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DEPARTMENT OF BIOLOGY
MARINE BIOLOGY SECTION

Academic Year 1998-1999

THE USE OF MACROBENTHIC COMMUNITIES IN THE EVALUATION OF ENVIRONMENTAL CHANGE

BY

JOHAN A. CRAEYMEERSCH

PROMOTOR: PROF. DR. C.H.R. HEIP
CO-PROMOTOR: DR. P.M.J. HERMAN

THESIS SUBMITTED IN PARTIAL FULFILMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
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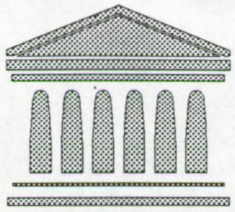

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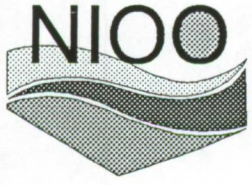

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CONTENT

CHAPTER 1

General introduction and outline

About two thirds of the world's human population live in the coastal areas of the continents. This ratio is increasing due to population growth, in combination with migration from inland areas. By the year 2025, about three-quarters of humanity, more than 6.3 billion people, will have made the coastal margins of the continents their home (Lindén and Granlund 1998). Humans use the coastal zone for transport, recreation, waste disposal, fish harvesting, mariculture, shore protection, coastal infrastructure, offshore industries, military activities, mineral mining, and sand and gravel extraction. Coastal zones receive and concentrate pollutants and suffer other negative impacts of activities taking place in the shorelands and hinterlands, such as changing nutrient and sediment loads. This may lead to physical changes of the system, to chemical and biological changes at different levels, from biochemical processes and genetic changes to species extinction and biodiversity loss (Cadée et al. 1994). Really heavy damage to coastal resources started in the 1960s and accelerated through the 1970s. In the 1980s and 1990s worldwide awareness of the need for conservation was achieved. The increased public awareness of the vulnerability of the marine environment has led to government legislation requiring operators to monitor the effects of their activities in the marine environment (Kingston and Riddle 1989, Clark 1998).

In 1984 the first International Conference on the Protection of the North Sea highlighted the need for an overall assessment of the extent to which the North Sea was affected by human activities, and was followed by several Quality Status Reports (NSTF 1993). Under the authority of the Oslo and Paris Commissions (OSPARCOM) a Joint Monitoring Program (JMP) was developed to review the condition of the sea and the effectiveness of the measures undertaken to improve this condition (van Zeijl 1995). For the Netherlands, the program includes biological effect monitoring, the assessment of the spatial distribution of pollution and temporal trends in organic contaminants in water, sediments, suspended matter and biota (van Zeijl 1998). In 1989

the Dutch Directorate-General of Public Works and Water Management (Rijkswaterstaat) initiated a biological monitoring program for the salt waters of the Netherlands. The primary goal of the program is to provide biological information in the framework of Monitoring of the National Water Systems, especially in relation to long-term developments (Heinis et al. 1995). At smaller scales, the planning and design of many activities nowadays include an Environmental Impact Assessment, and local monitoring programs are set up to assess impacts that have been predicted during the planning and assessment phase.

The general objectives of most monitoring programs are: to detect any disturbance of the system greater than that caused by natural environmental variability; to establish the magnitude, the spatial and temporal distribution of the disturbance; to identify the cause(s) of such disturbance, to ensure that human health is not threatened; to ensure that unacceptable harm is not done to the marine ecosystem or marine resources; and to supply managers with information that allows them to make informed decisions concerning continued, reduced, or expanded use of the sea (Hartley 1982, Bilyard 1987, Rees et al. 1990). Careful thought must be given therefore to sampling design prior to the initiation of the survey to allow distinctions to be drawn between natural and anthropogenically induced variability. Indeed, most populations are variable between sampling times and the temporal pattern is often not in phase from one place to another. Therefore, usually complex sampling designs are required (Underwood 1993).
In the case of a well-defined impact, most of the studies use so-called BACI designs (Before/After, Control/Impact). These studies involve data collection before and after a putative impact at replicated 'control' and 'impact' locations. In this way BACI designs take into account background variability which is common to both control and impacted sites (Stewart-Oaten and Murdoch 1986, Underwood 1992, 1993). Other monitoring programs, for instance the Dutch biological monitoring program mentioned above, do not focus on *a priori* known impacts. Rather, the aim is to test whether any differences between years occurred or changes in the fluctuations took place (Colijn and Akkerman 1990).

Environmental impact assessment and monitoring can be regarded as attempts to test the null hypothesis that a defined human action has no impact upon the environment (Fairweather 1991).

The null hypothesis of such tests of significance states that an observed difference just reflects chance variation. The statistical power of a test is defined as 1-ß, where ß is the probability of making a type II error (i.e. the conclusion that there is no difference, when in fact there is). Power thus reflects the probability of correctly rejecting the null hypothesis. Power depends on several factors, including the precision of the estimates – power decreases with increasing within-year variance -, the magnitude of the actual (rate of) change, and the level (α) of a type I error (i.e. the conclusion that there is a difference, when in fact there is none and an alternative hypothesis is true) (Sokal and Rohlf 1981, Peterman 1989, Freedman et al. 1991).

The point of the monitoring 'exercise' is, thus, to detect an impact if it exists and the optimal ways of detecting human impacts, including the norms of statistical hypothesis testing, must be found. Discussion of statistical power, i.e. the probability that a given change results in a statistically significant test, and how it might impinge upon environmental sampling is therefore relevant to the context and aims of monitoring if we are to improve the design and efficiency of monitoring programs.

Another important consideration is the type of environmental and biological data to be collected (Rees et al. 1990). The analysis of benthic infauna is a key element of many marine and estuarine monitoring programs for several reasons (Elmgren and Cederwall 1978, Pearson and Rosenberg 1978, Hartley 1982, Kingston and Riddle 1989, Rees et al. 1990, Holtmann et al. 1996). In contrast to other organisms (e.g. plankton, fishes, marine birds), benthic organisms are sedentary and must adapt to environmental stress or perish. The benthos is immediately dependent on the quality of the overlying water, but, being stationary, it integrates the effects of water quality over a considerable period of time – years to decades for the long-lived macrofauna. Benthic organisms are effective indicators of impacts at higher levels of biological organization (e.g. community level) because of their importance to overall ecosystem structure and function. Numerous species of fish, birds and mammals depend directly or indirectly on benthic infauna. Because they are important prey items, they have the potential to mediate the transfer of toxic substances to higher trophic levels. They are also important mediators of nutrient recycling from sediments to the water, influencing primary production. Benthic animals are very sensitive to

habitat disturbance, including organic enrichment of the sediments and contamination of the sediments by toxic substances. Because species vary in their sensitivity to pollutants, benthic communities can undergo dramatic changes in species composition and abundance in response to pollutant stresses (Pearson and Rosenberg 1978, Rygg 1985a, b, Dauvin and Ibanez 1986, Swartz et al. 1986, Bilyard 1987, Olsgard and Gray 1995).

The sedentary habits of benthic infauna, which permit statistical determination of spatial and temporal variability, facilitate a power analysis (Bilyard 1987). Spatial and temporal variability may be determined for any biological community, but other biological communities do not confer the same degree of site-specificity. The benthic infauna community is the only biological community that provides managers with quantitative data of biological variability at specific sites and over specific areas.

However, monitoring the benthos is very costly involving ship-time and laboratory analysis that is very intensive. And the time-consuming nature of the laboratory analysis leads to a lag phase between sampling and production of results. Moreover, many monitoring programs are constrained by e.g. the available resources and the minimum legislative requirement (Kingston and Riddle 1989, Colijn and Akkerman 1990, Rees et al. 1990). Therefore, there is the potential for a) a considerable waste of time and money if methods are not the most appropriate for the objectives of monitoring (Bilyard 1987, Kingston and Riddle 1989) and b) a decrease in the capacity to make sensible long-term decisions about matters having direct environmental effects (Underwood 1993).

Outline of this thesis

During the last 10 years, I have been involved in many inventorying and monitoring studies in the Netherlands. In this dissertation part of the macrobenthos data recorded during these surveys are re-analysed in the light of the items mentioned above.

Chapter 2 first gives an overview of the background and the data recorded during the different surveys. The amount of data resulting from these surveys required the use of a relational database. The need for such databases, allowing proper data management and fast access to the data, is more and more recognised. Therefore, I added a paragraph about the structure of the

database and some problems encountered during the design and maintenance. Finally, chapter 2 gives an overview of the multivariate techniques used in the following chapters.

Multivariate methods of data analysis prove to be very sensitive for detecting differences in community structure between samples in space, or changes over time (see e.g. examples given by Warwick & Clarke, 1991). Ordination techniques were primarily exploratory analyses, but with multivariate direct gradient analysis it became possible to rigorously test statistical hypotheses. There are, however, no good methods yet to estimate the power of ordination analysis. In **chapter 3** a first attempt is made to compare the power of ordination techniques with that of the univariate analysis of variance.

A major problem in monitoring studies is the appropriate spatial scale over which to assess the populations. The choice depends on the kind and scale of changes one wants to assess, and must be determined and justified in terms of the processes operating and of the dispersal and dispersion of the populations being sampled (Underwood 1993). It is further important to recognise the communities and the structuring forces that lead to their development at that chosen spatial scale. Changes in the spatial distribution of these communities may imply changes in the structuring forces. A proper sampling design based on this distribution will result in a reduction of the within-year variability within each community and, thus, in an increase of the possibility to detect changes within each area. Finally, when the structuring forces are known, their effects can be removed in a partial analysis focusing on the effect of the variables of interest.

In this dissertation we describe the changes in and relationships between species composition and some abiotic characteristics at two scales: that of several tens of kilometers (the Westerschelde estuary; **chapter 4**) and that of several hundreds of kilometers (the North Sea; **chapter 5**).

In the last four decades several studies already described the distribution of the macrobenthic fauna of the Westerschelde (Wolff 1973, Vermeulen and Govaere 1983, Meire et al. 1991, Ysebaert and Meire 1991, Ysebaert et al. 1993, 1998) but a complete review of the major gradients has been hampered by the biased selection of stations and sampling schemes. The monitoring surveys as realised since 1990 within the framework of the Dutch national monitoring program, covering more than 1500 samples of both the intertidal and the subtidal areas, enabled a re-examination of the relationship between species composition and the major

abiotic gradients. Chapter 4 also aims at defining biotopes. The mapping of marine biotopes is fundamental to management and nature conservation (Hiscock 1995, Sotheran et al. 1997).
In 1986 participants of the Benthos Ecology Working Group of ICES made a synoptic mapping of the macrobenthic infauna of the southern and northern North Sea. Together with a mapping of the infauna of the northern North Sea by Eleftheriou and Basford (1989) this provided a database for the description of the benthic macrofauna of the whole North Sea. Künitzer et al (1992) describe the macrofauna communities, Heip et al (1992) the trends in total biomass, total density and species diversity of the macrofauna, and Huys et al (1992) the copepod communities and trends in density and biomass. Chapter 5 summarises the results on the macrofauna.
Chapters 6, 7 and 8 focus on three impact studies. **Chapter 6** deals with the assessment of the impact of a land reclamation project in the northern part of the Voordelta, i.e. the coastal area in the southwest of the Netherlands formed by the ebb-tidal deltas of the rivers Rhine, Meuse and Scheldt. The results are discussed in the light of some problems encountered in monitoring programs (e.g. reference sites, spatial scale, and statistical procedures).
Demersal fishing has significant direct effects on the fauna. As the gears scrape the surface of the seabed, trawling causes mortality in target and non-target species. Direct mortality due to trawling occurs both among the caught and subsequently discarded animals as in the trawl path, among animals that are damaged or killed by the passing gear. Thus evidence is available of the direct effects of beam trawling (Collie et al. 1997, Jennings and Kaiser 1998, Lindeboom and de Groot 1998). The long-term impact on a particular species will depend on the direct mortality at each fishing event, the distribution of the fishing effort, the distribution of that species and its life history characteristics such as longevity and fecundity. The longer term effects of demersal fisheries are still a point of discussion. Recently, information of the spatial distribution of fishing effort became available at the scale of 1 by 1 nautical mile (Rijnsdorp et al. 1998). Before, information on fishing activities was limited to a scale of 30 by 30 mile. The authors reported that in the heavily fished southern North Sea, 47-71% of the seabed was swept 1-5 times a year, 9-44% less than once a year and 0-4% between 10-50 times a year. During the last decade, the macrofauna has been studied in great detail as well (Holtmann et al. 1996). In **chapter 7** spatial differences in the species composition of two subareas of the North Sea are related to differences in fishing effort.

Chapter 8 reports changes in the species composition at a station in the eastern part of the Oosterschelde in the period 1983-1986, i.e. during the construction of the storm surge barrier in the mouth of the estuary and two additional dams more inland. The chapter re-introduces the analytical method proposed by Feoli and Orlóci (1979) and Orlóci (1981): the Analysis of Concentration. The method offers a way to interpret the influences of environmental, community-wide changes on the density changes of single species. In the present dissertation it is used as an extension of Correspondence Analysis, but it could also be used with other ordination techniques.

Finally, in **chapter 9**, the results of the chapters are summarised and some general conclusions are drawn.

References

Bilyard, G. R. 1987. The value of benthic infauna in marine pollution monitoring studies. Marine Pollution Bulletin **18**:581-585.

Cadée, N., J. Dronkers, C. Heip, J.-C. Martin, and C. Nolan. 1994. ELOISE (European Land-Ocean Interaction Studies) Science Plan. Ecosystems Research Report Series of the Environmental Research Programme of the European Commission, Directorate-General for Science, Research and Development. Brussels, Luxembourg. 52 pp.

Clark, J. R. 1998. Coastal seas: the conservation challenge. Blackwell Science Ltd., Oxford. 76pp.

Colijn, F., and I. Akkerman. 1990. Biologisch monitoringsprogramma zoute wateren, stand van zaken 1990. Rijkswaterstaat, Dienst Getijdewateren. Nota GWAO-90.018. 30pp.

Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Marine Ecology Progress Series **155**:159-172.

Dauvin, J.-C., and F. Ibanez. 1986. Variations à long-terme (1977-1985) du peuplement des sables fins de la Pierre Noire (Baie de Morlaix, Manche occidentale): analyse statistique de l'évolution structurale. Hydrobiologia **142**:171-186.

Eleftheriou, A., and D. J. Basford. 1989. The macrobenthic infauna of the offshore northern North Sea. Journal of the Marine Biology Association of the United Kingdom **69**:123-143.

Elmgren, R., and H. Cederwall. 1978. Monitoring the Baltic ecosystem by means of benthic macrofauna sampling. Presented at the first Nordik Oikos conference, October 2-4, Uppsala.

Fairweather, P. G. 1991. Statistical power and design requirements for environmental monitoring. Australian Journal of Marine and Freshwater Research **42**:555-567.

Feoli, E., and L. Orlóci. 1979. Analysis of concentration and detection of underlying factors in structured tables. Vegetatio **40**:49-54.

Freedman, D., R. Pisani, R. Purves, and A. Adhikari. 1991. Statistics, 2nd Edition. W.W. Norton & Company, New York, London. 514pp.

Hartley, J. P. 1982. Methods for monitoring offshore macrobenthos. Marine Ecology Progress Series **13**:150-154.

Heinis, F., I. Akkerman, K. Essink, F. Colijn, and M. J. Latuhihin. 1995. Biologische monitoring zoute rijkswateren 1990-1993. Rijkswaterstaat, Rijksinstituut voor Kust en Zee. Rapport RIKZ-95.059. 80pp.

Heip, C., D. Basford, J. A. Craeymeersch, J.-M. Dewarumez, J. Dörjes, P. de Wilde, G. Duineveld, A. Eleftheriou, P. M. J. Herman, U. Niermann, P. Kingston, A. Künitzer, E. Rachor, H. Rumohr, K. Soetaert, and T. Soltwedel. 1992. Trends in biomass, density and diversity of North Sea macrofauna. ICES Journal of Marine Science **49**:13-22.

Hiscock, K., editor. 1995. Classification of benthic marine biotopes of the north-east Atlantic. Proceeding of a BioMar-Life workshop held in Cambridge, 16-18 November 1994. Joint Nature Conservation Committee, Peterborough. 105pp.

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijkswijk. 244pp.

Huys, R., P. M. J. Herman, C. H. R. Heip, and K. Soetaert. 1992. The meiobenthos of the North Sea: density, biomass trends and distribution of copepod communities. ICES Journal of Marine Science **49**:23-44.

Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on the marine ecosystems. Advances in Marine Biology **34**:201-352.

Kingston, P. F., and M. J. Riddle. 1989. Cost effectiveness of benthic faunal monitoring. Marine Pollution Bulletin **20**:490-496.

Künitzer, A., D. Basford, J. A. Craeymeersch, J. M. Dewarumez, J. Dörjes, G. C. A. Duineveld, A. Eleftheriou, C. Heip, P. Herman, P. Kingston, U. Niermann, E. Rachor, H. Rumohr, and P. A. J. de Wilde. 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES Journal of Marine Science **49**:127-143.

Lindeboom, H. J., and S. J. de Groot, editors. 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. NIOZ-RAPPORT 1998-1 / RIVO-DLO REPORT C003/98. 404pp.

Lindén, O., and A. Granlund. 1998. Building capacity for coastal management. Ambio **27**:589.

Meire, P. M., J. J. Seys, T. J. Ysebaert, and J. Coosen. 1991. A comparison of the macrobenthic distribution and community structure between two estuaries in SW Nehterlands. Pages 221-230 *in* M. Elliott and J.-P. Ducrotoy, editors. Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen & Olsen, Fredensborg.

NSTF. 1993. North Sea Quality Status Report 1993. Oslo and Paris Commissions. London. 132 pp.

Olsgard, F., and J. S. Gray. 1995. A comprehensive analysis of the effects of offshore oil and gas exploration and production on the benthic communities of the Norwegian continental shelf. Marine Ecology Progress Series **122**:277-306.

Orlóci, L. 1981. Probing time series vegetation data for evidence of succession. Vegetatio **46**:31-35.

Pearson, T. H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: an Annual Review **16**:229-311.

Peterman, R. M. 1989. Statistical power analysis can improve fisheries research and management. Canadian Journal of Fisheries and Aquatic Sciences **47**:2-15.

Rees, H. L., D. C. Moore, T. H. Pearson, M. Elliott, M. Service, J. Pomfret, and D. Johnson. 1990. Procedures for the monitoring of marine benthic communities at UK sewage sludge disposal sites. Department of Agriculture and Fisheries for Scotland. Scottish Fisheries Information Pamphlet Number **18**. 78 pp.

Rijnsdorp, A. D., A. M. Buys, F. Storbeck, and E. G. Visser. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES Journal of Marine Science **55**:403-419.

Rygg, B. 1985a. Distribution of species along pollution-induced diversity gradients in benthic communities in Norwegian fjords. Marine Ecology Progress Series **16**:469-474.

—. 1985b. Effects of sediment copper on benthic fauna. Marine Ecology Progress Series **25**:83-89.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research, 2nd Edition. Freeman and Co, San Francisco. 859pp.

Sotheran, I. S., R. L. Foster-Smith, and J. Davies. 1997. Mapping of benthic habitats using image processing techniques within a raster-based Geographic Information System. Estuarine, Coastal and Shelf Science **44 (Supplement A)**:25-31.

Stewart-Oaten, A., and W. W. Murdoch. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology **67**:929-940.

Swartz, R. C., F. A. Cole, D. W. Schultz, and W. A. DeBen. 1986. Ecological changes in the Southern California Bight near a large sewage outfall: benthic conditions in 1980 and 1983. Marine Ecology Progress Series **31**:1-13.

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology **161**:145-178.

—. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Australian Journal of Ecology **18**:99-116.

van Zeijl, W. J. M. 1995. National Comment of the Joint Monitoring Programme of The Netherlands 1993. Ministry of Transport, Public works and Water management / National Institute for Coastal and Marine management (RIKZ). Report RIKZ/95.009. 45pp.

—. 1998. National Evaluation Report of the Joint Assessment and Monitoring Programme of the Netherlands 1996. Ministry of Transport, Public works and Water management / National Institute for Coastal and Marine management (RIKZ). Report RIKZ - 98.009. 44 pp.

Vermeulen, Y. M., and J. C. R. Govaere. 1983. Distribution of benthic macrofauna in the Western Scheldt estuary (the Netherlands). Cahier de Biologie Marine **14**:297-308.

Warwick, R. M., and K. R. Clarke. 1991. A comparison of some methods for analysing changes in benthic community structure. Journal of the Marine Biology Association of the United Kingdom **71**:225-244.

Wolff, W. J. 1973. Zoölogische Verhandelingen, No. **126**: The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Brill, Leiden. 242pp.

Ysebaert, T., and P. Meire. 1991. Het macrozoöbenthos van de Westerschelde en de Beneden Zeeschelde. Rijksuniversiteit Gent, Laboratorium voor Ecologie der Dieren / Instituut voor Natuurbehoud. Rapport W.W.E. 12 / Rapport I.N. A92.085. 184pp.

Ysebaert, T., P. Meire, D. Maes, and J. Buijs. 1993. The benthic macrofauna along the estuarine gradient of the Schelde estuary. Neth. J. Aquat. Ecol **27**:327-341.

Ysebaert, T. G., P. Meire, J. Coosen, and K. Essink. 1998. Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. Aquatic Ecology **32**:53-71.

CHAPTER 2

Material and Methods: general aspects

2.1 Surveys

For this study we had access to data of several surveys, conducted at different spatial and temporal scales. All surveys have been carried out in the last fifteen years in the North Sea and adjacent estuaries in the Southwest of the Netherlands.

2.1.1.The Delta area

The so-called Delta area is the region in the Southwest of the Netherlands created by the rivers Rhine, Meuse and Scheldt (figure 2.1). Over the last era man reclaimed large areas and the outline is, nowadays, fixed by rigid seawalls and dikes. After the large storm flood in 1953 the Dutch government decided to close all estuaries except for the Westerschelde and the Nieuwe Waterweg, the shipping ways to respectively the harbours of Antwerpen and Rotterdam (Knoester 1984). The original plan for the Oosterschelde estuary was changed and a storm surge barrier was built instead of a dam. For an overview of the different phases of the 'Delta Project' we refer to Bijlsma and Kuipers (1989), Meire (1993), and Nienhuis and Smaal (1994).

The 'Delta Works' caused large changes in the aquatic environment of the enclosed estuaries and the Oosterschelde. The Haringvliet, the Hollandsch Diep, the Biesbosch, the Amer, the Nieuwe Merwede, the Markiezaat, the Volkerakmeer and the Zoommeer have been freshened. The Grevelingenmeer is managed as a stagnant saltwater basin, and the Veerse Meer is a brackish lake. The Oosterschelde changed into a tidal bay. The tidal range is reduced, the salinity increased, and the water is clearer now than before the building of the storm surge barrier.

The impact of these large engineering works on the ecosystems has been the subject of several studies, mostly including the effects on the macrozoobenthos of soft sediments. Smit (1995)

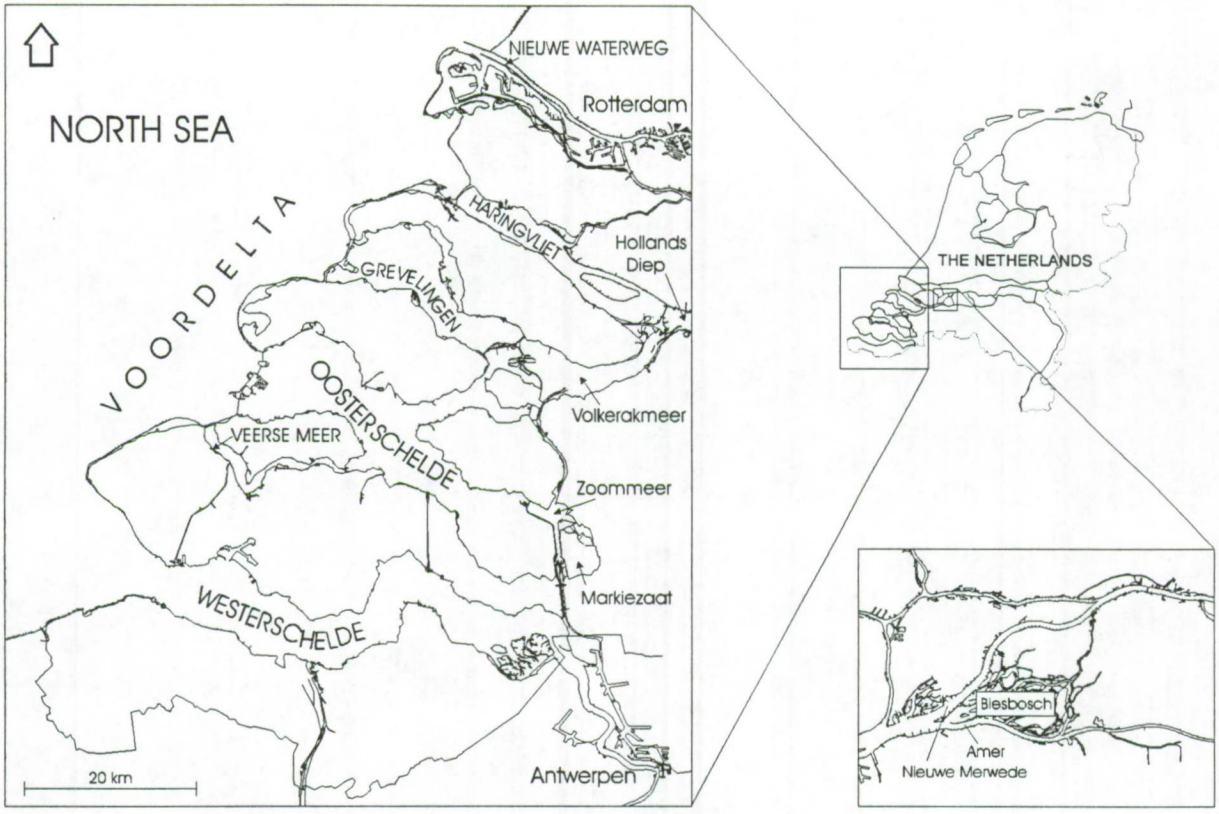


Figure 2.1. Map of the Delta area of the rivers Rhine, Meuse and Scheldt.

focused on the macrozoobenthos of the enclosed, freshened areas. Lambeck (1981, 1982, 1984) described changes in the benthic fauna of the Grevelingen, van Mansfeld (1978) and Seys and Meire (1988) the effects in the Veerse Meer.

Changes in the physical, chemical and ecological characteristics of the Oosterschelde are reported by Nienhuis and Smaal (1994). In this special volume of Hydrobiologia, four papers dealt with the macrobenthos of soft sediments (Coosen et al. 1994, Hummel et al. 1994, Meire et al. 1994, Seys et al. 1994). One of the studies aimed at a description of the spatial distribution before and after the construction of the barrier (project INTERECOS). The two other data sets came from two monitoring programs on the major tidal flats in the Oosterschelde: the Roggenplaat, the Verdronken Land van Zuid-Beveland (COST database) and the Slikken van Viane (VIANE database). In 1990 most of these stations became part of a national monitoring program. The primary goals of this program (EXP*BMN or BIOMON), co-ordinated by the

Dutch National Institute for Coastal and Marine Management (RIKZ), are (Colijn and Akkerman 1990, Colijn et al. 1992, Essink 1992, 1994, Heinis et al. 1995):

- to describe the biological condition of the different water systems;
- to describe long-term developments or trends in density and biomass;
- to signal shifts from the desired situation described in the Third Water Management Policy Document (RWS 1989);
- to advise on water management and policy making;
- to evaluate the effects of measures taken by the government;
- to discriminate between man induced changes and natural variability.

The program now covers the study of the benthic fauna in the Dutch sector of the North Sea, the Wadden Sea and, in the Delta area, the Westerschelde, the Oosterschelde, the Grevelingenmeer and the Veerse Meer.

In the Westerschelde, where the shipping channel will be dredged to a deeper level to allow the access of larger ships to Antwerp, an additional monitoring program (MOVE) has been set up in 1994 to study the influence of the expected changing sedimentation patterns on the benthic communities.

More information on the BIOMON and MOVE surveys in the Delta area is given in chapter 2.1.1.1.

The 'Delta Works' also induced major changes in the hydraulic conditions and the geomorphology of the shallow ebb-tidal areas of the rivers Rhine, Meuse and Scheldt, i.e. the area seawards of the dams known as the Voordelta. The tidal currents in the deltas of the Haringvliet and Grevelingen e.g. were reduced by 45 to 80 %. The development of this area between Zeebrugge and Europoort has been the subject of an integrated, multidisciplinary research project (VOORDELTA), aimed at predicting at an intermediate time scale the change in geomorphology and possible shift in ecological functioning of this area (Mulder 1990). Several papers and reports described the development and predicted changes (see e.g. Cattrijsse et al. 1993, Craeymeersch et al. 1990, Hallie et al. 1990, Hamerlynck and Mees 1991, Hamerlynck et al. 1990, 1992, Kohsiek 1988, Kohsiek and Mulder 1989, Mulder 1990, Mees

and Hamerlynck 1992, Postma et al. 1991a, b, c, d, Steijn et al. 1989, Vanreusel 1990, 1991), and the results are being used as a basic information in the development of an integral policy plan (van Alphen and Molendijk 1993).

The northern part of the Voordelta is situated near the industrial region of Rotterdam. In the early eighties it was decided to build a disposal site for contaminated dredged material from the lower reaches of the river Rhine (GLBB: 'Grootschalige Lokatie voor Baggerspecie uit het Benedenrivierengebied'). The depot construction was completed in 1986, another land reclamation scheme in this area realised. This project was the first in the Netherlands for which a so-called Environmental Impact Assessment (EIA) was made. The likely effects of the proposed development on the wider environment were considered as part of the planning and design of the engineering works. The results of this EIA were reported in an Environmental Impact Statement. Besides a full description of the proposed construction works, the EIS included a description of the existing environment (the macrobenthos was surveyed in 1983), a description of the options considered and a statement of the predicted environmental impacts. It was further decided that an environmental monitoring plan had to be carried out for a period of 30 years. The monitoring of the macrobenthos started in 1988. The predicted changes are being evaluated every five years. An overview of the first evaluation periods is given by Anonymous (1992, 1997). Chapter 2.1.1.2. gives more information on the monitoring surveys.

In this dissertation data were used from the COST program (chapter 7), the BIOMON program (chapters 3, 4 and 7), the MOVE program (chapter 4) and the GLBB program (chapter 6).

2.1.1.1. Monitoring the macrobenthos of the Delta Area

Sampling program

Within the framework of the national monitoring program (BIOMON), the benthic communities of the inter- and subtidal bottoms of the Westerschelde and the Oosterschelde, and the subtidal bottom of the Veerse Meer and the Grevelingenmeer are being surveyed. All water systems are being sampled twice a year, in spring and autumn.

At the start of the project in spring 1990, only the intertidal was surveyed (figure 2.2.a). The selected stations in the Oosterschelde had previously been part of monitoring studies (COST, VIANE; see above). At the COST-stations 15 cores were taken, sieved in the field over a 1mm mesh sieve, and the residues separately fixed with buffered formaline. At the VIANE-station 30 cores of 4.5 cm diameter and 15 cores of 15 cm diameter were taken to a depth of 30 cm. The smaller cores were fixed in the field with buffered formaline, brought to the laboratory and washed through a 1 mm mesh sieve. The larger cores were washed in the field through a 3 mm sieve, and the separate residues fixed with formaline. Before, the COST stations were sampled in a different way, and, in the first two years, 3-4 times a year. At each date samples consisted of three compound replicates of 5 cores of 83 cm^2, which were washed through a 1mm sieve in the field. To assess the density of the larger animals the top layer of a two squares meter sampling area was collected and washed through a 3 mm sieve. Subsequently the area was dug out to a depth of 50 cm and the organisms were picked out from the sediment by hand. The material was stored in 10% formaldehyde. Chapter 7 deals with changes at one of these COST stations (station 33; figure 2.2.a).

The stations in the Westerschelde estuary had been surveyed in 1987, part of them also in 1988 within the framework of a study on the bioaccumulation of chemical substances in benthic species (project SAWES) (Anonymous 1987, Meire and Develter 1988, Stronkhorst 1988, Vanhooren 1989, Meire et al. 1991). At each of the selected stations, 10 cores of 4.35 cm diameter were taken to a depth of 10 cm, and 5 cores of 15 cm diameter to a depth of 30 cm. The treatment of these cores was as described for the VIANE-station, except that the residues of all smaller respectively larger cores were put together.

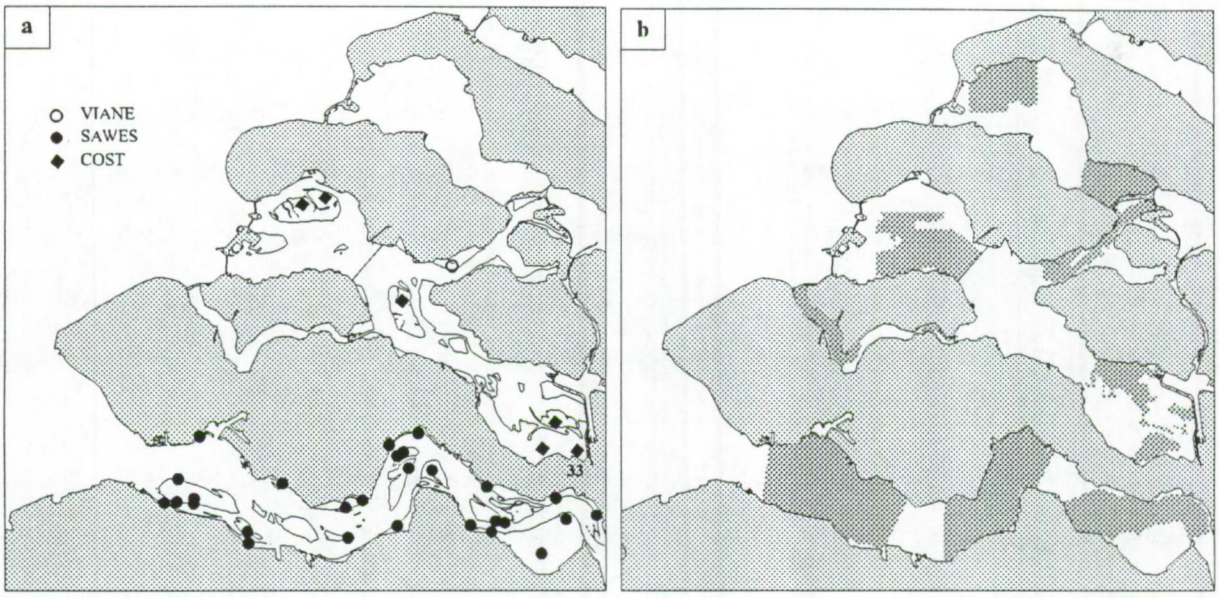


Figure 2.2. a. fixed stations sampled in the Oosterschelde and the Westerschelde during the first two years of the Dutch national monitoring program (BIOMON), indicating the original programs (COST, VIANE, SAWES); COST station 33 was no longer sampled after 1992, but part of the data are used in chapter 7;. b. subareas of the Westerschelde, the Oosterschelde, the Veerse Meer and the Grevelingen presently covered by the national monitoring program.

In autumn 1990, the study was extended to the subtidal areas. Within each water system, two or three subareas were chosen, divided into three depth strata. Within each stratum of each subarea, 10 randomly selected stations were sampled, except for the Grevelingenmeer. Here, sampling of the most shallow stratum was done along transects (with 4 to 7 stations) that had been monitored since 1982 (see e.g.Lambeck et al. 1989), and in the two other strata 15 stations were sampled. At most stations a compound sample of 3 cores of 8 cm diameter taken from a single box-core was obtained. The sediment was sieved aboard on a 1 mm mesh size and the residues were stored in buffered formaline. In the shallowest strata of the Grevelingenmeer and the Veerse Meer, however, sampling was done with either a flushing sampler (200 cm^2; van Arkel and Mulder 1975) or a corer of 180 cm^2. In the two other strata of the Veerse Meer, only one core was taken from the box-core, but the whole box-core was checked for larger specimen of *Mya arenaria* (length above 2 cm). Each survey new stations were chosen, except for the intertidal (fixed stations) and the most shallow parts of the Grevelingenmeer (transects).

In 1992 the sampling design was changed. In the intertidal no longer fixed stations were sampled, but stations randomly chosen within intertidal areas adjacent to the subtidal subareas already surveyed. As in the subtidal, 10 stations within each subarea were randomly selected at each survey. At each station, a compound sample of 3 cores of 8 cm diameter was taken, and sieved in the field. In the Veerse Meer, the two most westerly subareas were joined, reducing the total number of stations and samples taken. In the Grevelingenmeer the number of stations was reduced to 10 for each stratum. And in the Oosterschelde, one of the subareas was restricted to the northern branch of the estuary. Figure 2.2.b. gives an overview of all areas studied.
Following discussions on the power of the running monitoring programs (Duin 1994, van der Meer 1997), it was decided to stop, from spring 1995 onwards, choosing new stations at each survey but to revisit the stations randomly selected in autumn 1994. In the Westerschelde, however, we continued the old design. There, the power to detect changes in the density of selected species proved not to be higher when revisiting stations randomly chosen the first year than when randomly selecting stations each year, indicating that the patterns of change between stations in the Westerschelde were not synchronised (see chapter 3). The chosen design also has the advantage that the measurements made each survey are independent.

The program to evaluate the deepening of the Westerschelde (MOVE) was set up as an addition of the BIOMON program. Samples are taken in a) a fourth subarea and b) at 29 fixed stations where the sedimentation and erosion is being followed into detail (figure 2.3). The subarea is sampled as in the BIOMON program, except that 5 instead of 10 randomly chosen stations are sampled within each of the four strata. At the intertidal stations 15 cores of 4.5 cm diameter and 5 cores of 15 cm diameter were taken to a depth of 30 cm. The smaller cores were fixed in the field with buffered formaline, brought to the laboratory and washed through a 1 mm mesh sieve. The larger cores were washed in the field through a 3 mm sieve, and the separate residues fixed with formaline.

Sampling was done aboard of several vessels of the Ministry of Transport and Public Works, and with the RV Luctor of the Netherlands Institute of Ecology.

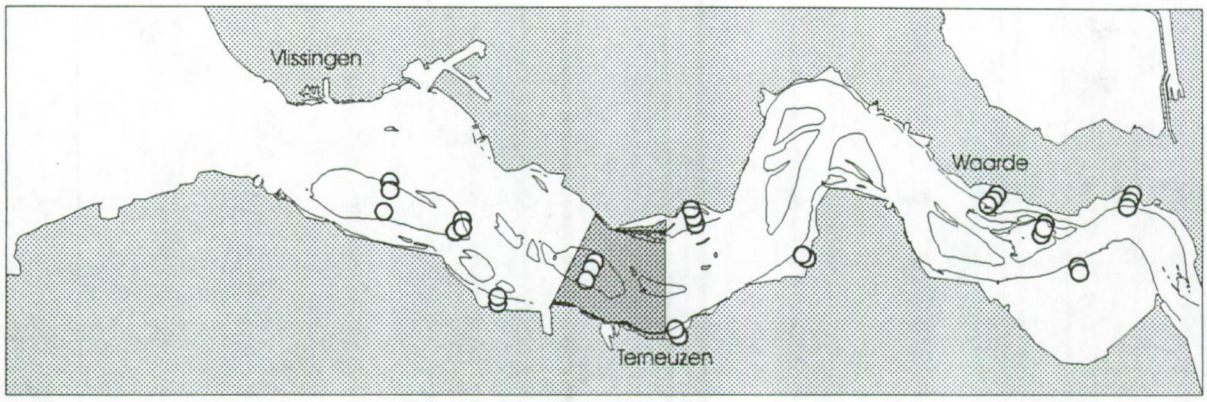


Figure 2.3. Project MOVE (Evaluation of the deepening of the Westerschelde): fixed sampling stations and subarea covered additionally to the national monitoring program (see fig. 2.2.b).

Laboratory methods

In the laboratory the organisms were sorted, identified to species level if possible and counted. Sizes were recorded for all molluscs and some polychaetes. Biomass of all species (except some small and rare ones) were determined as ash-free dry weight (AFDW) in one of the following ways:

- directly, as the difference between the dried (80°C for minimum 48 hours) and ashed (560-580°C for 2 hours) weights of the animals;
- indirectly, by means of length-weight relationships ($W=aL^b$, W=AFDW, L=length);
- indirectly by converting the (blotted) wet weight (determined with a Sartorius balance to the nearest 0.1 mg) into ash free dry weight;
- indirectly, by assigning an individual AFDW (exceptionaly; in a few cases where only a single, small specimen was found).

At the start of the program, all biomass measurements were made directly. At present, most measurements are based on length-weight relationships (molluscs, AFDW including the organic content of the shells) and factors converting wet weight into ash free dry weight. Separate conversion factors are used for spring and autumn. Each survey, new length-weight relationships are established. The AFDW/WW ratios were determined during the analyses of the 1993 surveys. First, ratios were determined at the lowest level of identification (mostly at the species level). Then, if variation proved to be small within a higher taxonomic level, a mean ratio was

determined for that taxon (mostly at the family level, but in some cases at the generic or order level). The ratios are given in the appendix.

In cases two types of corers were used to sample the intertidal (the 1990 and 1991 BIOMON surveys, fixed MOVE stations), most of the data on density and biomass are based on the smaller cores. The data on the polychaetes *Arenicola marina* and *Scolelepis foliosa*, however, are based on the larger cores. The data on the Nereidae, the Nephtyidae and bivalves are based on both. The density and biomass of small specimens (molluscs: length < 4 mm; polychaetes: mean individual AFDW < 0.003 g) are based on the smaller cores, the density and biomass of larger specimen on the larger cores. For the two deepest strata of the Veerse Meer, the density and biomass values of small *Mya arenaria* (length < 2 cm) are based on the core taken within the box-core for small individuals, the values of the larger individuals on the whole box-core.

2.1.1.2. Environmental Impact Assessment in the Haringvliet delta (GLBB)

Sampling program

Since 1988 the ebb-tidal delta of the Haringvliet (figure 2.4) is monitored to evaluate whether or not the predicted impact on the environment actually occurs. At present, data from five surveys are available (1988, 1989, 1990, 1992, 1994).

The program has the following sampling design (figure 2.5). Two subareas were selected: the intertidal flat near the city Voorne and the Brielse Meer, and a mainly subtidal area including the Hinderplaat, a sand bar south of the depot. Both subareas were divided in boxes and within each box, 3 to 5 stations were selected at random. At each station one sample was taken. The subtidal stations were sampled with a van Veen grab (0.192 m^2), one grab at each station. The sediment was washed aboard on a 1 mm mesh sieve, and the residue fixed with buffered formaline. In the intertidal area of the Westplaat, stations were sampled with a corer of 6 cm diameter. One core was taken at each station. The whole sample was fixed in buffered formaline and sorted in the laboratory. The intertidal part of the Hinderplaat was not surveyed in 1988.

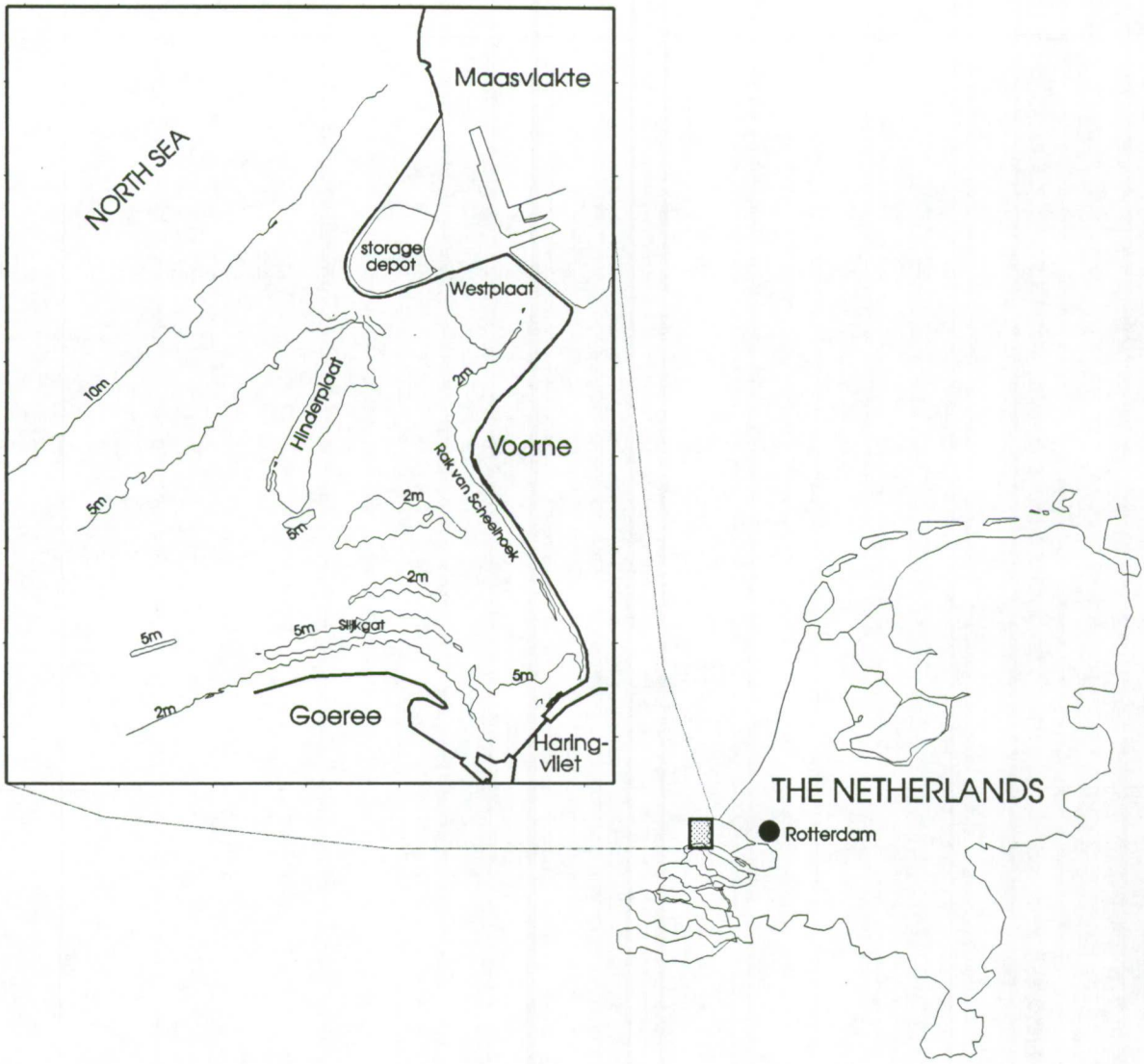


Figure 2.4. Map of the ebb-tidal delta of the Haringvliet.

Based on results of the 1988 survey, the subtidal area was enlarged to the south from 1989 onwards, and new stations were selected. On the Westplaat, a compound sample of three cores was taken instead of a sample of one core. In principle, the stations chosen in 1989 were revisited in the following surveys. In 1992, however, the stations of the 1988 survey were revisited. After the first evaluation (Anonymous 1992), it was decided to reduce the number of stations to be sampled west of the Hinderplaat to 1 instead of 3 per box. Different van Veen grabs were used, the surface area varying between 0.091 and 0.2 m^2.

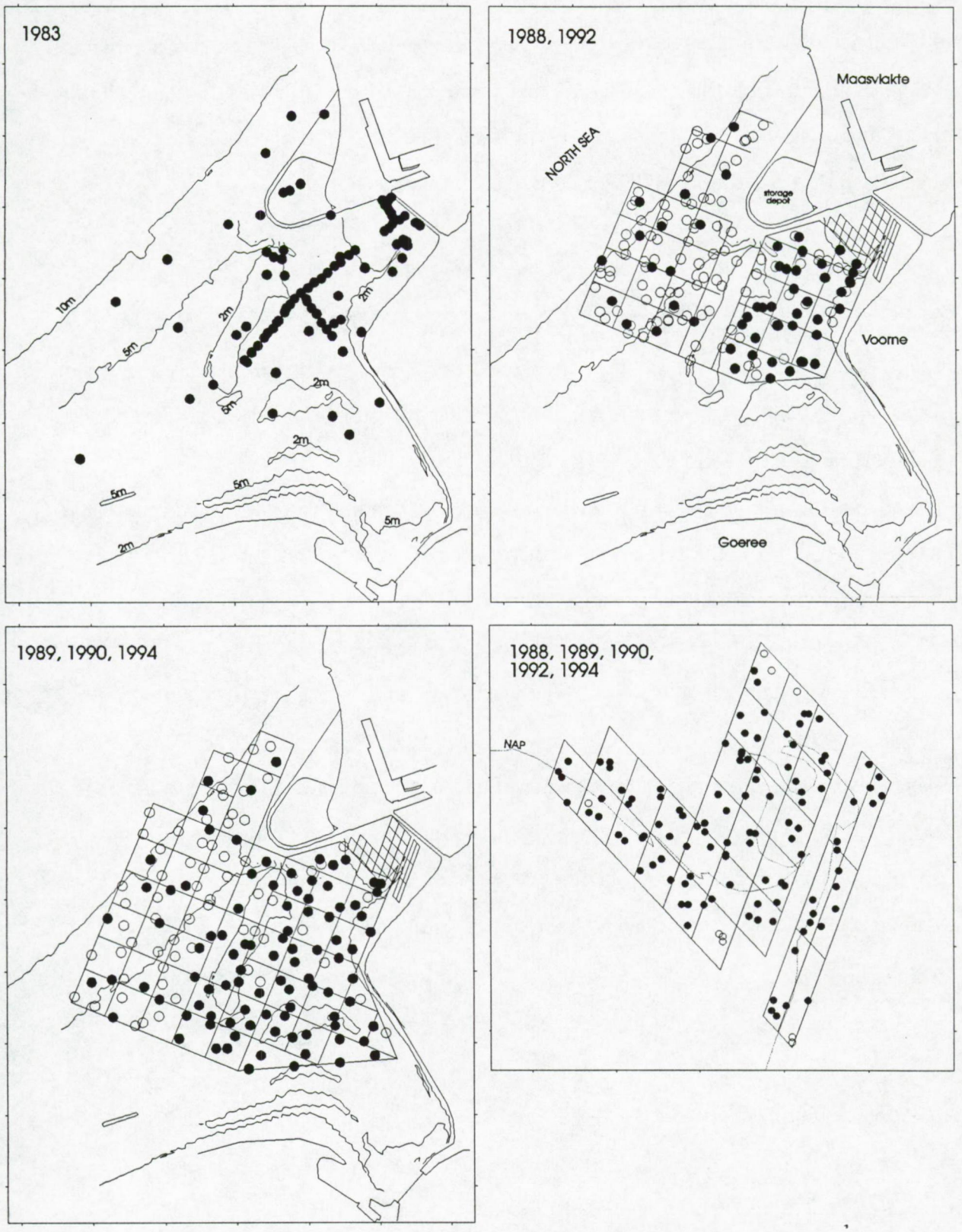


Figure 2.5. Sampling localities in the ebb-tidal delta of the Haringvliet (solid circles refer to stations sampled at all the years mentioned in the upper left corner of the figure; other stations only sampled at one or more of these years).

In 1989 and 1990, sampling on the Hinderplaat was as on the Westplaat: 3 cores (6cm diameter) at each station. In 1992, no samples were taken, and in 1994 sampling was done at high tide at only some of the selected stations with a van Veen grab.
The Ministry of Transport and Public Works took all samples.

Laboratory methods

In the laboratory the organisms were sorted, identified to species level if possible and counted. Biomass of all species (except some small and rare ones) were determined as ash-free dry weight (AFDW) in one of the following ways:
- directly, as the difference between the dried (70°C for minimum 48 hours) and ashed (520°C for 4 hours) weights of the animals (1988 survey);
- indirectly, by assigning an individual AFDW (1989 and 1990 surveys, except for *Nereis diversicolor*) (each survey mean individual weights were re-determined);
- indirectly, by means of length-weight relationships ($W=aL^b$, W=AFDW, L=length) (molluscs, 1992 and 1994 surveys);
- indirectly by converting the (blotted) wet weight (determined with a Sartorius balance to the nearest 0.1 mg) into ash free dry weight (1989 and 1990 surveys: *Nereis diversicolor*, ADW/WW conversion factors respectively 0.086 and 0.085; 1992 and 1994 surveys: all species except molluscs, conversion factors as determined during the monitoring studies mentioned in chapter 2.1.1.1.).

2.1.2. the North Sea

2.1.2.1. The North Sea Benthos Survey

In spring 1986 participants of the ICES Benthos Ecology Working Group carried out a North Sea-wide synoptic survey of macro- and meiobenthos. The North Sea Benthos Survey (NSBS)

was executed in April-May 1986 when 197 stations were sampled, covering the ICES grid from 51°N to 58°N and from 2°30' W to 8°15'E. The boxes in the ICES grid were defined by the intersection of whole degrees longitude and half degrees latitude. The stations were on the four corners of the boxes and in the centre. At each of these stations, five box cores when possible, but sometimes van Veen grabs, were taken. The complete list of replicates, dates, samples and stations has been reported to ICES (BEWG 1986). Most of the stations were analysed for macrobenthos biomass, density and species composition, for meiofauna density and copepod species composition, for sediment grain size analysis, protein content, plant pigment analysis and organic matter.

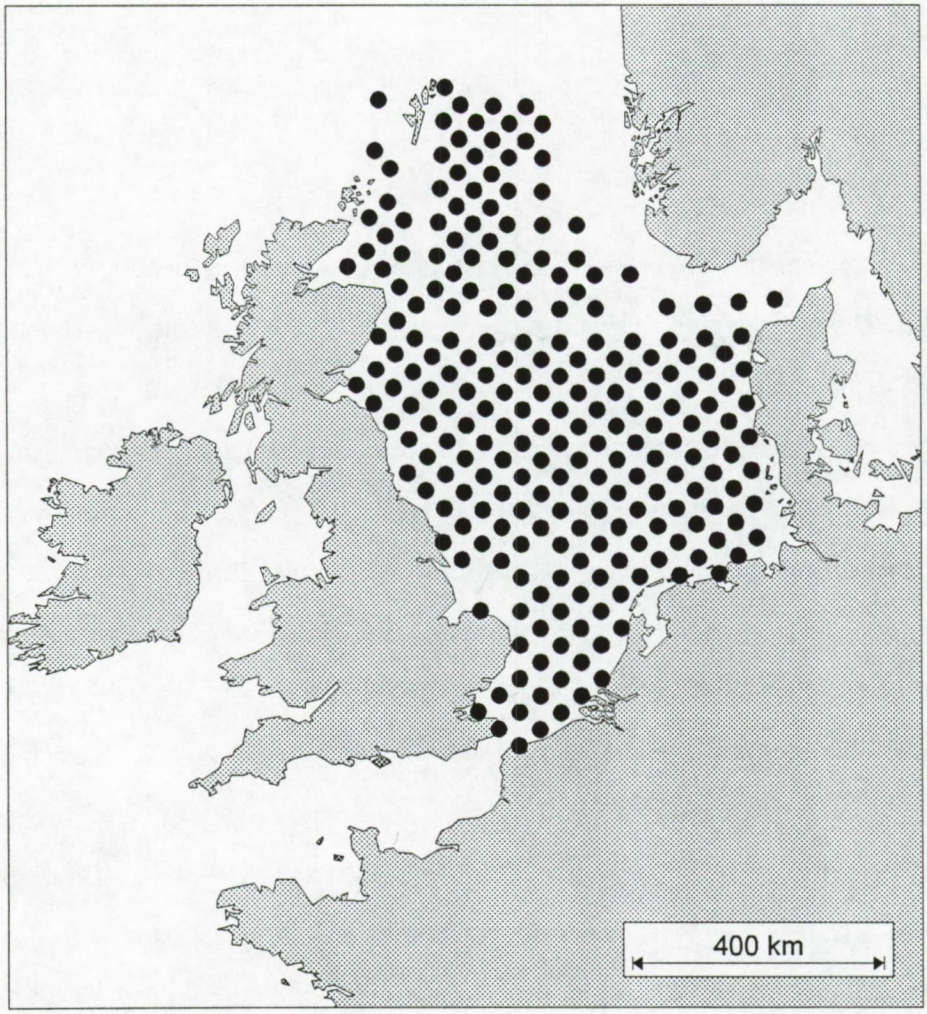


Figure 2.6. Stations sampled by participants of the North Sea Benthos Survey (NSBS) in 1986, and stations lying on an extrapolated ICES grid sampled between 1980 and 1985 by MAFF.

Data from the northern North Sea have been gathered during eight Ministry of Agriculture, Fisheries and Food cruises from 1980 to 1985 (MAFF Survey) always in spring and early summer (Basford and Eleftheriou 1988, Basford et al. 1989, Eleftheriou and Basford 1989). The area covered extends between 56°15'N and 60°45'N, and 3°30'W and 7°30' E. A total of 119 stations were sampled for macrofauna (Basford et al. 1990).

In chapter 5 data on the macrobenthos of those stations lying on an extrapolated ICES grid are analysed. The chapter summarises previous reports and papers (BEWG 1986, Duineveld et al. 1990, 1991, Heip et al. 1992, Künitzer et al. 1992, Heip and Craeymeersch 1995). The position of all stations used in these analyses is shown in figure 2.6.

2.3.1.2. Dutch Continental Shelf

In the period 1988-1993 the meio- and macrobenthic communities of the larger part of the Dutch continental shelf were sampled in much detail (project MILZON-Benthos). The stations were chosen according to a stratified sampling design. The area was divided into a number of compartments and in each compartment 3 to 7 randomly chosen stations were sampled with a Reineck box-corer. At each station the content of one box-corer was washed over a 1mm-sieve. The macrobenthic residue was stored in a buffered formaldehyde solution.

In the laboratory, the residue was stained with rose bengal and the animals were sorted. Density and biomass were, if possible, recorded on the species level. The ash-free dry weight (AFDW) biomass was either determined by drying the organisms at 60°C for at least 60 hours and subsequently incinerating them at 520°C for 4 hours or by conversion of the blotted wet weight. Some crustaceans (amphipods, isopods and cumaceans) were assigned an average individual AFDW. At each station, depth was recorded and samples were taken for grain size analysis.

More details on these surveys can be found in Groenewold and van Scheppingen (1989, 1990), Holtmann & Groenewold (1992, 1994), Holtmann et al (1996), and van Scheppingen and Groenewold (1990).

In chapter 8 part of the macrobenthic and sediment data were used in a study on the assessment of the impact of beam trawling.

2.2. Database

The need to store ecological information in a database is, nowadays, well recognised. The amount of information resulting from the ongoing monitoring studies is that large that analysis would be impossible without a proper data management. Moreover, there is the need to have access to data from the past to facilitate the possible effects of e.g. fishery impacts and eutrophication. Consequently, there is a large effort to incorporate published and non-published data from studies in the past. Given all data mentioned in the preceding chapter, we were forced to design a database ourselves.

At the Netherlands Institute for Ecology, we started with the development of a database storing information on the benthic fauna of the North Sea and adjacent estuaries in 1992. Data from the ICES North Sea Benthos Survey, the Monitoring Master Plan of the North Sea Task Force and the inventory of the benthos on the Dutch Continental Shelf (MILZON) were stored in Paradox®, a relational database management system that can be used either as a standalone system on a single computer or as a multi-user system on a network. Meanwhile, many additional data sets were added to this database (BEDMAN - Benthic Data MANagement), including the data of all the above mentioned projects. The majority of the data are concentrated around the Dutch coastline, but the data extend from the southern North Sea to north of the Shetland Islands. Most of data included are macrobenthic infauna data: numbers, density and biomass of individual species and/or species groups. The database now has information of more than 10000 samples. The design and maintenance has been discussed at several meetings of the ICES Benthos Ecology Working Group (BEWG 1994, 1995, 1996). Recently, the database resulted in an atlas of the zoobenthos of the Dutch Continental Shelf (Holtmann et al. 1996) and an atlas of the North Sea infauna based on the 1986 North Sea Benthos Survey of the ICES Benthos Ecology Working (Craeymeersch et al. 1997).

A major topic in discussions on database management concerns the way species are entered: full species names or coded names. Although, given computers' storage capacity nowadays, it's no longer necessary to use short names, the size of the data files and the time needed to perform queries is much shorter if short species codes are used. Over the years, several coding systems have been developed. Some are simply abbreviations of the species name (e.g. the RUBIN-code; Zetterberg 1992), others are alphanumerical or strictly numerical (e.g. the species code of the National Oceanographic Data Center (NODC) operated by NOAA, the National Oceanographic and Atmospheric Administration of the U.S, the Species Directory of the Marine Conservation Society (MCSSD) (Howson 1987), and the species code developed by the National Museum in Leiden (IAWM) and used in the database system of the Dutch Institute for Coastal Management (Lavaleye et al. 1995). All try to represent the Linnean system. The NODC taxonomic code, for instance, contains a maximum of 12 digits, partitioned into a series of 2-digit couplets. Each couplet represents one or more levels of the taxonomic hierarchy. Moreover, taxonomy is revised from time to time, and new species are found that don't fit in the existing system. Consequently, some codes have to be changed as well. These problems are well realised by the centres developing the coding systems.

While developing our database, we encountered the same problems. No existing system covered all species found in the North Sea and adjacent estuaries. But we could not wait till such code would exist. Therefore, we decided to give every species name an identification number. In a separate table (the species table) this name identification number is linked with the full Latin name, the authors who first described the name, and a species identification number (figure 2.7). Thus, synonyms have different name identification numbers but the same species identification number. In a third table (the taxonomy table) the species identification number is linked with the taxonomic position, and the different codes used. This set-up enables us to store the original name used by the scientist, which facilitates reference to published papers. It also simplifies the management of the database as the main file, storing the densities and biomasses for each

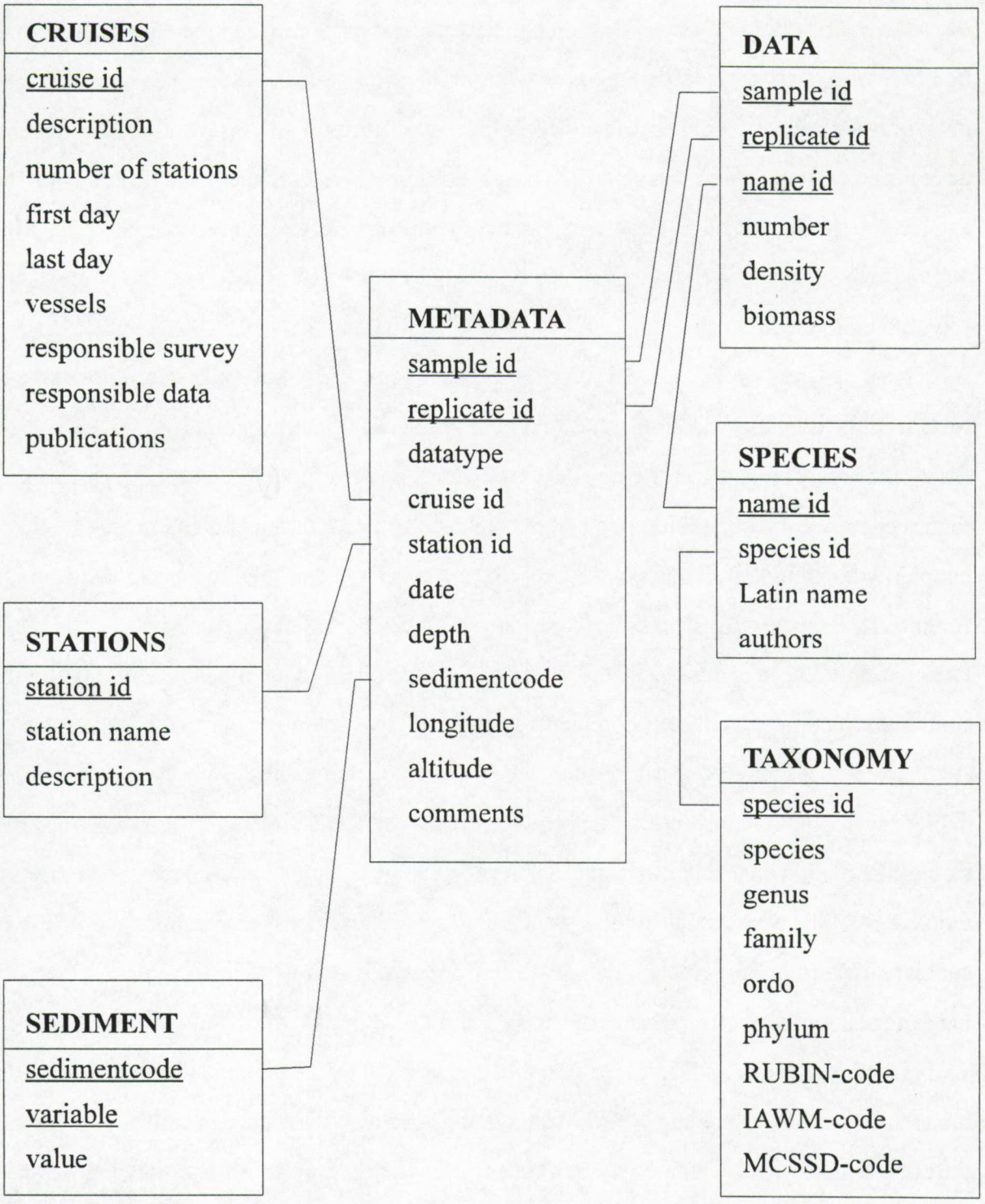


Figure 2.7. BEDMAN: database structure. The main data are arranged into 7 tables, linked by common fields. Fields defined as primary or composite keys are underlined.

species, don't have to be changed when e.g. new codes evolve or when the name turns out to be synonymous with a species already existing in the database. In the first case, codes in the taxonomy table have to be altered or added. In the second case, the species identification number in the species table has to be changed. Thus, it is simple to handle the instability (synonymy and re-classification) of names. Other information on species (e.g. taxonomic position, photographs, drawings or ecological information) can be stored in separate files in the same way, linked to the other files by the species identification number.

As for the species, we use an identification number for each sample (i.e. the total of one to several replicate grabs, cores or other basic entities at a particular station during a particular cruise) added to the database. Thus, the main data file (density and biomass per species for each replicate of a sample) basically has five fields: a sample identification number, a replicate number, a name identification number, the density (ind./m^2) and the biomass (g ash-free dry weight/m^2) (additionally, data on e.g. the wet weight can be added).

Information on each sample is stored in several, separate files. One gives information on the station sampled (station name, short description). A second one gives more information on the surveys or cruises (short description, number of stations sampled, the vessels used, first and last day of the survey, the responsible persons for the cruises and data, publications). A third one stores information on the date of sampling, the geographic position and the depth, and has some fields indicating whether the sample concerns macrobenthos or meiobenthos, and a link to another file storing the sediment data. All these files are linked by identification numbers for the samples, replicates, cruises and stations.

At present, we are adding new information to this database, namely information on the methodology of sampling and sediment analysis. For some cruises and species, we also added information on the density and biomass per length class. In the near future, data collected by dredges or trawls will be added. These data are now kept in separate databases.

2.3 Multivariate analyses

Ordination

Ordination may be defined as the ordering of entities (species and stations) in a one- to multidimensional space in such a manner that their arrangement will reveal some useful information about their relationships (Hermy 1988). Similar entities are close to each other and dissimilar entities are far apart (Gauch 1982). Therefore, ordination allows relating faunal change to environmental variables. The result of the ordination in two dimensions is a diagram in which sites are represented by points in two-dimensional space. The aim of ordination is to arrange the points such that points that are close together correspond to sites that are similar in species composition, and points that are far apart correspond to sites that are dissimilar in species composition (Jongman et al. 1987, ter Braak and Prentice 1988).

The axes of an ordination diagram could be thought of as hypothetical environmental gradients, which are subsequently interpreted in terms of measured environmental variables. If the measured environmental variables relate strongly to the first few ordination axes, they are sufficient to predict the main part of the variation in the species composition (ter Braak 1986). This two-step approach is an indirect gradient analysis. In a direct gradient analysis, species occurrences are related directly to environmental variables (Gauch 1982). A constrained multivariate (or canonical) ordination is a direct gradient analysis where the axes are constructed in such a way as to explicitly optimise the fit to supplied environmental data (ter Braak and Prentice 1988). In a partial canonical ordination, the effect of one or more co-variables can be partialled out. The result is an ordination of the residual variation in the species data that remains after fitting the effects of the co-variables.

Many ordination methods have been proposed (see e.g. Jongman et al. 1987, Hermy 1988, ter Braak and Prentice 1988, Legendre and Legendre 1998). In this dissertation we made use of Redundancy Analysis (RDA), Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA). RDA, the canonical form of Principal Components Analysis (PCA), is based on a linear response model of species with respect to environmental gradients. CA and CCA are ordination techniques based on an unimodal response model. Linear methods are appropriate

to community analysis when the species data are quantitative abundances (with few zeroes) and the range of environmental variation in the sample set is narrow. If the community variation is over a wider range, non-linear ordination methods are more appropriate (ter Braak and Prentice 1988). For more information on the different ordination methods and the algorithms used, we refer to Jongman et al. (1987) and Legendre and Legendre (1998).

Classification

In contrast to ordination classification aims at structuring data into groups (clusters) of similar entities. The emphasis here is more on discontinuities in the data. Classification techniques may be classified by a number of characteristics: non-hierarchical vs. hierarchical; divisive vs. agglomerative; formal vs. informal; mono- vs. polythetic (Jongman et al. 1987, Hermy 1988). In this study (chapters 5, 6 and 7), we used TWINSPAN, a polythetic divisive technique. A divisive strategy consists of progressively subdividing into groups of decreasing size. Polythetic classification methods divide clusters on the basis of several characteristics at the same time (Heip et al. 1985, Hermy 1988).

The TWINSPAN program (Hill 1979) constructs an ordered two-way table from a samples-by-species matrix. First, the samples are ordened by a division on the first ordination axis of a correspondence analysis (the "primary" ordination) and a subsequent refinement based on differential species that are preferential to each side of the dichotomy (the "refined" ordination). This refined ordination is used to determine the dichotomy. A third ordination based on the most highly preferential species (the "indicator" ordination) is used to see whether the dichotomy suggested can be reproduced by a division of the indicator ordination. Finally, the species are classified based on the classification of the samples. After completing the samples classification the species are classified in the light of the samples classification. It is based on the degree to which species are confined to particular groups of sites. As a result, a structured table is made in which similar species and similar samples are grouped (Hill 1979, Jongman et al. 1987). As TWINSPAN places the most similar samples together, the sample sequence could reflect an existing environmental gradient, and the differential species identified (called the

indicator species) may be classified according to their ecological preferences. TWINSPAN allows identifying differences in density as the species can be split up into pseudospecies according to chosen density classes.

2.4. References

Anonymous. 1987. Projectplan SAWES. Rijkswaterstaat, Dienst Getijdewateren. Nota GWAO-87.103. 40 pp.

—-. 1992. Evaluatie milieu effect rapportage Slufter over de periode 1986 tot en met 1990. Werkgroep Evaluatie Slufter. Gemeentewerken Rotterdam, Ministerie van Verkeer en Waterstaat. Rotterdam. 40 pp.

—-. 1997. Evaluatie milieu effect rapportage 'Slufter' over de periode 1986 tot en met 1996. Werkgroep Evaluatie Slufter. Gemeentewerken Rotterdam, Ministerie van Verkeer en Waterstaat. Rotterdam, 64 pp.

Basford, D., and A. Eleftheriou. 1988. The benthic environment of the North Sea (56° to 61°N). Journal of the Marine Biology Association of the United Kingdom **68**:125-141.

Basford, D. J., A. Eleftheriou, and D. Raffaelli. 1989. The epifauna of the northern North Sea (56°-61N). Journal of the Marine Biology Association of the United Kingdom **69**:387-407.

Basford, D., A. Eleftheriou, and D. Raffaelli. 1990. The infauna and epifauna of the northern North Sea. Netherlands Journal of Sea Research **25**:165-173.

BEWG. 1986. Fifth report of the Benthos Ecology Working Group. ICES C.M. 1986/L:27. 33 pp.

—-. 1994. Report of the Benthos Ecology Working Group, Yerseke, The Netherlands, 9-13 May 1994. ICES C.M. 1994/L:4. 178 pp.

—-. 1995. Report of the Benthos Ecology Working Group, Torshavn, Faroe Island, 3-6 May 1995. ICES CM 1995/L:3. 98 pp.

—-. 1996. Report of the Benthos Ecology Working Group. Aberdeen, Scotland, 1-4 May 1995. ICES CM 1996/L:5. 97 pp.

Bijlsma, L., and J. W. M. Kuipers. 1989. River water and the quality of the Delta waters. Pages 3-26 *in* J. C. Hooghart and C. W. S. Posthumus, editors. Hydro-ecological relations in the Delta Waters in the South-West Netherlands. Technical Meeting 46, Rotterdam, The Netherlands, 8 March 1989. TNO Committee on Hydrological Research, The Hague, Proceedings and information, TNO Committee on Hydrological Research, No. 41.

Cattrijsse, A., J. Mees, and O. Hamerlynck. 1993. The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary. Cahier de Biologie Marine **34**:187-200.

Colijn, F., and I. Akkerman. 1990. Biologisch monitoringsprogramma zoute wateren, stand van zaken 1990. Rijkswaterstaat, Dienst Getijdewateren. Nota GWAO-90.018.

Colijn, F., W. Snoek, and E. C. L. Marteijn. 1992. Biologische monitoring, een beheersinstrument voor de Nederlandse wateren? Pages 3-8 *in* Programma en samenvattingen van het symposium biologische monitoring in het aquatische milieu, 18 november 1992, Amsterdam. Rijkswaterstaat.

Coosen, J., J. Seys, P. M. Meire, and J. A. M. Craeymeersch. 1994. Effect of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde estuary (SW Netherlands) on distribution, density and biomass of five common macrobenthic species: *Spio martinensis* (Mesnil), *Hydrobia ulvae* (Pennant), *Arenicola marina* (L.), *Scoloplos armiger* (Muller) and *Bathyporeia* sp. Hydrobiologia **282/283**:235-249.

Craeymeersch, J. A., O. Hamerlynck, K. Hostens, A. Vanreusel, and M. Vincx. 1990. De ekologische ontwikkeling van de Voordelta. Deelrapport 1. De huidige ekologische situatie van de Voordelta. Delta Instituut voor Hydrobiologisch Onderzoek - Rijksuniversiteit Gent, Sektie Mariene Biologie. 92 pp.

Craeymeersch, J. A., C. H. R. Heip, and J. Buijs. 1997. Atlas of North Sea Benthic Infauna. ICES Cooperative Research Report No 218.

Duin, R. N. M. 1994. Poweranalyse bodemdieren Groninger Wad. Rijkswaterstaat, Rijksinstituut voor Kust en Zee. Werkdocument RIKZ/OS-94.121. 14 pp.

Duineveld, G. C. A., P. A. W. J. de Wilde, and A. Kok. 1990. A synopsis of the macrobenthic assemblages and benthic ETS activity in the dutch sector of the North Sea. Netherlands Journal of Sea Research **26**:125-138.

Duineveld, G. C. A., A. Künitzer, U. Niermann, P. A. W. J. de Wilde, and J. S. Gray. 1991. The macrobenthos of the North Sea. Netherlands Journal of Sea Research **28**:53-65.

Eleftheriou, A., and D. J. Basford. 1989. The macrobenthic infauna of the offshore northern North Sea. Journal of the Marine Biology Association of the United Kingdom **69**:123-143.

Essink, K. 1992. Macrozoobenthos trend monitoring in the Dutch sector of the North Sea. In: Report of the Benthos Ecology Working Group, Bergen, Norway 4-8 May 1992. ICES C.M. 1992/L:11, Annex 6, p.50-53. ICES, Copenhagen.

—. 1994. Ongoing monitoring studies in the Netherlands. In: Report of the Benthos Ecology Working Group, Yerseke, The Netherlands, 9-13 May 1994. ICES C.M. 1994/L:4, Annex 5, p. 41-46. ICES, Copenhagen.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. 298pp.

Groenewold, A., and Y. van Scheppingen. 1989. De ruimtelijke verspreiding van het benthos in de zuidelijke Noordzee. Voorjaar 1988. Rijkswaterstaat Directie Noordzee / Dienst Getijdewateren. MILZON-BENTHOS Rapport 89-05. 27pp.

—-. 1990. De ruimtelijke verspreiding van het benthos in de zuidelijke Noordzee. De noord-Nederlandse kustzone 1989. Rijkswaterstaat directie Noordzee / Dienst Getijdewateren. MILZON-benthos rapport nr. 90-01. 27pp.

Hallie, F. P., T. Louters, J. P. M. Mulder, and R. Postma. 1990. Geomorphological and ecological changes in the littoral zone of the south-west Netherlands: consequences for integrated coastal zone management. Pages 330-334 *in* R. E. Quelennec, E. Ercolani and G. Michon, editors. Symp. 1st Eurocoast, Littoral 1990, Marseille.

Hamerlynck, O., and J. Mees. 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. Oceanologica Acta **SP. N°. 11**:205-211.

Hamerlynck, O., J. Mees, P. Van de Vyver, E. Van Landtschoote, K. Hostens, and A. Cattrijsse. 1990. Eindverslag Hyperbenthosonderzoek Voordelta. Sektie Mariene Biologie, Instituut voor Dierkunde, Rijksuniversiteit Gent. 102pp.

Hamerlynck, O., K. Hostens, J. Mees, R. V. Arellano, A. Cattrijsse, P. Van de Vijver, and J. A. Craeymeersch. 1992. The ebb tidal delta of the Grevelingen: a man-made nursery for flatfish? Netherlands Journal of Sea Research **30**:191-200.

Heinis, F., I. Akkerman, K. Essink, F. Colijn, and M. J. Latuhihin. 1995. Biologische monitoring zoute rijkswateren 1990-1993. Rijkswaterstaat, Rijksinstituut voor Kust en Zee. Rapport RIKZ-95.059. 80pp.

Heip, C., and J. A. Craeymeersch. 1995. Benthic community structures in the North Sea. Helgoländer Meeresuntersuchungen **49**:313-328.

Heip, C., M. Vincx, and G. Vranken. 1985. The ecology of marine nematodes. Oceanography and Marine Biology: an Annual Review **23**:399-489.

Heip, C., D. Basford, J. A. Craeymeersch, J.-M. Dewarumez, J. Dörjes, P. de Wilde, G. Duineveld, A. Eleftheriou, P. M. J. Herman, U. Niermann, P. Kingston, A. Künitzer, E. Rachor, H. Rumohr, K. Soetaert, and T. Soltwedel. 1992. Trends in biomass, density and diversity of North Sea macrofauna. ICES Journal of Marine Science **49**:13-22.

Hermy, M. 1988. An introduction to multivariate analysis in biology. Bull. Soc. roy. bot. Belg. **121**:127-158.

Hill, M. O. 1979. TWINSPAN. A FORTRAN program for arranging Multivariate data in an Ordered Two-Way Table by Classification of the Individuals and Attributes. Ecology and Systematics, Cornell University, Ithaca, 90 pp.

Holtmann, S.E., and A. Groenewold. 1992. Distribution of the zoobenthos on the Dutch Continental Shelf: The Oyster Ground, Frisian Front, Vlieland Ground and Terschelling Bank (1991). Netherlands Institute of Sea Research, NIOZ-rapport 1992-8, Netherlands Institute of Ecology, NIOO-CEMO rapporten en verslagen 1992-6, 129 pp.

Holtmann , S.E., and A. Groenewold. 1994. Distribution of the zoobenthos on the Dutch Continental Shelf: The Western Frisian Front, Brown Bank and Broad Fourteens (1992/1993). Netherlands Institute of Sea Research, NIOZ-rapport 1994-1, Netherlands Institute of Ecology, NIOO-CEMO rapporten en verslagen 1994-1, 136 pp.

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijkswijk. 244pp.

Howson, C. M., editor. 1987. Directory of the British marine fauna and flora. A coded checklist of the marine fauna an flora of the British Isles and surrounding seas. Marine Conservation Society. 471pp.

Hummel, H., A. W. Fortuin, R. H. Bogaards, A. Meijboom, and L. de Wolf. 1994. The effects of prolonged emersion and submersion by tidal manipulation on marine macrobenthos. Hydrobiologia **282/283**:219-234.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen. 299pp.

Knoester, M. 1984. Introduction to the Delta case studies. Wat. Sci. Tech. **16**:1-9.

Kohsiek, L. H. M. 1988. Reworking of former ebb-tidal deltas into large longshore bars following the artificial closure of tidal inlets in the southwest of the Netherlands. Pages 113-122 *in* P. L. de Boer, A. van Gelder and S. D. Nio, editors. Tide-influenced sedimentary environments and facies. Reidel, Dordrecht.

Kohsiek, L. H. M., and J. P. M. Mulder, editors. 1989. De Voordelta. Een watersysteem verandert. Rijkswaterstaat, Dienst Getijdewateren, Middelburg. 24pp.

Künitzer, A., D. Basford, J. A. Craeymeersch, J. M. Dewarumez, J. Dörjes, G. C. A. Duineveld, A. Eleftheriou, C. Heip, P. Herman, P. Kingston, U. Niermann, E. Rachor, H. Rumohr, and P. A. J. de Wilde. 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES Journal of Marine Science **49**:127-143.

Lambeck, R. H. D. 1981. Effects of closure of the Grevelingen estuary on survival and development of macrozoobenthos. Pages 153-158 *in* N. V. Jones and W. J. Wolff, editors. Feeding and Survival Strategies of Estuarine Organisms. Plenum, New York.

—-. 1982. Colonization and distribution of *Nassarius reticulatus* (Mollusca: Prosobranchia) in the newly created saline Lake Grevelingen (SW-Netherlands). Netherlands Journal of Sea Research **16**:67-79.

—-. 1984. Dynamics, migration and growth of *Nassarius reticulatus* (Mollusca: Prosobranchia) colonizing saline Lake Grevelingen (SW-Netherlands). Netherlands Journal of Sea Research **18**:395-417.

Lambeck, R. H. D., E.G.J. Wessel, and A. Hannewijk. 1989. Het macrozoöbenthos in het Grevelingenmeer: een bestandsopname in voorjaar 1988. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke. Rapporten en Verslagen nr. 1989-5. 46 pp.

Lavaleye, M. S. S., A. Stroo, and J. P. H. M. Adema. 1995. Naamlijst van Zee- en Zoetwaterdieren van Nederland en omstreken met IAWM-codes. Nationaal Natuurhistorisch Museum, Leiden / Rijkswaterstaat, Rijksinstituut voor Kust en Zee, den Haag. Rapport RIKZ-95.031. 77pp.

Legendre, P., and L. Legendre. 1998. Developments in Environmental Modelling, 20: Numerical Ecology. Second English Edition. Elsevier B.V., Amsterdam. 853pp.

Mees, J., and O. Hamerlynck. 1992. Spatial community structure of the winter hyperbenthos of the Schelde estuary, the Netherlands, and the adjacent coastal waters. Netherlands Journal of Sea Research **29**:357-370.

Meire, P. 1993. Wader populations and macrozoobenthos in a changing estuary: the Oosterschelde (The Netherlands). PhD Thesis, University of Gent, Gent. 311pp.

Meire, P., and D. Develter. 1988. Macrozoöbenthos van de Westerschelde: eerste overzicht van de resultaten van de macrozoöbenthos bemonstering najaar 1987 in het kader van het projekt SAWES. Rijksuniversiteit Gent, Laboratorium voor Ekologie der Dieren. Rapport W.W.E. no. 9.

Meire, P. M., J. J. Seys, T. J. Ysebaert, and J. Coosen. 1991. A comparison of the macrobenthic distribution and community structure between two estuaries in SW Nehterlands. Pages 221-230 *in* M. Elliott and J.-P. Ducrotoy, editors. Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen & Olsen, Fredensborg.

Meire, P. M., J. Seys, J. Buijs, and J. Coosen. 1994. Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm-surge barrier? Hydrobiologia **282/283**:157-182.

Mulder, J. 1990. Beschrijving globale bodemkaart Voordelta en indicaties voor verwachte ontwikkelingen in de bodemsamenstelling op termijn 2010. Rijkswaterstaat, Dienst Getijdewateren. Notitie GWAO-90.13044. 7pp.

Nienhuis, P. H., and A. C. Smaal, editors. 1994. The Oosterschelde estuary: a case study of a changing ecosystem. Developments in hydrobiology 97, Kluwer Academic Publishers. 597pp.

Postma, R., J. Mulder, T. Louters, and F. Hallie. 1991a. Een prognose van de morfologie van de Grevelingen-buitendelta in 2010. Rijksuniversiteit Utrecht, rapport GEOPRO 1991.08 (notitie GWAO 90.1345). 37pp.

—. 1991b. Een prognose van de morfologie van de Haringvliet-buitendelta in 2010. Rijksuniversiteit Utrecht, rapport GEOPRO 1991.09 (notitie GWAO 90.13039). 25pp.

—. 1991c. Voorspelling van de morfologie en de sedimentbalans van de voordelta in 2010. Rijksuniversiteit Utrecht, rapport GEOPRO 1991.11 (notitie GWAO 90.13045). 37pp.

Postma, R., J. Mulder, T. Louters, F. Hallie, and F. de Vos. 1991d. Een kwalitatieve prognose van de morfologie van de Oosterschelde-buitendelta in 2010. Rijksuniversiteit Utrecht, rapport GEOPRO 1991.10 (notitie GWAO 90.13040). 14pp.

RWS. 1989. Water voor nu en later: derde Nota waterhuishouding. SDU, 's-Gravenhage. 297 p.

Seys, J., and P. Meire. 1988. Macrozoöbenthos van het Veerse Meer. Rijksuniversiteit Gent, Laboratorium voor Ecologie der Dieren. Rapport W.W.E. 4.

Seys, J. J., P. M. Meire, J. Coosen, and J. A. Craeymeersch. 1994. Long-term changes (1979-89) in the intertidal macrozoobenthos of the Oosterschelde estuary: are patterns in total density, biomass and diversity induced by the construction of the storm-surge barrier? Hydrobiologia **282/283**:251-264.

Smit, H. 1995. Macrozoobenthos in the enclosed Rhine-Meuse Delta. PhD Thesis, University of Nijmegen, Nijmegen. 192pp.

Steijn, R. C., T. Louters, A. J. F. van der Spek, and H. J. de Vriend. 1989. Numerical model hindcast of the ebb-tidal delta evolution in front of the deltaworks. Pages 255-264 *in* R. A. Falconer, P. Goodwin and R. G. S. Matthew, editors. Hydraulic and Environmental Modelling of Coastal, Estuarine and River Waters. Proceedings of the International Conference held at the University of Bradford, 19-21 September 1989. Gower Technical, Aldershot.

Stronkhorst, J. 1988. Microverontreinigingen in enkele soorten bodemdieren uit de Westerschelde, zomer 1987. Rijkswaterstaat, Dienst Getijdewateren. Nota GWWS-88.503. 46pp.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research **18**:272-318.

van Alphen, J., and R. Molendijk. 1993. Vorm in Verandering. Integraal Beleidsplan Voordelta. Ministerie van Verkeer en Waterstaat, Rijkswaterstaat, Secretariaat Bestuurlijk Overleg Voordelta. 75 p.

van Arkel, M. A., and M. Mulder. 1975. A device for quantitative sampling of benthic organisms in shallow water by means of a flushing technique. Netherlands Journal of Sea Research **9**:165-170.

van der Meer, J. 1997. Sampling design of monitoring programmes for marine benthos: a comparison between the use of fixed versus randomly selected stations. Journal of Sea Research **27**:167-179.

Vanhooren, H. 1989. Verspreiding van macrozoöbenthos in de Westerschelde: invloed van abiotische factoren en pollutie. Licentiaatsverhandeling, Rijksuniversiteit Gent. 187 pp.

van Mansfeld, M. J. M. 1978. Verandering in de samenstelling van het zoöbenthos van het zachte substraat in het Veerse Meer sinds 1959. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke. Studentenverslag D2. 100p.

Vanreusel, A. 1990. Ecology of the free-living marine nematodes from the Voordelta (Southern Bight of the North Sea). I. Species composition and structure of nematode communities. Cahier de Biologie Marine **31**:439-462.

—-. 1991. Ecology of free-living marine nematodes in the Voordelta (Southern Bight of the North Sea). II. Habitat preferences of the dominant species. Nematologica **37**:343-359.

van Scheppingen, Y., and A. Groenewold. 1990. De ruimtelijke verspreiding van het benthos in de zuidelijke Noordzee. De Noord-Nederlandse kustzone, overzicht 1988-1989. MILZON-benthos rapport nr. 90-03. 27 pp.

Zetterberg, G. editor 1992. Term List K1, Crustacea, version 920414-GUZ. Environmental Data Standardization, Term-List 1. Nordic Code Center, Swedisch Museum of Natural History, Stockholm.

Appendix

Ratios to convert wet weight to ash free dry weight Biomass of molluscs was mostly determined by length-weight relationships. For pectinariids, serpulids and flagelligerids, the ratios of ampharetids were used. For cossurids, ophiotrichids and glycerids, the ratios of respectively cirratulids, ophiolepids and nephtyids were used. Further remarks: (1) autumn ratio also used in spring; (2) spring ratio also used in autumn; (3) spring ratio as terebellids; (4) autumn ratio as petricolids.

phylum		Spring	Autumn	
Annelida	Ampharetidae	0.114	0.114	(1)
Annelida	Arenicolidae	0.100	0.094	
Annelida	Capitellidae	0.121	0.111	
Annelida	Cirratulidae	0.126	0.066	
Annelida	Hesionidae	0.153	0.159	
Annelida	Magelonidae	0.146	0.144	
Annelida	Nephtyidae	0.136	0.130	
Annelida	Nereis	0.121	0.092	
Annelida	Nereis virens	0.121	0.115	
Annelida	Oligochaeta	0.111	0.133	
Annelida	Opheliidae	0.094	0.118	
Annelida	Orbiniidae	0.128	0.121	
Annelida	Paraonidae	0.144	0.144	
Annelida	Phyllodocidae	0.139	0.135	
Annelida	Platynereis	0.134	0.150	
Annelida	Poecilochaetidae	0.131	0.131	
Annelida	Polynoidae	0.161	0.154	
Annelida	Sabellidae	0.114	0.097	
Annelida	Scalibregmidae	0.092	0.091	(3)
Annelida	Sigalionidae	0.149	0.131	
Annelida	Spionidae	0.130	0.110	
Annelida	Syllidae	0.131	0.131	(2)
Annelida	Terebellidae	0.092	0.097	
Arthropoda	Amphipoda	0.129	0.120	
Arthropoda	Chironomidae	0.106	0.120	
Arthropoda	Cumacea	0.131	0.120	
Arthropoda	Isopoda	0.132	0.119	
Arthropoda	Mysidacea	0.142	0.156	
Arthropoda	Natantia	0.129	0.131	
Arthropoda	Pycnogonida	0.194	0.194	(2)
Arthropoda	Reptantia	0.120	0.120	
Chordata	Chordata	0.039	0.040	
Cnidaria	Actiniaria	0.142	0.138	
Echinodermata	Asteriidae	0.076	0.110	
Echinodermata	Ophiolepidae	0.051	0.053	
Echinodermata	Spatangidae	0.018	0.018	
Mollusca	Calyptraeidae	0.047	0.047	(1)
Mollusca	Cardiidae	0.049	0.049	(2)
Mollusca	Corbulidae	0.046	0.046	(1)
Mollusca	Hydrobiidae	0.097	0.084	
Mollusca	Lepidopleuridae	0.116	0.116	
Mollusca	Littorinidae	0.067	0.051	
Mollusca	Macoma	0.043	0.056	
Mollusca	Mactridae	0.060	0.060	
Mollusca	Montacutidae	0.076	0.074	
Mollusca	Myacidae	0.048	0.054	
Mollusca	Mytilidae	0.054	0.054	
Mollusca	Nassariidae	0.072	0.079	
Mollusca	Nudibranchia	0.069	0.069	
Mollusca	Ostreidae	0.035	0.035	
Mollusca	Petricolidae	0.050	0.064	
Mollusca	Pholadidae	0.050	0.064	(4)
Mollusca	Retusidae	0.079	0.079	
Mollusca	Scrobiculariidae	0.043	0.043	
Mollusca	Solenidae	0.089	0.089	(1)
Mollusca	Tellina	0.056	0.056	
Mollusca	Veneridae	0.058	0.058	(2)
Nemertea	Nemertea	0.174	0.154	
Porifera	Porifera	0.044	0.044	

CHAPTER 3

Monitoring benthic communities: the power of univariate vs. multivariate analyses

Introduction

Monitoring programs focus on the change in chosen parameters over years. Because of their relative immobility and their intimate link with the sediment and the conditions immediately above the sediment, benthic organisms have become important targets for many long-term studies of the effects of natural and anthropogenic change in marine ecosystems (Holtmann et al. 1996, Pearson 1997). Whether or not biological changes can be detected and related to changes in environmental factors, depends on the accurate collection, collation and statistical analysis of the biological and environmental data (Pearson 1997). The effectiveness of detecting changes is defined in terms of statistical power, i.e. the probability of correctly rejecting a false null hypothesis (Cohen 1969, Fryer and Nicholson 1993).

Ideally, power should be used in the design and planning of monitoring studies to avoid wasted time and effort on a program that is unlikely to yield useful information. Power calculations can indicate the sample size needed to detect and environmental change and optimize the survey design, thus making sure that specified changes are likely to be detected (Bilyard 1987, Gerrodette 1987, Fairweather 1991, Nicholson and Fryer 1992, van der Meer 1997b). Power analysis is also important for the interpretation of results when the null hypothesis is not rejected, to evaluate the study for its sensitivity, realized power and detectable effect sizes. Otherwise, one might falsely conclude that nothing is going on (Toft and Shea 1983, Fairweather 1991, Stevens 1992). Several statistical power analyses from impact assessment and resource management show that current methods of estimating populations have a low probability of detecting a significant change in abundance, should one occur (Peterman and Bradford 1987, Nicholson and Fryer 1992). And, finally, power as the ability to detect change can guide researchers in the selection of the best statistical tests or indices (Fairweather 1991).

For a comparison of two means (*t*-test), the power can be calculated from (based on box 9.13 of Sokal & Rohlf 1981) :

$$t_{\upsilon}(\beta) = \frac{\delta * \sqrt{n}}{\sigma * \sqrt{2}} - t_{\upsilon}(\alpha / 2)$$

with $t_{\upsilon}(\beta)$ and $t_{\upsilon}(\alpha / 2)$ = values from a one-tailed *t*-table for υ degrees of freedom and corresponding to probabilities of β and $\alpha/2$; α is the probability of rejecting the null hypothesis when in fact it is true, β the risk of not rejecting the null hypothesis when it is in fact false (= 1 – P , the power of the analysis)

σ = the true standard deviation

$\upsilon = a(n-1)$, the degrees of freedom of the sample standard deviation *s* with *a* groups and *n* replications per group; and

δ = the smallest true difference desired to be detected.

Using *s* as an estimate of σ, δ/σ is estimated as the ratio of the detectable difference, expressed as a percentage of the mean ($100*\delta/\bar{x}$), and the coefficient of variation ($100*s/\bar{x}$ with $\bar{x}$ the sample mean).

In two experimental studies (April and November 1992) on the direct impact of bottom trawling on the benthos (Craeymeersch 1994), we used the above formula to estimate the effectiveness of detecting differences between the (log-transformed) mean densities of infauna species before and after fishing. The power was estimated at a significance level α set to 0.20 (instead of the generally used 0.05 and, thus, allowing a large probability of type I errors) and differences (δ) of 5, 10, 20 and 50% for a few selected species with different coefficients of variation.

Figure 3.1 gives the power for the numerically dominant species as a function of the differences set to be detected. In all cases the power was very low. For example, in April 1992 the probability to detect a 50% difference at the 20% level for *Ophiura albida* was about 30%. In the second experiment, the coefficients of variation ($cv = s/\bar{x}$) were lower than recorded in the April survey. But, as in April, a power of 80% for α= 0.20 (i.e. both the type I and type II error set to 0.20) was only reached for differences of 50% for species with a coefficient of variation below about 0.60: *Scoloplos armiger, Abra alba* and *Spiophanes bombyx*. It was concluded that, given the

low power of the *t*-tests, no conclusions could be made about the impact on the benthic animals and that further studies should try to minimize the sample variance to increase the power.

The accuracy of the biological estimates is to a large extent determined by the sampling design. Therefore, planning of experiments should include an *a priori* estimation of powers associated with alternative designs and sample sizes (Slob 1987). Van der Meer (1997b) recently analysed the statistical power of the *F*-tests in univariate analysis of variance (anova) accompanying three possible sampling designs:

(1) a few replicate samples are taken at non-random stations, each of them revisited each year (called the fixed model), the sampling design mostly used by benthic ecologists;

(2) one sample is taken at stations selected at random each year (nested model); and

(3) one sample is taken at stations randomly selected in the first year, and revisited in succeeding years (mixed model).

The probablity of a significant *F*-test outcome if the null hypothesis, i.e. all yearly means are equal, is false (the power) depends upon the significance level (level of Type 1 error), the degrees of freedom (df) and the magnitude of the different variance components. This is expressed in the non-centrality parameter Φ^2 (Slob 1987). A larger Φ^2 results in a larger power. For a nested, mixed and fixed model, the non-centrality parameter Φ^2 can be estimated by (van der Meer 1997b):

$$\text{nested model} : \Phi^2 = \frac{bn\sum \alpha_i^2}{a(\sigma_e^2 + n(\sigma_b^2 + (a-1)\sigma_{ab}^2 / a))}$$

$$\text{mixed model} : \Phi^2 = \frac{bn\sum \alpha_i^2}{a(\sigma_e^2 + n\sigma_{ab}^2)}$$

$$\text{fixed model} : \Phi^2 = \frac{bn\sum \alpha_i^2}{a\sigma_e^2}$$

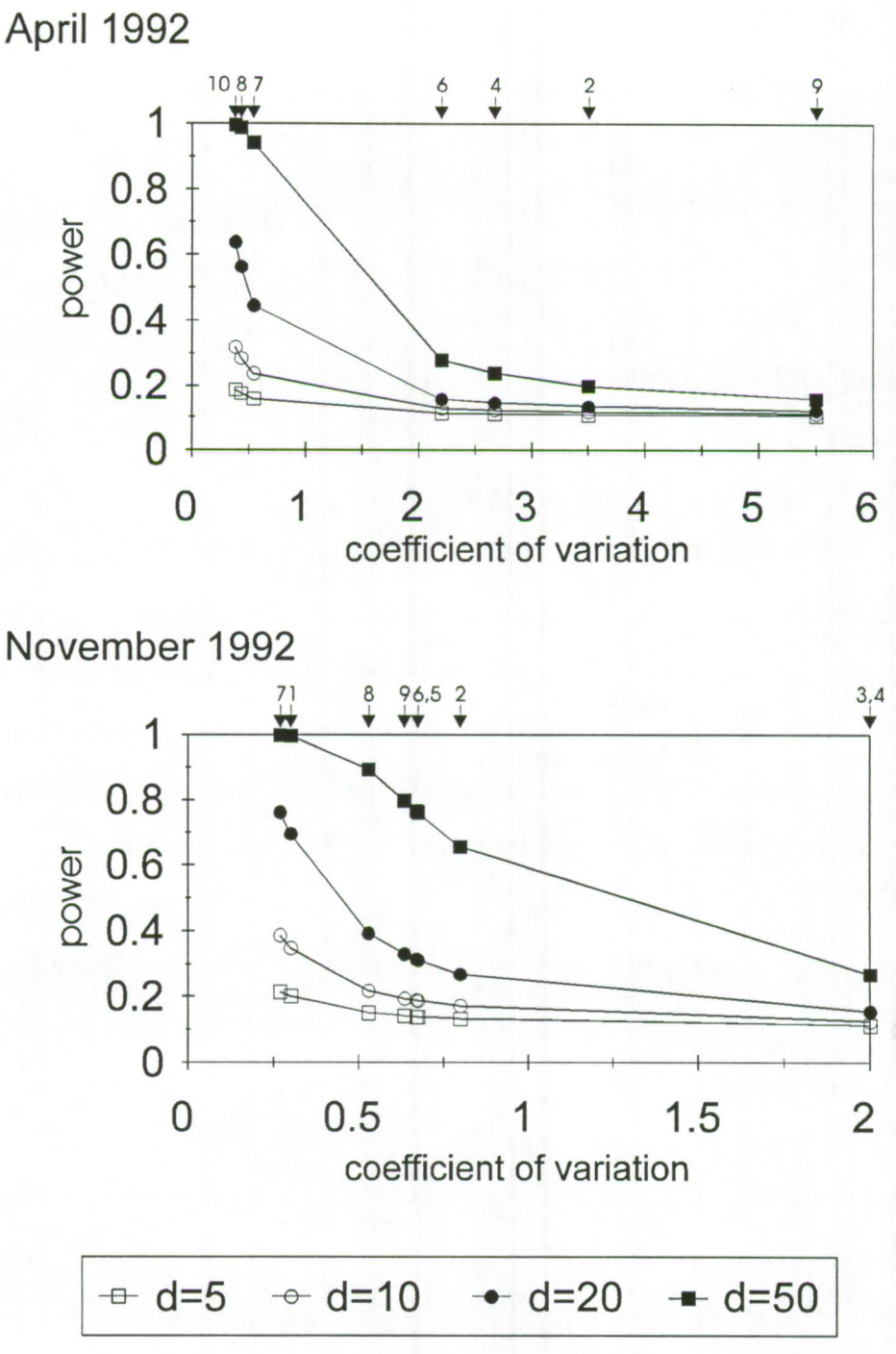


Figure 3.1. Power curves for a two-tailed *t*-test for different species (= different coefficients of variation) with $\alpha = 0.20$. Species: 1. *Abra alba* - 2. *Capitella capitata* - 3. *Eteone* spec. - 4. *Montacuta ferruginosa* - 5. *Mysella bidentata* - 6. *Ophiura albida* - 7. *Scoloplos armiger* - 8. *Spiophanes bombyx* - 9. *Urothoe brevicornis*.

with:

α_i = the difference between the mean value in a particular year *i* and the overall mean value,

a = the number of years,

b = the number of stations visited each year,

n = the number of replicates taken each year at each station,

σ_b^2= the among-stations variance component,

σ_{ab}^2 = the year*stations-interaction variance component, and

σ_e^2 = the residual within-stations variance component.

The null hypothesis tested is $\alpha_i = 0$ for all *i*. Only if $\sigma_b^2 = \sigma_{ab}^2 / a$ will the power of the mixed and nested models be equal. In case of synchronized patterns of change over years between stations, that is if $\sigma_b^2 - \sigma_{ab}^2 / a > 0$, the power of the mixed model will be greater than the power of the nested model. The power of the fixed model will always be larger than that of the other two models, unless $\sigma_{ab}^2 = 0$. The results arising from a fixed model design, however, only refer to the few sampled stations (van der Meer 1997b).

The analysis of van der Meer (1997b) was based upon data of the macrobenthic fauna of the Oysterground area (North Sea), data of some tidal flats in the Oosterschelde and data of the Balgzand, a tidal flat area in the Wadden Sea. It was concluded that a random selection of stations, which are revisited in the succeeding years, is the most appropriate design for a monitoring program for soft-bottom marine benthos, where the primary objective is detection of change. It was further concluded that monitoring programs should revisit many randomly selected stations (nested model) and make little effort per stations (only taking 1 replicate per station per year).

We made the same calculations for the tidal flats in the western part of the Westerschelde estuary as carried out in the first years of the monitoring programme (BIOMON; see chapter 2 for more information on the sampling scheme). The Autumn 1990 and 1991 log-transformed density data for the 16 most dominant species were used for a power estimation of a *t*-test (fixed model; a=2, b=10, n=1). At each station only a single estimate of the density was made and, hence, the within-station variance and, consequently, the power of the fixed model, could not be estimated

(unless assuming $\sigma_{ab}^2 = 0$, i.e. all stations have the same changes). The calculations were done with the DESIGN computer program (Dallal 1988), with a probability level α of 0.05. Following van der Meer (1997b), the effect size, defined as the back transformed difference between the true means, was supposed to be equal to 1.5, i.e. $|\alpha_1| = |\alpha_2| = \frac{1}{2}\log(1.5)$. Approximately, it means that the higher density was supposed to exceed the lower density with 50%. Besides the power, the number of stations needed to obtain a power of 0.80 with an effect size of 1.5, and the detectable effect size with a power of 0.80 and b = 10 (a=2; n=1) were calculated (table 3.1).

	Power		b		des	
	Nested	Mixed	nested	mixed	nested	mixed
A. marina	0.105	0.121	153	107	5.30	4.38
C. edule	0.061	0.060	720	740	37.28	49.65
C. volutator	0.079	0.074	283	312	9.71	12.67
E. longa	0.059	0.068	900	410	57.71	18.38
H. filiformis	0.059	0.100	910	150	59.14	5.75
M. balthica	0.058	0.066	1080	467	84.56	22.38
N. diversicolor	0.059	0.071	950	358	63.95	115.15
P. ligni	0.058	0.059	1090	860	86.39	67.46
P. elegans	0.060	0.066	800	461	45.77	21.97
S. armiger	0.184	0.137	65	89	30.18	3.82
S. subtruncata	0.072	0.173	379	64	13.91	3.11
T. marioni	0.055	0.061	1610	670	228.48	41.22

Table 3.1. Power of *t*-test (α = 0.05; effect size = 1.5), number of stations (b) required for a power of 0.80 and an effect size of 1.5, and detectable effect size (des) for a power of 0.80 and b=10 (n=1)

For many species the power of testing the hypothesis of no difference among the yearly means was very low. Consequently, the number of stations required for a power of 0.80 and the detectable effect were mostly very large. Notice that for many species the power of the mixed model was, in contrast to the results of van der Meer (1997b), not consistently larger than that of the nested model and, thus, the patterns of change at the selected stations seem to be unsynchronized.

Thus, both in the impact experiments and in the monitoring program the *F*-tests had very low power. The high variability, characteristic for many biological systems (Gittins 1985), does not seem to allow detecting reasonable changes in the density of the most dominant species. But ecosystems consist of many interacting biotic and abiotic components. Any study of

multidimensional data sets using univariate statistics assumes that the unidimensional variables are independent of one another, Univariate analyses do not take into account the covariance among descriptors. Statistical techniques based on such simple distributions as the unidimensional normal distribution are, therefore, not really appropriate for analysing complex ecological data sets. It is usually more interesting to describe the variability of the structure of the assemblage as a whole than to look at each species independently (Legendre and Legendre 1998). In such cases the need for multivariate analysis arises. The purpose of multivariate analysis is to treat multivariate data as a whole, summarizing the data and revealing their structure. The goal of multivariate analysis is to express data structure as faithfully as possible, with minimal expression of noise, that is the variation in a species' abundance not related in a systematic manner to variation in other species' abundances. Multivariate methods shift in focus away from the levels (averages) and distributions (variances) of the phenomena, concentrating instead upon the degree of relationships (correlations or covariances) among these phenomena (Sheth 1977, Gauch 1982). The most important dimensions (or gradients) in the data set are determined. In direct gradient analysis, one is interested from the beginning in particular environmental variables (Gauch 1982). Canonical ordination techniques are designed to detect the patterns of variation that can be explained 'best' by the observed environmental variables (Jongman et al. 1987). While ordination techniques were primarily exploratory analyses, with multivariate direct gradient analysis it became possible to rigorously test statistical hypotheses (Palmer, http://www.okstate.edu/artsci/botany/ordinate/motivate.htm). One can test the null hypothesis that species are unrelated to a postulated environmental factor, or that the community structure is not changing over time. In this chapter we want to evaluate if canonical ordination analysis indeed has a larger power to detect changes in time than univariate analyses of each species separately.

Material and methods

The power of univariate analyses (*F*-test in an anova) and multivariate analyses was compared by analyzing simulated data sets. Two types of trends were modeled:

- model 1: no change in the species composition; all species show the same trend in their abundances;
- model 2: the species composition changes with time; some species increase in density, others decrease.

The density changes of each species were calculated as:

$$N_{ti} = N_{1i} * (1 + f * (t\text{-}1)) + E_{ti}$$

with:

N_{ti} the logarithmically transformed density of species i at time t (with t = 1 to 10);

f the rate of change;

E_{ti} an error term reflecting the deviation from the expected value due to local differences in the abiotic and biotic environment (see further).

Table 3.2 gives the *f*-values used for each model simulation.

	simulation	*C. edule*	*P. elegans*	*T. marioni*	*A. marina*	*M. balthica*	*N. succinea*	*C. volutator*
model 1	1	0.1	0.1	0.1	0.1	0.1		
	2	0.05	0.05	0.05	0.05	0.05		
	3	0.03	0.03	0.03	0.03	0.03		
	4	0.01	0.01	0.01	0.01	0.01		
	5	0.001	0.001	0.001	0.001	0.001		
model 2	1	-0.05		-0.05	-0.05		0.05	0.05
	2	-0.01		-0.01	-0.01		0.01	0.01
	3	-0.1		-0.05	no change		0.05	0.1
	4	-0.05		-0.01	no change		0.05	0.1
	5	-003		0.03	-0.03		0.03	-0.03

Table 3.2. *f*-values used in the different simulations.

The observed mean densities at the 10 intertidal stations in the marine part of the Westerschelde estuary in autumn 1990 were used as the initial values N_{1i}. In model 1 five species with positive covariances were selected: *Cerastoderma edule*, *Tharyx marioni*, *Pygospio elegans*, *Arenicola marina* and *Macoma balthica*. In the second model, *C. edule*, *P. elegans*, *A. marina*, *Nereis succinea* and *Corophium volutator* were used. *N. succinea* and *C. volutator* have negative covariances with the other three species. Table 3.3 gives the correlation between these species and their (log-transformed) observed densities and standard deviations.

	N_{1i}	st.dev.	correlation coefficients						
			C.e.	P.e.	T.m.	A.m.	M.b.	N.s.	C.v.
C. edule	2.231	1.371	1.000						
P. elegans	2.849	1.407	0.802	1.000					
T. marioni	2.668	1.920	0.808	0.634	1.000				
A. marina	0.263	0.566	0.236	0.516	0.301	1.000			
M. balthica	1.284	1.395	0.591	0.857	0.523	0.516	1.000		
N. succinea	0.527	1.665	-0.102	-0.104	-0.488	-0.164	-0.324	1.000	
C. volutator	0.278	0.880	-0.102	-0.104	-0.488	-0.164	-0.324	1.000	1.000

Table 3.3. Mean (log-transformed) densities (and their standard deviations) and Pearson product moment correlations.

In model 1, the error term E_{ti} was calculated as the sum of the products of the component loadings of a Principal Components Analysis (PCA) and a random value generated from a normal distribution (z scores):

$$E_{ti} = b_{i1} * z_{1t} + b_{i2} * z_{2t} + b_{i3} * z_{3t} + b_{i4} * z_{4t} + b_{i5} * z_{5t}$$

with:

b_{ij} the species score (component loading) of species *i* on the *j*-th ordination axis;

z_{it} a z score.

PCA was run with the five selected species at the ten stations sampled as an input, factoring the covariance matrix. The principal components explained respectively 75.6%, 15.7%, 5.3%, 2.4% and 1.1% of the variance. As the z scores have unit variance and the sample scores are standardized in PCA, the error term is actually a random point in the multidimensional space

of the ordination diagram (figure 3.2). Doing so, the covariance structure at all sampling times is kept more or less equal.

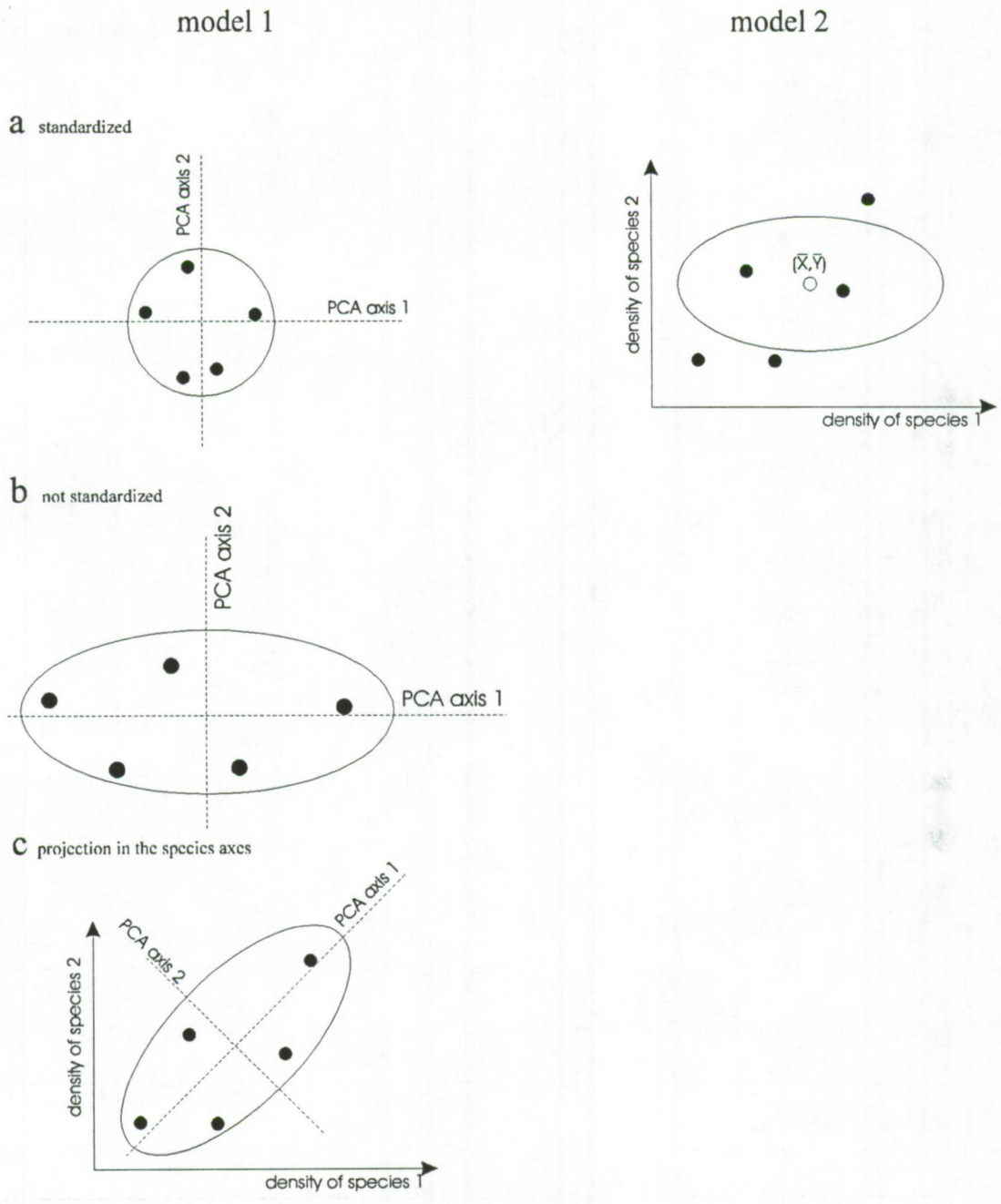


Figure 3.2. Schematic representation of the 95% confidence interval of the error terms in the model 1(left-hand side) and model 2 (right-hand side) simulations.

In the second model, the error term had to be calculated in a different way. Here, to keep the magnitude of the random error equal to the error in the initial data set, the error term was calculated as the product of the standard deviation and a z score:

$$E_{ti} = sd_i * z_{it}$$

For each year each model was run 1000 times, allowing 100 subsets of 10 'samples' to be further analysed. Changes in time of the individual species were analysed by means of a one-way anova. Overall changes in time in species composition were tested by a Redundancy Analysis (RDA), using the year as the single explanatory variable. SYSTAT (Wilkinson 1988) was used for PCA and ANOVA, CANOCO v. 3.12 (ter Braak 1988) for the RDA. The uncertainty of the ordination analyses was estimated by a Monte Carlo permutation test, restricted for time series, at the 5% significance level.

Results

Table 3.4 gives the results of the univariate (anova) and multivariate (RDA) analyses of the model 1 simulations. The number of subsets having significant differences ($p < 0.05$) among years for the five species, and the number of ordinations where the Monte Carlo permutation test led to a p-value of 0.05 or less.

f		0.10	0.05	0.03	0.01	0.001
ANOVA	*C. edule*	90	27	11	6	5
	P. elegans	100	56	18	5	4
	T. marioni	76	18	5	3	3
	M. balthica	37	12	9	3	3
	A. marina	10	6	5	4	5
	one species	100	65	27	17	15
	one species (bc)	99	29	7	2	3
	all species	4	0	0	0	0
RDA		100	76	45	16	9
	% EXPL.	5.3 à 26.4 %	2.4 à 13.5 %	1.3 à 8.9 %	1.2 à 5.1 %	1.2 à 4.9 %

Table 3.4. Number of significant ($p<0.05$) *F*-tests (anova) and permutation tests (RDA) in the model 1 simulations (one species = number of cases in which at least one of the selected species showed a significant trend; one species (bc) = the same but Bonferroni-adjusted; all species = number of cases in which all selected species showed a significant trend; %EXPL. = explained variance by constrained RDA-axis).

When the changes are very large, e.g. when the (logarithmically transformed) mean densities increase every year by 10% of the initial values, one could be very confident to find those changes with an ANOVA, at least when one uses the densities of the most dominant species in the analysis. But the chance of rejecting the null hypothesis of no difference among years is strongly decreasing with a decreasing *f*-value. Once the increase is less then 1%, the power of the *F*-test accompanying an anova is not higher than expected from chance. Moreover, the chance of rejecting the null hypothesis for all selected species is nearly always zero.

The decrease in power of a multivariate analysis is much slower than that of the univariate analyses. The power of the multivariate analyses is also much higher than the chance of finding at least one of the species showing the modeled trend. When the increase was 3%, RDA still had a power of 0.45 (although the percentage of the variance explained was lower than 10%) compared to a maximum of 0.18 for the separate species analyses (*P. elegans*). Only in 7% of the cases at least one of the species showed a significant trend (Bonferroni-corrected probability). Even without this correction the power was already much lower (0.27). When the increase was less then 3%, the non-corrected probabilities remained about 0.20, i.e. about the value expected from chance when species would be independent of one another.

	Simulation	1		2		3		4		5	
ANOVA	*C. edule*	5%↘	29	1%↘	2	10%↘	92	5%↘	29	3%↘	10
	T. marioni	5%↘	25	1%↘	10	5%↘	25	1%↘	10	3%↗	12
	A. marina	5%↘	3	1%↘	3	-	4	-	4	3%↘	3
	N. succinea	5%↗	4	1%↗	5	5%↗	4	5%↗	5	3%↗	5
	C. volutator	5%↗	3	1%↗	3	10%↗	5	10%↗	3	3%↘	3
	one species		51		18		93		46		31
	one species (bc)		22		7		78		17		7
	all species		0		0		0		0		0
RDA			81		21		99		50		42
	% EXPL.	2.5 à 13.5 %		1.3 à 4.7 %		2.3 à 13.3 %		1.2 à 5.8 %		1.5 à 6.1 %	

Table 3.5. Number of significant ($p<0.05$) *F*-tests (anova) and permutation tests (RDA) in the model 2 simulations (one species = number of cases in which at least one of the selected species showed a significant trend; one species (bc) = the same but Bonferroni-adjusted; all species = number of cases in which all selected species showed a significant trend; %EXPL. = explained variance by constrained RDA-axis).

The results of the simulations where the species composition is changing over time, are given in table 3.5. The arrows point to increasing or decreasing densities, as described in table 3.2.

The power to detect the modeled trends in the densities of the five species separately is low, except in cases of large changes of numerically dominant species (e.g. *C. edule* in simulation 3). In not a single case, changes were found significant for all species. The power of the multivariate analyses was much higher. Notice that the percentage of the variance explained by the time-constrained axis was maximum 13.5%.

Discussion

Although ordination techniques are nowadays widely used in ecological studies, to our knowledge no power considerations have been made yet. But, as expected, our results point to a larger effectiveness of direct gradient analysis to detect changes in time, even if only a minor part of the total variance could be explained. Even the non-corrected probability to find a significant change in at least one of the species by separate analyses of variance became lower than that of the multivariate analysis below a certain rate of change. The power of an analysis of variance only seems to follow that of a multivariate analysis when the rate of change is very large.

Thus, the results are in accordance with the few studies comparing univariate and multivariate methods of data analysis in cases of known anthropogenic effects. Warwick & Clarke (1991) and Clarke & Warwick (1994) give some examples in which multivariate and univariate methods are used for detecting differences in community composition between sites. Multivariate analysis was clearly more sensitive in detecting differences: in the community structure away from the center of drilling activity at the Ekofisk platform in the North Sea, in monitoring the recovery phase of reef corals, and in distinguishing differences in reef-fish assemblages due to mining activity. In a study on the impact of the storm-surge barrier on the benthic fauna of the Oosterschelde, the large year-to-year variations in benthos abundance made it impossible to evaluate the impact of the works on the benthos solely on the basis of observed densities and biomasses before and after the works. A direct gradient analysis, however, proved to be a useful instrument to evaluate how the macrobenthic fauna changed as a result of the

environmental alterations that took place. Particularly species living high or low in the tidal zone were affected by the reduction of the tidal volume (van der Meer 1997a).

The models and analyses considered in this study should be seen as a first contribution to an evaluation of the power of multivariate analysis. As mentioned in the introduction of this chapter, the power of a statistical test is dependent on several factors: the α level, the sample size and variance, the effect size, the scenario of change (Slob 1987, Stevens 1992, van der Meer 1997b).

In the present study we did not explore the influence of setting different type I errors. Using a more liberal type I error will result in a higher power. The coefficients of variation at the start of the modeled time-series varied between 0.5 and 3.2 ($cv = s / \bar{x}$) and are normal values for the Westerschelde estuary (figure 3.3). For many species the effect sizes, i.e. the back-transformed differences between the maximum and minimum density, were very large (table 3.6), some of them not to be expected in the real world. Only a linear change in log-transformed densities was considered. Different patterns of change have a different chance of being detected (Gerrodette 1987, Nicholson and Fryer 1992).

The power of multivariate analyses should not only be compared with that of analyses of variance of single species but other community quantities (total density, total biomass, productivity, for example) should be considered as well. These community parameters might have less long-term fluctuations than the densities of the constituent species, and the coefficients of variation are much smaller than those of the population densities (Heip and Herman 1985, Herman and Heip 1986).

f-value :	0.10	0.05	0.03	0.01	0.001
C. edule	170.22	13.05	4.67	1.67	1.05
P. elegans	706.32	26.58	7.16	1.93	1.07
T. marioni	465.59	21.58	6.32	1.85	1.06
A. marina	1.83	1.35	1.20	1.06	1.01
M. balthica	19.23	4.39	2.43	1.34	1.03

Table 3.6. Effect sizes of the model 1 simulations.

As the error terms in the model 2 simulations are unrelated to each other, in contrast to the model 1 simulations, we expected the data in the model 2 simulations to contain more unrelated information than in the model 1 simulations and, therefore, to find a larger power in the model 2 simulations. This was not the case (compare the model 2 simulations 1, 2 and 5 with the model 1 simulations 2, 4 and 3). The reason must be searched in the fact that the order of magnitude of the covariance matrix was more or less equal to that of the standard deviations. Indeed, using the error formula of model 2 in the model 1 simulations, did not markedly change the results of the Redundancy Analysis (e.g. with a *f*-value of 0.03, the power of the RDA-analysis was 0.44).

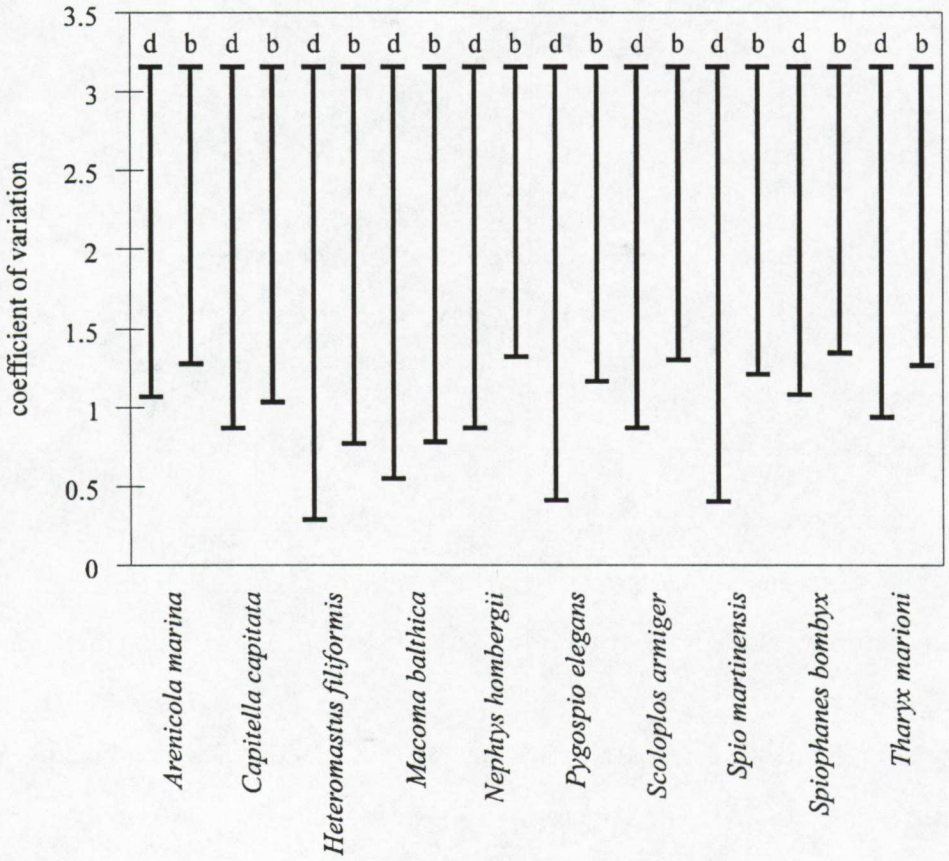


Figure 3.3. Range of coefficients of variation of (log) density (d) and (log) biomass (b) values recorded for some dominant species in the Autumn and Spring surveys in the Westerschelde estuary (data 1992-1997).

In canonical analysis using a single explanatory variable, the coordinates of the species along the first axis (species scores, loadings) provide a ranking along that variable. Tables 3.7 gives

the species scores for one the 2nd model 2 simulation (in cases of significant permutation tests). Thus, species that increased in density over the 10 years have the same sign as the variable year (year had always a zero score along the second axis), species decreasing in density the

T. marioni	*C. edule*	*A. marina*	*C. volutator*	*N. succinea*	Year
-0.0606	0.1456	0.0129	-0.251	0.0936	-
-0.2321	-0.2522	-0.0631	0.0135	0.03	+
0.1339	-0.02	0.0011	-0.0358	-0.1913	-
0.1956	0.0154	0.0632	0.0044	0.045	-
0.2264	-0.0882	0.066	0.067	0.0851	-
0.2158	0.0009	0.1904	0.0797	0.0507	-
-0.1706	-0.1671	0.0193	-0.0499	0.0044	+
-0.1882	-0.1433	0.0259	-0.027	-0.0813	+
0.1368	0.0471	0.0395	-0.033	-0.1551	-
-0.1406	0.1057	-0.0643	-0.2652	0.1323	-
-0.1727	-0.1219	-0.005	0.1882	0.0159	+
0.2357	0.0581	0.0059	-0.1066	0.2628	-
0.2732	0.0593	0.2837	-0.0925	0.0543	-
0.1414	-0.1264	-0.0367	0.0114	-0.2171	+
0.1605	0.2162	0.1053	0.0425	0.1131	-
-0.1876	-0.0137	0.0983	0.2283	-0.0302	-
0.0516	0.2165	0.1362	0.2362	0.0251	-
0.3088	0.0797	-0.0399	0.0621	0.0606	-
-0.1816	0.033	0.1517	0.0091	0.0949	+
-0.0762	0.2087	0.1367	-0.0023	-0.2044	-
0.2389	0.2277	0.05	-0.1361	0.0162	-

Table 3.7. RDA of model 2, simulation 2: species scores and sign of the 'environmental variable' year in the 21 cases with a significant permutation test

opposite sign. For species with low scores inferences are imprecise. The ranking must, therefore, be interpreted with caution. If, for instance, we consider species scores with an absolute value of above 0.1, we see that in most cases the sign of the species is correct (*T. marioni, C. edule* and *A. marina* have the opposite sign as 'year', *C. volutator* and *N. succinea* the same sign). In the 16th case, however, the ranking along the time axis is opposite to the modeled trends. Measures of the percentage fit due to the environmental variables per species and (for unimodal methods) the tolerances for species (the standard deviation for each species along an axis) provided by e.g. the program CANOCO may help in the interpretation (Legendre and Legendre 1998).

The model simulations presented were based on data from the monitoring program as performed in the different water systems of the southwest Netherlands. During each survey, 10 stations are sampled within three or four depth strata within quite large subareas of each water system. Thus, the sampling design does not take into account spatial variation in e.g. sediment structure, wave exposure, etc. Part of the within-year variability is, therefore, due to the spatial heterogeneity of the areas sampled. The power of a time series analysis might be increased using covariables, removing part of the error variance. Some of these covariables (e.g. sediment grain size distributions, pigment concentrations, organic C- and N-content, height, current velocity calculated from existing hydrodynamical models) might be obtained at a low cost compared to the cost of sampling and analysing the benthos. The efficiency of this approach should be tested with existing data. The approach to consider covariables also has the advantage that, in principle, the cause of any change detected could be traced more easily.

Alternatively, or in addition to the previous approach, one could reconsider the sampling design. The current design could be compared with one in which one monitors smaller, more homogeneous areas. The assignment of such areas could be based on the relationship between the biotic patterns and the environment. The data that became available during the years of monitoring certainly allow such analysis for the different water systems. They also add more information of the natural fluctuations of benthic populations. When smaller areas are monitored, more samples could be taken enabling higher precision of the estimates. Probably, several spatial scales should be considered as suggested by Underwood (1993). Monitoring a few indicator species at a limited number of fixed stations would allow sufficient power to detect changes and to relate them to changes in the environment. Monitoring a larger spatial scale would allow an extrapolation of the results obtained at the fixed stations to the whole system.

References

Bilyard, G.R. 1987. The value of benthic infauna in marine pollution monitoring studies. Marine Pollution Bulletin **18**:581-585.

Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth, 144 pp.

Cohen, J. 1969. Statistical power analysis for the behavioral sciences. Academic Press, London. 415pp.

Craeymeersch, J. A. 1994. Effects of a 4m beam trawl on the benthic fauna of the Belgian Continental Shelf (Flemish Banks). Pages 209-236 *in* S. J. de Groot and H. J. Lindeboom, editors. Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea.,, Netherlands Institute for Sea Research NIOZ RAPPORT 1994 - 11 / Netherlands Institute for Fisheries Research RIVO-DLO REPORT C026/94.

Dallal, G. E. 1988. Design: a supplementary module for SYSTAT and SYGRAPH. SYSTAT, Inc., Evanston, Il.

Fairweather, P.G. 1991. Statistical power and design requirements for environmental monitoring. Australian Journal of Marine and Freshwater Research **42**:555-567.

Fryer, R. J., and M. D. Nicholson. 1993. The power of a contaminant monitoring programme to detect linear trends and incidents. ICES Journal of Marine Science **50**:161-168.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. 298pp.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology **68**:1364-1372.

Gittins, R., editor. 1985. Canonical analysis: a review with applications in ecology. Springer, Berlin. 351pp.

Heip, C., and P. M. J. Herman. 1985. The stability of a benthic copepod community. Pages 255-264 *in* P. E. Gibbs, editor. Proceedings of the 19th European Marine Biology Symposium. Cambridge Univ. Press, Cambridge.

Herman, P. M. J., and C. Heip. 1986. The predictability of biological populations and communities: an example from the meiobenthos. Hydrobiologia **142**:281-290.

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijkswijk. 244pp.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen. 299pp.

Legendre, P., and L. Legendre, editors. 1998. Developments in Environmental Modelling, 20: Numerical Ecology. Second English Edition. Elsevier B.V., Amsterdam. 851pp.

Nicholson, M. D., and R. J. Fryer. 1992. The statistical power of monitoring programmes. Marine Pollution Bulletin **24**:146-149.

Pearson, T. H. 1997. Improvements to long term benthic studies. Pages 91-98 *in* B. F. Keegan, P. J. D. Lambshead, B. C. Coull, M. Overcash and C. Nolan, editors. Change in marine benthos: the case for long-term studies. Office for Official Publications of the European Communities, Luxembourg.

Pearson, T.H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: an Annual Review **16**:229-311.

Peterman, R.M., and M.J. Bradford. 1987. Statistical power of trends in fish abundance. Can. J. Fish. Aquat. Sci. **44**:1879-ÑÞ89.

>Sheth, J. N. 1977. What is multivariate analysis? Pages 3-10 *in* J. N. Sheth, editor. Multivariate methods for market and survey reserach. American Marketing Association, Chicago.

Slob, W. 1987. Strategies in applying statistics in ecological research. Ph.D. dissertation, Free University Press, Amsterdam. 112pp.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research, 2nd Edition. Freeman and Co, San Francisco. 859pp.

Stevens, J. 1992. Applied multivariate statistics for the social sciences, 2nd Edition. Lawrence Eribaum Associates, Inc., Hillsdale, New Yersey. 552pp.

ter Braak, C. J. F. 1988. CANOCO - an extension of DECORANA to analyze species-environment relationships. Vegetatio **75**:159-160.

Toft, C.A., and P.J. Shea. 1983. Detecting community-wide patterns: estimating power strengthens statistical inference. The American Naturalist **122**:618-625.

Underwood, A. J. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Australian Journal of Ecology **18**:99-116.

van der Meer, J. 1997a. A handful of feathers. Studies on the estimation and modelling of temporal and spatial fluctuations in the numbers of birds and their prey. PhD Thesis, Rijksuniversiteit Groningen, Groningen. 262pp.

—-. 1997b. Sampling design of monitoring programmes for marine benthos: a comparison between the use of fixed versus randomly selected stations. Journal of Sea Research **37**:167-179.

Warwick, R. M., and K. R. Clarke. 1991. A comparison of some methods for analysing changes in benthic community structure. Journal of the Marine Biology Association of the United Kingdom **71**:225-244.

Wilkinson, L. 1988. SYSTAT, the system for statistics. SYSTAT, Evanston, Illinois.

CHAPTER 4

Spatial patterns of the macrobenthic infauna of the Westerschelde estuary

Introduction

The Westerschelde is the estuarine part of the river Scheldt. It is the only remaining true estuary of the so-called delta region in the south-west of the Netherlands, formed by the rivers Rhine, Meuse and Scheldt. The other estuaries have been totally or partially enclosed and altered into freshwater, brackish and marine lakes or lagoons.

The Scheldt is the smallest of the three rivers with an average freshwater inflow of about 100 m^3s^{-1}. This low inflow results in a rather large residence time, about 75 days (Heip 1988, Soetaert and Herman 1995). Consequently the salinity zones in the estuary are relatively stable, shifts occurring according to the freshwater inflow. In the most maritime zone complex sediment transport occurs through a system of flood and ebb channels. Every tide sediment is resuspended, resuspension being highest with incoming tides The tidal currents are strongest in the eastern part of the Westerschelde. The turbidity maximum caused by the flocculation of organic matter is situated at the low salinity part of the estuary downstream Antwerpen (Postma 1976, Heip 1988, 1989).

The Scheldt estuary is heavily contaminated with heavy metals and organic micropollutants as a result of large domestic, industrial and agricultural waste-water discharges (Billen et al. 1988, van Zoest and van Eck 1991, Zwolsman and van Eck 1993). Close to the turbidity maximum, the oxygen concentration is very low (0-20% saturation), mainly due to the heavy loading with ammonia and organic material, causing high microbial activity (Duursma et al. 1988, Heip 1988, Hummel et al. 1988, Heip and Herman 1995).

The estuary has an important function for navigation. Thus, there is an intense dredging in the Westerschelde to maintain the channel to the port of Antwerpen. Yearly, about 8 million m^3 of sediment has to be dredged (Vroon et al. 1997). As the main channel will be deepened in the next years, dredging activities will further increase.

The estuarine gradients result in differences in the major biological processes and biota. Spatial patterns related to differences in salinity, water depth, turbidity, dissolved oxygen and sediment composition have been reported for the zooplankton (Soetaert and van Rijswijk 1993), the meiobenthos (Van Damme et al. 1980, Li and Vincx 1993, Soetaert et al. 1994, 1995), the hyperbenthos (Mees and Hamerlynck 1992, Mees et al. 1993), and the epibenthic invertebrates and demersal fish (Hamerlynck et al. 1993).

The distribution of macrobenthic animals has been studied by Wolff (1973), Vermeulen and Govaere (1983), Meire et al. (1991) and Ysebaert et al. (1993, 1998). Ysebaert and Meire (1991) summarised all data obtained in the period 1965-1990, but the consequent analysis was hampered by the different sampling methodologies used and the low spatial resolution. The data obtained since 1990 within the framework of two ongoing monitoring programmes now allow a re-evaluation of the conclusions of these studies on two items: which communities can be recognised and what are the structural forces which lead to their development. The study also aims at defining biotopes in the Westerschelde estuary.

Mapping of marine biotopes is fundamental to management and nature conservation. A simplified classification of the marine biotopes can help to (Hiscock 1995, Sotheran et al. 1997):

- select and designate specific areas as being of conservation importance;
- identify vulnerable or threatened habitats and associated communities;
- identify sensitive habitats in relation to different human activities;
- assess and compare e.g. species richness between similar biotopes.

Material and methods

Sampling and laboratory analysis

Since 1990, the benthic communities of the inter- and subtidal of the Westerschelde are being surveyed twice a year within the framework of the Dutch national monitoring program. In three subareas divided into four depth strata, samples were taken at 10 stations per depth stratum

during each survey. In spring 1990, only the intertidal was surveyed. During the first two years, the intertidal stations were fixed stations; the subtidal ones were randomly selected with new stations being selected each survey. From 1992 onwards, all stations were randomly selected. Since 1994 the same strategy is followed in a fourth subarea (5 stations per depth stratum), and another 30 intertidal (fixed) stations are being monitoring as well. Thus, almost the whole estuary is covered (fig. 4.1). In total, the dataset used covered 1518 samples taken in the period 1990-1995. More information on the different sampling schemes and the laboratory methods can be found in chapter 2.

Abiotic variables

At all subtidal stations, depth (relative to NAP, the Dutch ordnance level) was recorded at the time of sampling. The depth (or height) of the intertidal stations was obtained from a Geographical Information System (GIS), storing all bathymetric data in the area. Salinity and current velocity estimates were estimated for an average tide with the hydrodynamical model SCALDIS (van der Meulen and Sileon 1997) with a spatial resolution of respectively 400 and 100 meters. Salinity estimates were made for a maximum, a minimum and an average discharge of the river Scheldt. Finally, information on the water depth, the salinity and the tidal currents was available for 1368 stations (figure 4.1).

At 296 of these stations, samples have been taken for sediment analysis. The grain size distribution was determined using a Malvern particle size analyser, and the median grain size estimated. Most of the sediment samples were taken in spring.

All GIS-based estimates and sediment analyses were done at the National Institute of Coastal and Marine Management (Middelburg, the Netherlands).

Data analysis

Samples were classified using TWINSPAN (Hill 1979) based on (non-transformed) species abundances. Cutlevels used were 0, 50, 100, 500, 2500 and 10000. The relationship between species composition and the measured or estimated environmental variables was analysed using

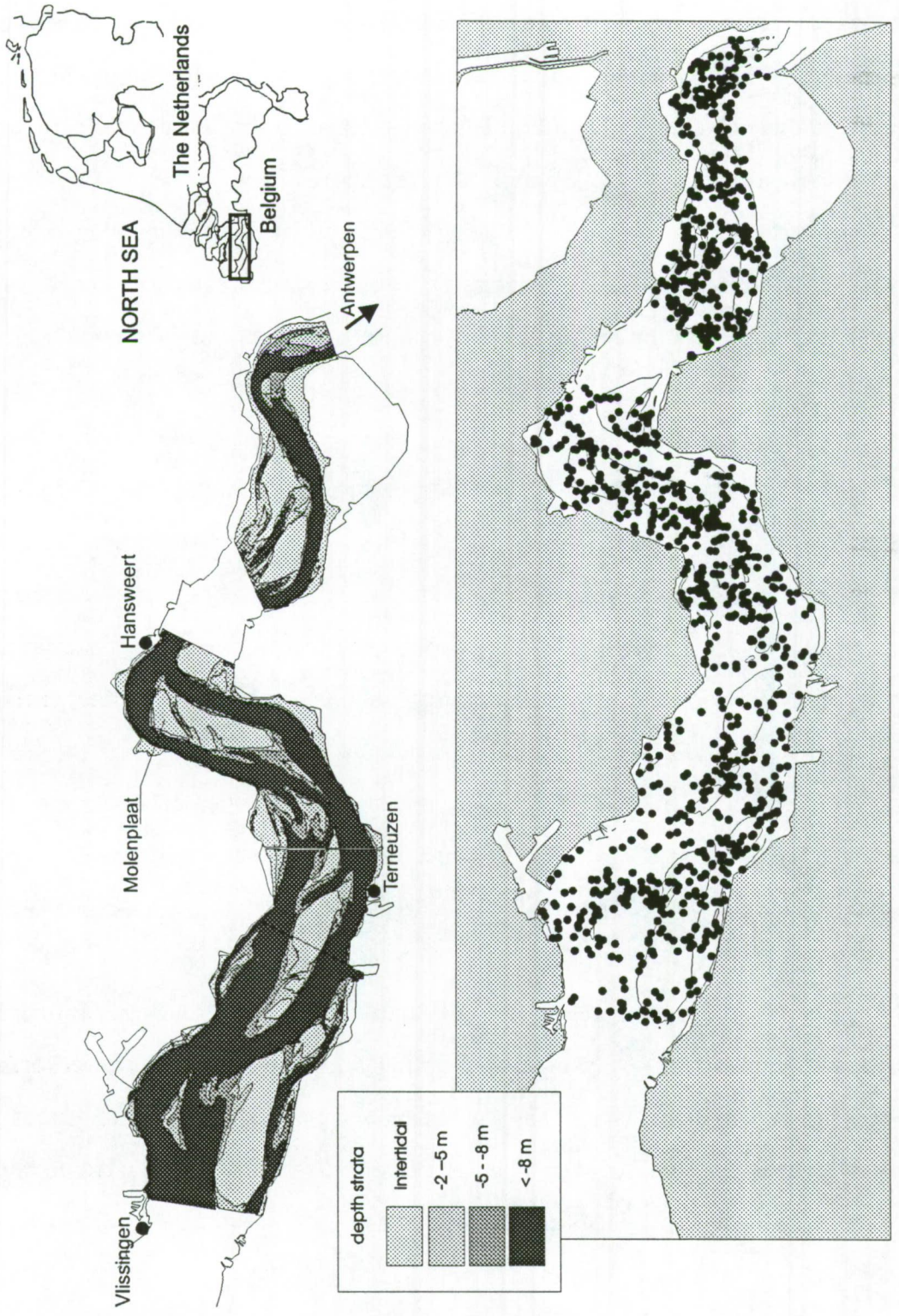


Figure 4.1. Map of the Westerschelde estuary showing the sampling scheme (depth strata) and the sampling localities.

the ordination technique Canonical Correspondence Analysis (CCA) (ter Braak 1986) on the logarithmically transformed density data. The analysis was done twice: once with and once without the sediment variable. More information on these multivariate techniques can be found in chapter 2.

At 148 out of the 1368 sampling locations no macrobenthic animals were found and, thus, these stations were not used in the multivariate analyses. Also, samples with less then 4 species and dominated by mysids (51 samples) and a single station where only a small ophiuroid was found, were excluded from the multivariate analyses. Only species found in at least 10 samples were used. All higher taxa, except for oligochaetes and nemertines (always identified at the phylum level only), were excluded from the multivariate analyses. This resulted in a further exclusion of 7 stations.

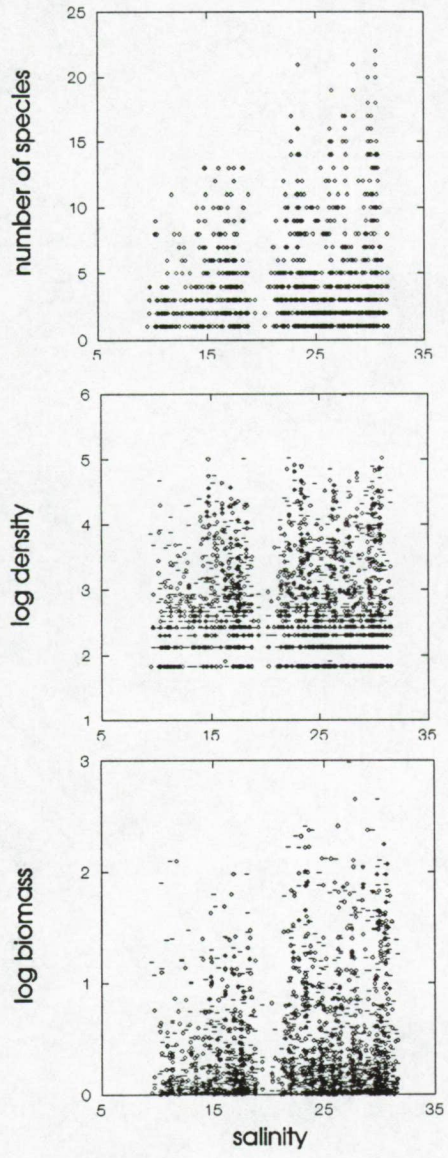


Figure 4.2. Diversity (number of species), (log) total density (ind m^{-2}) and (log) total biomass (gAFDW m^{-2}) along the salinity gradient (stations where no animals were found are omitted).

Results

A total of 110 species were identified. Half of them were polychaetes, a third were arthropods (mostly amphipods) and a fifth were molluscs. Only two echinoderms were found: one individual of the starfish *Asterias rubens*, and one small specimen of an unidentified ophiuroid.

The number of species found in a single sample (including species identified at the generic, family or even a higher taxonomic level) varied between 0 and 22. Almost 90% of the samples had less than 10 species, almost 70% less then 5 species. The most common species were *Heteromastus filiformis* (found in about 50% of the samples), *Pygospio elegans* and *Macoma balthica* (both found in 25% of the samples). The total density ranged from 0 to a maximum of 106000 ind/m^2; 70% of the samples had less then 1000 ind/m^2. The total biomass values ranged from 0 to 445 gAFDW/m^2. The highest values of diversity, total density and total biomass were found in the marine part, decreasing with decreasing salinity (figure 4.2).

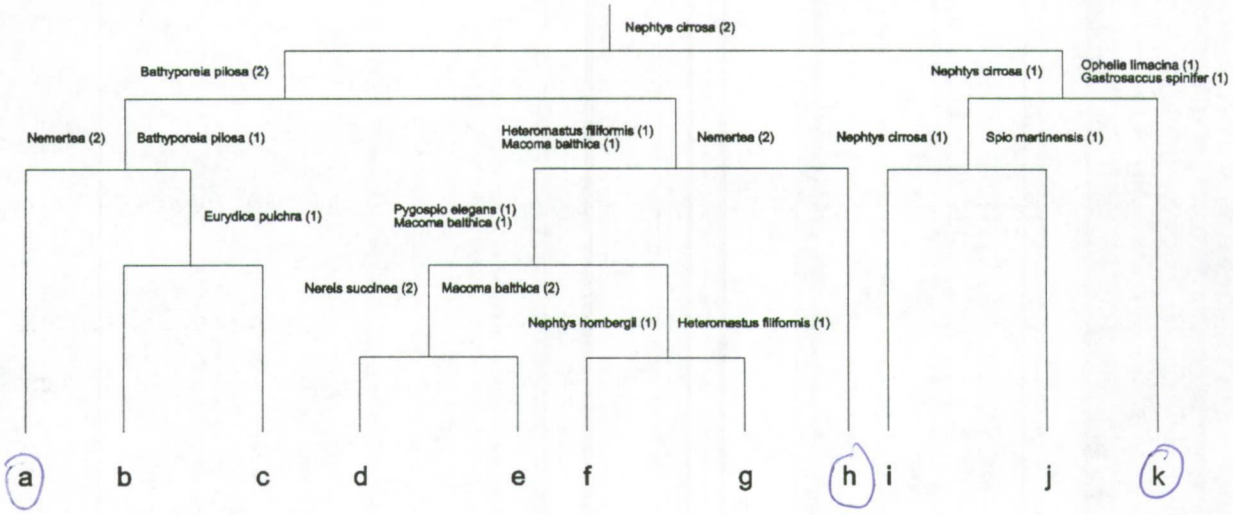


Figure 4.3. TWINSPAN dendrogram based on species densities showing the indicator (pseudo)species.

The results of the TWINSPAN analysis are given in figures 4.3. Figure 4.4 shows the geographical distribution of the identified clusters. The mean densities of the indicator species are given in table 4.1.

First, 266 samples are separated from the rest. Indicator species is *Nephtys cirrosa*. In a further division 17 samples with indicator species *Ophelia limacina* and *Gastrosaccus spinifer* (cluster k) are separated from the rest. Cluster k also has much lower densities of *N. cirrosa* than the

Cluster	a		b		c		d		e		f	
Number of stations	18		149		70		50		310		126	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Bathyporeia pilosa	7	5.1	380	50	1500	300	0	0	83	83	0	0
Eurydice pulchra	15	8.6	7.7	2.16	230	34	0	0	7	3.0	0	0
Gastrosaccus spinifer	11	8.1	8	3.1	23	10.8	0	0	1.1	.93	2.0	1.14
Heteromastus filiformis	11	11.1	86	18.2	14	3.5	910	250	2000	350	180	11
Macoma balthica	0	0	4.8	1.85	15	5.4	7.9	2.70	560	89	30	5.4
Nemertinae indet.	89	10.8	7.7	2.27	9	3.0	1.4	1.39	21	5.0	4.6	1.94
Nephtys cirrosa	0	0	.5	.48	0	0	0	0	2.9	.94	8.0	2.54
Nephtys hombergii	0	0	1.0	.68	2.5	1.45	0	0	16.6	2.94	77	8.2
Nereis succinea	0	0	5	3.7	0	0	580	91	42	11.0	2.0	1.98
Ophelia limacina	7	5.1	0	0	1.0	0.95	0	0	0.23	0.227	0	0
Pygospio elegans	0	0	1.1	.62	50	20.6	440	117	3500	490	130	77
Spio martinensis	0	0	4.3	1.55	2.9	1.63	4.5	2.23	20	5.4	200	47

Cluster	g		h		i		j		k	
Number of stations	148		24		142		107		7	
	mean	se	mean	se	mean	se	mean	se	mean	se
Bathyporeia pilosa	.5	.45	0	0	3.3	2.05	.7	.75	0	0
Eurydice pulchra	2.7	1.41	0	0	3.8	1.30	0	0	13	8.9
Gastrosaccus spinifer	2.7	1.90	0	0	14	8.4	2.2	1.28	113	24.4
Heteromastus filiformis	310	40	4	3.5	26	9.4	20	7.1	0	0
Macoma balthica	1.4	.77	0	0	2.8	1.48	4.5	2.08	0	0
Nemertinae indet.	6.8	2.19	116	20.7	3.3	1.82	4.5	2.33	170	116
Nephtys cirrosa	2.7	1.08	0	0	86	3.5	58	8.1	20	10.2
Nephtys hombergii	2.3	1.18	7	4.8	1.9	.94	8.2	2.78	0	0
Nereis succinea	0	0	0	0	.5	.47	0	0	0	0
Ophelia limacina	0	0	19	6.7	0	0	0	0	75	17.0
Pygospio elegans	1.8	.89	0	0	1.4	.82	0	0	0	0
Spio martinensis	32	14.8	7	4.8	1.4	1.05	360	126	0	0

Table 4.1. Mean density (ind. m^{-2}) and standarderror (se) of the TWINSPAN indicator species.

other samples. The latter further separate into a group with high densities of *Spio martinensis* (cluster j), and a group with the highest densities of *N. cirrosa* (cluster i).

The remaining 895 samples after the first division are separated in a first group of 237 samples and a second group of 658 samples with indicator species *Bathyporeia pilosa*. In the next division of the first group, 18 samples (cluster a) are separated from the rest. They are characterised by nemertines, while *B. pilosa* is almost absent. Also in the next division of the second group, a few samples (24) characterised by nemertines (cluster h) are separated from the rest. The latter group is characterised by *Heteromastus filiformis* and *Macoma balthica.*

The 219 samples remaining from the first group are further separated into a group of 149 samples (cluster b) and a group of 70 samples (cluster c). Indicator species is *Eurydice pulchra*. The 634 samples remaning from the second group are split into a group of 360 samples and a group of 274 samples. Indicator species are *Pygospio elegans* and *Macoma balthica*. This first group can further be divided in a group of 50 samples characterised by *Nereis succinea* (cluster d) and a group of 310 samples (cluster e) with high densities of *Macoma balthica*. The second group is further divided in a group of 126 samples (cluster f) and a group of 148 samples (cluster g) based on differences in the densities of *Nephtys hombergii* and *Heteromastus filiformis*.

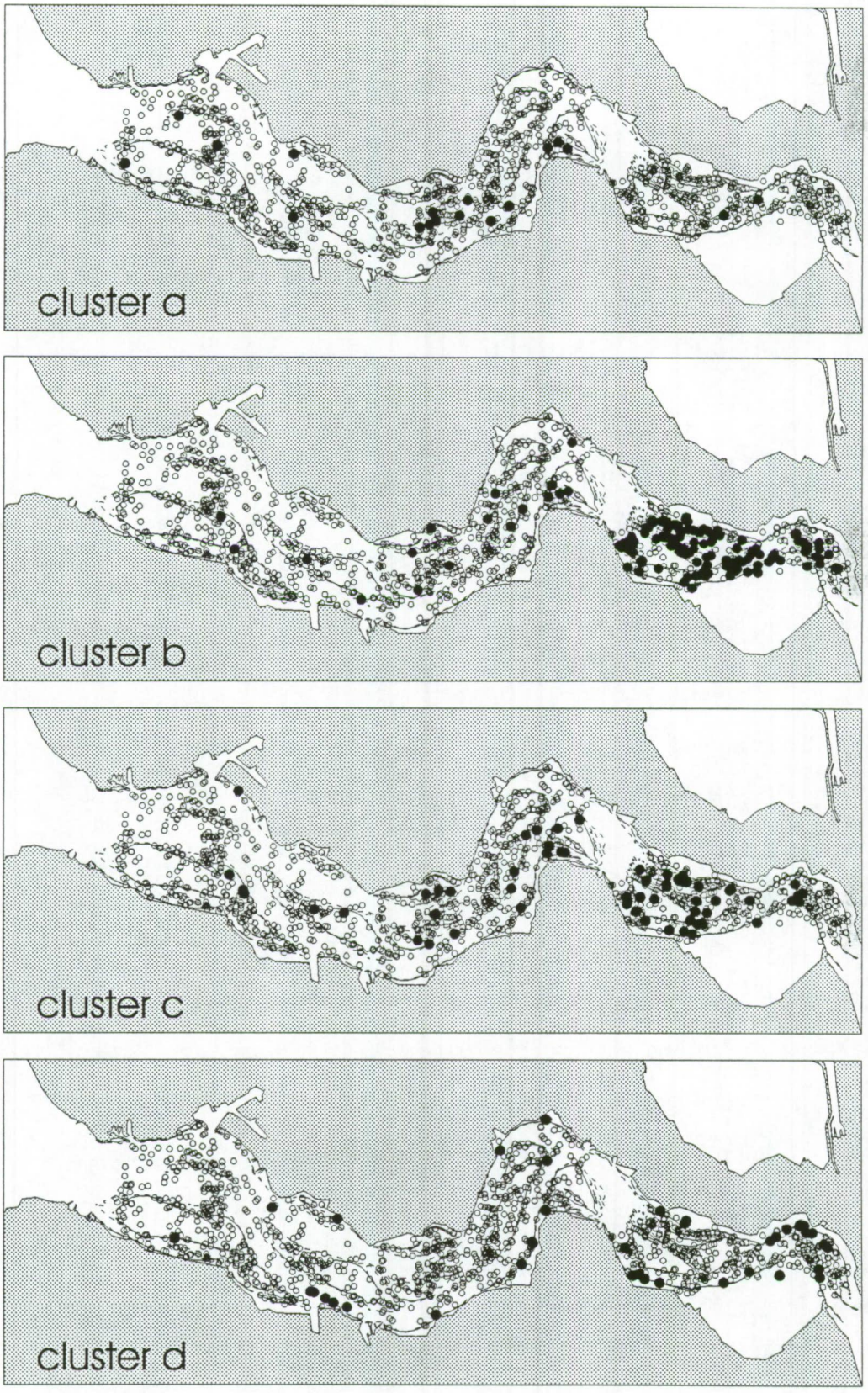


Figure 4.4. Geographical distribution of the TWINSPAN clusters. Each window shows the location of the samples of one cluster (filled circles) and all other samples (open circles).

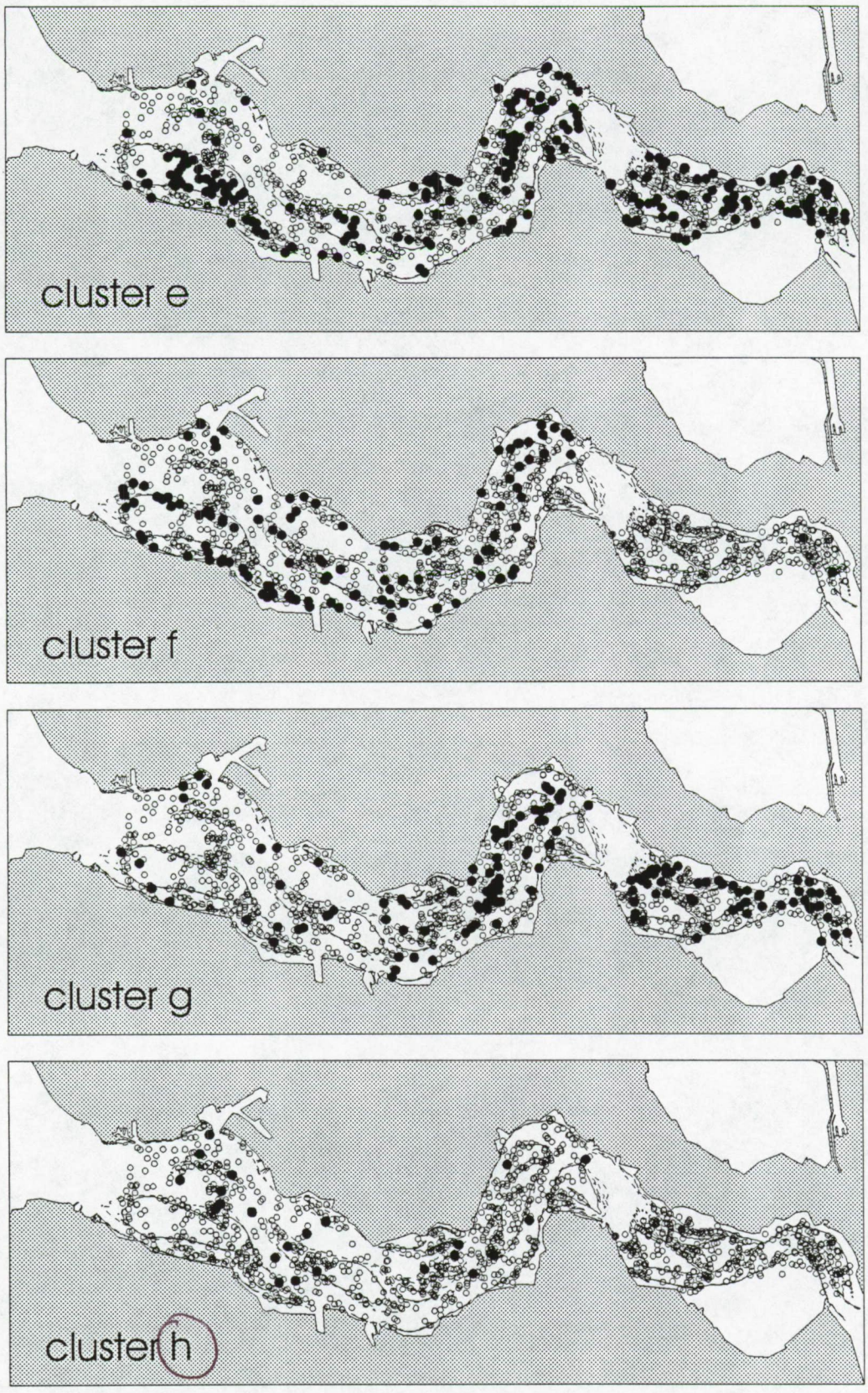


Figure 4.4. Continued.

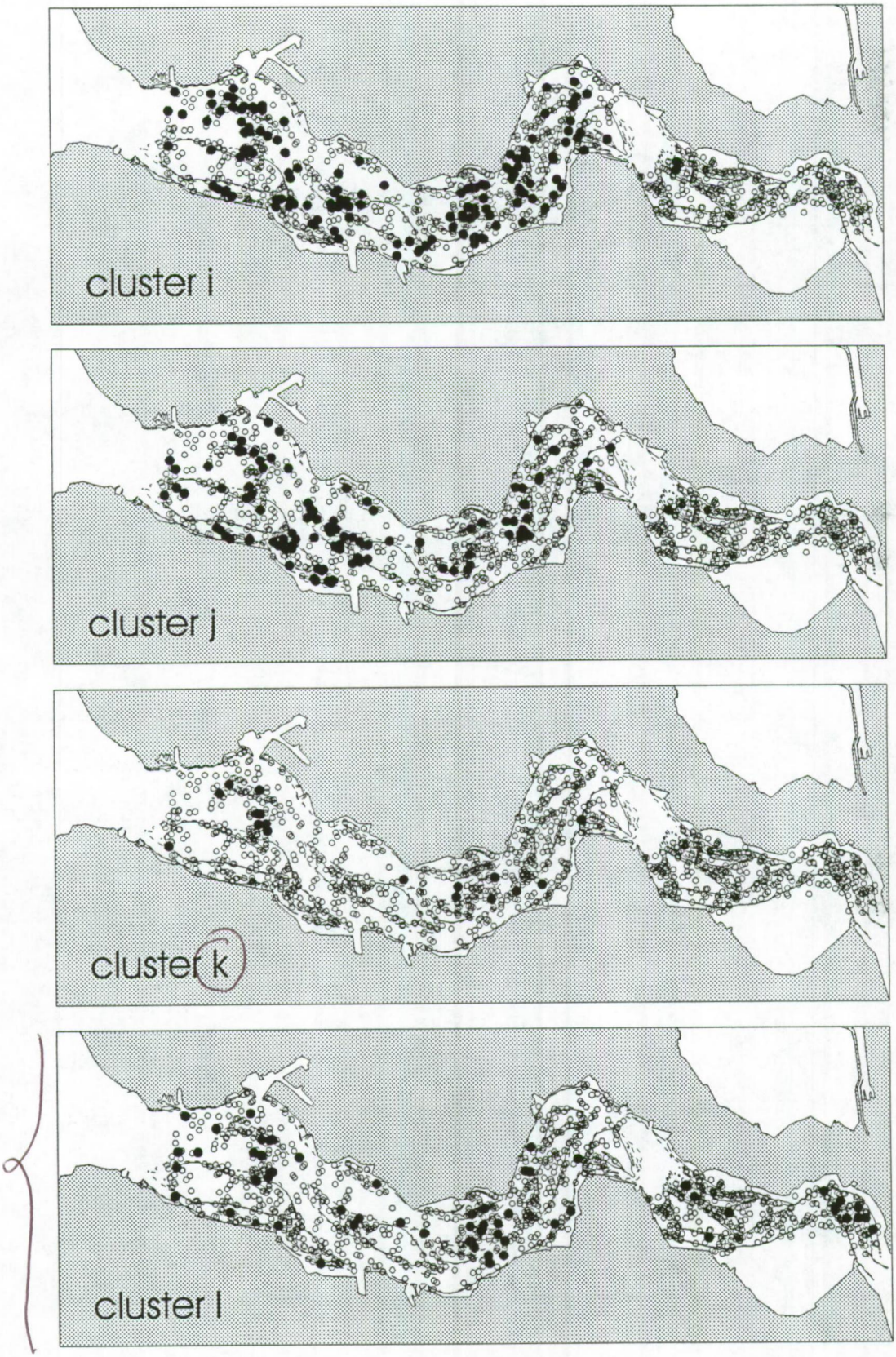


Figure 4.4. Continued.

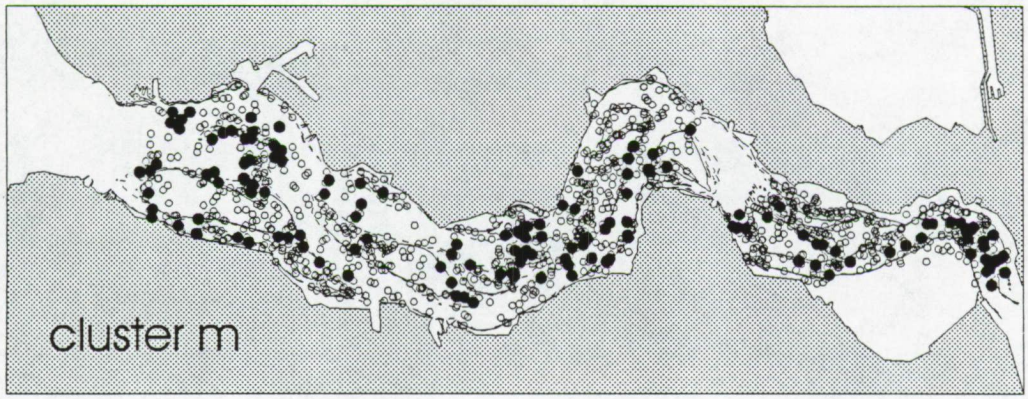


Figure 4.4. Continued.

The stations belonging to clusters a, h and k are mainly found subtidally in the western and middle part of the estuary (figure 4.4). The current velocities are mostly high, and the sediment is much coarser than at stations of the other clusters (figure 4.5). Cluster b is mainly restricted to the brackish zone, and contains shallow locations. Most of the stations of cluster c are situated in the middle and eastern part, and located in the intertidal and shallow subtidal. Cluster e is mainly restricted to the intertidal areas. Current velocities at these stations are generally low, and the sediment is finer than at stations of the other clusters. The cluster is not restricted to a particular area with respect to salinity. Cluster d is, compared to cluster e, situated at locations with coarser sediments and higher current velocities. Cluster g mainly contains subtidal stations; most of them are located in the middle and eastern part. Cluster f is restricted to the western and middle part of the Westerschelde, and current velocities are somewhat lower than at stations of cluster g. Cluster i is restricted to the deeper parts of the marine and transition zone. Compared to cluster i, cluster j is found at locations with lower current velocities and finer sediments. Stations of cluster l (species poor locations, mainly dominated by mysids), are mainly found subtidally, and not restricted with respect to salinity. The same holds for cluster m (stations where no species were found).

The intertidal clusters d and e are by far the richest in species composition, and have the highest densities and biomasses (figure 4.6). Clusters i and l have the lowest diversity and densities, cluster a the lowest biomass.

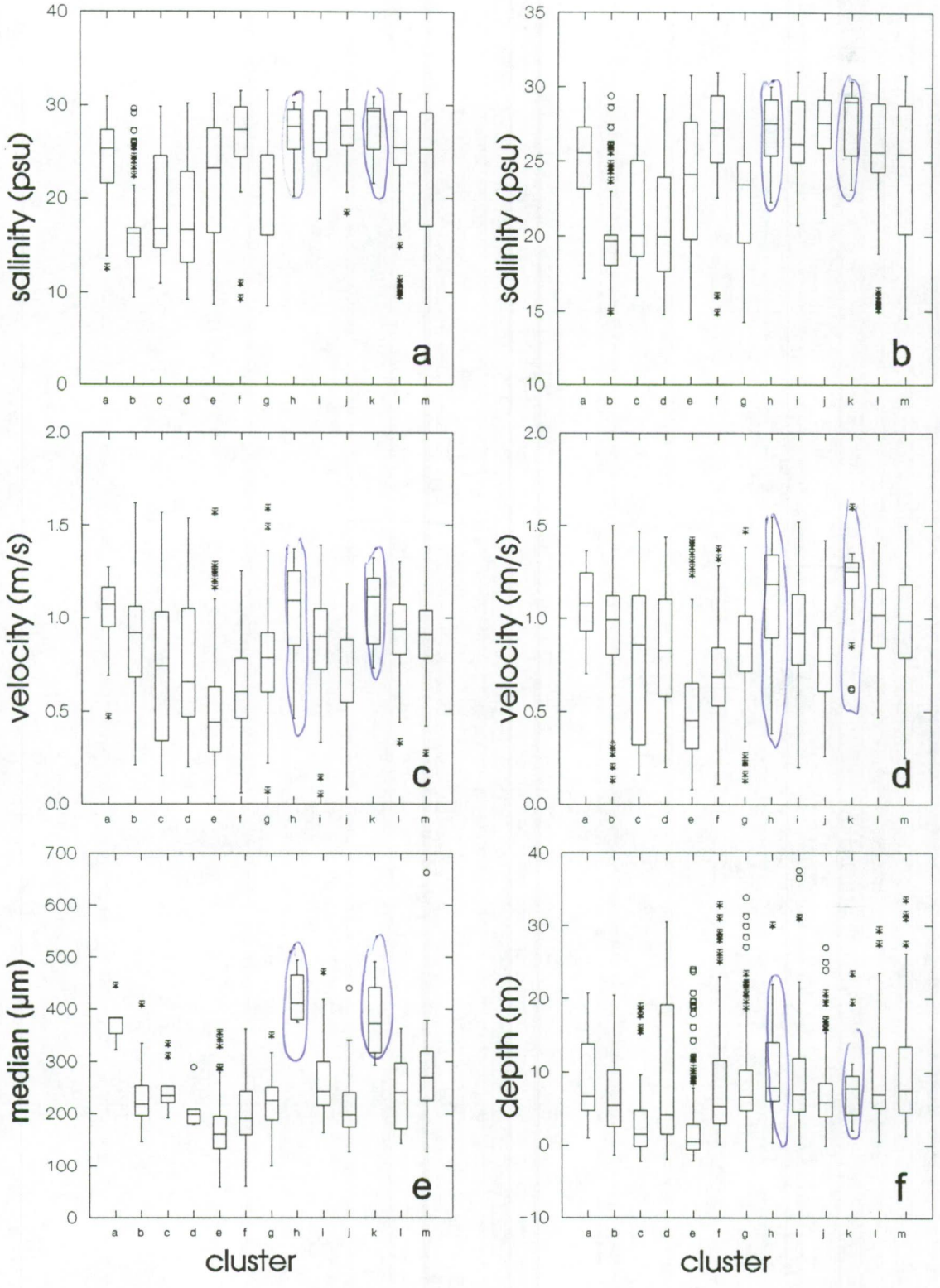


Figure 4.5. Box-and-whisker plots of salinity at maximum (a) and minimum (b) river discharges, maximum current velocities at ebb (c) and flood (d), median grain size (e) and depth (f) for each TWINSPAN cluster.

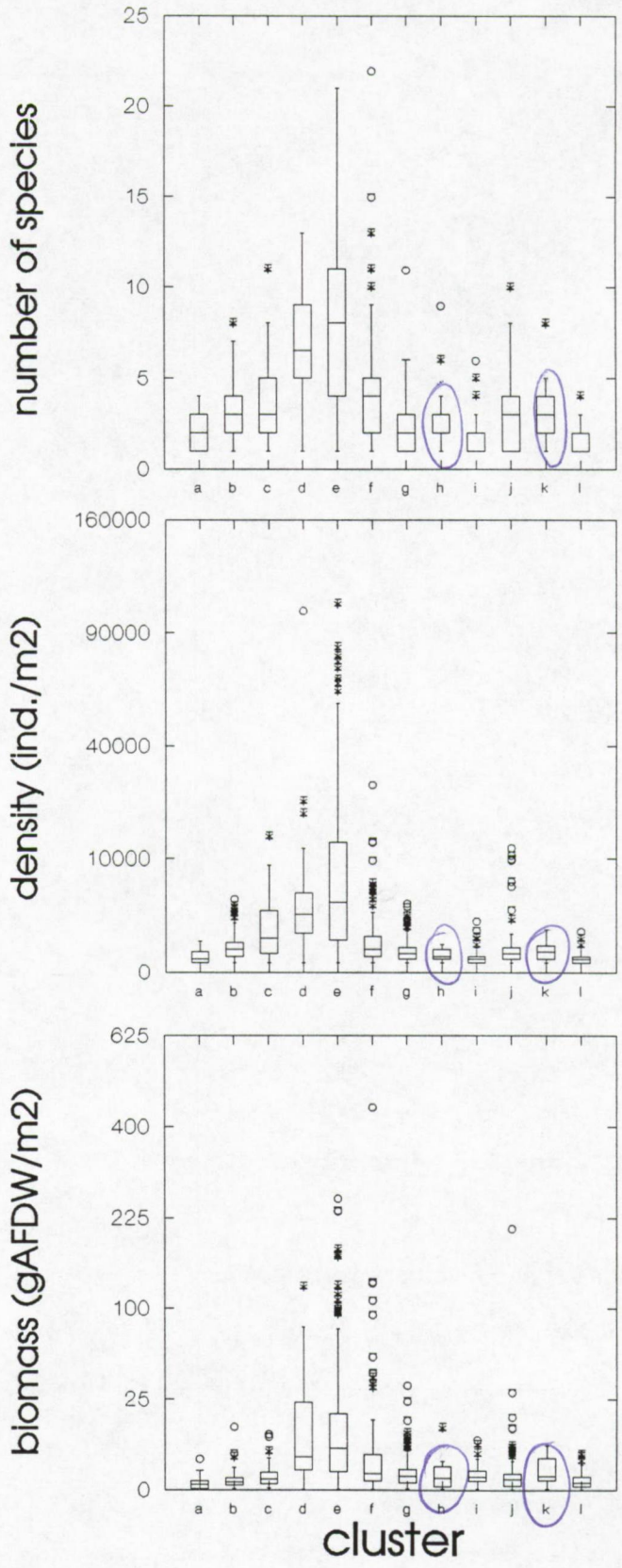
Figure 4.6.

Box-and-whisker plots of

(a) the number of species,

(b) total density, and

(c) total biomass.



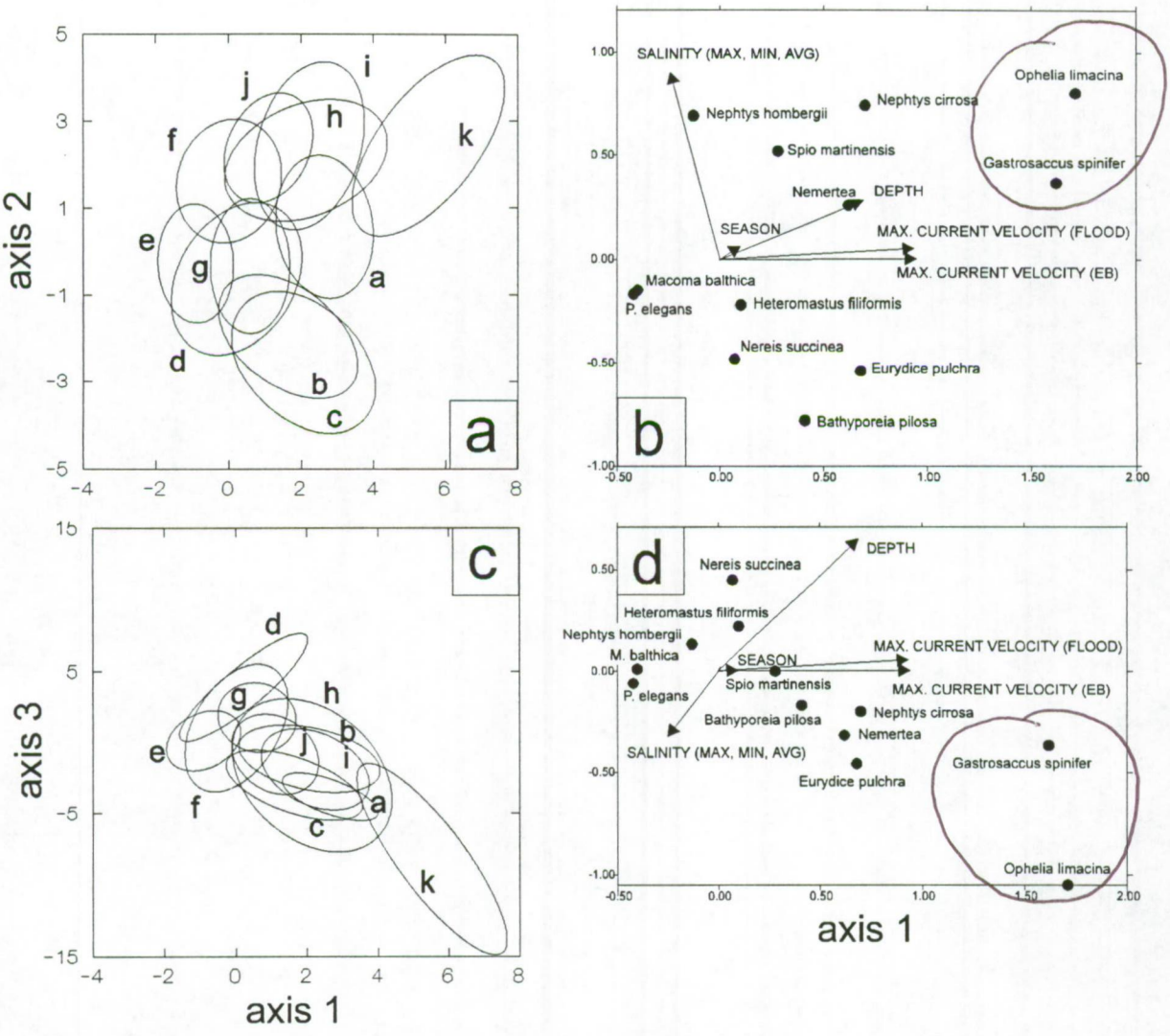


Figure 4.7. CCA ordination diagrams based on the analysis without sediment data. The figures on the left show the 75 percent confidence regions of the sample scores for each cluster; the figures on the right show the indicator species scores and the environmental axes.

The results of the Canonical Correspondence Analyses (CCA) are shown in figures 4.7 (without sediment data) and 4.8 (restricted dataset with grainsize data). The three salinity estimates had almost the same scores and are, therefore, not shown separately.

The total variance explained by the ordination diagrams is very low. The first three axes explained 2.4, 2.1 and 0.8 % in the first analysis, 3.2, 2.8 and 1.5 % in the second analysis. The diagrams show, however, clearly the gradually changing species composition along the measured environmental variables: there is no clear cut between the different TWINSPAN

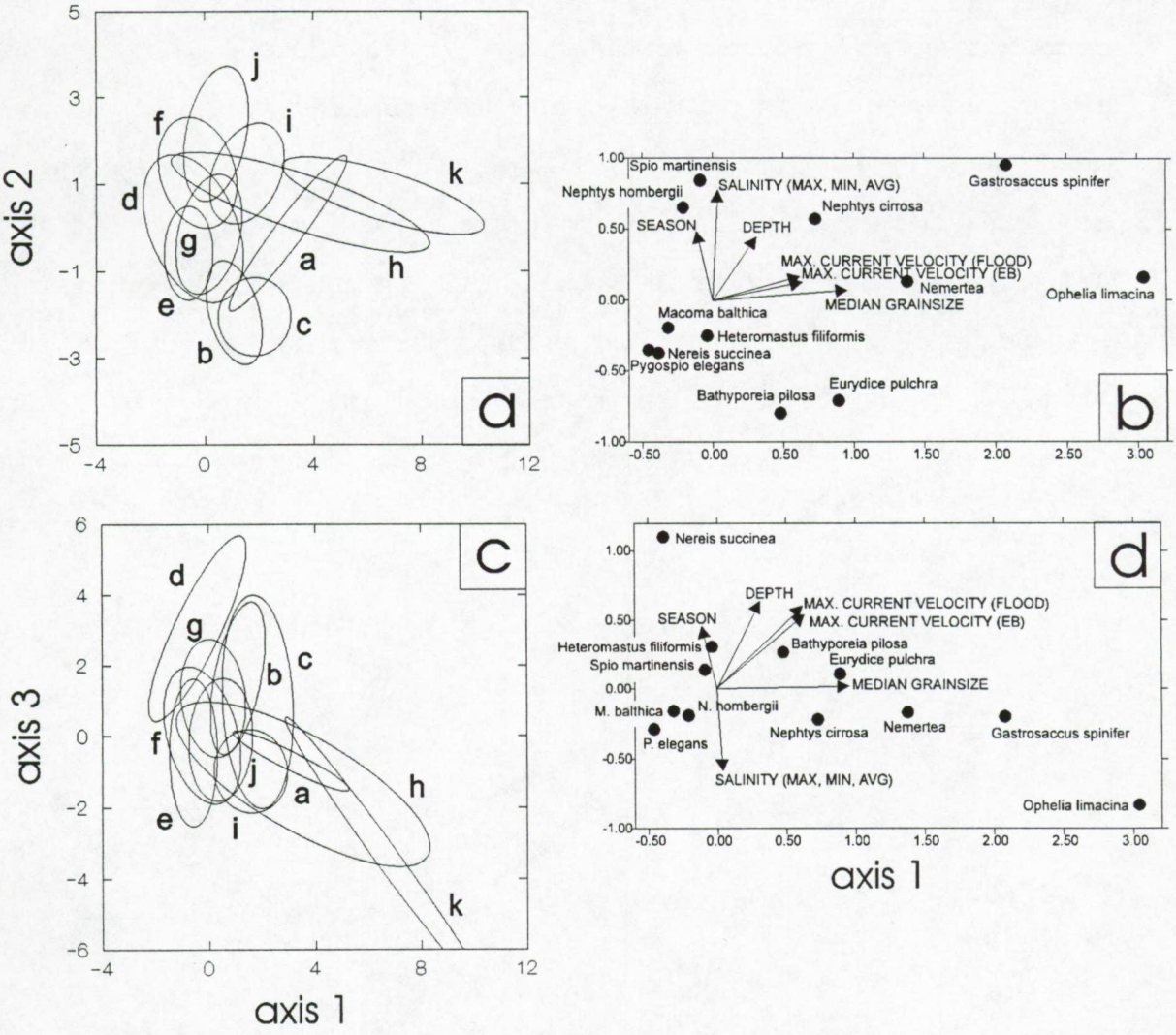


Figure 4.8. CCA ordination diagrams based on the analysis with sediment data. The figures on the left show the 75 percent confidence regions of the sample scores for each cluster; the figures on the right show the indicator species scores and the environmental axes.

clusters. Clusters grouping together at a higher dichotomy (see TWINSPAN dendrogram) largely overlap (e.g. cluster b and c).

The main gradients are a sediment gradient and a salinity gradient. Current velocity strongly correlates with the first CCA axis ($r \approx 0.6$ in the 1st analysis, 0.5 in the second analysis), as does median grain size ($r \approx 0.7$ in the 2nd analysis). Salinity strongly correlates with the second axis ($r \approx 0.6$ in both analyses). The correlation of the third axis is less obvious. There is no strong correlation with any of the environmental variables measured: $r \approx 0.3$ with depth in the 1st analysis, $r \approx 0.3$-0.4 with any variable in the 2nd analysis. The median grain size correlates very

well with the maximum current velocity (fig. 4.8.b): the higher the currents, the coarser the sediment (see also figure 4.9). Salinity and current velocity are not correlated. Only in the lower salinity range (up to 15 psu) maximum values of the maximum current velocity increase with increasing salinity (fig. 4.9). In the ordination diagrams both gradients are nearly perpendicular (figure 4.7 and 4.8). Maximum current velocities also increase with increasing depth (fig. 4.9), but the depth range where specific current velocities are found is larger for higher currents than for lower currents. Maximum depth increases with salinity: the deepest stations are located near the mouth of the estuary. Thus, the depth gradient is nearly parallel with either the current velocity gradient (same direction) or the salinity gradient (opposite direction).

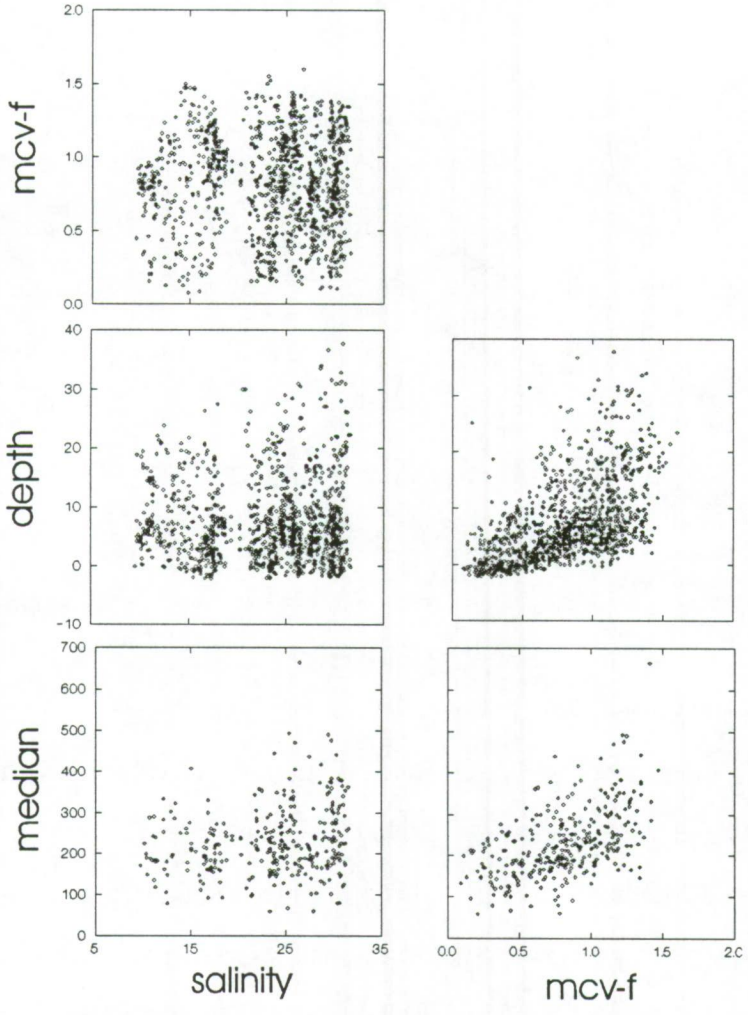


Figure 4.9. Scatterplots of maximum current velocity at flood (mcv-f; m/sec) against salinity (psu), and median grainsize (μm) and depth (m) against salinity and maximum current velocity at flood.

As the ordination diagrams are very similar, further interpretation has been done on the largest dataset (fig. 4.7). The first axis (explaining most of the variance) correlates with the maximum current velocities and, thus, represents a gradient in the hydrodynamical conditions at the locations sampled. Stronger currents, and, hence, coarser sediments, are found at deeper locations. The second axis represents the salinity gradient. In the first ordination plane (formed by axis 1 and 2), the deeper stations with the highest current velocities (cluster k) are situated in the upper right corner. The most brackish stations with intermediate currents (clusters b and c) are located in the lower part of the ordination diagram, the stations with the lowest hydrodynamics (cluster e) are situated left in the CANOCO space. Clusters j and i differ along the depth and currents gradients, clusters f and g along the salinity gradient. Seasonal changes are not important in explaining the main differences in species composition.

Specific preferences of the species for an environmental variable can be extracted from the ordination diagrams by orthogonally projecting the species position on the environmental axis. A species as *Ophelia limacina* is restricted to the coarser sediments in the marine part of the estuary, *Bathyporeia elegans* to the more dynamical sediments in the brackish part. *Macoma balthica* and *Pygospio elegans* are mainly found intertidally, and have a broad tolerance for salinity. The specific preferences are represented as box-and-whisker plots in figure 4.10, showing the median distribution, the 10% and 90% occurrences as well as the total range along which the species were observed.

Discussion

The majority of the benthic macrofaunal species have a pelagic larval stage. But, although many of the adults can swim, they all depend on the seabed. Thus, there is a strong relationship between the species composition and the environmental conditions at the seabed. Estuaries have strongly pronounced gradients of many physico-chemical parameters. They show a large temporal variability in these gradients induced by factors such as tides and river discharge. The most obvious is the salinity gradient. Many abiotic factors (nutrients, suspended matter) change in parallel with this in an upstream/downstream fashion. The magnitude of fluctuations is larger

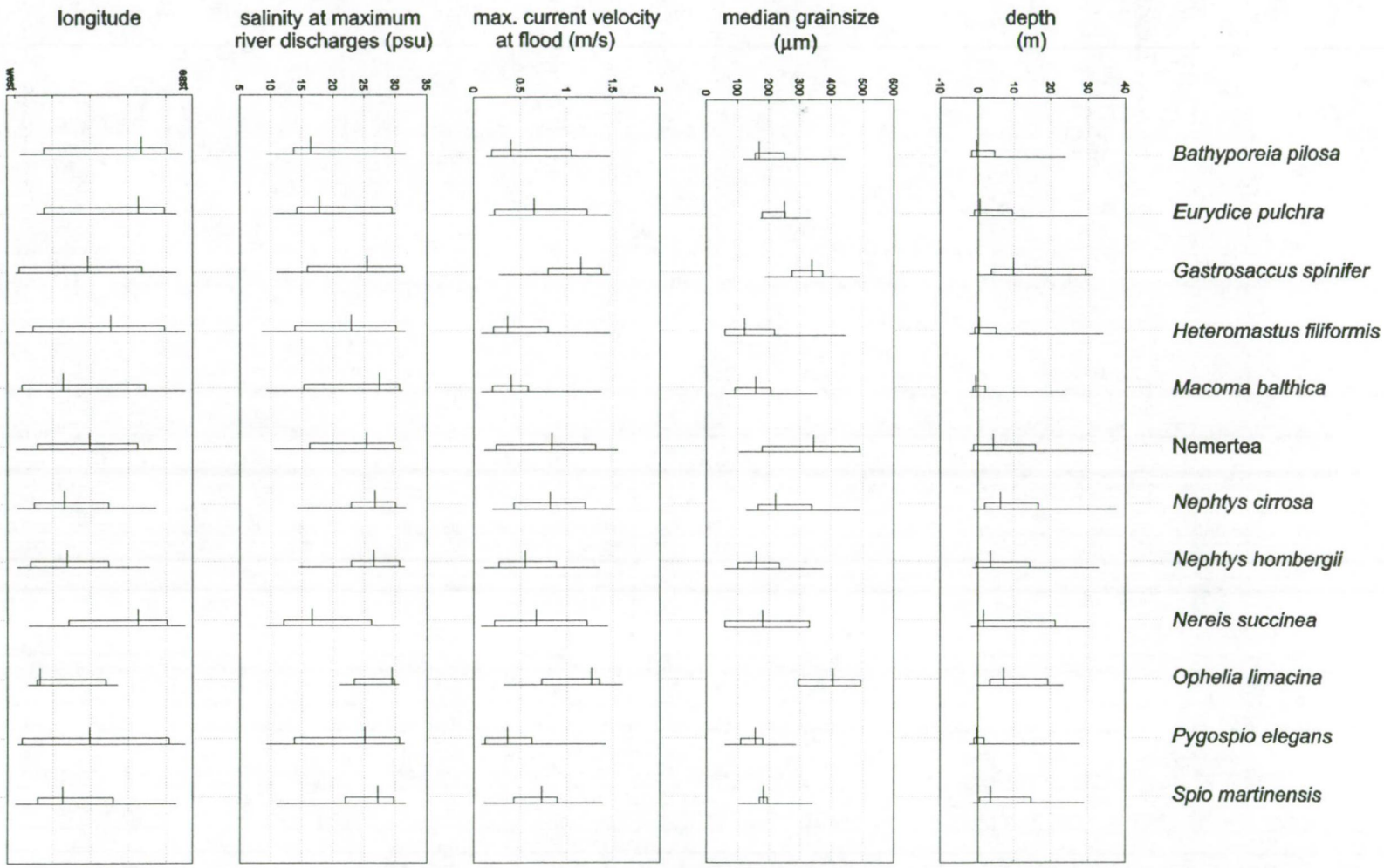


Figure 4.10. Distributional characteristics of the TWINSPAN indicator species. Indicated are the total range (horizontal line), the median occurrence (vertical dash) and the 10 to 90% occurrence (horizontal bar).

upstream than downstream. Other gradients are related to depth and sediment conditions. Not all macrobenthic species are adapted to the same specific conditions. Several publications have shown trends in diversity, density, biomass and species composition along the salinity gradient. The highest diversity and density are found in the more saline parts. In most studies there is also a trend from lower biomass in the upper estuarine regions to higher biomass in the more downstream parts (see e.g. review by Heip et al. 1995). These trends are also found in the Westerschelde estuary (figure 4.2). It should be noticed that locations with low diversity, density and biomass values or even without macrobenthic life are found along the whole estuarine gradient (figures 4.2 and 4.4, TWINSPAN cluster m).

A complete review of the major gradients in the Westerschelde estuary, and in estuarine benthic habitats in general (Heip et al. 1995), was difficult to make up to now because of a biased selection of stations and sampling schemes. The monitoring surveys in the estuary as realised since 1990 covered both the intertidal and the subtidal, and enabled a re-examination of the relationship between species composition and the major abiotic gradients. The CCA confirmed the strong relationships between the macrobenthic assemblages and the natural gradients in the Westerschelde estuary. The main forces are the hydrodynamic conditions (resulting in differences in sediment stability and composition) and salinity. As a result, some of the identified assemblages are restricted to either the brackish or marine part of the estuary, or to the inter- or subtidal sediments, or to a particular sediment type. But, as can be seen in the ordination diagrams, there are no abrupt changes in the species composition. Therefore, seriation is a more appropriate term to describe the benthic community structure then the more common term zonation (Clarke et al. 1993).

The importance of salinity and sediment in structuring the macrobenthic communities of the Westerschelde has been reported previously (Wolff 1973, Vermeulen and Govaere 1983, Meire et al. 1991, Ysebaert and Meire 1991, Ysebaert et al. 1993, 1998), as has been shown for other estuaries (Sanders et al. 1965, Boesch 1973, Holland et al. 1987, Jones et al. 1990, Warwick et al. 1991, Mannino and Montagna 1997, Rakocinski et al. 1997). This study shows that, in the

Westerschelde estuary, the hydrodynamical regime, determining sediment stability and sediment characteristics such as grain size and organic content, is even more important than the salinity gradient. The first CCA axis clearly represents a current velocity/sediment gradient. The second CCA axis, nearly orthogonal to the first one, represents a salinity gradient.
The fact that the reduced space only accounts for a small fraction of the variance does not mean it is useless and non-representative for the main gradients (Legendre and Legendre 1998). When picking 100 times a random sample of 100 samples, the first three axes of a CCA without sediment data explained 7.1 – 10.4 % of the total variance. When picking out random samples of 10 samples, the variance explained increased to 42.1 – 69.6%. However, in 55 cases the relationship between the species and the environmental variables was not statistically significant.

In estuaries with different physical conditions, the relative importance of both gradients might be different. Thus, Warwick et al. (1991) related changes in species composition within the Severn estuary to differences in sediment granulometry. Also Boesch (1973) related spatial patterns of species distribution in the Hampton Roads Area, Virginia, USA to differences in the substrate. In other estuaries, the community structure was more strongly correlated with salinity distribution than sediment characteristics (Jones et al. 1990, Mannino and Montagna 1997, Rakocinski et al. 1997). However, most of these studies were restricted to either the intertidal or to the subtidal; at least in part of these studies, this may have influenced conclusions on the relative importance of hydrodynamics and salinity. Indeed, focussing only on the intertidal macrobenthos of the Westerschelde, Ysebaert et al. (1993) concluded that the distribution of the species was mainly controlled by salinity.

Management and conservation of the estuarine environment requires information on the habitats and biotopes (Hiscock 1995, Sotheran et al. 1997). In the Westerschelde estuary, the clusters identified can be summarised into 5 biotopes. The mean density and biomass of all species in each biotope are given in appendices 1 and 2.
A first biotope (clusters a, h, k, l and m) is found subtidally along the whole estuary. Current velocities are highest, preventing small particles from settling there (Oenema et al. 1988).

Species diversity, total density and total biomass are very low. At many locations, no animals were found. At others, mainly hyperbenthic animals such as mysids were observed. The most coarse sediments (clusters a, h and k) are also characterised by nemerteans, the mysid *Gastrosaccus spinifer* and, restricted to the more saline waters, the polychaete *Ophelia limacina*. *G. spinifer* lives near or partially buried in the bottom (Tattersall and Tattersall 1951), and is a typical member of the hyperbenthic fauna of the shallow coastal waters and the Westerschelde (Mees 1994). *O. limacina* typically lives in clean sands devoid of fine particles (Bellan and Dauvin 1991, Dauvin et al. 1993).

A second biotope is found subtidally in the marine part of the estuary up to Hansweert (clusters i and j). Compared to biotope 1, current velocities are lower. The characteristic species, *Nephtys cirrosa,* is also typical for the sandy areas with a low mud content in the Southern Bight down to about 20m depth (Holtmann et al. 1996). As such, this biotope can be seen as an intrusion of the North Sea biotope. As in biotope 1, the diversity, total density and total biomass are low. A further subdivision of this cluster can be made along the hydrodynamical gradient. The shallower, less dynamic parts are characterised by *Spio martinensis*.

Most of the stations of a third biotope (clusters b and c) are situated in the intertidal and shallow subtidal of the brackish part of the estuary. The biotope is characterised by the very mobile amphipod *Bathyporeia pilosa*. It lives in the upper sediment layer and is able to swim (Nicolaisen and Kanneworff 1969, Khayrallah and Jones 1980a, b). Current velocities and grain size are as in biotope 2. Diversity, density and biomass are low.

The latter also holds for the fourth biotope (clusters f and g) situated mainly subtidally along the whole estuary. Current velocities are lower than in biotopes 1 and 2. This biotope can be further divided along the salinity gradient, with *Nephtys hombergii* as characteristic species for the more marine subdivision. Densities of *Heteromastus filiformis* are highest in the brackish subdivision.

The fifth biotope (cluster d and e) is situated intertidally. Here, current velocities are the lowest, sediments the finest. Diversity, density and biomass are much higher than in the other biotopes. It has been shown previously that the intertidal flats of the Westerschelde harbour most of the benthic life (e.g. Meire et al. 1991), and, apparently, hydrodynamic conditions are better there than subtidally (Heip et al. 1995).

Biotope five correlates with the low dynamic, intertidal areas as defined by Huijs (1995) (her geomorphological groups P1b and P1c). The high dynamic areas (P2) appear to fall into biotopes 3 and 4. Huijss (1995) further divided both types according to differences in morphology and sediment composition (silt content). The spatial resolution of the data used in the present study does not allow a comparison of the species composition within these geomorphological units. In a recent study on the Molenplaat, an intertidal flat in the middle of the Westerschelde, a first division could be made between stations characterised by a very dynamic sandy substrate where megaripples were found, and the rest of the tidal flat (Herman et al. 1996). The first group of stations is situated in the high dynamic areas of Huijs (1995), and falls into biotope 4 (cluster f) identified in this study. The second group - fitting into our biotope 5 (and, more specific, cluster e) - could further be divided according to the bottom shear stress. Benthic suspension feeders are most abundant in the zone of lowest bottom shear stress (and lowest current velocities) probably depending on the sinking material (Herman et al. 1996). Deposit feeders dominate the other stations. Thus, also at lesser current speeds benthic animals are influenced by hydrodynamics, probably through a control on food supply.

The present study provided insight in the structure of the intertidal and subtidal macrobenthos of the Westerschelde on a macro-scale, i.e. on the scale of the whole estuary. The patterns of the Molenplaat study on a meso-scale (1-100 m) fit well with ours, probably because both appear generated by physical processes. Future studies should, therefore, examine whether the results of the Molenplaat can be extrapolated to other tidal flats or not. The positive relationship that has been suggested between the suspension-feeders' biomass and current velocities might not be generally valid. Legendre et al. (1997), for instance, found greater abundances of most size classes of two bivalve species where flood shear stress was higher. The best hydrodynamical conditions for suspension feeders might, thus, not always be the same. Spatial patterns might also be the result of local biological processes (e.g. activity of predators, adult/juvenile interactions). There is, however, increasing evidence that biologically generated patterns are important at a micro-scale (1m) but are unlikely to appear at a macro- or meso-scale (Herman et al. 1996, Legendre et al. 1997, McArdle et al. 1997, Thrush et al. 1997).

Land reclamation and dredging activities in the last decades, resulted in an increase of the total area and height of the banks along the central axis of the estuary, but in less low dynamic, silty intertidal areas (Mol et al. 1997, Vroon et al. 1997). Further geomorphological changes can be expected with an increase in dredging activities in the near future. In this paper, we documented that the hydrodynamic regime appears to be the main structuring force. Thus, we might be able to predict the impact on the benthos.

However, the relationships found in this study might not longer be valid under the new conditions. Many benthic species, for instance, show a post-settlement movement following primary settlement. In the Westerschelde estuary the most important factor determining a successful primary settlement of the bivalves *Cerastoderma edule* and *Macoma balthica* is most likely the local hydrodynamic regime (Bouma and Herman 1998). Primary settlement is almost restricted to areas with low current velocities. Secondary settlement is possible in the more dynamic areas where, probably, feeding conditions are better. Thus, the most favourable areas for primary and secondary settlement differ. If the loss of suitable areas for primary settlement is restricted, secondary settlement could still occur by active or passive migration from other areas. If favourable conditions for primary settlement are missing, this will certainly have influences on the overall community structure.

Changes in the community structure could also be due to changes of a factor not included in the present study. The system-averaged benthic biomass, mostly dominated by suspension feeders, is strongly dependent on the system primary production (Herman et al. in press). If the total suspended matter for some reason strongly decreases, the total primary production would increase, as might the biomass of suspension feeders. Moreover, high-above sediment concentrations of algae will no longer be restricted to areas with relatively low current velocities. Consequently, suspension feeders too could have a wider or even a different distribution. The most favourable areas under the new regime could differ from those under the present regime. Finally, macrobenthic populations are not passively undergoing the influence of their environment. The animals change their own environment and interact between each other. More information is, therefore, needed about the processes and mechanisms leading to the spatial distribution of benthic communities.

References

Bellan, G., and J.-C. Dauvin. 1991. Phenetic and biogeographic relationships in *Ophelia* (Polychaeta, Opheliidae). Bulletin of Marine Science **48**:544-558.

Billen, G., C. Lancelot, E. De Becker, and P. Servais. 1988. Modelling microbial processes (phyto- and bacterioplankton) in the Schelde estuary. Hydrobiological Bulletin **22**:43-55.

Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads Area, Virginia. Marine Biology **21**:226-244.

Bouma, H., and P. M. J. Herman. 1998. De invloed van fysische omgevingsfactoren op de vestiging, handhaving en groei van bodemdieren. Inzichten voor inrichting- en beheermaatregelen op basis van veld- en literatuuronderzoek. Rijksuniversiteit Groningen, Vakgroep Mariene Biologie; Nederlands Instituut voor Oecologisch Onderzoek, Centrum voor Estuariene en Mariene Oecologie. Rapportage in kader van het project SEBES in opdracht van Rijkswaterstaat, RIKZ. 82 pp.

Clarke, K. R., R. M. Warwick, and B. E. Brown. 1993. An index showing breakdown of seriation, relation to disturbance,in a coral-reef assemblage. Marine Ecology Progress Series **102**:153-160.

Dauvin, J.-C., D. Bellan-Santini, and G. Bellan. 1993. Les genres *Ophelia* et *Ampelisca* de la région de Roscoff: exemples d'allotopie et de syntopie dans les communautés marines de substrat meuble. Cahier de Biologie Marine **34**:1-15.

Duursma, E. K., A. G. A. Merks, and J. Nieuwenhuize. 1988. Exchange processes in estuaries such as the Westerschelde, an overview. Hydrobiological Bulletin **22**:7-20.

Hamerlynck, O., K. Hostens, R. V. Arellano, J. Mees, and P. A. Van Damme. 1993. The mobile epibenthic fauna of soft bottoms in the Dutch Delta (South-West Netherlands): spatial structure. Neth. J. Aquat. Ecol **27**:343-358.

Heip, C. 1988. Biota and abiotic environment in the Westerschelde estuary. Hydrobiological Bulletin **22**:31-34.

—. 1989. The ecology of the estuaries of Rhine, Meuse and Scheldt in The Netherlands. *In* J. D. Ros, editor. Topics in Marine Biology. Scientia marina **53**: 531-541.

Heip, C., and P. M. J. Herman. 1995. Major biological processes in European tidal estuaries: a synthesis of the JEEP-92 Project. Hydrobiologia **311**:1-7.

Heip, C. H. R., N. K. Goosen, P. M. J. Herman, J. Kromkamp, J. J. Middelburg, and K. Soetaert. 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanography and Marine Biology: an Annual Review **33**:1-149.

Herman, P., M. de Vries, P. Thoolen, M. Vonk, A. Baart, and J. Boon. 1996. Micro-macro. Een onderzoek naar de relatie tussen hydrodynamische factoren en kleinschalige verspreiding van macrobenthos. BEON Rapport nr. 96-5, part 4.

Herman, P. M. J., J. J. Middelburg, J. van de Koppel, and C. H. R. Heip. in press. Ecology of estuarine macrobenthos. Advances in Ecological Research.

Hill, M. O. 1979. TWINSPAN. A FORTRAN program for arranging Multivariate data in an Ordered Two-Way Table by Classification of the Individuals and Attributes. Ecology and Systematics, Cornell University, Ithaca, 90 pp.

Hiscock, K., editor. 1995. Classification of benthic marine biotopes of the north-east Atlantic. Proceeding of a BioMar-Life workshop held in Cambridge, 16-18 November 1994. Joint Nature Conservation Committee, Peterborough. 105pp.

Holland, A. F., A. T. Shaughnessy, and M. H. Hiegel. 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. Estuaries **10**:227-245.

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijkswijk.

Huijs, S. W. E. 1995. Geomorfologische ontwikkeling van het intergetijdegebied van de Westerschelde, 1935-1989. Rapport R 95-3, Universiteit Utrecht, Fakulteit Ruimelijke Wetenschappen, Vakgroep Fysische Geografie. 56pp.

Hummel, H., G. Moerland, and C. Bakker. 1988. The concomitant existence of a typical coastal and a detritus food chain in the Westerschelde estuary. Hydrobiological Bulletin **22**:35-41.

Jones, K. K., C. A. Simenstad, D. L. Higley, and D. L. Bottom. 1990. Community structure, distribution, and standing stock of benthos, epibenthos, and plankton in the Columbia River Estuary. Prog. Oceanog. **25**:211-241.

Khayrallah, N. H., and A. M. Jones. 1980a. The ecology of *Bathyporeia pilosa* (Amphipoda: Haustoriidae) in the Tay estuary. I. Factors influencing the distribution on Tayport and Tentsmuir beaches. Proceedings of the Royal Society of Edinburgh **78B**:109-119.

—. 1980b. The ecology of *Bathyporeia pilosa* (Amphipoda: Haustoriidae) in the Tay estuary. II. Factors affecting the micro-distribution. Proceedings of the Royal Society of Edinburgh **78B**:121-130.

Legendre, P., and L. Legendre, editors. 1998. Developments in Environmental Modelling, 20: Numerical Ecology. Second English Edition. Elsevier B.V., Amsterdam. 853pp.

Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. Journal of Experimental Marine Biology and Ecology **216**:99-128.

Li, J., and M. Vincx. 1993. The temporal variation of intertidal nematodes in the Westerschelde. I. The importance of an estuarine gradient. Neth. J. Aquat. Ecol **27**:319-326.

Mannino, A., and P. A. Montagna. 1997. Small-scale spatial variation of macrobenthic community structure. Estuaries **20**:159-173.

McArdle, B. H., J. E. Hewitt, and S. F. Thrush. 1997. Pattern from process: it is not as easy as it looks. Journal of Experimental Marine Biology and Ecology **216**:229-242.

Mees, J. 1994. The hyperbenthos of shallow coastal waters and estuaries: community structure and biology of the dominant species. PhD Thesis, University of Gent, Zoology Institute, Marine Biology Section. 212pp.

Mees, J., and O. Hamerlynck. 1992. Spatial community structure of the winter hyperbenthos of the Schelde estuary, the Netherlands, and the adjacent coastal waters. Netherlands Journal of Sea Research **29**:357-370.

Mees, J., A. Dewicke, and O. Hamerlynck. 1993. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. Netherlands Journal of Aquatic Ecology **27**:359-376.

Meire, P. M., J. J. Seys, T. J. Ysebaert, and J. Coosen. 1991. A comparison of the macrobenthic distribution and community structure between two estuaries in SW Nehterlands. Pages 221-230 *in* M. Elliott and J.-P. Ducrotoy, editors. Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen & Olsen, Fredensborg.

Mol, G., A. M. van Berchum, and G. M. Krijger. 1997. De toestand van de Westerschelde aan het begin van de verdieping 48'/43'. Beschrijving van trends in de fysische, biologische en chemische toestand. Rijkswaterstaat. Rapport RIKZ-97.049. 51pp.

Nicolaisen, W., and E. Kanneworff. 1969. On the burrowing and feeding habits of the amphipods *Bathyporeia pilosa* Lindström and *Bathyporeia sarsi* Watkin. Ophelia **6**:231-250.

Oenema, O., R. Stekener, and J. Reynders. 1988. The soil environment of the intertidal area in the Westerschelde. Hydrobiological Bulletin **22**:21-30.

Postma, H. 1976. Sediment transport and sedimentation in the estuarine environment. Pages 158-179 *in* G. H. Lauff, editor. Estuaries. American Association for the Advancement of Science Publication, Washington.

Rakocinski, C. F., S. S. Brown, G. R. Gaston, R. W. Heard, W. W. Walker, and J. K. Summers. 1997. Macrobenthic responses to natuaral and contaminant-related gradients in northern Gulf of Mexico estuaries. Ecological Applications **7**:1278-1298.

Sanders, H. L., P. C. J. Mangelsdorf, and G. R. Hampson. 1965. Salinity and faunal distribution in the Pocasset River, Massachusetts. Limnology and Oceanography (Suppl.) **10**:R216-R229.

Soetaert, K., and P. M. J. Herman. 1995. Estimating estuarine residence times in the Westerschelde (The Netherlands) using a box model with fixed dispersion coefficients. Hydrobiologia **311**:215-224.

Soetaert, K., and P. van Rijswijk. 1993. Spatial and temporal patterns of the zooplankton in the Westerschelde estuary. Marine Ecology Progress Series **97**:47-59.

Soetaert, K., M. Vincx, J. Wittoeck, M. Tulkens, and D. Van Gansbeke. 1994. Spatial patterns of Westerschelde meiobenthos. Estuarine, Coastal and Shelf Science **39**:367-388.

Soetaert, K., M. Vincx, J. Wittoeck, and M. Tulkens. 1995. Meiobenthic distribution and nematode community structure in five European estuaries. Hydrobiologia **311**:185-206.

Sotheran, I. S., R. L. Foster-Smith, and J. Davies. 1997. Mapping of benthic habitats using image processing techniques within a raster-based Geographic Information System. Estuarine, Coastal and Shelf Science **44 (Supplement A)**:25-31.

Tattersall, W. M., and O. S. Tattersall. 1951. The British Mysidacea. The Ray Society, London. 460pp.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

Thrush, S. F., V. J. Cummings, P. K. Dayton, R. Ford, J. Grant, J. E. Hewitt, A. H. Hines, S. M. Lawrie, R. D. Pridmore, P. Legendre, B. H. McArdle, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult/juvenile interactions. Journal of Experimental Marine Biology and Ecology **216**:153-169.

Van Damme, D., R. Herman, Y. Sharma, M. Holvoet, and P. Martens. 1980. Benthic studies of the Southern Bight of the North Sea and its adjacent continental estuaries. Progress Report II: fluctuations of the meiobenthic communities of the Westerschelde estuary. ICES CM/L 23: 131-170.

van der Meulen, A., and M. Sileon. 1997. Overzicht van modellenin gebruik bij het RIKZ en het RIZA. Rijkswaterstaat, Rapport RIKZ-97.008. 109pp.

van Zoest, R., and G. T. M. van Eck. 1991. Occurrence and behaviour of several groups of organic micropollutants in the Scheldt estuary. The Science of the Total Environment **103**:57-71.

Vermeulen, Y. M., and J. C. R. Govaere. 1983. Distribution of benthic macrofauna in the Western Scheldt estuary (the Netherlands). Cahier de Biologie Marine **14**:297-308.

Vroon, J., C. Storm, and J. Coosen. 1997. Westerschelde, stram of struis? Eindrapport van het Project Oostwest, een studie naar de beïnvloeding van fysische en verwante biologische patronen in een estuarium.Rijkswaterstaat, Rijksinstituut voor Kust en Zee. Rapport RIKZ-97.023. 106 pp.

Warwick, R. M., J. D. Goss-Custard, R. Kirby, C. L. George, N. D. Pope, and A. A. Rowden. 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn estuary different? Journal of Animal Ecology **28**:329-345.

Wolff, W. J. 1973. Zoölogische Verhandelingen, No. 126: The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Brill, Leiden. 242pp.

Ysebaert, T., and P. Meire. 1991. Het macrozoöbenthos van de Westerschelde en de Beneden Zeeschelde. Rijksuniversiteit Gent, Laboratorium voor Ecologie der Dieren / Instituut voor Natuurbehoud. Rapport W.W.E. 12 / Rapport I.N. A92.085. 184pp.

Ysebaert, T., P. Meire, D. Maes, and J. Buijs. 1993. The benthic macrofauna along the estuarine gradient of the Schelde estuary. Netherlands Journal of Aquatic Ecology **27**:327-341.

Ysebaert, T. G., P. Meire, J. Coosen, and K. Essink. 1998. Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. Aquatic Ecology **32**:53-71.

Zwolsman, J. J. G., and G. T. M. van Eck. 1993. Dissolved and particulate trace metal geochemistry in the Scheldt estuary, S.W. Netherlands (water column and sediments). Netherlands Journal of Aquatic Ecology **27**:287-300.

Appendix 1. Mean density (ind./m^2) and standarderror (se) in the five biotopes identified in the Westerschelde.

Biotope	1		2		3		4		5	
Number of samples	266		249		219		274		360	
	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	.5	.38	0	0	9	6.3	1.1	.69
Abra spec.	0	0	0	0	0	0	0	0	.4	.37
Abra tenuis	0	0	0	0	0	0	0	0	6	5.7
Achelia echinata	.10	.097	0	0	0	0	0	0	0	0
Actiniaria indet.	1.2	.81	.27	.269	0	0	12	6.2	10	4.0
Amphitrite spec.	0	0	0	0	0	0	.24	.243	0	0
Anaitides mucosa	0	0	.5	.38	0	0	.7	.42	6.5	2.59
Anaitides spec.	0	0	.27	.269	0	0	0	0	.32	.231
Anoplodactylus petiolatus	0	0	0	0	0	0	.24	.243	0	0
Arenicola marina	0	0	.5	.38	0	0	2.4	.76	10.7	1.74
Asterias rubens	0	0	0	0	0	0	.24	.243	0	0
Autolytus langerhansi	0	0	0	0	0	0	0	0	.29	.185
Autolytus spec.	0	0	0	0	0	0	1.5	1.46	0	0
Barnea candida	0	0	0	0	0	0	.5	.34	.9	.68
Bathyporeia elegans	0	0	0	0	1.5	1.10	0	0	0	0
Bathyporeia pelagica	0	0	0	0	5.5	1.69	1.2	.64	1.9	1.00
Bathyporeia pilosa	1.0	.50	2.2	1.20	210	107	.24	.243	270	68
Bathyporeia sarsi	.8	.75	0	0	4.3	2.54	1.5	.91	29	6.3
Bathyporeia spec.	.25	.251	.8	.46	39	9.4	.24	.243	2.1	.65
Bivalvia indet.	.25	.251	.27	.269	0	0	.5	.34	5.5	2.63
Bodotria pulchella	0	0	0	0	0	0	.5	.34	.37	.262
Bodotria scorpioides	0	0	.27	.269	0	0	.24	.243	0	0
Capitella capitata	.25	.251	8.1	2.75	3.3	1.31	30	8.3	33	6.6
Capitellidae indet.	0	0	.27	.269	.3	.30	0	0	.30	.216
Caprellidae indet.	0	0	0	0	0	0	0	0	.29	.185
Carcinus maenas	0	0	.27	.269	.20	.100	.24	.243	3.9	.91
Caridea indet.	0	0	.5	.38	0	0	0	0	4	3.9
Cerastoderma edule	0	0	.8	.81	1.0	.48	5	3.3	280	50
Cerastoderma spec.	0	0	0	0	0	0	.24	.243	0	0
Corophium arenarium	0	0	0	0	3.7	1.76	0	0	230	61
Corophium bonnelli	0	0	0	0	0	0	0	0	.7	.74
Corophium insidiosum	0	0	0	0	0	0	0	0	1.5	1.14
Corophium lacustre	0	0	0	0	0	0	0	0	.22	.222
Corophium spec.	0	0	0	0	0	0	0	0	1.9	.79
Corophium volutator	0	0	.27	.269	.6	.61	0	0	440	145
Crangon crangon	.25	.251	1.6	.75	2.2	1.43	4.6	1.03	23	4.6
Crangon spec.	.8	.43	0	0	0	0	0	0	0	0
Crassostrea spec.	0	0	0	0	0	0	0	0	.29	.185
Crepidula fornicata	0	0	0	0	0	0	.24	.243	.29	.185
Cumacea indet.	.25	.251	.27	.269	0	0	0	0	.29	.187
Cumopsis goodsiri	0	0	.27	.269	0	0	0	0	.30	.217
Cyathura carinata	0	0	0	0	0	0	0	0	9	4.6
Dodecaceria concharum	0	0	0	0	0	0	.24	.243	0	0
Dyopedos spec.	0	0	0	0	0	0	.5	.34	0	0
Ensis directus	0	0	0	0	0	0	1.5	.68	.7	.45
Ensis spec.	4.3	2.04	110	51	0	0	60	34	6	3.7
Eteone flava	0	0	0	0	0	0	0	0	.29	.187
Eteone longa	0	0	.8	.46	.3	.30	1.2	.54	98	25.9
Eteone picta	0	0	0	0	0	0	0	0	.7	.53
Eteone spec.	.8	.43	1.6	.65	2.1	.74	3.6	1.25	43	6.6
Eumida sanguinea	0	0	.27	.269	0	0	1.0	.97	0	0
Eumida spec.	0	0	0	0	0	0	.24	.243	0	0
Eurydice pulchra	1.8	.75	2.2	.75	77	13.0	1.5	.77	6.1	2.47
Eurydice spec.	0	0	.27	.269	0	0	0	0	0	0
Gammaridea indet.	0	0	0	0	0	0	.24	.243	.11	.111
Gammarus salinus	1.5	1.28	0	0	0	0	0	0	23	5.9
Gammarus spec.	1.3	.83	.5	.38	0	0	.24	.243	2.0	1.21
Gastrosaccus spec.	1.3	.66	.27	.269	0	0	.24	.243	0	0
Gastrosaccus spinifer	28	6.4	9	4.8	12	4.0	2.2	1.11	.9	.76
Gattyana cirrosa	0	0	0	0	0	0	.24	.243	.9	.76
Glycera alba	0	0	0	0	0	0	0	0	.6	.41
Glycera spec.	0	0	.5	.38	0	0	.7	.42	.29	.185
Glycera tridactyla	0	0	0	0	0	0	0	0	1.0	.48
Harmothoe imbricata	0	0	0	0	0	0	.24	.243	0	0
Harmothoe impar	0	0	.5	.38	0	0	1.7	.87	.29	.185
Harmothoe lunulata	0	0	0	0	0	0	.7	.42	.29	.185
Harmothoe spec.	.15	.146	.5	.38	0	0	.5	.34	.7	.45
Haustorius arenarius	1.8	1.52	1.6	.85	39	5.5	1.9	.90	.37	.262
Heteromastus filiformis	2.3	.96	22	5.9	59	11.8	232	27.3	1790	288
Hydrobia ulvae	0	0	1.3	.71	7.8	2.56	1.7	.80	440	89
Insecta indet.	0	0	0	0	0	0	0	0	.29	.185
Lanice conchilega	0	0	1.6	.85	0	0	18	14.0	6.9	2.64
Macoma balthica	0	0	3.2	1.12	7.8	2.10	11.7	2.20	460	74
Magelona papillicornis	.25	.251	10.2	1.91	.3	.30	1.0	.48	.37	.262
Malacoceros fuliginosus	0	0	0	0	0	0	.24	.243	2.5	1.58
Malacoceros spec.	0	0	0	0	0	0	0	0	.30	.216
Malacoceros tetracerus	0	0	0	0	0	0	0	0	.22	.157
Manayunkia aestuarina	0	0	0	0	0	0	0	0	3.0	2.52
Melita palmata	0	0	0	0	0	0	0	0	.7	.74
Melita spec.	0	0	0	0	0	0	0	0	1.3	1.30
Mesopodopsis slabberi	.25	.251	.5	.38	4.9	1.64	1.0	.48	.7	.45
Microphthalmus fragilis	2.8	1.85	.27	.269	0	0	.25	.246	0	0
Microdeutopus gryllotalpa	0	0	0	0	.3	.30	0	0	0	0
Microphthalmus listensis	.25	.251	0	0	0	0	0	0	0	0
Microprotopus maculatus	.05	.049	0	0	0	0	.24	.243	0	0
Microphthalmus similis	1.5	.86	.27	.269	0	0	0	0	0	0
Microphthalmus spec.	2.5	1.32	.27	.269	0	0	.5	.49	.29	.185
Mya arenaria	0	0	0	0	1.8	1.03	.24	.243	.7	5.9
Mysella bidentata	0	0	0	0	.3	.30	1.2	.64	6.6	2.59
Mysidacea indet.	1.0	.50	2.7	2.18	.3	.30	.5	.34	.5	.30
Mytilus edulis	2.0	1.12	1.1	.66	.3	.30	13	4.8	250	241

Appendix 1. Continued.

Biotope	1		2		3		4		5	
Number of samples	266		249		215		274		360	
	mean	se	mean	se	mean	se	mean	se	mean	se
Nemertinae indet.	22	5.3	3.5	1.33	7.6	1.74	5.4	1.38	18	4.1
Neoamphitrite figulus	0	0	0	0	0	0	.5	.49	1.1	.83
Neomysis integer	1.3	.56	0	0	3.0	1.28	.5	.34	.6	.41
Neoamphitrite spec.	.29	.291	0	0	0	0	.24	.243	0	0
Nephtys caeca	2.8	1.43	.27	.269	0	0	1.2	.64	0	0
Nephtys cirrosa	3.3	1.02	69	3.8	.3	.30	4.4	1.11	2.4	.77
Nephtys hombergii	.8	.43	4.0	1.15	1.4	.63	30	3.8	13.6	2.42
Nephtys longosetosa	0	0	0	0	.3	.30	0	0	0	0
Nephtys spec.	.8	.56	4.3	1.40	.6	.61	1.7	.64	.9	.42
Nereis diversicolor	.5	.35	0	0	.5	.34	0	0	126	20.1
Nereis longissima	0	0	.27	.269	0	0	1.0	.59	.6	.32
Nereis spec.	0	0	0	0	.3	.30	.7	.42	12	4.1
Nereis succinea	.25	.251	.27	.269	3.1	2.33	.7	.73	111	17.9
Nereis virens	0	0	0	0	0	0	.24	.243	.19	.185
Notomastus latericeus	0	0	.27	.269	0	0	.5	.34	0	0
Oligochaeta indet.	.9	.47	1.3	.60	9	5.1	19	6.6	590	120
Ophelia limacina	7.3	1.74	0	0	.3	.30	0	0	.19	.185
Ophelia rathkei	0	0	0	0	1.4	.98	0	0	.8	.77
Ophelia spec.	.8	.43	0	0	.3	.30	0	0	0	0
Ophiuridae indet.	.25	.251	0	0	0	0	0	0	0	0
Pazaonis fulgens	.25	.251	.5	.38	.9	.91	3.4	1.13	.19	.185
Pazajassa pelagica	2.5	1.41	.8	.46	.3	.30	.5	.34	0	0
Pectinaria koreni	0	0	0	0	0	0	.5	.34	0	0
Pectinaria spec.	0	0	0	0	0	0	.24	.243	0	0
Petricola pholadiformis	0	0	.8	.46	.9	.68	40	33	27	8.2
Pholoe minuta	0	0	0	0	0	0	1.0	.69	.8	.77
Phyllodocinae indet.	0	0	0	0	0	0	.24	.243	.19	.185
Platynereis dumerilii	0	0	0	0	.3	.30	0	0	.19	.187
Pleusymtes glaber	0	0	0	0	0	0	0	0	8	4.2
Polychaeta indet.	0	0	.27	.269	0	0	3	3.2	.6	.32
Polydora ligni	0	0	.8	.46	.18	.183	19	17.8	350	81
Polydora spec.	0	0	0	0	.18	.183	.24	.243	1.2	.79
Polycirrus spec.	0	0	0	0	.3	.30	0	0	0	0
Pontocrates altamarinus	.25	.251	.8	.60	0	0	0	0	0	0
Portumnus latipes	.25	.251	0	0	.3	.30	0	0	0	0
Proceraea cornuta	.05	.049	0	0	0	0	0	0	0	0
Pseudocuma longicornis	.25	.251	0	0	0	0	0	0	0	0
Pseudopolydora pulchra	0	0	0	0	0	0	.24	.243	0	0
Pycnogonum littorale	0	0	0	0	0	0	1.5	1.46	0	0
Pygospio elegans	.25	.251	.8	.46	17	6.7	50	28.7	2900	410
Retusa alba	0	0	.27	.269	0	0	0	0	.6	.32
Schistomysis kervillei	0	0	.27	.269	0	0	.5	.34	0	0
Schistomysis spiritus	.25	.251	0	0	0	0	0	0	0	0
Scoloplos armiger	1.0	.50	8.3	1.45	.9	.52	15	3.7	32	8.2
Scolelepis foliosa	0	0	0	0	0	0	0	0	.03	.031
Scolelepis squamata	0	0	1.1	.53	3.2	1.49	0	0	4.0	1.94
Scrobicularia plana	0	0	.27	.269	.6	.59	.21	.243	80	25.5
Spiophanes bombyx	0	0	8.1	2.64	.3	.30	1.7	.94	1.2	.47
Spio filicornis	0	0	0	0	0	0	0	0	2.8	2.81
Spio martinensis	1.0	.50	130	47	3.7	1.12	90	19.8	17	4.4
Spionidae indet.	1.0	.50	.8	.46	0	0	.5	.34	.9	.36
Spisula spec.	0	0	0	0	0	0	0	0	.9	.76
Spisula subtruncata	0	0	40	36	0	0	38	16.8	4	3.9
Sthenelais boa	0	0	0	0	0	0	.7	.54	0	0
Tellinacea indet.	0	0	0	0	0	0	0	0	2.6	1.44
Tellina spec.	0	0	.27	.269	0	0	.24	.243	.6	.32
Tellina tenuis	0	0	2.2	.75	0	0	.24	.243	1.2	.52
Terebellomorpha indet.	0	0	.27	.269	0	0	0	0	.7	.46
Tharyx marioni	0	0	2.7	1.06	1.1	.56	140	54	840	170
Thecata indet.	0	0	0	0	0	0	2.2	2.19	0	0
Urothoe spec.	0	0	0	0	0	0	.24	.243	0	0
Venerupis pullastra	0	0	0	0	0	0	.24	.243	0	0
Total	110	43	480	189	1050	201	900	330	9700	2030

Appendix 2. Mean biomass (gAFDW/m^2) and standarderror (se) in the five biotopes identified in the Westerschelde.

Biotope	1		2		3		4		5	
Number of samples	266		249		219		274		360	
	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	.0018	.00133	0	0	.019	.0164	.00022	.000136
Abra spec.	0	0	0	0	0	0	0	0	.00025	.000250
Abra tenuis	0	0	0	0	0	0	0	0	.005	.0051
Achelia echinata	**********		0	0	0	0	0	0	0	0
Actiniaria indet.	.010	.0098	.00012	.000121	0	0	.41	.243	.46	.200
Amphiuride spec.	0	0	0	0	0	0	.005	.0049	0	0
Anaitides mucosa	0	0	.0009	.00066	0	0	.00044	.000257	.014	.0073
Anaitides spec.	0	0	.00028	.000282	0	0	0	0	**********	
Anoplodactylus petiolatus	0	0	0	0	0	0	**********		0	0
Arenicola marina	0	0	.021	.0161	0	0	.26	.136	.82	.140
Asterias rubens	0	0	0	0	0	0	.0011	.00113	0	0
Autolytus langerhansi	0	0	0	0	0	0	0	0	**********	
Autolytus spec.	0	0	0	0	0	0	.00001	.000036	0	0
Barnea candida	0	0	0	0	0	0	.00004	.000037	.00008	.000062
Bathyporeia elegans	0	0	0	0	.00041	.000292	0	0	0	0
Bathyporeia pelagica	0	0	0	0	.00087	.000256	.00012	.000082	.0005	.00032
Bathyporeia pilosa	.00026	.000135	.0007	.00039	.103	.0127	.00004	.000036	.045	.0112
Bathyporeia sarsi	.00026	.000263	0	0	.0018	.00152	.0007	.00048	.0067	.00190
Bathyporeia spec.	.00004	.000038	.00016	.000098	.0071	.00185	**********		.00031	.000107
Bivalvia indet.	**********		.015	.0149	0	0	.0021	.00212	.0007	.00045
Bodotria pulchella	0	0	0	0	0	0	.00008	.000073	**********	
Bodotria scorpioides	0	0	**********		0	0	.00001	.000036	0	0
Capitella capitata	**********		.0013	.00059	.0013	.00064	.010	.0054	.0081	.00194
Capitellidae indet.	0	0	.00004	.000040	.00005	.000046	0	0	**********	
Caprellidae indet.	0	0	0	0	0	0	0	0	**********	
Carcinus maenas	0	0	.8	.84	.0042	.00239	.00026	.000255	.17	.142
Caridea indet.	0	0	**********		0	0	0	0	.0009	.00092
Cerastoderma edule	0	0	.00012	.000121	.10	.062	.31	.217	5.4	1.18
Cerastoderma spec.	0	0	0	0	0	0	**********		0	0
Corophium arenarium	0	0	0	0	.0011	.00051	0	0	.030	.0113
Corophium bonnelli	0	0	0	0	0	0	0	0	**********	
Corophium insidiosum	0	0	0	0	0	0	0	0	**********	
Corophium lacustre	0	0	0	0	0	0	0	0	**********	
Corophium spec.	0	0	0	0	0	0	0	0	.00020	.000083
Corophium volutator	0	0	.00004	.000040	.00005	.000046	0	0	.10	.036
Crangon crangon	.00001	.000038	.019	.0161	.019	.0176	.08	.031	.039	.0148
Crangon spec.	.007	.0068	0	0	0	0	0	0	0	0
Crassostrea spec.	0	0	0	0	0	0	0	0	.04	.044
Crepidula fornicata	0	0	0	0	0	0	.00026	.000255	**********	
Cumacea indet.	**********		**********		0	0	0	0	.00006	.000056
Cumopsis goodsiri	0	0	.00004	.000040	0	0	0	0	**********	
Cyathura carinata	0	0	0	0	0	0	0	0	.0051	.00300
Dodecaceria concharum	0	0	0	0	0	0	**********		0	0
Dyopedos spec.	0	0	0	0	0	0	.00007	.000052	0	0
Ensis directus	0	0	0	0	0	0	2.0	1.21	.5	.35
Ensis spec.	.0023	.00139	.24	.121	0	0	.7	.48	.027	.0142
Eteone flava	0	0	0	0	0	0	0	0	.00006	.000056
Eteone longa	0	0	.00012	.000070	.00005	.000046	.0010	.00051	.044	.0123
Eteone picta	0	0	0	0	0	0	0	0	.00039	.000275
Eteone spec.	.0005	.00035	.0017	.00106	.005	.0032	.0016	.00073	.10	.035
Eumida sanguinea	0	0	.00012	.000121	0	0	.0015	.00146	0	0
Eumida spec.	0	0	0	0	0	0	.00004	.000036	0	0
Eurydice pulchra	.00034	.000202	.0013	.00072	.031	.0064	.00055	.000288	.0018	.00073
Eurydice spec.	0	0	.00004	.000040	0	0	0	0	0	0
Gammaridea indet.	0	0	0	0	0	0	.00007	.000073	.00006	.000056
Gammarus salinus	.0011	.00082	0	0	0	0	0	0	.010	.0047
Gammarus spec.	.0013	.00093	**********		0	0	**********		.00025	.000154
Gastrosaccus spec.	.00005	.000038	**********		0	0	.00026	.000255	0	0
Gastrosaccus spinifer	.052	.0115	.014	.0072	.021	.0108	.009	.0072	.0012	.00114
Gattyana cirrosa	0	0	0	0	0	0	.0026	.00263	.011	.0067
Glycera alba	0	0	0	0	0	0	0	0	.0018	.00181
Glycera spec.	0	0	.0013	.00101	0	0	.0005	.00035	.00011	.000111
Glycera tridactyla	0	0	0	0	0	0	0	0	.0016	.00066
Harmothoe imbricata	0	0	0	0	0	0	.0010	.00099	0	0
Harmothoe impar	0	0	.00008	.000057	0	0	.0028	.00266	**********	
Harmothoe lunulata	0	0	0	0	0	0	.0005	.00033	.00006	.000056
Harmothoe spec.	**********		.0004	.00044	0	0	.00011	.000110	**********	
Haustorius arenarius	.005	.0036	.0030	.00237	.047	.0079	.0026	.00133	.0008	.00073
Heteromastus filiformis	.0054	.00254	.070	.0256	.099	.0161	.68	.115	2.39	.288
Hydrobia ulvae	0	0	.0006	.00032	.0016	.00051	.00058	.000299	.121	.0225
Insecta indet.	0	0	0	0	0	0	0	0	**********	
Lanice conchilega	0	0	.05	.034	0	0	.12	.100	.021	.0096
Macoma balthica	0	0	.015	.0082	.054	.0204	.18	.062	1.94	.196
Magelona papillicornis	.0012	.00124	.020	.0048	.00027	.000274	.00022	.000136	.00028	.000251
Malacoceros fuliginosus	0	0	0	0	0	0	.00007	.000073	.00028	.000166
Malacoceros spec.	0	0	0	0	0	0	0	0	**********	
Malacoceros tetraceros	0	0	0	0	0	0	0	0	.00006	.000039
Manayunkia aestuarina	0	0	0	0	0	0	0	0	**********	
Melita palmata	0	0	0	0	0	0	0	0	.00025	.000250
Melita spec.	0	0	0	0	0	0	0	0	**********	
Mesopodopsis slabberi	**********		.00017	.000167	.0012	.00046	.00015	.000115	.00006	.000056
Microphthalmus fragilis	.00012	.000065	.00004	.000040	0	0	.00004	.000036	0	0
Microdeutopus gryllotalpa	0	0	0	0	**********		0	0	0	0
Microphthalmus listensis	**********		0	0	0	0	0	0	0	0
Microprotopus maculatus	**********		0	0	0	0	**********		0	0
Microphthalmus similis	**********		**********		0	0	0	0	0	0
Microphthalmus spec.	.00009	.000053	**********		0	0	**********		**********	
Mya arenaria	0	0	0	0	.0035	.00244	**********		.33	.168
Mysella bidentata	0	0	0	0	**********		.00026	.000159	.0017	.00073
Mysidacea indet.	.0010	.00102	.0023	.00214	.0013	.00132	.00004	.000037	.0007	.00067
Mytilus edulis	.00005	.000038	**********		**********		.00068	.000250	.9	.47

Appendix 2. Continued.

Biotope	1		2		3		4		5	
Number of samples	266		249		219		274		360	
	mean	se	mean	se	mean	se	mean	se	mean	se
Natantia indet.	0	0	0	0	0	0	.00011	.000109	0	0
Nemertinae indet.	.017	.0052	.0047	.00232	.0061	.00191	.022	.0100	.022	.0062
Neoamphitrite figulus	0	0	0	0	0	0	.05	.048	.12	.121
Neomysis integer	.0009	.00060	0	0	.0012	.00085	.00011	.000082	.0006	.00056
Neoamphitrite spec.	**********		0	0	0	0	.017	.0173	0	0
Nephtys caeca	.05	.037	.0010	.00097	0	0	.0039	.00260	0	0
Nephtys cirrosa	.035	.0180	.40	.042	.00014	.000137	.019	.0058	.008	.0030
Nephtys hombergii	.010	.0090	.043	.0168	.0018	.00105	.22	.046	.14	.030
Nephtys longosetosa	0	0	0	0	.00027	.000274	0	0	0	0
Nephtys spec.	.0014	.00108	.0020	.00103	.00009	.000091	.00019	.000096	.0004	.00032
Nereis diversicolor	.002	.00249	0	0	.0018	.00133	0	0	.45	.065
Nereis longissima	0	0	.00016	.000161	0	0	.006	.0050	.0018	.00091
Nereis spec.	0	0	0	0	.00014	.000137	.00030	.000258	.0015	.00072
Nereis succinea	.010	.0098	.00004	.000040	.004	.0032	.005	.0047	.155	.0268
Nereis virens	0	0	0	0	0	0	.06	.061	.0015	.00147
Notomastus latericeus	0	0	.0003	.00032	0	0	.0018	.00129	0	0
Oligochaeta indet.	.00005	.000038	.00017	.000080	.0005	.00033	.0021	.00090	.058	.0120
Ophelia limacina	.13	.039	0	0	.00009	.000091	0	0	.00014	.000139
Ophelia rathkei	0	0	0	0	.0007	.00073	0	0	.0005	.00050
Ophelia spec.	.0019	.00188	0	0	.00005	.000046	0	0	0	0
Ophiuridae indet.	**********		0	0	0	0	0	0	0	0
Paraonis fulgens	.00004	.000038	.00012	.000090	.00014	.000137	.0009	.00032	.00006	.000056
Parajassa pelagica	.00031	.000205	.00017	.000114	**********		.00004	.000037	0	0
Pectinaria koreni	0	0	0	0	0	0	.005	.0049	0	0
Pectinaria spec.	0	0	0	0	0	0	.00004	.000036	0	0
Petricola pholadiformis	0	0	.00012	.000070	**********		.014	.0127	.8	.32
Pholoe minuta	0	0	0	0	0	0	.00018	.000131	**********	
Phyllodocinae indet.	0	0	0	0	0	0	**********		**********	
Platynereis dumerilii	0	0	0	0	**********		0	0	.0017	.00169
Pleusymtes glaber	0	0	0	0	0	0	0	0	.0008	.00044
Polychaeta indet.	0	0	**********		0	0	.00018	.000131	**********	
Polydora ligni	0	0	.00005	.000041	**********		.0022	.00194	.038	.0128
Polydora spec.	0	0	0	0	**********		**********		**********	
Polygirrus spec.	0	0	0	0	**********		0	0	0	0
Pontocrates altamarinus	.00004	.000038	.00012	.000090	0	0	0	0	0	0
Portumnus latipes	.0011	.00105	0	0	.0015	.00146	0	0	0	0
Proceraea cornuta	**********		0	0	0	0	0	0	0	0
Pseudocuma longicornis	.00008	.000075	0	0	0	0	0	0	0	0
Pseudopolydora pulchra	0	0	0	0	0	0	.0004	.00044	0	0
Pycnogonum littorale	0	0	0	0	0	0	.019	.0185	0	0
Pygospio elegans	**********		.00005	.000041	.0015	.00080	.0036	.00209	.230	.0292
Rctusa alba	0	0	.00008	.000081	0	0	0	0	.00011	.000088
Schistomysis kervillei	0	0	.00024	.000242	0	0	.00015	.000103	0	0
Schistomysis spiritus	.0003	.00034	0	0	0	0	0	0	0	0
Scoloplos armiger	.010	.0080	.056	.0154	.0006	.00042	.044	.0118	.096	.0234
Scolelepis foliosa	0	0	0	0	0	0	0	0	.0019	.00192
Scolelepis squamata	0	0	.00037	.000288	.014	.0080	0	0	.019	.0097
Scrobicularia plana	0	0	.00008	.000081	.00005	.000046	.00022	.000219	1.9	.63
Spiophanes bombyx	0	0	.015	.0056	**********		.0031	.00271	.0008	.00052
Spio filicornis	0	0	0	0	0	0	0	0	.0005	.00050
Spio martinensis	.0020	.00170	.016	.0066	.0011	.00036	.013	.0030	.0021	.00056
Spionidae indet.	.00016	.000106	.00008	.000057	0	0	.00004	.000037	**********	
Spisula spec.	0	0	0	0	0	0	0	0	**********	
Spisula subtruncata	0	0	.018	.0142	0	0	.5	.31	.006	.0058
Sthenelais boa	0	0	0	0	0	0	.006	.0061	0	0
Tellinacea indet.	0	0	0	0	0	0	0	0	.00034	.000218
Tellina spec.	0	0	**********		0	0	**********		**********	
Tellina tenuis	0	0	.033	.0167	0	0	.0012	.00124	.0013	.00089
Terebellomorpha indet.	0	0	.00008	.000081	0	0	0	0	**********	
Tharyx marioni	0	0	.00029	.000120	.00032	.000209	.026	.0103	.140	.0295
Thecata indet.	0	0	0	0	0	0	.006	.0060	0	0
Urothoe spec.	0	0	0	0	0	0	**********		0	0
Venerupis pullastra	0	0	0	0	0	0	.00007	.000073	0	0
Total	.36	.177	1.9	1.23	.54	.192	6	3.2	18	4.7

********** : mean biomass < 0.00003 gAFDW.m^{-2}

CHAPTER 5

The benthic infauna of the North Sea: spatial trends in species composition, density, biomass and diversity

This chapter is based on:

Heip, C., D. Basford, J. A. Craeymeersch, J.-M. Dewarumez, J. Dörjes, P. de Wilde, G. Duineveld, A. Eleftheriou, P. M. J. Herman, U. Niermann, P. Kingston, A. Künitzer, E. Rachor, H. Rumohr, K. Soetaert, and T. Soltwedel. 1992. Trends in biomass, density and diversity of North Sea macrofauna. ICES Journal of Marine Science **49**:13-22.

Künitzer, A., D. Basford, J. A. Craeymeersch, J. M. Dewarumez, J. Dörjes, G. C. A. Duineveld, A. Eleftheriou, C. Heip, P. Herman, P. Kingston, U. Niermann, E. Rachor, H. Rumohr, and P. A. J. de Wilde. 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES Journal of Marine Science **49**:127-143.

Heip, C., and J. A. Craeymeersch. 1995. Benthic community structures in the North Sea. Helgoländer Meeresuntersuchungen **49**:313-328.

Craeymeersch, J. A., C. H. R. Heip, and J. Buijs. 1997. Atlas of North Sea Benthic Infauna. ICES Cooperative Research Report No 218. 86 pp.

Introduction

Macrobenthos of the North Sea has been the subject of investigation since the early years of the century, when Gilson (1907) and Petersen (1914) studied Belgian and Danish coastal waters respectively. The studies of Petersen have had an especially important impact on marine ecology in general, mainly through the introduction of the concept of marine communities. This concept has found wide application in ecological monitoring. The fact that spatially coherent species assemblages can be delimited using objective methods has proved to be of great significance in monitoring the impact on the sedimentary environment of human activities through pollution

by oil and sewage, dredging, beam trawling, and sand and gravel exploitation (see e.g. Olsgard and Gray 1995; Kenny and Rees 1994; Lindeboom and de Groot 1998). Whether these species assemblages are structured through species interactions or by common environmental requirements has been the subject of a long and intense debate, but is immaterial in the context of monitoring. The question that arises is whether such patterns are sufficiently constant to serve as yardsticks against which the magnitude and sign of changes can be evaluated. However, elucidation of the causal factors will strengthen the explanatory power of these synecological, multivariate analyses.

Besides changes in the distribution of the species assemblages, human activity also causes changes in other community attributes such as density, biomass and diversity. An intermediate disturbance seems to raise both biomass (e.g. Beukema and Cadée 1986; Cederwall and Elmgren 1980) and diversity (e.g. Lambshead 1986; Pearson et al. 1983). As the magnitude of the disturbance further increases, dramatic changes in the benthos may occur in which species diversity decreases but abundance of smaller species increases, until with still further increasing disturbance a total collapse occurs (e.g. Pearson and Rosenberg, 1978; Rosenberg 1985, Niermann et al. 1990). Monitoring the benthos gives a direct way of quantifying these effects. Moreover, the measurement of benthic abundance and biomass is important for more fundamental studies of energy flow through ecosystems.

Most of the North Sea surveys were carried out in coastal areas, not farther north than the Dogger Bank area. A review of the infauna assemblages of the North Sea was given by Kingston & Rachor (1982), showing the scarcity of benthic surveys in the central and northern North Sea. Investigations in the vicinity of oil platforms suggested that infauna assemblages north of the Dogger Bank might be similar to those south of it. On the other hand, Glémarec (1973) developed a concept of three different étages of benthic assemblages along the European North Atlantic Continental shelf, according to differences in annual variation of temperature in bottom waters. He divided the North Sea into three étages: the southern North Sea up to the northern edge of the Dogger Bank; the central North Sea from 40 to 100m depth; and the northern North

Sea from 100 to 200m depth. The assemblages of these étages should be further structured by the sediment composition.

In 1981, the International Council for the Exploration of the Sea established a Working Group on North Sea Benthos. One of the aims of the working group was to provide synoptic maps of qualitative and quantitative aspects on the status of the benthic communities in the North Sea. After reviewing the state-of-the-art of benthos investigations, the Working Group concluded that the available data were not sufficient to produce such a complete review of the faunal assemblages and to prove or reject Glémarec's concept. The group therefore recommended that a large scale benthos survey, covering the whole North Sea and using standard sampling and processing techniques, be initiated to solve this problem (NSBWG 1982, BMWG 1983). The program was planned into more detail at their meetings in 1984 and 1985 (BMWG 1984, BEWG 1985). The North Sea Benthos Survey was completed in early 1986 owing to the commitment of several marine institutes, covering an area between 51° and 58°N, 3°W and 9°E. Samples were taken by grab and box-corer for macrobenthic infauna with additional samples for epifauna and meiobenthic infauna. Data from the northern North Sea have been gathered during eight cruises from 1980 till 1985, always in spring and early summer (Eleftheriou and Basford 1989). The area covered extends between 65°15'N and 60°45'N.

This chapter describes the faunal assemblages and patterns in biomass, density and diversity of the macrobenthic infauna. The spatial trends in the whole North Sea, with a characteristic length scale of the order of tens of hundreds of kilometres, are a necessary background information for more localised impact studies.

Material and methods

Sampling

The present results are part of the North Sea Benthos Survey executed in April-May 1986 when 181 stations were sampled covering the ICES grid from 51°N to 58°N and from 2°30'W to 8°15'E. The complete list of replicates, dates, samples and stations can be found in BEWG (1986) and Craeymeersch et al. (1997). At each of these stations five box cores if possible but sometimes Van Veen grabs were taken. Most of the stations were analysed for macrofauna biomass, density and species composition, for meiofauna density and copepod species composition, for sediment grain size analysis, protein content, plant pigment content, organic matter and a series of heavy metals. Data on the meiofauna density and copepod species composition have been published by Huys et al. (1992). Data on the sedimentary environment are reported by Basford et al. (1993).

The data from the northern North Sea have been gathered during eight cruises from 1980 to 1985, always in spring or early summer (Basford and Eleftheriou 1988, Basford et al. 1989, Eleftheriou and Basford 1989). The area covered extends between 56°15'N and 60°45'N and 3°30'W and 7°30'E. A total of 119 stations were sampled for macrofauna (Basford et al. 1990).

The data presented here are based on the 177 stations of the ICES North Sea Benthos Survey where macrobenthos samples have been taken (43 of them sampled by two different laboratories), and 61 stations of the northern North Sea, viz. those stations laying on an extrapolated ICES grid (7 of them overlapping with ICES stations). Thus, the species composition was determined for 281 samples taken at 231 stations (fig. 5.1). At 214 of these stations (266 samples) the biomass of the major phyla was determined. For the analysis of trends in total density, total biomass and diversity, average values per station have been used.

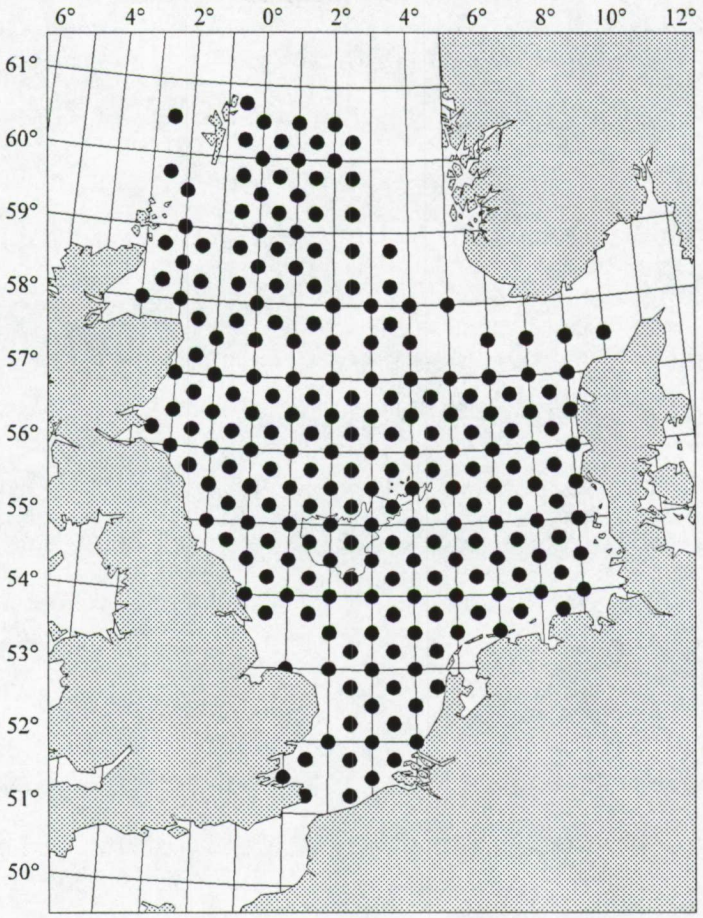


Figure 5.1. Stations sampled by participants of the North Sea Benthos Survey in 1986. Stations in the northern North Sea were sampled between 1980 and 1985 by the Marine Laboratory, Aberdeen (see text).

Intercalibration

Two intercalibration exercises have been performed, the results of both have been presented to ICES (Heip et al. 1985, Duineveld and Witte 1987) and will be briefly repeated here.

The first intercalibration exercise aimed at intercomparison of sampling gear and processing methods (sieving, washing, fixation etc.). Samples were taken at two stations, Molengat (53°01.8'N and 4°41.4'E, depth 8.5 m, sand) and Meta II (53°42.2'N and 4°30'E, depth 37 m, muddy sand) with the usual gear of each institute and with one standardised set. The routinely used gear varied from 30 kg Van Veen grabs to 700 kg box-corers. The processing of the sample

on board the vessel was also very different (fixation prior to sieving or not, round woven holes or square punched holes in the sieve etc.). The results clearly showed that the different procedures used by different laboratories resulted in different results even when the same macrofauna community was sampled (drift of the ship while sampling may have caused some of these differences). In the case of total density, the penetration of the gear was clearly the crucial factor in the sandy station Molengat. Neither density nor biomass estimates differed significantly in the muddy sand station Meta II, irrespective of using a 30 kg Van Veen or a 700 kg box-corer. Measures of diversity depend on taxonomic skill but also on gear used. The small Reineck box-corer consistently gave lower estimates of species number. When it was eliminated from the analysis the results for Molengat did not differ significantly, but the difference for Meta II remained very highly significant. This was due to taxonomic processing and to different sieving methods.

The results from this intercalibration exercise clearly showed that comparisons of macrofauna data are very difficult and that standardisation of gear and processing as well as taxonomic intercalibration will be essential for future comparative studies.

Ash-free dry weight was standardised after an intercalibration exercise, which again clearly showed the necessity of a standardised method. When the different methods traditionally used in each laboratory were applied to samples of the mollusc *Macoma balthica*, both the slope and the intercept of the regression line between weight and length were significantly different. When the standard method proposed by the Benthos Ecology Working Group of ICES (Rumohr et al. 1987) was used, results between laboratories did not differ (Duineveld and Witte 1987).

Generation of the species list

A main problem encountered in the data treatment was taxonomic. A species list integrating all species names found by the different participants (including species sampled by box-corer, grab or trawl surveys, and some species recorded in earlier years) was circulated at the meeting of the ICES Benthos Ecology Working Group in 1989. The list was checked for a) typing errors

and different spellings, and b) synonyms. Spelling and synonyms were checked using the Marine Conservation Society species directory, a coded checklist of the marine fauna and flora of the British Isles and its surrounding seas (Howson 1987). The directory includes most of the species recorded during the NSBS. Further uniformization was achieved by e.g. eliminating the second i at the end of the species names (e.g. *hartmanni* instead of *hartmannii*), using the abbreviation "sp." if the species names were unknown, and "indet." for all higher taxa. If there is only one species (genus,...) within a genus (family,...), the lowest taxonomic level was used.

At a final workshop in Texel (1989) the remaining taxonomic problems were resolved. For this workshop a list of "suspect" species was drawn up by calculating an index of particularity, expressing the degree to which species were found exclusively by one or a few laboratories. Depending on the number S_{obs} of stations in which a species is found, one can calculate the number L_{exp} of laboratories that should have found the species, if the latter were homogeneously distributed over the whole North Sea:

$$L_{\exp} = \sum_{i=1}^{L_{tot}} \left\{ 1 - \left(\frac{S_{obs}}{S_{tot} - S_i} \right) \Big/ \left(\frac{S_{tot}}{S_{obs}} \right) \right\}$$

where S_{obs} = total number of stations, S_i = number of stations sampled by laboratory i, L_{tot} = total number of laboratories. The index of particularity describes the degree of digression from this hypothesis of homogeneity by calculating

$PISP = L_{exp} - L_{obs}$

where L_{obs} = number of laboratories that have found the species. The assumption of homogeneous distribution over the North Sea is in itself nonsensical, but the index provided a basis for a thorough discussion of taxonomy used between the participants. An auxiliary basis for this discussion was a computerised atlas showing the spatial distribution of all species, genera, families and phyla (Craeymeersch et al. 1997).

The list of 'suspect' species proved very useful. Several species had to be lumped together. For, first, different laboratories used different identification keys and not every key differentiates all species. *Pholoe pallida* of Chambers (1985), for instance, is not mentioned in other keys (e.g. Hartmann-Schröder 1971, Fauvel 1923)and there is confusion between this species, *P. inornata*

and *P. minuta*. Consequently, they were all lumped at the genus level. Secondly, some laboratories identified taxa as e.g. the sipunculids and the nemerteans to the species level while others did not. Further, even well established laboratories have different opinions on the taxonomy of some species. It was felt that at least some of these taxa need a review (e.g. Capitellidae, Sabellidae, and Cirratulidae) before accurate identification can be made.
It was decided to remove those species from the dataset for which the sampling gear (box-corer or grab) has clearly been inappropriate: all fishes, meiobenthic species or groups (as e.g. Kinorhyncha indet., Platyhelminthes indet., Copepoda indet., Ostracoda indet.), other species only/mostly retained by a 0.5mm sieve (e.g. *Ophelina modesta*, Oligochaeta indet.), larval stages of crustaceans, all hyperiids (genera *Themisto, Euthemisto, Parathemisto*) as they are pelagic, all hyper- and epibenthic species or groups (all shrimps, pagurids, starfish, the mysid *Schistomysis kervillei*, the euphausiid *Thyanoessa inermis*, and *Thia scutella*).

The revised species list finally contained 954 different taxa. Before, there had been 1270 taxa. In the NSBS and Aberdeen stations a total of 709 infauna macrobenthic taxa was found. The list can be found in Craeymeersch et al. (1997). The taxonomic position of the species mentioned later on in this chapter are given in the appendix.

Diversity

As measures of faunal diversities the following Hill's diversity numbers (Hill 1973) were used:

N_0 : the number of species (species richness)
N_1 : exp(H') where H' is the Shannon-Wiener diversity (calculated with natural logarithms)
N_2 : 1/SI where SI is Simpson's dominance index (calculated with the revised formula of Pielou 1969 - see Heip et al 1988)
N_∞ : 1/DI where DI is the dominance index (relative abundance of the most common species)

As sample size influences the different measures in a different way (Soetaert and Heip 1990) these diversity measures were calculated both on the raw, purified data set (see above) as well

as for a standard sample size. From each sample 50 individuals were drawn at random, and the diversity indices calculated. This was repeated 50 times. Arithmetic means of the 50 values were used as the standardised diversity estimate for the sample.

Biomass

Depending on the institute the biomass was measured either directly as ash-free dry weight or calculated from wet weight using appropriate conversion factors (Rumohr et al. 1987).

Statistical analysis

Total biomass, total density, individual weight and diversity were compared with the environmental variables (latitude, longitude, depth, median grain size and silt, chlorophyll *a* and POC content of the sediment) by multiple linear regression.

Samples were grouped according to their similarity in species composition using TWINSPAN analysis (Hill 1979). This program divides the ordinated samples into two groups and proceeds by dividing each group into two further groups and so on (see chapter 2). TWINSPAN also identifies one to several differential species that are particularly diagnostic of each division (twin group) in the dendrogram (indicator analysis). This analysis was run twice; firstly solely with presence or absence of species data and secondly taking into account the (logarithmically transformed) abundance of the species (cutlevels used were: 0, 1.5, 2.5 and 3.5).

The relationship between species composition and the environment was analysed using Canonical Correspondence Analysis (CCA) (ter Braak 1986) on the logarithmically transformed density data. Environmental variables used were depth, latitude and longitude, percentage silt (sediment 62 µm) and median grain size of the sand fraction. Data were available for 242 samples. The resulting ordination diagram reflects the major relationships between the species (and stations) and each of the given environmental variables. In the ordination diagram, the stations are positioned as points and arrows represent the environmental variables.

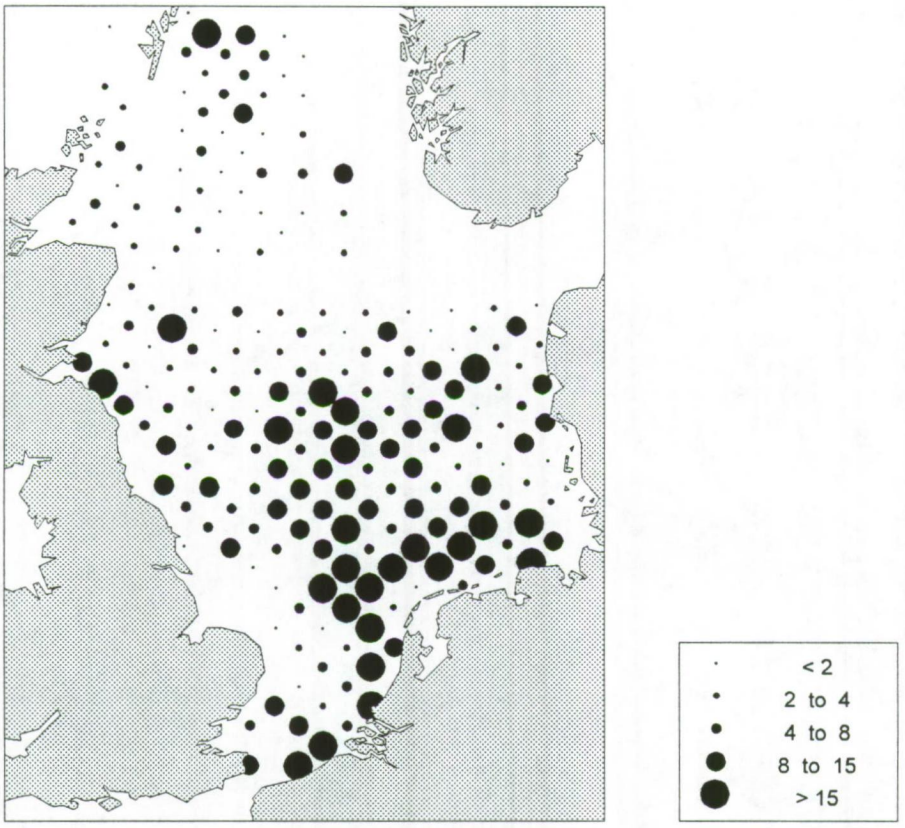


Figure 5.2. Total biomass of macrofauna (g ash-free dry weight m^{-2})

Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and therefore more closely related to the pattern of variation of species composition shown in the ordination diagram. Arrows that point in the same direction indicate positively correlated variables, perpendicular arrows indicate lack of correlation and arrows pointing in the opposite direction indicate negatively correlated variables.

Results

Abundance and biomass

The total macrofauna biomass and the biomass of the major phyla (Annelida, Mollusca, Arthropoda, Echinodermata, Rest) at each station are shown in figures 5.2 and 5.3. The average

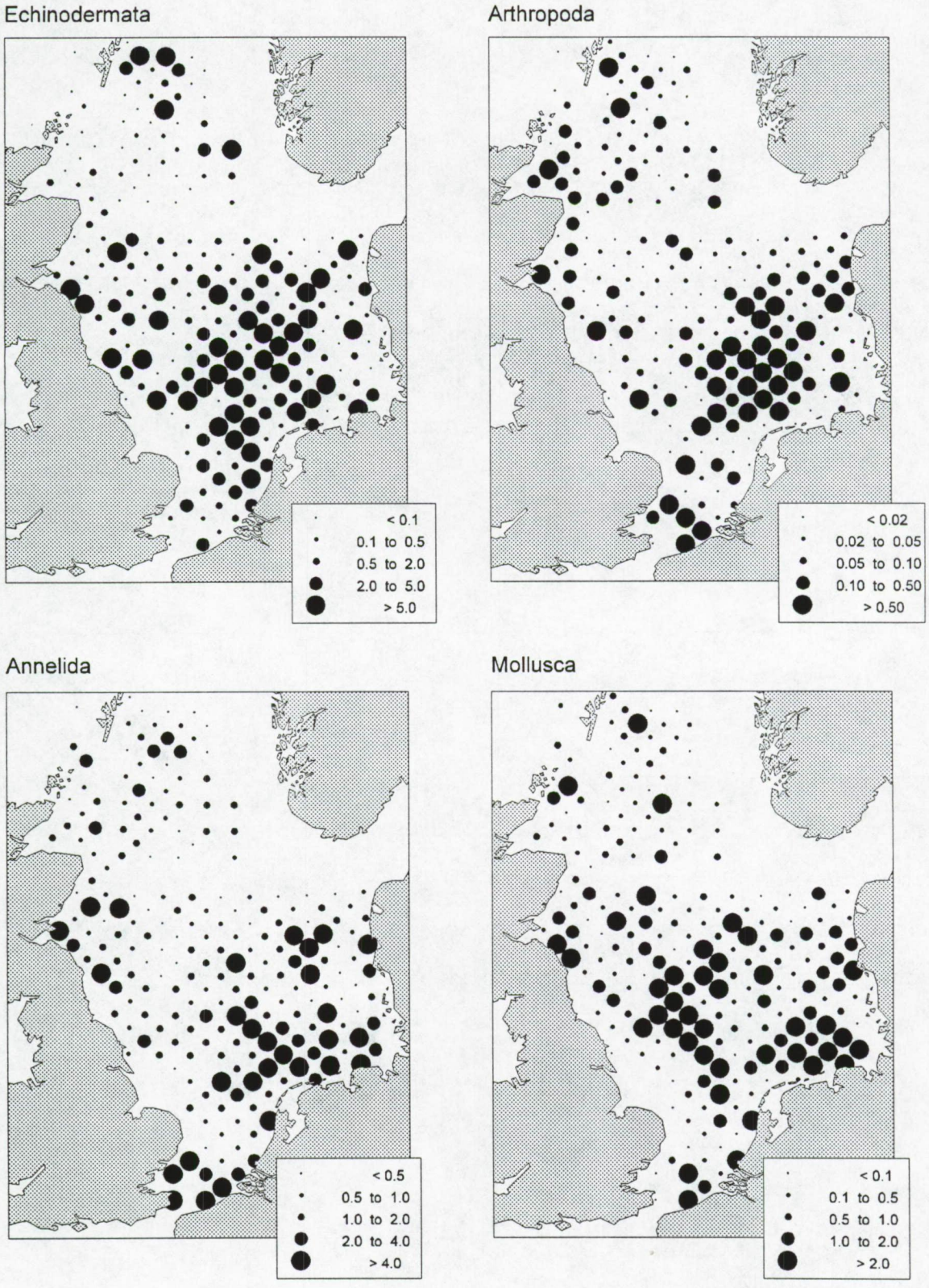


Figure 5.3 Total biomass of the major taxonomical groups of the macrobenthos (gAFDW m^{-2})

total biomass is 7 g ash-free dry weight (AFDW) per m^2, the maximum 38.85 g AFDW/m^2, the minimum 0.10 g AFDW/m^2.

Total biomass (after log transformation) shows a clear and significant trend with latitude. This is shown in fig. 5.4 where for each degree latitude the mean ± standard error of the biomass is expressed. Towards the north biomass decreases considerably. One major taxonomical group overtaking another as one goes north (fig. 5.5) does not cause this major shift. Rather, the same trends seem to be operating in the different groups.

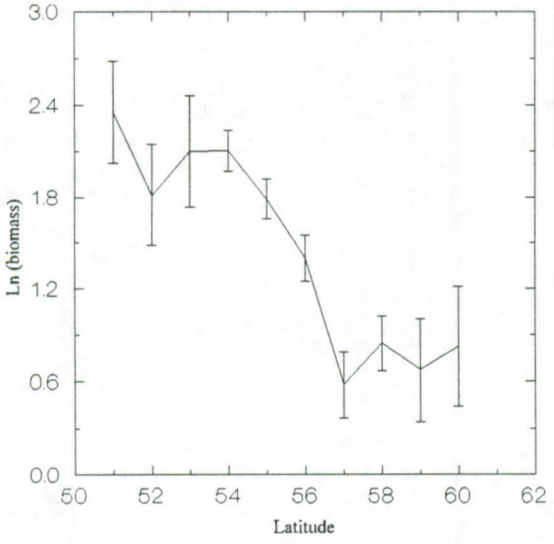


Figure 5.4. Total macrofauna biomass (gAFDW m^{-2}) as a function of latitude.

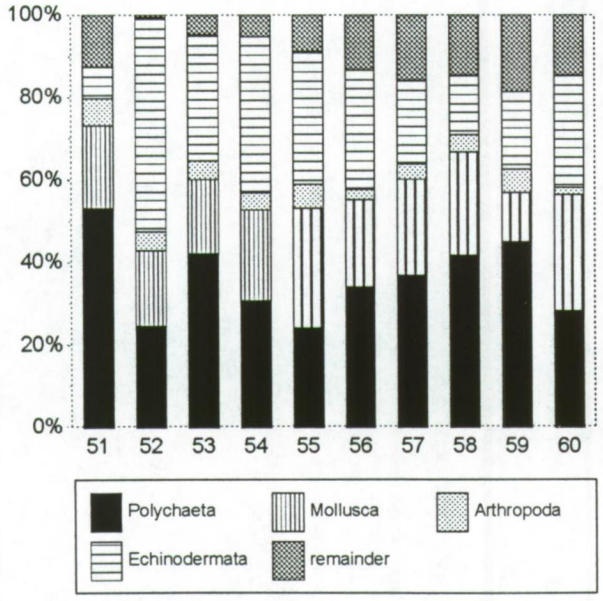


Figure 5.5. Fraction of total biomass represented by the major taxonomical groups of the macrofauna.

Apart from latitude sediment composition (logarithm of fraction smaller than 62 μm) and chlorophyll *a* content of the sediment also influence the total biomass, and the biomass of most separate groups significantly (table 5.1). In these regressions the following variables were tested: longitude, latitude, median grain size, silt content, percentage organic carbon, chlorophyll *a* content and depth. The best model in most cases was using latitude plus one or two sediment variables, in which case latitude accounts always for a larger part of the variance. For biomass of molluscs, the model with latitude and chlorophyll *a* accounted for a smaller proportion of variance (squared multiple r = 0.100) than the model with silt content and chlorophyll *a* as predictors (squared multiple r = 0.147).

	Latitude	Chlorophyll *a*	log (silt)	Depth
Total	*	*	*	
Mollusca		*		*
Annelida	*	*	*	
Echinodermata	*	*		
Arthropoda	*		*	
Rest		*		

Table 5.1. Multiple linear regression of (log transformed) biomass and environmental variables; * indicates that the environmental variable has a significant (5%) independent contribution to the explanation of the dependent variable in the "best" model (i.e. the model with all partial regression coefficients different from zero and the highest squared multiple r).

Especially with silt content of the sediment, the relation may be non-linear. Figure 5.6 shows this relation, clarified by a smoothing technique called distance weighted least squares smoothing (McLain 1974, Wilkinson 1988). The locally weighted smooth line clearly suggests that biomass increases with silt content between 0.1 and 1%, remains relatively uncorrelated for silt content between 1 and 10%, and decreases with silt content for very fine sediments (silt content 10%). This type of relationship is not uncommon in macrobenthos. The relationship of (log transformed) total biomass with (log transformed) chlorophyll *a* content of the sediment is relatively linear (fig. 5.7).

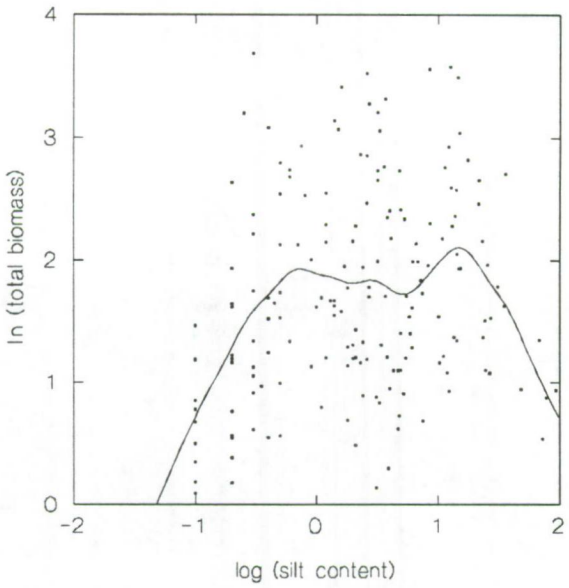


Figure 5.6. Relationship of (ln transformed) total biomass (gAFDW m^{-2}) with (log transformed) % sediment <62µm. The smooth line is obtained by distance weighted least squares smoothing.

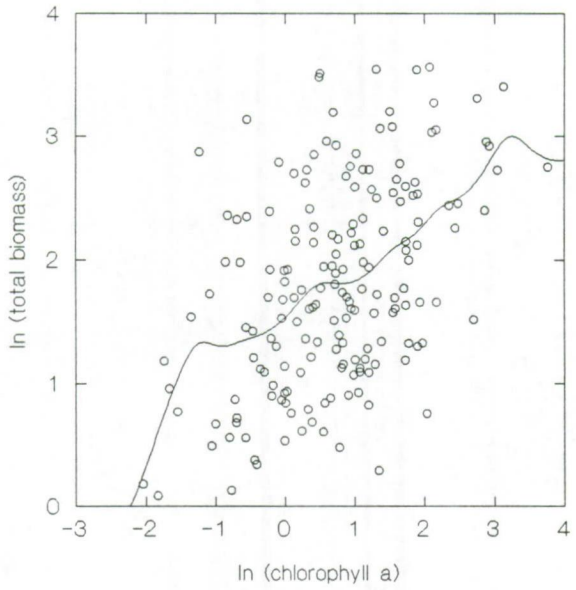


Figure 5.7. Relationship of (ln transformed) total biomass (gAFDW m^{-2}) with (ln transformed) chlorophyll *a* content in the sediment (µg chla per 5 cm^2 sediment). The smooth line is obtained by distance weighted least squares smoothing.

Density shows a less clear gradient with latitude. There is a tendency for density to increase towards the north (fig. 5.8), but the trend is less clear and less linear than for biomass and

diversity. Using latitude, chlorophyll *a* content and median grainsize as predictors gives the 'best' model, and sediment accounts for a larger part of the variance than latitude.

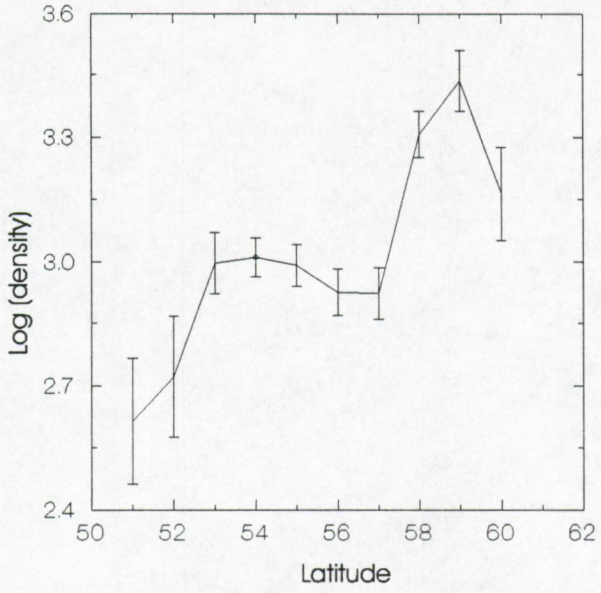


Figure 5.8. Total density (number m^{-2}) as a function of latitude.

Body weight

The mean weight of the individuals, obtained by dividing total biomass by total density in each sample, also shows a very clear gradient with latitude (fig. 5.9). Towards the northern part of the North Sea, individual size becomes considerably smaller: the difference in mean weight is much more than one order of magnitude. Adding sediment as predictor variable does not increase the squared multiple r (0.371 for the model with latitude and chla, 0.364 using only latitude).

Diversity

Diversity, as measured by Hill's diversity index N_1, shows a significant trend with latitude (fig. 5.10). Towards the north of the North Sea diversity increases considerably. The trend is found within each 'laboratory zone', and is about as strong everywhere. Analysis of covariance showed

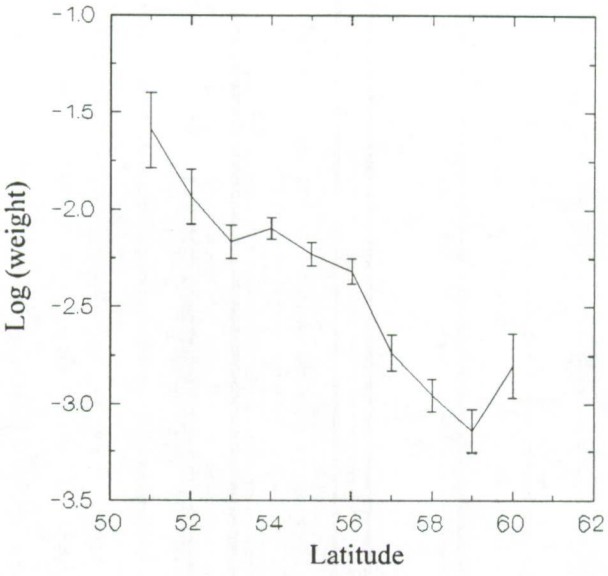


Figure 5.9. Individual weight (gAFDW ind^{-1}) as a function of latitude.

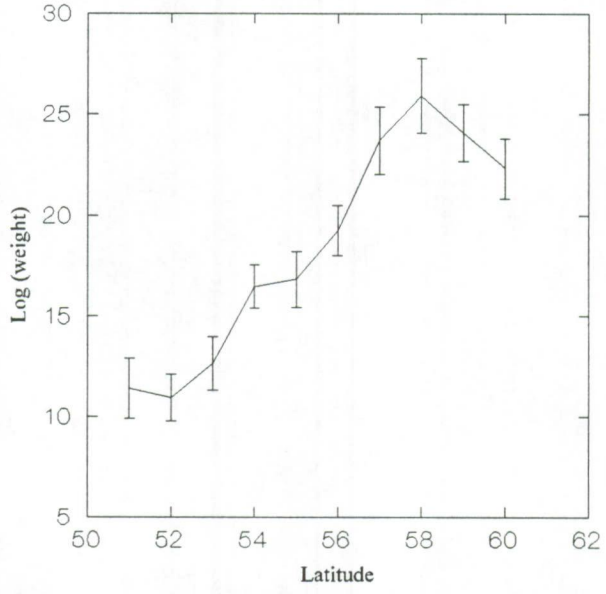


Figure 5.10. Diversity (Hill number N_1 expressed in equivalent number of species) as a function of latitude.

no significant (0.05 level) interaction between laboratory and slope of the regression on latitude. On the other hand, different laboratories had significantly different intercepts for the relation with latitude, In view of the non-random distribution of the laboratory zones over the North Sea, it is not clear, however, whether this reflects true differences between the laboratories. Besides latitude, both depth and longitude show an effect in the separate regressions. Other environmental variables have no clear influence. The 'best' model has both latitude and

longitude as predictors. Other diversity measures (N_0, N_2, N_∞) show the same trend (they are strongly correlated) but are subject to more variability then N_1.

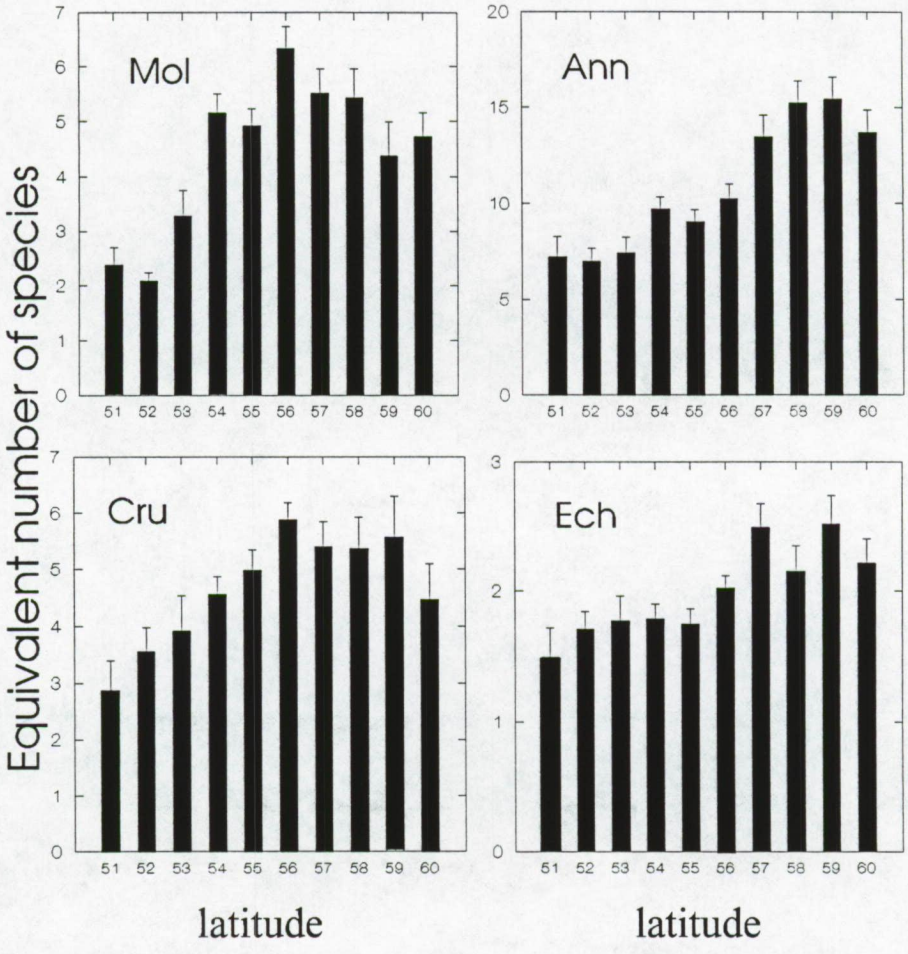


Figure 5.11. Diversity of the major taxonomic groups (Hill number N_1 expressed in equivalent number of species) as a function of latitude. Mol: Mollusca; Ann: Annelida; Art: Arthropoda; Ech: Echinodermata.

The effect of different sample sizes on the estimation of diversity indices was not very important for N_1. After standardisation to 50 individuals, its relation with latitude was not too different from the relationship shown in figure 5.10. In accordance with the conclusions of Soetaert and Heip (1990), the effect was more pronounced on N_0, the number of species. Here much variability was taken away by standardisation, and a very clear relationship with latitude ensued. Both latitude, longitude and depth show an effect on the standardised number of species, and all regression coefficients remain significantly different from zero in a multiple regression.

The increase of diversity also exists within the four main macrofaunal groups (fig. 5.11). Mollusc diversity seems to peak at 56°N, whereas echinoderm and annelid diversity increases more to the north.

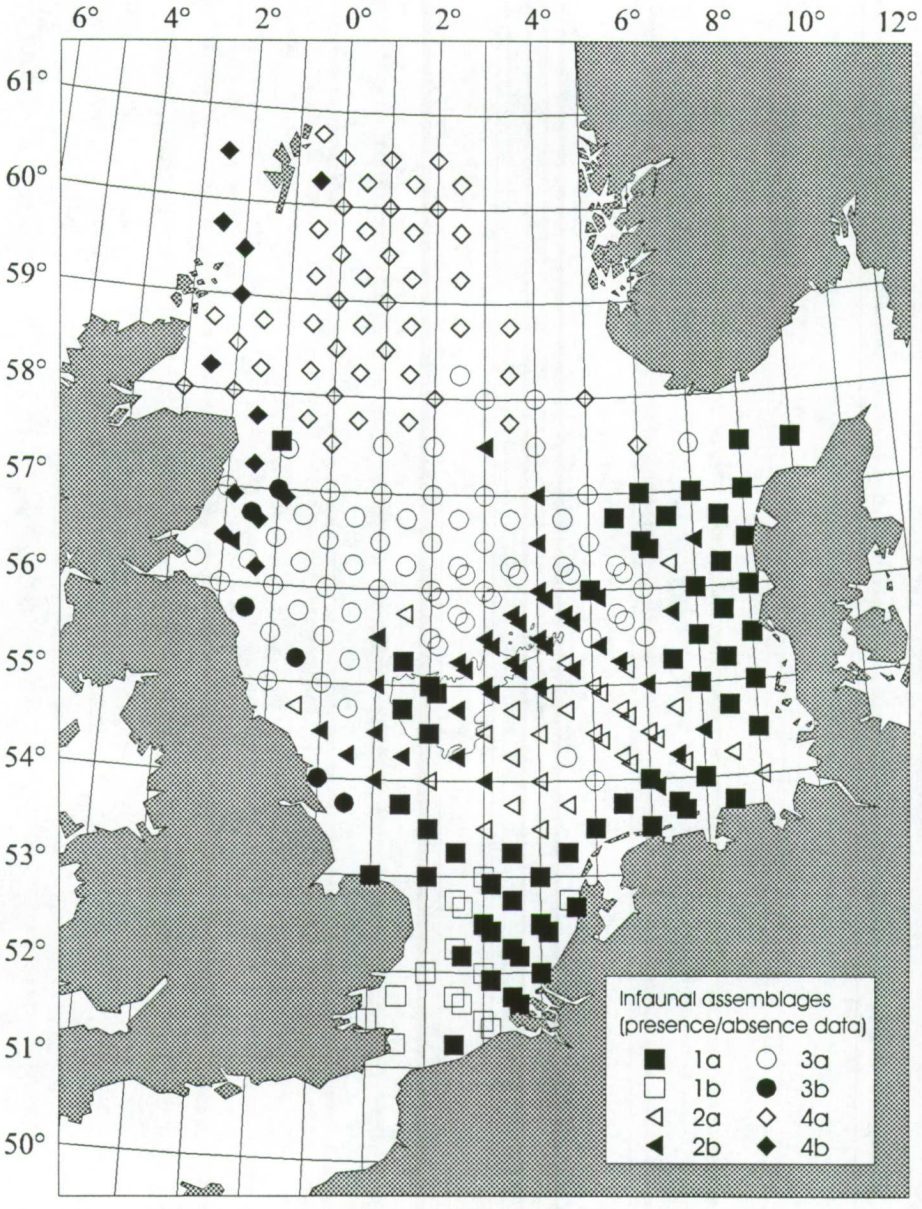


Figure 5.12. Classification of stations by TWINSPAN, using only species present/absence data.

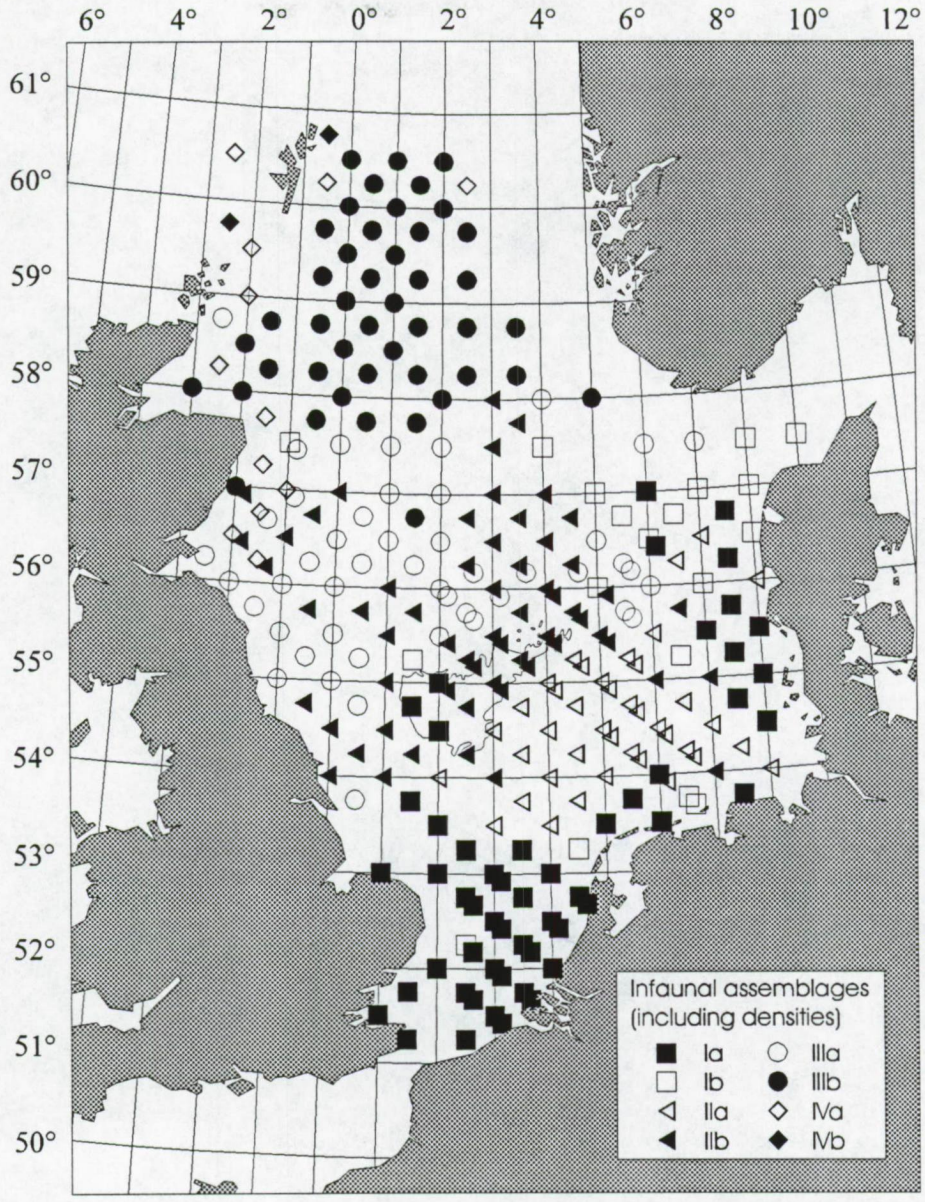


Figure 5.13. Classification of stations by TWINSPAN, incorporating species abundances.

Species assemblages

Figure 5.12 shows the stations of similar species composition based on presence/absence data. Figure 5.13 shows the similarity in species composition when densities are taken into account. The assemblages in the North Sea remain more or less the same in both cases but the similarity of assemblages is different between the central and northern North Sea.

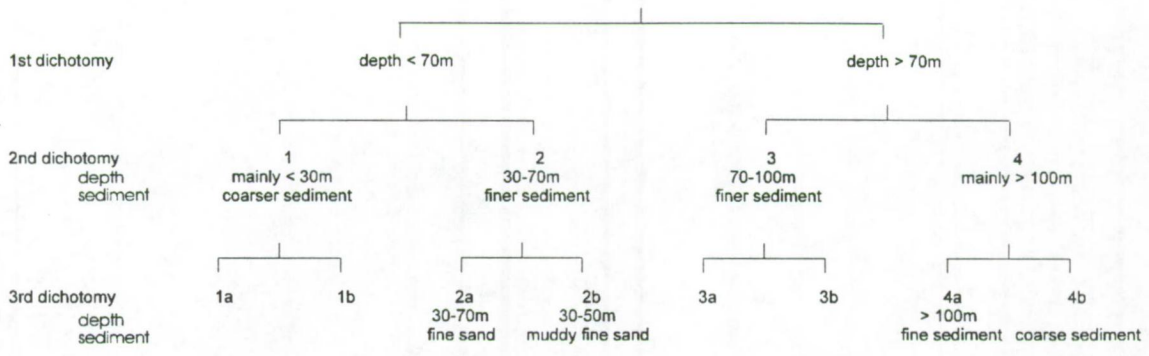


Figure 5.14. Scheme of TWINSPAN classification based on thespecies presence/absence data.

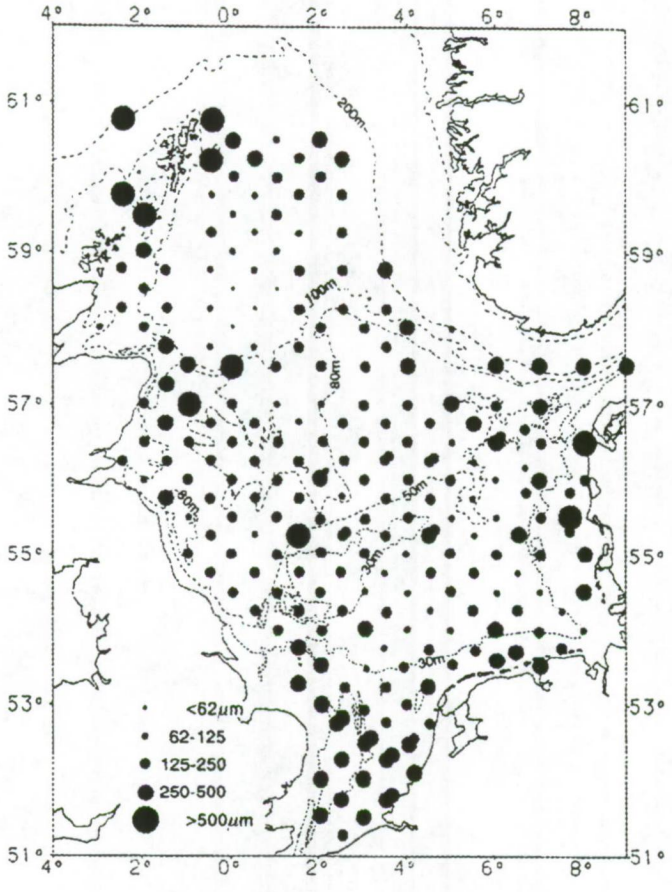


Figure 5.15. Median grain size of the sediment at each station (analysed by Irion, Wilhemshaven and Basford, Aberdeen) and depth distribution in the North Sea

Figure 5.14 gives the scheme of TWINSPAN classification for the eight different assemblages (twin groups) which are shown in figure 5.12. The classification was based on presence/absence data. The infauna assemblages of the North Sea are determined by the depth and by the sediment type. The type of sediment at each station is shown in figure 5.15.

At the first dichotomy most stations north of the Dogger Bank (indicator species: *Spiophanes kröyeri, Myriochele* sp., *Minuspio cirrifera, Antalis entalis*) were separated from the stations south of the 70m depth contour (indicator species: *Magelona* sp., *Echinocardium cordatum*). The benthic fauna of the deeper northern half of the North Sea is different from the fauna of the shallower southern half.

At the second dichotomy the stations south of the 70m depth contour were divided along the 30m depth contour into those with coarser sediment mainly shallower than 30m (group 1, no indicators) and those with a sediment of fine sand and with a depth generally greater than 30m (group 2, indicators: *Amphiura filiformis, Phoronis* sp., *Pholoe* sp., *Mysella bidentata, Nephtys hombergi, Cylichna cylindracea, Harpinia antennaria*). The stations north of the 70m depth contour were divided mainly by the 100m depth contour into those in the central North Sea (group 3, indicators: *Mysella bidentata, Scoloplos armiger, Chaetoderma nitidulum*) and those in the northern North Sea (group 4, indicators: *Exogone verugera*).

At the third dichotomy stations near the English Channel (group 1b, indicators: *Glycera lapidum, Polycirrus medusa*) were separated from the other stations on coarse sediment in the southern North Sea (group 1a, indicators: *Fabulina fabula, Lunatia poliana*). The stations on fine sand were further divided into stations on muddy fine sand south of the Dogger Bank (group 2b, indicators: *Eudorella truncatula, Callianassa subterranea, Ampelisca tenuicornis, Nucula nitidosa, Harpinia antennaria, Chaetopterus variopedatus*) and those on clean fine sands in the central North Sea mainly north of the Dogger Bank (group 2a, no indicators).

In the central North Sea some stations along the English coast (group 3b, indicators: *Glycera lapidum, Leptochiton asellus*) have a different fauna than the other stations (group 3a, no indicators). Within the northern North Sea, stations along the Scottish coast including the Orkneys and Shetlands, being mainly shallower than 100m depth and with coarse sediment

(group 4b, no indicators), were different from those deeper than 100m on muddy fine sand (twin group 4a, indicators: *Thyasira* sp.).

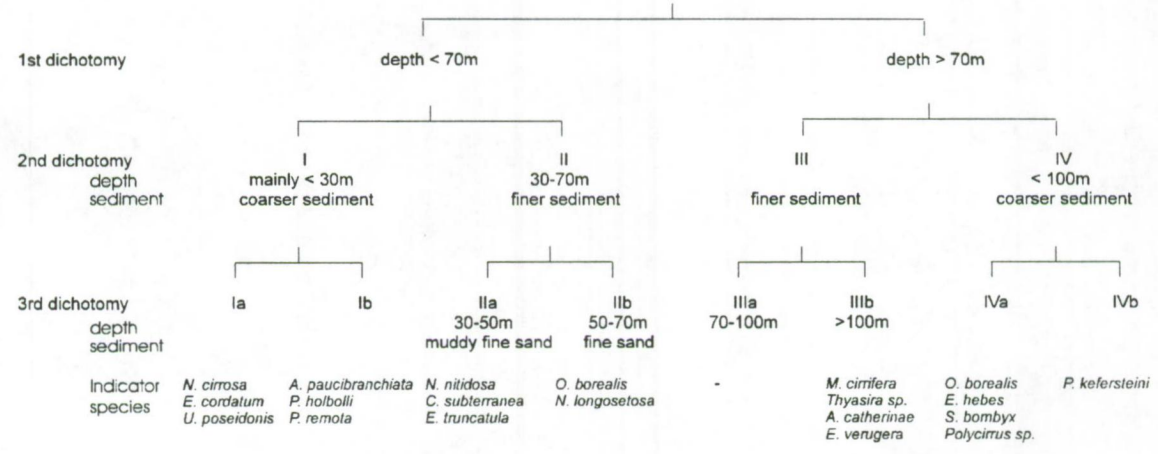


Figure 5.16. Scheme of the TWINSPAN classification based on species abundance data

Figure 5.16 gives the scheme of TWINSPAN classification based on species abundances, for the assemblages that are shown in figure 5.13. The classification gave about the same results as the analysis with presence/absence of species. In comparison to the analysis described before,the assemblages of the northern and central North Sea seem to be more similar. The borderline between southern and northern assemblages is shifted slightly towards the north. A list of the most frequent species of every group is given in table 5.2. A list of the ten most abundant species per group is given in table 5.3.

At the first dichotomy stations were separated along the 70m depth contour into stations to the north (indicator species: *Spiophanes kröyeri, Minuspio cirrifera, Myriochele* sp.) and stations to the south of it (indicator species*: Echinocardium cordatum, Magelona* sp., *Bathyporeia elegans*).

At the second dichotomy among the stations south of the 70m depth contour, those on coarse sediment (group I, no indicators) were separated from those on fine sand (group II, indicators: *Amphiura filiformis, Pholoe* sp., *Phoronis* sp., *Mysella bidentata, Harpinia antennaria, cylichna cylindracea, Nephtys hombergii*). Among the northern stations those along the Scottish coast on coarse sediment (group IV, indicators: *Sphaerosyllis bulbosa, Hesionura elongata*)

TWIN Ia	(54 stations)	TWIN IIIa	(47 stations)
44	*Spiophanes bombyx*	44	*Goniada maculata*
41	*Bathyporeia elegans*	44	*Myriochele* sp.
41	*Nephtys cirrosa*	40	*Amphiura filiformis*
41	*Scoloplos armiger*	38	*Scoloplos armiger*
38	*Ophelia borealis*	38	*Spiophanes bombyx*
38	*Spio filicornis*	36	*Spiophanes kroyeri*
36	*Echinocardium cordatum*	35	*Nephtys hombergi*
35	*Magelona* sp.	31	*Antalis entalis*
31	*Lunatia poliana*	31	*Pholoe* sp.
30	*Bathyporeia guilliamsoniana*	30	*Chaetozone setosa*
TWIN Ib	(19 stations)	TWIN IIIb	(45 stations)
19	*Ophelia borealis*	41	*Spiophanes kroyeri*
16	*Aonides paucibranchiata*	40	*Prionospio cirrifera*
14	*Scoloplos armiger*	38	*Pholoe* sp.
11	*Chaetozone setosa*	37	*Myriochele* sp.
11	*Echinocyamus pusillus*	35	*Thyasira* sp.
11	*Phoxocephalus holbolli*	34	*Levinsenia gracilis*
11	*Pisione remota*	33	*Amphiura filiformis*
10	*Bathyporeia elegans*	32	*Owenia fusiformis*
9	*Abra prismatica*	30	*Notomastus latericeus*
9	*Spiophanes bombyx*	29	*Aricidea catherinae*
TWIN IIa	(40 stations)	TWIN IVa	(12 stations)
38	*Amphiura filiformis*	11	*Sphaerosyllis bulbosa*
38	*Nephtys hombergi*	10	*Echinocyamus pusillus*
37	*Pholoe* sp.	9	*Anonides paucibranchiata*
36	*Phoronis* sp.	9	*Exogone hebes*
35	*Chamelea gallina*	9	*Ophelia borealis*
35	*Mysella bidentata*	8	*Hesionura elongata*
35	*Nucula nitidosa*	8	*Polycirrus* sp.
34	*Lunatia poliana*	8	*Spiophanex bombyx*
33	*Echinocardium cordatum*	7	*Abra prismatica*
33	*Spiophanes bombyx*	7	*Angulus pygmeus*
TWIN IIb	(62 stations)	TWIN IVb	(2 stations)
57	*Spiophanes bombyx*	2	*Aonides paucibranchiata*
54	*Pholoe* sp.	2	*Glycera lapidum*
53	*Amphiura filiformis*	2	*Hesionura elongata*
53	*Goniada maculata*	2	*Pisione remota*
53	*Scoloplos armiger*	2	*Protodorvillea kefersteini*
49	*Mysella bidentata*	1	All other species
45	*Phoronis* sp.		
44	*Bathyporeia elegans*		
44	*Nephtys longosetosa*		
43	*Magelona* sp.		

Table 5.2. Number of stations in each TWINSPAN group at which a species has been found (based on species abundance data) for theten most frequent species.

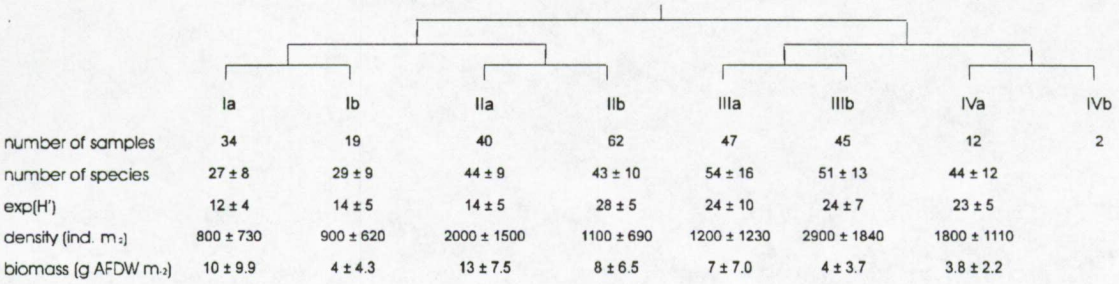
were separated from the other stations in the central and northern North Sea (group III, indicators: *Levinsenia gracilis, Thyasira* sp.).

TWIN Ia		TWIN IIIa	
70	*Bathyporeia elegans*	333	*Myriochele* sp.
69	*Magelone* sp.	131	*Amphiura filiformis*
53	*Scoloplos armiger*	48	*Diastylis lucifera*
48	*Urothoe poseidonis*	25	*Scoloplos armiger*
36	*Ophelia borealis*	20	*Goniada maculata*
34	*Angulus fabulus*	20	*Eudorella emarginata*
31	*Nicomache* sp.	17	*Spiophanes bombyx*
28	*Spisula subtruncata*	15	*Mysella bidentata*
27	*Bathyporeia guilliamsoniana*	14	*Spiophanes kroyeri*
27	*Spiophanex bombyx*	12	*Rhodine gracilior*
TWIN Ib		TWIN IIIb	
128	*Pisione remota*	215	*Thyasira* sp.
71	*Protodorvillea kefersteini*	195	Capitellidae indet.
60	*Ophelia borealis*	158	*Myriochele* sp.
43	*Goniadella bobretzki*	123	Ophiuroidea indet.
36	*Scoloplos armiger*	114	*Spiophanes kroyeri*
36	*Aonides paucibranchiata*	112	*Owenia fusiformis*
23	*Branchiostoma lancelolatum*	81	*Prionospio cirrifera*
21	*Goodallia triangularis*	68	*Pholoe* sp.
21	*Echinocyamus pusillus*	65	*Paradoneis lyra*
18	*Chaetozone setosa*	62	*Amphiura filiformis*
TWIN IIa		TWIN IVa	
469	*Amphiura filiformis*	344	*Ophelia borealis*
270	*Mysella bidentata*	139	*Exogone hebes*
112	*Myriochele* sp.	108	*Glycera lapidum*
95	*Phoronis* sp.	93	*Prionospio malmgreni*
91	*Pholoe* sp.	81	*Echinocyamus pusillus*
91	*Magelona* sp.	78	Ophiuroidea indet.
70	*Scoloplos armiger*	58	*Sphaerosyllis bulbosa*
51	*Chaemelea gallina*	48	*Spiophanes bombyx*
50	*Spiophanes bombyx*	48	Spiunculida indet.
43	*Nucula nitidosa*	46	*Pisione remota*
TWIN IIb		TWIN IVb	
93	*Spiophanex bombyx*	145	*Pisione remota*
85	*Bathyporeia elegans*	135	*Protodrilus* sp.
81	*Amphiura filiformis*	75	*Glycera lapidum*
56	*Magelona* sp.	71	*Echinocyamus pusillus*
55	*Mysella bidentata*	71	Sabellidae indet.
51	*Phoronis* sp.	45	*Aonides paucibranchiata*
49	*Myriochele* sp.	45	*Goniada norvegica*
38	*Scoloplos armiger*	40	*Owenia fusiformis*
34	Anthozoa indet.	35	*Hesionura elongata*
29	*Ophiura albida*	25	Sipunculida indet.

Table 5.3. Average density (ind./m^2) per TWINSPAN group of the ten most abundant species.

At the third dichotomy stations north-west of Denmark (group Ib, indicators*: Aonides paucibranchiata, Phoxocephalus holbolli, Pisione remota*) were separated from the other stations on coarser sediment (group Ia, indicators: *Nephtys cirrosa, Echinocardium cordatum,*

Urothoe poseidonis). The stations on fine sand were divided into those south of the Dogger Bank (group IIa, indicators: *Nucula nitidosa, Callianassa subterranea, Eudorella truncatula*)



	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb
number of samples	34	19	40	62	47	45	12	2
number of species	27 ± 8	29 ± 9	44 ± 9	43 ± 10	54 ± 16	51 ± 13	44 ± 12	
exp(H')	12 ± 4	14 ± 5	14 ± 5	28 ± 5	24 ± 10	24 ± 7	23 ± 5	
density (ind. m_{-2})	800 ± 730	900 ± 620	2000 ± 1500	1100 ± 690	1200 ± 1230	2900 ± 1840	1800 ± 1110	
biomass (g AFDW m_{-2})	10 ± 9.9	4 ± 4.3	13 ± 7.5	8 ± 6.5	7 ± 7.0	4 ± 3.7	3.8 ± 2.2	

Figure 5.17. Biotic parameters (mean ± s.d.) of the assemblages as identified by TWINSPAN using abundance data.

and those on fine sand in the central North Sea at 50-70m depth (group IIb, indicators: *Ophelia borealis, Nephtys longosetosa*). Stations deeper than 70m were divided along the 100m depth contour into those of the northern North Sea (group IIIb, indicators: *Minuspio cirrifera, Thyasira* sp., *Aricidea catherinae, Exogone verugera*) and those of the central North Sea at about 70-100m depth (group IIIa, no indicators).

The difference in biotic parameters among the assemblages is shown in figure 5.17 for the species number, diversity, density and biomass.

Species number and diversity gradually increase from the assemblages shallower than 30m (group Ia, Ib) to the assemblages in 30-70m depth (group IIa, IIb) and are highest in the assemblages in areas deeper than 70m (group IIIa, IIIb). Towards the Scottish coast (group IV) species number and diversity decrease again.

The variation in densities is too high to show differences between assemblages. Densities seem to be lower in the assemblages on shallow coarse sediment (Ia, Ib). They seem to be highest in twin group IIIb but at stations in this group a finer mesh of 0.5mm instead of 1.0mm was used. Also at the stations of group IV the 0.5mm mesh was used, and therefore densities are higher than they would have been by using a 1mm mesh and are not directly comparable to the densities in group I and II.

The variation in biomass is also very high. The mean biomass per assemblage is lowest in the northern North Sea (groups IIIb and IV). The biomass increases towards the shallower southern North Sea and reaches highest values south of the Dogger bank (group Ia, IIa).

Species distributions

Since it is impossible to show the distribution of all species in the North Sea, only a few examples will be given here to show the main patterns. The species chosen are typical of individual assemblages identified by the TWINSPAN analysis. Typical for an assemblage means that the species occur at most stations of this assemblage but at nearly no stations of the adjacent assemblages. Not all indicator species mentioned above are shown because they are only indicators for the division and must not be typical for an assemblage.

On each map, the radiuses of the circles in the map are proportional to the ln-transformed abundances of the species. The box-and-whisker plots express the frequency distribution of the non-zero observations on a logarithmic scale. Each plot shows the median observation as a vertical line. Its (back-transformed) value is written on top of the box (e.g. 63 in the case of *Amphiura filiformis* in figure 5.18). The box is determined, to its left- and right-hand sides, by the first and third quartiles of the data. To either side of the box extend the whiskers. These are limited by the most extreme observation lying within the bound quartile value ± 1.5 times the interquartile distance. Their value (also back-transformed) is given under the box-and-whisker plot (2 and 2142, respectively, in the case of *A. filiformis*). The number of observations falling beyond the whiskers, called outliers, is given by the numbers to the left and right of the plot (twice 0 for *A. filiformis*).

The distributions of individual species vary, some species being more cosmopolitan than other species. Species with more restricted distributions can be used to describe the found assemblages that inhabit specific areas. In the North Sea some species, e.g. *Spiophanes bombyx, Goniada maculata* and *Amphiura filiformis* (fig. 5.18), occur widely at nearly all depths and in a wide variety of sediments. Most species are either distributed south of a line parallel to the northern edge of the Dogger Bank (50m depth contour) or north of it.

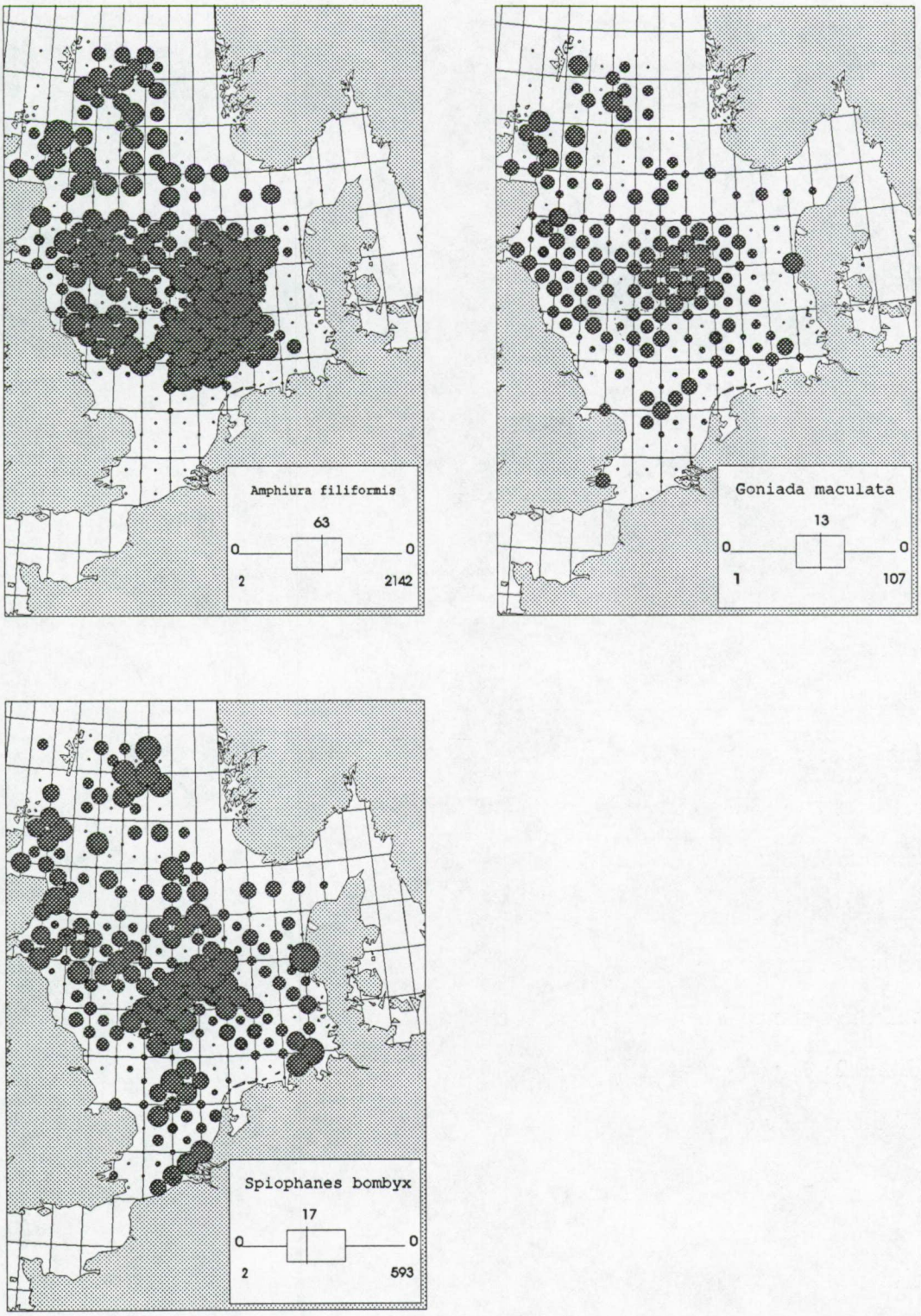


Figure 5.18. Distribution and density of species with a wide occurrence.

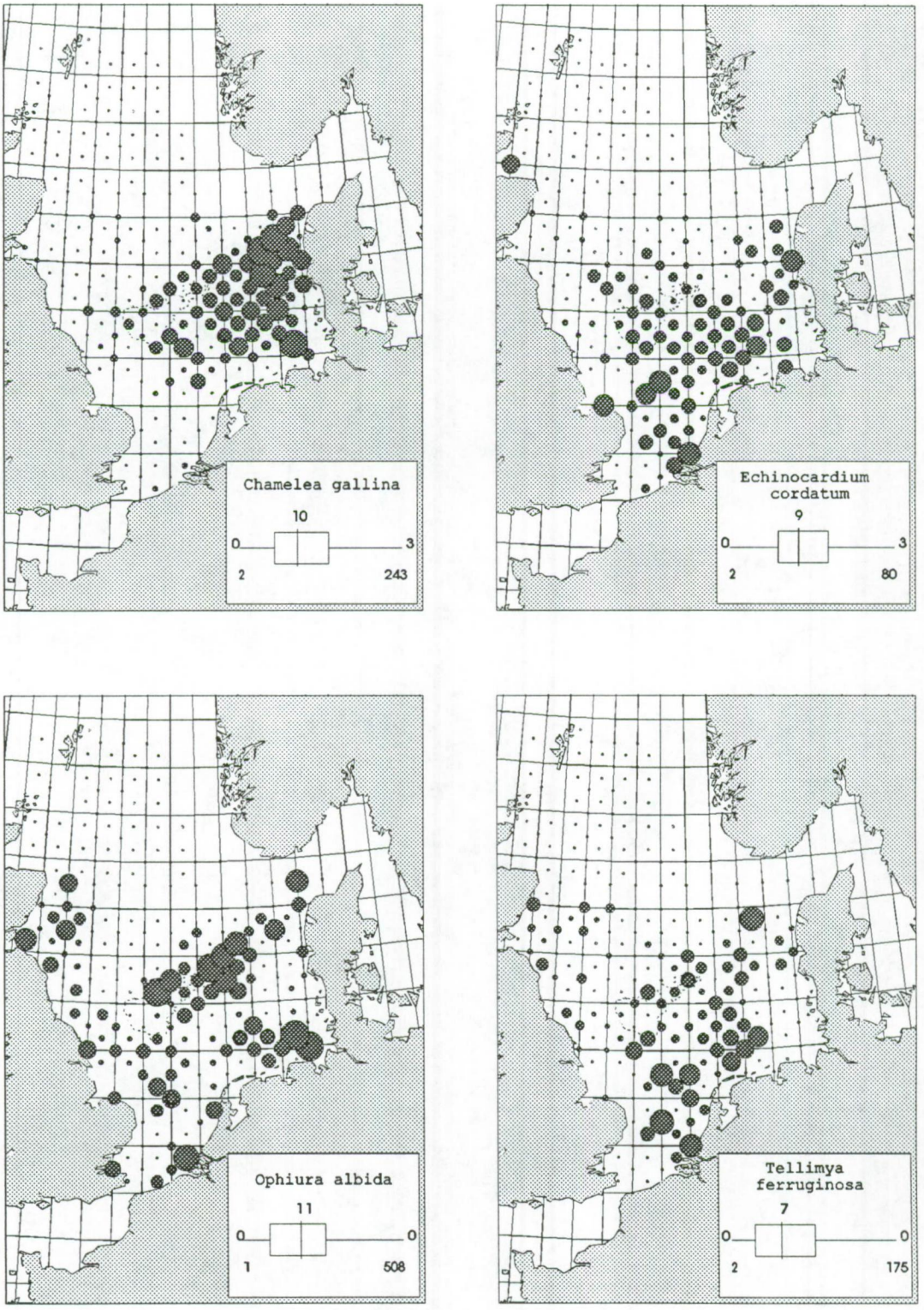


Figure 5.19. Distribution and density of species with a southern occurrence.

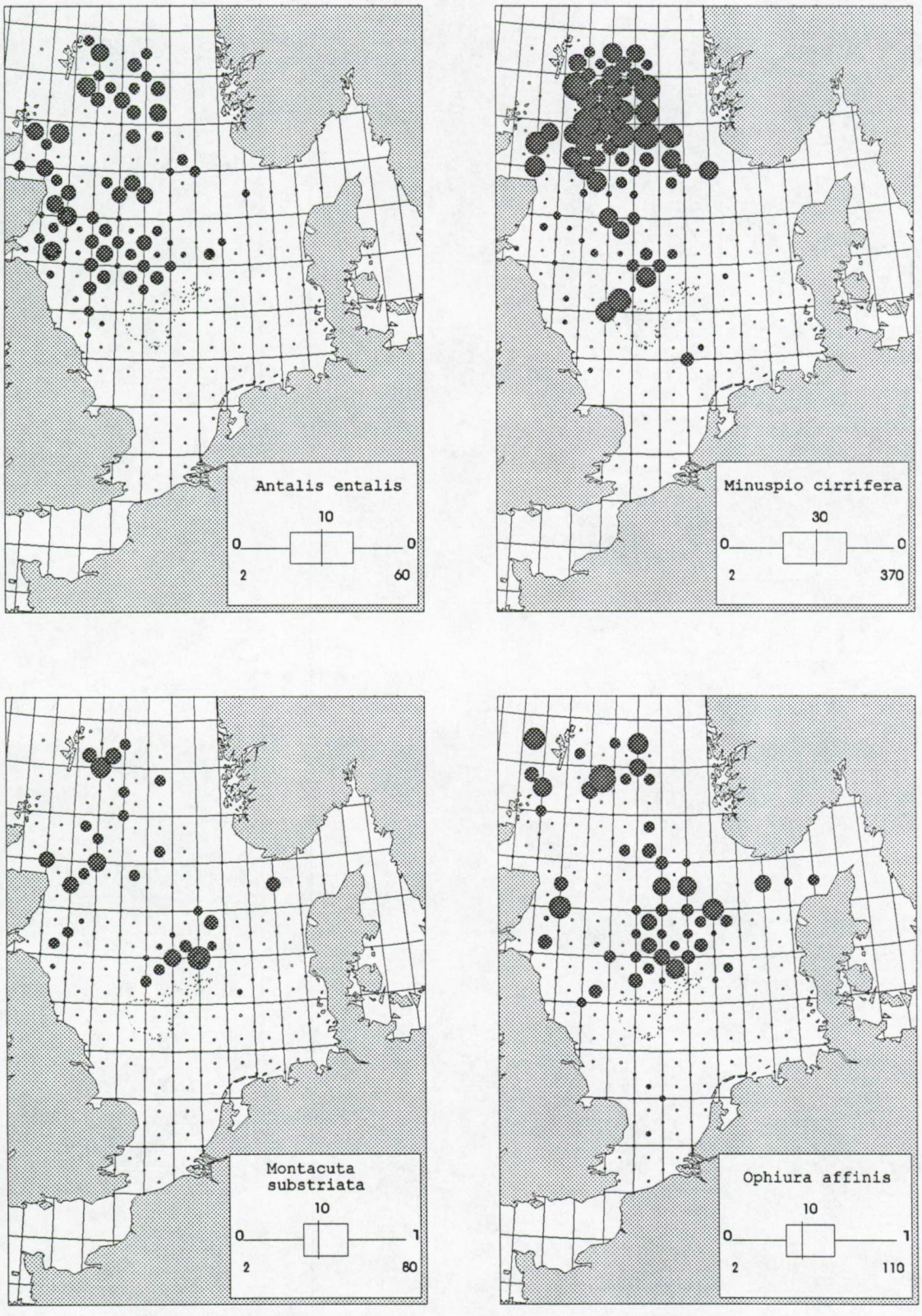


Figure 5.20. Distribution and density of species with a northern occurrence.

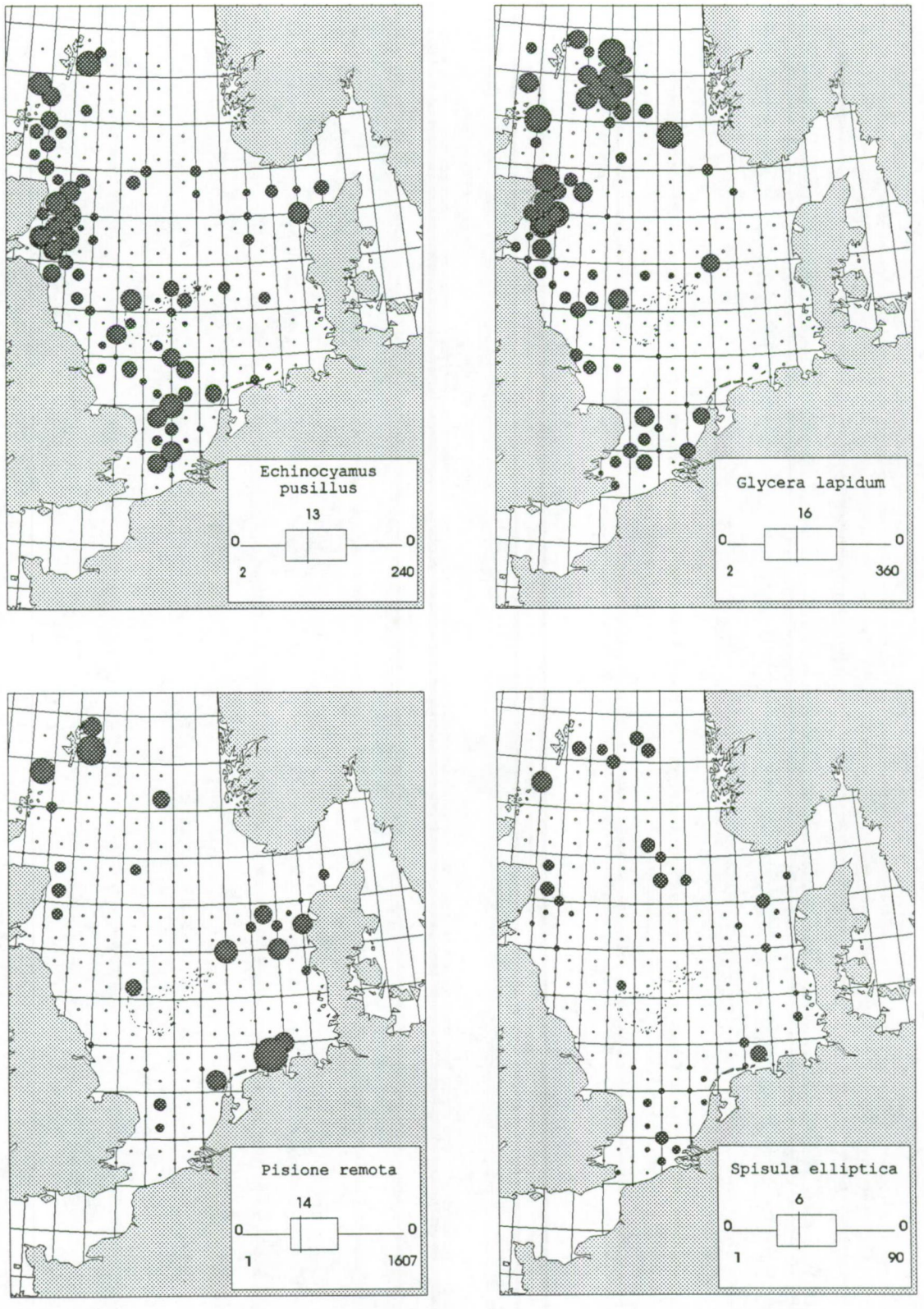


Figure 5.21. Distribution and density of species with a wide occurrence on coarse sediments.

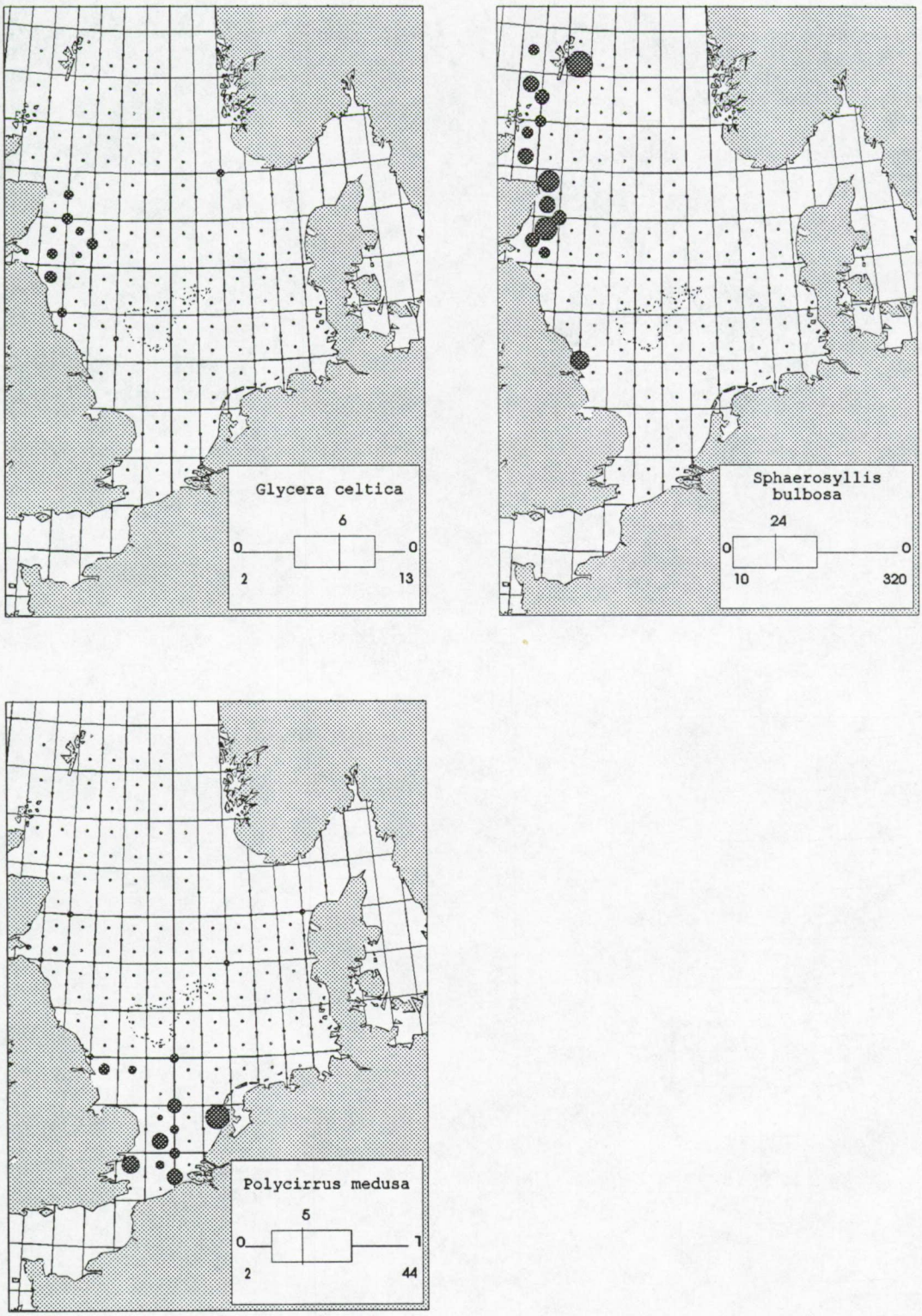


Figure 5.22. Distribution and density of species with a restricted occurrence on coarse sediments.

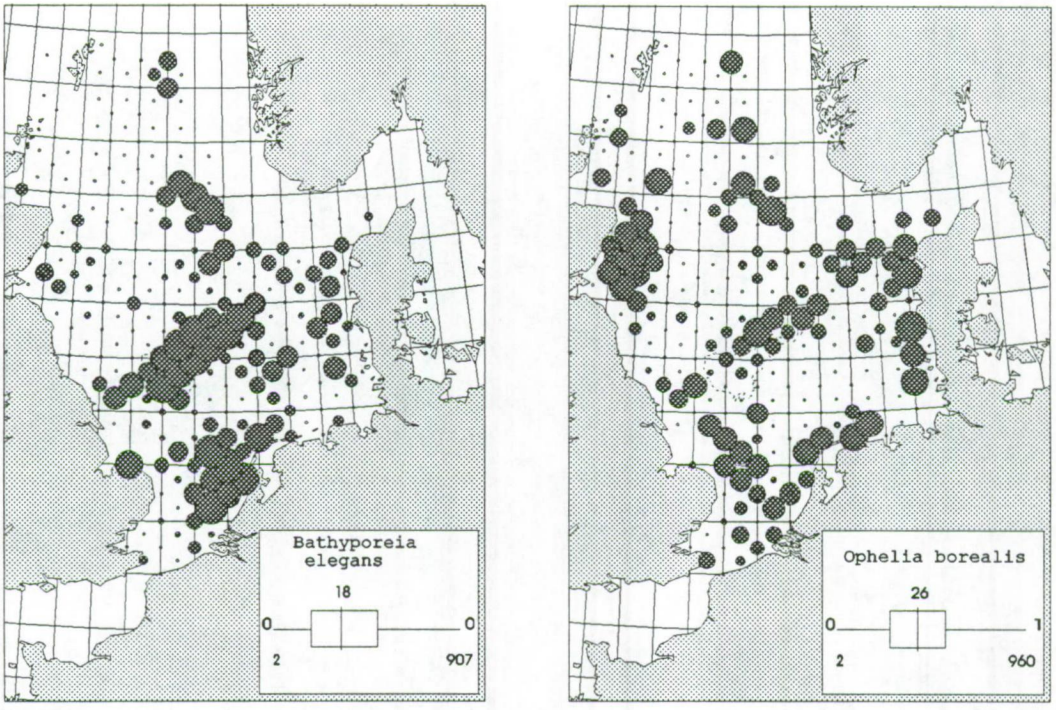


Figure 5.23. Distribution and density of species with a wide occurrence on fine sand.

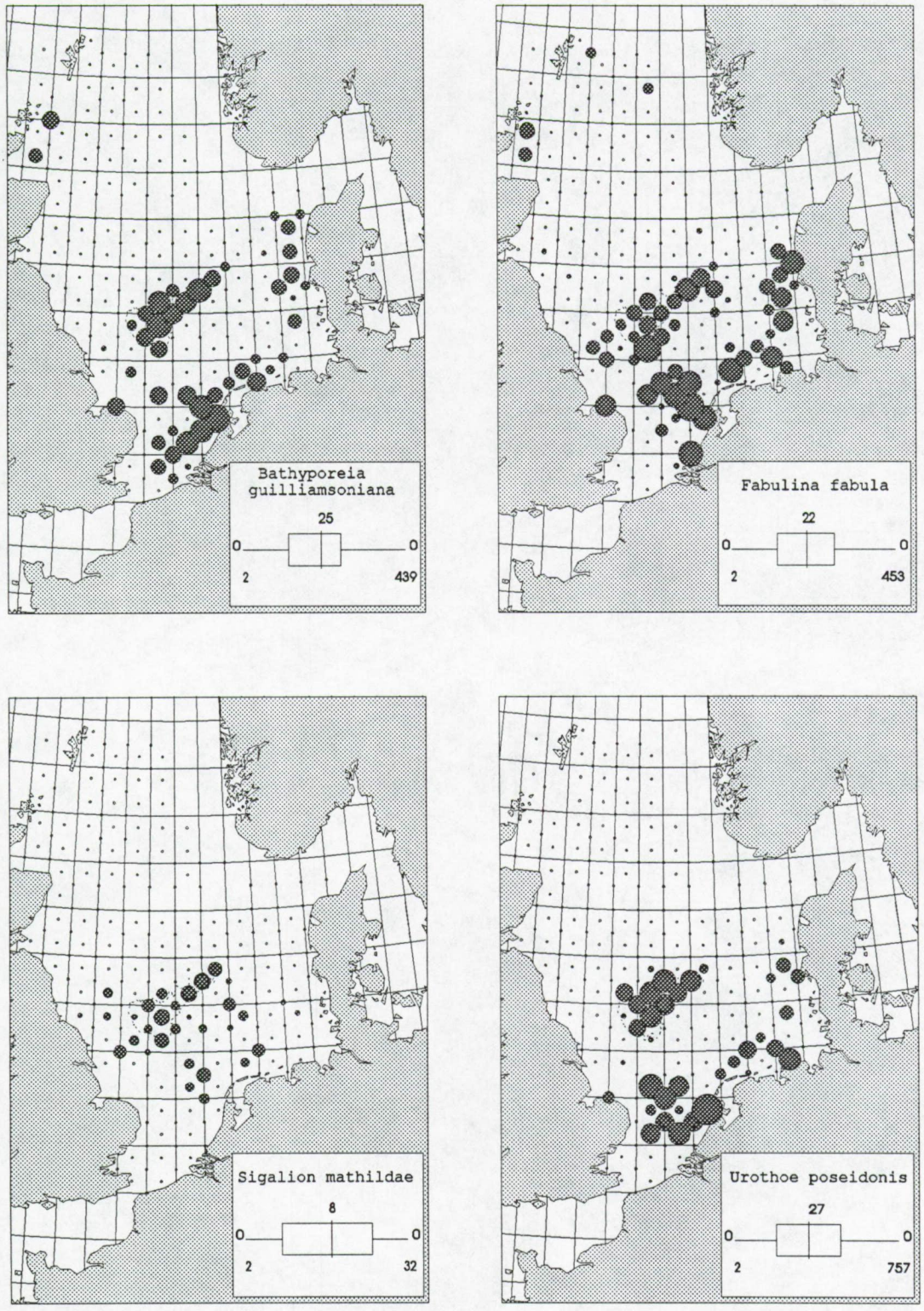


Figure 5.24. Distribution and density of species with a restricted occurrence on fine sand in the southern North Sea.

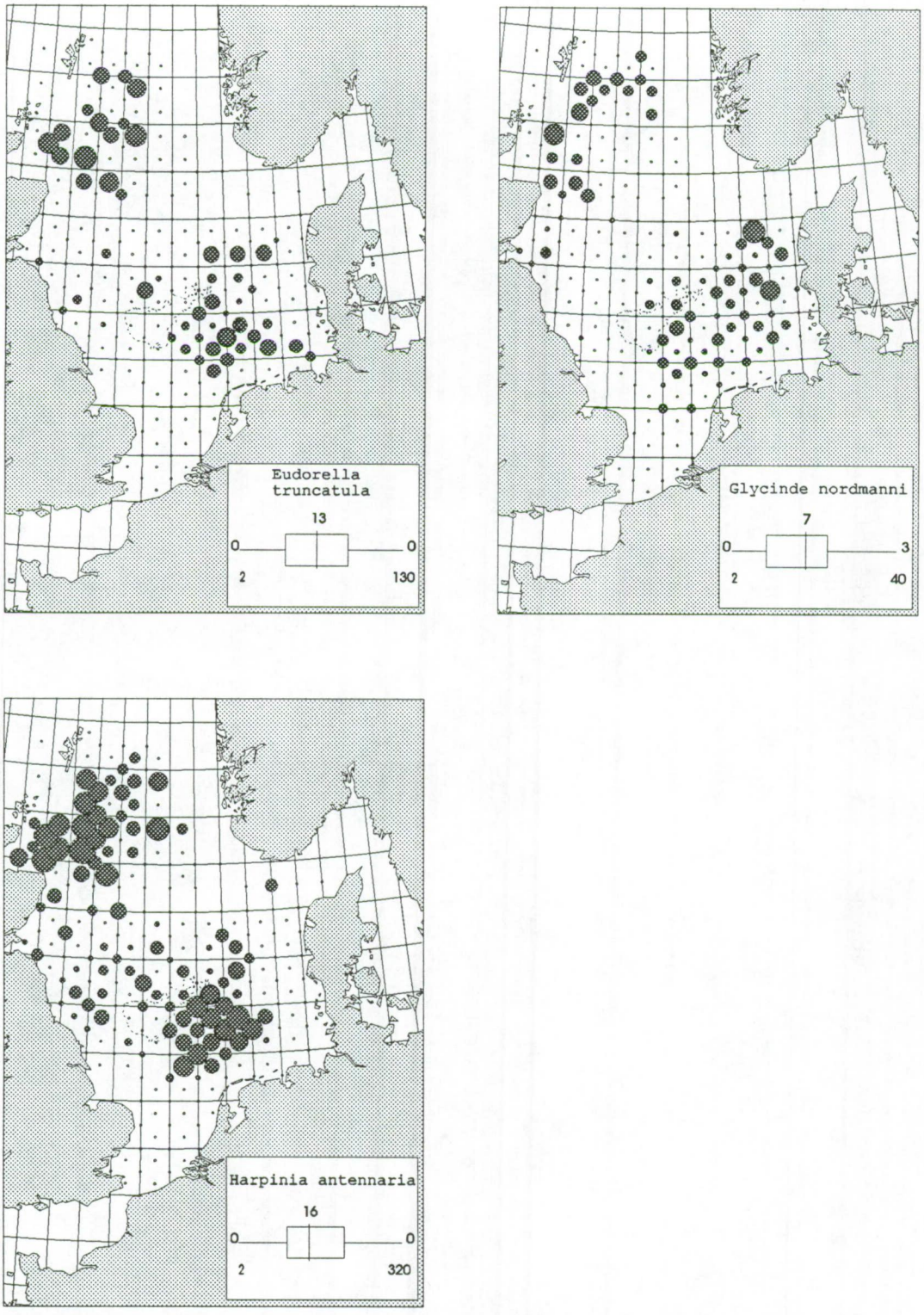


Figure 5.25. Distribution and density of species with a wide occurrence on muddy fine sand.

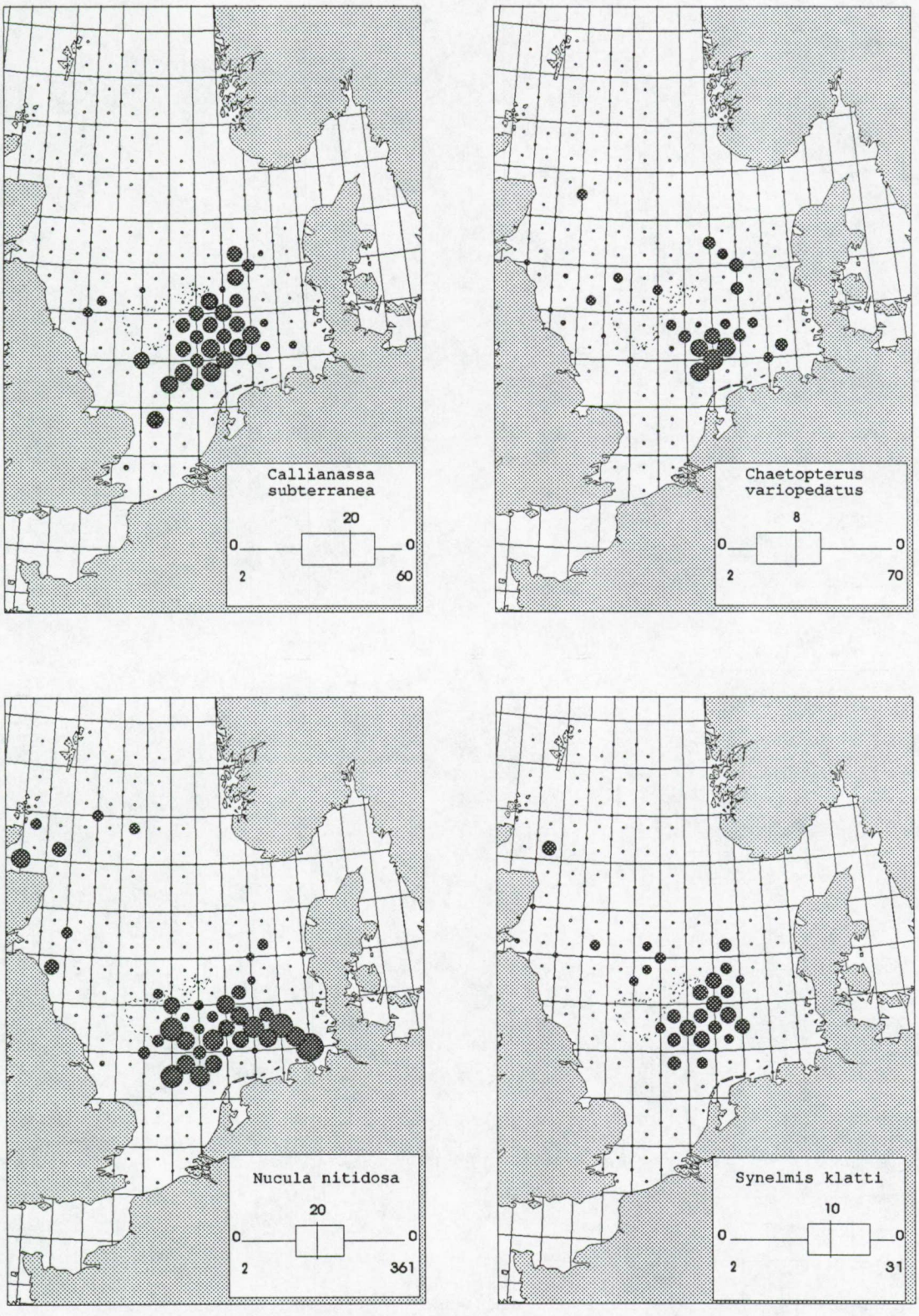


Figure 5.26. Distribution and density of species with a restricted occurrence on muddy fine sand in the southern North Sea.

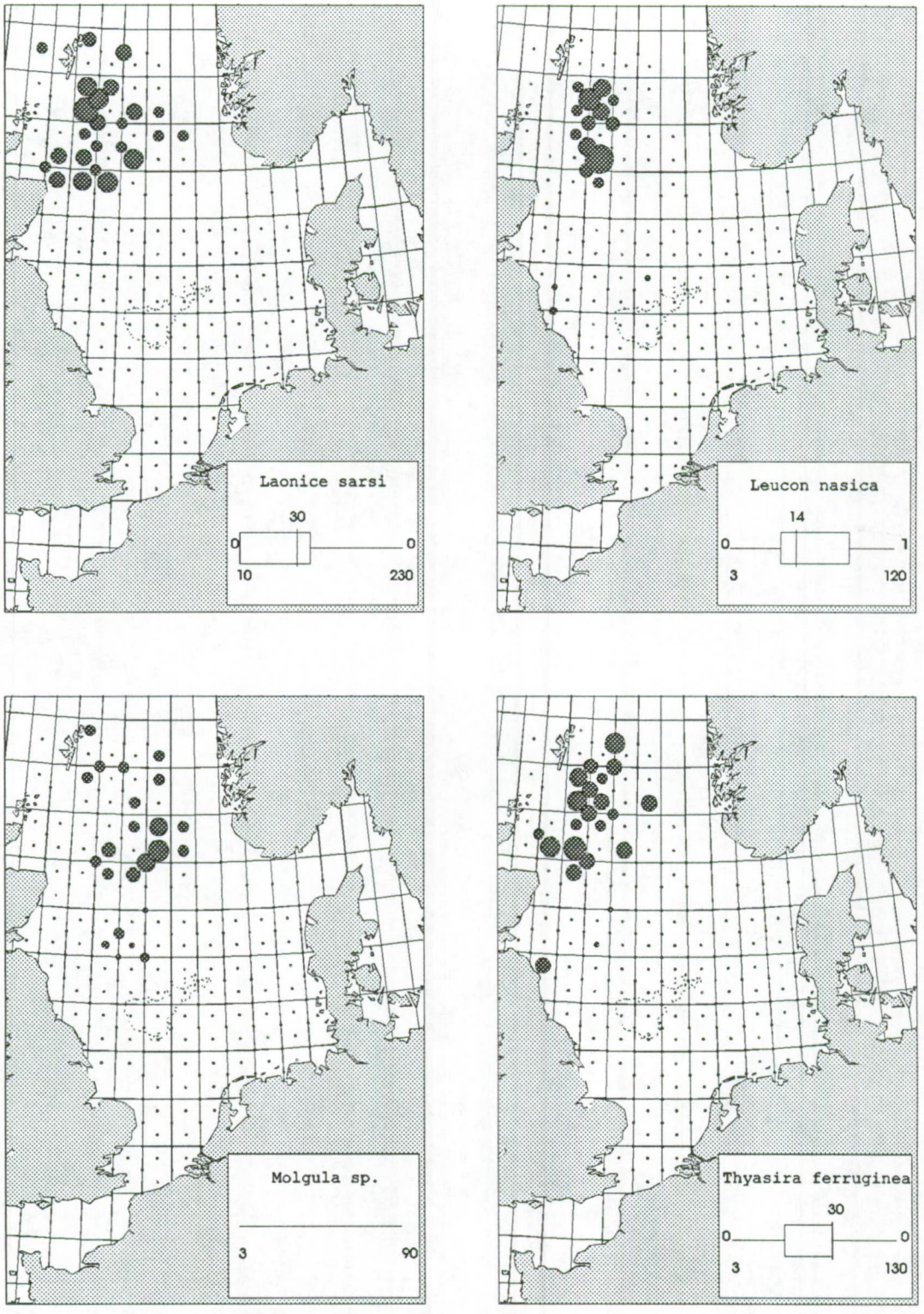


Figure 5.27. Distribution and density of species with a restricted occurrence on muddy fine sand in the northern North Sea.

Species with a southern distribution may occur also in the central North Sea but never north of the 100m contour at 57-58°N: examples are *Ophiura albida, Echinocardium cordatum, Chamelea gallina* and *Tellimya ferruginosa* (fig. 5.19). Some of these species mainly occur in the central North Sea, like *Chaetoderma nitidulum* and *Ampelisca tenuicornis* (not shown here).

Species with a northern distribution were almost never found south of the 50m depth contour, e.g. *Ophiura affinis, Montacuta substriata, Antalis entalis* and *Minuspio cirrifera* (fig. 5.20). Species with northern and southern distributions respectively, caused the division into northern and southern assemblages along the 70m depth contour.

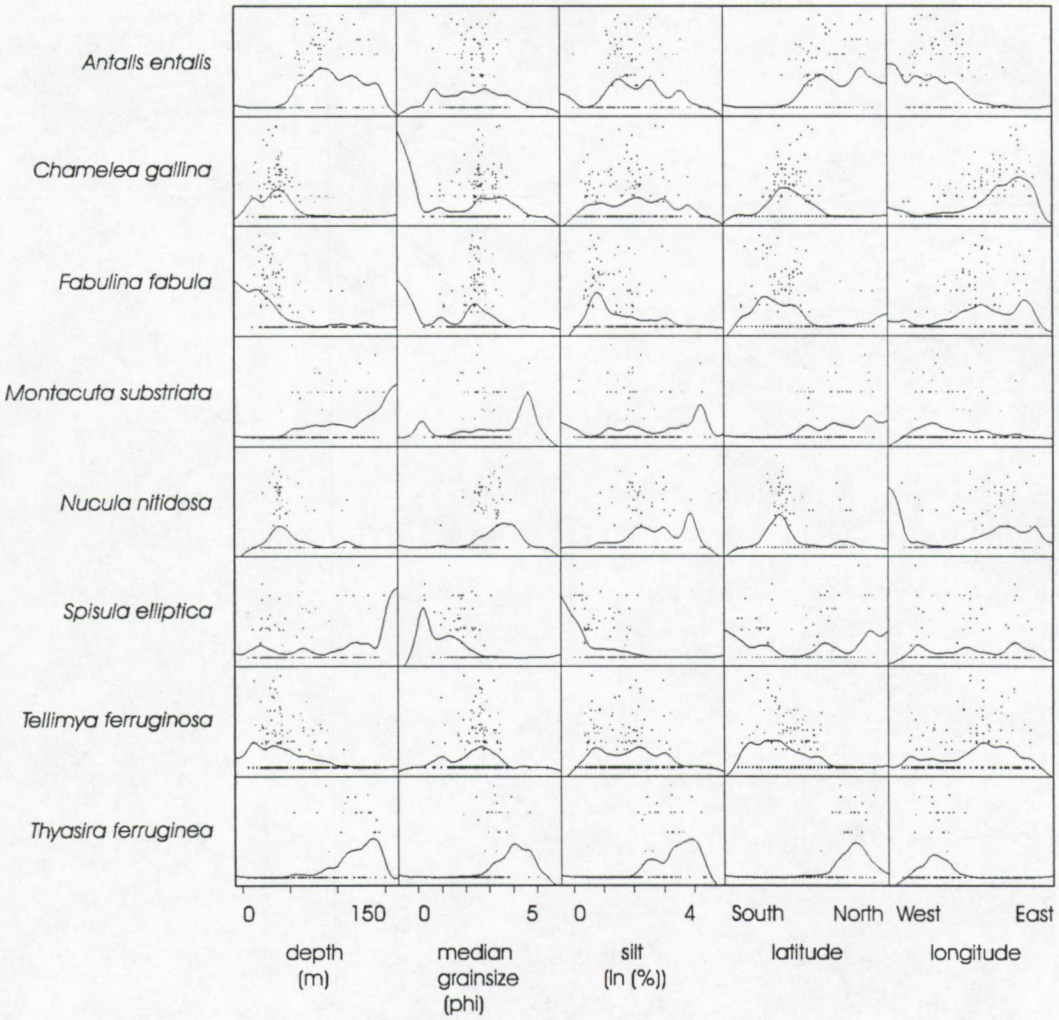


Figure 5.28. Matrix of scatterplots of (ln transformed) densities of selected mollusks against environmental variables. The smooth line is obtained by distance weighted least squares.

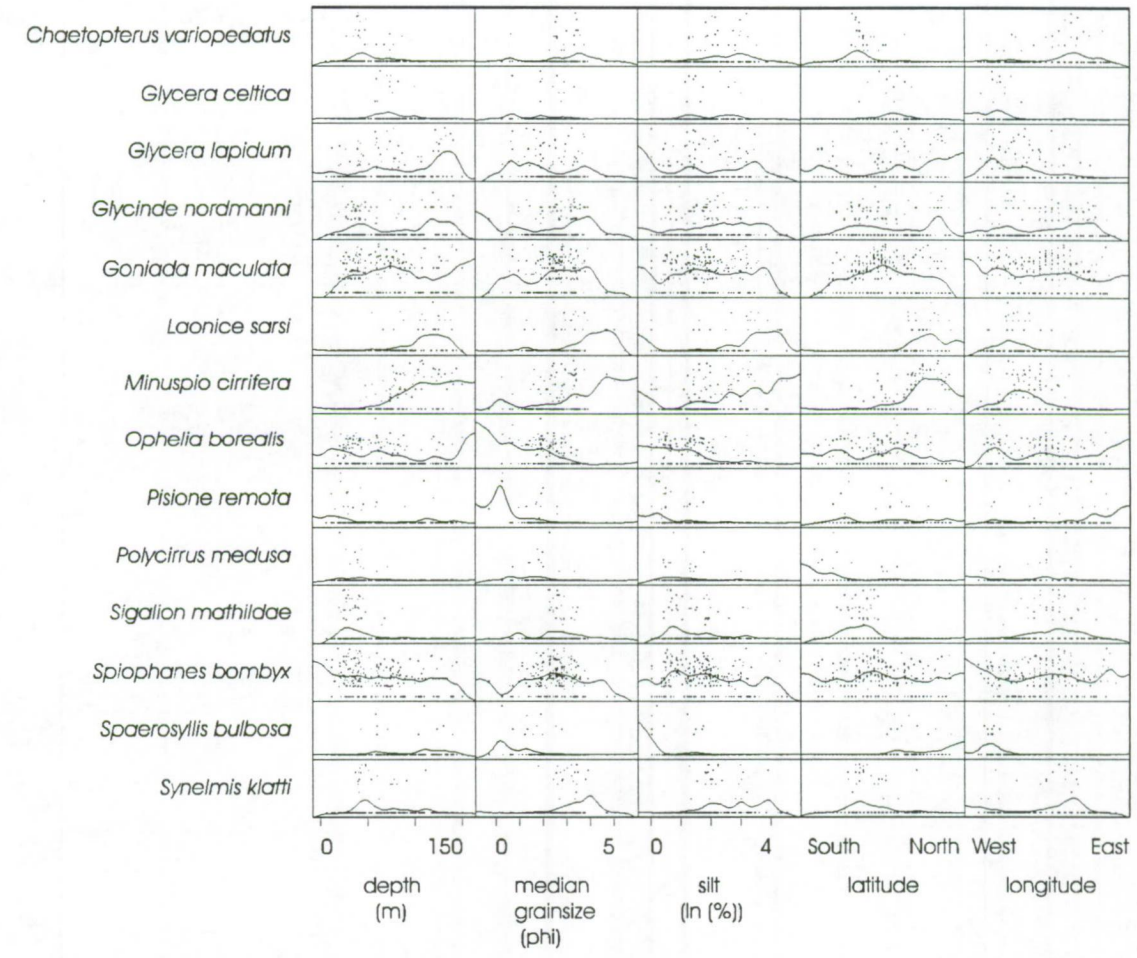


Figure 5.29. Matrix of scatterplots of (ln transformed) densities of selected annelids against environmental variables. The smooth line is obtained by distance weighted least squares smoothing.

The distribution of the species also seems to be determined by the sediment. On coarse sediments *Echinocyamus pusillus, Pisione remota, Glycera lapidum* and *Spisula elliptica* occur all over the North Sea (fig. 5.21), while *Sphaerosyllis bulbosa* and *Glycera celtica* are restricted to coarse sediments along the Scottish coast and *Polycirrus medusa* to coarse sediments in the south of the North Sea (fig. 5.22). On fine sand *Aricidea minuta, Bathyporeia elegans* and *Ophelia borealis* occur all over the North Sea (fig. 5.23), but *Bathyporeia guilliamsoniana, Fabulina fabula, Urothoe poseidonis* and *Sigalion mathildae* were only found in the southern North Sea on fine sand at depths less than 30m (fig. 5.24). Sediments of muddy fine sand occur mainly in the southern North Sea at 30-50m depth and in the west of the northern North Sea (fig. 5.15). Species with a wide distribution on this sediment are *Eudorella truncatula, Glycinde nordmanni* and *Harpinia antennaria* (fig. 5.25). *Callianassa subterranea, Nucula nitidosa, Chaetopterus*

variopedatus and *Synelmis klatti* are restricted to the southern North Sea (fig. 5.26) and *Leucon sarsi, Thyasira ferruginea, Laonice sarsi* and *Molgula* sp. are restricted to the northern North Sea (fig. 5.27).

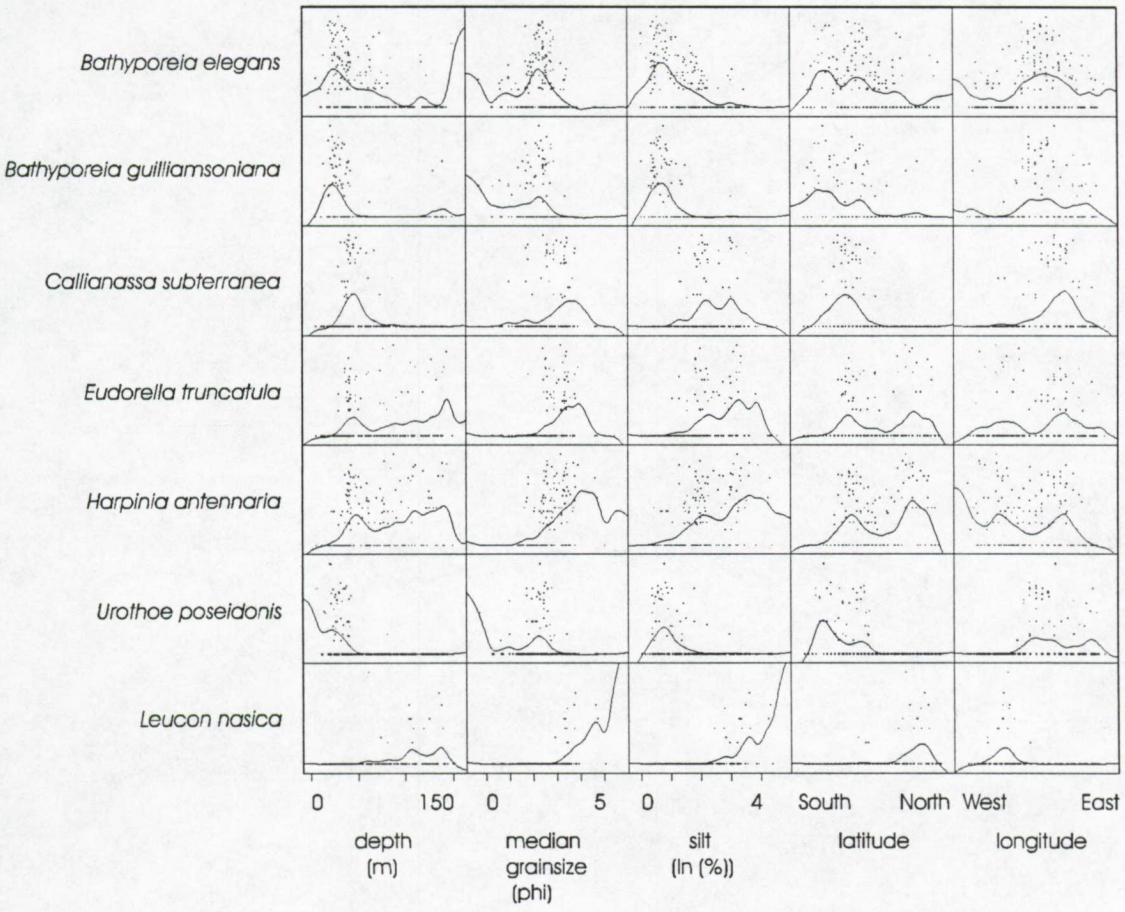


Figure 5.30. Matrix of scatterplots of (ln transformed) densities of selected arthropods against environmental variables. The smooth line is obtained by distance weighted least squares smoothing.

The relationship between the distribution of the species mentioned above and depth, sediment characteristics and geographical position is also obvious from figures 28 to 31, showing scatterplots of (ln-transformed) densities against each environmental variable. *Antalis entalis*, for example, is restricted to the northwest of the North Sea – also the deepest part of the area investigated – but seems not to be affected by the median grainsize or silt content of the sediment. *Spisula elliptica*, on the contrary, occurs over the whole North Sea but is restricted to the coarser sediments.

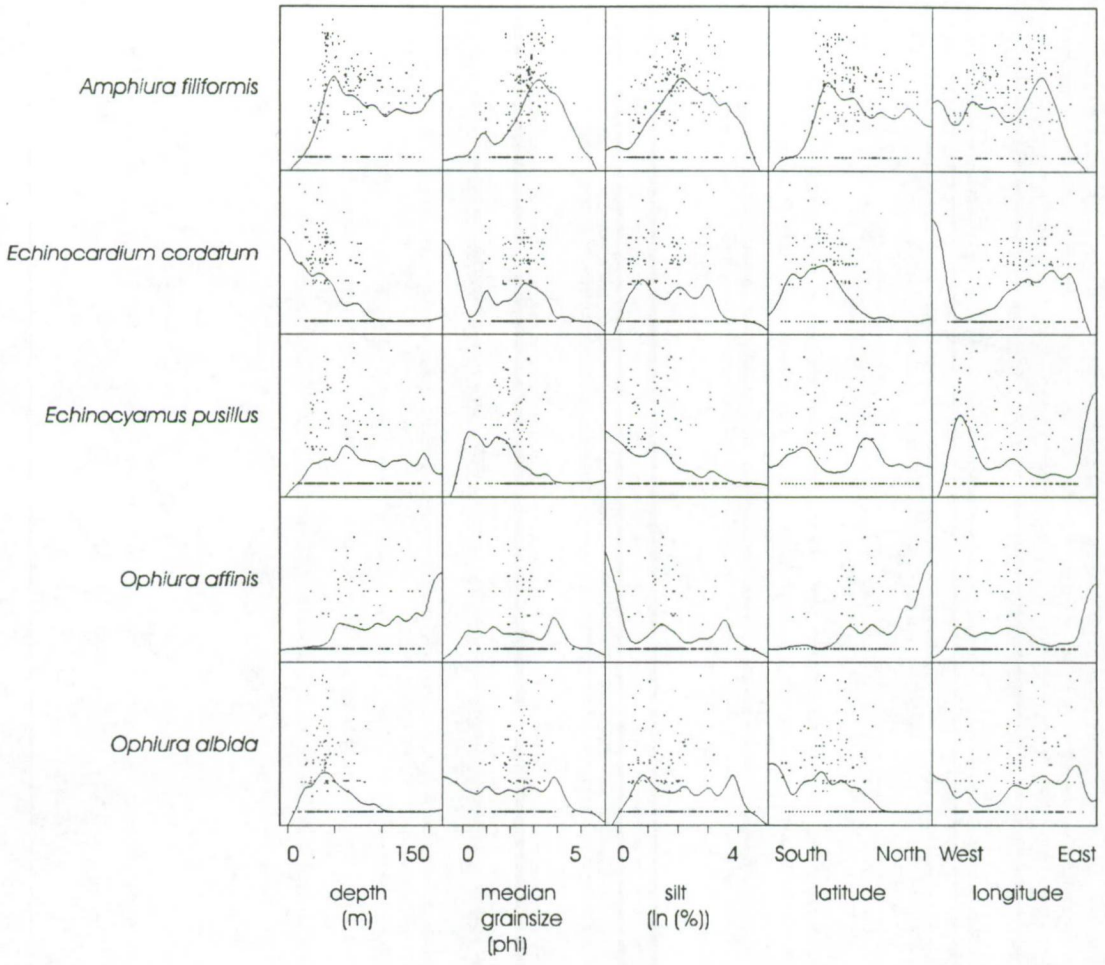


Figure 5..31. Matrix of scatterplots of (ln transformed) densities of selected echinoderms against environmental variables. The smooth line is obtained by distance weighted least squares smoothing.

Ordination

The results of the Canonical Correspondence Analyses (CCA) are shown in figure 5.33 (the two stations of cluster IVb were not incorporated in this analysis).

Depth and longitude are negatively correlated; the deepest locations were found in the west. Latitude is closely related to depth – there is a general trend of increasing water depth to the north – but is hardly correlated to the species compositon. Median grainsize (expressed in phi-units) and silt content are positively correlated. There seems to be almost no correlation between sediment characteristics and depth.

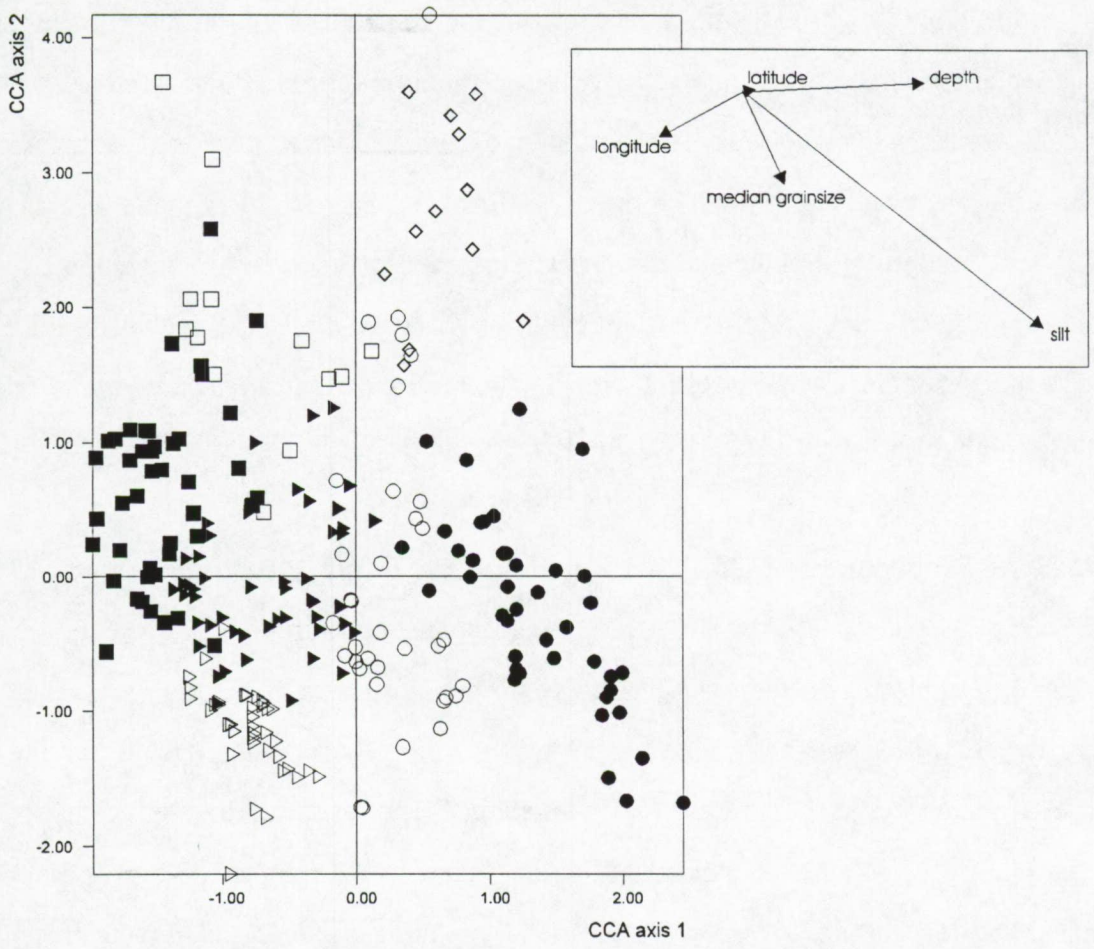


Figure 5.32. CCA ordination diagram of the TWINSPAN groups based on species abundance data (symbols as in figure 5.13).

The identity of the TWINSPAN groups is clearly expressed. The coarsest sediments are found in clusters Ib and IVa. The deepest stations are found in cluster IIIb, the shallowest stations in cluster Ib. The stations of several the clusters (e.g. IIa, IIIa and IIIb) are further arranged along a gradient of grain size (increasing mud content and median grain size expressed in phi-units).

Discussion

The North Sea is situated on the continental shelf of northwest Europe. The depth gradually increases from less than 30 m in the south to about 200 m in the northern part. In the northeast, parallel to the Norwegian coast and curving southwards into the Skagerrak, the sea floor steeply slopes down to more than 700 m. The 100 m depth contour (approximately 57.3°N) separates

two hydrographic zones. Atlantic waters entering the North Sea from the north do not reach the continental coastline but turn gradually eastwards along the 100 m depth contour towards the Jutland coast and the Skagerrak. To the south of the 100 m contour there is a residual southerly flow along the English coast which meets the English Channel inflow water and then flows northeast through the Southern Bight and German Bight eventually to enter the Skagerrak, where it merges with the northern Atlantic inflow. All water masses leave the North Sea along the west coast of Norway. The general direction of the circulation varies only little with seasons (Basford and Eleftheriou 1988, Backhaus 1989, NSTF 1993).

The North Sea sediments are mainly of Holocene age. During the Quaternary glacial period, the whole area was covered by ice. After the last glacial period around 15000 years ago (Wurm or Weichsel glaciation), the sea penetrated into the North Sea area from the north, and the northern part of it became part of a glacial sea known as the Yoldia sea. Between the Boreal and Atlanticum (5500 BC), the sea level was about 17 metres lower than today, the North Sea was a shallow basin with several shoals and the Channel was not open. As late as 2000 BC the Channel was still a small river-like water. In the beginning of the Atlanticum the present shape of the North Sea formed, except for the west coast of Jutland and the Dutch and German coast. Subsequently the sea level rose 15 metres, the Dogger Bank disappeared and the Channel reached its full extent (Nio et al. 1981). The distribution of the sediments reflects the glacial history and more recent hydrodynamic processes. In the northern North Sea sedimentary inputs are negligible, and due to the greater depths in this region hydrographic redistribution of the sediments is limited to the shallower areas with stronger tides (e.g. Orkney-Shetland Channel) (Basford et al. 1993). In contrast, in the southern part of the North Sea particulate material is introduced and deposited from the major rivers and via the English Channel. In this shallow area of the North Sea, intensive sediment movements and associated transport occur frequently, owing to wind-induced currents, tides, and/or wave action (NSTF 1993). The counterclockwise residual currents transport the fine-grained material in suspension from the Southern Bight along the eastern boundaries of the North Sea towards the Skagerrak (Eisma and Kalf 1987). Therefore, the coarsest sandy sediments are found in the Southern Bight. Strong tidal currents and wave action have swept the glacial and fluvial sandy sediments into elongated sand waves

and ridges (e.g. in the Brown Bank area). Relict glacial deposits can locally be found near the sediment surface (e.g. at the Cleaver Bank). As the maximum current velocities decrease in northward direction, the median grain size gradually decreases northward as well. Mud deposition characterises deeper areas such as the Oyster Ground, the Skagerrak and the Norwegian Trench. The sediment of the Oyster Ground area was mainly deposited in the last glacial. Recent accumulation of fine particles in that area mainly takes place along the southern border at the Frisian front (Holtmann et al. 1996).

The same forces that influence sediment transport also determine the distribution of the organic matter. The distribution of organic carbon closely follows that of the fine-grained material (Basford et al. 1993). The labile organic material reaching the sediment in the Southern Bight, which originates from direct deposition of phytoplankton blooms, becomes progressively more refractory during its transport northwards (Dauwe and Middelburg 1998). Ultimately the major fraction of the total suspended matter of the North Sea is deposited in the Skagerrak (Eisma 1990), the area with the slowest bottom water movements (NSTF 1993).

Most areas of the North Sea are vertically well mixed in winter months. In the northern North Sea the water is thermally stratified throughout the summer The strength of the thermocline depends on the heat input and the turbulence generated by the tides and the wind. Large areas of the southern North Sea remain well mixed throughout the year owing to strong tidal action (Tomczak and Goedecke 1964, NSTF 1993) and therefore the summer temperature of bottom waters is high (10°C) (Tomczak and Goedecke 1962). In the stratified areas north of the Dogger Bank summer temperatures are less than 7°C. In winter the southern North Sea is colder (4°C) than the rest of the North Sea (5-7°C).

The main patterns of species distribution show that the bottom fauna of the North Sea is composed of northern elements that do not extend further south than the north of the Dogger Bank, and southern elements going not further north than the 100 m contour. Northern and southern species mix in the central North Sea. The occurrence of cold water species north of the Dogger Bank and of warm water species in the southern North Sea was already recognised

by Ursin (1960), Kirkegaard (1969) and Petersen (1977). None of these authors, however, showed that the southern species occurred as far north as the 70-100 m depth contour. The separation of the fauna into a northern and a southern one might be a result of the current pattern in the North Sea. The northern North Sea and part of the central North Sea is influenced by a different type of water than the rest of the North Sea. The distribution of the larger epifauna has been shown to be likewise determined by these two different water masses (Frauenheim et al. 1989). The epifauna north of the Dogger Bank is different from the one in the southern North Sea.

The productivity of temperate, shallow areas such as the North Sea is generally high. Bottom topography, water circulation and nutrient discharges by rivers seem to be crucial in explaining spatial differences in primary production and biomass. Coastal regions generally keep a higher level of nutrients during the whole year, allowing a more sustained phytoplankton growth. Production is known to have strong seasonal variation. It starts in the nutrient-rich areas just outside the largest continental river mouths and spreads offshore and north as the daily irradiance (and temperature) increases with season. The differences in time of onset are associated with increasing water depth, and the delay must be a consequence of later stabilisation. In the southern North Sea the cycle peaks in early April, in the central North Sea perhaps slightly later. In the northern North Sea production reaches its maximum at the beginning of May. Whereas in the southern North Sea production appears to be continuous throughout summer, in the northern North Sea the blooms are restricted to the spring. Thus, the riverine inputs of nutrients result both in a higher and longer lasting phytoplankton spring bloom and a higher biomass during the summer (Colebrook and Robinson 1965, Cushing 1983, Lancelot et al. 1987, Owens et al. 1990, Joint and Pomroy 1993, Skogen et al. 1995, Varela et al. 1995).

The correlation between benthic biomass and chlorophyll *a* in sediments certainly indicates a link with surface productivity, especially since the correlation does not exist with total pigment concentration. However, the total biomass is influenced both by the quantity as the quality of the organic matter. In the shallower, coarse-grained areas in the southern North Sea, the physical stress excerted by tidal currents and storms on the bottom will inhibit larval settlement or erode

settlers (Jenness and Duineveld 1985). Many dominant species exhibit dramatic variations in their abundance coinciding with severe storms (Hall, 1994). Other species are able to withstand erosion of the bottom by burrowing (e.g. *Echinocardium cordatum*) (Duineveld et al. 1991). The dominant species are often small, mobile, actively burrowing deposit feeding crustaceans such as the genus *Bathyporeia* (Hall, 1994). The low content of organic matter of coarse-grained sediments is reflected in very low macrobenthic biomass (Dauwe et al. 1998). The higher biomass in the areas with finer sediments suggests a decreased physical stress and an improved food input. Sediments with a prolonged season input of organic matter (e.g. the Frisian Front area) are populated by both subsurface-deposit and suspension-interface feeders. Subsurface deposit-feeder dominated communities populate sediments with a high supply of low quality organic matter (e.g. the Skagerrak), suspension-interface feeding communities sediments with a high amount of high quality organic matter (e.g. the German Bight) (Dauwe et al. 1998). In systems with little stress from hydrodynamic disturbance, an increase in macrobenthic biomass with increased primary production have been reported (Rachor 1990, Beukema and Cadée 1997).

The mean biomass appears to be at least – because April is commonly assumed to be the moment of minimum biomass – twice as high as estimated before (3.2 gAFDW/m^2) by Rachor (1982). The present study likely still underestimates the biomass. Less abundant, usually larger species that may occur at frequencies of less than one per square meter are infrequently found in grab samples. Larger quantitative samples of the sea bed biota can only be taken by dredges such as developed by the Netherlands Institute for Fisheries Research to assess shellfish stocks (van Stralen 1992) and the Netherlands Institute for Sea Research (Bergman and van Santbrink 1994). However, some predicted features such as highest biomass stocks in the whole infralittoral étage (Glémarec 1973) and in the coastal étage near the Scottish coast and south and east of the Shetlands have been confirmed.

The influence of physical stress is also reflected in differences in diversity. Areas where strong tidal currents exist and where the wave action reaches the bottom are in general characterised by a lower diversity. Diversity shows a clear increase with latitude and, thus, with depth. North

of the 58 degree latitude almost all stations sampled are situated to the west of the 2nd degree longitude, in the southern North Sea (i.e. south of the 54°N) the stations are situated east of the 2nd degree longitude. This can explain the effect of longitude on diversity.
The northern North Sea data have been obtained over different years and using a sieve of 0.5 mm mesh size. Especially the effect of mesh width may complicate the comparison with the NSBS data. Except for density, there is, however, no abrupt change north of the 58°N latitude, i.e. the northern limit of the NSBS.

Trends in individual body weight or in diversity on a global scale have been documented mainly for fauna from the terrestrial environment, but why these trends exist is not really understood (Clarke 1992). Thorsen (1946) noted a pronounced increase in the species richness of epifauna from hard substrates towards the tropics, but the number of macrofaunal species in sediments appeared to be roughly the same for arctic, temperate and tropical seas. On the other hand, Stehli et al. (1967) clearly demonstrated a decrease in diversity of bivalve molluscs at species, genus and family level from the tropics to the poles, and in a later study (Stehli et al. 1972, cited in Clarke 1992) demonstrated the same for foraminifers. These appear to be the only detailed work on the problem of diversity trends, and, since both groups form calcareous skeletons, Clarke (1992) suggested that perhaps such trends do not exist in other taxa. In our study it is clearly demonstrated that trends in several characteristics do indeed exist on large scales (about 1000 km). These trends can, however, vary in different groups. Thus the individual weight and diversity of copepods (figures 5.33 and 5.34) display trends opposite to the trends observed for the macrofauna.

Although human impact around point sources such as sewage outlets and oil platforms is known to affect the benthos (see e.g. Daan et al. 1990, 1991, 1992), these effects are localised. Effects of fisheries are probably much more widespread but difficult to quantify. Especially beam-trawling is thought to have large effects on benthic communities. Effects of fishing on benthic communities have been described by e.g. Graham (1955), Bridger (1970), Houghton et al. (1971), de Groot and Apeldoorn (1971), Margetts and Bridger (1971), Rees and Dare (1993), de Groot and Lindeboom (1994), WGECO (1996), and Lindeboom and de Groot (1998).

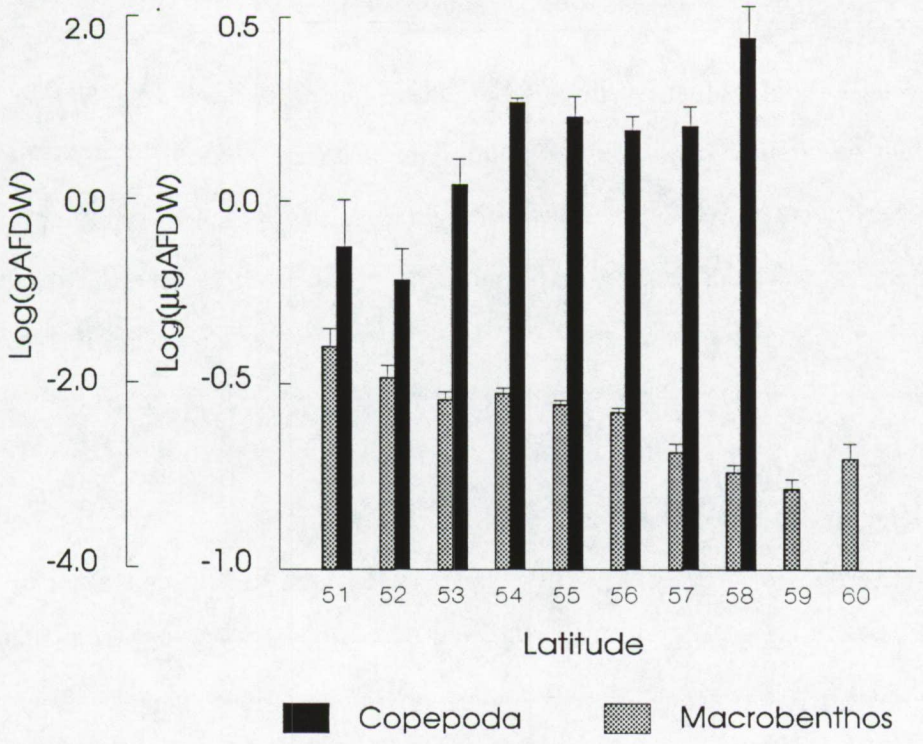


Figure 5.33. Individual weight of macrofauna (log g AFDW) and copepods (log µg AFDW) as a function of latitude.

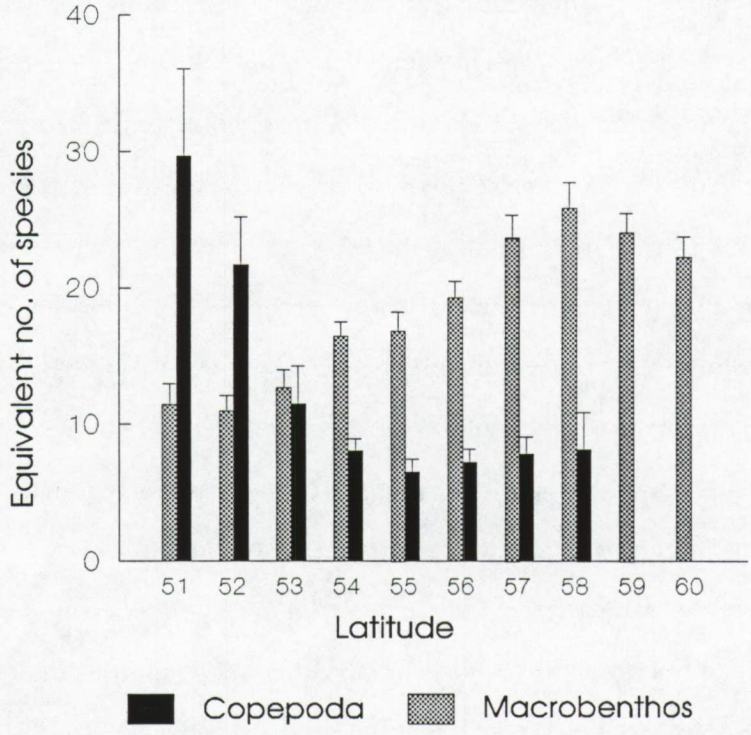


Figure 5.34. Diversity of macrobenthos and harpacticoid copepods (Hill N_1 expressed in equivalent number of species) as a function of latitude.

Damage, mortality and reduction in numbers have been reported for *Arctica islandica, Echinocardium* sp., *Lanice conchilega, Ophiura ophiura, Lagis koreni, Liocarcinus holstus, Corystes cassivelaunus and Spiophanes bombyx*. On local scales the loss of target populations, such as oysters, and the destruction of physical structures such as *Sabellaria* reefs is well documented. The disappearance of species such as *Ostrea edulis, Modiolus modiolus, Dosinia exoleta, Glycymeris glycymeris, Arctica islandica* and *Neptunea antiqua* has been ascribed as being caused by the beam trawl fishery.

Organic enrichment leads to an increase in macrobenthic biomass (see above), but only to a certain point. Eutrophication may lead to oxygen deficiency of the bottom waters and sediment may become anoxic which then lead to the death of the benthos (NSTF 1993). In several areas, a shift towards greater dominance of small, opportunistic, short-lived species has been reported. On the Dogger Bank, polychaete species such as *Spiophanes bombyx* and *Scoloplos armiger* have increased in numbers (Kröncke 1992). In muddy areas in the inner German Bight, *Echinocardium cordatum* and *Nucula nitidosa* have become less important. The ophiurid *Amphiura filiformis* was found in increasing densities in several studies related to enrichment of organic matter. Duineveld et al. (1987) suggested that the increase of *A. filiformis* in the shallower parts of the North Sea (1938/1950–1986) could indicate an enhanced food supply for the benthic, which may have some relation to the eutrophication in nearshore areas. The decomposition of organic matter may result in low oxygen concentrations or even oxygen deficiencies, causing mortality of benthic organisms. Dyer et al. (1983) found many dead macrobenthic animals (*Echinocardium cordatum, Aphrodite aculeata, Corystes cassivelaunus* and *Astropecten irregularis*) in his dredge samples (emergence behaviour). Niermann et al. (1990) found *Owenia fusiformis, Lanice conchilega, Spio filicornis*, juvenile bivalves, and especially juveniles of the echinoderms *Ophiura albida* and *Echinocardium cordatum* either reduced in abundance or not occurring at all under the hypoxic conditions in the German Bight in the summer of 1983. But recovery may be rapid (Niermann et al. 1990).

The utility of benthic communities as tools for biological monitoring of the marine environment is now generally accepted. The confirmation that the entire North Sea may be subdivided into areas based on benthic species composition is important in view of the management of the North

Sea, since it permits choices of representative stations to be made. Spatial patterns are sufficiently constant in time to permit prediction of the species composition. However, to increase predictive strength, the causal mechanisms leading to changes in size and relative abundance have to be better understood. Any further study should take into account the main factors affecting the benthic communities: differences in the hydrodynamic conditions, differences in productivity and organic flux to the benthos, and the impact of human disturbances.

References

Backhaus, J. O. 1989. The North Sea and the climate. Dana **8**:69-82.

Basford, D., and A. Eleftheriou. 1988. The benthic environment of the North Sea (56E to 61EN). Journal of the Marine Biology Association of the United Kingdom **68**:125-141.

Basford, D. J., A. Eleftheriou, and D. Raffaelli. 1989. The epifauna of the northern North Sea (56E-61EN). Journal of the Marine Biology Association of the United Kingdom **69**:387-407.

Basford, D., A. Eleftheriou, and D. Raffaelli. 1990. The infauna and epifauna of the northern North Sea. Netherlands Journal of Sea Research **25**:165-173.

Basford, D. J., A. Eleftheriou, I. M. Davies, G. Irion, and T. Soltwedel. 1993. The ICES North Sea benthos survey: the sedimentary environment. ICES Journal of Marine Science **50**:71-80.

Bergman, M. J. N., and J. W. van Santbrink. 1994. A new benthos dredge ('triple-D') for quantitative sampling of infauna species of low abundance. Netherlands Journal of Sea Research **33**:129-133.

Beukema, J. J., and G. C. Cadée. 1986. Zoobenthos responses to eutrophication of the dutch Wadden Sea. Ophelia **26**:55-64.

—. 1997. Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only locally a limiting factor. Limnology and Oceanography **42**:1424-1435.

BEWG. 1985. Fourth report of the Benthos Methodics Working Group. ICES C.M. 1985/L:33. 39pp.

—. 1986. Fifth report of the Benthos Ecology Working Group. ICES C.M. 1986/L:27. 33pp.

BMWG. 1983. Second report of the Benthos Methodics Working Group. ICES C.M. 1983/L:38. 37pp.

—. 1984. Third report of the Benthos Methodics Working Group. ICES C.M. 1984/L:36. 27pp.

Bridger, J. P. 1970. Some effects of the passage of a trawl over a seabed. ICES C.M.1970/B:10. 10pp.

Cederwall, H., and R. Elmgren. 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. Ophelia **(Suppl.) 1**:287-304.

Chambers, S. 1985. Polychaetes from Scottish waters. Part 2. Families Aphroditidae, Sigalionidae and Polyodontidae. Royal Scottish Museum Studies. 38pp.

Clarke, A. 1992. Is there a latitudinal diversity cline in the sea? Tree **7**:286-287.

Colebrook, J. M., and G. A. Robinson. 1965. Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north-eastern Atlantic and the North Sea. Bulletin of Marine Ecology **6**:123-139.

Craeymeersch, J. A., C. H. R. Heip, and J. Buijs. 1997. Atlas of North Sea Benthic Infauna. ICES Cooperative Research Report No 218. 86pp.

Cushing, D. H. 1983. Sources of variability in the North Sea ecosystems. Pages 498-516 *in* J. Sünderman and W. Lenz, editors. North Sea dynamics. Springer-Verlag, Berlin.

Daan, R., W. E. Lewis, and M. Mulder. 1990. Biological effects of discharged oil-contaminated drill cuttings in the North Sea. Netherlands Institute for Sea Research, Report 1990-5: 1-77.

—. 1991. Biological effects of washed OBM drill cuttings discharged on the Dutch Continental Shelf. Nederlands Instituut voor Onderzoek der Zee. NIOZ-Rapport 1991-8. 33 pp.

Daan, R., M. Mulder, and W. E. Lewis. 1992. Long-term effects of discharges of washed and unwashed OBM drill cuttings on the Dutch Continental Shelf. Nederlands Instituut voor Onderzoek der Zee. NIOZ-Rapport 1992-9. 39 pp.

Dauwe, B., and J. J. Middelburg. 1998. Amoni acids and hexosamines as indicators of organic matter degradation state in North Sea sediments. Limnology and Oceanography **43**:782-798.

Dauwe, B., P. M. J. Herman, and C. H. R. Heip. 1998. Community structure and bioturbation potential of macrofauna at four North Se stations with contrasting food supply. Marine Ecology Progress Series **173**:67-83.

de Groot, S. J., and J. M. Apeldoorn. 1971. Some experiments on the influence of the beamtrawl on the bottomfauna. ICES C.M.1971/B:2.

de Groot, S. J., and H. J. Lindeboom. 1994. Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Fisheries Research (RIVO-DLO) Report CO26/94, Netherlands Institute for Sea Research (NIOZ) Report 1994-11. 257 pp.

Duineveld, G. C. A., and H. J. Witte. 1987. Report on an intercalibration excercise on methods for determining ashfree dry weight of macrozoobenthos. ICES C.M./L:39. 6pp.

Duineveld, G. C. A., A. Künitzer, and R. P. Heyman. 1987. *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. Netherlands Journal of Sea Research **21**:317-329.

Duineveld, G. C. A., A. Künitzer, U. Niermann, P. A. W. J. de Wilde, and J. S. Gray. 1991. The macrobenthos of the North Sea. Netherlands Journal of Sea Research **28**:53-65.

Dyer, M. F., J. G. Pope, P. D. Fry, R. J. Law, and J. E. Portmann. 1983. Changes in fish and benthos catches off the Danish coast in September 1981. Journal of the Marine Biology Association of the United Kingdom **63**:767-775.

Eisma, D. 1990. Transport and deposition of suspended matter in the North Sea and the relation to coastal situation, pollution and bottom fauna distribution. Aquatic Sciences **3**:181-216.

Eisma, D., and J. Kalf. 1987. Dispersal, concentration and deposition of suspended matter in the North Sea. Journal of the Geological Society, London **144**:161-178.

Eleftheriou, A., and D. J. Basford. 1989. The macrobenthic infauna of the offshore northern North Sea. Journal of the Marine Biology Association of the United Kingdom **69**:123-143.

Fauvel, P. 1923. Polychètes errantes. Faune de France, **5**. 488pp.

Frauenheim, K., V. Neumann, H. Thiel, and M. Türkay. 1989. The distribution of the larger epifauna during summer and winter in the North Sea and its suitability for environmental monitoring. Senckenbergiana maritima **20**:101-118.

Gilson, G. 1907. Exploraiton de la mer sur les côtes de la Belgique. Mémoires du Musée Royal d'Historie Naturelle de Belgique **4**:1-87.

Glémarec, N. 1973. The benthic communities of the European North Atlantic continental shelf. Oceanography and Marine Biology: an Annual Review **11**:263-289.

Graham, M. 1955. Effects of trawling on animals of the sea-bed. Deep-Sea Research **3**:1-6.

Hall, S.J. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogrphy and Marine Biology: a Review **32**:179-239.

Hartmann-Schröder, G. 1971. Tierwelt Deutschlands, 58: Annelida, Borstenwürmer, Polychaeta. Fischer, Jena. 594pp.

Heip, C., T. Brey, F. Creutzberg, J. Dittmer, J. Dörjes, G. Duineveld, P. Kingston, H. Mair, E. Rachor, H. Rumohr, L. Thielemans, and C. Vanosmael. 1985. Report on an intercalibration exercise on sampling methods for macrobenthos. ICES C.M./L:19. 4pp.

Heip, C., R. M. Warwick, M. R. Carr, P. M. J. Herman, R. Huys, N. Smol, and K. Van Holsbeke. 1988. Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord. Marine Ecology Progress Series **46**:171-180.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology **54**:427-432.

—. 1979. TWINSPAN. A FORTRAN program for arranging Multivariate data in an Ordered Two-Way Table by Classification of the Individuals and Attributes. Ecology and Systematics, Cornell University, Ithaca, 90 pp.

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijkswijk. 244pp.

Houghton, R. G., T. Williams, and R. W. Blacker. 1971. Some effects of double beam trawling. ICES C.M. 1971/B:5. 16pp.

Howson, C. M., editor. 1987. Directory of the British marine fauna and flora. A coded checklist of the marine fauna an flora of the British Isles and surrounding seas. Marine Conservation Society. 471pp.

Huys, R., P. M. J. Herman, C. H. R. Heip, and K. Soetaert. 1992. The meiobenthos of the North Sea: density, biomass trends and distribution of copepod communities. ICES Journal of Marine Science **49**:23-44.

Jenness, M. I., and G. C. A. Duineveld. 1985. Effects of tidal currents on chlorophyll *a* content of sandy sediments in the southern North Sea. Marine Ecology Progress Series **21**:283-287.

Joint , I., and A. Pomroy. 1993. Phytoplankton biomass and production in the southern North Sea. Marine Ecology Progress Series **99**:169-182.

Kenny, A. J., and H. L. Rees. 1994. The effects of marine gravel extraction on the macrobenthos: early post-dredging recolonization. Marine Pollution Bulletin **28**:442-447.

Kingston, P. F., and E. Rachor. 1982. North Sea level bottom communities. ICES C.M. 1982/L:41. 19pp.

Kirkegaard, J. B. 1969. A quantitative investigation of the central North Sea polychaeta. Spolia Zoologica Musei Hauniensis **29**:1-285.

Kröncke, I. 1992. Macrofauna standing stock of the Dogger Bank. A comparison: III. 1950-54 versus 1985-1987. A final summary. Helgoländer Meeresuntersuchungen **46**:137-169.

Lambshead, P. J. D. 1986. sub-catastrophic sewage and industrial waste contamination as revealed by marine nematode faunal analysis. Marine Ecology Progress Series **29**:247-260.

Lancelot, C., G. Billen, A. Sournia, T. Weisse, F. Colijn, M. J. W. Veldhuis, A. Davies, and P. Wassman. 1987. *Phaeocystis* blooms and nutrient enrichment in the continental coastal zones of the North Sea. Ambio **16**:38-46.

Lindeboom, H. J., and S. J. de Groot (editors) 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. NIOZ-RAPPORT 1998-1 / RIVO-DLO REPORT C003/98. 404pp.

Margetts, A. R., and J. P. Bridger. 1971. The effect of a beamtrawl on the sea bed. ICES C.M.1971/B:8. 9pp.

McLain, D. H. 1974. Drawing contours from arbitrary data points. The Computer Journal **17**:318-324.

Niermann, U., E. Bauerfeind, W. Hickel, and H. V. Westernhagen. 1990. The recovery of benthos following the impact of low oxygen content in the German Bight. Netherlands Journal of Sea Research **25**:143-154.

Nio, S.D., R.T.E. Shüttenhelm, and T.C.E. van Weering (editors) 1981. Holocene Marine Sedimentation in the North Sea Basin. Species Publication 5 of the International Association of Sedimentologists. Blackwell Oxford, London. 515pp.

NSBWG. 1982. First report of the North Sea Benthos Working Group. ICES C.M. 1982/L:39. 21pp.

NSTF. 1993. North Sea Quality Status Report 1993. Oslo and Paris Commissions. London. 132 pp.

Olsgard, F., and J. S. Gray. 1995. A comprehensive analysis of the effects of offshore oil and gas exploration and production on the benthic communities of the Norwegian continental shelf. Marine Ecology Progress Series **122**:277-306.

Owens, N. J. P., E. M. S. Woodward, J. Aiken, I. E. Bellan, and A. P. Rees. 1990. Primary production and nitrogen assimilation in the North Sea during July 1987. Netherlands Journal of Sea Research **25**:143-154.

Pearson, T. H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: an Annual Review **16**:229-311.

Pearson, T. H., R. Rosenberg, and P. J. Johannessen. 1983. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. 2. Data analyses. Marine Ecology Progress Series **12**:237-255.

Peterse n, C. G. J. 1914. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. Rep. Dan. Biol. Stn. **21**:1-44.

Petersen, G. H. 1977. The density, biomass and origin of the bivalves of the central North Sea. Meddelser fra Danmarks Fiskeri- og Havundersøgelser **7**:221-273.

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York. 286pp.

Rachor, E. 1982. Biomass distribution and production estimates of macro-endofauna in the North Sea. ICES C.M.1982/L:2. 11pp.

—. 1990. Changes in sublittoral zoobenthos in the German Bight with regard to eutrophication. Netherlands Journal of Sea Research **25**:209-214.

Rees, H. L., and P. J. Dare. 1993. Sources of mortality and associated life-cycle traits of selected benthic species: a review. MAFF, Lowestoft. Fisheries Research Data Report Number 33.

Rosenberg, R. 1985. Eutrophication - the future marine coastal nuisance? Marine Ecology Progress Series **16**:227-231.

Rumohr, H., T. Brey, and S. Ankar. 1987. A compilation of biometric conversion factors for Baltic invertebrates. Baltic Marine Biology Publication **9**:1-56.

Skogen, M. D., E. Svendsen, J. Berntsen, D. Aksnes, and K. B. Ulvestad. 1995. Modelling the primary production in the North Sea using a coupled three-dimensional physical-chemical-biological ocean model. Estuarine, Coastal and Shelf Science **41**:545-565.

Soetaert, K., and C. Heip. 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Marine Ecology Progress Series **59**:305-307.

Stehli, F. G., A. L. McAlester, and C. E. Helsley. 1967. Taxonomic diversity of recent bivalves and some implications for geology. Geological Society of America Bulletin **78**:455-466.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Φresund). Medelelser fra Kommissionen for Danmarks Fiskeri- og Havundersϕgelser (Plankton) **4**:1-523.

Tomczak, G., and E. Goedecke. 1962. Monatskarten der Temperatur er Nordzee, dargestellt für verschiedene Tiefenhorizonte. Deutsche Hydrographische Zeitschrift, Ergäzungsheft, B(4E), No.7.

—. 1964. Die thermische Schichtung der Nordzee auf Grund des mittleren Jahresgangs der Temperatur in 1/2E- und 1E-Feldern. Deutsche Hydrographische Zeitschrift, Ergäzungsheft, B(4E), No.8.

Ursin, E. 1960. A quantitative investigation of the echinoderm fauna of the central North Sea. Meddelser fra Danmarks Fiskeri- og Havundersϕgelser **2**:1-204.

van Stralen, M. R. 1992. Het bestand mosselzaad in de Waddenzee in het voorjaar 1992. Rijksinstituut voor Visserijonderzoek RIVO-DLO. Rapport AQ 92-610.

Varela, R. A., A. Cruzado, and J. E. Gabaldon. 1995. Modelling primary production in the North Sea using the European Regional Seas Ecosystem Model. Netherlands Journal of Sea Research **33**:337-361.

WGECO. 1996. Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES Headquarters, 13-21 March 1996. ICES CM 1996/Assess/Env:1.

Wilkinson, L. 1988. SYGRAPH. SYSTAT, Inc., Evanston, IL.

Appendix. Taxonomic position of the species mentioned in chapter 5.

Phylum	Familia	Genus	Species
Annelida	Chaetopteridae	*Chaetopterus*	*Chaetopterus variopedatus*
	Glyceridae	*Glycera*	*Glycera celtica*
			Glycera lapidum
	Goniadidae	*Glycinde*	*Glycinde nordmanni*
		Goniada	*Goniada maculata*
	Magelonidae	*Magelona*	*Magelona* sp.
	Nephtyidae	*Nephtys*	*Nephtys cirrosa*
			Nephtys hombergi
			Nephtys longosetosa
	Opheliidae	*Ophelia*	*Ophelia borealis*
	Orbiniidae	*Scoloplos*	*Scoloplos armiger*
	Oweniidae	*Myriochele*	*Myriochele* sp.
		Owenia	*Owenia fusiformis*
	Paraonidae	*Aricidea*	*Aricidea catherinae*
		Levinsenia	*Levinsenia gracilis*
	Pectinariidae	*Lagis*	*Lagis koreni*
		Hesionura	*Hesionura elongata*
	Pilargiidae	*Synelmis*	*Synelmis klatti*
	Pisionidae	*Pisione*	*Pisione remota*
	Sigalionidae	*Pholoe*	*Pholoe* sp.
		Sigalion	*Sigalion mathildae*
	Spionidae	*Aonides*	*Aonides paucibranchiata*
		Laonice	*Laonice sarsi*
		Minuspio	*Minuspio cirrifera*
		Spiophanes	*Spiophanes bombyx*
			Spiophanes kroeyeri
	Syllidae	*Exogone*	*Exogone verugera*
		Sphaerosyllis	*Sphaerosyllis bulbosa*
	Terebellidae	*Lanice*	*Lanice conchilega*
		Polycirrus	*Polycirrus medusa*
Arthropoda	Ampeliscidae	*Ampelisca*	*Ampelisca tenuicornis*
	Callianassidae	*Callianassa*	*Callianassa subterranea*
	Corystidae	*Corystes*	*Corystes cassivelaunus*

Phylum	Familia	Genus	Species
Arthropoda	Haustoriidae	*Bathyporeia*	*Bathyporeia guilliamsoniana*
		Bathyporeia	*Bathyporeia elegans*
	Leuconidae	*Eudorella*	*Eudorella truncatula*
		Leucon	*Leucon nasica*
	Phoxocephalidae	*Harpinia*	*Harpinia antennaria*
		Phoxocephalus	*Phoxocephalus holbolli*
	Portunidae	*Liocarcinus*	*Liocarcinus holsatus*
Chordata	Molgulidae	*Molgula*	*Molgula* sp.
Echinodermata	Amphiuridae	*Amphiura*	*Amphiura filiformis*
	Fibulariidae	*Echinocyamus*	*Echinocyamus pusillus*
	Ophiolepidae	*Ophiura*	*Ophiura affinis*
			Ophiura albida
			Ophiura ophiura
	Spatangidae	*Echinocardium*	*Echinocardium cordatum*
Mollusca	Buccinidae	*Neptunea*	*Neptunea antiqua*
	Chaetodermatidae	*Chaetoderma*	*Chaetoderma nitidulum*
	Cyprinidae	*Arctica*	*Arctica islandica*
	Dentaliidae	*Antalis*	*Antalis entalis*
	Glycymeridae	*Glycymeris*	*Glycymeris glycymeris*
	Lepidopleuridae	*Leptochiton*	*Leptochiton asellus*
	Mactridae	*Spisula*	*Spisula elliptica*
	Montacutidae	*Montacuta*	*Montacuta substriata*
		Mysella	*Mysella bidentata*
		Tellimya	*Tellimya ferruginosa*
	Mytilidae	*Modiolus*	*Modiolus modiolus*
	Naticidae	*Lunatia*	*Lunatia poliana*
	Nuculidae	*Nucula*	*Nucula nitidosa*
	Scaphandridae	*Cylichna*	*Cylichna cylindracea*
	Tellinidae	*Fabulina*	*Fabulina fabula*
	Thyasiridae	*Thyasira*	*Thyasira ferruginea*
			Thyasira sp.
	Veneridae	*Chamelea*	*Chamelea gallina*
Phoronida	Phoronidae	*Phoronis*	*Phoronis* sp.

CHAPTER 6

Evaluation of the impact of a land reclamation project on the macrozoobenthos in the nearby coastal area

Introduction

In 1986 the construction of a disposal site for dredged material from the lower reaches of the river Rhine (GLBB: 'Grootschalige Locatie voor Baggerspecie uit het Benedenrivierengebied') in the northern part of the Voordelta was completed. This project was the first in the Netherlands for which a so-called Environmental Impact Assessment (EIA) was made. For the first time the expected effects of the proposed development on the wider environment were considered as part of the planning and design of the engineering works. The results of this EIA were reported in an Environmental Impact Statement (Anonymous 1984). Besides a full description of the proposed construction works, the EIS included a description of the existing environment, a description of the options considered and a statement of the predicted environmental impacts.

In general, the EIS expected a decrease in the current velocities and wave impact in the area between the depot and the coast of Voorne (see figure 6.1). As a consequence the morphology was expected to adapt. An increased sedimentation would result in a decrease of the depth of the subtidal zone and an increase in surface area of the intertidal zone. Once the equilibrium was reached, 80-95% of the area between the depot and the coast of Voorne would be emersed at ebb. The changes in hydrodynamical conditions would also result in changes in the grain size composition of the sediment. The intertidal areas would become siltier. All these changes were expected to have an impact on the vegetation, the benthic organisms and the bird populations.

Based on a baseline survey in 1983, eight subareas (stations groups) characterised by a different species composition were described (figure 6.1) (Anonymous 1984). The groups were named

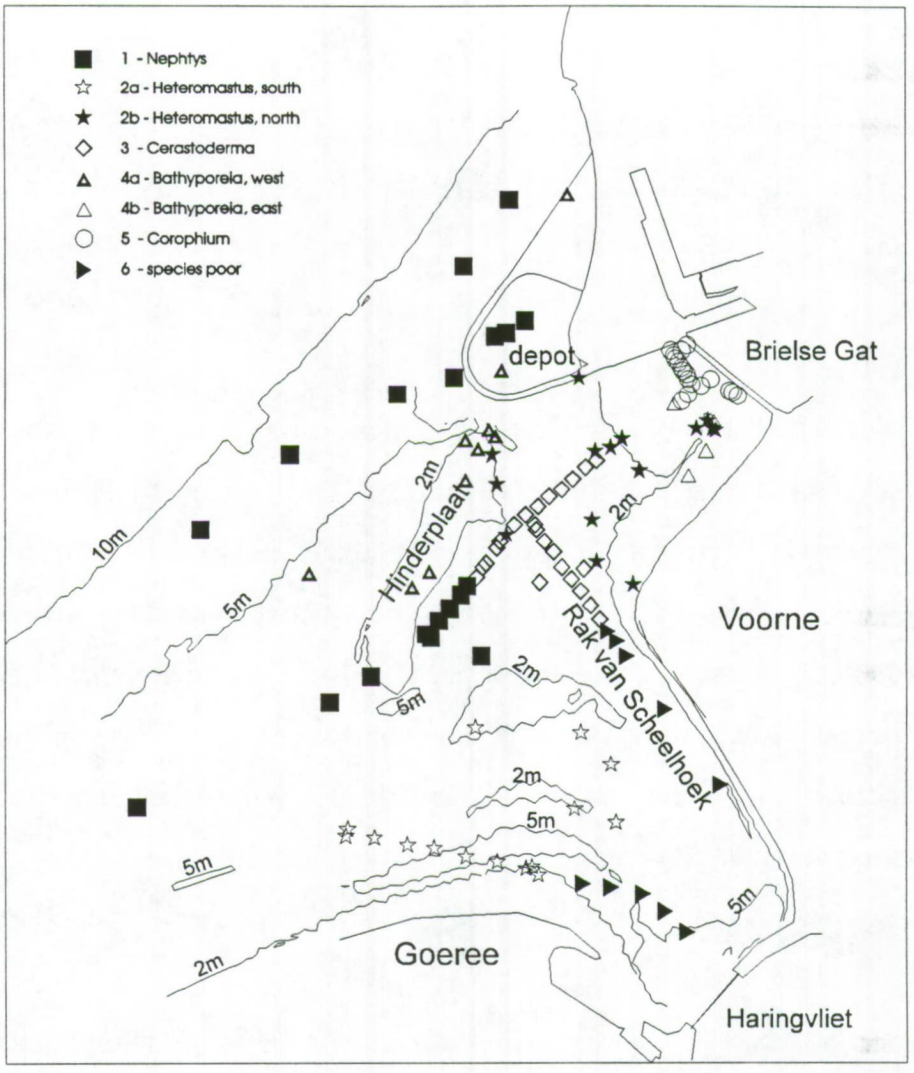


Figure 6.1. Map showing the spatial pattern of the different TWINSPAN groups based on the 1983 data (based on Anonymous 1984).

after the most characteristic or dominant species. It was predicted that, due to the increase of the silt percentage, the intertidal area characterised by the amphipod *Corophium volutator* would increase, while the area dominated by *Bathyporeia pilosa* would decrease. The southwards shift of the tidal channel north of the Hinderplaat, which before the construction was situated at the location of the disposal site, was expected to result in a decrease of the cockle *Cerastoderma edule* in favour of the polychaete *Heteromastus filiformis*.

The EIA considered four alternative locations for the disposal site. The option finally chosen was considered to have the smallest impact: the sedimentation rate and the increase in intertidal areas were the slowest, the increase in silt content and the decrease of the cockle-assemblage area the smallest.

The EIA further proposed that an environmental monitoring plan had to be carried out for a period of 30 years to verify the predicted impact. The following items have to be monitored: the geomorphology, the grain size of the sediment, the macrobenthic organisms, the bird populations, the salt spray intrusion into the dunes, and the vegetation.

This chapter presents the results of the monitoring of the macrobenthic infauna up to 1994. The aim is to evaluate if the faunal assemblages identified in the base-line study in 1983 have been persistent over time, if the spatial distribution of these assemblages has changed or not and if the characteristic and dominant species have remained the same. Results of the other monitoring programmes have been presented in Anonymous (1992, 1997).

The program is also indicative for the many problems encountered in detecting anthropogenic disturbances: which sampling design to use, what are good reference sites, at which spatial scale or scales the monitoring should be done, which statistical procedure should be followed, etc. The discussion aims at suggesting improvements of the future monitoring programmes.

Material and methods

Sampling program

Data from five surveys are available (1988, 1989, 1990, 1992, 1994). All surveys were carried out in Autumn. Sampling was done in two subareas: the intertidal area near the Brielse Gatdam and a mainly subtidal area including the Hinderplaat, a sand bar south of the depot. Both areas were divided in boxes (see chapter 2, figure 2.5) and within each box, 1 to 5 stations were

randomly selected. At each station a sample was taken and washed on a 1mm mesh-size sieve. In the laboratory, the samples were sorted and the abundance and biomass of all species were determined. More information on the sampling design and the laboratory methods is given in the second chapter (Material and Methods).

Statistical analysis

In this study we analysed all data obtained in the period 1988-1994 and those of 1983 (except for the most southern stations lying outside the area monitored; compare figures 6.1 and 6.4). To evaluate changes in the species composition, both in time and space, all 1293 samples were classified using TWINSPAN (Hill 1979). The cut-levels used in the TWINSPAN analysis were 0, 10, 100, 500, 1000, 5000 and 99999. Two taxonomical remarks should be made. First, the 1983 study did not discriminate between *Pygospio elegans* and *Spio martinensis*, which were clustered as *P. elegans*. Secondly, in the 1983 and 1988 studies all *Bathyporeia* species were identified as *B. pilosa*, also the specimens found west of the Hinderplaat (respectively at 1 and 29 stations). In later years, the most common *Bathyporeia* species found in that area was *B. elegans*. In a few cases *B. guilliamsoniana* was found as well. Haustoriid amphipods show a definite vertical zonation, although there is a seasonal variation and the zones overlap to some extent (Watkin 1939, Vader 1965, Fincham 1971). *B. pilosa, B. sarsi* and *B. pelagica* are mostly typical for the intertidal, *B. elegans* and *B. guilliamsoniana* are almost exclusively recorded subtidally. Therefore, we renamed all *Bathyporeia* specimens found west of the Hinderplaat as *B. elegans*.

It should further be noticed that the 1992 survey and part of the 1994 survey took place after fishing for cockles in the area east of the Hinderplaat. Thus, the density and biomass estimates of this species are underestimated. The latter might also hold for two other bivalves living near the surface of the seabed, *Macoma balthica* and young *Mya arenaria*, as both species are likely affected by the dredging activities (Craeymeersch 1997).

Results

Fluctuations in density and biomass

Tables 6.1, 6.2 and 6.3 give the total density, the total biomass and the density and biomass values of a few selected species (density 100 ind/m^2 or biomass 1 gAFDW/m^2 during one of the surveys) for the intertidal area near the Brielse Dam, the subtidal area east of the Hinderplaat and the subtidal area west of the Hinderplaat. The Hinderplaat was not included because this sandbar was not sampled every year and when sampled only a few samples were taken. We made the distinction between the three areas because of their different species composition (see further). For 1983, the samples taken in May were omitted.

At the intertidal area near the Brielse Dam, the most striking change is the decrease in density of *Corophium*. In 1983, maximum densities of 132.000 ind./m^2 were recorded; in 1994, a maximum of only 35.000 ind./m^2 was found. The decrease is most pronounced in the southwestern part (figure 6.2). Moreover, from 1992 onwards, two species are found: *Corophium volutator* and *Corophium arenarium*. In 1994 both species showed a clear spatial segregation (figure 6.3).

	1983	1988	1989	1990	1992	1994
Density						
Corophium volutator	23000 ± 8500	20000 ± 4200	10000 ± 1110	5300 ± 680	6900 ± 660	4500 ± 670
Hydrobia ulvae	480 ± 144	2800 ± 940	2600 ± 360	2100 ± 340	1850 ± 236	330 ± 72
Spio martinensis *	680 ± 279	190 ± 50	23 ± 9.0	44 ± 14.0	0 ± 0	9 ± 3.5
*Pygospio elegans**		2100 ± 380	14100 ± 1990	6500 ± 660	3500 ± 420	1900 ± 510
Total	26000 ± 9600	34000 ± 7700	33000 ± 4200	21000 ± 2690	18700 ± 2560	18100 ± 2900
Biomass						
Nereis diversicolor	12 ± 20.9	14.4 ± 1.27	7.6 ± 0.77	3.3 ± 0.30	0.78 ± 0.113	5.4 ± 0.43
Scrobicularia plana	5.9 ± 2.33	5 ± 3.4	0.05 ± 0.032	0.15 ± 0.057	0.10 ± 0.043	1.2 ± 0.59
Corophium volutator	5.8 ± 1.56	5.7 ± 1.02	2.00 ± 0.222	1.58 ± 0.203	0.87 ± 0.124	1.22 ± 0.0116
Mya arenaria	2.1 ± 1.50	1.8 ± 1.61	1.0 ± 0.34	0.43 ± 0.183	0.15 ± 0.099	5.2 ± 0.83
Macoma balthica	0.13 ± 0.065	1.0 ± 0.44	0.46 ± 0.103	0.61 ± 0.164	1.11 ± 0.181	1.23 ± 0.262
Heteromastus filiformis	0.14 ± 0.047	0.73 ± 0.181	0.096 ± 0.0256	0.063 ± 0.0170	0.029 ± 0.0138	0.75 ± 0.120
Total	27 ± 8.0	31 ± 8.6	14.4 ± 2.15	9.9 ± 1.68	5.7 ± 1.40	16.7 ± 2.83

Table 6.1. Density (ind./m^2) and biomass (gAFDW/m^2) (mean ± s.e.) on the intertidal area near the Brielse dam (* in 1983 no distinction was made between *P. elegans* and *S. martinensis*).

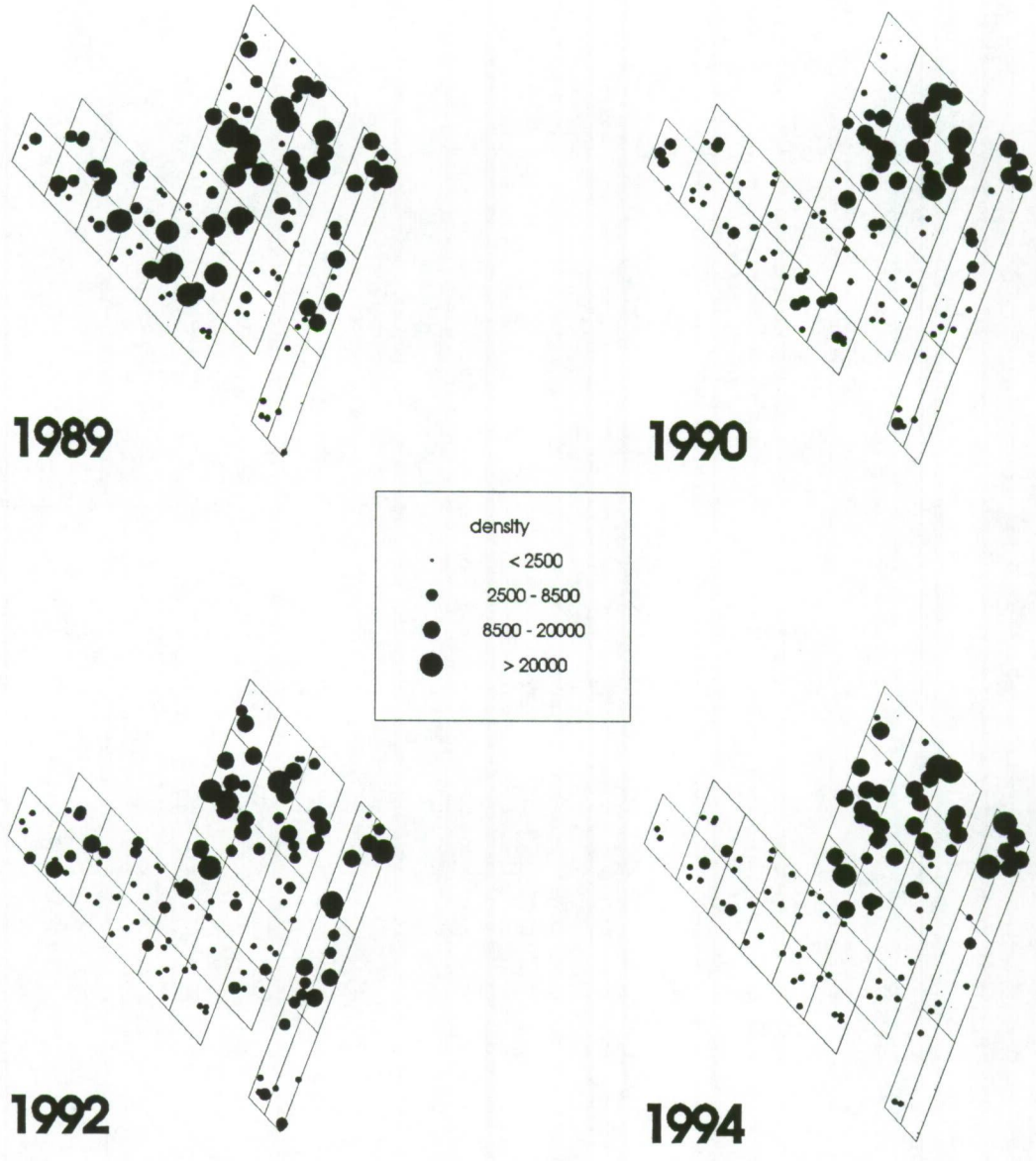


Figure 6.2. Distribution and density (ind./m^2) of *Corophium* species (*C. volutator, C. arenarium*) in the period 1989-1994 on the intertidal area near the Brielse dam (boxes refer to the sampling scheme; see figure 2.5).

From 1988 to 1992, the total biomass decreased. In 1994, the total biomass was again higher. This trend followed that of the most important species, *N. diversicolor*. Also other species such as *Scrobicularia plana*, *C. volutator* and *Mya arenaria* showed the same trend.

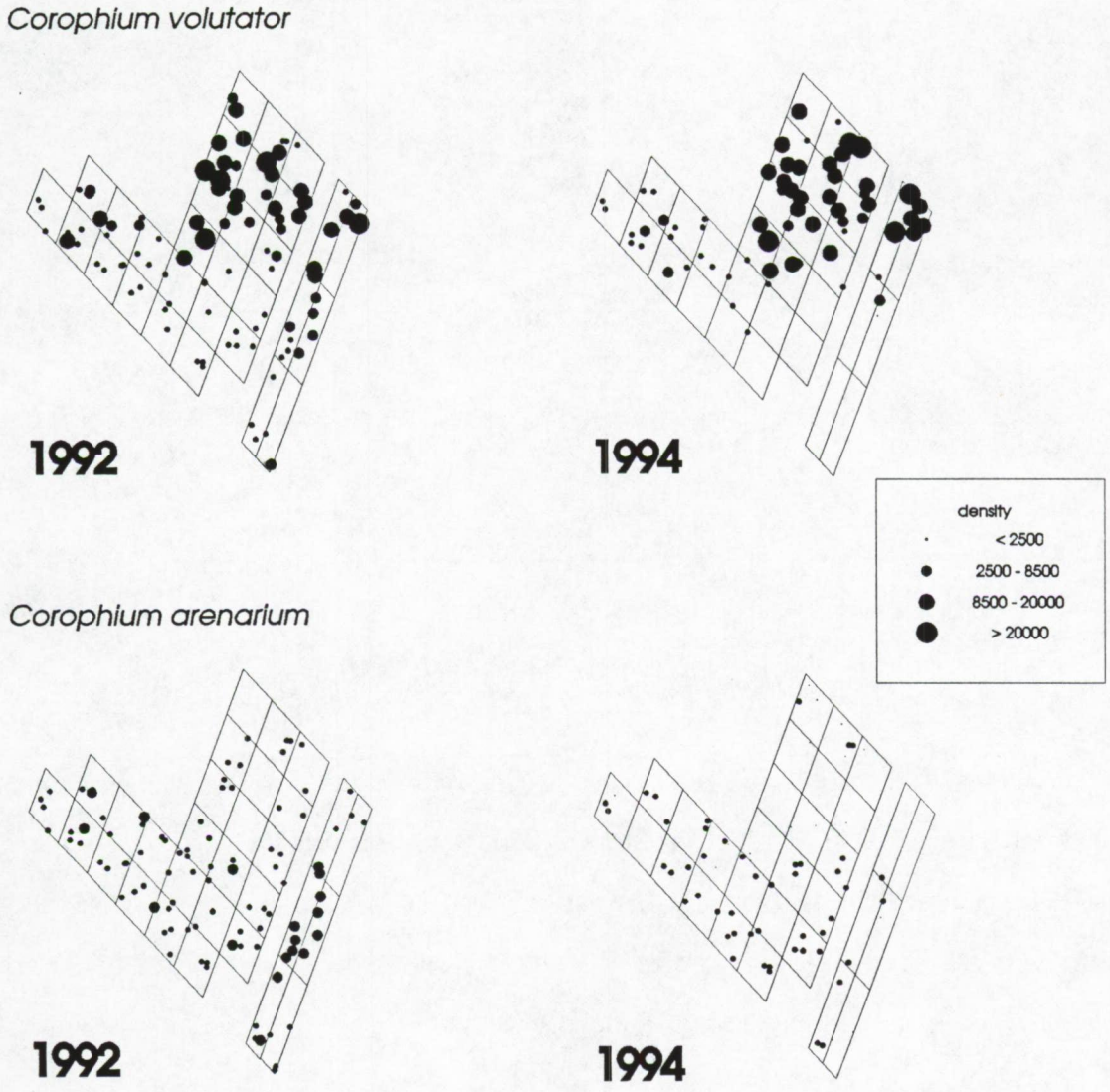


Figure 6.3. Distribution and density (ind./m^2) of *C. volutator* and *C. arenarium* in 1992 and 1994 on the intertidal area near the Brielse dam.

In the subtidal area east of the Hinderplaat, the total densities recorded during the last four surveys were much higher than values recorded in 1983 and 1988. This pattern coincided with that of *Heteromastus filiformis* and *Pygospio elegans.* Most of the other species showed more variation. They showed peak values during only one or two surveys. *Mya arenaria*, for instance, showed a dramatic increase in 1994 due to a very good recruitment.

	1983	1988	1989	1990	1992	1994
Density						
Heteromastus filiformis	170 ± 55	129 ± 27.4	740 ± 155	280 ± 78	340 ± 83	390 ± 102
Pygospio elegans *	} 60 ± 36	30 ± 6.9	440 ± 120	350 ± 133	250 ± 119	230 ± 48
Spio martinensis *		340 ± 71	670 ± 135	290 ± 72	240 ± 76	990 ± 272
Tharyx marioni	32 ± 9.6	56 ± 26.0	990 ± 299	260 ± 84	1400 ± 370	39 ± 20.7
Mya arenaria	1.5 ± 0.81	2.8 ± 1.18	60 ± 25.2	22 ± 11.9	48 ± 14.4	2000 ± 410
Bathyporeia pilosa	0.33 ± 0.171	0.4 ± 0.33	130 ± 130	60 ± 54	7 ± 5.0	1.5 ± 0.77
Cerastoderma edule	260 ± 58	41 ± 17.3	16 ± 5.5	12 ± 4.9	90 ± 28.6	260 ± 82
Echinocardium cordatum	0 ± 0	0 ± 0	160 ± 60	0.5 ± 0.36	0 ± 0	0 ± 0
Oligochaeta indet.	0.8 ± 0.35	1.5 ± 0.93	1.7 ± 1.69	0 ± 0	140 ± 56	19 ± 6.7
Polydora ligni	0.07 ± 0.067	5.7 ± 1.89	30 ± 11.5	49 ± 29.1	8 ± 3.7	210 ± 57
Total	670 ± 236	760 ± 208	3700 ± 1130	1700 ± 650	3200 ± 1150	4800 ± 1180
Biomass						
Cerastoderma edule	33 ± 7.2	16 ± 7.3	1.7 ± 0.64	3.3 ± 1.77	13 ± 4.0	1.4 ± 0.57
Mya arenaria	1.1 ± 0.85	0.027 ± 0.0107	0.27 ± 0.132	0.12 ± 0.081	1.4 ± 0.66	9.0 ± 2.42
Spisula subtruncata	0 ± 0	0.012 ± 0.0061	1.5 ± 0.68	0.09 ± 0.032	7 ± 4.3	1.2 ± 0.30
Echinocardium cordatum	0 ± 0	0 ± 0	1.2 ± 0.43	0.027 ± 0.0231	0 ± 0	0 ± 0
Mytilus edulis	3.2 ± 2.01	0.17 ± 0.169	< 0.0003	< 0.0003	0.09 ± 0.093	< 0.0003
Total	38 ± 10.6	18 ± 7.9	6.8 ± 2.56	4.8 ± 2.37	24 ± 10.7	13 ± 3.7

Table 6.2. Density (ind./m^2) and biomass (gAFDW/m^2) (mean ± s.e.) in the subtidal area east of the Hinderplaat (* in 1983 no distinction was made between *P. elegans* and *S. martinensis*).

The total biomass decreased from 1983 to 1990 followed by higher biomass values in 1992 and 1994. In all years, except in 1994, the most important species was the cockle *Cerastoderma edule*. As mentioned before, the 1992 and part of the 1994 surveys took place after or during fishing activities. Thus, the biomass of *C. edule* and, consequently, the total biomass was probably of the same magnitude as in 1983 or 1988.

In the subtidal area seawards from the Hinderplaat, the highest total density values were noticed in 1988 and 1989. In 1988 this was due to a very high density of *Spisula subtruncata*. Many other bivalve and polychaete species showed high values in 1988 as well. In 1989 *Spio martinensis* was numerically the most dominant species. Its density increased from 1983 to 1989 followed by a decrease in 1990. In the last investigation years the density of *S. martinensis* remained at the same level.

Mean total biomass was usually at about 3 gAFDW/m^2. In 1988 and 1992 much higher values were found, which can be explained by the high density and biomass of the bivalve *S. subtruncata*. In 1992 there were also high biomass values of Actiniaria (sea anemones) and *Carcinus maenas*.

	1983	1988	1989	1990	1992	1994
Density						
Abra alba	0 ± 0	110 ± 51	33 ± 28.3	3.9 ± 2.14	0.7 ± 0.67	16 ± 7.6
Anaitides mucosa	0 ± 0	180 ± 70	15 ± 6.4	0.32 ± 0.227	19 ± 7.1	25 ± 17.9
Eumida sanguinea	0 ± 0	300 ± 99	52 ± 21.9	20 ± 8.6	0 ± 0	0 ± 0
Lanice conchilega	11 ± 7.1	120 ± 43	100 ± 71	12 ± 7.1	29 ± 20.7	56 ± 23.2
Magelona papillicornis	71 ± 25.6	24 ± 3.2	59 ± 10.3	13 ± 4.0	8.7 ± 2.56	390 ± 139
Pygospio elegans *	} 39 ± 17.7	0 ± 0	0.26 ± 0.183	0.16 ± 0.162	0 ± 0	0.24 ± 0.238
*Spio martinensis**		1170 ± 210	2300 ± 510	440 ± 151	550 ± 182	600 ± 163
Spisula subtruncata	0 ± 0	5700 ± 1880	320 ± 133	150 ± 109	90 ± 38	80 ± 32
Spiophanes bombyx	1400 ± 560	110 ± 34	170 ± 53	10 ± 4.0	120 ± 50	140 ± 47
Total	1700 ± 710	8200 ± 2530	3600 ± 990	1100 ± 470	1400 ± 540	1700 ± 650
Biomass						
Spisula subtruncata	0 ± 0	15.3 ± 2.76	0.49 ± 0.198	1.3 ± 0.48	2.9 ± 1.52	0.6 ± 0.32
Actiniaria indet.	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.3 ± 1.22	0.32 ± 0.222
Carcinus maenas	0 ± 0	0.0021 ± 0.00182	< 0.0003	< 0.0003	2.3 ± 1.59	0.0006 ± 0.00061
Total	3.1 ± 1.53	19 ± 4.3	2.6 ± 0.97	2.8 ± 1.08	8 ± 5.2	2.8 ± 1.66

Table 6.3. Density (ind./m^2) and biomass (gAFDW/m^2) (mean ± s.e.) in the subtidal area west of the Hinderplaat (* in 1983 no distinction was made between *P. elegans* and *S. martinensis*).

Multivariate analysis

The spatial distribution of the different assemblages is shown in figures 6.4 and 6.5. In figure 6.4 no distinction is made between clusters 2 and 3; this is done separately in figure 6.5. All samples were analysed together, but the spatial distribution of the withdrawn clusters is shown separately for each survey. The depth lines indicated on these maps are all from 1990, except the NAP-line in figure 6.5, which is from 1987. In figure 6.6 the relative densities of the indicator species are represented. The actual mean densities of all species in each cluster are given in the appendices (appendix 1: overall mean density per cluster; appendix 2: yearly mean density per cluster).

Spatial patterns in species composition

All samples have been grouped by a single cluster analysis to separate areas of similar species composition. At the first dichotomy of the TWINSPAN analysis most of the stations on the intertidal areas (the Hinderplaat and the area near the Brielse dam) and the shallowest parts east of the Hinderplaat (assemblages 1-5) are separated from the deeper stations (assemblages 6-8).

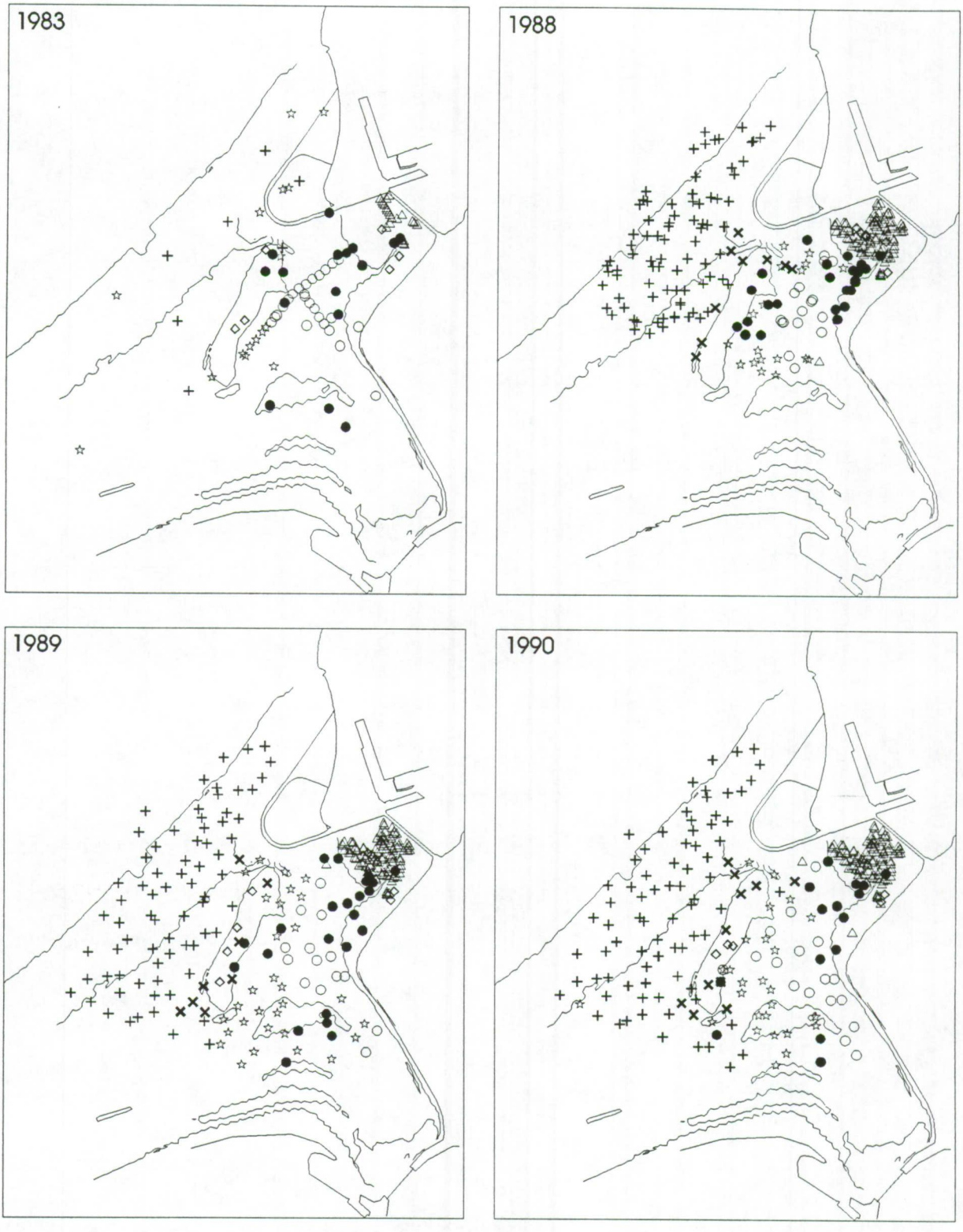


Figure 6.4. See next page.

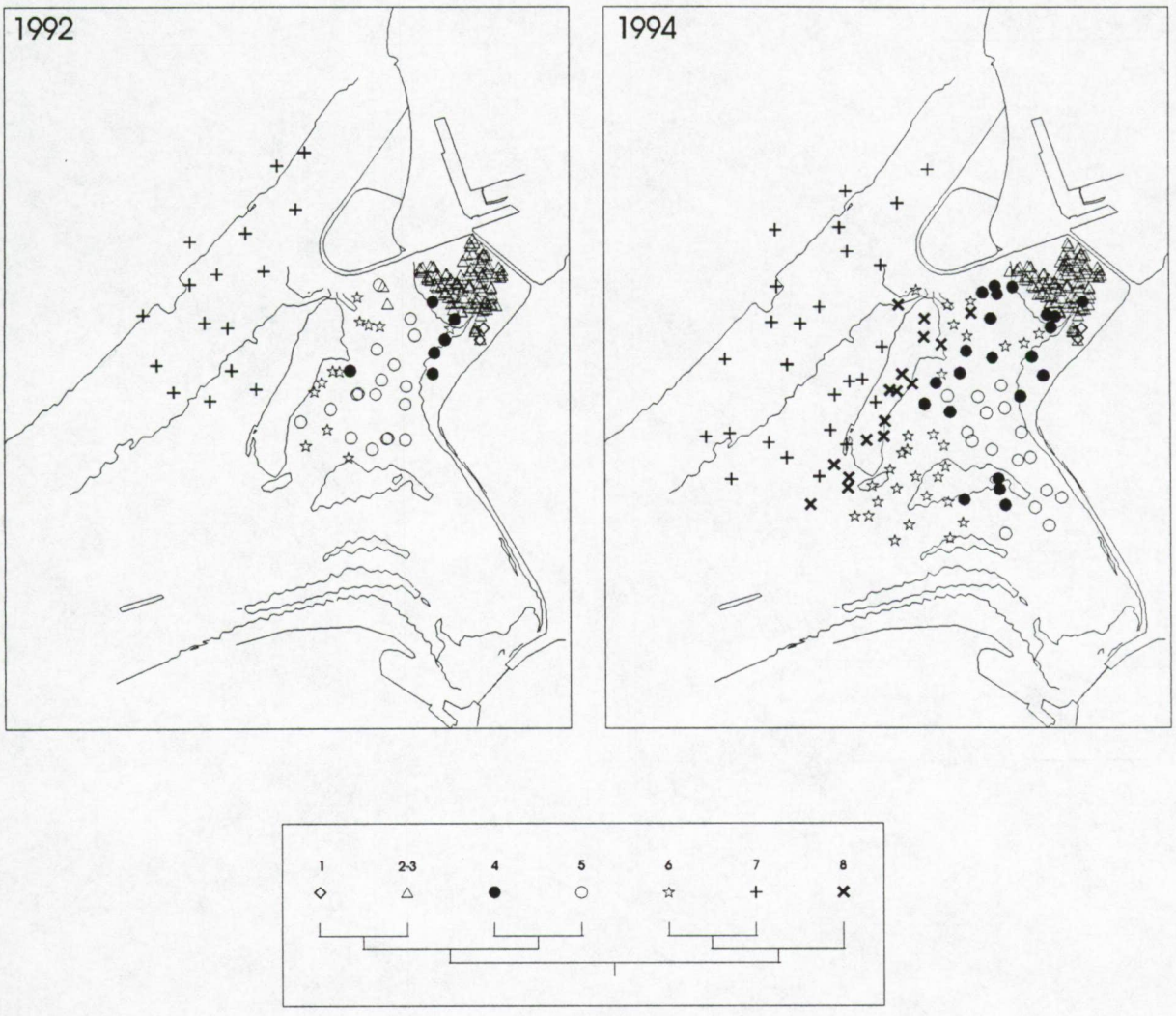


Figure 6.4. Dendrogram of TWINSPAN divisions and maps showing the spatial pattern of the different TWINSPAN groups based on the data of 1983-1994. For a distinction between groups 2 and 3: see figure 6.5.

Indicator species for assemblages 1-5 are *Nereis diversicolor, Pygospio elegans, Corophium volutator* and *Hydrobia ulvae.* Indicator species for assemblages 6-8 are *Spio martinensis, Nephtys cirrosa* and *Nephtys hombergii.*

At the second dichotomy both groups are further divided according to water depth. *Nereis diversicolor*, *Corophium volutator*, *Hydrobia ulvae* and Oligochaeta all occur in larger densities in assemblages 1, 2 and 3 then in assemblages 4 and 5. *Tharyx marioni*, on the other hand, is an indicator species for assemblages 4 and 5. Indicator species for assemblages 6 and 7 are *Spisula subtruncata, Magelona papillicornis* and *Spiophanes bombyx. Paraonis fulgens,*

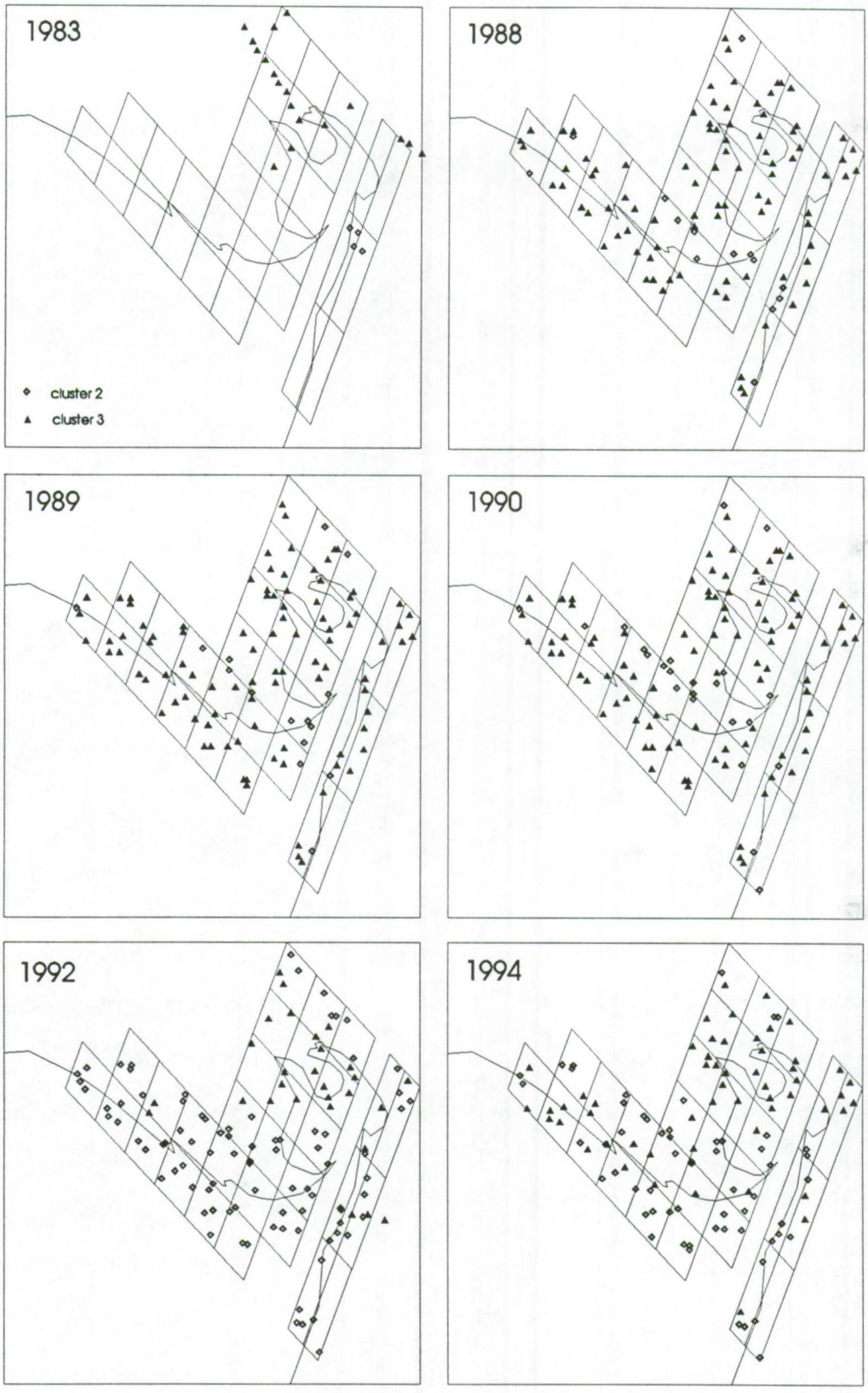


Figure 6.5. Maps showing the spatial distribution of the TWINSPAN groups 2 and 3 on the intertidal area near the Brielse dam.

Scolelepis squamata and *Nephtys hombergii* are indicators for assemblage 8, situated on and near the Hinderplaat.

Most of the stations of assemblage 6 (indicators: *Pygospio elegans, Heteromastus filiformis*) are situated east of the Hinderplaat, stations of assemblage 7 (indicators*: Bathyporeia elegans, Nephtys cirrosa, Urothoe poseidonis, Eumida sanguinea*) mainly west and south of the Hinderplaat.

Assemblage 4 and 5 differ in the densities of *Pygospio elegans, Spio martinensis* and *Cerastoderma edule*. The two spionids are found in higher densities in assemblage 4, cockles (*C. edule*) in higher densities in assemblage 5.

Assemblage 1 (indicator species: *Bathyporeia pilosa*) is found on the Hinderplaat and a small area near the coast of Voorne. Assemblages 2 and 3 (indicators*: Hydrobia ulvae, Nereis diversicolor, Corophium volutator, Pygospio elegans,* Oligochaeta, *Mya arenaria*) are almost exclusively found on the Westplaat.

Assemblage 2 differs from assemblage 3 in its higher densities of *Bathyporeia pilosa* and *Corophium arenarium*, and its much lower densities of *Corophium volutator* and *Nereis diversicolor*.

The main pattern of the species distributions in 1983 as described here (figure 6.4) is similar to the one described in the baseline study in 1984 (figure 6.1). Assemblage 1 is the *Bathyporeia* community, but because of the low number of stations we didn't make the difference between an eastern and western group. Moreover, part of the stations of the *Bathyporeia* group on the Hinderplaat now grouped with assemblage 4. Assemblages 2 and 3 together are similar to the *Corophium* group. Assemblage 4 is the northern *Heteromastus* group. Assemblage 5 is similar to the *Cerastoderma* group, and assemblages 6 to 8 form the *Nephtys* group. As in the baseline study we didn't find a distinct spatial distribution of the latter assemblages in 1983. This might be due to the low number of stations sampled at that time. *Paraonis fulgens* and *Scolelepis squamata*, the most important indicator species for assemblage 8, were respectively not found or only found at very low densities in 1983.

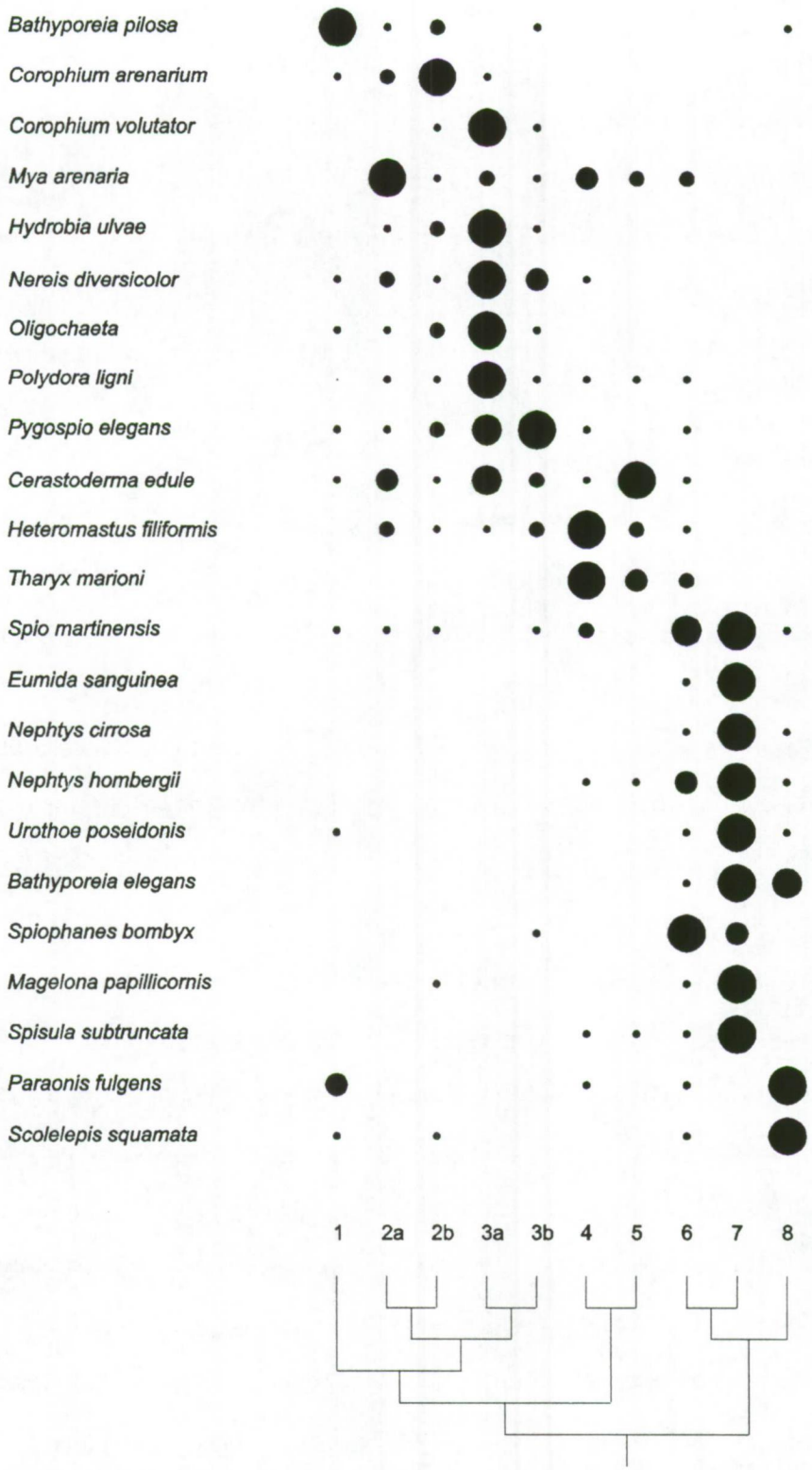


Figure 6.6. Relative densities of the indicator species within each TWINSPAN group.

Faunistic changes with time

The general pattern in species composition has remained the same over the years. The fauna of the intertidal areas (Hinderplaat, area near the Brielse dam) differs from the fauna in the subtidal area. The fauna of the Hinderplaat differs from the fauna of the area near the Brielse dam. The subtidal area west of the Hinderplaat is characterised by other species than the shallower area east of this sand bar. There is an intrusion of the former into the latter north and south of the Hinderplaat. The subtidal area between the Hinderplaat and the coast of Voorne can be further divided into two assemblages, mainly based on differences in the density of *Heteromastus filiformis* and *Tharyx marioni*. Cockles (*Cerastoderma edule*), if present, are found in the area with the lowest values of both polychaetes. The few stations belonging to the 'species poor' assemblage as identified in 1983 (figure 6.1) are now part of assemblage 5 in figure 6.4.

Some important changes in time were noted. The largest changes took place on the intertidal area near the Brielse dam. The differences between the southwestern and northeastern parts of this area were more pronounced in 1992 and 1994 than before. In the period 1988-1990 the differences in species composition and densities were mainly the distinction between assemblages 3a and 3b of the TWINSPAN analysis (figure 6.7). In 1992 and 1994 the differences were expressed at one level higher in the TWINSPAN dendrogram. Till 1990 assemblage 2 was only found in a small part of this area (figure 6.5). In 1992 and 1994, however, it was found on about half of the intertidal area, more specifically on the southwestern part of it, while assemblage 3 was restricted to the northeastern part. Assemblages 2 and 3 mainly differ in the densities of *Bathyporeia pilosa*, *Corophium volutator* and *Corophium arenarium*. In 1992, *Bathyporeia pilosa* was recorded at most of the southwesterly stations. And, as mentioned before, *C. arenarium* was not found before 1992. In 1994 both *Corophium* species had a clear spatial segregation.

The species composition of assemblage 2 changed as well. In a further division of assemblage 2, most of the 1994 stations were grouped into a separate group (assemblage 2a; figure 6.7). Assemblage 2a was characterised by higher densities of *Heteromastus filiformis, Mya arenaria*

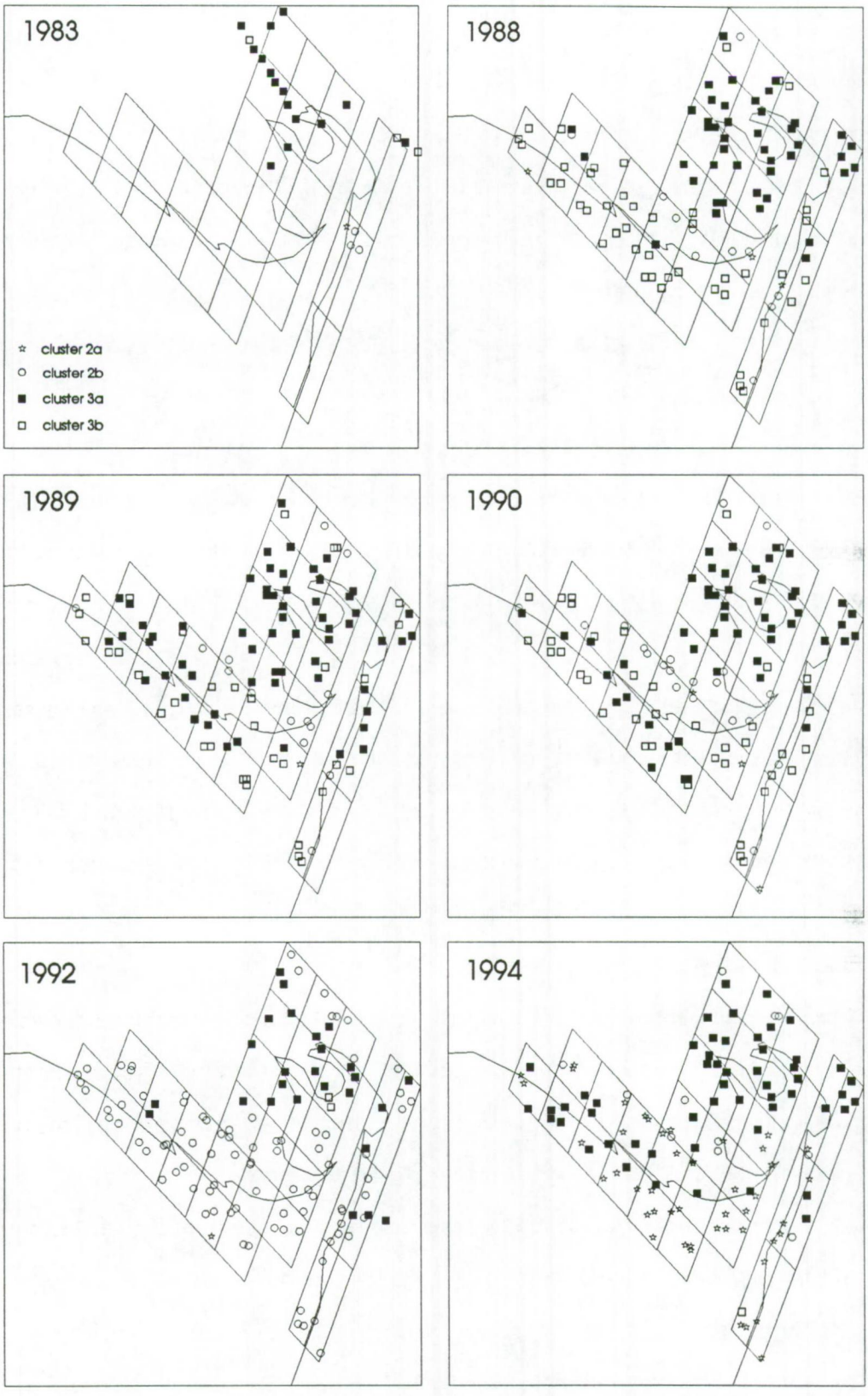


Figure 6.7. Maps showing the spatial distribution of groups resulting from a further division of TWINSPAN groups 2 and 3.

and *Cerastoderma edule*, but lower densities of *Corophium volutator* and *Pygospio elegans* (see appendix 1).

In the subtidal area the difference in spatial distribution of assemblages 6 and 7 was not found in 1983, although all stations east of the Hinderplaat do belong to assemblage 6. And no 1983 stations were grouped into assemblage 8. This is in agreement with the baseline study (Anonymous 1984; figure 6.1) where no further division of the *Nepthys* group was made.

Within most of the assemblages there was a large variability in the relative abundance of species. Different species became the dominant ones (see appendix 2). Till 1992, assemblage 2 was dominated by *Pygospio elegans*. In 1994, however, Oligochaeta became the dominant taxon.
In 1983 and 1988, *Corophium volutator* was by far the most abundant species of assemblage 3. In 1989 and 1990, *Pygospio elegans* became dominant. In 1992 and 1994, when the assemblage was restricted to the northeastern part of the intertidal, *C. volutator* again and, as in assemblage 2, Oligochaeta became the two dominant taxa.
In most years *Heteromastus filiformis* and *Tharyx marioni* were the most abundant species of assemblage 4. In 1994, however, *Mya arenaria* became numerically dominant after an immense spatfall. That large spatfall was not restricted to assemblage 4 but also recorded in the other assemblages east of the Hinderplaat.
In 1983, *Cerastoderma edule* was the most dominant species of assemblage 5 (which was therefore named after this species). As for assemblage 4, *Mya arenaria* was the dominant species in 1994. In the years in between, *Tharyx marioni* and *Heteromastus filiformis* were the two most abundant species but with lower densities than in assemblage 4.
In assemblage 6, *Spio martinensis* was the most abundant species except for 1983 (*Spiophanes bombyx*) and 1992 (*Tharyx marioni*).
Assemblage 7 was dominated by *Spiophanes bombyx* in 1983. In 1988 *Spisula subtruncata* became dominant due to the presence of many recently settled specimen. In later years, *Spio martinensis* was the most abundant species.
The dominant species of assemblage 8 was *Spio martinensis* in 1988, *Bathyporeia pilosa* in 1989, *Paraonis fulgens* in 1990 and *Spio martinensis* again in 1994.

Discussion

Spatial patterns

The observed pattern in benthic community structure presented here clearly shows differences in species composition between the intertidal and the subtidal areas. The intertidal fauna of the area near the Brielse dam differs from the one of the Hinderplaat. The subtidal fauna east of the

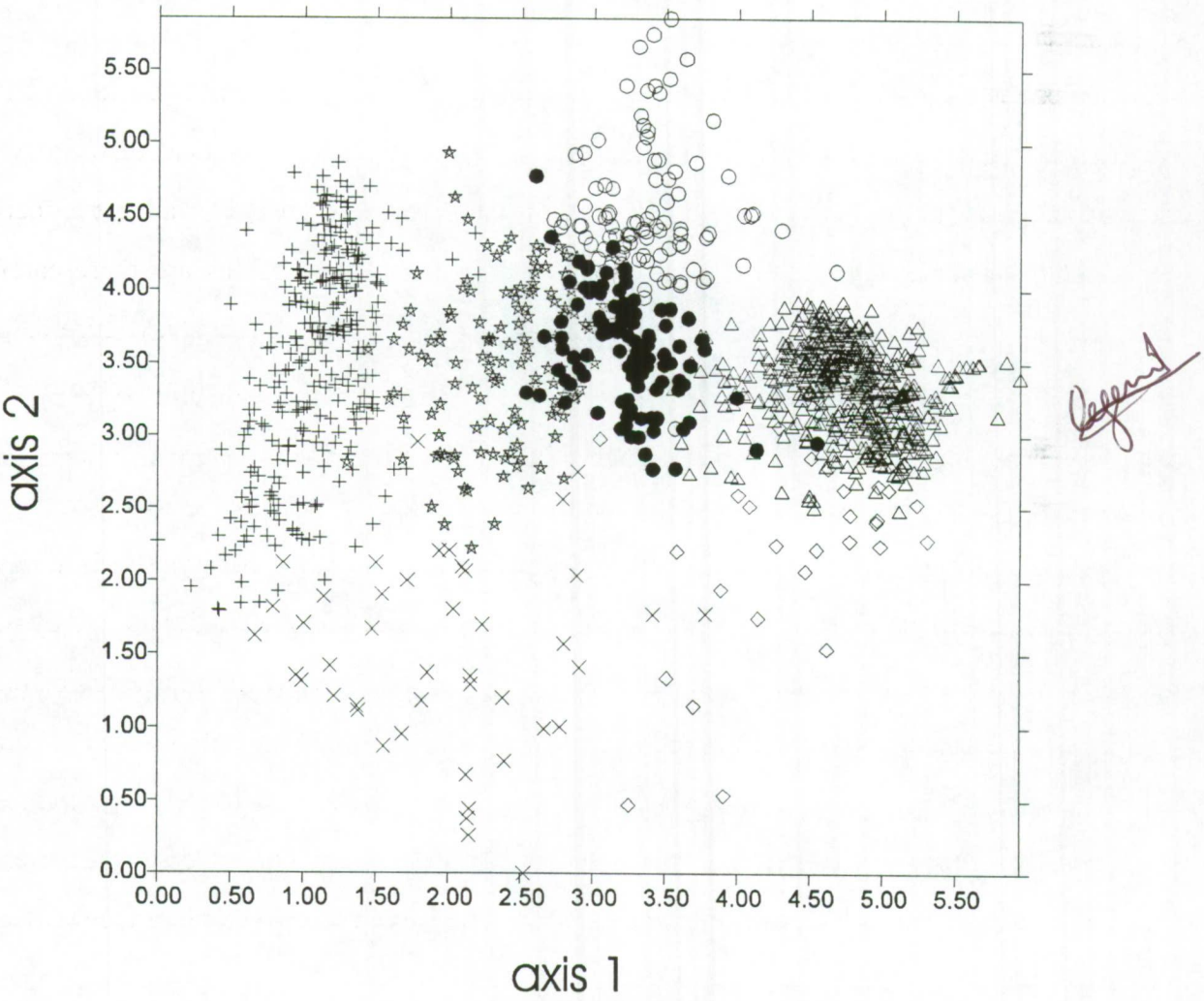
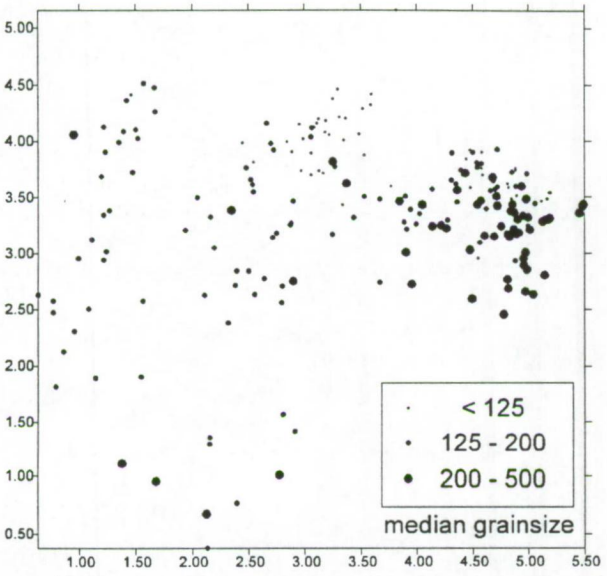


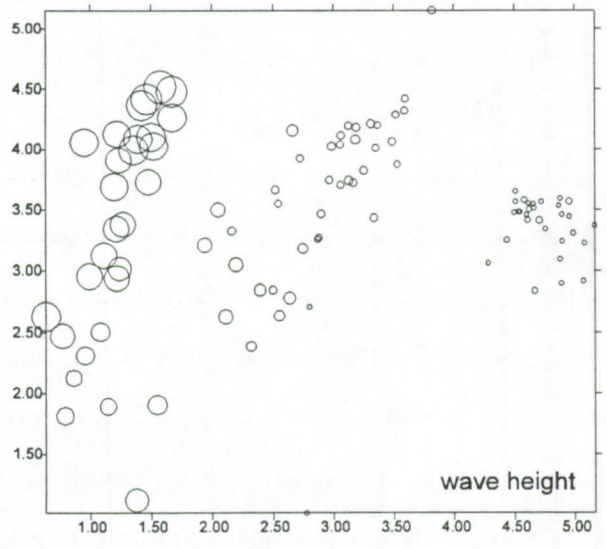
Figure 6.8. Scatterplot of the first two axes of a Detrended Correspondence Analysis. Symbols as in figure 6.4.

Hinderplaat differs from that of the area west of this sandbar. These changes are not as abrupt as the results of the cluster analysis might suggest. TWINSPAN forces the data into distinct classes even when continua exist (Field et al. 1982). Ordination provides a more accurate representation of gradual changes in species composition (McRae et al. 1998). In figure 6.8, assemblages 2-7 are situated in the upper part, assemblages 1 and 8 in the lower part of the ordination diagram. The intertidal area near the Brielse dam (assemblage 2-3) is situated on the right-hand side, the subtidal area west of the Hinderplaat (assemblage 7) on the left-hand side. Assemblages 4 and 5 are situated in between and are separated along the second axis.

The most important environmental variables determining the species composition in our study area are most likely related to differences in depth or height, wave impact, sediment characteristics and salinity fluctuations. Data on median grain size were only available for half of the intertidal samples of 1989 and 1990 and the subtidal samples of 1994. Data on the wave height and the orbital velocity, a function of depth and wave height, were only available for part of the 1994 samples. In figure 6.9 differences in these abiotic variables are represented graphically, superimposing the environmental data onto the ordination diagram (figure 6.8). Assemblage 5 has the finest sediments. There is a gradient in wave height from left to right. The orbital velocity is the highest in the assemblages 1 and 8. Indeed, the characteristic species found here (*Bathyporeia elegans*, *Paraonis fulgens*, *Scolelepis squamata*) are highly adapted to the dynamic conditions on or in the swash zone of sandbars or beaches. *Bathyporeia* is highly mobile and able to dig and swim (Watkin 1939). *P. fulgens* lives anchored in the bottom by its corkscrew-shaped posterior end while the foremost part is in strong wave motion searching the surface of the bottom for food, mainly plant debris and small dead animals washed ashore (Rasmussen 1973). *S. squamata* lives in the sediment inside vertical, loosely constructed burrows. It uses its long palps, helically coiled with their frontal surfaces oriented into the current flow to catch suspended and resuspended particles above the sediment-water interface (Dauer 1983).

No data on salinity were available. In general, the nearshore area is influenced by a high freshwater input at low tide through the Haringvliet sluices at high Rhine discharges (above





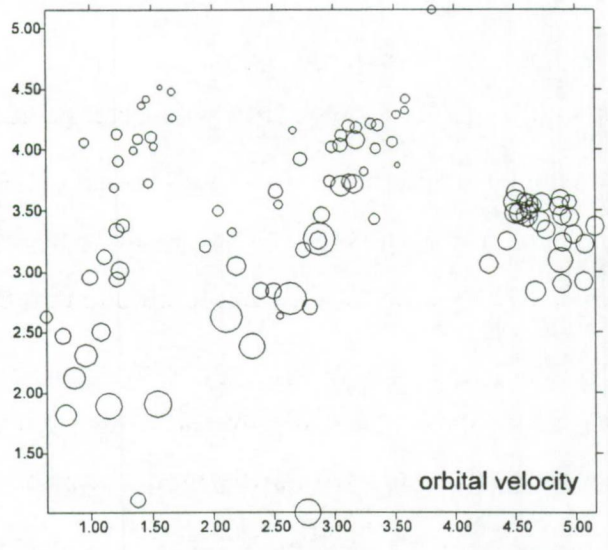


Figure 6.9. DCA-scatterplot with superimposed symbols representing:

- median grainsize (μm);
- wave height that is exceeded in 1 percent of the year (at low water and southwestern wind (max:1.7 m); and
- orbital velocity (velocity at the bottom resulting from the orbital motion in a wave) (max:1.3 m/sec).

1700 m^3/s) (de Hoog and Steenkamp 1989). Many marine species cannot live there but for a short time and the species composition resembles therefore that of an estuary. The subtidal area between the Hinderplaat and Voorne (assemblages 4 and 5) has, therefore, a distinct fauna compared to the rest of the Voordelta (Craeymeersch et al. 1990). Even in an analysis of the whole Dutch Continental Shelf, this area is separated from the rest of the near coast stations (Holtmann et al. 1996). The fauna of the Hinderplaat is similar to that of other sandbanks in the Voordelta. Craeymeersch et al. (1990) further distinguished two strata west of the Hinderplaat. A further division of assemblage 7 indeed followed the depth gradient but was, for comparison with the baseline study, not reported in our study.

Temporal changes

The changes in community structure as revealed by the TWINSPAN analysis are in general small. This is in agreement with the minor environmental changes. At present the expected increase of the silt percentage in the intertidal area has not occurred (Anonymous 1997). Consequently we should not expect an increase of the *Corophium* assemblage at the expense of the *Bathyporeia* assemblage. There has been a yearly change in the area of assemblages 4 (*Heteromastus*) and 5 (*Cerastoderma*) (figure 6.4), but no indication that assemblage 5 decreased as was expected. Cockles were not present every year but that is mainly due to irregular recruitment.

Nevertheless, it is still expected that the intertidal area near the Brielse dam will increase, but that the increase will be slower than predicted. The area between the Hinderplaat and Voorne has already become much shallower. The Hinderplaat itself is, more than expected, moving to the south while the northern part becomes deeper and fragmented. These geomorphological changes were already going on before the construction of the depot. The Hinderplaat, for instance, only developed after the Haringvliet was closed in 1970. The influence of the land-reclamation on these phenomena is unclear (Anonymous 1997). A new morphodynamic equilibrium is not yet reached. As the generation times of many macrobenthic species are

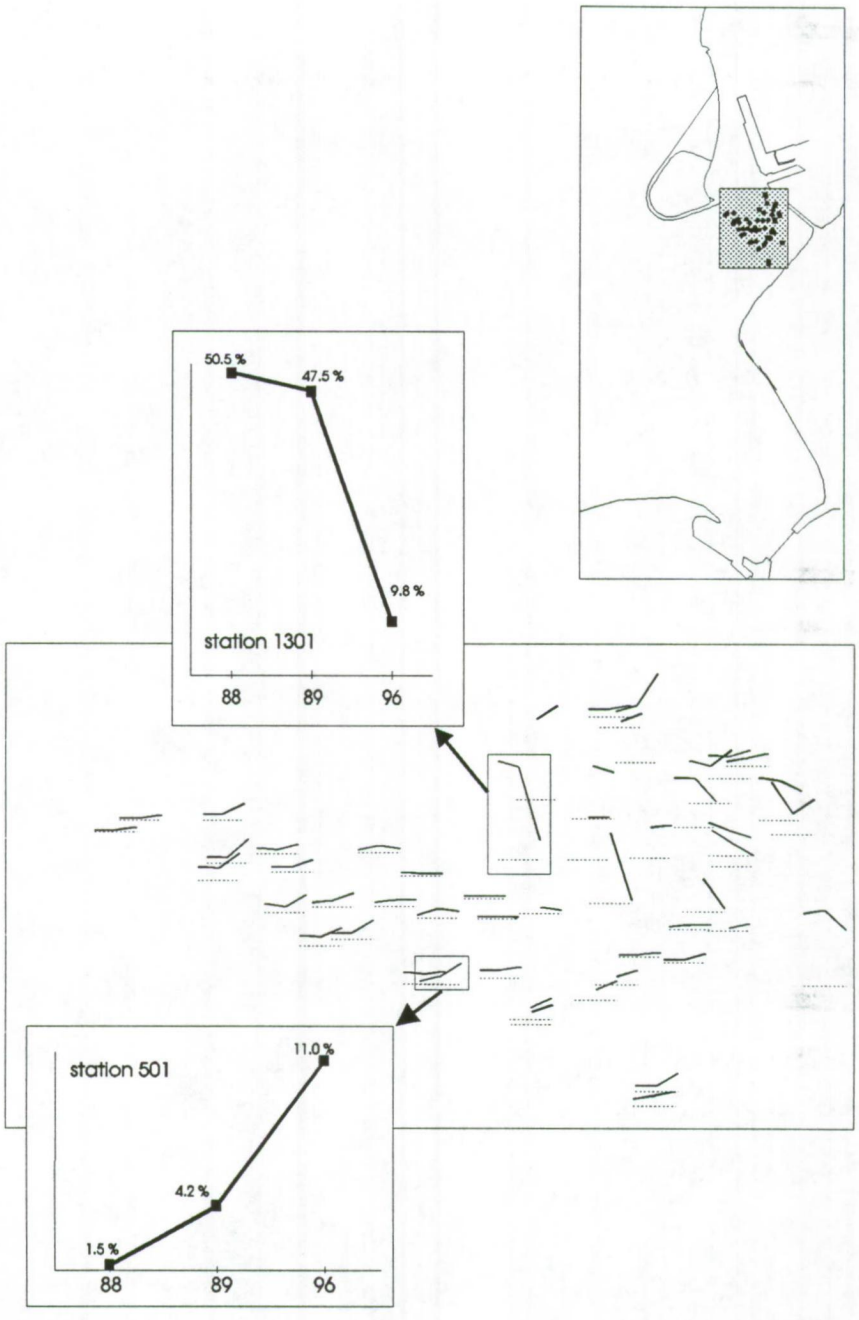


Figure 6.10. Changes in silt content at selected stations on the intertidal area near the Brielse dam.

measured in years, the full establishment of a community characterising the new environmental conditions may take several years. Consequently, on the long term, larger effects on the benthos still might occur.

The only major changes recorded in our study were those on the intertidal area near the Brielse dam. Assemblage 2, at the beginning of the study only found in a small part of the area, covered half of the area in 1994. The changes are probably due to changes in the sediment composition of the southwestern part. A spatial segregation of *C. arenarium* and *C. volutator* has been found in the Wadden Sea in areas where muddy sediment is found in the upper zone and the lower zone is sandy (Flach 1993, 1996). *C. arenarium* inhabits the sandy sediments (% silt < 10%), *C. volutator* the more muddy sediments (% silt > 10%). We might, therefore, expect the sediment of the southwestern part of the Westplaat to have become sandier. The larger area where *Bathyporeia pilosa* was found in 1992 also points to a sandier sediment than before. Sediment data are, unfortunately, only available for 1988, 1989 and 1996 (figure 6.10). Between 1989 and 1996, there is a decrease in silt content in a large part of the northeastern zone, but a small increase in the southwestern parts. It is, therefore, likely that the reported changes were only temporarily. Indeed, in 1996 *C. arenarium* was only found at a few stations (unpublished data).

Cluster analysis can reveal major changes and is, thus, a tool to check the main aims of the study: have the faunal assemblages identified in the base-line study in 1983 been persistent over time, has the spatial distribution of these assemblages changed? Ordination methods are better tools to analyse changes and patterns in detail. Moreover, these methods allow to recognise gradual changes (see e.g. the response of the macrobenthos in the Bay of Morlaix to the Amoco Cadiz oil-spill - Dauvin 1984, Dauvin & Ibanez 1986).

Figure 6.11 shows the temporal fluctuation of the sample scores of three geographically defined areas (more ore less coinciding with assemblages 3a, 5 and 7) along the first two ordination axes (figure 6.8).

The mean positions of the samples taken in area 1 fluctuate along the first axis but without a general trend. The position of the samples along this axis is about the same at the end of the observation period as at the beginning of the observation period. Similar fluctuations occur in area 2 along the first axis and in area 3 along the second axis. These fluctuations reflect interannual variations in the species composition. Such year-to-year variations in benthic communities are well known (see e.g. Essink and Beukema 1986; Heip et al. 1987; Beukema 1989; Keegan 1991, Coosen et al. 1994), although the factors causing them are rarely known.

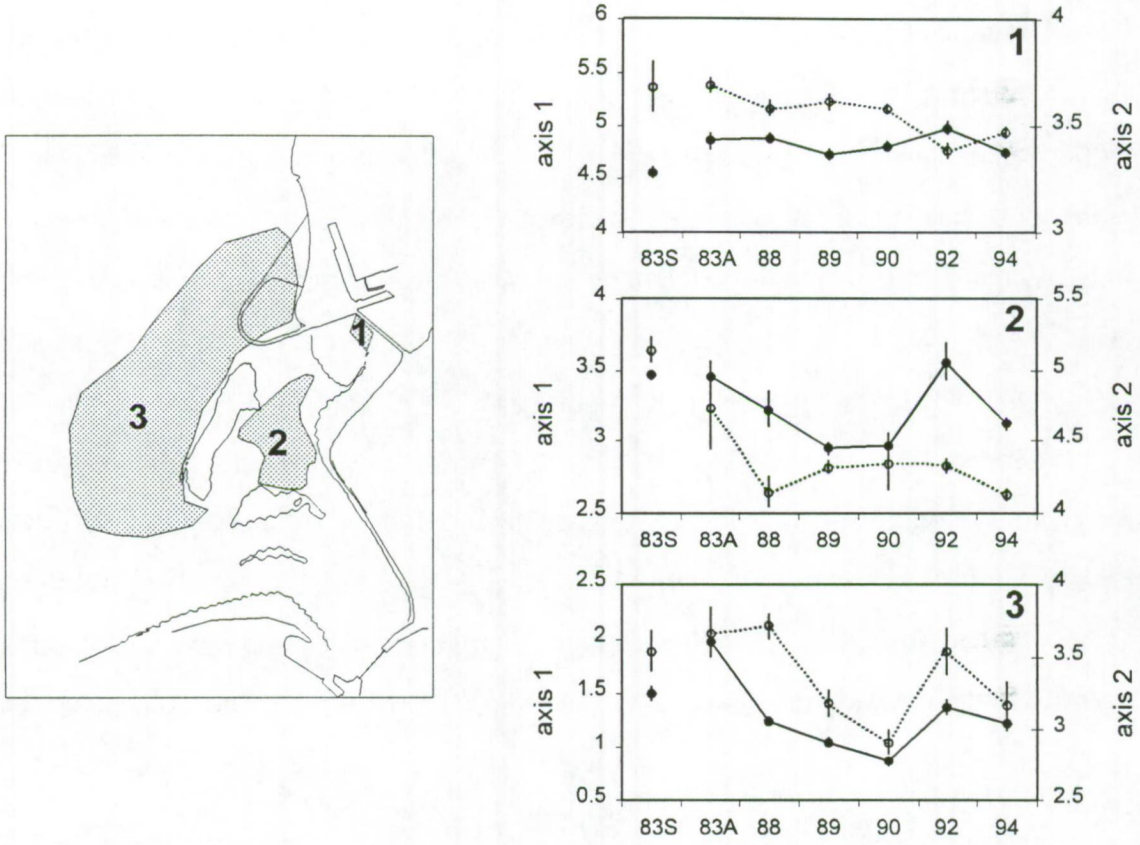


Figure 6.11. Temporal changes in the mean sample scores (± s.e.m.) of three selected areas along the first (solid line) and second (dotted line) ordination axis (83S = Spring 1983; 83A = Autumn 1983).

In a few cases fluctuations in numbers and/or biomass have been observed to be a response to interannual fluctuation in the environment (winter temperature, duration of immersion, food availability) (Beukema 1979, Holme 1983, Rumohr and Krost 1991, Johnson and Wiederholm 1992, Buchanan 1993, Josefson et al. 1993)

All three areas also show some displacement along one of the axes. On the uppershore of the intertidal flat near the Brielse dam (area 1), the 1992 and 1994 samples have lower scores along the second axis then samples of the other surveys. The Autumn 1983 samples of area 2 had higher values along the second axis, the Autumn 1983 samples of area 3 had higher values along the first axis. The amplitude of the fluctuations is rather small (a maximum of ±1 along the second axis in area 2), especially when compared to the spatial variation of the study area (figure 6.8). It is also difficult to make inferences about the species involved: the characteristic species of a particular area remain the same. Moreover, temporal changes within subareas might be different and, consequently, reflected along different ordination axes.

Thus, the spatial scale at which the ordination analysis was done, i.e. the whole study area, might be too large to detect trends within subareas. It might be better to analyse chosen subareas separately. As an example, a Detrended Correspondence Analysis was performed with the data of area 2 (figure 6.12). There is a major shift in 1988 along the first axis and in 1989 along the second axis (fig. 6.12.a and c). In the plot of the species scores (figure 6.12.b) the species corresponding to the stations can be found. The 1983 samples, for instance, are characterised by mussels *Mytilus edulis* and associated species such as *Nereis virens*. The bivalves *Mya arenaria* and *Spisula subtruncata* had higher densities from 1989 onwards. In conclusion, a separate analysis of particular areas indeed gives a better picture of the temporal fluctuations and trends. The choice of the subareas should be determined and justified in terms of the processes operating, the dispersal and dispersion of the populations being sampled, some managerial requirement or some natural feature of the landscape (Underwood 1993). Also, as

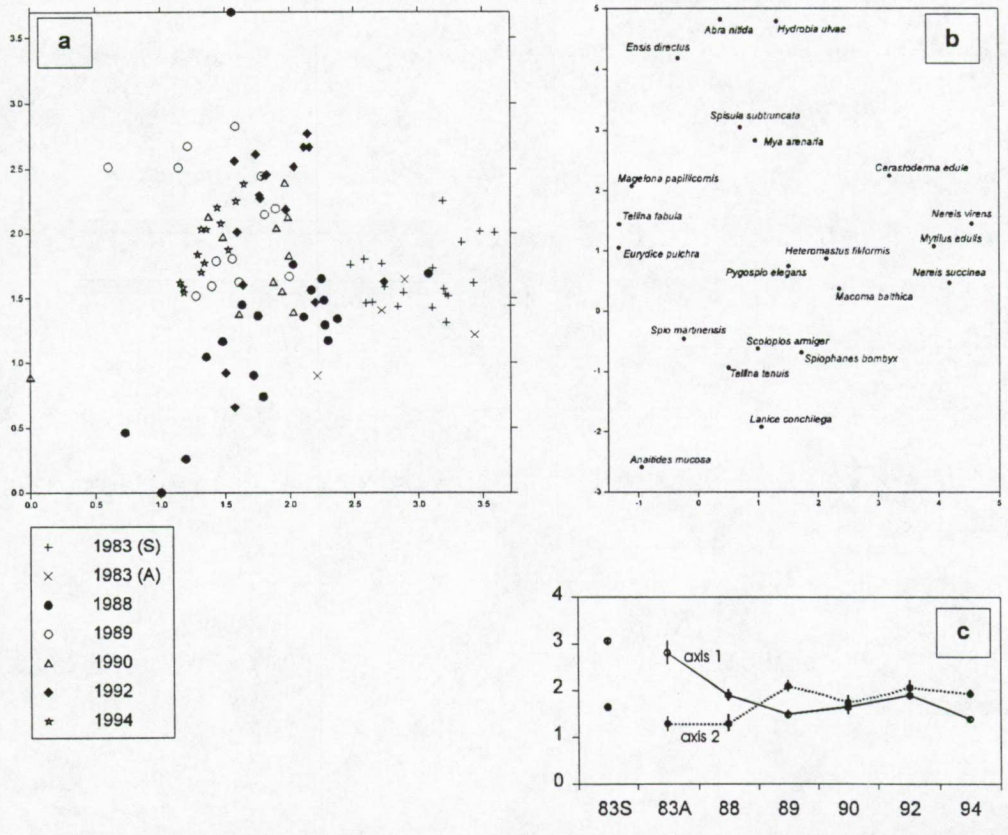


Figure 6.12. DCA of samples taken in area 2 (see figure 6.11); a. scatterplot of the sample scores in the first ordination plane; b. scatterplot of selected species; c. temporal changes along the first and second ordination axis (83S = Spring 1983; 83A = Autumn 1983).

mentioned in the same paper, one should not restrict sampling to a single station. There must be appropriate replication to ensure that the spatial variation within a non-homogeneous subarea is tackled. This variation can be quite large (see e.g. the 1992 sample scores in figure 6.12). Besides spatial replication, monitoring programmes also need replicated sampling in time: both before a proposed development takes place and after it has happened (Stewart-Oaten and Murdock 1986, Underwood 1992). In the study presented here only two surveys took place before the land-reclamation, both in 1983 (Spring and Autumn). It is, therefore, difficult to judge whether mussels disappeared after the construction of the depot or whether the presence in 1983 was an exceptional situation. It is unclear whether or not the 1983 situation was representative for the pre-depot situation.

Another problem in monitoring studies is that ideally several control locations should be sampled (e.g. Underwood 1993). According to Underwood, there should be a series of sites, randomly chosen out of a set of possible sites that have similar features as the one where the development is being proposed. This was certainly not planned when the present monitoring programme started. Given the different species composition in several subareas, no reference areas could be found within our study area. However, some of the changes recorded could be compared with data from other studies. The decrease of *Spiophanes bombyx*, for instance, in the area west of the Hinderplaat was not restricted to this area but also recorded more southerly in the ebb-tidal deltas of the Grevelingen and the Oosterschelde (unpublished data) and, consequently, not caused by the land reclamation. At present, monitoring programmes are running in all marine waters of the Netherlands (the Delta area in the south, the Wadden Sea, the North Sea) providing good reference situations.

Monitoring programmes should not only aim at detecting trends, but also relate them to changes in the environment. In the present study an explanation for the changes recorded was difficult to made. Hardly any data were available on the fluctuations of the most important environmental variables. Thus, there is no proof that the changes on the intertidal flat of the Brielse gat are indeed due to changes in the sediment composition, only a hypothesis based on the changes in the species composition. In fact, data were already too limited to correlate the main gradients

in species composition with abiotic data and, thus, to determine the most important abiotic factors. The different aspects of the monitoring programmes should have been incorporated into a single multidisciplinary programme. Other important variables (e.g. tidal currents, water waves) were measured at the start of the programme but abandoned in an early stage due to the high costs. A solution might be to consider several hierarchically arranged spatial and temporal scales (Underwood 1993). At several, independent times of sampling, a detailed analysis of the macrobenthos and all relevant environmental variables should be done at selected stations. Experimental work should help to understand the processes going on at these stations. The environmental measurements should be incorporated into models generating data of the whole area of interest. Changes in the community structure of the whole area, and any changes in the coverage of the different assemblages, should be followed at larger time intervals. These data could also be used as calibration data.

In conclusion, the monitoring programme as run was certainly not optimal. Consequently, the programme has major limitations for understanding the fluctuations in the macrobenthic communities and, thus, in discriminating between natural changes and changes due to construction of the disposal site. At present, changes in the abiotic environment are believed to be minor, but the area is far from a morphodynamic equilibrium (Anonymous 1997). Therefore, a revision of the monitoring programme is needed.

References

Anonymous. 1984. Grootschalige locatie voor de berging van baggerspecie uit het bendenrivierengebied. Projectnota/Milieu-effectrapport. Gemeente Rotterdam / Openbaar Lichaam Rijnmond / Rijkswaterstaat, Rotterdam.

—-. 1992. Evaluatie milieu effect rapportage Slufter over de periode 1986 tot en met 1990. Werkgroep Evaluatie Slufter. Gemeentewerken Rotterdam, Ministerie van Verkeer en Waterstaat. Rotterdam. 40 pp.

—-. 1997. Evaluatie milieu effect rapportage 'Slufter' over de periode 1986 tot en met 1996. Werkgroep Evaluatie Slufter. Gemeentewerken Rotterdam, Ministerie van Verkeer en Waterstaat. Rotterdam. 64 pp.

Beukema, J. J. 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the dutch Wadden Sea: effects of a severe winter. Netherlands Journal of Sea Research **13**:203-233.

—-. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. Helgoländer Meeresuntersuchungen **43**:405-415.

Buchanan, J. B. 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. Journal of Experimental Marine Biology and Ecology **172**:1-10.

Coosen, J., J. Seys, P. M. Meire, and J. A. M. Craeymeersch. 1994. Effect of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde estuary (SW Netherlands) on distribution, density and biomass of five common macrobenthic species: *Spio martinensis* (Mesnil), *Hydrobia ulvae* (Pennant), *Arenicola marina* (L.), *Scoloplos armiger* (Muller) and *Bathyporeia* sp. Hydrobiologia **282/283**:235-249.

Craeymeersch, J. A. 1997. Effekten van de schelpdiervisserij op het bodemleven in de Voordelta. Nederlands Instituut voor Oecologisch Onderzoek, Centrum voor Estuariene en Mariene Oecologie. 63 pp.

Craeymeersch, J. A., O. Hamerlynck, K. Hostens, A. Vanreusel, and M. Vincx. 1990. De ekologische ontwikkeling van de Voordelta. Deelrapport 1. De huidige ekologische situatie van de Voordelta. Delta Instituut voor Hydrobiologisch Onderzoek - Rijksuniversiteit Gent, Sektie Mariene Biologie. 92 pp.

Dauer, D. M. 1983. Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). Marine Biology **72**:279-285.

Dauvin, J. C. 1984. Revue des principales techniques utilisées pour l'étude expérimentale de l'établissement de peuplements macrobenthiques subtidaux de sédiment meuble. Premiers résultats des expérimentations réalisées en Baie de Morlaix. Océanis **10**:237-258.

Dauvin, J.-C., and F. Ibanez. 1986. Variations à long-terme (1977-1985) du peuplement des sables fins de la Pierre Noire (Baie de Morlaix, Manche occidentale): analyse statistique de l'évolution structurale. Hydrobiologia **142**:171-186.

de Hoog, J. E. W., and B. P. C. Steenkamp. 1989. Eutrophication of the fresh waters of the Delta. Pages 27-47 *in* J. C. Hooghart and C. W. S. Posthumus, editors. Hydro-ecological relations in the Delta Waters of the South-West Netherlands: Technical Meeting 46, Rotterdam, The Netherlands, 8 March 1989. TNO Committee on Hydrological Research, The Hague, Proceedings and information / TNO Comittee on Hydrological Research; no 41.

Essink, K., and J. J. Beukema. 1986. Long-term changes in intertidal flat macrozoobenthos as an indicator of stress by organic pollution. Hydrobiologia **142**:209-215.

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series **8**:37-52.

Fincham, A. A. 1971. Ecology and population studies of some intertidal and sublittoral sand-dwelling amphipods. Journal of the Marine Biology Association of the United Kingdom **51**:471-488.

Flach, E. C. 1993. The distribution of the amphipod *Corophium arenarium* in the dutch Wadden Sea: relationships with sediment composition and the presence of cockles and lugworms. Netherlands Journal of Sea Research **31**:281-290.

—. 1996. Distribution of *Corophium* at different scales. Senckenbergiana maritima **27**:119-127.

Heip, C., B. F. Keegan, and J. R. Lewis, editors. 1987. Developments in Hydrobiology, 38: Long-term changes in coastal benthic communities. Proceedings of a symposium, held in Brussels, Belgium, December 9-12, 1985. Dr. W. Junk Publishers, Dordrecht.

Hill, M. O. 1979. TWINSPAN. A FORTRAN program for arranging Multivariate data in an Ordered Two-Way Table by Classification of the Individuals and Attributes. Ecology and Systematics, Cornell University, Ithaca, 90 pp.

Holme, N. A. 1983. Fluctuations in the benthos of the western English Channel. Pages 121-124 *in* Proceedings of the 17th EMBS (Brest, France, 1982). Oceanologica Acta N°SP..

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijswijk. 244pp.

Johnson, R. K., and T. Wiederholm. 1992. Pelagic-benthic coupling - the importance of diatom interannual variability for population oscillations of *Monoporeia affinis*. Limnology and Oceanography **37**:1596-1607.

Josefson, A. B., J. N. Jensen, and Æ rtebjerg. 1993. The benthos community structure anomaly in the late 1970s and early 1980s - a result of a major food pulse? Journal of Experimental Marine Biology and Ecology **172**:31-45.

Keegan, B. F., editor. 1991. Space and time series data analysis in coastal benthic ecology. An analytical exercise organised within the framework of the COST 647 Project on Coastal Benthic Ecology. Commission of the European Communities. Directorate-General for Science, Research and Development, Brussels. 581pp.

McRae, G., D. K. Camp, W. G. Lyons, and T. L. Dix. 1998. Relating benthic infaunal community structure to environmental variables in estuaries using nonmetric multidimensional scaling and similarity analysis. Environmental Monitoring and Assessment **51**:233-246.

Rasmussen, E. 1973. Systematics and ecology of the Islefjord marine fauna (Denmark). Ophelia **11**:1-507.

Rumohr, H., and P. Krost. 1991. Experimental evidence of damage to benthos by bottom trawling with special reference to *Arctica islandica*. Meeresforschung **33**:340-345.

Stewart-Oaten, A., and W. W. Murdock. 1986. Environmental impact assessment: "Pseudoreplication" in time? Ecology **67**:929-940.

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populqations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology **161**:145-178.

—-. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Australian Journal of Ecology **18**:99-116.

Vader, W. J. M. 1965. Intertidal distribution of haustoriid amphipods in the Netherlands. Botanica Gothoburgensia **3**:233-246.

Watkin, E. E. 1939. The pelagic phase in the life history of the amphipod genus *Bathyporeia*. Journal of the Marine Biology Association of the United Kingdom **23**:467-481.

Appendix 1. Overall mean density (ind./m^2) and standarderror (se) per cluster.

Cluster	1		2a		2b		3a		3b	
Number of stations	30		60		148		257		127	
	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	0	0	.8	.80	0	0	0	0
Abra nitida	0	0	0	0	0	0	0	0	0	0
Actiniaria indet.	0	0	0	0	0	0	0	0	0	0
Ampelisca brevicornis	0	0	0	0	0	0	0	0	0	0
Ampelisca spinipes	0	0	0	0	0	0	0	0	0	0
Amphilochus neapolitanus	0	0	0	0	0	0	0	0	0	0
Anaitides groenlandica	0	0	0	0	0	0	0	0	0	0
Anaitides mucosa	0	0	0	0	.8	.80	.5	.46	0	0
Anaitides rosea	0	0	0	0	0	0	0	0	0	0
Anaitides spec.	0	0	0	0	0	0	0	0	0	0
Anthozoa indet.	0	0	0	0	0	0	0	0	0	0
Aoridae indet.	0	0	0	0	0	0	0	0	0	0
Arenicola marina	0	0	0	0	0	0	.08	.078	0	0
Asterias rubens	0	0	0	0	0	0	0	0	0	0
Astropecten irregularis	0	0	0	0	0	0	0	0	0	0
Atylus falcatus	0	0	0	0	0	0	.5	.46	0	0
Atylus swammerdami	0	0	0	0	0	0	0	0	0	0
Autolytus langerhansi	0	0	0	0	0	0	0	0	0	0
Autolytus spec.	0	0	0	0	0	0	0	0	0	0
Barnea candida	0	0	0	0	0	0	0	0	0	0
Bathyporeia elegans	0	0	0	0	0	0	0	0	0	0
Bathyporeia guilliamsoniana	0	0	0	0	0	0	0	0	0	0
Bathyporeia pelagica	0	0	0	0	0	0	0	0	0	0
Bathyporeia pilosa	3600	690	670	183	1510	208	8	3.7	90	42
Bathyporeia sarsi	0	0	.5	.37	0	0	0	0	0	0
Bathyporeia spec.	0	0	0	0	.8	.80	0	0	0	0
Bivalvia indet.	0	0	6	3.3	8.0	2.69	1.4	.79	0	0
Bodotria scorpioides	0	0	0	0	0	0	0	0	2.7	2.74
Capitella capitata	0	0	.17	.167	0	0	9	6.0	0	0
Caprellidae indet.	0	0	0	0	.8	.80	0	0	0	0
Carcinus maenas	.4	.43	.17	.167	2.6	1.38	26	4.8	4.7	2.43
Caridea indet.	0	0	0	0	0	0	0	0	0	0
Cerastoderma edule	4	3.9	230	45	8	3.1	290	41	80	15.2
Cerastoderma spec.	0	0	0	0	10	5.6	.5	.46	0	0
Chaetozone setosa	0	0	0	0	0	0	0	0	0	0
Cirratulidae indet.	0	0	0	0	0	0	0	0	0	0
Corbula gibba	0	0	0	0	0	0	0	0	0	0
Corophium arenarium	16	12.3	290	39	920	113	30	17.5	0	0
Corophium lacustre	0	0	0	0	0	0	0	0	0	0
Corophium spec.	0	0	16	9.1	3	3.2	29	12.3	0	0
Corophium volutator	56	21.3	140	82	2000	390	18600	1960	3800	650
Crangon crangon	4	3.9	12	6.6	3.0	1.43	38	7.5	32	10.3
Crangon spec.	0	0	0	0	0	0	0	0	0	0
Crepidula fornicata	0	0	0	0	0	0	0	0	0	0
Cumacea indet.	0	0	0	0	0	0	0	0	0	0
Cumopsis goodsiri	0	0	.5	.37	0	0	0	0	0	0
Decapoda indet.	0	0	0	0	0	0	0	0	0	0
Diastylis bradyi	0	0	0	0	0	0	0	0	0	0
Diastylis rathkei	0	0	0	0	0	0	0	0	0	0
Diastylis spec.	0	0	0	0	0	0	0	0	0	0
Diogenes pugilator	0	0	0	0	0	0	0	0	0	0
Donax vittatus	0	0	0	0	0	0	0	0	0	0
Echinocardium cordatum	0	0	0	0	0	0	0	0	0	0
Ensis directus	0	0	0	0	0	0	0	0	0	0
Ensis spec.	0	0	0	0	0	0	0	0	1.0	.93
Eteone flava	0	0	0	0	0	0	0	0	0	0
Eteone longa	0	0	0	0	2.4	1.78	6.4	1.79	20	4.5
Eteone spec.	0	0	13	1.6	11	3.1	1.8	.91	0	0
Eumida sanguinea	0	0	0	0	0	0	0	0	0	0
Eumida spec.	0	0	0	0	0	0	0	0	0	0
Eurydice pulchra	4	3.9	.17	.167	0	0	0	0	0	0
Eurydice spec.	8	5.5	0	0	0	0	0	0	0	0
Gammarus crinicornis	0	0	0	0	0	0	0	0	0	0
Gammarus locusta	0	0	0	0	0	0	0	0	0	0
Gammarus salinus	0	0	0	0	0	0	.004	.0039	0	0
Gammarus spec.	0	0	0	0	0	0	0	0	0	0
Gammarus tigrinus	0	0	0	0	0	0	.30	.300	0	0
Gastrosaccus spinifer	0	0	0	0	0	0	0	0	0	0
Harmothoe imbricata	0	0	0	0	0	0	0	0	0	0
Harmothoe lunulata	0	0	0	0	0	0	0	0	0	0
Harmothoe spec.	0	0	0	0	0	0	0	0	0	0
Haustorius arenarius	4	3.9	0	0	0	0	0	0	0	0
Heteromastus filiformis	5	4.0	230	69	22	7.7	97	15.8	230	39
Hydrobia ulvae	4	3.9	230	94	1120	248	3400	450	790	103
Idotea linearis	0	0	0	0	0	0	0	0	0	0
Ingolfiellidae indet.	0	0	0	0	0	0	0	0	0	0
Lamprops fasciata	0	0	0	0	0	0	0	0	0	0
Lanice conchilega	0	0	0	0	0	0	0	0	.09	.087
Leucothoe incisa	0	0	0	0	0	0	0	0	0	0
Liocarcinus holsatus	0	0	0	0	0	0	0	0	0	0
Liocarcinus spec.	0	0	0	0	0	0	0	0	0	0
Lysianassidae indet.	0	0	0	0	0	0	0	0	0	0
Macoma balthica	0	0	61	16.7	90	11.0	254	29.8	78	18.8
Mactra corallina	0	0	0	0	0	0	0	0	0	0
Magelona papillicornis	0	0	0	0	.8	.80	.5	.46	0	0
Malacoceros fuliginosus	0	0	0	0	0	0	0	0	0	0
Manayunkia aestuarina	0	0	0	0	2.4	1.78	10	4.5	.9	.93
Melita obtusata	0	0	0	0	0	0	0	0	0	0
Melita palmata	0	0	0	0	0	0	0	0	0	0
Melita spec.	0	0	0	0	0	0	0	0	0	0
Mesopodopsis slabberi	0	0	0	0	0	0	0	0	0	0

Appendix 1. Continued.

Cluster	1		2a		2b		3a		3b	
Number of stations	30		60		143		257		127	
	mean	se	mean	se	mean	se	mean	se	mean	se
Microphthalmus listensis	0	0	0	0	0	0	0	0	0	0
Microprotopus maculatus	0	0	0	0	0	0	0	0	0	0
Montacuta ferruginosa	0	0	0	0	0	0	0	0	0	0
Mya arenaria	8	7.9	1110	179	25	6.2	510	80	21	5.1
Mysella bidentata	0	0	0	0	.8	.80	.5	.46	7	3.3
Mysidacea indet.	0	0	0	0	0	0	0	0	0	0
Mytilus edulis	0	0	2.0	1.96	0	0	0	0	0	0
Natica alderi	0	0	0	0	0	0	0	0	0	0
Nemertinae indet.	4	3.9	0	0	2.4	1.37	2.8	1.29	3.7	2.26
Neomysis integer	0	0	0	0	0	0	0	0	0	0
Nephtys caeca	0	0	0	0	0	0	0	0	0	0
Nephtys cirrosa	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	0	0	0	0	0	0	0	0	0	0
Nephtys longosetosa	0	0	0	0	0	0	0	0	0	0
Nephtys spec.	0	0	0	0	0	0	0	0	0	0
Nereis diversicolor	140	42	1350	123	750	74	4200	500	3030	205
Nereis longissima	0	0	0	0	0	0	2.5	1.80	0	0
Nereis spec.	0	0	1280	265	190	30	430	61	5	4.6
Nereis succinca	.4	.43	0	0	0	0	0	0	0	0
Nereis virens	.4	.43	0	0	.5	.54	1.4	1.30	0	0
Notomastus latericeus	0	0	0	0	0	0	0	0	0	0
Nudibranchia indet.	0	0	0	0	0	0	0	0	0	0
Oligochaeta indet.	250	138	1200	420	2200	310	6000	440	570	146
Ophiura albida	0	0	0	0	0	0	0	0	0	0
Ophiuridae indet.	0	0	0	0	0	0	0	0	0	0
Ophiura spec.	0	0	0	0	0	0	0	0	0	0
Ophiura texturata	0	0	0	0	0	0	0	0	0	0
Orchomene humilis	0	0	0	0	0	0	0	0	0	0
Orchomene nana	0	0	0	0	0	0	0	0	0	0
Pagurus bernhardus	0	0	0	0	0	0	0	0	0	0
Paraonis fulgens	80	75	0	0	0	0	0	0	0	0
Paraonis gracilis	0	0	0	0	0	0	0	0	0	0
Paraonidae indet.	0	0	.17	.167	0	0	0	0	0	0
Pectinaria koreni	0	0	0	0	0	0	0	0	0	0
Pectinaria spec.	0	0	0	0	0	0	0	0	0	0
Perioculodes longimanus	0	0	0	0	0	0	0	0	0	0
Petricola pholadiformis	0	0	0	0	0	0	0	0	0	0
Pholoe minuta	0	0	0	0	.8	.80	0	0	0	0
Phyllodocinae indet.	0	0	0	0	0	0	0	0	0	0
Platynereis dumerilii	2.6	2.57	0	0	0	0	.10	.101	0	0
Polychaeta indet.	0	0	0	0	.8	.80	.4	.39	0	0
Polydora ciliata	0	0	0	0	0	0	0	0	0	0
Polydora ligni	0	0	14	8.9	15	10.2	630	69	15	6.2
Polydora spec.	0	0	0	0	0	0	0	0	0	0
Pontocrates altamarinus	0	0	0	0	0	0	0	0	0	0
Pontocrates arenarius	0	0	0	0	0	0	0	0	0	0
Pontophylus trispinosus	0	0	0	0	0	0	0	0	0	0
Portumnus latipes	0	0	0	0	0	0	0	0	0	0
Proceraea cornuta	0	0	0	0	0	0	0	0	0	0
Pseudocuma longicornis	0	0	0	0	0	0	0	0	0	0
Pseudopolydora pulchra	0	0	0	0	0	0	0	0	0	0
Pseudocuma spec.	0	0	0	0	0	0	0	0	0	0
Pygospio elegans	500	320	560	88	3400	320	6600	970	8600	870
Schistomysis kervillei	0	0	0	0	0	0	0	0	0	0
Scoloplos armiger	100	72	0	0	.8	.80	0	0	0	0
Scolelepis bonnieri	4	3.9	0	0	0	0	0	0	0	0
Scolelepis squamata	12	6.6	.17	.167	.8	.80	0	0	0	0
Scrobicularia plana	0	0	2.0	1.96	4.0	2.63	26	4.5	.9	.93
Sigalion mathildae	0	0	0	0	0	0	0	0	0	0
Spiophanes bombyx	0	0	0	0	1.6	1.12	.5	.46	2.8	2.78
Spio martinensis	12	8.7	53	27.1	17	10.4	8	3.6	170	41
Spionidae indet.	0	0	0	0	0	0	0	0	0	0
Spisula spec.	0	0	0	0	0	0	0	0	0	0
Spisula subtruncata	0	0	0	0	11	11.2	0	0	1.1	.94
Stenothoe marina	0	0	0	0	0	0	0	0	0	0
Sthenelais boa	0	0	0	0	0	0	0	0	0	0
Streblospio shrubsolii	0	0	10	6.4	18	10.8	570	166	70	38
Talitrus saltator	0	0	0	0	.8	.80	0	0	0	0
Tellina fabula	0	0	0	0	0	0	0	0	0	0
Tellinacea indet.	0	0	0	0	0	0	0	0	0	0
Tellina pygmaeus	0	0	0	0	0	0	0	0	0	0
Tellina spec.	0	0	.17	.167	0	0	0	0	0	0
Tellina tenuis	0	0	0	0	0	0	0	0	0	0
Tharyx marioni	0	0	3.9	2.76	0	0	4.1	1.35	6.6	2.40
Urothoe poseidonis	.4	.43	0	0	0	0	0	0	0	0
Urothoe spec.	0	0	0	0	0	0	0	0	0	0
Vaunthompsonia cristata	0	0	0	0	0	0	0	0	0	0
Venerupis pullastra	0	0	0	0	0	0	0	0	0	0
Venus striatula	0	0	0	0	0	0	0	0	0	0
Total	4800	1440	7500	1680	12300	1800	42000	4900	17600	2210

Appendix 1. Continued.

Cluster	4		5		6		7		8	
Number of stations	107		106		131		283		44	
	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	4.1	2.93	1.5	.92	1.6	.73	42	16.0	0	0
Abra nitida	0	0	.05	.047	0	0	0	0	0	0
Actiniaria indet.	0	0	0	0	.04	.038	.8	.51	0	0
Ampelisca brevicornis	0	0	0	0	0	0	.47	.163	0	0
Ampelisca spinipes	0	0	0	0	0	0	0	0	.25	.250
Amphilochus neapolitanus	0	0	0	0	0	0	.018	.0177	0	0
Anaitides groenlandica	0	0	0	0	0	0	2.4	.44	0	0
Anaitides mucosa	1.8	1.14	0	0	1.9	.62	58	20.4	0	0
Anaitides rosea	0	0	0	0	.15	.102	1.8	.55	0	0
Anaitides spec.	.09	.093	0	0	.5	.40	.08	.057	0	0
Anthozoa indet.	0	0	0	0	.07	.069	.32	.097	0	0
Aoridae indet.	.7	.45	.19	.133	.38	.274	.6	.31	0	0
Arenicola marina	0	0	0	0	0	0	0	0	0	0
Asterias rubens	.4	.38	0	0	.23	.229	.11	.056	0	0
Astropecten irregularis	0	0	.09	.094	0	0	0	0	0	0
Atylus falcatus	.7	.68	.05	.049	.37	.169	10.5	1.34	0	0
Atylus swammerdami	.5	.32	.05	.047	.53	.293	2.5	.78	0	0
Autolytus langerhansi	0	0	0	0	0	0	.5	.34	0	0
Autolytus spec.	0	0	0	0	.07	.069	.60	.224	0	0
Barnea candida	0	0	0	0	.23	.142	.018	.0177	0	0
Bathyporcia elegans	.08	.084	0	0	.52	.269	23.6	2.99	18	7.3
Bathyporeia guilliamsonian	0	0	0	0	0	0	.30	.142	0	0
Bathyporeia pelagica	0	0	0	0	0	0	.04	.035	.9	.60
Bathyporeia pilosa	19	16.8	0	0	.7	.39	.29	.170	400	300
Bathyporeia sarsi	0	0	.09	.094	0	0	0	0	0	0
Bathyporcia spec.	.4	.37	0	0	0	0	.7	.32	.23	.159
Bivalvia indet.	0	0	.19	.133	.23	.161	.04	.035	0	0
Bodotria scorpioides	.09	.093	.09	.094	0	0	0	0	0	0
Capitella capitata	19	3.3	2.3	1.36	101	21.5	31	4.1	1.4	.57
Caprellidae indet.	2.1	2.06	.09	.094	1.3	.63	9.3	1.67	0	0
Carcinus maenas	1.4	.42	2.7	1.14	.19	.107	.9	.35	0	0
Caridea indet.	0	0	.09	.094	.04	.038	0	0	0	0
Cerastoderma edule	45	13.0	320	63	8	3.4	.05	.037	0	0
Corastoderma spec.	0	0	0	0	0	0	0	0	0	0
Chaetozone setosa	0	0	0	0	0	0	.83	.264	0	0
Cirratulidae indet.	0	0	0	0	0	0	.04	.035	0	0
Corbula gibba	.05	.047	0	0	.04	.038	0	0	0	0
Corophium arenarium	.8	.45	0	0	0	0	0	0	0	0
Corophium lacustre	0	0	.19	.133	0	0	0	0	0	0
Corophium spec.	0	0	0	0	.04	.038	.018	.0177	0	0
Corophium volutator	2.0	1.77	.21	.207	.24	.140	.4	.39	0	0
Crangon crangon	4.1	.60	4.2	1.28	5.3	.93	6.8	.63	.5	.33
Crangon spec.	0	0	.19	.133	0	0	0	0	0	0
Crepidula fornicata	0	0	0	0	0	0	.018	.0177	0	0
Cumacea indet.	0	0	0	0	.16	.113	.04	.035	0	0
Cumopsis goodsiri	0	0	.09	.094	.31	.189	0	0	0	0
Decapoda indet.	0	0	0	0	0	0	.04	.037	0	0
Diastylis bradyi	0	0	.10	.104	0	0	7.6	1.12	0	0
Diastylis rathkei	0	0	0	0	.04	.040	0	0	0	0
Diastylis spec.	.028	.0280	0	0	.50	.185	.35	.144	0	0
Diogenes pugilator	0	0	0	0	0	0	.14	.066	.11	.114
Donax vittatus	0	0	0	0	.08	.076	.07	.046	0	0
Echinocardium cordatum	0	0	0	0	90	33	2.9	.63	.24	.237
Ensis directus	.09	.066	.05	.047	.23	.194	.11	.061	0	0
Ensis spec.	1.8	.59	.8	.40	1.8	.61	21	8.0	0	0
Eteone flava	.15	.084	0	0	0	0	0	0	0	0
Eteone longa	8.5	2.85	0	0	1.7	.65	1.4	.34	0	0
Eteone spec.	.61	.227	.47	.237	1.11	.283	.12	.081	.45	.273
Eumida sanguinea	.08	.084	0	0	2.1	1.85	102	29.3	0	0
Eumida spec.	0	0	0	0	.23	.170	5	3.3	0	0
Eurydice pulchra	.14	.104	0	0	0	0	0	0	2.7	2.68
Eurydice spec.	0	0	0	0	0	0	0	0	0	0
Gammarus crinicornis	.05	.049	.05	.047	.04	.038	.018	.0177	0	0
Gammarus locusta	0	0	0	0	0	0	.8	.57	0	0
Gammarus salinus	0	0	.6	.36	.29	.172	0	0	0	0
Gammarus spec.	0	0	0	0	.12	.092	0	0	0	0
Gammarus tigrinus	0	0	.4	.32	0	0	0	0	0	0
Gastrosaccus spinifer	0	0	0	0	.08	.084	.27	.101	.23	.159
Harmothoe imbricata	.15	.146	0	0	0	0	0	0	0	0
Harmothoe lunulata	.19	.187	0	0	.56	.273	14	3.2	0	0
Harmothoe spec.	.19	.187	.05	.047	.04	.038	.22	.099	0	0
Haustorius arenarius	0	0	0	0	.06	.046	.8	.36	3.5	2.70
Heteromastus filiformis	810	116	270	59	160	35	.19	.070	.9	.80
Hydrobia ulvae	.9	.35	3.9	1.66	0	0	0	0	0	0
Idotea linearis	0	0	0	0	0	0	.06	.041	0	0
Ingolfiellidae indet.	0	0	0	0	.27	.232	.14	.086	.23	.159
Lamprops fasciata	0	0	0	0	.04	.040	.83	.173	0	0
Lanice conchilega	.7	.38	.19	.189	4.9	1.94	68	21.5	0	0
Leucothoe incisa	0	0	0	0	0	0	.07	.050	0	0
Liocarcinus holsatus	0	0	0	0	.25	.128	1.3	.33	0	0
Liocarcinus spec.	0	0	0	0	0	0	.12	.053	0	0
Lysianassidae indet.	0	0	0	0	0	0	.04	.035	0	0
Macoma balthica	21	8.7	14	4.6	8.0	1.28	1.25	.260	.49	.295
Mactra corallina	0	0	.20	.140	.08	.054	4.4	1.26	0	0
Magelona papillicornis	.37	.273	0	0	7.2	2.17	55	11.9	.20	.205
Malacoceros fuliginosus	.05	.047	0	0	0	0	0	0	0	0
Manayunkia aestuarina	0	0	0	0	0	0	0	0	0	0
Melita obtusata	0	0	0	0	.4	.34	1.1	.47	0	0
Melita palmata	0	0	.2	.114	0	0	.04	.035	0	0
Melita spec.	0	0	0	0	.08	.076	0	0	0	0
Mesopodopsis slabberi	.05	.047	.028	.0283	0	0	0	0	0	0

Appendix 1. Continued.

Cluster	4		5		6		7		8	
Number of stations	107		106		131		283		44	
	mean	se	mean	se	mean	se	mean	se	mean	se
Microphthalmus listensis	0	0	0	0	0	0	0	0	.11	.114
Microprotopus maculatus	2.1	1.35	0	0	5.6	2.77	12.8	2.49	.5	.36
Montacuta ferruginosa	0	0	0	0	19	7.8	1.6	.44	0	0
Mya arenaria	600	274	410	182	430	171	.036	.0255	.6	.47
Mysella bidentata	3.8	1.66	1.7	1.44	3.8	2.78	9.1	2.06	0	0
Mysidacea indet.	0	0	0	0	0	0	.19	.118	0	0
Mytilus edulis	.55	.220	5.6	2.23	.40	.212	.37	.174	0	0
Natica alderi	0	0	0	0	0	0	4.2	1.25	0	0
Nemertinae indet.	.6	.33	.08	.055	2.9	.68	35	21.0	.55	.277
Neomysis integer	0	0	0	0	.023	.0229	0	0	0	0
Nephtys caeca	0	0	0	0	0	0	.018	.0177	0	0
Nephtys cirrosa	.15	.112	.10	.104	9.7	1.74	53	3.1	11.4	2.51
Nephtys hombergii	9.2	2.97	2.4	.95	26	4.3	41	3.7	.9	.62
Nephtys longosetosa	0	0	0	0	.07	.069	.03	.032	0	0
Nephtys spec.	.28	.146	.05	.047	.23	.119	2.3	.90	0	0
Nereis diversicolor	100	35	.38	.290	3.4	2.51	.10	.069	0	0
Nereis longissima	.05	.047	0	0	1.6	.85	1.7	.63	0	0
Nereis spec.	5.6	2.43	.09	.094	0	0	.035	.0249	.11	.114
Nereis succinea	.12	.122	1.4	.57	.15	.108	.018	.0184	0	0
Nereis virens	5	5.4	.028	.0283	0	0	0	0	0	0
Notomastus latericeus	0	0	0	0	.04	.038	0	0	0	0
Nudibranchia indet.	.19	.187	0	0	0	0	0	0	0	0
Oligochaeta indet.	6	3.2	59	21.7	2.6	.99	.25	.182	2.7	2.68
Ophiura albida	0	0	.9	.93	0	0	.04	.035	0	0
Ophiuridae indet.	.09	.093	0	0	0	0	0	0	0	0
Ophiura spec.	.09	.066	0	0	.08	.084	0	0	0	0
Ophiura texturata	.08	.084	1.3	1.35	.8	.43	.13	.062	.5	.50
Orchomene humilis	0	0	0	0	0	0	.07	.074	0	0
Orchomene nana	0	0	0	0	0	0	.9	.74	0	0
Pagurus bernhardus	0	0	0	0	0	0	.46	.158	0	0
Paraonis fulgens	7	4.6	0	0	26	6.7	1.0	.55	140	47
Paraonis gracilis	0	0	0	0	.04	.038	0	0	0	0
Paraonidae indet.	0	0	0	0	0	0	.04	.035	0	0
Pectinaria koreni	3.8	1.28	3.7	1.07	.96	.274	7	4.2	0	0
Pectinaria spec.	0	0	0	0	.11	.085	.04	.035	0	0
Perioculodes longimanus	0	0	0	0	.29	.174	7.5	1.01	0	0
Petricola pholadiformis	1.1	1.10	.33	.204	.6	.34	.9	.76	0	0
Pholoe minuta	0	0	0	0	.08	.084	.43	.172	0	0
Phyllodocinae indet.	0	0	0	0	.15	.153	.04	.035	0	0
Platynereis dumerilii	0	0	.05	.047	0	0	0	0	0	0
Polychaeta indet.	0	0	0	0	0	0	0	0	0	0
Polydora ciliata	0	0	.52	.260	0	0	.04	.035	0	0
Polydora ligni	130	37	33	24.4	28	10.1	3.4	1.57	0	0
Polydora spec.	0	0	0	0	.04	.038	.34	.226	0	0
Pontocrates altamarinus	0	0	0	0	.9	.70	9.8	1.08	3.4	1.32
Pontocrates arenarius	0	0	0	0	0	0	1.6	.36	.12	.118
Pontophylus trispinosus	0	0	.05	.047	0	0	0	0	0	0
Portumnus latipes	0	0	.05	.047	0	0	.60	.270	.6	.37
Proceraea cornuta	.05	.047	0	0	.04	.038	.04	.035	0	0
Pseudocuma longicornis	0	0	0	0	0	0	.14	.084	0	0
Pseudopolydora pulchra	.23	.139	0	0	.7	.62	.19	.104	0	0
Pseudocuma spec.	0	0	0	0	.08	.076	.42	.273	0	0
Pygospio elegans	620	135	16	6.6	160	31	.31	.187	50	51
Schistomysis kervillei	.29	.166	0	0	.7	.31	1.90	.274	.8	.45
Scoloplos armiger	31	16.6	1.2	.72	27	7.1	22	4.6	.49	.295
Scolelepis bonnieri	0	0	0	0	0	0	.07	.050	0	0
Scolelepis squamata	.10	.067	.19	.189	1.1	.40	.09	.053	53	12.1
Scrobicularia plana	.19	.132	.24	.140	0	0	0	0	0	0
Sigalion mathildae	0	0	0	0	0	0	.04	.035	0	0
Spiophanes bombyx	.8	.37	.28	.210	180	99	105	20.1	.5	.37
Spio martinensis	440	112	.8	.31	940	153	1140	150	110	40
Spionidae indet.	0	0	0	0	.04	.038	0	0	.11	.114
Spisula spec.	.09	.093	.09	.094	.08	.076	0	0	0	0
Spisula subtruncata	110	33	92	22.3	100	30	1700	550	.12	.118
Stenothoe marina	.05	.049	0	0	0	0	0	0	0	0
Sthenelais boa	0	0	0	0	0	0	.20	.109	0	0
Streblospio shrubsolii	320	56	2.6	1.40	27	22.3	0	0	0	0
Talitrus saltator	0	0	0	0	0	0	0	0	0	0
Tellina fabula	2.2	1.34	0	0	1.6	.59	38	6.4	0	0
Tellinacea indet.	.09	.093	.28	.283	0	0	0	0	0	0
Tellina pygmaeus	0	0	0	0	0	0	.011	.0106	0	0
Tellina spec.	1.1	.94	0	0	5.2	1.86	.5	.33	0	0
Tellina tenuis	.23	.122	0	0	1.4	.40	.66	.139	.36	.272
Tharyx marioni	710	210	430	116	210	71	.21	.082	.11	.114
Urothoe poseidonis	0	0	0	0	1.5	.89	39	6.3	1.2	.80
Urothoe spec.	0	0	0	0	0	0	.018	.0177	0	0
Vaunthompsonia cristata	0	0	0	0	0	0	.04	.035	0	0
Venerupis pullastra	.42	.258	.09	.066	.04	.038	.018	.0177	0	0
Venus striatula	0	0	0	0	0	0	.037	.0260	0	0
Total	4100	1010	1700	540	2600	740	3800	930	800	480

Appendix 2. Yearly mean density (ind./m^2) and standarderror (se) per cluster.

Cluster 1

Year	1983		1988		1989		1990		1992		1994	
Number of stations	8		7		8		5		2		2	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Bathyporeia pilosa	1200	160	4400	1600	6600	1600	2300	690	1200	710	1900	1180
Carcinus maenas	2.2	2.17	0	0	0	0	0	0	0	0	0	0
Cerastoderma edule	0	0	0	0	0	0	0	0	0	0	60	59
Corophium arenarium	0	0	0	0	0	0	0	0	240	118	0	0
Corophium volutator	9	8.5	150	70	70	38	0	0	0	0	0	0
Crangon crangon	0	0	0	0	0	0	24	23.6	0	0	0	0
Eurydice pulchra	0	0	0	0	0	0	24	23.6	0	0	0	0
Eurydice spec.	0	0	0	0	29	19.3	0	0	0	0	0	0
Haustorius arenarius	2.2	2.17	0	0	0	0	24	23.6	0	0	0	0
Heteromastus filiformis	7	1.4	0	0	0	0	24	23.6	0	0	0	0
Hydrobia ulvae	0	0	0	0	0	0	24	23.6	0	0	0	0
Mya arenaria	1.2	1.17	0	0	0	0	0	0	0	0	120	118
Nemertinae indet.	2.2	2.17	0	0	15	14.7	0	0	0	0	0	0
Nereis diversicolor	140	51	250	146	150	76	24	23.6	60	59	180	177
Nereis succinea	2.2	2.17	0	0	0	0	0	0	0	0	0	0
Nereis virens	2.2	2.17	0	0	0	0	0	0	0	0	0	0
Oligochaeta indet.	0	0	1000	520	60	59	0	0	0	0	0	0
Paranais fulgens	0	0	0	0	280	278	0	0	0	0	0	0
Platynereis dumerilii	13	12.8	0	0	0	0	0	0	0	0	0	0
Pygospio elegans	110	86	50	30	350	236	2000	1930	60	59	180	177
Scoloplos armiger	500	340	0	0	0	0	0	0	0	0	0	0
Scolelepis bonnieri	0	0	0	0	15	14.7	0	0	0	0	0	0
Scolelepis squamata	0	0	0	0	44	21.6	0	0	0	0	0	0
Spio martinensis	0	0	0	0	29	29.5	0	0	0	0	60	59
Urothoe poseidonis	2.2	2.17	0	0	0	0	0	0	0	0	0	0
total	1900	970	5900	2380	7600	2430	4400	2760	1500	940	2500	1770

Cluster 2

Year	1983		1988		1989		1990		1992		1994	
Number of stations	4.00		15.00		16.00		23.00		91.00		59.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Anaitides mucosa	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Bathyporeia pilosa	900	310	1200	430	1700	580	2900	740	1200	246	650	173
Bathyporeia sarsi	0	0	0	0	0	0	0	0	.33	.245	0	0
Bathyporeia spec.	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Bivalvia indet.	0	0	0	0	0	0	0	0	13	4.3	6	3.4
Capitella capitata	0	0	0	0	0	0	0	0	.11	.110	0	0
Caprellidae indet.	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Carcinus maenas	7	6.5	0	0	15	10.1	0	0	1.4	1.30	0	0
Cerastoderma edule	0	0	23	23.2	15	10.1	5	5.1	6.3	2.68	230	46
Cerastoderma spec.	0	0	0	0	0	0	0	0	17	9.1	0	0
Corophium arenarium	0	0	0	0	0	0	0	0	1450	159	370	50
Corophium spec.	0	0	0	0	0	0	0	0	5	5.2	16	9.2
Corophium volutator	380	228	190	67	1000	520	720	246	2200	500	1200	590
Crangon crangon	27	12.5	23	23.2	0	0	10	7.1	1.3	1.30	6	3.4
Cumopsis goodsiri	0	0	0	0	0	0	0	0	.33	.245	0	0
Eteone longa	0	0	0	0	0	0	0	0	3.9	2.68	0	0
Eteone spec.	0	0	0	0	0	0	0	0	15	4.9	12	4.7
Eurydice pulchra	0	0	0	0	0	0	0	0	.11	.110	0	0
Heteromastus filiformis	80	61	420	268	130	63	21	12.1	17	5.7	108	20.4
Hydrobia ulvae	0	0	90	41	440	149	1600	1300	1380	236	140	35
Macoma balthica	0	0	23	23.2	45	21.1	21	9.5	126	15.7	68	17.1
Magelona papillicornis	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Manayunkia aestuarina	0	0	0	0	0	0	0	0	3.9	2.68	0	0
Mya arenaria	0	0	23	23.2	0	0	21	9.5	30	8.9	1160	181
Myaella bidentata	0	0	0	0	0	0	5	5.1	0	0	0	0
Mytilus edulis	0	0	0	0	0	0	0	0	0	0	2.0	2.00
Nemertinae indet.	0	0	0	0	0	0	0	0	3.5	2.22	0	0
Nereis diversicolor	830	266	1600	410	1400	320	1090	131	310	33	1500	113
Nereis spec.	0	0	0	0	0	0	0	0	280	44	1350	266
Nereis virens	20	20.0	0	0	0	0	0	0	0	0	0	0
Oligochaeta indet.	0	0	50	46	280	91	1200	410	2600	430	2000	540
Paranaidae indet.	0	0	0	0	0	0	0	0	.11	.110	0	0
Pholoe minuta	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Polychaeta indet.	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Polydora ligni	0	0	0	0	0	0	0	0	23	16.5	14	9.1
Pygospio elegans	1300	810	1600	560	4100	1120	3500	840	3300	410	860	250
Scoloplos armiger	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Scolelepis squamata	0	0	0	0	7	7.4	0	0	.11	.110	0	0
Scrobicularia plana	0	0	0	0	0	0	0	0	6	4.3	2.0	2.00
Spiophanes bombyx	0	0	0	0	7	7.4	0	0	1.3	1.30	0	0
Spio martinensis	0	0	190	126	90	48	30	31	1.8	1.65	10	5.2
Spisula subtruncata	0	0	0	0	0	0	0	0	18	18.1	0	0
Streblospio shrubsolii	0	0	0	0	0	0	0	0	29	17.5	10	6.6
Talitrus saltator	0	0	0	0	0	0	0	0	1.3	1.30	0	0
Tellina spec.	0	0	0	0	0	0	0	0	.11	.110	0	0
Tharyx marioni	0	0	0	0	0	0	0	0	0	0	4.0	2.80
total	3500	1710	3500	2040	9300	2950	11000	3800	13100	2200	9800	2340

Appendix 2. Continued.

Cluster 3

Year	1983		1988		1989		1990		1992		1994	
Number of stations	18.00		90.00		96.00		94.00		29.00		57.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Anaitides mucosa	0	0	0	0	1.2	1.23	0	0	0	0	0	0
Arenicola marina	1.1	1.11	0	0	0	0	0	0	0	0	0	0
Atylus falcatus	0	0	0	0	1.2	1.23	0	0	0	0	0	0
Bathyporeia pilosa	0	0	70	54	47	17.5	34	16.8	8	5.6	2.2	2.07
Bivalvia indet.	0	0	0	0	0	0	0	0	12	6.8	0	0
Bodotria scorpioides	0	0	4	3.9	0	0	0	0	0	0	0	0
Capitella capitata	2.8	2.83	0	0	23	15.9	0	0	0	0	2.1	2.07
Carcinus maenas	4.0	2.19	23	10.7	25	6.0	16	5.2	16	7.7	12	5.7
Cerastoderma edule	9	6.2	380	104	190	34	126	22.9	130	41	270	59
Cerastoderma spec.	0	0	0	0	0	0	0	0	4	4.1	0	0
Corophium arenarium	0	0	0	0	0	0	0	0	230	150	17	13.0
Corophium spec.	0	0	0	0	0	0	0	0	0	0	130	54
Corophium volutator	28000	8900	24000	5100	12000	1260	6500	800	13200	1300	8100	1060
Crangon crangon	40	12.1	77	21.8	14	5.2	25	6.9	8	5.6	37	14.2
Ensis spec.	0	0	0	0	0	0	1.4	1.26	0	0	0	0
Eteone longa	0	0	0	0	27	5.7	16	4.8	4	4.1	0	0
Eteone spec.	0	0	0	0	0	0	0	0	8	5.6	4.1	2.90
Gammarus salinus	.06	.056	0	0	0	0	0	0	0	0	0	0
Gammarus tigrinus	4	4.3	0	0	0	0	0	0	0	0	0	0
Heteromastus filiformis	90	30	170	37	130	41	93	25.9	69	29.0	250	49
Hydrobia ulvae	1000	245	3400	1150	3100	420	2270	293	3400	550	530	141
Lanice conchilega	0	0	0	0	0	0	.12	.117	0	0	0	0
Macoma balthica	18	4.5	330	79	152	20.4	98	12.0	170	34	280	49
Magelona papillicornis	0	0	0	0	0	0	0	0	4	4.1	0	0
Manayunkia aestuarina	0	0	0	0	0	0	0	0	33	18.4	31	17.6
Mya arenaria	48	9.7	100	33	210	52	110	17.6	94	25.8	1600	310
Mysella bidentata	0	0	0	0	1.2	1.23	9	4.5	0	0	0	0
Nemertinae indet.	0	0	0	0	6	3.2	1.3	1.25	12	9.0	2.1	2.07
Nereis diversicolor	1830	180	5900	1360	4900	310	2860	148	1280	193	1980	142
Nereis longissima	36	25.0	0	0	0	0	0	0	0	0	0	0
Nereis spec.	0	0	0	0	0	0	0	0	570	132	1650	186
Nereis virens	20	18.5	0	0	0	0	0	0	0	0	0	0
Oligochaeta indet.	70	36	2500	620	3600	630	3600	530	11000	1290	7000	900
Platynereis dumerilii	1.4	1.44	0	0	0	0	0	0	0	0	0	0
Polychaeta indet.	6	5.6	0	0	0	0	0	0	0	0	0	0
Polydora ligni	0	0	370	82	690	137	380	88	530	183	240	60
Pygospio elegans	480	255	2300	450	16300	2360	7400	780	4100	1140	3000	1010
Scrobicularia plana	39	9.8	12	6.6	9	4.0	28	8.6	28	11.2	12	5.7
Spiophanes bombyx	0	0	0	0	4	3.7	0	0	0	0	2.1	2.07
Spio martinensis	0	0	190	57	9	5.3	51	16.2	0	0	4	4.1
Spisula subtruncata	0	0	0	0	0	0	1.5	1.27	0	0	0	0
Streblospio shrubsolii	4	3.1	0	0	6	4.4	230	91	450	240	2100	700
Tharyx marioni	0	0	0	0	16	4.1	2.6	1.77	4	4.1	0	0
Total	31000	9800	40000	9200	42000	5400	23800	2880	35000	5400	27000	4800

Cluster 8

Year	1988		1989		1990		1994	
Number of stations	9.00		8.00		11.00		16.00	
	mean	se	mean	se	mean	se	mean	se
Ampelisca spinipes	0	0	0	0	1.0	1.00	0	0
Bathyporeia elegans	0	0	45	29.2	31	18.1	6	3.9
Bathyporeia pelagica	0	0	0	0	0	0	2.5	2.19
Bathyporeia pilosa	21	11.8	2400	1560	0	0	5	3.5
Bathyporeia spec.	0	0	0	0	0	0	.6	.43
Capitella capitata	1.2	.77	1.1	1.13	1.0	1.00	1.9	1.28
Crangon crangon	0	0	0	0	1.0	1.00	.6	.63
Diogenes pugilator	0	0	0	0	0	0	.3	.31
Echinocardium cordatum	1.2	1.16	0	0	0	0	0	0
Eteone spec.	0	0	0	0	0	0	1.3	.72
Eurydice pulchra	0	0	0	0	11	10.7	0	0
Gastrosaccus spinifer	0	0	0	0	0	0	.6	.43
Haustorius arenarius	0	0	16	14.6	1.0	1.00	.9	.94
Heteromastus filiformis	0	0	0	0	0	0	2.5	2.19
Ingolfiellidae indet.	0	0	0	0	0	0	.6	.43
Macoma balthica	1.2	.77	0	0	1.0	1.00	0	0
Magelona papillicornis	0	0	1.1	1.13	0	0	0	0
Microphthalmus listensis	0	0	0	0	0	0	.3	.31
Microprotopus maculatus	0	0	0	0	0	0	1.3	.97
Mya arenaria	0	0	0	0	0	0	1.6	1.27
Nemertinae indet.	.6	.58	1.1	1.13	0	0	.6	.43
Nephtys cirrosa	12	3.9	16	6.1	18	7.7	4.7	1.85
Nephtys hombergii	.6	.58	0	0	1.0	1.00	1.6	1.56
Nereis spec.	0	0	0	0	0	0	.3	.31
Oligochaeta indet.	0	0	15	14.7	0	0	0	0
Ophiura texturata	0	0	0	0	2.0	2.00	0	0
Paraonis fulgens	36	12.8	180	82	340	167	32	11.8
Pontocrates altamarinus	.6	.58	11	5.0	5	3.1	0	0
Pontocrates arenarius	.6	.58	0	0	0	0	0	0
Portumnus latipes	.6	.58	0	0	0	0	1.3	.97
Pygospio elegans	0	0	0	0	210	203	1.9	1.88
Schistomysis kervillei	2.9	1.76	0	0	1.0	1.00	0	0
Scoloplos armiger	1.2	.77	0	0	1.0	1.00	0	0
Scolelepis squamata	70	33	120	35	51	23.1	8	3.2
Spiophanes bombyx	1.7	1.74	0	0	0	0	.3	.31
Spio martinensis	140	56	170	103	18	7.0	110	93
Spionidae indet.	0	0	0	0	0	0	.3	.31
Spisula subtruncata	.6	.58	0	0	0	0	0	0
Tellina tenuis	0	0	0	0	1.0	1.00	.3	.31
Tharyx marioni	0	0	0	0	0	0	.3	.31
Urothoe poseidonis	1.2	1.16	1.1	1.13	3.0	3.00	0	0
Total	290	128	3000	1850	700	450	190	136

Appendix 2. Continued.

Cluster 4

Year	1983		1988		1989		1990		1992		1994	
Number of stations	16.00		24.00		23.00		15.00		7.00		22.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	.22	.217	1.2	.65	0	0	1.4	1.43	18	14.1
Anaitides mucosa	0	0	.9	.87	7	5.1	0	0	2.9	2.86	0	0
Anaitides spec.	0	0	0	0	0	0	0	0	1.4	1.43	0	0
Aoridae indet.	0	0	0	0	0	0	0	0	11	5.9	0	0
Asterias rubens	0	0	.22	.217	0	0	0	0	6	5.7	0	0
Atylus falcatus	0	0	3	3.0	0	0	0	0	0	0	0	0
Atylus swammerdami	0	0	0	0	0	0	0	0	7	4.2	0	0
Bathyporeia elegans	0	0	0	0	.4	.39	0	0	0	0	0	0
Bathyporeia pilosa	120	112	0	0	6	5.1	.7	.73	0	0	.23	.227
Bathyporeia spec.	2.5	2.50	0	0	0	0	0	0	0	0	0	0
Bodotria scorpioides	0	0	0	0	0	0	0	0	1.4	1.43	0	0
Capitella capitata	19	8.4	6.9	2.56	28	11.0	6	5.9	36	9.7	28	6.9
Caprellidae indet.	0	0	0	0	0	0	0	0	30	31	0	0
Cardinia hamata	1.3	.85	1.3	1.10	.8	.54	1.5	1.00	7	3.6	.23	.227
Cerastoderma edule	1.6	.77	11	8.0	29	15.3	3.7	2.97	11	6.7	170	54
Corbula gibba	0	0	0	0	0	0	0	0	0	0	.23	.227
Corophium arenarium	0	0	0	0	0	0	0	0	0	0	4.1	2.07
Corophium volutator	.19	.188	0	0	8	8.2	0	0	0	0	.9	.72
Crangon crangon	2.9	1.48	3.3	1.46	5.1	1.37	3.7	1.38	2.9	1.84	5.7	1.33
Diastylis spec.	.19	.188	0	0	0	0	0	0	0	0	0	0
Ensis directus	0	0	0	0	0	0	0	0	0	0	.5	.31
Ensis spec.	0	0	0	0	1.2	.65	1.5	1.00	0	0	6.4	2.51
Eteone flava	0	0	.7	.36	0	0	0	0	0	0	0	0
Eteone longa	2.1	1.87	0	0	30	11.7	7	3.7	14	11.3	0	0
Eteone spec.	0	0	0	0	0	0	0	0	1.4	1.43	2.5	.92
Eumida sanguinea	0	0	0	0	.4	.39	0	0	0	0	0	0
Eurydice pulchra	0	0	0	0	0	0	0	0	1.4	1.43	.23	.227
Gammarus crinicornis	0	0	.22	.217	0	0	0	0	0	0	0	0
Harmothoe imbricata	0	0	.7	.65	0	0	0	0	0	0	0	0
Harmothoe lunulata	0	0	0	0	0	0	0	0	2.9	2.86	0	0
Harmothoe spec.	0	0	0	0	0	0	0	0	2.9	2.86	0	0
Heteromastus filiformis	420	145	200	76	1900	340	390	94	740	267	890	292
Hydrobia ulvae	.6	.63	0	0	2.0	1.26	.7	.73	1.4	1.43	.9	.72
Lanice conchilega	0	0	1.1	1.09	0	0	0	0	6	4.3	.23	.227
Macoma balthica	14	4.7	10.6	2.25	34	9.7	15	8.3	60	12.3	15	5.4
Magelona papillicornis	.19	.188	0	0	1.2	.65	0	0	0	0	.5	.45
Malacoceros fuliginosus	0	0	0	0	0	0	0	0	0	0	.23	.227
Mesopodopsis slabberi	0	0	0	0	0	0	0	0	0	0	.23	.227
Microprotopus maculatus	0	0	0	0	.8	.54	1.5	1.47	26	19.5	0	0
Mya arenaria	1.9	1.36	1.3	.57	170	73	17	8.5	11	8.3	2700	680
Myaella oideatata	0	0	0	0	10	5.4	10	8.0	2.9	2.86	.23	.227
Mytilus edulis	0	0	.7	.65	.8	.54	0	0	1.4	1.43	.7	.35
Nemertinae indet.	1.3	1.25	0	0	1.6	1.22	0	0	1.4	1.43	0	0
Nephtys cirrosa	0	0	0	0	0	0	.7	.73	0	0	.23	.227
Nephtys hombergii	.38	.256	0	0	10	6.2	2.2	1.17	0	0	33	11.8
Nephtys spec.	0	0	0	0	0	0	0	0	2.9	1.84	.5	.31
Nereis diversicolor	.4	.38	160	130	170	82	51	28.9	34	18.8	210	46
Nereis longissima	0	0	0	0	0	0	0	0	0	0	.23	.227
Nereis spec.	0	0	0	0	0	0	0	0	4.3	2.02	26	10.9
Nereis succinea	.8	.81	0	0	0	0	0	0	0	0	0	0
Nereis virens	40	36	0	0	0	0	0	0	0	0	0	0
Nudibranchia indet.	0	0	0	0	0	0	0	0	0	0	.9	.91
Oligochaeta indet.	0	0	0	0	0	0	0	0	16	14.1	25	14.5
Ophiuridae indet.	0	0	0	0	0	0	0	0	1.4	1.43	0	0
Ophiura spec.	0	0	0	0	0	0	0	0	0	0	.5	.31
Ophiura texturata	0	0	0	0	.4	.39	0	0	0	0	0	0
Paranaitis fulgens	0	0	0	0	25	20.8	0	0	0	0	5	5.5
Pectinaria koreni	0	0	.9	.60	7	3.3	.7	.73	0	0	10	4.9
Petricola pholadiformis	0	0	0	0	5	5.1	0	0	0	0	.23	.227
Polydora ligni	0	0	8	4.0	90	32	170	128	19	13.7	420	141
Proceraea cornuta	0	0	0	0	0	0	0	0	0	0	.23	.227
Pseudopolydora pulchra	0	0	0	0	0	0	0	0	0	0	1.1	.65
Pygospio elegans	210	97	64	15.7	1800	540	550	199	420	149	430	103
Schistomysis kervillei	0	0	0	0	.4	.39	1.5	1.00	0	0	0	0
Scoloplos armiger	150	100	0	0	5	3.1	40	45	13	9.7	.23	.227
Scolelepis squamata	0	0	.22	.217	0	0	0	0	0	0	.23	.227
Scrobicularia plana	0	0	0	0	0	0	0	0	2.9	1.84	0	0
Spiophanes bombyx	1.3	1.25	0	0	2.0	1.26	0	0	1.4	1.43	.7	.68
Spio martinensis	0	0	320	73	970	284	80	40	150	62	730	420
Spisula spec.	0	0	0	0	0	0	0	0	1.4	1.43	0	0
Spisula subtruncata	0	0	1.5	.58	210	97	13	8.5	9	8.6	310	111
Stenothoe marina	0	0	.22	.217	0	0	0	0	0	0	0	0
Streblospio shrubsolii	21	14.1	130	30	490	143	470	186	1100	310	240	114
Tellina fabula	0	0	0	0	9	6.1	0	0	0	0	1.6	.95
Tellinacea indet.	0	0	0	0	0	0	0	0	0	0	.5	.45
Tellina spec.	0	0	0	0	0	0	0	0	1.4	1.43	5	4.5
Tellina tenuis	0	0	0	0	0	0	0	0	1.4	1.43	.7	.37
Tharyx marioni	2.6	1.64	23	13.5	2200	760	260	163	2600	1480	110	70
Venerupis pullastra	0	0	0	0	0	0	0	0	0	0	2.0	1.22
Total	1000	530	900	370	8300	2480	2100	940	5300	2490	8330	2130

Appendix 2. Continued.

Cluster 5

Year	1983		1988		1989		1990		1992		1994	
Number of stations	25.00		16.00		14.00		17.00		18.00		16.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	.3	.33	0	0	0	0	.6	.56	9	5.9
Abra nitida	0	0	0	0	0	0	0	0	0	0	.3	.31
Aoridae indet.	0	0	0	0	0	0	0	0	1.1	.76	0	0
Astropecten irregularis	.4	.40	0	0	0	0	0	0	0	0	0	0
Atylus falcatus	0	0	.3	.33	0	0	0	0	0	0	0	0
Atylus swammerdami	0	0	0	0	0	0	0	0	0	0	.3	.31
Bathyporeia sarsi	0	0	0	0	0	0	0	0	.6	.56	0	0
Bivalvia indet.	0	0	0	0	0	0	0	0	1.1	.76	0	0
Bodotria scorpioides	0	0	0	0	0	0	0	0	.6	.56	0	0
Capitella capitata	0	0	1.0	.71	0	0	1.9	1.41	2.2	1.29	9	8.7
Caprellidae indet.	0	0	0	0	0	0	0	0	.6	.56	0	0
Cardinus maenas	10	4.5	0	0	0	0	.6	.65	1.1	.76	.3	.31
Caridea indet.	0	0	0	0	0	0	0	0	.6	.56	0	0
Cerastoderma edule	510	88	150	63	28	9.4	41	17.6	170	56	900	330
Corophium lacustre	0	0	0	0	0	0	0	0	1.1	.76	0	0
Corophium volutator	0	0	0	0	0	0	1.3	1.29	0	0	0	0
Crangon crangon	5.4	1.95	1.0	.71	1.3	.87	10	7.0	.6	.56	5.6	1.98
Crangon spec.	0	0	0	0	0	0	0	0	1.1	.76	0	0
Cumopsis goodsiri	0	0	0	0	0	0	0	0	.6	.56	0	0
Diastylis bradyi	0	0	0	0	0	0	.6	.65	0	0	0	0
Ensis directus	0	0	0	0	0	0	0	0	0	0	.3	.31
Ensis spec.	0	0	0	0	0	0	0	0	0	0	5.6	2.41
Eteone spec.	0	0	0	0	0	0	0	0	1.7	1.21	1.3	.72
Gammarus crinicornis	0	0	0	0	0	0	0	0	0	0	.3	.31
Gammarus salinus	2.4	1.49	0	0	0	0	0	0	0	0	0	0
Gammarus tigrinus	1.7	1.36	0	0	0	0	0	0	0	0	0	0
Harmothoe spec.	.20	.200	0	0	0	0	0	0	0	0	0	0
Hetermastus filiformis	90	37	170	88	270	151	480	255	230	106	420	189
Hydrobia ulvae	.20	.200	0	0	0	0	8	4.4	11	7.7	6	4.7
Lanice conchilega	0	0	0	0	0	0	0	0	1.1	1.11	0	0
Macoma balthica	6.7	2.55	67	26.3	3.2	2.60	0	0	5.0	2.18	3.8	1.80
Mactra corallina	0	0	0	0	0	0	.6	.65	.6	.56	0	0
Nelita palmata	3	4.8	0	0	0	0	0	0	0	0	0	0
Nesopodopsis slabberi	.12	.120	0	0	0	0	0	0	0	0	0	0
Mya arenaria	1.4	1.18	9	4.3	25	8.2	70	46	57	23.7	2500	1080
Mysella bidentata	0	0	0	0	0	0	0	0	10	8.4	0	0
Mytilus edulis	20	8.9	0	0	0	0	1.3	.89	2.8	1.58	1.3	.72
Nemertinae indet.	.32	.229	0	0	0	0	0	0	0	0	0	0
Nephtys cirrosa	0	0	0	0	0	0	.6	.65	0	0	0	0
Nephtys hombergii	0	0	0	0	1.3	1.29	0	0	8	5.0	6.3	2.17
Nephtys spec.	0	0	0	0	0	0	0	0	0	0	.3	.31
Nereis diversicolor	1.2	1.20	0	0	0	0	0	0	0	0	.6	.43
Nereis spec.	0	0	0	0	0	0	0	0	0	0	.6	.63
Nereis succinea	5.6	2.23	0	0	0	0	0	0	0	0	.3	.31
Nereis virens	.12	.120	0	0	0	0	0	0	0	0	0	0
Oligochaeta indet.	1.4	.61	4	3.6	0	0	0	0	290	113	56	22.5
Ophiura albida	0	0	0	0	0	0	6	5.8	0	0	0	0
Ophiura texturata	0	0	0	0	0	0	8	8.4	0	0	0	0
Pectinaria koreni	0	0	8.2	1.19	3.9	2.26	2.6	1.17	4	3.9	-	5.0
Petricola pholadiformis	0	0	0	0	0	0	0	0	0	0	2.2	1.29
Platynereis dumerilii	.20	.200	0	0	0	0	0	0	0	0	0	0
Polydora ciliata	2.2	1.05	0	0	0	0	0	0	0	0	0	0
Polydora ligni	.12	.120	6	3.9	8	7.7	1.3	1.29	0	0	210	159
Pontophylus trispinosus	.20	.200	0	0	0	0	0	0	0	0	0	0
Portumnus latipes	0	0	0	0	0	0	0	0	0	0	.3	.31
Pygospio elegans	4.3	1.71	7	7.1	14	9.1	6	6.5	14	10.5	60	40
Scoloplos armiger	0	0	0	0	0	0	6	4.2	1.7	1.21	0	0
Scolelepis squamata	0	0	0	0	0	0	0	0	1.1	1.11	0	0
Scrobicularia plana	1.0	.58	0	0	0	0	0	0	0	0	0	0
Spiophanes bombyx	0	0	0	0	0	0	0	0	1.7	1.21	0	0
Spio martinensis	0	0	1.3	1.01	0	0	.6	.65	1.7	1.21	1.3	.97
Spisula spec.	0	0	0	0	0	0	0	0	.6	.56	0	0
Spisula subtruncata	0	0	1.6	1.03	93	23.3	54	29.0	120	68	330	102
Streblospio shrubsolii	0	0	9	8.4	1.9	1.93	0	0	3.9	2.44	2.2	2.19
Tellinacea indet.	0	0	0	0	0	0	0	0	0	0	1.9	1.88
Thaiyx marioni	56	15.7	190	98	1100	630	360	196	1100	390	28	15.3
Venerupis pullastra	0	0	0	0	0	0	0	0	0	0	.6	.43
Total	900	257	600	310	1500	840	1100	580	2000	810	4600	1990

Appendix 2. Continued.

Cluster 6

Year	1983		1988		1989		1990		1992		1994	
Number of stations	16.00		18.00		30.00		26.00		12.00		29.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	0	0	0	0	1.3	.93	3.3	1.88	5	3.1
Actiniaria indet.	0	0	0	0	0	0	0	0	0	0	.17	.172
Anaitides mucosa	0	0	1.4	.71	.9	.50	2.5	1.76	5	5.0	2.6	.85
Anaitides rosea	0	0	0	0	.3	.30	0	0	.8	.83	0	0
Anaitides spec.	4	3.1	0	0	0	0	0	0	.8	.83	0	0
Anthozoa indet.	0	0	0	0	.3	.30	0	0	0	0	0	0
Aoridae indet.	0	0	0	0	0	0	0	0	4.2	2.88	0	0
Asterias rubens	0	0	0	0	0	0	0	0	2.5	2.50	0	0
Atylus falcatus	.19	.188	1.2	.90	.3	.30	.4	.42	0	0	.17	.172
Atylus swammerdami	0	0	0	0	0	0	0	0	5.8	2.88	0	0
Autolytus spec.	0	0	0	0	.3	.30	0	0	0	0	0	0
Barnea candida	0	0	0	0	0	0	0	0	0	0	1.0	.63
Bathyporeia elegans	0	0	0	0	.9	.50	.4	.42	2.5	2.50	0	0
Bathyporeia pilosa	4	3.0	0	0	0	0	0	0	0	0	.7	.41
Bivalvia indet.	0	0	0	0	0	0	0	0	1.7	1.67	.34	.239
Capitella capitata	120	93	150	63	80	53	43	11.0	190	93	97	28.6
Caprellidae indet.	0	0	0	0	0	0	5	3.0	2.5	1.31	.3	.34
Carcinus maenas	.38	.256	0	0	.3	.30	0	0	.8	.83	0	0
Caridea indet.	0	0	0	0	0	0	0	0	0	0	.17	.172
Cerastoderma edule	2.4	1.13	0	0	2.7	1.38	1.3	.93	15	7.4	26	14.6
Corbula gibba	0	0	0	0	0	0	0	0	0	0	.17	.172
Corophium spec.	0	0	0	0	0	0	0	0	0	0	.17	.172
Corophium volutator	0	0	0	0	0	0	.8	.59	.8	.83	0	0
Crangon crangon	1.6	.72	2.0	.75	3.9	.93	7.6	2.71	12	5.8	6.2	2.06
Cumacea indet.	0	0	0	0	0	0	.4	.42	.8	.83	0	0
Cumopsis goodsiri	0	0	0	0	0	0	.4	.42	2.5	1.79	0	0
Diastylis rathkei	0	0	.29	.289	0	0	0	0	0	0	0	0
Diastylis spec.	3.5	1.16	0	0	0	0	0	0	.8	.83	0	0
Donax vittatus	.6	.63	0	0	0	0	0	0	0	0	0	0
Echinocardium cordatum	.6	.63	0	0	380	131	1.3	.93	0	0	0	0
Ensis directus	0	0	0	0	0	0	0	0	0	0	1.0	.87
Ensis spec.	0	0	0	0	.3	.30	2.1	1.06	.8	.83	5.7	2.44
Eteone longa	1.3	1.25	.29	.289	1.5	.76	6	4.1	0	0	0	0
Eteone spec.	0	0	0	0	0	0	0	0	2.5	1.79	4.0	.84
Eumida sanguinea	0	0	0	0	.6	.60	10	9.3	0	0	0	0
Eumida spec.	0	0	0	0	0	0	0	0	2.5	1.79	0	0
Gammarus crinicornis	0	0	0	0	0	0	0	0	0	0	.17	.172
Gammarus salinus	0	0	.6	.58	.9	.66	0	0	0	0	0	0
Gammarus spec.	0	0	0	0	0	0	.4	.42	0	0	.17	.172
Gastrosaccus spinifer	0	0	0	0	0	0	.4	.42	0	0	0	0
Harmothoe lunulata	0	0	0	0	.6	.42	.4	.42	3.3	2.56	.17	.172
Harmothoe spec.	0	0	0	0	0	0	0	0	0	0	.17	.172
Haustorius arenarius	.19	.188	.29	.289	0	0	0	0	0	0	0	0
Heteromastus filiformis	1.0	.65	140	36	200	102	210	99	300	134	100	47
Ingolfiellidae indet.	0	0	0	0	0	0	0	0	2.5	2.50	.17	.172
Lamprops fasciata	0	0	.29	.289	0	0	0	0	0	0	0	0
Lanice conchilega	19	13.5	.6	.40	1.5	.62	2.5	2.14	18	9.1	.52	.288
Liocarcinus holsatus	0	0	0	0	.6	.42	0	0	.8	.83	.17	.172
Macoma balthica	11	5.1	6.9	2.34	5.7	1.46	5.5	1.85	28	8.6	3.3	.83
Mactra corallina	0	0	0	0	0	0	0	0	0	0	.34	.239
Magelona papillicornis	37	15.6	2.9	.96	3.3	1.40	.4	.42	.8	.83	6.0	1.86
Melita obtusata	0	0	0	0	.3	.30	1.7	1.69	0	0	0	0
Melita spec.	0	0	0	0	0	0	0	0	.8	.83	0	0
Microprotopus maculatus	0	0	0	0	1.8	1.52	19	13.4	15	5.8	0	0
Montacuta ferruginosa	0	0	0	0	80	32	2.5	1.86	0	0	0	0
Mya arenaria	1.3	1.25	.6	.40	2.7	2.12	3.4	1.18	55	29.9	1900	720
Mysella bidentata	0	0	0	0	.6	.60	17	13.9	3.3	1.42	.17	.172
Mytilus edulis	0	0	0	0	0	0	.8	.85	2.5	1.31	0	0
Nemertinae indet.	1.3	1.25	0	0	6.6	2.07	5.1	2.04	0	0	.9	.36
Neomysis integer	.19	.188	0	0	0	0	0	0	0	0	0	0
Nephtys cirrosa	22	10.0	5.2	2.06	7.2	2.42	14	4.4	9	3.6	5.0	1.94
Nephtys hombergii	27	5.5	1.4	1.01	4.8	1.60	12	3.2	21	6.7	76	15.1
Nephtys longosetosa	0	0	0	0	.3	.30	0	0	0	0	0	0
Nephtys spec.	0	0	0	0	0	0	0	0	1.7	1.12	.34	.239
Nereis diversicolor	0	0	19	18.2	0	0	1.7	.79	2.5	1.79	1.2	.64
Nereis longissima	.6	.63	0	0	4	3.3	3.0	1.78	1.7	1.67	0	0
Nereis succinea	0	0	0	0	0	0	0	0	.8	.83	.3	.34
Notomastus latericeus	0	0	0	0	0	0	0	0	0	0	.17	.172
Oligochaeta indet.	12	7.0	1.4	1.01	0	0	0	0	8	4.1	1.4	.65
Ophiura spec.	0	0	0	0	0	0	.4	.42	0	0	0	0
Ophiura texturata	.19	.188	0	0	.3	.30	3.0	2.07	.8	.83	0	0
Paraonis fulgens	0	0	3.5	1.74	36	14.7	20	8.2	2.5	1.79	58	23.9
Paraonis gracilis	0	0	0	0	0	0	0	0	0	0	.17	.172
Pectinaria koreni	1.3	1.25	1.7	.94	.3	.30	.4	.42	0	0	1.9	.68
Pectinaria spec.	0	0	0	0	0	0	0	0	.8	.83	.17	.172
Perioculodes longimanus	0	0	0	0	.9	.66	.4	.42	0	0	0	0
Petricola pholadiformis	0	0	0	0	0	0	0	0	.8	.83	2.6	1.44
Pholoe minuta	0	0	0	0	0	0	.4	.42	0	0	0	0
Phyllodocinae indet.	0	0	0	0	0	0	0	0	1.7	1.67	0	0
Polydora ligni	0	0	4.3	2.57	2.1	.83	30	13.5	16	8.5	90	42
Polydora spec.	0	0	0	0	0	0	0	0	0	0	.17	.172
Pontocrates altamarinus	0	0	0	0	4	3.0	0	0	0	0	0	0
Proceraea cornuta	0	0	0	0	0	0	0	0	0	0	.17	.172
Pseudopolydora pulchra	0	0	0	0	0	0	0	0	8	6.6	.17	.172
Pseudocuma spec.	0	0	0	0	0	0	0	0	.8	.83	0	0
Pygospio elegans	120	76	34	18.7	100	54	230	83	180	98	260	86
Schistomysis kervillei	0	0	0	0	.9	.66	1.7	1.32	.8	.83	.17	.172
Scoloplos armiger	14	8.2	3.2	1.53	29	9.5	90	31	11	3.4	.17	.172
Scolelepis squamata	3.1	1.45	0	0	.3	.30	0	0	0	0	2.8	1.52
Spiophanes bombyx	1400	770	10	4.3	21	5.1	.8	.59	20	9.1	4.7	1.66
Spio martinensis	0	0	830	194	830	207	560	142	670	196	2100	580
Spionidae indet.	0	0	0	0	0	0	0	0	0	0	.17	.172
Spisula spec.	0	0	0	0	0	0	0	0	.8	.83	0	0
Spisula subtruncata	0	0	.9	.47	9	3.1	27	9.0	70	31	410	120
Streblospio shrubsolii	4	4.4	2.0	2.03	0	0	0	0	240	242	19	13.1
Tellina fabula	0	0	0	0	4.2	2.15	0	0	3.3	2.56	1.6	.93
Tellina spec.	0	0	0	0	0	0	0	0	5.0	2.30	21	7.7
Tellina tenuis	.4	.38	0	0	1.5	.76	.4	.42	3.3	1.88	2.9	1.30
Tharyx marioni	.8	.64	1.7	1.03	90	56	300	154	1300	600	4.7	1.77
Urothoe poseidonis	11	7.0	0	0	.3	.30	.4	.42	0	0	0	0
Venerupis pullastra	0	0	0	0	0	0	0	0	0	0	.17	.172
Total	1800	1030	1200	360	1900	700	1600	630	3300	1570	5200	1730

Appendix 2. Continued.

Cluster 7

Year	1983		1988		1989		1990		1992		1994	
Number of stations	7.00		83.00		73.00		78.00		16.00		26.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Abra alba	0	0	110	49	31	26.8	3.4	1.87	.6	.63	13	6.2
Actiniaria indet.	0	0	0	0	0	0	0	0	11	8.7	1.9	.79
Ampelisca brevicornis	0	0	1.4	.53	.12	.123	0	0	0	0	.19	.192
Amphilochus neapolitanus	0	0	0	0	0	0	0	0	0	0	.19	.192
Anaitides groenlandica	0	0	6.1	1.31	2.1	.60	.14	.141	.6	.63	0	0
Anaitides mucosa	0	0	180	68	14	6.0	.42	.241	18	6.7	20	14.5
Anaitides rosea	0	0	1.1	.46	5.1	2.02	.42	.241	.6	.63	0	0
Anaitides spec.	.4	.43	0	0	0	0	0	0	0	0	.8	.60
Anthozoa indet.	0	0	.38	.174	.49	.262	.28	.198	0	0	0	0
Aoridae indet.	0	0	0	0	0	0	0	0	11	4.8	0	0
Asterias rubens	0	0	.13	.088	.12	.123	.14	.141	0	0	0	0
Atylus falcatus	0	0	21	3.7	9.6	1.77	5.2	1.66	2.5	1.94	1.2	.50
Atylus swammerdami	0	0	0	0	0	0	.6	.40	34	10.8	5.0	1.92
Autolytus langerhansi	0	0	0	0	0	0	0	0	1.9	1.88	5	3.5
Autolytus spec.	0	0	1.3	.60	.7	.52	0	0	0	0	.19	.192
Barnea candida	0	0	0	0	0	0	0	0	0	0	.19	.192
Bathyporeia elegans	13	13.1	3.1	.62	10	6.6	39	7.9	9	5.9	8.1	2.57
Bathyporeia guilliamsonian	0	0	0	0	0	0	.14	.141	4.4	2.23	.19	.192
Bathyporeia pelagica	0	0	0	0	0	0	0	0	.6	.63	0	0
Bathyporeia pilosa	0	0	.9	.56	0	0	0	0	.6	.63	0	0
Bathyporeia spec.	.4	.43	0	0	.12	.123	.14	.141	11	5.1	0	0
Bivalvia indet.	0	0	0	0	0	0	0	0	.6	.63	0	0
Capitella capitata	10	10.0	22	4.4	49	11.6	13	1.0	66	27.5	47	16.2
Caprellidae indet.	0	0	24	5.1	.12	.123	4.2	1.68	9.4	2.95	6.3	1.95
Carcinus maenas	.4	.43	1.6	1.09	.12	.123	1.0	.50	1.3	.85	.38	.266
Cerastoderma edule	0	0	.06	.063	.12	.123	0	0	0	0	0	0
Chaetozone setosa	0	0	.9	.34	.9	.66	1.1	.62	.6	.63	0	0
Cirratulidae indet.	0	0	0	0	0	0	0	0	.6	.63	0	0
Corophium spec.	0	0	0	0	0	0	0	0	0	0	.19	.192
Corophium volutator	0	0	0	0	0	0	1.4	1.41	0	0	0	0
Crangon crangon	1.9	1.42	9.2	1.50	1.1	.77	7.3	1.07	10	3.9	4.8	1.18
Crepidula fornicata	0	0	0	0	0	0	0	0	0	0	.19	.192
Cumacea indet.	0	0	0	0	0	0	0	0	.6	.63	0	0
Decapoda indet.	0	0	.13	.126	0	0	0	0	0	0	0	0
Diastylis bradyi	0	0	13	3.3	2.7	.65	8.9	1.64	4.4	1.57	2.7	1.45
Diastylis spec.	1.4	1.43	0	0	0	0	0	0	4.4	2.23	.8	.36
Diogenes pugilator	0	0	0	0	0	0	0	0	.6	.63	1.2	.58
Donax vittatus	0	0	0	0	0	0	.14	.141	0	0	.38	.266
Echinocardium cordatum	.4	.43	1.8	.79	5.1	1.69	3.9	1.37	0	0	0	0
Ensis directus	0	0	0	0	0	0	0	0	0	0	1.2	.64
Ensis spec.	0	0	29	8.3	10	29.1	6.2	1.98	2.5	1.94	6.3	2.05
Eteone longa	0	0	2.9	.86	1.9	.82	.28	.198	0	0	0	0
Eteone spec.	0	0	0	0	0	0	0	0	1.3	1.25	.6	.42
Eumida sanguinea	0	0	290	95	50	20.7	18	7.6	0	0	0	0
Eumida spec.	0	0	0	0	0	0	0	0	3.1	1.20	50	35
Gammarus crinicornis	0	0	0	0	0	0	0	0	0	0	.19	.192
Gammarus locusta	0	0	2.8	1.93	0	0	0	0	0	0	0	0
Gastrosaccus spinifer	0	0	.25	.123	0	0	0	0	3.1	1.51	.19	.192
Harmothoe impar	0	0	25	8.7	4.7	1.97	9	3.6	13	7.6	24	15.2
Harmothoe spec.	1.9	1.42	0	0	.25	.173	.14	.141	1.3	1.25	0	0
Haustorius arenarius	0	0	2.9	1.21	0	0	0	0	0	0	0	0
Heteromastus filiformis	.4	.43	.19	.107	.25	.173	.14	.141	0	0	.19	.192
Idotea linearis	0	0	.19	.140	0	0	0	0	0	0	0	0
Irgolfiellidae indet.	0	0	0	0	0	0	0	0	.6	.63	1.2	.85
Lamprops fasciata	0	0	2.8	.53	0	0	0	0	0	0	0	0
Lanice conchilega	2.9	2.86	120	42	180	68	11	6.2	27	14.2	45	19.1
Leucothoe incisa	0	0	0	0	0	0	0	0	1.3	.85	0	0
Liocarcinus holsatus	0	0	3.1	1.00	1.0	.38	.56	.276	0	0	.19	.192
Liocarcinus spec.	0	0	0	0	0	0	0	0	0	0	1.3	.52
Lysianassidae indet.	0	0	0	0	0	0	0	0	.6	.63	0	0
Macoma balthica	0	0	1.6	.48	1.2	.59	1.3	.53	1.3	.85	.6	.42
Mactra corallina	0	0	11	3.9	1.0	.57	3.8	1.42	0	0	.19	.192
Magelona papillicornis	39	24.7	23	3.1	56	9.9	12	3.5	8.1	2.45	320	116
Melita obtusata	0	0	.9	.64	0	0	3.8	1.55	0	0	0	0
Melita palmata	1.4	1.43	0	0	0	0	0	0	0	0	0	0
Microphthalmus fragilis	0	0	0	0	0	0	0	0	0	0	.19	.192
Microprotopus maculatus	0	0	25	6.4	1.9	.68	2.3	.97	59	22.3	11	5.8
Montacuta ferruginosa	0	0	1.3	.52	1.4	.91	3.0	1.21	0	0	.8	.46
Mya arenaria	0	0	.06	.063	0	0	0	0	0	0	.19	.192
Mysella bidentata	0	0	11	3.9	11	5.8	4.9	2.14	25	9.4	3.8	2.39
Mysidacea indet.	0	0	0	0	0	0	0	0	3.1	1.98	.19	.192
Mytilus edulis	0	0	.50	.230	0	0	.6	.56	.6	.63	.38	.266
Natica alderi	0	0	9	3.6	3.7	2.02	2.4	.71	0	0	.19	.192
Nemertinae indet.	15	14.2	6.6	1.68	26	4.4	90	76	7	3.3	10	4.0
Nephtys caeca	0	0	0	0	0	0	0	0	0	0	.19	.192
Nephtys cirrosa	27	11.9	38	5.7	42	4.3	82	6.3	49	12.8	42	10.0
Nephtys hombergii	9	8.7	57	8.3	39	6.2	24	6.1	70	21.7	31	7.6
Nephtys longosetosa	0	0	0	0	.12	.123	0	0	0	0	0	0
Nephtys spec.	0	0	0	0	0	0	0	0	3.8	1.80	23	8.9
Nereis diversicolor	0	0	.13	.088	.25	.247	0	0	0	0	0	0
Nereis longissima	.4	.43	3.5	1.93	1.9	.96	.42	.241	0	0	.8	.60
Nereis spec.	0	0	0	0	0	0	0	0	0	0	.38	.266
Nereis succinea	0	0	.06	.063	0	0	0	0	0	0	0	0
Oligochaeta indet.	6	7.1	0	0	0	0	0	0	.6	.63	.19	.192
Ophiura albida	0	0	0	0	0	0	0	0	.6	.63	0	0
Ophiura texturata	0	0	.31	.163	0	0	.14	.141	0	0	0	0
Orchomene humilis	0	0	.25	.251	0	0	0	0	0	0	0	0
Orchomene nana	0	0	0	0	3.3	2.86	0	0	0	0	0	0
Pagurus bernhardus	0	0	.9	.43	.12	.123	.28	.282	.6	.63	.38	.266
Paraonis fulgens	0	0	.13	.088	1.0	.54	.7	.70	0	0	6	5.4
Paraonidae indet.	0	0	0	0	0	0	0	0	.6	.63	0	0
Pectinaria koreni	1.4	1.43	22	14.1	.37	.211	.6	.44	0	0	.4	.38
Pectinaria spec.	0	0	0	0	0	0	0	0	.6	.63	0	0
Perioculodes longimanus	0	0	9.6	1.62	7.3	1.59	9.6	2.79	2.5	1.94	0	0
Petricola pholadiformis	0	0	2.8	2.57	0	0	.28	.198	0	0	.19	.192
Pholoe minuta	0	0	1.1	.55	.37	.211	0	0	0	0	0	0
Phyllodocinae indet.	1.4	1.43	0	0	0	0	0	0	0	0	0	0
Polydora ciliata	0	0	0	0	0	0	0	0	.6	.63	0	0
Polydora ligni	0	0	1.8	1.23	7	4.7	0	0	2.5	2.50	11	10.0
Polydora spec.	0	0	0	0	0	0	0	0	0	0	3.7	2.41
Pontocrates altamarinus	0	0	0	0	13.3	2.56	18.3	2.54	12.5	2.96	2.9	.74
Pontocrates arenarius	0	0	5.3	1.12	0	0	0	0	0	0	.19	.192
Portumnus latipes	0	0	1.5	.89	0	0	0	0	0	0	1.7	.62
Processa cornuta	0	0	0	0	0	0	0	0	0	0	.4	.38
Pseudocuma longicornis	0	0	.25	.152	0	0	0	0	1.3	1.25	0	0

Appendix 2. Continued.

Cluster 7

Year	1987		1988		1989		1990		1992		1994	
Number of stations	7.00		83.00		73.00		78.00		16.00		26.00	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Pseudopolydora pulchra	0	0	0	0	0	0	0	0	0	0	2.1	1.08
Pseudocuma spec.	0	0	0	0	0	0	0	0	8	4.6	0	0
Pygospio elegans	9	7.0	0	0	.25	.173	0	0	0	0	.38	.266
Schistomysis kervillei	0	0	1.5	.43	1.2	.44	3.1	.69	3.1	1.51	1.2	.58
Scoloplos armiger	5.4	2.51	20	4.9	39	14.0	8.7	2.59	2.5	1.94	38	24.8
Scolelepis bonnieri	0	0	0	0	0	0	0	0	1.3	.85	0	0
Scolelepis squamata	0	0	.06	.063	.12	.123	.14	.141	0	0	0	0
Sigalion mathildae	0	0	0	0	0	0	0	0	.6	.63	0	0
Spiophanes bombyx	500	440	100	33	170	50	10	3.5	110	48	110	39
Spio martinensis	0	0	2150	203	2300	480	430	135	510	174	580	141
Spisula subtruncata	0	0	5500	1810	300	126	130	95	80	36	66	26.9
Sthenelais boa	0	0	.38	.279	0	0	0	0	1.3	1.25	.19	.192
Tellina fabula	0	0	57	17.1	50	13.2	27	7.1	13	7.1	3.8	1.97
Tellina pygmaeus	.4	.43	0	0	0	0	0	0	0	0	0	0
Tellina spec.	0	0	0	0	0	0	0	0	6	3.6	2.5	.97
Tellina tenuis	0	0	.31	.137	.37	.211	1.1	.38	1.3	.85	1.0	.39
Tharyx marioni	0	0	0	0	.25	.173	.28	.198	.6	.63	.38	.266
Urothoe poseidonis	3.7	1.70	19	6.4	80	18.6	44	12.3	3.8	1.55	4.4	1.72
Urothoe spec.	0	0	0	0	0	0	0	0	0	0	.19	.192
Vaunthompsonia cristata	0	0	0	0	0	0	0	0	.6	.63	0	0
Venerupis pullastra	0	0	0	0	0	0	0	0	0	0	.19	.192
Venus striatula	0	0	.13	.089	0	0	0	0	0	0	0	0
Total	700	560	8000	2410	3500	930	1100	420	1300	500	1500	550

CHAPTER 7

Distinction between man-induced and natural changes in macrobenthic communities: application of the Analysis of Concentration

Introduction

Extensive hydraulic engineering projects, carried out over the last 25 years to secure the south west of the Netherlands against flooding, have resulted in a compartmentalization and closure of three of the four estuaries. The Oosterschelde Barrier Project started in 1978 and was completed in April 1987. A storm-surge barrier across the mouth (completed in 1986) along with three secondary dams (Markiezaatsdam, closed in 1983; Philipsdam, closed in 1986; and Oesterdam, closed in 1987) in the northern and eastern part of the estuary were constructed (fig. 7.1). Since this barrier was expected to cause significant changes to the ecosystem (see e.g. Elgershuizen 1981; Smies & Huiskes 1981) a series of investigations has been set up to evaluate possible effects. Changes in the hydrodynamics of the estuary are reported in Wetsteyn et al. (1990), Wetsteyn and Kromkamp (1994), Bakker et al. (1990, 1994), Vroon (1994) and Mulder and Louters (1994). Mean tidal amplitude and mean maximum current velocities decreased. In the eastern part, a clear vertical salinity gradient emerged, residence time increased, suspended matter contents declined and water transparency rose. The consequences for the ecosystem were evaluated by several authors, and comprised in a special volume of Hydrobiologia (Nienhuis and Smaal 1994).

In the present paper more detailed attention is paid to changes in an intertidal macrobenthic community in the eastern part of the estuary during the period 1983-1986, thus covering a period before and during the construction works. In the period mid-1985 to mid-1986, there was a marked reduction in tidal range (ten Brinke 1994).

The analytical technique used is Analysis of Concentration (AOC). The method was introduced

by Feoli and Orlóci (1979). They developed AOC to measure the sharpness of group structure in data tables (as e.g. obtained by cluster analysis), and to identify factors that influence variation among the groups. The latter was done by an indirect gradient analysis: an eigenanalysis was performed and given environmental variables were subsequently related to the canonical scores. Orlóci (1981) adapted AOC for analysing trends in density fluctuations. First, the existence of global density trends in community structure was tested. If the time series incorporated one or more trends, the latter were decomposed into independent components by ordination, and the components related to changes in the environment. Finally, the influence of these components on the density trends of the individual species was measured to evaluate how an environmental variable affects the single species. The method is an extension of Correspondence Analysis (CA), as it uses this ordination technique to extract the dominant patterns of variation in the community composition. To our knowledge, the technique has not been used till now in other investigations.

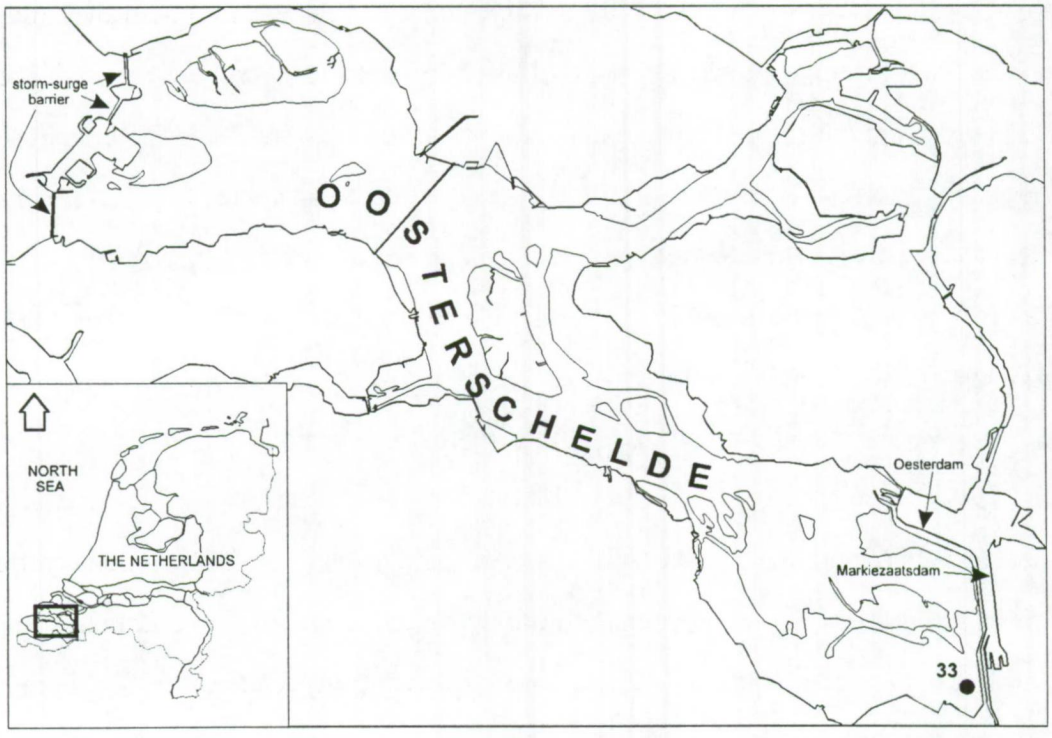


Figure 7.1. Map of the Dutch Delta region indicating the study location (station 33).

Material and methods

Study area and sampling

Since Spring 1983 the macrobenthic fauna of the Oosterschelde was monitored at selected stations on the major tidal flats of the estuary. This paper is concerned with data from a station situated on the mudflats of the Verdronken Land van Zuid-Beveland (figure 7.1, station 33). The plot has an average height of NAP + 0.60m (NAP = Dutch ordnance level). At the start of the investigations the sediment was a well sorted muddy sand (median grain size: 3.30-3.58 Φ; sorting coefficient 0.27-0.37 Φ). The upper 1 cm of the sediment contained 6.4-12.9 % silt (53μm), the subsurface sediment (2-25cm) 4.7-8.3 %.

The plot was sampled three times in 1983, four times in 1984, and twice in 1985 and 1986. At each date samples consisted of 3x5 cores of 83 cm^2, which were sieved through a 1mm sieve in the field. To assess the density of the larger animals the top layer of a two square meters sampling area was collected and sieved through a 3 mm sieve. Subsequently the area was dug out to a depth of 50 cm and the organisms were picked out from the sediment by hand. The material was stored in 10% formalin. In the laboratory the samples were sorted and the abundance of the following species was determined: *Cerastoderma edule, Macoma balthica, Mya arenaria, Scrobicularia plana, Hydrobia ulvae, Nereis diversicolor, Nephtys hombergii, Scoloplos armiger, Arenicola marina* and *Heteromastus filiformis*.

Numerical analysis

Trends in density fluctuations were analysed by Analysis of Concentration (AOC) (Feoli and Orlóci 1979, Orlóci 1981). AOC incorporates testing of global community density trends, decomposing these mostly complex trends into independent components, and measuring the influence of each component on the density trends of the single species.

Existence of community trends is tested by evaluating

$$\chi^2 = \sum_h \sum_j ((F_{hj} - F^{\circ}_{hj})^2 / F^{\circ}_{hj}$$

where $h = 1,\ldots,t$ (number of species);

$j = 1,\ldots,q$ (number of recording periods);

F_{hj} the observed density of species h at time j; and

F°_{hj} the expected density of species h at time j.

The expected density is calculated as (Feoli and Orlóci 1979):

$$F^{\circ}_{hj} = F_{h.}F_{.j} / F_{..}$$

where $F_{h.} = \sum_{j} F_{hj}$

$F_{.j} = \sum_{h} F_{hj}$

$F_{..} = \sum_{h} \sum_{j} F_{hj}$, i.e. the grand total of the data.

Global community trends exist if $\chi^2 > \chi^2_{\nu,\tau}$, the ν probability point of the chi square distribution with $\tau = (q\text{-}1)(t\text{-}1)$ degrees of freedom. If the time series shows trend, further analysis can be undertaken.

The first step is an indirect gradient analysis. The principal community trends are extracted from the data matrix by ordination, and interpreted in terms of variation in the environment. In our case we analysed changes in dominance structure, since the data emphasise fluctuations in abundance rather than differences in species composition. Patterns of the changes in dominance structure of the 10 major species were obtained by correspondence analysis of the log(x+1)-transformed data matrix. The most important community trends are described by the variation in time of the scores for recording periods along the main ordination axes. They were related to environmental variables by Spearman rank correlation (Siegel 1956). The variables examined are summarised in table 7.1. Temperature and wind velocity are important in determining reproduction and survival success (e.g. Thorson 1946; Beukema 1982). Visibility and seston concentration are indicators of food content and/or quality. Parameters of hydrological changes are: mean tidal levels, period and length of immersion or emersion, height of water column. The variables we have chosen surely do not make a complete list of all abiotic variables that may affect the benthos community, but data about other variables that might

change the community structure (e.g. sediment characteristics, current velocities) were not available.

Variable name	Unit	Description
MA	°C	monthly average of daily mean air temperature
MD	°C	monthly average of daily minimum air temperature
W	°C	water temperature
L<0	#	number of days daily mean air temperature ≤ 0°C
ML<0	#	number of days daily minimum air temperature ≤ 0°C
DZ	dm	visibility
ZW	mg/l	seston content
HW	cm	monthly average high tide
LW	cm	monthly average low tide
TA	cm	monthly average tidal amplitude
WV	0.5m/s	monthly average wind velocity
PTT + 60CM	%	period of immersion of NAP+60cm
MSE + 200CM	#	maximum number of successive tides of emersion of NAP+200cm
MSI - 175CM	#	maximum number of successive tides of immersion of NAP-175cm

Table 7.1. Variables used as 'predictor variables' (NAP = Nieuw Amsterdams Peil, the Dutch ordnance level, ca. 9 cm above mean sealevel in Den Helder, the Netherlands).

In the second step the influence of the community trends on the density trends of the single species is measured. Global density trends of the single species are given by the evolution in time of the deviations from expectation:

$$\Delta_{hj} = F_{hj} - F^{\circ}_{hj}$$

The sign of the deviation indicates the rate of enhancement (positive sign) or suppression (negative sign) of the species representation in the community (Feoli and Orlóci 1985). The contribution of each community component *i*, extracted by ordination, to this deviation is given by (see appendix):

$$\Delta_{hj(i)} = Y_{hi} X_{ji} R_i F^{\circ}_{hj} = Y_{hi} X_{ji} R_i \frac{F_{h.} F_{.j}}{F_{..}}$$

where R_i is the square root of the *i*-th eigenvalue of the ordination;

X_{ji} the *i*-th ordination co-ordinate for recording period *j*; and

Y_{hi} the *i*-th ordination co-ordinate for species *h*.

Results

Density fluctuations

The abundances per sampling period of the different species are given in figure 7.2 (left side), their (dominant) feeding mode and larval development type in table 7.2.

In 1985 and 1986 the density values of *Scrobicularia plana* were much lower than before. Although *Nephtys hombergii* never reached high densities, it did not show the usual peak abundance in autumn during the years 1985 and 1986. *Scoloplos armiger*, *Macoma balthica* and *Mya arenaria* had exceptionally high densities in Autumn 1985, while the density values of *Cerastoderma edule* and *Hydrobia ulvae* were very low compared with the other Autumn values. The autumn value of 1986 for *Nereis diversicolor* was very high compared with the other years. *Heteromastus filiformis* showed highest densities in autumn and winter over the entire period of investigation.

species	feeding category	larval development	references
Cerastoderma edule	SF	Pl	1,3,7,8
Mya arenaria	SF	Pl	1,3,8
Arenicola marina	DF	N	1,3,5,8
Heteromastus filiformis	DF	Le	3,7
Scoloplos armiger	DF	N	1,3,5
Macoma balthica	DF	Pl	1,3,8
Scrobicularia plana	DF	Pl	1,8
Hydrobia ulvae	DF/G	N	1,8
Nephtys hombergii	P	Pl	1,3,4,8
Nereis diversicolor	P	N	1,2,3,5,8

Table 7.2: Feeding mode and larval development type; SF: suspension feeder; DF: deposit feeder; G: grazer; P: omnivorous or predatory species; Le: lecitotrophic pelagic development; Pl: planktotrophic pelagic development; N: non- or semi-pelagic development. References: 1. Wolff 1973; 2. Heip & Herman 1979; 3. Beukema et al. 1983; 4. Hily 1983; 5. Thorson, 1964; 6. Hartmann-Schröder 1971; 7. Josefson 1986; 9. Newell 1979.

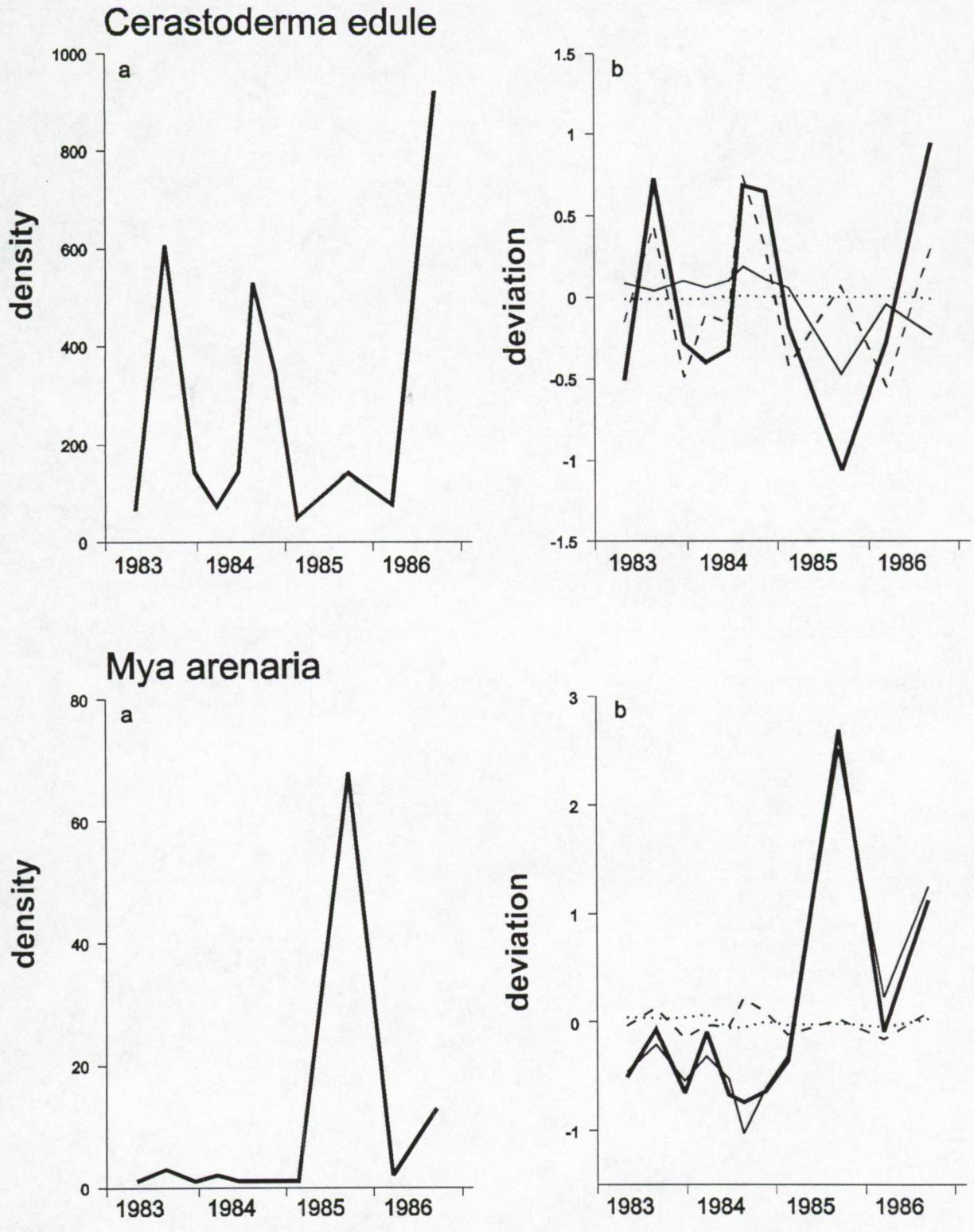


Figure 7.2. Time series of a) density (N/m^2) and b) global trend (bold solid line) and main components of density changes (C1: thin solid line; C2: dashed line; C3: dotted line).

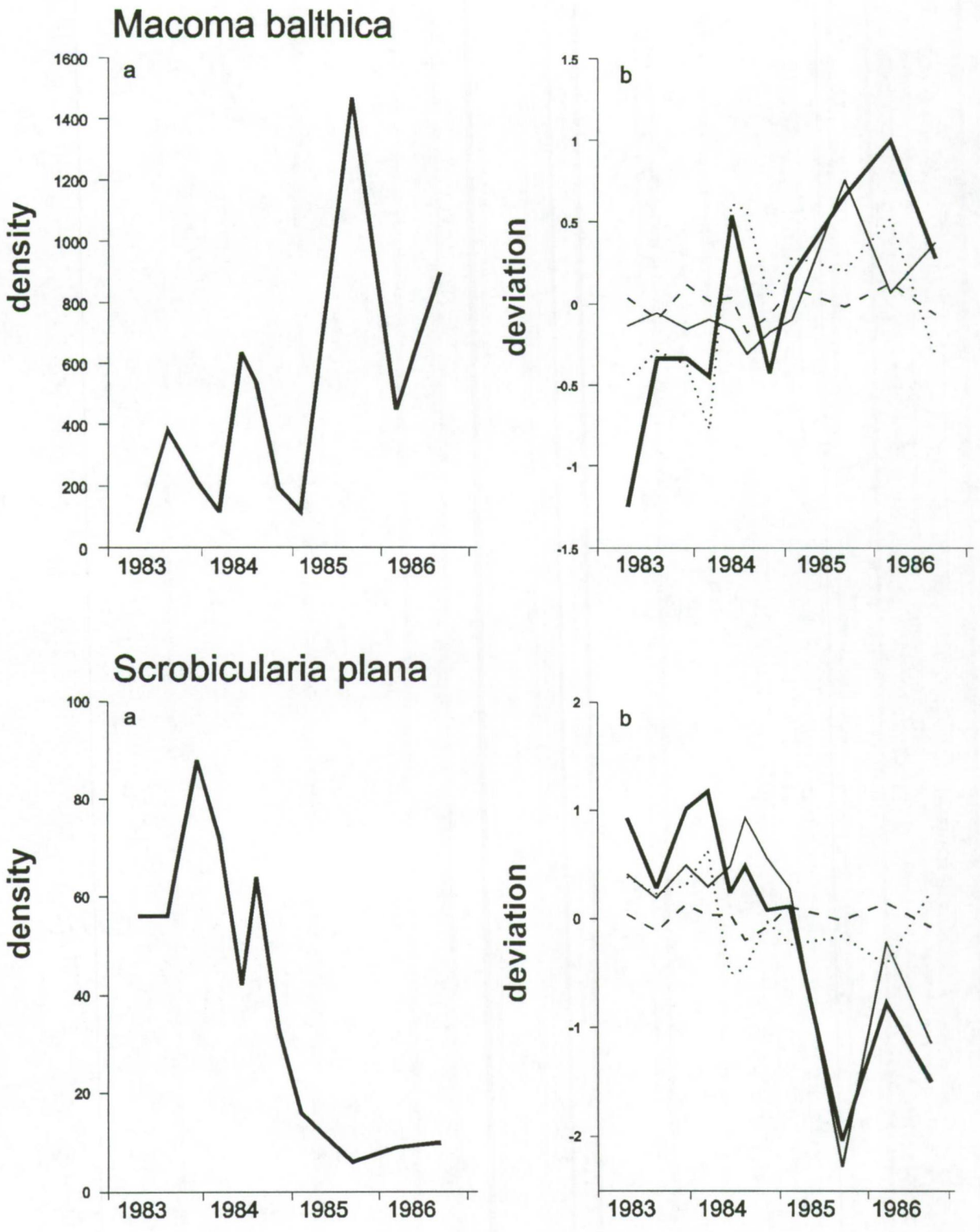
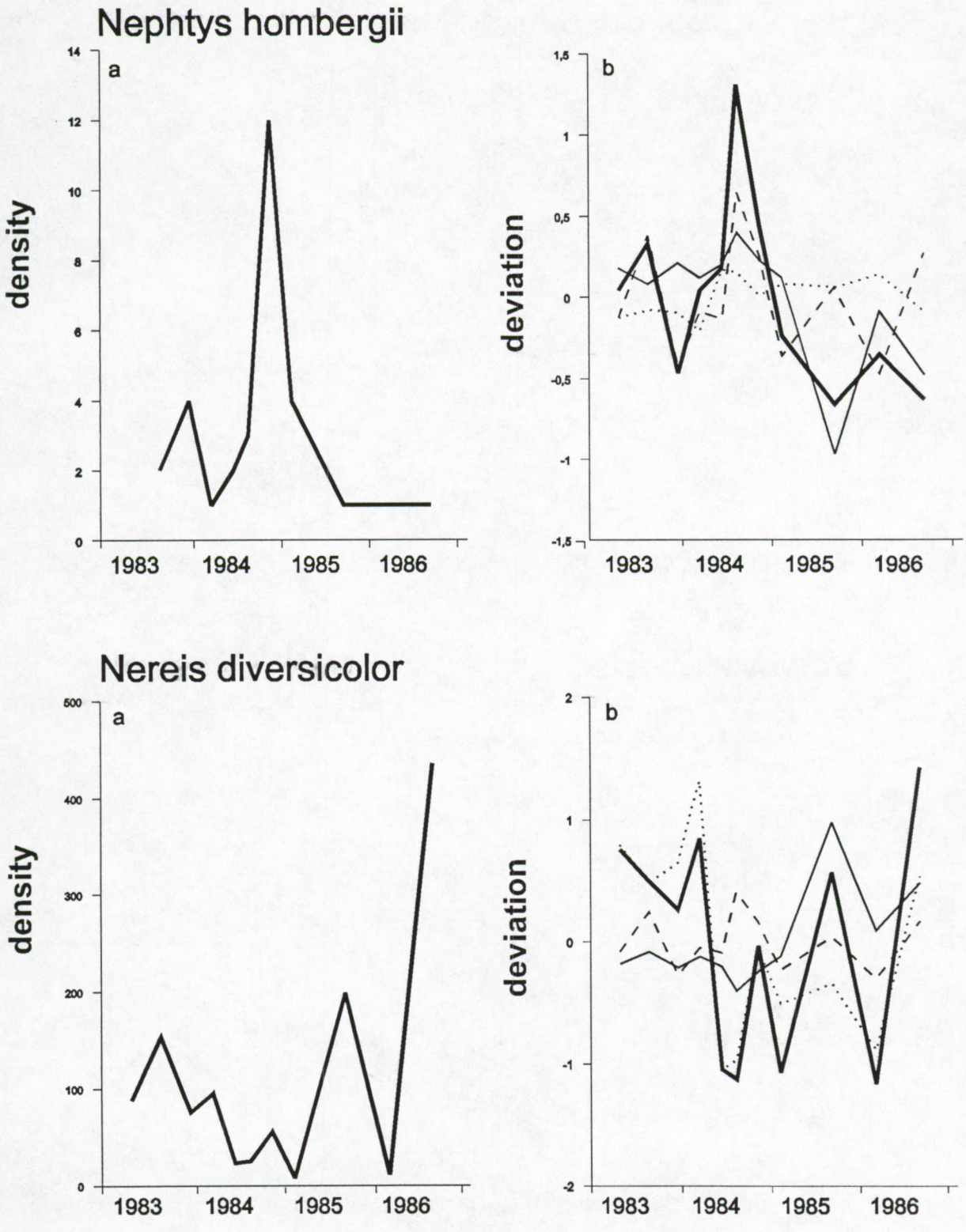


Figure 7.2. Continued.



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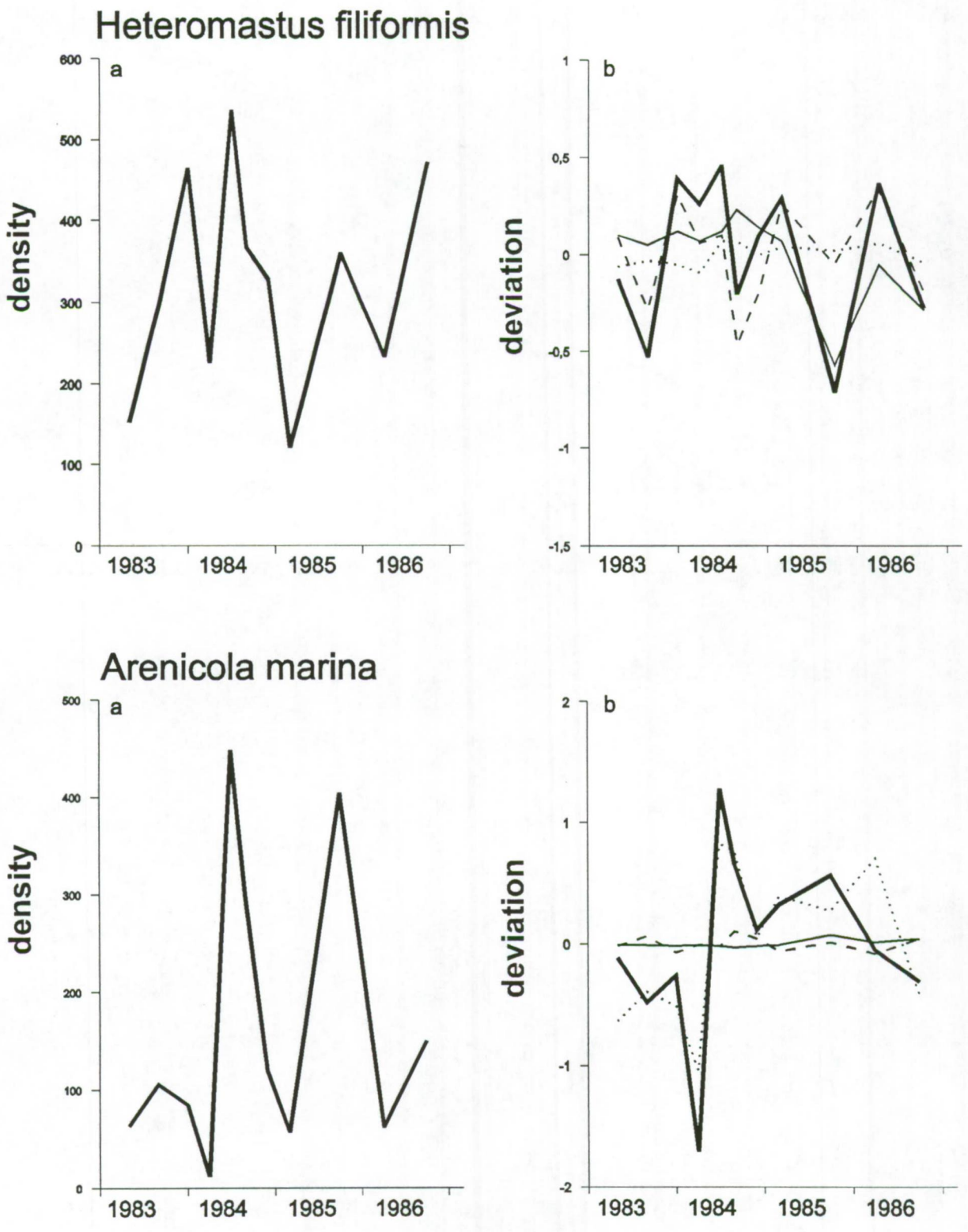

Table 7.2. Continued.

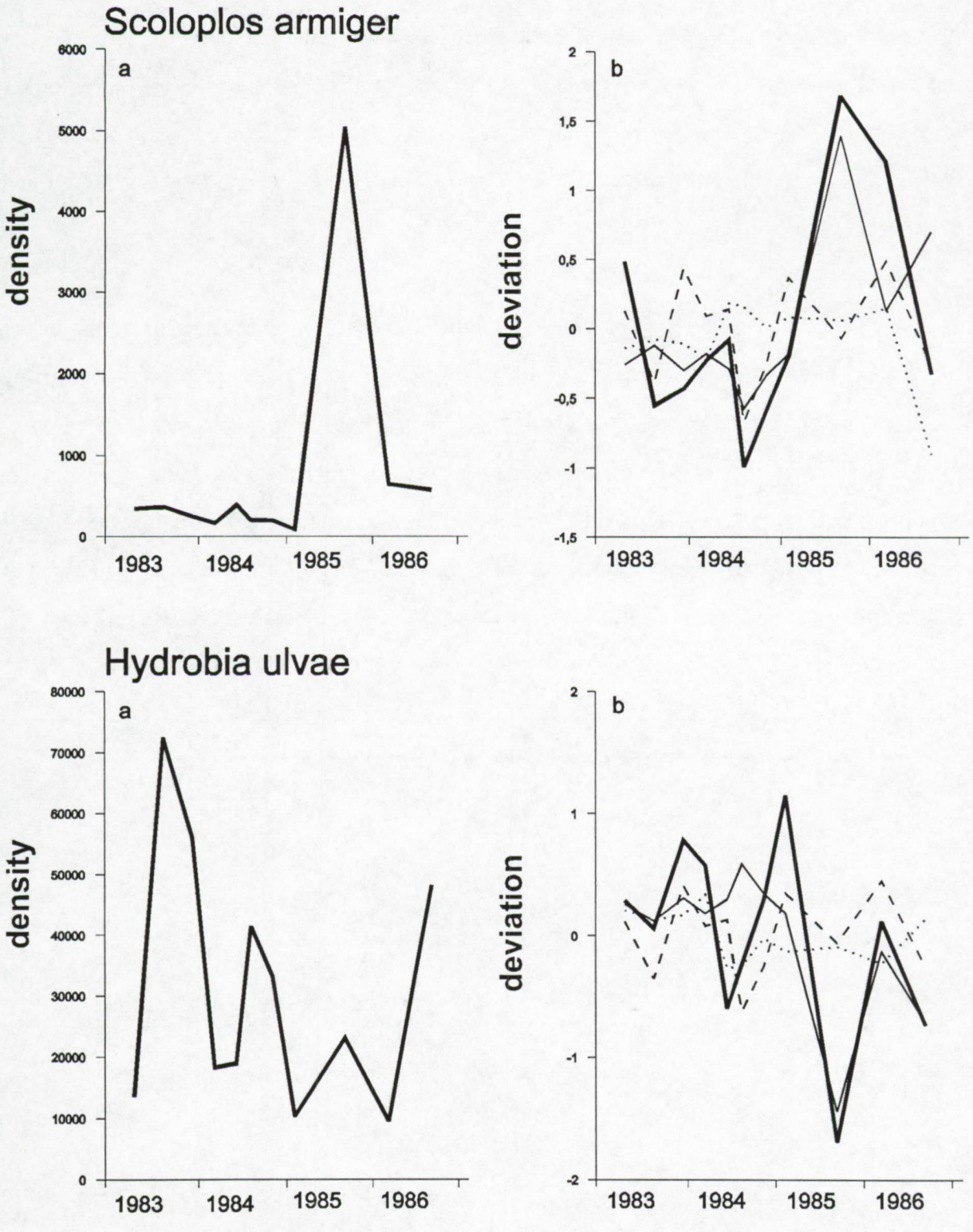

Figure 7.2. Continued.

The observed χ^2 value (43219.80) was very large ($\chi^2_{.005,90}$ = 128.30). Thus the series incorporated one or more trends, and further analysis was carried out. The first three axes of the ordination explained almost 90% of total variance. Figure 7.3 shows the projection of the sampling periods and species in the first and second plane. A clear temporal pattern appeared with two major breaks: a first between March and June 1984, a second between March and September 1985 (fig. 7.3a).

The first axis, which explains 60% of the variability, correlated with the maximum number of successive tides NAP + 200 cm was not immersed (table 7.3). Changes in this variable are indicative for changes in the water height at high tide, and express in this way changes in water displacement over the tidal flat. The second axis (18%) could not be related to any of the measured environmental variables. The third axis (11%) correlated with the monthly mean water temperature, mean air temperature, and the number of days the mean and minimum air temperature was lower than 0°C (table 7.3). It expresses the seasonal changes in the community.

variable	axis 1		axis 2		axis 3	
MSE+200CM	0.866	**	-0.348	ns	-0.170	ns
MSI-175CM	0.500	ns	-0.464	ns	0.125	ns
PTT+60CM	-0.262	ns	0.286	ns	-0.119	ns
MA	-0.180	ns	0.082	ns	-0.855	**
MD	-0.180	ns	0.082	ns	-0.855	**
W	-0.103	ns	0.055	ns	-0.806	**
L<0	0.255	ns	0.155	ns	0.773	**
ML<0	0.255	ns	0.155	ns	0.773	**
DZ	-0.252	ns	0.427	ns	-0.403	ns
ZW	-0.202	ns	0.238	ns	0.560	ns
HW	-0.470	ns	-0.124	ns	0.246	ns
LW	-0.227	ns	-0.161	ns	-0.270	ns
TA	-0.370	ns	0.042	ns	-0.115	ns
WV	-0.059	ns	-0.286	ns	0.541	ns

Table 7.3: Spearman rank correlation between ordination axes and environmental variables (**: $p < 0.05$; ns: not significant; abbreviations of the variables as in table 7.1).

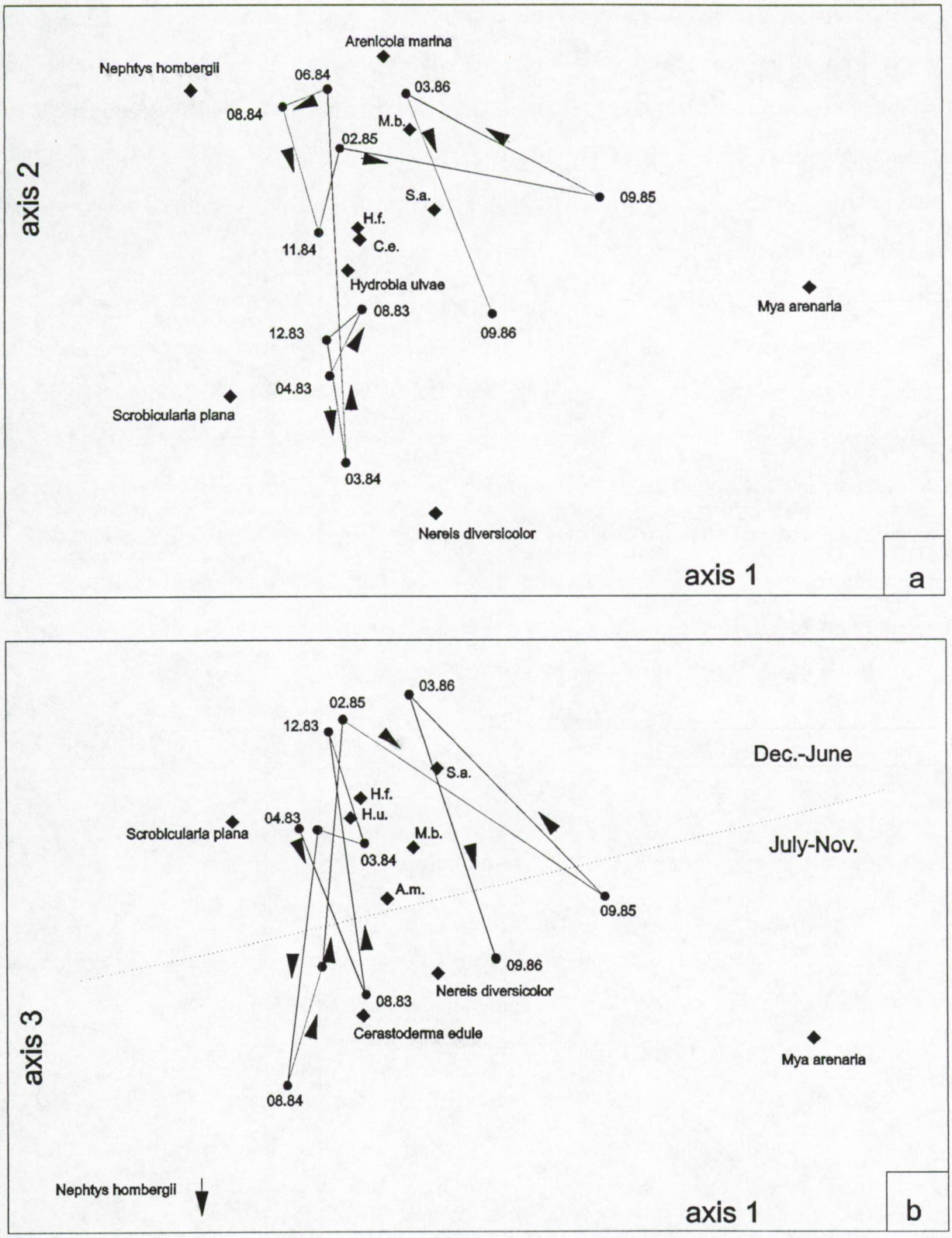

Figure 7.3. Correspondence analysis: projection of the dates of sampling and species in the plane of a) axis 1 and 2, and b) axis 1 and 3. H.f.: *Heteromastus filiformis*; M.b.: *Macoma balthica;* S.a.: *Scoloplos armiger*; C.e.: *Cerastoderma edule*; A.m. *Arenicola marina*; H.u.: *Hydrobia ulvae*.

Global trends and components within single species are shown in figure 7.2 (right hand side). In this figure the global density trends of the individual species ($\Delta_{hj} = F_{hj} - F^{\circ}_{hj}$) and the influence of the three main components on this global trend are shown. It should be noticed that global trends do not always follow actual changes. Indeed, as noticed by Orlóci (1981), actual increases can be too slow to prevent the proportional representation of the species from declining and density, while increasing, can drop below random expectation. From this figure it can be seen that the most important trend (first ordination axis) affected all species except *Arenicola marina* in 1985, resulting in a decline of the dominance of *C. edule, H. ulvae, N. hombergii, S. plana* and *H. filiformis*, and an increase of the dominance of *S. armiger, M. balthica* and *N. diversicolor*. The global density trend of *Mya arenaria* was totally determined by the first component. For the other species, global density trends were, except for 1985, largely affected by either the second (e.g. *C. edule*) or the third component (e.g. *N. diversicolor*). *C. edule* showed a regular seasonal pattern with maximum, positive Δ-values in August/September following recruitment. From June 1984 onwards, the density of *N. diversicolor* dropped below expectation and remained low up to August 1986. *A. marina*, on the other hand, showed the opposite trend: positive Δ-values between June 1984 and 1986.

Discussion

Many benthic species show seasonal fluctuations in their frequency of occurrence or abundance (related to e.g. their reproductive cycle, temperature resistance and the seasonal appearance of predators). Seasonality in total density (e.g. Kühlmorgen-Hille 1965; Stripp 1969; Watling 1975; Rudnick et al. 1985; Coull 1986) and diversity (e.g. Heip and Herman 1985; Boesch 1973) has been described. Changes in species composition or abundances result from a complex of influencing abiotic and biotic factors, and only multivariate analyses can demonstrate the distinct patterns affecting the species assemblage properly. In many cases multivariate analysis showed a type of seasonal succession within the benthic communities (Bodiou and Chardy 1973, Boesch 1973, Levings 1975, Chardy and Glémarec 1977, Warwick 1977, Desprez et al. 1986). To our knowledge, only Warwick (1977) interpreted the seasonal groups resulting from cluster

analysis with respect to feeding type. But seasonal changes in the relative abundance of the feeding groups are well known (e.g. Maurer et al. 1979; Pearson et al. 1982; Kojima and Ohta 1990). In our case, the displacement along the third ordination axis is related to such a seasonal pattern. Regrouping the species with respect to the influence of the third axis of ordination (correlated with temperature) to their global density trends, the species exhibit one of two patterns:

year	1983			1984				1985		1986	
month	4	8	12	3	6	8	11	2	9	3	9
pattern 1	-	+	-	-	-	+	+	-	+	-	+
pattern 2	+	-	+	+	+	-	-	+	-	+	-

where + and - respectively indicates a deviation above or below expectation (see fig. 7.2). The first group (*Cerastoderma edule, Nephtys hombergii, Mya arenaria, Nereis diversicolor* and *Arenicola marina*) are shifted to a higher dominance in autumn, the second group (*Scoloplos armiger, Hydrobia ulvae, Heteromastus filiformis, Macoma balthica* and *Scrobicularia plana*) to a higher dominance in spring. The first group consists of suspension feeders and omnivores/predators (*A. marina* excepted, which is, however, almost not influenced by the third component), the second group of grazers and deposit feeders. The two groups can also be separated in the ordination diagram (fig. 7.3b). One should look for a possible explanation in the changing circumstances for different feeding guilds in different seasons, including seasonality in food availability, food quality and predation.

The second axis could not be related clearly to any of the measured environmental factors. But as the changed hydrodynamics changed the behaviour of fine sediments (ten Brinke et al. 1994), and species such as *N. diversicolor, S. plana* and *M. arenaria* have the lowest scores on the second axis, one might think of changes in (not monitored) sediment characteristics. Recent information on the distribution characteristics of the silt content and the median grainsize of the sediment, however, doesn't show much differences between the species studied (figure 7.4). Nevertheless, there are some indications that the shift along the second axis is caused by the construction of the different barriers. From 1984 onwards, the construction works changed the

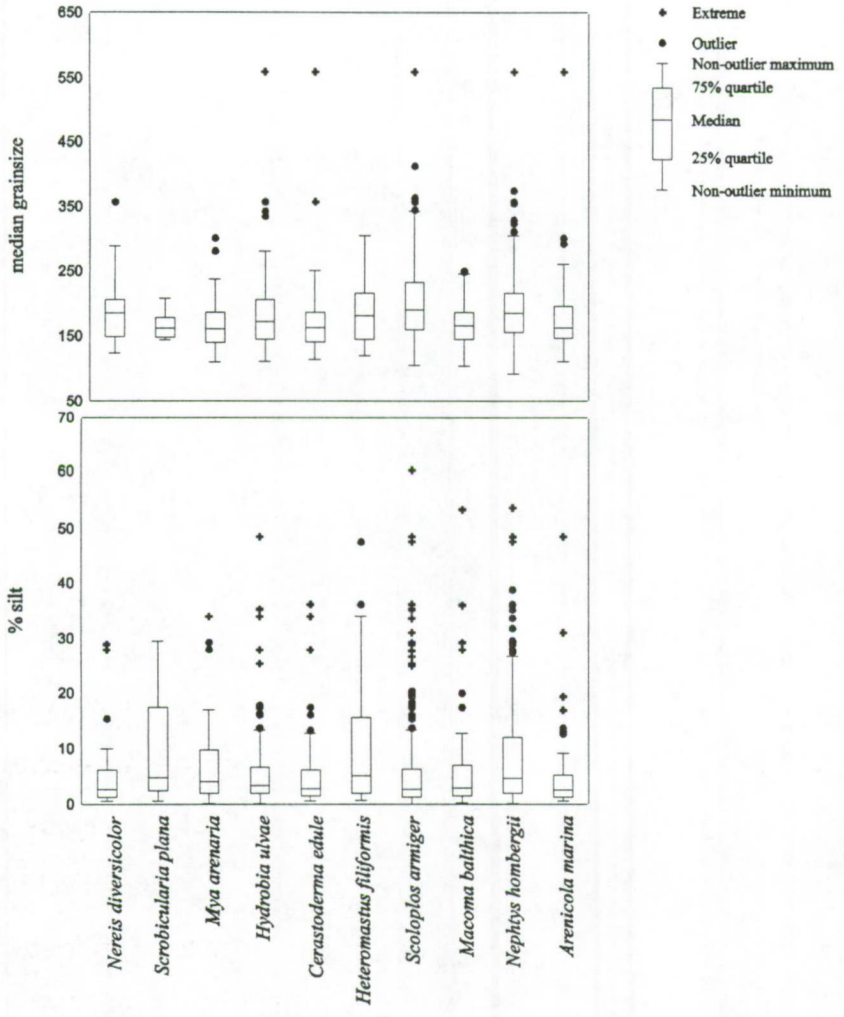

Figure 7.4. distribution characteristics of silt content and median grain size (box-and-whisker plots; values weighted in proportion to density) based on data from the monitoring program in the Oosterschelde (1990-1996). Species are arranged according to their score along the second ordination axis (see fig. 7.3).

hydrodynamical conditions and water quality in the eastern part of the estuary. Sedimentation enhanced and suspended matter concentrations decreased (Wetsteyn and Kromkamp 1994), and the changed light and turbidity conditions affected the phytoplankton composition (Bakker et al. 1990, 1994). This may have changed the food-supply to the benthos. Surprisingly, global density trends of the suspension feeders (*Cerastoderma edule* and *Mya arenaria*) were not affected at all by the second component of deviation.

During the first two years of investigation (1983-1984), global density trends of several species (*Cerastoderma edule, Heteromastus filiformis, Hydrobia ulvae* and *Nephtys hombergii*) were largely affected by the third component of deviation (fig. 7.2). The global density trends of these species showed a seasonal cycle. Global density trends of other species *(Arenicola marina, Macoma balthica, Nereis diversicolor*) were above all influenced by the second component (fig. 7.2). *Scrobicularia plana* and *Scoloplos armiger* showed a complex trend, reflecting the combined influence of several components. But in autumn 1985, the dominance structure was mainly determined by changes in tidal movement (first component), disturbing the normal dominance pattern of all species but *Arenicola marina*. This indicates that the effect of hydrodynamical changes was much stronger than any effect of another factor. One such factor may have been the winter of 1984, which was quite severe, compared with the two previous winters. It has been shown that the effect of a severe winter is not restricted to heavy mortalities (Beukema and de Vlas 1979) but may include an enhancement of recruitment in several species during the subsequent summer (Beukema 1982). And, indeed, six of the species studied (*Cerastoderma edule, Nephtys hombergii, Heteromastus filiformis, Scoloplos armiger, Hydrobia ulvae* and *Nereis diversicolor*) had lowest density values during the period 1983-1986 in spring 1985. Only the first two of these have previously been shown to be affected by severe winters, the others are relatively tolerant (Beukema and de Vlas 1979). Beukema (1982) noticed an enhanced recruitment of all bivalve species (*Cerastoderma edule, Mytilus edulis, Mya arenaria* and Macoma *balthica*). In our study heavy spatfall in 1985 was noted for *Macoma balthica* and *Mya arenaria*, but *Cerastoderma edule* and *Scrobicularia plana* had poor recruitment. Therefore, we can conclude that, if there was any effect of the severe winter, it has been overshadowed by the effect of hydrodynamical changes. Changes in the length of the immersion period, in the frequency of immersion, or in the water level must have influenced the populations by changes in predation pressure, wave action, temperature extremes, desiccation, and amount of feeding particles and/or success of spatfall.

Especially the density fluctuations of the bivalves were affected directly by a changed recruitment success. *Mya arenaria* is a typical case. From literature (e.g. Spear & Glude 1957; Matthiessen 1960; Kossler 1968; Munch-Petersen 1973; Winter and Gray 1985; Emerson et al. 1988) it is known that the majority of the newly settled clams are found seaward of the zone

inhabited by the previous year classes. Matthiessen (1960) and Kossler (1986) concluded that hydrodynamical forces are primarily responsible for this aggregated distribution pattern. Gaucher (1965) suggested a different mortality of spat in certain sediment types. Rowell (pers. comm.) observed that a thin flocculant silt layer covering the substrate can prevent settlement. Whatever mechanism leads to that typical distribution pattern, it is clear that some intertidal zones are 'seed' areas, others are 'growth' areas (Spear and Glude 1957). As the length of the few animals found during the first two years of investigation ranged from 31 to 64 mm, our sampling plot was obviously located in such a growth area. In autumn 1985 and 1986 old individuals were no longer found. On the other hand, a higher spatfall appeared during the years 1985 and 1986. We suppose the changed hydrodynamics caused an alteration of our study plot from a growth area to a seed area. Whether the mechanism leading to this change was a direct or an indirect one (e.g. by a changed substrate composition) could not be detected from this study.

Increase in dominance of some species is indirectly influenced by the hydrodynamical changes. For instance, the increased dominance, and density, of *Scoloplos armiger* in 1985 may be caused by the reduction in the *Nephtys hombergii* population. In the Wadden Sea, Beukema (1987) showed that *N. hombergii* is an important predator controlling, in part, abundances of *S. armiger* and *Heteromastus filiformis*. No major changes in density or biomass of the latter species were observed in our study.

We cannot explain in every detail all the observed density fluctuations. For instance, we do not know why some years were successful for recruitment for some species, but poor years for others. Success of spatfall is determined by the presence and abundance of larvae, and the complex interaction of physical and biological processes (see e.g. Jackson 1986; Levin 1986; Woodin 1986). But we showed that, at least during the construction of the storm-surge barrier, the species composition of the tidal flats in the eastern part of the Oosterschelde was influenced by changes in the hydrodynamics. This impact may have been temporary, as studies covering data up to 1989 do not suggest any influence of the changed hydrodynamics (Meire et al. 1994, Seys et al. 1994). But their conclusions might have been biased by the large year-to-year variations in benthos abundance. A recent re-analysis of data gathered at 300 stations on the

three major tidal flats of the estuary in 1985 and 1989, indeed suggest that particularly species that are related to the tidal zone were affected by the reduced tidal range (van der Meer 1997).

The results of this study support the conclusion of Orlóci (1981) that AOC is an appropriate method in time series analysis. Besides testing the existence of trends, and extracting the dominant patterns within the community structure, it offers the possibility to interpret in a simple way the influences of environmental changes, man-induced and natural, on the density changes of the single species.

References

Bakker, C., P. M. J. Herman, and M. Vink. 1990. Changes in seasonal succession of phytoplankton induced by the storm-surge barrier in the Oosterschelde (S.W. Netherlands). Journal of Plankton Research **12**:947-972.

—-. 1994. A new trend in the development of the phytoplankton in the Oosterschelde (SW Netherlands) during and after the construction of a storm-surge barrier. Hydrobiologia **282/283**:79-100.

Beukema, J. J. 1982. Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. Netherlands Journal of Sea Research **16**:37-45.

—-. 1987. Influence of the predatory polychaete *Nephtys hombergii* on the abundance of other polychaetes. Marine Ecology Progress Series **40**:95-101.

Beukema, J. J., and J. de Vlas. 1979. Population dynamics of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. Netherlands Journal of Sea Research **13**:331-353.

Beukema, J. J., G. C. Cadée, and H. Hummel. 1983. Differential variability in time and space of numbers in suspension and deposit feeding benthic species in a tidal flat area. Oceanologica Acta **N°SP**:21-26.

Bodiou, J.-Y., and P. Chardy. 1973. Analyse en composantes principales du cycle annuel d'un peuplement de copépodes harpacticoïdes des sables fins infralittoraux de Banyuls-sur-Mer. Marine Biology **20**:27-34.

Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads Area, Virginia. Marine Biology **21**:226-244.

Chardy, P., and M. Glémarec. 1977. Evolution dans le temps des peuplements des sables envasés en Baie de Concarneau (Bretagne). Pages 165-172 *in* B. F. Keegan, P. O. Ceidigh and P. G. S. Boaden, editors. Biology of Benthic Organisms. Proc. 11th European Marine Biology Symposium. Pergamon Press, Oxford.

Coull, B. C. 1986. Long-term variability of meiobenthos: value, synopsis, hypothesis generation and predictive modelling. Hydrobiologia **142**:271-279.

Desprez, M., J.-P. Ducrotoy, and B. Sylvand. 1986. Fluctuations naturelles et évolution artificielle des biocénoses macrozoobenthiques intertidales de trois estuaries des côtes françaises de la Manche. Hydrobiologia **142**:249-270.

Elgershuizen, J. H. B. W. 1981. Some environmental impacts of a storm surge barrier. Marine Ecology Progress Series **12**:265-271.

Emerson, C. W., T. E. Minchinton, and J. Grant. 1988. Population structure, biomass, and respiration of *Mya arenaria* L. on temperate sandflat. Journal of Experimental Marine Biology and Ecology **115**:99-111.

Feoli, E., and L. Orlóci. 1979. Analysis of concentration and detection of underlying factors in structured tables. Vegetatio **40**:49-54.

—-. 1985. Species dispersion profiles of anthropogenic grasslands in the Italian Eastern Pre-Alps. Vegetatio **60**:113-118.

Gaucher, T. A. 1965. Dispersion in a subtidal *Mya arenaria* (Linnaeus) population. Proceedings of the National Shellfisheries Association **56**:3-4.

Hartmann-Schröder, G. 1971. Tierwelt Deutschlands, 58: Annelida, Borstenwürmer, Polychaeta. Fischer, Jena.

Heip, C., and P.M.J. Herman. 1985. The stability of a benthic copepod community. Pages 255-264 *in* P.E. Gibs, editor. Proceedings of the 19th European Marine Biology Symposium. Cambridge University Press, Cambridge.

Hily, C. 1983. Macrozoobenthic recolonization after dredging in a sandy mud area of the Bay of Brest enriched by organic matter. Oceanologica Acta **N°SP**:113-120.

Jackson, G. A. 1986. Interaction of physical and biological processes in the settlement of planktonic larvae. Bulletin of Marine Science **39**:202-212.

Josefson, A. B. 1986. Temporal heterogeneity in deep-water soft-sediment benthos - an attempt to reveal temporal structure. Estuarine, Coastal and Shelf Science **23**:147-169.

Kojima, S., and S. Ohta. 1990. Seasonal variations of the deep-sea macrobenthos communities in the coastaland bathyal zones off Sanriku, Northeastern Japan. Journal of the Oceanographical Society of Japan **45**:250-260.

Kossler, A. 1968. Distributional patterns of the eulitoral fauna near the isle of Hiddensee (Baltic Sea, Rugia). Marine Biology **1**:266-268.

Kühlmorgen-Hille, G. 1965. Quantitativen Untersuchungen der Bodenfauna in der Kieler Bucht und ihre jahreszeitlichten Veränderungen. Kieler Meeresforschung **21**:167-191.

Levin, L. A. 1986. The influence of tides on larval availability in shallow waters overlying a mudflat. Bulletin of Marine Science **39**:224-233.

Levings, C. D. 1975. Analyses of temporal variation in the structure of a shallow-water benthic community in Nova Scotia. International Revue der gesamten Hydrobiologie **60**:449-470.

Matthiessen, G. C. 1960. Intertidal zonation in populations of *Mya arenaria*. Limnology and Oceanography **5**:381-388.

Maurer, D., L. Watling, W. Leathem, and P. Kinner. 1979. Seasonal changes in feeding types of estuarine benthic invertebrates from Delaware Bay. Journal of Experimental Marine Biology and Ecology **36**:125-155.

Meire, P. M., J. Seys, J. Buijs, and J. Coosen. 1994. Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm-surge barrier? Hydrobiologia **282/283**:157-182.

Mulder, J. P. M., and T. Louters. 1994. Changes in basin geomorphology after implementation of the Oosterschelde estuary project. Hydrobiologia **282/283**:29-39.

Munch-Petersen, S. 1973. An investigation of a population of the soft clam (*Mya arenaria* L.) in a Danish estuary. Meddelelser fra Danmarks Fiskeri- og Havundersøgelser **7**:47-73.

Newell, R. C. 1979. Biology of Intertidal Animals, 3rd Edition. Marine Ecological Surveys, Faversham, Kent.

Nienhuis, P. H., and A. C. Smaal, editors. 1994. Developments in Hydrobiology, **97**: The Oosterschelde estuary: a case study of a changing ecosystem. Kluwer Academic Publishers, Dordrecht. 597 pp.

Orlóci, L. 1981. Probing time series vegetation data for evidence of succession. Vegetatio **46**:31-35.

Pearson, T. H., G. Duncan, and J. Nuttall. 1982. The Eil Project: population fluctuations in the macrobenthos. Journal of Experimental Marine Biology and Ecology **56**:305-321.

Rudnick, D. T., R. Elmgren, and J. B. Frithsen. 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. Oecologia (Berlin) **67**:157-168.

Rumohr, H. 1990. Soft bottom macrofauna: collection and treatment of samples. ICES, Techniques in marine environmental sciences No. **8.** 18 pp.

Seys, J. J., P. M. Meire, J. Coosen, and J. A. Craeymeersch. 1994. Long-term changes (1979-89) in the intertidal macrozoobenthos of the Oosterschelde estuary: are patterns in total density, biomass and diversity induced by the construction of the storm-surge barrier? Hydrobiologia **282/283**:251-264.

Siegel, S. 1956. Nonparametric Statistics for the Bahavioural Sciences. McGraw-Hill Kogakusha Ltd, Tokyo. 312pp.

Smies, N., and A. H. L. Huiskes. 1981. Holland's Eastern Scheldt estuary barrier scheme: some ecological considerations. Ambio **10**:158-165.

Spear, H. S., and J. B. Glude. 1957. Effect of environment and heredity on growth of the soft clam (*Mya arenaria*). Fish. Bull. Fish. Wildl. Serv. **57**:279-292.

Stripp, K. 1969. Jahreszeitliche Fluktuationen von Makrofauna und Meiofauna in der Helgoländer Bucht. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven **12**:65-94.

ten Brinke, W. B. M. 1994. Hydrodynamic and geomorphological changes in the tidal system. Hydrobiologia **282/283**:15-16.

ten Brinke, W. B. M., J. Dronkers, and J. P. M. Mulder. 1994. Fine sediments in the Oosterschelde tidal basin before and after partial closure. Hydrobiologia **282/283**:42-56.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Φresund). Medelelser fra Kommissionen for Danmarks Fiskeri- og Havundersφgelser (Plankton) **4**:1-523.

van der Meer, J. 1997. A handful of feathers. Studies on the estimation and modelling of temporal and spatial fluctuations in the numbers of birds and their prey. PhD Thesis, Rijksuniversiteit Groningen, Groningen. 262pp.

Vroon, J. 1994. Hydrodynamic characteristics of the Oosterschelde in recent decades. Hydrobiologia **282/283**:17-27.

Warwick, R. M. 1977. The structure and seasonal fluctuations of phytal marine nematode associations on the Isles of Scilly. Pages 577-585 *in* B. F. Keegan, P. O. Ceidigh and P. G. S. Boaden, editors. Biology of Benthic Organisms. Proc. 11th European Marine Biology Symposium. Pergamon Press, Oxford.

Watling, L. 1975. Analysis of structural variations in a shallow estuarine deposit-feeding community. Journal of Experimental Marine Biology and Ecology **19**:275-313.

Wetsteyn, L. P. M. J., and J. C. Kromkamp. 1994. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980-1990). Hydrobiologia **282/283**:61-78.

Wetsteyn, L. P. M. J., J. C. H. Peeters, R. N. M. Duin, F. Vegter, and P. R. M. de Visscher. 1990. Phytoplankton primary production and nutrients in the Oosterschelde (The Netherlands) during the pre-barrier period 1980-1984. Hydrobiologia **195**:163-177.

Winter, V., and J. S. Gray. 1985. The biology of *Mya arenaria* (Bivalvia) in the eutrophic inner Oslofjord. Sarsia **70**:1-9.

Wolff, W. J. 1973. Zoölogische Verhandelingen, No. 126: The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Brill, Leiden.

Woodin, S. A. 1986. Settlement of infauna: larval choice? Bulletin of Marine Science **39**:401-407.

Appendix

U_{hj} is the abundance value of species h at time j transformed into probabilities and centred by species and stations:

$$U_{hj} = (F_{hj}F_{..} - F_{h.}F_{.j})/(F_{..}\sqrt{F_{h.}F_{.j}})$$

or:

$$U_{hj} = \frac{F_{hj}}{\sqrt{F_{h.}F_{.j}}} - \frac{\sqrt{F_{h.}F_{.j}}}{F_{..}}$$

where F_{hj} = the observed density of species h at time j;

$$F_{.j} = \sum_{h} F_{hj}$$

$$F_{h.} = \sum_{j} F_{hj}$$

$$F_{..} = \sum_{h} \sum_{j} F_{hj}$$

and $h = 1,\ldots,t; j = 1,\ldots,q$

The matrices of the species and station co-ordinates (coefficients, scores) extracted by component analysis are given by:

$$[X_{ji}] = \alpha D(F_{.j}/F_{..})^{-1/2} \qquad (1)$$

and

$$[Y_{hi}] = \hat{\alpha}\, D(F_{h.}/F_{..})^{-1/2} \qquad (2)$$

with

X_{ji} the i-th ordination co-ordinate for recording period j

Y_{hi} the i-th ordination co-ordinate for species h

$D(F_{.j}/F_{..})$ a matrix with diagonal elements $F_{.j}/F_{..}$ and elsewhere zeros

$D(F_{h.}/F_{..})$ the diagonal matrix of $F_{h.}/F_{..}$

α is the matrix of the eigenvectors of the cross product matrix $S_1 = U'U$, and

$\hat{\alpha}$ is the matrix of the eigenvectors of the matrix $S_2 = UU'$, U' being a transpose of U .

If Λ represents the diagonal matrix of the eigenvalues of the matrices S_1 and S_2, then:

$$\hat{\alpha} = U\alpha\Lambda^{-1/2}$$

and

$$U = \hat{\alpha}\,\alpha^{-1}\Lambda^{1/2}$$

As α is an orthogonal matrix, $\alpha^{-1} = \alpha'$, a transpose of α , and:

$$U = \hat{\alpha}\,\alpha'\Lambda^{1/2}$$

or, from formulae (2) and (3):

$$U_{hj} = \sum_i Y_{hi} X_{ji} R_i \frac{\sqrt{F_{h.} F_{.j}}}{F_{..}}$$

and not the formula

$$U_{hj} = \sum_i Y_{hi} X_{ji} R_i$$

as published by Orlóci (1981).

CHAPTER 8

Distribution of macrofauna in relation to the micro-distribution of trawling effort

This chapter is based on:

J.A. Craeymeersch, G.J. Piet, A.D. Rijnsdorp & J. Buijs, in press. Distribution of macrofauna in relation to the micro-distribution of trawling effort. In: *Effects of fishing on non-target species and habitats. Biological, Conservation and Socio-Economic Issues* (eds. Kaiser, M.J. & de Groot, S.J.). Fishing News Books, Blackwell Science, Oxford.

Introduction

Benthic invertebrates comprise a large proportion of the catch of mobile demersal fishing gears. For the beam trawl used in the North Sea to target flatfish, the by-catch of in- and epifaunal species is several times the amount of marketable fish. The species composition largely depends on the faunal composition at the trawling site, but tends to be dominated by starfish, heart urchins and crabs (Lindeboom and de Groot 1998). Of all these species which are discarded into the sea, a fraction will not survive their stay in the net and the sorting on board of the trawler. This mortality is species dependent: 10% for starfish and brittlestars, 50-70% for most crustaceans and almost 90% for the bivalve *Arctica islandica.* However, the catch efficiency of commercial trawls for these species is low and therefore the overall mortality is very low when expressed as a percentage of the initial density of these animals. A larger fraction of the mortality occurs in the trawl path because many animals not caught in the net are damaged or killed by the fishing gear as it passes over the seabed. Thus, the total direct mortality varies from 10 - 80%, with fragile or superficially living species showing the highest mortalities (Lindeboom and de Groot 1998, Bergman and van Santbrink 1999).

The long-term impact of bottom fisheries on a particular species will depend on the direct mortality at each fishing event, the distribution of the fishing effort, the distribution of that

species and its life history characteristics such as longevity and fecundity. Long-living species with a low fecundity will be affected more than short-living species with high fecundity. Benthic scavengers may benefit from the additional food supply from discards or animals damaged in the trawl path (Kaiser and Spencer 1994, Collie et al. 1997, Lindeboom and de Groot 1998, Fonds 1999, Ramsay et al. 1999, Groenewold and Fonds submitted). The longer term effects of fisheries on the benthic communities may be evaluated from long term trends in benthos or by-catch data (Philippart 1998, Schroeder and Knust submitted). They may also be inferred from comparisons between fished and un-fished areas (Hall et al. 1993, Lindeboom and de Groot 1998, Tuck et al. 1998).

Since 1993, the spatial distribution of the Dutch beam trawl fleet has been studied on a scale of 1x1 nautical mile (Nm) squares (Rijnsdorp et al. 1998. Piet et al. submitted). Previously, information on fishing activities was limited to a scale of 30 x 30 mile (ICES rectangles). Rijnsdorp et al (1998) showed that in eight of the most heavily fished ICES rectangles of the North Sea 47-71% of the surface area was trawled 1-5 times a year; 9-44% less than once a year and 0-4% between 10-50 times a year. This detailed information on the distribution of fishing effort offers a new opportunity to compare the benthic fauna of areas under different levels of fishing disturbance. This paper reports a first evaluation of differences in the macrobenthic infauna with respect to differences in fishing effort. First, we will focus on changes in species composition along the gradient in fishing effort. Secondly, we will focus on differences in the density of Spionidae, a polychaete family of which many species are known to be opportunists, often being the first species to colonise disturbed sediments (Gudmundsson 1985).

Material and methods

Trawling effort

The micro-scale distribution of the beam trawling activities of a representative sample of the Dutch fleet has been studied since 1993 (Rijnsdorp et al 1998). In the period 1993-1995, 25 beam trawl vessels (24 of them with an engine power > 300 Hp or ≈ 221 kW) were equipped

with an automated position registration system (APR) which records position every 6 minutes at an accuracy of 180 m. In 1996 another 6 vessels (5 of them with an engine power < 300 Hp) were equipped with an APR. By calculating vessel speed it is possible to estimate the fishing position of the sampled vessels, assuming a fishing speed of respectively 4.3 and 6 $Nm.h^{-1}$ for ships with an engine power of respectively less and more then 300 Hp. For the present study the total number of APR data recorded in each 1x1 Nm rectangle during a 4-year period (1-4-1993 until 31-3-1997) were used.

Macrobenthos

During the last decade the macrobenthic infauna on the Dutch Continental Shelf was surveyed in great detail. In the period 1985-1993, samples were taken at about 800 stations. All surveys were carried out in spring and used the same type of sampling equipment. In most surveys a Reineck boxcorer was used and sometimes Van Veen grabs. The content of the boxcorer or grab was washed over a sieve with round holes of 1 mm diameter. The work resulted in an atlas describing the occurrence and distribution of the most common species, together with relevant information on their ecology (Holtmann et al. 1996b). We refer to this atlas for more information on the different surveys.

Statistical analysis

For the purpose of this study, subareas were selected for further analyses based on following conditions. First, the fishing effort within an area was not randomly distributed in space. Secondly, the faunal composition within an area had to be more or less similar. Based on the macrobenthos data mentioned above, the Dutch Continental Shelf can be divided into 4 subareas (Holtmann et al. 1996a): the southern part of the Dogger Bank, the Oyster Ground, the southern offshore area and the coastal area. This spatial pattern has been consistent over time (Holtmann et al. 1998). The coastal area, generally fished by smaller vessels (< 300 hp), was excluded for this study because before 1996 only a single small vessel was sampled and because different gear types might be used by smaller vessels during the year. On the relatively small Dogger

Bank area macrobenthic data were too sparse to allow further analysis. Finally, two subareas, one situated in the Oyster Ground and one in the Offshore area, were chosen. Figure 8.1 gives the location of the infauna sampling locations (79 samples in the offshore area, 129 samples in the Oyster Ground area) superimposed by the fishing effort.

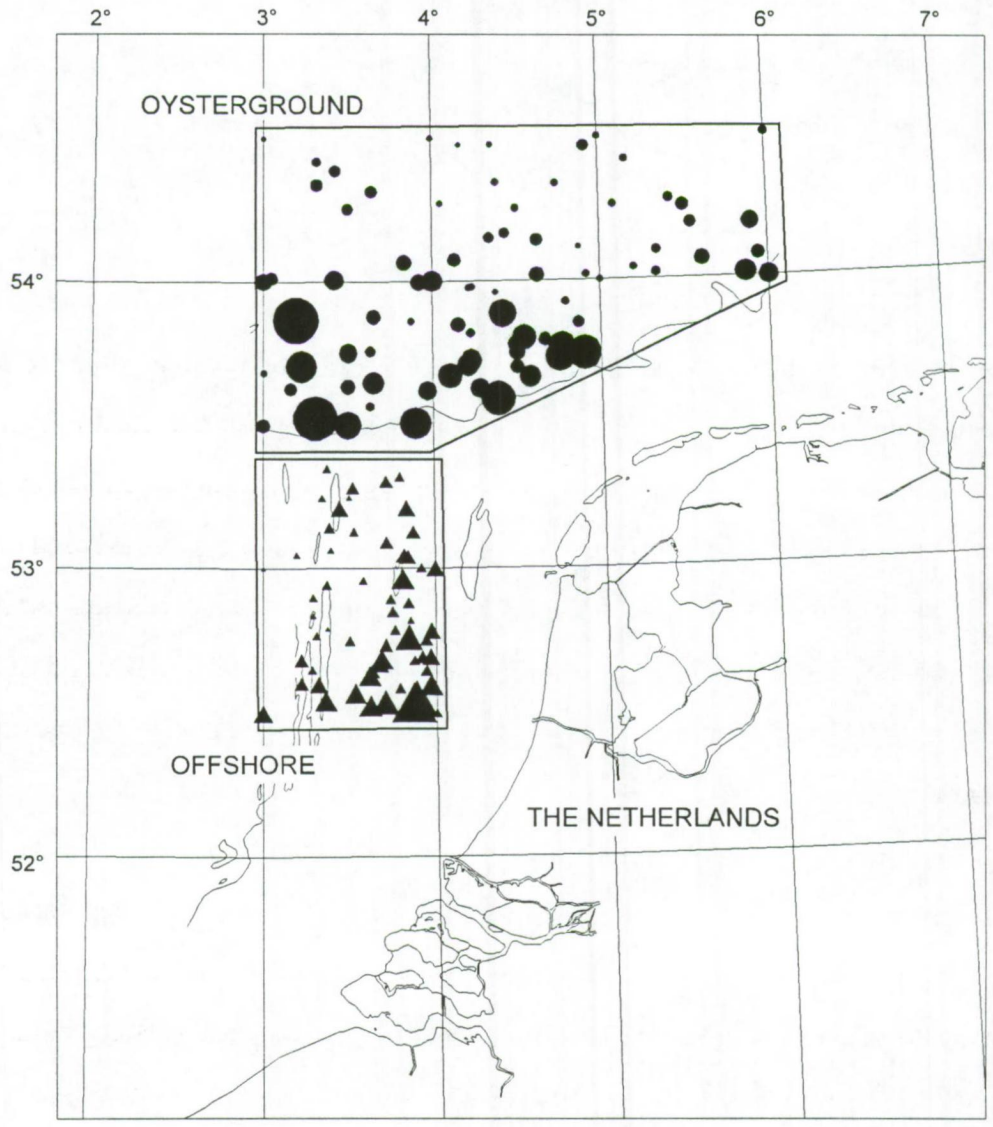

Figure 8.1. Location of the sampling locations with superimposed symbols representing subarea (circles = Oysterground area; triangels = Offshore area); the size of the symbols is increasing with increasing fishing effort.

The relation between the (log-transformed) total density of spionids and fishing effort was measured by a linear regression, and the significance tested. The few stations without spionids

(respectively 2 and 15 in the Offshore and Oysterground area) were excluded from the analyses.

To determine whether there is a relationship between fishing effort distribution and infaunal community structure, a direct gradient analysis was performed. In a direct gradient analysis the species composition is directly related to measured environmental variables: the first axes of the ordination are constructed in such a way as to explicitly optimise the fit to the supplied environmental data (ter Braak and Prentice 1988). In a partial canonical ordination, the effect of one or more covariables can be factored out. The result is an ordination of the residual variation in the species data that remains after fitting the effects of the covariables. This is especially interesting in our study, as we are not interested in environmental variation but want to focus on the species responses to fishing disturbance. Here we removed possible effects of depth and sediment characteristics (silt content, median grainsize). We used two ordination methods: partial Canonical Correspondence Analysis (CCA) and partial Redundancy Analysis (RDA). RDA, the canonical form of Principal Components Analysis (PCA), is based on a linear response model between species and environmental variables (as e.g. expected in short segments of ecological gradients); CCA is based on an unimodal response model. RDA and CCA allow measuring the amount of variation in the species data that can be explained by the environmental variables. The significance of this relation was tested by a Monte Carlo permutation test. For more information about these techniques we refer to Jongman et al. (1987), ter Braak (1988b), ter Braak and Prentice (1988), Borcard et al (1992) and Palmer (1993). Macrobenthic abundance data were log-transformed. Species found at less than 10 stations were excluded from the analyses, resulting in respectively 50 and 92 species in the Offshore and Oysterground area. All analyses were done with the CANOCO program of ter Braak (1988a), version 3.10.

Results

Spionidae

The (log-transformed) total density of spionids increased significantly with increasing fishing effort, both in the Offshore area ($R^2 = 0.120$; $p < 0.001$) and in the Oysterground area ($R^2 = 0.034$; $p = 0.027$) (figure 8.2).

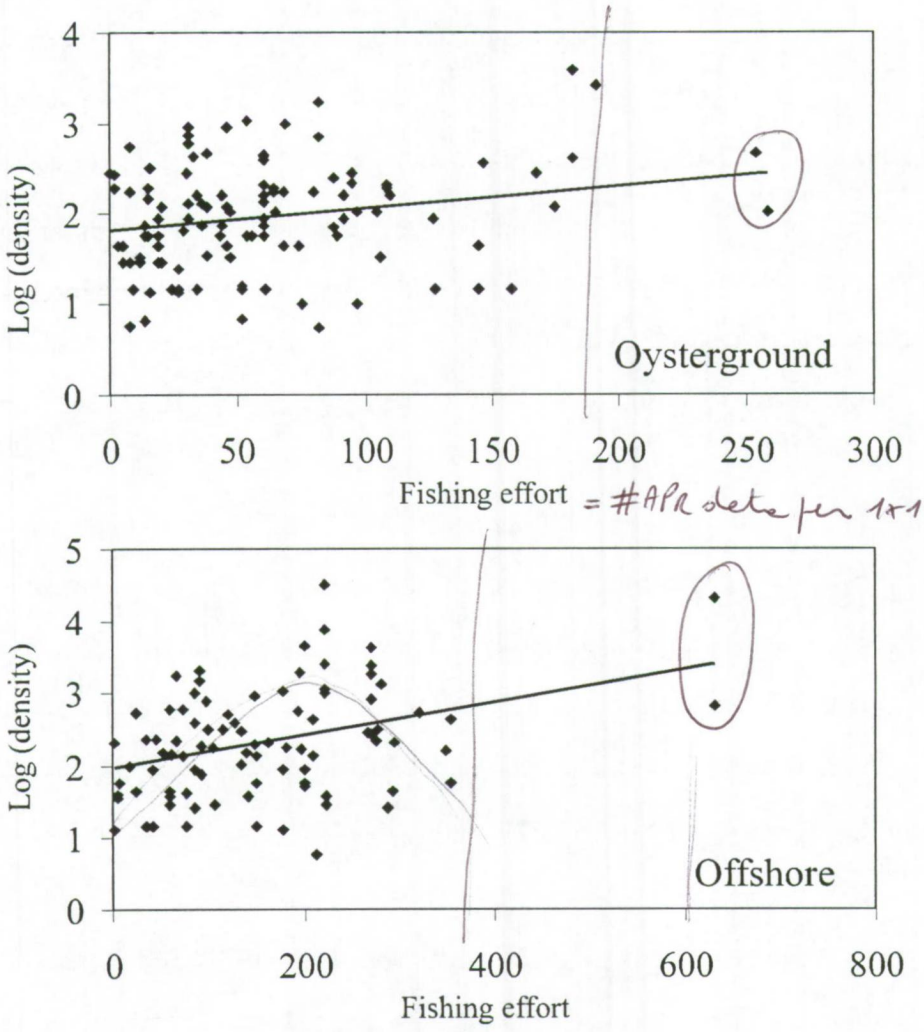

Figure 8.2. Relationship between fishing effort and density (ind. m^{-2}) of spionids.

Community structure

Figure 8.3 shows the ordination diagrams (site scores) resulting from the partial RDA and partial CCA analyses. In these plots stations with a similar species composition are closest to each other, stations that are dissimilar in species composition far apart. Stations represented by larger circles experienced a higher level of fishing disturbance. In the Offshore area, fishing effort accounted for 2.0% (RDA) and 2.2% (CCA) of the variance remaining after removing the effect of depth and sediment characteristics (silt content, median grainsize). The Monte Carlo permutation test on the 1st axis was significant at a probability level of respectively 0.00 and 0.01. In the Oysterground area, fishing effort accounted for 0.9% (RDA) and 1.5% (CCA) of the residual variance. For both RDA and CCA analyses, the Monte Carlo permutation test on the 1st axis was significant at a probability level of 0.00. The covariables explained 6-10% of the total variance in the species data.

Discussion

The assessment of the impact of trawling on the benthic fauna of the North Sea has previously been seriously hampered by the low resolution of information on the spatial distribution of fishing (ICES rectangles of 30 * 30 miles). Estimated trawling frequencies (Welleman 1989, Lindeboom 1995) have been based on the assumption that fishing effort in a rectangle was homogeneously distributed. In reality however, this is not the case and fishing activities tend to be concentrated in small areas, as is shown for the Dutch fleet by Rijnsdorp et al. (1998).
On the Dutch Continental Shelf also data on the benthic fauna are available on a fine spatial resolution (Holtmann et al. 1996b) and, thus, we now had the opportunity to check whether the small scale patterns in fishing effort are reflected in the benthic community.

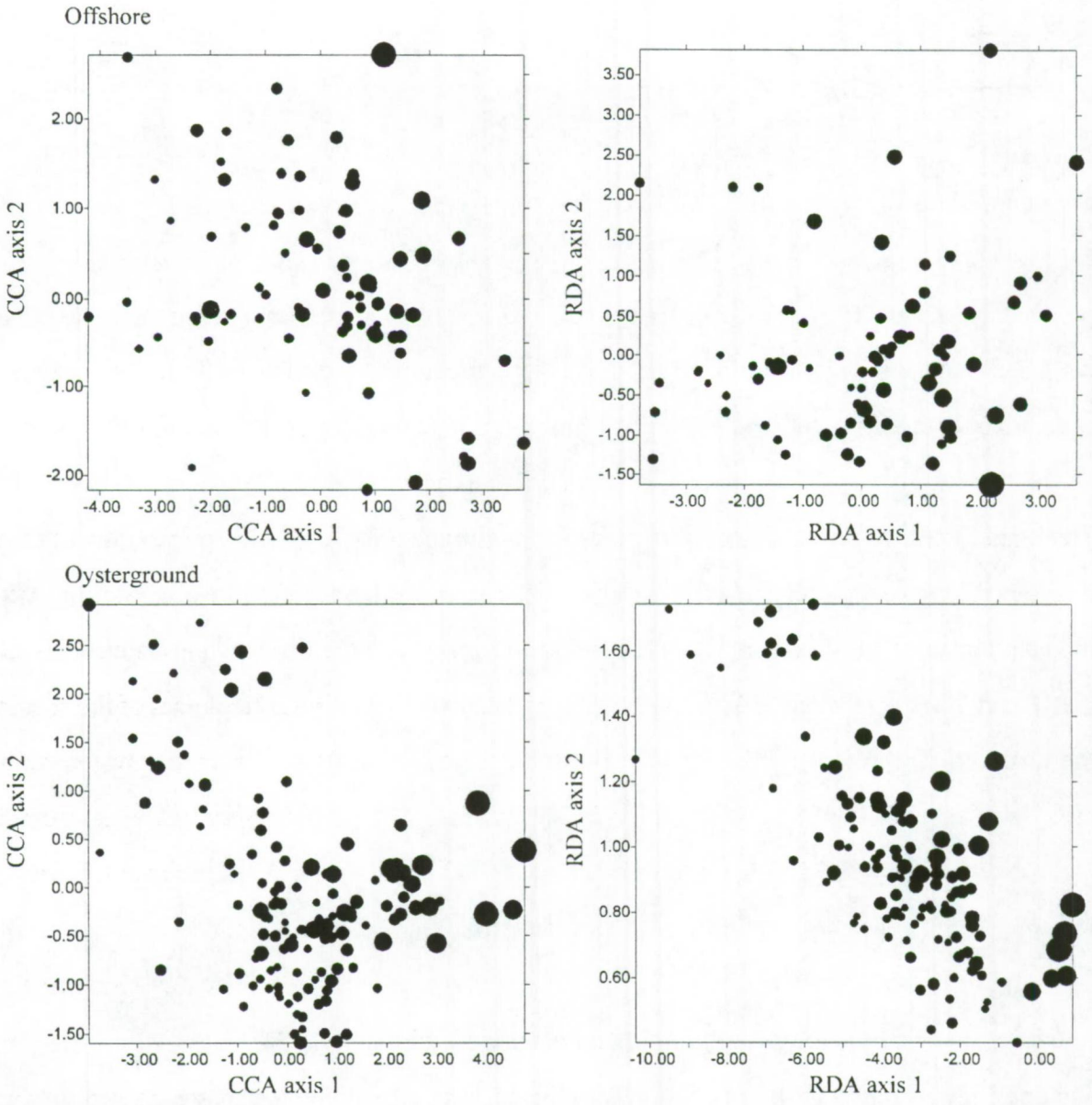

Figure 8.3. Sample scores in the ordination planes formed by the first and second canonical axes of the CCA and RDA of the two subareas. Symbol size represents fishing effort.

The present study certainly has some limitations. First, we only considered infaunal species, while epifaunal taxa may be more vulnerable suffering direct damage by the passage of a trawl. Secondly, the most vulnerable species may have decreased earlier this century due to trawling (Lindeboom and de Groot 1998). Finally, our analysis might have suffered from the fact that the benthos data and the effort data did not cover the same period. In the period 1993-1996 the micro-distribution of the sampled vessels showed, however, a remarkable similarity (Rijnsdorp

et al. 1998). In a study of all data from the Dutch Continental Shelf in the period 1986-1997, Holtmann et al (1998) found that species composition in 1986 and 1990 was different from that in later years. However, most of the data used in this study were from 1991 to 1993. Thus, our implicit assumption that the trawling effort distribution within each area was similar during the period macrobenthic sampling took place, is most likely not violated.

The results of our study at first seem to point to a significant impact of bottom trawling. The total density of spionids increases with increasing fishing disturbance. In addition, there is a significant, although small, relationship between the species composition and fishing effort.

The direct gradient analyses point to a globally significant difference in species composition between intensively fished and less heavily fished locations. In the Offshore area, stations with high abundances of species such as *Pseudocuma longicornis* and *Urothoe brevicornis* are situated on the left side of the ordination diagrams, stations with high abundances of the species *Sigalion mathildae* and *Atylus swammerdami* are situated on the right side. In the Oysterground area, stations with high abundances of species such as *Sigalion mathildae, Ampelisca brevicornis* and *Arctica islandica* are located on the left side, stations with high abundances of *Urothoe poseidonis* on the right side. The fishing effort gradient is from left to right, suggesting that population sizes of for instance *A. islandica* are decreasing in response to increasing fishing pressure, while those of e.g. *A. swammerdami* are increasing.

Ampelisca brevicornis is a tube-dwelling amphipod. The tubes may rise above the surrounding bottom surface (see e.g. fig. 6.B in Valente et al. 1992). Females reproduce once and carry the eggs in their marsupium. It is clear that bottom trawling will destroy the tubes. Although it is possible that only a part of the population is affected, as *A. brevicornis* can swim (Klein et al. 1975), frequent trawling will certainly inhibit re-colonisation.

The quahog *Arctica islandica* only occurs north of the 30 m depth contour. The effect of beam trawling on populations of *A. islandica* was clearly illustrated by Witbaard and Klein (1994) and Witbaard (1997). In the Oysterground area, only few specimens have undamaged shells and the mortality rate seems to be higher than that in the northern North Sea or western Atlantic. Witbaard and Klein (1994) observed an increase in the occurrence of scars in the 1980s,

coincident with an increase of larger fishing vessels. The quahog is a slow growing species with a high longevity and low, irregular recruitment (Rees and Dare 1993). This makes the population very sensitive to disturbance.

Thus, for the two species mentioned above the observed negative relationship with fishing effort is to be expected. For *A. islandica*, however, most of the specimen were very small (zero year class). Thus, the differences in distribution is very likely due to differences in spatfall. For the other species mentioned above, the relationship with fishing effort is hard to explain. *Atylus swammerdami, Pseudocuma longicornis, Urothoe brevicornis* and *Urothoe poseidonis* are highly mobile and can swim free (Watkin 1939, Jones 1976, Holme 1983, Holtmann et al. 1996b) and hence are not directly vulnerable to sediment disturbance. Moreover, these species have a short life cycle and at least one of them, the cumacean *P. longicornis*, breeds twice a year. Thus, their life-cycle strategy ensures a long-term survival. Surprisingly, *A. swammerdami* and *U. poseidonis* are found in higher densities in the most intensively trawled areas, *P. longicornis* and *U. brevicornis* have higher abundances in the less heavily trawled areas.

It is further striking that in the Offshore area the densities of the polychaete *Sigalion mathildae* are higher at the most intensively trawled locations, while in the Oystergrond area their abundances are lowest at these locations. As *S. mathildae* lives 15 to 20 cm beneath the sediment surface, we don't expect it to be sensitive to fishing impact.

For most benthic species, however, it is difficult to indicate whether they are likely to be vulnerable or not. Data on the life-history parameters are either lacking or are scattered through often grey literature. The data on the species discussed above suggest that in the areas studied the relation between fishing effort and community structure may be largely correlative and not causal. The patterns found are, therefore, likely to be due to one or more environmental variables not included in our study. These structural differences in the environment may affect the fishing strategies of skippers directly or indirectly, i.e. if some parts of the studied areas might be more attractive to fish than others. Thus, as noted by Hall et al. (1993), the fact that 'unfished' areas are usually unfished precisely because they differ from real fishing grounds, makes the interpretation very difficult. Probably, the same actors determine both species composition and fishing effort distribution. In such cases it is probably impossible to discriminate between environmental impact and fishery impact. If the environmental actors are factored out in a partial

canonical analysis, the effect of fishing effort will at least be underestimated. This may already have been the case in our study, partialling out depth and grain size. However, this is very unlikely as the first axis in canonical analyses with fishing effort as the only environmental variable but without covariables did not explain a larger part of the variance compared to the partial analyses.

Opportunistic species, including most members of the polychaete family Spionidae, are characterised by high growth rates, a short life span, a low reproductive age and a large reproductive output. These enable them to rapidly adapt to environmental perturbation and quickly re-colonise empty habitats (Grassle and Grassle 1974, Gudmundsson 1985). For several areas of the North Sea an increase in the abundance of opportunistic species has been reported and has been explained as an effect of eutrophication, pollution and fisheries (Suess 1980, Rachor 1990, Olsgard and Gray 1995, Schroeder and Knust submitted). However, benthic communities often show a high natural variability and it is mostly not possible to distinguish the different influences. This is certainly true for highly dynamic areas such as the Offshore area, already characterised by relatively opportunistic species (Holtmann et al. 1998). Nevertheless, a positive relationship between spionid density and fishing effort was also found here.

Another important factor causing a shift in the benthic community from low-productive, long-lived species to high-productive, short-lived species is eutrophication (Rachor 1990). The importance of both eutrophication and beam trawling in the benthic community shift can be inferred from changes in growth of plaice and sole (Rijnsdorp and van Beek 1991, Rijnsdorp and van Leeuwen 1996). The overall changes in growth suggest increased food availability in the southern North Sea. They can be broken down into effects of eutrophication (decreasing with increasing distance from the shore) on juveniles and of beam trawling (of minor importance within the 12 miles zone) on older fishes, whereas both factors may play a role during an intermediate life phase. Therefore, in the subareas studied differences in the fishing effort are the most likely explaining factor in the differences in spionid densities.

References

Bergman, M. J. N., and J. W. van Santbrink. 1999. Fishing mortality of invertebrate species due to bottom trawling. *in* M. J. Kaiser and S. J. de Groot, editors. Fishing New Books: Effects of fishing on non-target species and habitats. Biological, conservation and socio-economic issues. Blackwell Science, Oxford.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology **73**:1045-1055.

Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Marine Ecology Progress Series **155**:159-172.

Fonds, M. 1999. Food produced by beam trawling for scavenging benthic carnivores. *in* M. J. Kaiser and S. J. de Groot, editors. Fishing New Books: Effects of fishing on non-target species and habitats. Biological, conservation and socio-economic issues. Blackwell Science, Oxford.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. Journal of Marine Research **32**:253-284.

Groenewold, S., and M. Fonds. submitted. The importance of damaged fauna and discards, produced by beamtrawling in the southern North Sea, as food source for scavenging species in the benthic ecosystem. ICES Journal of Marine Science.

Gudmundsson, H. 1985. Life history patterns of polychaete species of the family Spionidae. Journal of the Marine Biology Association of the United Kingdom **65**:93-111.

Hall, S. J., M. R. Robertson, D. J. Basford, and S. D. Heaney. 1993. The possible effects of fishing disturbance in the northern North Sea: an analysis of spatial patterns in community structure around a wreck. Netherlands Journal of Sea Research **31**:201-208.

Holme, N. A. 1983. Fluctuations in the benthos of the western English Channel. Pages 121-124 *in* Proceedings of the 17th EMBS (Brest, France, 1982). Oceanologica Acta, N°SP.

Holtmann, S. E., J. J. M. Belgers, B. Kracht, and R. Daan. 1996a. The macrobenthic fauna in the Dutch sector of the North Sea in 1995 and a comparison with previous data. Netherlands Institute of Sea Research, NIOZ-Rapport 1996-8. 102 pp.

Holtmann, S. E., A. Groenewold, K. H. M. Schrader, J. Asjes, J. A. Craeymeersch, G. C. A. Duineveld, A. J. van Bostelen, and J. van der Meer. 1996b. Atlas of the zoobenthos of the Dutch Continental Shelf. Ministry of Transport, Public Works and Water Management, North Sea Directorate, Rijkswijk. 244pp.

Holtmann, S. E., G. C. A. Duineveld, M. Mulder, and P. A. W. J. de Wilde. 1998. The macrobenthic fauna in the Dutch sector of the North Sea in 1997 and a comparison with previous data. Netherlands Institute of Sea Research, NIOZ-Rapport 1998-5. 103 pp.

Jones, N. S. 1976. British Cumaceans (Synopses of British Fauna (New Series) No. 7). Academic Press, London. 63pp.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen. 299pp.

Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behaviour in recently trawled areas. Marine Ecology Progress Series **112**:41-49.

Klein, G., E. Rachor, and S. A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. Ophelia **14**:139-159.

Lindeboom, H. J. 1995. Protected areas in the North Sea: an absolute need for future marine research. Helgoländer Meeresuntersuchungen **49**:591-602.

Lindeboom, H. J., and S. J. de Groot, editors. 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems.NIOZ-RAPPORT 1998-1 / RIVO-DLO REPORT C003/98. 404pp.

Olsgard, F., and J. S. Gray. 1995. A comprehensive analysis of the effects of offshore oil and gas exploration and production on the benthic communities of the Norwegian continental shelf. Marine Ecology Progress Series **122**:277-306.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology **74**:2215-2230.

Philippart, C. J. M. 1998. Long-term impact of bottom fisheries on several by-catch species of demersal fish and benthic invertebrates in the south-eastern North Sea. ICES Journal of Marine Science **55**:342-352.

Piet, G. J., A. D. Rijnsdorp, M. J. N. Bergman, J. W. van Santbrink, J. A. Craeymeersch, and J. Buijs. submitted. fishing mortality in invertebrate populations: the effect of spatial resolution. ICES Journal of Marine Science.

Rachor, E. 1990. Changes in sublittoral zoobenthos in the German Bight with regard to eutrophication. Netherlands Journal of Sea Research **25**:209-214.

Ramsay, K., M. J. Kaiser, A. D. Rijnsdorp, J. A. Craeymeersch, and S. I. Rogers. 1999. The impact of beam trawling on the benthic scavenger *Asterias rubens* L. *in* M. J. Kaiser and S. J. de Groot, editors. Fishing New Books: Effects of fishing on non-target species and habitats. Biological, conservation and socio-economic issues. Blackwell Science, Oxford.

Rees, H. L., and P. J. Dare. 1993. Sources of mortality and associated life-cycle traits of selected benthic species: a review. MAFF, Lowestoft. Fisheries Research Data Report Number 33. 34pp.

Rijnsdorp, A. D., and F. A. van Beek. 1991. Changes in the growth of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in the North Sea. Netherlands Journal of Sea Research **27**:441-457.

Rijnsdorp, A. D., and P. I. van Leeuwen. 1996. Changes in the growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. ICES Journal of Marine Science **53**:1199-1213.

Rijnsdorp, A. D., A. M. Buys, F. Storbeck, and E. G. Visser. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organismes. ICES Journal of Marine Science **55**:403-419.

Schroeder, A., and R. Knust. submitted. Long term changes in the benthos of the German Bight (North Sea) - possible influences of fisheries ? ICES Journal of Marine Science.

Suess, E. 1980. Particulate organic carbon flux in the oceans: surface productivity and oxygen utilization. Nature (London) **288**:260-263.

ter Braak, C. J. F. 1988a. CANOCO - an extension of DECORANA to analyze species-environment relationships. Vegetatio **75**:159-160.

—-. 1988b. Partial canonical correspondence analysis. Pages 551-558 *in* H. H. Bock, editor. Classification and related methods of data analysis. Elsevier Science Publishers B.V., Amsterdam.

ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research **18**:272-318.

Tuck, I., S. J. Hall, M. R. Robertson, E. Armstrong, and D. J. Basford. 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Marine Ecology Progress Series **162**:227-242.

Valente, R. M., D. C. Rhoads, J. D. Germano, and V. J. Cabelli. 1992. Mapping of benthic enrichment patterns in Narragansett Bay, Rhode Island. Estuaries **15**:1-17.

Watkin, E. E. 1939. The pelagic phase in the life history of the amphipod genus *Bathyporeia*. Journal of the Marine Biology Association of the United Kingdom **23**:467-481.

Welleman, H. 1989. Literatuurstudie naar de effecten van de bodemvisserij op de bodem en het bodemleven. The Netherlands Institute for Fisheries Research (RIVO-DLO), MO 89-201, 58 pp.

Witbaard, R. 1997. Trea of the sea. The use of internal growth lines in the shell of *Arctica islandice* (Bivalvia, Mollusca) for the retrospective assessment of marine environmental change. PhD Thesis, Rijksuniversiteit Groningen, , Groningen. 149pp.

Witbaard, R., and R. Klein. 1994. Long-term trends on the effects of the southern North Sea beamtrawl fishery on the bivalve mollusc *Arctica islandice* (L.) (Mollusca, Bivalvia). ICES Journal of Marine Science **51**:99-105.

CHAPTER 9

Summary

Benthic animals are a key element of many marine and estuarine monitoring programs. They are, in contrast to e.g. plankton or fishes, sedentary and must adapt to environmental and human-induced disturbances or perish. They are immediately dependent on the quality of the overlying water and very sensitive to habitat disturbance. The benthos integrates the effects over a considerable period of time. Many fishes, birds and mammals depend directly or indirectly on the benthic fauna. However, monitoring the benthos is very costly involving ship-time and laboratory analysis that is very intensive. The time-consuming nature of the laboratory analysis leads to a lag phase between sampling and production of results. Therefore, the most appropriate methods should be used for both sampling the benthic fauna and analysing the data in the light of the objectives of the monitoring program.

During the last 10 years, I have been involved in several inventorying and monitoring studies in the Netherlands. In this dissertation part of the macrobenthos data recorded during these surveys are re-analysed in the light of some problems encountered when evaluating biological changes in the marine environment. Chapter 2 gives a detailed description of the surveys and the macrobenthos data used in chapter 3 to 8. All surveys have been carried out in the last fifteen years in the North Sea and adjacent estuaries in the Southwest of the Netherlands. To allow proper data management of the huge amount of data resulting from these surveys, the data have been stored in a relational database. In chapter 2 the structure of the database and some problems encountered during the design and maintenance are reported. Chapter 2 finally gives an overview of the multivariate techniques used in the other chapters.

Multivariate methods of data analysis describe the variability of the structure of the assemblages as a whole. In contrast to univariate methods, such as the analysis of variance, they take into account the covariance among the descriptors (species) (Legendre and Legendre 1998). The methods proved to be very sensitive for detecting differences in community structure between

samples in space, or changes over time (Clarke and Warwick 1994). Classification methods aim at structuring data into groups of similar entities. Ordination methods arrange the samples such that in the resulting diagram, samples with a similar species composition are situated close together, samples that are dissimilar far apart. While ordination techniques were primarily exploratory, with multivariate direct gradient analysis it became possible to test statistical hypotheses. Environmental impact assessment and monitoring can be regarded as attempts to test the null hypothesis that a defined human action has no impact upon the environment (Fairweather 1991). The outcome of any statistical test, however, not only depends on the true state of the phenomenon but also on the magnitude of the change and the quality of the experiment such as design of the experiment and precision of the measurements (Slob 1987, van der Meer 1997b). The effectiveness of detecting changes is defined in terms of statistical power, i.e. the probability of a significant test outcome if the null hypothesis is false. In contrast to the univariate analysis of variance, power considerations of ordination techniques have, to our knowledge, not been made yet. In chapter 3 a first attempt is made to compare the power of ordination techniques with that of the univariate analysis of variance by analysing simulated data sets. The results indeed point to a larger effectiveness of direct gradient analysis to detect changes in time. The power of an analysis of variance only seems to follow that of a multivariate analysis when the rate of change is very large. Further studies should incorporate other community parameters (such as total biomass) and consider different patterns of change.

The confirmation that the marine environment may be subdivided into areas based on benthic species composition is important in view of the management. Changes in the spatial distribution of the assemblages may imply changes in the structural forces that lead to their development. A division of the water systems according to the species composition permits choices of representative areas or stations to be made for monitoring. Effects of anthropogenic changes might differ between the various assemblages. A sampling design based on the distribution of benthic assemblages will result in a reduction of the within-year variability and, thus, in an increase of the power. Changes in the marine environment may occur on different spatial (and temporal) scales. It is, therefore, important to recognise the structuring forces that lead to the species distribution at the scale considered. Chapter 4 describes the changes in and relationships between species composition and some abiotic characteristics at the scale of several tens of

kilometres (the Westerschelde estuary), chapter 5 those at the scale of several hundreds of kilometres (the North Sea).

The distribution of the macrobenthic animals in the Westerschelde estuary has been studied before (Wolff 1973, Vermeulen and Govaere 1983, Meire et al. 1991, Ysebaert and Meire 1991, Ysebaert et al. 1993, 1998) but a complete review of the major gradients has been hampered by the biased selection of stations and sampling schemes. The monitoring surveys as realised since 1990 within the framework of the Dutch national monitoring program, covering both the intertidal and the subtidal areas, enabled a re-examination of the relationship between species composition and the major abiotic gradients. A Canonical Correspondence Analysis confirmed the strong relationships between the macrobenthic assemblages and the natural gradients in the Westerschelde estuary. The main forces are the hydrodynamic conditions (resulting in differences in sediment stability and composition) and salinity. As a result, some of the identified assemblages and biotopes are restricted to either the brackish or marine part of the estuary, to the inter- or subtidal sediments, or to a particular sediment type. The patterns of a study at the Molenplaat on a smaller spatial scale (Herman et al. 1996) fit well with ours, probably because both appear generated by physical processes.

In 1986 participants of the Benthos Ecology Working Group of ICES made a synoptic mapping of the macrobenthic infauna of the southern and central North Sea. Together with a mapping of the infauna of the northern North Sea by Eleftheriou and Basford (1989) this provided a database for the description of the benthic macrofauna of the whole North Sea. Division of the macrobenthic infauna into assemblages separated northern assemblages from southern assemblages along the 70m depth contour line. Assemblages were further separated by depth and sediment type. Northern species extend south to the northern margins of the Dogger Bank, southern species north to the 100 m depth line. The central North Sea is an area of overlap of southern and northern species. The factors structuring species distributions and assemblages seem to be temperature, the influence of different water masses, the type of sediment and the stability of the bottom and the food supply to the benthos. The differences in diversity, total density and total biomass between the benthic assemblages are reflected in the general trends in these quantities. There exists a clear and significant decreasing trend in biomass with latitude, both in total biomass and for the different taxonomic groups. Biomass further increases

consistently in finer sediments and sediments with a higher chlorophyll *a* content. Towards the north of the North Sea diversity, as measured by Hill's diversity index N_1, increases considerably. Also longitude and depth show an effect on diversity. Total density tends to increase towards the north, but sediment related variables have a larger influence. Mean individual weight becomes considerably smaller towards the northern part of the North Sea.

The three other chapters deal with three impact studies: the impact of a land reclamation project (chapter 6), the construction of the storm-surge barrier in the mouth of the Oosterschelde (chapter 7) and the effects of beam trawling in the North Sea (chapter 8).

In 1986 the construction of a disposal site in the northern part of the Voordelta (SW Netherlands) for dredged material from the lower reaches of the river Rhine was completed. A so-called Environmental Impact Assessment considered four alternative locations for the disposal site. The option finally chosen was considered to have the smallest impact. The EIA further proposed that an environmental monitoring plan had to be carried out, including the macrobenthic organisms. The aim was to evaluate if the faunal assemblages identified in a baseline study in 1983 have been persistent over time, if the spatial distribution of these assemblages has changed or not and if the characteristic and dominant species have remained the same. In chapter 6 the data of the baseline study and five surveys carried out after the construction of the depot (1988, 1989, 1990, 1992, 1994) are analysed. The temporal changes in community structure are in general small, as are the environmental changes. Nevertheless, geomorphological changes are still expected and, consequently, on the long term larger effects on the benthos still might occur.

Chapter 7 describes the density fluctuations of the dominant macrobenthos species at a mid-tidal station on a mudflat in the eastern part of the Oosterschelde in the period 1983-1986. During that period dams were constructed in the eastern, western and northern part of the estuary. Density fluctuations were analysed by Analysis of Concentration (Orlóci 1981), an extension of Correspondence Analysis, and related to environmental variables. In 1983 and 1984 density changes were most clear on the second and third ordination axes. The third axis expressed seasonal fluctuations. The interpretation of the second axis is less clear. In 1985 all species (except one) shifted position along the first axis. This correlated with changes in tidal amplitude. Depending on the species, these changes intensified, weakened or overrided the influences correlated with the second and third axes. In a comparison of the before- (1985) and

after-the-works (1989) surveys at some tidal flats in the Oosterschelde, van der Meer (1997a) also concluded that particularly species that are related to the tidal zone axis were affected. The results of this study further support the conclusion of Orlóci that Analysis of Concentration is an appropriate method in time series analysis.

Chapter 8 focuses on the impact of beam trawling on the Dutch Continental Shelf. As the gears scrape the surface, trawling causes mortality in target and non-target species. Direct mortality due to trawling occurs both among the caught and subsequently discarded animals as in the trawl path, among animals that are damaged or killed by the passing gear. Thus, evidence is available of the direct effects of beam trawling (Collie et al. 1997, Jennings and Kaiser 1998, Lindeboom and de Groot 1998) The longer term effects of demersal fisheries on benthic marine ecosystems are still a point of discussion. The long-term impact on a particular species will depend on the direct mortality at each fishing event, the distribution of the fishing effort, the distribution of that species and its life history characteristics such as longevity and fecundity. The longer-term effects may be evaluated from long term trends in benthos or by-catch data. They may also be inferred from comparisons between fished and un-fished areas. The detailed information of fishing effort that recently became available (Rijnsdorp et al. 1998) offered the opportunity to compare benthic fauna of areas under different levels of fishing disturbance. The study focused on two subareas on the Dutch Continental Shelf. A direct gradient analysis pointed to a globally significant difference in species composition between intensively fished and less heavily fished locations. It is, however, very likely that a major part of this differences are not related to differences in trawling effort. On the contrary, differences in spionid densities are most likely explained by differences in fishing effort. The total density of spionids, mostly opportunistic species, increased with increased fishing disturbance.

In order to accurately evaluate biological changes in the marine environment, it is necessary to know the spatial and temporal scales of natural variability. At the scale of the North Sea (chapter 5) only the spatial variability was studied. The ongoing monitoring study on the Dutch Continental Shelf shows, however, that there exists indeed a fundamental difference in species composition in different parts of the North Sea (Holtmann et al. 1998). The Westerschelde study (chapter 4) incorporated six years of monitoring. Temporal fluctuations were largely overrided

by spatial fluctuations. The same was noticed in chapter 6. The faunal assemblages identified in the base-line study have been persistent over time, but there were large year-to-year fluctuations in the density and biomass of the dominant species of each assemblage.

Because of the natural variability of aquatic systems, monitoring studies should ideally include several affected and control locations or areas. Without knowledge of the temporal fluctuations at such control locations it is difficult to judge whether an observed pattern of change in the potentially disturbed area is really due to the anthropogenic disturbance. In the study of a land reclamation project (chapter 6) only a single survey was carried out before the construction works. It is, therefore, unclear whether or not that year was representative for the pre-construction situation. In the study no spatial control was planned as well. Luckily, some comparison could be made with other monitoring studies ongoing in the coastal area.

The same study points to another problem in monitoring studies. The study has major limitations for understanding the spatial and temporal fluctuations, as data on the fluctuations of the most important abiotic variables were hardly available. Despite the intimate link of the benthic animals with the sediment, sediment characteristics such as the median grain size, known to affect species composition (chapter 4, chapter 5) are not included in many monitoring programs. The power of a time series would, however, be increased if the variability due to year-to-year and/or seasonal fluctuations in median grain size or silt content could be removed from the analysis (e.g. in a partial canonical analysis as done in chapter 8). Other important variables such as current velocity can nowadays be calculated from existing hydrodynamical models (see e.g. chapter 4). Thus, important information on the changes in natural conditions might be obtained at a low cost compared to the cost of sampling and analysing the benthos.

Finally, it is necessary to understand the community dynamics to allow prediction of the consequences to the whole community of changes in the abundance of individual species as a result of natural factors or human disturbances (Keegan 1991). In the case of the Westerschelde (chapter 4), it might be possible to predict the impact of future geomorphological changes expected with the increase in dredging activities as the macrobenthic structure appears to be generated by the local hydrodynamic conditions. However, the relationships found might not longer be valid under the new conditions. There is, for instance, not enough knowledge on the most favourable conditions for primary and secondary settlement of bivalves. If favourable

conditions for primary settlement are missing, this will certainly influence the overall community structure. Changes in the community structure could also be due to changes of a factor not included in the present study such as the system primary production, for a large part determining the system-averaged benthic biomass (Herman et al. in press). More information is, therefore, needed about the processes and mechanisms leading to the spatial distribution of benthic communities and their characteristics.

Samenvatting

Macroscopische bodemdieren vormen een belangrijk onderdeel van veel monitorprogramma's in mariene en estuariene watersystemen. Veel bodemdieren zijn direct of indirect een belangrijke voedselbron voor veel vissen, vogels en zoogdieren. Bodemdieren zijn, in tegenstelling tot bijvoorbeeld plankton en vissen, veelal niet of weinig mobiel. Ze zijn daarom afhankelijk van de lokale waterkwaliteit. Ook moeten ze zich kunnen aanpassen aan verstoringen van hun leefmilieu, of deze nu van natuurlijke oorsprong zijn of als gevolg van menselijke activiteiten.

Het monitoren van bodemdieren is echter niet goedkoop. Het vraagt de inzet van schepen en de analyse van de genomen monsters vraagt veel tijd. Dit laatste leidt er overigens toe dat er een aanzienlijke periode kan bestaan tussen het nemen van de monsters en het ter beschikking komen van de gegevens. Daarom is het noodzakelijk dat er, in het licht van de doelstellingen van het programma, voldoende aandacht besteed wordt aan zowel de wijze waarop gemonsterd wordt als aan de gebruikte analysemethodes.

Sinds ik in 1986 in Nederland werkzaam ben, ben ik er bij veel inventarisaties en monitorprogramma's betrokken. In dit proefschrift word de analyse van een deel van de macrobenthos gegevens die tijdens deze programma's verzameld zijn, gepresenteerd en bediscussieerd in het licht van een aantal problemen waartegen men aanloopt bij de evaluatie van biologische veranderingen in het mariene milieu. Hoofdstuk 2 geeft een uitgebreide

beschrijving van de programma's waarvan de gegevens in de hoofdstukken 3 tot en met 8 gebruikt worden. Al deze programma's zijn gedurende de laatste vijftien jaar in de Noordzee en de estuaria in het zuidwesten van Nederland uitgevoerd. De hoeveelheid gegevens vereiste het opzetten van een systeem waarbij alle gegevens uniform ingevoerd en opgeslagen werden. In hoofdstuk 2 wordt de struktuur van de database en enige problemen bij het ontwerp en onderhoud van zo'n database besproken. Verder wordt in hoofdstuk 2 een overzicht gegeven van de multivariate analyses die in de overige hoofdstukken gebruikt worden.

Multivariate technieken beschrijven de variabiliteit binnen gemeenschappen. In tegenstelling tot univariate methodes, zoals bijvoorbeeld variantie-analyses, houden ze daarbij rekening met de covariantie tussen soorten (Legendre en Legendre 1998). De methodes blijken ruimtelijke en temporele verschillen in de soortensamenstelling goed te kunnen weergeven (Clarke en Warwick 1994). Classificatietechnieken verdelen de genomen monsters in groepen met een gelijkaardige soortensamenstelling. Ordinatietechnieken schikken de monsters op zo'n manier dat in het resulterende ordinatiediagram monsters met eenzelfde soortensamenstelling dicht bij elkaar liggen, monsters met een verschillende soortensamenstelling ver uit elkaar. De nieuwste technieken laten ook toe hypotheses te testen. Het meten van effecten en monitoring kunnen daarbij gezien worden als het testen van de nulhypothese dat een vooraf gedefinieerde menselijke activiteit geen invloed heeft (Fairweather 1991). De uitkomst van een statistische toetst hangt niet alleen af van het al of niet bestaan van een effect, maar ook van de grootte van de verandering, de kwaliteit van het experiment en de precisie van de metingen (Slob 1987, van der Meer 1997b). De mogelijkheid om veranderingen statistisch aan te tonen is gedefinieerd in termen van statistisch onderscheidingsvermogen. Dit is de kans dat de nulhypothese verworpen wordt als deze inderdaad ook fout is; kortom, de kans om werkelijk opgetreden veranderingen ook daadwerkelijk te constateren. In tegenstelling tot de univariate variantie-analyses is aan het onderscheidingsvermogen van ordinatietechnieken voor zover we weten nog geen aandacht besteed. In hoofdstuk 3 pogen we het onderscheidingsvermogen van ordinaties te vergelijken met dat van variantieanalyses. We gebruiken daarbij gesimuleerde veranderingen in de dichtheid van een beperkt aantal soorten. De resultaten wijzen op een groter onderscheidingsvermogen van de ordinatietechnieken. Enkel wanneer de veranderingen erg groot zijn, is het onderscheidingsvermogen van variantie-analyses niet lager dan dat van de

ordinaties. Vervolgstudies moeten bij dit soort vergelijking ook andere gemeenschapskenmerken (bijvoorbeeld de totale biomassa) betrekken en niet alleen lineaire veranderingen beschouwen.

Het feit dat het mariene leefmilieu onderverdeeld kan worden op basis van verschillen in de soortensamenstelling van de bodemdieren is een belangrijk gegeven voor het beheer. Veranderingen in de ruimtelijke verspreiding van gemeenschappen kan wijzen op belangrijke veranderingen in het leefmilieu. Een verdeling van de watersystemen op basis van de soortensamenstelling laat een betere keuze toe van gebieden of locaties die men wil monitoren. Menselijke activiteiten kunnen op de verschillende gemeenschappen een andere invloed hebben. Een monitorprogramma gebaseerd op de ruimtelijke verspreiding van gemeenschappen zal resulteren in een vermindering van de variabiliteit binnen iedere campagne en dus tot een hoger onderscheidingsvermogen. Veranderingen in het mariene milieu kunnen op verschillende ruimtelijke (en temporele) schalen plaatsvinden. Het is daarom belangrijk op dezelfde schalen inzicht te hebben van de voor de verspreiding van soorten meest belangrijke omgevingsvariabelen. Hoofdstuk 4 beschrijft de veranderingen en relaties tussen soorten en enkele omgevingsvariabelen op de schaal van enige tientallen kilometers (de Westerschelde), hoofdstuk 5 op de schaal van enkele honderden kilometers (de Noordzee).

De verspreiding van macrobenthische dieren in de Westerschelde is reeds vroeger bestudeerd (Wolff 1973, Vermeulen en Govaere 1983, Meire et al. 1991, Ysebaert en Meire 1991, Ysebaert et al. 1993, 1998), maar een volledig overzicht van de belangrijkste gradiënten was niet mogelijk door de veelheid aan gebruikte monstermethoden. Het monitorprogramma zoals dat sinds 1990 in de Westerschelde gerealiseerd is in het kader van het Nederlands nationaal monitorprogramma van de zoute wateren, dat zowel het intergetijdegebied als de onderwaterbodem omvat, liet een analyse van de relatie tussen soorten en de belangrijkste abiotische omgevingsvariabelen toe. Een Canonische Correspondentie Analyse bevestigde de sterke relatie tussen de macrobenthische gemeenschappen en natuurlijke gradiënten in het Westerschelde estuarium. De belangrijkste factoren zijn de hydrodynamische omstandigheden (resulterend in verschillen in de stabiliteit van de sedimenten en verschillen in korrelgrootteverdeling) en de saliniteit. Als gevolg van verschillen in deze factoren zijn een aantal gemeenchappen en biotopen beperkt tot het brakke of mariene deel van de Westerschelde,

tot het intergetijdegebied of tot de onderwaterbodems, of tot een bepaald type sediment. Verschillen in de structuur die op een kleinere ruimtelijke schaal gevonden zijn op de Molenplaat (Herman et al. 1996) passen heel goed in de in hoofdstuk 4 beschreven structuur, waarschijnlijk omdat op beide schalen fysische processen de belangrijkste structurende factor zijn.

In 1986 hebben deelnemers van de Benthos Ecology Working Group van ICES een programma uitgevoerd waarbij de macrobenthische infauna in de gehele zuidelijke en centrale Noordzee bemonsterd werd. Eleftheriou en Basford (1989) hadden enkele jaren voordien al de noordelijke Noordzee bemonsterd. Dit liet de beschrijving van de gehele Noordzee toe. De 70m dieptelijn verdeelde de Noordzee in noordelijke en zuidelijke gemeenschappen. Verschillen in diepte en sediment resulteerden in een verdere verdeling. Noordelijke soorten komen niet verder zuidwaarts dan de noordelijke randen van de Doggerbank, zuidelijke soorten niet noordelijker dan de 100m dieptelijn. In de centrale Noordzee overlappen zuidelijke en noordelijke soorten. De verdeling lijkt een gevolg van verschillen in temperatuur, de invloed van verschillende watermassa's, sediment, stabiliteit van de bodem en voedseltoevoer naar het benthos. De verschillen in diversiteit, totale dichtheid en totale biomassa tussen de gemeenschappen is ook in de globale trends in deze parameters terug te vinden. Zowel de totale biomassa als de biomassa van de verschillende taxonomische groepen nemen naar het noorden toe af. De biomassa is verder hoger in de fijnere sedimenten en sedimenten met een hoger gehalte chlorofyl *a*. Naar het noorden toe neemt de diversiteit (Hills diversiteitsindex N_1) toe. Ook verandert de diversiteit met de lengtegraad en de diepte. De totale dichtheid lijkt naar het noorden toe te nemen, maar met sediment gerelateerde variabelen zijn belangrijker. Het gemiddeld individueel gewicht wordt veel kleiner in het noordelijk deel van de Noordzee.

De andere drie hoofdstukken beschrijving de invloed van een landwinning in zee ten behoeve van de haven van Rotterdam (hoofdstuk 6), de bouw van de stormvloedkering in de mond van de Oosterschelde (hoofdstuk 7) en de effecten van het vissen met boomkorren in de Noordzee (hoofdstuk 8).

In 1986 was in het noordelijk deel van de Voordelta aan de zeezijde van het Rotterdamse haven- en industriegebied de bouw van een depot voor de berging van baggerspecie uit het benedenrivierengebied klaar. In een milieu-effectrapport werden vier alternatieve locaties voor

dit depot in beschouwing genomen. Van de uiteindelijk gekozen locatie werd verondersteld dat deze het geringste effect op de natuur had. Het milieu-effectrapport stelde verder als voorwaarde dat de effecten gedurende 30 jaar onderzocht moesten worden. Doel was o.a. na te gaan of de ruimtelijke verspreiding van de macrobenthische gemeenschappen, zoals vastgesteld in 1983, zou veranderen, en of de karakteristieke en dominante soorten van deze gemeenschappen dezelfde zouden blijven. In hoofdstuk 6 worden de gegevens van 1983 en de eerste vijf campagnes na de bouw van het depot (1988, 1989, 1990, 1992, 1994) geanalyseerd. De gemeenschapsstructuur blijkt over de tijd maar weinig te veranderen, zoals overigens ook de omgeving zelf. Maar het is te verwachten dat de geomorfologie van het gebied nog wel degelijk zal veranderen en dat er dus ook veranderingen in het benthos zullen optreden.

Hoofdstuk 7 beschrijft de veranderingen van enkele belangrijke bodemdieren op een slik in het oosten van de Oosterschelde in de periode 1983-1986. Tijdens deze periode werden in het oosten, het westen en het noorden van het estuarium dammen gebouwd in het kader van het zogenaamde Deltaproject. De dichtheidsveranderingen werden geanalyseerd met een 'Analysis of Concentration' (Orlóci 1981), een uitbreiding van een correspondentie analyse, en gerelateerd aan veranderingen in enkele omgevingsvariabelen. In 1983 en 1984 waren de dichtheidsfluctuaties het meest gerelateerd aan de tweede en derde ordinatie-as. De derde as was gerelateerd aan temperatuur, en gaf dus seizoenale verschillen weer. De interpretatie van de tweede as was minder duidelijk. In 1985 vertoonden alle soorten op één na een verschuiving langs de eerste as. Dit correleerde met veranderingen in de getij-amplitude. Naargelang de soort werden de veranderingen gerelateerd aan de tweede en derde as geïntensifieerd, verzwakt of overtroffen. Dit resultaat is in overeenstemming met de bevindingen van van der Meer (1997a) die, bij een vergelijking van de situatie voor (1985) en na (1989) de werken op enkele intergetijdegebieden in de Oosterschelde, vond dat vooral soorten die hoog of laag op de platen en slikken voorkomen door de werken beïnvloed waren. De resultaten van ons onderzoek duiden er verder op dat de gevolgde analysemethode (Analysis of Concentration) ten onrechte niet meer gebruikt wordt bij de analyse van tijdsseries.

Hoofdstuk 8 gaat in op de effecten van boomkorvisserij op het Nederlands Continentaal Plat. Het vissen met boomkorren leidt tot sterfte van verschillende bodemdieren, zowel van gevangen als van niet gevangen dieren. Over het directe effect van deze vorm van visserij is ondertussen

veel geweten (Collie et al., 1997, Jenings en Kaiser 1998, Lindeboom en de Groot 1998). De lange-termijneffecten hangen af van de directe mortaliteit, de verspreiding van de visserij, de verspreiding van de soorten en de populatiedynamische kenmerken van de soorten. Kennis over de lange-termijneffecten kan verkregen worden uit analyses van veranderingen in het benthos zelf of van veranderingen in de bijvangst van de visserij. Ook een vergelijking van beviste en niet beviste gebieden kan bijdragen tot een betere kennis van de effecten. De recent beschikbaar gekomen informatie over de bevissingsintensiteit op een schaal van 1 bij 1 mijl (Rijnsdorp et al. 1998), bood de gelegenheid de bodemfauna van gebieden met een verschillende verstoring door visserij te vergelijken. De studie heeft zich toegespitst op twee gebieden op het Nederlands Continentaal Plat. Een ordinatie-analyse wees op een significant verschil in soortensamenstelling tussen erg beviste en minder beviste gebieden. Het is echter heel waarschijnlijk dat deze verschillen niet aan verschillen in visserij-intensiteit te wijten zijn. De verschillen in de totale dichtheid van Spionidae zijn echter hoogstwaarschijnlijk wel een gevolg van verschillen in de intensiteit van bevissing. De totale dichtheid van deze groep polychaeten, meestal opportunistische soorten, neemt toe naarmate er meer gevist is.

Om biologische veranderingen in het mariene milieu te kunnen evalueren, is kennis over de ruimtelijke en temporele fluctuaties nodig. Op de schaal van de Noordzee (hoofdstuk 5) is enkel het ruimtelijk aspect bestudeerd. Het monitorprogramma op het Nederlands Continentaal Plat toont echter aan dat er een fundamenteel verschil in soortensamenstelling bestaat tussen verschillende delen van de Noordzee (Holtmann et al. 1998). De studie in de Westerschelde (hoofdstuk 4) omvatte zes jaar monitoring. Temporele fluctuaties waren echter kleiner dan ruimtelijke variaties. Hetzelfde werd waargenomen in hoofdstuk 6. De gemeenschappen onderscheiden vóór de bouw van het depot zijn blijven bestaan, maar er waren grote jaarlijkse fluctuaties in de dichtheid en de biomassa van de verschillende soorten binnen iedere gemeenschap.

Juist vanwege de grote natuurlijke variabiliteit van watersystemen zouden monitorprogramma's ook altijd verschillende locaties of gebieden moeten volgen, zowel gebieden waar een effect mogelijk is als controlegebieden. Zonder kennis van de temporele fluctuaties in deze laatste gebieden is het moeilijk te oordelen of veranderingen in de mogelijk beïnvloede gebieden wel

degelijk een gevolg zijn van menselijke activiteiten. In de studie bij de haven van Rotterdam (hoofdstuk 6) is slechts één bemonstering uitgevoerd voor de aanvang van de bouw van het depot. Het is daarom onduidelijk of de situatie zoals dan vastgesteld wel representatief is voor de pre-depot situatie. In deze studie was ook geen ruimtelijke controle gepland. Gelukkig kon enige vergelijking gemaakt worden met gegevens van andere monitorprogramma's in de kustzone.

Deze laatste studie heeft nog een andere tekortkoming. Het is immers erg moeilijk om de gevonden ruimtelijke en temporele fluctuaties te begrijpen gezien gegevens over de meest belangrijke omgevingsvariabelen nauwelijks beschikbaar waren. Ondanks de nauwe relatie tussen bodemdieren en het sediment, zijn sedimentkarakteristieken waarvan bekend is dat ze de soortensamenstelling beïnvloeden (hoofdstuk 4 en 5) niet in het monitorprogramma opgenomen. Het onderscheidingsvermogen van de tijdsanalyse zou echter veel hoger zijn als rekening gehouden kon worden met de variabiliteit te wijten aan jaarlijkse en seizoenale fluctuaties in bijv. mediane korrelgrootte of slibgehalte (bijv. in een partiële canonische analyse zoals gebruikt in hoofdstuk 8). Andere belangrijke omgevingsvariablelen als de stroomsnelheid kunnen tegenwoordig modelmatig berekend worden (zie bijv. hoofdstuk 4). Belangrijke informatie over veranderingen in de omgeving waarin bodemdieren leven kan tegen relatief lage kosten (in vergelijking met de kosten van bemonsteren en laboratoriumanalyses) verkregen worden.

Tenslotte is een betere kennis van de gemeenschapsdynamiek nodig om de gevolgen van veranderingen in de dichtheid van afzonderlijke soorten op de gehele gemeenschap te kunnen voorspellen (Keegan 1991). In het geval van de Westerschelde (hoofdstuk 4) is het misschien mogelijk de impact van de geplande verdere verdieping en dus van verwachte geomorfologische veranderingen op de macrobenthische structuur te voorspellen gezien de soortensamenstelling vooral afhangt van de hydrodynamische omstandigheden. Anderzijds is de gevonden relatie misschien niet meer geldig onder de nieuwe omstandigheden. Er is, bijvoorbeeld, niet genoeg kennis over de meest gunstige omstandigheden voor de primaire en secundaire vestiging van tweekleppigen. Als gunstige omstandigheden voor de primaire vestiging ontbreken, kan dit grote gevolgen hebben voor de gehele gemeenschapsstructuur. Veranderingen in de structuur kunnen ook veroorzaakt worden door veranderingen in een variabele die niet in de huidige studie

meegenomen is, zoals bijv. in de primaire productie die voor een groot deel de gemiddelde biomassa van een watersysteem bepaald (Herman et al. in press). Meer kennis is dus nodig over de processen en mechanismen die tot de ruimtelijke verspreiding van gemeenschappen leiden.

References

Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth, 144 pp.

Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Marine Ecology Progress Series **155**:159-172.

Eleftheriou, A., and D. J. Basford. 1989. The macrobenthic infauna of the offshore northern North Sea. Journal of the Marine Biology Association of the United Kingdom **69**:123-143.

Fairweather, P. G. 1991. Statistical power and design requirements for environmental monitoring. Australian Journal of Marine and Freshwater Research **42**:555-567.

Herman, P., M. de Vries, P. Thoolen, M. Vonk, A. Baart, and J. Boon. 1996. Micro-macro. Een onderzoek naar de relatie tussen hydrodynamische factoren en kleinschalige verspreiding van macrobenthos. BEON Rapport nr. 96-5, part 4.

Herman, P. M. J., J. J. Middelburg, J. van de Koppel, and C. H. R. Heip. in press. Ecology of estuarine macrobenthos. Advances in Ecological Research.

Holtmann, S. E., G. C. A. Duineveld, M. Mulder, and P. A. W. J. de Wilde. 1998. The macrobenthic fauna in the Dutch sector of the North Sea in 1997 and a comparison with previous data. Netherlands Institute of Sea Research, NIOZ-Rapport 1998-5. 103 pp.

Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on the marine ecosystems. Advances in Marine Biology **34**:201-352.

Keegan, B. F., editor. 1991. Space and time series data analysis in coastal benthic ecology. An analytical exercise organised within the framework of the COST 647 Project on Coastal Benthic Ecology. Commission of the European Communities. Directorate-General for Science, Research and Development, Brussels. 582pp.

Legendre, P., and L. Legendre, editors. 1998. Developments in Environmental Modelling, 20: Numerical Ecology. Second English Edition. Elsevier B.V., Amsterdam. 853pp.

Lindeboom, H. J., and S. J. de Groot, editors. 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems.,, NIOZ-RAPPORT 1998-1 / RIVO-DLO REPORT C003/98.404 pp.

Meire, P. M., J. J. Seys, T. J. Ysebaert, and J. Coosen. 1991. A comparison of the macrobenthic distribution and community structure between two estuaries in SW Nehterlands. Pages 221-230 *in* M. Elliott and J.-P. Ducrotoy, editors. Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen & Olsen, Fredensborg.

Orlóci, L. 1981. Probing time series vegetation data for evidence of succession. Vegetatio **46**:31-35.

Rijnsdorp, A. D., A. M. Buys, F. Storbeck, and E. G. Visser. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organismes. ICES Journal of Marine Science **55**:403-419.

Slob, W. 1987. Strategies in applying statistics in ecological research. Ph.D. dissertation, Free University Press, Amsterdam. 112pp.

van der Meer, J. 1997a. A handful of feathers. Studies on the estimation and modelling of temporal and spatial fluctuations in the numbers of birds and their prey. PhD Thesis, Rijksuniversiteit Groningen, Groningen. 262pp.

—-. 1997b. Sampling design of monitoring programmes for marine benthos: a comparison between the use of fixed versus randomly selected stations. Journal of Sea Research **37**:167-179.

Vermeulen, Y. M., and J. C. R. Govaere. 1983. Distribution of benthic macrofauna in the Western Scheldt estuary (the Netherlands). Cahier de Biologie Marine **14**:297-308.

Wolff, W. J. 1973. Zoölogische Verhandelingen, No. 126: The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Brill, Leiden. 242pp.

Ysebaert, T., and P. Meire. 1991. Het macrozoöbenthos van de Westerschelde en de Beneden Zeeschelde. Rijksuniversiteit Gent, Laboratorium voor Ecologie der Dieren / Instituut voor Natuurbehoud. Rapport W.W.E. 12 / Rapport I.N. A92.085. 184pp.

Ysebaert, T., P. Meire, D. Maes, and J. Buijs. 1993. The benthic macrofauna along the estuarine gradient of the Schelde estuary. Neth. J. Aquat. Ecol **27**:327-341.

Ysebaert, T. G., P. Meire, J. Coosen, and K. Essink. 1998. Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. Aquatic Ecology **32**:53-71.

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