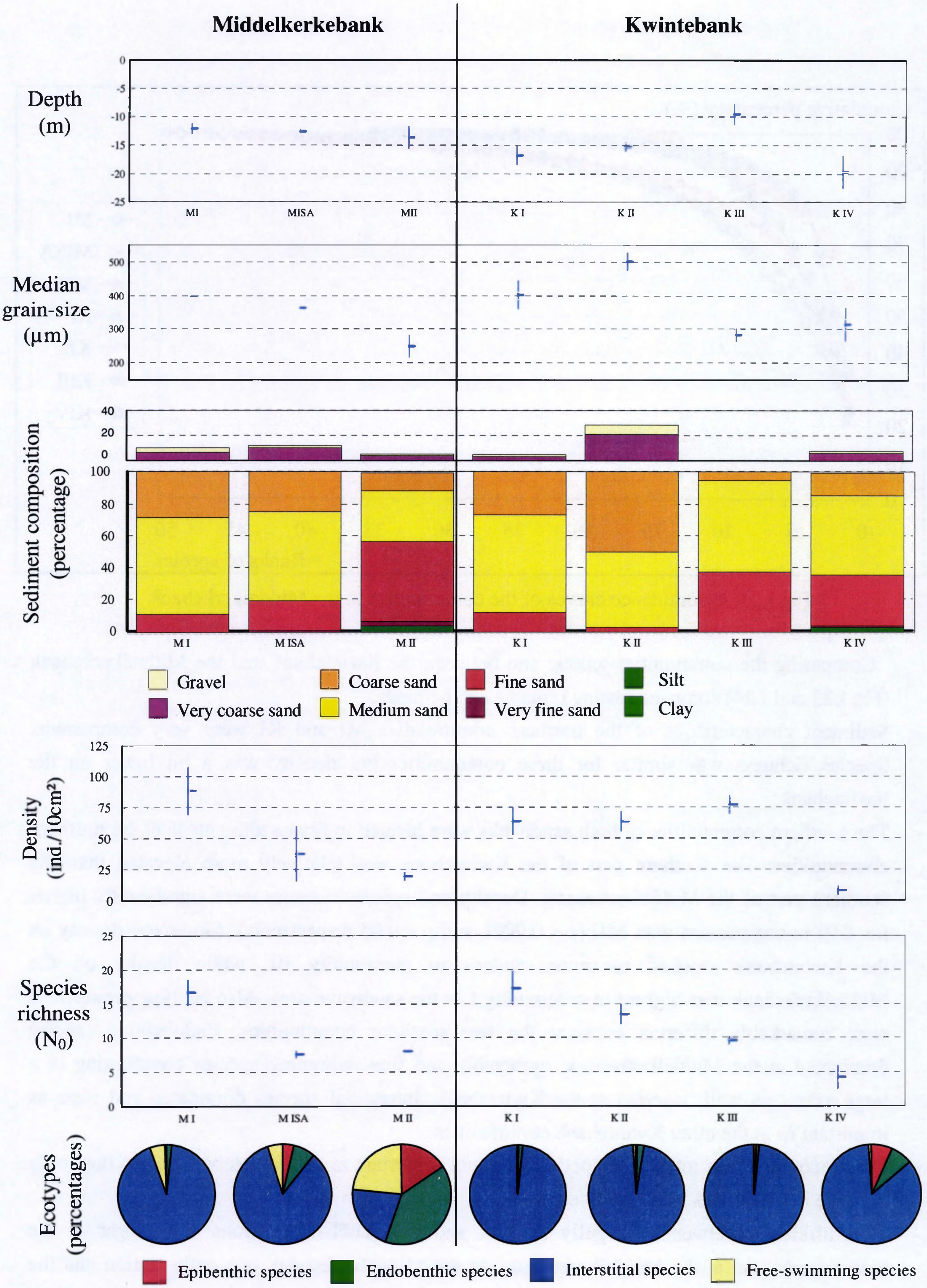


Fig.I.23: Abiotic variables (depth (a), median grain-size (b) and sediment composition (c)) and biotic variables (density (d), species richness (e) and ecotype proportion (f)) of the different communities at the Middelkerkebank and the Kwintebank

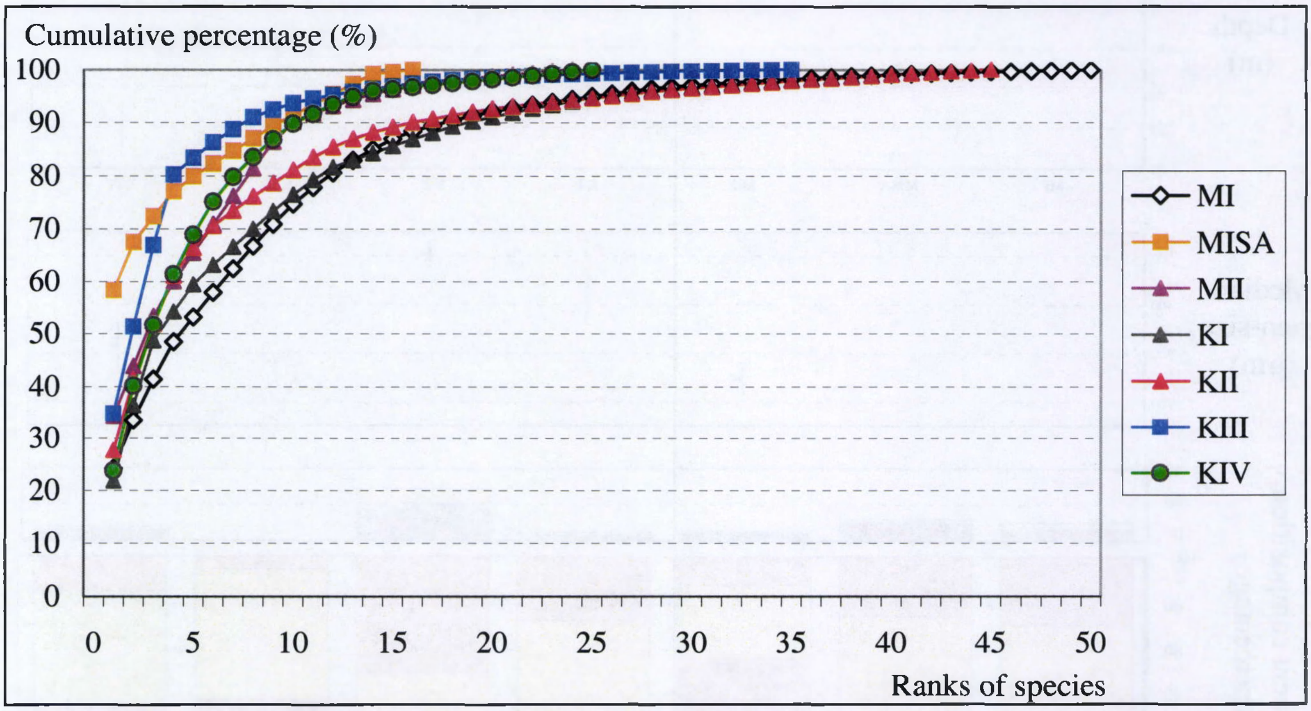


Fig.I.24: k-dominance curves of the communities at the Middelkerkebank

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 cm^2)	N_0	N_1	Sampling area	Sampling period
	minimum and maximum per station				
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 cm^2)	N_0	N_1	Sampling area	Sampling period
	minimum and maximum per station or mean per station				
				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)	N_0	N_1	Sampling area	Sampling period
	minimum and maximum per station or mean per station				
	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		TiO^2-waste dumping site	June 1984
Herman, 1989	5-206	2-22	1.65-14.9	TiO^2-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	N_0	Sampling area/ Sampling period	Depth	Sediment class/ Grain size
	minimum and maximum per station or mean per station				
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	N_0	Sampling area/ Sampling period	Depth	Sediment class/ Grain size
	minimum and maximum per station or mean per station				
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
Moore, 1979d	**47-102**	**6-7** (ES_{50})	Isle of Man, U.K August and December 1973	0-1.3 m	Shallow fine sand
	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	N_0	Area	Sediment class/ Grain size	Period
	minimum-maximum per station or mean per station				
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.

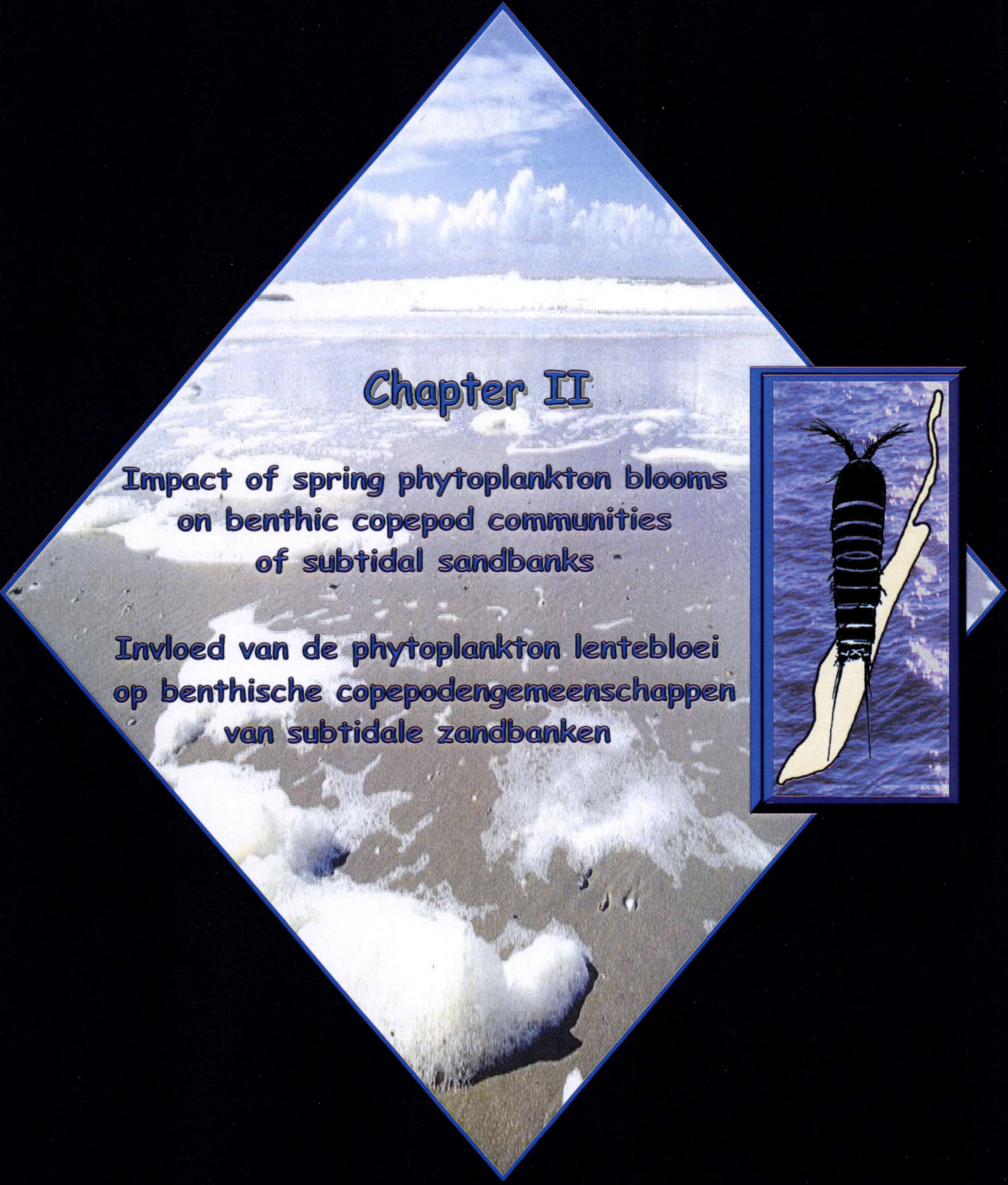
The reduced density at the Kwinte gully station compared to the Uitdiep station may be attributed to seasonal differences, although the greater depth of the Kwinte gully station may induce environmental differences as well. A high variability among replicates at the Uitdiep and Kwinte stations indicated 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.



Chapter II

Impact of spring phytoplankton blooms on benthic copepod communities of subtidal sandbanks

Invloed van de phytoplankton lentebloei op benthische copepodengemeenschappen van subtidale zandbanken

Impact of spring phytoplankton blooms on benthic copepod communities of subtidal sandbanks

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Veronique Rousseau, Jean-Yves Parent & Magda Vincx

1 Introduction

The marine eutrophication in the North Sea is characterized by a shift from moderate early spring diatom growth to a non-siliceous *Phaeocystis* dominated phytoplankton community (Gieskes & Kraay, 1977; Lancelot *et al.*, 1987; Reid *et al.*, 1990; Rousseau, 2000). *Phaeocystis* has been estimated to comprise up to 96 % of the total phytoplankton biomass in the North Sea during that bloom (Zevenboom *et al.*, 1991). As the bloom progresses, nutrient depletion (Lancelot & Mathot, 1987), ciliate grazing (Moll, 1997) and virus infections (Jacobsen *et al.*, 1996) increasingly cause *Phaeocystis* mortality. Diatoms are the main constituent of the planktonic copepod's diet (Rousseau *et al.*, 2000) but a lot of controversy exists on the trophic fate of *Phaeocystis* and its predation by copepods in the water column (Weisse *et al.*, 1994). Even though *Phaeocystis* colonies were not an important food source for copepods of the zooplankton in the Southern Bight of the North Sea (Gasparini *et al.*, 2000; Rousseau *et al.*, 2000), dissolved organic carbon produced by a *Phaeocystis* bloom through excretion and lysis has been demonstrated to be a main source of carbon for the microbial foodweb in the water column, including copepods (Van Boekel *et al.*, 1992; Rousseau *et al.*, 2000). In accordance with this finding, the accumulation of *Phaeocystis* derived organic matter at the bottom may also indirectly induce changes in the community structure of the benthic fauna. Sinking of decaying *Phaeocystis* colonies and organic carbon to the bottom results in large amounts of bottom detritus (Riebesell, 1993). Osinga *et al.* (1996) also observed a continuously high sedimentation of living *Phaeocystis* cells. The natural deposition of organic matter is the primary source of food for sublittoral marine benthos (Gee *et al.*, 1985). In offshore areas it is principally derived from phytoplankton (Smetacek, 1984) and zooplankton faecal pellets and exuvia (Angel, 1984). Settling diatoms are an important food source for the benthos (Brown & Sibert, 1977; Montagna, 1984; Decho, 1988) but the role of the benthos in the remineralization pathway of deposited *Phaeocystis* derived detritus is unknown (Rousseau *et al.*, 2000).

The increased food availability due to organic enrichment often causes a significant increase in harpacticoid densities (Gee *et al.*, 1985). Changes in biodiversity patterns are less straightforward and clear. Species richness of epibenthic and endobenthic detritus feeders may increase in case the deposited organic matter (settling diatoms or *Phaeocystis* detritus) is directly consumable (Fig.II.1). If the bottom detritus is an appropriate food source for benthic microfauna which copepods feed upon, an organic enrichment may result in an increased bacterial productivity and hence an increase in species richness and a decrease in dominance of interstitial bacteria-grazing copepods (Hockin, 1983). Diversity of diatom or detritus feeders or bacteria-grazers may follow a monotonous increasing trend if diversity continuously increases with increasing productivity, possibly reaching a maximum. Due to an enhanced primary production however diversity may decrease if it follows a unimodal relationship. This explains why harpacticoid communities were characterized by an increase in species richness in a low-dose treatment but showed an increase in dominance and a decrease in species richness with increasing organic enrichment (Gee *et al.*, 1985). Also Marcotte & Coull (1974) observed decreasing diversities of a subtidal harpacticoid community with increasing organic enrichment. The response of natural communities depends on the kind of primary production, the amount of organic mattter and the composition of the community, i.e. the proportion of bacteria-grazing and microalgae consuming species (Hockin, 1983). Consequently, eutrophication may cause an increase in biodiversity in specific areas, an impoverishment in others. To examine this hypothesis, an intensive sampling campaign was performed at two subtidal stations in the southern North Sea from the beginning of March until the beginning of July in 1999. Temporal changes in harpacticoid density, diversity and community structure in relation to the diatom and *Phaeocystis* spring bloom have been examined. Also temporal fluctuations in the vertical distribution of harpacticoids in the sediment have been studied. Special attention has been paid to the different response of epi- and endobenthic and interstitial species in order to describe the influence of organic enrichment on the functional biodiversity of harpacticoid communities. Temporal and vertical distribution patterns of the different life history stages were examined to reveal a potential interrelation between migratory behaviour and reproductive activity as a result of organic enrichment. Finally, differences are discussed between the two sandbank stations, since a decreasing trend of organic enrichment was expected with distance from the coast.

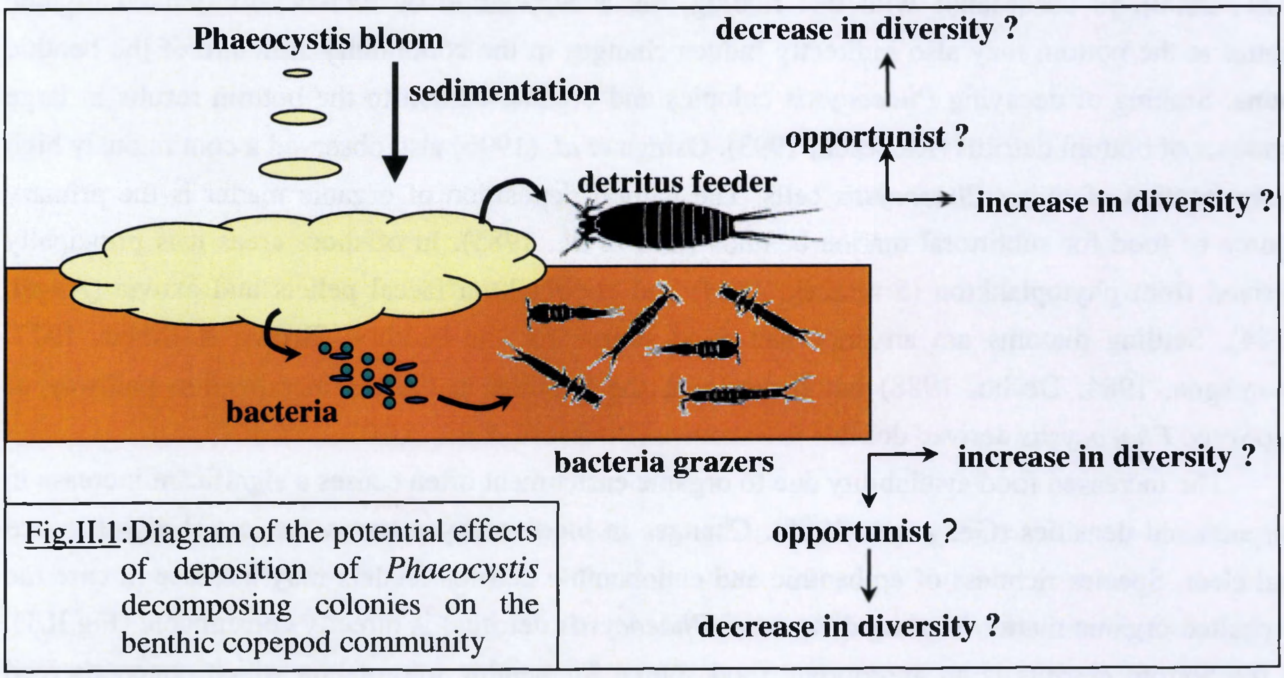
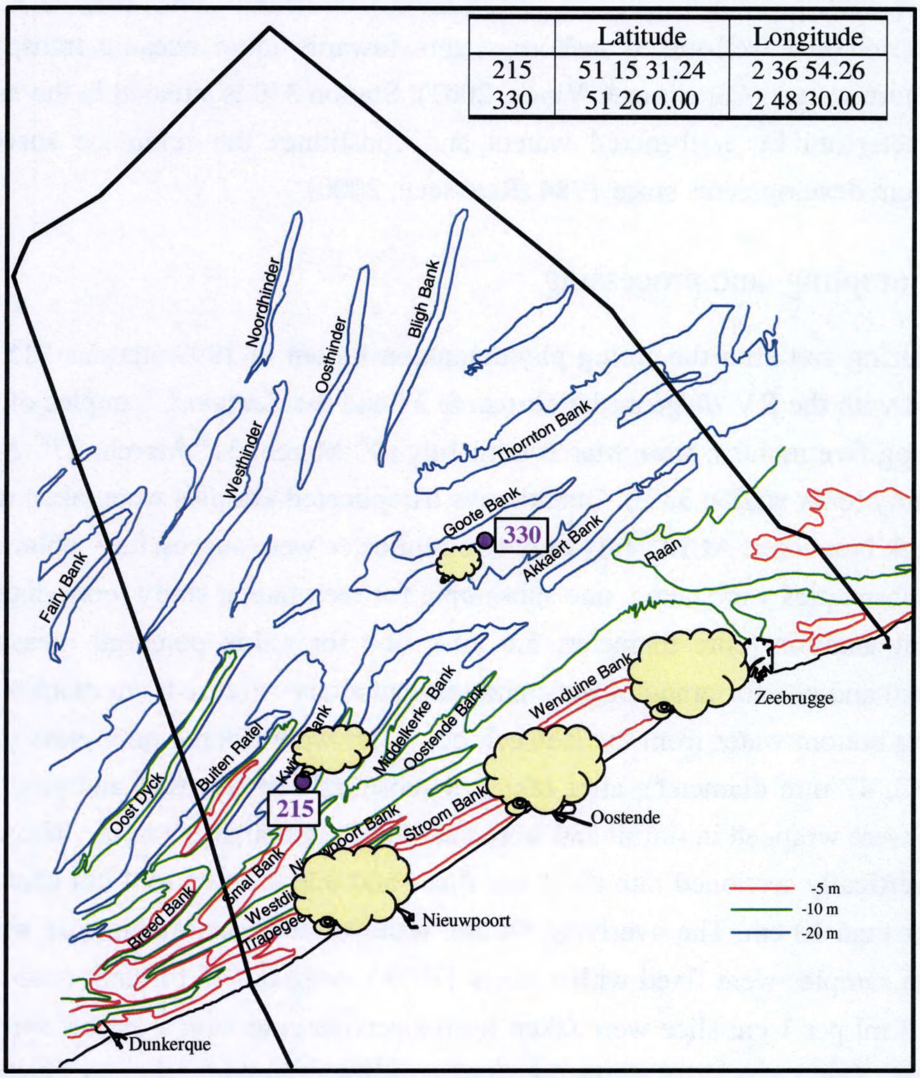


Fig.II.1:Diagram of the potential effects of deposition of *Phaeocystis* decomposing colonies on the benthic copepod community

2 Materials and methods

2.1 Description of the study area



	Latitude	Longitude
215	51 15 31.24	2 36 54.26
330	51 26 0.00	2 48 30.00

Fig.II.2: Location of the sampling stations

Two stations were sampled at the Belgian Continental Shelf (Fig.II.2). Station 215 is located at 12 m depth on the southern part of the Kwintebank, belonging to the Flemish Banks. An extensive description of the Kwintebank and the Flemish Banks area is given in chapter I. Station 330 is situated at greater depth (24 m) on the southern flank of the Gootebank. Just as the Kwintebank, the Gootebank is rectilinear at a large scale, but the direction is parallel to the coastline. The outlines of the bank are not streamlined to the same degree as the Flemish Banks. (Vlaeminck *et al.*, 1989) The Gootebank belongs to the Zeeland Ridges, a group of shelf sandbanks which are mainly located in Dutch territorial waters. The Gootebank has a length of 15 km and a maximum width of 2 km. It shows a relative elevation above the seafloor of 6 m at the ends and up to 10 m at the centre, which corresponds with a low water depth of 12 m. In comparison with the Flemish Banks, its height is less pronounced, although they occur at approximate similar water depths. (Lanckneus *et al.*, 1993) The topography of the bank is not very explicit and rather smooth: the southwestern part of the bank is only 1 m higher than the surrounding channels (Vlaeminck *et al.*, 1989). In general, it has very mild slopes to the NW and a more steeper slope to the SE (Lanckneus *et al.*, 1993). The physical, chemical and biological characteristics of the Belgian Continental Shelf display a gradient from turbid, nutrient rich and well-mixed inshore waters towards more oceanic transparent and less productive offshore waters (Cattrijsse & Vincx, 2001). Station 330 is situated in the latter zone. This station is characterized by well-mixed waters and constitutes the reference survey station for *Phaeocystis* bloom developments since 1984 (Rousseau, 2000).

2.2 Sampling and processing

Before, during and after the spring phytoplankton bloom in 1999 stations 215 and 330 were regularly visited with the RV *Belgica*, the *Oostende XI* and the *Zeehond*. Samples of six dates were analyzed covering five months, from March until July (9th March, 31st March, 27th April, 12th May, 28th June, 12th July (only station 330)). Quantitative trireplicated samples were taken with a modified 0.017 m² Reineck box corer. At 12th July only two replicates were successfully obtained. From each replicate four subsamples were taken, one subsample for meiofaunal study (core diameter: 3.6 cm), one for pigment analysis (core diameter: 3.6 cm), one for redox potential measurements (core diameter: 3.6 cm) and one for granulometric and nutrient analysis (core 6 cm diameter). Aliquots of 0.5-1 l overlying bottom water from the Reineck box corer were filtered on a glass microfibre filter (Whatman GF/C, 47 mm diameter), after taking a subsample for nutrient analysis. The filters for HPLC analysis were wrapped in tinfoil and stored at –20°C until analysis in the laboratory. The core samples were vertically sectioned into ten 1 cm slices and one slice up to 4 cm containing the core sediment deeper than 10 cm. The overlying bottom water of each meiofauna core was preserved as well. Meiofauna samples were fixed with a warm (70 %), neutral 4 % formaline tap water solution. Subsamples of 1 ml per 1 cm slice were taken from a second core with a cut off syringe for further pigment analysis. The 1 cm slices from the third core for granulometric and nutrient study were preserved in Petri dishes in the freezer, as well as the sample units for pigment analysis. The redox potential was measured, on board, by means of a micro-platinum electrode which was connected to a pH-millivoltmeter. Seawater temperature and salinity were measured aboard with a thermosalinometer (Beckman). On each sampling event, a vertical profile of temperature, salinity, turbidity and irradiance was obtained by means of a CTD-cast.

In the lab, the same procedure was followed to elutriate the harpacticoids from the sediment as described in chapter I. A distinction was made between males, egg carrying and non egg-carrying females and copepodites. Densities are expressed as ind./10 cm², referring to the surface area of the core but actually a volume is concerned, comprising the whole core up to 10 cm of depth for total densities and a volume of 10 cm² x 1 cm for densities per depth layer to describe the vertical distribution of the copepods.

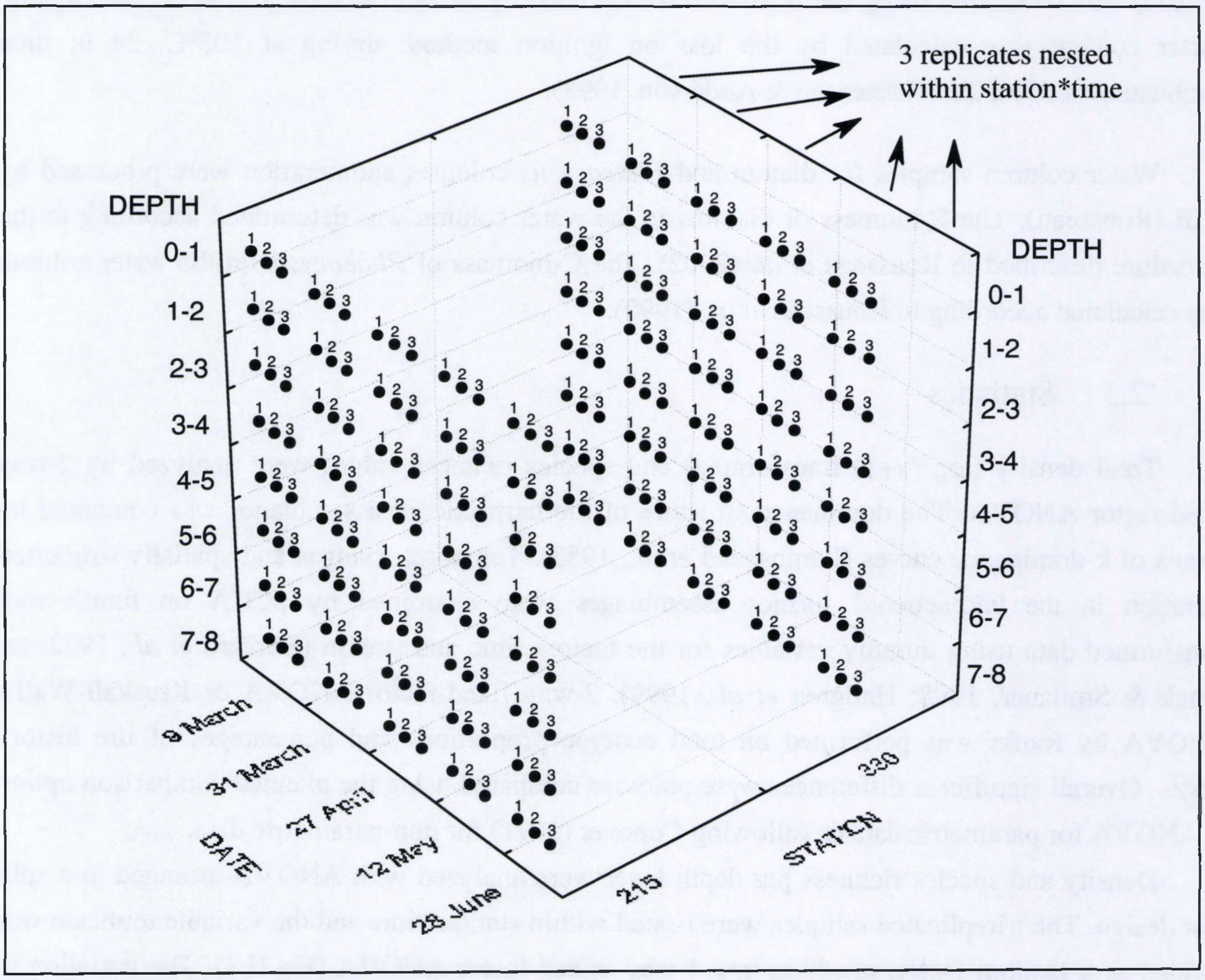
Sediment granulometry was analyzed with a Coulter LS100 Particle Size Analyzer using laser light of 750 nm. The sediment fractions are listed according to the Wenthworth scale (Buchanan, 1984). For nutrient analysis (silicate, nitrate plus nitrite and ammonia) the overlying water or the interstitial water extracted from the sediment were analyzed through an automatic chain SKALAR SAN^{plus} Segmented Flow Analyzer using a photometric method. The filters for chlorophyll *a* analysis were cut into small pieces and placed in tubes (10 ml) containing 5 ml of 90 % acetone and were sonicated for 30 seconds. Reverse-phase high-performance liquid chromatography (RP-HPLC) (Gilson) was conducted using the method recommended by Wright & Jeffrey (1997). The organic matter content was calculated by the loss on ignition method: drying at 105°C, 24 h; then combusting at 550°, 2h. (Kristensen & Anderson, 1993).

Water column samples for diatom and *Phaeocystis* colonies enumeration were processed by ULB (Rousseau). The C-biomass of diatoms in the water column was determined according to the procedure described in Rousseau *et al.* (2002). The C-biomass of *Phaeocystis* in the water column was calculated according to Rousseau *et al.* (1990).

2.3 Statistics

Total density (log (x+1) transformed) and species richness values were analyzed by 2-way fixed-factor ANOVA. The dominance structure of the harpacticoid assemblages was compared by means of k-dominance curves (Lambshead *et al.*, 1983). Temporal changes and spatially structured variation in the harpacticoid species assemblages were examined by pCCA on fourth root transformed data using dummy variables for the factors time and station (Borcard *et al.*, 1992; ter Braak & Smilauer, 1998; Hallgren *et al.*, 1999). 2-way fixed-factor ANOVA or Kruskall-Wallis ANOVA by Ranks was performed on total ecotype proportions and percentages of life history stages. Overall significant differences were pairwise compared using the planned comparison option in ANOVA for parametric data or following Conover (1971) for non-parametric data.

Density and species richness per depth layer were analyzed with ANOVA arranged in a split plot design. The trireplicated samples were nested within station*time and the variable replicate was defined as a random factor, resulting in a 4-way mixed-factor ANOVA (Fig.II.3). The variation in the dataset due to the vertical zonation of harpacticoids was defined by pCCA on fourth root transformed data. Replicate A from depth layer 0-1 cm taken on 27th April at station 215 and replicate B from the overlying water on 28th June at station 330 were outliers and excluded from this analysis. Significant effects of the variables station, time, depth and the interactions between them on the species composition were examined with Monte-Carlo permutation tests restricted for split-plot design using pCCA in CANOCO for Windows (Table II.1) (ter Braak & Smilauer, 1998). Since after transformation of the ecotype proportions and percentages of life history stages none of the assumptions for ANOVA were met, these data (arcsin(x/100) transformed) were also analyzed with Monte-Carlo permutation tests restricted for split-plot design using pRDA (Table II.2). This technique was also applied to univariate log (x+1) data such as the densities of selected species. Forward selection using Monte-Carlo permutation tests restricted for split-plot design in pCCA and pRDA selected the variables significantly contributing to the effect of time or depth or the interactions between the factors station, time and depth. The results of the 4-way mixed-factor ANOVA on total densities and species richness were compared with the Monte-Carlo permutation tests restricted for split-plot design.



<u>Fig.II.3</u>: Representation of the statistical design (4-way mixed-factor ANOVA) to define significant effects of the variables station, time, depth and the interactions between these variables on density and species richness

				Monte-Carlo permutation test restricted for split-plot design			
	Analysis	Explanatory variables (as dummy variables)	Covariables (as dummy variables)	covariables as blocks	whole plots (in one block, if defined) (one sample per whole plot)	split plots in one whole plot	permuted
Total variation	CA	none	none				
Spatial + temporal + depth structured variation	CA	stations + dates + depth layers	none				
Spatially structured variation	CCA	stations	none	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-temporal spatial variation	pCCA	stations	dates	dates	samples of both stations on one date	7 depth layers of one sample	whole plots
Non-depth related spatial variation	pCCA	stations	depth layers	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-temporal and non-depth related spatial variation = effect station	pCCA	stations	dates + depth layers	dates	samples of both stations on one date	7 depth layers of one sample	whole plots
Temporally structured variation	CCA	dates	none	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-spatial temporal variation	pCCA	dates	stations	stations	samples on all dates at one station	7 depth layers of one sample	whole plots
Non-depth related temporal variation	pCCA	dates	depth layers	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-spatial and non-depth related temporal variation = effect time	pCCA	dates	stations + depth layers	stations	samples on all dates at one station	7 depth layers of one sample	whole plots
Depth structured variation	CCA	depth layers	none	none	samples of both stations on all dates	7 depth layers of one sample	split plots
Non-spatial depth structured variation	pCCA	depth layers	stations	stations	samples on all dates at one station	7 depth layers of one sample	split plots
Non-temporal depth structured variation	pCCA	depth layers	dates	dates	samples of both stations on one date	7 depth layers of one sample	split plots
Non-temporal and non-spatial depth variation = effect depth	pCCA	depth layers	dates + stations	stations	samples on all dates at one station	7 depth layers of one sample	split plots
Spatially temporal structured variation = effect time*station	pCCA	all possible interactions of date*station	dates + stations	dates	samples of both stations on one date	7 depth layers of one sample	whole plots
Spatially depth structured variation = effect depth*station	pCCA	all possible interactions of depth layer*station	depth layers + all possible interactions of depth layer*date	samples	samples of both stations on all dates = blocks	7 depth layers of one sample	split plots
Temporally depth structured variation = effect depth*time	pCCA	all possible interactions of depth layer*date	depth layers + all possible interactions of depth layer*station	samples	samples of both stations on all dates = blocks	7 depth layers of one sample	split plots
Spatially and temporally depth structured variation = effect station*time*depth	pCCA	all possible interactions of depth layer*date*station	all possible interactions of date*station, depth layer*station and depth layer*date	samples	samples of both stations on all dates = blocks	7 depth layers of one sample	split plots

Table II.1: Statistical design to define significant effects of the variables station, time, depth and of the interactions between these variables on species composition, the sample values are mean values of 3 replicates

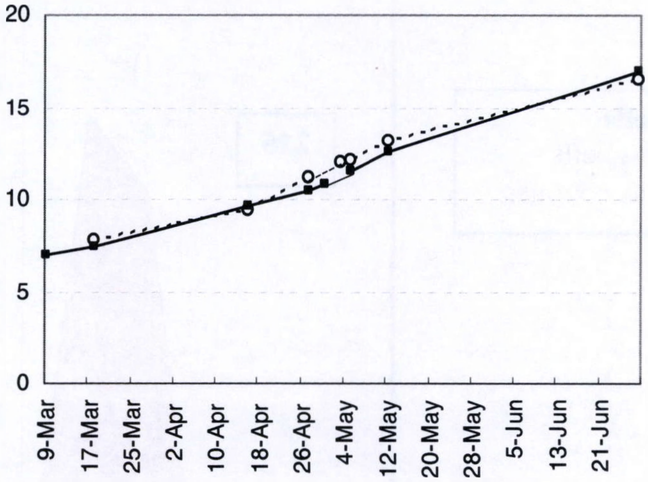
				Monte-Carlo permutation test restricted for split-plot design			
	Analysis	Explanatory variables (as dummy variables)	Covariables (as dummy variables)	covariables as blocks	whole plots (in one block, if defined) (one replicate per whole plot)	split plots in one whole plot	permuted
Non-temporal and non-depth related spatial variation	pRDA	stations	dates + depth layers	dates	3 replicates of both stations on one date	8 depth layers of one sample	whole plots
Non-spatial and non-depth related temporal variation	pRDA	dates	stations + depth layers	stations	3 replicates of one station on all dates	8 depth layers of one sample	whole plots
Non-temporal and non-spatial depth variation	pRDA	depth layers	dates + stations	stations	3 replicates of one station on all dates	8 depth layers of one sample	split plots
Spatially temporal structured variation = effect time*station	pRDA	all possible interactions of date*station	dates + stations	dates	3 replicates of both stations on one date	8 depth layers of one sample	whole plots
Spatially depth structured variation = effect depth*station	pRDA	all possible interactions of depth layer*station	depth layers + all possible interactions of depth layer*date	replicates	3 replicates of both stations on all dates = blocks	8 depth layers of one sample	split plots
Temporally depth structured variation = effect depth*time	pRDA	all possible interactions of depth layer*date	depth layers + all possible interactions of depth layer*station	replicates	3 replicates of both stations on all dates = blocks	8 depth layers of one sample	split plots
Spatially and temporally depth structured variation = effect station*time*depth	pRDA	all possible interactions of depth layer*date*station	all possible interactions of date*station, depth layer*station and depth layer*date	replicates	3 replicates of both stations on all dates = blocks	8 depth layers of one sample	split plots

Table II.2: Statistical design to define significant effects of the variables station, time, depth and of the interactions between these variables on density, species richness, ecotype proportions and percentages of life history stages

3 Results

3.1 Environmental data

3.1.1 Temperature and salinity



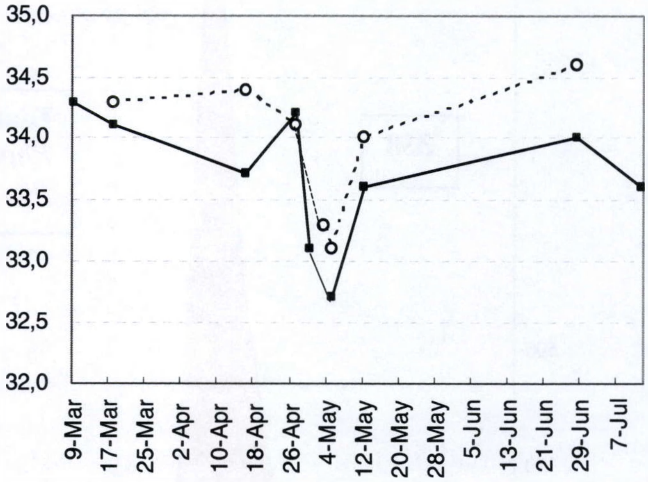


Fig.II.4: Temperature measurements at stations 215 (open circles + dotted line) and 330 (closed squares + full line) during the sampling period

Fig.II.5: Salinity measurements at stations 215 (open circles + dotted line) and 330 (closed squares + full line) during the sampling period

Temperature linearly increased from 7°C on 9th March up to 17°C on 12th July (Fig.II.4). During approximately two weeks (27th April-12th May) temperature was almost 1°C higher at station 215 than at station 330. This period coincides with a drop in salinity at both stations (Fig.II.5). Between 27th April and 30th April salinity dropped with one unit, further decreasing toward 3rd May and increasing again afterwards. Through the whole period salinity was slightly higher at station 215 than at station 330.

3.1.2 Description of the diatom and *Phaeocystis* spring bloom

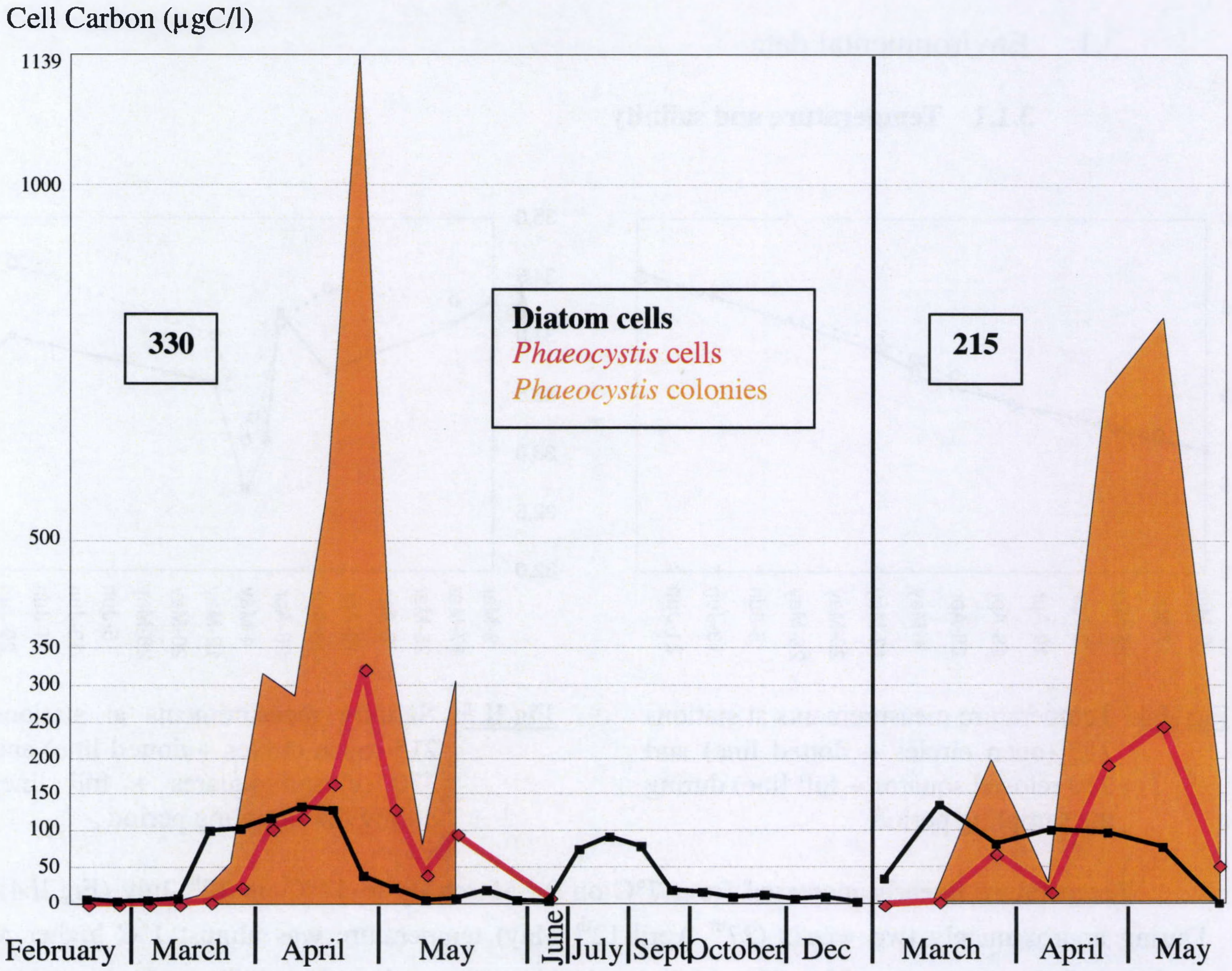


Fig.II.6: Carbon content in the water column, derived from diatom cells, *Phaeocystis* cells and *Phaeocystis* colonies (mucilage included) during the sampling period, measured at stations 330 and 215 in 1999

From 19th March (100 µg/l) until 27th April a high carbon content, derived from diatom cells, was measured in the water column at station 330, reaching a maximum of 132 µg/l on 23rd April (Fig.II.6). During this spring diatom bloom the onset of the *Phaeocystis* bloom was observed on 19th March. *Phaeocystis* derived cell carbon increased during April and peaked after the diatom bloom terminated on 29th April. *Phaeocystis* derived colonial carbon (including mucilage) amounted to 1139 µg/l at this date. During May *Phaeocystis* cell carbon content decreased to 11 µg/l on 2nd June. Diatoms showed a second moderate bloom in July. At station 215 the diatom bloom started at the same moment as at station 330 but lasted a bit longer until 3rd May. In the water column lower values were recorded for *Phaeocystis* derived carbon at station 215 than at station 330, the peak of *Phaeocystis* derived cell carbon (244 µg/l) and colonial cell carbon (782 µg/l) being less pronounced and occurring on 3rd May whereas on 29th April at station 330.

3.1.3 Chlorophyll *a* and total organic matter

3.1.3.1 Station 330

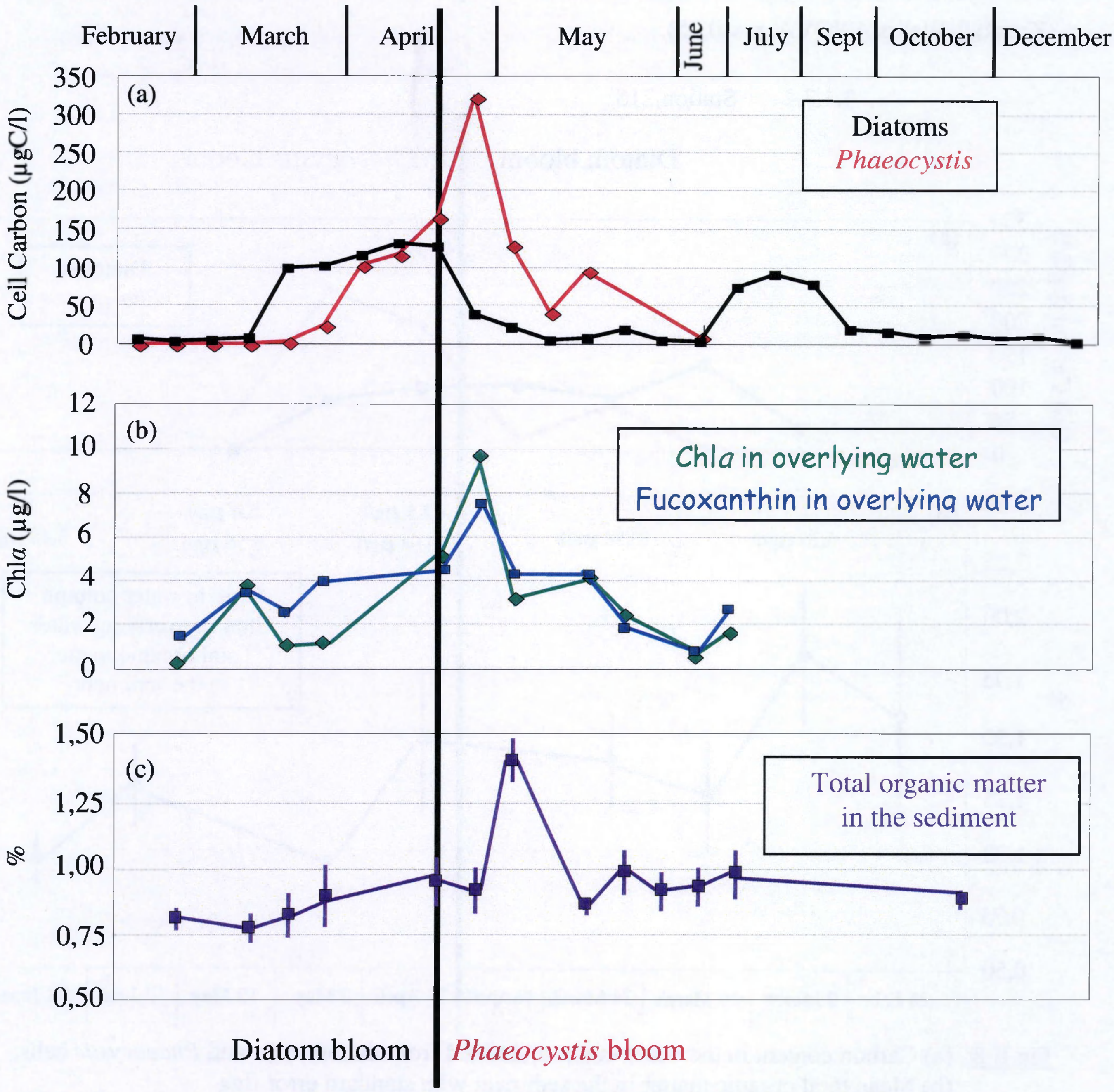


Fig.II.7: (a) Carbon content in the water column, derived from diatom cells and *Phaeocystis* cells; (b) Chlorophyll *a* content in water column and overlying water; (c) Mean total organic matter in the sediment with standard error measured at station 330 in 1999

Chlorophyll *a* content in the water column and in the overlying water started to rise during the diatom bloom and peaked at the same moment as the *Phaeocystis* bloom (Fig.II.7.b). In May chlorophyll *a* content in the overlying water showed the same trend as the *Phaeocystis* bloom.

Elevated values for chlorophyll *a* were also recorded in the overlying water on 9th May whereas this increase was not recorded in the water column (Rousseau, unpubl. data). Total organic matter (Fig.II.7.c) showed a distinct peak on 3rd May, indicating that 4 days after the peak of the *Phaeocystis* bloom a significant higher amount of organic matter was present in the sediment (Kruskall-Wallis ANOVA, $p < 0.05$).

3.1.3.2 Station 215

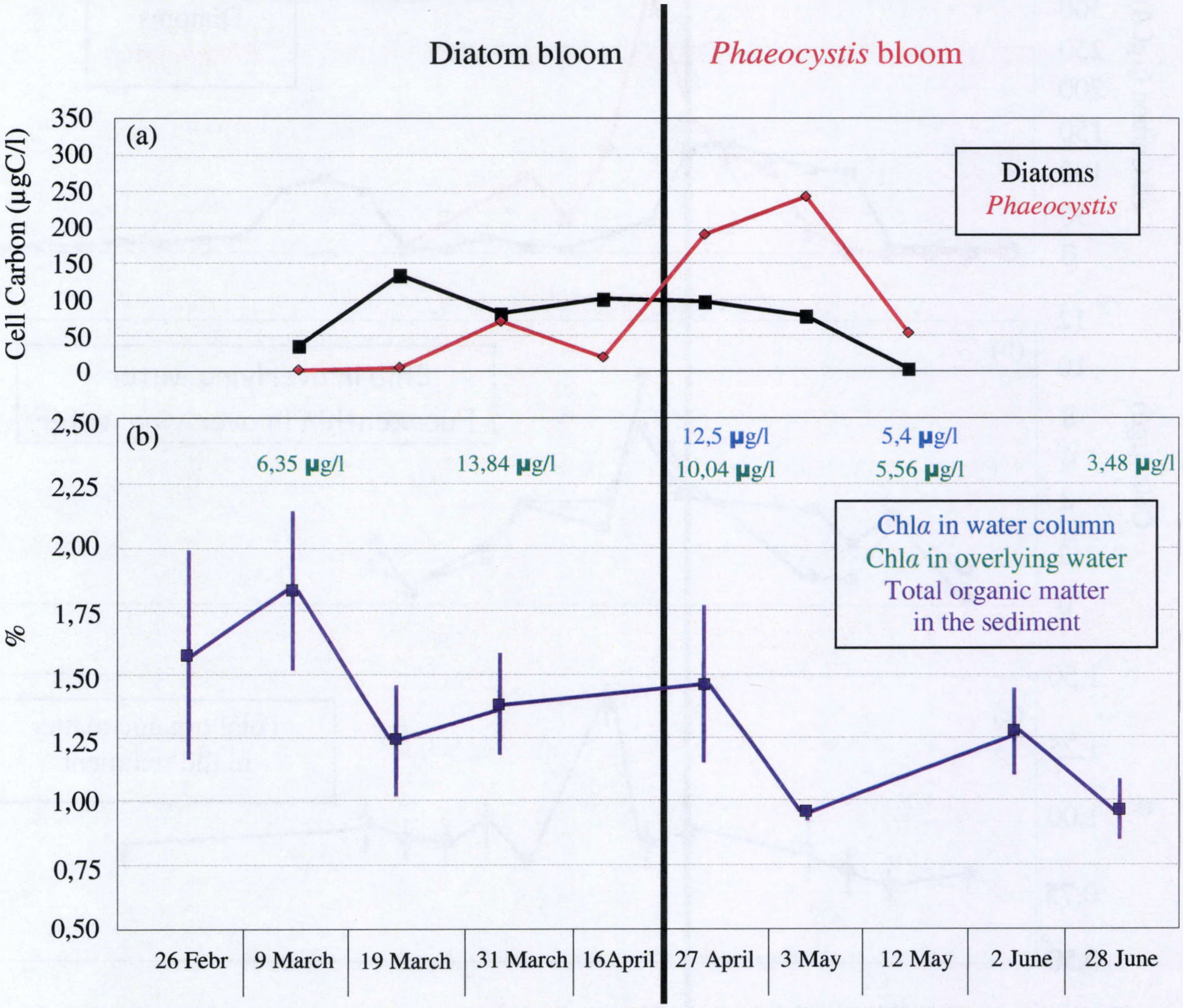


Fig.II.8: (a) Carbon content in the water column, derived from diatom cells and *Phaeocystis* cells; (b) Mean total organic matter in the sediment with standard error flag measured at station 215 in 1999
Measurements of chlorophyll *a* content in water column and overlying water are given in the graph of total organic matter.

At station 215 the few measurements of chlorophyll *a* indicate that the concentration of chlorophyll *a* in the water column was nearly the same as in the overlying water. The highest value for chlorophyll *a* near the bottom was measured on 31st March. This value even exceeded the measurement during the *Phaeocystis* bloom on 27th April.

On any date, the total organic matter content in the sediment was higher at station 215 than at station 330, resulting in a significant difference between both stations (Kruskall-Wallis ANOVA, $p < 0.001$). At station 215 the highest percentages of total organic matter were recorded at the end of February and the beginning of March while the lowest percentages were measured in the beginning of May and at the end of June. In contrast with station 330, a peak in total organic matter was not found on 3rd May.

3.1.4 Nutrients

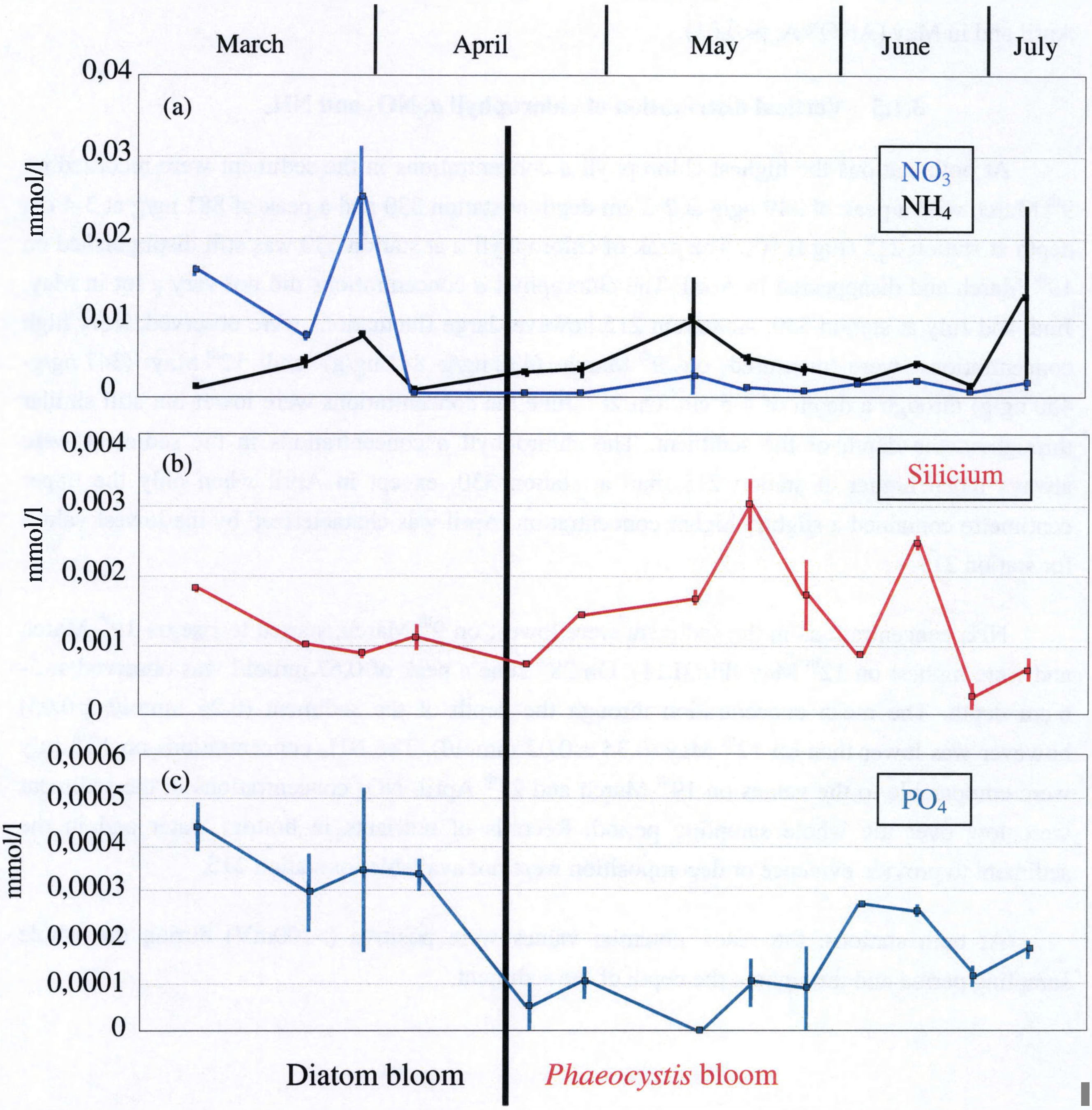


Fig.II.9: (a) NO_3 and NH_4 concentrations; (b) silicium concentrations and (c) PO_4 concentrations measured at station 330 in 1999

At station 330 the highest NO_3 concentrations (Fig.II.9.a) were measured in March with two distinct peaks on 9th March (0.016 mmol/l) and 31st March (0.026 mmol/l) (Kruskall-Wallis ANOVA, $p < 0.05$). Low values were recorded throughout the following sampling period. NH_4 concentrations showed three significant peaks at station 330 (Kruskall-Wallis ANOVA, $p < 0.05$). The first peak appeared on 31st March (0.008 mmol/l), the second on 12th May (0.010 mmol/l) and the third on 12th July (0.013 mmol/l). Silicium concentrations (Fig.II.9.b) were low in March and April and significantly higher on 20th May (0.003 mmol/l) and 16th June (0.002 mmol/l) (Kruskall-Wallis ANOVA, $p < 0.05$). PO_4 concentrations (Fig.II.9.c) were significantly lower at the end of April and in May (ANOVA, $p<0.01$).

3.1.5 Vertical distribution of chlorophyll *a*, NO_3 and NH_4

At both stations the highest chlorophyll *a* concentrations in the sediment were recorded on 9th March with a peak of 349 ng/g at 2-3 cm depth at station 330 and a peak of 881 ng/g at 3-4 cm depth at station 215 (Fig.II.10). The peak of chlorophyll *a* at station 330 was still distinguished on 19th March and disappeared in April. The chlorophyll *a* concentrations did not vary a lot in May, June and July at station 330. At station 215 however large fluctuations were observed. Very high concentrations were measured on 9th March (438 ng/g- 881 ng/g) and 12th May (347 ng/g-450 ng/g) through a depth of 4-5 cm. On 28th June the concentrations were lower but still similar throughout the depth of the sediment. The chlorophyll *a* concentrations in the sediment were always much higher at station 215 than at station 330, except in April when only the upper centimetre contained a slightly higher concentration. April was characterized by the lowest values for station 215.

NH_4 concentrations in the sediment were lowest on 9th March, started to rise on 19th March and were highest on 12th May (Fig.II.11). On 28th June a peak of 0.67 mmol/l was observed at 5-6 cm depth. The mean concentration through the depth of the sediment (0.26 mmol/l ± 0.05) however was lower than on 12th May (0.34 ± 0.02 mmol/l). The NH_4 concentrations on 12th July were comparable to the values on 19th March and 27th April. NO_3 concentrations in the sediment were low over the whole sampling period. Records of nutrients in bottom water and in the sediment to provide evidence of decomposition were not available for station 215.

At both stations, the redox potential values were positive (>100mV) during the whole sampling period and throughout the depth of the sediment.

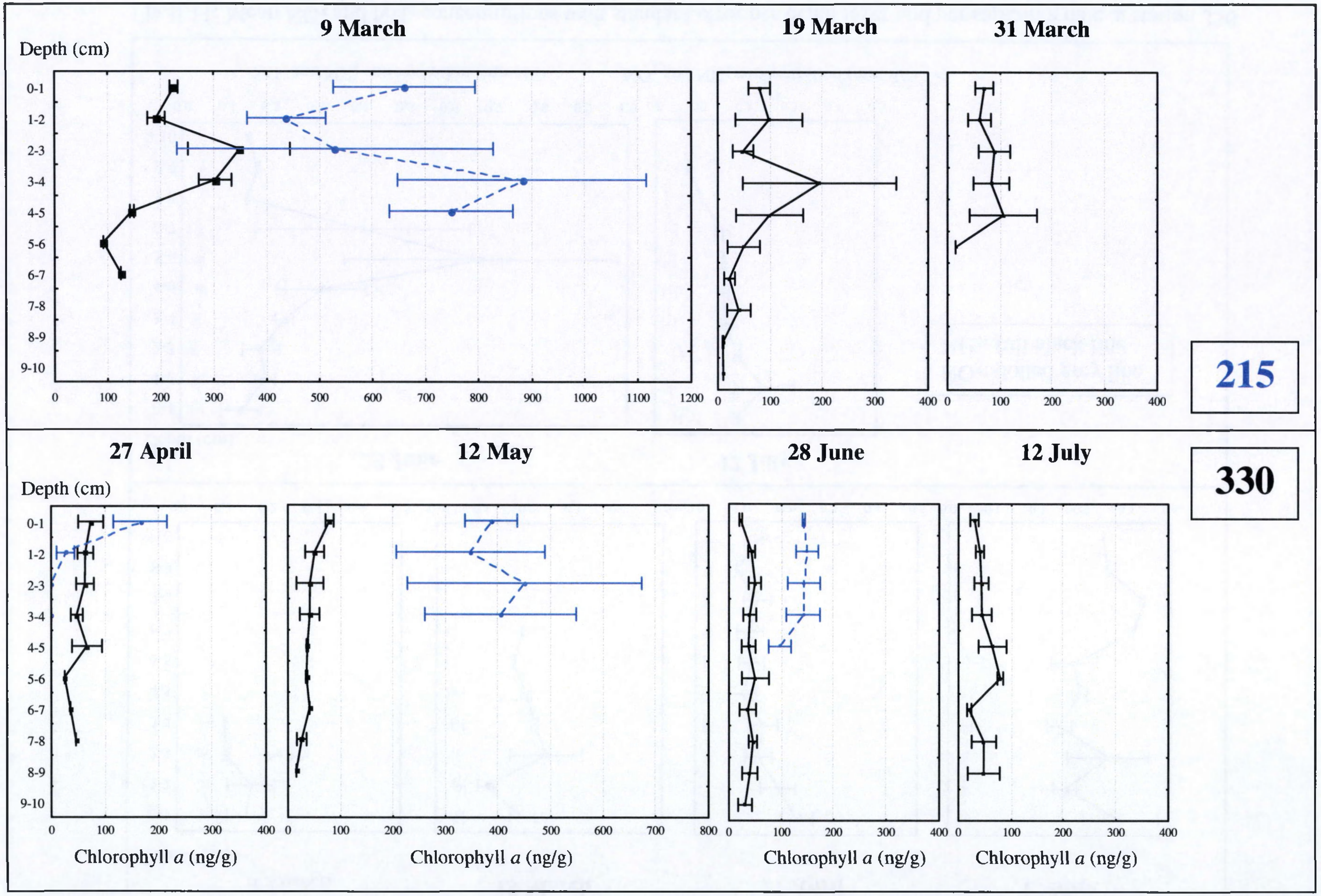


Fig.II.10: Mean chlorophyll *a* concentration with standard error per depth layer and per sampling date at station 215 and station 330, on 19th March, 31st March and 12th July chlorophyll *a* measurements were not available for station 215

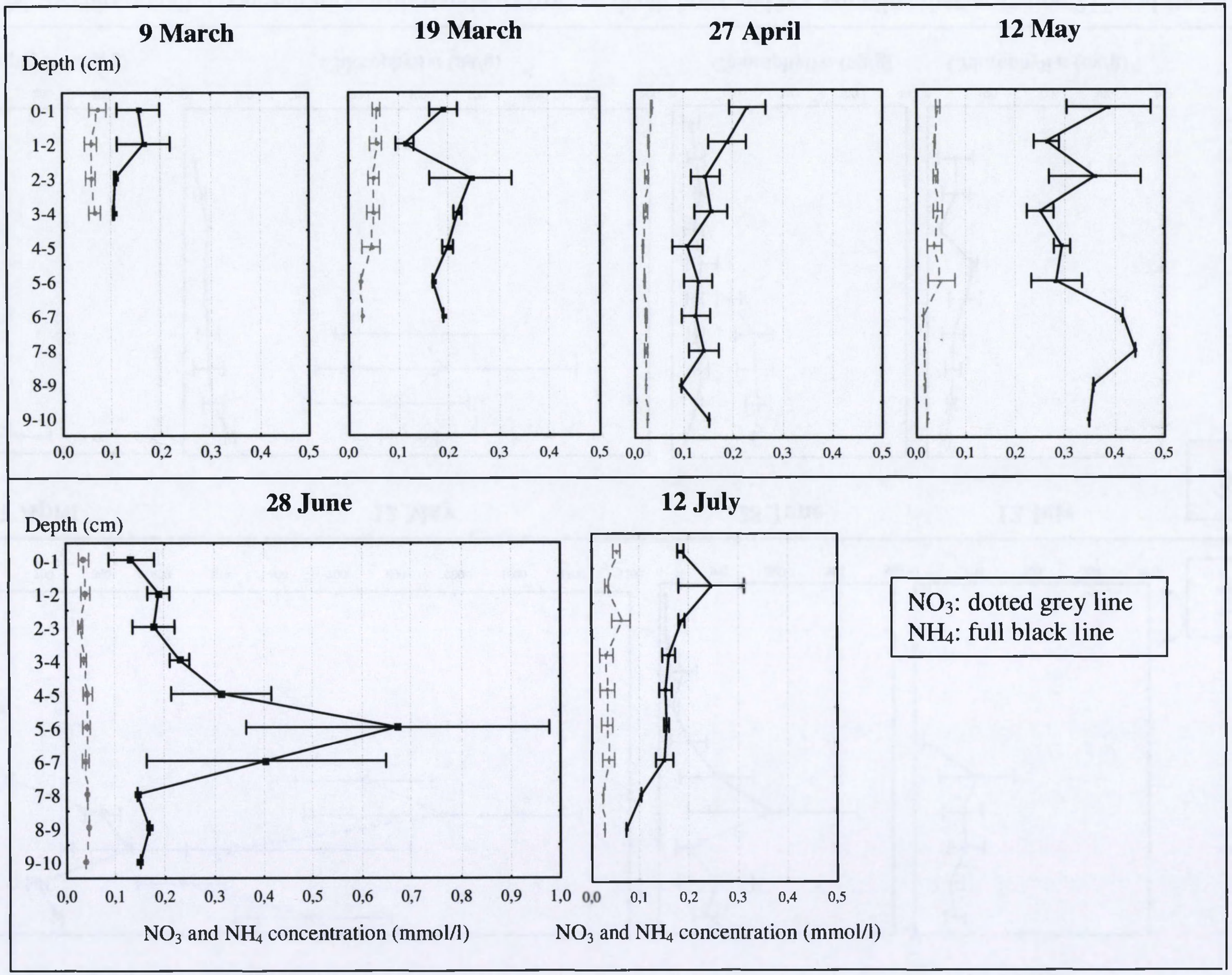


Fig.II.11: Mean NO_3 and NH_4 concentrations with standard error per depth layer and per sampling date at station 330

3.1.6 Sediment characteristics

Medium sand dominated at both stations. The mean median grain size over the whole period was 310 ± 24 µm at station 215 and amounted to 350 ± 10 µm at station 330. Sediment composition was very constant at station 330 throughout the whole period, except for a slight increase in coarse and very coarse sand on 27th April. Because of the low variance between the replicates at station 330 an increase in median grain size of 40 µm on 27th April resulted in a significant difference in comparison with the other sampling dates (ANOVA, $p < 0.01$). At station 215 the median grain size was significantly higher on 9th March in comparison with the median grain size in April and June (Kruskall-Wallis ANOVA, $p < 0.01$), due to a significant higher contribution of coarse sand on 9th March (ANOVA, $p < 0.001$). At station 330 the sediment is very well sorted and predominated by medium sand (69 % ± 1 %) (Fig.II.12), whereas at station 215 the sediment is rather poorly sorted, containing a lot of fine (35 % ± 6 %) as well as very coarse sand (11 % ± 1 %).

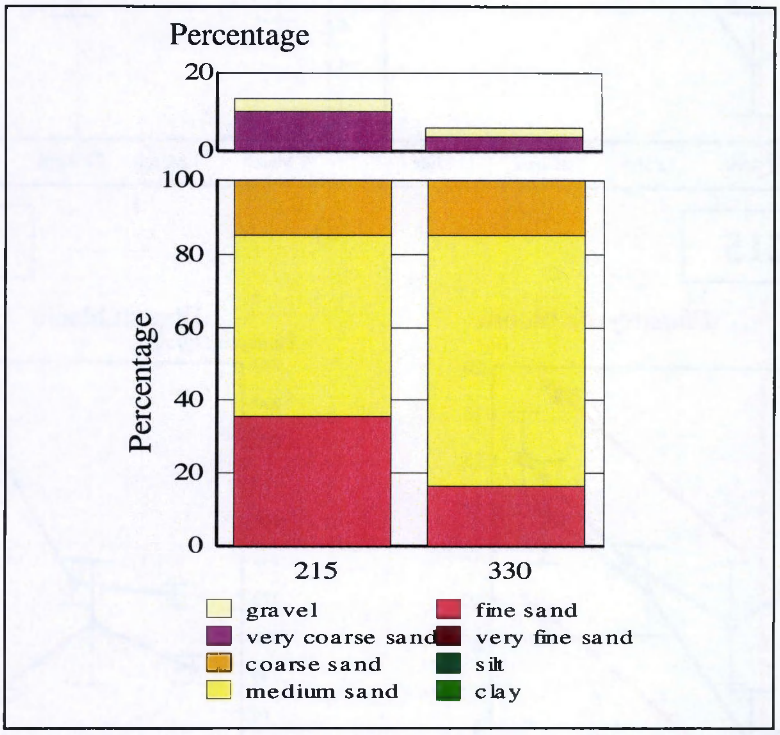


Fig.II.12: Mean sediment composition over the whole sampling period at station 215 and 330

3.2 Time series of harpacticoid data

3.2.1 Total harpacticoid density and diversity

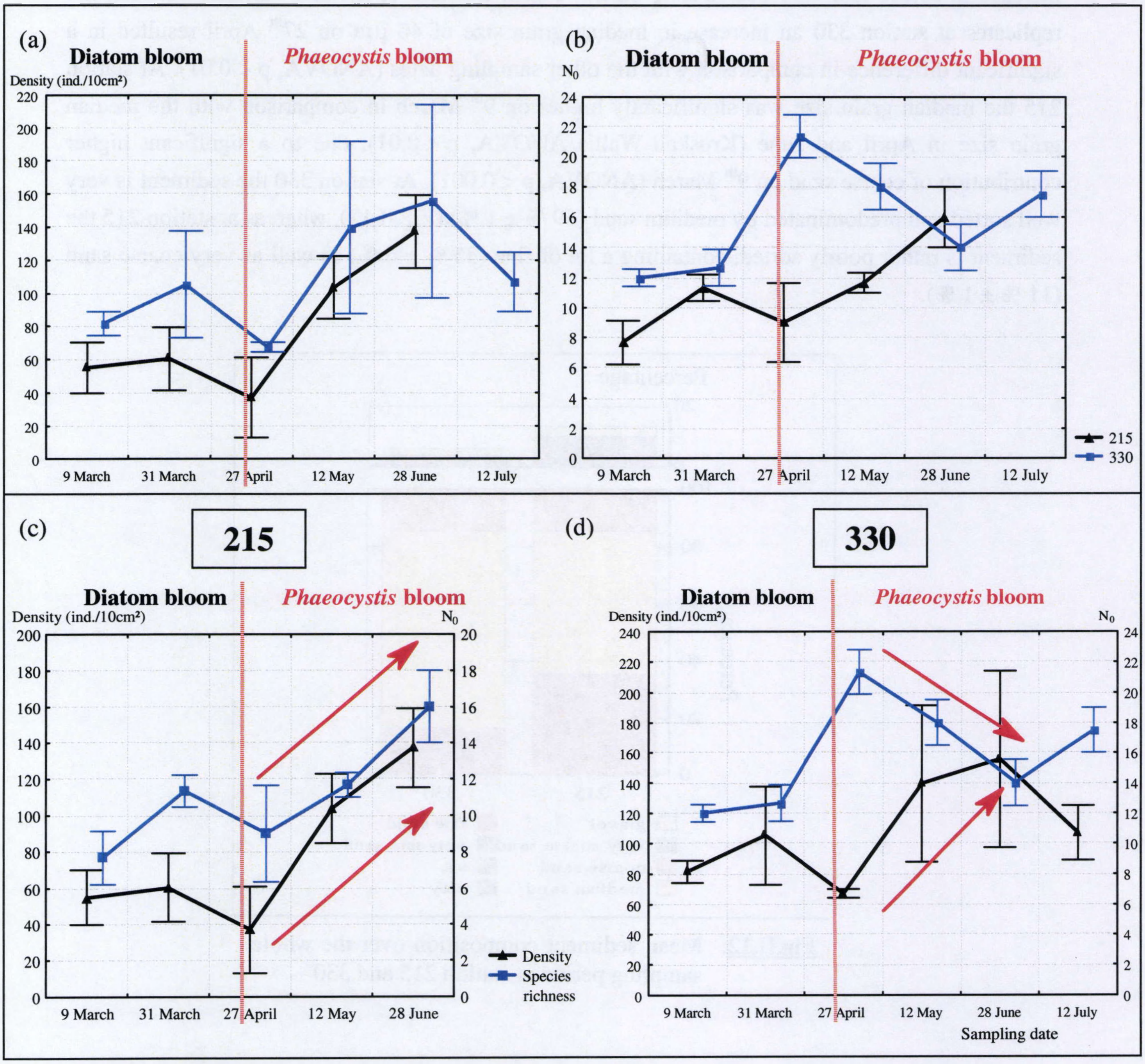


Fig.II.13:(a) Mean total densities with standard error at stations 215 and 330;
(b) Mean total number of species with standard error at stations 215 and 330;
(c) Mean total densities and number of species with standard errors at station 215;
(d) Mean total densities and number of species with standard errors at station 330

Harpacticoid total density showed a very similar trend at both stations. A slight increase from the beginning toward the end of March was followed by a decrease in April at the end of the diatom bloom (Fig.II.13.a). Total densities rose during the *Phaeocystis* bloom to a maximum in June. At station 330 total density decreased again in July. The significant temporal pattern (Table II.3) resulted from significant differences between April and May or June (twice $p < 0.01$) and between 9th March and June ($p < 0.05$).

ANOVA	df	df	Density		Species richness	
	Effect	Error	F ratio	p value	F ratio	p value
Station	1	20	4.18334	0.05421	*21.7913*	*0.00015*
Time	4	20	*3.7476*	*0.01967*	*4.89563*	*0.00645*
Station*Time	4	20	0.68955	0.60771	*6.39078*	*0.00176*

Table II.3: Results of the 2-way fixed-factor ANOVA analyzing the effect of station, time and the interaction term station*time on total densities and number of species

Species richness revealed exactly the same pattern as density at station 215, reaching maximum values in June at the end of the *Phaeocystis* bloom (Fig.II.13.c). An opposite trend of density and species richness typified station 330 (Fig.II.13.d). At station 330 a huge increase in species richness was observed between the end of March and the end of April, whereas density decreased in this period. In April density was even lowest while species richness was highest. Species richness decreased during the *Phaeocystis* bloom as long as density was rising. When density dropped in July, species richness increased again. Consequently, species richness showed an opposite course at station 215 and 330 (Fig.II.13.b), reflected in the significant effect of the interaction term station*time (Table II.3). Both stations also significantly differed in overall species richness (Table II.3), which was generally higher at station 330 than at station 215. In June however more species were encountered at station 215 than at station 330. The significant temporal pattern (Table II.3) reflected significant differences in species richness between 9th March and April or May or June (3x $p < 0.01$) and between 31st March and April ($p < 0.05$).

3.2.2 Harpacticoid community changes

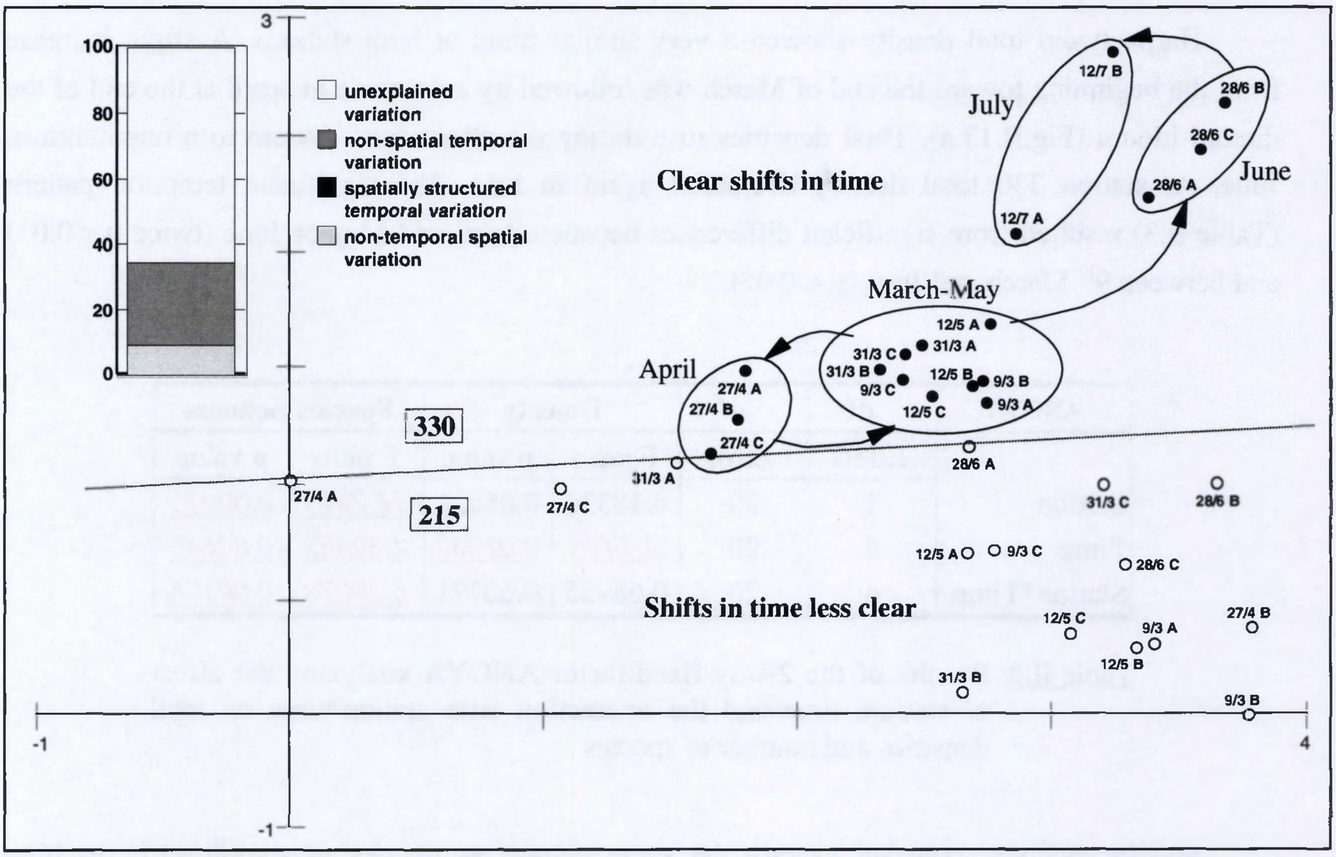


Fig.II.14: Plot of the replicates of each date for stations 215 and 330 in a DCA based on total absolute species abundances, the different proportions of variation in the pCCAs are represented in the upper left corner.

Overall analysis	Analysis	Explanatory variables (dummy variables !)	Covariables (dummy variables !)	Eigenvalue	% of total variation	p value	
Total variation	CA	none	none	4.237			1
Total explained variation	CCA	stations and dates	none	1.488	35	< 0.001	2
Spatially structured variation = effect station + station*time	CCA	stations	none	0.399	9	< 0.001	3
Temporally structured variation = effect time + station*time	CCA	dates	none	1.094	26	< 0.001	4
Non-temporal spatial variation = effect station	pCCA	stations	dates	0.394	9	< 0.001	5
Non-spatial temporal variation = effect time	pCCA	dates	stations	1.089	26	< 0.001	6
Spatially structured temporal variation = effect station*time				0.005	0		= 4 -6
Unexplained variation				2.749	65		= 2 -1

Table II.4: Results of the pCCA analyzing the effect of station, time and the interaction term station*time on total absolute species abundances

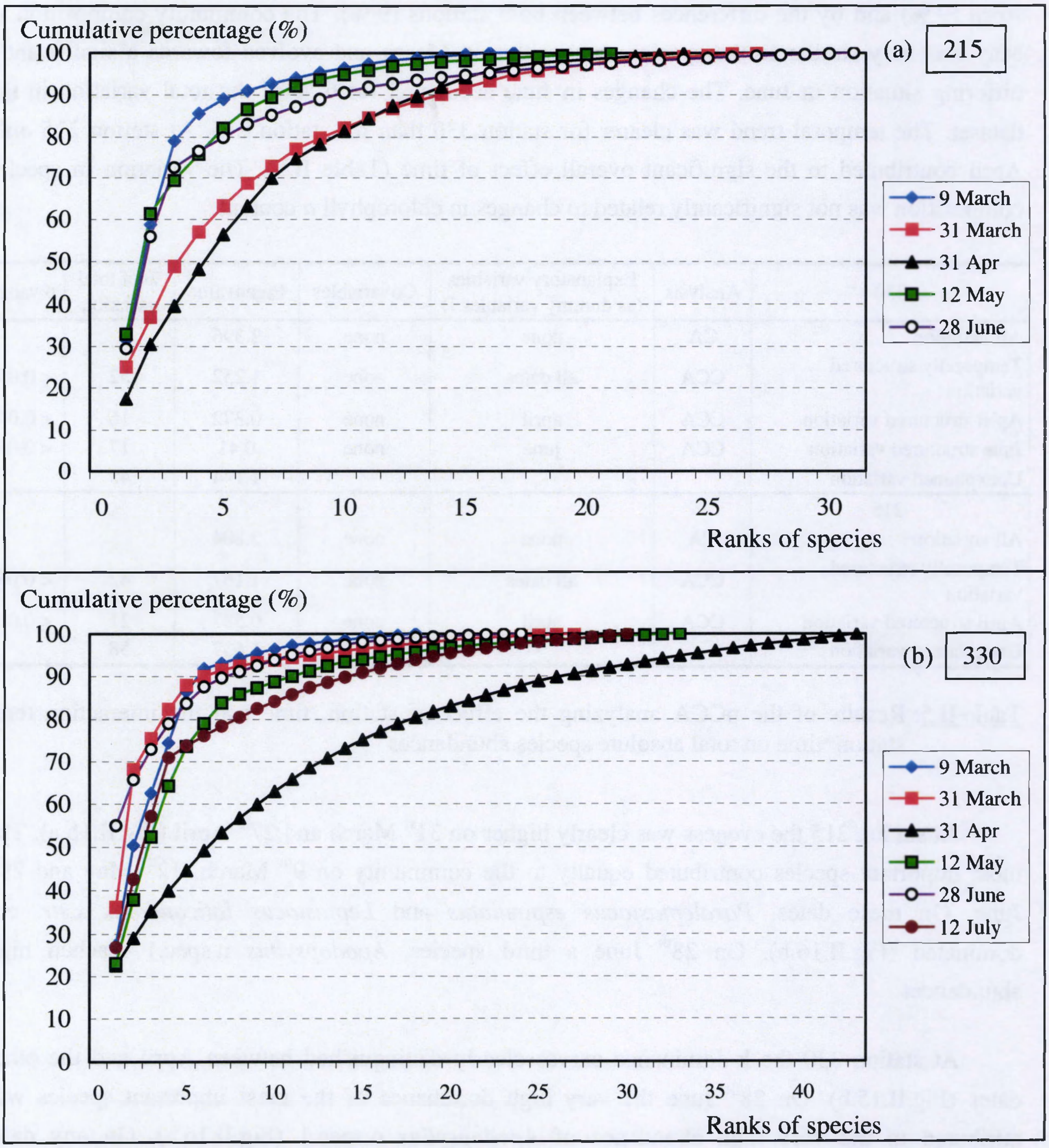
The harpacticoid fauna significantly varied by station and significantly changed through time (Table II.4, Fig.II.14). The highest proportion of variation was induced by community changes in April (9 %) and by the differences between both stations (9 %). The community composition in May was very similar to the species composition in March and evolved towards a significantly differing situation in June. The changes in June accounted for 6 % of the total variation in the dataset. The temporal trend was clearer for station 330 than for station 215. At station 215 only April contributed to the significant overall effect of time (Table II.5). The variation in species composition was not significantly related to changes in chlorophyll *a* content.

330	Analysis	Explanatory variables (as dummy variables !)	Covariables	Eigenvalue	% of total variation	p value
All variation	CA	none	none	2.396		
Temporally structured variation	CCA	all dates	none	1.252	52	< 0.05
April structured variation	CCA	april	none	0.372	16	< 0.05
June structured variation	CCA	june	none	0.41	17	< 0.05
Unexplained variation				1.144	48	
215						
All variation	CA	none	none	2.804		
Temporally structured variation	CCA	all dates	none	1.167	42	< 0.05
April structured variation	CCA	april	none	0.587	21	< 0.05
Unexplained variation				1.637	58	

Table II.5: Results of the pCCA analyzing the effect of station, time and the interaction term station*time on total absolute species abundances

At station 215 the eveness was clearly higher on 31st March and 27th April (Fig.II.15.a). The most important species contributed equally to the community on 9th March, 12th May and 28th June. On these dates, *Paraleptastacus espinulatus* and *Leptastacus laticaudatus s.str.* co-dominated (Fig.II.16.b). On 28th June a third species, *Apodopsyllus* n.spec.1 reached high abundances.

At station 330 the k-dominance curves clearly distinguished between April and the other dates (Fig.II.15.b). On 28th June the very high dominance of the most important species was attributed to the very high abundance of *Apodopsyllus* n.spec.1 (Fig.II.16.a). On any date, *Leptastacus laticaudatus s.str.* and *Kliopsyllus* n.spec. 2 reached similar densities and co-dominated on 9th March and 31st March, while *Arenosetella* n.spec.1 was the second most abundant species on 12th May.



<u>Fig II.15</u>: k-dominance curves of each date for station 215 (a) and 330 (b)

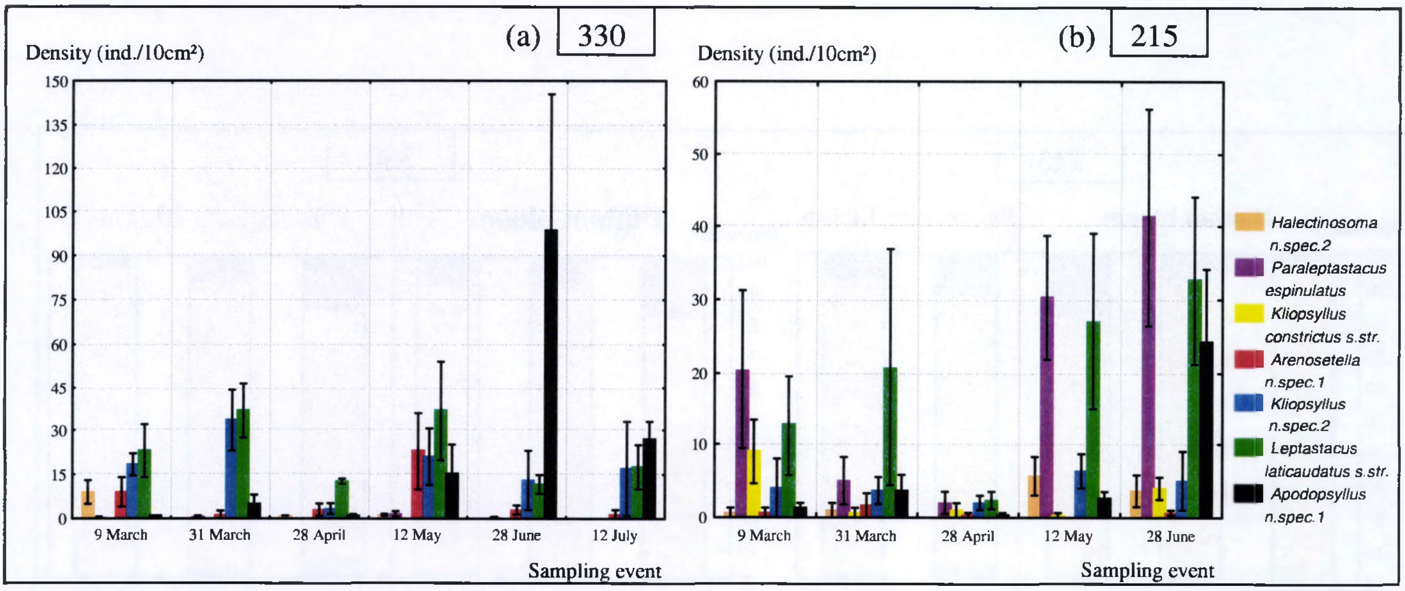


Fig II.16: Mean absolute abundances of the most important species on each date at stations 330 (a) and 215 (b)

3.2.3 Ecotype proportions

Ecotype	Analysis	Effect	df Effect	df Error	F	p value
Epibenthic species	Kruskal-Wallis ANOVA	Station	1	28		0.1399
		Time	4	25		0.4759
Endobenthic species	Kruskal-Wallis ANOVA	Station	1	28		*0.0396*
		Time	4	25		0.5311
Intersitial species	2-way ANOVA	Station	1	20	0.80262	0.3810
		Time	4	20	0.93156	0.4656
		Station*Time	4	20	1.15061	0.3618
Free-swimming species	Kruskal-Wallis ANOVA	Station	1	28		0.5949
		Time	4	25		*0.0364*

Table II.7: Results of the analyses of the effect of station, time and the interaction term station*time if possible on ecotype proportions

Ecotype proportions did not significantly change through time during the spring phytoplankton bloom (Table II.7). The significant temporal pattern for free-swimming species resulted from significant differences in May and June in relation to 9th March ($p < 0.05$), caused by the presence of *Temora longicornis* on top of the sediment in May (5 % at both stations) and other planktonic species in June (2 % at both stations). Throughout the whole period endobenthic species were more abundant at station 330 than at station 215 (Fig. II.17; Table II.7). At station 215 epi- and endobenthic species increased during the diatom bloom to a maximum at the end of April (19 % epibenthic and 11 % endobenthic species) and decreased again during the *Phaeocystis* bloom (Fig.II.17). At station 330 the highest percentages of interstitial species were found in June and July (90 % and 95 % respectively).

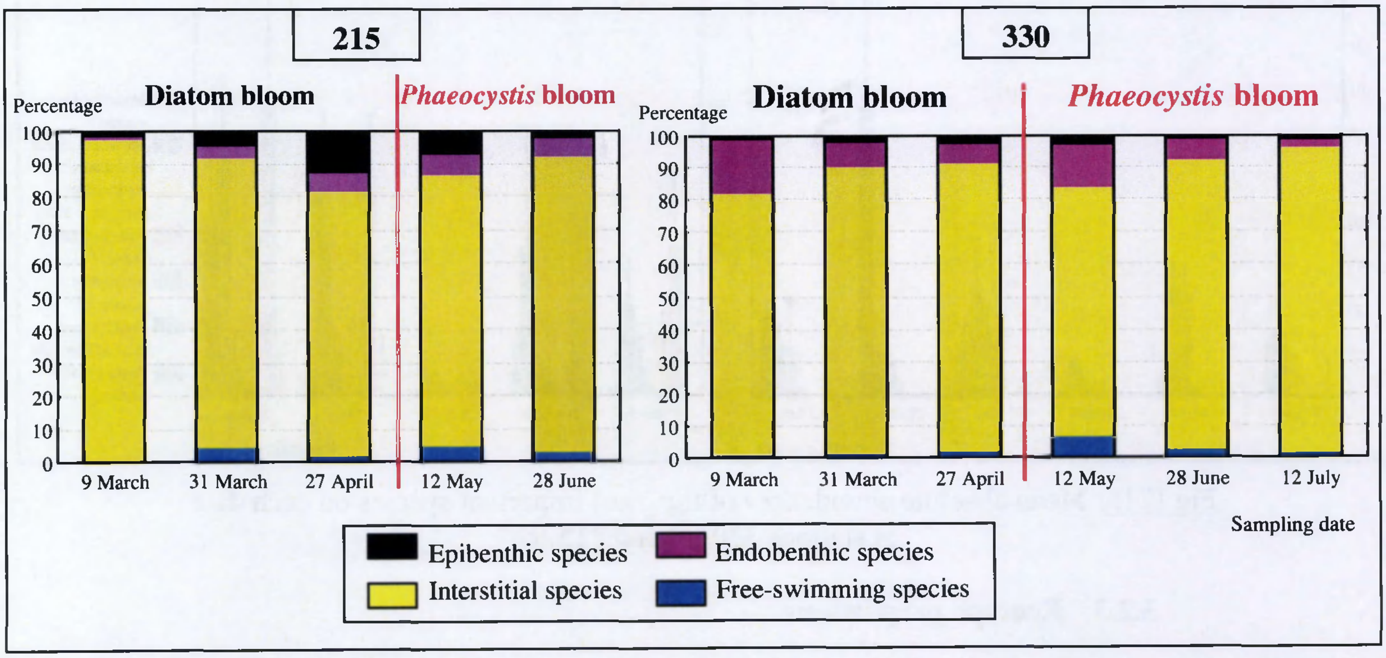


Fig.II.17: Mean relative abundances of different ecotypes at stations 215 and 330

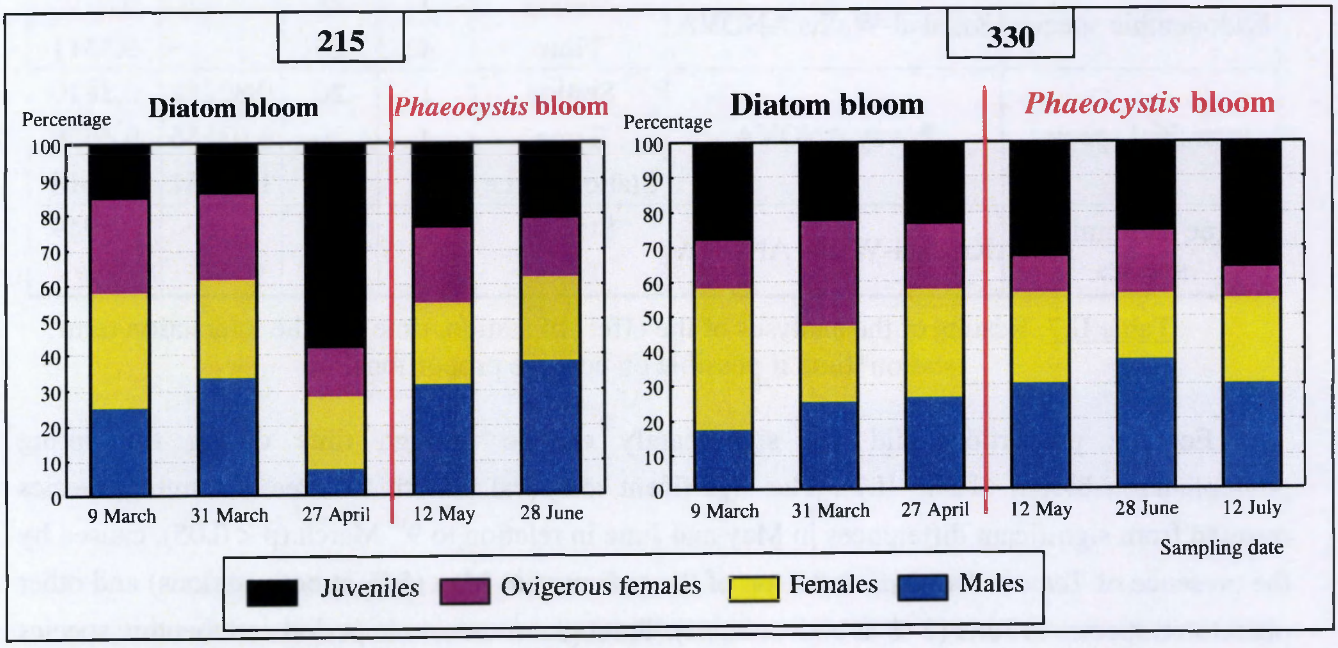


Fig.II.18: Mean relative abundances of different life history stages at stations 215 and 330

3.2.4 Life history stages

Life history stages	Analysis	Effect	df Effect	df Error	F	p-level
Males	2-way ANOVA	Station	1	20	1.18659	0.2890
		Time	4	20	2.93588	0.0463
		Station*Time	4	20	0.83805	0.5171
Females	2-way ANOVA	Station	1	20	0.43692	0.5162
		Time	4	20	2.99884	0.0433
		Station*Time	4	20	0.81345	0.5314
Ovigerous females	2-way ANOVA	Station	1	20	2.59215	0.1231
		Time	4	20	3.17546	0.0358
		Station*Time	4	20	1.68518	0.1928
Copepodites	Kruskal Wallis ANOVA	Station	1	28		0.0294
		Time	4	25		0.1687

Table II.8: Results of the analyses of the effect of station, time and the interaction term station*time if possible on the proportions of life history stages

Significant temporal gradients were discerned for males, females and ovigerous females (Table II.8). The contribution of females significantly decreased from 9th March in relation to all succeeding months ($p < 0.05$) whereas the relative abundance of males significantly increased between 9th March ($p < 0.01$) or 31st March ($p < 0.05$) and June. The percentage of ovigerous females dropped significantly between 31st March and May or June (twice $p < 0.01$). Fig.II.18 shows that a very high mean relative abundance of juveniles (59 %) was recorded at the end of April at station 215.

3.3 Vertical distribution of harpacticoids

3.3.1 Density

Throughout the whole period a minimum of about 60 % harpacticoids was present in the upper 5 cm of the sediment, with a mean of 75 % over the whole period. Only on 9th March at station 215 the major proportion of the population (53 %) was recorded from deeper levels. Figure II.19 illustrates that harpacticoids are more concentrated in the upper sediment layers in May and June at both stations and on 31st March at station 330 relative to 9th March and 27th April, when harpacticoids were more evenly distributed among depth layers. The temporal differences in vertical distribution were not defined as significant (effect time*depth, Table II.9). Only the effect of depth unrelated to time was judged significant at both stations (Table II.9), attributed to overall higher densities in the depth layers 0-1 cm and 1-2 cm (2x $p < 0.001$).

Station 215 + 330	ANOVA in a split-plot design					pRDA(1)
Effect	Error	df Effect	df Error	F ratio	p value	p value
Station	Replicate{station*time}	1	20	2.49111	0.130	0.057
Time	Replicate{station*time}	4	20	*2.99000*	*0.044*	*0.016*
Depth	Depth*replicate{station*time}	7	140	*14.71677*	*0.000*	*0.001*
Time*Station	Replicate{station*time}	4	20	2.80628	0.054	0.930
Depth*Station	Depth*replicate{station*time}	7	140	*2.48000*	*0.020*	*0.001*
Depth*Time	Depth*replicate{station*time}	28	140	1.19167	0.250	0.063
Station*Time*Depth	Depth*replicate{station*time}	28	140	1.15889	0.283	0.417
Station 215		df	df			
Effect	Error	Effect	Error	F ratio	p value	
Time	Replicate{station*time}	4	10	*4.022039*	*0.034*	
Depth	Depth*replicate{station*time}	7	70	*2.715466*	*0.015*	
Time*Depth	Depth*replicate{station*time}	28	70	0.928577	0.574	
Station 330		df	df			
Effect	Error	Effect	Error	F ratio	p value	
Time	Replicate{station*time}	4	10	1.22296	0.361	
Depth	Depth*replicate{station*time}	7	70	*18.53903*	*0.000*	
Time*Depth	Depth*replicate{station*time}	28	70	1.59214	0.060	

(1) Monte-Carlo permutation tests restricted for split-plot design

Table II.9: Results of the analyses of the effect of station, time, depth and the interactions between these factors on densities per depth layer

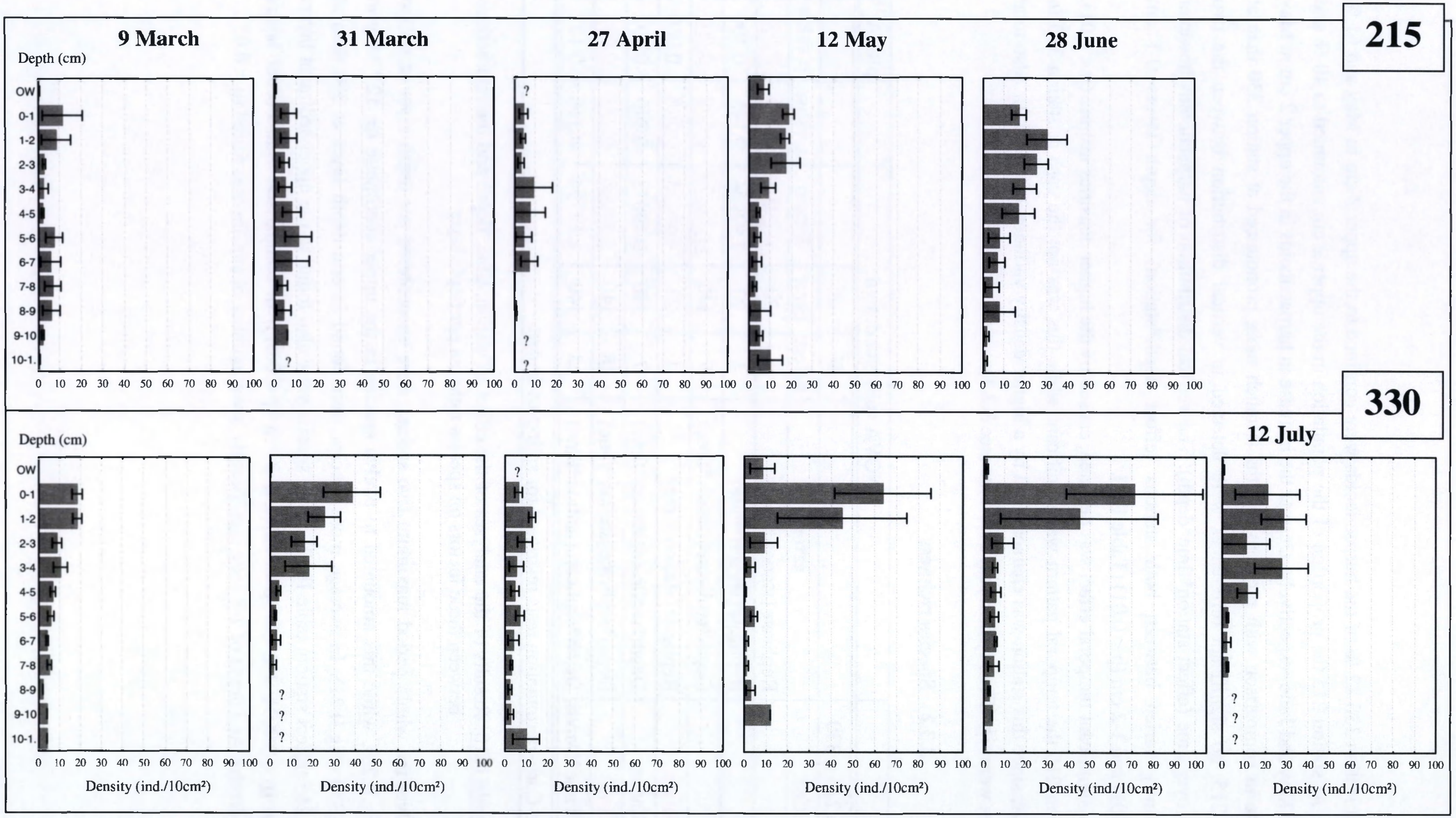


Fig.II.19: Total mean density with standard error per depth layer and per sampling date at stations 215 and 330
A question mark indicates that no data are available from that depth layer.

At station 330 82 % of the harpacticoids were confined to the upper 2 cm in May and 61 % in June. At station 215 the proportion of the population in the upper 2 cm amounted to 40 % and 26 % in May and June respectively. Despite the increase in harpacticoids in the upper 2 cm in May and June in comparison with previous months is much more pronounced at station 330 than at station 215, no significant differences were detected in vertical distribution between the two stations over time (effect station*time*depth). The vertical distribution of harpacticoids however significantly varied between both stations (effect depth*station) for depth layers 0-1 cm ($p < 0.001$) and 1-2 cm ($p < 0.01$) (Table II.9).

A significant temporal effect was detected, caused by the higher densities in June ($p < 0.01$). At station 215 the temporal pattern was significant while this was not the case at station 330 in ANOVA, since this station was characterized by a higher density variation (Table II.9). Also total densities were significantly different over time (see 3.2.1).

3.3.2 Species richness

	ANOVA split plot design					pRDA(1)
Station 215 + 330		df	df			
Effect	Error	Effect	Error	F ratio	p value	p value
Station	Replicate{station*time}	1	20	*10.29592*	*0.004*	*0.006*
Time	Replicate{station*time}	4	20	1.92964	0.145	0.409
Depth	Depth*replicate{station*time}	7	140	*11.81873*	*0.000*	*0.001*
Time*Station	Replicate{station*time}	4	20	*4.66785*	*0.008*	0.060
Depth*Station	Depth*replicate{station*time}	7	140	0.49072	0.840	0.292
Depth*Time	Depth*replicate{station*time}	28	140	*1.64090*	*0.033*	*0.002*
Station*Time*Depth	Depth*replicate{station*time}	28	140	1.12794	0.316	0.122

(1) Monte-Carlo permutation tests restricted for split-plot design

Table II.10: Results of the analyses of the effect of station, time, depth and the interactions between these factors on species richness per depth layer

Over the whole period maximum five species were encountered per depth layer at station 215 (Fig.II.20), while this amounted to twelve species in the upper centimetre on 12th May at station 330 (Fig.II.21). In average more species were found in one depth layer at 330 than at station 215 (effect station, table II.10). More species were also found in the upper sediment layers (0-1 cm ($p < 0.001$), 1-2 cm ($p < 0.001$), 2-3 cm ($p < 0.01$)) in comparison with deeper layers (effect depth). At a depth of 7-8 cm a significantly lower number of species was found ($p < 0.05$).

215

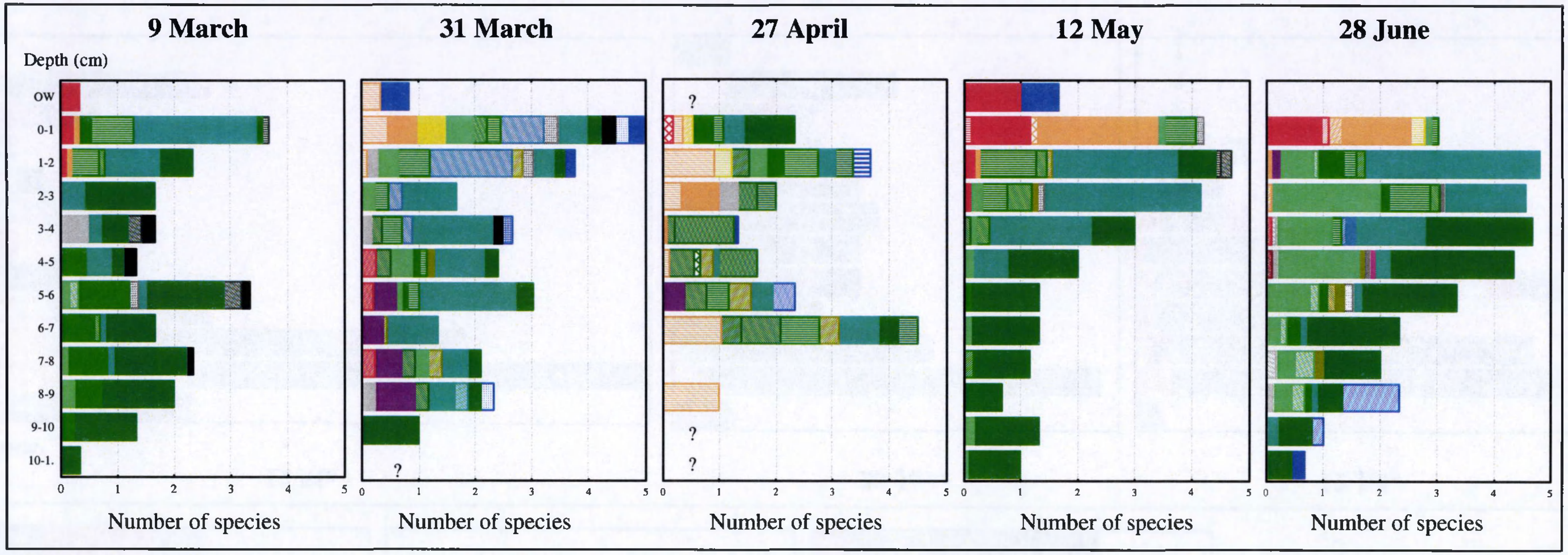


Fig.II.20: Mean species richness per depth layer and per sampling date at station 215 is represented by the total bars. The different colours within the bars reflect the evenness or the importance of each species per depth layer, mean density of each species being represented as a proportion of the species richness. Hence it is clear how many species were present in the three replicates, contributing to the mean species richness per depth layer. Red coloured patterns are epibenthic species, orange coloured patterns are endobenthic species, bright blue coloured patterns are phytal or free-swimming species and all other colours point to interstitial species. A question mark indicates that no data are available from that depth layer.

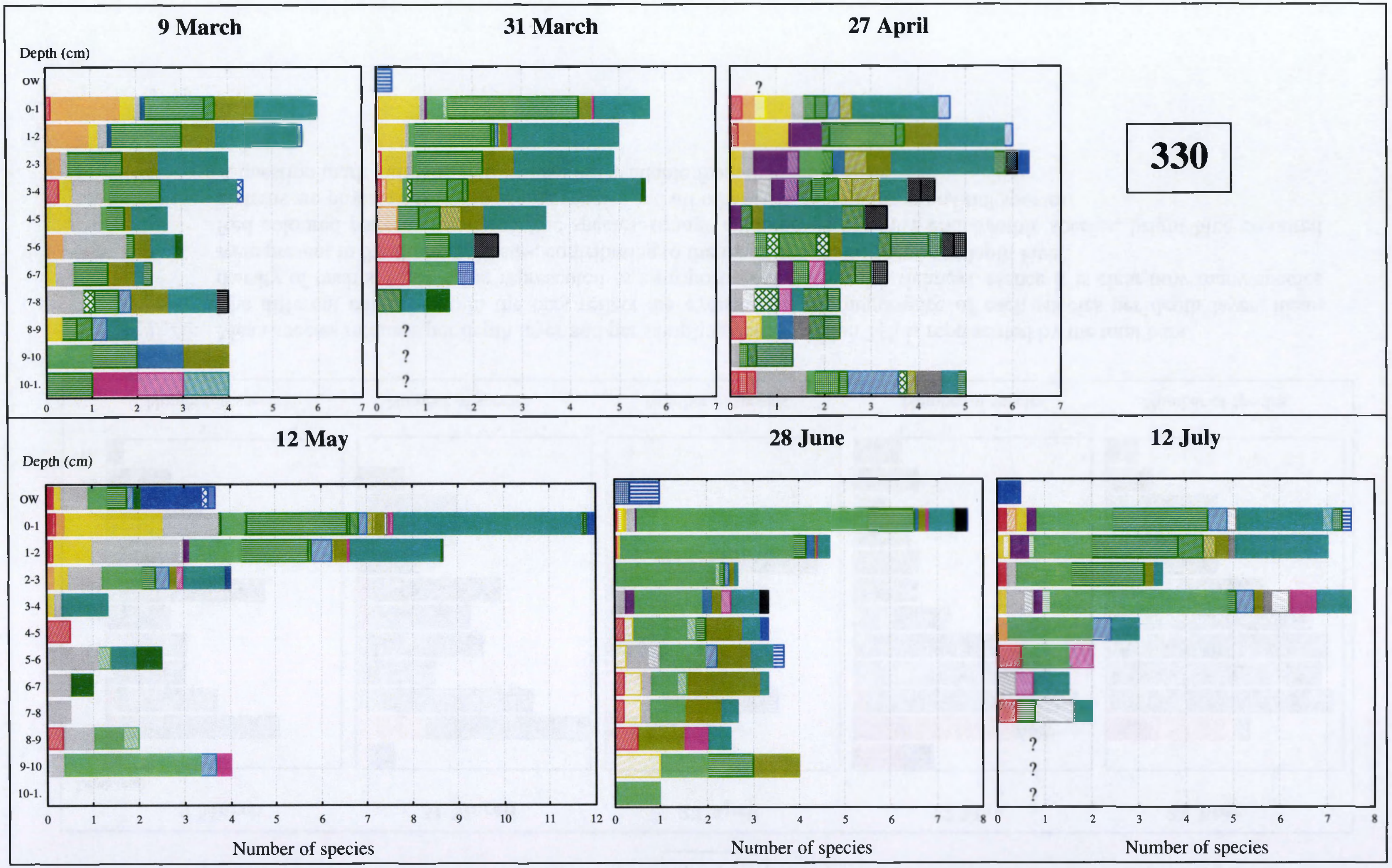


Fig.II.21: Mean species richness per depth layer and per sampling date at station 330 is represented by the total bars.

The different colours within the bars reflect the eveness or the importance of each species per depth layer, mean density of each species being represented as a proportion of the species richness. Hence it is clear how many species were present in the three replicates, contributing to the mean species richness per depth layer.

Red coloured patterns are epibenthic species, orange coloured patterns are endobenthic species, bright blue coloured patterns are phytal or free-swimming species and all other colours point to interstitial species.

A question mark indicates that no data are available from that depth layer.

A clear temporal trend in mean species number per depth layer was not observed. For specific depth layers however significant changes were recorded through time (effect depth*time). In May more species were present in the upper 3 cm of the sediment (0-1 cm ($p < 0.001$), 1-2 cm ($p < 0.01$), 2-3 cm ($p < 0.01$)). In April the upper cm yielded a lower number of species ($p < 0.05$) while more species were concentrated in the deeper layers (6-7 cm ($p < 0.05$)). More copepod species also preferred to stay deeper in the sediment on 9th March in comparison with the succeeding months (7-8 cm ($p < 0.05$). The effect time*station reflected the different trend in species richness between both stations.

3.3.3 Species composition

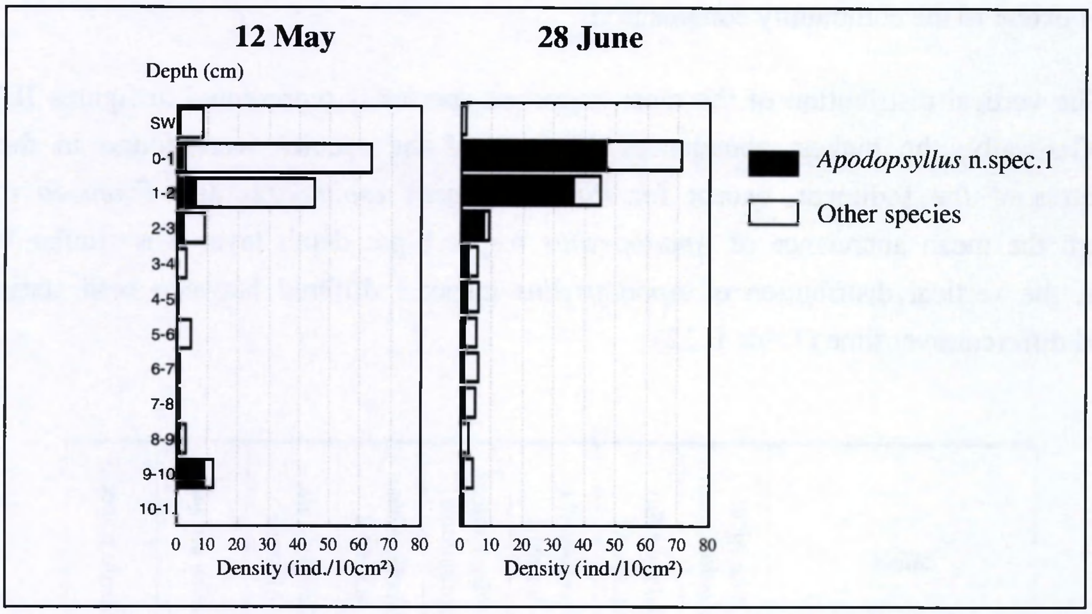


Fig.II.22: Mean absolute densities of *Apodopsyllus* n.spec.1 per depth layer in relation to the importance of other species on 12th May and 28th June at station 330

Fig.II.20 and II.21 illustrate that the species composition between both stations differed considerably and that a lot of species appeared only in April and were not encountered at any other date. April was also characterized by a higher eveness of the species, detected in all depth layers. Below 2 cm depth the variation between the replicates was much higher than at any other moment, while the mean number of species per depth layer was not higher than for the other recordings. The unique characteristics of the harpacticoid community in April applied to both stations.

At station 215 the harpacticoid community of 9th March, 12th May and 28th June was characterized by a high proportion of a few and largely the same species through the depth of the sediment. On 31st March an intermediate species assemblage between 9th March and 28th April was discerned. Especially in the surface layers of the sediment most of the species varied between the replicates. One species (*Leptastacus laticaudatus s.str.*) dominated the community through the depth of the sediment but eveness was already higher at this time.

In June *Apodopsyllus* n.spec.1 became very abundant (17 % of the total density) and preferred the upper 5 cm of the sediment. The same happened in June at station 330, *Apodopsyllus* n.spec. 1 accounting for 55 % of the total density. This species made up 67 % and 54 % in the 0-1 cm and 1-2 cm depth layer respectively (Fig.II.22).

At station 330 the species assemblage on 31st March was very similar to the situation on 9th March, in contrast with station 215. At station 330 the species assemblage in May and June also deviated from that on 9th March. On 12th May a lot of species occur in the upper 3 cm while the deeper layers were impoverished. In June a lot of the species had withdrawn to deeper levels while *Apodopsyllus* n.spec. 1 dominated the upper centimetres. In July more species contributed again in a higher extent to the community composition.

The vertical distribution of the most important species is represented in figures II.23 upto II.30. Generally, the highest abundances of most of the species were found in the upper centimetres of the sediment, except for *Paraleptastacus espinulatus* and *Evansula* n.spec.1. Although the mean abundance of *Apodopsyllus* n.spec.1 per depth layer was similar for both stations, the vertical distribution of *Apodopsyllus* n.spec.1 differed between both stations and behaved different over time (Table II.12).

effect	*Leptastacus laticaudatus s.str.*	*Apodopsyllus* n.spec.1	*Arenosetella* n.spec.1	*Paraleptastacus espinulatus*	*Halectinosoma* n.spec.2	*Thompsonula hyaenae*	*Ameira parvula*	*Evansula* n.spec.3
station	n.s.	n.s.	* *	* *	n.s.	*	* *	* *
time	n.s.	* *	n.s.	* *	n.s.	*	n.s.	n.s.
depth	* *	* *	n.s.	n.s.	* *	* *	* *	n.s.
depth x time	n.s.	n.s.	n.s.	n.s.	*	* *	*	*
depth x station	n.s.	* *	n.s.	n.s.	n.s.	* *	* *	* *
time x station	n.s.	n.s.	*	* *	*	n.s.	n.s.	n.s.
station x time x depth	* *	* *	*	n.s.	* *	*	* *	*

Table II.12: Results of the Monte-Carlo permutation tests restricted for split-plot design using pRDA testing the effect of station, time, depth and the interactions between these factors on the absolute densities of the most important species, * $p < 0.05$, ** $p < 0.01$

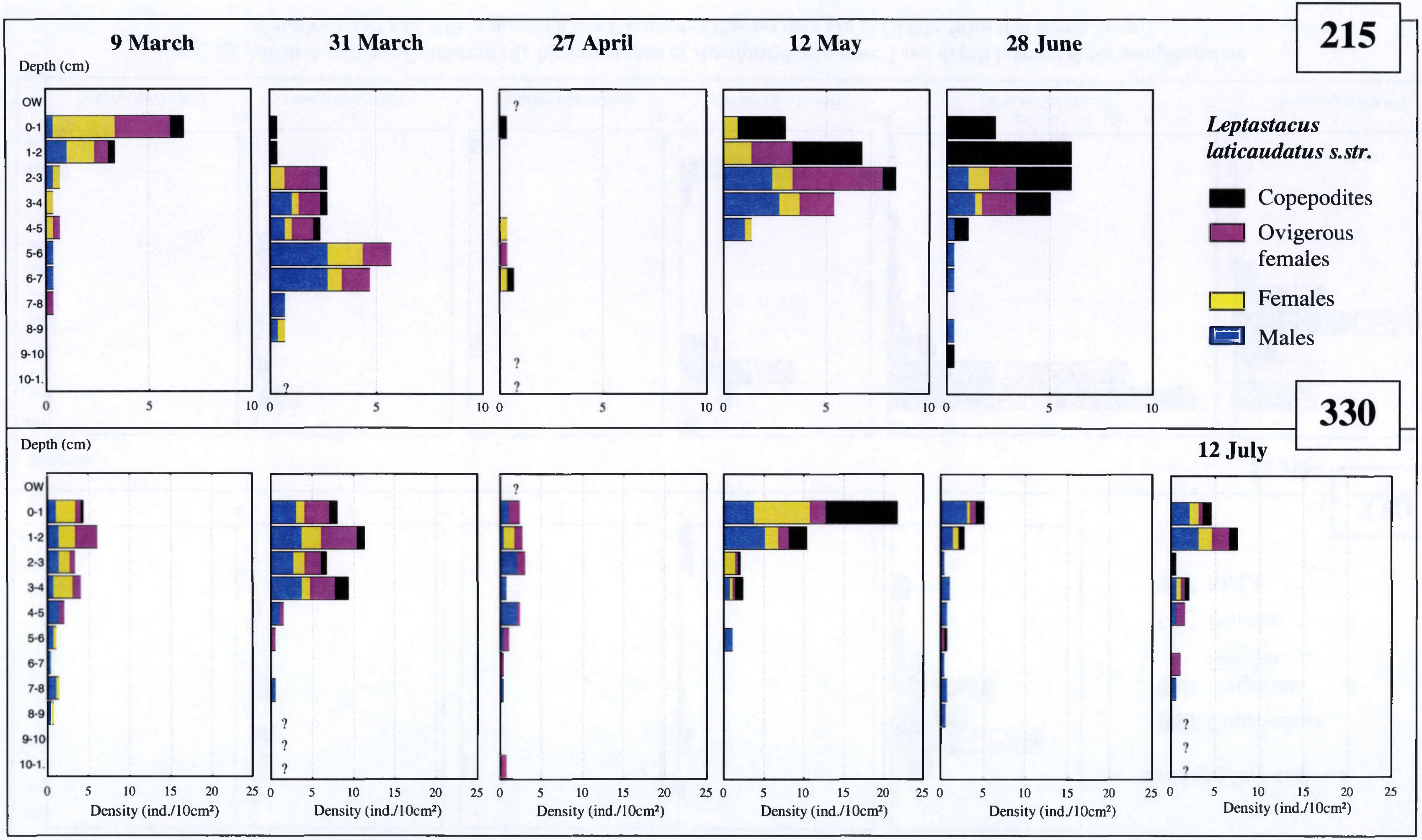


Fig.II.23: Mean densities of different life history stages of *Leptastacus laticaudatus s.str.* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

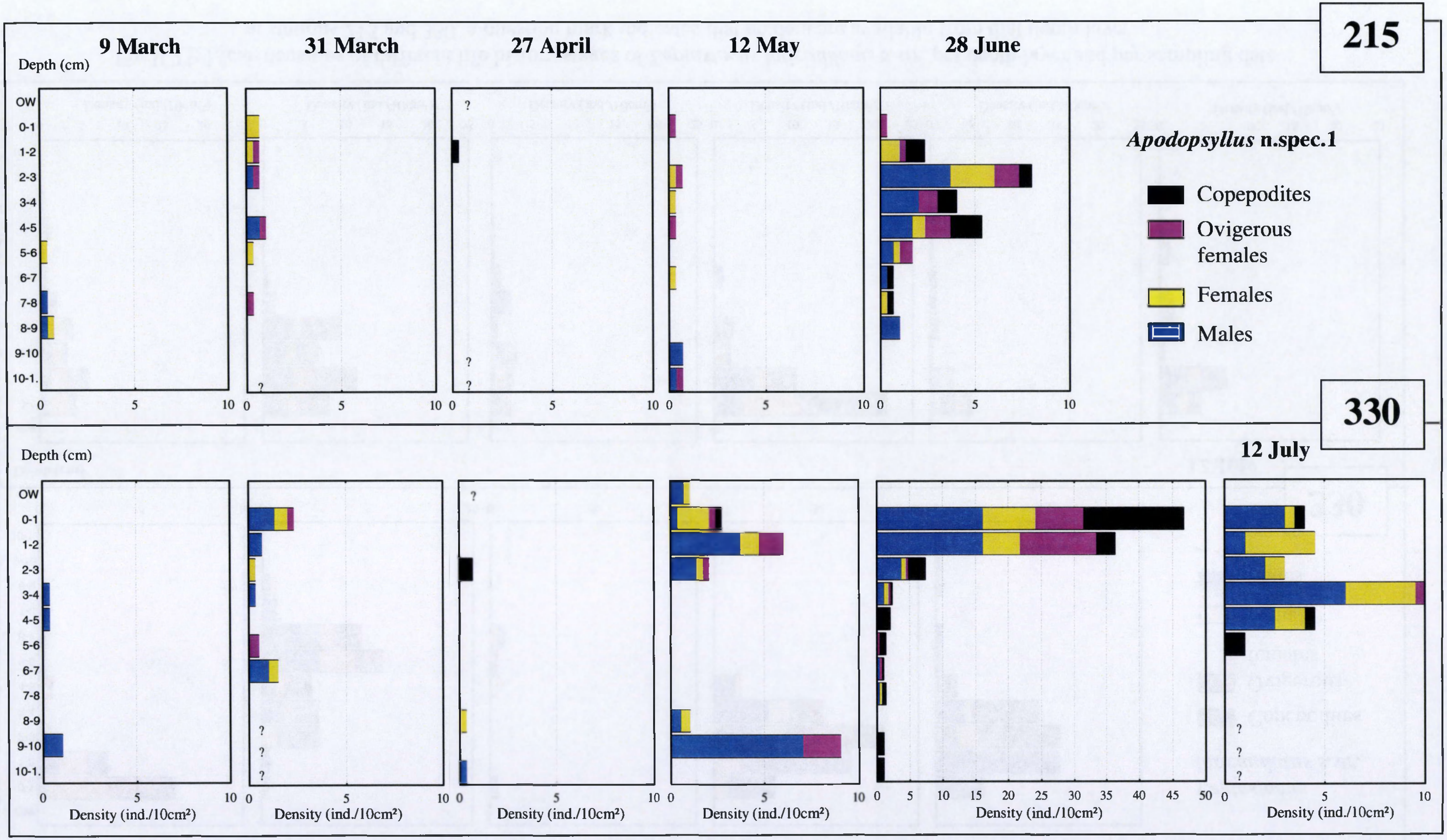


Fig.II.24: Mean densities of different life history stages of *Apodopsyllus* n.spec.1 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

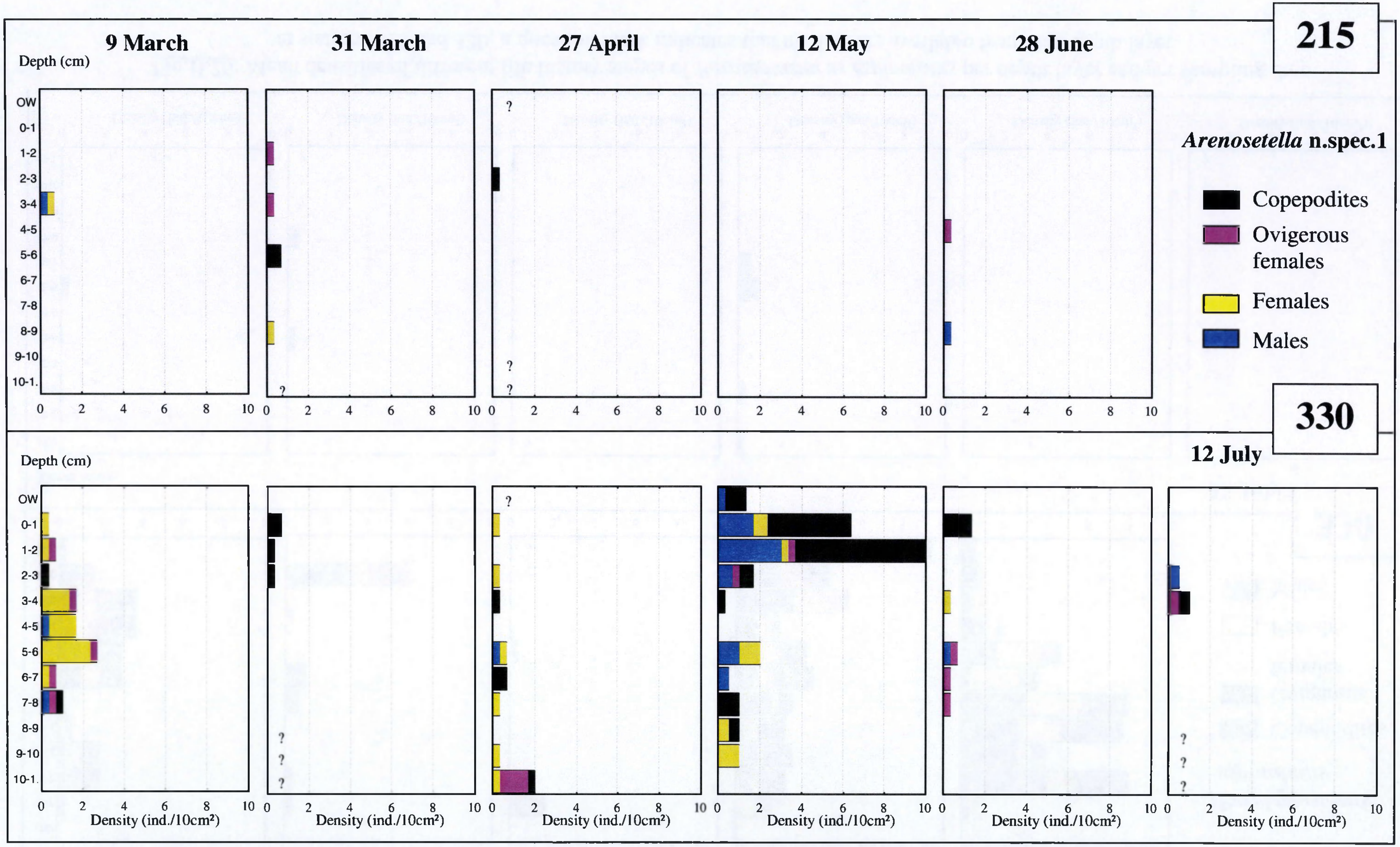


Fig.II.25: Mean densities of different life history stages of *Arenosetella* n.spec.1 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

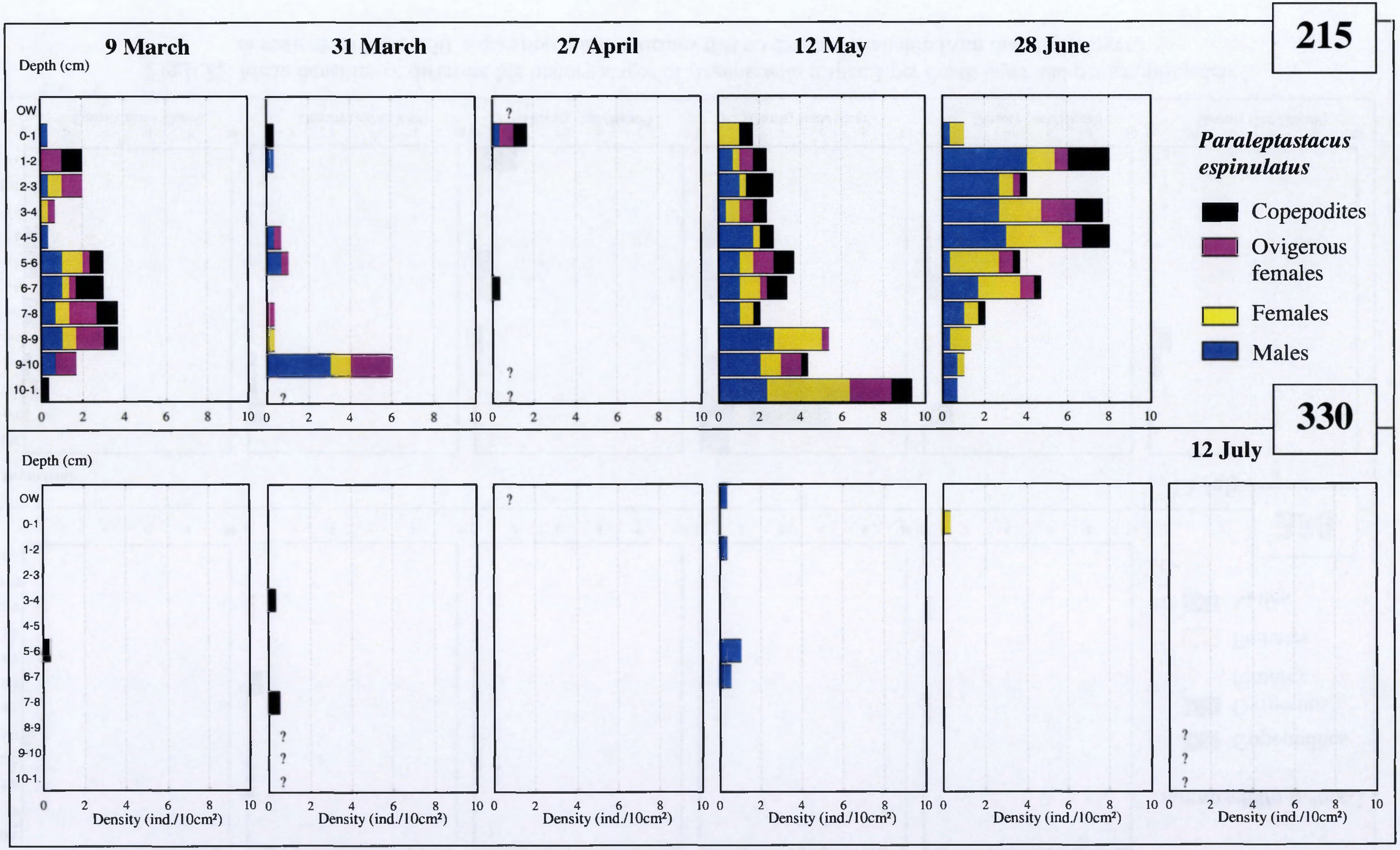


Fig.II.26: Mean densities of different life history stages of *Paraleptastacus espinulatus* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

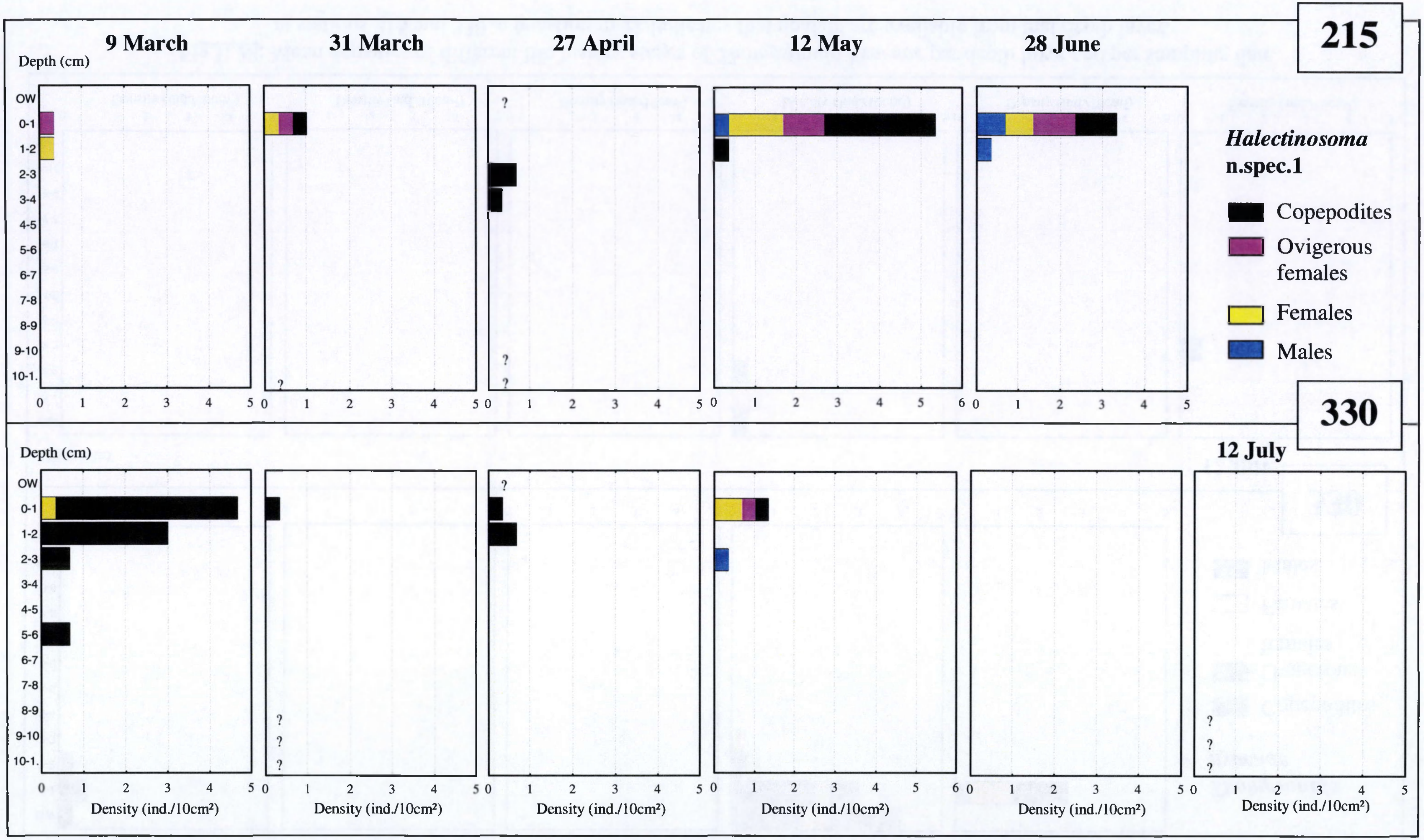


Fig.II.27: Mean densities of different life history stages of *Halectinosoma* n.spec.1 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

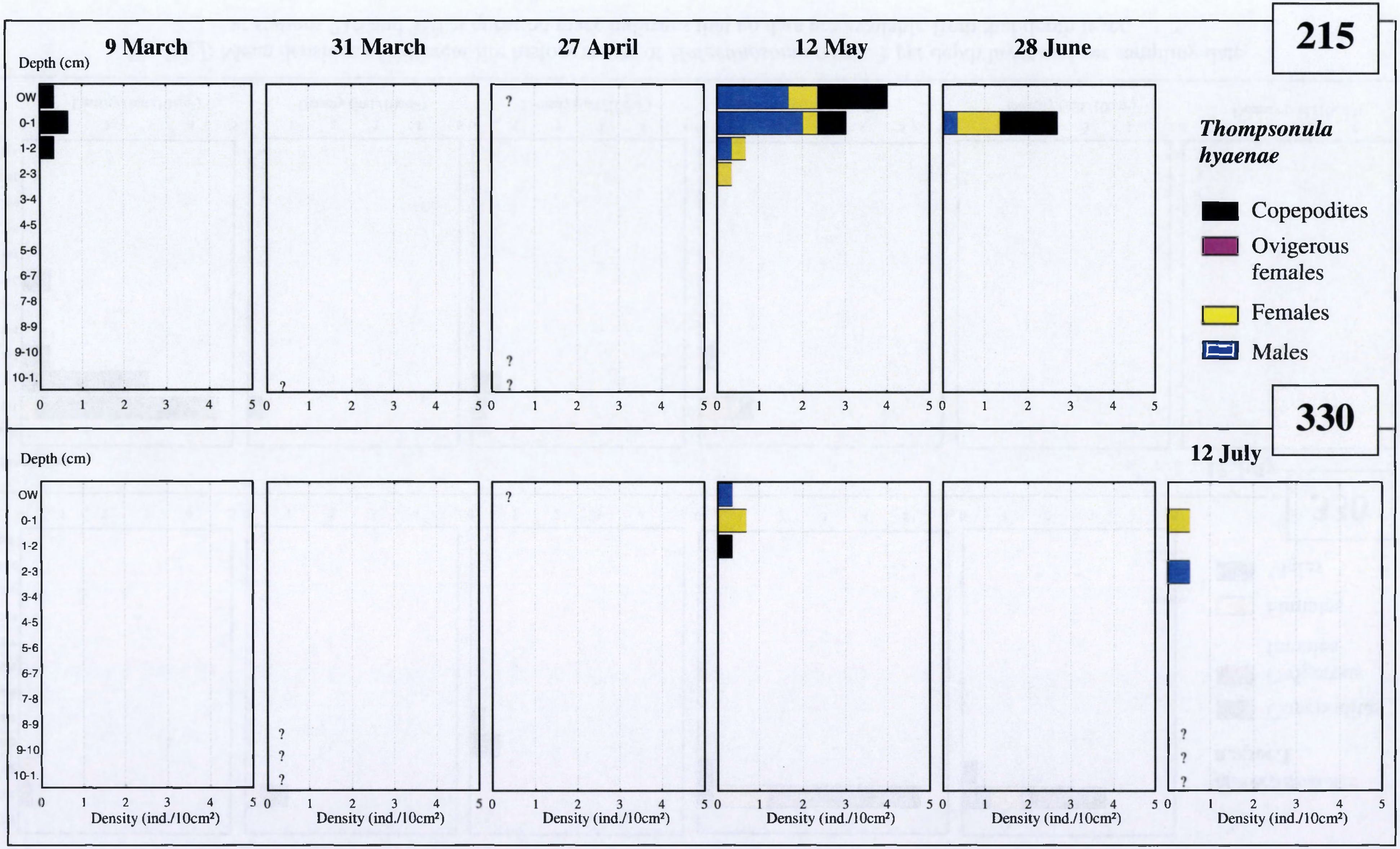


Fig.II.28: Mean densities of different life history stages of *Thompsonula hyaenae* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

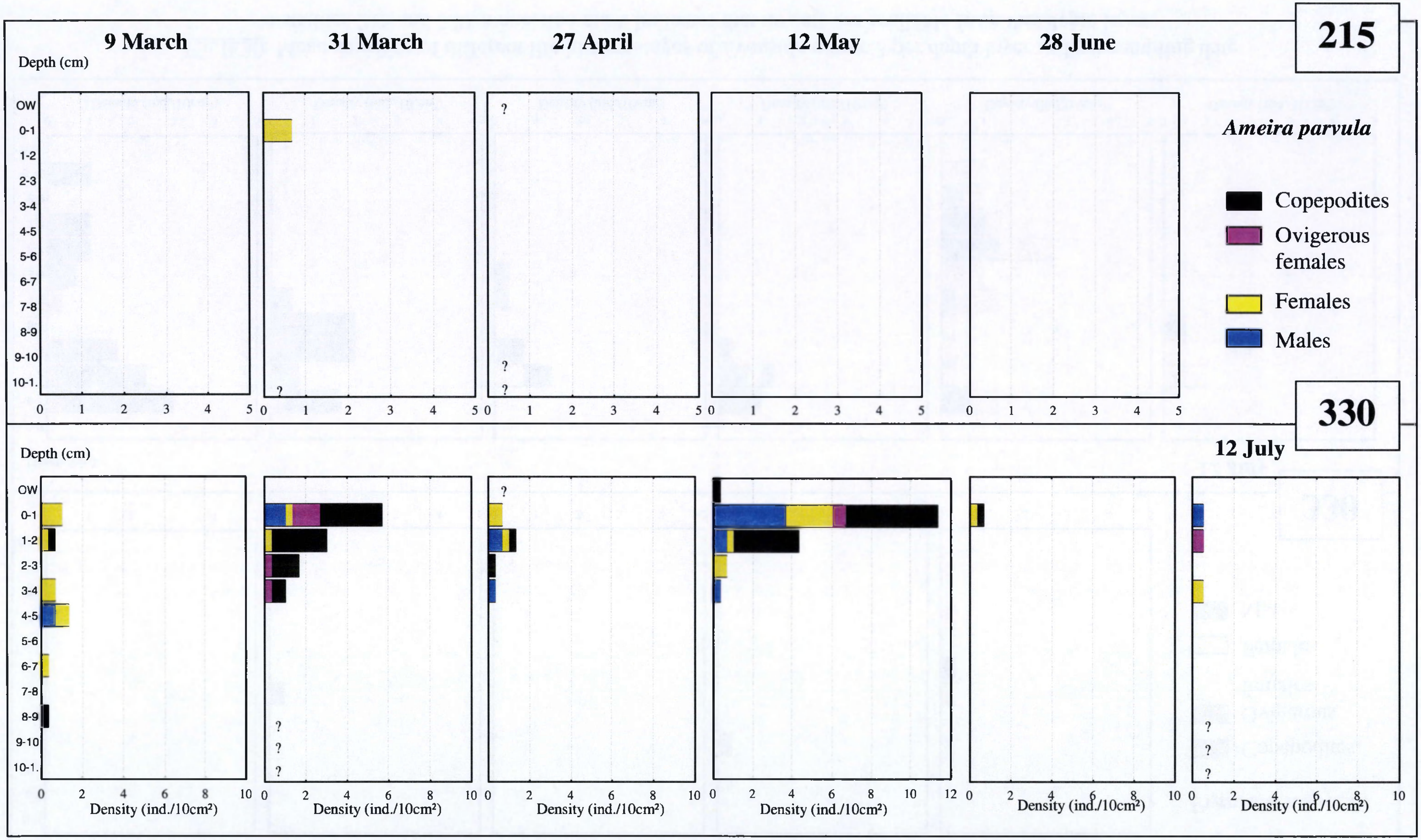


Fig.II.29: Mean densities of different life history stages of *Ameira parvula* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

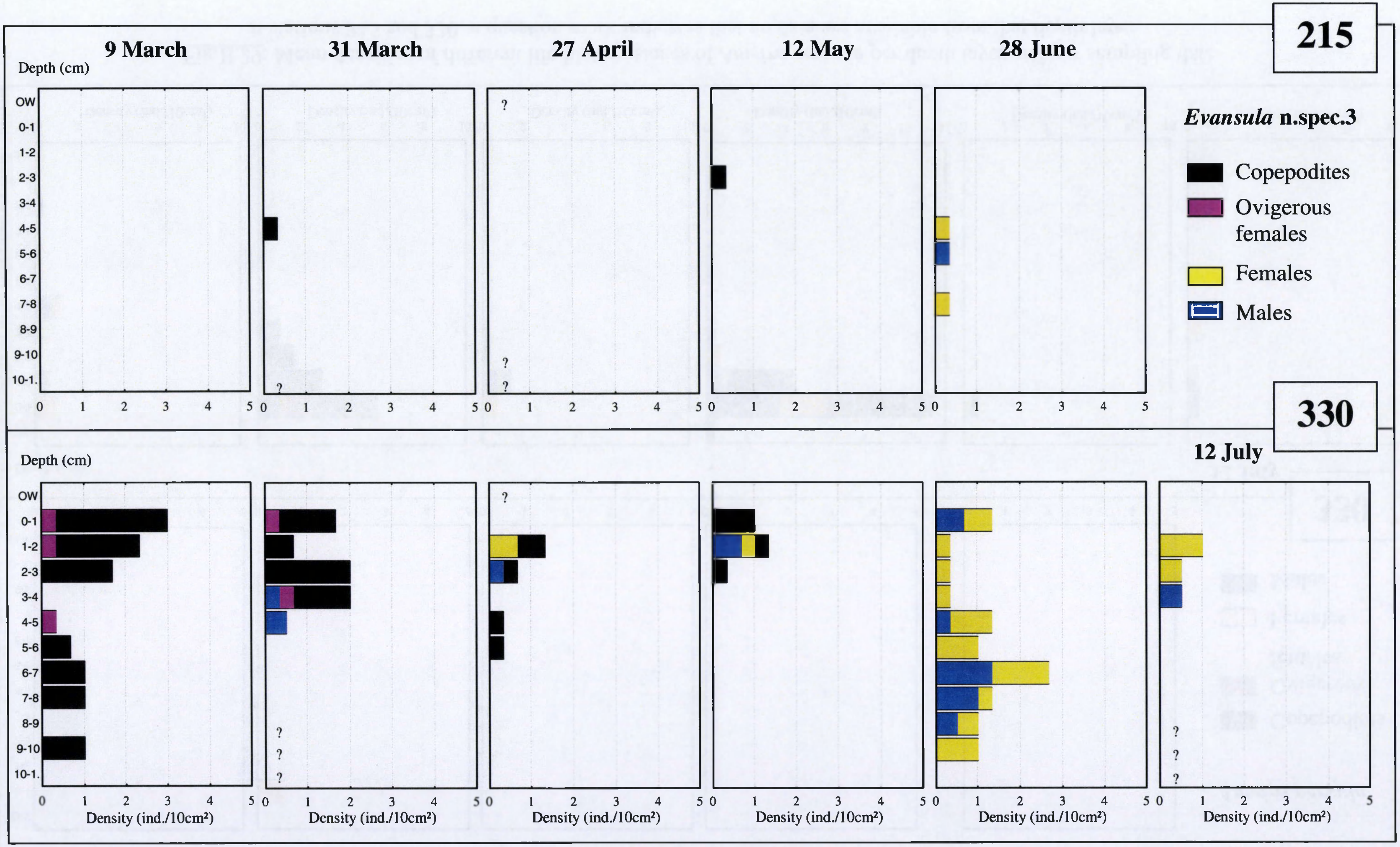


Fig.II.30: Mean densities of different life history stages of *Evansula* n.spec.3 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

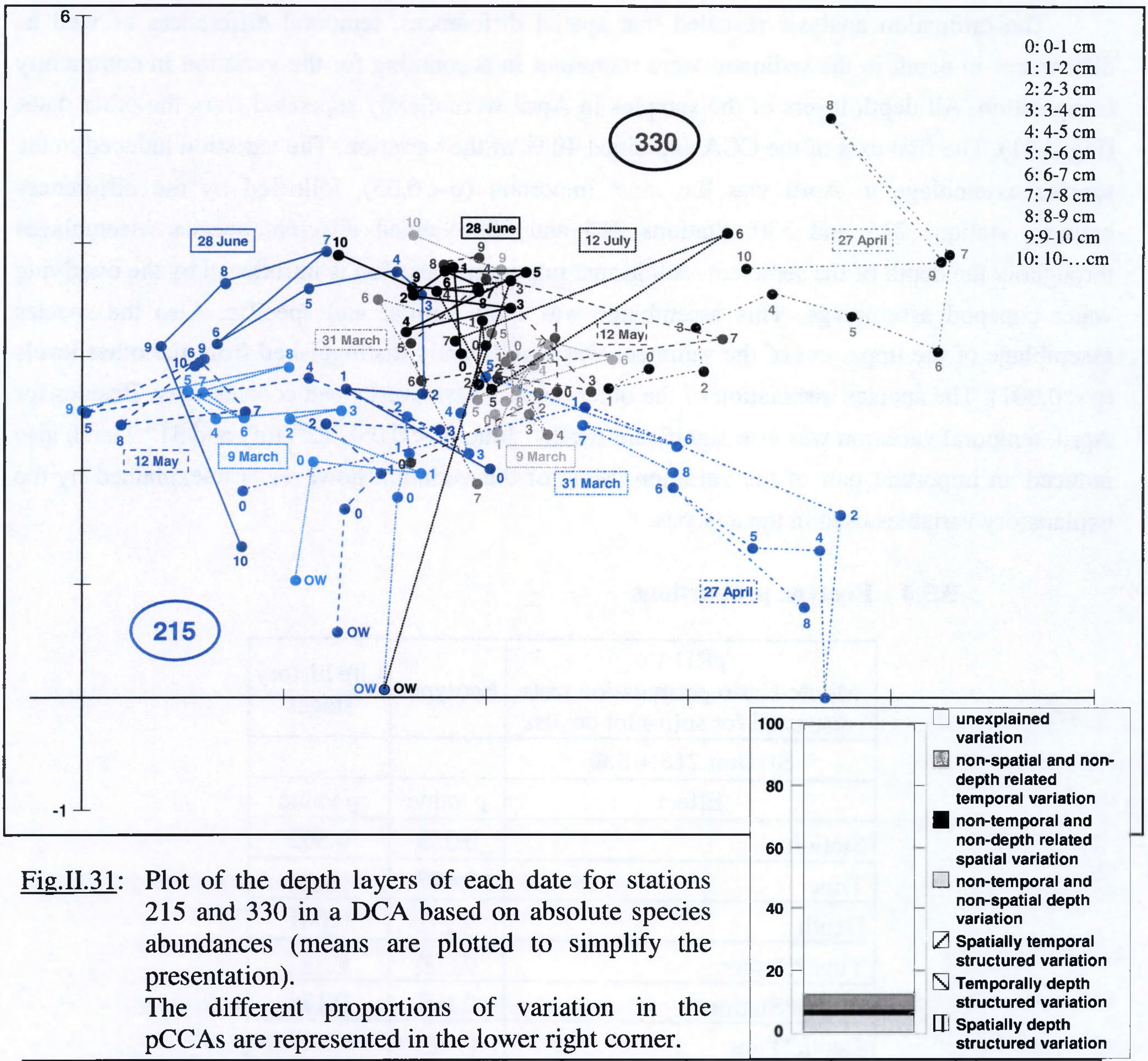


Fig.II.31: Plot of the depth layers of each date for stations 215 and 330 in a DCA based on absolute species abundances (means are plotted to simplify the presentation).
The different proportions of variation in the pCCAs are represented in the lower right corner.

	Analysis	Eigenvalue	% of total variation	p value [(1)]
Total variation	CA	19.509		
Spatial + temporal + depth structured variation	CA	2.464	12.63	
Non-temporal and non-depth related spatial variation	pCCA	0.352	1.80	0.026
Non-spatial and non-depth related temporal variation	pCCA	0.933	4.78	0.001
Non-temporal and non-spatial depth variation	pCCA	1.131	5.80	0.002
Spatially temporal structured variation = effect station*time	pCCA	0.005	0.03	0.029
Spatially depth structured variation = station*depth	pCCA	0.009	0.05	0.097
Temporally depth structured variation = time*depth	pCCA	0.034	0.17	0.465
Spatially and temporally depth structured variation = effect station*time*depth	pCCA	0.002	0.01	0.259
(1) Monte-Carlo permutation tests restricted for split-plot design				

Table II.12: Results of the analyses of the effect of station, time, depth and the interactions between these factors on species composition

The ordination analysis revealed that spatial differences, temporal differences as well as differences in depth in the sediment were important in accounting for the variation in community composition. All depth layers of the samples in April were clearly separated from the other dates (Fig.II.31). The first axis of the CCA explained 40 % of the variation. The variation induced in the species assemblage in April was the most important ($p < 0.05$), followed by the differences between stations 215 and 330. Stations 215 and 330 yielded different species assemblages throughout the depth of the sediment. Additional important variation is introduced by the overlying water copepod assemblage. This assemblage was quite similar and specific. Also the species assemblage of the upper cm of the sediment was significantly distinguished from the other levels ($p < 0.001$). The species association of the other depth layers overlapped considerably. Besides for April, temporal variation was also significant for 28th June ($p < 0.05$). 12th July and 31st March also induced an important part of the variation. Most of the variation however is unexplained by the explanatory variables used in the analysis.

3.3.4 Ecotype proportions

pRDA Monte-Carlo permutation tests restricted for split-plot design	Ecotypes	Life history stages
Station 215 + 330		
Effect	p value	p value
Station	0.583	0.302
Time	0.477	*0.004*
Depth	*0.001*	0.061
Time*Station	*0.006*	*0.043*
Depth*Station	0.102	0.184
Depth*Time	*0.044*	0.127
Station*Time*Depth	*0.002*	*0.027*

Table II.13: Results of the analyses of the effect of station, time, depth and the interactions between these factors on ecotype proportions and on the proportions of life history stages

Depth was an important structuring variable for ecotype distribution (Table II.13). Endobenthic species were significantly more abundant in the upper cm of the sediment in comparison with deeper levels, whereas it was the other way around at 7-8 cm depth. Yet, the typical sediment surface inhabiting epi- and endobenthic species were not restricted to the upper sediment layers (Fig.II.32 and II.33). Especially epibenthic species often occurred in deeper layers of the sediment, reducing the relative abundance of the interstitial species. These fluctuations in vertical distribution were responsible for the significant effect of depth*time. The presence of epibenthic species in deeper levels was more important at station 330 than at station 215, resulting in the significant effect of station*time*depth. The endobenthic species were more restricted to the upper sediment layers than the epibenthic species at station 215, where they were not encountered anymore below 3 cm depth. They were very abundant in the upper cm in May and June. At station 330 they were also frequently found in the surface layers of the sediment in May but their abundance in the upper 2 cm was reduced in June. They were still frequently found in the deeper layers from 4 to 10 cm depth at that moment, contributing to the significant effect station*time*depth. The higher relative abundances of epi-and endobenthic species at station 215 in comparison with station 330 in April explain the significant effect of time*station ($p < 0.01$ for April). A significant effect of the interaction between time and station was also observed in May ($p < 0.05$) because more epi- and endobenthic species were then found at station 330. Some free-swimming species were also encountered in the deeper layers of the sediment. Another peculiarity is that in May even interstitial species were present in the overlying water.

3.3.5 Life history stages

Depth does not influence the distribution of males, (ovigerous) females or juveniles of the total species assemblage in the sediment (Table II.13). In general adults do not make excursions into the sediment or to the surface over time and copepodites were not found to be concentrated at the surface layers (Fig.II.34). In April the latter were even more abundant in the deeper layers of the sediment. In April the lower contribution per depth layer of all adults in favour of copepodites at station 215 in comparison with station 330 resulted in a significant effect time*station ($p < 0.01$ for April). This kind of interaction also comprised differences in May ($p < 0.05$) between both stations due to the higher contribution of males at the expense of females and ovigerous females at station 330. The significant temporal pattern was already illustrated by the total percentages per sample (see 3.2.4) and was confirmed by the proportions per depth layer ($p < 0.05$ for 31st March). On 31st March more ovigerous females and less females and copepodites were encountered per depth layer than at the other sampling dates ($p < 0.05$).

The distribution of the life history stages of the most important species is illustrated in figures II.23 up to II.30. *Leptastacus laticaudatus s.str.*, *Apodopsyllus* n.spec.1 and *Arenosetella* n.spec.1 showed enhanced recruitment in May and/or June. At station 330 the highest number of juneniles of *Evansula* n.spec.3 and *Halectinosoma* n.spec.1 was found on 9th March. Juveniles of *Leptastacus laticaudatus s.str.* and *Arenosetella* n.spec.1 are concentrated in the upper layers of the sediment, whereas the relative distribution of the different life history stages of *Apodopsyllus* n.spec.1, *Paraleptastacus espinulatus* and *Evansula* n.spec.3 was similar throughout the depth of the sediment.

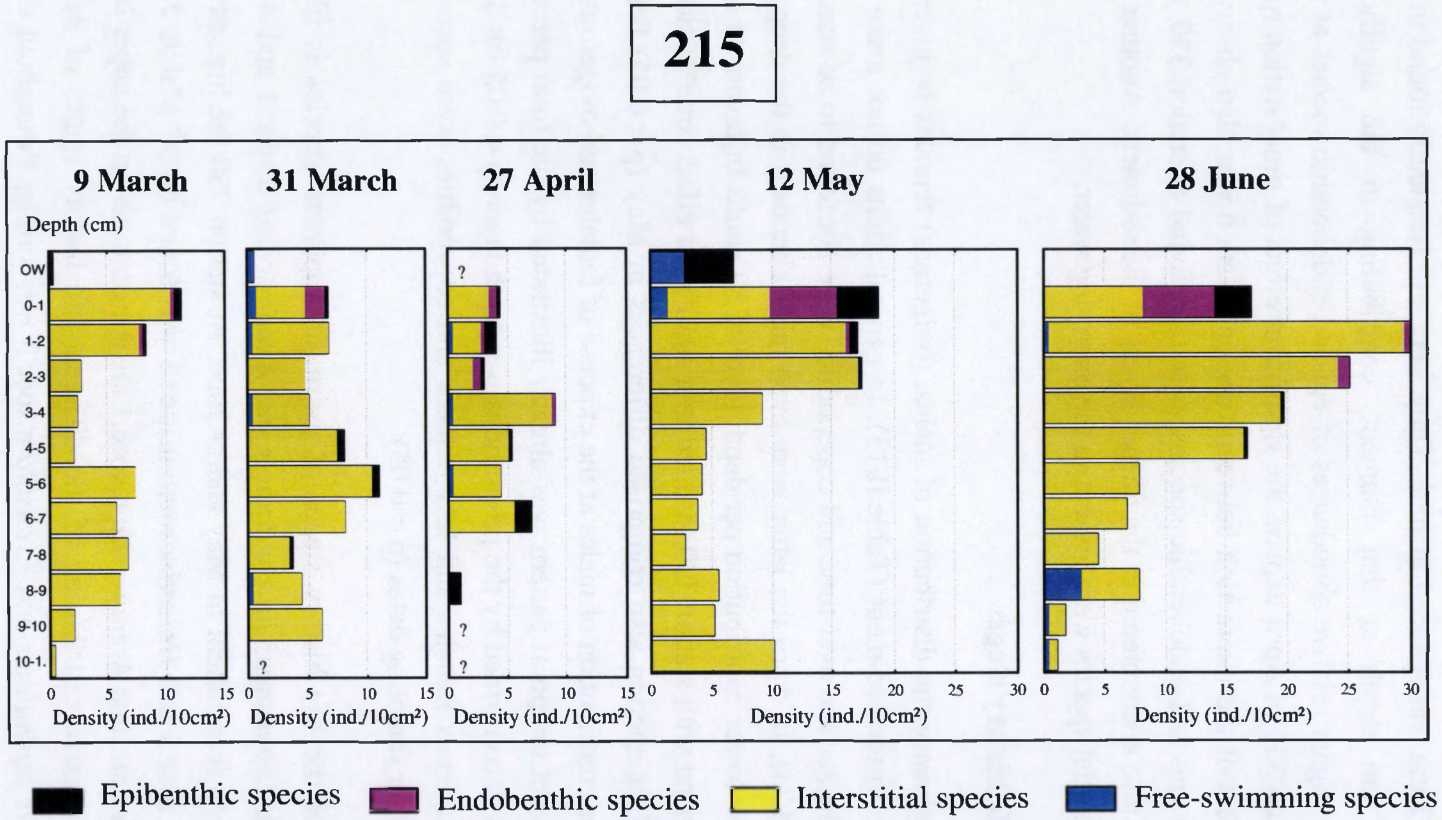


Fig.II.32: Mean relative abundances of different ecotypes per depth layer and per sampling date at station 215, a question mark indicates that no data are available from that depth layer.

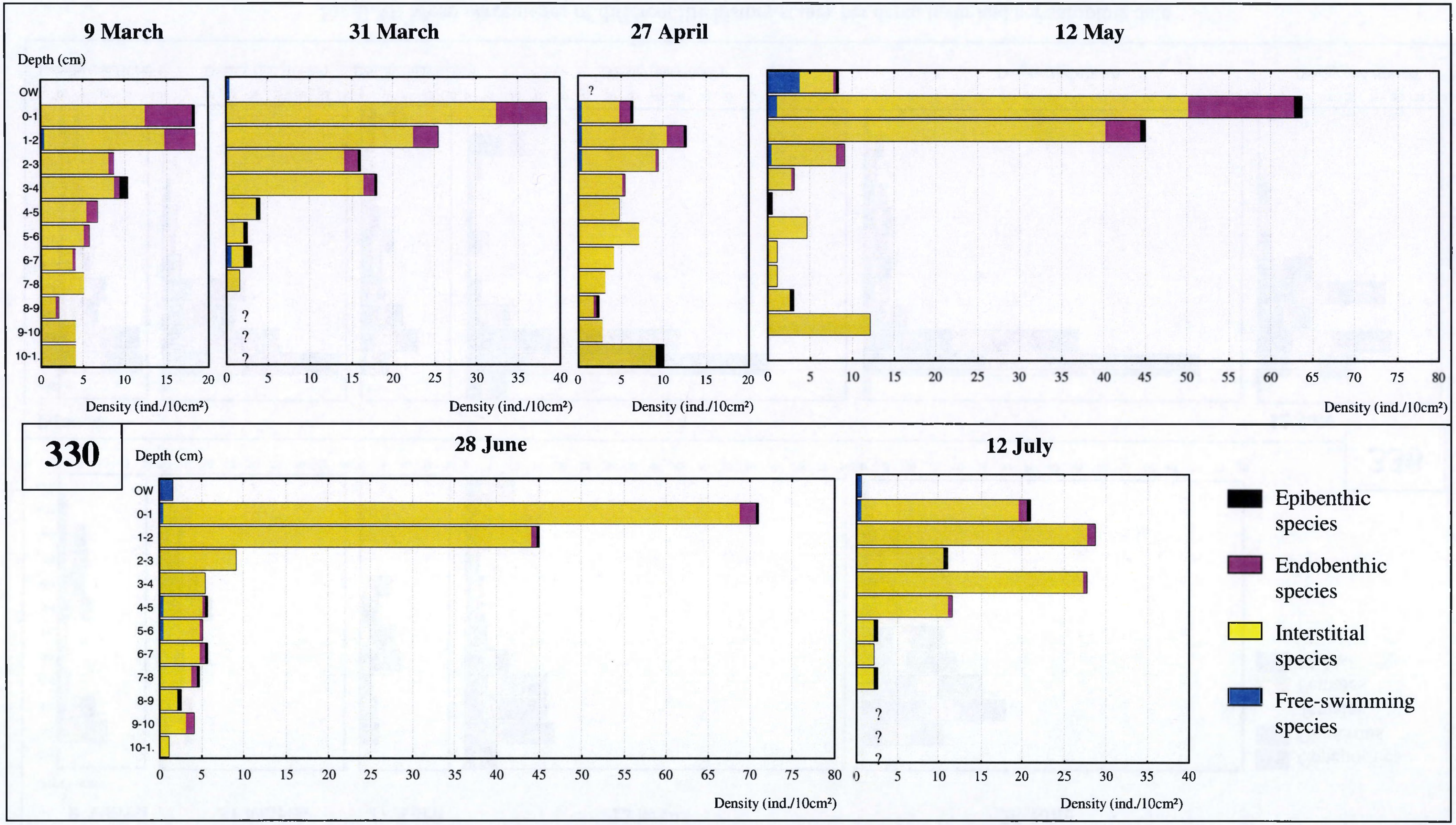


Fig.II.33: Mean relative abundances of different ecotypes per depth layer and per sampling date at station 330, a question mark indicates that no data are available from that depth layer.

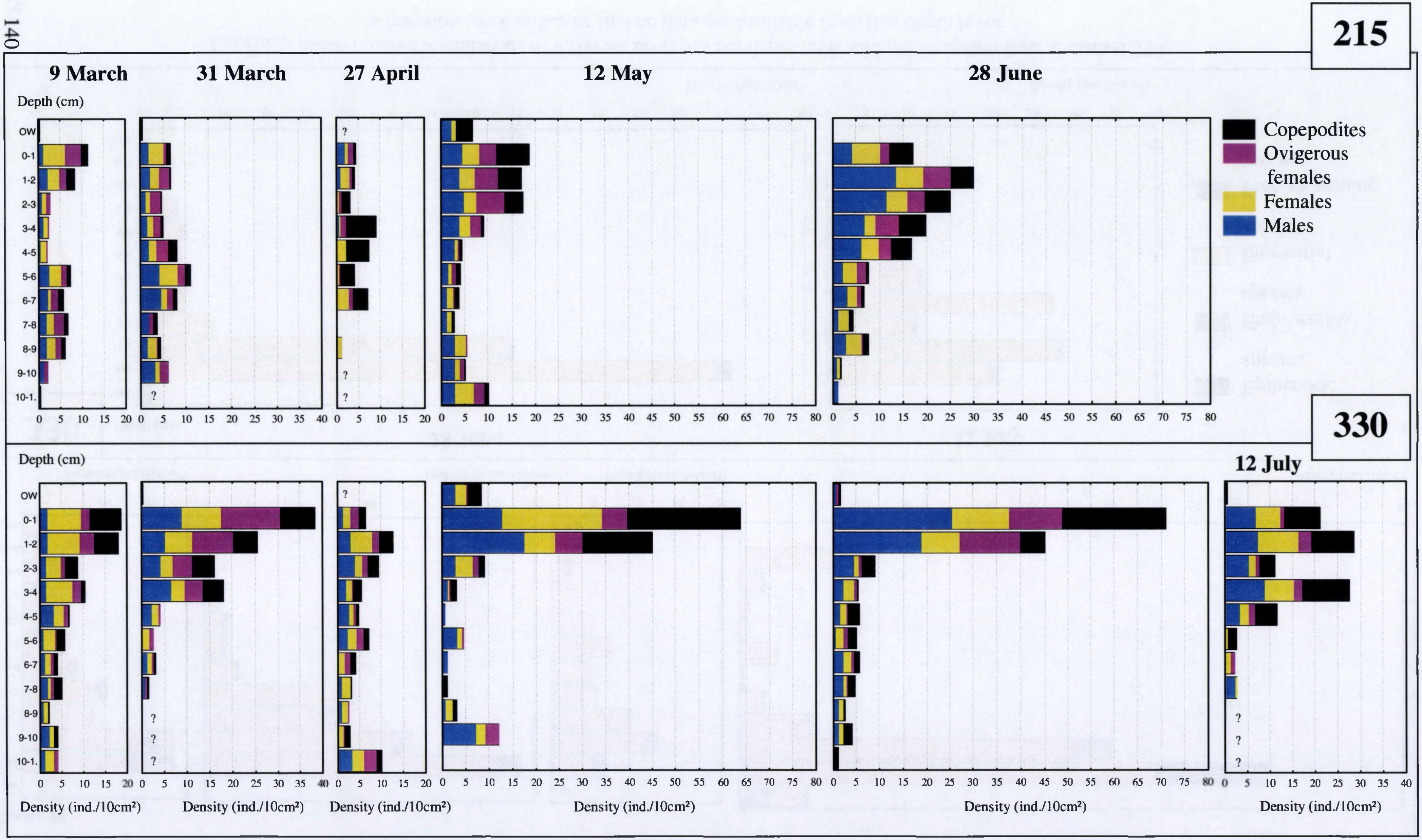


Fig.II.34: Mean percentages of different life history stages per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

4 Discussion

4.1 Environmental data

4.1.1 High chlorophyll *a* background signature near and in the sediment

Surprisingly, the highest chlorophyll *a* concentration in the sediment was recorded on 9th March at both stations. At station 330, the chlorophyll *a* and fucoxanthin concentration in the overlying water showed a peak as well, whereas this was not visible in the surface water. The chlorophyll *a* and fucoxanthin concentrations point to the presence of diatoms, Chrysophyceae, Prymnesiophyceae or brown macroalgae. Several reasons may explain elevated chlorophyll *a* and fucoxanthin concentrations near and in the bottom unrelated to primary production in the water column: 1) lateral advection of deposited organic matter such as macroalgae (Graf, 1992); 2) benthic primary production of bottom-dwelling algae such as diatoms or 3) presence of diatom spores in the sediment.

Lateral advection and accumulation of a great amount of deposited phytoplankton from the water column is impossible as diatoms or *Phaeocystis* cells (Prymnesiophyceae) were not observed yet (in high numbers for diatoms) in the water column at that time. Vanaverbeke (2003) ascribed the high chlorophyll *a* concentration at station 330 on 9th March to the deposition of slowly decaying macroalgae, because the phytopigment signature disappeared slowly. Macroalgae increase organic matter content in sediments during winter, when thalli are torn off by storms and are transported to deeper areas (Price & Hylleberg, 1982; Graf *et al.*, 1983; Abele, 1988). In the Kiel Bight sediments 73 % of the organic matter is derived from macrophytes (Liebezeit, 1986). The Kiel Bight is a relatively non-turbulent enclosed body (Smetacek, 1984; Boon & Duineveld, 1996), where macroalgae may accumulate and sink. The sandbank system is definitely not. At station 215 still much higher chlorophyll *a* concentrations were reported on 9th March, throughout the depth of the sediment. The recurrence of this observation cast doubt on the possibility of the deposition of macroalgae. Deposition and burying of macroalgae would happen rather exceptionally because of the high hydrodynamics of the area and the remoteness of areas with dense patches of macroalgae. An accumulation of macrophytes might occur at places with reduced current velocity in the gullies but very unlikely on the sandbanks themselves. Both observations at station 215 and station 330 may also be unrelated and caused by a different kind of organic supply.

At a depth of 12 m at station 215 there might also be an effect of benthic primary production (Rosenfeld, 1979). In shallow areas benthic algae sometimes overrule the phytoplankton: in the Wadden Sea, for instance, the mean benthic primary production is of the same magnitude as the phytoplankton production (Postma, 1982). Sufficient light intensity reaching the bottom is the ultimate requirement for autotrophic activity on the bottom. Euphotic depths in the Belgian and Dutch coastal waters range respectively between 70 and 8 m in offshore areas (Gieskes & Kraay, 1975, 1977; Lancelot & Mathot, 1987). Gieskes & Kraay (1975) observed that the onset of the growing season was related to a mean light intensity over the mixed water column of 0,03 gcal/cm²min. In general this is attained in February-March in the Belgian and Dutch offshore waters. Irradiance measurements on 9th March at station 215 show that the euphotic depth was 9.5 m, i.e. approximately 2 meters above the bottom and benthic diatoms were not observed in the sediment samples (Bonne & Muylaert, pers. obs.). Benthic primary production could hence not have been important. Moreover, benthic primary production would only take place at the sediment surface, whereas the high concentrations were found through the depth of the sediment.

Yet, pelagic diatoms and a lot of tychopelagic diatoms were frequently encountered in the sediment samples (Bonne, Muylaert & Sabbe, pers. obs.). The exact life form of the latter kind of diatoms is little known (Sabbe, 1997). A lot of diatoms rely on physical mixing to sustain production and some of them are known to migrate with the tide between sediment and water column in estuaries (Lauria *et al.*, 1999). The presence of these diatoms have contributed to the fluctuations in the pigment signature but the observed amount of tychopelagic diatoms is probably not high enough to explain the high values of the pigment profile on 9th March (Bonne & Muylaert, pers. obs.). Diatom spores cannot give such a strong pigment signature either (Muylaert, pers. comm.).

A high background level of organic matter may also be related to non-active autotrophs. Hansen & Josefson (2003) found comparable concentrations in aphotic sediments prior to the spring phytoplankton bloom in the Baltic, due to the presence of predominantly spore-forming diatoms. The diatom pool sizes supported the idea that diatoms do survive for long periods in sediments and that diatoms buried in the sediment have very slow degradation rates (Hansen & Josefson, 2001). Upon the death of diatoms, remineralization of the frustules occurs slowly in aerobic conditions (Van Bennekom *et al.*, 1974). The grazing upon diatoms somewhat enhances Si remineralization (Johnston, 1973). Finally Sun *et al.* (1991) suggested that more than one pool of chlorophyll exists and that some of the chlorophyll in the sediment is unrelated to fresh phytodetritus. The present organic matter may constitute a non-reactive, refractory fraction which has already reached the maximum degree of degradation (Graf, 1992). It is concluded that the background level on 9th March is mainly due to older buried phytoplankton derived material. This phytodetritus may have accumulated during autumn and winter and not have been processed completely due to low temperatures (Rudnick *et al.*, 1985). Yet, under oxic conditions it is most likely that a settling autumn bloom can be completely consumed by a well established benthic community (Graf *et al.*, 1983).

4.1.2 Diatom and *Phaeocystis* bloom

Diatom and *Phaeocystis* C biomass data expressed a diatom bloom from mid March until the end of April, followed by a *Phaeocystis* bloom from mid April until mid May in 1999. This succession is common in the southern North Sea (Nelissen & Stefels, 1988; Reid *et al.*, 1990; Lancelot *et al.*, 1987; Lancelot *et al.*, 1998; Rousseau, 2000). The developing diatom bloom was also reflected by the declining Si concentrations from the beginning of March to the end of April in the bottom water at station 330 (Lancelot & Mathot, 1987; Rousseau *et al.*, 2000). Si concentration increased again through remineralization from the end of April to mid June, being processed again in a second moderate diatom bloom in July. Very low nitrate and phosphate concentrations in the surface water at the end of April confirmed the *Phaeocystis* bloom peaked at that moment and also marked the end of the bloom (Van Bennekom *et al.*, 1975; Gieskes & Kraay, 1975; Veldhuis *et al.*, 1987). The drop in salinity at both stations indicated a high input of fresh water from the river Scheldt (Yang, 1998; Rousseau, 2000) and Yser (for station 215), probably enhanced by heavy rainfall (Rousseau, 2000). The high input of river water may be enhanced by the storm on 27th April and probably even increased the biomass of *Phaeocystis* offshore, as these runoff waters are characterized by a high nutrient load (Nelissen & Stefels, 1988).

4.1.3 Sedimentation of primary production

Direct sedimentation of phytoplankton cells in the North Sea has been shown to be very important, particularly during and at the end of phytoplankton blooms (Fransz & Gieskes, 1984; Gieskes & Kraay, 1984; Cadée, 1985). Sedimentation of *Phaeocystis* colonies has already been described in the Southern Bight of the North Sea for long time (Savage & Hardy, 1934). Sedimentation was also found to be the main loss factor in other areas (Wassmann *et al.*, 1990; Wassmann, 1994; Riebesell, 1993). Not only at the end of the bloom but also during bloom periods higher diatom as well as *Phaeocystis* concentrations were recorded near the bottom than in the surface water (Peperzak *et al.*, 1998). Settling rates of *Phaeocystis* colonies were probably enhanced by pinnate colonization because these diatoms have a higher specific density than *Phaeocystis* colonies (van Ierland & Peperzak, 1984). Sedimentation has even been proposed to be an important factor in the life cycle of *Phaeocystis* (Peperzak, 1993). Nevertheless, Rousseau *et al.* (2000) calculated that at station 330, the organic material originating from the *Phaeocystis* bloom was consumed before reaching the benthic system and that all organic material was remineralized in the water column. According to these findings, no effect of the spring bloom would have been observed in the benthos. The observations and measurements in the present study however point in the direction of substantial fluxes of phytoplankton derived material toward the bottom. An accurate estimate of phytoplankton sedimentation is essential from an ecological point of view as it determines available food for higher trophic levels in the seabed. Interpretation of the existing field data on primary production and pigment and nutrient concentrations near and in the bottom is however complicated, due to the interplay of environmental and physiological factors.

4.1.3.1 Sedimentation of diatom blooms

The ammonium concentration is one of the most obvious indicators of the extent of organic matter decomposition (Nelissen & Stefels, 1988). A peak of NH_4 near the bottom was recorded on 31st March at station 330. NH_4 must have been recently formed because this N compound is an unstable intermediate form (Johnston, 1973). Fauna activity may have enhanced this benthic ammonification (Postma *et al.*, 1984). The highest concentration of NO_3 at this time reflected the stock of nitrate enriched in the water column during winter (Rousseau *et al.*, 2000). NO_3 concentration decreased during the sampling period as the phytoplankton bloom progressed.

The spring diatom bloom started between the 9th and 19th March and lasted until 27th April. Smetacek (1980) estimated that the time interval between a bloom in the water column and material arriving on the bottom was one to two weeks. The settling of diatoms after bloom development has been discussed as a seeding behaviour of these organisms, i.e., diatoms leave the euphotic zone and settle rapidly as clumped aggregates, which disintegrate at the sediment surface and release spores (Smetacek, 1985). Graf *et al.* (1983) observed that there was a considerable loss of cells already during early to mid March, when the diatom bloom was still growing vigorously. At least in shallow waters, diatoms reach the sediment surface as intact cells providing high quality food for benthic organisms (Graf, 1992). Zooplankton grazing is low at the beginning of the diatom bloom (Rousseau *et al.*, 2000) and with low temperatures, the rapidly sinking diatoms are not susceptible to extensive bacterial decomposition in the water column (Smayda, 1970; Iturriaga, 1979; Hobbie & Cole, 1984). This scenario is consistent with the presence of pelagic as well as tychopelagic diatoms in the sediment samples from 9th March until 12th May (Bonne, pers. obs.). Graf *et al.* (1982) demonstrated that the benthic response to such pelagic events is immediate. As a result an efflux from the sediment by diffusion includes in the liquid phase dissolved organic matter as well as dissolved inorganic nutrients derived from decomposition products (Graf, 1992). In mesocosms response in terms of ammonia release of the sediment was recorded in less than 5 days (Kelly & Nixon, 1984). Consequently, the increased ammonium concentrations at the end of March may reflect decomposition of diatoms on the sediment in the early stage of the diatom bloom, whereas decomposition processes near the bottom were less important during April.

The apparently lower decomposition activity near the bottom in April may be attributed to increased grazing pressure in the water column, most of the sinking diatoms being eaten before reaching the bottom. Rousseau *et al.* (2000) described the food web structure in the water column at station 330, activated by the early spring diatom and *Phaeocystis* production. Bacterial production increased in early March 1998 almost in concert with diatom production, utilising organic products derived from the diatoms. Microprotozooplankton started their growth and reached a first peak at the end of the diatom bloom. Mesozooplankton grazing was also stimulated by the early spring diatom bloom, with a short delay as well. This finding is consistent with the presence of *Temora longicornis* and *Acartia clausi* at the end of March at the sediment surface at station 215 and 330 respectively. Whether phytoplankton settles out in the form of fresh algal material or as degraded material may also vary from year to year depending on the abundance and composition of the zooplankton (Reigstad *et al.*, 2000). On 27th April a moderate storm (wind force 7 beaufort, wind speed 14.7 m/s) may have washed away any evidence of potentially deposited material near the bottom.

In the sediment the background signature of chlorophyll *a* completely disappeared at both stations in April. At station 330 the older organic matter present in the sediment was metabolized during March, reflected in the higher NH_4 concentration at that moment near the depth of the earlier measured peak in chlorophyll *a* in the sediment. If a part of the background signature at station 215 may have been attributed to primary production of tychopelagic diatoms, this may have been hampered by the huge proliferations of *Phaeocystis* in the water column at the end of April, because light penetration in the water column is determined by suspended matter content and phytoplankton biomass (Reid *et al.*, 1990).

Another peak of NH_4 concentration near the bottom at station 330 was observed on 12th July, coinciding with high numbers of diatoms and elevated values for fucoxanthin and chlorophyll a in the water column as well as near the bottom. The organic decomposition in July was probably mainly derived from the moderate diatom bloom at that moment.

4.1.3.2 Sedimentation of *Phaeocystis* colonies

4.1.3.2.1 Station 330

The highest chlorophyll *a* concentration near the bottom was recorded at the same moment as the *Phaeocystis* bloom peaked (29th April), followed by a clear peak in total organic matter at the bottom on 3rd May at station 330. The latter observation has to be treated with caution, as this measure may not reflect organic carbon that is not consumed yet by benthic organisms. The highest density of macrobenthic organisms during the sampling campaign (2480 ind./m²) was recorded in the macrobenthic samples of 3rd May, due to the very high abundance of *Spiophanes bombyx* (1102 ind./m²) and juveniles of *Scoloplos armiger* (347 ind./m²), both deposit feeders (Van Hoey, 2000). The highest density of juveniles of *Ophelia limacina* (deposit feeder), *Lanice conchilega* (deposit feeder, grazer and filter feeder), *Anaitides maculata-mucosa* (predator) and *Pectinaria koreni* (deposit feeder or grazer) was also found at this moment. Some of these polychaetes may have been present in the sediment that was burned to measure total organic carbon in the sediment. Their high abundances however point to the presence of a lot of detrital material. Van Hoey (2000) excluded this sampling event from the analyses because of the finer sands that were sampled, assuming that another area was sampled in comparison with other dates. The sampling point on 3rd May was indeed located at 200 m from the exact coordinates of station 330 but it was situated in between the areas sampled at 19th March and 31st March. The latter samples were not characterized by another community than at station 330 proper. Moreover the species and juveniles abundantly found on 3rd May were also encountered at succeeding sampling events, though in lower numbers. The sampling point on 3rd May was not situated in a large pit where finer material could have been accumulated, because depth on 3rd May was the same as the surrounding points sampled. On 3rd and 6th May the nets were completely clogged with *Phaeocystis* colonies and a thick layer of living and dead *Phaeocystis* colonies were observed on top of the sediment in the core samples (Bonne, pers. obs.). The huge increase of deposit feeders indicates enhanced food availability through the settlement of this phytoplankton material (Widbom & Frithsen, 1995). Larval settlement of some polychaetes seems to be timed so that the population can significantly benefit from the sedimentation of the phytoplankton bloom (Rumohr, 1980). Although *Spiophanes bombyx* is often spatially distributed, sudden and huge increases in densities following the spring phytoplankton bloom have recently been observed at the Middelkerkebank as well (Van Hoey, unpubl. data). Phytoplankton can be readily assimilated by the benthos, without needing bacterial intermediaries (Tenore *et al.*, 1982; Findlay & Tenore 1982). Davies & Payne (1984), Graf *et al.* (1984) and De Wilde *et al.* (1984) assumed that the sedimentation of the spring phytoplankton bloom acted as a triggering mechanism for the lifecycle of macrobenthic fauna. The peak in organic carbon at 3rd May, probably including some polychaete biomass, is regarded as a result of phytoplankton deposition. At station 330 sedimentation most probably occurred en masse in the beginning of May. No doubt exists whether the majority of the settled material is derived from the *Phaeocystis* colonies, as the peaks of chlorophyll *a* at the bottom coincided with the peaks of chlorophyll *a* and *Phaeocystis* biomass in the water column and because *Phaeocystis* colonies were observed at the bottom. On 12th and 20th May the nets were still clogged with *Phaeocystis*. Still, some diatom biomass may be deposited at that time as well.

Fucoxanthin concentration peaked at the same moment in the water column as chlorophyll *a* and *Phaeocystis* biomass (Bonne & Van Gansbeke, unpubl.data). The same was observed near the bottom. Fucoxanthin has been widely accepted to be a diatom-specific pigment (Hansen & Josefson, 2003) but the close relation between fucoxanthin and chlorophyll *a* concentrations indicates dominance of fucoxanthin-containing microflagellates such as Prymnesiophyceae (Gieskes & Kraay, 1984), which class *Phaeocystis* belongs to. Consequently it is not clear which portion is made up by diatom sedimentation in the beginning of May as a result of the end of the diatom bloom. Si concentrations near the bottom peaked at 20th May, indicating the end of remineralization processes of diatom material through the food web. With the available data it is impossible to define when these diatoms must have been consumed. Silicon is not rapidly recycled (Reid *et al.*, 1990), so a considerable time span between uptake of diatoms and release of silicon is assumed. It's possible that diatoms still settled in May, as the species taking over the lead after an initial diatom bloom cannot reduce the diatoms to ecologically negligible quantities (Van Bennekom *et al.*, 1975; Officer & Ryther, 1980). Diatoms are always present and contribute significantly to the phytoplankton community throughout the vegetative season including periods of *Phaeocystis* occurrence (Lancelot *et al.*, 1998; Rousseau *et al.*, 2000). In the present study low abundances of diatoms in the water column were still recorded until 12th May. Pelagic diatoms were also present in the sediment samples of 12th May but were absent in the samples of 28th June (Bonne, pers. obs.). Van Ierland & Peperzak (1984) demonstrated that diatoms are also associated with decaying *Phaeocystis* colonies.

High NH_4 concentrations near the bottom on 12th May indicated an increased decomposition of organic material, most probably originating from decaying *Phaeocystis* colonies. A fluff layer was discerned on top of the sediment in the cores at that moment (Bonne, pers. obs.). Also in the sediment NH_4 concentrations increased in May and June.

4.1.3.2.2 Station 215

The clogging of nets and the presence of *Phaeocystis* colonies on top of the sediment in the beginning of May was observed at station 215 as well. Yet, the peak in total organic matter in the sediment was not observed on 3rd May, implying that deposition of *Phaeocystis* derived material would not have taken place in a similar extent as at station 330 or that deposition had taken place at another moment. Currents and bottom topography create advection and non-synchronisation of bulk sedimentation of the spring bloom causing uneven deposition in different water masses (Graf, 1992; Hansen & Josefson, 2003). Considerable variability in the supply of organic matter to the sediment also results from spatial and temporal differences in rates of primary production, zooplankton grazing and chemical regimes in the water column (Gee *et al.*, 1985). Resuspension could be another mechanism by which the material was removed from the sediment surface just after deposition (Hansen & Josefson, 2003). Although no evidence was found near the bottom for phytodetritus deposition, contrasting observations were made in the sediment. On 12th May chlorophyll *a* concentrations greatly exceeded all maximum recordings of station 330 and were comparable to the concentrations in the beginning of March at station 215. This pigment signature may be a sum of *Phaeocystis* derived detritus and tychopelagic diatoms, since the latter were also very numerous in the sediment at that moment. *Phaeocystis* colonies accompanied by amphipods and cumaceans were present in the overlying water on 12th May (Bonne, pers. obs.).

4.1.4 Tidal induced resuspension and redeposition

Chlorophyll *a* concentrations at station 215 were always higher than at station 330, except on 27th April when almost no chlorophyll *a* was observed beneath 1 cm depth at station 215. On any date (except 27th April) the chlorophyll *a* profile was uniform to a depth of about 5 cm at station 215, whereas this was not observed at station 330. Evidence exists that wave action, hydrodynamics and tidal sediment transport create a more dynamic environment on the southern part of the Kwintebank than at the investigated site at the Gootebank (Langhorne, 1982, Vlaeminck *et al.*, 1989; Lanckneus *et al.*, 1993; De Moor *et al.*, 1993). As a result, the sediment at station 215 in the sandwave area (Lanckneus *et al.*, 1992a) may be subject to continuous tidal depositions and resuspensions. The different hydrodynamic activity may be reflected in the poorer sorted sediments at station 215 in comparison with the well-sorted sediment at station 330, situated in a flattened area (Vlaeminck *et al.*, 1989). At station 215 high concentrations of chlorophyll *a* may have been rapidly homogenised through the top 5 cm of the sediment due to more intensive hydrodynamics. At beaches the chlorophyll per g of sand was uniform to a depth of about 20 cm as a result of the sand being mixed to a depth of between 2 and 10 cm on any tide (McIntyre *et al.*, 1970). Also in estuarine waters, the concentration of organic matter is kept constant, since currents and waves often rework the top centimetres of the sediments (Rice & Rhoads, 1989). In regions where tidal mixing is important, sediment resuspension and redeposition will serve to complicate the picture of sedimentation events (Smetacek, 1984). Jennes & Duineveld (1985) provided marvelous evidence of the effect of the tidal cycle on the amount and composition of near-bottom suspended material in offshore sandy habitats. During flood the current velocity is strong enough to erode the sediment, whereas algae and other particles are deposited during the slack following the flood. Ebb current velocities move the sediment but they are not strong enough to resuspend the sediment. As a result, deposited algae and particles are buried in the sediment down to a depth of 5 cm. The presence of sand ripples enhance this process, since algae and other particles tend to move towards the lee side of the ripple where they are buried by heavier sand particles descending from the crest of the ripple. This process is repeated when the stronger flood current velocities resuspend buried algae and particles again. Resuspension during high tidal currents and resedimentation was also observed by Boon & Duineveld (1998) in the German Bight.

Weather conditions and tide of the sampling events are illustrated in table II.14. The highest chlorophyll *a* values at station 215 were observed in samples taken at low water. At station 215 the previously mentioned tychopelagic diatoms were more abundant on 9th March and 12th May in comparison with other dates, with the highest numbers on 12th May. At station 330 they were most numerous on 31st March, sampled with low water as well, but the amount was not as high as on 12th May at station 215. The estimates of diatom quantities are very rough since the samples were not processed for diatom enumeration. The higher abundances of tychopelagic diatoms might result from sinking under stable conditions during the tide, while they are mixed throughout the water column during periods of intense mixing. This process will be enhanced with good weather whereas no settling will take place during bad weather, as was indeed recorded on 27th April. Hence, the interpretation of the chlorophyll *a* and nutrient concentrations are very likely influenced by fluctuations resulting from tidal currents, especially at station 215. It will be hardly possible to report sedimentation of phytoplankton near the bottom at high current velocities during flood. Yet, phytoplankton may have settled and have been buried in the sediment at other moments of the day. Jennes & Duineveld (1985) performed an experiment in which they observed that algae soon became buried even though no surface deposit could be detected. This may be the reason why a peak in organic matter or chlorophyll *a* was not found near the sediment in the beginning of May at station 215, whereas elevated chlorophyll *a* concentrations were present in the sediment. The concentrations of chlorophyll *a* that can be buried in this way range from 400 µg/l to 3500 µg/l sediment (Jennes & Duineveld, 1985). These values are consistent with the high concentrations found in this study at station 215, ranging between 347 ng/g and 881 ng/g, which is similar to 1509 µg/l and 3830 µg/l. It can be concluded that tidal processes buried tychopelagic diatoms and some older detritus on 9th March and buried tychopelagic diatoms and *Phaeocystis* detritus on 12th May at station 215.

The resemblance with the observations of Jennes & Duineveld (1985) confirm that this mechanism might be quite widely spread on the sandbanks of the North Sea.

	215			330	
	sampling	wind speed		sampling	wind speed
9th March	at low water	3 beaufort (4.0 m/s)	9th March	2 h. before low water	3 beaufort (3.5 m/s)
31st March	3 h. before low water	2 beaufort (3.0 m/s)	31st March	at low water	2 beaufort (3.3 m/s)
28th April	3 h. before low water	?	27th April	2 h. before low water	7 beaufort (14.7 m/s)
11th May	at low water	4 beaufort (6.7 m/s)	12th May	2.5 h. after low water	6 beaufort (13.7 m/s)
29th June	2.5 after high water	6 beaufort (13 m/s)	29th June	1.5 h. before low water	6 beaufort (13.8 m/s)
12th July	/		12th July	0.5 h. before high water	5 beaufort (10.2 m/s)

Table II.14: Weather conditions and sampling moment in relation to the tidal cycle for the samples at stations 215 and 330

Whereas at station 215 frequent resuspension of the upper sediment layer most likely determines the distribution of chl *a* and chemical compounds in the sediment, the sediment at station 330 is not reworked that intensively and other mechanisms regulating pore water flow and particle concentrations may be more important than tidal resuspension and redeposition. Sedimentological structures such as ripples, which are present in the study area, may influence the boundary layer flow by creating advective transport processes through the sediment near the ripples (Ziebis *et al.*, 1996; Thibodeaux & Boyle, 1987). The transport is driven by pressure gradients generated when bottom flows are deflected by small surface structures of e.g. hydrodynamical origin (Huettel *et al.*, 1996) and is much faster than diffusional transport (Ziebis *et al.*, 1996). In natural sands, particulate organic matter constitutes the most fine-grained and easily suspendable part of the sediment and is therefore likely to follow pore water flows through the sand matrix (Rusch *et al.*, 2000). Hence, the topography-related interfacial particle transport can be a key process for organic matter uptake and cycling in seabeds with sandlike permeabilities. The layers of advective pore-water flows may produce zones of enhanced microbial decomposition activities (Huettel *et al.*, 1996), resulting in the higher NH_4 concentrations in the top layers of the sediment in comparison with deeper layers, as clearly distuinguished on 27th April and 12th July at station 330. This mechanism may also have been responsible for the increased availability of diatoms and bacteria and particles originating from the decaying *Phaeocystis* colonies, into the upper layers of the sediment, resulting in a reaction of the interstitial fauna. The spatial pattern of the ripples introduces spatial variability of the advective porewater flows (Huettel & Gust, 1992) and may explain why different vertical concentration patterns are also observed.

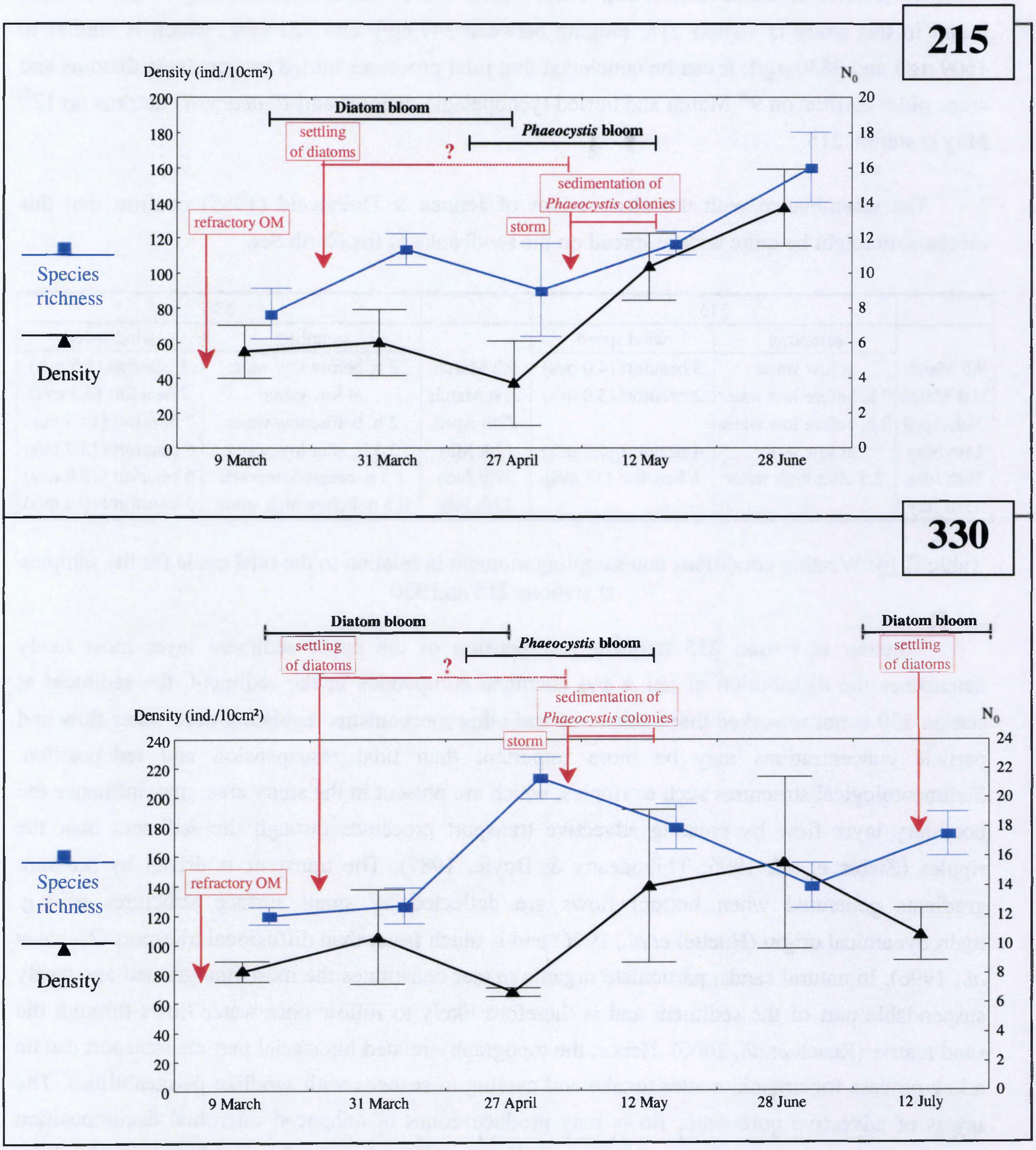


Fig.II.35: Representation of phytoplankton sedimentation and observed (storm) processes during the sampling period, plotted on the graph of density and diversity at stations 215 and 330.

4.2 Response of the harpacticoid community

While sandy sediments of low organic-matter content are widely distributed in high-energy nearshore and offshore areas, little is known of the response of benthic fauna in low organic-content sands to the deposition of phytodetrital organic matter to the sediment surface (Webb, 1996). The majority of studies investigating the response of harpacticoids to diatom or phytodetrital sedimentation have been conducted in fine, often organic-rich sediments with significant silt-clay contents in both field (e.g. Rudnick *et al.*, 1985; Decho & Fleeger, 1988a; Fleeger & Shirley, 1990; Olafsson & Elmgren, 1997) and laboratory settings (e.g. Montagna, 1984; Decho & Castenholz, 1986; Gee *et al.*, 1985; Rudnick, 1989; Widbom & Elmgren, 1988; Widbom & Frithsen, 1995). Some field records also exist from harpacticoid responses on very high organic loads such as sludge disposal (e.g. Moore & Pearson, 1986). The response of harpacticoids in sandy sediments was investigated in an experiment with sediments from a salt marsh (Webb, 1996) or in a field study in an estuary (Montagna *et al.*, 1983) and on beaches (Hockin, 1983). Field studies of the harpacticoid response on sedimentation of primary production in comparable offshore clean sands are lacking.

The previously discussed phytoplankton sedimentation events are represented in Fig.II.35 as potential triggering mechanisms responsible for the changes in the harpacticoid communities. Direct correlations were not detected and it is not known for how long specific conditions had prevailed but an attempt is made to indicate the varying importance of the changing physical environment and the food supply to the benthos within the entire period observed. Although the underlying processes cannot be identified from the available data, the analyses give some information about important shifts in community composition during the spring phytoplankton bloom.

4.2.1 Winter population

In the beginning of March a typical winter population was found at station 215 in comparison with the species assemblage of January 1997 at the same station (Chapter I). *Halectinosoma* n.spec.2, *Arenosetella* n.spec.1, *Kliopsyllus constrictus s.str.*, *Kliopsyllus* n.spec.2, *Kliopsyllus* n.spec.4, *Leptastacus laticaudatus s.str.*, *Paraleptastacus espinulatus*, *Arenocaris bifida*, *Arenocaris reducta* and *Membranastacus* n.spec.1 were common species for both sampling events, accounting for 71 % of the species and 92 % of the total density in March 1999. A stable community was outlined in the southern part of the Kwintebank, encompassing spatial sediment differences from fine to medium median grain size (Chapter I). The species assemblage of the even coarser sediments on 9th March (median grain size 384 µm with 13 % very coarse sand and 4 % gravel) did not deviate from this previously defined community pattern. The comparable medium sand (median grain size 351 µm) at station 330 yielded a similar density and species richness as station 215 in the beginning of March. They had half of the species in common but the very high dominance of *Paraleptastacus espinulatus* at station 215 resulted in a clearly lower eveness than at station 330 throughout the depth of the sediment. Both communities were evenly distributed among the different depth layers. Deeper levels yielded significantly more copepods in comparison with later sampling events. During periods of adversity, interstitial species have an avoidance advantage by vertical migration into deeper sand layers (Hicks, 1979). Though the subsurface feeding benthos may depend upon detritus that is buried during winter in order to survive (Rudnick *et al.*, 1985), the present organic material is unlikely to be palatable food for the present community. At both stations the highest chlorophyll *a* concentrations were measured on 9th March and corresponded with a quite low density and species richness. Despite the much higher chlorophyll *a* values in the sediment at station 215 in comparison with station 330, the former even yielded less individuals and species than the latter. Beneath the surface flocculent layer, detrital particles are generally in a compacted form within faecal pellets or bulk sediment (Moore, 1931; Young, 1971; Rhoads, 1974) and are certainly, on average, of greater age and poorer nutritional quality than surface particles. Nevertheless, benthic heterotrophic bacteria, associated with the buried detritus, may have acted as a trophic buffer providing some food for the present community during this season of low primary production.

4.2.2 Early spring population during diatom bloom

From the end of March to the end of April a completely different community evolved at both stations. At station 215 an intermediate situation between the beginning of March and the end of April was already observed on 31st March, diversity in the upper sediment layers being increased, whereas this was not the case yet at station 330. At station 330 diversity increased dramatically at the end of April. Sediment composition differences and the occurrence of a storm however render the interpretation of the changed community characteristics in April more difficult. At station 215 finer sands were sampled, while the median grain size at station 330 was significantly coarser than the other samples at this station. The community typical of the southern part of the Kwintebank occurs over a range of sediments with a median grain size from fine to medium sand (Chapter I). The sediments sampled in April at station 215 fell into this range. The same community should therefore be expected, all the more since this community was also encountered on 9th March in coarser sediments.

The variation in the harpacticoid species assemblage between April and the other sampling events was more important than the differences between both stations, belonging to two different sandbanks. The observed changes thus exceed clear spatial differences and are therefore not only attributed to slight changes in sediment characteristics but very likely to other environmental changes as well. Adverse effects of disturbances by the storm may have impoverished the fauna but cannot have changed the species assemblage completely. The insignificant lower abundances may be related to these environmental conditions.

The community shift may be related to the developing diatom bloom in the water column, diatoms settling rapidly (Graf *et al.*, 1983; Smetacek, 1985). Several epibenthic (Sellner, 1976; Ustach, 1982; Decho, 1986, 1988; Decho & Fleeger, 1988a) and endobenthic harpacticoids (Decho & Fleeger, 1988b) are found to feed upon diatoms as well as phytodetritus (Rudnick, 1989). Even interstitial species are observed to ingest diatoms and diatom exudates (Decho & Castenholz, 1986). Moreover, harpacticoids are able to exponentially increase feeding rates as a function of increased microphytobenthos (Montagna *et al.*, 1995). Nevertheless, no evidence was found for associations between diatoms and total harpacticoid abundances in correlative field studies (Montagna *et al.*, 1983) or in laboratory experiments (Webb, 1996). This finding is confirmed in the present study since harpacticoid abundances did not show a clear trend in early spring. Species composition however changed dramatically. The sudden increase of subordinate species may explain the emergence of a different community. Numerically subordinate species which are incapable of feeding flexibility, are likely to be constrained to a narrow specialized range of food items which might only be available at certain times of the year. Inflexible species will therefore tend towards a lower numerical carrying capacity with breeding seasons limited to surplus periods of preferred foods (Hicks, 1979). The otherwise dominant species is both incapable of the utilization of the food resource and of outcompeting the subordinates (Hicks & Coull, 1983).

Lee *et al.* (1977) found some interstitial harpacticoids to be highly selective in forming patches around certain types of algae. They suggested that algal colonies or blooms can selectively attract specific species and may be a factor causing the non-random distribution of these harpacticoids. Yet, Montagna *et al.* (1983) only found one out of four dominant species to be strongly correlated with the standing stock of diatoms at a sand site. Although diatoms are implicated in the feeding of interstitial and epibenthic species, it has also been shown that bacteria are important dietary constituents (Rieper, 1978), which may be more important as food than the diatoms proper. Feeding data of an interstitial harpacticoid species suggest that attraction to algae (diatoms) may be only to find bacteria associated with the algal patch, since the animals ingested diatoms with associated heterothrophs but only retained the heterothrophic fraction (Decho & Castenholz, 1986).

Graf (1992) has put forward that the response of the small organisms, bacteria (Meyer-Reil, 1983) and foraminiferans (Altenbach, 1985) may be so fast that no food remains for the slower larger animals. The high conversion efficiency of this first response, especially of bacteria, however provides significant amounts of bacterial food to higher trophic levels. Although harpacticoids are able to grow and reproduce on an exclusive diet of bacteria (Rieper, 1978), some of them produced more eggs on a mixed diet of algae and bacteria than either diet alone (Heinle *et al.*, 1977). Montagna (1984) found copepods ingesting diatom carbon faster than bacterial carbon. Although assimilation rates of bacteria were 8-10 times that of diatoms in other laboratory experiments (Heinle *et al.*, 1977; Brown & Sibert, 1977), the species may be highly dependent on diatoms for the provision of necessary trace nutrients required for breeding – emphasizing food quality rather than quantity as the necessary prerequisite for successful reproductive performance (Hicks, 1979). Intact diatoms may still have been available in the early phase of the diatom bloom when heterotrophic activity in the sediment is minimal (Nixon *et al.*, 1976; Hobbie & Cole, 1984). The presence of diatoms in the sediment and of ovigerous diatom eating *Enhydrosoma* (Hicks & Coull, 1983) indicate that nutritional requirements were probably met. High diversity of food particles, including diatoms, diatom exudates, bacteria and other heterothrophs, faecal pellets and other organic compounds may have contributed to the diversity of the community. With the sedimentation of the *Phaeocystis* bloom the favourable conditions for many of the subordinate species may have vanished and these species disappeared again.

4.2.3 Late spring - early summer population after Phaeocystis sedimentation

In May a clear response was observed in the upper layers of the sediment, being even more pronounced in June, when the community characteristics were significantly different. At the sediment surface the significant higher number of *Temora longicornis* in May may have been feeding on *Phaeocystis* colonies (Jones & Haq, 1963; Weisse, 1983). The presence of a thick fluff layer of *Phaeocystis* colonies was also reflected in the presence of even interstitial species in the overlying water, probably feeding on the rich bacteria or heterotrophic cultures on the decaying colonies.

After sedimentation lysis of the *Phaeocystis* cells is an important mechanism for release of dissolved organic carbon (Osinga *et al.*, 1996). Van Duyl *et al.* (1992) and Osinga *et al.* (1995) found that bacteria responded rapidly to addition of fresh *Phaeocystis* material in experimental benthic systems. Also in the field, sedimentation of phytoplankton blooms increased bacterial biomass significantly (Meyer-Reil, 1983, 1987). Bacterial utilization of the carbon substrates and microheterotroph grazing of bacteria and uptake of dissolved organic carbon may form an important link to higher trophic levels (Davidson & Marchant, 1992).

The surface feeders observed in the upper centimetres of the sediment (e.g. the epibenthic harpacticoid *Thompsonula hyaenae* and the endobenthic *Halectinosoma* species) in May may have been directly assimilating sedimented phytodetritus (Rudnick, 1989). Yet, the significantly increased abundance of these species did not result in a significant effect of the sedimentation process on total epi- or endobenthic densities or on total harpacticoid densities in May. A high degree of utilization of fresh detritus was also shown by harpacticoids in a mesocosm experiment of Widbom & Frithsen (1995), whereas they did not respond quantitatively within the 5 months of the experiment.

Significantly higher total harpacticoid densities and an altered species composition were reported more than one month later, in June. At that moment the more abundant harpacticoids were concentrated in the upper 2 cm and strongly dominated by a single interstitial species, *Apodopsyllus* n.spec.1. This bacteria grazer may have increased bacterial consumption and reproduction as a result of increased food density (Rieper, 1978). Gray (1969) and Decho & Castenholz (1986) found a strong experimental or field relationship between the distribution of specific harpacticoid species and certain microbial flora. Very high densities of *Apodopsyllus* n.spec.1 in spring were also recorded at coastal stations along the Belgian coast (Herman, 1989) and this species was frequently found in sand enriched with silt (Willems, 1989). The high reproductive potential, the small body size and the large fluctuations in population size are characteristics of a typical r-strategist and provide a selective advantage in unpredictable or short-lived environments (Heip, 1995). *Apodopsyllus* n.spec.1 has probably a capacity for the utilization of a wide variety of food sources of different origin, including *Phaeocystis*. Opportunists of organic enrichment have been found among the epibenthic and phytal copepods (*Bulbamphiascus* and *Tisbe* (Moore & Pearson, 1986; Marcotte & Coull, 1974, Gee *et al.*, 1985)). *Apodopsyllus* n.spec.1 is an interstitial representative of an opportunist utilizing an increased organic input through an indirect pathway. *Apodopsyllus* n.spec.1 may be the harpacticoid counterpart of *Capitella capitata* and *Polydora* species. These opportunistic macrobenthic species are able to persist in areas where periodic anoxic conditions exist (Heip, 1995). *Apodopsyllus* species also display preference for anoxic environments (Wieser *et al.*, 1974; Moore, 1979b, Willems, 1989). Anoxic conditions may not have favoured this species in the present study since the sediment was oxidized at any time.

Increased reproductive effort in May and June in the present study was observed for other interstitial species as well. Also Fleeger & Shirley (1990) found that the reproductive cycles in the dominant harpacticoid species were related to the spring bloom sedimentation event. While not denying the role of temperature, the results suggest that breeding periodicity is also strongly related to food resource availability as a result of phytoplankton deposition. For some species migratory behaviour and reproductive activity were interrelated, egg development taking place in the surface layers of the sand (Huys *et al.*, 1986a), whereas the total distribution of life history stages per depth layer did not reveal any changes in the vertical distribution over time. A lack of response at major taxon level (Fleeger *et al.*, 1989) may be misleading, if individual species within the taxon react differently to environmental change (Warwick *et al.*, 1988; Olaffson, 1992).

The dense interstitial fauna in the upper sediment layers reflects that deposited organic matter is effectively assimilated and incorporated in the sediment, very likely through the microbial food web since the main source of energy for the interstitial harpacticoids is the bacterial flora (McIntyre *et al.*, 1970). Also the increase in nematode selective deposit feeders was suggested to be the result of increased numbers of bacteria and protozoa in the sediment following the spring bloom (Olafsson & Elmgren, 1997). The significant vertical migration took place after the bloom reached the sediment surface in May and June, animals from deeper sediment layers moving to the sediment surface attracted by the fresh food supply (Schulz, 1983). In June deeper levels harboured more harpacticoids than in May as a result of particle and pore-water transport by bioturbation, providing food particles at greater depth (Graf, 1992). A significant structuring effect is thus recorded in the interstitial community, which relies indirectly on sedimented phytoplankton, and not in the directly assimilating epibenthic harpacticoids, although these copepods are regarded as very mobile and may colonize food patches very quickly (Decho & Fleeger, 1988a).

Changes in total densities were not regarded as significant at station 330 due to the considerable patchiness. Yet, organic matter reaching the bottom is patchy distributed as well (Plante *et al.*, 1986) and the high variability in densities was reported in these months in which a clear sinking of organic matter was demonstrated.

With the available data it is impossible to define how important the contribution of diatoms must have been in May and June. It is very likely that the most important contribution to the bacterial production was based on *Phaeocystis* sedimentation. The clear response in the upper centimetres in June may also be partly due to post-bloom sedimentation of largely amorphous carbon-rich material, accumulated in the surface layer in the course of the bloom. Post-bloom mucilage sedimentation could be a secondary pathway for the vertical flux of *Phaeocystis*-derived organic matter (Riebesell *et al.*, 1995).

4.2.4 Similarities and differences between the stations

The response of the harpacticoid fauna observed in June was clearly different from the community changes in April at both stations. The high eveness in April after the moderate diatom sedimentation contrasts with the high dominance in June after the clear and more extensive *Phaeocystis* sedimentation. A clear picture emerges of increasing dominance and decreasing diversity with increased organic enrichment and potentially with the change in nutritive value of the deposited organic matter.

Species richness was however not negatively affected at station 215 after *Phaeocystis* deposition. Species richness increased from the beginning of March toward the end of June, implying an increasing positive effect of the sedimentation events on species richness. Species richness patterns differed significantly between both stations. At station 330 species richness increased dramatically from the beginning of March toward the end of April, whereas it decreased after the sedimentation of the *Phaeocystis* bloom. Densities increased during the entire period at both stations. The trend in species richness at station 330 is consistent with the results of the laboratory experiments of Gee *et al.* (1985), while abundances behaved differently. His experiments showed that, at levels of organic enrichment common in nature, not only the abundances of many species increased but also the number of species, compared with the controls. At high levels of organic enrichment there was a decrease in both the abundance and species richness and an increase in species dominance. Harpacticoids also showed negative responses in abundance in organic enrichment experiments of Widbom & Elmgren (1988) and Widbom & Frithsen (1995). Van Damme *et al.*, (1984) also recorded a drastic decrease in harpacticoid fauna along the Dutch and Belgian coast as a result of intensive organic enrichment. In the present study however organic enrichment was not that severe yet to negatively affect densities.

According to the scenario at station 330 and in Gee *et al.* (1985) the increasing species richness at station 215 suggests that organic enrichment was less intensive at this station. Yet, chlorophyll *a* concentrations in the sediment at station 215 were much higher than at station 330 on 12th May and 28th June, whereas the faunal responses to high organic loads (increased abundance versus decreased diversity) were clearer at station 330. This apparent discrepancy may be refuted by the hypothesis that the response on organic enrichment is also dependent on mixing in the sediment. One consequence of tidal mixing is that very little of the primary production in the water column becomes incorporated in the sediment (Jennes & Duineveld, 1985) and may hamper an efficient assimilation of the organic matter by the benthos. In areas where the top centimetres of the sediments are often reworked by currents and waves, the total concentration of metabolizable organic matter in the sediments is critically dependent on how fast the animals work the organic matter into the sediment (Rice & Rhoads, 1989). Despite the higher chlorophyll *a* concentrations at station 215, the fauna may not have been fast enough to incorporate as much organic matter as at station 330. Consequently, the interstitial fauna was not as densely concentrated in the top centimetres of the sediment as at station 330 after phytoplankton deposition.

Resuspension and advection of deposited organic matter at station 215 may also result from sand extraction activities (Newell *et al.*, 1998), since the Kwintebank is a heavily exploited sandbank (Chapter III). Station 215 however is located in an area of low sand extraction intensity. Table II.15 illustrates the extraction activities in spring 1999 near station 215. Extraction activity was most frequent in April but still fairly low to rework the sediment considerably. Just before sampling on 28th April a sand extraction vessel had been in the neighbourhood only for a very short while. Yet, on more heavily exploited areas on the Kwintebank (Chapter III) the importance of resuspension and redeposition may be significant in diluting the organic enrichment in the sediment at specific places and concentrating it at other places. On top of the bill, these extractions do not only reduce the food availability by resuspension but also directly impact fauna densities by removing the fauna. The possible confusion between effects of increased organic matter inputs and effects of sand extraction (or fisheries in Heip, 1995) is an unexplored problem that requires careful consideration in a number of other dredged areas as well.

1999	January	February	March		April	May	June	July
Days	14,20,28	4	23,30,31		6,7,16,21, 22,23,28,29	5,6,10	0	0
Number of days	3	1	3		8	3	0	0
Mean duration of disturbance (min.)	4,5	1	0,5		1,7	1,7	0	0
m² disturbed	540	120	60		204	204	0	0
Sampling	/	/	9th March	31st March: sand extraction on 31st March after sampling	28th April	11th May	29th June	/
Last sand extraction event before sampling			35 days before sampling	23 h. before sampling	5 h. before sampling	20 h. before sampling	50 days before sampling	

Table II.15: Sand extraction activities in spring 1999 near station 215 on the Kwintebank

4.2.5 Differences between meiofaunal taxa

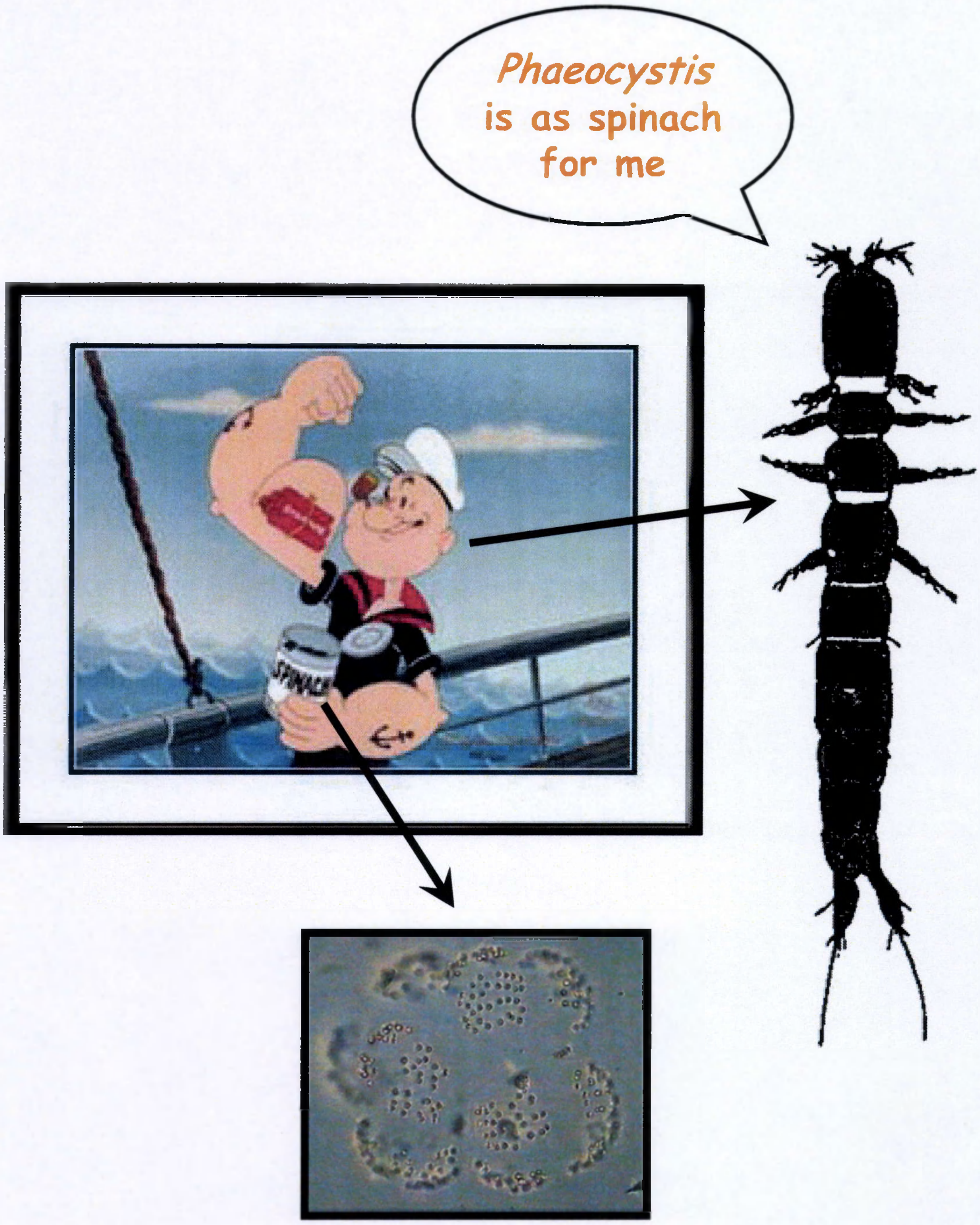
The obvious differences in harpacticoid community structure in April were not as clearly observed for other meiofaunal organisms such as nematodes. For nematode abundances and community structure at station 330 significant differences were found between 9th March and later sampling events (Vanaverbeke, 1993). Differences in density and community structure between April and succeeding months were also observed but they were not as pronounced as for harpacticoids. Copepod community structure was more sensitive to low dose enrichment than the nematode species assemblage, in agreement with the findings of Gee *et al.* (1985). They demonstrated that there were no detectable differences in nematode community structure between different levels of organic enrichment but that there was a clear response in the high dose treatments. The copepods, on the other hand, separated out into well-defined communities and were obviously the most important group in determining the total meiofaunal community pattern Gee *et al.* (1985).

Yet, in April nematode densities increased significantly in comparison with 9th March, whereas this was not the case for harpacticoid densities. Nematodes reached maximum densities in May whereas harpacticoids in June. Montagna *et al.* (1989) suggested that the two groups occupy different trophic niches, nematodes being linked to a short, detrital/bacterial-based food chain. In the case of organic enrichment their number would increase rapidly. In the present study nematode abundances responded more rapidly to the pulses of organic matter in April as well as in May, while copepods lacked behind but were also able to assimilate a considerable amount of the detrital/bacterial-based food sources. The differences in abundance maxima between nematodes and copepods may be due to competition, both being dependent on the same input from the water column. During the diatom bloom, nematodes and polychaetes may have more quickly assimilated diatoms than (epibenthic) harpacticoids. Montagna *et al.* (1983) found positive correlations between diatoms and ciliates or nematodes or polychaetes but not between diatoms and harpacticoids. Nematodes may also suffer from competition with polychaetes, like harpacticoids. Widbom & Elmgren (1988) and Widbom & Frithsen (1995) found that the meiofauna showed remarkably little response to the increased organic input to the sediment because they were limited by biotic interactions with the opportunistic polychaete species that completely dominated the benthic fauna in the eutrophied mesocosms. Their results suggest that a few opportunistic species may, at least temporarily, prevent species that are more dependent on fresh detritus from utilizing an increased input of such phytodetritus to population growth (Widbom & Frithsen, 1995). Experimental evidence that such negative interactions occur, and can be more important than predation or physical disturbance, has been presented by Alongi & Tenore (1985); additions of a subsurface feeding polychaete decreased surface meiobenthic abundance.

5 Conclusions

During the spring phytoplankton bloom temporal changes in the harpacticoid community were clearly discerned with high diversity in April and high density and dominance in June. Changes in community structure and density followed the same pattern while diversity behaved differently at both stations. At station 215 the organic matter is probably mixed trough the upper layers of the sediment and reworked continuously. A great part of the deposited matter is resuspended during flood and hence not assimilated in a great extent by the infauna. The fraction of the deposited matter that is consumed by the harpacticoids continuously increased density and species richness. Yet, the *Phaeocystis* derived material increased the dominance in the community. At station 330 the deposited organic matter is not reworked as intensively, resulting in a more stable food supply to the benthos. The harpacticoid fauna was more concentrated in the upper centimetres of the sediment at this station. Diversity increased remarkably during the diatom bloom, whereas the community was completely dominated by the most successful opportunistic interstitial species, *Apodopsyllus* n.spec.1, which exploits the detrital/bacterial food sources after *Phaeocystis* deposition.

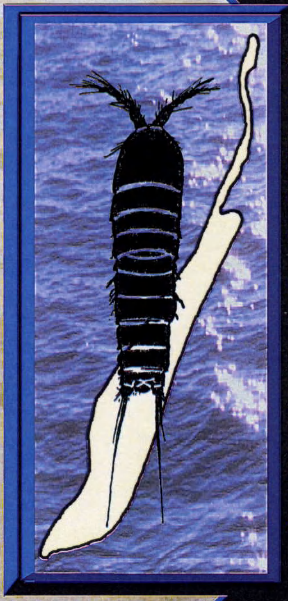
Popeye of the North Sea = *Apodopsyllus*



Chapter III

The impact of marine sand extraction on benthic copepod communities of a subtidal sandbank

De invloed van zandontginning op benthische copepodengemeenschappen van een subtidale zandbank



The impact of marine sand extraction on benthic copepod communities of a subtidal sandbank

Wendy Bonne & Magda Vincx

1 Introduction

Sand extraction and dredging in general is one of the most important human impacts on the marine benthic environment (Rumohr & Krost, 1991). Dredges directly impact species that live on or near the seafloor, as the tubes of the extraction ship physically disturb the habitat when they are dragged across the seafloor. Indirect changes in benthic communities, which are strongly determined by sediment structure (Sanders, 1968, 1969; Sanders & Hessler, 1969; Coull, 1972, 1985; Giere, 1993), may result from sediment removal through erosion and changing sediment characteristics causing habitat modifications. The spatial extent and frequency of habitat disturbance influences the degree of ecological impact, but it is a difficult task to detect specific ecological effects due to sand extraction. Dredging statistics are usually not appropriate to determine the dredging intensity at specific sites because the available information is collected over much too broad a scale. Dredgers effectively target sand quality and exploit the habitat in a patchy manner, causing a great deal of spatial variation in dredging effort. Also it is very difficult to detect the effect of human-induced physical disturbance in areas exposed to extreme natural disturbances (Hall *et al.*, 1990; Kaiser & Spencer, 1996). Additionally adequate knowledge of baseline pre-disturbance conditions is often lacking, in order to evaluate the extent of change caused by human-induced disturbance. The assessment of the impact of anthropogenic disturbances on the marine environment depends on the possibility of prediction by the analysis of changes in suitable biological communities. Soft-bottom benthic infauna is most frequently used to monitor the biological effects of environmental change. As a group they are largely sedentary and so must withstand the extremes of their local environment or perish. (Schratzberger *et al.*, 2000) Most studies on the impacts of marine sand and gravel extraction focused on macrofauna (Kenny & Rees, 1996; Newell *et al.*, 1998; van Dalfsen *et al.*, 2000; Sarda *et al.*, 2000; Boyd *et al.*, 2003), which can readily be counted and identified, whereas no studies have been conducted yet on the impacts on the meiobenthos. Meiofauna and in particular harpacticoid copepods react quickly on changes in the environment, making them suitable for ecological monitoring (Heip, 1980; van Damme *et al.*, 1984; Vincx & Heip, 1987; Moore & Bett, 1989).

Marine aggregate extraction is a growing industry. Sand and gravel extraction on the Belgian Continental Shelf increased fivefold from 0.37 million m³ sand in 1979 to 1.69 million m³ in 1999. 95 % of the sand mined in the Belgian waters originates from the Kwintebank, because of its location near the coast, the appropriate grain size and low calcium content of the sand. This intense mining activity makes the Kwintebank a valuable but also a potentially threatened area. The communities of sandbanks and sandwaves in areas with a high amount of exposure, as is the case for the Kwintebank, are adapted to continuous changing conditions. Such communities of high-stress areas are more adept to readjustement to the impact of dredging operations than communities of more stable environments (Desprez, 2000). When stress becomes too severe, however, physical disturbances may decrease community complexity and increase the abundance of opportunistic species (Rzonzef, 1993). Relating the structure of the different harpacticoid communities of the Kwintebank to environmental factors necessitates data on dredging intensity, as this may be an important structuring factor. Since 1978 the Kwintebank has been the subject of several benthic research projects, making it possible to compare the present day communities with the situation of the seventies (Claeys, 1979; Willems *et al.*, 1982b).

In this chapter the following hypothesis has been put forward: sand extraction activities can be associated with changes in sediment characteristics and harpacticoid communities observed between 1978 and 1997. In order to test this hypothesis the different harpacticoid communities on the Kwintebank have been determined and the importance of dredging pressure has been assessed in accounting for variation in community composition across a number of sites that differ in a variety of environmental characteristics. The possible impact of the extraction activities is discussed by comparing the results of 1997 with species distribution data collected in 1978 prior to intensive sand extraction.

2 Material & Methods

2.1 Sand extraction

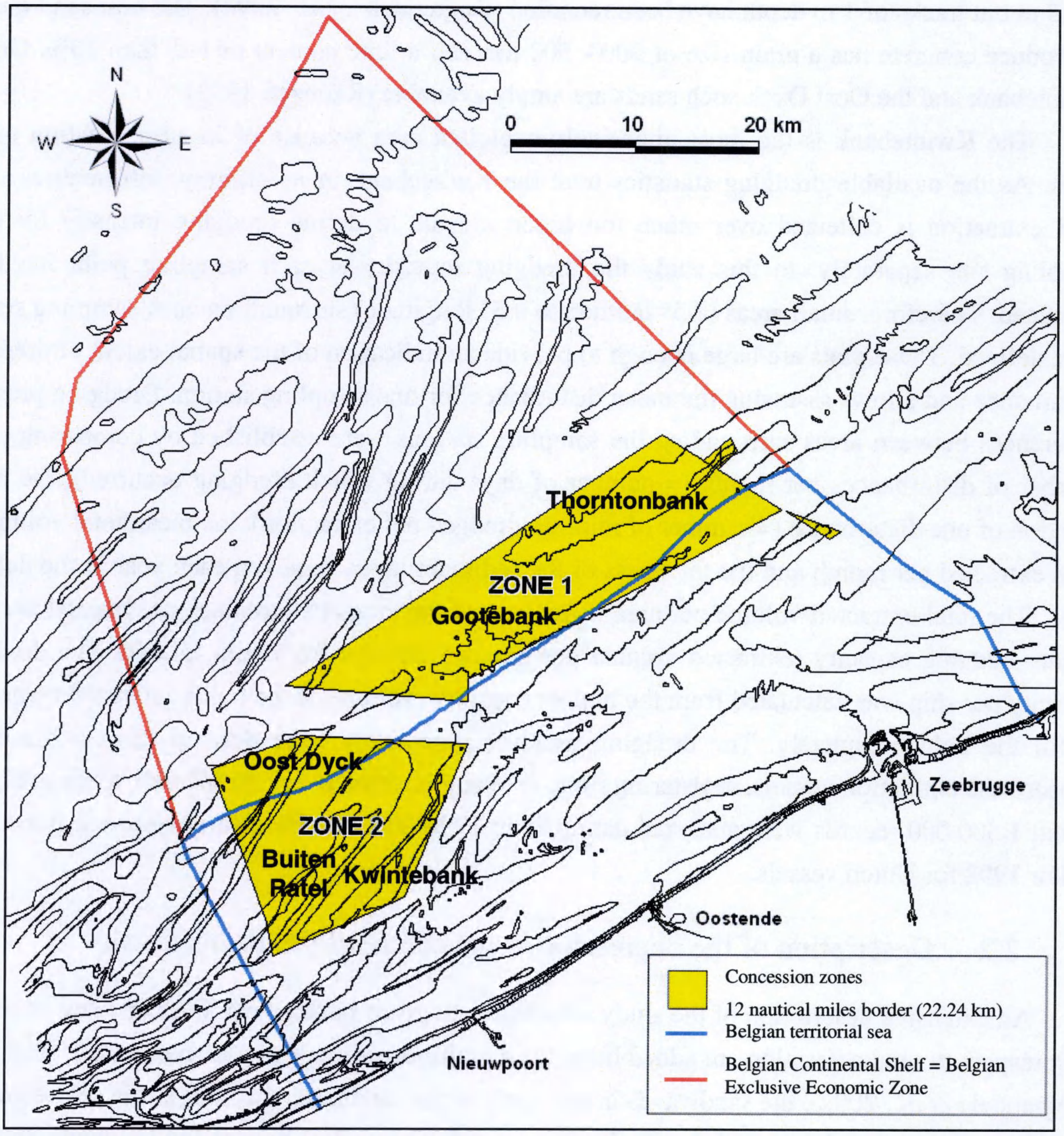


Fig.III.1: Sand extraction concession zones on the Belgian Continental Shelf (Fund For Sand Extraction)

In Belgium marine dredging activities started in 1976 to provide sand for the building industry, for road construction, for beach supplements to slow down erosion of the Belgian coast and exceptionally for land reclamation (Rzonzef, 1993). Two concession zones for sand extraction exist on the Belgian Continental Shelf: concession zone I comprises the Gootebank and the Thorntonbank and is reserved for exploitation in favour of public works. Consession zone II is open to exploitation by private companies and includes the Kwintebank, the Buiten Ratel and the Oost Dyck (Fig.III.1). Since 1996 anchor dredging is banned and trailer suction hopper dredging is the only allowed method in the concession areas of the Belgian Continental Shelf. During trailer suction hopper dredging, a tube at both sides of the extraction vessel is dragged across the seafloor, creating two tracks of 2 m wide and 20 to 30 cm deep (Rzonzef, 1993). The maximum depth is set at 0.5 m but tracks of 1 m depth have been recorded (Degrendele *et al.*, 2002). The best sand quality to produce concrete has a grain size of 300 - 500 µm and a lime content of less than 30%. On the Kwintebank and the Oost Dyck such sands are amply available (Rzonzef, 1993).

The Kwintebank is the most intensively exploited area because of its near location to the coast. As the available dredging statistics treat the Kwintebank in its entirety, information about sand extraction is collected over much too broad a scale to define dredging intensity for each sampling site separately. In this study the dredging intensity at each sampling point has been estimated. Therefore, small areas (0.5° latitude to 0.5° longitude) surrounding each sampling station were defined. These plots are large enough to provide an indication of the spatial extent of dredging disturbance and allows assessing the mean disturbance for one sampling station. Dredging pressure differences between areas surrounding the sampling stations were established by comparing mean number of disturbances per month (= number of days during which dredging occurred), the mean duration of one disturbance (= number of minutes dredged per extraction), the mean total volume of sand extracted per month and the thickness of the sediment layer, removed each year in the defined areas. The total extracted volume per area is the sum of the extracted volumes determined per ship as the dredging capacity (extracted volume per minute) differed from ship to ship. The dredging capacity per ship was calculated from the hopper capacity (volume of the hold) and the time needed to fill the hold completely. The dredging pressure parameters were derived from a black-box onboard the extraction vessels, registering time, date and position every 30 seconds when dredging. About 1 500 000 records were analyzed dating from 1996-2000 for Belgian vessels and from 1997 and/or 1998 for Dutch vessels.

2.2 Description of the depression in the centre of the Kwintebank

An extensive description of the study area has been given in chapter I. Further relevant details with respect to sand extraction are added here. On a multibeam-image of the Kwintebank (Fig.III.2) (Degrendele *et al.*, 2002), the sandwaves in the north of the sandbank, the kink in the centre and the flat elevated plateau of the south are easily recognized. The central part of the sandbank shows a disturbed topography. A depression is formed in the centre beneath the kink in the longitudinal profile of the sandbank. The southern tip of the depression shows a gap in the steep slope of the western flank. The depression runs parallel to the western flank of the centre of the sandbank while the eastern side of the depression forms a continuation of the western flank of the southern plateau. The crests of the large sand dunes situated in the central part of the sandbank display a less pronounced elevation when traversing the depression. The height of the sandwaves is remarkably lower than in the surrounding area.

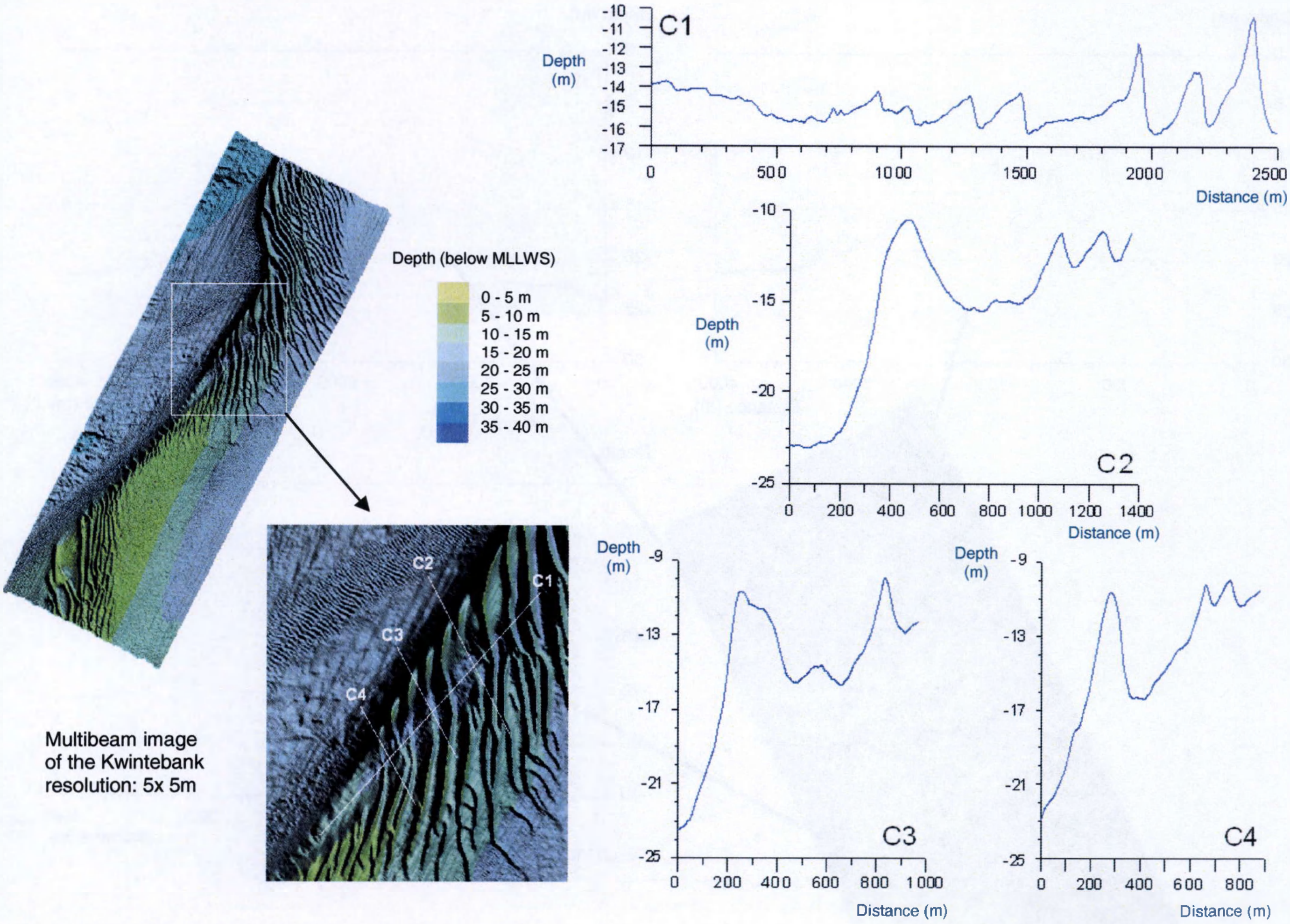


Fig.III.2: Multibeam image of the Kwintebank and cross-sections through the depression in the central part (Degrendele *et al.*, 2002)

Cross-sections through the sandbank were derived from a singlebeam-recording of 1994 and multibeam-pictures of 2000 in order to compare depth profiles (Fig.III.3). By comparing the same cross-section (situated between the meiofauna sampling stations 5 and 6 in the centre) between 1994 and 2000, it was estimated that over a five-year period depth had increased by approximately 5 m in the depression. Cross-sections at most other places along the sandbank did not show such depth differences but only natural oscillations. One cross-section beneath the depression at the centre indicated a decrease of 1 m depth at the eastern side of the sandbank. This decrease is also interpreted to be a result of sand extraction. The depression in the centre is very obvious on the multibeam-image but in the northern top of the sandbank a weaker deepening can also be distinguished in between the sandwaves.

Additional to the geomorphological information concerning the depression in the centre of the sandbank, a rough estimation could be made of the depth differences over 20 years, concerning the entire sandbank. This very rough analysis was based upon the bathymetric charts of 1980, 1995 and 2000 of the Coastal Waterways Division, the Hydrographic Office of the Flemish Region, Belgium (Addendum III.1, 2 & 3).

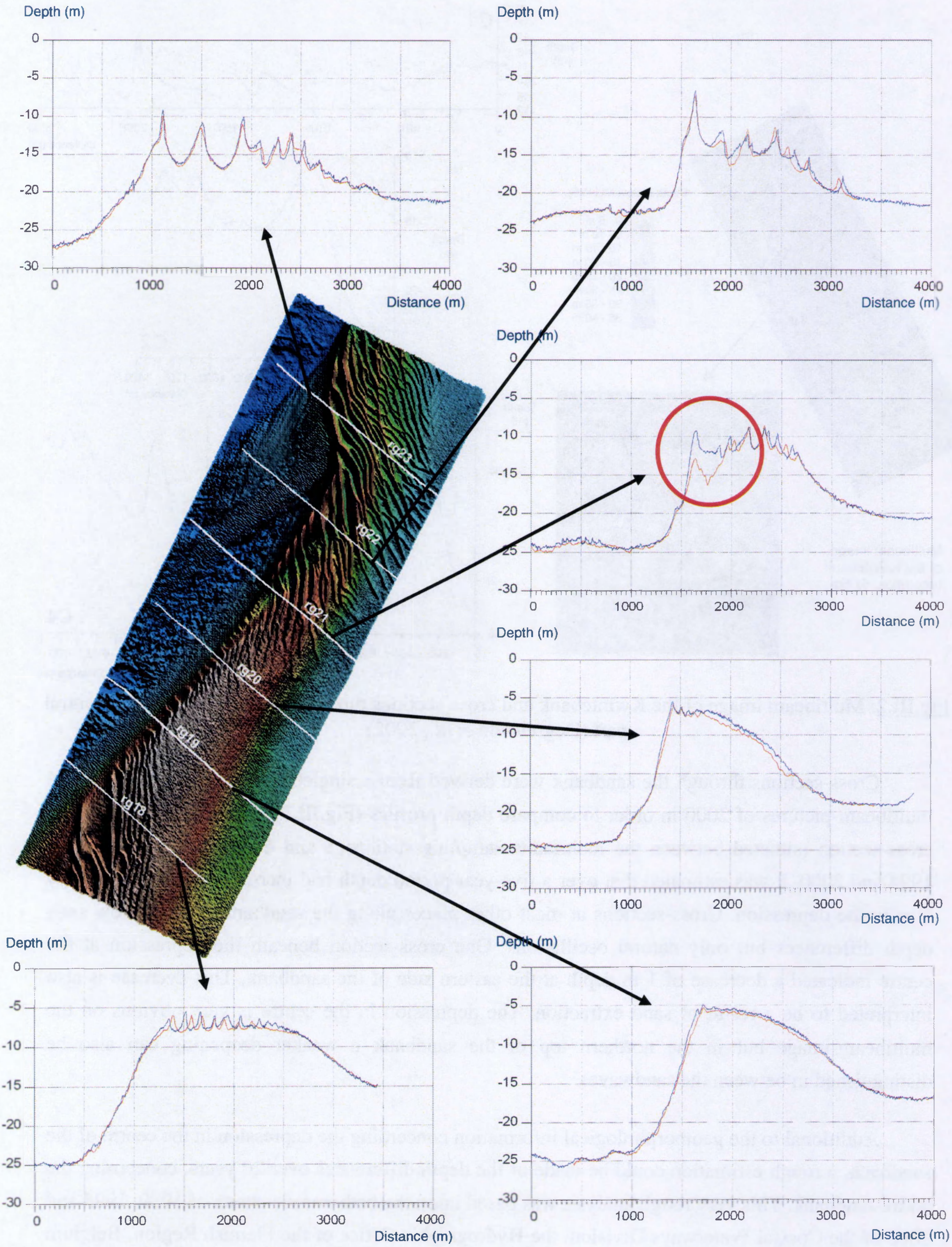


Fig. III.3: Cross-sections through the Kwintebank: singlebeam 12/1994 (red lines) and multibeam 11/1999 – 05/2000 (blue lines), depth below MLLWS (Degrendele *et al.*, 2002)

2.3 Sampling and processing

Meiofauna sampling methods and sample processing are described in chapter I. Additional data used in this chapter originate from a sampling at station 5 on the Kwintebank in 2000 and data of 1978 recalculated and reanalyzed from Claeys (1979). Species richness was also compared with values given in Willems *et al.* (1982b).

In order to compare sediment composition between 1978 and 1997, sediment samples of 1997 had to be submitted to a standard dry-sieving procedure (Wentworth, 1972) for granulometric analysis. Sediment fractions were defined according to the Wenthworth scale (Buchanan, 1984) and expressed as mass percentages.

2.4 Statistics

Hill's numbers (Hill, 1973) were used to calculate diversity. In order to compare densities and diversity indices within 1997 and between 1978 and 1997, ANOVA's were performed on untransformed or log (x+1) transformed data if needed to meet the assumptions for ANOVA. In some cases Kruskall-Wallis ANOVA by Ranks was preferred as relative abundances of some ecotypes and copepodites were still not normally distributed after arcsin (x/100) transformation. A t-test was performed in order to compare a single observation of 1978 with the mean of a sample of 1997 for normally distributed data. If these data were not normally distributed, no comparison could be made because the degrees of freedom were too low to perform a z-test and non-parametric tests are not powerful enough to compare a single observation with a mean. Spearman Rank Order Correlations were used to unravel correlations between densities or diversity indices and granulometric characteristics and Product-moment correlations to search for relationships between sand extraction intensity and total densities or relative copepodite densities. Correlations between individual species presence/absence and parameters of sand extraction intensity were examined by logistic regressions. All univariate analyses (ANOVA, t-tests, Kruskall-Wallis ANOVA by Ranks, Product-moment correlations, Spearman Rank Order Correlations and logistic regressions) were performed with STATISTICA^{TM} software (Microsoft, StatSoft, Inc., 2000).

A Canonical Correspondence Analysis (CCA, Hill, 1974) on fourth root transformed data was applied to describe the structure of the harpacticoid communities of 1997 in relation to environmental factors (granulometric information, depth and sand extraction intensity). 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 harpacticoid community structure of 1978 and 1997 was analyzed by means of multivariate classification and ordination techniques. A Cluster Analysis based on the Bray-Curtis similarity index and Group Average Sorting (Clifford & Stephenson, 1975), a TWINSPAN (TWo-way INdicator SPecies Analysis) (Hill, 1979a) and a Correspondence Analysis (CA, Hill, 1974) were performed on the compiled dataset (fourth root transformed) of the seventies and the nineties. The ordination analyses were performed with CANOCO for Windows (ter Braak & Smilauer, 1998). In order to compare the results of 1997 with the species dataset of 1978, the dataset of 1997 had to be reduced because taxonomical resolution was lower in 1978 and because some representatives of some families (especially Ectinosomatidae and Ameiridae) were not identified down to species level in 1978. In this way, *Kliopsyllus varians* identified in 1978 was lumped with the species *Kliopsyllus* n.spec.2, n.spec.3, n.spec.4 and *Kliopsyllus* spec. defined in 1997. The other species of this genus could be retained. Further taxonomic reductions were performed for the genera *Arenosetella*, *Apodopsyllus*, *Leptopontia*, *Arenopontia*, *Evansula* and *Arenocaris* of which the species identified in 1997 were pooled to genus level.

Different classes of sand extraction intensity were defined using the classification technique Cluster Analysis (Clifford & Stephenson, 1975).

3 Results

3.1 Sand extraction intensity

According to the analysis of sand extraction intensity in the 0.5° latitude x 0.5° longitude (600 x 900m) areas surrounding the sampling stations, three levels of sand extraction intensity can be distinguished (Table III.1): 1) the centre (stations 5 and 6) and the northern top (stations 1 and 2) of the sandbank are very intensively exploited areas, 2) station 3 and the southern part (stations 7 to 10) of the sandbank are exploited much less frequently and 3) at station 4 and the gully stations (almost) no extraction occurs. The centre of the sandbank is disturbed almost every day during the week by the same extraction vessel, for a duration of one hour around station 6 and half an hour around station 5 (Table III.1). In the northern tip sand is extracted every 3 days, during one hour per day around station 1 and three quarters of an hour around station 2. In the centre and the north often two ships or sometimes even three ships visited the same area the same day. Every year an average amount of 62.000 m^3 of sand is removed around stations 1, 2 and 5 and 100.000 m^3 of sand around station 6. This means that a sediment layer of respectively 12 cm and 19 cm of depth is removed every year of the entire area around the station. The less intensively exploited area (station 3 and the southern part) is disturbed 5 to 6 days a month or about once a week. Stations 8, 9 and 10 are characterized by a disturbance duration of 6 minutes per day, a removal of 4.000 m^3 of sand per year or of a sediment layer of 0.3 to 1.3 cm per year. For the stations 3 and 7 these extraction intensity parameters amount to 11 minutes per day, 16.000 m^3 of sand per year and 3 cm of sediment per year. In the gully stations no sand is extracted, only one record was registered in station 12. In station 4 no exploitation occurs because the lime content is too high because of the presence of a lot of shell debris. Sand extraction is seasonal: lower values are recorded for December, January and July in comparison with the rest of the year.

Sand extraction intensity	Stations		Frequency (days/month)	Duration (min./day)	Volume of sand removed (m³/month)	Surface removed (cm/year)
1) very high	1 - 2 - 5 - 6	mean ±se	15 ± 2	51.8 ± 6.5	6000 ± 800	13.2 ± 1.7
		range	12 - 19	35.3 - 63.9	5000 - 8300	11.2 - 18.5
2) high	3 - 7	mean ±se	6 ± 1	11.6 ± 1.4	1330 ± 60	2.9 ± 0.1
		range	5 - 7	10.2 - 13.0	1270 - 1380	2.8 - 3.0
low	8 - 9 - 10	mean ±se	5 ± 1	6.4 ± 0.5	360 ± 120	0.8 ± 0.3
		range	3 - 6	5.6 - 7.3	150 - 570	0.3 - 1.3
3) very low	4 - 11 - 12	mean ±se	0.2 ± 0.2	0.2 ± 0.2	9 ± 9	0.02 ± 0.02
		range	0.0 - 0.5	0.0 - 0.7	0 - 28	0.00 - 0.06

Table III.1: Sand extraction intensity on the Kwintebank expressed as mean frequency, mean duration, mean volume of sand removed per month and mean sediment surface layer removed per year

3.2 Sediment characteristics

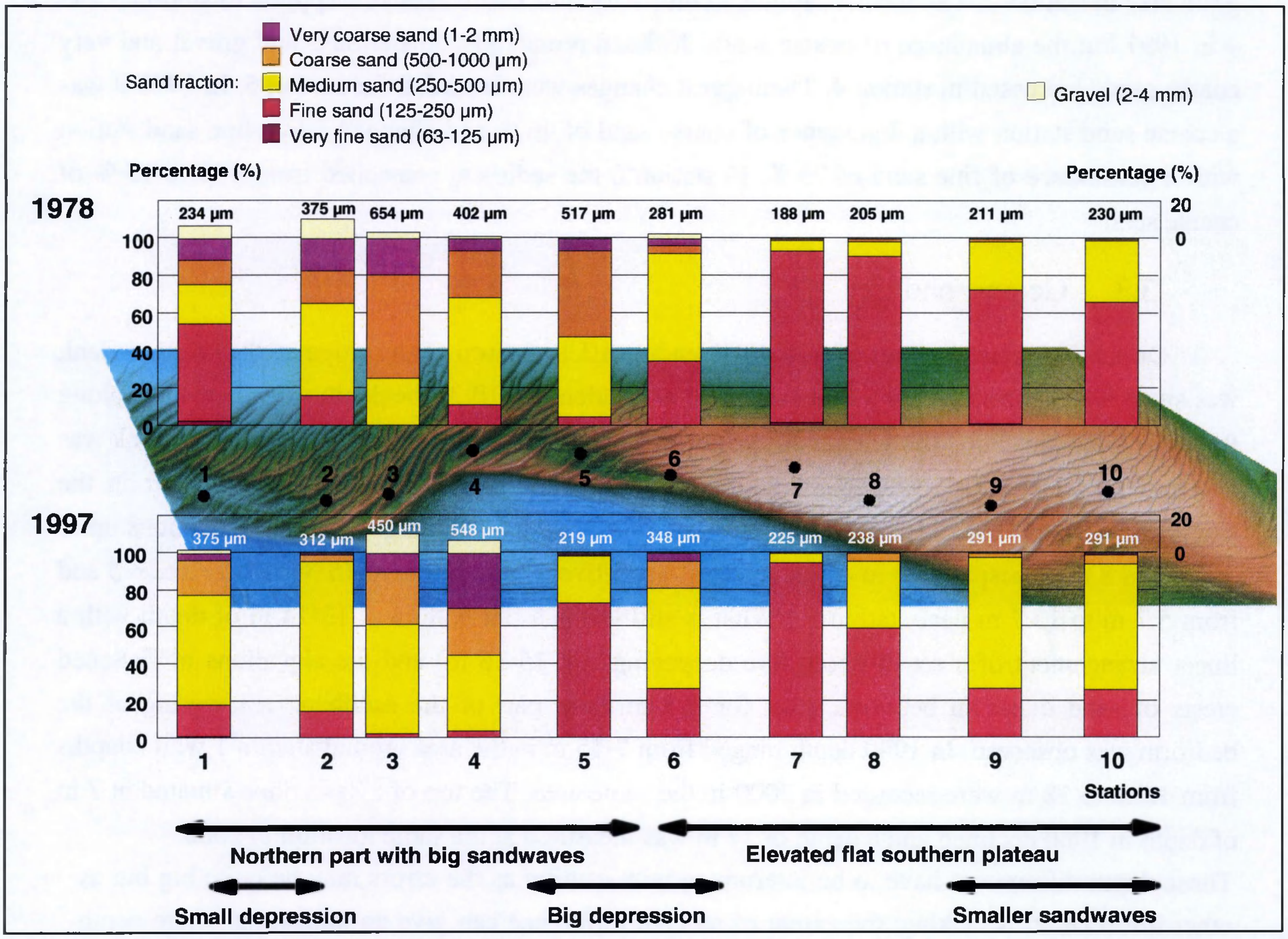


Fig.III.4: Sediment composition on the Kwintebank, the different sediment classes being expressed as mass percentages of the sand fraction and mass percentage of gravel being considered separately. Grain size values are given on top of the bars. Sampling stations are plotted on a multibeam image of the Kwintebank.

In 1978 the median grain size showed a linear trend and decreased from north to south (Willems *et al.*, 1982b). The gradient still existed in 1997 (Fig.III.4) but the difference in grain size between north and south in 1997 was not as pronounced as in 1978, mainly because of dramatic changes at station 5 and because the percentage of medium sand increased to a great extent in the south of the sandbank (from 18 % to 45 %). The domination of this area by fine sands was reduced from 71 % in 1978 to 47 % in 1997. Moreover, the importance of medium sand increased over the entire sandbank from a mean of 33 % in 1978 to 50 % in 1997. The mean percentage of fine sands decreased from 44 % to 35 %. The mean grain size over the entire sandbank, however, did not change at all because the coarsening was counterbalanced by a refining at stations 2, 3 and 5. In 1978 the sandwaves of the north of the Kwintebank consisted mainly of coarse and medium sands (Fig.III.4), while a low content of fine sands was found as well. At the deepest station 1 in the north, fine sands were more abundant in 1978 but also gravel and very coarse material was present, creating a very diverse biotope for meiofaunal organisms. However, the heterogeneous sediment of stations 1 and 2 is much more homogenised in 1997. The gravel, very coarse and fine sands were replaced by medium sands, resulting in a higher median grain size in station 1 and a lower median grain size in station 2. The former sediment composition of sandwaves still applied to station 3 and 4 in 1997 but the abundance of coarse sands declined remarkably in station 3 and gravel and very coarse sands increased in station 4. The biggest changes were recorded for station 5. In 1978 it was a coarse sand station with a dominance of coarse sand of 46 % and changed into a fine sand station with a dominance of fine sand of 73 %. In station 6 the sediment coarsened from 4 % to 15 % of coarse sand.

3.3 Geomorphology

On the bathymetric chart of 1980 (Addendum III.1) the top of the slope of the western flank was situated at approximately 6 m depth, in 2000 (Addendum III.3) the depth measured 14 m along the same boundary line. The bathymetric chart of 1980 shows that the gap in the western flank was not present yet twenty years ago. The large dunes, situated in the western central part in the beginning of the 1980s, were much reduced in 2000. They have undergone height reductions up to 7.4 m and 8 m corresponding to depth changes respectively from 7.9 m to 15.3 m near station 5 and from 5.7 m to 13.7 m near station 6 ! What is still left is a flat bottom at 13-14 m of depth with a linear arrangement of a set of about five deepenings (at 15-16 m) and the elevations of flattened crests of sand dunes in between. Also for the northern part of the sandbank a lowering of the bedform was observed. In 1980 depth ranged from 7-15 m in the area around station 1 while depths from 16 m to 18 m were recorded in 2000 in the same area. The top of a sand dune situated at 7 m of depth in 1980 declined and a depth of 17 m was measured at the same location in 2000.

These depth differences have to be interpreted with caution as the errors may be quite big but as other information is lacking, the extent of a depth difference can give an indication where depth changes really have taken place. The stations for which an increase in depth was found are all situated in the erosion areas as defined by De Moor & Lanckneus (1994) (Fig.III.13.c) while depth didn't change much at the other stations.

3.4 Harpacticoid density and diversity

Densities were significantly lower ($p < 0.001$) in 1997 than in 1978. In 1978 the lowest densities were recorded at the only two stations (7 and 8) with a very high percentage of fine sands (92 %). Density was highest at station 5, characterized by the highest percentage of coarse sand (46 %). Densities at stations 3, 5, 6, 9 and 10 in 1997 were significantly lower than the values of these stations respectively in 1978 (Fig.III.5).

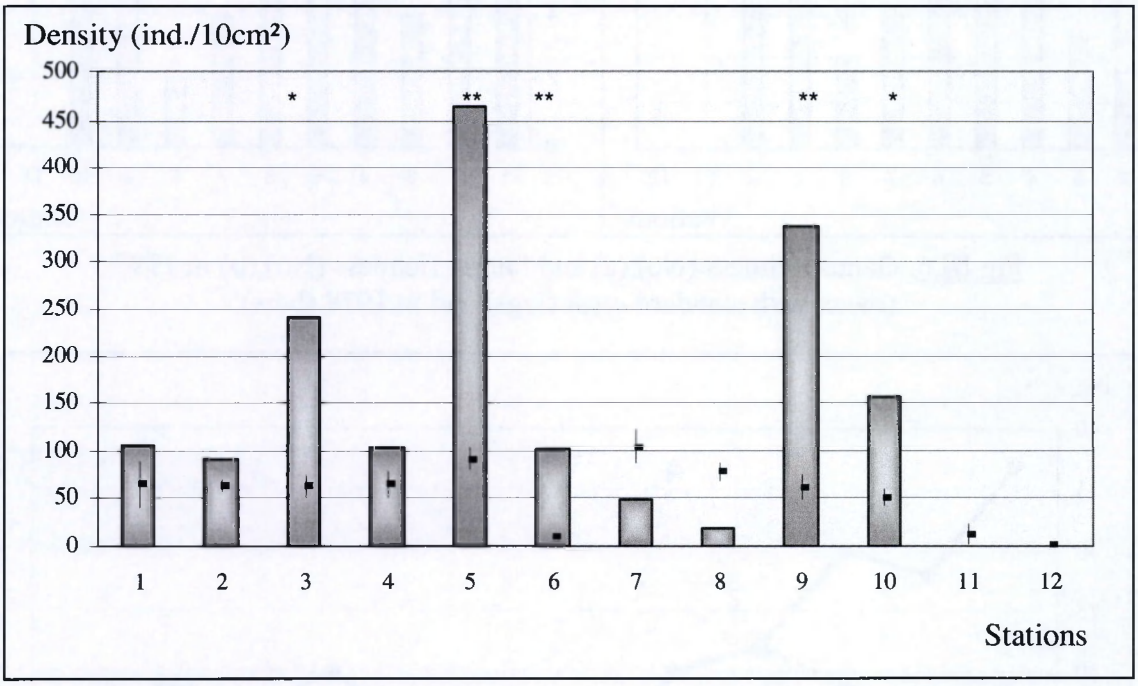


Fig.III.5: Densities in 1997 (mean with standard error flags) and in 1978 (bars), significant differences between 1978 and 1997 at the same station are indicated by *: $p < 0.05$ and **: $p < 0.01$

Although taxonomic resolution was much higher in 1997 than in 1978, species richness was lower near and in the centre of the sandbank (stations 4, 5 and 6) in 1997 than in 1978. Comparing species diversity of 1997 with 1978 accurately was impossible because the bulk of the Ectinosomatidae and Ameiridae were not identified in the available dataset of Claeys (1979). Therefore diversity indices of Hill of both years were compared at genus and family level, although this still resulted in a strong underestimation of genus diversity at station 3 in 1978 because of a high percentage of Ectinosomatidae in this station.

In 1997 genus and family richness were lower in the centre of the sandbank ($p < 0.05$ for station 4 (genus level) and $p < 0.01$ for station 5 (genus and family level)) compared to 1978 (Fig.III.6). Family richness in 1997 was also significantly lower at station 1 ($p < 0.05$).

Between intensively extracted (stations 1, 2, 5 and 6) and not intensively extracted stations a significant decrease ($p < 0.05$) of families was recorded with a loss of 3 families in the north and 4 families in the centre of the bank from 1978 to 1997. In the centre (stations 5 and 6) also the decrease in genera from 1978 to 1997 is significantly different ($p < 0.05$) from the not intensively exploited stations on the bank.

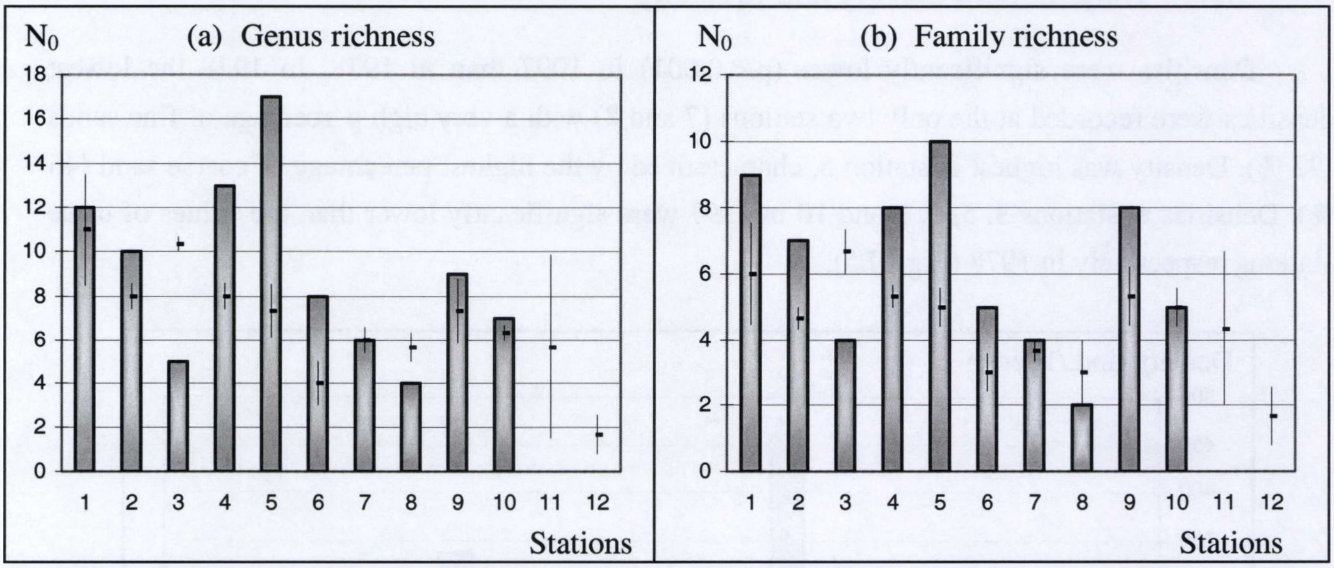


Fig.III.6: Genus richness (No) (a) and family richness (No) (b) in 1997 (mean with standard error flags) and in 1978 (bars)

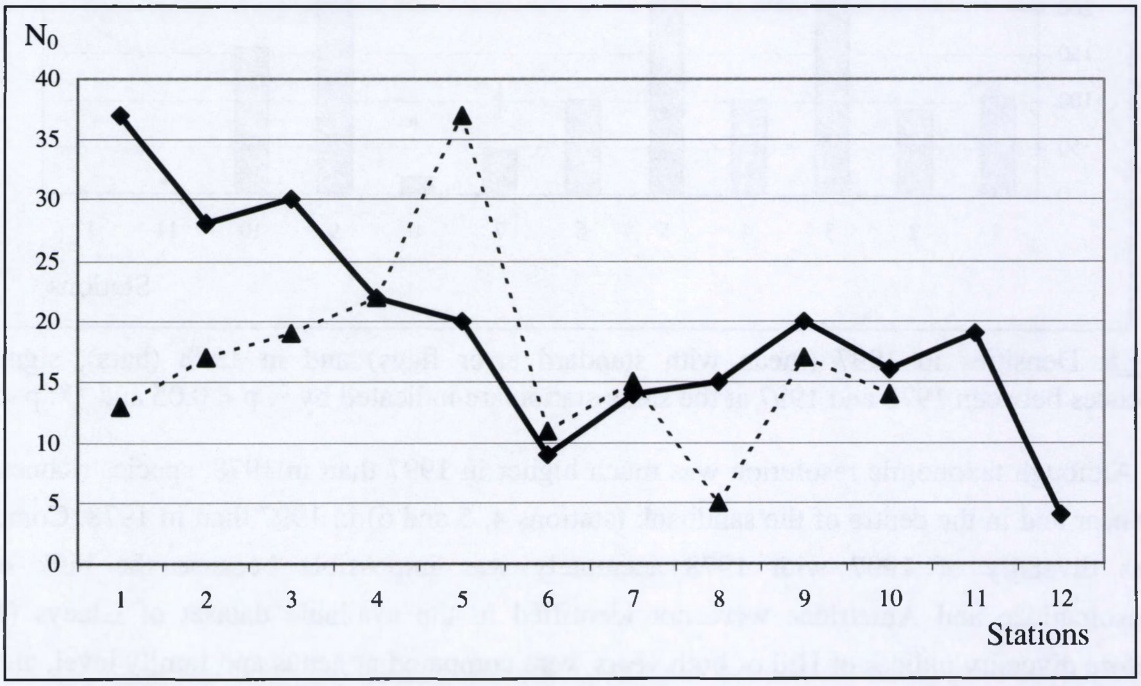


Fig.III.7: Species richness in 1997 (solid line) and in 1978 (dotted line)

In Willems *et al.* (1982b) the total number of species is given for two replicates combined, Ectinosomatidae and Ameiridae also being identified to species level. Comparing these values with the total number of species for three replicates in the nineties, it is clear that stations 1, 2 and 3 yield much more harpacticoid species in the nineties than in the seventies, whereas species richness remained exactly the same at station 4. At station 5 in the centre of the sandbank, the number of species is much lower in the nineties. Species richness at the southern part of the Kwintebank was similar for both periods, except for a rise in the number of species at station 8.

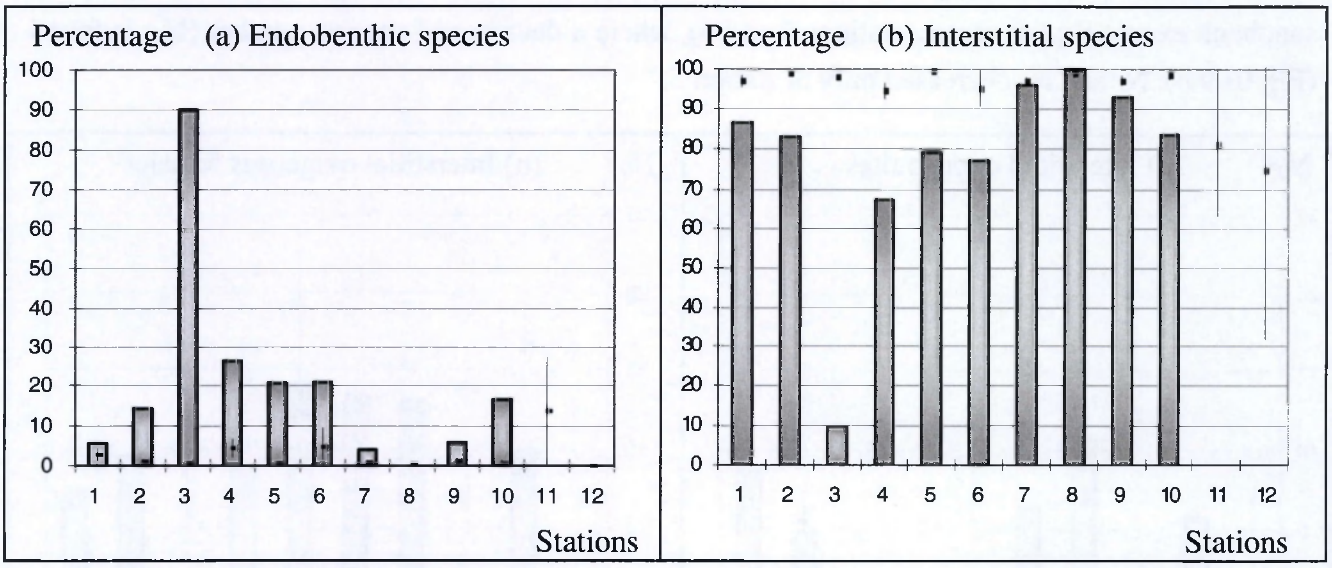


Fig.III.8: Relative abundance of endobenthic (a) and interstitial species (b) in 1997 (mean with standard error flags) and in 1978 (bars)

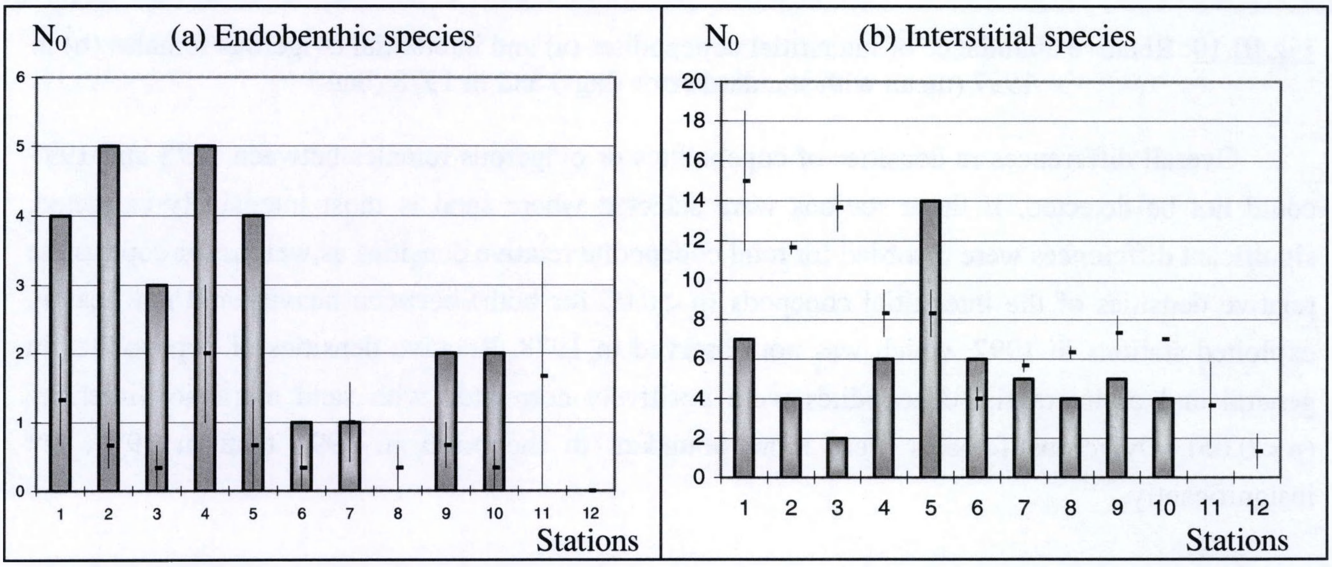


Fig.III.9: Species richness (No) of endobenthic (a) and interstitial species (b) in 1997 (mean with standard error flags) and in 1978 (bars). Species richness of endobenthic species in 1978 is strongly underestimated at station 3.

In the northern tip (station 1) density and species richness of epibenthic copepods were significantly lower in 1997 than in 1978 ($p < 0.01$ and $p < 0.05$ respectively). The decrease in epibenthic species was significant ($p < 0.01$) between the northern most exploited stations and the other categories of stations, grouped by sand extraction intensity. Relative densities (Fig.III.8a), species richness (N_0) (Fig.III.9.a) and N_2 of endobenthic species were significantly lower ($p < 0.001$, $p < 0.05$ and $p < 0.05$ respectively) in 1997 compared to 1978, while the relative densities of interstitial species were significantly higher ($p < 0.001$) in 1997 (Fig.III.8.b). In 1997 the proportion of interstitial species was equal over the entire sandbank with a minimum of 95 %.

Within the interstitial group the diversity indices of Hill increased significantly for the entire sandbank except for the centre (stations 5 and 6), where a decrease of species number (N_0) is found (Fig.III.9.b). N_1 and N_2 decreased only in station 5.

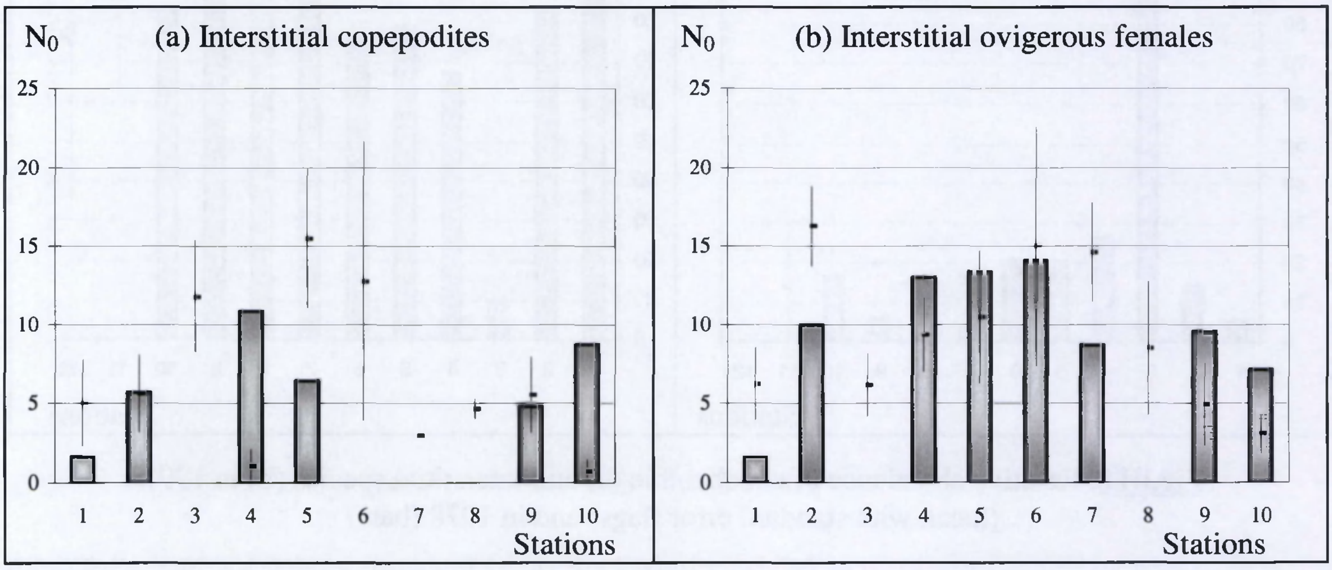


Fig.III.10: Relative abundance of interstitial copepodites (a) and interstitial ovigerous females (b) in 1997 (mean with standard error flags) and in 1978 (bars)

Overall differences in densities of copepodites or ovigerous females between 1978 and 1997 could not be detected. If these stations were selected where sand is most intensively extracted, significant differences were recorded for total copepodite relative densities as well as for copepodite relative densities of the interstitial copepods ($p < 0.05$ for both) between heavily and not heavily exploited stations in 1997, which was not observed in 1978. Relative densities of copepodites in general and of interstitial copepodites were positively correlated with sand extraction intensity ($p < 0.05$). Ovigerous females were more abundant in the north in 1997 than in 1978, but insignificantly.

3.5 Harpacticoid community structure

Fig.III.11 shows that the first axis of the CCA, of length 3.41 SD and explaining 53 % of the variation, is interpreted as a granulometric gradient from coarse to fine sands along the sandbank and the second axis, of length 4.28 SD (eigenvalue 0.39), as a gradient in depth and sand extraction intensity. When the gully stations were excluded, depth was not important anymore but sand extraction intensity was the only important environmental variable with statistical significance ($p < 0.05$) along the second axis.

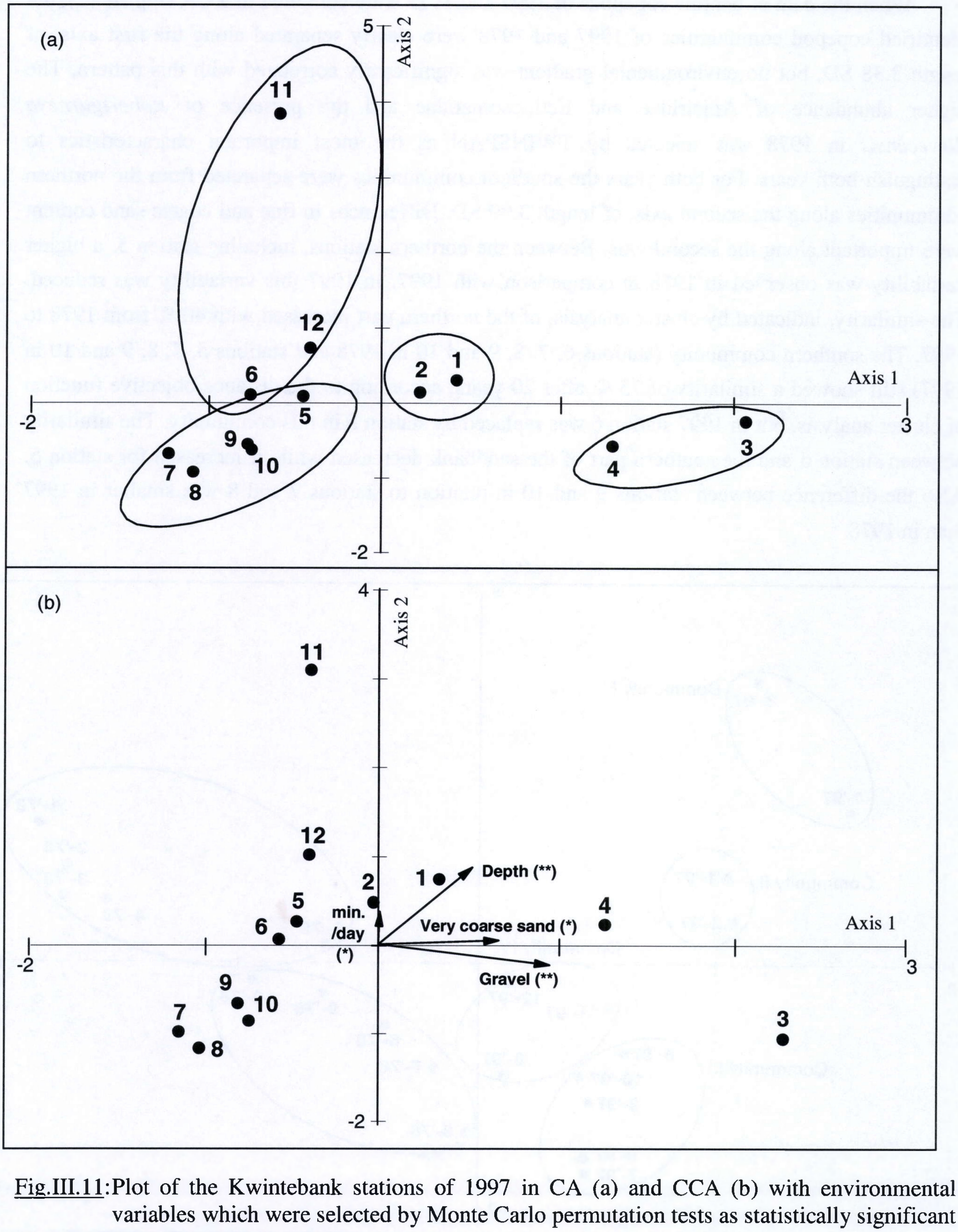


Fig.III.11: Plot of the Kwintebank stations of 1997 in CA (a) and CCA (b) with environmental variables which were selected by Monte Carlo permutation tests as statistically significant (** $p < 0.01$, * $p < 0.05$).

When the data of benthic copepods of 1997 and 1978 were compiled in a CA (Fig.III.12), the identified copepod communities of 1997 and 1978 were clearly separated along the first axis, of length 3.38 SD, but no environmental gradient was significantly correlated with this pattern. The higher abundance of Ameiridae and Ectinosomatidae and the presence of *Robertgurneya ilievecensis* in 1978 was selected by TWINSPAN as the most important characteristics to distinguish both years. For both years the southern communities were separated from the northern communities along the second axis, of length 3.99 SD. Differences in fine and coarse sand content were important along the second axis. Between the northern stations, including station 5, a higher variability was observed in 1978 in comparison with 1997. In 1997 this variability was reduced. The similarity, indicated by cluster analysis, of the northern part increased with 40 % from 1978 to 1997. The southern community (stations 6, 7, 8, 9 and 10 in 1978 and stations 5, 7, 8, 9 and 10 in 1997) still showed a similarity of 75 % after 20 years, according to the distance objective function of cluster analysis, but in 1997 station 6 was replaced by station 5 in this community. The similarity between station 6 and the southern part of the sandbank decreased while it increased for station 5. Also the difference between stations 9 and 10 in relation to stations 7 and 8 was smaller in 1997 than in 1978.

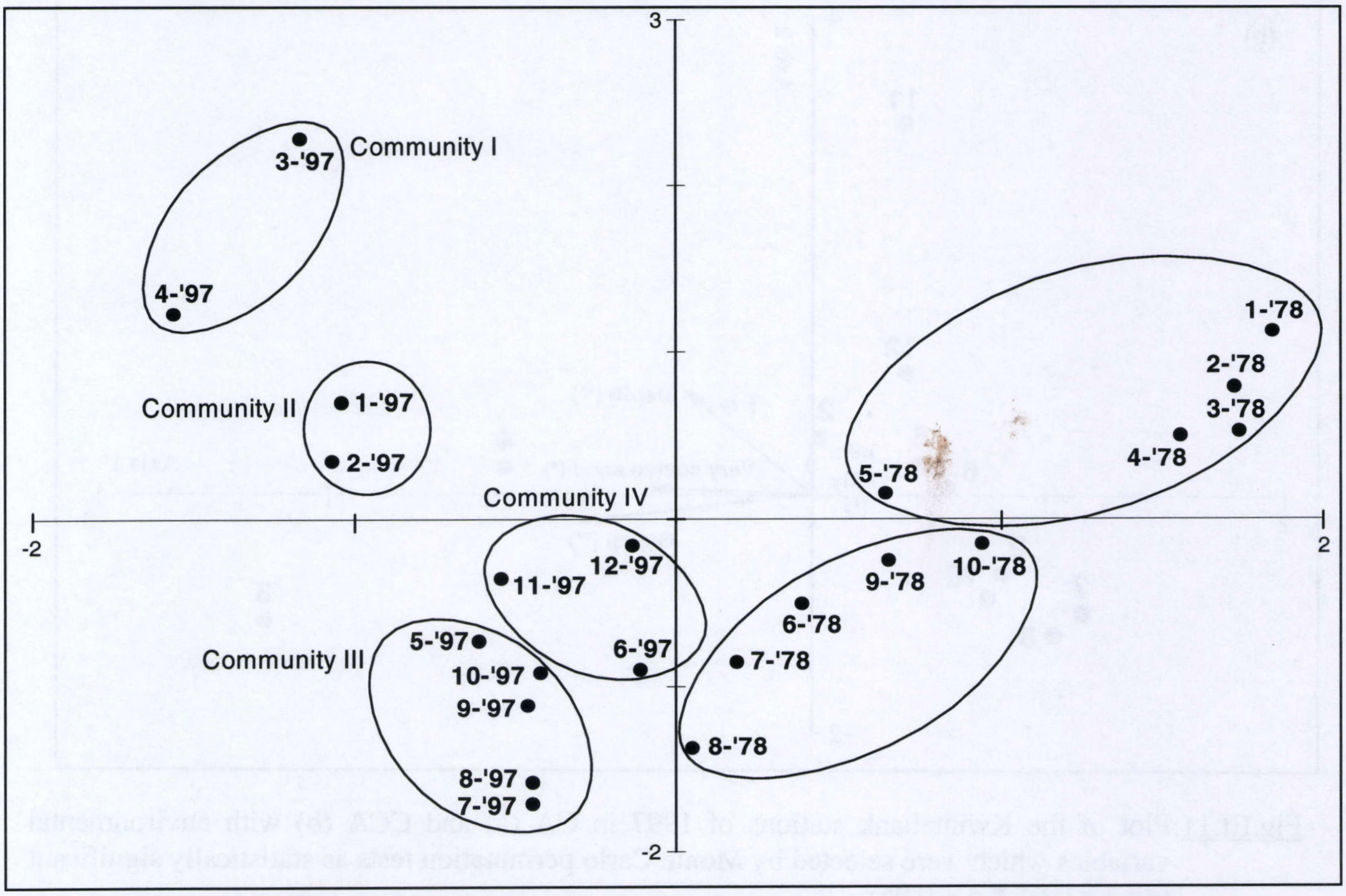


Fig.III.12: Plot of the stations in a CA, based on absolute species densities of the pooled dataset of 1978 and 1997

In the nineties the northern part of the Kwintebank was split up in two easily distinguished communities while in the seventies strong affinities existed neither between station 1 and 2 nor between stations 3 and 4. In the seventies only a high variable northern part was defined with the biggest differences between station 1 and the other northern stations. In 1997 stations 1 and 2 were very similar. In 1978 *Apodopsyllus* n.spec.1 (47 %) and *Stenocaris pontica* (22 %) predominated at station 1 while *Leptastacus laticaudatus s.str.* (18 %), *Paraleptastacus moorei* (10 %) and *Apodopsyllus* n.spec.1 (7 %) were the most abundant species in 1997 (Addendum III.4). *Leptastacus laticaudatus s.str.* (43 %) and *Kliopsyllus holsaticus varians* (25 %) were the two codominant species at station 2 in 1978 while the relative abundance of *Leptastacus laticaudatus s.str.* (11 %) decreased and *Paraleptastacus moorei* (34 %) was dominant in 1997. The latter species was not present at all in the seventies, the lower taxonomical resolution taken into account. In 1997 *Paraleptastacus moorei* was the dominant species and an indicator species of the most northern community but it was not restricted to the community in the northern top, it occurred in station 5 as well. The presence of *Paraleptastacus moorei* was not correlated with any sediment characteristics but positively correlated with all sand extraction intensity parameters ($p < 0.05$).

The southern community was stable in time as for stations 7, 8, 9 and 10 still a uniform species composition was found after 20 years (Addendum III.5). All the species present in 1978 still occurred in 1997. Also the dominant species and the proportional distribution were still comparable. Only Ectinosomatidae and Ameiridae, which were important in 1978 at stations 9 and 10 respectively, were represented in a less extent at these stations in 1997. Of all the stations on the Kwintebank, the species assemblage of station 8 in 1997 showed the highest similarity with its situation in 1978.

3.6 Comparison of the results of 1978 and 1997 (2000) in the depression in the centre of the Kwintebank

	Depression in the centre				
	Station 5			**Station 6**	
	1978	1997		1978	1997
Very coarse sand (%)	6	0.3		3	4
Coarse sand (%)	46	1		4	14
Medium sand (%)	43	25		57	54
Fine sand (%)	5	73		35	27
Very fine sand (%)	0.1	0.5		0.5	0.2
Sediment change	refining (by accretion of fine sediments in the recently formed depression ?) ⬇			coarsening (by erosion ?) ⬇	
	1978	1997	2000	1978	1997
Density (ind./10cm²)	463	100	39	101	10
Number of species	20 (1)	10	10	8 (2)	4
Epi- and endobenthic species (%)	21	1	0	21	5
Interstitial species (%)	79	99	100	77	95
***Paraleptastacus espinulatus*:**					
• abundance (%)	0	64	5	27	25
• copepodites (%)	0	19	0	0	20
	• decreasing density and diversity • community shift • impoverishment			• decreasing density and diversity • impoverishment	

(1) 13 % of individuals were not identified
(2) 21 % of individuals were not identified

Table III.2: Differences in granulometric and biological characteristics between 1978, 1997 and 2000 at stations 5 and 6, situated in the depression in the centre of the Kwintebank

In the central part of the sandbank beneath the kink in the longitudinal profile of the sandbank, a depression was formed, in which stations 5 and 6 were situated and which was not present in the seventies. Station 5 was located in the centre of the depression, while station 6 was situated in the south of the depression near the gap in the steep slope of the western flank of the sandbank. In this area density and diversity decreased dramatically and the abundance of big epi- and endobenthic species decreased in favour of interstitial species.

At station 5 very coarse and coarse sands almost disappeared, the quantity of medium sands halved and fine sands predominated in 1997. As a result of these changes in sediment characteristics a shift was recorded from a species rich northern community to a less divers southern community. This change was reflected by the dominance of *Paraleptastacus espinulatus* and the presence of *Kliopsyllus constrictus s.str.* in 1997, which were typical for the southern community. *Kliopsyllus constrictus s.str.* was absent in 1978 and from *Paraleptastacus espinulatus* only one specimen was found. In 2000 the relative abundance of *Paraleptastacus espinulatus* decreased again but then, *Leptastacus laticaudatus s.str.* reached a relative abundance of 33 %. Yet, the station was still characterized by a southern community fauna since *Paraleptastacus espinulatus, Leptastacus laticaudatus s.str.* and *Kliopsyllus constrictus s.str.* replace each other as most dominant species in this community. *Arenosetella* n.spec.1 increased to a large extent in 1997 and two of the dominant species (*Interleptomesochra eulitoralis* and *Sicameira leptoderma*) in 1978 disappeared in 1997.

At station 6 the sediment coarsened. A big loss of Ectinosomatidae species was observed but there was no clear shift in the dominant interstitial species. Remarkable as well was the increased abundance of juveniles at both stations in 1997, almost exclusively due to the high relative importance of *Paraleptastacus espinulatus* juveniles (20%).

4 Discussion

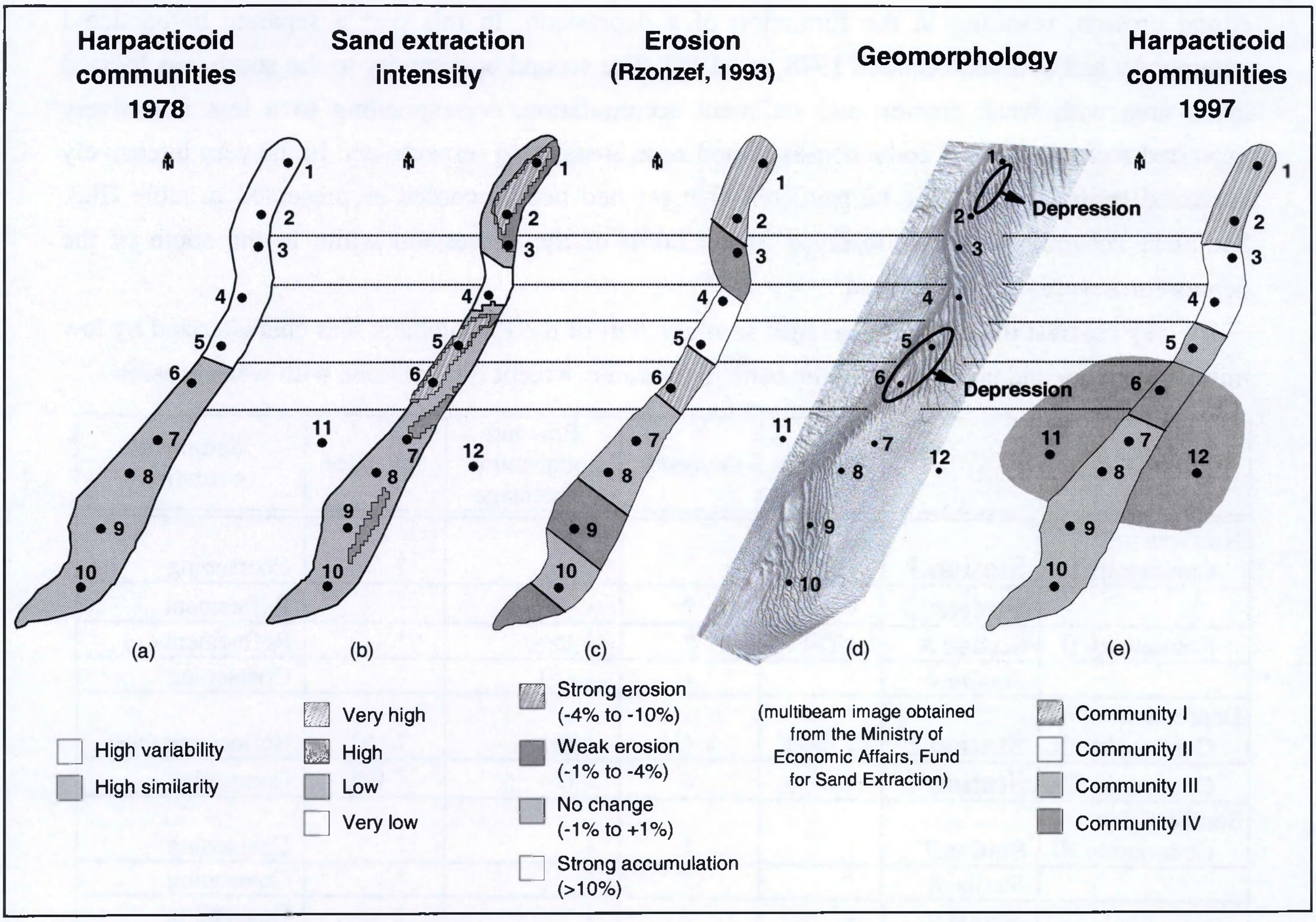


Fig.III.13: Correspondence between sand extraction intensity (b), erosion (c), geomorphology (d) and harpacticoid communities in 1997 (e), compared with harpacticoid communities in 1978 (a) on the Kwintebank

Analogies were found in the occurrence of erosion (Fig.III.13.c) and extraction areas (Fig.III.13.b) and the distribution of harpacticoid communities (Fig.III.13.e) on the Kwintebank. Community analyses of the harpacticoid dataset of the seventies distinguished between a northern part, with a highly variable species composition in the coarser deposits, and a southern community, characterized by a high similarity in the finer sands. This pattern was much different in 1997. The northern part was split up in two communities, while station 5 showed more similarities to the southern community than to the northern part. Station 6 was separated from the southern community due to low densities and the similarities with the gully stations. Stations more to the south remained nearly unchanged.

This community pattern corresponded with different erosion trends and mining intensity patterns. The northern top of the Kwintebank was subject to very intensive sand extraction and strong erosion, resulting in the formation of a depression. In this part a separate harpacticoid community had evolved between 1978 and 1997. The second community to the south was located in an area with weak erosion and sediment accumulation, corresponding to a less intensively exploited zone at station 3 and a non-exploited zone at station 4 respectively. In the very intensively exploited central part drastic harpacticoid changes had been recorded as presented in table III.2. Sediment accumulation was observed in the north of the depression while in the south of the depression severe erosion occured.

By contrast the nearly unchanged southern part of the Kwintebank was characterized by low mining intensity and no changes in the bank top volume, except for one zone with weak erosion.

		Density	Diversity	Epi- and endobenthic percentage	Juveniles	Sediment evolution
Northern top Community I	**Station 1**	↓	↑	↓	↑	Coarsening
	Station 2	↓	↑	↓	↑	Refinement
Community II	**Station 3**	↓ (>)	?	↓ (>>)	↑	Refinement (>)
	Station 4	↓	↓	↓ (>)	↓	Coarsening
Depression Community III	**Station 5**	↓ (>>)	↓ (>)	↓ (>)	↑ (>)	Refinement (>>)
Community IV	**Station 6**	↓ (>>)	↓	↓ (>)	↑ (>)	Coarsening
Southern part Community III	**Station 7**	↑	↑	↓	↑	Coarsening
	Station 8	↑	↑	↑	↑	Coarsening
	Station 9	↓	?	↓	↑	Coarsening
	Station 10	↓	?	↓ (>)	↓	Coarsening

Table III.3: Changes in 1997 relative to 1978 in density, diversity, percentage of epi- and endobenthic species, percentage of juveniles and grain size per station on the Kwintebank; > indicates changes exceeding maximum seasonal differences recorded in other studies along the Belgian coast, >> points to differences exceeding the maximum seasonal fluctuations 1.5 times or more. Sand extraction intensity is expressed as different type fonts of the stations: **Bold 13: very high**; **Bold 11**: **high**; Regular 11: low; *Italic 11: very low*

Although obvious links were observed between the harpacticoid community pattern and sand extraction and erosion zones, table III.3 clearly shows that biological parameters such as density, diversity and ecotype proportion are not closely related to sand extraction intensity nor to sediment evolution. Apart from the percentage of juveniles, correlations could not be detected between biological characteristics and sand extraction intensity. A relationship between sediment evolution and sand extraction intensity was not found either. This does not mean that sand extraction did not impact the fauna because the degree of the impact of extraction activities is site specific and depends on numerous factors, including sediment type and mobility, bottom topography and current strength and the nature of the pre-disturbance community (Desprez, 2000). A similar sand extraction intensity may induce different environmental and biological changes and hence blur an overall analysis of sediment evolution or density and diversity. A lot of observed changes, especially in the centre of the sandbank, clearly surpassed potential seasonal fluctuations and did not clearly correspond to a consistent sediment evolution. These changes will be discussed in detail in relation to sand extraction but attention will also be paid to changes minor to seasonal fluctuations.

4.1 Impacts in the depression in the centre of the Kwintebank

Dredging statistics indicated that a great deal of spatial variation exists in dredging effort on the Kwintebank, as dredgers effectively target sand quality and exploit the habitat in a patchy manner. At the centre and the northern top the most intensive sand extraction was recorded. So far, Vanosmael *et al.* (1979) and De Moor & Lanckneus (1991) considered only the northern top of the Kwintebank to be intensively exploited. This study revealed that the centre of the Kwintebank is even more intensively exploited. In this area, sand extraction affects not only geomorphological and sedimentological but also biological characteristics.

4.1.1 Geomorphological characteristics

Near station 6 the centre corresponds with an area of strong erosion (Fig.III.13.c) (De Moor & Lanckneus, 1994). A multibeam survey (Fig.III.13.d) showed the existence of a depression in this area that was not present in the seventies (Degrendele *et al.*, 2002). Sandwaves are very stable structures (De Moor, 1985; De Moor & Lanckneus, 1994; Lanckneus & De Moor, 1995) but in the centre of the Kwintebank they were almost entirely destroyed, although evidence for quick recovery exists. In 1992 De Moor & Lanckneus (1994) observed a depression of 6 m depth and 100 m wide in the northern part of the Kwintebank, made by anchor hopper dredging, which is not allowed anymore. After nine months the pit was completely filled, illustrating the potential for recovery by sediment fluxes. De Moor & Lanckneus (1991) stated that dynamic sandbanks can withstand extraction activities because of the residual sediment transport from the gullies towards the top of the sandbanks. Infilling of the pits and furrows depends upon the type of substratum and the ability of local currents to transport the surrounding sediment (Desprez, 2000), but also on the frequency of extraction. Due to the continuous and intensive extraction concentrated in the centre of the Kwintebank, this area had no time to recover from sediment losses. This proofs that sandbanks can be significantly affected by continuous and long-term sand exploitation. Storms may destroy small (max. height of 50 cm) and medium dunes on the summit of a sandbank. Even crests of large dunes (max. 8 m heigh) may be lowered with up to 1.2 m under storm conditions (Houthuys *et al.*, 1994). The original shape of small, medium and large dunes are however reconstructed by the fair-weather tidal flows. Depth differences up to 8 m, as recorded in the centre of the Kwintebank on the bathymetric chart of 2000 in comparison with the one of 1980, are therefore considered unnatural. Probably most of the deepening occurred in the nineties as depth had increased by approximately 5 m in the depression between 1994 and 2000 (Degrendele *et al.*, 2002). Depth may change rapidly due to extraction activities. Kenny & Rees (1996) estimated that over a five-day period depth had increased by approximately 2 m in areas where the draghead had followed the same path several times.

4.1.2 Granulometric characteristics

Not only the morphology of a sandbank but also granulometric characteristics are mainly maintained by tidally induced forces (Stride, 1982). Grain size changes can occur after some rough weather crossed a sandbank (Houthuys *et al.*, 1994) but in general grain size distribution of the Flemish sandbanks is regarded as stable (De Moor & Lanckneus, 1994; M. Roche, pers. comm.). Natural hydrodynamics cannot account for the obvious changes in sediment composition between 1997 and 1978 at station 5. De Moor & Lanckneus (1994) found that near station 5 the centre was characterized by a strong accumulation of sediment (Fig.III.13.c). The altered sediment composition at station 5 may result from an accretion of fine sediments, as a consequence of changed current velocities due to the increased depth in the depression. According to several authors (Kaplan *et al.*, 1975; Hily, 1983; Van der Veer *et al.*, 1985; Desprez & Duhamel, 1993) a further implication of the formation of depressions by dredging is a local drop in current strength associated with the increased water depth, resulting in deposition of finer sediments than those of the surrounding substrate. The fine sediments potentially originate both from overflow and from the large natural tidal transport of sediments in the area. Infilling by sediment transport is the most rapid and dominant process if the dredge site is located in an area of active sand transport (Desprez, 2000), like the Kwintebank. Extraction progressively eliminates the original coarse sand and causes the dredged area to fill in with a different sediment type. Similar observations are reported in the dredging site of Dieppe along the French coast by Desprez (2000) and by Van der Veer *et al.* (1985) in the Dutch Waddensea. Sediments filling dredge tracks are generally finer than the original ones and the fauna colonizing the new substrate may differ from the biota present in the adjacent undredged coarser substrates (Shelton & Rolfe, 1972; Millner *et al.*, 1977). The difference between the fauna is proportional to the refinement of the sediment, which itself is linked to the dredging intensity (Desprez, 2000).

The observed refinement and the continued high extraction intensity seem to contradict each other, since dredgers are looking for coarser sands (300-500 µm). It is however not clear how widespread the refinement at station 5 took place. During three later sampling campaigns fine sediments were encountered again at station 5, whereas at other sampled places in the depression the typical coarser sediments were found. Patches of finer sediments along the dredging tracks probably do not matter as long as the total cargo is coarse enough. At station 6 a coarsening is observed and according to detailed dredging statistics the amount of extracted sand is still higher at this station than at station 5, probably reflecting the intention to get the right mixture of sand.

4.1.3 Biological characteristics

4.1.3.1 Harpacticoid communities

4.1.3.1.1 Station 5

The infilling with much finer sediment than originally present has lead to the development of a different harpacticoid community on the Kwintebank. At station 5 a shift was recorded from a species rich northern community in 1978 to a less diverse southern community with a high dominance of *Paraleptastacus espinulatus* in 1997, the density of which was still negligible in 1978. *Interleptomesochra eulittoralis* was the second most abundant species in September 1978 but absent in January 1997. Along the Belgian coast this species reaches its maximum density in January (Huys *et al.*, 1986a). Low values have been recorded in January on a beach on the North Sea Island Sylt while densities were highest in the preceding months November and December (Mielke, 1975). This decline was the result of a temperature drop down to below zero on the beach. On a sublitoral sandbank such a steep temperature drop will not occur and reproduction of *Interleptomesochra eulittoralis* will not be affected because of this reason. This winter breeder should have been recorded in 1997 if the conditions would have been favourable. Comparison of earlier studies in the Southern Bight (Huys *et al.*, 1986b; Huys *et al.*, 1992) revealed that the interstitial harpacticoid community in sandy habitats is stable in time. Yet, changes in species dominance were only observed when they were related with sediment changes (Huys *et al.*, 1986b).

The community shift in the depression contradict the statement of Van der Veer *et al.* (1985) that on sandbanks, excavated sites are filled with sediment similar to that removed by the dredger and hence the colonizing benthic community is similar in composition to that originally present. Indirect impacts of sand extraction are possible due to habitat modification, changes in sedimentation pattern or benthic algal production and nutrient cycling, as similar to the changes induced by trawling (Thrush *et al.*, 1998). The community shift in station 5 in the northern part of the depression can be clearly defined as mainly an indirect impact of sand extraction, acting through sediment changes. Sand extraction may lead to direct changes in the meiofauna through removal or crushing of individuals. The refinement at station 5 may have induced the shift in species dominance but also the direct effect of the frequent removal of the fauna by the extraction activities may not be overlooked.

4.1.3.1.2 Station 6

While an impoverishing community shift was recorded at station 5, even a more extensive impoverishment was observed at station 6. At the border of the depression, near the gap in the steep slope of the western flank, conditions must be too harsh for harpacticoid life to maintain successfully. Surprisingly the lowest density and species richness were recorded here in 1997, although higher values were expected due to the considerable amount of coarse sands (Coull, 1985). The sediment even coarsened from 4 % in 1978 to 15 % coarse sand in 1997. Although sediment characteristics were very similar to the richest station on the bank, station 6 showed more affinities to the poor gully inhabiting community.

The northern part of the central depression has been subject to deposition of fine sediments, while the southern part around station 6 was characterized by strong erosion (Fig.III.13.d). A sediment layer of a minimum depth of 20 cm is removed 4 times a year at exactly the same location, each time eliminating the present fauna. Due to intensive sand extraction a gap may have been created in the western flank. The strong flood stream may have a stronger impact on the southern part of the depression than it had before the gap existed. These currents may carry finer sands more northwards in the depression, where the fine material is deposited as a result of decreasing current velocity. The depression is very sensitive to further erosion because the flood dominant transport in the western gully may cause a residual erosion on the steep bank flank (De Moor & Lanckneus, 1991), reinforcing the erosion due to the intensive sand extraction. Only a poor harpacticoid community is able to sustain, due to the direct impact of the frequent removal of the existing fauna and the indirect impact of strong erosion processes. The changes in the harpacticoid fauna in the depression confirm that biological community composition reflects changes in sediment composition, but is also in equilibrium with seabed disturbance, either from human-induced physical disturbance or from tidal currents and wave action, both of which show spatial variations and interactions with water depth (Newell *et al.*, 1998). Disturbance by currents and agitation of superficial bottom layers have been shown to considerably affect harpacticoids (Giere, 1993). For the Belgian and Dutch Continental Shelf Govaere *et al.* (1980) already clarified the importance of hydrodynamic and related forces, which regulate the distribution of finer sediments, suspended materials and nutrients, and hence the dynamics of the benthic system. We may expect that the basic composition and occurrence of the respective communities will remain stable as long as the currents and the amount of suspended material carried will not drastically change (Govaere *et al.*, 1980). This is not only valid at a large scale, but also on a small scale. Sand extraction may have induced unfavourable habitat changes and hence a mediate to strong impoverishment in the harpacticoid fauna.

4.1.3.2 Harpacticoid densities

The decreased densities in the depression relative to 1978 may be a direct result of the removal of sediment and the inhabiting fauna. Throughout most of the year the harpacticoid community of a sandy station at the Belgian Continental Shelf was concentrated at the sediment surface, with over 70 % present in the upper 6 cm (Huys *et al.*, 1986a). Removing the surface layers by sand extraction up to 20 cm (maximum 50 cm and sporadically 1 m) depth is expected to impact harpacticoid abundances drastically. Indeed, density dropped by 78 % at station 5 in the northern part and by 90 % at station 6 in the southern part of the depression. Seasonal fluctuations may also account for the observed differences. The autumn/winter ratio of harpacticoid densities ranges from 1/1 to 3/1 at the sandy stations investigated in Huys *et al.* (1986a) and in Herman (1989). Ratios of 4.6/1 (for station 5) and 10/1 (for station 6) comparing autumn 1978 with winter 1997 are never recorded as seasonal fluctuations along the Belgian coast. However, in a study along the Dutch coast (Huys *et al.*, 1986b) an interstitial harpacticoid community with very high densities in autumn collapsed totally in spring. Density decreased tenfold but the next autumn the community re-established and density was as high again as the previous autumn. In contrast, densities at station 5 on the Kwintebank were even lower in late autumn 2000 than in January 1997. Also year-to-year variation between September samples amount to ten times (Herman, 1989). This holds for coastal muddy and fine sand stations, which are more subject to density fluctuations than the sandbank communities. The large fluctuations at the coastal stations were mainly caused by *Microarthridion littorale*, an epibenthic copepod which is common along the coast and shows a patchy but dense distribution. Comparison of earlier studies in the Southern Bight (Huys *et al.*, 1986b; Huys *et al.*, 1992) revealed that the community in sandy habitats is stable in time. Furthermore it is very unlikely that a big difference in harpacticoid density due to yearly variation at a specific site would not be recorded in the surrounding area as well, even if it is populated with a different community. Yearly variation is not found to be site-specific. In a study of Herman in 1989 yearly variation was detected at a group of sites, some of which populated with different communities. Nevertheless, the lack of available data on seasonal and yearly variation is definitely a shortcoming in this study to compare 1978 and 1997.

4.1.3.3 Ecotype proportions

The changes in species assemblage in the centre imply an increased importance of small interstitial species between 1978 and 1997. Seasonal fluctuations may account for the observed differences. On the southern part of the Kwintebank and on the Gootebank, endobenthic species showed a seasonal density variation of respectively 5 % and 15 % between winter and summer in 1999 (Chapter II). Comparing autumn 1978 with winter 1997, it's unlikely that a decline of 20 % endobenthic species will only be generated by seasonal fluctuations, all the more since the community at station 5 was completely dominated by interstitial species in late autumn 2000. Additional information on seasonal and year-to-year variation in the proportions of epi- and endobenthic to interstitial species are only available from muddy and fine sand stations in the coastal area (Herman, 1989). These oscillations can be very extensive because of the patchy and momentary high abundance of individual epi- and endobenthic species in this area. The population dynamics of an epi- and endobenthic species assemblage can however not easily be extrapolated to an interstitial sandbank community.

Interstitial harpacticoids are able to hide deeper into the sediment than the bigger epi- and endobenthic species. Harris (1972b) found interstitial species migrating down to a depth of 65 cm on an intertidal sandy beach. Such behaviour may be more beneficial than the swimming activity of the epi- and endobenthic species when coping with extreme disturbance. Epi- and endobenthic species do not hide deeper into the sediment to avoid suspension when exposed to physical reworking of the sediment (Thistle *et al.*, 1995). Being suspended they risk to be damaged, expatriated or exposed to water-column predators (D'Amours, 1988) or their energy stores can become depleted (Thistle *et al.*, 1999). The highly mobile epibenthic species and the endobenthic diggers may be able to withstand sand extractions, as long as they are not too intensive (Rzonzef, 1993). The epi- and endobenthic species were present in 1978 but may have disappeared as the extractions became too intensive. Also Thistle *et al.* (1999) found a reduced proportion of surface-living epi- and endobenthic species and a higher proportion of interstitial harpacticoids, which were distributed deeper into physically reworked sediments, in comparison with more quiescent sites.

4.1.3.4 Juveniles

According to Hall *et al.* (1994) the increased abundance of small opportunistic species is a common response of marine soft-sediment communities to increasing disturbance frequency and intensity. The same holds for an increased abundance of juvenile life-history stages (Hall *et al.*, 1994). In 1997 20 % of the *Paraleptastacus espinulatus* specimens were copepodites while no juveniles of this species were found in 1978. Juveniles of *Arenosetella* n.spec.1 and *Evansula* species were only present in the intensively exploited stations and not encountered at other stations in 1997 or in 1978. Egg carrying females and copepodites of *P. espinulatus* in January are remarkable, since this species was found to have a protracted breeding activity from April to December (Huys *et al.*, 1986a). This indicates that *P. espinulatus* has a prolonged egg bearing period and produces a higher percentage of copepodites in the depression than would be the case in an undisturbed environment. At station 8, a much less disturbed area on the Kwintebank, *P. espinulatus* was also the dominant harpacticoid with a relative density of 55 % (the highest percentage on the Kwintebank) but the juveniles of this species accounted only for 4 % of the total density of this species. The capacity to control output, periodicity, and duration of reproduction in response to a stressful environment would incur great adaptability and might be the basis for marked colonizing abilities of opportunistic species (e.g. Marcotte & Coull, 1974, Castel & Lasserre, 1979; Hicks, 1980, 1982). A high investment in gametes makes evolutionary sense in stressed habitats (Hicks & Coull, 1983). However, no juveniles of the abundant species *Leptastacus* *laticaudatus s.str.* were recorded in 1997. Along the Belgian coast this species was found to breed at the same time as *Paraleptastacus espinulatus* with a seasonal breeding activity lasting up to 7 or 8 months, but spawning was much less pronounced (Huys *et al.*, 1986a). In the study of Huys *et al.*, (1986a) *Interleptomesochra eulittoralis* had egg production for only 4 months and was the last of the dominant copepods to start breeding in the year, reaching maximum densities in January. The restricted breading season of this species may be the reason why it was not present in 1997, being faced with the frequent removal of the population by sand extraction. Females predominating during periods of low population density are also an adaptation for survival at low densities. This would ensure a sufficiently large number of females in reproductive condition (Hicks & Coull, 1983). A significant increasing trend in ovigere females however was not observed between 1978 and 1997 at the most intensively extracted stations. The significant increase in juveniles in the most exploited stations is remarkable because January is one of the least productive months of the year, falling out of the reproductive period of most interstitial species (Hicks & Coull, 1983). These indications however cannot ensure a clear relationship with sand extraction since the comparison is based on one observation in the nineties.

4.1.3.5 Recolonization

On the eastern flank of the depression, near the northern tip of the southern plateau, a very rich community was present in 2000 (Bonne, unpubl. data). Stephenson *et al.* (1978) and Jones & Candy (1981) both documented the enhanced diversity and abundance of benthic fauna near to dredged channels. Disturbance of sediments by dredging may release sufficient organic matter to enhance species diversity and population density outside the immediate zone of disturbance (Newell *et al.*, 1998). The rich communities may recolonize the affected areas on the Kwintebank if sand extraction is ceased to make recovery possible. Due to the detection of the depression, the Ministry of Economic Affairs has decided to close the central part of the Kwintebank for sand extraction in the beginning of 2003 for a period of 5 years.

In spite of the general sensitivity of harpacticoids, also illustrated in the present study, harpacticoids are the most commonly and rapidly recovering taxon due to their active emergence. In contrast, the usually more “sediment-bound” nematodes have a lower potential of recolonization (Giere, 1993). Passive suspension (Bell & Sherman, 1980; Palmer 1988) combined with active emergence (Armonies, 1989) are regular phenomena and lead to rapid dispersal and recolonization of disturbed habitats (Giere, 1993). Mainly diatom-eating species have been recorded to perform excursions in the water column and especially epibenthic harpacticoids are passively transported through suspension by regular tidal currents (Giere, 1993). Recolonization by the interstitial community will last longer, as the vermiform interstitial species are not able to swim (Hicks & Coull, 1983; Bonne, pers. obs.).

The natural communities of gravels and sands contain varying proportions of slow-growing K-selected equilibrium species depending on the degree of disturbance by waves and currents. These communities are held in a transitional state by natural environmental disturbance and are likely to recover within a period of 2-3 years after cessation of dredging. This holds for macrobenthos, meiobenthos will likely recover at a faster rate (Newell *et al.*, 1998). A 9 m^2 defaunated area of intertidal mud was recolonized by harpacticoids within one day (Sherman & Coull, 1980). The rate of recovery is highly variable depending on the type of community that inhabits the deposits in the dredged area and surrounding deposits, the latitude and the extent to which the community is naturally adapted to high levels of sediment disturbance and suspended particulate load (Newell *et al.*, 1998). The community inhabiting the depression in 1997 is predominated by small interstitial species with a high percentage of juveniles. They are typical r-strategists with a short life cycle so this community will be able to increase densities very rapidly. According to Rees (1987), colonization by a range of infaunal species in soft sediments will occur within weeks or months depending on season, largely through larval recruitment. Also diversity will increase by immigration of the invading species of the rich communities living at the border of the depression. Recolonization by populations of motile epifaunal browsers and predators will depend on the availability of suitable food, but may occur opportunistically through migration of adults into the area or via larval recruitment (Rees, 1987).

The readjustement of the benthic new community after cessation of dredging is not only linked to parameters such as the larval and adult pool of potential colonizers and the nature and intensity of stress usually endured by the community, but also to the nature and stability of the sediment exposed or accumulated at the extraction site (ICES, 1992; Newell *et al.*, 1998). The recovery of the original community depends on the evolution of the sediments present in the depression. It 's unclear whether the original western bank flank in the centre will be restored after cessation of dredging as the current directions and velocities may have changed too much and may hamper the deposition of sediments transported by tidal currents. Natural infill of the dredging site is limited by currents and depends on bottom morphology. In the deepest and narrowest part of a dredging site (dredged to 12 m below original bottom level) in the Seine estuary (France), an acceleration of tidal bottom currents had prevented any restoration, whereas in the larger and shallower part (maximum deepening of 5 m) fine sediments were deposited that were five times more silty than in the reference area (Desprez, 2000). Different levels of recolonization were also observed in the dredging site off Dieppe (France). Recolonization nearly achieved 2 years and 4 months after cessation of dredging in the western part, where intrusion of mobile coarse sands had occurred. Recolonization was in progress in the median sector of the dredging site with increasing number of coarse sand species and decreasing number of fine sand species, whereas the deposition area in the eastern part was still dominated by clean fine sands with the lowest species richness, abundance and biomass (Desprez, 2000). This contrasts with a study at the Catalan coast (Spain), where large quantities of medium to coarse sand were dredged for beach nourishment. After a short period of heterogeneous sediment composition and presence of organic debris, the depressions were gradually replenished by new sand deposits and mean grain size composition reached pre-dredging values in less than one year (Sardá *et al.*, 2000). The recovery of the central part of the Kwintebank is doubtful. Accurate monitoring will have to point out in which direction the area evolves and which further implications are to be expected.

4.2 Impacts in the northern part of the Kwintebank

4.2.1 Geomorphological characteristics

At the northern top of the sandbank (stations 1 and 2) sand extraction intensity is as high as at station 5 in the depression of the sandbank. At station 3 extraction intensity is four times less while at station 4 no extraction activities are taking place (Fig.III.13.b). The northern top is subject to strong erosion, while station 3 is characterized by weak erosion and station 4 is situated in an area of sediment accumulation (Fig.III.13.c) (De Moor & Lanckneus, 1994). Comparing the bathymetric charts of 1980 and 1995 large depth differences could be detected at the northern top. On the multibeam-image a disturbed topography with a depression was observed in this area. Stations 1 and 2 are situated just north and south respectively at the border of this depression. The origin and the dynamics of this depression are not studied yet by geologists but the link with sand extraction is obvious (Fig.III.13), just as in the centre of the sandbank.

4.2.2 Granulometric characteristics

The homogenisation of the sediment at stations 1 and 2 between 1978 and 1997 is confirmed by data gathered by the Ministry of Economic Affairs (Fund For Sand Extraction) from 1989 to 1999 (Degrendele, unpubl. data). The sediment composition (with 68 % medium sand) of a station situated in the depression and about 200 m SE from station 1, was stable in these ten years and very similar to the sediment composition at station 1 in 1997. A second station was located about 100 m NW from station 1 and characterized by much coarser sediment (10 % very coarse and 28 % coarse sand) in 1989. During the following ten years the sediment composition evolved towards that of station 1 in 1997 since the medium sand content increased to 73 %. These evolutions may indicate that medium sand accumulates in the depression and that the depression is probably expanding. In Lanckneus *et al.* (1992a) granulometric data are available from the area around station 1 from 1989-1991, in De Moor & Lanckneus (1994) from 1991-1993 and in Vernemmen (2001) from 1996-1997. Median grain size was defined with the same methodology as in the present study. In September 1978 station 1 had a median grain size of 234 µm while it was roughly assigned to the class of 300-500 µm in November 1989 and in 1991 more precisely to the class of 400-500 µm (in June as well as in December). It is not possible to detect any differences comparing the classifications of 1989 and 1991 but Lanckneus *et al.* (1992a) specified a coarsening in this area not exceeding 200 µm. In May 1993 station 1 was characterized by a mean grain size between 300-

400 µm, reaching a value between 400 and 450 µm in May 1996, while it was assigned to the class of 350-400 µm in 1997. Indeed, the median grain size at station 1 was 375 µm in the present study.

Lanckneus *et al.* (1992a) concluded that grain size parameters on the northern Kwintebank vary through time. Yearly and seasonal variation were clearly detected but the residual difference between 1978 and 1997 was a coarsening of the sediment from fine to medium sand, because in the area of 1 km² surrounding the station a grain size below 300 µm was not recorded anymore since the end of the eighties. The grain size measurements for macrobenthos sampling in seventies and nineties also indicated a significant increase in grain size (Rekecki, 2002, chapter IV).

Conversely, the coarsest patches at 1.5 km northwest of station 1 are subject to a refining. In 1989 these patches had a mean grain size up to 1500 µm. The maximum grain size measured in the same area was 921 µm in June 1991, 870 µm in December 1991, 780 µm in 1993 and 760 µm in 1996. Mean grain size increased again to 847 µm in 1997. In this particular area a grain size decrease up to 600 µm was observed from 1989 to 1991 (Lanckneus *et al.*, 1992a). It was unclear whether the decrease was related to either seasonal processes or to sand dredging operations, because the examined area was located in the northern exploited area and not compared with a non-exploited area. The whole time series indicates that the very coarse patches are more subject to fluctuations than areas with finer sediments and that a residual refinement of the sediment is detected anyhow. The two opposite long-term trends result in a homogenisation of the sediment in the total area, which was already postulated from the increased dominance of medium sand by comparing the samples of 1997 and 1978 at stations 1 and 2 in the present study.

At stations 3 and 4 it's more difficult to distinguish between natural and unnatural sediment changes because the changes are not as abrupt as at station 5 and no extensive additional information is available from other studies as for stations 1 and 2. The observed changes in sediment composition may result from (1) the sampling of small-scale spatial variation proper or from a number of factors inducing sediment changes on sandwaves: seasonal or yearly variation (2), small-scale spatial variation as a result of the movement of the crests of sandwaves (3) and influences by storms (4).

(1) Differences may exist between sandwave tops and depressions because in ripple mark areas crests contain coarser sediments than troughs. In troughs, fine sand and often a flocculent surface layer tend to accumulate, resulting in a higher content of organic material. This varying small-scale sediment pattern represents different microhabitats for meiobenthic animals (Eckman, 1979; Hogue & Miller, 1981; Hicks, 1989). This small-scale difference is not verified yet for sandwave systems but may be responsible for observed differences. Taking replicated samples reveal this spatial variability. The first and third replicate of a station can be 130 m remote from each other and the maximum difference between the mean grain size of 3 replicates at station 3 was 70 µm, the maximum difference of the coarse sand fraction 18 %. Therefore, the difference between 1978 and 1997 at station 3 is higher than this observed small-scale spatial variation.

(2) Coarse sands are subject to considerable seasonal and yearly fluctuations but in the vicinity of station 3 grain size changes recorded in Lanckneus *et al.* (1992a) between 1989 and 1991 were less than 200 µm, while this threshold is exceeded for station 3 in the present study.

(3) The displacement of the crests of large dunes on the Kwintebank has been studied for many years (De Moor, 1985) but no net movement has ever been detected. The positions of the crest lines of the large dunes can however change on a short-term basis. Between February and June 1989 a net movement of 30 m was recorded but in November 1989 the crests were returned to roughly the same positions they had 11 months earlier. The bank always seems to recover from such abrupt changes and the oscillatory movement of the crest lines is probably determined by wind- and swell-induced processes (Lanckneus & De Moor, 1995).

(4) The impact of storm events on the morphology and movement of large dunes was studied by Houthuys (1993). A comparison of the pre- and post-storm results showed that crest lines migrated a maximum distance of 5 m.

A movement of 5 m (due to storms) to 30 m (displacement on short-term basis) of a large dune crest will not be important in inducing differences between 1978 and 1997 as a larger area is covered by taking replicated samples. It is improbable that natural variation induced the sediment changes at station 3. Sand extraction may have reduced the high percentage of coarse sands by homogenising the sediment but this definitely needs more investigation. The changes at station 4 are smaller and may be due to natural variation. An accretion of shell debris may have resulted in the coarsening as the area around station 4 is an accumulation point of material (including shell gravel) coming from the gullies and this process may be enhanced by storm events (Tytgat, 1989).

4.2.3 Biological characteristics

4.2.3.1 Density and diversity

Copepod density dropped by 39 % and 31 % at stations 1 and 2 respectively. The observed sediment changes are not responsible for this decline because two opposite trends in sediment change at stations 1 and 2 both resulted in a decrease in density. Harpacticoids become more abundant as the particle size of the sediment increases (Hicks & Coull, 1983; Huys *et al.*, 1986b). According to this relation, density in station 1 should have increased while the opposite trend had to be observed in station 2, which was not the case. It is unclear whether the decline may be explained by seasonal fluctuations or by the intense extraction activities. The density drop is confined within the range of seasonal variations but extraction activities may also have contributed to the decreasing trend by the removal of fauna, consistent with the results in the depression in the centre. Densities at stations 1 and 2, however, were not as seriously affected by the same frequency of extractions as in the central depression of the Kwintebank.

Also diversity remained high (the highest values of the sandbank in 1997) but the abundance of big epi- and endobenthic species decreased and species composition altered in favour of interstitial species. At station 1 the increase and subsequent predominance of medium sands in the nineties may have caused this trend, since more interstitial species will develop with increasing grain size (from very fine to coarse sand) (Huys *et al.*, 1986b). In contrast, a decrease of coarse sand at station 2 coincided with an increase in interstitial species as well. The observed differences do not exceed seasonal fluctuations already recorded along the Belgian coast, but a link with sand extraction intensity can also be demonstrated. The smaller interstitial species have a shorter life cycle and reproduce much faster. A common response of the northern top and the central depression to the extraction activities is the significant increase of juvenile life-history stages of the small opportunistic interstitial species in both areas. In the northern top, diversity of interstitial species even increased, while it decreased in the central depression. General benthic ecology, but also meiobenthology, could show that disturbance and diversity are not necessarily negatively correlated (Warwick *et al.*, 1986). The natural communities of gravels and sands are held in a transitional state by natural environmental disturbance (Newell *et al.*, 1998). Such a natural ecosystem with its incessant cases of disturbance is never completely stable (Huston, 1979), because disturbances interfere with the established ecological balance and create new niches. Consequently, even in areas with disturbances of predominantly abiotic origin, a considerable meiofauna diversity can be maintained, provided the interferences are not too drastic (Giere, 1993). Due to the high hydrodynamical stress the community in the north is used to frequent physical disturbances and can resist intensive extraction better than the community in the centre in terms of density and diversity. Communities of high stress areas (e.g. shallow areas exposed to strong tidal currents and periodic storm disturbance) are more adept to readjustement to the impact of dredging operations than communities in more stable environments (Desprez, 2000).

4.2.3.2 Harpacticoid communities

Clear changes in harpacticoid communities were detected. Two separate harpacticoid communities I and II have evolved between 1978 and 1997 in the northern part, which was not subdivided in 1978. *Apodopsyllus* n.spec. 1 became less important in the habitat predominated by medium sand in station 1 and a newly appearing species *Paraleptastacus moorei* became dominant in community I whereas it was absent in community II. This species is not restricted to the community in the northern top but occurs in station 5 as well. The presence of *P. moorei* is positively correlated with sand extraction intensity. *Paraleptastacus* species appear to be adapted to different biotopes (Whybrew, 1984). In the intertidal areas of temperate sandy beaches, where they are often important or even dominant (Noodt, 1957; Mielke, 1976; Moore, 1979b), the sympatric occurrence of *Paraleptastacus* species is defined by the conditions of varying exposure (Whybrew, 1984). *P. supralitoralis* was restricted to the upper beach face of high energy beaches. With decreasing exposure its optimal environment and hence the scope of its population becomes increasingly limited. *P. spinicauda* preferred grain sizes between 200 and 450 µm but required more constant environmental conditions for optimal population development than *P. supralitoralis* (Whybrew, 1984). *P. spinicauda* also occurs on the Kwintebank in 1997 being restricted to the coarse sands of community II (stations 3 and 4). *P. moorei* may be the counterpart of *P. supralitoralis* on the Kwintebank. Like *P. supralitoralis,* the fitness and competitive abilities of *P. moorei* may be higher in environments of increasing disturbance (e.g. by sand extraction). As sediment characteristics are appropriate for *P. spinicauda* to occur in community I, it may be restricted to community II because of the elevated sand extraction intensity at stations 1 and 2.

More characteristics reflect the differences between community I and II in 1997. According to Huys *et al.* (1992) the interstitial community of the Southern Bight of the North Sea contains the interstitial families Canthocamptidae, Leptopontiidae, Leptastacidae and Paramesochridae, associated with small Ameiridae and vermiform Diosaccidae and Ectinosomatidae. These associations existed in 1978 and are still more obvious in community II than in community I in 1997. The important species of the northern community in 1978 listed in Willems *et al.* (1982b) are still found in community II. Remarkably the decrease in endobenthic species between 1978 and 1997 is highest at stations 3 and 4 relative to all the other stations on the sandbank. In 1997 the proportion of interstitial species amounted to 98 % and 95 % at stations 3 and 4 respectively.

In 1978 station 3 did not yield a typical interstitial community as endobenthic Ectinosomatidae predominated with 71 % and were associated with 19 % big sized Diosaccidae. Station 3 had an extremely high median grain size of 654 µm in 1978. Especially Ectinosomatidae and Diosaccidae tend to be very abundant in very coarse sands such as Amphioxus sand (Guille & Soyer, 1966). Willems *et al.* (1982b) pointed out that the community of the coarse sands of the Kwintebank contained many coarse sand indicator species previously described from Amphioxus sand (Monard, 1935; Por, 1964a,b; Soyer, 1970). Of these, the ectinosomatids *Ectinosoma reductum*, *Pseudobradya beduina* and *Hastigerella monniotae* were still found in community II in 1997 though not in high numbers anymore, while the abundant diosaccids *Robertgurneya ilievecensis* and *Rhyncholagena* disappeared. Representatives of the following genera in Amphioxus sand were also found in the coarse sands of the Kwintebank in 1978 (but not at stations 3 and 4): *Bulbamphiascus*, *Leptomesochra confluens*, *Phyllopodopsyllus bradyi* and *Pteropsyllus*. They were all absent in 1997. As Ectinosomatidae and Diosaccidae are so typical for very coarse sands, their strong reduction in 1997 may be attributed to the decrease of coarse and very coarse sands at station 3, associated with weak erosion (De Moor & Lanckneus, 1994) and potentially induced by sand extraction. Sand extraction (though not that severe) may have exerted a direct impact by the removal of the fauna as well. The presence of a lot of endobenthic forms in the coarse sands in 1978 implies that organic matter must have been available for this ecotype in 1978, whereas the harpacticoid fauna was dominated by interstitial bacteria-feeders in 1997, because the amount of suspended material was minimal (Govaere *et al.*, 1980). The sediment at station 3 contained 3.5 % organic matter in 1978 (Vanosmael *et al.*, 1982). Food availability is lower in winter than in autumn but the differences in epi-and endobenthic species densities at station 3 clearly exceed the seasonal variation ever recorded in sandy stations with a mean grain size exceeding 250 µm (Herman, 1989). Vanosmael *et al.* (1979) calculated that about 70 500 tons of slib per year were resuspended by the sand extraction activities at that time. A fivefold increase in sand extraction since then results in 352 500 tons of resuspended slib. Physical disturbances such as tidal mixing decrease the incorporation of organic matter into the sediment (Jennes & Duineveld, 1985). Hence sand extraction may have decreased the organic matter content in the dredged area, while silt is deposited in adjacent areas (Newell *et al.*, 1998).

At station 4 sand extraction activities are not taking place, the percentage of very coarse sand and gravel increased and still a decrease of the endobenthic Ectinosomatidae and Diosaccidae was observed. Hence the dynamics of these harpacticoids have to be interpreted with caution in order to draw conclusions on an impact of anthropogenic disturbances. Their decrease in the nineties is remarkable but cannot be defined with certainty to dredging impacts yet. An increase of the smaller and more frequently reproducing interstitial species strongly suggest a relation with enhanced disturbances but the comparison with similar non-dredged areas has to be documented more into detail.

4.2.3.3 Nematode communities

The coarser sediments in the north induced the separation of the Kwintebank nematode assemblages into a northern and a southern group (Vanaverbeke *et al.*, 2002). The presence of the coarser sediments was assigned to the impact of intensive sand extraction activities, whereas no attention was paid to the natural occurrence of coarser sediments in the north (Lanckneus, 1989), previously described as the reason for the existence of two nematode groups on the Kwintebank (Willems *et al.*, 1982b). Evaluating the effect of extraction activities on sediment characteristics and communities necessitates a comparison with the pre-dredging situation, which was not included in the study of Vanaverbeke *et al.* (2002). Coarse sands cover the entire northern part of the Kwintebank while it contains intensively dredged as well as non-dredged areas. The present study revealed that coarsening as well as a refinement is recorded in the exploited areas in the northern part, resulting in a homogenisation of the sediment. These differences, however, have not been assigned yet with absolute certainty to sand extraction activities by geologists. Erosion due to sand extraction may lead to a coarsening of the sediment but important changes also result from the infilling of newly created depressions with finer sediment than those of the surrounding substrate. This is very likely also the case in the depression in the northern top. Moreover, the most extensive coarsening in relation to the seventies took place in a non-dredged area. For such a complex system as the Kwintebank, care has to be taken not to jump to conclusions.

4.3 Impacts in the southern part of the Kwintebank

4.3.1 Geomorphological characteristics

The southern part of the Kwintebank is the least exploited part, in which the same area is disturbed only about once a week. The sand extraction intensity at station 7 is similar as at station 3, removing approximately 3 cm sediment per year. The extracted volume of sand at the stations more to the south is 4 times less than at stations 3 and 7 (Table III.1). This removal is compensated by natural sediment transport as the topography of the southern plateau of the Kwintebank did not show clear abnormalities. No changes were recorded in the top volume of the sandbank between 1987 and 1994 (De Moor & Lanckneus, 1994; Fig.III.13.c), except for the area around station 9, which had been subject to weak erosion. In 2002 weak erosion was also detected SE of the central depression, where the bedform was lowered by 1 m over a time period of 6 years (Fig.III.3). The lowering was linked to sand extraction intensity (Degrendele *et al.*, 2002). Station 7 was situated at the border of this area. The cross-sections south of this area only showed some natural variation in the displacement of sandwaves (Fig.III.3).

4.3.2 Biological characteristics

Harpacticoid communities of the southern plateau of the Kwintebank were stable in time. Dominant species were still the same after twenty years and proportional distribution remained very similar. The species assemblage of station 8 in 1997 showed the highest similarity with the species composition in 1978, relative to all other stations on the Kwintebank. Station 8 is characterized by the weakest sand extraction intensity, station 4 (no exploitation because of the shell debris) not taken into account. Yet, some remarkable differences were recorded between 1997 and 1978 at stations 9 and 10. Density decreased due to a considerable drop of the *Leptastacus laticaudatus s.str.* population and in the second place of a *Kliopsyllus* population. In a sandy station along the Belgian coast *L. laticaudatus s.str.* has repeatedly been recorded in high densities in September/October and always in association with a *Kliopsyllus* species second in dominance (Herman, 1989). Densities in winter from Herman (1989) were similar to the values found in 1997. On an intertidal sandy beach in England *L. laticaudatus s.str.* reached a very high density of 242 ind./10 cm² in September while the lowest value was recorded in January (Harris, 1972b). Also in that habitat *L. laticaudatus s.str.* was accompanied by a *Kliopsyllus* species, alternated with *Psammotopa phyllosetosa*, as second dominant species. These studies proved that reproduction of *L. laticaudatus s.str.* can be very pronounced in autumn, though not every year. The same holds for the accompanying *Kliopsyllus* species. So for these species, the differences on the Kwintebank may be explained by seasonal fluctuations, which is improbable for the decrease in *Interleptomesochra eulitoralis* density in the centre of the sandbank. The density drop at stations 9 and 10 is not clearly associated with a drastic change in an environmental factor. The only change that was measured is a replacement of some fine into medium sand. This change may be the reason why many endobenthic copepods are replaced by interstitial forms at station 10 (Huys *et al.*, 1986b), which cannot be completely explained by seasonal variation. Govaere *et al.* (1980) and Willems *et al.* (1982b) suggested that a stable *Leptastacus laticaudatus* community can be described for well-sorted clean, fine to medium sands of the Southern Bight of the North Sea. The data of 1997 showed that this community in the southern part of the sandbank remained about unchanged and is indeed stable in time. Sand extraction intensity is low in this area and these extraction activities may have washed away some fine sands but this did not affect the species composition in a great extent.

4.4 Comparison between Kwintebank and Middelkerkebank

A very similar interstitial community inhabits the sandwave area, covering a surface of approximately 9 x 1 km on the Middelkerkebank. Outside the area with sandwaves a totally different community is encountered in the fine sands of the southern topographically flat region and in the gullies. The pre-disturbance situation of the Kwintebank in the seventies revealed the same pattern: a 7 x 2 km sized sandwave area was defined as one unit with a variable species assemblage of predominantly interstitial copepods and the southern community was clearly distinguished from the northern part. The occurrence of two distinct groups at the northern and the southern part of the Flemish banks was thus illustrated by the species distributions on the Middelkerkebank as well as on the Kwintebank prior to intensive sand extraction. In the nineties enhanced similarities and dissimilarities between species assemblages subdivided the northern part of the Kwintebank in distinct communities. Environmental disturbance was unevenly distributed on the Kwintebank, which probably lead to a mosaic of communities and partly accounted for the patchiness of the harpacticoid communities (Newell *et al.*, 1998).

Not only the general community pattern but also the density pattern showed a striking correspondence between the Middelkerkebank and the Kwintebank prior to intensive sand extraction. Sandwaves yielded significantly higher numbers of copepods while low numbers were typical of flat areas and gullies. In the nineties lower densities were recorded in the northern part of the Kwintebank than in the flat area of the southern part, which yielded least copepods in the seventies. The inversed relation between the northern and the southern part in the nineties may be induced by sand extraction, as densities between pre-dredging and post-dredging situation dropped from 31 % to 90 % in the most intensively exploited stations and clearly surpassed potential seasonal fluctuations at 3 of the 5 impacted stations. Remarkably, density even increased in the southern flat area of the Kwintebank relative to the seventies and was comparable with densities recorded in the sandwave area of the Middelkerkebank. A common feature of the sandwave areas of the Middelkerkebank and the Kwintebank in the seventies is the high proportion of interstitial juveniles, indicating an enhanced productivity in hydrodynamically stressed areas relative to calmer regions. At heavily exploited stations of the Kwintebank the percentage of juveniles is higher in winter 1997 than in autumn 1978 and almost as high as the values in autumn 1997 at the sandwave area of the Middelkerkebank, although a lower productivity is expected in winter (Hicks & Coull, 1983). At the non-exploited station the percentage of juveniles was indeed lower in winter than in autumn.

In contrast with the Middelkerkebank, the sandwave area of the Kwintebank also contained very coarse sediments, harbouring a dense endobenthic species assemblage in the seventies. This typical coarse sand assemblage disappeared in the nineties, potentially extinguished by direct or indirect effects of sand extraction activities.

5 Conclusions

When the harpacticoid data of the Kwintebank are compared with information of sand extraction intensity and erosion, analogies could be found in the occurrence of erosion and extraction areas and the occurrence of harpacticoid communities on the sandbank (Fig.III.13). In the nineties the Kwintebank was split up in four communities while only two parts could be distinguished in the seventies: a high variable northern part and a southern part with a high similarity. The latter community is found to be stable in time, while the northern part was split up in different entities in the nineties. In the central part of the bank, the most intensive exploited area, community structure changed completely and copepod density and diversity decreased dramatically. By contrast, in the northern intensively exploited area, diversity remained high in the nineties but the species composition altered in favour of interstitial species like in the centre. Similar sand extraction intensities (in the centre and the north) induced different environmental changes and hence different harpacticoid community changes, resulting in enhanced community patchiness in 1997 relative to 1978 on the Kwintebank.

In Fig.III.14 conclusions are summarized in a scheme with hypothetical harpacticoid-environment interactions. Natural conditions define which harpacticoid species and communities occur but sand extraction may influence species composition both on a direct and an indirect way. The sand exploitation on the Kwintebank is very patchy and much too intensive in the centre. The northern tip and the centre of the Kwintebank are strongly impacted areas. The extension of the present central depression due to sand extraction can become quite problematic if these human-induced physical disturbances may cause a continuing erosion and impoverishment. Spreading the extraction activities over the different sandbanks in the concession zone will help decreasing disturbance frequency and intensity.

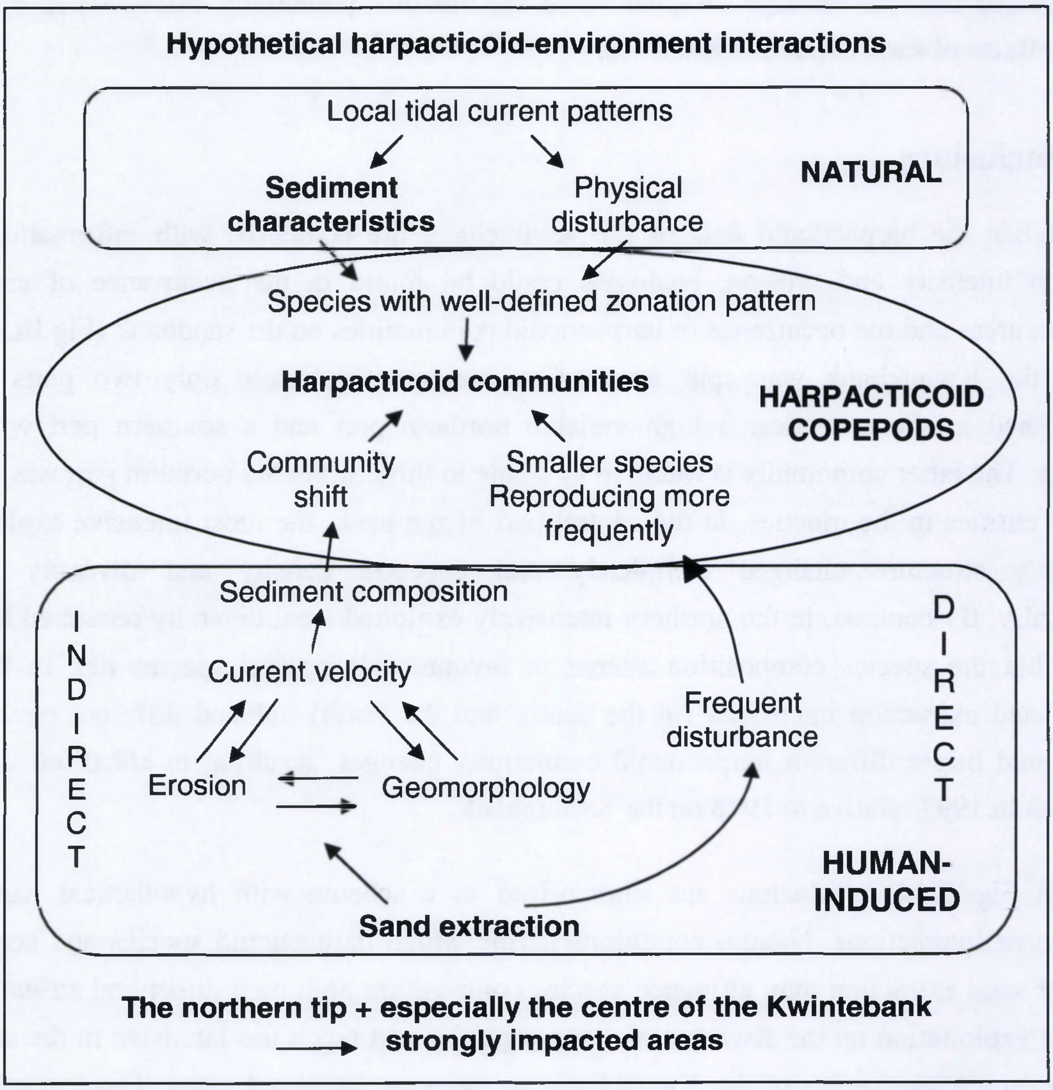
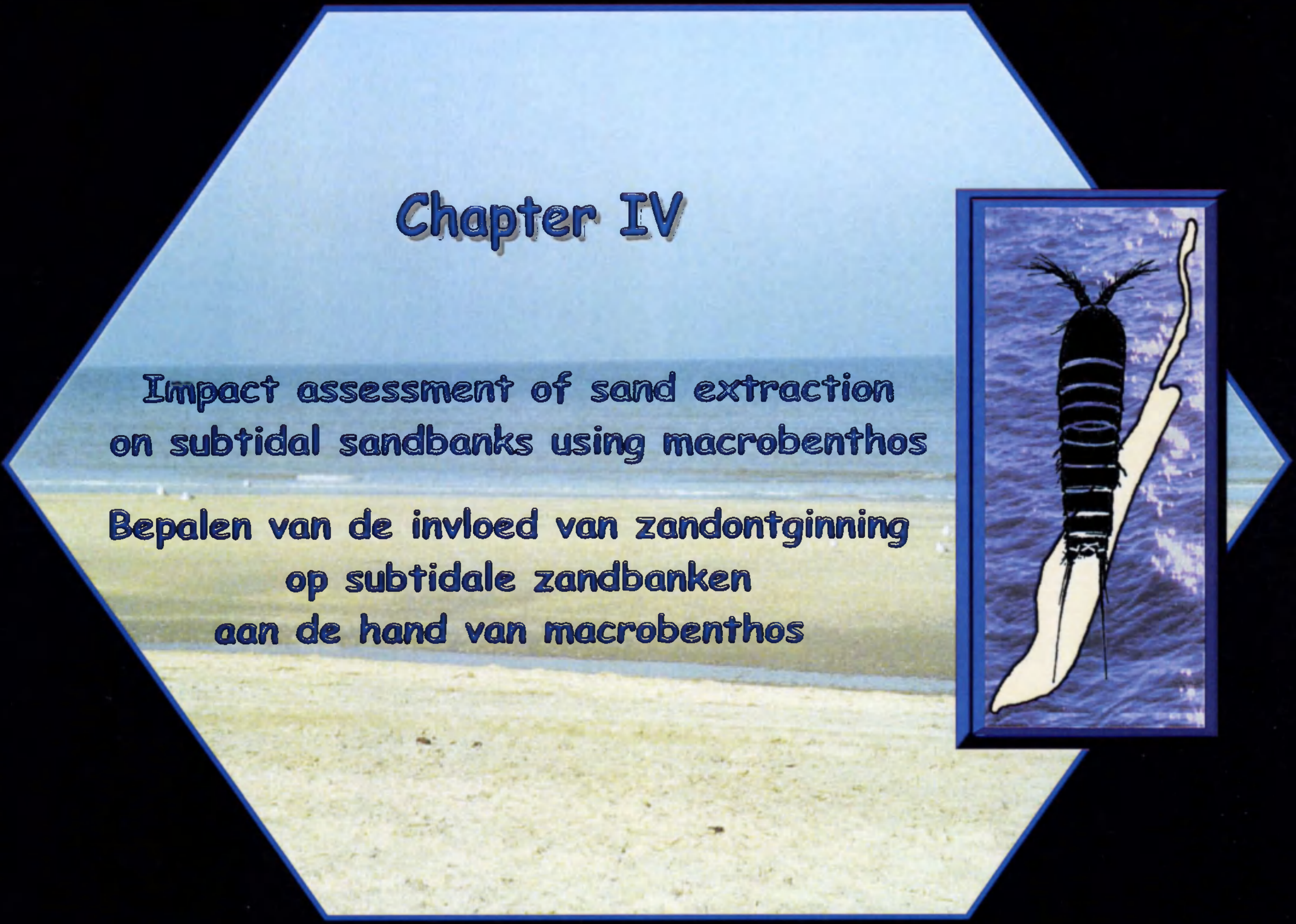


Fig.III.14: hypothetical harpacticoid-environment interactions

Be aware if you build a house in Europe !



Chapter IV

Impact assessment of sand extraction on subtidal sandbanks using macrobenthos

Bepalen van de invloed van zandontginning op subtidale zandbanken aan de hand van macrobenthos

Impact assessment of sand extraction on subtidal sandbanks using macrobenthos

Wendy Bonne, Annamaria Rekecki & Magda Vincx

1 Introduction

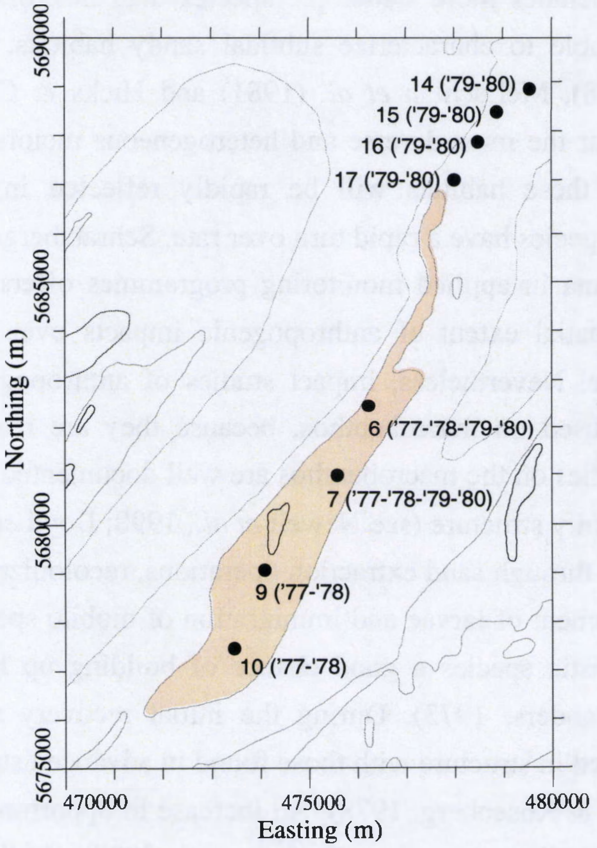
Remane (1933) assumed that meiofauna includes more stenotopic species than macrofauna and that meiofauna communities are more suitable to characterize subtidal sandy habitats. Por (1964b), Coull & Herman (1970), Fenchel (1978), McLachlan *et al.* (1981) and Hicks & Coull (1983) demonstrated that sandy sediments harbour the most diverse and heterogeneous meiofauna communities. Small environmental changes in these habitats will be rapidly reflected in the meiofauna community structure, because a lot of species have a rapid turn over rate. Schratzberger *et al.*, 2000) clarified that the inclusion of meiofauna in applied monitoring programmes offers the potential for improving the resolution of the spatial extent of anthropogenic impacts over that achievable from macrofauna investigations alone. Nevertheless, impact studies of anthropogenic alterations of the environment have mainly focused on macrobenthos, because they are readily counted and identified. Impacts of dredging activities on the macrobenthos are well documented and describe changes in density, diversity and community structure (see Newell *et al.*, 1998; Boyd *et al.*, 2003 for references). When areas are depopulated through sand extraction operations, recolonization of the disturbed area will depend largely on settlement of larvae and immigration of mobile species (van Dalfsen *et al.*, 2000). This gives opportunistic species a good chance of building up large populations in such open spaces (Grassle & Sanders, 1973). During the initial recovery after dredging benthic communities closely corresponded in structure with those found in advanced stages of organic pollution (Pagliai *et al.*, 1985; Pearson & Rosenberg, 1978). An increase in opportunistic species after sand extraction was observed in the Mediterranean (van Dalfsen *et al.*, 2000). Pagliai *et al.* (1985) found that the distribution of the individuals among species also departs from the log-normal model in the same way as found in many cases of organic pollution (Gray & Mirza, 1979; Bonsdorff & Koivisto, 1982). This convergence in community structure, following such different environmental disturbances is probably determined by a general rule occurring any time after many of the niches became suddenly unoccupied (Pagliai *et al.*, 1985).

Biotic indices have been proposed to provide useful tools to measure ecological quality in the marine environment, mainly as a response to organic enrichment (Hily, 1984; Majeed, 1987; Grall & Glémarec, 1997; Weisberg *et al.*, 1997). Hence, Borja *et al.* (2000) proposed that different anthropogenically changes in the environment, including alterations to the natural system such as dredging, engineering works, sewerage plans and the dumping of polluted waters, can be detected through the use of the Biotic Coefficient. The Biotic Coefficient as defined by Borja *et al.* (2000)

was applied to the macrobenthic data of an intensively exploited sandbank in order to assess the applicability of this kind of biotic indicators to reveal changes in the macrobenthic community as a result of sand extraction. A comparison of macrobenthic density and diversity measurements as well as community analyses were performed on a spatial and temporal scale and compared with the results of an impact study on harpacticoid copepods on the same sandbank.

2 Material & methods

2.1 Sampling stations



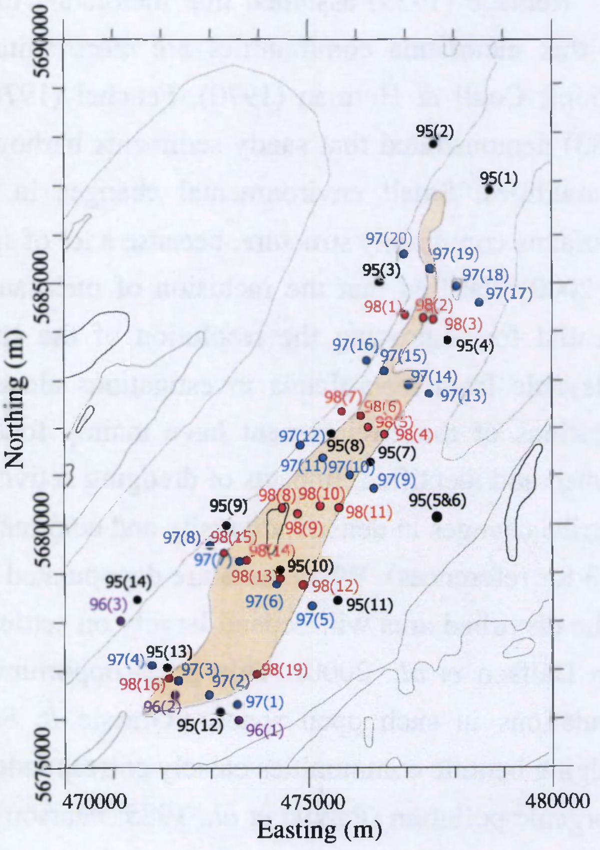


Fig.IV.1: Stations on the Kwintebank sampled for the macrobenthos in the late seventies (1977, 1978, 1979 and 1980)

Fig.IV.2: Stations on the Kwintebank sampled for the macrobenthos in the mid nineties (1995, 1996, 1997 and 1998)

Within the framework of different studies (Rappé, 1978; Vanosmael *et al.*, 1979; Waeterschoot, 1984; Vanosmael *et al.*, 1982; Willems *et al.*, 1982a; Coenjaerts, 1997; Cattrijsse & Vincx, 2001; Philips, 1998; Taverniers, 2000), the Kwintebank has been repeatedly sampled for macrobenthos between 1977 and 2001. A total of 144 samples were collected on the sandbank top, slope and in the gullies next to the bank. The time span of macrobenthos sampling on the Kwintebank covers three major periods: late seventies, mid nineties and 2001. No samples were taken in between these periods.

The sampling strategy differs a lot between the late seventies and the nineties, since the data were gathered within the frame of different research projects. In the late seventies (1977, 1978, 1979, 1980) three replicates were taken at different stations on the sandbank top (Fig.IV.1). In 1979 and 1980 the stations were sampled twice a year (in spring and autumn). In the mid nineties single samples were taken along different transverse transects covering the whole sandbank and including some gully stations (Fig.IV.2). In December 2001 five replicates were taken at stations 1, 6 and 9, corresponding with the stations sampled for meiofauna. Stations 6 and 9 were taken at the same location as in the seventies, whereas station 1 is situated near to station 16 sampled in the seventies.

2.2 Sampling and processing

Samples were taken with a Van Veen grab (sampling surface area: 0.1 m² or 0.12 m² and weight: ± 50 kg). A subsample taken with a small tube was used for sediment analysis. In the seventies sieving over a 0.87 mm mesh-sized sieve was done after fixation in a 7 % formaldehyde seawater solution. Very coarse samples were rinsed in a gutter. The lighter organisms were washed towards the end of the gutter and caught on a sieve of 250 µm mesh size, while the heaviest organisms like *Spisula* were picked out of the sediment directly. In the nineties the samples were sieved alive over a 1 mm mesh-sized sieve. After staining with Rose Bengal, macrobenthic organisms were picked out. Anthozoa, Oligochaeta and Nemertea were counted as groups and representatives of the Polychaeta, Mollusca, Archiannelida, Crustacea and Echinodermata were identified to species level under a stereoscopic microscope.

Water depth at each sampling station was recorded *in situ* and standardized to the mean low water spring level (MLWS) using the M2 reduction model (AWK). Sediment subsamples were dried in the oven and sieved in the lab over a set of sieves of different mesh size in the seventies. In the nineties and in 2001 they were analysed with a LS Coulter particle size analyser (measuring range: 0.4 – 850 µm). The median grain size and mud content (volume percentage < 64 µm) were used as granulometric parameters. Sediment classification was defined according to the Wenthworth scale (Buchanan, 1984).

2.3 Statistics

The extensive dataset of the nineties was used separately for macrobenthic community analysis in order to reveal spatially structured variation. The community structure was investigated by means of classification and ordination techniques. Two-Way Indicator Species Analysis (TWINSPAN, cutlevels 0, 1.682, 2.115, 2.660, 3.122, 8.409) (Hill, 1979a; Gauch & Whittaker, 1981) and CA (Hill, 1974) were conducted on fourth root transformed data. A separate TWINSPAN (cutlevels 0, 1.682, 2.000, 2.237, 2.660, 8.409) was performed on the data of one community. The program TWINDEND (Gauch & Whittaker, 1981) was used to define the TWINSPAN groups worth retaining.

Temporal changes were studied by selecting and comparing specific stations from the different datasets. From the dataset of the seventies station 16, station 6 and station 9 were selected and compared with the results of 2001 at stations 1, 6 and 9 respectively. Station 6 could also be compared with station 6 sampled in 1998 and station 9 was compared with stations 6 and 7 sampled in 1997 and stations 13 and 14 sampled in 1998. Two of the three replicates at station 6 in October 1977 were not taken into account as the very high values were obtained from the gully next to the bank (22 m depth) since the ship drifted off a lot while sampling (Rappé, 1978). Grain size and density values at station 1 in September 1978 were taken from Vanosmael *et al.* (1982). Species richness of Vanosmael *et al.* (1982) was not included, since the total number of species per station was listed instead of the mean number of species per station. In this way station 1 in the intensively exploited northern part, station 6 in the intensively exploited central part and station 9 in the relatively undisturbed southern part of the Kwintebank could be compared over time. Mean densities, species richness and grain size were analysed by means of ANOVA or Kruskall-Wallis ANOVA by Ranks, using STATISTICA^{TM} software (Microsoft, StatSoft, Inc., 2000). Overall significant differences were compared pairwise using the planned comparison option in ANOVA for parametric data or following Conover (1971) for non-parametric data.

The continuous Biotic Coefficient was calculated for stations 1, 6 and 9 for each sampling event, according to the formula Biotic Coefficient (BC) = {(0 x % GI) + (1.5 x % GII) + (3 x % GIII) + (4.5 x % GIV) + (6 x % GV)}/100, based upon the percentages of abundance of each ecological group (Borja *et al.*, 2000). The classification of the ecological groups is based upon Hily's model (Hily, 1984; Hily *et al.*, 1986; Majeed, 1987): GI stands for ecological Group I: species very sensitive to pollution, GII = Group II: species indifferent to pollution, GIII = Group III: tolerant species, GIV = Group IV: second-order opportunistic species and GV = Group V: first-order opportunistic species. The species encountered on the Kwintebank were assigned to the different ecological groups according to the species lists given in Borja *et al.* (2000). For stations 1, 6 and 9 the BC was calculated based on all species present, whereas for the different communities on the Kwintebank, the BC was calculated for the 12 most abundant species only, comprising at least 80 % of the total community density. Temporal changes were also tracked by TWINSPAN (cutlevels 0, 1.627, 1.733, 2.237, 2.784, 8.409) and CA for the total dataset of seventies, nineties and 2001 (fourth root transformed data). The ordination analyses were performed with CANOCO for Windows (ter Braak & Smilauer, 1998).

3 Results

3.1 Comparison between harpacticoids and macrobenthos

3.1.1 Macrobenthic communities on the Kwintebank

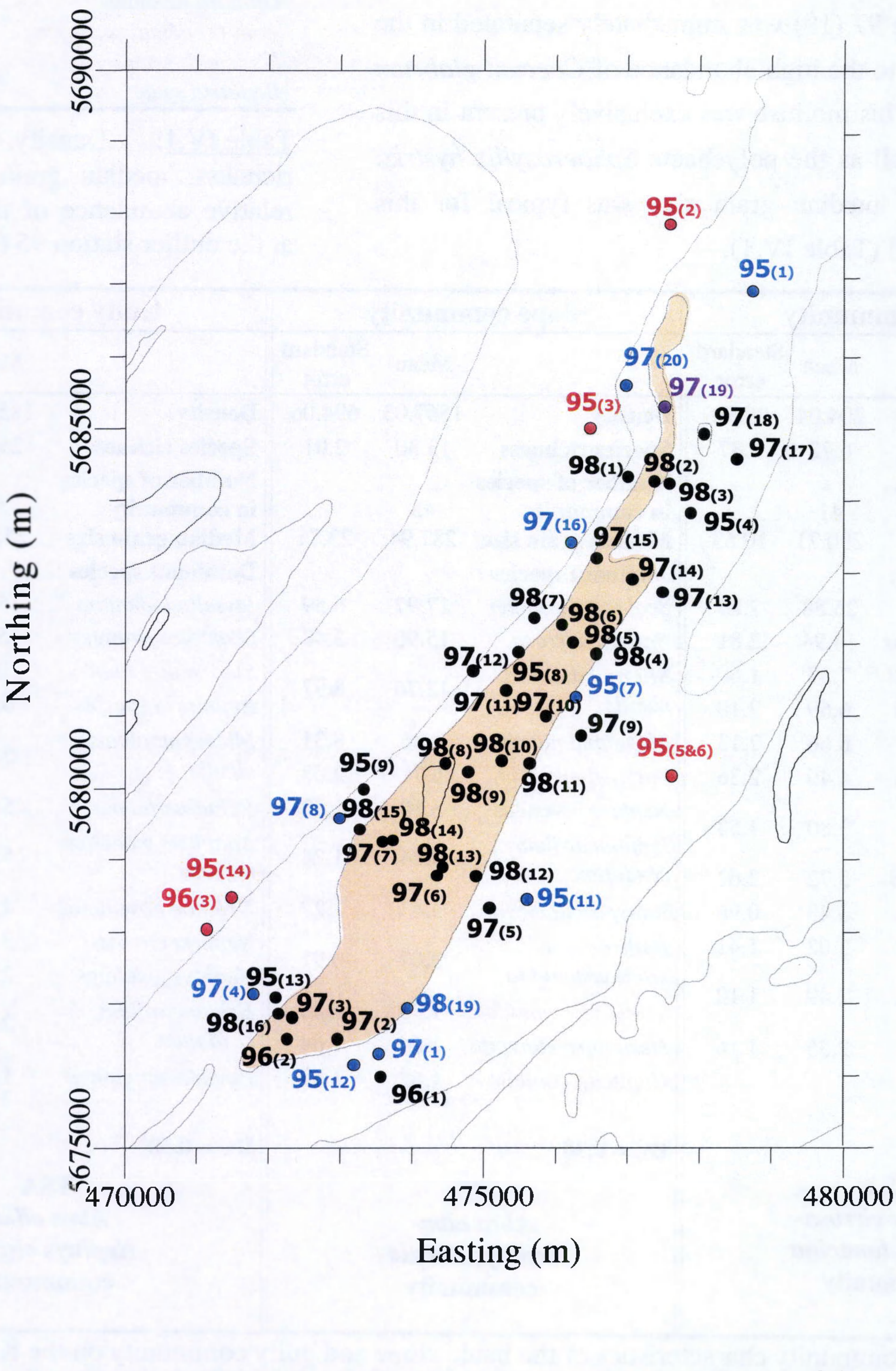


Fig.IV.3: Communities on the Kwintebank, based on the macrobenthos dataset of the mid nineties

TWINSPAN and CA of the dataset of the mid nineties revealed three different communities on the Kwintebank (Fig IV.3). A bank community covering the whole sandbank from north to south (36 stations), a slope community including 10 stations on the slopes and a gully community consisting of 5 gully stations. The outlier station 97 (19) was immediately separated in the analyses due to the high abundance of *Caecum glabrum* (Mollusca). This mollusc was exclusively present in this station, as well as the polychaete *Sphaerosyllis hystrix*. A very high median grain size was typical for this station as well (Table IV.1).

	97(19)
Density	282
Species richness	8
Median grain size	607,1
Dominant species:	
Caecum glabrum	44,33
Sphaerosyllis hystrix	17,73
Glycera convoluta	17,73
Hesionura elongata	8,87
Ophiura juveniles	2,84
Aonides paucibranchiata	2,84
Scolelepis bonnieri	2,84
Bodotria spec.	2,84

Table IV.1: Density, species richness, median grain size and relative abundance of the species at the outlier station 95 (19)

Bank community			**Slope community**			**Gully community**		
	Mean	Standard error		Mean	Standard error		Mean	Standard error
Density	204.04	29.90	**Density**	1567.03	694.06	**Density**	1850.33	388.95
Species richness	6.72	0.37	**Species richness**	13.30	2.01	**Species richness**	25.17	2.83
Number of species in community	41		**Number of species in community**	45		**Number of species in community**	58	
Median grain size	290.71	10.63	**Median grain size**	287.94	23.71	**Median grain size**	252.58	11.99
Dominant species :			**Dominant species :**			**Dominant species :**		
Nephtys cirrosa	26.88	2.85	*Scoloplos armiger*	17.97	6.59	*Mysella bidentata*	15.96	4.94
Bathyporeia elegans	14.94	2.81	*Nephtys cirrosa*	15.90	5.48	*Scoloplos armiger*	15.45	7.37
Urothoe brevicornis	7.37	1.60	*Microphthalmus similis*	12.76	8.57	*Spiophanes bombyx*	10.37	3.85
Magelona mirabilis	6.69	2.10	*Magelona mirabilis*	9.86	8.31	*Actiniaria species*	6.41	4.21
Scoloplos armiger	6.66	2.13	*Spiophanes bombyx*	6.71	2.08	*Microphthalmus similis*	5.83	2.80
Urothoe poseidonis	4.49	2.36	*Nephtys* juveniles	5.18	1.72	*Fabulina fabula*	5.09	1.70
Bathyporeia guilliamsoniana	3.80	1.53	*Echinocardium cordatum*	3.44	1.74	*Anaitides maculata-mucosa*	5.05	3.25
Hesionura elongata	3.72	2.62	*Bathyporeia elegans*	3.43	1.27	*Urothoe poseidonis*	4.96	4.48
Scolelepis bonnieri	3.43	0.96	*Bathyporeia guilliamsoniana*	2.07	0.91	*Nephtys cirrosa*	3.47	1.81
Spio goniocephala	3.02	1.41	*Scolelepis bonnieri*	1.93	0.80	*Nephtys* juveniles	2.17	0.75
Echinocardium cordatum	2.49	1.12	*Hesionura elongata*	1.64	1.64	*Echinocardium cordatum*	2.06	1.00
Ophelia limacina	2.35	1.16	*Capitella capitata*	1.62	1.57	*Eumida sanguinea*	1.83	1.58
BC = 0.65			**BC = 0.70**			**BC = 0.50**		
TSA ***Nephtys cirrosa-Ophelia limacina*** **community**			**TSA** ***Abra alba-Nephtys cirrosa-*** **community**			**TSA** ***Abra alba-Nephtys cirrosa*** **community**		

Table IV.2: Community characteristics of the bank, slope and gully community on the Kwintebank Ecological groups: species very sensitive to pollution (Group I), species indifferent to pollution (Group II), tolerant species (Group III), second-order opportunistic species (Group IV), first-order opportunistic species (Group V) and species which the ecological group was not available from in black; TSA = Transitional Species Association

In the overall TWINSPAN of the nineties the variance within the bank community was negligible in comparison with the high variance between and among the slope and gully community stations. The similarity among the bank stations was also illustrated by a separate TWINSPAN of the bank community. The TWINSPAN data table with the species arranged in order of their final scores did not reveal a clear gradient in species absence/presence or abundance along the sites. The stations are mainly grouped according to the different years and reflect slight temporal variability but no clear spatial structure on the bank (Fig.IV.4).

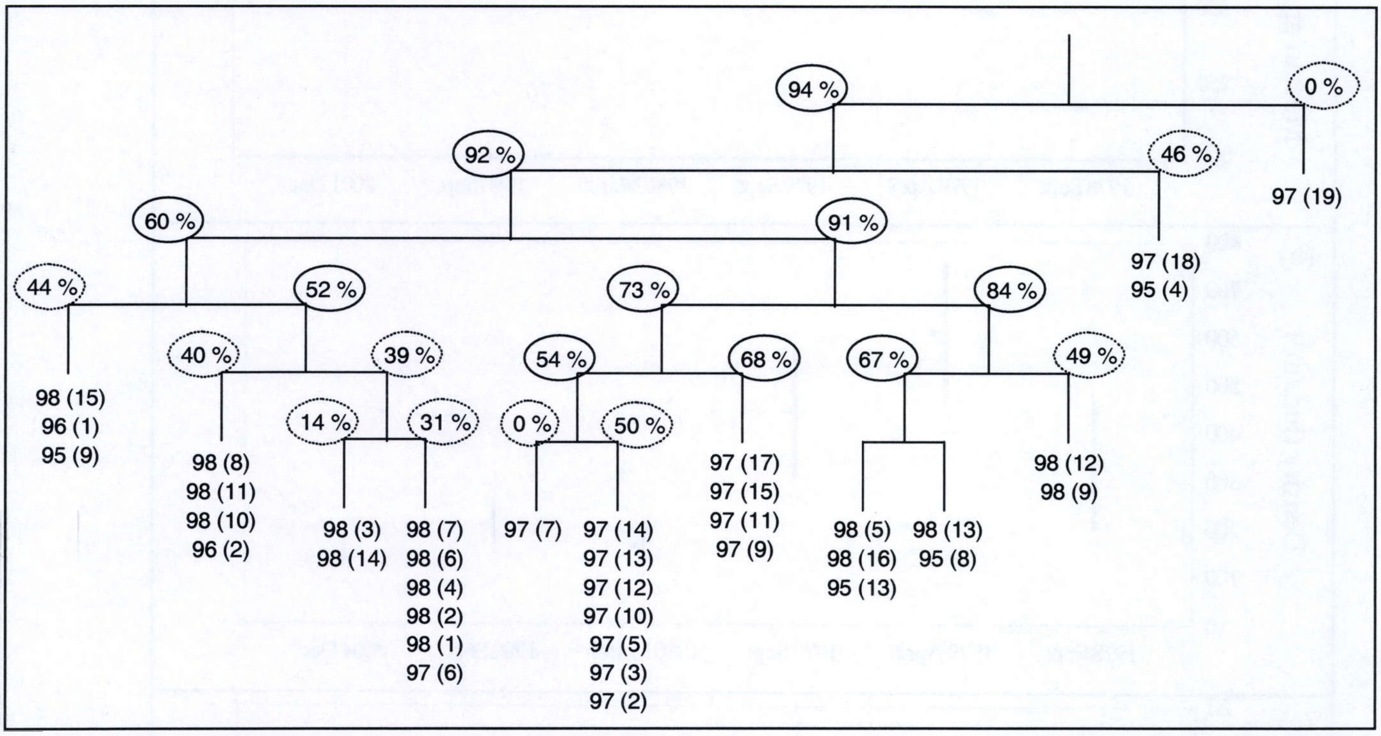


Fig. IV.4: TWINSPAN diagram of the macrobenthic samples belonging to the bank community on the Kwintebank. The percentages listed are the mean within-group variances or dispersions (Dp) expressed as a percentage of the total Dp of the data (Dt). Only the percentages exceeding 50 % indicate that the concerned division can still be subdivided. The percentages within dotted circles indicate that further divisions are not worth retaining.

3.1.2 Temporal changes in macrobenthos

3.1.2.1 Station 1

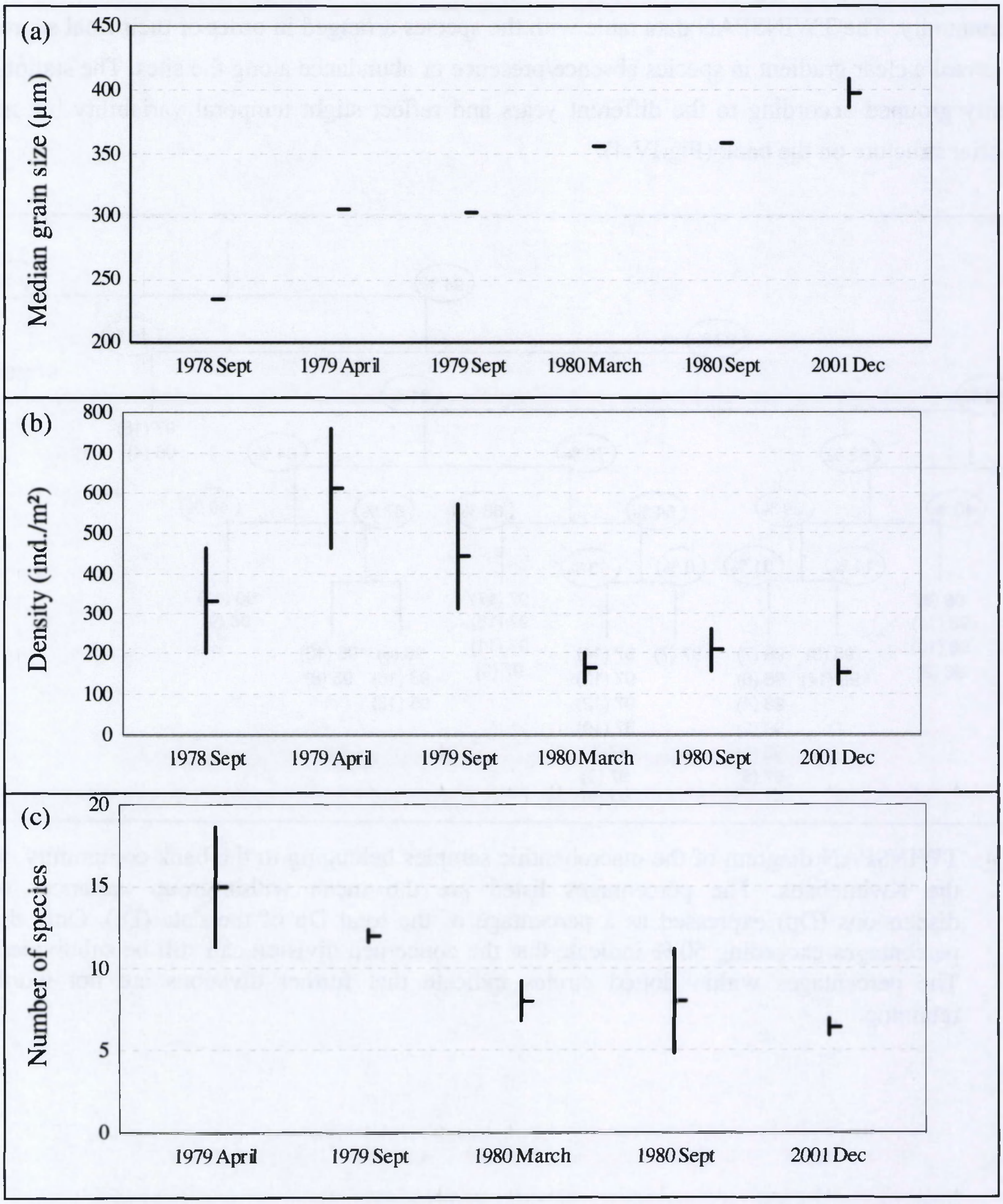


Fig. IV.5: Median grain size (a), density (b) and number of species (c) at station 1 for each sampling event between the seventies and 2001

Median grain size at station 1 significantly ($p < 0.05$) increased between the late seventies and 2001 (Fig.IV.5.a). The increasing trend was already observed in the short time span between 1978 and 1980. The sediment evolved from fine sand in 1978 toward medium sand in 1979-1980. The situation in the eighties and nineties is however unknown.

Density was significantly lower in 2001 in relation to both values of 1979 ($p < 0.05$) (Fig.IV.5.b). Already in March 1980 a significant lower density was recorded in comparison with 1979 ($p < 0.05$). The values in March 1980 were comparable with the densities recorded in 2001.

The number of species dropped between 1979 and 1980 but significant differences could not be detected between the sampling events (Fig.IV.5.c).

3.1.2.2 Station 6

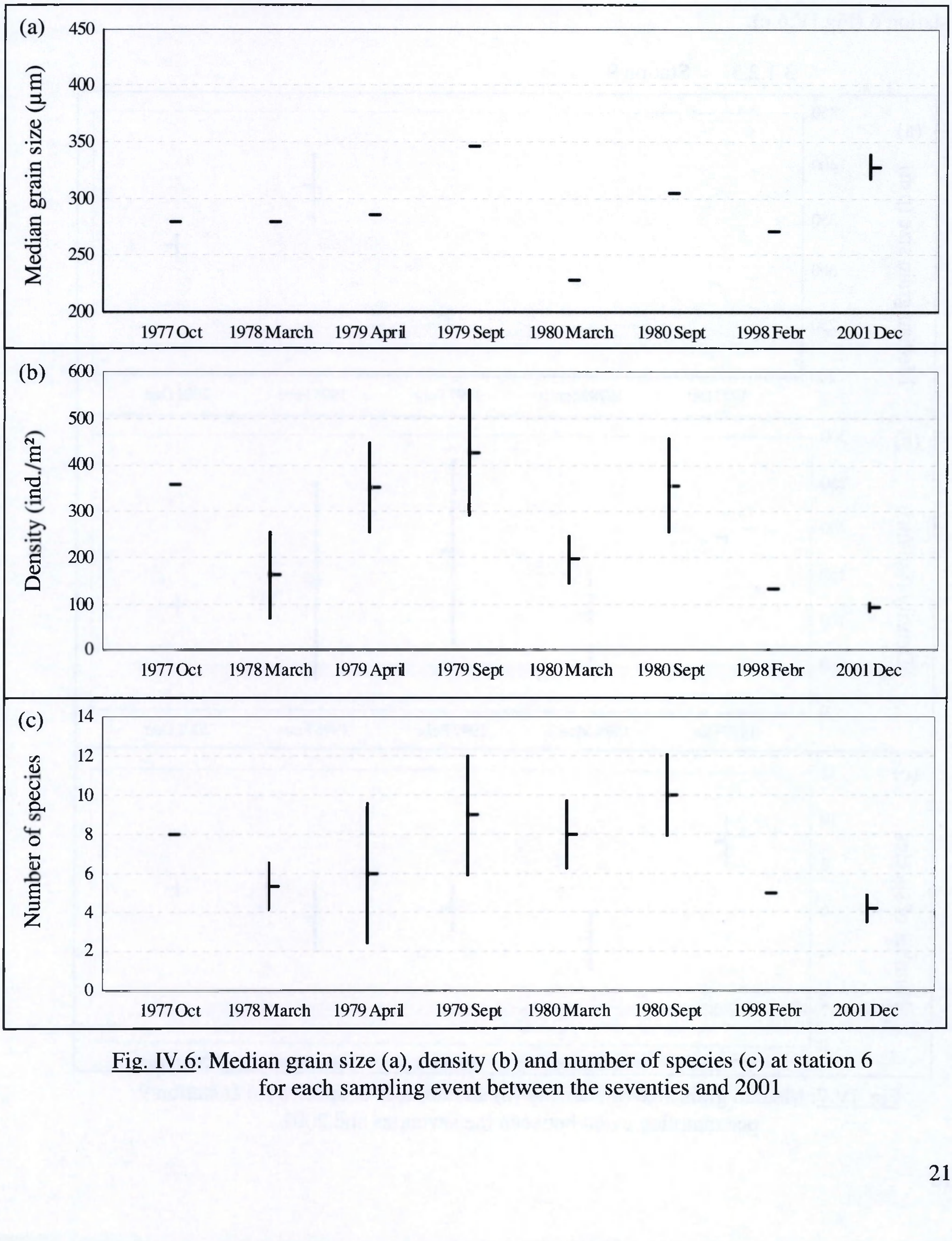


Fig. IV.6: Median grain size (a), density (b) and number of species (c) at station 6 for each sampling event between the seventies and 2001

Median grain size fluctuated around 300 µm through the whole period (Fig.IV.6.a). Slightly higher values were measured in September 1979 and in December 2001, whereas fine sands were sampled in March 1980. The densities of March 1978, March 1980, February 1998 and December 2001 were significantly lower than the densities in September 1979 ($p < 0.01$, $p < 0.05$, $p < 0.05$ and $p < 0.001$ respectively) (Fig.IV.6.b). The values in March 1978 and December 2001 were also lower in relation to September 1980 ($p < 0.05$ and $p < 0.01$). A lower density was also recorded in December 2001 in comparison with April 1979 ($p < 0.05$). Species richness did not reveal any trend at station 6 (Fig.IV.6.c).

3.1.2.3 Station 9

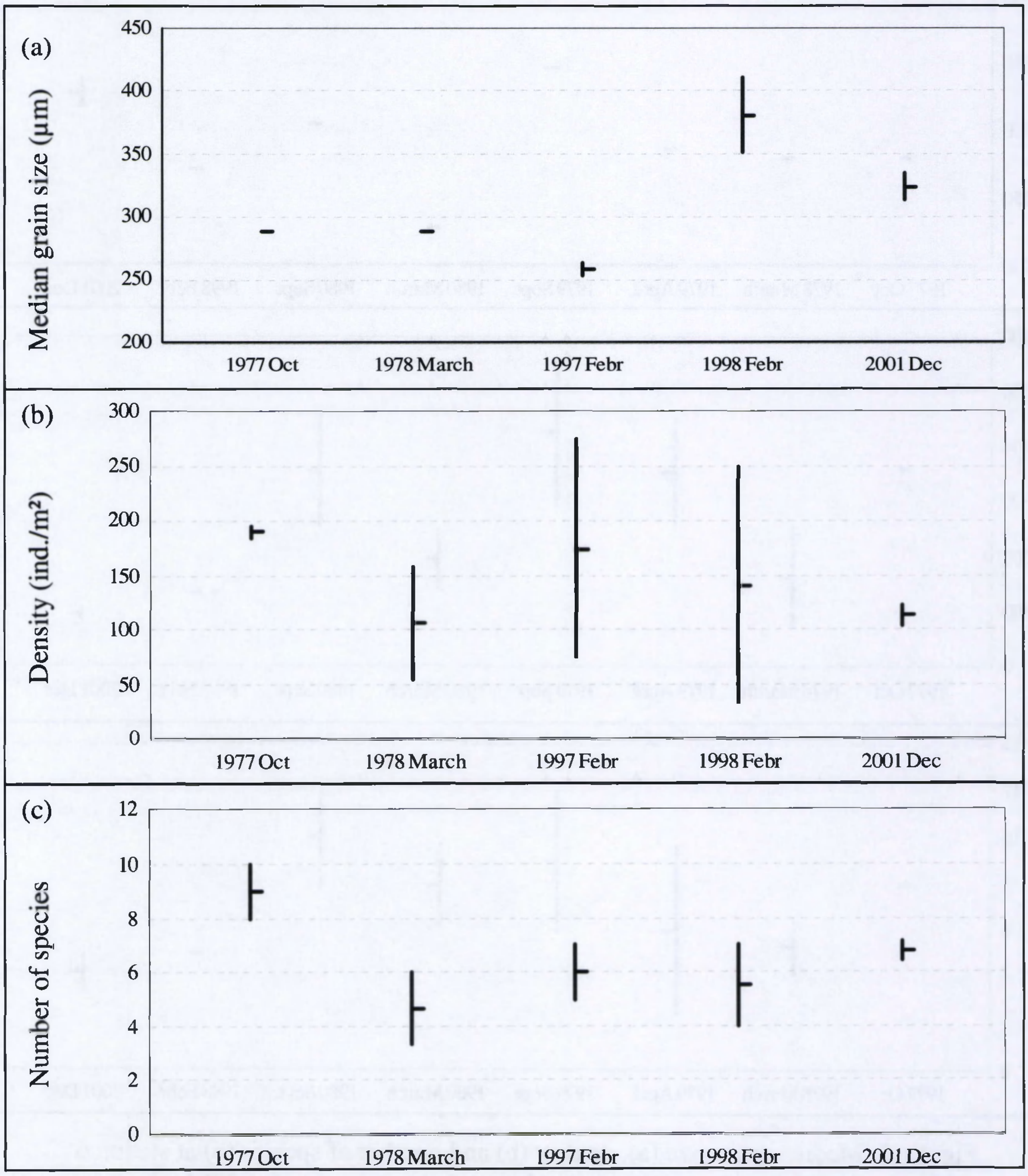


Fig. IV.7: Median grain size (a), density (b) and number of species (c) at station 9 per sampling event between the seventies and 2001

In February 1998 median grain size was significantly higher than at all the other sampling events (Fig.IV.7.a). In February 1997 a slightly lower median grain size was recorded, significantly differing from the measurements in December 2001. In general, however, no clear trend could be derived from the comparison between the seventies, nineties and 2001. Density and species richness did not change through time (Fig.IV.7.a & b).

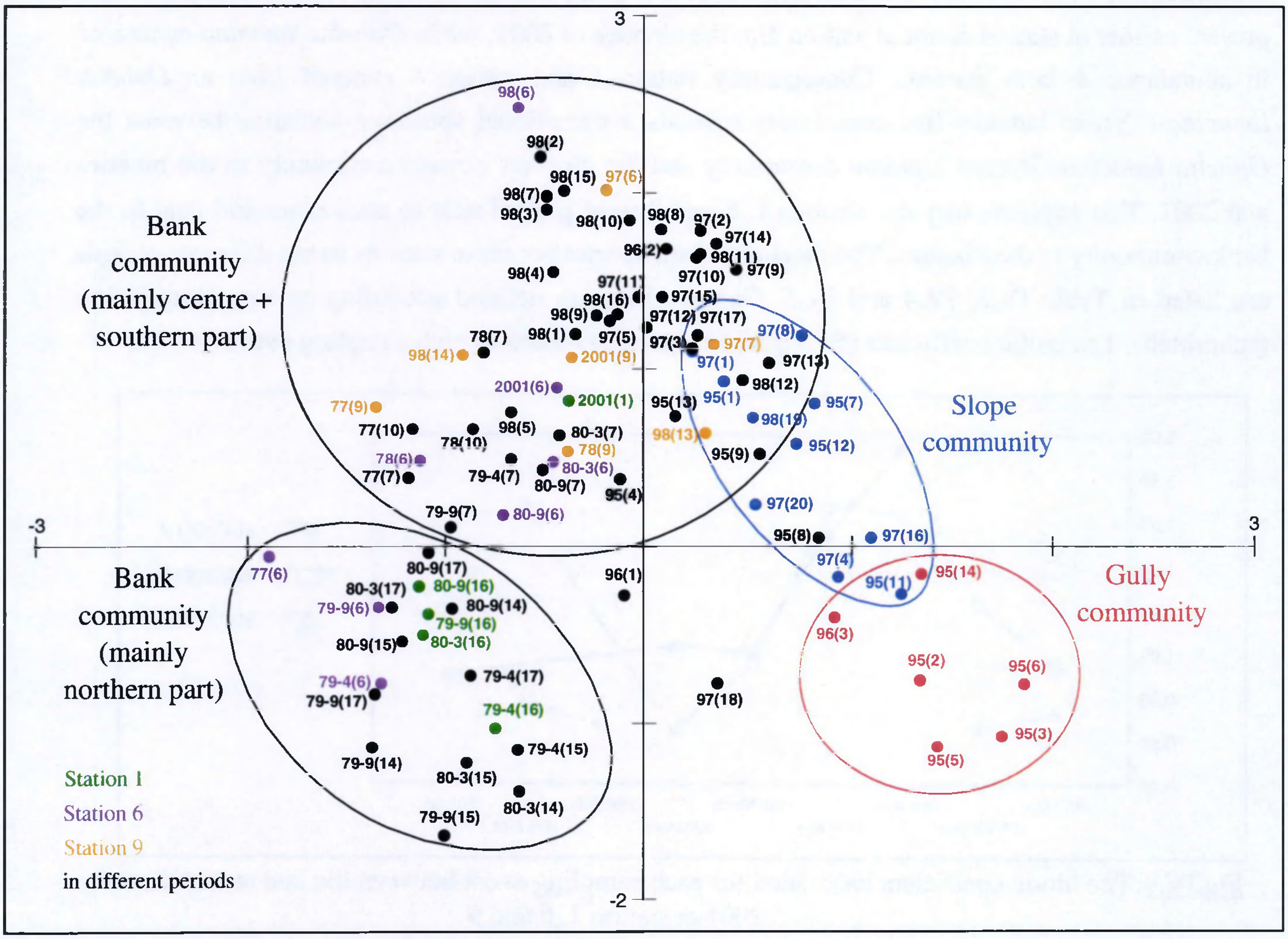


Fig.IV.8: CA plot of the macrobenthic samples taken on the Kwintebank between the late seventies and 2001, based on fourth root transformed absolute species abundances. The sample code includes the year of sampling (+ month if indicated) and the station number between brackets.

In the TWINSPAN (not depicted) and CA (Fig.IV.8) of the total dataset of the different periods, the gully, slope and bank communities were clearly distinguished, as described previously. A distinct difference also existed between the northern part of the Kwintebank (stations 14, 15, 16 and 17) in the seventies and the bank, slope and gully communities in the nineties. This northern part is distinguished due to the high abundances of *Ophelia limacina*, *Spisula solida*, *Spio filicornis* and Oligochaeta. Samples in this northern area are not available from the nineties. In 2001 however, station 1 in the northern part was resampled. This station was not plotted among the other northern stations in the seventies but near to the bank community from the nineties. Moreover, the different stations sampled in 2001 (situated in the northern part (1), as well as the centre (6) and the southern part (9) of the bank) were very similar in the plot. In the seventies similarities were also detected between station 6 and the northern part of the bank, due to the high abundance of the characteristic species *Spio filicornis* and *Ophelia limacina* and the presence of some *Spisula*'s and oligochaetes. In the nineties *Spisula* was only found in some slope and gully stations. *Spio filicornis* and *Spisula* were present neither at station 6, nor at station 1 in the nineties or 2001, while *Ophelia limacina* decreased in abundance at both stations. Consequently station 1 and station 6 evolved from an *Ophelia limacina-Glycera lapidum*-like community towards a transitional species association between the *Ophelia limacina-Glycera lapidum* community and the *Nepthys cirrosa* community in the nineties and 2001. This explains why the stations 1, 6 and 9 were plotted near to each other and near to the bank community in the nineties. The most abundant species for these stations in the different periods are listed in Table IV.3, IV.4 and IV.5. Communities are defined according to Van Hoey *et al.* (submitted). The biotic coefficient (BC) is added for each station at each sampling event.

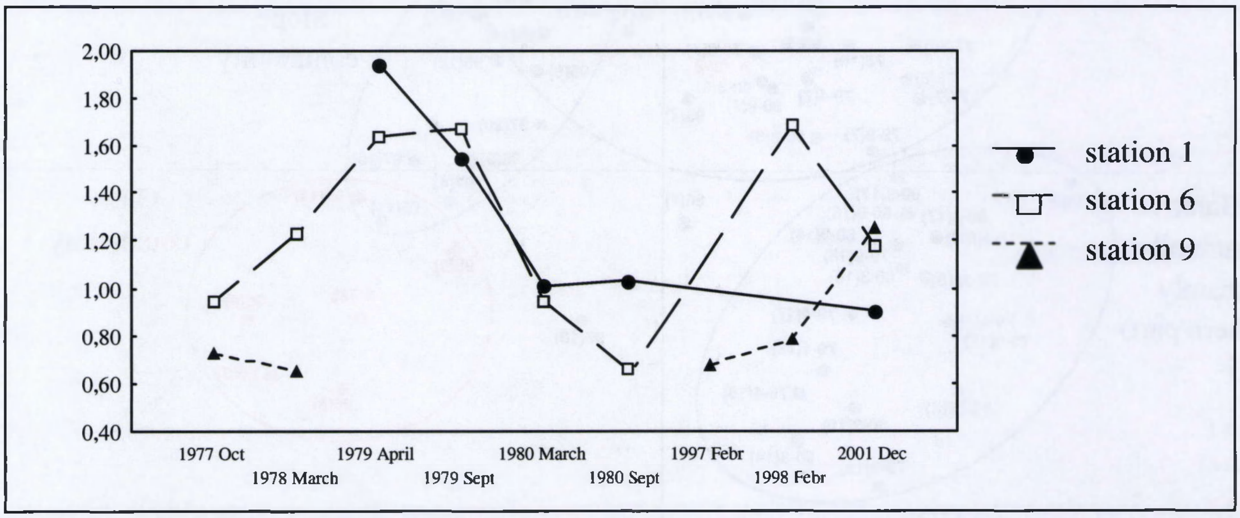


Fig.IV.9: The biotic coefficient calculated for each sampling event between the late seventies and 2001 at station 1, 6 and 9

The biotic coefficient fluctuated between 0.66 and 1.94, corresponding to an impoverished community or to a slightly polluted site (Fig.IV.9).

At station 1 the tolerant species (group III) were most important in April and September 1979, followed by the sensitive species (group I). In March and September 1980 and 2001 the sensitive species accounted for the highest relative abundance, followed by the indifferent species (group II). These changes resulted in a decrease of the BC between 1979 and 1980-2001.

At station 6 indifferent species dominated through the whole period, except in September 1980 when sensitive species were most abundant. Sensitive species were mostly second in abundance, except in September 1979 and February 1998. No clear trend in the BC was discerned through the time series.

At station 9 indifferent species were most abundant in 1977 and 2001, followed by sensitive species, while sensitive species dominated in the other periods with the indifferent species second in abundance. A slight increase of the BC was observed between the nineties and 2001. One second order opportunistic species (group IV) was encountered in the nineties at station 9, i.e. *Cirratulus* spec. in February 1997.

The fluctuations in the BC do not point to an increased abundance of opportunistic species between the seventies and the nineties and 2001 as a result of severe disturbances in the environment. Increasing sand extraction intensity from the late seventies onwards did not result in clear changes of the biotic coefficient. Moreover, the BC did not differ between the stations, characterized by different sand extraction intensity. The BC of the sporadically exploited station 9 was even higher than the two intensively exploited stations in 2001.

Station 1

1979 April		1979 September		1980 March		1980 September		2001 December	
Spio filicornis	27.20	*Spio filicornis*	41.22	*Nephtys cirrosa*	18.07	*Ophelia limacina*	27.14	*Urothoe brevicornis*	22.22
Spiophanes bombyx	21.66	*Ophelia limacina*	15.09	*Ophelia limacina*	16.27	*Spio filicornis*	19.05	*Nephtys cirrosa*	15.41
Scoloplos armiger	12.54	*Bathyporeia elegans*	11.26	*Spio filicornis*	13.86	*Nephtys cirrosa*	14.29	*Ophiura albida*	15.25
Ophelia limacina	8.63	*Glycera capitata*	5.18	*Scoloplos armiger*	12.05	*Spisula solida*	8.10	*Echinocardium cordatum*	11.12
Nephtys cirrosa	5.37	*Nephtys cirrosa*	5.18	*Eteone longa*	12.05	*Hesionura augeneri*	6.19	*Spio goniocephala*	9.38
Spisula elliptica	3.75	*Spisula spec.*	5.18	*Spisula solida*	10.24	*Gastrosaccus spinifer*	6.19	*Scoloplos armiger*	8.75
Heteromastus filiformis	2.77	*Eteone longa*	3.83	*Glycera capitata*	6.02	*Eteone longa*	4.76	*Ophelia limacina*	7.11
Eteone longa	2.12	*Gastrosaccus spinifer*	3.83	*Gastrosaccus spinifer*	4.22	*Atylus falcatus*	3.33	*Glycera capitata*	2.51
Lanice conchilega	2.12	*Hesionura augeneri*	2.93	*Goniadella bobretzkii*	1.81	*Scoloplos armiger*	3.33	*Crepidula fornicata*	2.22
Hesionura augeneri	1.63	*Nephtys spec.*	1.58	*Anaitides mac-muc*	1.81	*Polygordius appendiculatus*	3.33	*Thia scutellata*	1.74
Anaitides maculata-mucosa	1.63	*Microphthalmus similis*	0.68	*Tellina fabula*	1.81	*Bathyporeia guilliamsoniana*	1.43	*Lanice conchilega*	1.38
Anaitides subulifera	1.14	*Anaitides mac-muc*	0.68	*Atylus falcatus*	1.81	*Bathyporeia elegans*	1.43	*Psammechinus miliaris*	1.18
Oligochaeta spec.	1.14	*Spiophanes bombyx*	0.68			*Oligochaeta spec.*	1.43	*Gastrosaccus spinifer*	0.87
Goniadella bobretzkii	1.14	*Spisula elliptica*	0.68					*Eteone longa*	0.87
Spisula solida	1.14	*Brachyura spec.*	0.68						
Aonides paucibranchiata	1.14	*Spisula solida*	0.68						
Pagurus bernnardus	0.49	*Bathyporeia guilliamsoniana*	0.68						
Pariambus typicus	0.49								
Ophiura albida	0.49								
Pholoe minuta	0.49								
Megaluropus agilis	0.49								
Bathyporeia guilliamsoniana	0.49	**BC = 1.55**		**BC = 1.01**		**BC = 1.04**		**BC = 0.91**	
Magelona papillicornis	0.49								
Eumida sanguinea	0.49								
Natica alderi	0.49								
Chaetozona setosa	0.49								
BC = 1.94									
***Ophelia limacina-Glycera lapidum* community**		***Ophelia limacina-Glycera lapidum* community**		***Ophelia limacina-Glycera lapidum* community**		***Ophelia limacina-Glycera lapidum* community**		**TSA** ***Nephtys cirrosa-Ophelia limacina* community**	

Table IV.3: Community, biotic coefficient and relative abundances of the species assigned to different ecological groups per sampling event at station 1: species very sensitive to pollution, species indifferent to pollution, tolerant species, second-order opportunistic species, first-order opportunistic species and species which the ecological group was not available from in black, TSA = Transitional Species Association

Station 6

1977 October	
Hesionura augeneri	54.85
Archiannelida	24.86
Gastrosaccus spinifer	9.30
Macrochaeta helgolandica	3.08
Spio filicornis	1.85
Nephtys cirrosa	1.13
Pontocrates altamarinus	0.93
Spisula spec.	0.93
Oligochaeta spec.	0.74
Microphthalmus listensis	0.63
Mysella bidentata	0.47
Glycera capitata	0.43
Spisula solida	0.27
Modiolus modiolus	0.13
Oridia armandi	0.13
Ophelia limacina	0.08
Goniadella bobretzkii	0.08
Streptosyllis arenae	0.08
Notomastus latericeus	0.04

BC = 0.95

TSA
***Nephtys cirrosa*-*Ophelia limacina* community**

1978 March	
Hesionura augeneri	49.60
Nephtys cirrosa	11.79
Scolelepis bonnieri	9.29
Gastrosaccus spinifer	5.56
Spisula solida	5.56
Bathyporeia elegans	4.17
Pontocrates altamarinus	4.17
Scoloplos armiger	4.17
Archiannelida	1.90
Ophelia limacina	1.90
Paraonis fulgens	0.95
Spiophanes bombyx	0.95

BC = 1.23

TSA
***Nephtys cirrosa*-*Ophelia limacina* community**

1979 April	
Ophelia limacina	25.50
Hesionura augeneri	25.50
Spio filicornis	18.98
Glycera capitata	11.33
Oligochaeta spec.	6.52
Nephtys cirrosa	5.67
Scoloplos armiger	2.83
Goniadella bobretzkii	1.98
Nephtys caeca	0.85
Polygordius appendiculatus	0.85

BC = 1.64

***Ophelia limacina*-*Glycera lapidum* community**

1979 September	
Hesionura augeneri	37.38
Spio filicornis	28.74
Gastrosaccus spinifer	9.35
Ophelia limacina	7.71
Nephtys cirrosa	7.01
Scolelepis bonnieri	3.04
Spisula elliptica	1.64
Bathyporeia elegans	1.64
Anaitides maculata	0.70
Spisula spec.	0.70
Chaetozona setosa	0.70
Bodotria scorpioides	0.70
Dyastilis rathkei	0.70

BC = 1.67

1980 March	
Nephtys cirrosa	32.14
Ophelia limacina	15.31
Bathyporeia elegans	13.78
Scoloplos armiger	10.20
Anaitides maculata	6.63
Eteone longa	6.63
Spio filicornis	3.57
Scolelepis bonnieri	3.57
Nephtys longosetosa	3.57
Tellina fabula	1.53
Dyastilis bradyi	1.53
Bathyporeia guilliamsoniana	1.53

BC = 0.95

TSA
***Nephtys cirrosa*-*Ophelia limacina* community**

1980 September	
Ophelia limacina	28.93
Nephtys cirrosa	27.25
Bathyporeia elegans	17.70
Gastrosaccus spinifer	6.46
Echinocardium cordatum	4.78
Spio filicornis	3.65
Eteone longa	2.81
Scolelepis bonnieri	1.97
Hesionura augeneri	1.97
Scoloplos armiger	1.97
Pectinaria koreni	0.84
Anaitides maculata	0.84
Oligochaeta spec.	0.84

BC = 0.66

TSA
***Nephtys cirrosa*-*Ophelia limacina* community**

1998 February	
Nephtys cirrosa	50.00
Spio goniocephala	31.25
Bathyporeia elegans	6.25
Paraonis fulgens	6.25
Urothoe brevicornis	6.25

BC = 1.69

TSA
***Nephtys cirrosa*-*Ophelia limacina* community**

2001 December	
Nephtys cirrosa	54.03
Urothoe brevicornis	13.82
Gastrosaccus spinifer	10.15
Spiophanes bombyx	5.17
Ophelia limacina	4.00
Echinocardium cordatum	2.67
Thia scutellata	2.50
Scolelepis bonnieri	2.00
Nephtys spec.	2.00
Spio spec.	2.00
Eteone longa	1.67

BC = 1.18

TSA
***Nephtys cirrosa*-*Ophelia limacina* community**

Table IV.4: Community, biotic coefficient and relative abundances of the species assigned to different ecological groups per sampling event at station 6: species very sensitive to pollution, species indifferent to pollution, tolerant species, second-order opportunistic species, first-order opportunistic species and species which the ecological group was not available from in black, TSA = Transitional Species Association

Station 9

1977 October		1978 March		1997 February		1998 February		2001 December	
Nephtys cirrosa	22.39	*Nephtys cirrosa*	21.67	*Bathyporeia elegans*	39.02	*Scoloplos armiger*	31.67	*Nephtys cirrosa*	34.29
Gastrosaccus spinifer	18.32	*Tellina tenuis*	21.67	*Nephtys cirrosa*	20.50	*Nephtys cirrosa*	22.50	*Echinocardium cordatum*	15.03
Tanaissus lilljeborgi	17.31	*Mysella bidentata*	16.67	*Urothoe brevicornis*	11.49	*Spio filicornis*	14.17	*Scolelepis bonnieri*	9.22
Scolelepis bonnieri	6.93	*Scoloplos armiger*	13.33	*Bathyporeia guilliamsoniana*	9.95	*Urothoe brevicornis*	12.50	*Ophelia limacina*	7.13
Bathyporeia spec.	5.26	*Ophelia limacina*	10.00	*Scolelepis bonnieri*	7.64	*Gastrosaccus spinifer*	12.50	*Gastrosaccus spinifer*	6.40
Bathyporeia elegans	5.19	*Spiophanes bombyx*	6.67	*Bathyporeia spec.*	5.41	*Magelona mirabilis*	1.67	*Spiophanes bombyx*	5.54
Ophelia limacina	3.61	*Scolelepis bonnieri*	3.33	*Cirratulus spec.*	3.09	*Nephtys hombergi*	1.67	*Ophiura albida*	5.08
Spio filicornis	3.42	*Bathyporeia elegans*	3.33	*Magelona mirabilis*	1.45	*Urothoe poseidonis*	1.67	*Thia scutellata*	4.21
Bathyporeia guilliamsoniana	1.85	*Paraonis fulgens*	1.67	*Crangon crangon*	1.45	*Bathyporeia*	1.67	*Urothoe brevicornis*	4.05
Eteone cfr. flava	1.85	*Eteone longa*	1.67			*guilliamsoniana*	1.67	*Nephtys spec.*	2.00
Scoloplos armiger	1.85							*Spio goniocephala*	2.00
Pontophilus trispinosus	1.75							*Spio spec.*	1.54
Pseudocuma longicornis	1.75							*Nephtys caeca*	1.18
Nototropis swammerdami	1.75							*Hyale nilssoni*	1.18
Megaluropus agilis	1.75							*Bathyporeia*	
Hesionura augeneri	1.67							*guilliamsoniana*	1.18
Paraonis fulgens	1.67								
Magelona papillicornis	1.67	**BC = 0.65**		**BC = 0.68**		**BC = 0.79**		**BC = 1.25**	
BC = 0.73									
TSA ***Nephtys cirrosa-Ophelia limacina* community**		**TSA** ***Nephtys cirrosa-Ophelia limacina* community**		**TSA** ***Nephtys cirrosa-Ophelia limacina* community**		**TSA** ***Nephtys cirrosa-Ophelia limacina* community**		**TSA** ***Nephtys cirrosa-Ophelia limacina* community**	

Table IV.5: Community, biotic coefficient and relative abundances of the species assigned to different ecological groups per sampling event at station 9: species very sensitive to pollution, species indifferent to pollution, tolerant species, second-order opportunistic species, first-order opportunistic species and species which the ecological group was not available from in black, TSA = Transitional Species Association

4 Discussion

4.1 Community structure, density and diversity

The macrobenthic samples in the nineties included the centre and the southern part of the Kwintebank and some stations (‘97(17,18,19, 20)) in the northern part. Station ’97(19) was located in coarse sand and immediately separated from all the other stations in the analyses, due to the high abundance of *Caecum glabrum*, *Sphaerosyllis hystrix* and *Glycera convoluta*. The other stations from fine to medium sand in the centre and the southern part of the bank were defined as one bank community.

Vanosmael *et al.* (1982) discerned two major communities on the Kwintebank: a rich community including stations 2, 3 and 4 in the northern part of the bank (see meiofauna sampling stations on the Kwintebank) and a poorer southern bank community. *Sphaerosyllis* was abundantly present in the northern community and *Caecum glabrum* was exclusively found at station 4 (Willems *et al.*, unpubl. report). Station ’97(19) is situated very near to this station 4, which is devoid of any sand extraction activity because of the high content of shell debris and thus the coarseness of the sediment. The dominant species in this particular area did not change a lot between the seventies and the nineties. However, species richness probably decreased since 47 species were found in three replicates in the seventies (Willems *et al.*, unpubl. report) and only 8 species were encountered in one replicate in the nineties. The difference between sieving the samples alive or after fixation may account for the loss of some interstitial polychaetes in the nineties, but not for the loss of some molluscs. At the undredged station 4 the harpacticoid community of the nineties showed still similarity with the species assemblage of the northern part in the seventies, but the loss of some bigger harpacticoids was also observed (Chapter III). Unfortunately, in the nineties macrobenthic samples were not available from stations 2 or 3, which belonged to the rich northern macrobenthic community in the seventies. These stations are exploited for sand extraction and showed some differences with the seventies according to the harpacticoid species composition (Chapter III).

The presence of different *Spisula* species was a common characteristic of station 1, station 6 and the northern community in Willems *et al.* (unpubl. report) as well as in the analyses of the seventies in the present study, whereas *Spisula* was absent at station 1 and 6 in the nineties and 2001. In the seventies station 6 even harboured the mollusc *Caecum glabrum* (Willems *et al.*, unpubl. report). Station 1 and station 6 were also characterized by a high abundance of *Ophelia limacina* and *Spio filicornis* in the seventies, while these species clearly decreased in the nineties and 2001. Sieving the samples alive or after fixation cannot account for differences in presence/absence of *Spisula* or *Ophelia* species, whereas *Spio filicornis* may escape alive through the meshes of the 1 mm sieve (Degraer, pers. comm.). Although *Spio filicornis* was still encountered at a few stations in different years in the nineties, indicating that at least some *Spio filicornis* individuals are retained during sieving alive, no conclusions can be drawn from these quantitative differences.

Stations 1 in the northern part and station 6, situated in the depression in the centre of the Kwintebank, are heavily exploited stations, as was revealed in Chapter III. The disappearance of *Spisula* at these stations may be related to the sand extraction activities. *Spisula* was still encountered next to the depression in 2001, at the same station where a rich harpacticoid community was encountered in 2000 (Chapter III). Hence sand extraction may also have affected the macrobenthic fauna on the Kwintebank. Vanosmael *et al.* (1979) already suggested that *Spisula* may be affected by sand extraction activities on the Kwintebank, because this is a slowly growing species with a long life span. This statement was also applied to *Nephtys* species, whereas no indications were found of decreasing *Nephtys* densities in the present study. Sand extraction may initially also favour bivalve recruitment (*Spisula* species and *Tellina* species) (van Dalfsen *et al.*, 2000) but these species may fail to establish lasting populations due to continuous disturbances as on the Kwintebank.

The potential impact of sand extraction on the macrobenthos of the Kwintebank is however not confirmed by clear changes in other biological characteristics. As a result of sand extraction a decrease in macrobenthic density and species richness is expected (Newell *et al.*, 1998; Desprez, 2000). The direct impacts through removal of the fauna are undeniable. Vanosmael *et al.* (1979) studied the removal of macrobenthic organisms by sand extraction *in situ* and followed the dumping of dead and alive organisms by the sand extraction vessel. 45 % of the animals, which were retained on the sieve aboard the vessel and dumped in the sea, were deadly damaged, accounting for 70 % of the biomass. Mainly molluscs contributed to this percentage of deadly damaged fauna. Sampling the extraction site before and after dredging revealed a reduction in macrobenthic abundance by 80 % (Vanosmael *et al.*, 1979).

At station 1 and 6 significant differences were found between densities of different sampling events. Yet, these differences may result from seasonal fluctuations, since the densities in winter (February, December) and early spring (March) differed generally from samples in April or September. The very high macrofauna density in April 1979 at station 1 was attributed to the high abundance of *Spiophanes bombyx* (133 ind./m²) and *Spio filicornis* (167 ind./m²). Very high densities of *Spiophanes bombyx* have been frequently observed, probably as a response on the sedimentation of the spring phytoplankton bloom at the end of April (Van Hoey, unpubl. data and Chapter II). At station 9 densities were very similar, all the samples being taken in winter or early spring.

Species richness did not change through time at station 9 or at station 6, whereas a slight decreasing trend was observed at station 1. Station 1 was also characterized by a decreasing density and a coarsening of the sediment. The latter trend was also deduced from the comparison of meiofauna samples between the nineties and the seventies and from some time series of geologic surveys at this station, as was discussed in Chapter III. Harpacticoid density also showed a decreasing but non-significant trend at station 1, whereas significant changes were recorded for diversity.

Although macrobenthic density and species richness did not change a lot at any station, the species composition at station 1 and station 6 changed and became very similar to the poor macrobenthic bank community. Hence, the extraction activities may have caused a homogenisation of the macrobenthic on the Kwintebank. Except for one coarse station, the macrobenthic community analysis in the nineties did not distinguish between different parts on the sandbank top. Intensively exploited stations in the depression (station 6 as well as other stations in the nineties) or in the north (station 1) of the bank were not distinguished from less disturbed areas on the sandbank, whereas the harpacticoid community analysis clearly showed different communities, corresponding with different erosion and sand extraction areas (Chapter III).

Macrobenthic densities and diversities on the sandbank top are low, which is typical for well-sorted mobile sands (Elliott *et al.*, 1996) and characterized by mobile polychaetes (e.g. *Nephtys cirrosa*) and crustaceans (e.g. *Bathyporeia* spp.). The *Nephtys cirrosa* community is typically found in well-sorted medium sandy sediments and shows a lot of overlap with several transitional species associations (Van Hoey *et al.*, submitted). On the Kwintebank a transitional species association between the *Nepthys cirrosa* and the *Ophelia limacina-Glycera lapidum* community was generally defined. Slight differences between several combinations of transitional species assemblages may be hard to find and may not be detected in an overall community analysis.

4.2 Biotic Coefficient

In order to investigate the changes of macrobenthic species belonging to different ecological groups more accurately, the biotic coefficient was calculated according to Borja *et al.* (2000). This continuous index allows detecting changes in macrobenthic species with different sensitivity to a pollution gradient, giving a different weight to species with a different sensitivity. The biotic coefficient did not change markedly due to increased sand extraction activities since the late seventies. The highest biotic coefficient was recorded in April 1979 at station 1 and in September 1979 at station 6. The high co-dominance of the tolerant species *Spio filicornis* and *Spiophanes bombyx* accounted for the higher value in April 1979 at station 1. These deposit feeders may have increased in abundance due to enhanced food availability after the sedimentation of the spring phytoplankton bloom (Widbom & Frithsen, 1995). Hence the biotic coefficient measured an impact of slight organic enrichment.

The biotic coefficient is widely used in organic pollution assessment, the increase in opportunistic species being mainly related to this kind of environmental change. Borja *et al.* (2000) assumed that the increase in the biotic coefficient in the inner part of an estuary was related to dredging activities. The dredging probably increased the abundance of suspended matter and hence the abundance of opportunistic species. In Spain the increase in fine sands also resulted in an increase in opportunistic species (van Dalfsen *et al.*, 2000). As long as dredging activities cause an increased organic load through resuspension and resettling of organic matter, the biotic coefficient may be used to assess changes as a result of dredging but this study revealed that its applicability should not be overestimated. Reworking organic poor sediments of subtidal sandbanks (Vanosmael *et al.*, 1979; Vanosmael *et al.*, 1982) does not seem to favour typical opportunistic macrobenthic species. The competitive ability of opportunistic species responding to organic enrichment is probably not advantageous in organically poor and naturally physically stressed environments such as subtidal sandbanks. The naturally occurring species may just recruit more frequently to cope with the more intense disturbances but their species composition may not be altered in poor habitats. In Chapter II it was suggested that the impact of tidal mixing is important on the Kwintebank. In this kind of turbulent environment benthic macrofauna are apt to be less abundant and not as diverse as in more stable regions (Jennes & Duineveld, 1985). It is very difficult to detect the effect of human-induced physical disturbance in areas exposed to extreme natural disturbances (Hall *et al.*, 1990; Kaiser & Spencer, 1996) because the communities of high-stress areas are characterized by higher growth rates (Jennes & Duineveld, 1985) and hence more adept to readjustement to the impact of dredging operations (Desprez, 2000).

Some former species-richer areas (such as the northern top of the Kwintebank) may however have impoverished and have become similar to the surrounding area. This homogenisation hampers the distinction between extracted and non-extracted sites at a fixed moment in time. The use of a biotic coefficient, designed for organic pollution assessment, is not appropriate to measure dredging impacts in clean sands. A suggestion might be to modify the classification of the ecological groups used for the biotic coefficient, focusing on differences between the different (interstitial) polychaetes and amphipods prevailing in these habitats or to examine the percentages of juveniles or biomasses. If groups of species are used to characterize a certain degree of enrichment or disturbance, rather than single species, and such groupings are related to other environmental variables then a more useful system must be defined. Analysis of the ecological principles underlying the used model should remain the chief aim of those biologists concerned with the examination of the effects of enrichment or disturbance, and the use of any indicator schemes must be accompanied by a detailed knowledge of both the abundance and range of species in the area concerned (Pearson & Rosenberg, 1978). Swartz (1972) and Eagle & Rees (1973) pointed out that any attempts to use the presence of macrobenthic species in a sample as indicative of the enrichment or disturbance of the area must always be qualified by a consideration of the full species range present and the environmental conditions prevailing at the time of sampling.

Yet, differences in the macrofauna between areas of different levels of human disturbance are not easily detected on the Kwintebank at a fixed moment in time, because of potential homogenisation by the extractions, the poverty and wide niche width of the community and the extent to which the community is adapted to high levels of sediment disturbance in these dynamic systems. The poverty of samples so far is definitely an additional problem and comparisons with the macrofauna of similar undisturbed areas should be made. Hence a clear picture can be given on the presence/absence of the naturally occurring K- and r-strategists against which the community of the Kwintebank can be tested.

Further considerations and suggestions

Verdere beschouwingen en suggesties

Further considerations and suggestions

Wendy Bonne

This Ph.D. research started as an exploratory ecological study focusing on benthic copepods in offshore habitats. Sediment characteristics and organic enrichment as a result of the spring phytoplankton bloom were suggested to play an important role in defining the spatial and temporal variations in harpacticoid communities. Due to explorations on the Kwintebank and the Middelkerkebank, deviating species assemblages were detected which could not be attributed to sediment characteristics. One of the most likely causes on the Kwintebank was sand extraction. Consequently, much attention has been drawn to sand extraction impacts as well, although sampling strategy was not designed for this purpose. The conclusions drawn in the study on this topic suffer from incomplete knowledge on spatial and temporal variation. From the shortcomings of the conducted analyses, some useful proposals can therefore be made to improve research on the impacts of human-induced disturbances, and for the study of the Kwintebank in relation to sand extraction in particular.

1 Phytoplankton blooms

Strong evidence exists for a response in the benthic system on diatom and *Phaeocystis* sedimentation, though the mechanism and the food web interactions through which it acts are unclear so far. A fine-tuning of measurements of the relevant keys in the bacterial/detrital food chain is really necessary. The benthic system is affected but not in the same way at different places. Near the Gootebank a rapid but relatively clear response was observed, whereas on the Kwintebank this reaction was much less clear due to a probably strong interplay of hydrodynamics and other environmental factors. Large differences were detected in chlorophyll *a* measurements while these concentrations could not always be the result of sedimentation of primary production in the water column. Fluctuating levels of chlorophyll *a* may result from tidal currents. From the observations of quite a high amount of bentho-pelagic diatoms it is assumed that settlement behaviour of these organisms at shallower depth on sandbanks may be important for meiofauna, especially harpacticoids. When anchoring at the same station for a whole day, tidal surveys in an interdisciplinary study of zoologists, botanists, geologists and physicists during different weather conditions may reveal the different conditions of the sediment surface and the corresponding behaviour of diatoms and endobenthos. As tidal mixing may be a rather universal process, it could have a major influence on the study of bio-energetics in turbulent ecosystems, particularly in regard to the energy flow between the pelagic and the benthic system (Jennes & Duineveld, 1985). One of the reasons of the relatively wide distribution of the southern community on the Kwintebank and the community in the northern part of the Middelkerkebank may be related to repeated colonisation events through these resuspensions.

As harpacticoids include epibenthic as well as interstitial forms, their species assemblages may also reveal a tight interplay between hydrodynamic conditions and sediment mobility, more than the exclusively interstitial nematodes. Irrespective of depth and sediment composition (though in a specific range) the dominance of interstitial or larger epi- and/or endobenthic species may also be defined by bottom current velocities, bottom topography and consequently turbulence, pore water flow, maybe related with different bacterial or diatom growth/behaviour. A much tighter coupling between sedimentological, hydrodynamical and biological investigations is encouraged.

Some of the interactions responsible for the changes in relation to the phytoplankton bloom at station 330 may be imitated in experiments to study them more in detail but variations such as at station 215 will hardly be obtained in an experimental setup in the lab as the different causes of hydrodynamic stress are not known yet in an appropriate extent. Jennes & Duineveld (1985), however, performed already an interesting experiment in which they imitated tidal mixing.

On sandbanks the turbulence is thus not only of geological meaning but also of biological meaning. It releaves the benthos from severe sedimentation events and probably high growth rates of a poor macrobenthic community make it more resilient to sand extraction activities.

2 Sand extraction

Marine environments are dynamic and complex, the knowledge base is small, and many changes are not noticed until it is too late for a rigorous demonstration of cause and effect (Thrush *et al.*, 1998). This frustration appeared in the study of the Kwintebank as well. With the available data up till now, an effort was made to explain the harpacticoid community patterns using background data about sediment characteristics, topography and sand extraction intensity in order to asses the impact of sand extraction activities. Harpacticoid community structure varies with sediment composition, but is also in equilibrium with seabed disturbance, either from human-induced physical disturbance or from tidal currents and wave action, both of which show spatial variations and interactions with water depth. These environmental variables varied along the sandbank in a different extent, sand extraction being concentrated in two hydrodynamic different areas. Environmental disturbance was unevenly distributed on the Kwintebank, which may lead to a mosaic of communities and may partly account for the patchiness of marine communities in dredged areas (Newell *et al.*, 1998). The impact of extraction activities is site specific and depends on numerous factors, including sediment type and mobility, bottom topography and current strength (Desprez, 2000). Because of this environmental interdependence, similar sand extraction intensities (in the centre and the north) induced different environmental changes and hence different harpacticoid community changes, resulting in enhanced community patchiness in 1997 in relation to 1978 on the Kwintebank. These different responses make it difficult to unravel cause and effect in univariate and multivariate analyses and blur the results of correlation analyses. Nevertheless a relationship, either direct or indirect, between regional-scale changes in harpacticoid community structure and habitat disturbance by sand extraction was demonstrated.

The most serious physical impacts of marine aggregate extraction relate to substratum removal, alteration of the bottom topography and re-deposition of material (De Groot, 1996; Newell *et al.*, 1998). The indirect impact of fine sands deposited in the extraction site on the harpacticoid fauna, was very clear in the central depression and was more obvious as the direct effects. This effect may however not be generalized for the whole depression. Some biological changes could not be dedicated with certainty to sand extraction activities because of the lack of information about seasonal and yearly variation. Especially in the northern part it is very difficult to distinguish between the intense natural dynamics and the human-induced disturbances. Also in the dredging site off Dieppe in France the intense hydrodynamics explained why the effects of dredging were almost absent in the westernmost station, while a gradient of increasing impact was always observed from West to East within the extraction site (Desprez, 2000).

Unequivocally linking structural changes to their cause is difficult. Several authors (Messieh *et al.*, 1991; Gislason, 1994; Hall, 1994) already explained that biological effects are difficult to identify due to the complexity and variability in benthic communities. On the Belgian Continental Shelf the potential importance of changes in benthic communities due to habitat disturbance by dredging is discounted so far because impacts have not been well documented. An additional difficulty is the probably high resilience of the fauna adapted to frequent (tidal) disturbances. Nevertheless the weight of evidence should be of concern to resource managers. It is not because scientific conclusions do not deal with uncertainties, that science would have no place in debate, as suggested by Gray (Eleftheriou, 2000). Gray affirmed that government decisions can be driven by scientifically sound principles. However, the problem of identifying cause-and-effect relationships over broad scales emphasizes the value of a precautionary approach to environmental or dredging management. Caution is called for dredgers getting the benefit of the doubt over scientists.

The northern community on the Kwintebank is subject to severe stress conditions as a result of the extraction activities, like the fauna in the depression. However, in terms of density and diversity, the community in the northern part of the sandbank is more resilient to disturbances than the central part, probably due to different adaptive abilities to extreme hydrodynamic disturbances.

This knowledge may help in taking decisions on allowing a specific frequency of extraction activities. To meet the needs of the dredgers it is important to exploit the area in the most beneficial way by tuning the frequency of extraction activities to the capacity of the area, not only from a geological point of view but also from a biological viewpoint. This means that the northern part of the sandbanks can probably be exploited more frequently than the central and southern part. It is important to pay special attention to the area around a kink in the sandbank as in such an area current velocities and direction may be rapidly changed due to initial erosion by sand extraction. Further recovery of this area may consequently be hampered.

Sustainable management of renewable natural resources should include a balance between exploitation and adverse effects on other components of the ecosystem (Thrush *et al.*, 1998). The results of van Moorsel (1994), Kenny & Rees (1996) and Desprez (2000) illustrated that extensive dredging may only modify the sediment slightly but alter benthic communities seriously. This suggests that it would be preferable to concentrate dredging in small areas. However, prolonged extraction in limited sites affects seabed morphology and sediment quality more seriously (Desprez, 2000). There exists a threshold scale and a frequency of disturbance events at which lasting ecological effects may occur, even against a background of natural disturbance (Kaiser & Spencer, 1996). The results obtained at the Kwintebank support this conclusion. Every single spot in an area of about 0.7 km² being dredged 1 to 4 times a year, like in the depression, is too much to allow for a restoration of geological and biological features. Also in the northern top of the Kwintebank the consequences of intensive extractions are becoming obvious.

However, the comparisons in this study would be improved significantly by re-surveying more of the sites originally sampled. Seasonal fluctuations in harpacticoid densities are expected. Therefore surveys throughout the year have to be carried out to test accurately for seasonal patterns, instead of extrapolating data from other areas, as was done in this study. Studies from a variety of habitats suggest that the conclusions drawn from studies of habitat patches at one spatial scale may not necessarily be relevant to patches at another scale (for references see Thrush *et al.*, 1996). So more spatially extended appropriate data need to be collected to document the ecological changes with more certainty. As this involves finding more appropriate controls against which to assess effects of dredging pressure, non-exploited sandbanks with the same characteristics as the Kwintebank are very useful, such as the Middelkerkebank. Further monitoring is now recommended and proposed to refine the conclusions and to examine how disturbance of sand extraction acts upon the stability and diversity of a community.

An accurate monitoring is necessary more than ever since an effect on biota or sediments may be quickly blurred by the natural dynamics (Morton, 1977) and difficulty or insignificantly measured after a short time span. They may however act cumulatively through time and impacts may only be clearly measured when the negative trend is already going on for a long time, just as on the Kwintebank. At the moment the damage is noticed, it may be too late to get a complete recovery of the predisturbed situation.

Sandbanks are very dynamic study areas and the challenge in the future is to define the extent of natural fluctuations in order to be able to set the limit for extraction activities. When compared with the undisturbed sandbank, the Middelkerkebank, and in comparison with the Gootebank, the Kwintebank shows more heterogeneity, fluctuations and deviations. If this variation is an interplay of sand extraction activities and normally occurring natural dynamics, will have to be confirmed and entangled further in the future. If it can be defined when natural variation is exceeded, it will be possible to set a limit on sand extraction intensity. Monitoring the evolution of the bank more accurately should be priority, since except for some attempts in the late seventies, the Kwintebank is inadequately monitored from a biological viewpoint. Unless recommended in the past (De Moor & Lanckneus, 1991) no accurate monitoring occurred on the Kwintebank to follow up any biological evolution as a consequence of the exploitation. It is puzzling that the authorities have not undertaken research initiatives to investigate the closure of the centre of the Kwintebank in detail, preceding the closure, at the moment of the closure and at a regular basis afterwards. Such an excellent opportunity to examine the speed of meio- and macrobenthos changes due to the closure is just missed. The efforts in biologic research in Belgium have shortcomings. The organization and control of biologic research on the impacts need some special attention in the future. I would like to recommend to the Belgian Government the great functioning of the institutional organisation CEFAS in England concerning the impact assessment of extraction activities. Governmental tasks as the follow up of sand extraction impacts should be evaluated and reorganized in Belgium in order to obtain the quality of results of impact studies as obtained by CEFAS. They use standards of service which are included within agreements and contracts, *e.g.* the advice, data or other outputs required, how they will be achieved, the timetable for achievement, progress reports and final delivery of the service, which are all lacking at the moment in Belgium in respect to sand extraction. Nevertheless, the concession holder is required to pay an amount towards research costs in Belgium. The concession may be suspended if research results show negative effects on the marine environment. This was recently the case in 2002, due to a report of the Fund For Sand Extraction, when the depression was detected in the central area of the Kwintebank. It would be nice if the same effectiveness in biological research could be achieved as this example of geomorphological monitoring shows.

Monitoring of the morphological setting of the Kwintebank also revealed that the northern part of the Kwintebank is lowering since years and that the southern part is rising (Degrendele, pers. comm.). It is suggested that the strong near-bottom flood currents are channelled through the gap in the western bank flank and the depression, reinforcing hydrodynamic stress in the area north of the depression and preventing the uppiling of sediment to former levels in the northern part. This may explain why the difference in depth between the stations of the northern and the southern part of the Kwintebank measured 8 m in 1997 and only 2 m in 1978 in the present study. This hypothesis is however very speculative and will hopefully be further investigated in the future.

Geo(morpho)logical surveys have a firm and distinct value to understand indirect effects of sand extraction on the fauna. Still, dynamics of sandbanks are not known yet in an appropriate extent to assess the consequences of the extraction activities. Some promising initiatives have been undertaken to better understand these evolutions, such as the MAREBASSE project for Belgium and EUMARSAND for Europe.

3 Role of harpacticoids

Harpacticoids seem to be useful monitoring tools displaying a spatial variation at an appropriate scale (one sandbank) to detect community changes that are related to small-scale changes induced by sand extraction. Harpacticoid responses to environmental changes can be detected because harpacticoid communities of clear sands on sandbanks are very rich, containing a lot of species differing in fitness and competitive abilities. Community changes are more difficult to detect if dealing with a faunal group consisting of a poor community of very mobile species, as is the case for the macrofauna on the Kwintebank. Coull (1972) already expressed that meiofauna, because of their small size, can probably react on minor environmental alterations more acutely than their larger macrobenthic counterparts. Thus, the diversity relationships of these abundant organisms may be a better indicator of environmental complexity than that of the more easily studied macrofauna. The importance of meiofauna in marine benthic community analysis cannot continue to be overlooked. Coull also voiced concern that a more complete understanding of marine benthic ecosystems must include the numerically abundant meiofauna. And herewith the following conclusion of Heip (1980) can be added: stability in the number of species and in the nature of these species is a character of harpacticoid copepod taxocenes, which makes them particularly suitable for monitoring purposes.

Species richness and density measurements, however, were not appropriate to assess extraction effects at each impacted area in a simple way, but community analyses revealed more accurately the complexity of the responses. Controversy still exists on the interpretation of diversity and density measurements in relation to impact assessment of physical disturbances and organic enrichment. Also Moore & Bett (1989), Warwick & Clarke (1991), McRae *et al.* (1998) and Thrush *et al.* (1994) found that multivariate analyses, that identify changes to a suite of taxa with various life-history characteristics and sensitivities to disturbance, are often more sensitive than univariate analysis in discriminating between sites or times.

4 Research for sustainable management in the future

The results of this thesis indicate that it is necessary to perform the following objectives to allow a solid policy for the use of the aggregate resources of the Belgian Continental Shelf:

1. Sampling the Kwintebank in more detail
2. Repeatedly comparing the intensively exploited Kwintebank with the unexploited Middelkerkebank
3. Investigating seasonal and year-to-year fluctuations
4. As often as possible coupling biological information with hydrodynamical, sedimentologi-cal and morphological information of the sandbank
5. Defining the indicator value of the most important size classes of the benthos in relation to sand extraction (meio- and macrofauna at different taxon levels) in order to perform further research more specifically
6. Following recolonization and impoverishment
7. Gathering background knowledge of areas which will be intensively exploited in the future

These objectives are practically translated in the following plan:

1. Performing a complete screening of the Kwintebank and the Middelkerkebank only once, for meio- as well as macrofauna on a detailed spatial scale
2. Monitoring meio- and macrofauna of well-selected areas on the Kwintebank (definitely the depression) and the Middelkerkebank twice a year, preferably simultaneously with multibeam soundings
3. Performing a complete screening of the Buiten Ratel, Oost Dyck and Thornton Bank in order to assess the impacts of more intensive exploitation in these areas in the future
4. Processing and analyzing available bottom samples, stored in the basements, in order to get a better idea on the evolution in the past, on temporal variability and in order to test relationships which have not been examined yet in respect to sand extraction

This plan will allow getting a better idea on:

1. vulnerable areas on sandbanks (such as the kink on the Kwintebank) in order to limit extraction frequency in these areas
2. the recovery capacity of the benthos in order to tune the extraction frequencies to this characteristic
3. the indicator value of meio- and macrobenthos to indicate the degree of disturbance and potential consequences

5 Available bottom samples

An overview of the available (processed and unprocessed) bottom samples for meio- and macrofauna of the Marine Biology Section is given below. Analyzing a selection of these samples will be useful to complete the knowledge on the situation and the evolution in the past in relation to sand extraction.

a. Meiobenthos dataset

		Flemish Banks					Zeeland Banks		Hinderbanks			
		Oostendebank	*Middelkerkebank*	*Kwintebank*	*Buiten Ratel*	*Oost Dyck*	*Gootebank*	*Thorntonbank*	*Westhinder*	*Oosthinder*	*Noordhinder*	*Bligh Bank*
1977	October			13 (x3)								
1978	March			13 (x3)								
	May			13 (x3)								
	June			13 (x3)								
	September			13 (x3)								
	December			13 (x3)								
1979	April			13 (x3)								
	June			13 (x3)								
1981	March				5 (x4)		3 (x4)	2 (x4)				
	April			3 (x4)	1 (x4)							
	July		2 (x4)	2 (x4)	2 (x4)	2 (x4)	2 (x4)	2 (x4)				
	November			2 (x4)								
	December			2 (x2)								
1982	April			2 (x2)								
	June			3 (x2)								
	November			2 (x2)								
1983	April			2 (x2)								
	June			1 (x2)								
	September			2 (x2)								
	December			2 (x2)								
1984	March			1 (x2)								
	April			1 (x4)								
	December			1 (x2)								
1985	September			X								
1986	June			X								
1997	February			17 (x3)								
	October	7 (x3)	7 (x3)	12 (x3)					7 (x3)	7 (x3)		
1998	February					7 (x3)	7 (x3)	7 (x3)			7 (x3)	7 (x3)
	October						7 (x3)	7 (x3)			7 (x3)	7 (x3)
1999	February until July			1(x3) x13 (*)			1(x3) x12 (*)					
2000	October			4								
2001	December			13 (x3)								
2002	December			14 (x3)								

Table 1: Bottom samples for meiobenthos taken between 1978 and 2002 on different sandbanks on the Belgian Continental Shelf. The number of stations is given with the number of replicates for each station between brackets. Samples taken in the coastal area (Coast Banks and beaches) are not included.

(*) Samples taken in 1999 are part of a time series between February and July at three stations: one on the Kwintebank (sampled 13 times during that sampling period), one on the Gootebank (sampled 12 times) and one in the Westdiep (not given in the table).

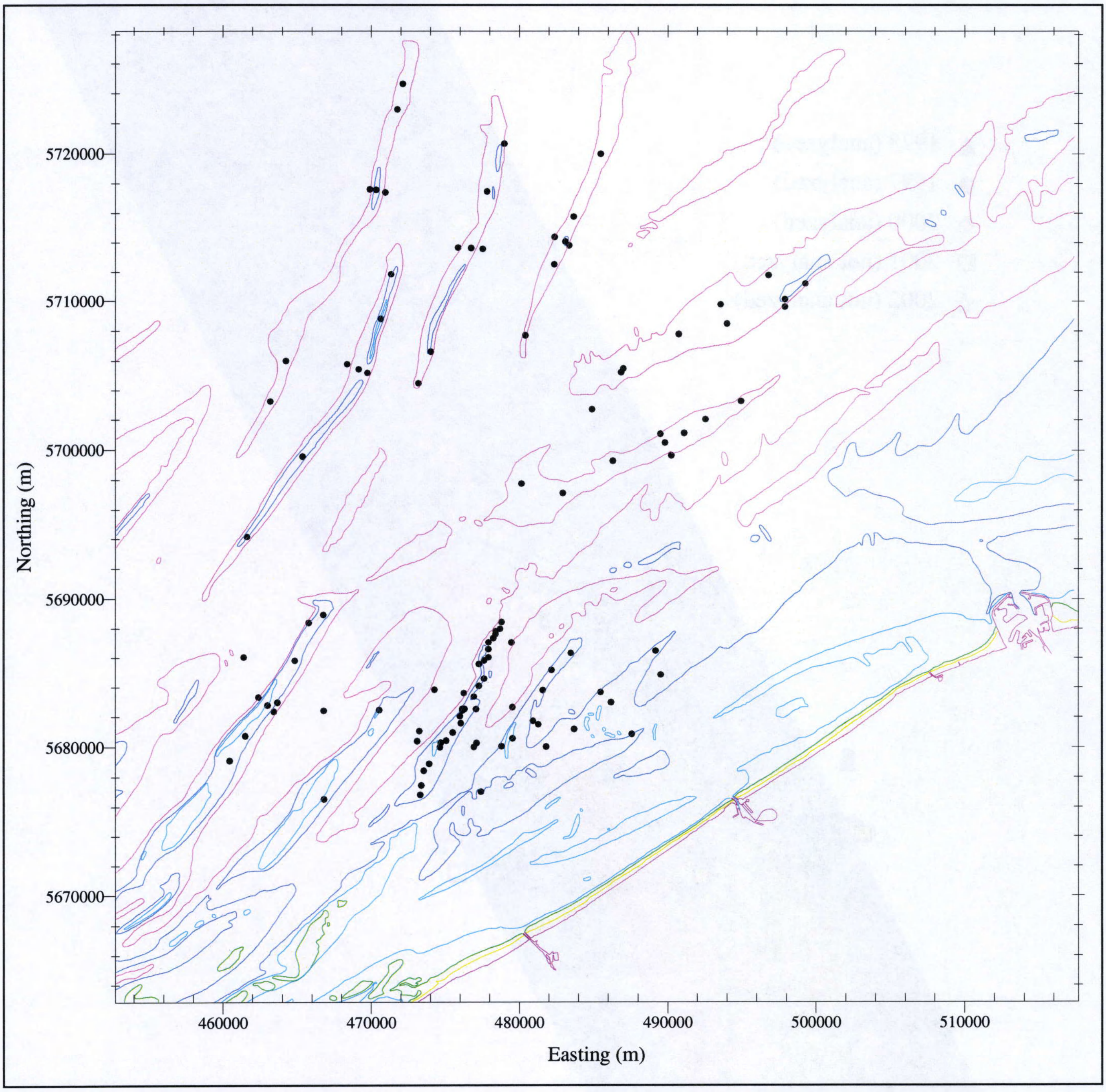


Fig. 1: Location of the meiobenthos stations sampled between 1978 and 2002 on different sandbanks on the Belgian Continental Shelf

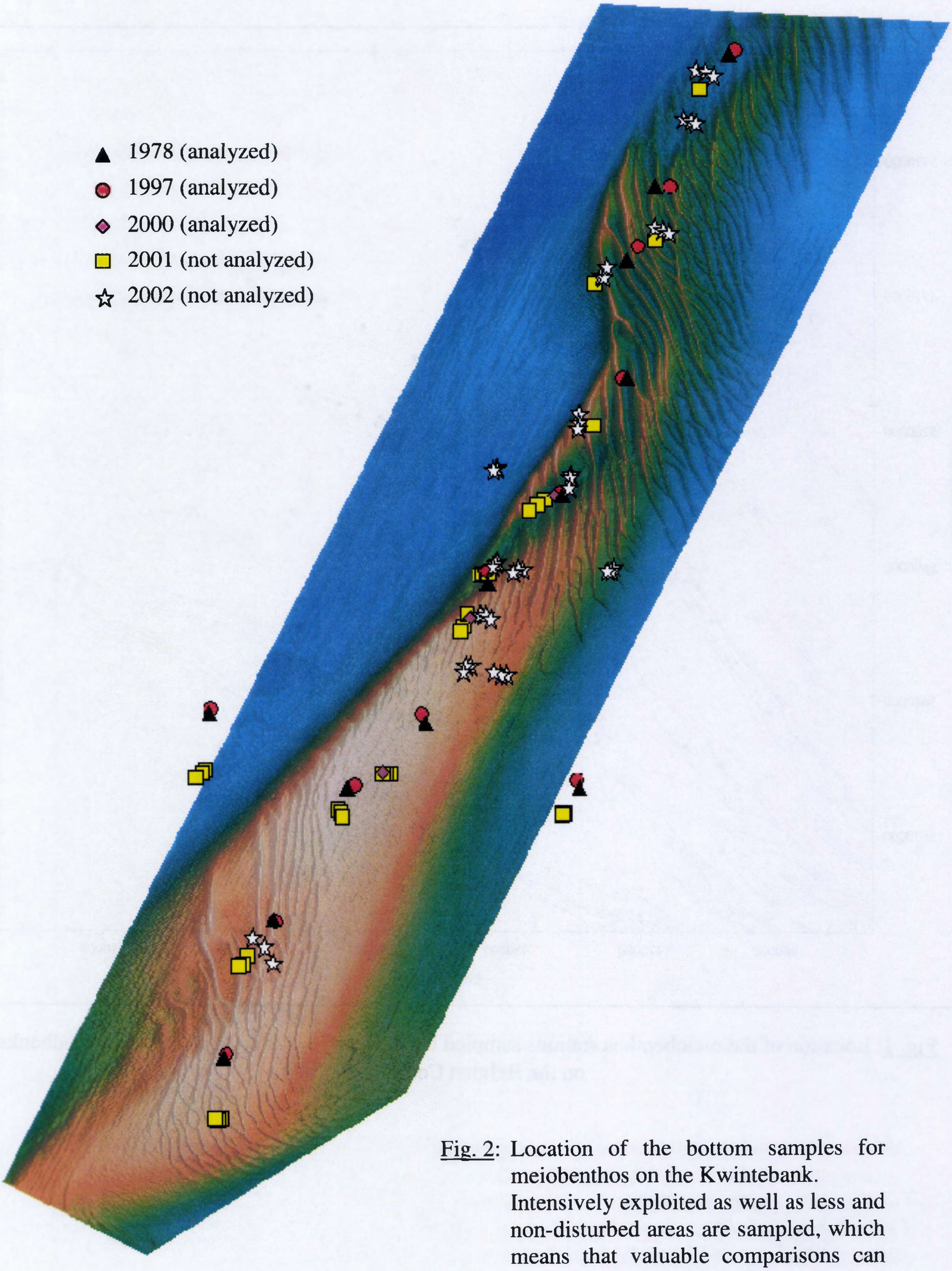


Fig. 2: Location of the bottom samples for meiobenthos on the Kwintebank. Intensively exploited as well as less and non-disturbed areas are sampled, which means that valuable comparisons can be made in future research.

b. Macrobenthos dataset

Part I		Flemish Banks					Zeeland Banks		Hinderbanks			
		Oostende Bank	*Middelkerke Bank*	*Kwintebank*	*Buiten Ratel*	*Oostdyck*	*Goote Bank*	*Thornton Bank*	*West Hinder*	*Oost Hinder*	*Noordhinder*	*Bligh Bank*
1977	October			4 (x3)	6 (x3)							
1978	March			16 (x3)	6 (x3)							
	May			13 (x3)								
	June			13 (x3)								
	September			13 (x3)								
	December			13 (x3)								
1979	April			16 (x3)								
	June			11 (x3)								
	September			17 (x3)								
	December		5 (x3)									
1980	February		2 (x4)	2 (x3)	6 (x6)	2 (x3)						
	March			11 (x3)	2 (x3)		3 (x4)	2 (x3)				
	June			11 (x3)								
	September		2 (x3)	24 (x3)	6 (x3)	2 (x3)	3 (x3)	2 (x3)				
1981	March			4 (x3)	6 (x3)		3 (x3)					
	May			10 (x3)	1 (x3)		2 (x3)					
	July			10 (x3)								
	October		2 (x3)	2 (x3)	6 (x3)		3 (x3)					
	November			7 (x3)	2 (x3)		3 (x3)	1 (x3)				
	December			11 (x3)								
1982	April		5 (x3)	11 (x3)	2 (x3)		3 (x3)					
	June		2 (x3)	11 (x3)								
	October		1 (x3)	9 (x3)	2 (x3)		1 (x3)					
	November		2 (x3)	9 (x3)	4 (x3)	1 (x3)	1 (x3)					
1983	April		2 (x3)	11 (x3)	2 (x3)		3 (x3)					
	June			11 (x3)								
	September		2 (x3)	11 (x3)	4 (x3)		3 (x3)	2 (x3)				
	December			11 (x3)								
1984	April		2 (x3)	3 (x3)	2 (x3)		2 (x3)					
	October			3 (x3)	2 (x3)	2 (x3)	4 (x3)	2 (x3)				
	December			6 (x3)	3 (x3)		2 (x3)					
1985	March			4 (x3)								
	May			4 (x3)			2 (x3)					
	September			6 (x3)	2 (x3)		5 (x3)	2 (x3)				
	November			7 (x3)								
1986	March		1 (x3)				4 (x3)					
	June											

Part II		Flemish Banks					Zeeland Banks		Hinderbanks			
		Oostende Bank	*Middelkerke Bank*	*Kwintebank*	*Buiten Ratel*	*Oostdyck*	*Goote Bank*	*Thornton Bank*	*West Hinder*	*Oost Hinder*	*Noordhinder*	*Bligh Bank*
1987	October			2 (x3)								
1994					20		20		20			
1995			19	20		13						
1996			22	12		12						
1997	February	20	20	20		12			20	20		
	October	18	20	19					20	20		
1998	February			17			20	20			21	21
	October						20	20			21	21
1999	February until July			1 (x3) x13 (*)			1 (x3) x13(*)					
2001	December			5 (x5)								
2002	December			5 (x5)								
2002-2003	March '02-October'03 each month		5 (x3) in de geulen									

Table 2: Bottom samples for macrobenthos taken between 1977 and 2002 on different sandbanks on the Belgian Continental Shelf. The number of stations is given with the number of replicates for each station between brackets. Samples taken in the coastal area (Coast Banks and beaches) are not included.

(*) Samples taken in 1999 are part of a time series between February and July at three stations: one on the Kwintebank (sampled 13 times during that sampling period), one on the Gootebank (sampled 13 times) and one in the Westdiep (not given in the table).

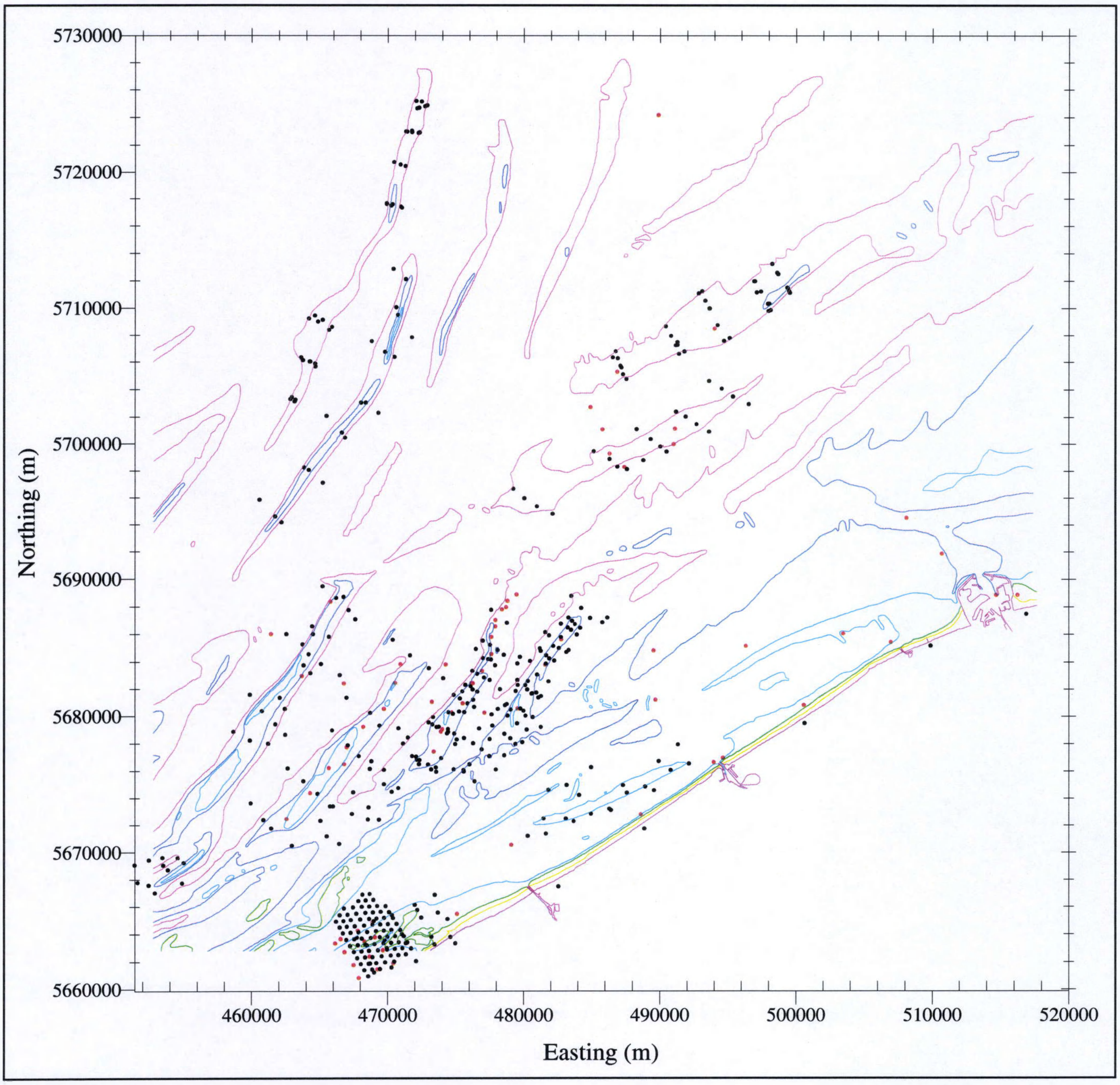


Fig. 3: Location of the macrobenthos stations sampled between 1977 and 2002 (1977-1987 in red, 1995-2002 in black) on different sandbanks on the Belgian Continental Shelf

The macrobenthos datasets will be used in the project BALANS 'balancing human activities in the Belgian part of the North Sea' co-ordinated by Prof. F. Maes of the Maritime Institute (Faculty of Law, University of Gent). This project partly adresses the use of the available macrobenthos data to model any potential effects on the existing communities, according to impacts recorded in literature.

Fig. 3: Location of the macrobenthos stations sampled between 1977 and 2002 (1977-1997 in red, 1997-2002 in black) on different sediments of the Belgian Continental Shelf

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Addenda

Addendum I.1: Species list of 12 replicated samples on the Kwintebank from January 1997

Harpacticoida		Eco-type			Eco-type
Ectinosomatidae	*Ectinosoma reductum*	2	Paramesochridae	*Scottopsyllus Scottopsyllus* n. spec. 1	3
	Halectinosoma canaliculatum	2		*Scottopsyllus Intermedopsyllus intermedius*	3
	Halectinosoma n. spec. 1	2		*Scottopsyllus Wellsopsyllus* n .spec. 1	3
	Halectinosoma n. spec. 2	2		*Scottopsyllus* spec.	3
	Pseudobradya beduina	2		*Diarthrodella secunda*	3
	Pseudobradya spec.	2	Canthocamptidae	*Evansula incerta*	3
	Arenosetella n. spec. 1	3		*Evansula pygmaea*	3
	Hastigerella cfr. leptoderma	3		*Evansula* n.spec. 1	3
	Hastigerella psammae	3		*Evansula* n.spec. 2	3
	Hastigerella cfr. monniotae	3		*Evansula* n.spec. 3 (*)	3
	Hastigerella n.spec. 1	3		*Evansula* n.spec. 4 (*)	3
	Hastigerella n. spec. 2	3	Leptopontiidae	*Leptopontia curvicauda*	3
Thompsonulidae	*Thompsonula hyaenae*	1		*Leptopontia dovpori*	3
Diosaccidae	*Amphiascus hirtus*	1		*Leptopontia* n.spec. 1	3
	Amphiascus spec.	1		*Arenopontia nesaie*	3
	Amphiascoides subdebilis	1		Leptopontiidae genus	3
	Psammotopa phyllosetosa	3	Leptastacidae	*Leptastacus laticaudatus s. str.*	3
	Psammotopa n. spec. (m.)	3		*Leptastacus laticaudatus intermedius*	3
	Psammotopa n. spec. 1 (vr.)	3		*Leptastacus uncinatus*	3
	Psammotopa n. spec. 2 (vr.)	3		*Leptastacus cfr. coulli*	3
	Protopsammotopa norvegica	3		*Paraleptastacus spinicauda*	3
	genus cfr. *Balucopsylla* n. spec. 1	3		*Paraleptastacus espinulatus*	3
Ameiridae	*Ameira parvula*	2		*Paraleptastacus moorei*	3
	Nitocra hibernica s. str.	2		*Paraleptastacus* n. spec. 1	3
	Psyllocamptus minutus minutus	2		*Paraleptastacus* n. spec. 2	3
	Sarsameira cfr. propinqua	2		*Arenocaris bifida*	3
	Sicameira leptoderma	2		*Arenocaris reducta*	3
	Sicameira n. spec. 1	2		*Membranastacus* n. spec. 1	3
	Interleptomesochra eulitoralis	3		Leptastacidae n. genus n. spec. (*)	3
	Praeleptomesochra africana	3	Cletodidae	*Enhydrosoma propinquum*	1
Paramesochridae	*Paramesochra helgolandica*	3	Argestidae	*Eurycletodes (Oligocletodes)* n. spec. 1	1
	Paramesochra mielkei	3	Laophontidae	*Paralaophonte* n. spec. 1	4
	Paramesochra n. spec. 1	3		*Pilifera* n. spec. 1	4
	Apodopsyllus n. spec. 1	3	**Cyclopoida**		
	Apodopsyllus n. spec. 2	3	Oithonidae	*Oithona spec.* copepodiet	4
	Kliopsyllus holsaticus s. str.	3	Cyclopinidae	*Metacyclopina* spec.	1
	Kliopsyllus coelebs	3		spec. cfr. *Cyclopina* copepodiet	4
	Kliopsyllus constrictus s. str.	3		spec. 1	4
	Kliopsyllus n. spec. 1	3		spec. 2	4
	Kliopsyllus n. spec. 2	3			
	Kliopsyllus n. spec. 3	3		Harpacticoida: 80 species (30 new species → 37.5 %) 36 genera (1 new genus) 11 families	
	Kliopsyllus n. spec. 4	3			
	Kliopsyllus spec.	3			

(*) *cfr.* respectively *Evansula cumbraensis*, *Evansula spinosa* en *Aquilastacus serratus* in HUYS, 1995.

Addendum I.2: Species list of 7 replicated samples on the Middelkerkebank from October 1997

Calanoida		Eco-type			Eco-type
Acartiidae	*Acartia clausi*	4	Leptopontiidae	*Leptopontia dovpori*	3
Harpacticoida				*Leptopontia flandrica*	3
Canuellidae	*Canuella perplexa*	1		*Leptopontia punctata*	3
Ectinosomatidae	*Ectinosoma* n.spec. 1	2		*Leptopontia* n.spec. 1	3
	Halectinosoma canaliculatum	2		*Leptopontia* n.spec. 2	3
	Halectinosoma clavatum	2	Leptastacidae	*Leptastacus laticaudatus s. str.*	3
	Halectinosoma n. spec. 2	2		*Leptastacus laticaudatus intermedius*	3
	Pseudobradya beduina	2		*Leptastacus uncinatus*	3
	Pseudobradya cfr. minor	2		*Leptastacus cfr. uncinatus*	3
	Arenosetella n. spec. 1	3		*Paraleptastacus espinulatus*	3
	Hastigerella spec.	3		*Paraleptastacus moorei*	3
Euterpinidae	*Euterpina acutifrons*	4		*Paraleptastacus* n. spec. 1	3
Peltiidae	*Alteutha oblonga*	4		*Psamathea cfr. brittanica*	3
Diosaccidae	*Amphiascus* n.spec. 1	1		*Arenocaris reducta*	3
	Psammotopa phyllosetosa	3		*Membranastacus* n. spec. 1	3
	Psammotopa n.spec. 1	3		Leptastacidae n. genus n. spec. (*)	3
	Psammotopa n.spec. 2	3	Cletodidae	*Enhydrosoma propinquum*	1
Thalestridae	*Dactylopusia vulgaris s. str.*	4	**Cyclopoida**		
Ameiridae	*Ameira parvula*	2	Oithonidae	*Oithona robusta*	4
	Ameira (parvula) scotti	2	Cyclopinidae	Cyclopina spec. ?	4
	Psyllocamptus Psyllocamptus minutus minutus	2		*Metacyclopina brevisetosa*	3
Paramesochridae	*Paramesochra mielkei*	3		*Metacyclopina* n.spec. 1	3
	Leptopsyllus n.spec. 1	3			
	Apodopsyllus n. spec. 1	3			
	Apodopsyllus n. spec. 4	3			
	Apodopsyllus n. spec. 5	3			
	Kliopsyllus holsaticus s. str.	3			
	Kliopsyllus n. spec. 2	3			
	Kliopsyllus n. spec. 3	3			
	Kliopsyllus n. spec. 4	3			
	Scottopsyllus Scottopsyllus minor	3			
	Scottopsyllus Intermedopsyllus intermedius	3			
	Scottopsyllus Intermedopsyllus n.spec. 1	3			
Canthocamptidae	*Epactophanes richardi*	1			
	Evansula n.spec. 1	3			
	Evansula n.spec. 2	3			
	Evansula n.spec. 3 (*)	3			
	Bolbotelos longisetosus	3			
	Boreovermis bilobata	3			
	Canthocamptidae n. genus n. spec.	1			

Harpacticoida:
55 species (23 new species → 42 %)
31 genera (2 new genera)
12 families

(*) *cfr.* respectively *Evansula cumbraensis* en *Aquilastacus serratus* in HUYS, 1995.

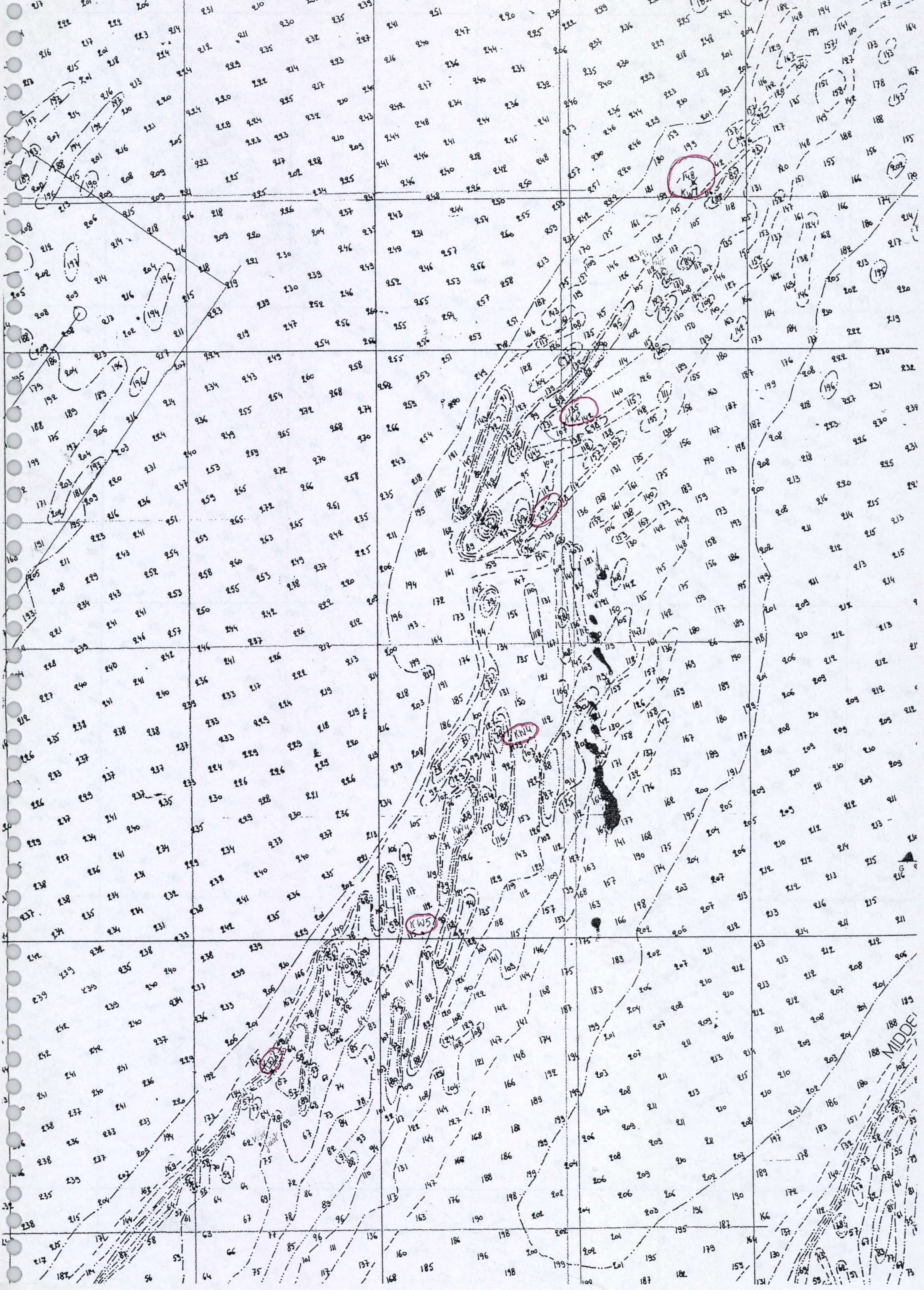
Addendum III.1: bathymetric chart of 1980 of the Kwintebank: p. 279-280

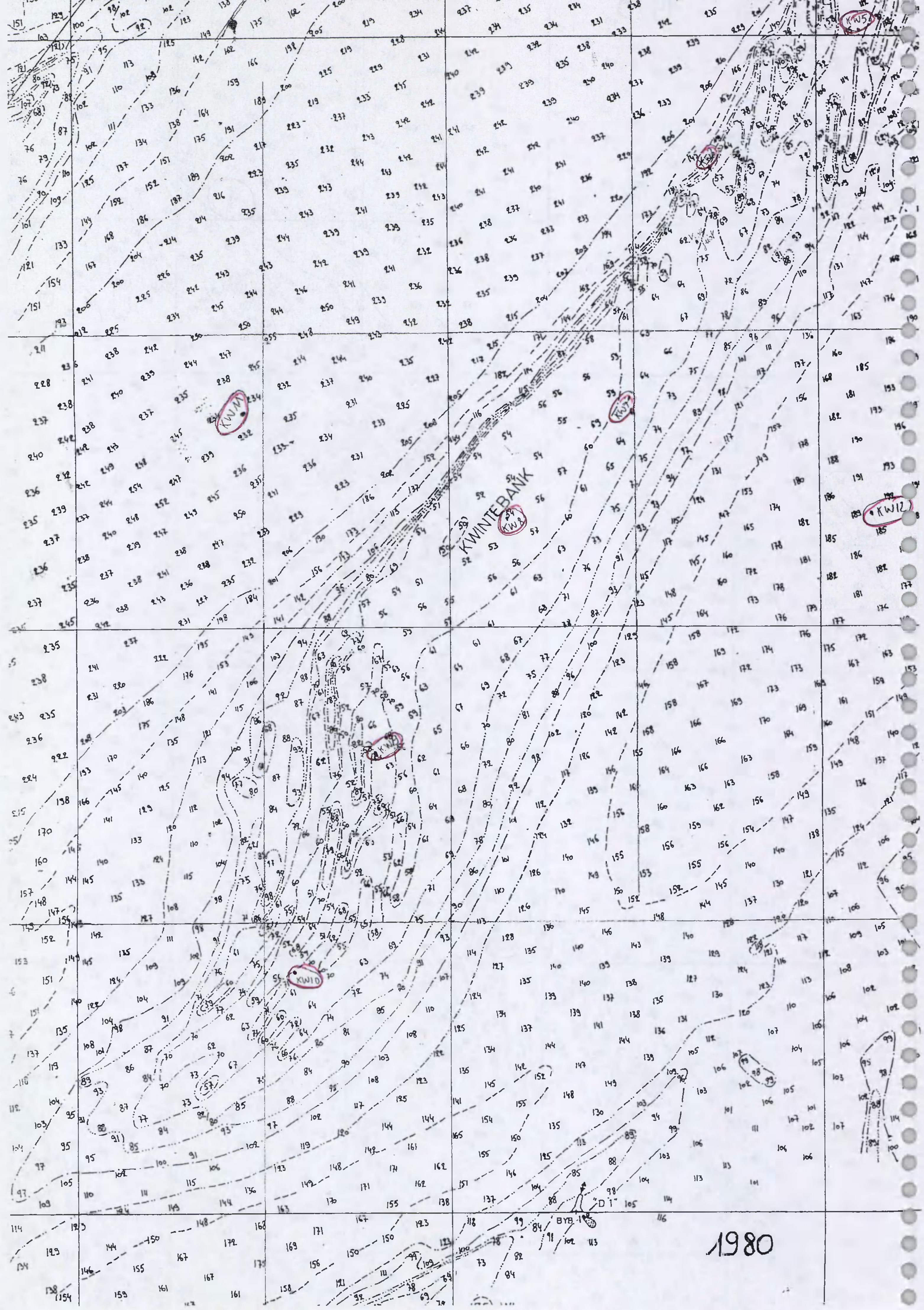
Addendum III.2: bathymetric chart of 1995 of the Kwintebank: p. 281-282

Addendum III.3: bathymetric chart of 2000 of the Kwintebank: p. 283-284

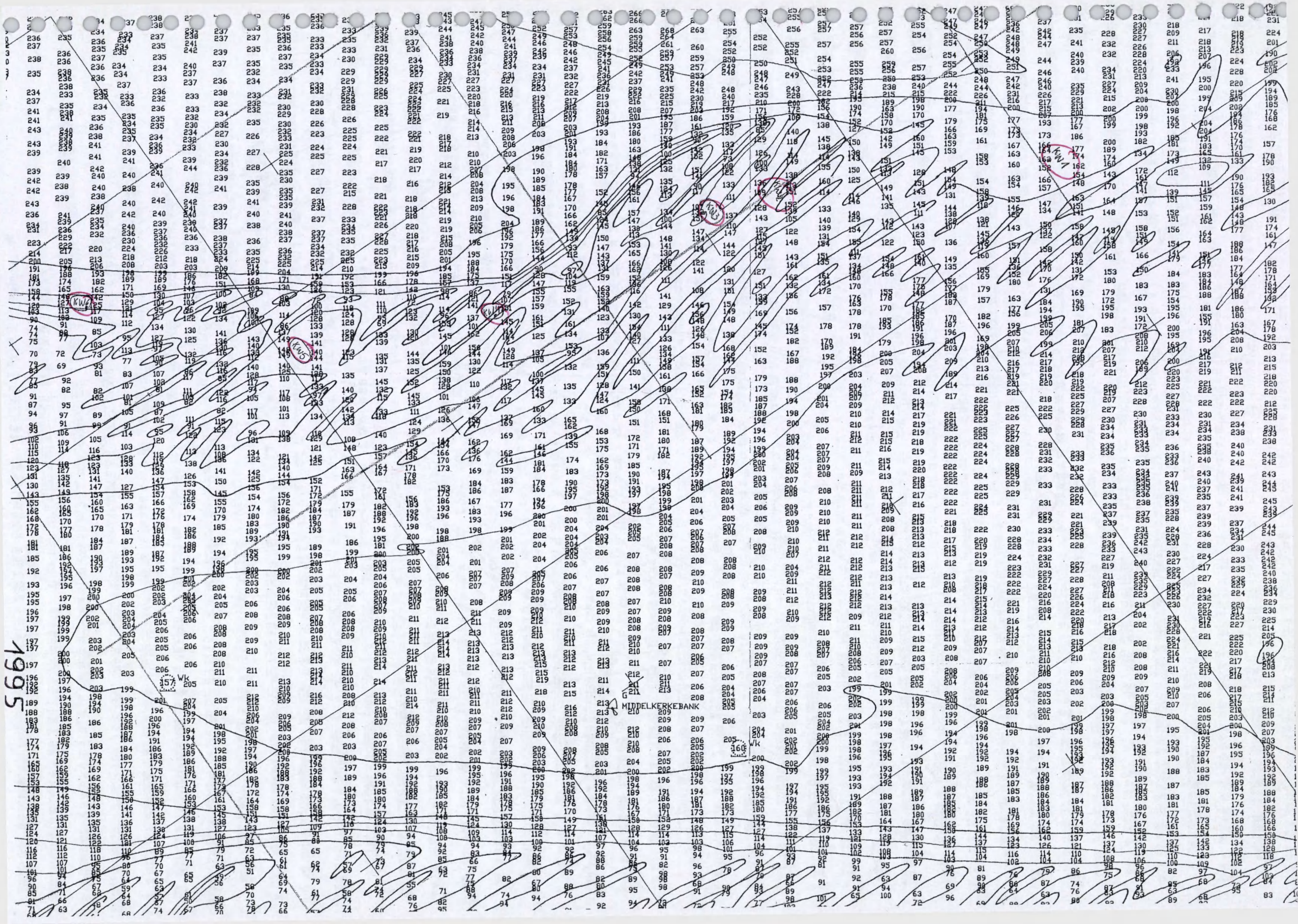
obtained from the Coastal Waterways Division, the Hydrographic Office of the Flemish Region, Belgium
Water depth measurements were standardized to Mean Low Water Spring (MLWS) using the M2 reduction model.

1980

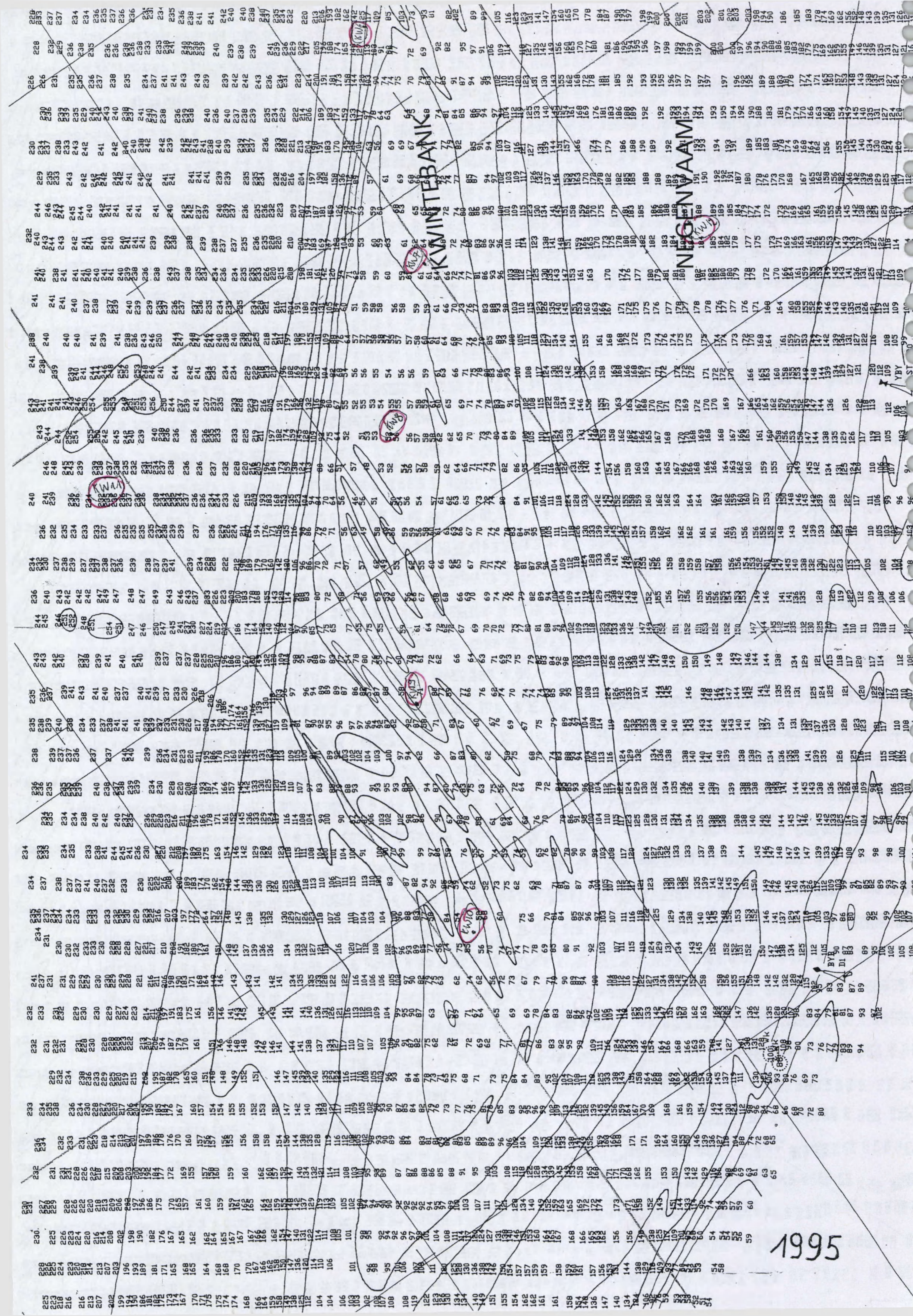


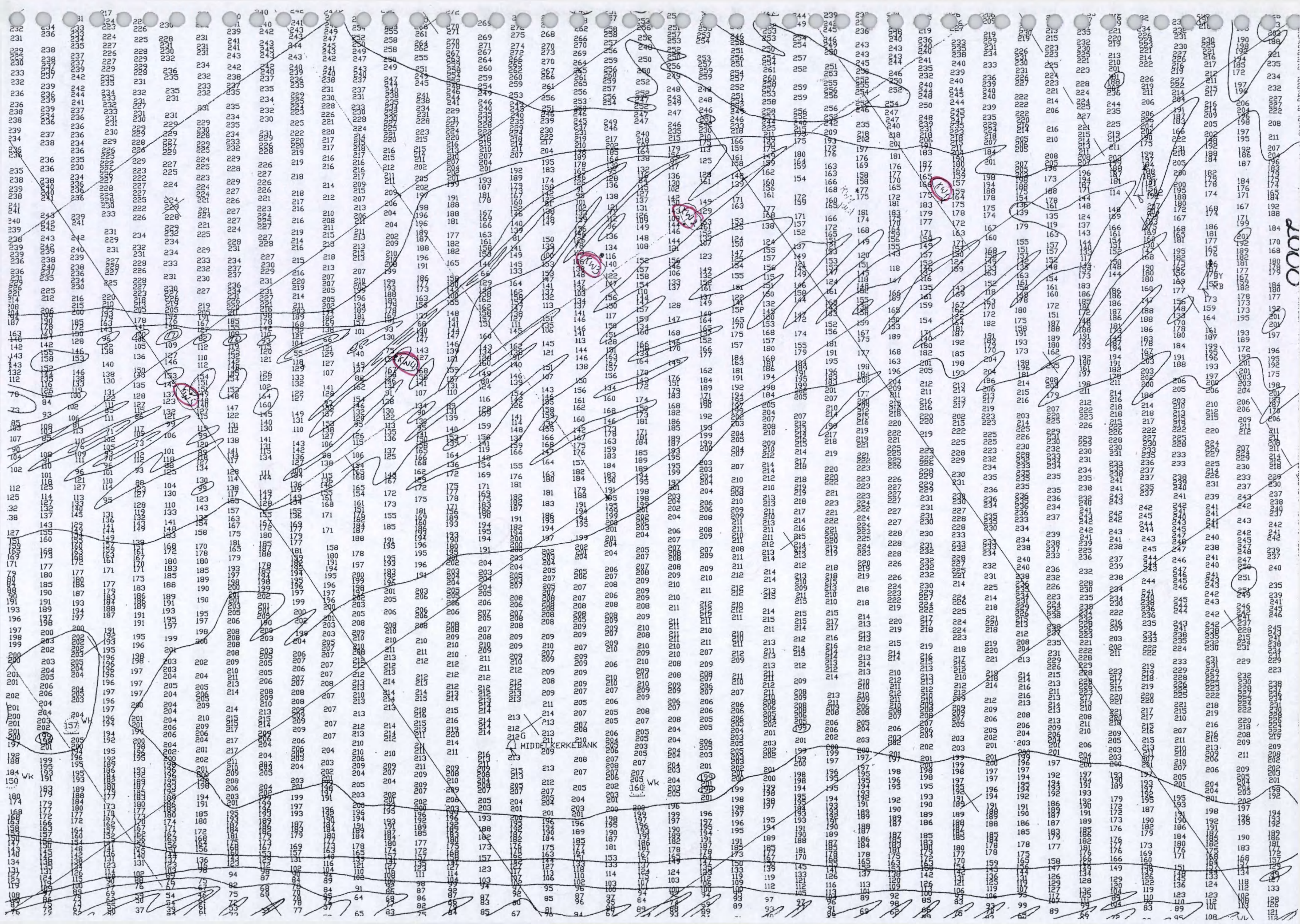


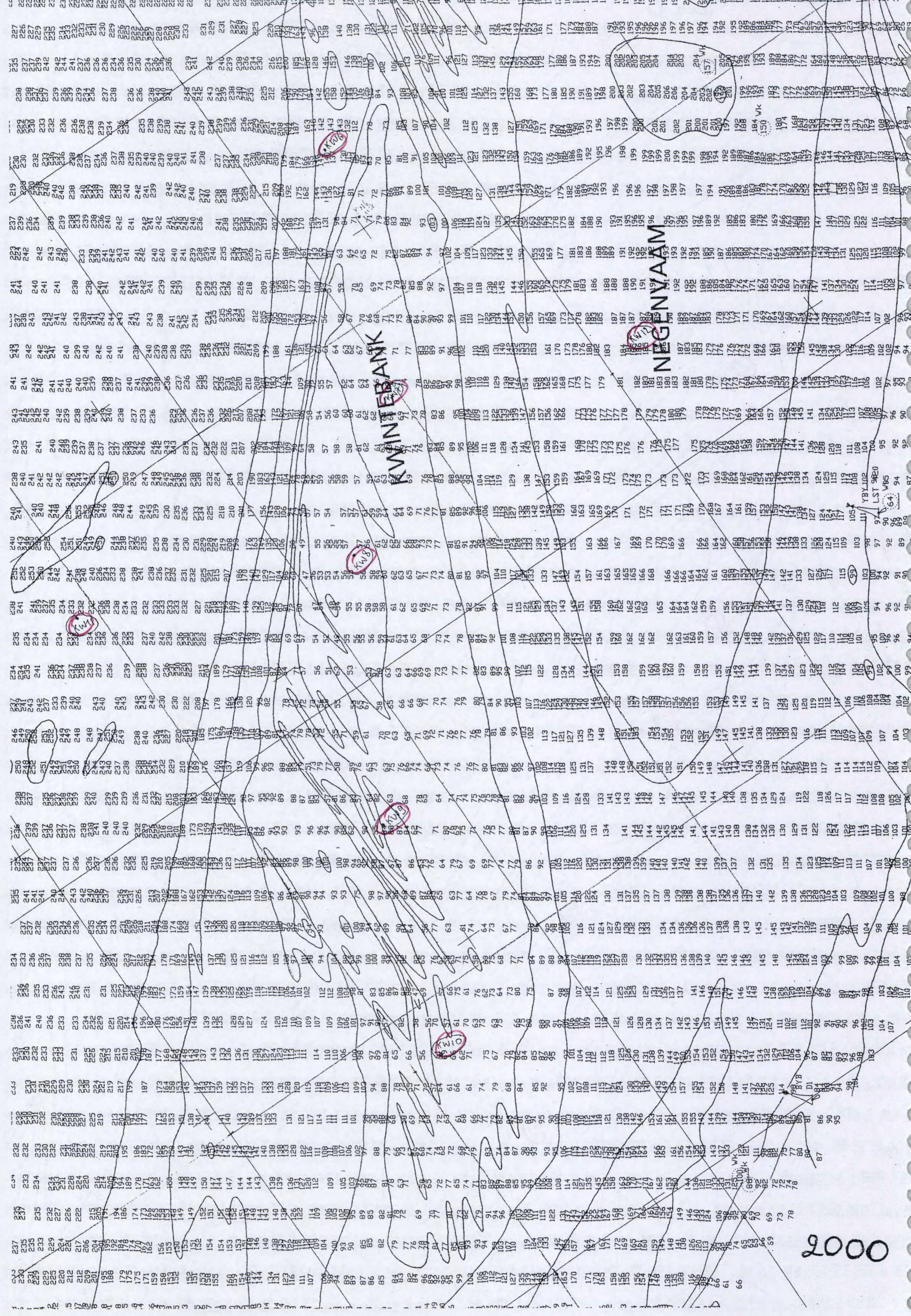
1980



1995


KWINTEBANK
NEGENVAAM
KW11
KW8
KW9
KW7
KW13
KW10
KW12
YBY
BYB
1995


2000
MIDDELKERKEBANK
212G
KWJ
Wk
160
157
BY
KB


KWINEBANK
NEGENVAAM
KW6
KW7
KW8
KW9
KW10
KW11
KW12
YBY 102
LST 9820
WBS
64
BYB
D1
WK
157
150
100

2000

Addendum III.4: Mean relative abundances of the species of the Kwintebank samples from September 1978 and January 1997 (northern part)

Year	1978					1997			
Stations	1	2	3	4	5	1	2	3	4
Harpacticoida									
Canuellidae *Canuella perplexa*	0,94	0	0	0	0	0	0	0	0
Ectinosomatidae									
Ectinosoma reductum	0	0	0	0	0	0	0	0,56	0
Halectinosoma herdmani	0	0	0	1,03	0	0	0	0	0
Halectinosoma gothiceps	0	0	0	1,03	0	0	0	0	0
Halectinosoma sarsi	0,47	0	0	0	0	0	0	0	0
Halectinosoma spec.	0	1,10	0	0	0	0	0	0	0
Halectinosoma n. spec. 2	0	0	0	0	0	0	0	0	1,80
Pseudobradya beduina	0	0	0	0	0	0	0	0	1,32
Arenosetella n.spec.1	0	0	0	0	0,22	3,87	7,17	0,78	0,48
Hastigerella cfr. leptoderma	0	0	0	0	0	0,34	0	0	0
Hastigerella psammae	0	0	0	0	0	0	0	0	0,48
Hastigerella cfr. monniotae	0	0	0	0	0	0	0	0	1,32
Hastigerella n.spec. 1	0	0	0	0	0	0	0	0,78	0
Hastigerella n. spec. 2	0	0	0	0	0	0	0,62	0,56	0
Ectinosomatidae algemeen	0	2,20	70,95	7,22	6,05	0	0	0	0
Ectinosomatidae copepodieten	1,41	1,10	0	0	0	0	0	0	0
Euterpinidae *Euterpina acutifrons*	0	0	0	0	0,22	0	0	0	0
Diosaccidae									
Amphiascus paracaudaespinosus	0	1,10	0	0	0	0	0	0	0
Amphiascus spec.	0	0	0	0	0	0,34	0	0	0,39
Amphiascoides subdebilis	0	0	0	0	0	0	0	0	0
Bulbamphiascus spec.	5,63	0	0	0	0	0	0	0	0
Robertgurneya ilievecensis	0	2,20	16,60	7,22	0,22	0	0	0	0
Rhyncholagena spec.	0	0	2,49	0	0	0	0	0	0
Psammotopa phyllosetosa	0	5,49	0	1,03	1,73	0,43	0	0,56	0
Psammotopa n. spec. (m.)	0	0	0	0	0	0,68	0	4,90	0
Psammotopa n. spec. 1 (vr.)	0	0	0	0	0	0	0	0,95	0
Psammotopa n. spec. 2 (vr.)	0	0	0	0	0	0	0	1,11	0
Protopsammotopa norvegica	0	0	0	0	0	0	0	0,56	0
Psammotopa copepodieten	0	0	0	0	0	0	0	10,70	0
genus cfr. *Balucopsylla* n. spec. 1	0	0	0	0	0	0	0	0,78	0
Diosaccidae copepodieten	0	0	0	0	0	0	0	0,39	0
Ameiridae									
Sarsameira cfr. propinqua	0	0	0	0	0	0	0	0	0,48
Sarsameira exilis	3,29	0	0	0	0	0	0	0	0
Sicameira leptoderma	0	0	0	0	9,72	0,77	0,62	0	0
Sicameira n. spec. 1	0	0	0	0	0	1,55	0	0	0,83
Leptomesochra confluens	0	0	0	0	3,24	0	0	0	0
Interleptomesochra eulitoralis	0	0	0,83	0	27,00	0	0	0	0
Ameiridae copepodiet 1	0	0	0	0	0	0,43	0	0	0
Ameiridae copepodiet 2	0	0	0	0	0	0	0,45	0	0
Ameiridae algemeen	0,47	6,59	0	9,28	0	0	0	0	0
Paramesochridae									
Paramesochra helgolandica	0	0	0	0	0	2,57	0	0	5,43
Paramesochra mielkei	0	0	0	0	0	4,21	2,71	0	0
Paramesochra n. spec. 1	0	0	0	0	0	0	0	0,78	0
Paramesochra copepodieten	0	0	0	0	0	0	0,55	0	0
Apodopsyllus n. spec. 1	46,48	0	0	3,09	0	6,73	0	0,56	0
Apodopsyllus n. spec. 2	0	0	0	0	0	0	0	0,78	0
Kliopsyllus holsaticus s. str.	0	0	0	0	0	0	0	0,56	54,77
Kliopsyllus coelebs	0	0	0	0	0	2,43	0	0	0
Kliopsyllus constricus s.str.	0	0	0	0	0	0,43	0	0	0

Year	1978					1997			
Stations	1	2	3	4	5	1	2	3	4
Paramesochridae									
Kliopsyllus n. spec. 1	0	0	0	0	0	4,75	0	0	0,48
Kliopsyllus n. spec. 2	0	0	0	0	0	2,32	5,13	0	0
Kliopsyllus n. spec. 3	0	0	0	0	0	5,07	1,61	2,06	3,60
Kliopsyllus spec.	0	0	0	0	0	0,34	0	0	0
Kliopsyllus holsaticus varians + Metacyclopina	3,76	25,27	9,13	36,08	28,94	0	0	0	0
Scottopsyllus Intermedopsyllus intermedius	0	0	0	0	0	5,81	0,45	2,50	0
Scottopsyllus Wellsopsyllus n .spec. 1	0	0	0	0	0	2,09	0,55	0	0
Scottopsyllus Scottopsyllus n. spec. 1	0	0	0	0	0	0	0	0,78	0
Diarthrodella secunda	0	0	0	0	0	0,77	0,55	0	4,99
Paramesochridae copepodieten	0	0	0	0	0	0,43	0	0	0
Tetragonicipitidae									
Phyllopodopsyllus bradyi	0,47	0	0	0	0	0	0	0	0
Pteropsyllus consimilis	0	0	0	0	0,22	0	0	0	0
Canthocamptidae									
Evansula incerta	0	0	0	0	0	0	0,62	0,78	2,28
Evansula pygmaea	0,47	0	0	0	0,43	1,30	1,45	0	0
Evansula n.spec. 1	0	0	0	0	0	14,96	9,76	0	0
Evansula n.spec. 2	0	0	0	0	0	0,34	1,00	0	0
Evansula n.spec. 3	0	0	0	0	0	3,46	7,03	0	0,48
Evansula n.spec. 4	0	0	0	0	0	0	0	0	3,86
Evansula copepodieten	0	0	0	0	0	0,68	1,16	0	0
Stenocaris pontica	22,07	0	0	0	0	0	0	0	0
Stenocaris spec.	7,51	0	0	0	0	0	0	0	0
Leptopontiidae									
Leptopontia curvicauda	0	3,30	0	1,03	0,22	0	0	0,56	0
Leptopontia dovpori	0	0	0	0	0	0	0	0,78	0
Leptopontia n.spec. 1	0	0	0	0	0	1,64	0	0	0
Arenopontia spec.	0	0	0	0	2,16	0	0	0	0
Leptopontiidae genus	0	0	0	0	0	0	0	0	0,39
Leptastacidae									
Leptastacus macronyx	0	0	0	0	0,86	0	0	0	0
Leptastacus laticaudatus s. str.	6,10	42,86	0	5,15	10,58	17,83	11,16	3,95	0,83
Leptastacus laticaudatus intermedius.	0	0	0	0	0,65	0,77	0,45	14,70	12,66
Leptastacus uncinatus	0	0	0	0	0	0	1,61	0	0
Leptastacus cfr. coulli	0	0	0	0	0	0	0,45	0	0
Leptastacus copepodieten	0	0	0	0	0	0,43	2,16	0	0
Paraleptastacus spinicauda	0	0	0	0	0	0	0	18,69	2,15
Paraleptastacus espinulatus	0	0	0	1,03	0,22	0,87	4,68	0	0
Paraleptastacus moorei	0	0	0	0	0	9,47	34,24	0	0
Paraleptastacus n.spec. 1	0	0	0	0	0	0,34	2,06	8,24	0
Paraleptastacus n. spec. 2	0	0	0	0	0	0,43	0	0	0
Arenocaris bifida	0	0	0	0	0,22	0	0,55	0	0
Arenocaris reducta	0	0	0	0	0	0	0,62	0	0
Membranastacus n. spec. 1	0	0	0	0	0	0,34	0	0	0
Leptastacidae n. genus n. spec. (*)	0	0	0	0	0	0	0	1,94	0
Leptastacidae copepodieten	0	0	0	0	0	0,34	0,62	0	0,48
Cylindropsyllidae spec.	0	0	0	0	0,65	0	0	0	0
Cletodidae copepodieten	0,94	1,10	0	0	0	0	0	0	0
Rhizothricidae *Rhizothrix minuta*	0	0	0	1,03	0	0	0	0	0
Laophontidae									
Paralaophonte n. spec. 1	0	0	0	0	0	0	0	0	0,48
algemeen	0	7,69	0	13,40	6,48	0	0	0	0
Cyclopoida									
Metacyclopina spec.	0	0	0	0	0	0,433	0	18,60	0
cyclopoide	0	0	0	3,09	0	0	0	1,17	0
copepodieten	0	0	0	1,03	0	0	0	0	0

Addendum III.5: Mean relative abundances of the species of the Kwintebank samples from September 1978 and January 1997 (southern part)

	1978					1997					
	6	7	8	9	10	5	7	8	9	10	6
Harpacticoida											
Ectinosomatidae											
Halectinosoma canaliculatum	0	0	0	0	0	0	0,30	0	0	0	0
Halectinosoma n. spec. 2	0	0	0	0	0	0,29	0,55	0,54	1,19	0	0
Pseudobradya spec.	0	0	0	0	0	0	0	0	0	0	4,76
Arenosetella n.spec.1	0	0	0	0	0	8,71	0,50	0	3,52	2,80	0
Hastigerella leptoderma	0	0	0	0	0	0,29	0	0	0	0	0
Ectinosomatidae algemeen	20,79	4,17	0	5,65	1,27	0	0	0	0	0	0
Euterpinidae											
Euterpina acutifrons	1,98	0	0	0,30	0	0	0	0	0	0	0
Thompsonulidae											
Thompsonula hyaenae	0	0	0	0,60	0	0	1,60	0,54	0,39	0,68	0
Diosaccidae											
Amphiascoides subdebilis	0	0	0	0	0	0	0,48	0	0	0	0
Psammotopa phyllosetosa	0	0	0	1,49	0	0	0	0	1,37	0,68	0
Ameiridae											
Nitocra hibernica s. str.	0	0	0	0	0	0	0	0	0	0,68	0
Sicameira leptoderma	0	0	0	0	0	0,29	0	0	0	0	0
Interleptomesochra eulitoralis	0	0	0	0	0	0	0	1,08	0	0	12,30
Ameiridae algemeen	0	0	0	0,30	14,65	0	0	0	0	0	0
Paramesochridae											
Paramesochra mielkei	0	0	0	0	0	0	0	0	1,19	0	4,76
Apodopsyllus africanus list.	0,99	0	0	0	0	0	0	0	0	0,51	15,87
Kliopsyllus holsaticus s. str.	0	0	0	0	0	0	0	2,48	0	2,04	0
Kliopsyllus constricus s.str.	2,97	2,08	5,00	23,81	26,75	2,28	16,34	6,11	3,92	53,86	10,00
Kliopsyllus n. spec. 2	0	0	0	0	0	2,03	1,20	1,06	2,76	0	0
Kliopsyllus n. spec. 3	0	0	0	0	0	1,38	0	0,35	8,43	1,95	8,89
Kliopsyllus n. spec. 4	0	0	0	0	0	0	17,69	6,73	25,75	16,63	0
Kliopsyllus copepodieten	0	0	0	0	0	0	0	0,71	0,39	0	0
Scottopsyllus Intermedopsyllus intermedius	0	0	0	0	0	0,40	0	0	0	0	0
Paramesochridae copepodieten	0	0	0	0	0	0,29	0,30	0	0	0	3,33
Canthocamptidae											
Evansula pygmaea	2,97	2,08	0	3,87	5,73	0	0	0	0	0	0
Evansula n.spec. 1	0	0	0	0	0	0,40	0	0	1,76	0,93	0
Evansula n.spec. 2	0	0	0	0	0	0,43	0	0	0,39	0,51	0
Evansula n.spec. 3	0	0	0	0	0	0,80	0	0	1,95	0	0
Evansula copepodieten	0	0	0	0	0	0,83	0	0	0	0	0
Leptopontiidae											
Arenopontia spec.	0	0	0	0	0	1,67	0	0	0	0,93	0
Leptastacidae											
Leptastacus laticaudatus s. str.	42,57	41,67	10,00	63,69	38,85	14,15	6,77	6,62	36,76	13,39	15,08
Paraleptastacus espinulatus	26,73	41,67	70,00	0	0	63,92	49,52	54,92	4,33	1,36	25,00
Paraleptastacus moorei	0	0	0	0	0	0,43	0	0	0	0	0
Arenocaris bifida	0,99	8,33	15,00	0,30	8,92	0	1,58	7,69	2,75	2,53	0
Arenocaris reducta	0	0	0	0	0	0,69	2,55	6,84	0,79	0,51	0
Arenocaris copepodieten	0	0	0	0	0	0	0	0,54	0	0	0
Membranastacus n. spec. 1	0	0	0	0	0	0,40	0,61	3,81	1,18	0	0
Cletodidae											
Enhydrosoma propinquum	0	0	0	0	0	0	0	0	0,79	0	0
copepodieten algemeen	0	0	0	0	3,82	0	0	0	0	0	0
Cyclopoida											
Metacyclopina spec.	0	0	0	0	0	0,29	0	0	0	0	0
copepodieten	0	0	0	0	0	0	0	0	0,39	0	0