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STRUCTURE AND DYNAMICS OF THE NORTH SEA BENTHOS

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Structure and dynamics of the North Sea benthos

Report of the ICES Study Group on the North Sea Benthos Project 2000

1 Executive Summary

Overview

The ICES Study Group on the North Sea Benthos Project 2000 undertook to integrate recent (1999–2002) macrobenthic infaunal and environmental data from various national sources.

The main aim was to compare the outcome with that of the ICES North Sea Benthos Survey conducted in 1986, to identify any significant changes and their likely causes.

In the process, the exercise yielded valuable lessons for the conduct of international collaborative programmes, as well as insights into the utility of a range of interpretational tools. These are timely in view of increasing requirements for periodic, sea-wide assessments of quality status to meet international obligations, such as those under OSPAR, ICES, HELCOM, and EU auspices for European waters.

Data sources/management

- i) A combination of new sampling effort at a proportion of the 1986 ICES North Sea Benthos Survey stations, along with contributions of existing data from several other sources, provided good coverage of the North Sea, especially of the southern part. Data from inshore environments and the eastern English Channel extended the scope of the earlier survey.
- ii) Much effort was committed to the harmonization of datasets on the macrobenthic infauna and associated environmental variables from different sources, which included desk-based evaluation of combined species lists and some laboratory work to resolve identification problems.
- iii) A database dedicated to the outputs from the ICES North Sea Benthos Project (NSBP) 2000 was constructed at the Flanders Marine Institute, underpinned by a national resource commitment. This was indispensable in serving the needs of the present collaborative assessment and will continue to act as an international repository for relevant biological and environmental data.

Analyses of NSBP 2000 data

- i) The structure and distribution of North Sea benthic communities can be explained largely by the measured (or modelled) natural environmental variables. These include temperature, salinity, tidal/wave-induced bed stress, stratification, depth, and sediment type. Their relative importance varies spatially, and many are intercorrelated.
- ii) Increased hydroclimatic variability, reduced salinity, and human-induced perturbations may account for the reduced diversity of the fauna of soft sediments in the shallowest parts of the southern North Sea. Distance from the richer Atlantic species pool may also contribute to a west-to-east decline in diversity in the southern North Sea.
- iii) Coarser substrata especially in the southwestern North Sea and eastern English Channel generally supported species-rich communities, which contrasted with a latitudinal (south-to-north) trend towards higher diversity in finer sediments.
- iv) Interface feeders were proportionately the dominant trophic group across most North Sea stations, while suspension-feeders predominated on the Oyster Ground.
- v) North Sea-wide distributional patterns for the macro-infauna, epifauna, plankton, and fish indicated relative uniformity in the responses to environmental forcing at this level, though responses on smaller scales were more variable.

- vi) For the southwestern North Sea, similar distributional patterns were observed for the meiofauna, macro-infauna, epifauna, and fish, again reflecting uniformity in the responses to environmental influences, especially habitat type and the hydrodynamic regime.
- vii) The relationship between fishing activities and benthic communities was considered to be largely correlative rather than causative. For example, comparisons of heavily and lightly fished areas may be confounded by environmental distinctions, which themselves account for the absence of commercially exploitable stocks.
- viii) NSBP 2000 data are unsuitable for evaluating the effects of fishing activities on larger (and rarer) infaunal species, which are not sampled adequately by conventional grabs or corers.
- ix) Trace metal concentrations in sediments reflect the historical legacy of industrialization, but there was no evidence of any adverse consequences for the benthic macrofauna at the levels encountered in the southwestern North Sea in 2000.
- x) There was no evidence of cumulative “footprints” associated with widely distributed industrial activities, especially oil and gas exploitation, in the southern North Sea. (Coverage was too sparse in the northern North Sea).
- xi) Illustrations of the wider utility of NSBP 2000 data were provided by a case study of the ecological role of the sand mason worm, *Lanice conchilega*, and the development of “habitat suitability models” for predicting species occurrences.
- xii) Analyses of the NSBP 2000 dataset are continuing, and additional insights will be reported in the peer-reviewed literature.

Comparisons between the 1986 and 2000 ICES North Sea benthos surveys

- i) Methodological differences between (and within) surveys were confounding variables in some assessments.
- ii) North Sea-wide patterns in sediment type were similar, and there was no significant difference in median grain sizes between datasets for matched stations.
- iii) Major distinctions between macrofaunal communities across the North Sea (especially along the 50 m contour line) were broadly similar.
- iv) There were significant differences within or at the boundaries of communities, especially in areas of the northwestern and southeastern North Sea. In some areas, these may be accounted for by recent wind-induced changes in sediment stability, e.g. in the vicinity of the Dogger Bank.
- v) Recent increases in sea surface temperature (SST) and associated food availability may account for species compositional changes, for example, in the German Bight and the southwestern North Sea approaching the English Channel.
- vi) Trends in univariate measures of the benthos at matching stations were very similar. For example, biomass and mean individual weights decreased with increasing latitude, and there was close concordance in the data from the 1986 and 2000 surveys.
- vii) Changes in the distributions or densities of selected species across the North Sea appeared in combination to reflect a dynamic equilibrium, with no evidence of a consistent directional trend.
- viii) Some species may be responding to increased SST, e.g. the brittlestar *Acrocnida (Amphiura) brachiata*, which, in 2000, occurred more frequently in the eastern North Sea, especially the German Bight, and on the Dogger Bank.
- ix) Using North Sea-wide averages, there was a marginal increase in densities and a marginal decrease in diversity. For individual communities, most univariate measures were lower in 2000, although in many cases the differences were not

statistically significant. Using multimetric indices, the quality status of all communities could be described as “good to high”, according to recently evolved classification schemes.

- x) North Sea-wide patterns in the distribution of the dominant (interface and suspension) feeding types were similar. There were significant differences in the proportional numerical contribution of feeding types within communities. However, the direction of change was inconsistent, and the causes remain speculative.
- xi) There was no evidence that changes in the benthos between the two sampling occasions were attributable to changes in fishing effort.
- xii) Comparisons of the 1986 and 2000 datasets are continuing, and additional insights will be reported in the peer-reviewed literature.

Review of other relevant information (1986–2000)

- i) There was no evidence from the available literature of a consistent directional trend over time in the densities or diversity of the benthic macrofauna at various North Sea locations. However, a number of studies identified responses to climatic changes (exemplified by correlations with the NAO Index), the nature and timing of which varied with locality.
- ii) Although the effects of commercial fishing may (through gear impact or predator removal) induce structural changes in benthic communities, there was as yet no evidence from the available literature of adverse consequences for the overall process of energy transfer through the benthic ecosystem.

Conclusions

- i) North Sea benthic communities remain in equilibrium with natural environmental forces, which account for most of the observed variability in space and time. Traits of resilience and adaptability help to explain patterns and changes in the benthic communities at the level of the entire North Sea and more locally, respectively. This conclusion can be applied to the responses both to natural and human influences.
- ii) Periodic sea-wide synoptic surveys are important to underpin the interpretation of local environmental assessments, e.g. to evaluate the significance of species distributional changes, which may not be readily identifiable over smaller scales. Future observations in a North Sea-wide setting will also be important to identify the range of ecological consequences of any directional climatic changes.
- iii) The NSBP 2000 initiative provided an excellent example of the willingness of many data providers to cooperate under ICES auspices. Practical lessons for the conduct of future collaborative survey and data compilation exercises included the importance of harmonized survey and sampling methodologies, the wider conduct of ring-testing and certification of taxonomic identification skills, the better documentation of individual datasets, and improved incentives for the submission of data to repositories to avoid data loss.
- iv) Although opportunistic exploitation of existing data is not a substitute for new survey work, it has the potential to increase the frequency of periodic assessments on large scales that are increasingly required to address issues such as the consequences of global warming or ocean acidification.
- v) The NSBP 2000 initiative demonstrates the capability of ICES to facilitate assessments of the marine environment across larger spatial scales and over longer periods than are feasible by most other organizations.

Recommendations

- i) Recommendations are made for the conduct of a coordinated interdisciplinary synoptic survey of the North Sea in 2010 under ICES auspices.
- ii) Other recommendations relate to the extension of synoptic surveys into other sea areas, the integration of outcomes with parallel information from other contemporary studies, the provision of long-term support for the North Sea Benthos database, and the establishment of links with other (European and global) databases to promote wider access.

2 Introduction

Macroinfaunal communities are especially suited to comparative investigations of the status of benthic ecosystems, because many of the constituent species are of low mobility, relatively long-lived, and integrate effects of environmental changes over time. Sampling and analytical methodologies, and accompanying frameworks for the interpretation of patterns or trends, are now well established. The macrobenthos of the North Sea has been studied on localized scales for many years and, because it is relatively easy to sample quantitatively and consistently over time, it is the mainstay of many biological trend monitoring programmes. However, the initiative to conduct a synoptic sampling exercise for the entire North Sea was only taken in 1986, under ICES auspices (e.g. Heip and Craeymeersch, 1995; Heip *et al.*, 1992; Künitzer *et al.*, 1992; Craeymeersch *et al.*, 1997). Five countries collaborated (Belgium, the Netherlands, Germany, France, and the UK) in the sampling of the southern North Sea in April 1986. The data were supplemented by an earlier extensive grid survey of the northern part conducted by Scotland (see e.g. Eleftheriou and Basford, 1989). In addition to analysis of the benthic macrofauna from grabs, data were also generated on the physico-chemical status of sediments (Basford *et al.*, 1993; Irion and Müller, 1987), on the meiofauna (principally copepods: see Huys *et al.*, 1992), and on the epifauna from small trawls or dredges (e.g. Duineveld *et al.*, 1991).

Following the success of this work, the ICES Benthos Ecology Working Group recommended that a survey be repeated to identify any changes to the status of communities identified in 1986 and their relationship with natural or human influences. A decision was made to promote national resampling of stations from the 1986 North Sea Benthos Survey or, alternatively, to seek contributions from ongoing national research and monitoring efforts that, collectively, might allow a holistic assessment comparable with that achieved in 1986.

This report documents the outcome of a collaborative exercise to reappraise the status of the North Sea macrofauna, involving seven countries and 14 data contributors. The work was conducted under the auspices of the ICES Study Group on the North Sea Benthos Project (NSBP) 2000, with the following objectives:

- i) Revisit as many stations as possible sampled during the 1986 ICES North Sea Benthos Survey;
- ii) Augment this targeted sampling effort with information from other sources collected during the period 1999–2002 in order to maximize coverage of the North Sea area;
- iii) Establish a dedicated NSBP 2000 database at the Flanders Marine Institute;
- iv) Work through annual ICES study group meetings, intersessional workshops, and via the ICES Benthos Ecology Working Group to resolve problems affecting the compatibility of datasets from different sources;
- v) Determine patterns in contemporary North Sea benthic communities and the causal influences by reference to supporting environmental data from NSBP 2000 and other sources;
- vi) Compare the outcome of NSBP 2000 with that of the 1986 ICES North Sea Benthos Survey and to postulate causes for any observed differences;
- vii) Report findings to ICES and to produce peer-reviewed papers;
- viii) Provide a strategic evaluation of the utility of the collaborative exercise for sea-wide quality assessments and to make recommendations for the timing and coordination of any future work.

In this report, we distinguish between earlier and recent synoptic survey effort as follows: the ICES North Sea Benthos Survey conducted (mainly) in 1986 is referred to as NSBS 1986, and the ICES North Sea Benthos Project 2000 is referred to as NSBP 2000. The report begins with an account of data quality and management issues (Section 3), including approaches to the

resolution of problems arising from the syntheses of data from disparate sources. This is accompanied by a description of the NSBP 2000 database, links with other international data repositories, and future data access. A description of the North Sea environment, and especially the physico-chemical status of sediments sampled alongside the macrofauna (Section 4), is followed by an evaluation of patterns and changes in the benthos (Section 5). The latter are explored in relation to community structure, species distributions, functional derivations, indices of ecological status, and links with measured or modelled environmental variables, including climatic influences. Relationships with other ecosystem components are explored in greater detail in Section 6, along with an evaluation of the consequences of demersal fishing practices for the benthic fauna. Examples are also given of the application of elements of the NSBP 2000 data in predicting habitat suitability, and in determining the structuring role of ecologically important benthic species. The main conclusions from this assessment of contemporary status and changes over time (Section 7) are followed by recommendations of both a practical and strategic nature (Section 8), which are designed to maximize the value of future international collaborative work.

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3 NSBP 2000 data management

E. Vanden Berghe, H. L. Rees, and J. D. Eggleton

3.1 Sources of data

3.1.1 Macrobenthos species distribution data

Data for the macrobenthic fauna, i.e. animals retained on a 1 mm mesh sieve, together with associated data on sediment particle size and (where available) trace metal concentrations for the ICES North Sea Benthos Project 2000, were provided by the Netherlands Institute for Sea Research (NIOZ)/Rijkswaterstaat–RIKZ Haren, TNO IMARES, the Alfred Wegener Institute for Polar and Marine Research (AWI), the Senckenberg Institute, Wilhelmshaven, the University of Kiel, the Bundesanstalt für Gewässerkunde, the Marine Station, Wimereux (University of Lille), the Centre for Environment, Fisheries and Aquaculture Science (Cefas), Marine Ecological Surveys Ltd (on behalf of a UK dredging consortium), Marine Biology section, University of Ghent, Institute for Agricultural and Fisheries Research, Oostende, FRS Marine Laboratory, Aberdeen, Akvaplan NIVA, Tromsø, and the Norwegian Institute for Water Research (NIVA), Grimstad. Also, the data from the 1986 North Sea Benthos Survey were available for analysis and comparison with the NSBP 2000 data.

A summary of those contributing benthic macrofaunal and associated sediment data is given in Table 3.1.1. Further information on the contribution of additional environmental data derived from computer models of the North Sea by the University of Hamburg and Cefas is given in Section 3.1.3.

Table 3.1.1. Contributing institutions and contact person for datasets. Note the two-letter codes, which are used later in the account to distinguish between individual datasets.

| DB | INSTITUTE | CONTACT PERSON | AREA |
|----|------------------|---------------------------------|-----------------------------|
| co | Akvaplan-NIVA | Sabine Cochrane | Norwegian waters |
| dg | Ghent University | Steven Degraer | Belgian waters |
| di | MES | Richard Newell | English Channel |
| do | TNO | Jan van Dalfsen | Dogger Bank |
| dr | Lille University | Nicolas Desroy (now at IFREMER) | French coastal waters |
| du | NIOZ/RIKZ | Gerard Duineveld | Dutch waters |
| dw | Lille University | Jean-Marie Dewarumez | English Channel |
| ee | MES | Richard Newell | English Channel |
| gl | MES | Richard Newell | English Channel |
| hi | ILVO | Hans Hillewaert | Belgian waters |
| md | MES | Richard Newell | English Channel |
| ne | BfG | Stefan Nehring | German estuaries |
| ns | ICES | 1986 North Sea Benthos Survey | North Sea (NS) |
| ou | NIVA | Eivind Oug | South-Norwegian fjords |
| ra | AWI/Senckenberg | Eike Rachor; Ingrid Kroencke | Central and southeastern NS |
| re | Cefas | Hubert Rees | English waters |
| ro | FRS | Mike Robertson | North Sea |
| ru | Kiel University | Heye Rumohr | Eastern German Bight |
| wb | MES | Richard Newell | English Channel |

Sampling occurred mainly in spring and early summer 2000 and covered almost the whole North Sea from the English Channel to about 60°N. The Norwegian dataset (*co*) contained information mainly from studies around offshore oil and gas platforms. Sampling locations are illustrated in Figure 3.1.1.

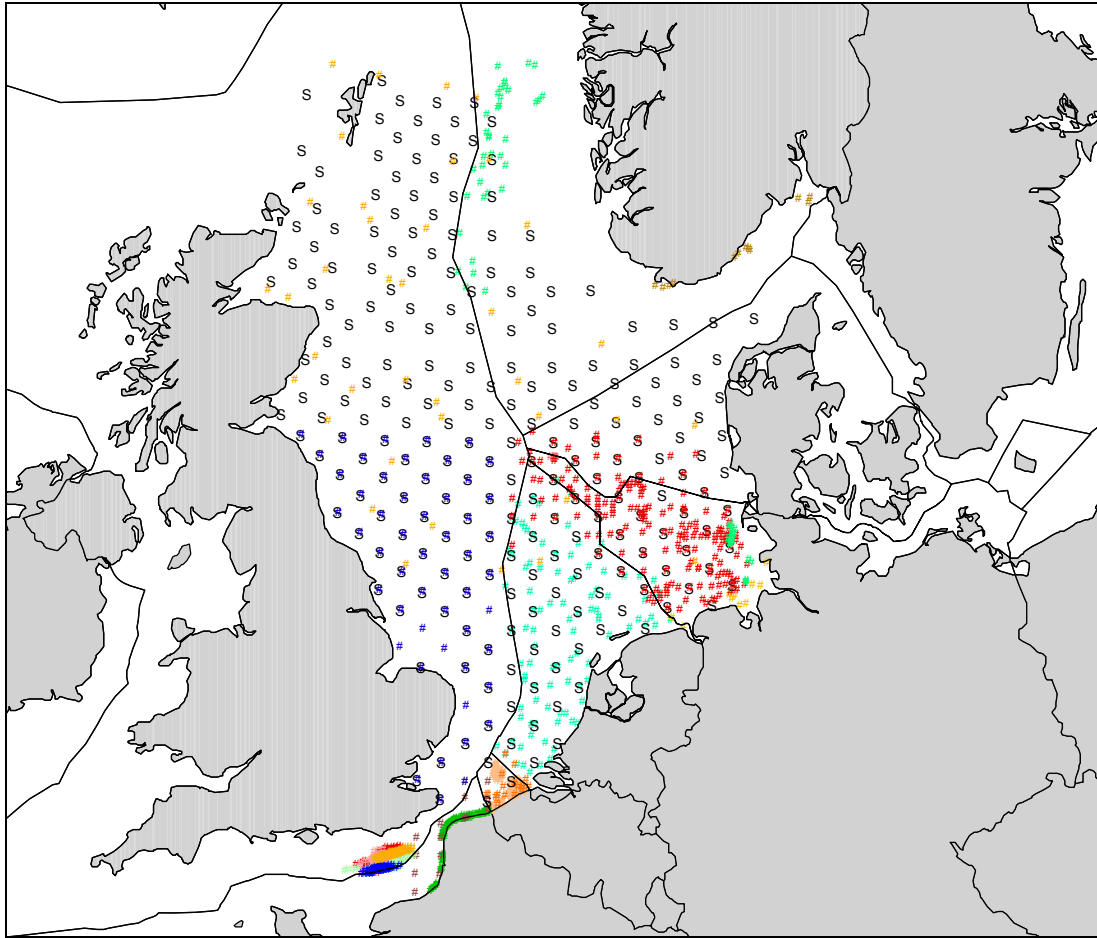


Figure 3.1.1. Location of sampling stations (1986 and 2000 surveys). The different datasets contributing to NSBP 2000 are colour-coded (e.g. red = *ra*). The NSBS 1986 stations are indicated by the letter *S*.

Sampling in UK waters was spread evenly over the area for the southern half of the North Sea (dataset *re*), with stations corresponding with those of NSBS 1986. Northern UK waters were sampled less intensively, but again locations were relatively evenly spaced (*ro*); additional stations in this dataset extend into other national waters. One of the Norwegian datasets (*co*) was collected as part of an extensive monitoring programme around offshore oil platforms. A separate smaller dataset (*ou*) was obtained for inshore southern and western Norwegian waters. Therefore, except for occasional stations from dataset *ro*, no data were available for the area between the Norwegian west coast and the offshore monitoring stations. Only a limited amount of data (*ra*/AWI) could be obtained for Danish waters.

Several datasets were available for German estuarine and marine waters (*ne*, *ra*, *ru*). A single dataset from the Netherlands (*du*) covered the entire Dutch continental shelf. However, because of the relatively small surface area covered by the corer (see Table 3.1.2), samples collected in 2000 were supplemented with those from 2001 at comparable locations, and employed as “pseudo-replicates”. A separate small dataset was available from the Dogger Bank (*do*). Two datasets were available from Belgian waters (*dg*, *hi*), one of which consisted of large numbers of stations in a relatively confined area, sampled within a proposed marine protected area in the southern part of the Belgian Economic Exclusion Zone (EEZ). Of two French contributions (*dr*, *dw*), the first was coastal and the second comprised a regular grid extending into the English Channel, including UK waters. Finally, a series of five UK datasets (*di*, *ee*, *gl*, *md*, *wb*) comprised several stations in the central part of the eastern English

Channel, which were sampled by a consortium of dredging companies to generate baseline data in the vicinity of proposed aggregate extraction sites.

Figure 3.1.2 illustrates the sampling intensity as a function of latitude, longitude, and depth. Obviously, the pattern is dictated by the bathymetry of the North Sea. The deeper samples are from Norway (*co, ou*). The two areas most heavily sampled (the southern part of the Belgian EEZ – *dg* – and the central part of the eastern English Channel – *di, ee, gl, md, wb*) clearly influence the pattern.

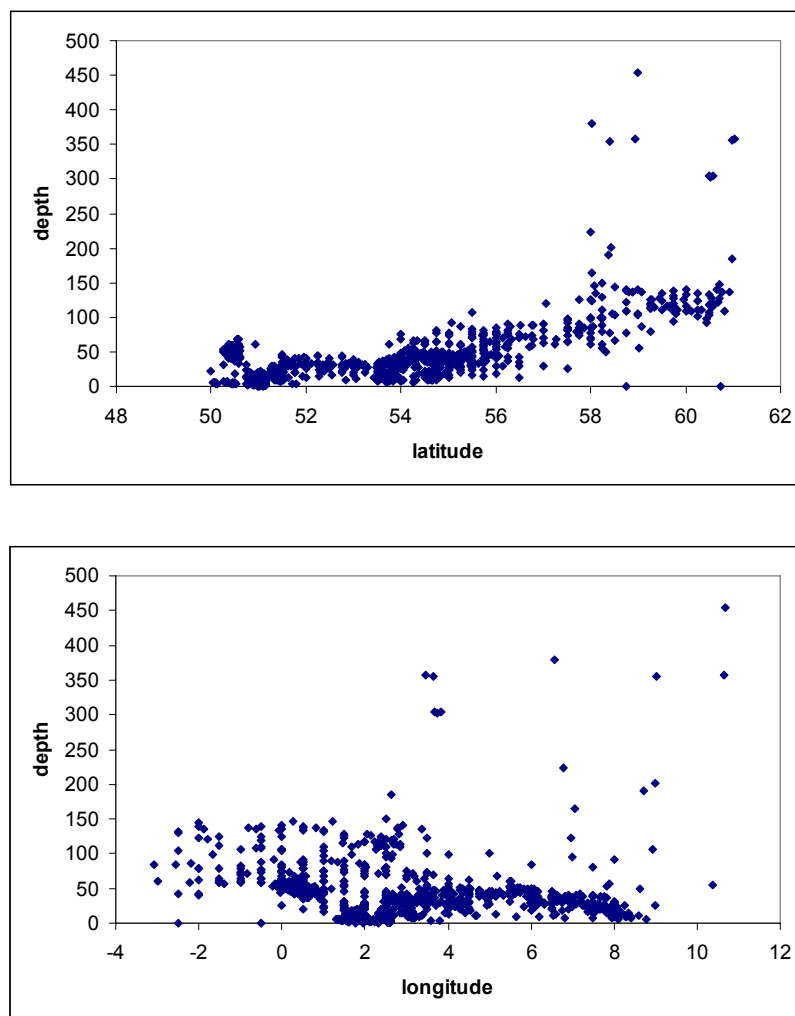


Figure 3.1.2. Variation of depth with latitude and longitude.

Most of the sampling for NSBP 2000 was conducted with a 0.1 m² van Veen grab; Dutch (*du*) and Scottish (*ro*) samples were obtained with boxcorers, English ones (*re*) mostly with a 0.1 m² Day or Hamon grab, depending on the sediment type (Table 3.1.2). Samples were sieved over a 1 mm mesh. Sieving was done before fixing, except for the samples from ILVO (*hi*) and a proportion of the samples from Ghent University (*dg*), where they were fixed before sieving. Generally, two to three replicates per station were taken; only one sample per station was taken by, e.g. Ghent University and NIOZ-RIKZ. Dutch samples were collected as part of an annual monitoring programme. Further details of sampling and subsequent treatment of the samples are given in Table 3.1.2.

Table 3.1.2. Sampling equipment used for the different datasets and availability of biomass data.

| DB | EQUIPMENT | REPLICATES | BIOMASS |
|----|--|------------|---|
| co | 0.1 m ² van Veen grab | 5 or 10 | Not available. |
| dg | 0.1 m ² van Veen grab | 1 | Not available. |
| di | 0.2 m ² Hamon grab | 1–3 | Biomass per grab–Polychaeta, Mollusca, Crustacea, Echinodermata, misc. |
| do | 0.1 m ² van Veen grab | 5 | Not available. |
| dr | 0.2 m ² Hamon grab | 2 | Replicates pooled–Polychaeta, Nemertea, Mollusca, Crustacea, Echinodermata, misc. |
| du | 0.068 m ² boxcore | 2 | To species. |
| dw | 0.1 m ² van Veen grab | 2 | To species. Data for the one pooled station was estimated per replicate from the densities recorded in each. Data reported in mg per 0.1 m ² . |
| ee | 0.1 m ² Hamon grab | 1–3 | Biomass per grab–Polychaeta, Mollusca, Crustacea, Echinodermata, misc. |
| gl | 0.1 m ² Hamon grab | 1–3 | Biomass per grab–Polychaeta, Mollusca, Crustacea, Echinodermata, misc. |
| hi | 0.1 m ² van Veen grab | 3 | Complete, to species. |
| md | 0.1 m ² Hamon grab | 1 | Biomass per grab–Polychaeta, Mollusca, Crustacea, Echinodermata, misc. |
| ne | 0.1 m ² van Veen grab | 6 | Not available. |
| ns | Cores; van Veen/Smith-McIntyre grabs | 2–12 | Replicates separate. Polychaeta, Mollusca, Crustacea, Echinodermata, misc. |
| ou | 0.1 m ² Day or van Veen grab | 4 | Not available. |
| ra | 0.1 m ² van Veen grab | 1–4 | Replicates separate. Polychaeta, Mollusca, Crustacea, Echinodermata, Chordata, Bryozoa, Cnidaria, misc. |
| re | 0.1 m ² Hamon, Day or van Veen grab | 2–3 | Replicates separate, to species. |
| ro | 0.25 m ² NIOZ core | 1–3 | Replicates separate, to species. |
| ru | 0.1 m ² van Veen grab | 1 | Not available. |
| wb | 0.2 m ² Hamon grab | 1 | Biomass per grab–Polychaeta, Mollusca, Crustacea, Echinodermata, misc. |

Sampling in the southern North Sea for NSBS 1986 was conducted in April/May, 1986, employing a 1 mm mesh sieve to extract the macrofauna. However, sampling in the northern North Sea was conducted between 1980 and 1985, using a 0.5 mm mesh sieve, as part of an earlier synoptic survey of this area by FRS (Scotland). Further details are given in Eleftheriou and Basford (1989), Heip *et al.* (1992), and Kunitzer *et al.* (1992). The samples for NSBP 2000 were mostly collected in 2000 but, as is apparent from Table 3.1.3, some data for 1999, 2001, and 2002 were also included in the combined dataset to improve the evenness of the coverage. Three samples from 2002 were included in the *ra* dataset because these locations were not visited in 2000. Likewise, 20 samples from 2002 were included in the *re* dataset, to complete a synoptic survey of English waters, employing the same stations as in 1986 NSBS. To compensate for the under-representation of samples in Dutch waters, samples collected in 2001 were included as pseudo-replicates.

In comparisons with earlier (NSBS 1986) sampling in April/May for the southern North Sea, there is the potential for confounding influences associated with the wider (spring/early summer) sampling window for NSBP 2000. However, the use of a 1 mm mesh sieve might be expected to limit any effects on density and diversity estimates arising from new recruitment in this period, compared with the use of a smaller (0.5 mm) mesh sieve.

Table 3.1.3. Number of samples, per year and per dataset.

| DB | 1980–1985 | 1986 | 1999 | 2000 | 2001 | 2002 |
|----|-----------|------|------|------|------|------|
| co | | | | 192 | 105 | |
| dg | | | | 183 | 73 | |
| di | | | | | 138 | |
| do | | | | 12 | | |
| dr | | | | 179 | | |
| du | | | | 100 | 100 | |
| dw | | | | 31 | | |
| ee | | | | | 165 | |
| gl | | | | | 83 | |
| hi | | | | 56 | | |
| md | | | 89 | | | |
| ne | | | | 60 | | |
| ns | 62 | 219 | | | | |
| ou | | | | 48 | | |
| ra | | | | 339 | | 3 |
| re | | | | 78 | 50 | 20 |
| ro | | | | | 75 | |
| ru | | | | 30 | 25 | |
| wb | | | 94 | | | |

Biomass was estimated by most of the laboratories, ranging from wet weight to ash-free dry weight (AFDW). Conversion factors can be used to standardize biomass for all datasets. AFDW and wet weight data are available from NIOZ–RIKZ and Wimereux to calculate conversion factors; conversions by Rumohr *et al.* (1987) are also commonly used. Some laboratories determined biomass for individual species, others for phyla only (or other high rank taxon). The availability of biomass data, along with an indication of the taxonomic levels at which they were determined, is illustrated in Figure 3.1.3 and Table 3.1.2.

Samples for analysis of the meiofauna were taken only by Cefas and FRS. An account of the meiobenthic (mainly nematode) communities of the southwestern North Sea is given in Section 6.4.

3.1.2 Other species distribution data

The ICES International Bottom Trawl Survey (IBTS) in the North Sea has been undertaken annually during January/February since about 1970. Part of this survey includes hydrochemical measurements at each station, which has resulted in a comprehensive dataset for the North Sea. Prior to 1993, the IBTS surveys were known as the International Young Fish Surveys (IYFS). Selected trawl data are publicly available on the ICES website (www.ices.dk/ocean/project/IBTS/).

A survey under ICES and EU auspices was carried out in 2000, in which five nations sampled the epibenthic and fish fauna at 270 stations throughout the North Sea. The aim of the survey was to investigate the diversity and community structure of epibenthic and fish communities and to identify relationships with environmental factors, including the frequency of commercial otter and beam trawling disturbance. The data have been analysed and published by Callaway *et al.* (2002).

A comparison of the results of the present study, in terms of distribution of communities, with the results of these epibenthos and demersal fish studies is given in Section 6.1.

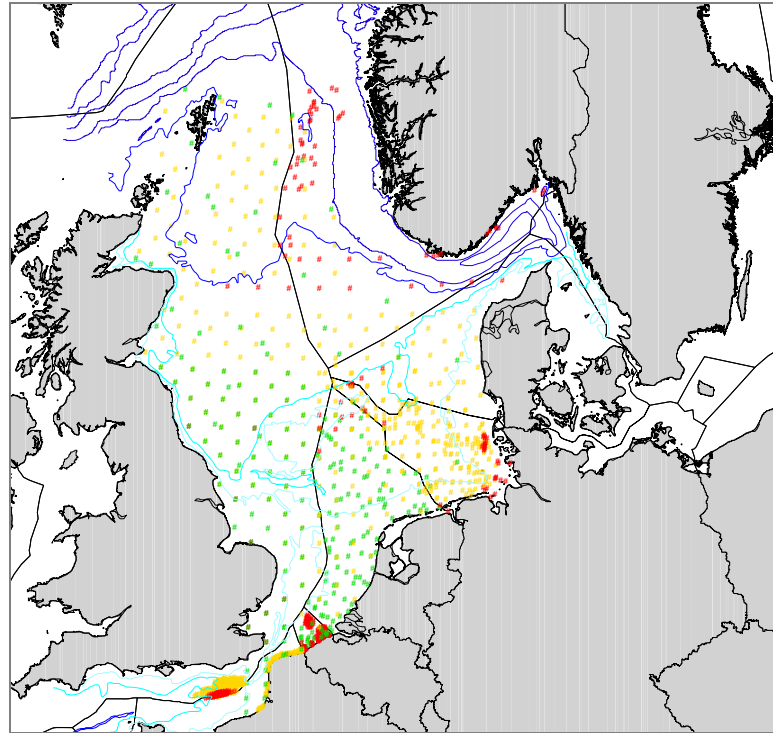


Figure 3.1.3. Available biomass data for 1986 and 2000. Red: no data; yellow: available per phylum; green: available per species.

3.1.3 Environmental data

Most data contributors collected information on the abiotic environment. The parameters measured varied widely, and procedures were not standardized. Depth and sediment granulometry were two parameters that were retained in the integrated database for analysis (see Section 4.2 for an account of the latter). However, data on contaminant concentrations in sediments were more limited (see Section 4.3). Data on salinity, temperature, and chlorophyll, along with tidal and wave stress, were derived from computer models. We are grateful to T. Pohlmann (University of Hamburg) and J. Aldridge (Cefas) for providing the following summaries.

Temperature and salinity (HAMSOM)

The hydrodynamic **Hamburg Shelf Ocean Model (HAMSOM)** is a three-dimensional, baroclinic primitive equation model for simulations of oceanic and coastal and shelf sea dynamics. It has a resolution of 5 minutes in latitude and longitude and a vertical resolution of ten layers. The numerical scheme of HAMSOM was developed at the Institute of Marine Research (University of Hamburg) by Backhaus (1985). For details about the HAMSOM model, see Pohlmann (1991). More information is available on a dedicated website (www.ifm.uni-hamburg.de/~wwwsh/res/HAMSOM/hamsom.html).

Primary production (ECOHAM1)

The model **ECOHAM1 (ECOLOGical North Sea Model, HAMBURG)** is a computer model that can be used to calculate annual and long-term phytoplankton dynamics for shelf seas in a three-dimensional physical environment (Moll, 1997). It is the simplest model for the analysis of the phytoplankton dynamics, nutrient transport, and primary productivity in the North Sea. The model, based on a simple phosphorus/nitrogen cycle, takes four state variables into account, namely three pelagic variables: phytoplankton, phosphate (DIP), nitrogen (DIN), and one for benthic detritus. The model uses the simplest parameterization for pelagic and benthic regeneration. The horizontal grid size of the numerical model is 20×20 km, the vertical

resolution is 5 m for the upper 50 m and increasing layer thickness below 50 m up to a maximum of 19 layers. The ECOHAM1 model was validated using observed chlorophyll (Moll, 1998), phosphate concentrations (Moll, 2000), and primary production values (Skogen and Moll, 2000). More information is available on the website www.ifm.uni-hamburg.de/~wwwem/dow/Ecoham/index.html.

Tide and wind data

Tidal parameters were generated at Cefas using a three-dimensional hydrodynamic model (Davies and Aldridge, 1993), run in depth-integrated form on an approximately 3.5-km resolution grid covering the European continental shelf. A formal validation procedure was not carried out. However, distributions of tidal amplitude and phase were plotted and found to be in close visual agreement with known distributions of these quantities (e.g. Pingree and Griffiths, 1979). Tidal bed stress was derived from the M_2 tidal constituent, the largest component on the European continental shelf. The amplitude of the depth mean M_2 tidal ellipse at the grid point nearest to the survey station was calculated. The peak M_2 velocity (that aligned along the major axis of the tidal ellipse) was converted to a bed shear stress using a standard quadratic formulation with drag coefficient $C_D = 0.0025$.

The stratification parameter S was derived from the formulation presented in Pingree and Griffiths (1979), using modelled M_2 tidal velocities and measured depths at the benthic stations.

Average and peak wave stress were calculated from a one-year model run covering the period September 1999 to September 2000, on an approximately 12-km grid, using the WAM spectral wave model run at the Proudman Oceanographic Laboratory (Osuna and Wolf, 2004). Again, no formal validation has been undertaken. Instantaneous wave stress was calculated from the significant orbital velocity at the bed using a standard quadratic formulation with friction factor (f_w) as given for rough beds by Swart (1974). A constant bed grain-size roughness corresponding to 0.1 mm of sand was assumed. Average and peak values of the wave stress were calculated at the grid point nearest the benthic station to obtain the values used in this study.

Although no validation of the tidal predictions has been carried out, we are confident that the relative distribution of tidal bed stresses is sufficiently accurate for the present interpretation. There is greater uncertainty in the predictions of wave parameters; nevertheless, we believe the relative distribution of wave-generated stress is adequate for the present task.

3.2 Sampling locations and replication

In 1986, funding was available to organize dedicated cruises in the central and southern North Sea, and to arrange for common sampling procedures. The survey design consisted of a regular grid, based on ICES rectangles. No comparable funding for a collaborative North Sea-wide survey was available in 2000, and much of the data employed in the present report was collected for other purposes, for example, to meet national monitoring, regulatory, or research needs. This resulted in more uneven coverage, e.g. a concentration of stations in parts of Belgian waters (dataset *dg*) and high replication at stations in Norwegian waters (dataset *co*).

To facilitate comparison between the NSBS 1986 and NSBP 2000 stations, a set of “standard pairs” was calculated. The number of stations in the NSBP 2000 dataset was much higher than in NSBS 1986. For each NSBS 1986 station, the closest NSBP 2000 station was calculated using ArcView. Each station from NSBP 2000 was allowed to be included in the list only once. In the resulting table, distances between station pairs were often very small, but, especially towards the north, much larger, which limits accurate interpretation.

The position of the nearest neighbour stations is illustrated in Figure 3.2.1. No stations are located in the English Channel, because this area was not part of the 1986 survey. Only a few

station pairs are available in the northern North Sea, mainly because of the limited geographical coverage of the available data for the 2000 period.

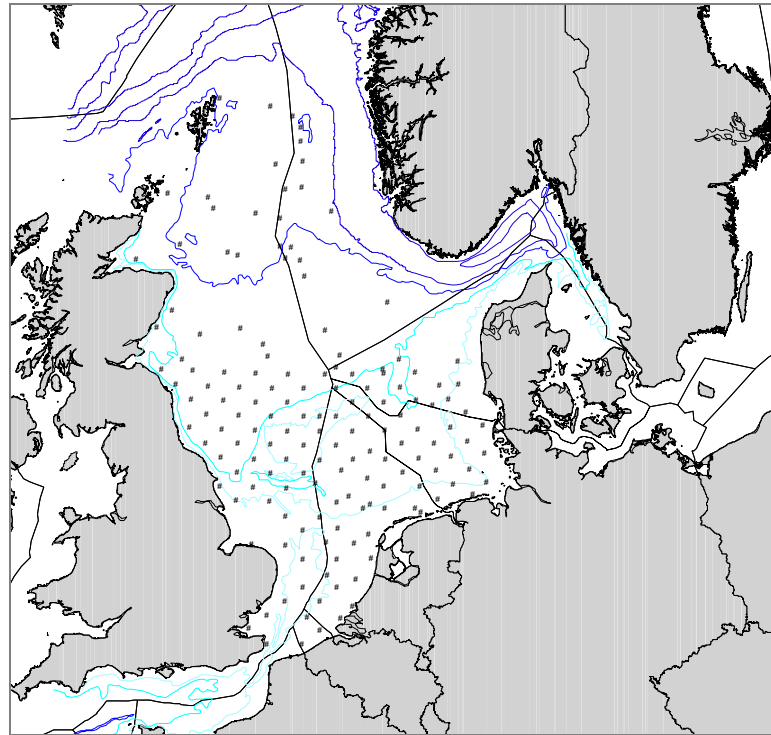


Figure 3.2.1. Location of “nearest neighbour” station pairs.

3.3 Taxonomic problems

After excluding spelling variations, the database (1986 and 2000 data combined) contained 1954 taxonomic entities, of which 939 (48%) were unique to individual datasets. However, the incidence of species found only once within any individual dataset was much smaller; e.g. for Akvaplan NIVA: 110 from a total of 629; for NIOZ–RIKZ: 56/218; and for the ICES North Sea Benthos Survey conducted in 1986: 201/1004. The high incidence of occurrences unique to individual datasets indicated that there could be differences in interpretation of the taxonomic literature between the different data contributors.

Taxonomic names were initially checked using the database Integrated Taxonomic Information System (ITIS; www.itis.org). It was found that 2% of the genera and 18% of the species in the NSBP 2000 list were missing in ITIS. So clearly, the problems described above seemed to have come from inconsistencies in the identification of species, rather than problems with nomenclature *per se*.

Taxonomic/nomenclatural problems were addressed during workshops held at AWI, Bremerhaven (September 2002), RIVO, Yerseke (March 2003), and VLIZ, Oostende (November 2003). During the Bremerhaven workshop, specimens from problem species were looked at by several data contributors, and some differences in interpretation resolved. The result was a significant reduction of errors in the taxa list.

3.4 Database

Data received from the project participants were uploaded into a central database. The database itself is a Microsoft SQL server database, with a front end developed in MS Access. For the taxonomy/species lists, no separate database was developed, but the existing species register at the Flanders Marine Institute (VLIZ) was used.

The structure for the taxonomic information was adapted from the structure of the ITIS database. The taxonomic hierarchy is implemented as an open-ended hierarchy, where every taxonomic name or name part is stored in a single record, together with a pointer to a parent record. In contrast to the ITIS structure, this open-ended hierarchy is consistently implemented for all taxonomic ranks: in ITIS, name parts for everything below genus are stored in a single record with a maximum of four name parts per record. The structure of the database is illustrated in Figure 3.4.1.

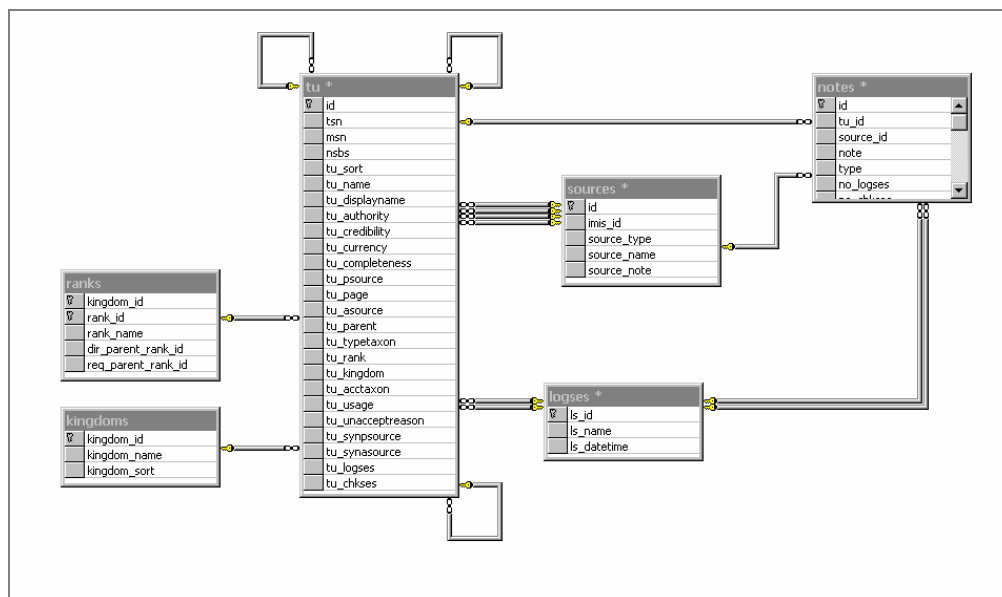


Figure 3.4.1. Structure of the taxonomic part of the database.

Data were sent to VLIZ either as MS Excel spread sheets, or as structured text or MS Word documents. Information was then first converted into separate MS Access mdb databases. After an initial quality check, the data were uploaded to the central database described above.

All taxonomic names were checked against the VLIZ taxonomic register, and an entry was created in this register when necessary. As a quality control procedure, all names were checked against the ITIS database. Synonyms were identified and linked with the valid name; often different names were in use for the same species in different component datasets. In the meantime, the European Register of Marine Species (ERMS) has become available; this register was compiled by a consortium of taxonomists funded by an EU project that ended in 1999. Funding from the EU Marine Biodiversity and Ecosystem Functioning network (www.marbef.org) and Species 2000 europa (www.sp2000europa.org) was used to convert the original MS Excel spread sheets into a database. All names from NSBP 2000 are now aligned with the names in ERMS, to facilitate integration in larger data collections.

Non-macrofauna (e.g. fish, other epifauna, and pelagic species) were flagged to allow exclusion from subsequent analysis.

In the data contributions, information on life stage was often lumped with the taxonomic information. This necessitated parsing this field into its taxonomic and life stage component. In the integrated database, the two kinds of information were stored separately.

Often, identifications were not done to species, or the identifier indicated doubt about the species; sometimes two species were mentioned. In all these cases, the taxonomy was reduced to the next higher formal taxonomic level.

An interface was built on the integrated database, allowing users to manipulate data prior to analysis and allowing fine-tuning (including inclusion/exclusion) of data on the level of dataset, species, or individual distribution records (Figure 3.4.2).

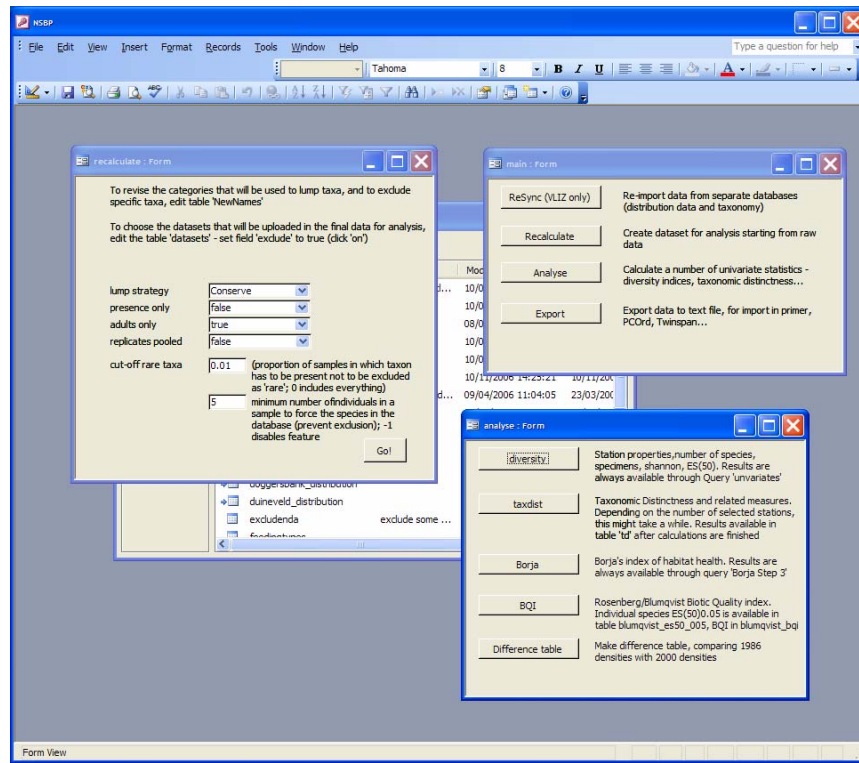


Figure 3.4.2. The user interface.

The NSBP 2000, data were collected for a variety of reasons (see above), and so resulted in a rather heterogeneous mix of datasets. For this reason, not all datasets were suitable for all types of analysis. Also, metadata were missing for a limited number of datasets, making it impossible to perform certain types of analysis.

The mix of incomplete and complete identifications, and various degrees of confidence in the accuracy of the identifications, necessitated building a system whereby different taxa could be lumped before being used in an analysis. If there are identifications to a genus in the database, but also identifications to several species within this genus, then it was felt that a choice should be made to either exclude the incomplete identifications or to aggregate the species with the genus. Two lumping strategies were built in to the interface that automated these exclusions or aggregations.

Another feature of the interface was the possibility to exclude rare species, which can be a useful option for certain interpretational needs. For this, a first criterion that could be set was to exclude any species from the analysis that occurred in less than a given fraction of the stations in the dataset. A second criterion could be set: if a species that would be excluded on the basis of the first criterion was very common at the few stations where it did occur, it could be retained in the analysis.

Several calculations were defined in the database: number of species and individuals per station, expected number of species, density, more commonly used conventional diversity indices, taxonomic distinctness (Warwick and Clarke, 1995), and two multimetric indicators of environmental quality: AMBI (Borja *et al.*, 2000) and BQI (Rosenberg *et al.*, 2004).

The modified dataset, after exclusions, lumping of taxa, etc., could be exported in a variety of formats to meet the needs of different analytical tools. Available were a generic list format, the condensed format for use with TWINSpan (Hill, 1979), and a generic matrix format that could be read by e.g. PRIMER (Clarke and Gorley, 2006). The last was especially important: none of the MS Office applications support tables with more than 256 columns. In our dataset, both the number of stations and the number of species were much larger than this. The export was done to a tab-delimited text file, getting round the limitation of the MS Office applications. PRIMER does not suffer the same limitations.

3.5 Summary statistics

The total number of distribution records for the NSBP 2000 dataset was 91 362, from 1570 stations, 2609 samples, and 1954 different taxa. The distribution of samples by species, and *vice versa*, is shown in Figure 3.5.1. A summary of the characteristics of the contributing datasets is given in Table 3.5.1.

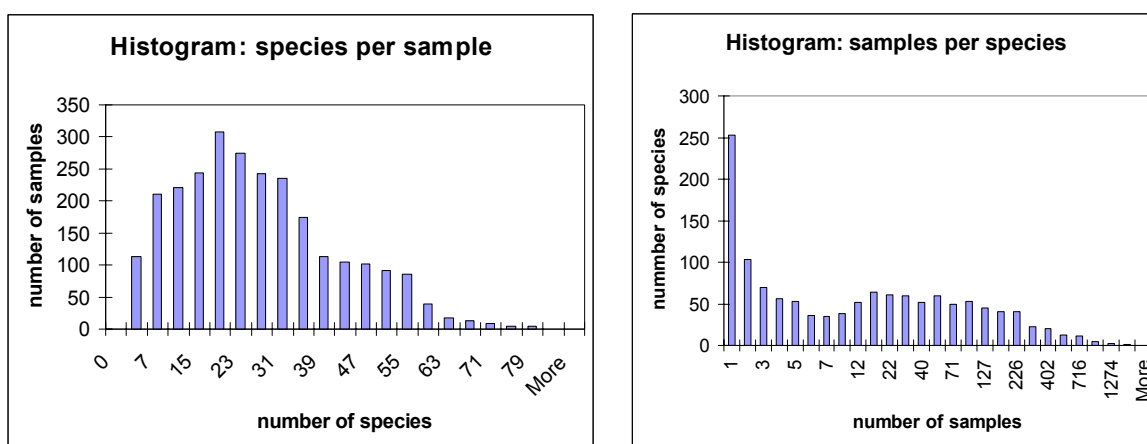


Figure 3.5.1. Number of species per sample and number of samples per species for the entire ICES NSBP 2000 dataset.

Table 3.5.1. Numbers of taxa, stations, and samples per contributing dataset.

| DB | RECORDS | TAXA | STATIONS | SAMPLES |
|----|---------|------|----------|---------|
| co | 14 891 | 576 | 37 | 297 |
| dg | 4057 | 177 | 256 | 256 |
| di | 12 088 | 360 | 106 | 138 |
| do | 566 | 114 | 12 | 12 |
| dr | 1073 | 111 | 94 | 179 |
| du | 4663 | 269 | 100 | 200 |
| dw | 493 | 167 | 15 | 31 |
| ee | 4433 | 347 | 137 | 165 |
| gl | 3251 | 244 | 67 | 83 |
| hi | 637 | 114 | 19 | 56 |
| md | 6360 | 377 | 89 | 89 |
| ne | 286 | 58 | 10 | 60 |
| ns | 11 820 | 709 | 231 | 281 |
| ou | 1918 | 280 | 12 | 48 |
| ra | 10 236 | 426 | 181 | 342 |
| re | 4230 | 666 | 53 | 148 |
| ro | 4680 | 555 | 38 | 75 |
| ru | 1026 | 123 | 19 | 55 |
| wb | 4654 | 279 | 94 | 94 |

Finally, in Figure 3.5.2a–c we present a comparison of summary statistics (total densities and ES(50) values: expected number of species in a hypothetical sample of 50 individuals) for the 1986 and 2000 North Sea benthos datasets at “matched” stations. The distributions of ranked densities are nearly identical (Figure 3.5.2a). Ranked ES(50) values are marginally though persistently lower in 2000, which may be an artefact of different sampling practices in 1986 and 2000: most of the stations in the central and southern North Sea were sampled by deeper-penetrating cores in 1986. Especially in sandy sediments, these may be more efficient at retaining species than grabs, which were used at most of the stations sampled in 2000 (see e.g. Rumohr, 1999). The relationship between ES(50) values and latitude, including the degree of variability around the fitted regression lines, was very similar in 1986 and 2000 (Figure 3.5.2c). We conclude that these broad comparisons of data structure provide reassuring evidence of the integrity of the NSBP 2000 dataset, despite reliance on more disparate sources than in 1986. Therefore, it provides a sound basis for an evaluation of the status of North Sea benthic assemblages in 2000, and of any changes since 1986, while recognizing that sampling and analytical influences must also be accounted for in ecological interpretations, and this is evident in the following sections.

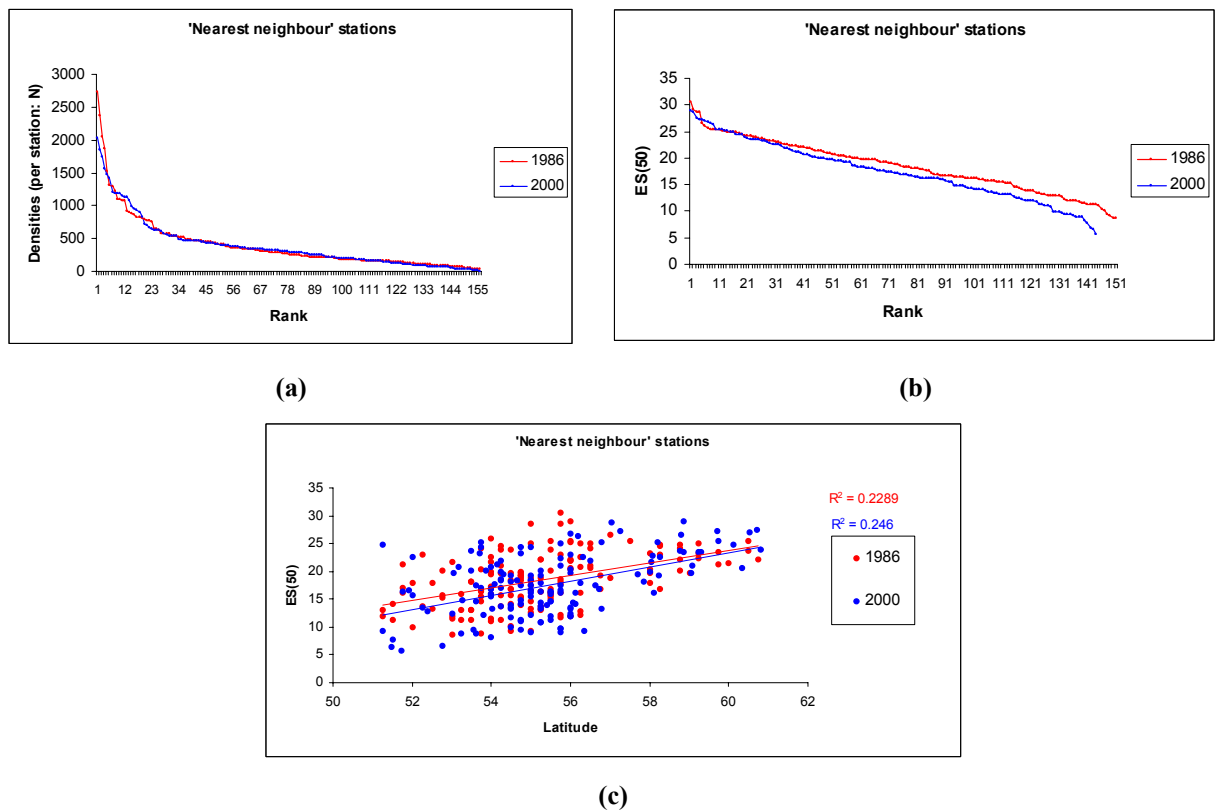


Figure 3.5.2a–c. Comparison of (a) ranked densities, (b) ranked ES(50) values, and (c) ES(50) values vs. latitude for the 1986 and 2000 ICES North Sea benthos datasets.

3.6 Access to NSBP 2000 data

Data policy, initially relating to access to data by non-data contributors, was discussed at several meetings of the ICES Study Group on the North Sea Benthos Project 2000 (ICES SG NSBP 2000). Although none of the contributors doubted the virtue of data sharing, it was felt that publication of the outcome of the collaborative ICES SG NSBP 2000 initiative to reflect the significant resource commitment of the participating institutes was reasonable, prior to complete transfer to the public domain. The data policies of MarBEF (see www.MarBEF.org) and other comparable international initiatives were reviewed, and the benefits of future collaboration were identified.

Arising from discussion at a final intersessional meeting of the ICES SG NSBP 2000 held in Oostende in November, 2006 and subsequent consultation with all data providers, the following was agreed:

- Permit unrestricted access to environmental data (granulometry, temperature, salinity, tidal and wave stress, heavy metal concentrations) at NSBP 2000 stations;
- Release species presence/absence data through the dedicated website after publication of the *ICES Cooperative Research Report (CRR)* summarizing the outcome of the NSBP 2000 initiative; this would be accompanied by a “terms of use statement,” along the lines of the MarBEF policy;
- Release species presence/absence data via EurOBIS after publication of the CRR, with links back to the NSB website;
- Release quantitative data via the NSB website after publication of follow-up research papers or after two years, whichever comes first.

The ICES NSBP 2000 database will continue to be supported by the Flanders Marine Institute (VLIZ) on behalf of ICES.

Note that the datasets contributing to the ICES NSBP 2000 database remain the property of the guardians or sponsors of the individual projects that led to their production. The release of these individual datasets for any other purposes clearly remains entirely at their discretion.

This policy now supersedes the data sharing statement that was agreed at the outset of the ICES NSBP 2000 initiative (see ICES, 2004).

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4 The North Sea environment

4.1 Synopsis and human influences

H. L. Rees, E. Rachor, and J. N. Aldridge

The Greater North Sea is defined (OSPAR Commission, 2000) by coordinates at 48° to 62°N, and 5°W to 12°E (Figure 4.1.1). To the south, it embraces the entire English Channel bordered by England, France, and Belgium, and to the east the waters of the Skagerrak and Kattegat, bounded by Denmark, Norway, and Sweden. These boundaries do not signify any isolation of the water mass, and exchange occurs principally through the influx of Atlantic water to the north and to a lesser extent via the Channel, and from the Baltic to the east, along with northward efflux, mainly along the Norwegian coast. An overall estimate of about one year for the flushing time of the entire North Sea disguises significant regional and temporal variations associated, *inter alia*, with prevailing depth, wave and tidal current regimes, and thermal stability of the water column.

The North Sea is relatively shallow, with depths generally not exceeding 100 m, except in the northern North Sea and in the Norwegian Trench (Figure 4.1.2).

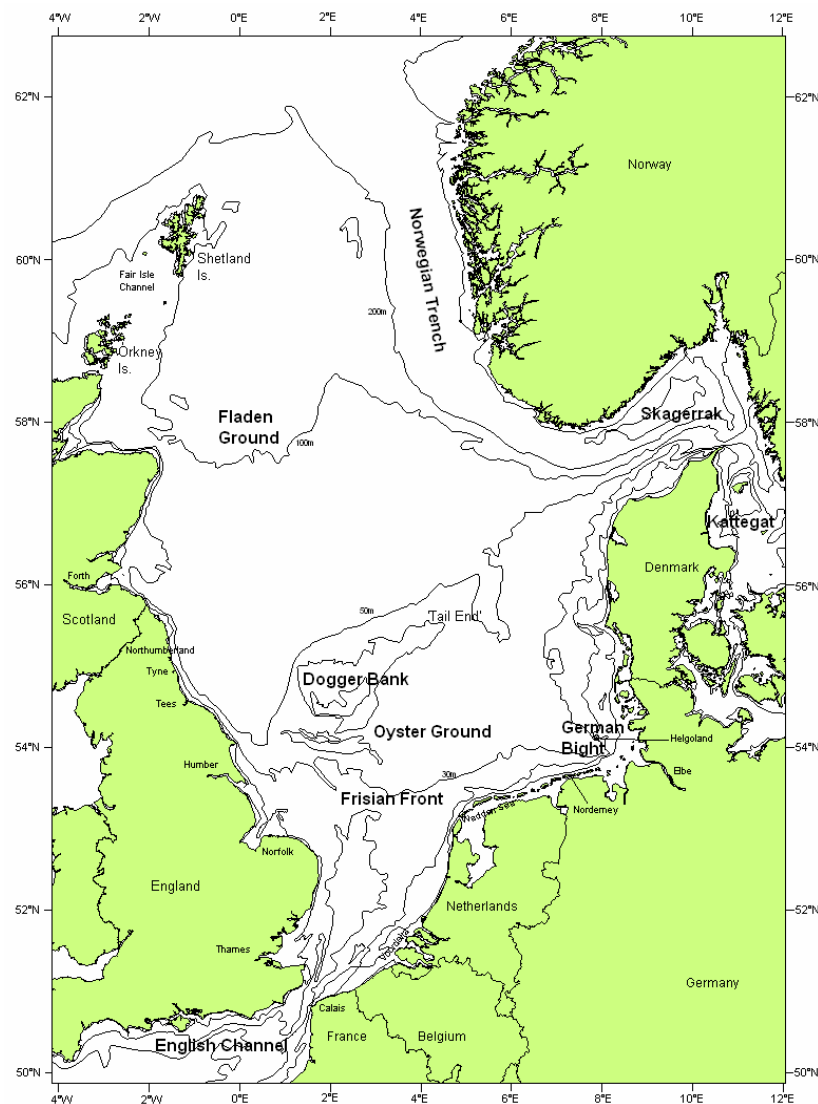


Figure 4.1.1 The North Sea with depth contours and selected locations referred to in this report. Courtesy of M. Curtis (Cefas).

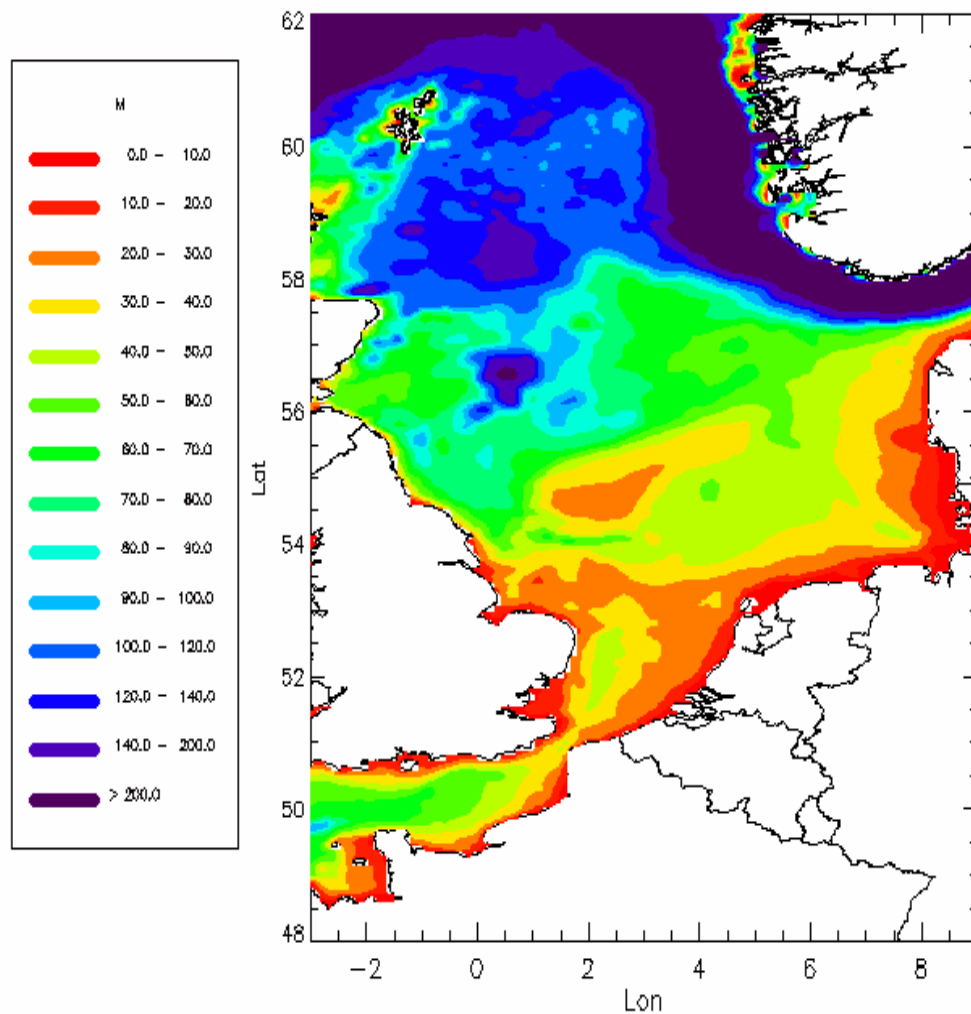


Figure 4.1.2. Bathymetry of the North Sea (source: Cefas).

Generally, depths do not exceed 50 m for most of the southern North Sea, including the eastern Channel. The northern boundary of the Dogger Bank in the central North Sea is defined approximately by the 50 m contour, which also serves to distinguish latitudinally between contrasting ecological and biogeographical domains.

Patterns in bottom-water temperature and salinity in winter (Figure 4.1.3) illustrate the influence of Atlantic water in the deeper northern North Sea, and of freshwater inflows from the larger river systems in the shallower southern part. As would be expected, the patterns vary vertically, seasonally, and annually and are summarized by (for example) the OSPAR Commission (2000). Information on annual temperature trends is also given below.

Most of the North Sea is mixed in winter, but is stratified in deeper offshore waters of the central and northern parts in summer. The waters of the southern part remain mixed throughout the year, owing to the shallow bathymetry and the influence of stronger tidal currents (OSPAR Commission, 2000; Figure 4.1.4). Spatial differences in the magnitude of tidal currents can also be expected to influence both the nature and stability of bottom sediments and hence the nature of the associated benthic communities.

Climatic influences on the North Sea ecosystem over various timescales (for example, changes in the North Atlantic Oscillation (NAO) index) have been linked to changes in circulation patterns, alterations to the composition and productivity of phyto- and zooplankton

with consequences for recruitment or migration of certain commercial fish species (Anon., 2001), as well as to changes to benthic communities (see Section 5.7).

As we have a special interest in identifying the causes of any changes to the status of benthic communities between 1986 and 2000, we show trends in the winter (December–March) NAO index for the Northeast Atlantic (Figure 4.1.5) and Sea Surface Temperature (SST; Figure 4.1.6) as expressions of climatic variability. The NAO index employed in Figure 4.1.5 is a measure of the difference of normalized sea level pressures between Gibraltar and Iceland. (The index is one of several permutations expressing contrasts in pressure data between weather stations in the vicinity of the subtropical Azores High and the polar Icelandic Low.) Positive values tend to be associated with warmer, wetter winters characterized by westerly airflows, while negative values reflect colder, more quiescent conditions characterized by northerly airflows. Following a period of persistently negative values in the 1960s, an upward trend encompassing the 1986 survey continued until the mid-1990s. After a drop in 1996, values remained near zero or positive until 2000. In the southern North Sea, annual mean values for SST were generally higher after 1986 than in preceding years, with a notable drop in 1996 (Figure 4.1.6a). This is also evident in the plot of seasonal SST anomalies (Figure 4.1.6b) and is consistent with a general warming trend in the North Atlantic over this time (ICES, 2006). The implications of changes in the NAO index and water temperatures for benthic communities are examined in Sections 5.2, 5.3, and 5.7.

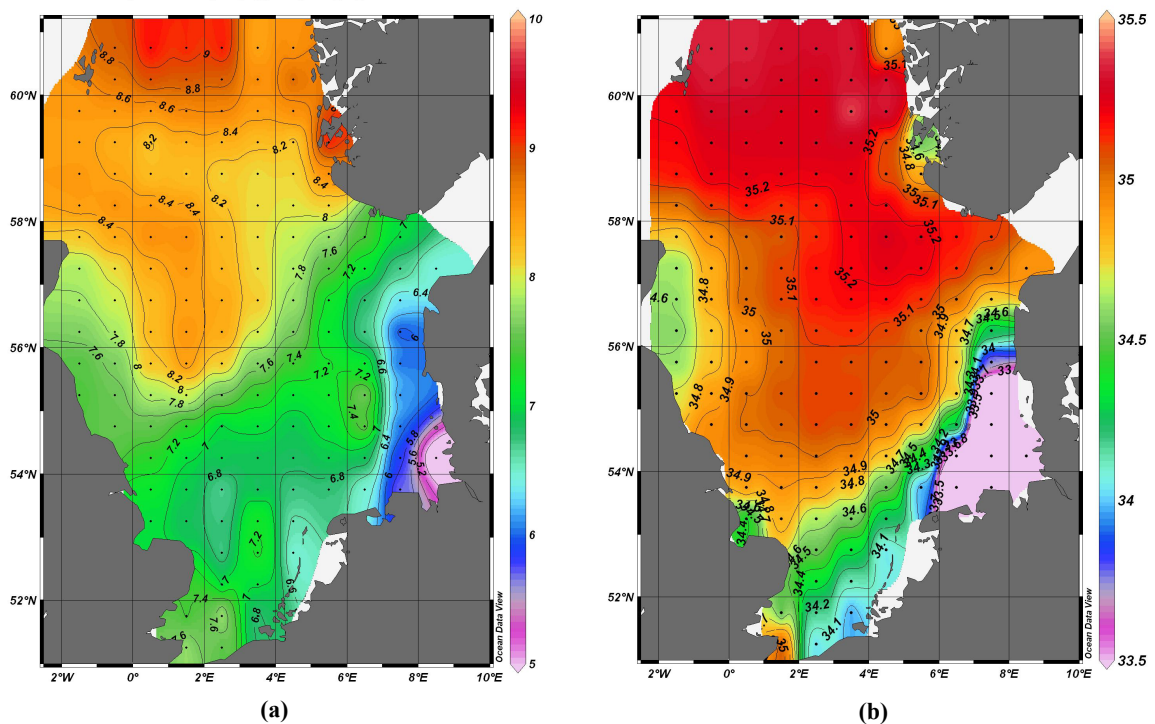


Figure 4.1.3. Winter (January–February) bottom-water temperature (a) and salinity (b) for the North Sea, collected during ICES International Bottom-Trawl Surveys in 2007 (from Skjoldal, 2007).

Variations in wind strength, persistence, and direction will be broadly reflected in changes to the NAO index and, mediated through the effects of wave action at the seabed, have the potential to directly influence the stability of subtidal benthic communities, especially in shallower waters. We examine spatial relationships from modelled output in Sections 5.3 and 6.1. Deducing causal relationships that might be associated with any longer term trends is complicated not only by spatial variation in the depth regime and the nature of the substratum but also, more generally, by wind-driven influences on circulation patterns in the North Sea and their demonstrable effects on system productivity (OSPAR Commission, 2000; see also

Section 5.2). Of course, storm events may occasionally result in wholesale destabilization of soft sediments and associated benthic communities in shallow waters on very short timescales (e.g. Rees *et al.*, 1977; Rachor and Gerlach, 1978).

There is an inconsistency between observations on storminess over the past 30 years (i.e. spanning the period between the 1986 and 2000 surveys), which appear to show no worsening trend and an increase in significant wave heights in the Northeast Atlantic (OSPAR Commission, 2000). In the North Sea, increased windspeeds over this time were also recorded off the Norwegian coast (reported in OSPAR Commission, 2000), which would be supported by trends in the NAO index (Figure 4.1.5). In the German Bight, Schroeder (2005) identified an increased frequency of windspeeds at or above 7 on the Beaufort scale in the 1990s. Increased wave heights may be explained partly by increased fetch (reflecting changes in average wind direction) or, more prosaically, by the absence of reliable data prior to about 1960 with which to provide a longer term historical perspective on the significance of recent changes (OSPAR Commission, 2000). Further consideration of possible links between changes in North Sea benthic communities and climatic influences is given in Sections 5 and 6.

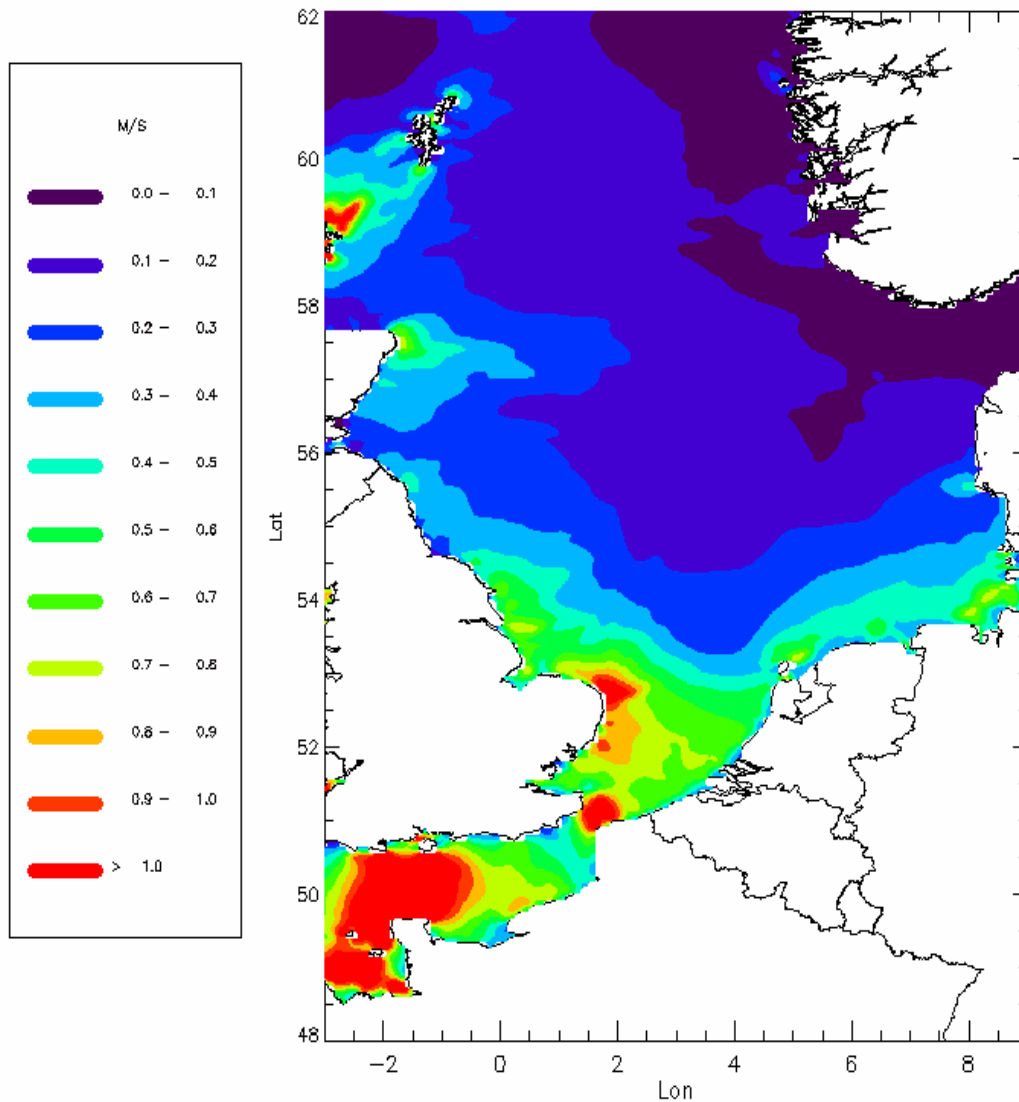


Figure 4.1.4. Peak M_2 tidal streams (m/s; source: Cefas).

Finally, in a recent review of the status of European seas, Frid *et al.* (2003) affirm that the ocean habitat is constantly changing on scales from seconds to thousands of years and hence does not have a “normal state”. As to current uncertainties about whether the recent warming trend reflects natural or human-influenced variability, they note that a better understanding should emerge in “10–15 years”.

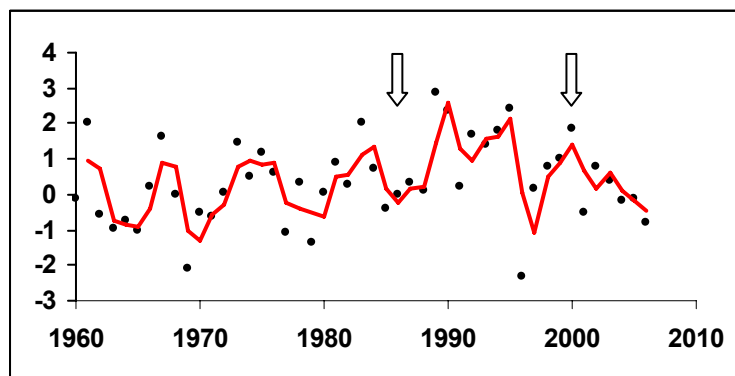


Figure 4.1.5. Trends in the winter (December–March) NAO index. Arrows show the timing of the 1986 and 2000 North Sea benthos surveys (www.cru.uea.ac.uk/cru/data/nao.htm).

The superficial bottom sediments of the North Sea reflect the modern reworking of fluvial and glacial deposits and consist mainly of sands or muds. Coarser deposits, typically gravel/sand admixtures in varying proportions, are patchily located along continental coastlines and, more extensively, along the English east coast and the Channel (see Section 4.2).

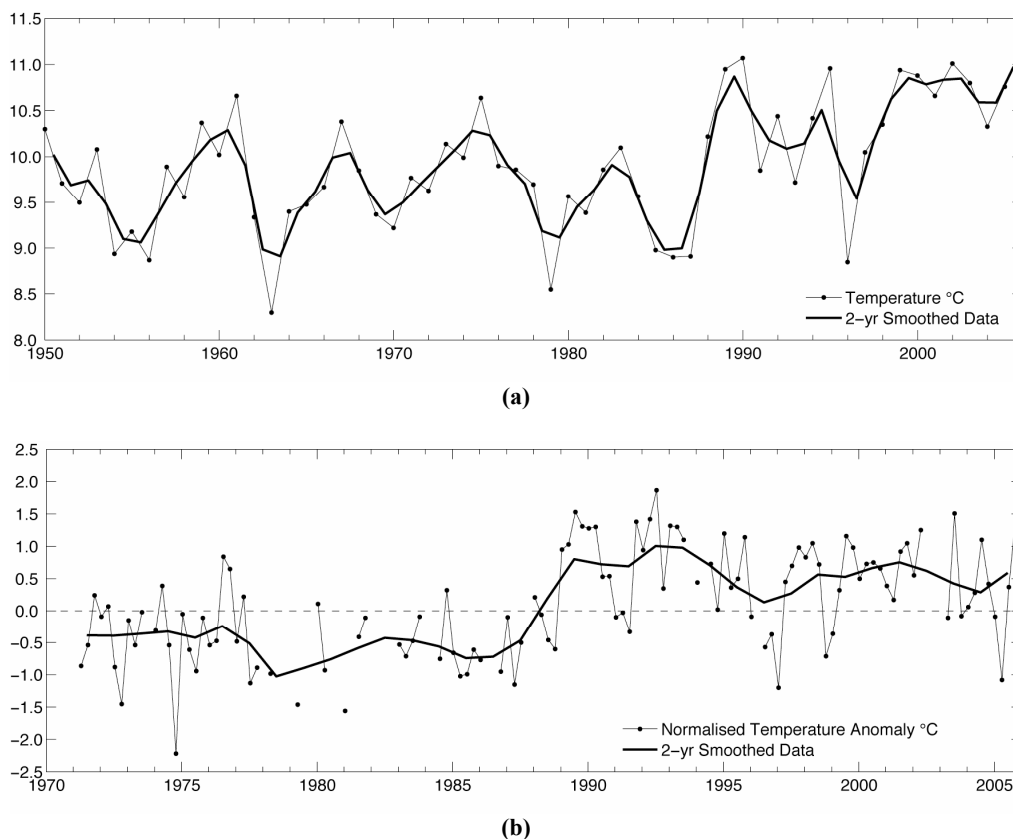


Figure 4.1.6. (a) Annual mean sea surface temperature in the German Bight (Station Helgoland Roads), southern North Sea (from ICES, 2006). (b) Normalized sea surface temperature anomalies relative to the period 1971–2000, derived from seasonal data along a regular ferry route at 52°N (ICES, 2006).

Recent proposals to subdivide European seas into ecoregions (Anon., 2004) are of special interest. For the North Sea, it was recommended to include the Kattegat to the east, while the western boundary was recommended to shift to ca. 2°W, i.e. to encompass the Channel as far as its central rather than farthest westerly point. Sampling of the eastern Channel in the present (NSBP 2000) survey therefore accounts for a significant proportion of this area of the greater North Sea, defined according to ecoregion.

Inputs to the North Sea of low salinity waters are dominated by outflow from the Baltic, which may have a significant influence on parts of the eastern North Sea coastal margin. Historically, inputs from the larger UK and continental river systems have also represented a significant source of nutrients and contaminants arising from agricultural, urban, and industrial developments along the estuaries and upriver catchment areas. Although there are continuing concerns over such inputs to parts of the North Sea, the general trend in trace element concentrations from anthropogenic sources has been downwards, reflecting concerted regulatory action to curb the quantities discharged at source, with the resolutions of the Second North Sea Conference in 1987 providing an important stimulus (Anon., 1988). Since NSBS 1986, implementation of the EU Urban Waste Water Treatment Directive (European Communities, 1991) has resulted in significant improvements to the quality of effluent discharged from sewage treatment works to estuaries and coastal waters. It also resulted in a ban on the disposal of sewage sludge to sea since 1998.

The range of human activities with the potential to influence the benthos of coastal and offshore waters includes:

- Commercial fishing/demersal fishing practices
- Oil and gas exploitation
- Shipping, including accidental oil spills, ballast-water introductions, and litter
- Coastal/offshore construction, including wind farms (larger scale developments occurring mainly since 2000)
- Dredging/disposal for port/harbour maintenance and development
- Urban/industrial discharges to estuaries and coastal waters
- Atmospheric inputs, including those via agricultural and motor vehicle emissions
- Climatic influences (to the extent that these may be affected by human activities)
- Agricultural practices/nutrient inputs via run-off
- Aquaculture
- Extraction of marine sand and gravel
- Coastal recreation/tourism/military-exercise areas
- Conservation measures

These activities are fully described in OSPAR Commission (2000) and in a more recent overview by Frid *et al.* (2003). A comprehensive and timely review of the status of North Sea benthic communities in relation to human activities and other influences is provided by Kröncke and Bergfeld (2003). Many of the studies identified by the authors are of a localized nature in accordance with the distribution of these activities. However, investigations of the effects of, for example, fishing, eutrophication, and climatic changes have a potentially more global relevance to the status of the North Sea benthos. Where appropriate, any relationships to changes evident from the 1986 and 2000 surveys are considered in the following sections.

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4.2 Sediment particle size

H. Hillewaert

This section provides a descriptive summary of the available sediment particle size data from samples collected for NSBP 2000 and compares it with earlier information, including a statistical evaluation of similarities between matching stations from the 1986 and 2000 North Sea benthos surveys. Examples of more detailed sources of sediment data derived from geological surveys of parts of the North Sea are given in Section 5.1.

4.2.1 Methods

All sediment datasets were collated into a uniform database containing percentages for mud content (grain size $<63 \mu\text{m}$), sand (grain size between $63 \mu\text{m}$ and $2000 \mu\text{m}$), gravel (grain size $>2000 \mu\text{m}$), median grain size, and sediment sorting coefficient, except the data for the Dutch continental shelf, for which only median grain size and mud content were available.

The datasets for which fractional data were available were reprocessed to yield uniformly calculated means, sorting coefficients, and descriptive assessments (see Figure 4.2.1).

The program GRADISTAT, Version 4.0 (Blott and Pye, 2001) was used for analyses.

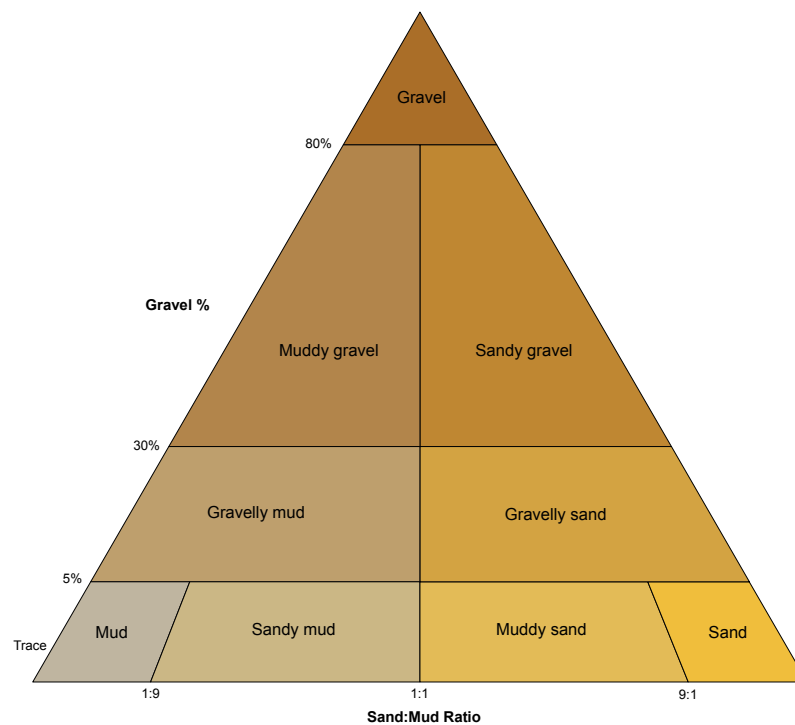


Figure 4.2.1. Standard descriptors of sediment type, according to % particle size contributions (after Folk, 1954).

4.2.2 Results and discussion

All the sediments sampled in the 2000 survey were relatively coarse grained, with 90% containing $<10\%$ silt/clay (Figure 4.2.2), and with most samples being predominantly sandy in nature. The proportion of silt/clay generally increased to the north. Gravelly sands and sandy gravels predominated in the south and east, and these are reflected in larger median grain sizes (Figure 4.2.3) and more poorly sorted sediments (Figure 4.2.4) in these areas.

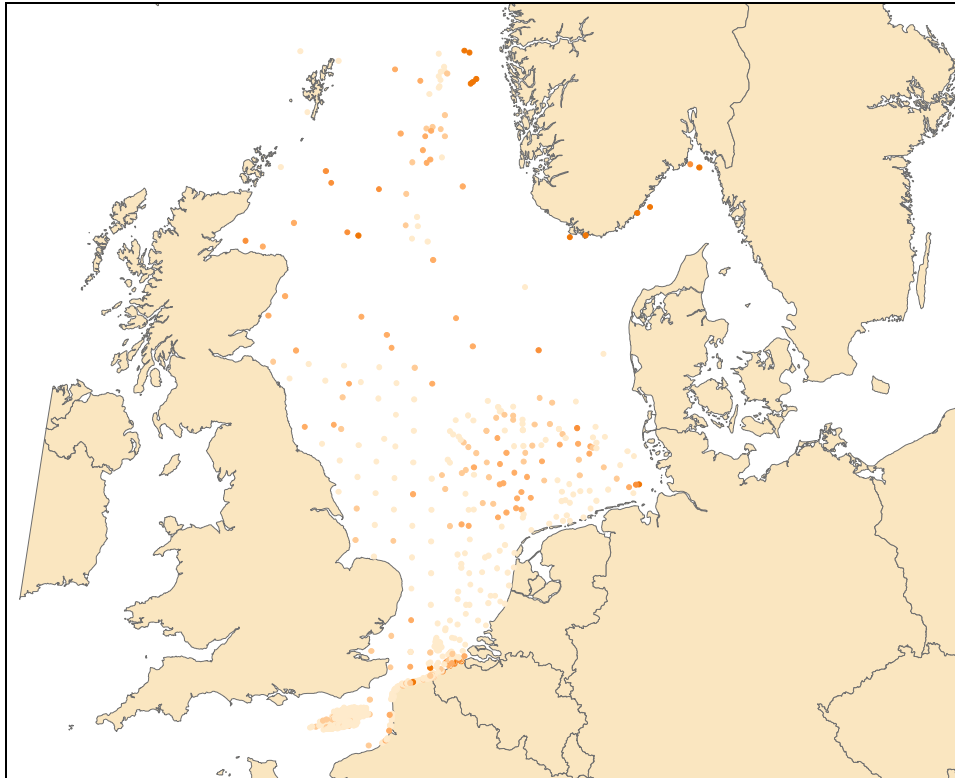


Figure 4.2.2. Percentage of mud content for NSBP 2000 stations. (Colour intensity increases with increasing % mud).

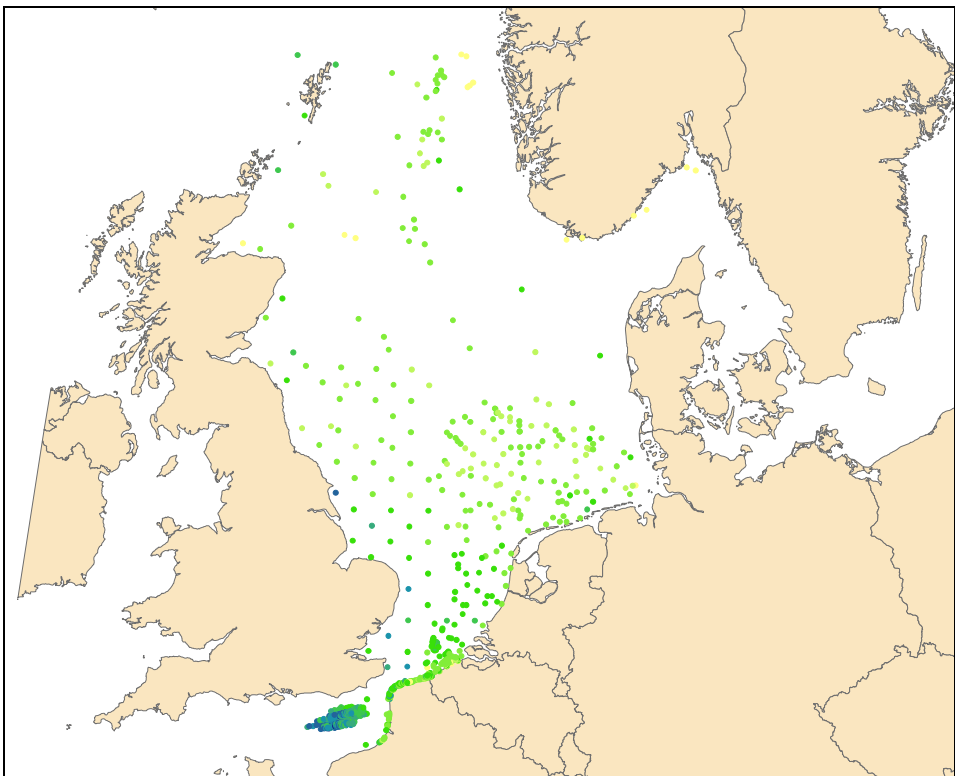


Figure 4.2.3. Median grain size for NSBP 2000 stations. (Colour intensity increases with increasing median size).

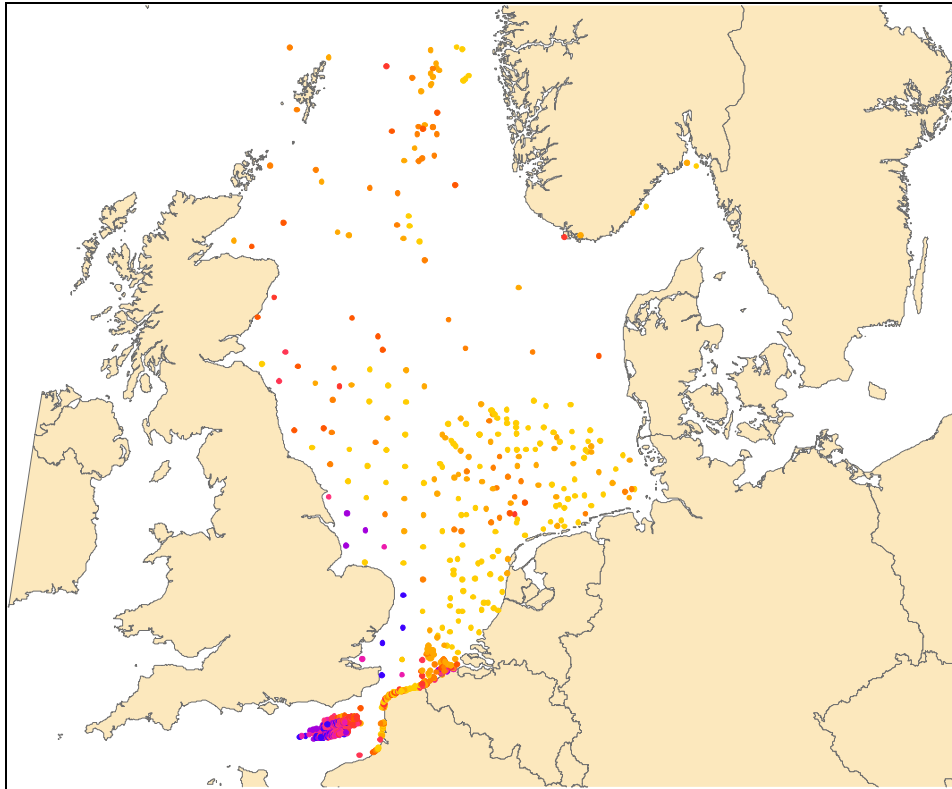


Figure 4.2.4. Particle sorting for NSBP 2000 stations. (Increasing colour intensity indicates increasingly poorly sorted sediments).

These patterns are consistent with earlier descriptions of the distribution of sediment types in the region (Figure 4.2.5) and correspond approximately to variations in bathymetry and tidal current velocities. The sources of sediment are varied, and the present distribution is the result of a complex interaction of modern processes (tides, waves, and surges) with the effects of glaciations, changes in relative sea level, active sediment erosion, particularly of older Quaternary deposits, and relict features (Goldberg, 1973; Nio *et al.*, 1981; Pantin, 1991; Basford *et al.*, 1993; Irion and Zöllmer, 1999).

Comparing 1986 and 2000

A reduced dataset consisting of 1986 and 2000 samples was constructed according to the paired-station algorithm (see Section 3), which identified those that lay relatively close together. In all, 146 station pairs were thus retained.

The median grain size (μm) was the only parameter that could be reliably compared (Table 4.2.1). A two-tailed *t*-test conclusively demonstrated no statistically significant difference between the two datasets ($P = 0.75 > 0.05$). The degree of correlation between the station pairs is illustrated in Figure 4.2.6.

Table 4.2.1. Mean and variance of median grain sizes in 1986 and 2000.

| | <i>MEDIANμm 1986</i> | <i>MEDIANμm 2000</i> |
|--------------|--|--|
| Mean | 189.19 | 192.28 |
| Variance | 13179.3 | 17245.9 |
| Observations | 146 | 146 |

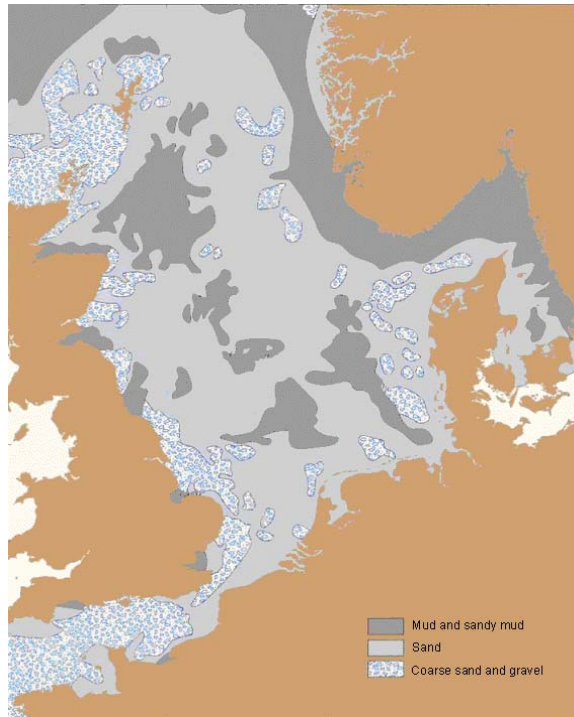


Figure 4.2.5. North Sea sediment types (after Eisma, 1981).

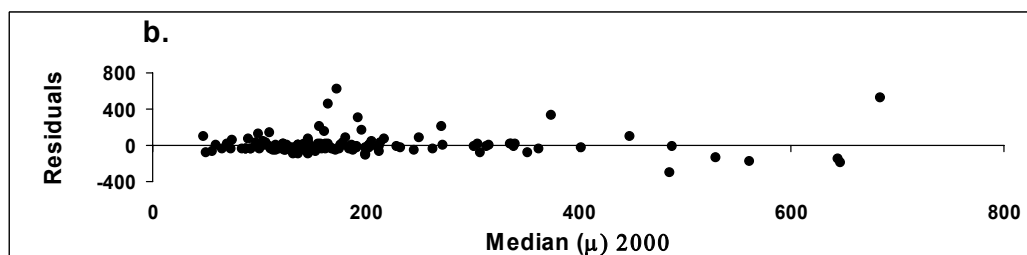
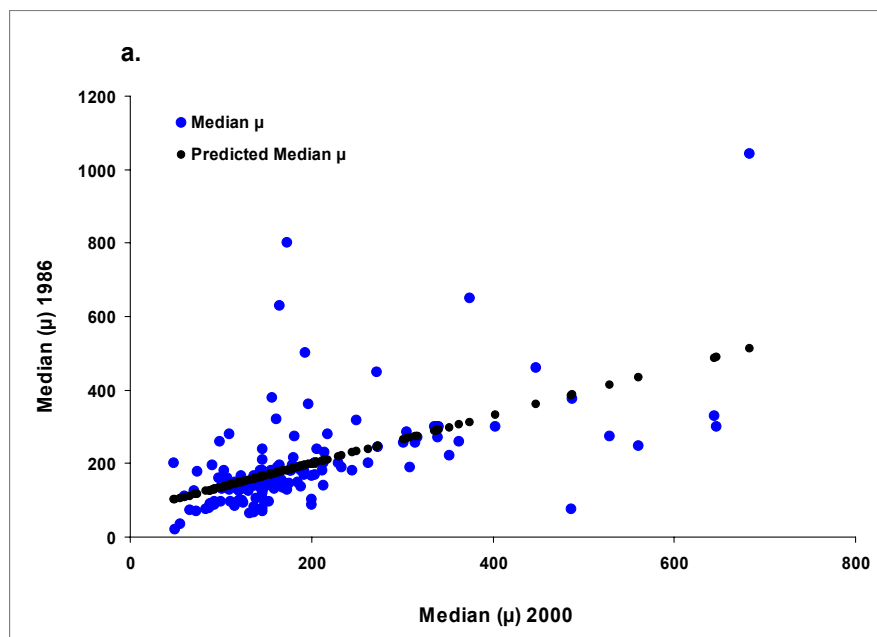


Figure 4.2.6. Top panel (a): relation between median grain sizes for 146 station pairs (1986 and 2000 data). Pearson correlation = 0.567, $P < 0.001$. Bottom panel (b): plot of residuals against median μ in 2000.

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4.3 Trace metal concentrations in sediments

P. J. Kershaw, C. Mason, G. Irion, T. Bolam, and R. Smith

4.3.1 Introduction

The North Sea has received relatively large additions of contaminants through riverine inputs (intensive agriculture and industrialization), atmospheric deposition (e.g. Pb from vehicle exhausts), and direct disposal (e.g. dredged material from industrialized estuaries). These are redistributed throughout the North Sea through wind and tidal mixing (Sündermann, 1994). Despite attempts to reduce these inputs (e.g. OSPAR, EU Directives), there remain appreciable quantities of contaminants in the North Sea ecosystem, partly as a result of continuing inputs and partly as a result of the legacy of past human activities (McGlade, 2002; Pedersen, 1996). As part of NSBP 2000, trace metal concentrations in sediments were investigated in two subregions: the UK sector of the western North Sea (Cefas) and the German Bight (AWI/Senckenberg).

Trace metal concentrations in shelf sediments usually show an inverse correlation with particle size, reflecting both variations in the geochemistry and mineralogy of the sediments, and the capacity for accumulation of contaminants (i.e. finer sediments have a much greater surface area for adsorption). This can be addressed either by analysing a defined size fraction or by normalizing the metal concentration against a non-contaminant element such as aluminium or lithium. The concentrations of these two elements tend to vary inversely with grain size (as the clay mineral content increases), so can be used as proxies to account for lithogenic variability (Loring, 1990). In contrast, coarser sediments tend to be dominated by quartz and to a lesser extent carbonates.

Unfortunately there has been no consensus on the most appropriate size fraction to use, leading to a number of different sizes being adopted: e.g. <2 mm (whole sediment), <63 µm, <20 µm, <16 µm, and <2 µm (Rowlatt and Lovell, 1994; Whalley *et al.*, 1999; Rowlatt, 1996; de Groot and Allersma, 1973; Basford *et al.*, 1993; Irion, 1994). In the present study, Cefas adopted the <63 µm fraction and Senckenberg the <20 µm fraction, reflecting standard practice in the respective laboratories. In contrast, NSBS 1986 used the <2 µm fraction.

The results were compared with the OSPAR recommended background concentrations (BCs) and background assessment criteria (BACs; OSPAR, 2005). These provided a means of assessing the overall contamination of the North Sea sediments.

4.3.2 Methods

Sample collection

Surface sediment samples were collected using a Day grab or, in coarser sampling areas, a Shipek grab from RV “Cirolana” between 2000 and 2002, as part of the UK contribution to NSBP 2000 (Figure 4.3.1) from sites previously occupied in 1986.

In addition, surface sediment samples were collected from the German Bight in 2000, using a van Veen grab, as part of the German (AWI/Senckenberg) contribution to NSBP 2000 (Figure 4.3.2). Spatial relationships between the two surveys completed in 2000 are shown in Figure 4.3.3.

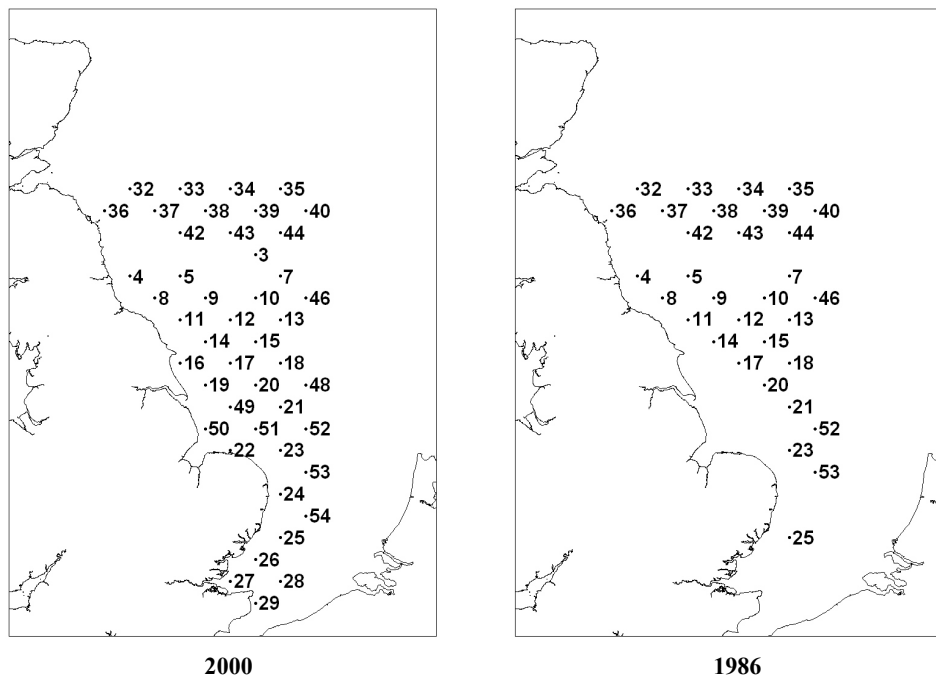


Figure 4.3.1. Sediment sampling locations for analysis of trace metals in the western North Sea, Cefas 2000 (left) and NSBS 1986 (right; fewer stations completed in 1986). Sampling locations labelled with station reference.

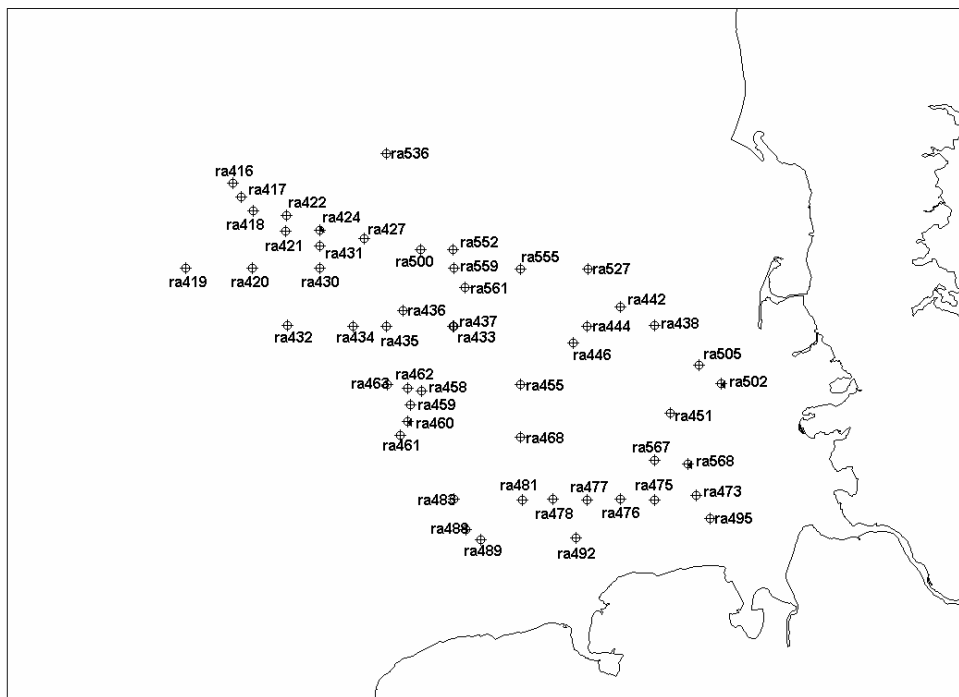


Figure 4.3.2. Sediment sampling locations for analysis of trace metals in the German Bight and offshore (AWI/Senckenberg) in 2000. Sampling locations labelled with station reference.

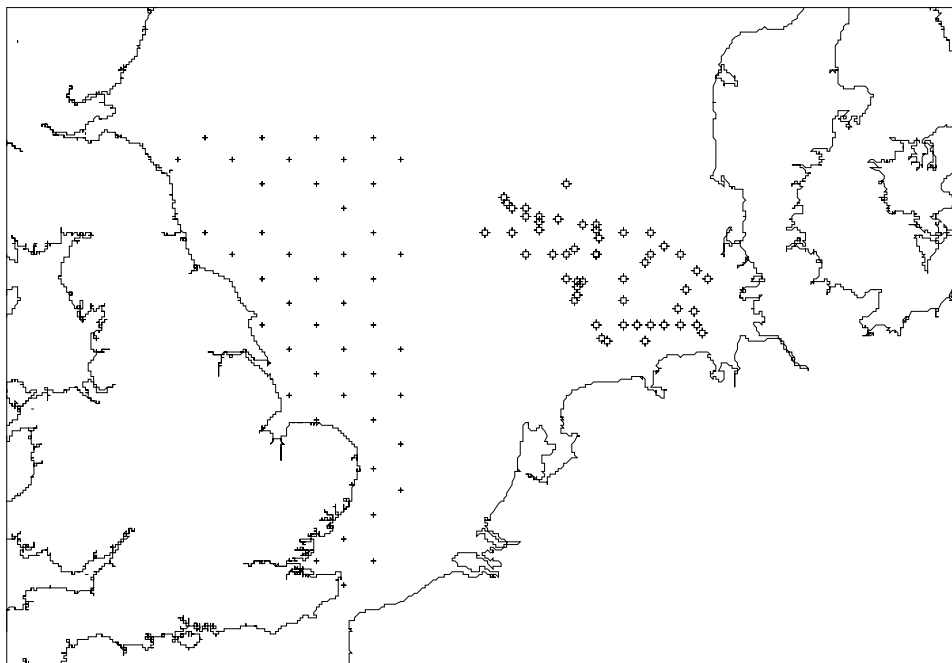


Figure 4.3.3. Sediment sampling locations from both surveys (Cefas (+) and AWI/Senckenberg) completed in 2000.

Particle size analyses (PSA)

At Cefas, the sediments were wet sieved at 63 μm . The >63 μm fraction was oven-dried at $\sim 80^{\circ}\text{C}$ for 24 h. It was then dry sieved at half phi intervals. The <63 μm fraction was freeze dried and analysed on a Coulter LS 130 laser sizer. The laser-sizer results were combined with the dry sieve results to give a full particle size distribution. The mean (phi), median (phi), sorting, skewness, kurtosis, and percentage of silt/clay (<63 μm fraction) were calculated from the full particle size distribution using established methods (Dyer, 1997; Folk, 1974).

At Senckenberg, the <20 μm fraction was separated using settling tubes, based on the principle of Stoke's Law to determine settling times (Atterberg, 1912). The separation was repeated five times to give >98% of the fraction; the suspension was collected in ceramic bowls, centrifuged, then evaporated in an oven at 80°C .

Contaminant analyses

At Cefas, samples were wet sieved to separate the <63 μm fraction. This fraction was dissolved in hydrogen fluoride (HF) and trace metal (and Al, Li, and Fe) concentrations determined using inductively coupled plasma mass spectrometry (ICP-MS; As, Cd, Cr, Cu, Hg, Ni, Pb, and Zn).

At Senckenberg, the <20 μm fraction was diluted in HNO_3 (65%) for analysis of Zn and Cu by atomic absorption spectrometry (AAS), with a precision of 1%.

In addition, at Cefas, tributyltin (TBT) concentrations were determined on unfractionated subsamples of the whole sediment by gas chromatography (GC). TBT was extracted from two grammes of sediment, using a mixture of methanol and 0.1% sodium hydroxide, and mechanical shaking. An internal standard of tripropyl tin was used for recovery. The sample was derivatized to the hydride with the addition of sodium borohydride. The samples were then centrifuged to separate the hexane layer, which was removed to a labelled GC vial using a Pasteur pipette. Determination was by GC-FPD, using a Hewlett Packard 6890GC with a 5% methyl silicone, 0.32 mm capillary column, with flame photometric detection.

4.3.3 Results

Sediment characterization (PSA)

All the sediments sampled in the NSBP 2000 survey were relatively coarse grained, with 90% containing <10% silt/clay (<63 μm), and with most samples being predominantly sandy in nature (Figure 4.3.4). Gravelly sands and sandy gravels predominated in the south and east with the proportion of silt/clay increasing to the north. This is consistent with the reported distribution of sediment types in the region and corresponds approximately to variations in bathymetry and tidal current velocities. The sources of sediment are varied, and the present distribution has resulted from a complex interaction of modern processes (tides, waves, and surges) with the effects of glaciations, changes in relative sea level, active sediment erosion – particularly of older Quaternary deposits – and relict features (Pantin, 1991; Basford *et al.*, 1993; Irion and Zöllmer, 1999).

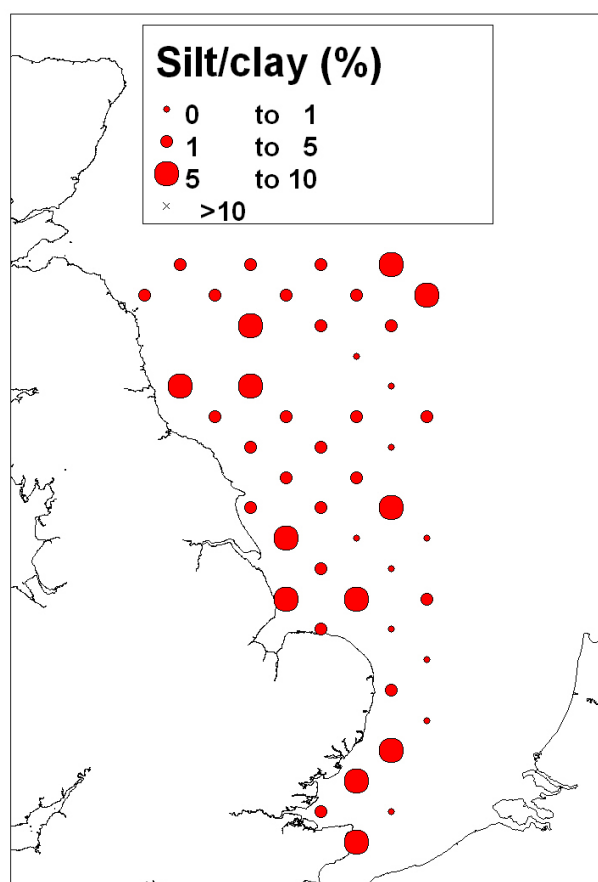


Figure 4.3.4. Distribution of the silt/clay fraction (<63 μm) in surface sediments in 2000.

Comparison of the median (μm) distributions in 1986 and 2000 (Figure 4.3.5) shows little difference in sediment type between 1986 and 2000, especially allowing for differences in methodologies used. Comparison of silt/clay (%) was not possible between 1986 and 2000 without more detailed PSD results from 1986. As described previously, most of the sediments have a median in the fine to medium sand range (>63 μm to 500 μm).

The distribution of trace metal concentrations from 2000 in the <63 μm fraction of surface sediments of the western North Sea set alongside their equivalents (mg kg^{-1}) in the <2 μm fraction of surface sediments from NSBS 1986 is shown in Figure 4.3.6. The distribution of copper and zinc in the <20 μm fraction of sediments in the German Bight, alongside the

<63 μm fraction of sediments of the western North Sea is shown in Figure 4.3.7. It was not possible to show similar distributions in the German Bight for 1986, because trace metals data for this area were not included in the datasets provided. The same ranges have been set for each trace metal to allow easy comparison of the different datasets, although this does not allow for differences in methodology used in the analyses.

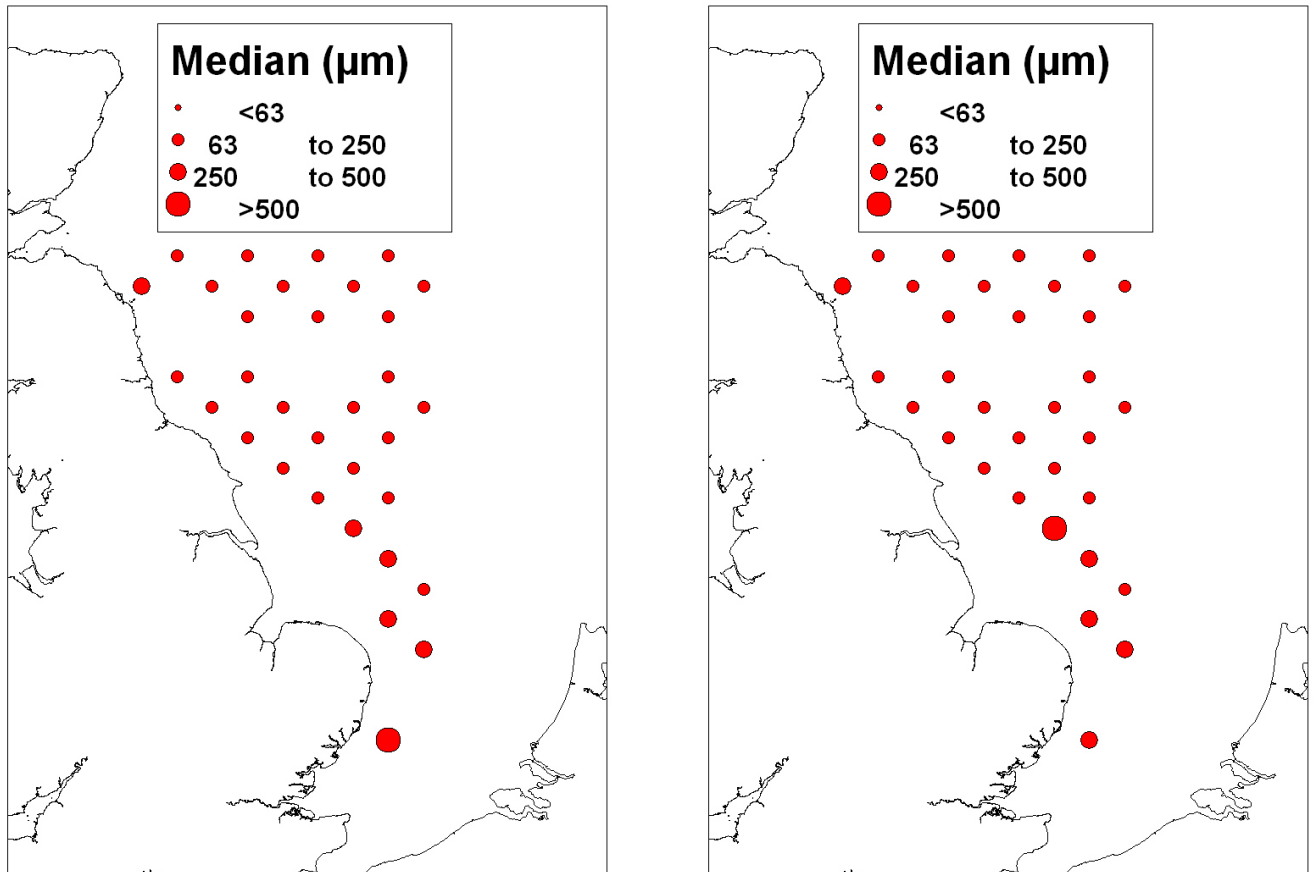


Figure 4.3.5. Median (μm) distribution in 2000 (left) and 1986 (right).

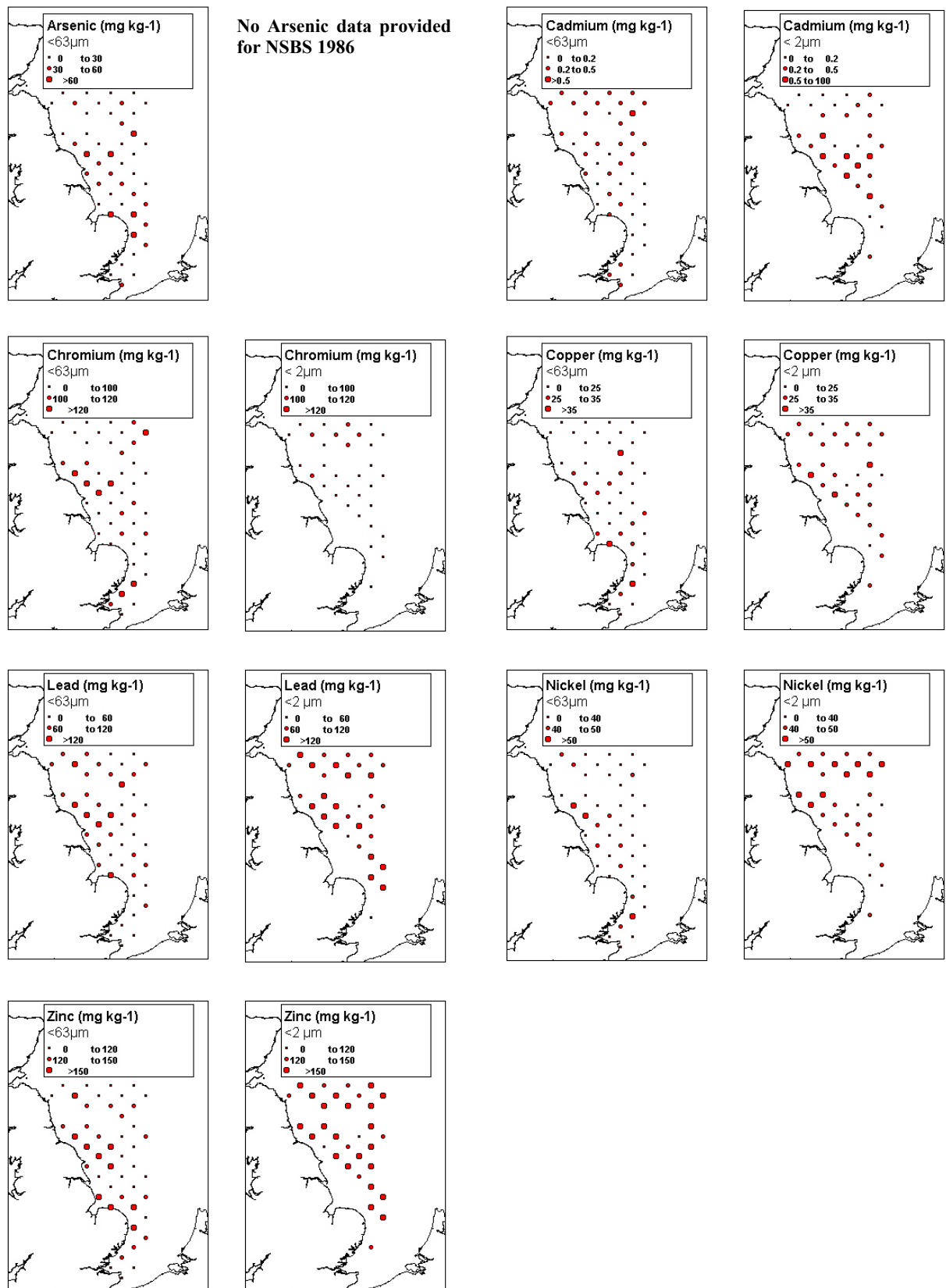


Figure 4.3.6. Grouped in pairs, showing the distribution of trace metal concentrations (mg kg⁻¹) in the <63 μm fraction of surface sediments from 2000 (left) set alongside their equivalents (mg kg⁻¹) in the <2 μm fraction of surface sediments from 1986 (right).

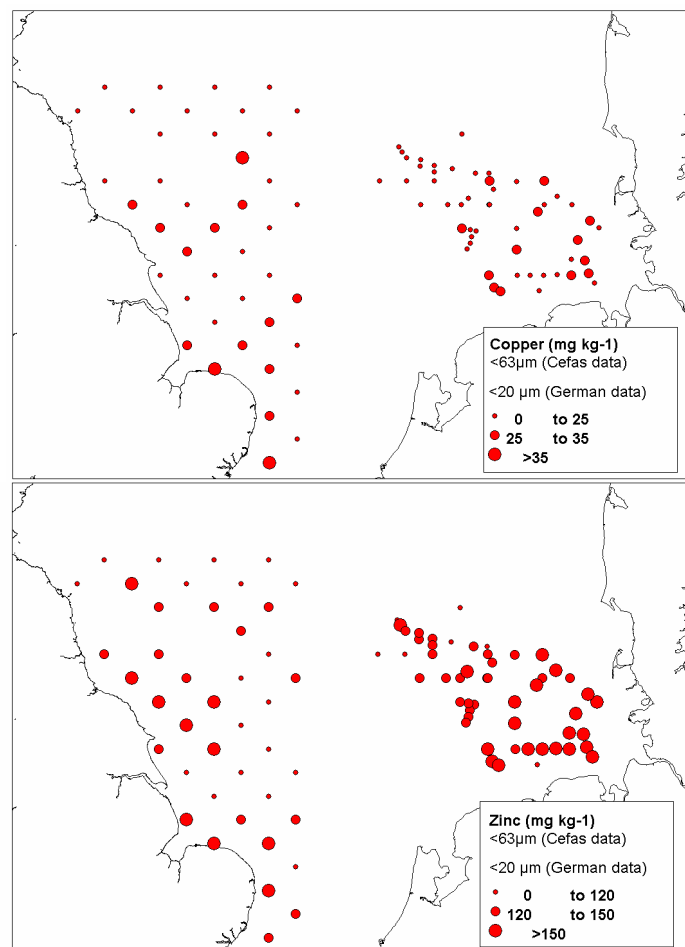


Figure 4.3.7. Distribution of trace metals (mg kg⁻¹) in the <20 μm fraction of surface sediments from the German Bight, and the <63 μm fraction of surface sediments from NSBP 2000.

The distribution of trace metals was uneven at the NSBP 2000 stations. Copper, chromium, and nickel showed a relatively uniform distribution. In contrast, lead and zinc showed a cluster of relatively high concentrations near the northeast coast of England, and arsenic, mercury, and cadmium had a rather patchy distribution.

In the German Bight (Senckenberg), the distribution of zinc showed a relatively uniform distribution, in contrast to copper with relatively high concentrations in sediments closer inshore.

The trace metal results were compared with the OSPAR recommended BCs and BACs (OSPAR, 2005). These have been developed, following extensive consultation, to provide a means of assessing the contamination status of sediments in the OSPAR region. The values are appropriate for fine-grained sediments or the fine fraction of sediments. In the present study, the observed concentrations in the separated fractions were used without further normalization.

The results for the western North Sea, 1986 and 2000, and the German Bight (NSBP 2000 data presented in Annex 1) indicated that the fine fraction is contaminated quite extensively. This was also shown by the percentage number of stations exceeding the OSPAR criteria (Table 4.3.1 and Table 4.3.2). Similarly, the fine fraction of sediments in the NSBS 1986 shows extensive contamination (Table 4.3.1 and Table 4.3.2). The potential sources of this additional trace metal burden are discussed below.

Table 4.3.1. Recommended BCs for fine sediments or fine fractions of sediments, and percentage of samples from each dataset that exceeded the BC values. (A dash (–) indicates that the metal was not measured).

| TRACE METAL | BC | 2000 CEFAS | 2000 SENCKENBERG | NSBS 1986 |
|-------------------------------|------|------------------------|------------------------|-----------------------|
| | | % EXCEEDING BC, <63 MM | % EXCEEDING BC, <20 MM | % EXCEEDING BC, <2 MM |
| As | 15 | 83 | – | – |
| Cd | 0.2 | 59 | – | 63 |
| Cr | 60 | 93 | – | 94 |
| Cu | 20 | 48 | 30 | 94 |
| Hg | 0.05 | 96 | – | – |
| Ni | 30 | 67 | – | 97 |
| Pb | 25 | 98 | – | 97 |
| Zn | 90 | 89 | 95 | 97 |
| Number of stations (n) | | 46 | 52 | 32 |

Table 4.3.2. Recommended BACs for fine sediments or fine fractions of sediments, and percentage of samples from each dataset that exceeded the BAC values. (A dash (–) indicates that the metal was not measured).

| TRACE METAL | BAC | 2000 CEFAS | 2000 SENCKENBERG | NSBS 1986 |
|-------------------------------|------|-------------------------|-------------------------|------------------------|
| | | % EXCEEDING BAC, <63 MM | % EXCEEDING BAC, <20 MM | % EXCEEDING BAC, <2 MM |
| As | 25 | 52 | – | – |
| Cd | 0.31 | 24 | – | 50 |
| Cr | 81 | 83 | – | 69 |
| Cu | 27 | 13 | 21 | 63 |
| Hg | 0.07 | 83 | – | – |
| Ni | 36 | 35 | – | 88 |
| Pb | 38 | 85 | – | 97 |
| Zn | 122 | 48 | 73 | 94 |
| Number of stations (n) | | 46 | 52 | 32 |

Tributyltin (TBT) concentrations for the western North Sea (NSBP 2000) were determined on the whole sediment subsamples, and all were below the detection limit, except for one station on the English east coast, where 0.013 mg kg⁻¹ TBT was recorded.

4.3.4 Discussion

Spatial variability and potential sources

Trace metal concentrations in the fine fraction of seabed sediments throughout the survey area were elevated compared with the OSPAR BAC recommended values. Enrichment values were calculated to show the spatial extent and degree of contamination (Figure 4.3.8), as follows:

$$\text{Enrichment value} = \text{Actual concentration} / \text{OSPAR BAC value}$$

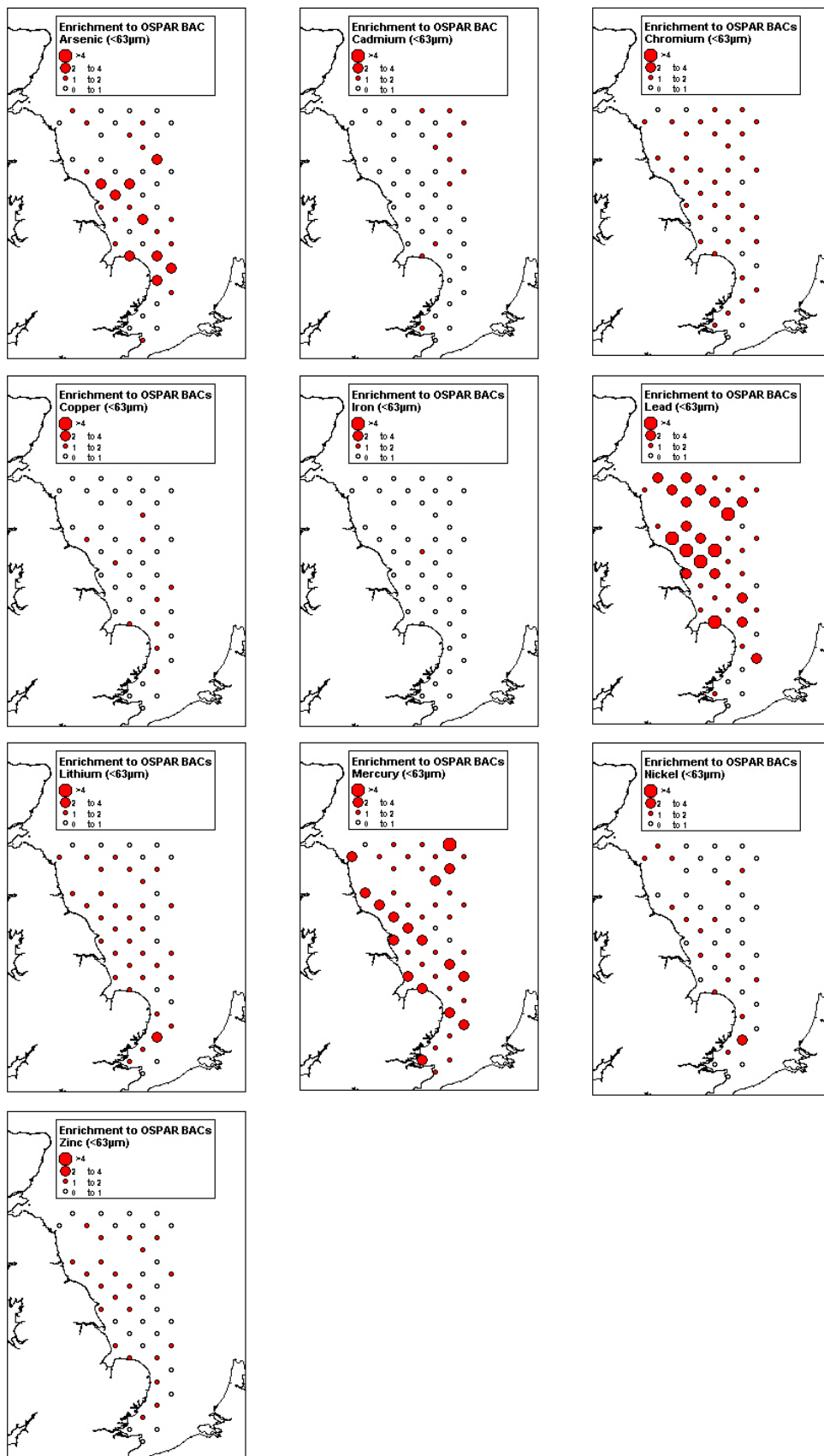


Figure 4.3.8. Enrichment of trace metals in the western North Sea (Cefas 2000), based on the OSPAR BACs (defined in Table 4.3.1).

This suggests widespread contamination, but it should not be taken to imply toxicity. Trace metals occur in the marine environment as a result of a number of natural processes and human activities. Contamination has resulted from the exploitation of natural resources and the processing and manufacturing industries. For example, Pb and Zn occurred in relatively high concentrations in parts of the western North Sea. This can be attributed, in part, to run-off from an extensive area of mineralization and consequent mining and industrial activity in northeast England from the 18th century onwards (Rowlatt and Lovell, 1994). Pb is also introduced into the North Sea through atmospheric fallout (Förstner and Witmann, 1979), giving a much wider distribution, although there have been substantial reductions as a result of the phasing out of lead additives in petrol. Trace metals are introduced directly through the disposal of contaminated material dredged from estuaries and harbours, and formerly from the dumping of industrial wastes and sewage sludge (Rowlatt and Lovell, 1994). Controls are in place to ensure that the most highly contaminated sediments are not disposed offshore, but there remains a measurable signal at and around the disposal sites. Levels of metals in contaminated dredged material have tended to decrease in recent years and this, combined with wave- and tide-induced dispersal, has resulted in lower concentrations observed in the nearshore environment. However, the spatial resolution in the NSBP 2000 survey was too coarse to reveal the influence of individual disposal sites.

The BIO-ENV (PRIMER) procedure was used to determine the combinations of environmental variables that are most responsible for structuring the benthic community. None of the trace metals used in the analyses showed any correlation with the patterns seen in the biota. Therefore, even though there are measured elevations in trace metal concentrations, these are not deemed to be responsible for the observed differences in community structure.

Temporal trends

There have been a number of studies of trace metal distributions in the western North Sea region in recent years. Direct comparison to establish trends is problematic in many cases because of differences in the particle size fraction used for the analysis. For example, the 2000 western North Sea benthos samples were taken from the same sites occupied in the 1986 survey, up to 2.5°E, but trace metal concentrations in the 1986 samples were determined in the <2 µm fraction (Irion and Müller, 1987; Basford *et al.*, 1993). To overcome this difficulty, multidimensional scaling (MDS) was used to establish the degree of similarity between the median grain size and trace metal concentrations (Cd, Cr, Cu, Ni, Pb, Zn) in both years (Figures 4.3.9 and 4.3.10), using the PRIMER software package. The relationship between the two similarity matrices was then compared using the RELATE (PRIMER) procedure. This produced a Rho value of 0.16, indicating a low degree of similarity between the two years. However, it is not clear whether the overall distribution of trace metal contamination has changed significantly or whether this difference simply reflects the effects of the different particle size fractions being analysed.

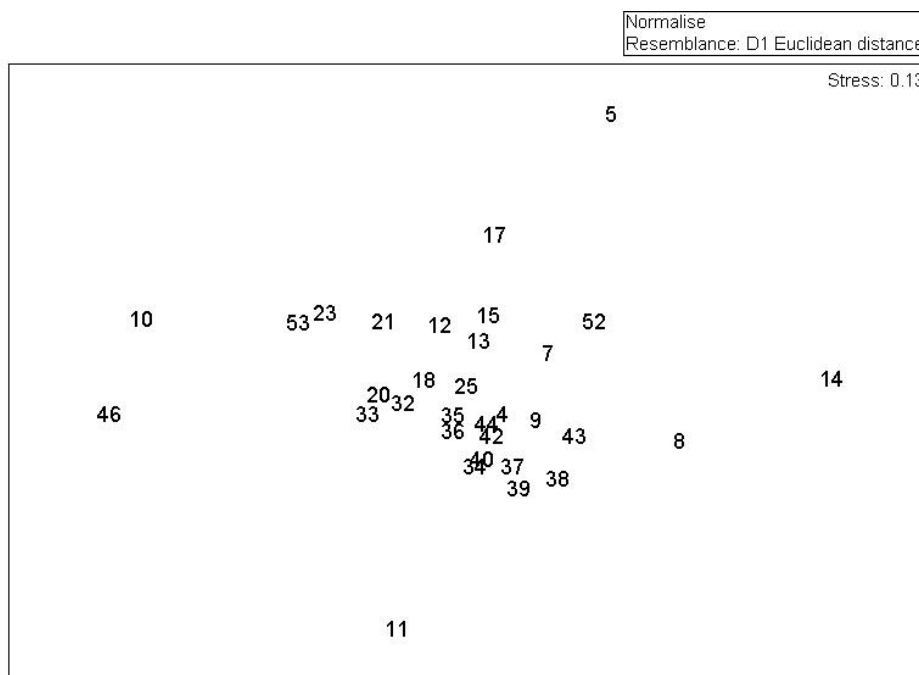


Figure 4.3.9. MDS of trace metal concentrations (Cd, Cr, Cu, Ni, Pb, Zn) for Cefas 2000. Numbers represent station locations as shown in Figure 4.3.1. Additional samples that were collected in 2000 have been excluded so that they are directly comparable with station locations measured in 1986.

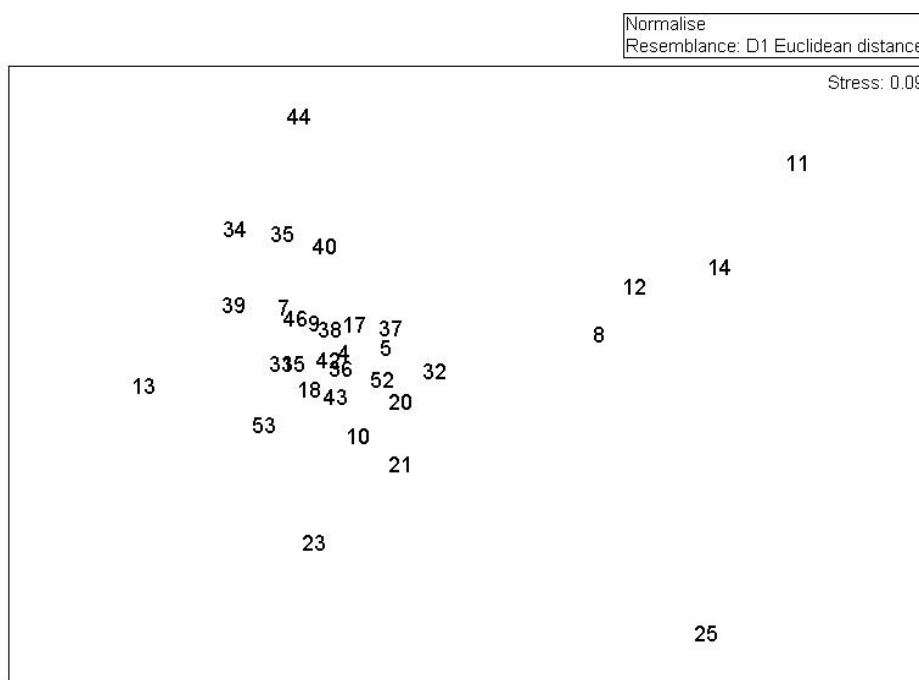


Figure 4.3.10. MDS of trace metal concentrations (Cd, Cr, Cu, Ni, Pb, Zn) for NSBS 1986. Numbers represent station locations as shown in Figure 4.3.1.

The 1990/1991 baseline survey for the North Sea Task Force covered the same region at a higher density of sampling locations, but metals were analysed on the <2 mm fraction (Rowlatt and Lovell, 1994; Rowlatt and Davies, 1995; Rowlatt, 1996). The study concluded that there were relatively high concentrations of lead and mercury off the northeast coast of England, that copper and nickel were distributed relatively uniformly, but that Al-normalized cadmium and chromium concentrations were higher on the northern edge of the Dogger Bank. A comprehensive investigation of metal distributions and behaviour on and around the Dogger

Bank concluded that cadmium cycling was associated with phytoplankton dynamics (Whalley *et al.*, 2002). A more detailed study of arsenic was carried out using the 1990/1991 baseline samples augmented by high-resolution sampling on the Dogger Bank in 1993 and 1995 (Whalley *et al.*, 1999), again using the <2 mm fraction. Arsenic has a high affinity with iron and tends to co-vary. Higher arsenic concentrations were observed off the northeast coast, in the Thames, and off northeastern Norfolk. The first two cases may have a direct industrial source, although the high discharges to the Humber are not reflected in high levels offshore. Higher levels of particulate iron observed off the Norfolk coast (Whalley *et al.*, 1999) may originate in the ironstone deposits exposed near Hunstanton, and sediments eroded on the Norfolk coast are transported eastwards (Irion and Zöllmer, 1999). This may provide a partial explanation for the higher arsenic levels, although transport from the Humber may be a contributing factor.

4.3.5 Conclusions

It is clear that the fine fraction of surface sediments over large areas of the North Sea is contaminated with trace metals, using the criteria recommended by OSPAR (i.e. BCs and BACs). It is likely that this is a consequence of the long history of industrialization and high population densities of the coastal fringe. The sediments act as a store for metals released over the past two centuries. It has not been possible to provide an adequate comparison of the contamination status in 2000 and in 1986 (Irion and Müller, 1987) owing to differences in the size fractions used for analysis. For the same reason, it has not been possible to compare directly the results from the German Bight and the western North Sea. It is suggested that such procedural differences be addressed and overcome before embarking on a similar collaborative exercise.

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5 Patterns and changes in the macro-zoobenthos (1986–2000)

5.1 Structure, distribution, and characterizing species of North Sea macro-zoobenthos communities in 2000

E. Rachor, H. Reiss, S. Degraer, G. C. A. Duineveld, G. Van Hoey, M. Lavaleye, W. Willems, and H. L. Rees

5.1.1 Introduction

This section describes spatial distribution patterns of North Sea macro-zoobenthos assemblages and general trends in structural features of the fauna. They allow comparison with earlier descriptions and their interpretations (see Section 5.2 ff.) and provide a renewed baseline for long-term comparison (see Section 5.7), mainly relating to possible climate-related changes and anthropogenic influences, such as eutrophication, pollution, acidification, sand and gravel extraction, and fisheries, as well as environmental and nature protection measures and their trends. In addition, they allow for better ecosystem understanding (see Section 5.5 ff).

5.1.2 Methods

Although quasi-synoptic sampling was intended for late spring to early summer in 2000, several parts of the North Sea could only be covered by including material from adjacent seasons and years (mainly 2001, see Table 3.1.3).

Most of the sampling was done by collecting infauna and slowly moving epifauna with grabs of the van Veen type (mostly two grabs of 0.1 m² at each station), sieving them alive on screens of 1 mm, and analysing the preserved material in detail in the home laboratories. Specific information, including the areas covered by the different laboratories and the sampling locations, is presented in Section 3.1.

Sediment distribution maps of the North Sea, derived from information obtained during sampling for the benthic infauna, are shown in Section 4.2. More detailed information can be found in large-scale regional sediment maps and overview maps such as the International Quaternary Map of Europe (1970); see also <http://gisweb2.awi-bremerhaven.de/Website/margis/viewer.htm>.

In the following account, a reduced dataset (950 stations, 521 taxa) was employed, after accounting for taxonomic inconsistencies and the exclusion of very rare species. The STATISTICA package (see e.g. www.statsoft.de) was used for univariate analyses. This includes diversity derivations from rarefaction curves to compensate for different sample sizes between stations and clusters (e.g. ES(100) = expected number of species in a hypothetical sample of 100 individuals).

Cluster analyses using the PRIMER 5.0 software package (Clarke and Warwick, 1994) were carried out using the Bray–Curtis similarity measure and group-average linkage. As initial results based on presence/absence and fourth-root transformed abundance data were similar, only the latter were used in subsequent analyses. Clusters were compared with the results of TWINSpan analyses (more information can be obtained at www.ceh.ac.uk/products/software/CEHSoftwareDECORANATWINSpan.htm), and a common grouping derived for comparative analyses (Figure 5.1.5). The characteristic species (see Salzwedel *et al.*, 1985; Rachor and Nehmer, 2003; Rachor *et al.*, in prep.) of each main cluster were determined using, among others, the SIMPER tool within the PRIMER work package. For their selection, fidelity in abundance, presence, fidelity in presence, numerical dominance, and rank of species contributing to dissimilarity (against all other stations) should be considered. These are defined as follows:

- 1) Fidelity in abundance (FA, total individual number of a species within a cluster/total individual number in the survey; highest ranks, >60%);
- 2) Presence (P, share of stations within a cluster where the species was found; highest ranks, >70%);
- 3) Fidelity in presence (FP, number of presence stations within a community/total number of presence stations in the survey; highest ranks, >60%);
- 4) Numerical dominance (ND, highest ranks, as a rule not less than 3%);
- 5) Rank of species contribution to dissimilarity of a cluster group compared with all other stations (RD, ranks 1–5 only considered).

For a characteristic species, at least three of the criteria have to be fulfilled, with ND as a rule not less than 3% and FP not less than 40%. The characterizing species are presented in Table 5.1.1.

5.1.3 Results

5.1.3.1 General trends – univariate analyses

Note: in the graphical outputs to accompany the following account, which complement those of Section 5.3, we have colour-coded the data points to highlight the different data sources used in NSBP 2000 and how they relate to the overall trends that were identified.

Diversity

Rarefaction analyses show increasing ES(100) values with latitude north of 51°N (Figure 5.1.1; see also Section 5.3). This is in accordance with the results from 1986 (Heip *et al.*, 1992). South of 53°N, elevated diversities in the eastern English Channel (Newell), and also along parts of the southeast English coast (Rees) that were not sampled so effectively in 1986, can be accounted for by the generally coarser substrata, which present greater small-scale heterogeneity. Biogeographical differences, with increasing species numbers to the west, may also account for elevated values in the Channel area (Figures 5.1.1 and 5.1.3; cf. Figure 5.3.5). Also notable are the elevated ES(100) values for samples collected by Robertson (FRS, Aberdeen) relative to the overall trend. These may be explained by the use of a large (0.25 m²) corer for sample collection which, because of deeper penetration than smaller cores or grabs, appear to be intrinsically more “biodiverse” than elsewhere at comparable latitudes. Finally, the depressed ES(100) values for the blue subcluster (Nehring) can be accounted for by estuarine influences.

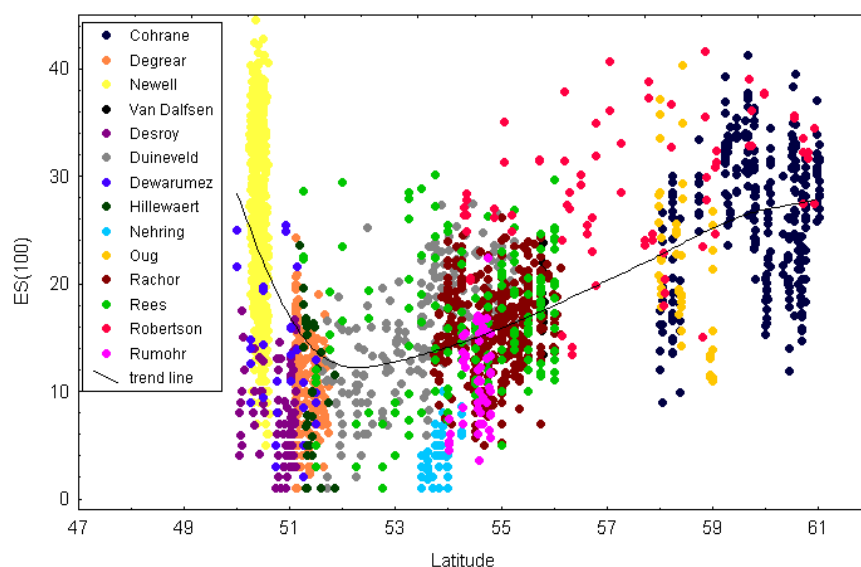


Figure 5.1.1. Diversities (rarefaction: ES(100), for individual grabs) vs. latitude.

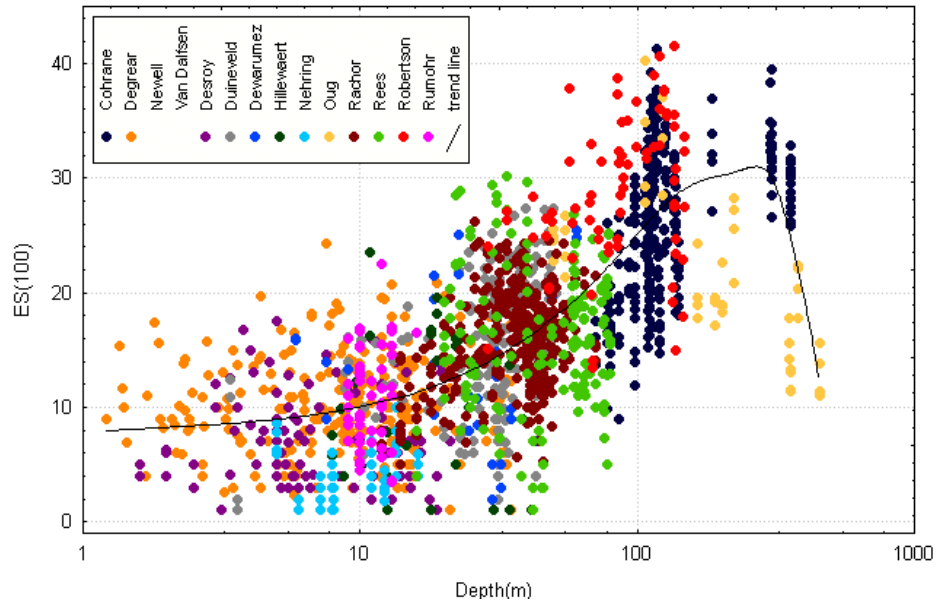


Figure 5.1.2. Diversities (rarefaction: ES(100)) vs. water depths; all data from individual grabs.

Similarly, diversity generally increases with depth (Figure 5.1.2), which may be explained by increasing environmental stability (e.g. decreased wave-induced or tidal turbulence and reduced temperature extremes; see Section 5.3) and the stronger influence of Atlantic inflow to the north. It is clear, therefore, that latitudinal gradients are matched by gradients in a number of influential environmental variables. Also notable are the depressed diversities of some of the deep-water Norwegian (Oug) samples (>350 m).

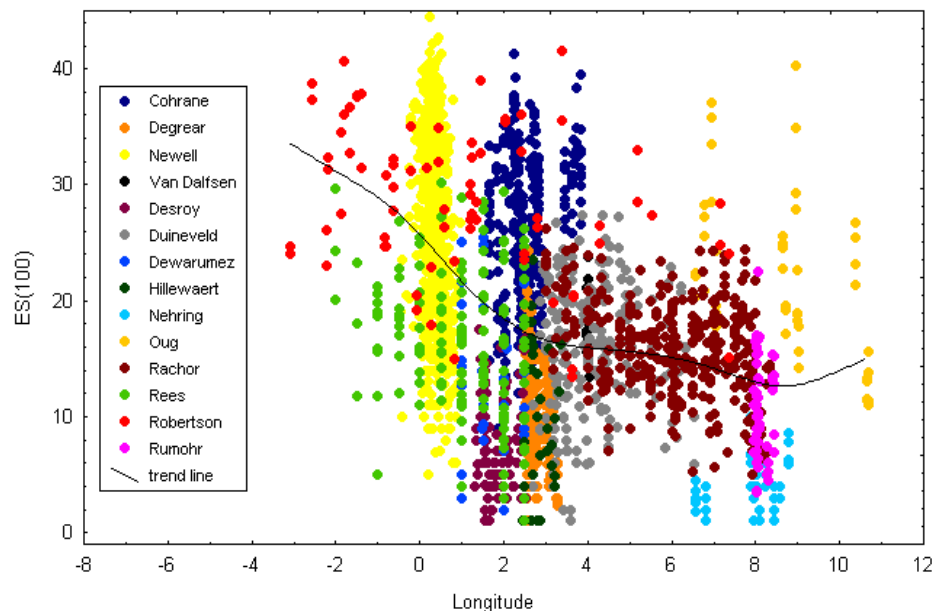


Figure 5.1.3. Diversities (rarefaction: ES(100), for individual grabs) vs. longitude.

Also, a longitudinal trend in diversity exists (Figure 5.1.3), with a decrease towards the eastern North Sea, where less saline water and more continental (climatic) influences prevail, and species adapted to warmer waters are rare. As expected, the lowest values were found in the estuaries (Nehring's data).

Abundance

Figure 5.1.4. shows increases from the Channel to the southeastern North Sea and slight increases from the southern to the central North Sea. The variability in these parts of the North Sea is high. From the central up to the northern North Sea, abundances are more or less stable, mostly at a relatively high level.

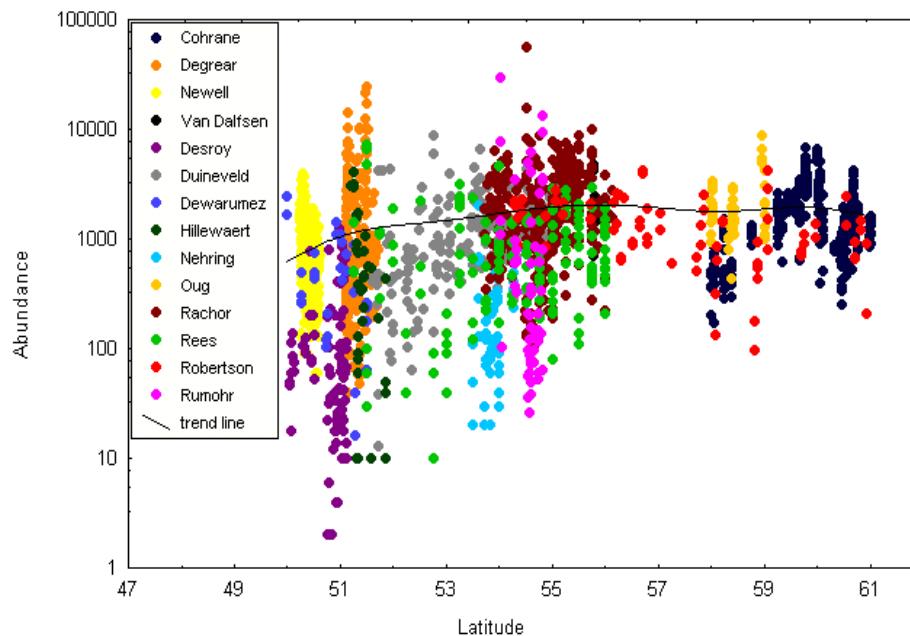


Figure 5.1.4. Abundances (ind. m⁻²; for individual grabs) vs. latitude.

5.1.3.2 Assemblages

Results of multivariate analyses

Both TWINSpan and PRIMER analyses employing fourth-root transformed abundance data produced similar results. Nevertheless, a number of stations in nearshore areas and several in transitional parts of the North Sea, such as in the vicinity of the Dogger Bank, were not assigned to the same groups by either method (Figure 5.1.5). Similar patterns were also found with presence/absence data.

Figure 5.1.6 shows the results of group-average clustering only; the cluster dendrogram is shown in Figure 5.1.7. The results of TWINSpan analysis are shown in Figure 5.1.8.

The main groups identified by both methods are related to water depths and distances from the shore (especially from south to north); differences between coarse and fine substrate types are also influential (assemblages B1 and B2 in the cluster dendrogram; Figure 5.1.7).

The quality of this clustering was also checked by looking at subsets of data that (from previous analyses) represented discrete communities – in particular, from a survey near the Belgian coast, which revealed well-defined trench and sandbank communities (see Degraer *et al.*, 2003, 2006) and from surveys in the German Bight (Rachor and Nehmer, 2003; Rachor, 2006).

The following descriptions relate to the outcome of clustering, using group-average linkage (Figure 5.1.6).

There is a clear separation of station clusters in mainly shallow inshore waters in the south from the French up to the German coastal-zones, in the Channel, as well as adjacent to the English east and southeast coasts, from those in deeper waters north of the Dogger Bank. In

between, the offshore assemblages of the sandy and muddy areas are also well distinguished, including the Oyster Ground and the sandy Dogger Bank and its more muddy slopes, which are inhabited by the same assemblage (D23) as is found in the Pleistocene Elbe valley extending from the inner German Bight to east of the sandbank.

The main separation of the deep-water cluster group (D21) is found near the 50 m depth contour north of the Dogger Bank, where it borders the assemblage D23.

B24 is a very specific cluster in the gravelly-to-muddy Helgoland Deep Trench, where faunal elements from the northern North Sea have their discrete outpost. These stations are similar to one outlier off the mouth of the Thames.

The characterizing features of each assemblage type identified from cluster analyses are shown in Table 5.1.1. In a few cases, very similar clusters are shown together.

Differences in diversity and densities of the assemblages are shown in Figure 5.1.9.

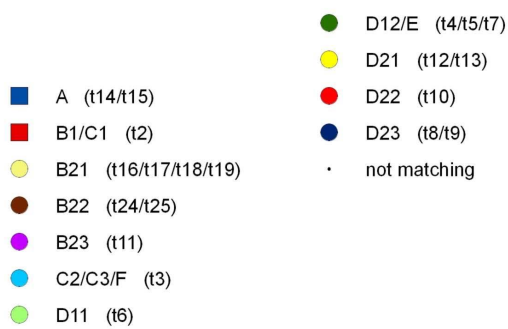
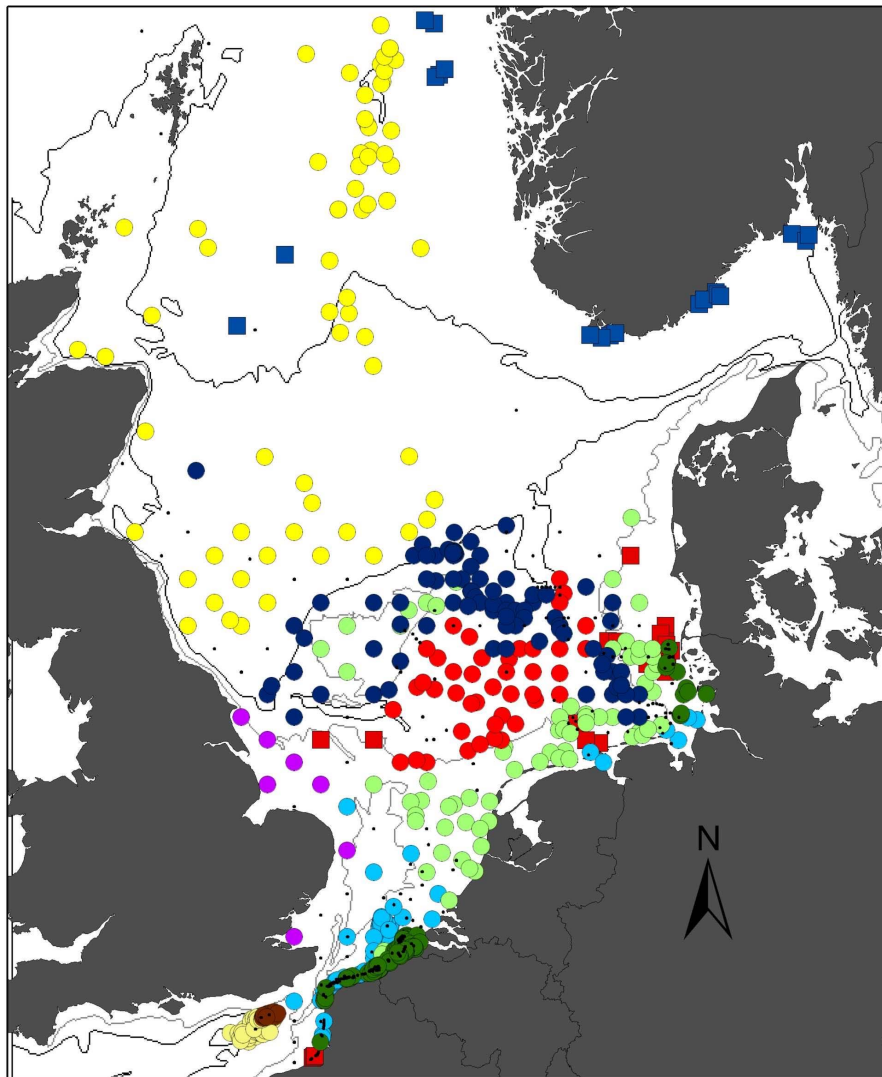


Figure 5.1.5. Common communities from PRIMER clustering and TWINSpan (all stations in 2000). Letters (A–D23) indicate clusters identified by PRIMER, and those in parentheses are the corresponding community clusters identified by TWINSpan. Stations from both analyses that did not correspond are illustrated by a black dot.

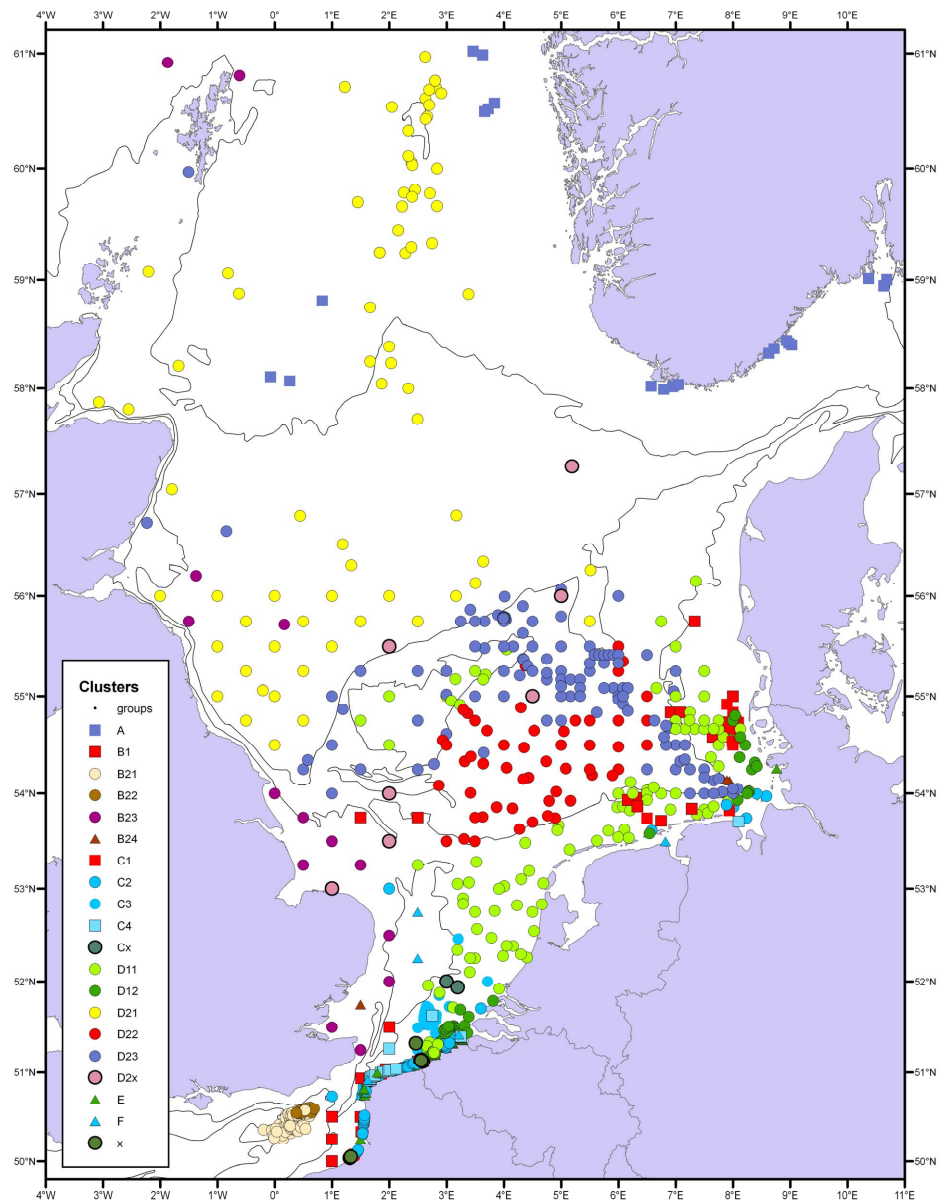


Figure 5.1.6. Distribution of assemblages in the North Sea in 2000 according to group-average cluster analysis (see also Figure 5.2.2).

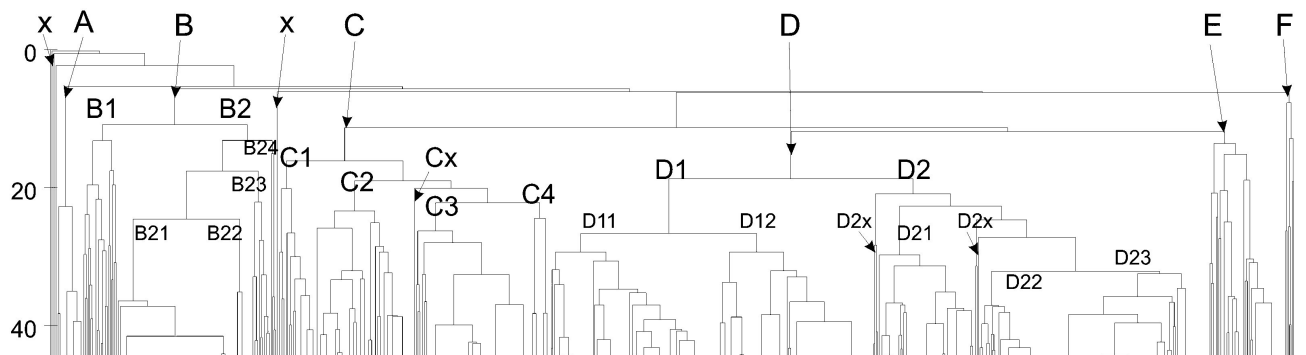


Figure 5.1.7. Cluster dendrogram (upper part only) of the groupings shown in Figure 5.1.6.

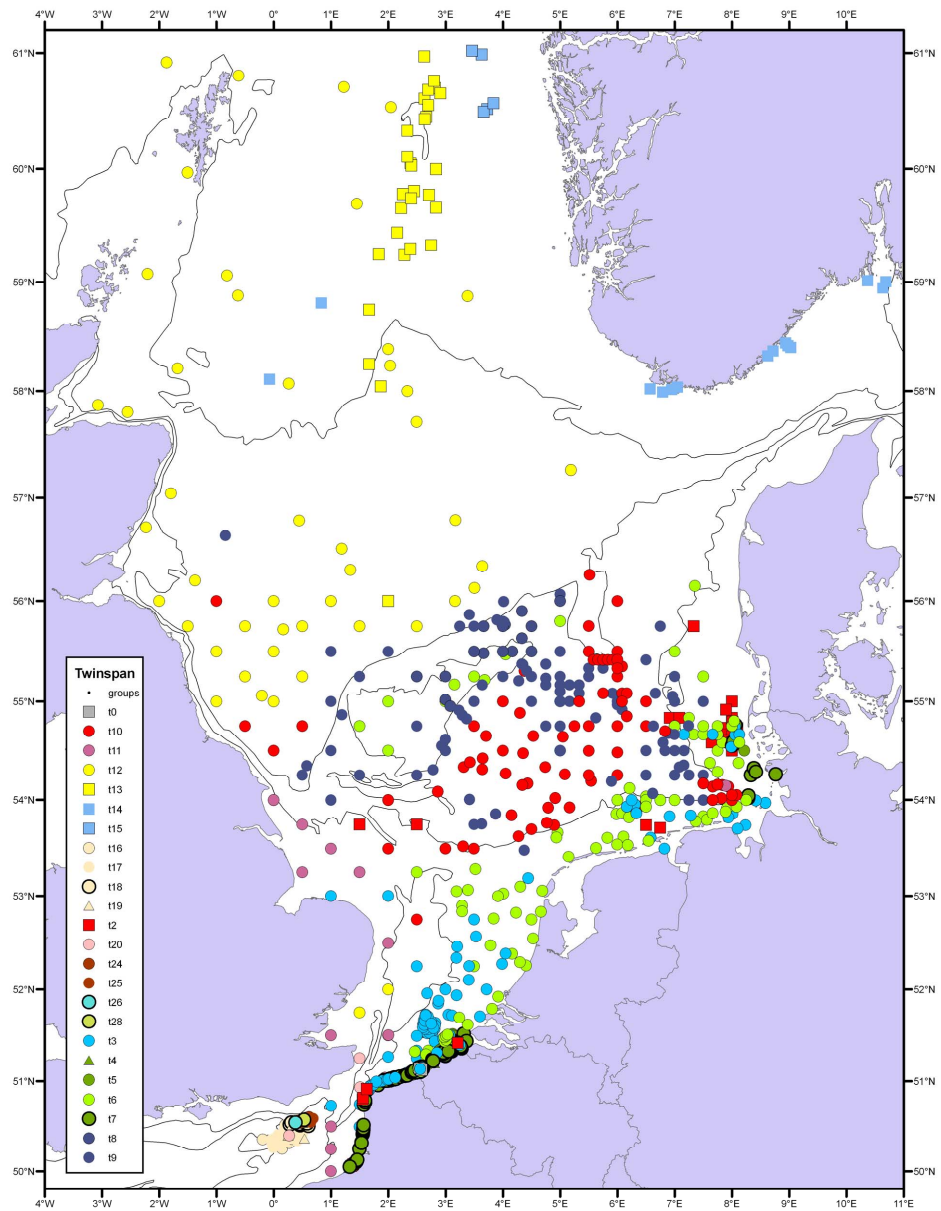


Figure 5.1.8. Assemblages (groupings) according to TWINSpan.

Table 5.1.1. Assemblages of macro-zoobenthos in the North Sea in 2000 with information on the area, the sediments/habitats, water depths, dominating and characterizing species as well as structural descriptors. In the second column, the comparable clusters of Figure 5.2.2 (2000) of Section 5.2 are indicated. Continued on next page.

| CLUSTER | IN SECTION 5.2 | AREA | PREDOMINANT WATER DEPTHS (M) | PREDOMINANT SEDIMENTS | ASSEMBLAGE TYPE (NAME-GIVING SPECIES) | DOMINANTS | CHARACTERIZING SPECIES (PRELIMINARY) | AV. SIM. | AV. DIVERSITY ES(50) | AV. DENSITY AND SD | NO. OF STATIONS |
|---------------------|----------------|--|------------------------------|--------------------------|--|---|---|-------------|----------------------|--------------------|-----------------|
| | | | | | | | | | | | |
| A | Bx | Near Norway and Fladen Ground | mainly >100 | Mud to muddy sand | <i>Thyasira equalis</i> | <i>Heteromastus filiformis</i> ; <i>Paramphinome jeffreysii</i> ; <i>Thyasira equalis</i> | <i>Thyasira equalis</i> ; <i>Eriopisa elongata</i> | 37.6 | 18.6 | 1655 1320 | 20 |
| D 21 | F1 and F2 | Northern and central NS | >50 | Muddy sand and fine sand | <i>Myriochele</i> with <i>Paramphinome</i> | <i>Myriochele</i> spp.; <i>Amphiura filiformis</i> ; <i>Spiophanes</i> spp. | <i>Paramphinome jeffreysii</i> | 36.6 | 19.4 | 1536 1146 | 74 |
| D 23 and D2x | E1 | Around Dogger Bank and in the Pleistocene Elbe valley (PEV) | 35–50 | Slightly muddy sand | <i>Amphiura</i> with <i>Spiophanes</i> | <i>Spiophanes bombyx</i> ; <i>Amphiura filiformis</i> ; <i>Mysella bidentata</i> | <i>Magelona filiformis</i> | 39.3 (24.0) | 14.1 | 2276 1386 | 121 |
| D 22 | G | Oyster Ground and outer part of the PEV | 35–50 | Muddy sand | <i>Amphiura</i> with <i>Corbula</i> | <i>Amphiura filiformis</i> ; <i>Corbula gibba</i> ; <i>Mysella bidentata</i> | <i>Corbula gibba</i> | 42.3 | 15.1 | 1520 838 | 55 |
| D 11 | E2 | Offshore sand areas in the southern NS (SNS) and Dogger Bank | 15–35 | Fine sand | <i>Tellina fabula</i> with <i>Urothoe poseidonis</i> | <i>Magelona johnstoni</i> ; <i>Spiophanes bombyx</i> ; <i>Urothoe poseidonis</i> | <i>Urothoe poseidonis</i> | 35.8 | 12.5 | 1177 1064 | 128 |
| D 12 | – | Sand areas nearer to coast in the SNS | 10–20 | Fine to medium sand | <i>Tellina fabula</i> with <i>Abra alba</i> | <i>Spiophanes bombyx</i> ; <i>Abra alba</i> ; <i>Magelona johnstoni</i> | None | 36.7 | 10.9 | 3578 4342 | 118 |
| E | – | Inshore SNS | 2–20 | Sandy mud to muddy sand | <i>Nephtys hombergii</i> with <i>Abra alba</i> | <i>Chaetozone Abra alba</i> ; <i>Nephtys hombergii</i> | None | 24.6 | 7.1 | 585 1454 | 58 |

| CLUSTER | IN SECTION 5.2 | AREA | PREDOMINANT WATER DEPTHS (M) | PREDOMINANT SEDIMENTS | ASSEMBLAGE TYPE (NAME-GIVING SPECIES) | DOMINANTS | CHARACTERIZING SPECIES (PRELIMINARY) | AV. SIM. | AV. DIVERSITY ES(50) | AV. DENSITY AND SD | NO. OF STATIONS |
|----------------------|----------------|---|------------------------------|--|---|--|--|----------|----------------------|----------------------|-----------------|
| B 1 | – | Banks with coarse sands (SNS) | 15–35 | Coarse sand, partly gravelly | <i>Branchiostoma</i> with <i>Echinocyamus</i> | <i>Aonides paucibranchiata</i> ; <i>Echinocyamus pusillus</i> ; <i>Branchiostoma lanceolatum</i> | <i>Branchiostoma lanceolatum</i> | 19.8 | 13.2 | 828 705 | 26 |
| C 1 | A | Southeastern NS banks with medium sands | 15 | Medium (with coarse) sand, partly gravelly | <i>Spisula</i> with <i>Ophelia</i> | <i>Nephtys cirrosa</i> ; <i>Spisula solida</i> ; <i>Ophelia borealis</i> | <i>Spisula solida</i> ; <i>Tellina tenuis</i> | 30.3 | 10.0 | 169 158 | 28 |
| C2, C3, and F | B | Southwestern NS SNS | <40 | Sand | <i>Nephtys cirrosa</i> | <i>Nephtys cirrosa</i> ; <i>Gastrosacchus spininifer</i> ; <i>Magelona johnstoni</i> | <i>Gastrosacchus spinifer</i> ; <i>Urothoe brevicornis</i> | 29–37 | 6.6, 8.5 | 209, 430 291, 280 | 75, 88 |
| C4 | – | Inshore SNS | mainly <20 | Sand | <i>Nephtys caeca</i> | <i>Nephtys caeca</i> | <i>Nephtys caeca</i> | 13.9 | 7.1 | 72 52 | 7 |
| B 23 | C | Western NS and north of Shetlands | 21–136 | Coarse to medium sands | <i>Sabellaria</i> with <i>Polycirrus</i> | <i>Glycera lapidum</i> ; <i>Polycirrus</i> spp.; <i>Sabellaria spinulosa</i> | <i>Sabellaria spinulosa</i> ; <i>Polycirrus</i> spp. | 29.3 | 19.7 | 1648 1394 | 14 |
| B 24 | – | Helgoland Deep Trench and outer Thames | 35–60 | Sand, gravel, mud, and shells | <i>Cerianthus</i> (formerly <i>Nucula nucleus</i>) | <i>Scalibregma inflatum</i> ; <i>Cerianthus lloydii</i> ; <i>Gattyana cirrosa</i> | <i>Gattyana cirrosa</i> ; <i>Cerianthus lloydii</i> | 26.2 | 12.5 | 2–3000 | 3–4 |
| B 21 and B 22 | – | Restricted to eastern English Channel | 41–68 | Sand to gravel | (Small polychaetes) | <i>Prionospio multibranchiata</i> ; <i>Aonides paucibranchiata</i> | <i>Prionospio multibranchiata</i> ; <i>Aonides paucibranchiata</i> | 51.1 | 24.0 | 823 283 | 91 |
| | – | | | | | <i>Hesionura elongata</i> ; <i>Aonides paucibra</i> | <i>Hesionura elongata</i> ; <i>Eurydice spinigera</i> | 50.7 | 12.1 | 536 295 | 12 |

Table 5.1.1 continued. Assemblages of macro-zoobenthos in the North Sea in 2000 with information on the area, the sediments/habitats, water depths, dominating and characterizing species as well as structural descriptors. In the second column, the comparable clusters of Figure 5.2.2 (2000) of Section 5.2 are indicated.

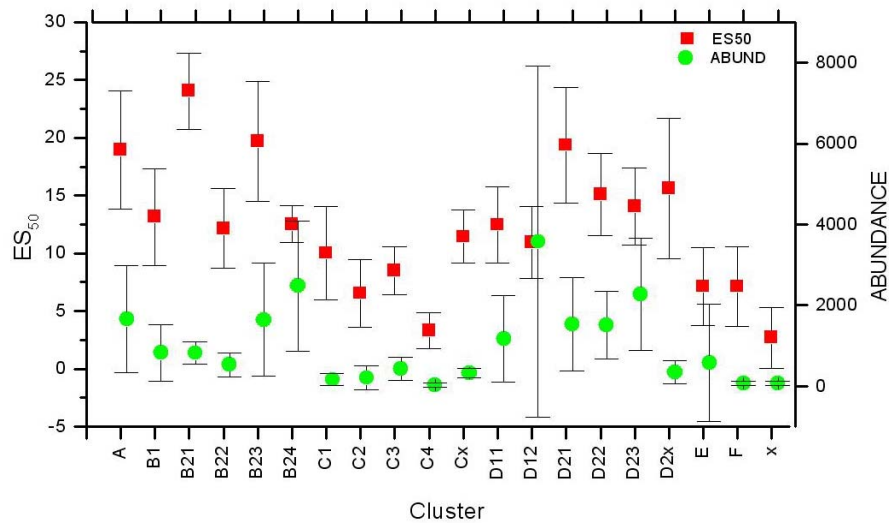


Figure 5.1.9. Diversity and densities of the assemblages.

The average macrobenthic density and diversity per cluster group (assemblage) ranged from approximately 35 to 3500 ind. m⁻² and ES(50) from 2.7 to 24.0, respectively. More information is presented in Section 5.3, e.g. Figures 5.3.5 and 5.3.10. Groups C1–C3, and Cx are characterized by a combination of low density and moderate diversity. High densities and diversities were found in groups D12 to D23 and also in A, B23, B24. Generally, several coarse sand to gravel assemblages had the highest diversities. Group C4 had both the lowest density and diversity (neglecting the outliers of “x”).

5.1.4 Discussion and conclusions

As in earlier descriptions (Künitzer *et al.*, 1992; Heip *et al.*, 1992), a main division of the macro-zoobenthos in the North Sea between its deeper northern and shallower southern parts again appears in the results of the NSBP 2000 survey. This division is seen clearly in the separation of assemblages along the Frisian Front at a depth of approximately 30 m and at the northern lower slope margin of the Dogger Bank. The latter occurs at depths of approximately 50–60 m, according to the outcome of cluster analysis (Figure 5.1.6), and at somewhat greater depths (60–70 m), in the outcome of TWINSPAN analysis (Figure 5.1.8), which is comparable with the results from 1986, also obtained with TWINSPAN.

Large-scale changes in comparison with earlier descriptions (especially from 1986) are discussed in Section 5.2. Here, we highlight changes in the community of the submerged Pleistocene Elbe valley (*Amphiura filiformis* with *Spiophanes bombyx*), which is also found at the outer margins of the Dogger Bank. The spreading of *Acrocynida* (*Amphiura*) *brachiata* towards the inner German Bight and on the Dogger Bank is discussed in Sections 5.2 and 5.4.

The relationship between spatial patterns in the infauna, epifauna, and fish are explored in Section 6.1. It is also interesting to note similarities in the distribution of the infauna and the plankton, namely a division between southern and northern communities with a transitional zone north of the Dogger Bank area. The northern community is especially influenced by the degree of north Atlantic inflow, while a third zone in the southwest North Sea is additionally characterized by stronger coastal-water influences (MAFF, 1981). Frasz *et al.* (1991) similarly highlighted the dominant effect of north Atlantic inflow on copepod species composition and abundance in stratified waters, in contrast to coastal mixed waters to the southeast where communities are more locally variable in character (see also Adams, 1987).

General latitudinal trends of increases in diversity and (less clearly) density from south to north as described for the 1986 data (Heip *et al.*, 1992) were again shown in 2000. They are at the same time related to water depths, which follows the same general trend. These depth-related zonation were also identified in early work by Spärck (1935), Remane (1940), and Jones (1950). Glémarec (1973) stressed the importance of increasing stability in the water temperature regime with increasing depths, which he defined in terms of zones or *étages*. However, other stress factors such as wind- and current-induced turbulence also decrease with depths. Stations in the Norwegian Skagerrak do not follow this rule, presumably because they are exceptionally deep and, thus, subject to reduced food inputs.

Lowest diversities were found in nearshore waters along the whole southern and southeastern North Sea (Figure 5.1.10). This may be related not only to the reduced salinities there, but also to the high climatic and hydrological variability and disturbing human influences, including pollution and eutrophication. The west-to-east trends shown with univariate methods (Figure 5.1.3) indicate that the eastern North Sea (especially a large part of the German Bight in the southeast) is generally impoverished in diversity. This part of the North Sea is most remote and biogeographically apart from the species-rich Atlantic Ocean and most strongly under the disturbing natural and anthropogenic “continental” (mainland) influences.

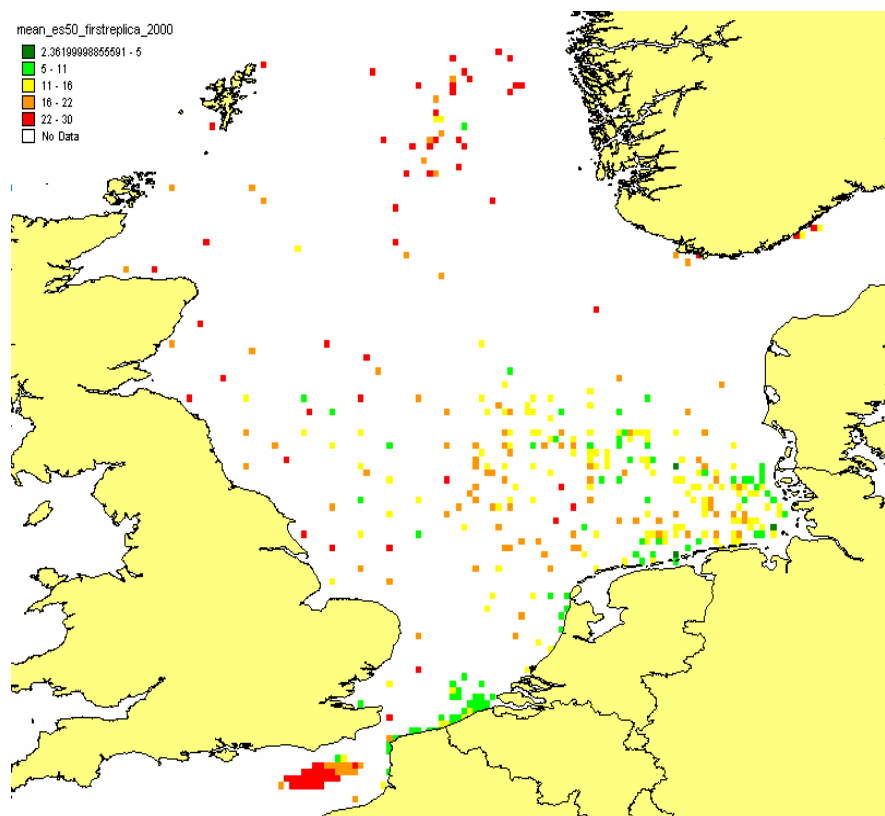


Figure 5.1.10. Distribution of diversities (ES(50)) of the first replicate samples per station.

Although some northern and central parts of the North Sea were poorly covered by sampling stations around 2000, the nearshore areas along the eastern English Channel and the French and Belgian North Sea coasts were sampled with very high spatial resolution. The groups identified there by both clustering and TWINSpan may be regarded as local sub-associations of larger communities (e.g. the well-known *Macoma* or the *Goniadella–Spisula* communities) reflecting the great spatial variability of environmental conditions in such waters.

Compared with the wider North Sea, these local variants appear to be of minor importance but, because inshore waters surrounding heavily populated areas are commonly subjected to a

wide range of human influences and are the target of many environmental or nature protection measures, they have been intensively studied (e.g. Degraer *et al.*, 2003, 2006; Van Hoey *et al.* 2004; Daan and Mulder, 2005; Rachor and Nehmer, 2003; Rachor, 2006; see also Rees and Eleftheriou, 1989; Kröncke and Bergfeld, 2003). Nevertheless, as for the wider North Sea, distinctions between these variants can be explained partly by responses to natural variation in sediment conditions, water depths, and longitude (see e.g. Figure 5.1.6).

Although the more offshore fine to medium sand areas in the Dutch and German waters, as well as the higher Dogger Bank, appear inhabited by a relatively homogenous community of the *Tellina fabula* type, areas off the English east coast (with water depths of less than approximately 30 m) are less uniform in substratum type and, accordingly, inhabited by different assemblages.

North of the “Frisian Front” with very muddy sediments at a depth of approximately 30 m, the Oyster Ground with mixed fine substrates up to the southern margin of the Dogger Bank is inhabited by the *Amphiura filiformis* community with *Corbula gibba*, partly extending across the Pleistocene Elbe valley in the east. This influence is more strongly expressed in the TWINSPAN results (Figure 5.1.8), while the clustering identifies a stronger relationship with the central North Sea *Myriochele* community in the depression east of the Dogger Bank Tail End. Thus, differences between group-average clustering and TWINSPAN outputs are mainly related to the above transitional areas.

A discussion of whether the few, more substantial changes between 2000 and 1986 are related to warming of the North Sea and/or more stable conditions in the years preceding 2000 appears in Section 5.2.

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5.2 Changes in community structure (1986–2000) and causal influences

I. Kröncke and H. Reiss

5.2.1 Introduction

The North Sea Benthos Project (NSBP) 2000 was initiated as a follow-up to the 1986 ICES North Sea Benthos Survey (NSBS, see Section 3). One major aim of NSBP 2000 was to compare the outcome with that of the NSBS 1986, in order to identify any significant changes and their likely causes. This section focuses mainly on an examination of any differences in the community structure. Thus, the 1986 data were re-analysed and compared with the 2000 data, and possible causal factors for observed differences are discussed.

5.2.2 Methods

For all analyses, only NSB data for the nearest matching stations in 1986 and 2000 were used (Figure 5.2.1). Thus, after excluding stations with a distance apart of more than 40 km, 156 matching stations were considered in the analyses. Instead of using the published results of the 1986 data (Künitzer *et al.*, 1992), they were re-analysed because both datasets had to be taxonomically adjusted to allow comparisons.

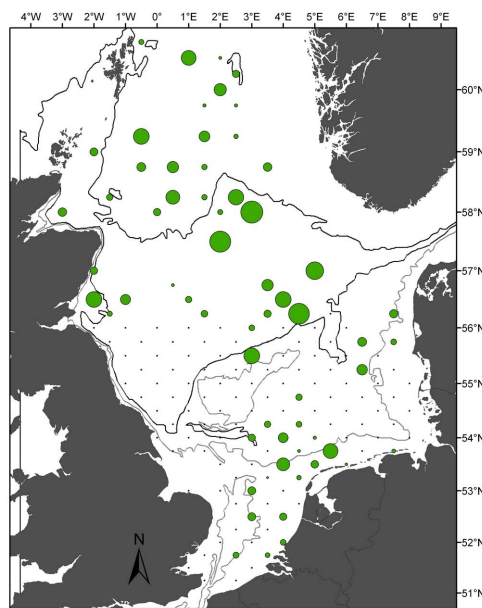


Figure 5.2.1. Location of matching stations with distances apart superimposed. Largest circles represent nearest matching stations of 40 km distance.

We used the PRIMER v5 program package to perform cluster analysis and multidimensional scaling for abundance data to reveal similarities between stations (Clarke and Warwick, 1994). Similarities were calculated using the Bray–Curtis coefficient. Fourth-root transformation was used prior to computation. Similarity, percentage analysis (SIMPER) was used to identify the main species that were responsible for differences in community structure. The significance of any differences in community structure at stations from 1986 and 2000 was tested with ANOSIM. The Hurlbert Index (Hurlbert, 1971) was calculated as an expression of species diversity.

The comparison between the univariate parameters and community structure in 1986 and 2000 was carried out using the clusters of 1986 as a starting point. Thus, stations within each of the 1986 clusters were compared with the matching stations sampled in 2000. Additionally, the datasets of 1986 and 2000 were combined in one cluster analysis to detect differences in the

cluster classification. If matching stations for both years belonged to one subcluster, we assumed a consistent classification.

5.2.3 Results

Figure 5.2.2 shows that the spatial distribution of the macrofaunal communities in 2000 was broadly similar to that in 1986 described by Kunitzer *et al.* (1992). The dendrogram outputs from cluster analysis for both years are shown in Figure 5.2.3. The comparison of the similarity matrices revealed a significant relationship between 1986 and 2000 data (Table 5.2.1). The major divisions in the communities of the North Sea still occur at the 50 m and 100 m depth contours. Also, greater heterogeneity of communities in the southern North Sea (<50 m) compared with the north is still evident.

Table 5.2.1. Correlation coefficients (Spearman rank) relating the similarity matrices of 1986 and 2000 infauna data for different transformation types (RELATE).

| | R ² | P |
|-------------------|----------------|-------|
| Fourth root | 0.533 | 0.001 |
| Square root | 0.527 | 0.001 |
| Presence/absence | 0.511 | 0.001 |
| No transformation | 0.421 | 0.001 |

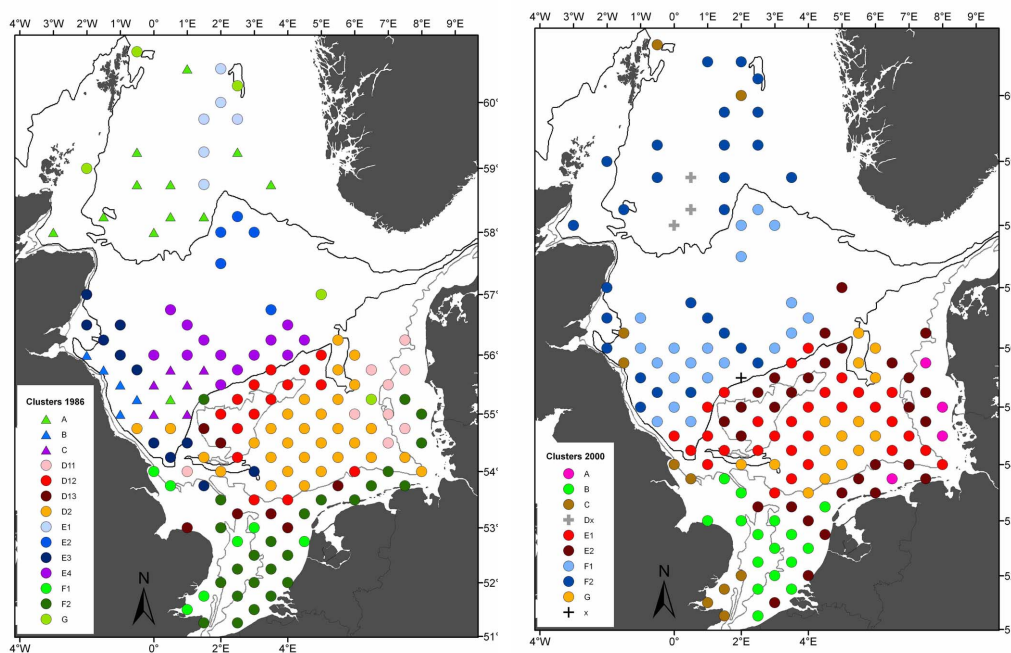


Figure 5.2.2. Spatial distribution of infaunal communities in 1986 (left) and 2000 (right), based on fourth-root transformed abundance data.

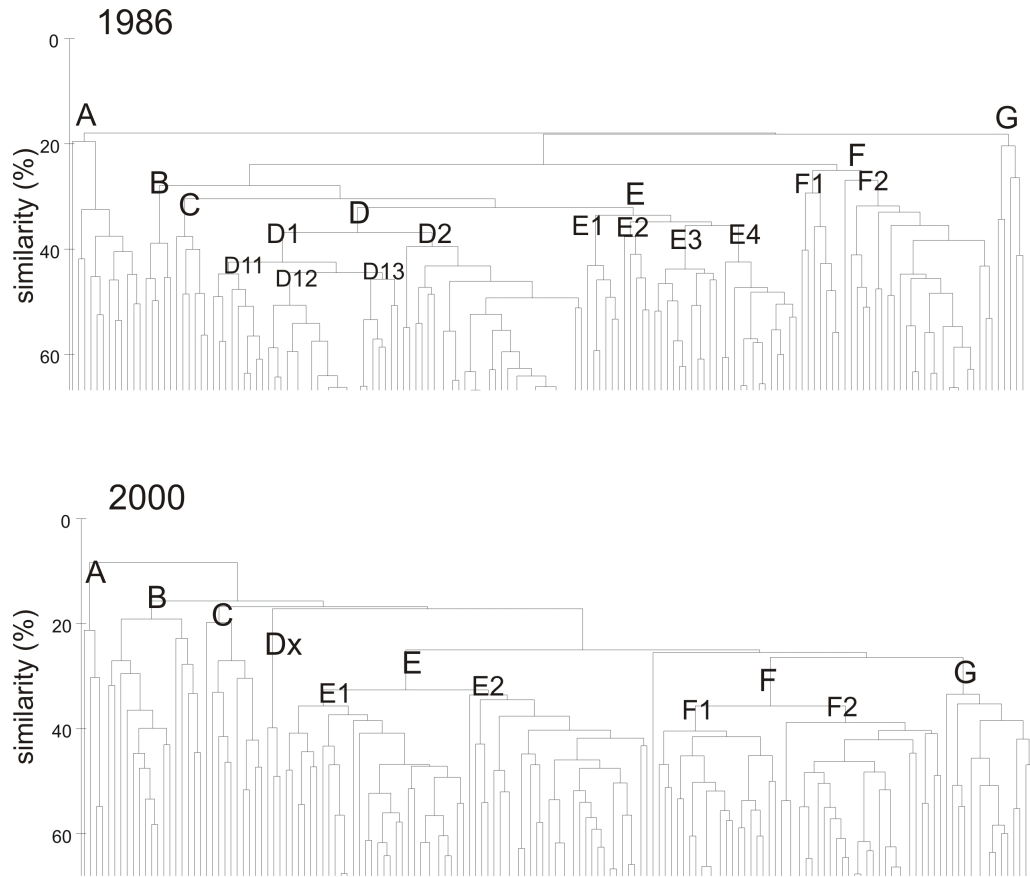


Figure 5.2.3. Cluster dendrograms and groupings shown in Figure 5.2.2 revealed with fourth-root transformed abundance data.

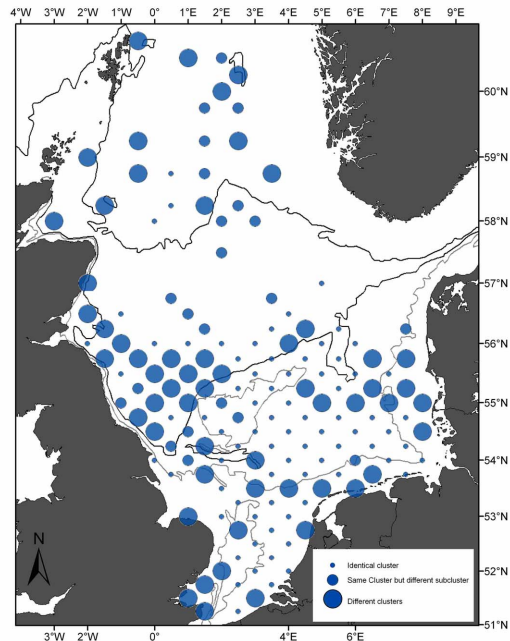


Figure 5.2.4. Distribution of differences in the cluster classification between 1986 and 2000, based on fourth-root transformed abundance data. Small-sized circles represent stations that were classified identically in 1986 and 2000. The largest circles represent stations classified in different main clusters.

However, on closer inspection, there are noticeable differences between the community structure in 1986 and 2000 in some areas of the North Sea. An evaluation of differences in the composition of stations within similar clusters in 1986 and 2000 demonstrates that these were greatest in the eastern North Sea, along the Frisian Front, towards the English Channel, and especially at depths of >50 m off the British north coast and at >100 m in the northern North Sea (Figure 5.2.4). These have been caused by differences in abundance and species numbers.

Deeper than 100 m, differences in community structure were caused mainly by a decrease in abundance but an increase in species numbers (Figure 5.2.5). In 2000, the community structure was similar to that in the central North Sea at 50–100 m depth (Figure 5.2.2). At some of the stations, *Paramphinome jeffreysii* occurred in considerably higher densities in 2000 (see also Section 5.4).

The differences in community structures off the British north coast (>50 m) seem to be caused by a general decrease in species numbers in parallel with an increase in abundance in 2000 (Figure 5.2.5). In 1986, this area was split into several clusters (mainly B, C, E4), while in 2000 the area was separated mainly into two clusters, F1 and F2 (Figure 5.2.2). The SIMPER analyses show that the differences in community structure have been caused by an increase in the small polychaete *P. jeffreysii*, and the interface-feeding polychaetes *Myriochele* spp. and *Spiophanes bombyx* (Annex 2).

In the eastern North Sea, differences in 2000 were caused by an increase in abundance of Phoronida and *S. bombyx*, and of the bivalves *Fabulina fabula* and *Corbula gibba*, the amphipod *Urothoe poseidonis*, and the brittlestar *Acrocnida (Amphiura) brachiata*.

In the southwest North Sea towards the English Channel, both a decrease and an increase in species numbers, as well as an increase in abundance occurred between 1986 and 2000. At the offshore stations, differences in communities were caused by an increase in *S. bombyx* and *Magelona* spp., but a decrease in e.g. *Ophelia borealis*. At the coastal stations, the abundance of the polychaetes *Lanice conchilega*, *S. bombyx*, and *Lagis koreni*, as well as the bivalve *Spisula* spp. increased considerably.

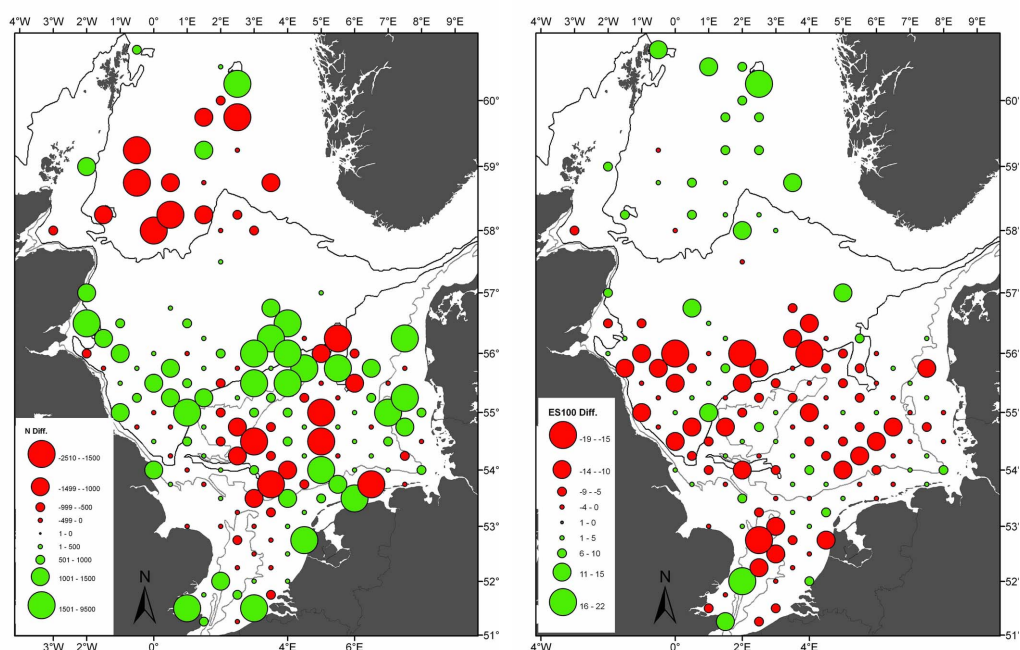


Figure 5.2.5. Differences in mean abundance (left) and mean ES(100) (right) between 1986 and 2000. Green dots indicate an increase and red dots a decrease in 2000 compared to 1986.

At the western part of the Frisian Front, differences in community structure could be explained by a general decrease in abundance, e.g. in *O. borealis*, while at the eastern part and at the East Frisian coast, total abundances increased owing to increases in *S. bombyx* and *Magelona* spp.

The community structure in the central Oyster Ground remained rather stable over time, but a decrease in total abundance was found at some stations. Also, the Dogger Bank community remained rather stable, even though the abundance of the polychaetes *O. borealis* and *Nephtys cirrosa* and the bivalve *Abra prismatica* decreased. At the Tail End, abundances of *L. conchilega* and *S. bombyx* increased, while at the South West Patch *Magelona* spp. and *S. bombyx* increased but *Bathyporeia* spp. decreased.

Table 5.2.2 shows that all of the changes in community structure evident, from Figure 5.2.6, are significant ($P < 0.05$). However, the highest R values (> 0.4) were found for the comparison of clusters from the northern North Sea (cluster A, B, C, E1, E2, and G).

Table 5.2.2. Differences between 1986 and 2000 data revealed with ANOSIM for the MDS-plots shown in Figure 5.2.6.

| CLUSTER | R | P |
|---------|-------|-------|
| A | 0.511 | 0.001 |
| B | 0.426 | 0.016 |
| C | 0.648 | 0.002 |
| D11 | 0.320 | 0.002 |
| D12 | 0.241 | 0.001 |
| D13 | 0.190 | 0.038 |
| D2 | 0.181 | 0.001 |
| E1 | 0.837 | 0.002 |
| E2 | 0.588 | 0.008 |
| E3 | 0.372 | 0.001 |
| E4 | 0.377 | 0.001 |
| F1 | 0.202 | 0.042 |
| F2 | 0.131 | 0.001 |
| G | 0.404 | 0.032 |

An additional factor contributing to the apparent decline in species number at many stations in the southern North Sea (Figure 5.2.5) may be the use of deeper penetrating core samples in 1986. Stations in 2000 were sampled mainly by 0.1 m² grabs (see Section 3).

Detailed maps comparing species distributions in 1986 and 2000 are given in Section 5.4. Section 5.3 presents detailed correlations of faunal and environmental parameters.

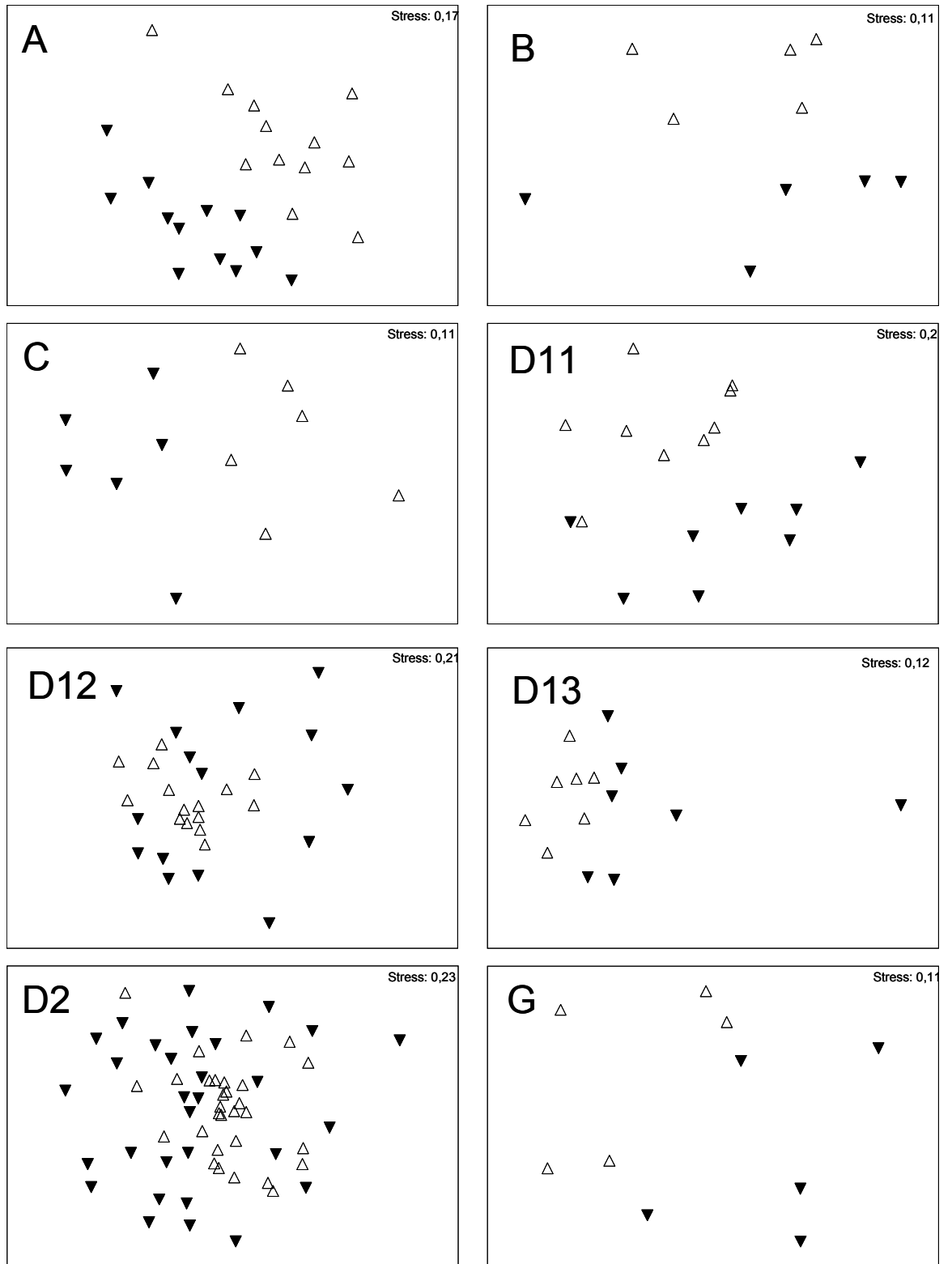


Figure 5.2.6 (continued on next page). MDS plots using fourth-root transformed abundance data for 1986 (Δ) and 2000 (\blacktriangledown) stations, corresponding to the clusters identified in Figure 5.2.3.

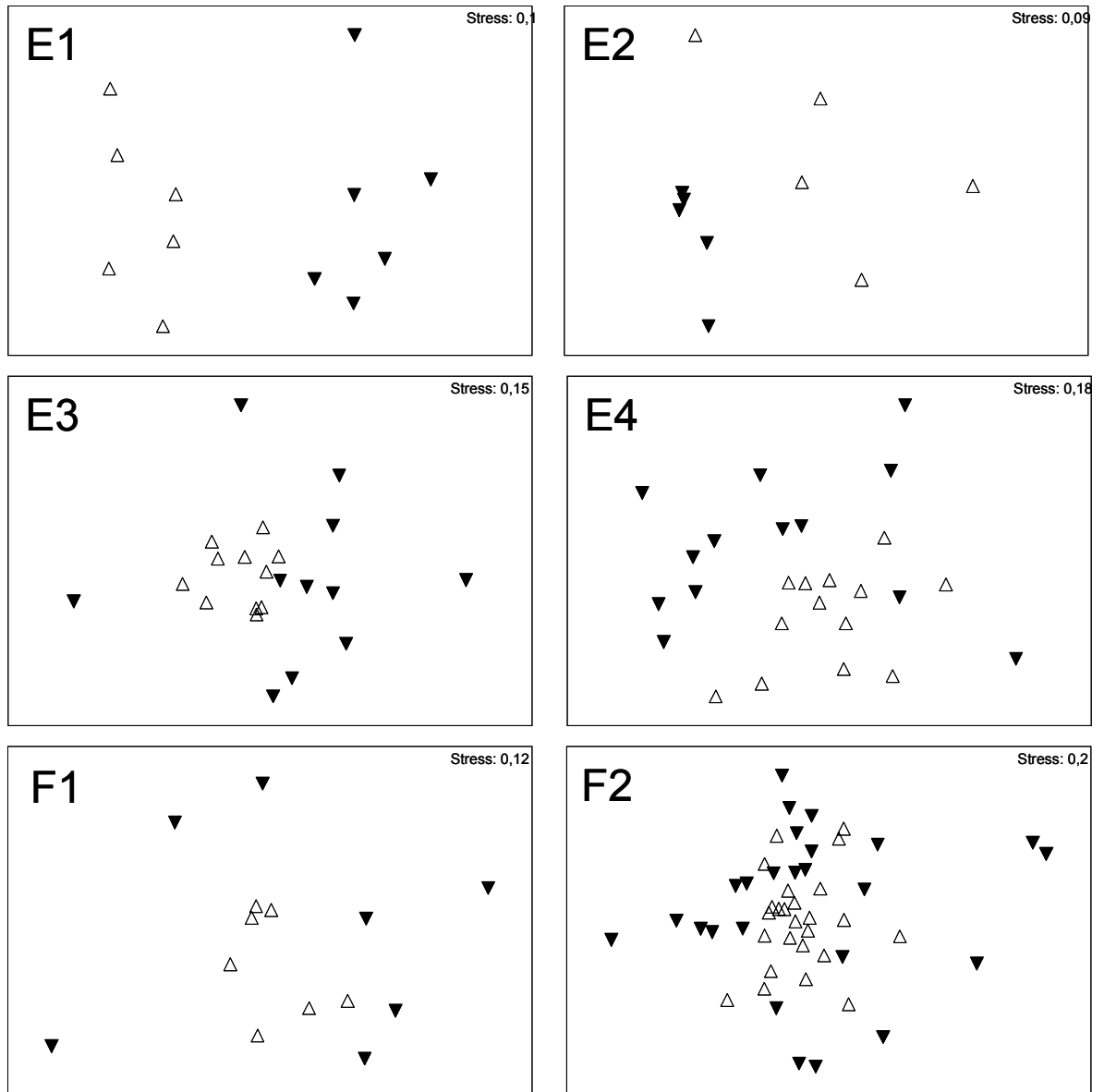


Figure 5.2.6 (continued). MDS plots using fourth-root transformed abundance data for 1986 (Δ) and 2000 (\blacktriangledown) stations, corresponding to the clusters identified in Figure 5.2.3.

5.2.4 Discussion

In general, the spatial distribution of the macrofaunal communities in 2000 was rather similar to that in 1986, as described by Künitzer *et al.* 1992. The major divisions in the structure of the communities of the North Sea still occur at the 50 m and 100 m depth contours, as also described by Glémarec (1973).

The decrease in total abundance found in the northern North Sea (>100 m) was influenced by the use of different mesh sizes in 1986 (0.5 mm) and 2000 (1 mm) as well as the spatial resolution of the station grid (Figure 5.2.1). The increase in species number in this region in 2000 might be to the result of improved taxonomic precision.

Thus “real” changes in community structure between 1986 and 2000 can be more confidently discussed for the southern North Sea. Changes in community structure north of the 50 m depth contour may be related to changes in the hydroclimate caused especially by changes in the North Atlantic Oscillation (NAO) which, in positive mode, results in an increase in SST, changes in sediment structure, and food availability, as described by Reid and Edwards (2001)

and Kröncke *et al.* (1998). Wieking and Kröncke (2001) described the NAO-influenced changes in hydrography, especially north and south of the Dogger Bank. The increase in inflow of Atlantic water masses through the Fair Isle channel strengthened the frontal system north of the bank creating a “strong” border between northern and southern water masses. High current velocities in the northern part of the Dogger Bank (Siegismund and Schrum, 2001) in addition to a seasonal jet (Brown *et al.*, 1999), limit the accumulation of particulate organic material in seabed sediments. Klein *et al.* (1999) showed that, during storms, fine sediments at the seabed are mobilized at a depth of up to 60 m at the northern slope of the Dogger Bank. Thus, the decrease in total species number and the increase in species such as the small polychaete *Paramphinome jeffreysii*, as well as the dominance of the interface-feeding polychaetes *Myriochele* spp. and *Spiophanes bombyx* north of the 50 m depth contour, provide supporting evidence for a change in hydrodynamics affecting sediment structure and stability, as confirmed by changes in the median grain size in this area associated with changes in food availability (Wieking and Kröncke, 2001). Since *P. jeffreysii* and *Myriochele* spp. are considered to be cold-temperate species, their increase in abundance north of the 50 m depth contour might be a hint of colder northern water masses north of the frontal system.

Changes observed in the communities at the offshore stations in the southwestern North Sea towards the English Channel and the eastern part of the Frisian Front indicate similar environmental influences. The decrease in the polychaete *Ophelia borealis* in these regions might be influenced by an increase in SST (*O. borealis* is a cold-temperate species) as well as by changes in the sediment composition as found by Wieking and Kröncke (2001) at the Dogger Bank. However, there was no evidence of a systematic change in sediment particle sizes between the 1986 and 2000 surveys (see Sections 4.2 and 4.3).

At the coastal stations in the southwestern North Sea towards the English Channel and at the western part of the Frisian Front, an increase in interface-feeding polychaetes such as *S. bombyx*, *Magelona* spp., and *Lanice conchilega*, as well as the bivalve *Spisula* spp., might be caused by greater food availability at the Flamborough and Frisian Fronts owing to an NAO-induced increase in SST and hydrodynamic forces. Owing to frontal conditions and enhanced primary production, food supply to the benthos (quality and quantity) will be higher than in non-frontal areas at comparable depths.

In the eastern North Sea in 2000, the increase in phoronids and other interface-feeding species such as the polychaete *S. bombyx* and the bivalves *Fabulina fabula* and *Corbula gibba* also indicate an NAO-induced increase in food availability owing to higher primary production in the German Bight, as described by Reid *et al.* (1998) and Reid and Edwards (2001). Current-induced changes in the sediment structure might have caused the increase in the brittlestar *Amphiura brachiata* and the sea urchin *Echinocyamus pusillus*, which prefers coarser sediments, but *A. brachiata* is also a warm-temperate species (Wieking and Kröncke, 2001). Further investigations of links between benthic community structure and environmental variables, including climatic influences, can be found in Sections 5.3, 5.7, 6.1, and 6.3.

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5.3 Relations and interactions between environmental factors and biotic properties

W. Willems, H. L. Rees, M. Vincx, P. Goethals, and S. Degraer

5.3.1 Introduction

This section examines in more detail the relationships between the biological and environmental data and highlights any differences between 1986 and 2000. The best way to express these relationships is identified. This work is designed to complement and extend the findings of Sections 5.1 and 5.4. Heip *et al.* (1992) performed a similar assessment of the relationship between biomass, density, diversity, and individual weight with abiotic variables for the NSBS 1986 dataset. The present analyses include the samples both from 1986 and 2000. Also, additional environmental variables, not available to Heip *et al.* (1992), were available (e.g. tidal stress, stratification; see Table 5.3.1).

This is a unique opportunity to search for trends on the scale of the whole North Sea, which measures 1000 by 600 km. Such a large-scale comparison of abiotic variables with the benthic fauna is rare. In the following account, a number of macro-ecological hypotheses are tested, including the relation between latitude and diversity, and temperature and individual weight. The outcome is summarized in a schematic overview to facilitate the communication of findings to a wider readership. The NSBP 2000 survey extended the geographical scope of the 1986 survey by including data for the eastern English Channel. Though a component of the greater North Sea as defined by OSPAR and the EU, the predominantly coarse substrata of the Channel provide a notable contrast to the generally finer sediments to the north.

5.3.2 Methodology

As a first step, the non-parametric Kendall’s tau correlation between all biotic and abiotic variables was calculated. Next, a principal components analysis (PCA) was performed to visualize the multivariate relations between the abiotic variables. For the 1986 and 2000 datasets, separate correlation analyses and PCA were conducted. The communities identified by Kunitzer *et al.* (1992) for the 1986 stations, and in this report (Section 5.1) for the 2000 samples, were superimposed on the PCA plots to facilitate interpretation of the outcome.

Table 5.3.1. Overview of the environmental and biological variables in the dataset.

| VARIABLE | 1986 | 2000 | VARIABLE | 1986 | 2000 |
|------------------------------|------|------|-----------------------|------|------|
| latitude | x | x | average salinity June | x | x |
| longitude | x | x | mode mm | – | x |
| depth | x | x | d10 mm | – | x |
| tidal stress | x | x | d50 mm | x | x |
| peak wave stress | x | x | d90 mm | – | x |
| stratification | x | x | ratio d10/d90 | – | x |
| chl a water | x | x | gravel % | – | x |
| chl a bottom | x | – | sand % | – | x |
| pigment total | x | – | mud % | x | x |
| protein | x | – | ES(50) | x | x |
| Org. C % | x | – | density | x | x |
| average temperature February | x | x | biomass | x | x |
| average temperature June | x | x | individual weight | x | x |
| average salinity February | x | x | | | |

Based on the outcome of correlation and PCA analyses, a subset of the most influential environmental variables was identified and relationships with biotic variables expressed as a

series of scatterplots. The first group of plots expresses relationships for the 1986 and 2000 datasets and include trend lines to aid interpretation. Because of their often distinctive character, samples from the eastern English Channel were identified separately and were not used in the construction of the linear trend line. The second group of plots allowed a comparison of the relation between the biotic and abiotic variables for 1986 and 2000. Variables that were the most strongly correlated with density, biomass, and diversity were determined from a combination of correlation analysis, PCA, and scatterplots. Because such a large ecological dataset was available, several macro-ecological hypotheses could be tested.

5.3.3 Results

5.3.3.1 Correlation 1986

Spatial relationships

There is a north–south decrease in the average winter bottom temperature and depth (see Figures 4.1.2 and 4.1.3), because both variables are negatively correlated with latitude (latitude–depth: $r = 0.55$; latitude–av. temp. feb86: $r = 0.71$). In the east–west direction, the peak wave stress increases towards the east (longitude–peak wave stress: $r = 0.57$). Winter and summer salinity decreases eastwards towards the Baltic (longitude–salinity feb86/jun86: $r = -0.75$ and -0.80). The density, biomass, individual weight, and ES(50) show no correlation with longitude or latitude.

Abiotic variables

At greater depth, the winter temperature was higher ($r = 0.67$), because shallow locations are less buffered for atmospheric temperature fluctuations. The temperature and salinity values are highly intercorrelated ($r = 0.38$ – 0.81). Overall, and as expected given the nature of the data, the sediment variables show a high correlation with each other. The percentage of sand and percentage of mud have the highest correlation ($r = -0.92$) and percentage of sand vs. d50 ($r = -0.60$), respectively. The water column chlorophyll *a*, the sediment chlorophyll *a*, total pigments, proteins, and organic carbon percentages show a very low correlation with each other and the other abiotic and biotic variables. Also, peak and tidal stress are totally unrelated according to the correlation analysis.

Relationships of abiotic and biotic variables

Diversity expressed as ES(50) correlates moderately with depth ($r = 0.42$) and temperatures (temp. February: 0.41 ; temp. June: $r = -0.43$). Other correlations between biotic and abiotic variables are low.

5.3.3.2 Correlation 2000

The tidal stress increases southwards (latitude–tidal stress: $r = -0.46$). As in 1986, the temperature and salinity values (from the same Pohlmann model) are highly intercorrelated. All sedimentological variables are highly correlated with each other and the average temperature in February ($r = 0.45$ – 0.63). Overall, the correlations between biotic and abiotic variables are very low.

5.3.3.3 Ordination

The PCA was performed on the abiotic variables per sample. Plots of the sample locations in the ordination space were colour-coded relative to the assigned community (Künitzer *et al.*, 1992; Section 5.1). By doing so, we could determine whether the abiotic clustering of the samples coincided with the biotic clustering of communities from the species abundance matrix. Overall, the communities occupied relatively well-defined regions in the PCA plots (see Figures 5.3.1 and 5.3.2).

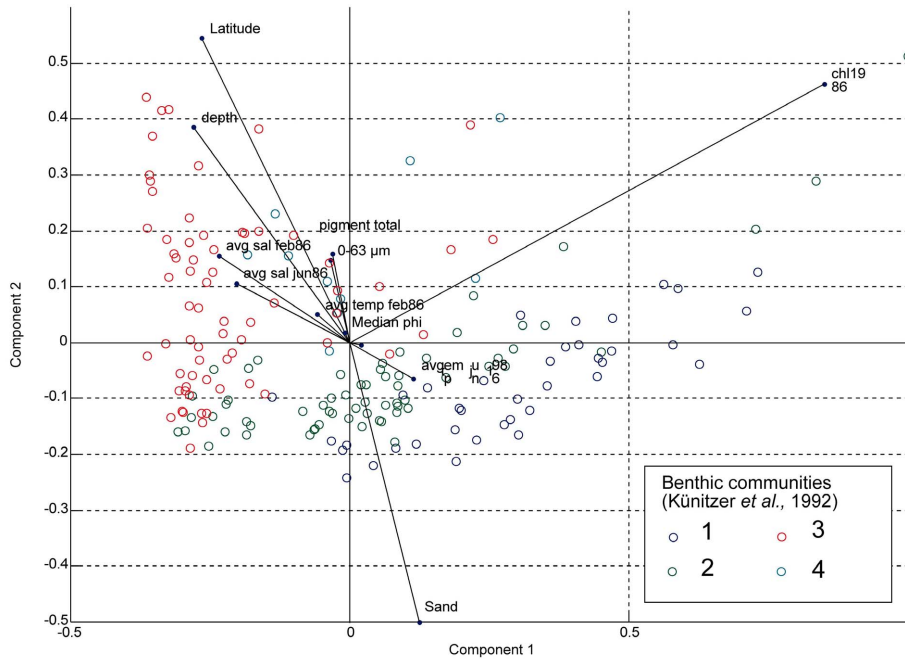


Figure 5.3.1. Principal components analysis of the NSBS 1986 samples (PC1 vs. PC2), colour-coded according to the benthic communities encountered (Künitzer *et al.*, 1992). Vectors indicate the orientation of the environmental variables in relation to the first two PCA components.

This illustrates that the communities can be separated largely according to the abiotic variables. The major separation in communities is perpendicular to the variables latitude, depth, and sand. Thus, for example, community 1 is generally found in sediments with a high percentage of sand in shallower waters and at lower latitudes. The first PCA component (PC1) is positively correlated with surface chlorophyll *a* and negatively with depth and latitude (Figures 5.3.1 and 5.3.2). PC2 is positively correlated with latitude and depth (Figure 5.3.1), and negatively with sand. PC3 is positively correlated with sand and latitude (Figure 5.3.2). Chlorophyll *a* shows no relation with any other variable. The variables latitude, depth, and percentage of sand are very similar in orientation, which illustrates their strong relationship. Thus, as expected, depth changes with latitude, and lower depths are associated with sediments having a higher percentage of sand. The total amount of pigment is highly correlated with the percentage of mud. The salinities in June and February are highly correlated and inversely related to the temperature in June.

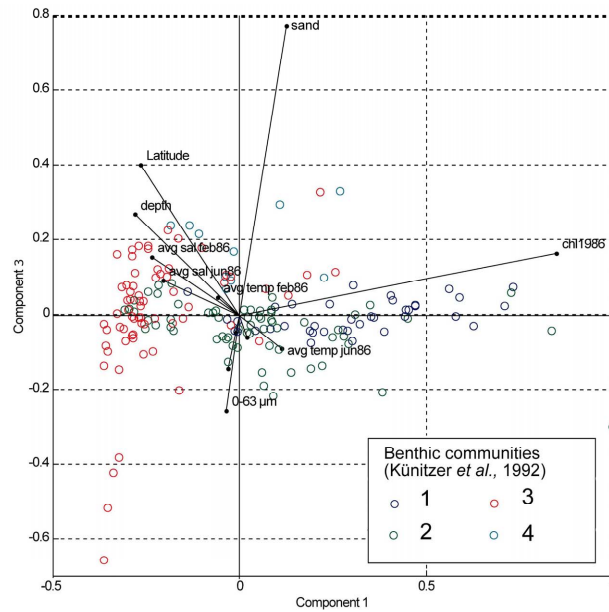


Figure 5.3.2. Principal components analysis of the NSBS 1986 samples (PC1 vs. PC3), colour-coded according to the benthic communities encountered (Künitzer *et al.*, 1992). Vectors indicate the orientation of the environmental variables in relation to the first and third PCA component.

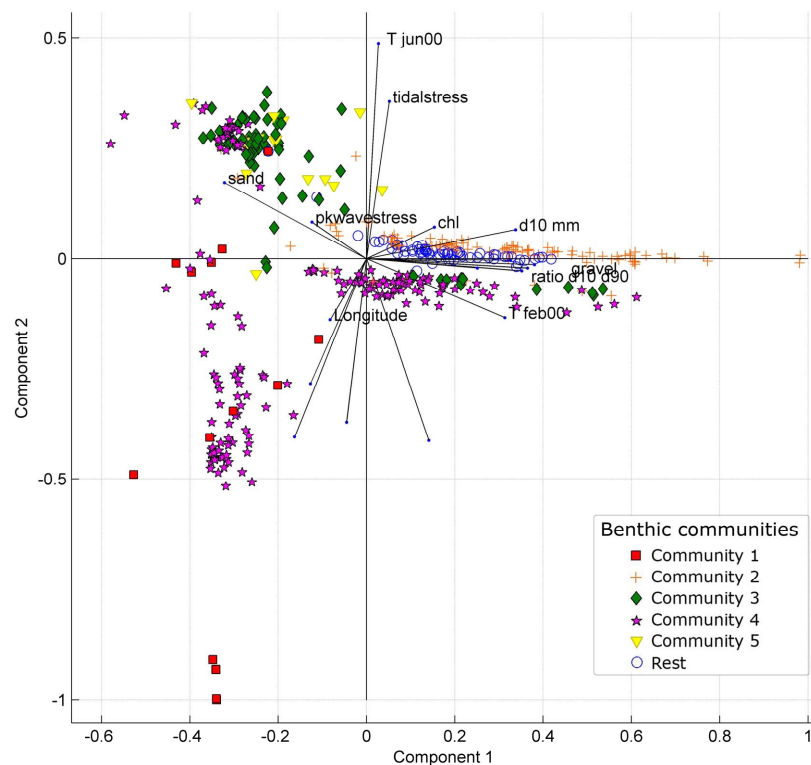


Figure 5.3.3. Principal components analysis of the NSBP 2000 samples (PC1 vs. PC2), colour-coded according to the benthic communities encountered in Section 5.1 (i.e. Community 1 = Cluster group A; Community 5 = Cluster group E; Rest = Group F and “x” samples). Vectors indicate the orientation of the environmental variables in relation to the first two PCA components.

In the PCA plots of the NSBP 2000 samples (Figure 5.3.3 and Figure 5.3.4), the spatial distinction between communities (Section 5.1) is also evident, though there is greater overlap than for the 1986 data. Thus, it is not possible to discriminate accurately between communities according to the available abiotic variables, but patterns can be identified. PC1 is positively

related with most sediment variables, the temperature in February, and the surface chlorophyll *a*, and negatively correlated with the percentage of sand. As expected, all sediment variables are linearly related. PC2 is positively related with the temperature in June and tidal stress, and negatively with the depth, latitude, and salinity in June. As in the 1986 samples, the depth increases with latitude over the North Sea basin. Finally, PC3 is positively related to longitude and chlorophyll *a*, and negatively with tidal stress and mud. The chlorophyll *a* increases eastwards, while the tidal stress, mud, and depth appear to increase westwards, according to the PCA output.

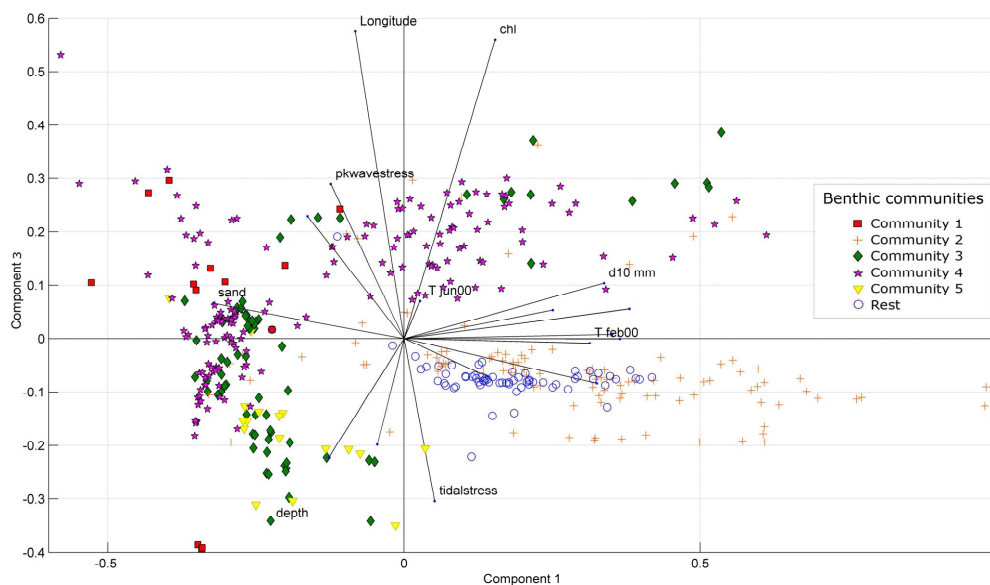


Figure 5.3.4. Principal components analysis of the NSBP 2000 samples (PC1 vs. PC3), colour-coded according to the benthic communities encountered (Section 5.1). Vectors indicate the orientation of the environmental variables in relation to the first and third PCA component.

5.3.3.4 Scatterplots

All abiotic variables were plotted against all biotic variables. For brevity, only a selection – principally those showing the strongest relationships – are presented here.

Diversity ES(50)

The Channel is clearly more diverse than other sites at low latitude (Dutch and Belgian coasts). The ES(50) rises almost linearly with latitude (Figure 5.3.5), if Channel samples are excluded from the trend line. The highest ES(50) values, however, are found on the German continental shelf. The trend of increasing ES(50) with latitude is similar in 1986 and 2000 (Figure 5.3.6). Heip *et al.* (1992) observed that, for the 1986 samples, diversity showed a trend with latitude, and the northern North Sea was more diverse. An effect of longitude and depth was observed by Heip *et al.* (1992), but not found for the combined 1986/2000 dataset in the present analysis.

Overall, there is a trend ($r^2 = 0.211$) of increasing ES(50) with increasing salinity in June (Figure 5.3.7). The lowest salinities are found in the Skagerrak where the ES(50) is intermediate. The lowest ES(50) values are found at a salinity of 34–34.5 psu. From this point, the ES(50) rises with rising salinity values. The ES(50) decreases almost linearly with the average temperature in June (Figure 5.3.8; $r^2 = 0.234$). The Channel has a much higher diversity relative to regions with similar temperatures. The 1986 and 2000 datasets show a similar trend of decreasing ES(50) with average temperature in June (Figure 5.3.9). However, the average temperature in June 2000 was significantly higher than in 1986 for each station (paired *t*-test; $p < 0.001$). The average temperature in 2000 was, on average, 1.07°C (stdev.

0.42) higher than in 1986. There is a positive relationship between stratification and ES(50) (not shown; $r^2 = 0.213$). The central part of the North Sea above 54° latitude is fully stratified and more diverse. The Channel is slightly more diverse and exhibits no to very little stratification. At low median grain sizes (median grain size $<1000 \mu\text{m}$), a range of diversities are encountered (Figure 5.3.10). Coarser samples, especially along the southeast English coast and the Channel show a much higher minimum and average ES(50). The coarsest (gravelly) Channel samples have a minimum ES(50) of 20 species.

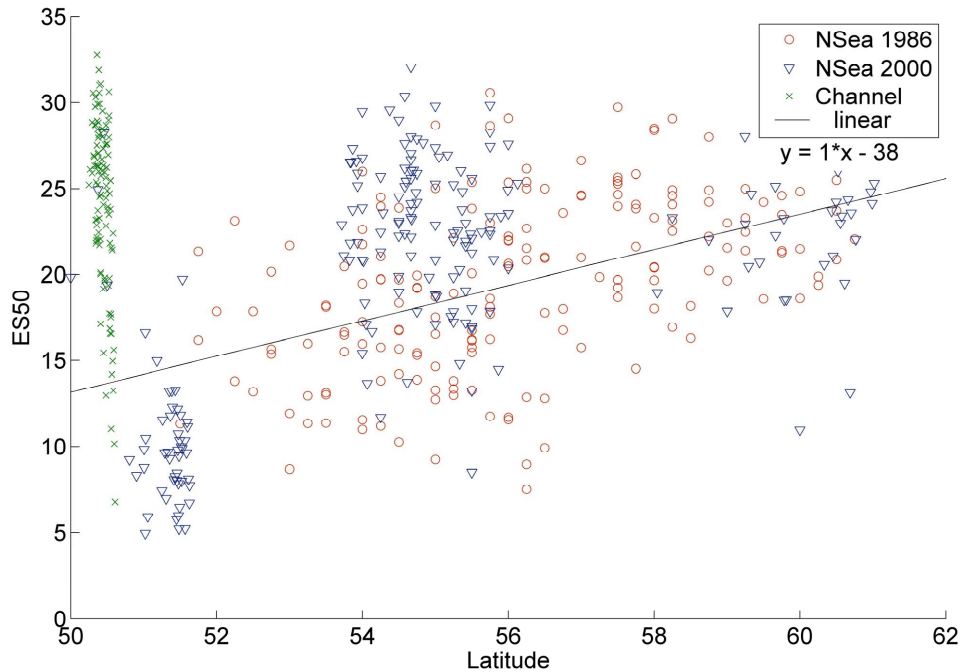


Figure 5.3.5. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. latitude for the 1986 and 2000 samples. The trendline $r^2 = 0.228$, excluding the Channel data.

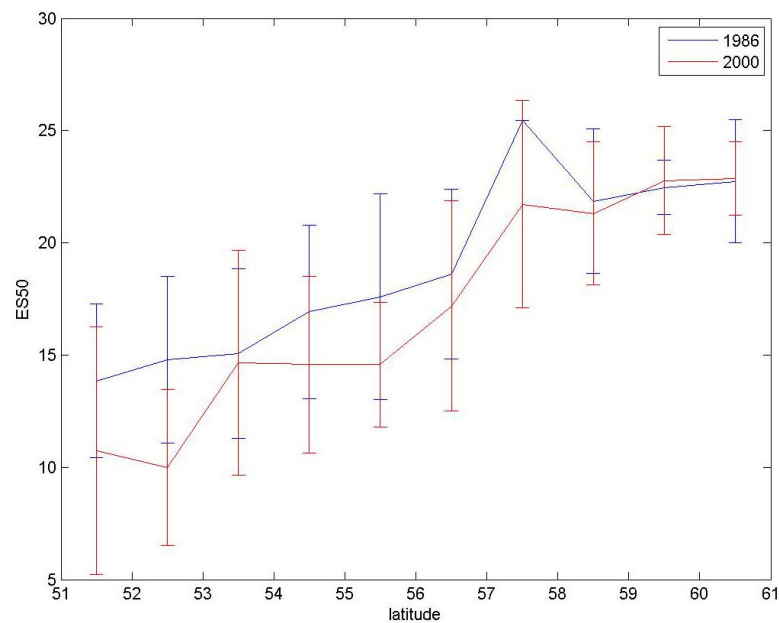


Figure 5.3.6. Plot of the average ES(50) for each degree of latitude. The error bars indicate the variance.

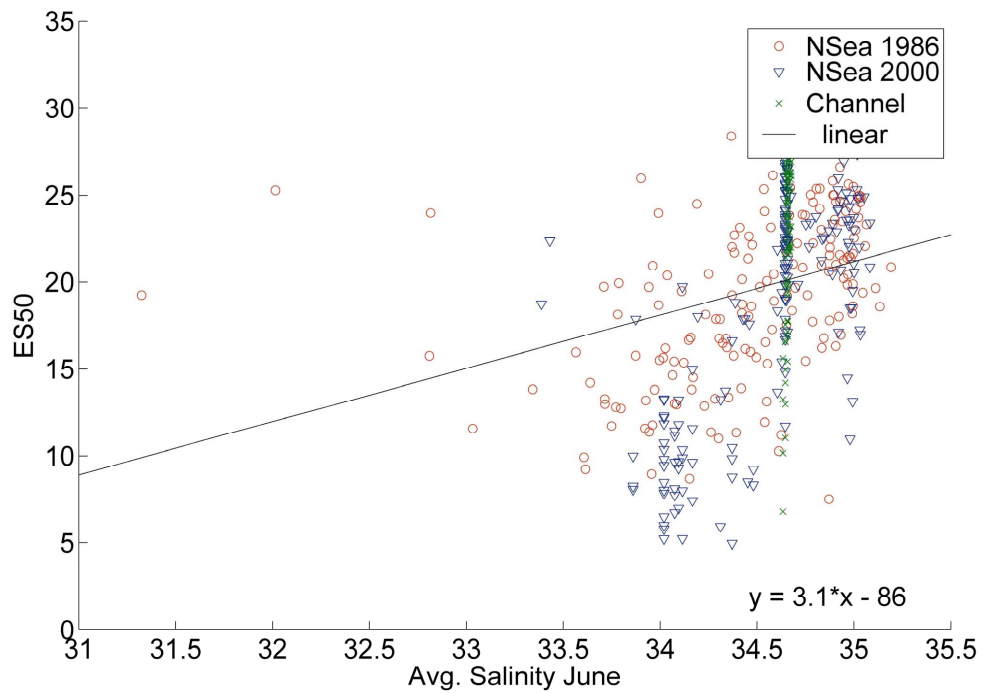


Figure 5.3.7. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. the average salinity in June for the 1986 and 2000 samples. The trendline $r^2 = 0.211$, excluding the Channel data.

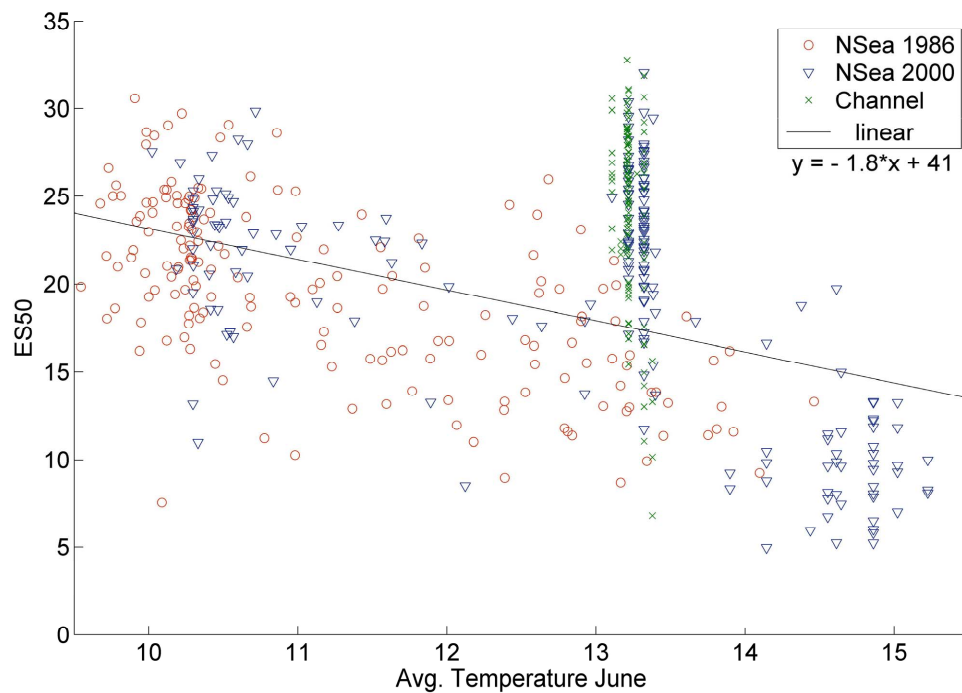


Figure 5.3.8. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. the average temperature in June for the 1986 and 2000 samples. The trendline $r^2 = 0.234$, excluding the Channel data.

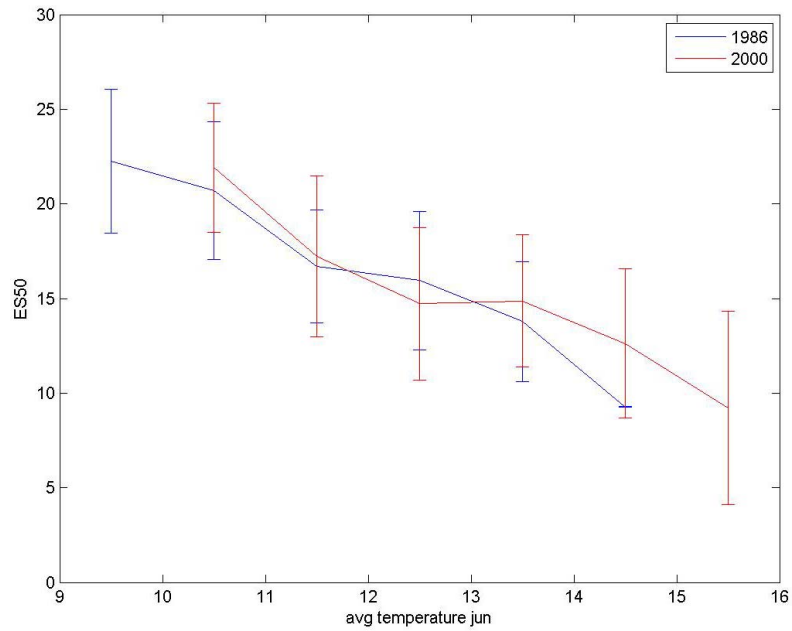


Figure 5.3.9. Plot of the average ES(50) for the average temperature in June. The error bars indicate the variance.

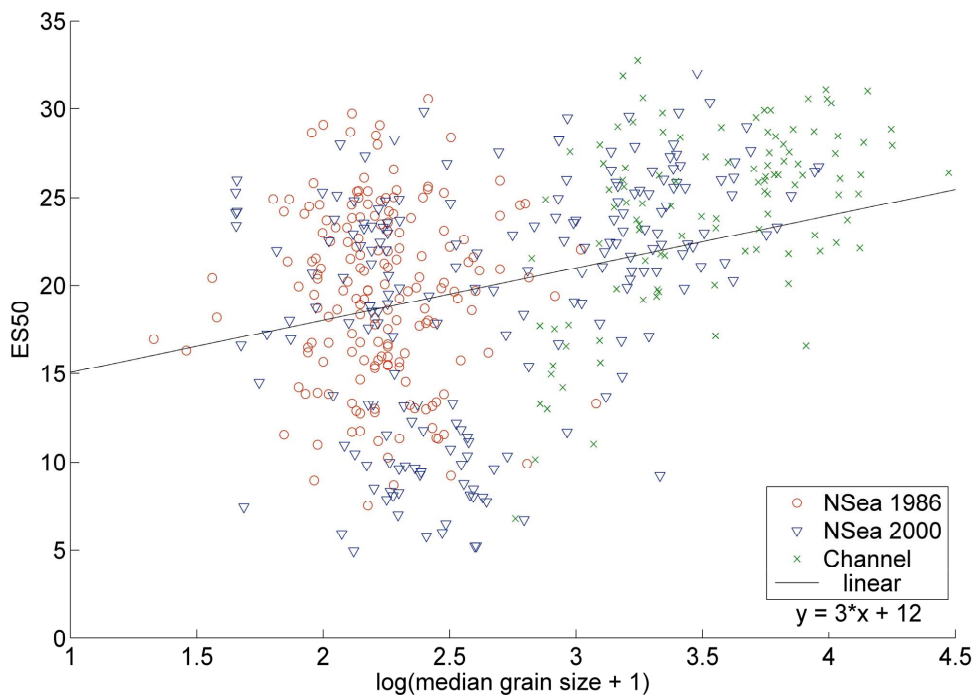


Figure 5.3.10. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. the median grain size (d50) for the 1986 and 2000 samples, excluding the Channel data.

Density

The logarithm of densities shows an almost linear relationship with latitude (Figure 5.3.11). However, samples with the highest densities were found in the Belgian part of the North Sea at low latitude (around 51.5°N). Samples close to the French coast (Calais–Dunkerque) have a low density. The samples in the Channel have a high density. The maximum and minimum densities were observed at shallow depths (not shown). At and above 50 m depth, the

minimum density is 200 ind. m⁻². At low median grain sizes (mud–sand), a range of densities are encountered (not shown). Coarser samples, especially gravelly substrata in the Channel, show a much higher average density. The coarsest Channel samples have a minimum density of 200 individuals. Density is negatively correlated with tidal stress (Figure 5.3.12). High levels of tidal stress are found near Dunkerque–Calais and in the Belgian part of the North Sea.

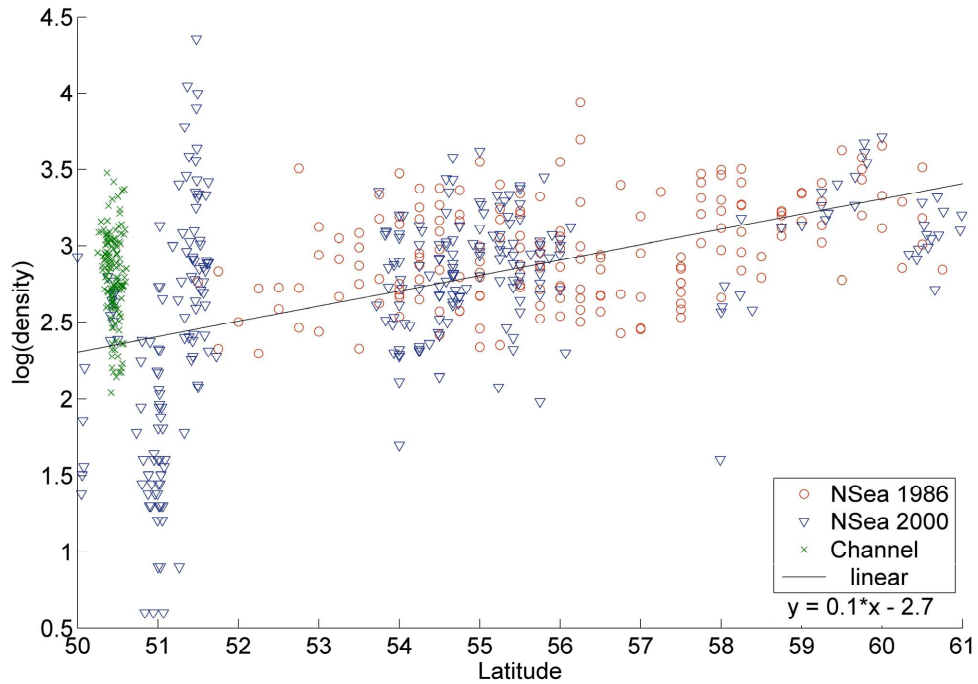


Figure 5.3.11. Scatterplot of the log(density) vs. the latitude for the 1986 and 2000 samples. The trendline $r^2 = 0.246$, excluding the Channel data.

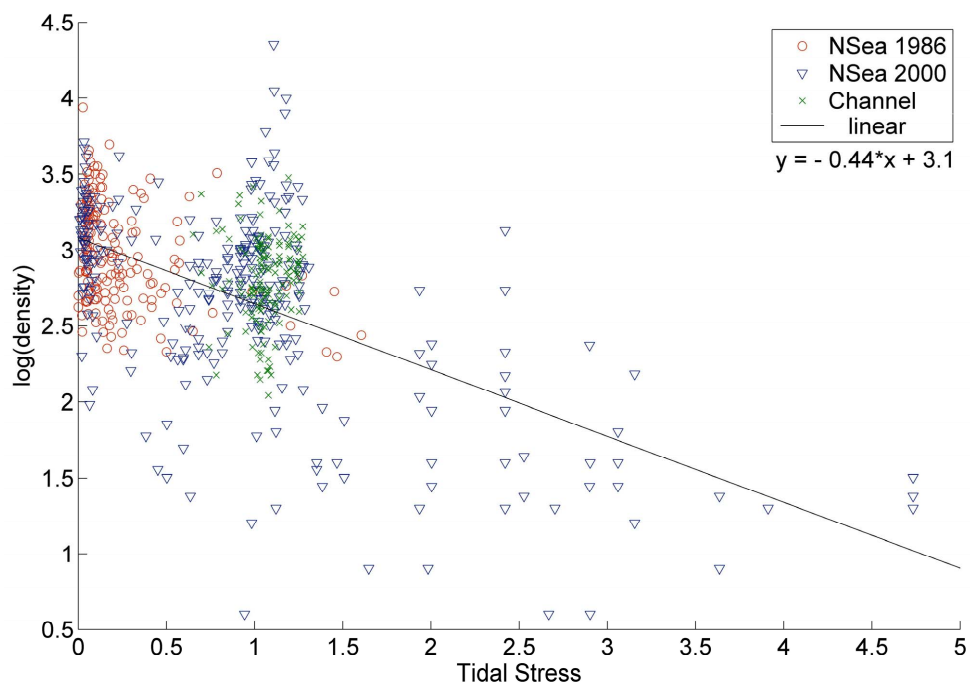


Figure 5.3.12. Scatterplot of the log(density) vs. the tidal stress for the 1986 and 2000 samples. The trendline $r^2 = 0.360$, excluding the Channel data.

Biomass

No clear trend with latitude was observed at low latitudes in or close to the Channel (Figure 5.3.13). Above 52°, the logarithm of the biomass decreases linearly with latitude. Below 52°, biomass was low close to Dunkerque–Calais and variable in the Belgian part of the North Sea.

The matching stations of the 1986 and 2000 datasets do show a relation with latitude (Figure 5.3.14), because the biomass decreases farther north. This can be explained by the exclusion of the Channel data and stations close to Dunkerque–Calais, because they were not sampled in 1986. The median grain size (not shown) shows the same pattern as for ES(50): at low median grain size (d50) both very high and very low biomasses occur. Above a median grain size of 5000 μm , the minimum biomass is about 0.1 g m^{-2} .

The logarithm of the biomass decreases almost linearly with the average temperature in February (Figure 5.3.15). Contrary to expectation, there is no relationship between benthic biomass and surface water chlorophyll *a* content (Figure 5.3.16). The latter data were derived from the HAMSOM model (Section 3.1.3). Bottom chlorophyll was only available for the 1986 samples and did show a relationship with benthic biomass (Heip *et al.*, 1992). The samples from 1986 and 2000 differed significantly, but identical trends were observed (Figure 5.3.17). The surface chlorophyll in 2000 was significantly higher than in 1986 for each station (paired *t*-test; $p < 0.001$). The chlorophyll was, on average, 89.96 $\mu\text{g l}^{-1}$ (s.d. 43.72) higher than in 1986.

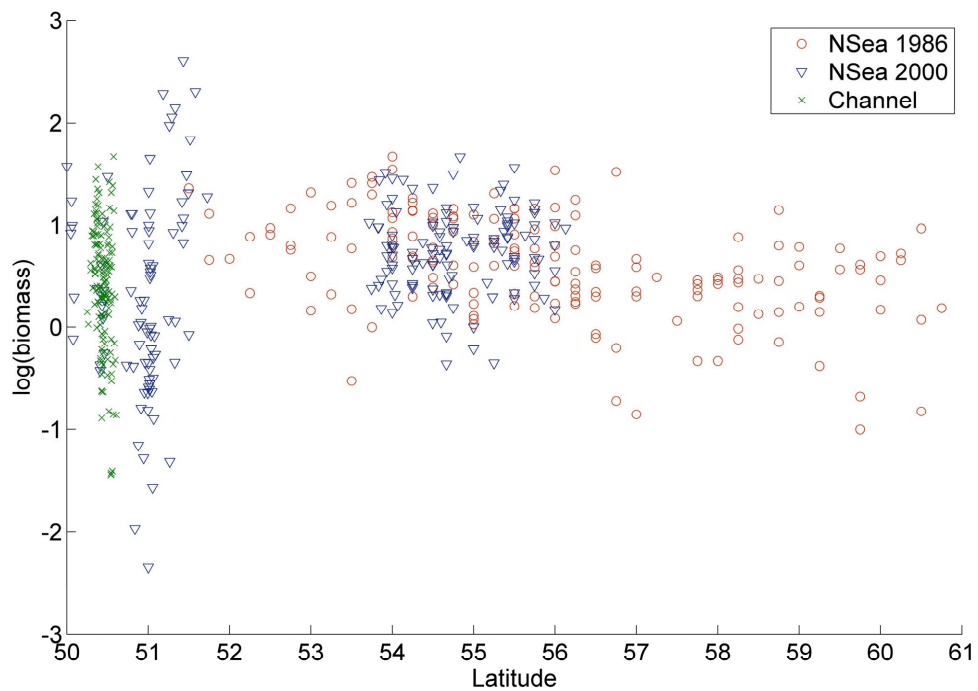


Figure 5.3.13. Scatterplot of the $\log(\text{biomass})$ vs. the latitude for the 1986 and 2000 samples.

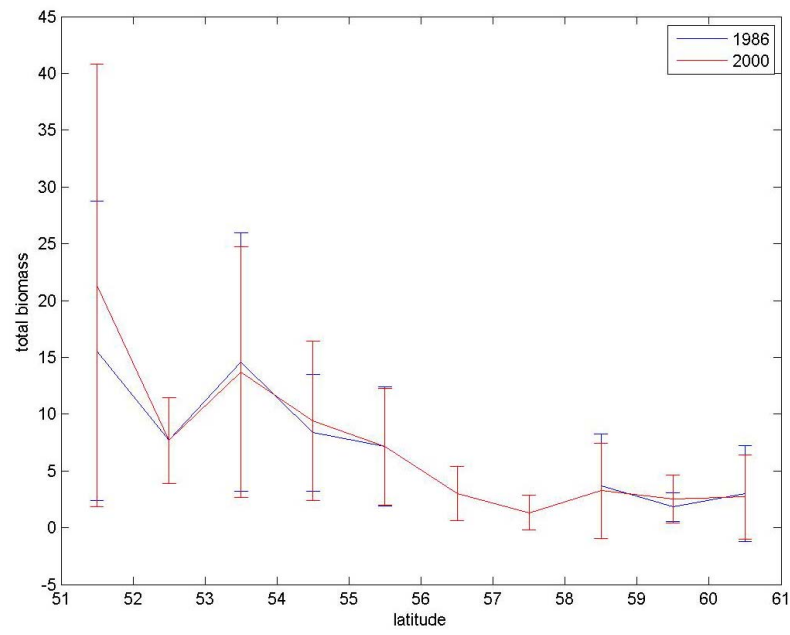


Figure 5.3.14. Plot of the average of the total biomass for each degree of latitude. The error bars indicate the variance.

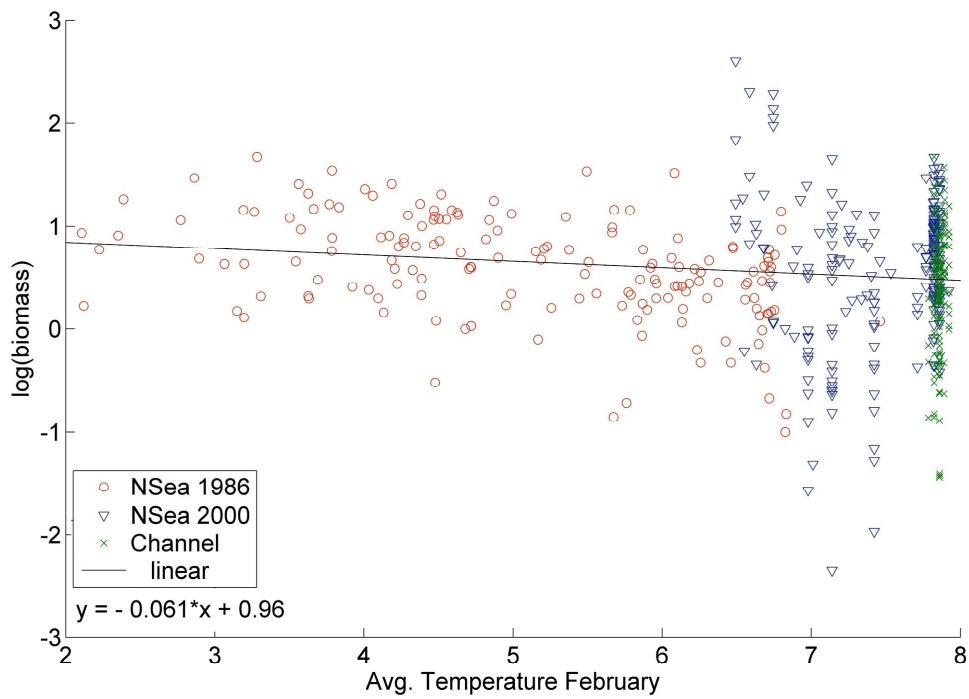


Figure 5.3.15. Scatterplot of the log(biomass) vs. the average temperature in February for the 1986 and 2000 samples.

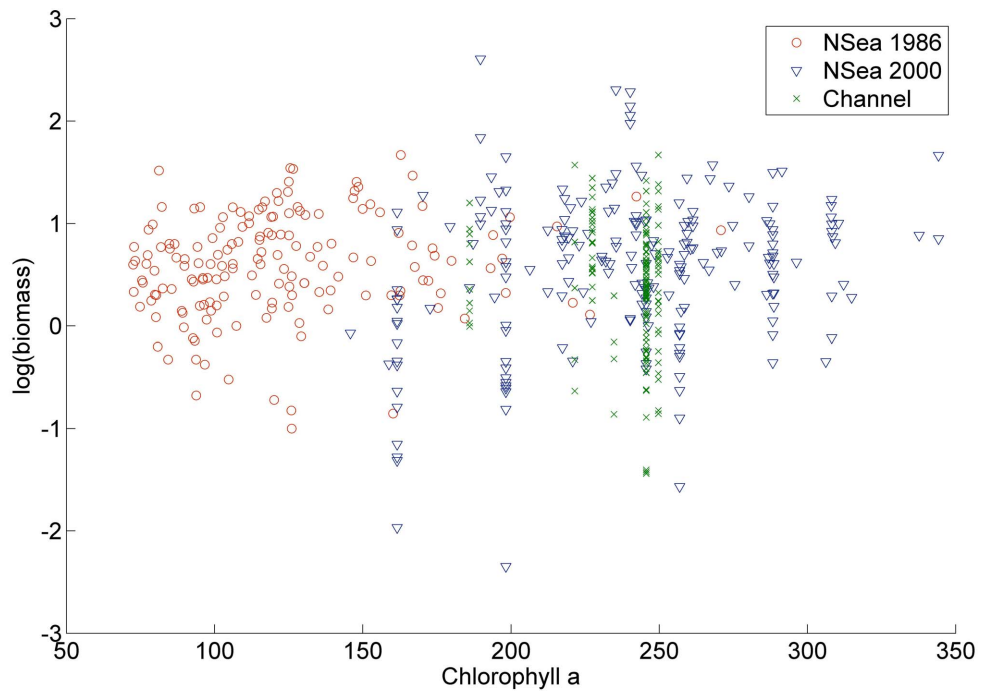


Figure 5.3.16. Scatterplot of the log(biomass) vs. the surface-water chlorophyll *a* for the 1986 and 2000 samples.

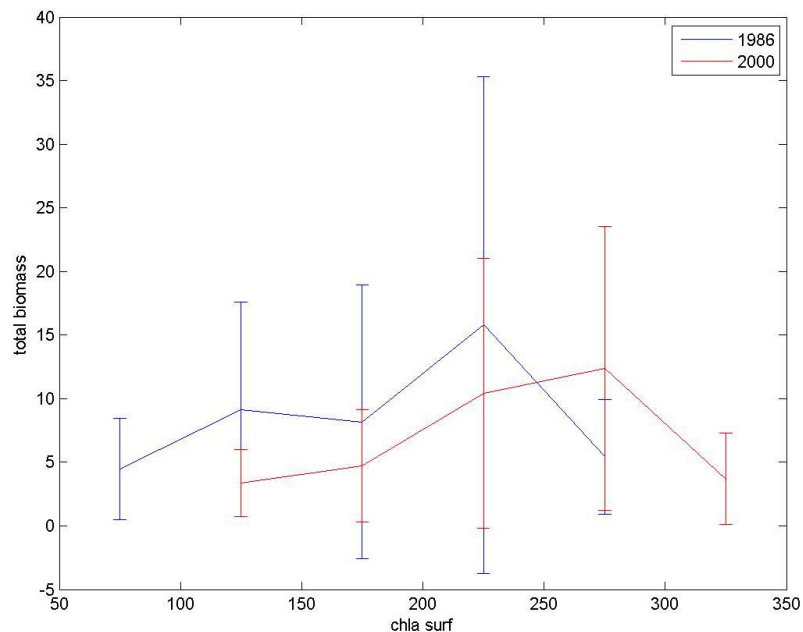


Figure 5.3.17. Plot of the average of the total biomass against the surface-water chlorophyll *a*. The error bars indicate the variance.

Individual Weight (IW)

The log(individual weight) (IW) shows a clear negative trend with latitude (Figure 5.3.18; $r^2 = 0.283$). The Channel samples have an IW below the trend line. In the reduced dataset with only the matching 1986/2000 samples, the pattern is clearer (Figure 5.3.19). The log IW shows a clear decreasing trend with depth (Figure 5.3.20; $r^2 = 0.198$). The Channel data also

follow this trend. The $\log(IW)$ shows a decreasing trend with the average salinity in June (not shown), while it increases with the temperature in June (Figure 5.3.21). It was also observed that $\log(IW)$ decreases linearly with stratification (Figure 5.3.22).

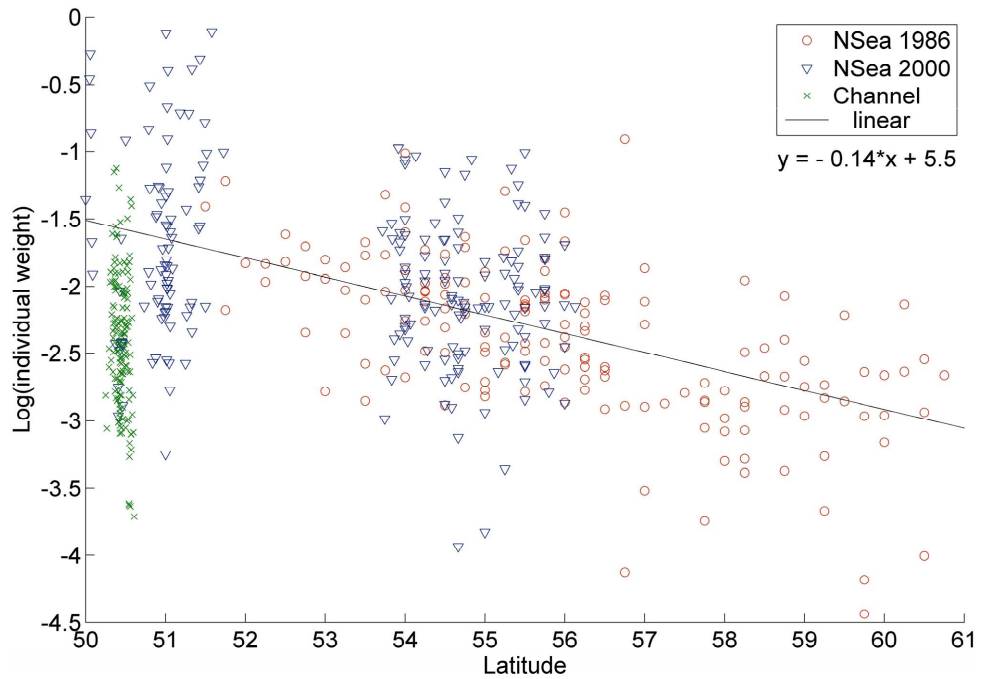


Figure 5.3.18. Scatterplot of the $\log(IW)$ vs. the latitude for the 1986 and 2000 samples. The trendline $r^2 = 0.283$, excluding the Channel data.

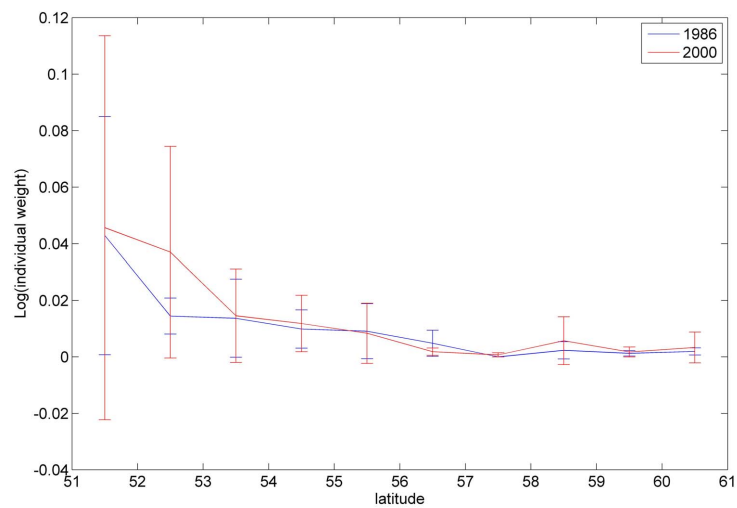


Figure 5.3.19. Plot of the average individual weight for each degree of latitude. The error bars indicate the variance.

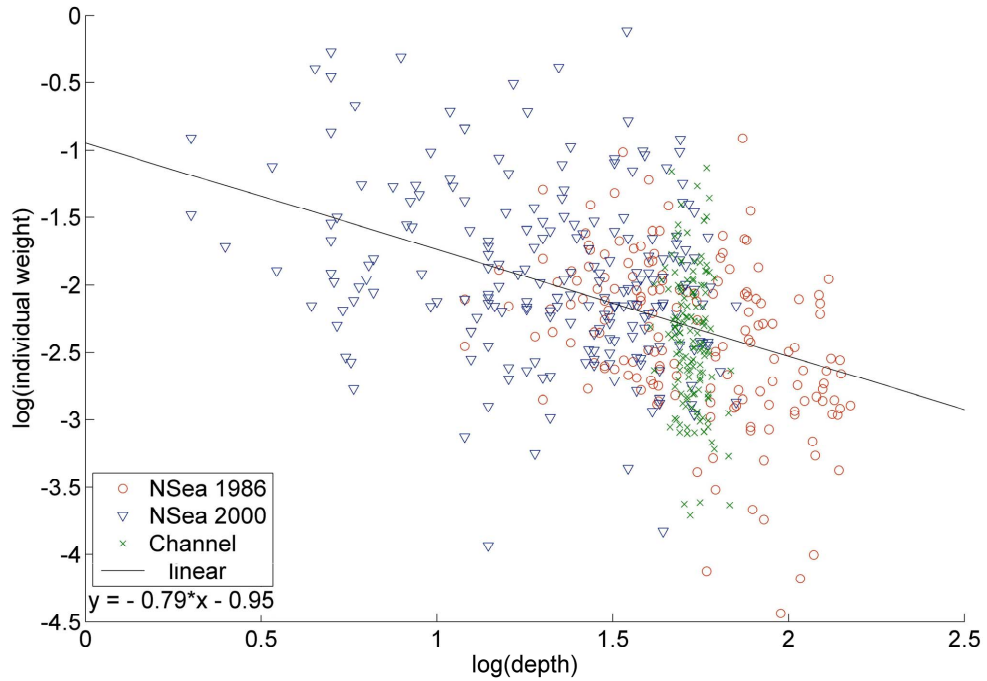


Figure 5.3.20. Scatterplot of the log(IW) vs. depth (m) for the 1986 and 2000 samples. The trendline $r^2 = 0.198$, excluding the Channel data.

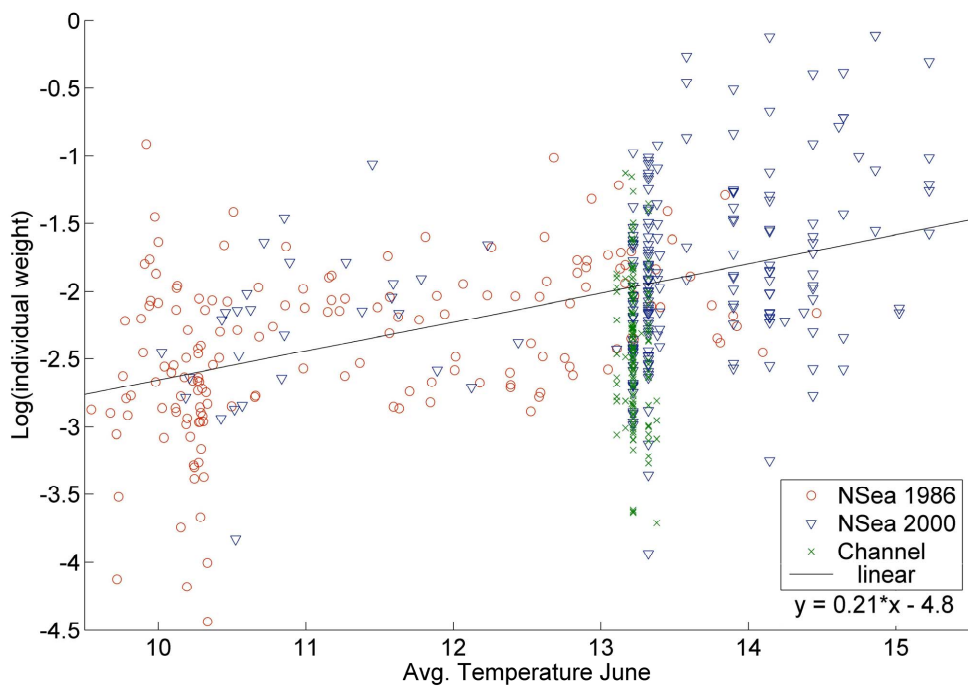


Figure 5.3.21. Scatterplot of the log(IW) vs. the average temperature in June for the 1986 and 2000 samples. The trendline $r^2 = 0.253$, excluding the Channel data.

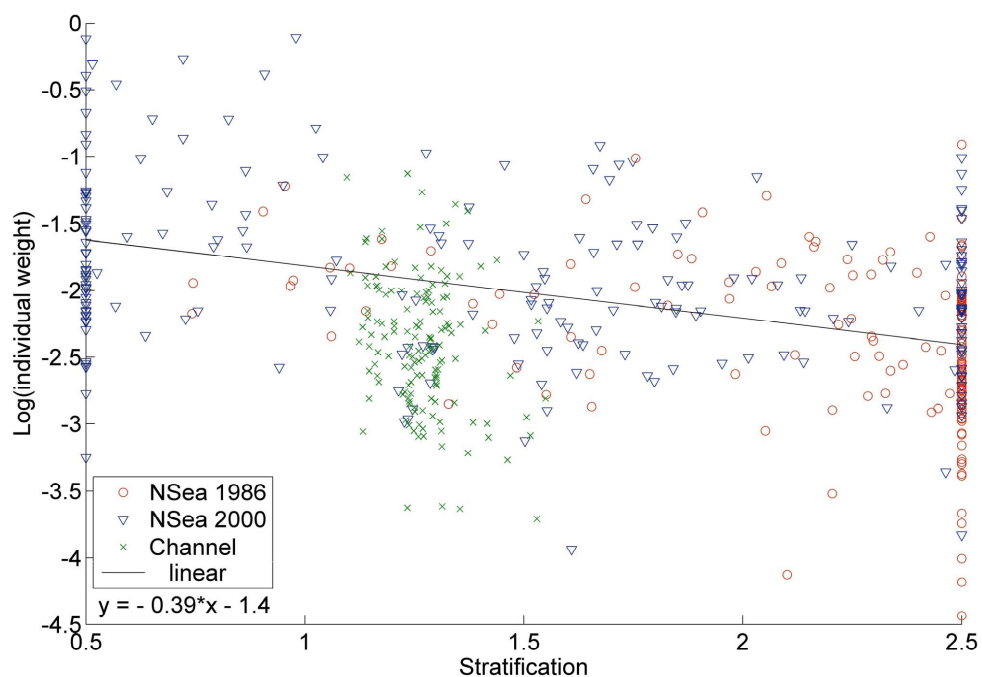


Figure 5.3.22. Scatterplot of the log(individual weight) vs. the stratification for the 1986 and 2000 samples.

5.3.4 Discussion

The comparison of biotic and abiotic variables showed that large-scale patterns exist and that a major part of the variance in the biotic variables can be explained by the abiotic variables. Although significant linear correlations with several variables were identified, it is generally not possible to determine their relative importance as causal influences because there is clearly scope for interaction among the variables, which is illustrated in the outcome of multivariate analyses (Figures 5.3.1–5.3.4). Overall, however, the outcomes of statistical analyses in this account advanced our insight into the mechanisms by which abiotic factors can influence the distribution of macrobenthic communities and species.

Correlation analysis provided an initial insight into the relationship between biotic and abiotic variables. The correlation coefficients were low overall, although some strong correlations were expected. The combined effect of interaction between environmental variables and the likelihood that the benthos was responding to multiple influences, therefore, complicated the search for cause–effect relationships. The PCA outputs identified related groups of variables, which was useful in selecting from the extensive list of available measures. By superimposing the outcome of earlier cluster analyses of the benthos data onto PCA plots of the environmental variables, useful insights were gained into the nature of the “realized niches” of the North Sea benthic communities.

Correlation and PCA analyses also highlighted differences between the 1986 and 2000 datasets, which were largely attributable to survey design and geographical scope. The 1986 dataset was derived from an evenly spaced sampling grid, while the 2000 dataset was highly clustered, with many more stations in the southern North Sea. Also, the 2000 survey extended into the eastern English Channel. The use of a reduced dataset, including only matched stations (see Section 5.2), was important in illustrating similarity in trends between the two sampling occasions.

Table 5.3.2. Strongest relationships observed between the biotic and abiotic variables in the NSBP dataset.

| | ES(50) | DENSITY | BIOMASS | IW |
|------------------------------|--------|---------|---------|----|
| latitude | + | + | - | - |
| depth | + | | | - |
| tidal stress | | - | | |
| chl _a water | - | | | |
| average temperature June | - | | | + |
| average temperature February | | | - | |
| average salinity June | + | | | - |
| stratification | + | | | |

+ = positive relation; - = negative relation.

Based on abiotic variables, the eastern English Channel clearly represented a different biotope, and this was evidenced by the discrete cluster that the stations occupied in several of the scatterplots. It is also evident that the Channel is more biodiverse than the rest of the North Sea. This can be ascribed to the coarser (gravelly) nature of the substrata here and also along parts of the southeast English coast which, combined with the interstitial sandy sediments, present a more complex habitat for colonization by an array of benthic species. This is in contrast to the predominantly soft sediments at the majority of stations in the North Sea, and explains why the trend lines for correlations between biotic and abiotic variables are generally higher after exclusion of the Channel samples.

Environmental variables

Most environmental variables are expected to interact: e.g. lower winter temperatures are expected in shallower areas, and these often have a different sediment composition, typically under the influence of stronger tidal currents and wave action. So, if a relationship between diversity and depth is observed, it is not necessarily clear which is the causative variable, if indeed a single cause is to be expected. It is essential, therefore, to explore interrelationships between the abiotic variables to help distinguish between correlative and causative influences on benthic communities.

Three types of environmental variables were identified by Austin *et al.* (1984): resource gradients are composed of matter and energy consumed (nutrients, water, and food); direct gradients have physiological importance (temperature, pH); while indirect gradients have no direct physiological relevance (slope, depth). Most variables in the present dataset represent indirect gradients (sediment type, currents, depth, and stratification). Indirect variables usually replace a combination of different resource and direct gradient variables in a simple way (Guisan *et al.*, 1999). For instance, depth (an indirect variable) is related to a number of resource and direct gradients (i.e. temperature, chlorophyll). The strongest relationships between biological and environmental variables are summarized in Table 5.3.2.

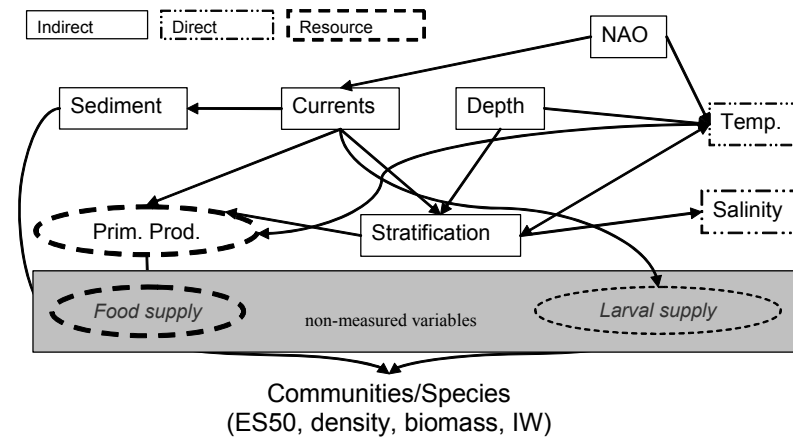


Figure 5.3.23. Simplified scheme of the expected relationships between the measured biotic and abiotic variables in the NSBP dataset. NAO = North Atlantic Oscillation; IW = individual weight (biomass/density). Food supply and larval supply were not measured in the NSBP dataset. The type of each variable is indicated: direct/indirect or resource gradient (*sensu* Austin *et al.*, 1984).

A conceptual model to represent the inferred relationships between the abiotic and biotic variables in the NSBP dataset is shown in Figure 5.3.23. For the NSBP dataset, the only resource gradient measured was chlorophyll *a*. Temperature and salinity influence the physiology and thus are direct gradients. Temperature determines the metabolism of macrobenthic animals. The other variables (sediment, currents, depth, and stratification) are indirect gradients. In predictive modelling studies, these indirect variables are often used because they are relatively easy to measure and, therefore, are widely available. However, only locally valid empirical models can be constructed with indirect variables (Guisan and Zimmerman, 2000).

The presence and biological properties of species/communities are dependent on the advection of food (Kröncke and Bergfeld, 2003) and the supply of larvae. The food supply is determined by how much of the primary production products reach the benthos. This downwards transport is governed mainly by currents/stratification. We expect primary production to be related to currents, stratification, and temperature in the NSBP dataset. Heip *et al.* (1992) hypothesized that the impact of stratification and current patterns on food input to the benthos might be one of the most important factors explaining large-scale patterns.

The North Atlantic Oscillation (NAO) is one of the most important drivers of climate fluctuations in the North Atlantic realm. The NAO index indicates the difference in atmospheric pressure between the Icelandic Low and the Azores High. The NAO controls the strength of westerly winds and storm tracks across the North Atlantic and surrounding continents and has a period of 7.3–8 years (Rogers, 1984). Persistently strong westerlies over middle latitudes in the Northeast Atlantic cause an increased transport of warm air and moisture into northern Europe, which results in milder winters as opposed to the more continental climate during low NAO periods (Gröger and Rumohr, 2006). Typically, positive NAO values will be associated with mild winters and reduced water column stratification. Macrofauna communities are severely affected by cold winters, with shallow stations affected the most (Reiss *et al.*, 2006).

The NAO index correlates with zooplankton, primary production, and macrobenthic abundances (Hagberg and Tunberg, 2000). In the western Baltic, Gröger and Rumohr (2006) observed that species richness was influenced positively by the winter NAO index and negatively by salinity (with a lag of four years for the salinity). Internal growth lines in shells of three suspension-feeding bivalves were correlated with monthly values of the NAO index, phytocolour, temperature, and wind (Witbaard *et al.*, 2005). Kröncke *et al.* (1998) found a strong positive relationship between abundance, species number, and (less clear) biomass in

the second quarter of the year and the NAO index. The mediator between the NAO and the benthos is probably the sea surface temperature (SST) in late winter and early spring (Kröncke *et al.*, 1998). Unfortunately, the NSBP dataset is not a time-series; therefore, the temporal relationships with NAO and temperature could not be tested.

Hagberg *et al.* (2003) found a relationship between macrobenthic communities and depth. Production–biomass ratios were negatively related to water depth and positively related to water temperature. Also, depth influences stratification, as shallow areas are rarely stratified, because mixing between all water depths can take place.

Tidal or wind-driven currents are known to influence food transport and availability (Herman *et al.*, 1999) and larval supply. However, microscale current measurements are rarely available in macrobenthic studies. In the NSBP dataset, the modelled bottom current (HAMSOM, Section 3.1.3) was available. Grain size is an important predictor of community type (van Hoey *et al.*, 2004) and species (Willems *et al.*, in press). Sediment distribution is determined by (a) the sediment source; (b) interactions between sediment particles; (c) hydrodynamic regime; (d) biological effects (Snelgrove and Butman, 1994). The sediment composition is in dynamic equilibrium with the bottom current regime. Regions with strong tidal currents tend to have coarser sediment, because finer particles do not settle. Similarly, larval transport and deposition and particulate flux are also governed by the benthic boundary-layer flow. Fine (muddy) sediments generally have higher levels of microbial abundance because they are typically encountered in more depositional environments, as well as providing a larger surface area for colonization (Snelgrove and Butman, 1994). Thus, sediment grain size can be used as a proxy for the strength of tidal currents or food supply.

Relation between biotic and abiotic variables

Abiotic variables and diversity (ES(50))

The diversity, expressed as expected number of species ES(50), increased with depth, salinity in June, and stratification. ES(50) decreased with chlorophyll *a* at the surface and the temperature in June. The analyses support the hypothesis of Heip *et al.* (1992) that the impact of stratification on food input to the benthos is one of the most important factors explaining large-scale patterns. In the NSBS 1986 dataset used by Heip *et al.* (1992), measures of stratification were not available. Heip *et al.* (1992) also identified a relationship between sediment type and diversity. However, depth and median grain size are positively related. At great depths and high median grain sizes, the diversity is high; at low depths and low grain sizes, there is a wide range of diversity. Deeper and coarser stations are thus more similar and exhibit a narrower range of diversity. Salinity had a large impact on diversity in the western Baltic according to Gröger and Rumohr, (2006). Kröncke *et al.* (1998) found a strong relationship between diversity and the sea surface temperature in late winter and early spring (Kröncke *et al.*, 1998). In the NSBP dataset, a negative relation of ES(50) with bottom summer temperature was found.

Latitudinal gradient and diversity

A regional decrease of biodiversity with increasing latitude has been observed in numerous studies across a range of biota and is one of the keystone observations of macro-ecology (Hillebrand, 2004). Although this pattern is observed frequently, there is a lack of consensus on the primary cause because several environmental variables are correlated with latitude. This was also evident in the analyses of NSBP data. In the present dataset, there is a latitudinal gradient of 11° (50–61°) representing a length of 1200 km (Figure 5.3.24). In addition to diversity, the relation between latitude, density, and biomass was also explored.

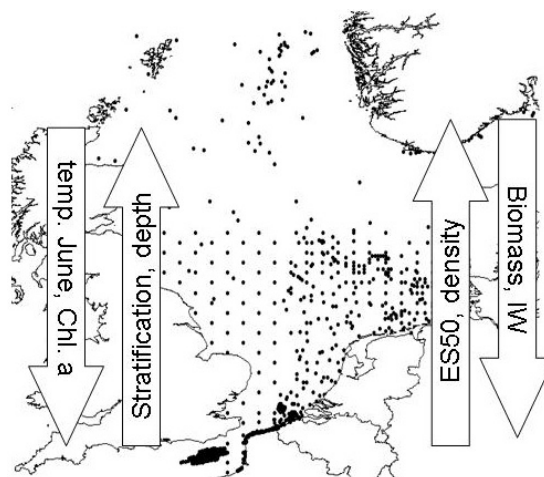


Figure 5.3.24. Schematic overview of the abiotic and biotic gradients. The arrows point in the direction of the highest values for the variables.

It was possible to test the global hypothesis of decreasing biodiversity with latitude at the regional level of the entire North Sea. For the combined dataset (1986/2000), there was an increase of diversity with latitude ($r^2 = 0.228$). For the 1986 and 2000 samples separately (Figure 5.3.6), the pattern was similar. This is contrary to the global pattern of increasing biodiversity towards the equator (Hillebrand, 2004). The northern North Sea was more diverse. However, the diversity gradient in the North Sea can be regarded as, at most, regional in scale, and the global diversity gradient in the macrobenthos remains to be explored. Most biotic variables correlate well with latitude. Density increased positively with latitude ($r^2 = 0.246$), while IW decreased with latitude ($r^2 = 0.283$).

Only biomass is less well correlated, mainly at low latitudes (Dutch and Belgian coasts). From a multiple regression analysis of the NSBS 1986 data, Heip *et al.* (1992) found that the $\log(\text{biomass})$ was significantly related to latitude, chlorophyll *a* in sediment, and $\log(\% \text{ mud})$. Latitude always accounted for the largest part of the variance. On the Norwegian shelf, species richness was highly variable (35–148 species), but showed no evidence of a relationship with latitude or other environmental variables (Ellingsen and Gray, 2002). Although latitude is clearly not a physical variable, it can be regarded as a “summarizing gradient”, because a number of variables are correlated with it. For example, stratification and depth increase northwards, while the summer temperature in June increases southwards. Latitude explained more variation than depth for biomass, density, and IW.

Biomass vs. water temperature

Temperature is one of the primary factors influencing metabolic rate of ectotherms; it also varies significantly over time and across microhabitats (Helmuth *et al.*, 2002). At low temperatures, metabolism, and thus respiration, is reduced, which (to a degree) can be beneficial to an organism in saving energy and increasing tolerance to lower oxygen levels. Biomass increased with decreasing winter temperatures in February. The summer temperature showed no clear relationship with biomass. Chapelle and Peck (2004) stated that size optima change with water temperature. In colder water, the metabolism is expected to decrease, which results in a lower food requirement, but also there is less food uptake (Chapelle and Peck, 2004). The balance between metabolism and uptake is important, but is not known for the studied species. Sebens (2002) stated that, with limited prey, the net result is that periods of lower temperature are energetically costly. For the NSBP dataset, the opposite seems to be true, as colder regions have higher biomass.

Abiotic variables and individual weight

Which abiotic variables correlate with average IW (community biomass divided by density)? For example, in a stable environment with lower temperature, one might expect a lower metabolism and a reduced oxygen demand and, thus, an individual may grow larger. On the other hand, the food supply might be limiting in colder environments.

IW decreased with depth, latitude, stratification, and salinity in June, and it increased with temperature in June. The resulting north–south pattern in IW is a result of the biomass decreasing moderately with latitude (Figure 5.3.13) and $\log(\text{density})$ increasing with latitude (slope = 0.1; Figure 5.3.11). The factors that increase IW (depth, latitude, stratification, and salinity) are all correlated and have a north–south gradient. This prevents us from disentangling the causal relationships with IW. The decrease of mean individual weight with latitude was also observed for the NSBS 1986 dataset by Heip *et al.* (1992).

Benthic biomass and surface chlorophyll *a*

Generally, one might expect high surface chlorophyll levels to be linked with high benthic biomass. However, several processes govern the transfer of primary production products to the seabed. Stratification can keep the food particles locked in the upper water layers, where they are constantly recycled. High water depths increase the sinking time and may cause the quality of the food input to the seabed to be lowered as the particles are consumed through microbial action during descent. Finally, water currents can divert the surface production leading to, for example, localized sinks of settled products away from the majority of organisms. In the present study, surface chlorophyll *a* levels from a model (ECOHAM1, Section 3.1.3) were compared with benthic biomass for the same location. Additionally, the relationship of chlorophyll *a* with density, diversity, and individual weight was also explored.

Contrary to expectation, no relationship between surface chlorophyll *a* and benthic biomass was found for the combined 1986/2000 dataset. The chlorophyll *a* level, however, was derived from a model and not from actual measurements. For the NSBS 1986 samples, Heip *et al.* (1992) found a relationship between sediment chlorophyll *a* and benthic biomass. However, no relationship was found between the sediment chlorophyll *a* content and the surface chlorophyll *a*. The coupling of surface and benthic chlorophyll *a* levels is complex and is determined by a number of factors (including water depth and stratification). Neither was a relationship found between chlorophyll *a* and density, diversity, or individual weight. The hypothesis of a link, therefore, was not supported by the available data.

5.3.5 Conclusions

Larger scale patterns exist in the structure (diversity and density) and functional attributes (biomass and mean individual weight) of the macrobenthos in the North Sea. The spatial trends could often be linked with one or more environmental variables. The variables measured were sometimes highly correlated, and the outputs from multivariate (PCA) analyses for 1986 and 2000, overlain with the main community types, were helpful in niche characterization. It was difficult to compare the 1986 and 2000 surveys in their entirety because the sampling grids differed significantly, but analysis of the reduced datasets based on matching stations revealed that, overall, the relationships between biotic and abiotic variables were similar for both years. Samples collected from the eastern English Channel and parts of the English east coast in 2000 were distinctive both in terms of the (coarser) substratum type and the benthic fauna. Most of the variation in biological properties of the North Sea benthos can be explained by the environmental variables. The diversity increased with increasing latitude, contrary to the general hypothesis. The biomass increased with decreasing winter temperatures in February. No relationship between surface chlorophyll *a* and biomass was found.

However, viewed on a global scale, it is possible that the observed relationships between the biotic and abiotic variables are only valid within the relatively limited geographical extent of the North Sea. A number of the relationships could therefore be correlative rather than causative. No resource gradient variables were available for the NSBP dataset, except surface chlorophyll *a*. However, the latter showed no relationship with the benthic biological variables. The other variables could be classified as having direct (e.g. temperature) or indirect (e.g. depth) physiological relevance (Austin *et al.*, 1984). Herman *et al.* (1999) state that food may be the most limiting factor over large spatial scales. In the NSBP dataset, environmental variables had to be used as proxies for food and larval availability. Human impacts were not considered in this analysis, but are also expected to play a role.

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5.4 Species distributions and changes (1986–2000)

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5.4.1 Introduction

Species distributions and abundances are governed by extrinsic factors, largely food availability, sediment composition and stability, temperature, salinity and hydrodynamics, and by intrinsic factors, mainly competition and predation. Explanations for changes in dominant or “indicator” species over time may therefore include recruitment success, feeding activities and lifestyle (burrowers/tube-builders), and competitive exclusion (Eagle, 1975; Snelgrove and Butman, 1994). Benthic communities can be subject to large changes on various timescales (seasonal, interannual, and multidecadal; Reiss and Kröncke, 2005; Schroeder, 2005; Reiss and Kröncke, 2006). Anthropogenic pressures such as fishing (Frid *et al.*, 2000; Rumohr and Kujawski, 2000; Bremner *et al.*, 2003), organic enrichment (Pearson and Rosenberg, 1978; Rees *et al.*, 2006), and chemical pollution also structure communities by excluding certain sensitive species and/or encouraging density increases in others.

The macroinfauna of the North Sea are generally categorized as northern species (extending down to the northern margins of the Dogger Bank) or southern species (extending north to the 100 m depth contour), with a mixture of both occurring in the central North Sea (Kröncke and Bergfeld, 2003). However, there are many species that are more cosmopolitan, being widely distributed in the North Sea and worldwide.

This section compares the distribution of selected species at the time of the 1986 North Sea Benthos Survey with data collected opportunistically by NSBP partners in 2000 to ascertain whether changes had occurred.

5.4.2 Methods

Indicator species were selected from TWINSPAN outputs, based on both 1986 and 2000 datasets. SIMPER outputs from PRIMER analyses of the same datasets were also used to select characterizing species from the main clusters. These species were displayed initially as separate maps for 1986 and 2000, using MapInfo (see Annex 3). Species were then selected where appreciable changes were apparent between sampling occasions or where species were characteristic of certain environmental conditions (e.g. northerly distributed, restricted to coarse gravels). Some of the species corresponded with those previously selected by Künitzer *et al.* (1992). Species were also included that are known to be fragile or sensitive to certain anthropogenic stressors such as mechanical disturbance (e.g. fishing) or smothering (Table 5.4.1).

A relatively large number of species has been introduced into European coastal waters, especially in the past 50 years or so. For the zoobenthos, Gollasch (2006) identified 563 non-indigenous species, of which about 50% have become established. For the North Sea, approximately 140 introduced species have been recorded. Familiar examples include the Pacific oyster *Crassostrea gigas*, the slipper limpet *Crepidula fornicata*, and the razor clam *Ensis americanus* (see also Reise *et al.*, 2005). Shipping and aquaculture appear to be the major introduction vectors; climatic conditions favourable to establishment or range expansion may also be important (Gollasch, 2006). Analyses of the NSBP 2000 data did not reveal any striking examples of recent introductions over larger (up to North Sea-wide) scales, and none is listed in Table 5.4.1. However, we recognize that the data might repay further examination for rarer or more localized occurrences of an unexpected nature.

Utilizing the NSBP 2000 database, the densities of selected species for only the matching stations in 1986 and 2000 (156 stations, up to 40 km apart) were mapped using MapInfo. Although most stations in the central and southern North Sea had directly matching stations in

both years (85 stations), those in the northern North Sea were opportunistically sampled in 2000, and therefore may not exactly represent the same sampling area or communities (see below). Species densities are represented as graduated (log) half pies where black represents presence in 1986 and white represents presence in 2000; species absences in both years are displayed as a cross symbol.

It must be recognized that a component of observed changes may be the result of the mismatches between stations in 1986 and 2000, especially in the northern North Sea. However, well matched stations may also be subject to small-scale changes in substratum type and benthic community composition. In addition, improvements in taxonomic sufficiency in 2000 may have been a confounding factor in the case of certain species. In general, we do not believe that these causes of error seriously compromise evaluations of distributional changes. In particular cases where they are thought to be important, they are referred to in the text.

5.4.3 Species distributions and changes since 1986

For convenience, species have been grouped according to their broad distributional similarities. These largely correspond to regions of the North Sea identified by Adams (1987; see also Eleftheriou and Basford, 1989). The offshore central and southern North Sea regions have been further subdivided to include specific areas such as the Dogger Bank and Oyster Ground. These areas have also been identified in previous sections as distinctive of particular communities.

Certain species illustrated below are restricted by sediment type, while others are more widespread in their distribution. Changes in species occurrences in the northern North Sea must be viewed with some caution because of inconsistencies in sampling between the two surveys.

Oyster Ground

The Oyster Ground is characterized as predominately shallow (<50 m) muddy sand, although it ranges from more sandy sediments in the south to muddy sediments in the north (Cadée, 1984; Duineveld *et al.*, 1991). Community analysis of the Oyster Ground showed stability over time (see Section 5.2 and Figure 5.2.2). However, there were changes in the distribution and abundance of some species at several stations in the area. The bivalves *Abra alba* (Figure 5.4.1c) and *Corbula gibba* (Figure 5.4.1e) both show increased abundance in 2000, with *C. gibba* also showing an extended spatial range to the west.

A. alba is a short-lived, fast-growing deposit feeder with strong seasonal reproduction and high year-to-year variability (Van Hoey *et al.*, 2005). Fromentin and Ibanez (1994) found a relationship between winter temperatures and *A. alba* densities. Maximum densities of the species always occurred with mild winters, whereas low densities were associated with cold winters. The distribution of this species may also be restricted by food availability. Organic matter was found to influence the distribution of the *A. alba* assemblage in the eastern English Channel (Thiebaut *et al.*, 1997). This may also explain the high densities of *A. alba* observed on the Oyster Ground compared with other areas of the North Sea. Van Hoey *et al.* (2005) noted that the species is also found in sandbank gullies along the whole of the Belgian coastal-zone, but not detected beyond the 14 mile zone on the Belgian continental shelf because of a change to coarser sediments. This would explain the apparent absence of this species when only matching stations in 1986 and 2000 are compared (see also Annex 3, which shows all data in 2000).

C. gibba is commonly found subtidally in coastal and estuarine silts and muddy gravels. Generally regarded as an invasive pest species, it colonizes organically enriched environments, where it acts as an efficient filter- and surface-deposit feeder. Holmes and Miller (2006) concluded that, for an invasive species, its dispersive capability was relatively

restricted and may be constrained by prevailing currents, such as exist at the Frisian Front. Dominance of this species is only thought to occur when local environmental conditions are perturbed (e.g. by oxygen deficiency caused by high temperatures) and competitive species are removed (Holmes and Miller, 2006). The species was only observed at a few stations on the eastern part of the Oyster Ground in 1986. However, its distribution had become more widespread by 2000. The Dutch Biological Monitoring programme (BIOMON) observed fluctuating densities of *C. gibba* on the Oyster Ground in 1991–2000, with highest average densities in 1996 (200 ind. m⁻²) and lowest in 1993 (2 ind. m⁻²; Daan and Mulder, 2006).

Table 5.4.1. Rationale for species selection.

| SPECIES OF INTEREST | REASON FOR SELECTION |
|--|---|
| <i>Abra alba</i> | Fragile to mechanical disturbance. ¹ |
| <i>Antalis entalis</i> * | Distributional changes. Characteristic of deep northern water. |
| <i>Exogone verufera</i> | Characteristic of deepwater and fine sediment in 1986. Distributional change in 2000. |
| <i>Myriochele</i> spp. | Indicator of deep northern water in 1986. Sensitive to hydrocarbons. ¹ |
| <i>Mysella bidentata</i> | In 1986, absent above 57.5°N. |
| <i>Nephtys longosetosa</i> | Distributional changes. Sensitive to hydrocarbons. ¹ |
| <i>Nucula nitidosa</i> | Spread west in 2000. Sensitive to physical disturbance. ¹ |
| <i>Nuculoma tenuis</i> | Absent from northern North Sea in 2000. |
| <i>Prionospio (Minuspio) cirrifera</i> * | One of the main indicators of deep northern North Sea waters in 1986 and 2000. |
| <i>Spiophanes krøyeri</i> | One of the main indicators of deep northern North Sea waters in 1986 and 2000. |
| <i>Paramphinome jeffreysii</i> | Northern distribution. Indicator species in both TWINSPAN and SIMPER clusters. |
| <i>Synelmis klatti</i> * | Restricted distribution. Found in southern muddy fine sand. |
| <i>Terebellides stroemi</i> | Change of distribution. Sensitive to chemical disturbance. ¹ |
| <i>Spiophanes bombyx</i> * | Wide occurrence. |
| <i>Chaetoderma nitidulum</i> | Increase of distribution in northern North Sea. |
| <i>Echinocardium cordatum</i> * | Southerly distributed. Sensitive to mechanical disturbance. ¹ |
| <i>Arctica islandica</i> | Sensitive to mechanical disturbance. ¹ |
| <i>Chamelea gallina</i> * | Characteristic of the central North Sea. ¹ |
| <i>Echinocyamus pusillus</i> * | Characteristic of coarse sandy sediment. |
| <i>Amphiura chiajei</i> | High sensitivity to hydrocarbons. ¹ |
| <i>Amphiura filiformis</i> * | High sensitivity to synthetic chemicals and hydrocarbons. ¹ |
| <i>Bathyporeia</i> spp. | <i>B. pelagica</i> is particularly sensitive to chemical contaminants. ¹ |
| <i>Amphiura (Acrocnida) brachiata</i> | Fragile to mechanical disturbance. ¹ |
| <i>Scoloplos armiger</i> | Widespread. Tolerant of most disturbances. ¹ |
| <i>Lanice conchilega</i> | Ecosystem engineers – tube builder. |
| <i>Callianassa subterranea</i> | Ecosystem engineers – burrower. |
| <i>Ophelia borealis</i> | Large decrease in abundance and distribution. |
| <i>Fabulina (Tellina) fabula</i> | Contributor to changes in eastern North Sea (see Section 5.2). |
| <i>Corbula gibba</i> | Large increases in abundance and distribution. |
| <i>Sabellaria spinulosa</i> | Important reef-forming polychaete. Increases community diversity. |
| <i>Urothoe poseidonis</i> | Abundance increases in the eastern North Sea. |

* As found in NSBS 1986 (Künitzer *et al.*, 1992).

¹ Information from ICES (2004a) and Hiscock *et al.* (2004).

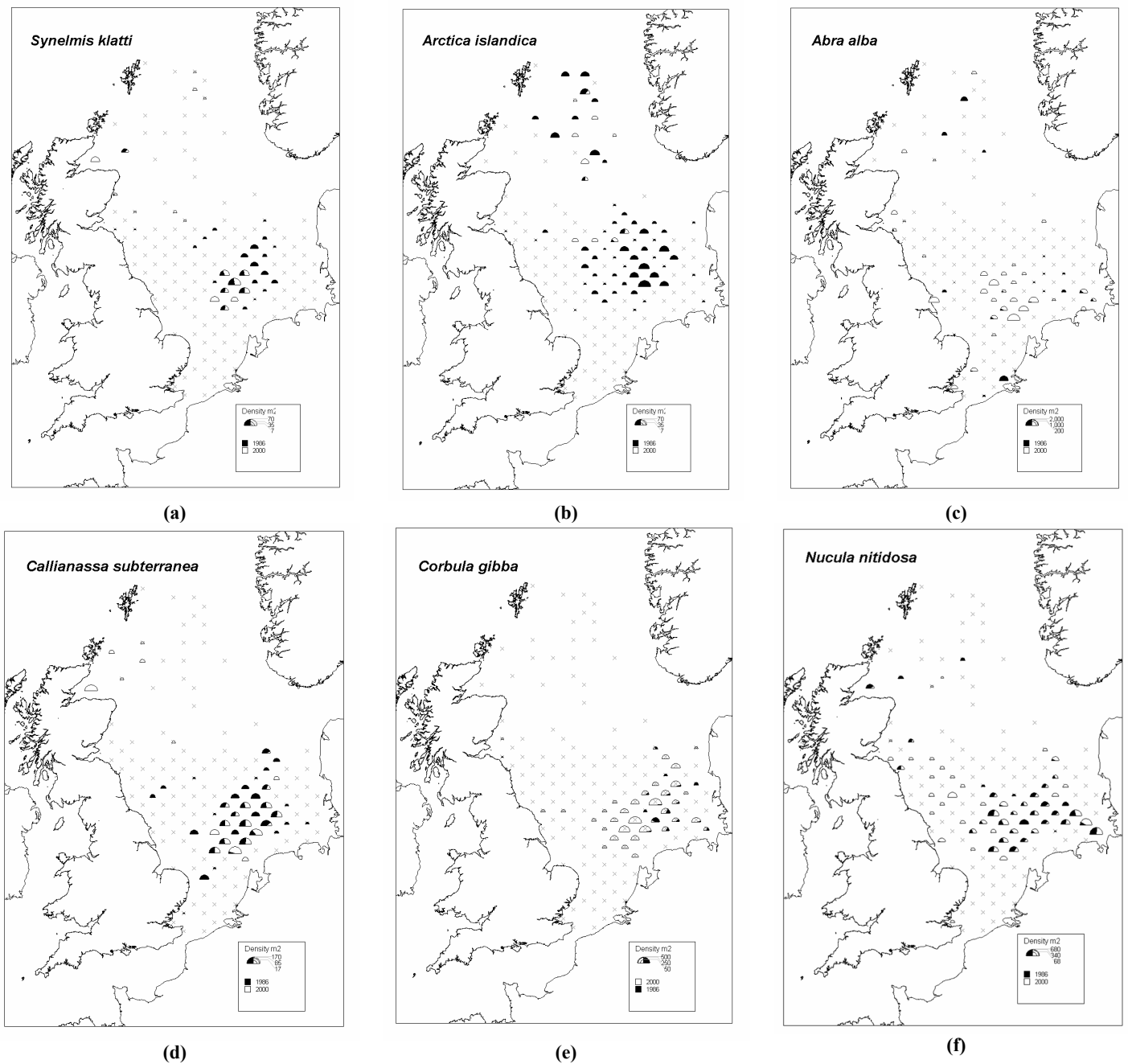


Figure 5.4.1a–f. Species strongly associated with the Oyster Ground (1986 and 2000). Species densities are represented as graduated (log) half pies where black represents presence in 1986 and white represents presence in 2000. Where a species was present at a station in both years, the half pies are proportionally divided accordingly. Species absences in both years are displayed as a cross.

The bivalve *Arctica islandica* (Figure 5.4.1b) was sparsely distributed on the Oyster Ground in 2000, although its northern range did not change significantly. This species is a slow-growing, long-lived (up to 100 years or more) filter-feeder, which is typically associated with sandy muds. It is more common in deeper areas of the central and northern North Sea, where it is less prone to sediment disturbance (Rees and Dare, 1993). Witbaard and Bergman (2003) indicated that the distribution and density of *A. islandica* in NSBS 1986 mainly included specimens <10 mm (spat), with only small representation by the larger animals. They also noticed that, in previous surveys, the use of smaller and shallower penetrating sampling gear

such as van Veen grabs appeared to miss the adults (>50 mm). Witbaard and Klein (1994) also described the increasing negative effects of the beam trawl fishery on this species.

The distribution of the polychaete *Synelmis klatti* (Figure 5.4.1a) was restricted to the southern North Sea in 1986. In 2000, its presence was reduced in the central part of the Oyster Ground with new occurrences of this species appearing in the northern North Sea. Distributions of the bivalve *Nucula nitidosa* (Figure 5.4.1f) are similar in both surveys on the Oyster Ground. The BIOMON programme also observed stable densities of this species over time in the area (Daan and Mulder, 2006). The species was also present at stations in the western North Sea off the Northumberland coast in 2000, where it had not been documented during the 1986 survey. Densities of *N. nitidosa* also increased in the inner German Bight. It has been suggested that the species may benefit from the high input of fresh organic matter in the area (Kröncke, 2006).

Overall, occurrences of the crustacean *Callianassa subterranea* (Figure 5.4.1d) appeared slightly reduced in 2000. The species was absent at several stations on the Oyster Ground and central North Sea, where it had previously been observed in 1986. However, there were increases at the Frisian Front and at stations off northern Scotland and east of the Orkneys. *C. subterranea* appears to favour the soft sediments of the Oyster Ground, where it creates deep-penetrating, three-dimensional burrows. Its burrowing activity oxygenates and reworks the sediment and therefore has a significant positive influence on the local benthic community. However, sediment instability also negatively affects certain species. The regime shift from an *A. filiformis*-dominated community to a *C. subterranea*-dominated community at the Frisian Front in the mid-1990s was largely attributed to sediment instability resulting from the burrowing of *C. subterranea* (van Nes *et al.*, 2007). Time-series data collected on the Oyster Ground as part of the BIOMON sampling programme showed that the species reached highest average densities (>120 ind. m⁻²) in 1990, then steadily declined by 1999 to levels similar to those observed in 1986. By 2000, densities had increased again (Daan and Mulder, 2006). The changes observed between the two NSB sampling occasions may reflect, in part, the different sampling gear used. Grabs such as the van Veen may only give limited information about the distribution of this species because of the deep penetration of *C. subterranea* into the sediment.

Dogger Bank and continental coast

The Dogger Bank is situated where Atlantic water from the north meets Channel inflow from the south. Depths on the Bank range from 18 to 40 m. Fine sand persists in the shallow areas, which becomes muddier in deeper parts around the Bank (Kröncke and Knust, 1995). Although community structure at the Dogger Bank was largely similar in 1986 and 2000, there were changes in both abundances and distributions of certain species. Densities of the tube-building polychaete *Lanice conchilega* (Figure 5.4.2d) were greatly increased in 2000, especially at the Tail End, where densities at one station exceeded 3000 ind. m⁻². *L. conchilega* is a dominant species of both intertidal and subtidal sands, where dense populations of the species can alter the benthic community by stabilizing the sediment, providing a settlement surface for larval recruits, a refuge from predators, and improving oxygen supply to the deeper sediment (Eagle, 1975; Callaway, 2006; see also Section 6.7). However, the species is more dynamic and ephemeral than some other habitat-structuring species, having the ability to recolonize an area rapidly after disturbance (Zühlke, 2001; Nicolaidou, 2003). Callaway (2006) observed a relationship between *L. conchilega* and the burrowing amphipod *Urothoe poseidonis*, which was found to inhabit deep sediment layers in close proximity to the *L. conchilega* tubes and may benefit from an improved oxygen supply generated by the polychaete. However, this relationship was not apparent from the NSB data. *U. poseidonis* (Figure 5.4.2b) exhibited reduced densities at stations on the western end of the Dogger Bank in 2000, but increases at stations in the southern North Sea off the Dutch coast.

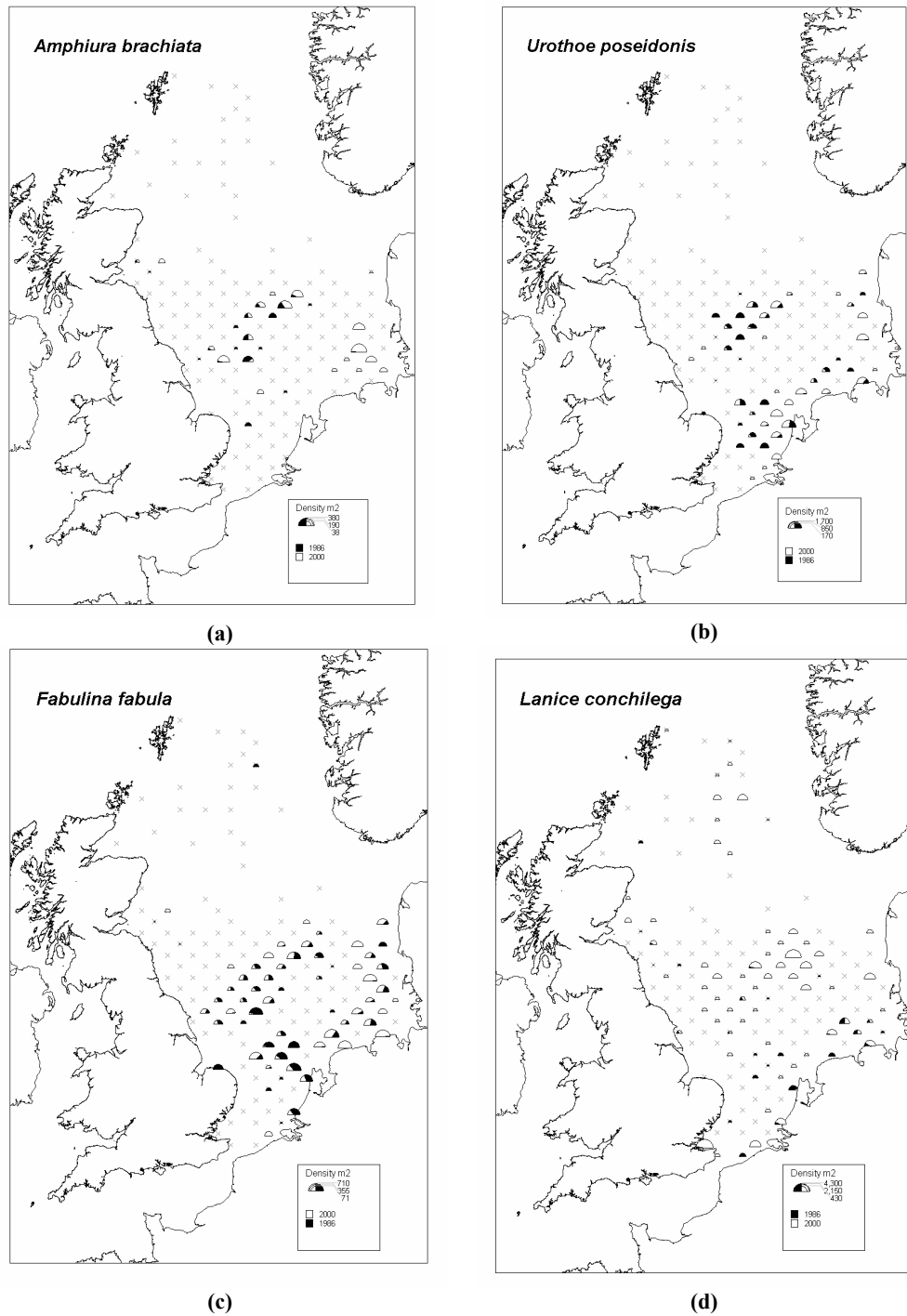


Figure 5.4.2a–d. Species strongly associated with the Dogger Bank and Continental Coast (1986 and 2000).

The echinoderm *Amphiura brachiata* (Figure 5.4.2a) and bivalve *Fabulina fabula* (Figure 5.4.2c) also showed slight increases in abundance, particularly along the continental coast and in the German Bight. *A. brachiata* is characteristic of fine sands in high energy environments (Bourgoin *et al.*, 1991). Temperature is thought to be an especially important limiting factor governing its distribution. Increased winter temperatures over the past 30 years may have contributed to the expansion of this species in the German Bight (Boos and Franke, 2006). *F. fabula* is also characteristic of fine sands at depths less than 30 m in the southern North Sea (Kröncke and Bergfeld, 2003). Increases in the densities of this species are apparent in the eastern North Sea, which may result from an increase in primary production (see Section 5.2).

Decreases in abundances are also noticeable at the Frisian Front. The *F. fabula* population on the Dogger Bank appears similar in both years, which concurs with the findings from the BIOMON programme (Daan and Mulder, 2006).

Central and southern North Sea

The echinoderms *Echinocardium cordatum* (Figure 5.4.3d) and *Amphiura filiformis* (Figure 5.4.3a) and the bivalve mollusc *Mysella bidentata* (Figure 5.4.3b) exhibited similar distributions in both 1986 and 2000. *E. cordatum* is a long-lived (10–20 years) species, found buried in sands or muddy sands and is widely distributed in the southern North Sea and English Channel (Rees and Dare, 1993). The species plays an important role in sediment bioturbation through its feeding activities. Wieking and Kröncke (2003) found that the abundance of *E. cordatum* on the Dogger Bank was affected by food quantity, while growth was determined by food quality. Its recruitment success may also depend on preceding winter temperatures in some areas (Beukema, 1985). Kirby *et al.* (2007) observed increases in the abundance and spatial distribution of *E. cordatum* larvae in the North Sea plankton (1988–2002), which they attributed to a pronounced increase in sea surface temperature after 1987. However, their conclusion that temperature increases also resulted in an extended range of the adult population in the German Bight in 2000 was based on a misinterpretation of NSB data presented in the 2004 ICES SGNSBP annual report (ICES, 2004b). Increases in sampling effort in 2000 (compared with 1986) appeared to have been mistaken for increased species distribution. Our comparison of matching stations in 1986 and 2000 shows that, although there appears to be significant density increases at many stations in 2000, there are also significant decreases at many others. The average density of *E. cordatum* adults per m² in the North Sea was similar in both sampling years (1986: 8.63(±3); 2000: 8.79(±3) (95%CI)). Furthermore, a time-series study at several stations in the German Bight reported by Schroeder (2005) also provided no evidence of an overall increase in distribution or densities. Of three long-term monitoring stations supporting *E. cordatum* populations, similar densities were recorded in both 1986 and 2000 at two, while a net increase against a background of significant annual fluctuations was only observed at one.

Densities of both *A. filiformis* and *M. bidentata* were highest on the Oyster Ground in both 1986 and 2000. *A. filiformis* lives with its disk buried to about 4 cm in the sediment and one or two arms protruding above the sediment for feeding. The species is principally a suspension feeder and therefore is largely dependent on the nature of bottom currents and suspended load for its food supply (Buchanan, 1964). However, *A. filiformis* is also known to switch feeding modes to surface deposit feeding, which may explain its distribution in the northern North Sea. Densities of *A. filiformis* were reduced at the Frisian Front in 2000, which may be the result of the influence of *C. subterranea*. *M. bidentata* exhibited similar distributional patterns, in the central and southern North Sea, to *A. filiformis*. Ockelmann and Muus (1978) suggested that *M. bidentata* is commensal with *A. filiformis*, living in its burrows and feeding on deposited detritus.

Densities of the bivalve mollusc *Chamelea gallina* (Figure 5.4.3c) were reduced in the eastern North Sea off the Danish and German coasts. There has been a decreasing trend in *C. gallina* in the German Bight since 1923, which has been attributed to demersal trawling (OSPAR Commission, 2000). Indeed, Bergman *et al.* (1998) found a negative correlation between abundances of *C. gallina* and trawling effort (see also Section 6.3). The bivalve mollusc *Nuculoma tenuis* (Figure 5.4.3e) was also reduced on the northern Oyster Ground, but densities increased in the western North Sea in 2000. *N. tenuis* is a subsurface deposit feeder that disturbs the top 2–3 cm of the sediment as it feeds. Although the bioturbating activities of this species may be limited compared with larger bioturbating organisms, it has been shown to promote diversity and hence plays an important role in structuring infaunal communities (Widdicombe *et al.*, 2000).

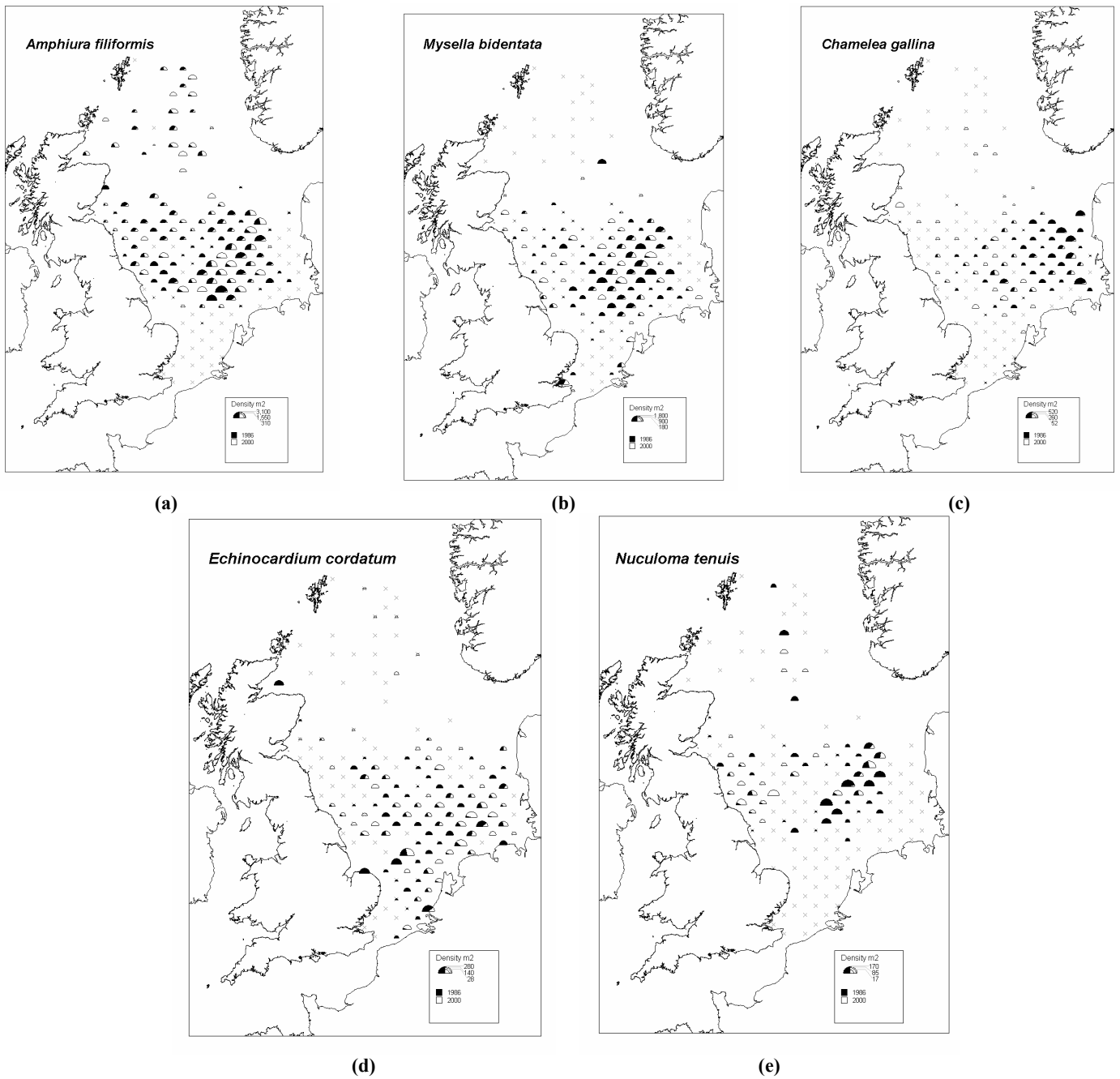


Figure 5.4.3a–e. Species predominantly associated with the central and southern North Sea (1986 and 2000).

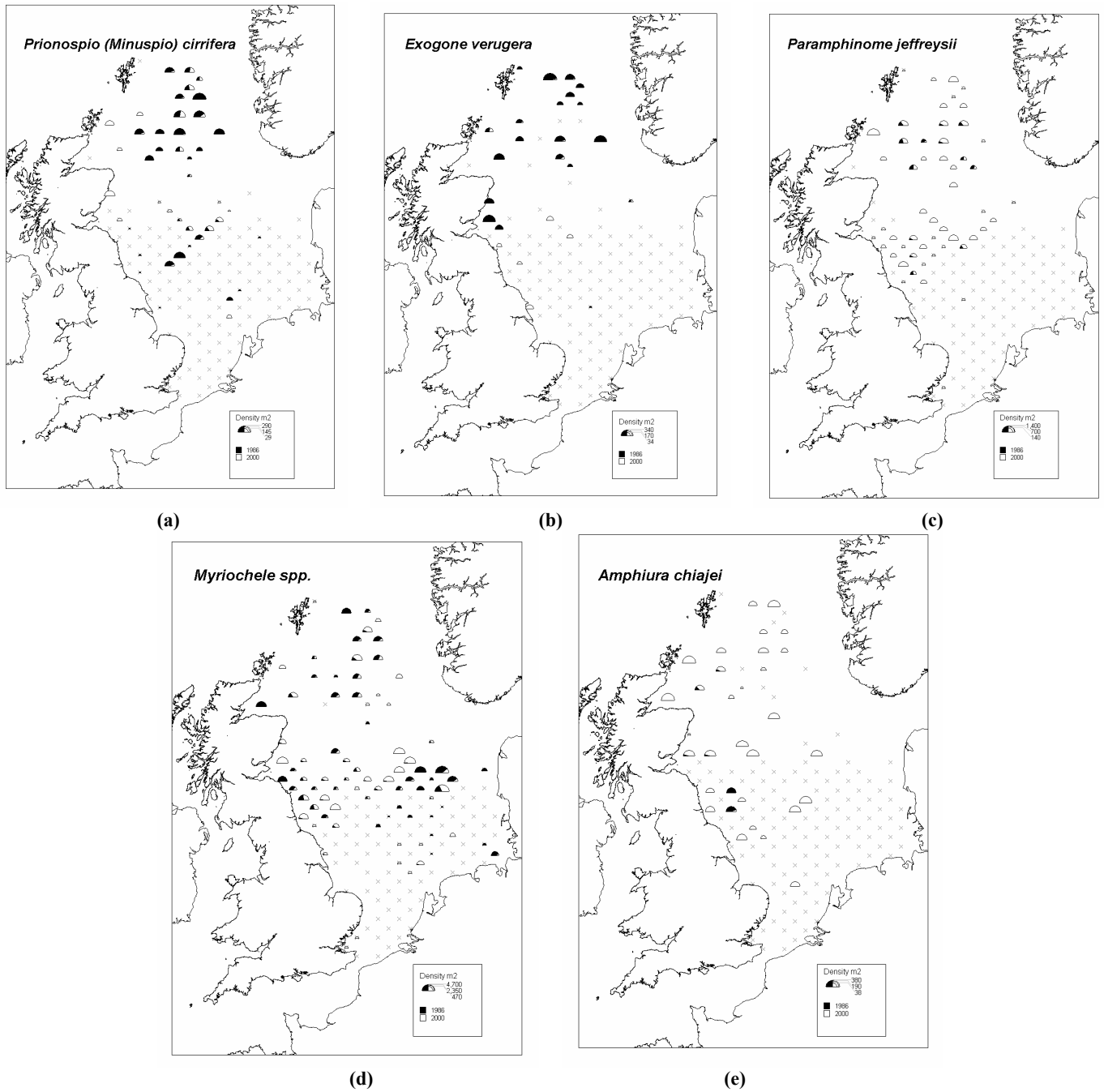


Figure 5.4.4a–g. Species occurring predominantly north of the Dogger Bank and in the northern North Sea (1986 and 2000). Continued on next page.

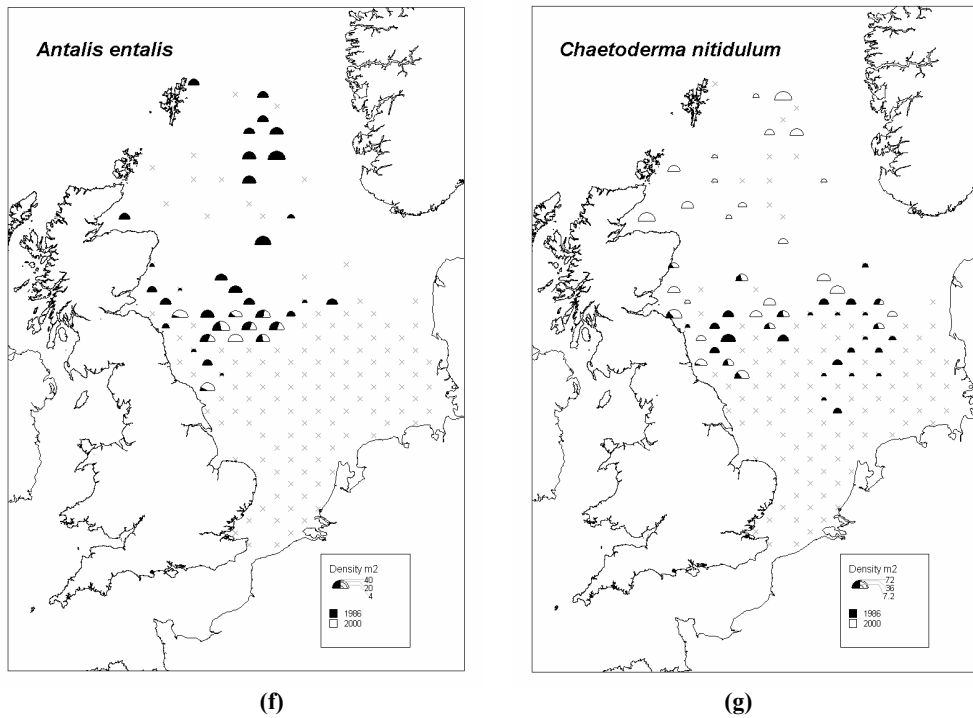


Figure 5.4.4a–g continued. Species occurring predominantly north of the Dogger Bank and in the northern North Sea (1986 and 2000).

North of Dogger Bank and northern North Sea

This region is mainly characterized by depths of >50 m and stable muddy sediments. Several of the species illustrated appear to have reduced abundances and restricted distribution in 2000 compared with 1986. The polychaetes *Prionospio (Minuspio) cirrifera* (Figure 5.4.4a) and *Exogone verugera* (Figure 5.4.4b) were indicators of depths greater than 70 m in 1986, but show substantially reduced presences in 2000. The distribution of *E. verugera* is documented as widespread and hence not restricted entirely to northern waters (Hayward and Ryland, 1995), while *P. cirrifera* is considered a cold-water Arctic-boreal species (see Maciolek, 1985). These small polychaetes may not have been adequately sampled by the 1 mm mesh sieve used in 2000 in the northern North Sea: a 0.5 mm mesh sieve was employed in 1986 (see Künitzer *et al.*, (1992)).

The mollusc *Chaetoderma nitidulum* (Figure 5.4.4g) shows an extended distribution to the north in 2000. This species was characteristic of the central North Sea in 1986. It is usually present in muddy or sandy sediments of 20–150 m in the North Sea (Salvini-Plawen, 1975). The polychaete *Paramphinome jeffreysii* (Figure 5.4.4c) is a species truly restricted to the deeper parts (>50 m) of the central and northern North Sea (George and Hartmann-Schroder, 1985). Records for the presence of this species at two stations south of the Dogger Bank and in the Thames area may result, therefore, from taxonomic error. The distribution and abundance of this species has increased, especially in the central North Sea. Frid *et al.* (1999) also observed “dramatic” abundance increases in *P. jeffreysii* in a time-series study off the Northumberland coast. Large increases were noticeable the year after large decreases of other organisms were observed, and it was thought that the polychaete was opportunistically scavenging on the dead remains. Kröncke and Reiss (Section 5.2) suggest that the abundance increases of both *P. jeffreysii* and *Myriochele* spp. (Figure 5.4.4d) may result from the presence of colder water masses in the northern North Sea.

The scaphopod mollusc *Antalis entalis* (Figure 5.4.4f) appears to have become restricted to the central North Sea between latitudes of 54–56°N in 2000. However, this may be an anomaly

owing to large distances between nearest matching stations in the northern North Sea in 1986 and 2000. Further interrogation of data from other surveys in this area will help clarify whether the apparent absence of this species is real. The polychaetes *Spiophanes krøyeri* and *Terebellides stroemi* (not shown) were both indicators of deep muddy sediment in 2000. *S. krøyeri* was also indicative of depths >70 m in 1986. Both species appeared more widespread in the central North Sea in 2000 (see Annex 3).

Amphiura chiajei (Figure 5.4.4e) exhibited significant density increases in 2000. The species replaces *A. filiformis* at depths of 70–100 m off the Northumberland coast in silty depositional areas. The life history traits of the two *Amphiura* species are considered to be a major factor in controlling their distribution. *A. chiajei* is a long-lived, slow-growing deposit feeder, whereas *A. filiformis* is a fast-growing, short-lived suspension feeder (Buchanan, 1964). *A. chiajei* lives buried up to 6 cm in the sediment using one or two arms to collect food particles at the surface, which are then transported along the arms to the mouth. Its feeding activities allow oxygen to penetrate deeper into the sediment, and the species is therefore considered an important bioturbator. For example, Widdicombe *et al.* (2004) found a positive relationship with the abundance of *A. chiajei* and species diversity, which they related to the bioturbating activities of this species.

Western North Sea

The echinoderm *Echinocyamus pusillus* (Figure 5.4.5a) and the “reef”-building polychaete *Sabellaria spinulosa* (Figure 5.4.5b) are species preferring the coarser sediment of the western North Sea. *E. pusillus* inhabits the interstices of gravelly substrata in areas exposed to extensive wave action and/or strong tidal currents (Telford *et al.*, 1983; Brown *et al.*, 2001). This species showed significant density decreases at many stations in the western North Sea in 2000. In contrast, the species exhibited density and distributional increases at the Tail End of the Dogger Bank and in the eastern North Sea. Holtmann *et al.* (1999) and Wiekling and Kröncke (2001) attributed density increases of this species at the northeastern Dogger Bank to changes in sediment composition caused by increases in current velocities.

S. spinulosa use large quantities of mobile sand to build tubes and “reef” structures, although they usually require a suitably firm substratum on which to establish a community (Schafer, 1972; Holt *et al.*, 1997). The reefs provide habitat for a wide variety of species (both infaunal and epifaunal), resulting in a rich and distinctive community that may not otherwise be found in the area (Rees *et al.*, 1999; UK Biodiversity Group, 1999). Although in some areas, reefs may be extensive and persist for several years, they are also known to be ephemeral (Schafer, 1972; Holt *et al.*, 1997). For example, extensive reefs have been previously identified in an area, only to disappear a few months later (R. Foster-Smith, pers. comm.). *Sabellaria* reefs are also prone to destruction by fishing gear (Riesen and Reise, 1982) as well as naturally by storms (Holt *et al.*, 1997). In the Wadden Sea, *Sabellaria* reefs are now completely absent possibly as a result of destruction by heavy demersal fishing gear (Riesen and Reise, 1982). The species showed an increase in distribution and densities in the western North Sea in 2000.

Cosmopolitan species

The polychaete *Ophelia borealis* (Figure 5.4.6c) is typical of mobile fine sands and is widely distributed throughout the North Sea (Künitzer *et al.*, 1992). The presence of this species was significantly reduced in 2000, except at a few stations in the western North Sea and the Dogger Bank. Wiekling and Kröncke (2001) also noticed dramatic decreases in this species between the mid-1980s and late 1990s on the northeastern Dogger Bank, which they attributed to increased grain size caused by an increase in current velocities in the area. Other species preferring fine sands, such as *Spiophanes bombyx* (Figure 5.4.6b) and *Bathyporeia elegans*, also showed decreased occurrences to the northeast of the Bank, which concurs with the NSB findings. Decreases in the densities of *Bathyporeia* spp. (Figure 5.4.6a) are also evident on the southwest of the Dogger Bank and in the southern North Sea. Towards the Tail End of the

Dogger Bank, densities of *Bathyporeia* spp. increased in 2000. Daan and Mulder (2005) observed greatest increases in *Bathyporeia elegans* in this area in 2000. Densities and distribution of the polychaete *Nephtys longosetosa* (Figure 5.4.6d) were reduced in 2000, particularly on the Dogger Bank. *N. longosetosa* was also a species indicative of fine sand at 50–70 m depths in the NSBS 1986. *S. bombyx* showed decreased presence on the Dogger Bank in 2000; however, densities generally increased on a North Sea-wide scale.

The overall abundances (matching stations only) of the polychaete *Scoloplos armiger* (Figure 5.4.6e) were slightly reduced in 2000. The species is found in all sediment types, but highest numbers are found in finer sediments with a high content of mud (Degraer *et al.*, 2006). The distribution of *S. armiger* appeared significantly reduced in offshore regions of the Belgian continental coast in 2000 compared with 1986 distributions. Degraer *et al.* (2006) found that *S. armiger* was mainly distributed nearer the western Belgian coast between 1994 and 2001 (see also Annex 3) and was scarcer in the offshore zone compared with earlier surveys (1976–1986). The apparent reduced densities in the German Bight may be the result of the patchiness of the species in this area (see Annex 3).

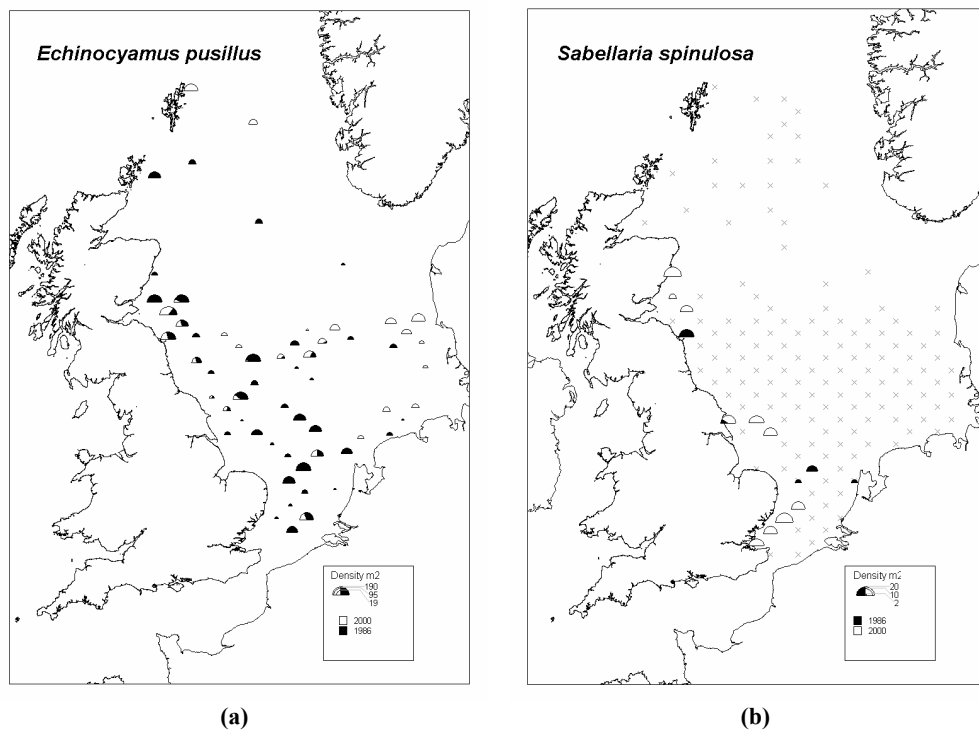


Figure 5.4.5.a–b. Species predominantly associated with the western North Sea.

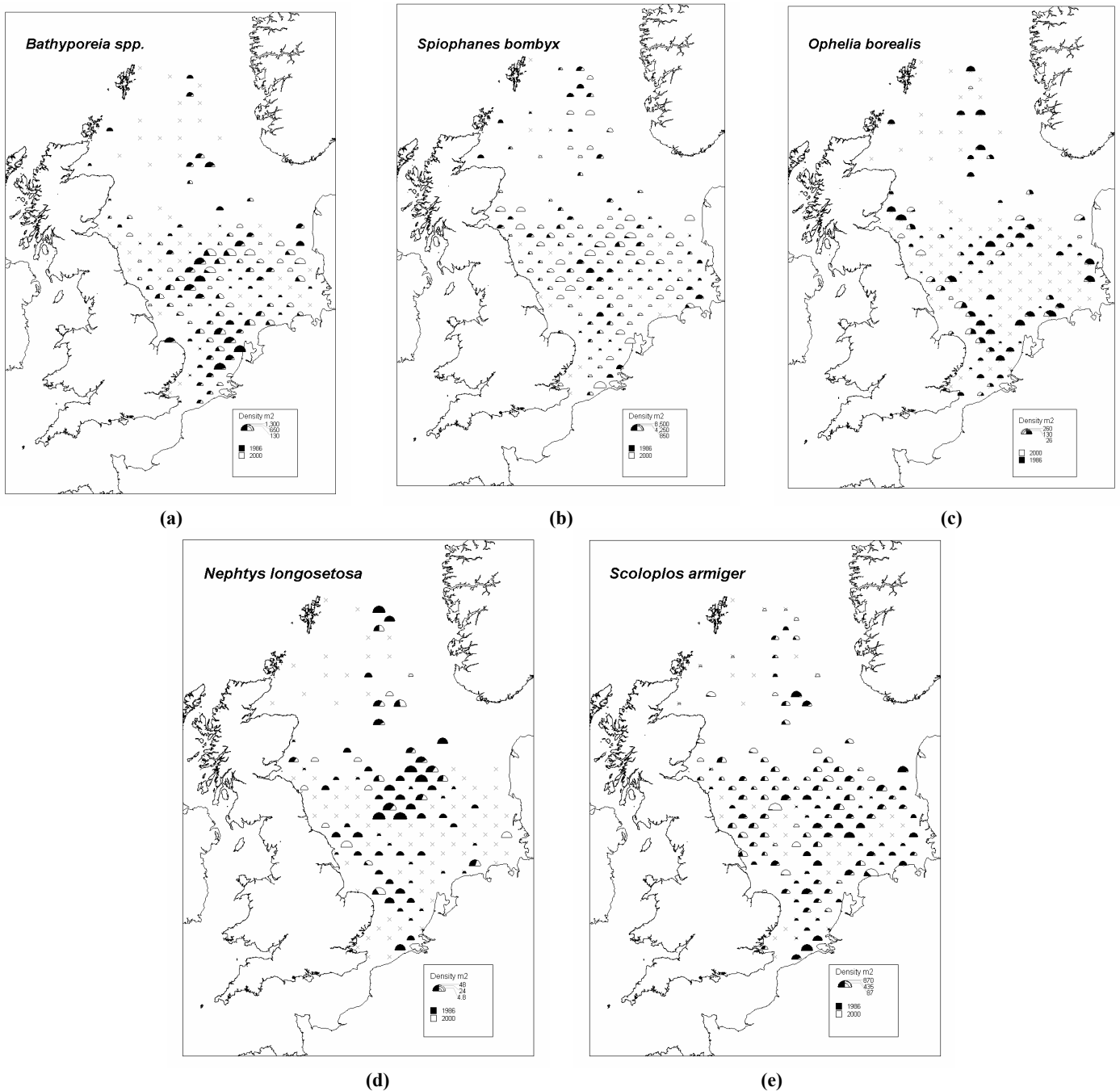


Figure 5.4.6a–e. Species with North Sea-wide distributions.

5.4.4 Conclusions

Table 5.4.2 summarizes the changes for the selected species. In general, the information suggests that, although there is some evidence of flux that may be attributable to natural variation in the recruitment process of relatively short-lived species, there is little indication of a consistent directional trend and, for the majority of species investigated in this section, the distributions remain broadly similar to those in 1986. This may be largely the result of the close association of many species with their sedimentary environment. Time-series studies undertaken between the two sampling occasions revealed that, although the densities of some species remained fairly stable, others tended to fluctuate widely, both on a seasonal and yearly basis (e.g. Reiss and Kröncke, 2005; Daan and Mulder, 2006). Understandably, food supply and quality have been suggested as major factors influencing species abundances (Schroeder, 2005; Wieking and Kröncke, 2005). Areas with contrasting food supply also differ in the

trophic structure of the benthic community (Wieking and Kröncke, 2005). Buchanan and Moore (1986) suggest that communities are also structured by density-dependent mortality through interspecific and intraspecific competition for a finite resource. A significant increase in organic matter may upset this competitive balance, resulting in opportunistic species reacting rapidly to the changing environmental conditions. Species that inhabit more exposed and unstable environments are also likely to show higher temporal variability than those in the deeper, stable environments. Direct competition for space may also structure species distributions. For example, the regime shift observed at the Frisian Front in the mid-1990s was mainly attributed to instability of the sediments, caused by the burrowing activity of *C. subterranea*, which resulted in a negative effect on *A. filiformis* populations (van Nes *et al.*, 2007).

In this study, there is some evidence to suggest that three species (*O. borealis*, *C. gallina*, *N. tenuis*) have shown movements away from the eastern North Sea in 2000, extending their distribution to the deeper waters of the western North Sea. Species such as *A. brachiata*, which require warmer temperatures in order to reproduce successfully, have shown an increasing presence in the eastern North Sea. The abundances of *C. gibba* and *A. alba* also increased significantly in 2000. Both species are known to predominate in warmer temperatures. In addition, demersal fishing may have resulted in the reduced distribution and abundances of the bivalves *A. islandica* and *C. gallina* in this study. This may repay further investigation via additional data sources.

Table 5.4.2. Summary of species changes between 1986 and 2000 (based on matching stations only).

| SPECIES | ABUNDANCE AND DISTRIBUTIONAL CHANGES IN 2000 | SPECIES | ABUNDANCE AND DISTRIBUTIONAL CHANGES IN 2000 |
|--------------------------------|--|--------------------------------|--|
| <i>Abra alba</i> | + | <i>Lanice conchilega</i> | + |
| <i>Amphiura chiajei</i> | + | <i>Myriochele</i> spp. | + |
| <i>Amphiura filiformis</i> | same | <i>Mysella bidentata</i> | same |
| <i>Amphiura brachiata</i> | + | <i>Nephtys longosetosa</i> | – |
| <i>Antalis entalis</i> | – | <i>Nucula nitidosa</i> | + |
| <i>Arctica islandica</i> | – | <i>Nuculoma tenuis</i> | – |
| <i>Bathyporeia</i> spp. | same | <i>Ophelia borealis</i> | – |
| <i>Callianassa subterranea</i> | same | <i>Paramphinome jeffreysii</i> | + |
| <i>Chaetoderma nitidulum</i> | + | <i>Prionospio cirrifera</i> | – |
| <i>Chamelea gallina</i> | – | <i>Sabellaria spinulosa</i> | + |
| <i>Corbula gibba</i> | + | <i>Scoloplos armiger</i> | – |
| <i>Echinocardium cordatum</i> | same | <i>Spiophanes bombyx</i> | + |
| <i>Echinocyamus pusillus</i> | + | <i>Spiophanes krøyeri</i> | + |
| <i>Exogone verugera</i> | – | <i>Synelmis klatti</i> | – |
| <i>Fabulina fabula</i> | + | <i>Terebellides stroemi</i> | + |
| | | <i>Urothoe poseidonis</i> | + |

+ = greater abundance and distribution in 2000.

– = reduced abundance and distribution in 2000.

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5.5 Functional diversity

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5.5.1 Introduction

The way in which benthic species acquire their food determines various other parameters of their lives and reflects their adaptation to the environment. Thus, differences in the environment will be reflected in the distribution of feeding types. The latter may also reflect differences in the energy transfer from surface production to the benthos. These are the reasons to focus on the feeding types as an aspect of the functional diversity of the benthos.

The main benthic feeding types can be divided in two ways: what they feed on and how they feed. The first category can be divided into herbivores, carnivores, and detritivores, and the second into suspension-feeders, filter-feeders, deposit-feeders, scavengers, and predators (www.aqualex.org).

Herbivores are organisms that feed on plant material. They live mainly on plants or on the sediment surface, usually in shallow areas, and have special mouth parts (e.g. radulae), which enable them to cut and chew vegetal material.

Carnivores/predators are organisms that feed on live individuals of various sizes. They have well-developed sensory organs, which enable them to detect prey; they are highly mobile in order to pursue their prey; and they have special mouth parts, jaws, teeth, and extendible pharynxes to capture and consume their prey. Scavengers can be considered as a subcategory of carnivores. They are of similar body construction and feed on dead bodies or remnants of either benthic or pelagic organisms.

Suspension-feeders have appendages covered by mucus to which suspended particles from the water column become attached. They are then carried by means of the cilia and antennae to the mouth. This category of organisms does not have much mobility and lives attached to the substrate; they prefer hard substrate and usually construct special hard cases or tubes into which they retreat when they sense danger. In hydrodynamically energetic areas, very fine sediment is not a favourable environment for suspension-feeders because resuspension causes their feeding appendages to clog up.

Filter-feeders find their food in much the same way as suspension-feeders: the only difference is that they themselves create water currents towards the special food retention appendages by means of siphons or articulated appendages. Their ecological preferences do not differ in general from those of suspension-feeders, with the only important difference being their ability to colonize environments with a sparser food supply.

Deposit-feeders feed on organic material contained in the soft sediments of the seabed. The ways in which they acquire their food are quite diverse and range from a simple swallowing of the sediment and the digestion of the organic material contained in it, to spreading mucus on the sediment surface and then the swallowing of particles of organic material and/or bacteria that become attached to it. They are differentiated as selective and non-selective deposit-feeders according to their ability to select the type and the size of the particles they swallow, and as surface and subsurface deposit-feeders according to their ability to feed on particles on the surface or to exploit food located deeper in the sediment (though not deeper than a few centimetres).

5.5.2 Material and methods

For all macrobenthic species/taxa recorded in 1986 and 2000, the feeding type was determined from the literature or by expert judgment. Only a small percentage of the total (1.5%) could not be allocated, based on current knowledge, while allocation to a further 5.9% was

inappropriate owing to taxonomic imprecision (e.g. unidentified bivalves). The feeding types were eventually divided into four main groups (Table 5.5.1). The parasites were put into a separate (fifth) group, but this was very small in terms of density and biomass and is not dealt with further in this account.

Table 5.5.1. Feeding groups.

| FEEDING GROUP | DESCRIPTION |
|---------------|---|
| I | Suspension- or filter-feeder |
| II | Interface-feeder, surface deposit-feeder, facultative suspension-feeder |
| III | Subsurface deposit-feeder, grazer |
| IV | Predator, omnivore, scavenger |
| V | Parasite |
| na | Not appropriate at the recorded taxonomic level |
| U | Unknown |

For the four main feeding guilds, distribution plots were made based on the data of 1986 and 2000 separately. The percentage of each feeding group was plotted for those stations where it exceeded 40% of the total density. For this reason, only two maps are needed to illustrate the distribution of the feeding guilds (Figure 5.5.1 and Figure 5.5.2).

The relationship between latitude and percentage of each feeding group was inspected using X-Y scatterplots, further visualized by adding a lowess smoother for both the 1986 and 2000 data.

Differences between 1986 and 2000 in the proportion of each feeding group were tested for significance using the following tests:

- unpaired and paired t-test
- analysis of similarities (ANOSIM)
- non-parametric MANOVA (NPMANOVA)

For these tests, the data (percentages) were arcsin transformed. Furthermore, for the last two multivariate analyses, the feeding groups were treated as variables, i.e. descriptors of the community. All the analyses were done for the three main areas of the North Sea as delineated by the community analysis of 1986 (TWINSPAN groups I, II, and III, based on species abundances; Künitzer *et al.*, (1992)).

5.5.3 Results

The percentage of suspension-feeders is large on the Oyster Ground and (in 2000) in parts of the German Bight (Figure 5.5.1 and Figure 5.5.2). On the Dogger Bank and to the north in the deeper water of the North Sea, filter-feeders form a minority of the macrobenthos. In the shallow part south of the Frisian Front, the percentage of suspension-feeders is also small. This is also the case along the Belgian and French coasts and in the English Channel, though there are some stations with large percentages. (Note that, in the last case, a large number of stations are situated close together).

Interface-feeders form the most important part of the infauna over the whole North Sea, except for the Oyster Ground. At many stations, the percentage of this feeding guild is larger than 50%. Subsurface deposit-feeders form a minority in the North Sea. Only in the German Bight, in the Channel, and along the Belgian and French coasts are they found in greater numbers, but not often exceeding 50%. Predators, scavengers, and omnivores together demonstrate a pattern similar to that of subsurface deposit-feeders, though with slightly larger percentages, especially in the coarser sediments along the UK coast.

The large proportion of suspension-feeders in the Oyster Ground is also apparent from the latitudinal gradient (Figure 5.5.3). Interface-feeders demonstrate a drop in their proportion in that area. Subsurface feeders fluctuate around a low value, but without obvious peaks or dips. The proportion of predators appears to be similar over the whole latitudinal range, except in the south where there is evidence of an increase. Overall, there was no evidence of a marked change in the proportion of feeding types along the latitudinal gradient in 1986 and 2000, and the lowest lines of both years (1986 and 2000) are quite similar for each feeding guild (Figure 5.5.3).

In all three North Sea assemblages (based on Künitzer *et al.*, 1992), there is a difference in the proportion of the feeding groups between 1986 and 2000 (ANOSIM, NPMANOVA: Table 5.5.2). The *t*-tests reveal that, in assemblage 1, covering the shallowest stations, there is a significant difference between the proportion of interface-feeders and subsurface deposit-feeders in 1986 and 2000 (Table 5.5.2). In the somewhat deeper (30–70 m) stations with finer sediments (assemblage 2), 1986 and 2000 differ in the proportion of all feeding groups. In the deeper area (assemblage 3), there is a difference in the proportion of subsurface deposit-feeders and carnivores.

Table 5.5.2. Differences between 1986 and 2000 in the proportion of each feeding group (I–IV), tested for significance using unpaired and paired *t*-tests and community analyses (ANOSIM, NPMANOVA). * = significantly different, ** = highly significantly different.

| ASSEMBLAGE | ANALYSIS | I | II | III | IV |
|------------|-------------------------|------------|-------------|-------------|------------|
| 1 | unpaired <i>t</i> -test | p = 0.305 | p = 0.005** | p <0.001** | p = 0.250 |
| | paired <i>t</i> -test | p = 0.268 | p <0.001** | p <0.001** | p = 0.120 |
| 2 | unpaired <i>t</i> -test | p = 0.06 | p <0.001** | p = 0.049* | p <0.001** |
| | paired <i>t</i> -test | p = 0.006* | p <0.001** | p = 0.018** | p <0.001** |
| 3 | unpaired <i>t</i> -test | p = 0.442 | p = 0.648 | p = 0.020* | p <0.001** |
| | paired <i>t</i> -test | p = 0.311 | p = 0.638 | p = 0.008* | p <0.001** |

| ASSEMBLAGE | ANALYSIS | P-VALUE |
|------------|----------|-------------|
| 1 | NPMANOVA | p <0.001** |
| | ANOSIM | p <0.001** |
| 2 | NPMANOVA | p = 0.002** |
| | ANOSIM | p = 0.001** |
| 3 | NPMANOVA | p = 0.005** |
| | ANOSIM | p = 0.001** |

5.5.4 Discussion

Surprisingly, in this comparison of the density of the different feeding types between 1986 and 2000, we found a statistically significant difference for the three main faunal assemblages (1–3) in the North Sea, as identified by Künitzer *et al.* (1992). However, the nature of the changes appears to be different between assemblages, and possible causes are considered below.

In assemblage 2, centred on the Oyster Ground at moderate depth (30–70 m) and with a high mud content, all feeding types exhibited change. The Oyster Ground is characterized by a high-density and a high-proportional contribution of suspension-feeders, which is the case for 1986 as well as 2000. This is caused mainly by the brittlestar *Amphiura filiformis*. From the yearly biomonitoring of the benthos in the Dutch sector covering the Oyster Ground, there is evidence that *Amphiura* has declined since the 1990s (Daan and Mulder, 2005). There are several possible explanations for this change, including fishing activity, increased resuspension caused by higher windstress, and an ecological “regime shift” as the *Amphiura* population at the low point of a natural cycle of variation in densities is displaced by larger

numbers of *Callianassa subterranea* and *Upogebia deltaura* (van Nes *et al.*, 2007). A large change in the *Amphiura* population can explain not only the difference in the proportion of suspension-feeders, but also of other feeding types because, expressed in this way, they are dependent variables. High densities of suspension-feeders in an area are often seen as an indication of an unpolluted or unstressed environment, and this is reflected in the scoring systems for many marine biotic indices (e.g. Borja *et al.*, 2000; Word, 1978). It follows that a decrease of suspension-feeders would point to increased stress.

In assemblage 1, covering mainly the southern part of the North Sea with sandy sediment and shallow depths, there was a significant change in the proportion of the interface-feeders and subsurface feeders. The interface-feeders increased, while the subsurface feeders decreased. For the interface-feeders, these changes were mainly caused by the greater numbers of *Spiophanes bombyx* and *Magelona* spp. in 2000. These short-lived polychaetes, however, can demonstrate large year-to-year differences in their populations. This is evident from long-term monitoring of the macrobenthic fauna in the Dutch sector of the North Sea (1990–2005: Daan and Mulder, 2006), and instead of an increase, they note a somewhat decreasing trend in *Spiophanes* densities. For *Magelona* spp., they cannot show a clear trend. *Scoloplos armiger* and *Ophelia borealis* were responsible for the decrease of subsurface feeders in our comparison between 1986 and 2000. Here the same argument applies as for *Spiophanes* and *Magelona*, namely that the changes are probably caused by normal year-to-year variations in the densities of these short-lived species, rather than pointing to a clear long-term trend.

In assemblage 3, located in the deeper area of the North Sea, a difference in the proportion of subsurface deposit-feeders and carnivores was found. The subsurface feeders demonstrated a proportional decrease from 1986 to 2000. Among the species causing this change, the Capitellidae had the highest contribution, but no single species could be held responsible for the change. The main species responsible for the increase of carnivores was *Paramphinoe jeffreysii*. As for the changes in assemblage 1, we argue that these are mainly caused by year-to-year fluctuations in the population of short-lived species.

We conclude that, based on the proportional contribution of the four feeding guilds, there is a clear change in the central North Sea (Oyster Ground and surroundings), which is backed up by annual monitoring. For the other parts of the North Sea, we noted a change, but could not designate this as a continuous trend over the years. It is unfortunate that these North Sea-wide quantitative exercises cannot be conducted on a more frequent (even annual) basis, because long-term trends can now be difficult to separate from annual fluctuations in the macrobenthic populations. We stress that, in response to increasing concerns over global warming, the possibility of declining fishery effort in the future (because of regulations or stock depletion) and the designation of marine protected areas in the North Sea, it is very important to monitor the consequences for the benthic fauna at appropriate frequencies. After decades of increasing fishing effort and concerns over pollution and other human activities, it is surprising that the first quantitative survey of the macrobenthic fauna of the whole North Sea was only carried out in 1986. Further, it has taken another 15 years to achieve a repeat assessment on a comparable scale. This seems to be an unacceptably low frequency, given the continued importance of the North Sea for mankind and nature.

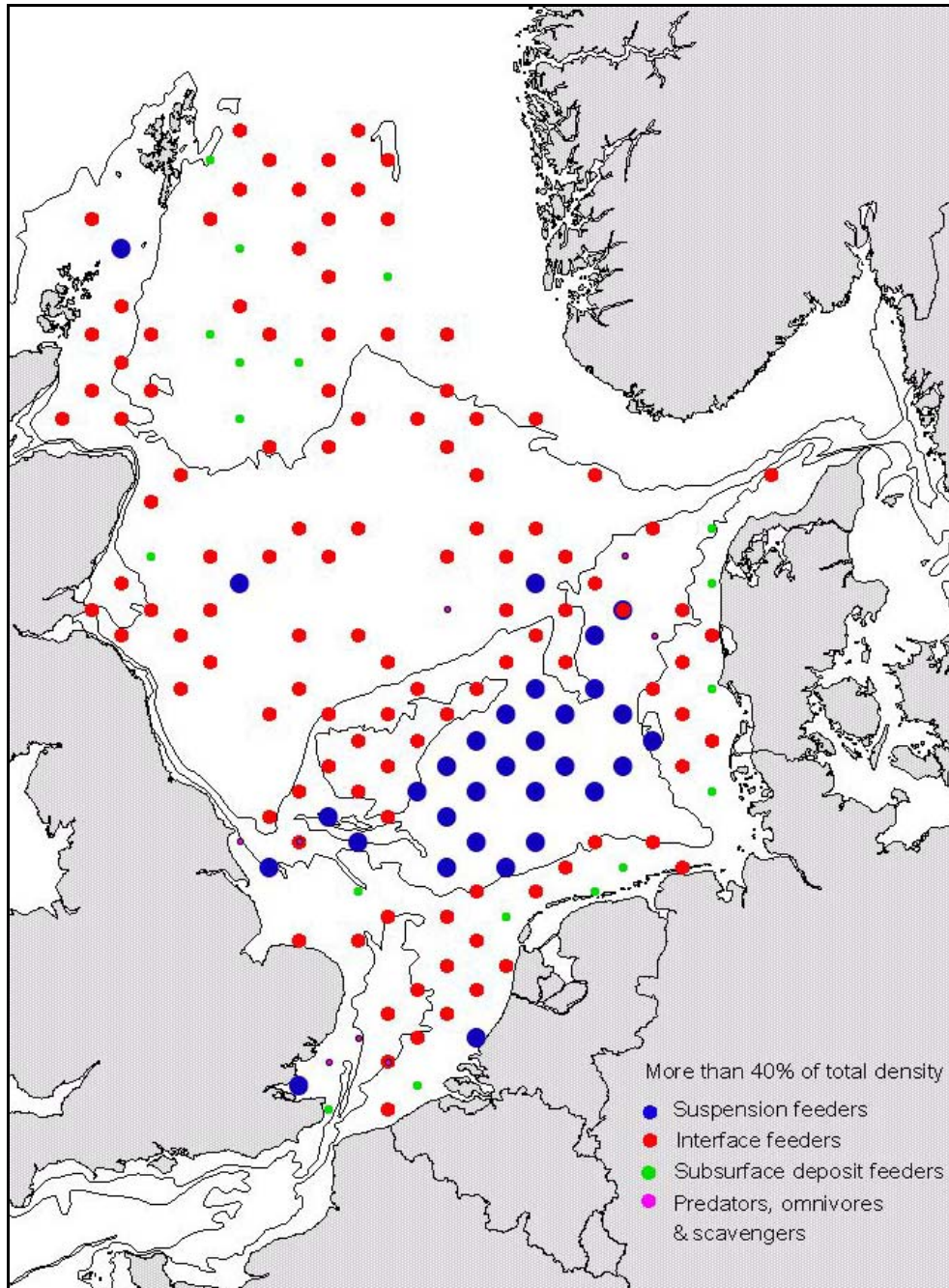


Figure 5.5.1. Distribution of the feeding groups for 1986. The feeding group per station is shown only if larger than 40%. The symbols representing the four different feeding types have different colours as well as different sizes to make a possible overlap visible in the case of two feeding types having more than 40% of the total density at the same station.

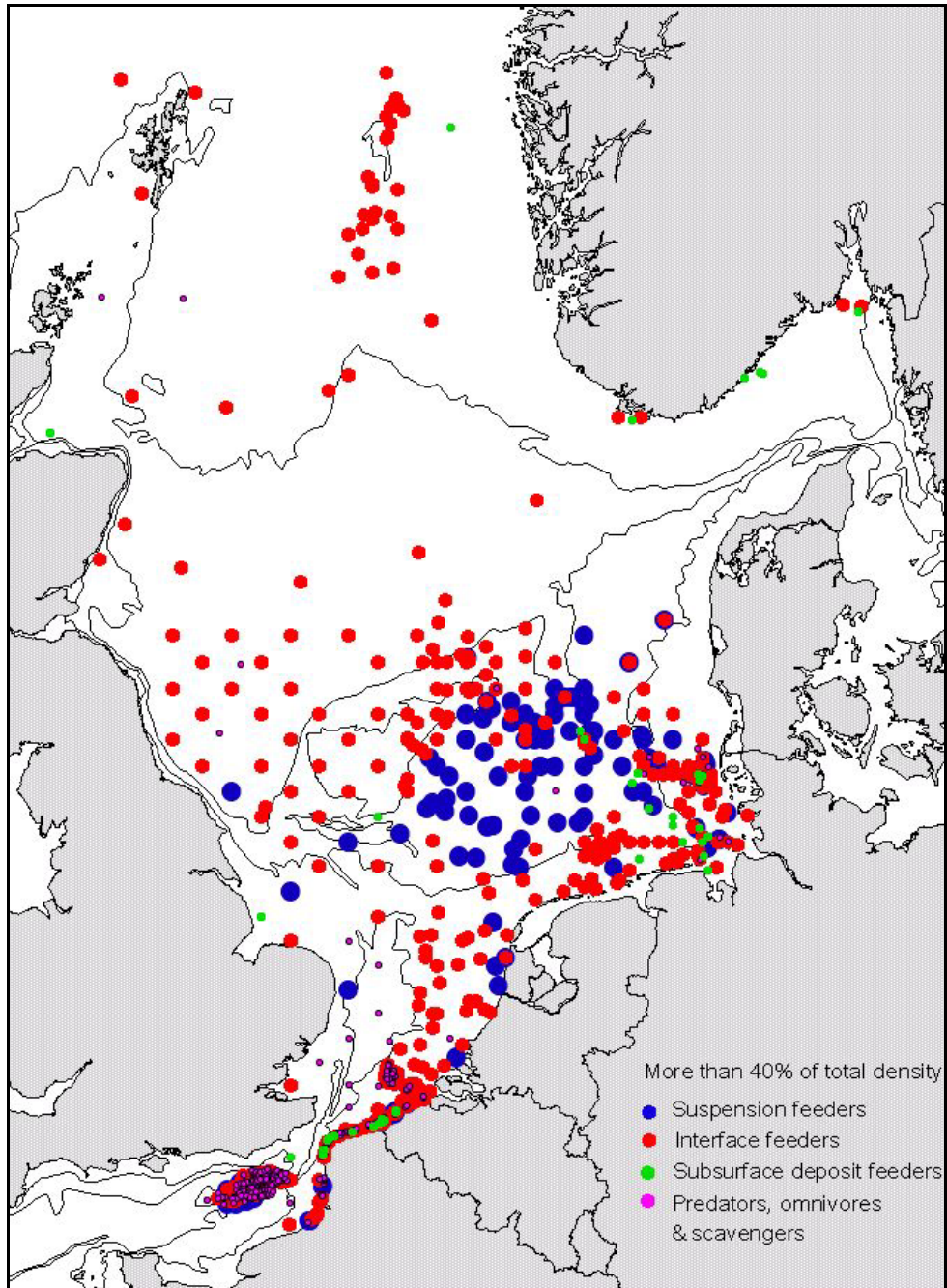


Figure 5.5.2. Distribution of the feeding groups for 2000. The feeding group per station is shown only if larger than 40%. The symbols representing the four different feeding types have different colours as well as different sizes to make a possible overlap visible in the case of two feeding types having more than 40% of the total density at the same station.

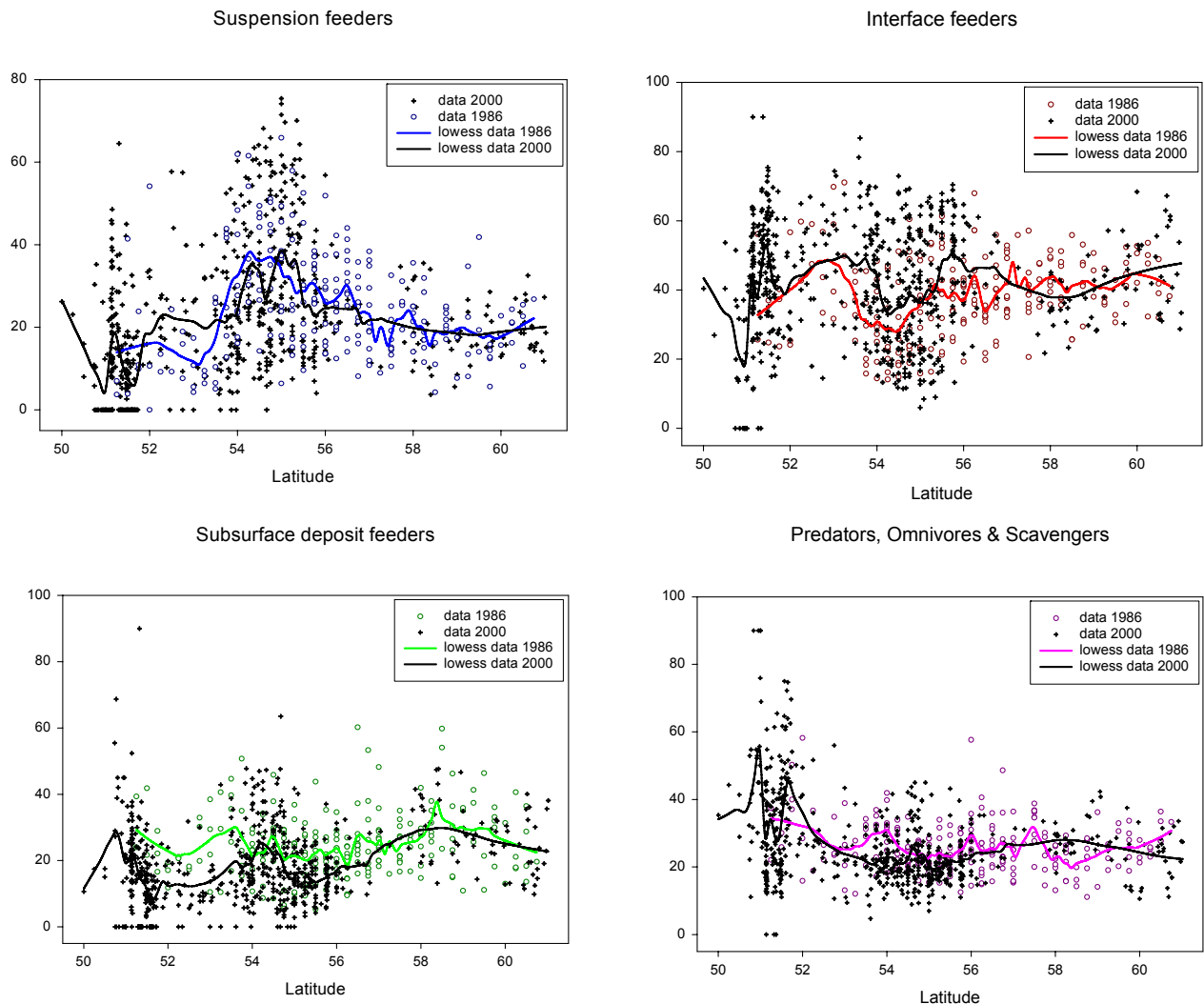


Figure 5.5.3. Latitudinal gradients in proportion of feeding groups (the Y axes are % feeding type). The lowess line is a locally weighted regression line used to smooth and visualize fluctuations.

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5.6 A comparison of indicators reflecting the status of the North Sea benthos

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5.6.1 Introduction

Interest in the use of summary measures (indicators) to quantify the responses of benthic communities to natural and human-induced changes has increased in recent years, especially to meet the requirements of initiatives such as the United Nations Convention on Biological Diversity (1992), the EU Water Framework Directive (European Communities, 2000), the European Marine Strategy (Commission of the European Communities, 2002), and OSPAR (see Lanteris *et al.*, 1999 and ICES, 2004). There exists a wide variety of measures to describe the biological status or changes (Diaz *et al.*, 2004). In their simplest form, the primary variables (typically the total numbers of individuals, species, or biomass) are employed as stand-alone summary measures. Derived univariate measures such as the Hill diversity series (Whittaker, 1972; Hill, 1973; Magurran, 1988) add an additional layer of complexity and typically combine the numerical dominance and species richness components of diversity. Finally, the multimetric methodologies (below) combine a variety of primary or derived univariate measures in one index or, in a more complex form, employ outputs from multivariate analysis.

In Europe, the development of multimetric methodologies has been stimulated by the requirements of the EU Water Framework Directive (Borja *et al.*, 2007). Many countries have used the AZTI Marine Biotic Index (AMBI) combined with other measures of diversity in their multimetric approach (including the UK, Spain, Portugal, Denmark, and Norway; Borja *et al.*, 2007). Other approaches include a method developed by Swedish scientists, based on Hurlbert's index (Rosenberg *et al.*, 2004), while the German approach is based on taxonomic spread (MarBIT; Meyer *et al.*, 2006). The Dutch methodology is based on a hierarchical approach incorporating three levels and aims to evaluate not only the benthos, but also the associated habitats and ecosystem functioning (NIOO-method; Ysebaert and Herman, 2004).

The NSB 1986/2000 datasets provide an opportunity to evaluate a range of commonly used measures over wider geographical and timescales than is normally feasible. The findings are intended to complement assessments elsewhere in this report. This section will investigate which of a range of univariate measures (employed singly or in combination as multimetric derivations) are the most suitable for identifying and quantifying any changes to the North Sea benthos between 1986 and 2000. Our aim was not to exhaustively test the relative efficiency of the wide range of measures currently available (we selected a subset; see Material and methods below). Some of our observations, nevertheless, may be useful in prioritizing the use of selected measures according to the objectives of different investigations, including evaluations of quality status under OSPAR/ICES auspices and the developing European Marine Strategy.

5.6.2 Material and methods

5.6.2.1 Data origin

For all analyses, only the NSB data for the nearest matching stations between 1986 and 2000 were used. Thus, after excluding stations separated by a distance of more than 40 km, 156 matching stations were selected. The assemblages employed in this account were based on those identified from the outcome of cluster analysis after fourth-root transformation as described in Section 5.2.

5.6.2.2 Selection of measures for evaluating indicator utility

Singular (i.e. unimetric) measures of community structure

The following commonly used summary measures were selected: density (N), species richness (S), the Shannon–Wiener index (H'), Simpson's index, and Hurlbert's index (ESn). Density is expressed as individuals per m^2 (ind. m^{-2}), and species richness as the number of species found at a station. The Shannon–Wiener (H') index (Shannon and Weaver, 1949) considers both species richness and the evenness component of diversity. Simpson's index is a more explicit measure of the latter, i.e. the proportional numerical dominance of species in a sample (Simpson, 1949). These two indices are sensitive to sample size while, in contrast, Hurlbert's is less so. This index determines the expected number of species (ES) in a randomly selected subset of individuals, e.g. 50 (hence ES(50)), as used in this section (Hurlbert, 1971).

Combined (multimetric) univariate measures

Only the multimetric approaches m-AMBI (Spain), IQI (UK), DKI (Denmark), NQI (Norway), and BQI (Sweden) will be described and discussed. The methodologies were, at the time of analyses, accepted by these countries as appropriate to meet the needs of the EU Water Framework Directive, though most were still undergoing a process of validation.

The incorporation of the AMBI (AZTI Marine Biotic Index) is common in the multimetric approaches m-AMBI, IQI, DKI, and NQI and, for that reason, we also examined its performance separately. For the AMBI index, benthic species are assigned to five ecological groups ranging from sensitive to highly tolerant of stress. The complementary Biotic Coefficient is calculated according to the percentage of each ecological group within a sample. Further details are described in Borja *et al.* (2000). The other measures employed within the multimetric approaches can differ depending on the formulations (below).

The Spanish methodology (m-AMBI) combines AMBI, species richness, and the Shannon–Wiener index in a multimetric approach based on factor analysis (FA), which was used to determine the Ecological Quality Ratio (EQR) for each of the “typologies”, with their corresponding references (Borja *et al.*, 2004; Bald *et al.*, 2005; Muxika *et al.*, 2007). The outcome of factor analysis was applied to the results of each station and in each sampling period, and virtual reference stations for “high” and “bad” ecological status were considered in the analysis. Data for analysis were $\log(1+x)$ -transformed and standardized by subtracting the mean and dividing by the standard deviation in order to achieve a normal distribution of the data. The FA solution was rotated (using the Varimax rotation method) in order to simplify the interpretation of the results, and the scores of the first three factors were extracted. After obtaining the sampling stations' relative positions (extracted FA scores), the projection of each sampling station in the axis connecting both reference stations was calculated in the new three-dimensional space created by the FA. The Euclidian distance of each projection to the virtual station possessing a “bad” status was measured.

The UK's IQI (Infaunal Quality index) used AMBI, Simpson's Index (as a measure of evenness in the apportioning of individuals among the species), and the number of taxa as parameters. The individual measures have been weighted and combined within the multimetric, in order to best describe the changes in the benthic invertebrate community caused by anthropogenic pressure (A. Miles, UK Environment Agency, pers. comm.).

$$IQI = (((0.38 \times AMBI^{IQI}) + (0.08 \times (1-\lambda')^{IQI}) + (0.54 \times S^{IQI} 0.1)) - 0.4) \div 0.6$$

where $AMBI^{IQI}$ is $(1 - (AMBI BC \div 7)) \div (1 - (AMBI BC \div 7))^{MAX}$; $(1-\lambda')^{IQI}$ is $(1 - \lambda') \div (1 - \lambda')^{MAX}$; and S^{IQI} is $S \div S^{MAX}$. Each metric is normalized to a maximum value expected for that metric. MAX parameters relate to the reference condition for that metric for a specific habitat which, in this exercise, is defined as the maximum value observed in the dataset for each benthic assemblage.

The Danish methodology (DKI) used a combination of the Shannon–Wiener index, AMBI, the number of species, and the number of individuals.

$$DKI = (((1 - (AMBI \div 7)) + (H \div H_{MAX})) \div 2 \times ((1 - (1 \div S)) + (1 - (1 \div N))) \div 2)$$

where H is the Shannon–Wiener index with log base 2; H_{MAX} is the reference value that H can reach in undisturbed conditions; N is the number of individuals; and S is the number of species. The factors N and S only have significant effect when the number of individuals and species are <10.

The Norwegian methodology (NQI) includes AMBI, the number of individuals, the Shannon–Wiener index, and the diversity index SN (combination of number of species and individuals) in its multimetric approach.

$$NQI = 0.5 \times (1 - AMBI_{63} \div 7) + 0.5 \times (SN_{63} \div 2.7) \times (N \div (N + 5))$$

where $SN = \ln(S) \div \ln(\ln(N))$: S number of species and N number of individuals.

In the BQI (Benthic Quality index) of Rosenberg *et al.* (2004), the Hurlbert index was used to categorize benthic species according to their sensitivity to disturbance. They assumed that tolerant species are mainly found in disturbed environments and so mainly occur at stations with low ES(50), whereas sensitive species mainly occur at stations with high ES(50). Based on this conclusion, a species tolerance level ($ES(50)_{0.05}$) was calculated, which reveals the minimum ES(50) value for 5% of each macrofauna population. On this basis, the BQI was proposed:

$$BQI = (\sum_{i=1}^n ((A_i \div \text{tot}A) \times ES50_{0.05i})) \times \log(S+1)$$

where A is the mean relative abundance of species i, and S is the number of species at the station.

Analysis

The changes observed in the selected measures between 1986 and 2000 for the entire North Sea and for the major assemblages were visualized using box plots (without outliers). The Kruskal–Wallis test was used for testing significant differences between the groups, and the Mann–Whitney U-test was used for pairwise testing between the groups.

5.6.3 Results

5.6.3.1 Overall values

There were no spectacular differences in the univariate measures between 1986 and 2000 (Figure 5.6.1). The average of the different diversity indices was slightly lower in 2000 compared with 1986, whereas the density was higher. However, only for ES(50) and density was the overall difference significant (Kruskal–Wallis; $p < 0.01$). The Biotic Coefficient (BC(AMBI)) showed a slight increase (not significant), but not a shift of status.

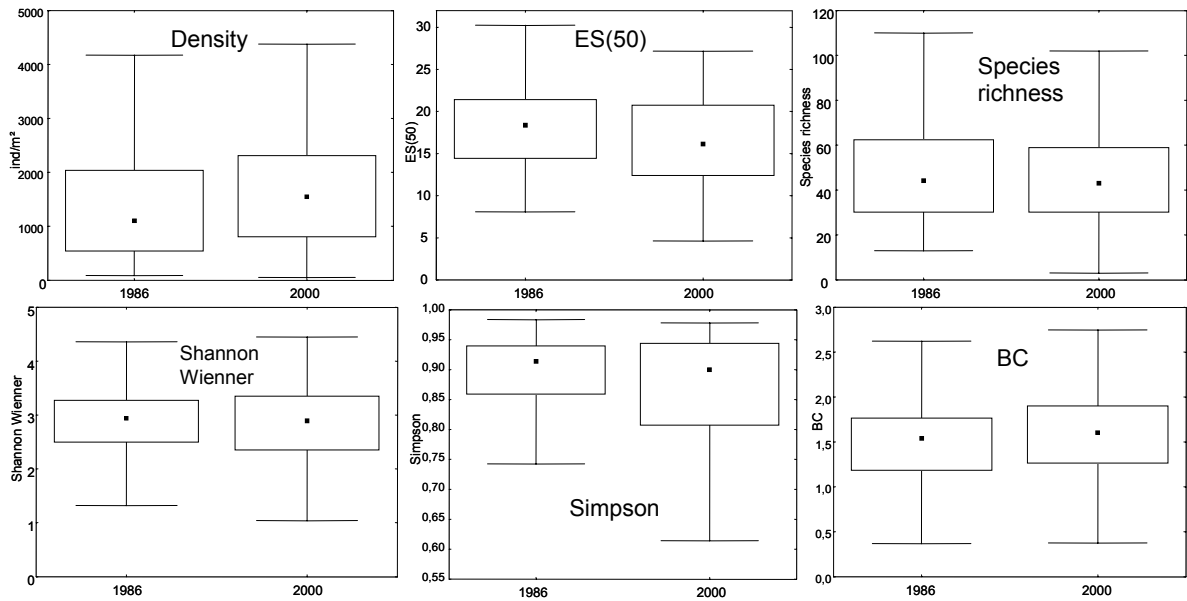


Figure 5.6.1. Box plots comparing different indices between the overall (i.e. North Sea-wide) data of 1986 and 2000.

The comparison between 1986 and 2000 in the multimetric methods demonstrates that all methodologies show a slight decrease of the average value in 2000, but only NQI and BQI give significant differences (Kruskal–Wallis, $p < 0.05$ and $p < 0.01$, respectively; Figure 5.6.2).

Calculations at the level of the entire North Sea may be too robust, i.e. insensitive to changes occurring on smaller spatial scales. Therefore, it is appropriate to examine for any changes at the benthic assemblage level (see Section 5.2).

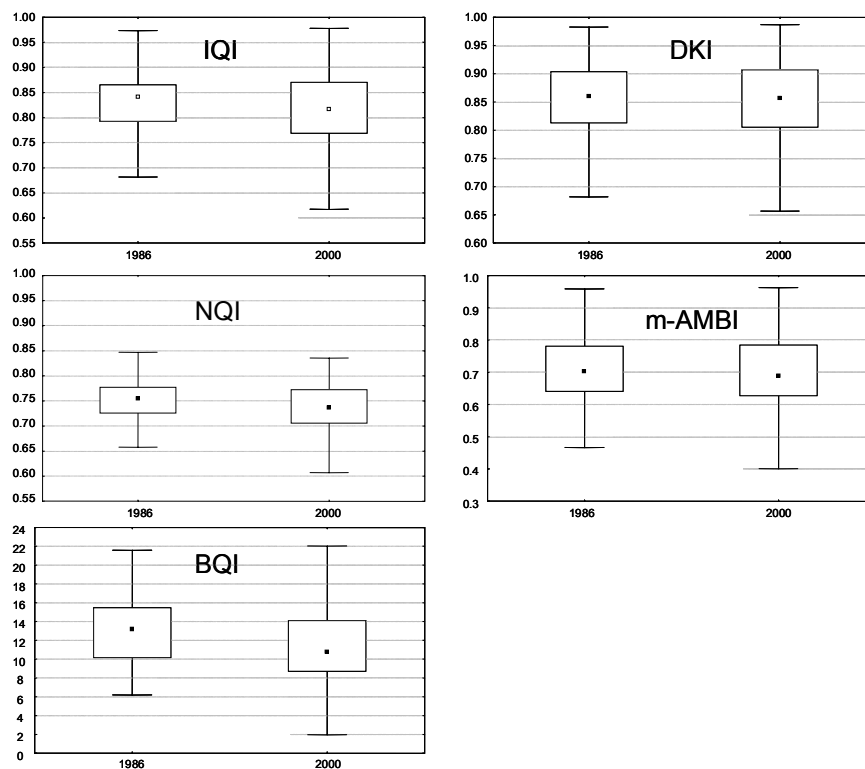


Figure 5.6.2. Box plots comparing different multimetric indices between the overall (i.e. North Sea-wide) data of 1986 and 2000.

5.6.3.2 Benthic assemblages

Density

In most assemblages, the average density was higher in 2000 compared with 1986 (Figure 5.6.3). In the assemblages of the central North Sea and Southern Bight, the density increased (Dogger Bank (D12), Oyster Ground (D2), Southern Bight (F1)), decreased (D13), or remained stable (Southern Bight (F2)). In the northern North Sea at a depth of >100 m, the density decreased or increased, depending on the assemblage type (A, E1, E2, and G). In the assemblages off the English east coast (B, C, E3, and E4), the density increased, as did the assemblage along the German–Danish coast (D11). In the rest of the North Sea, an increase in density was observed between 1986 and 2000. However, the differences were only significant for assemblages B, E2, and G ($p < 0.05$).

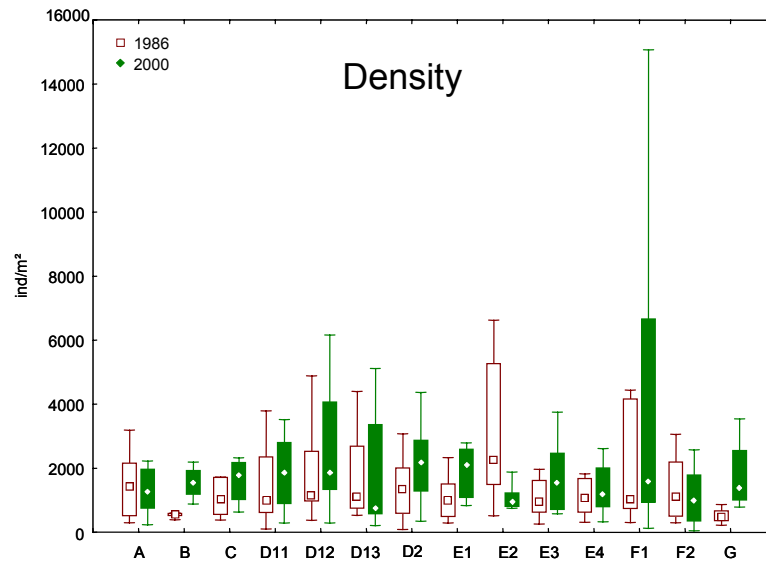


Figure 5.6.3. Box plots comparing density for 1986 (brown) and 2000 (green) across assemblages identified in Section 5.2.

ES(50)

In the Northern assemblages (A, E1, and G), an increase in expected number of species was observed (Figure 5.6.4). The other assemblages elsewhere in the North Sea were characterized by a decrease in expected number of species. Only the assemblage at the Oyster Ground (D2) showed no obvious changes in expected number of species. Overall, only the assemblages C, E4 (English east coast), and D12 (Dogger Bank) showed a significant decrease in expected number of species ($p < 0.05$).

Other measures of diversity (S, Shannon, Simpson)

Box plots for these measures are not shown, but the trends are summarized in Table 5.6.1. The averages were higher in 2000 compared with 1986 for the northern North Sea assemblages (significantly so for A and E1; for assemblage G, only the number of species differed significantly). This trend (though not significant) was also observed for the assemblages situated between 50–100 m depth (B, C, E2, E3, and E4). All the other assemblages showed a similar average value or a decrease for the different diversity measures.

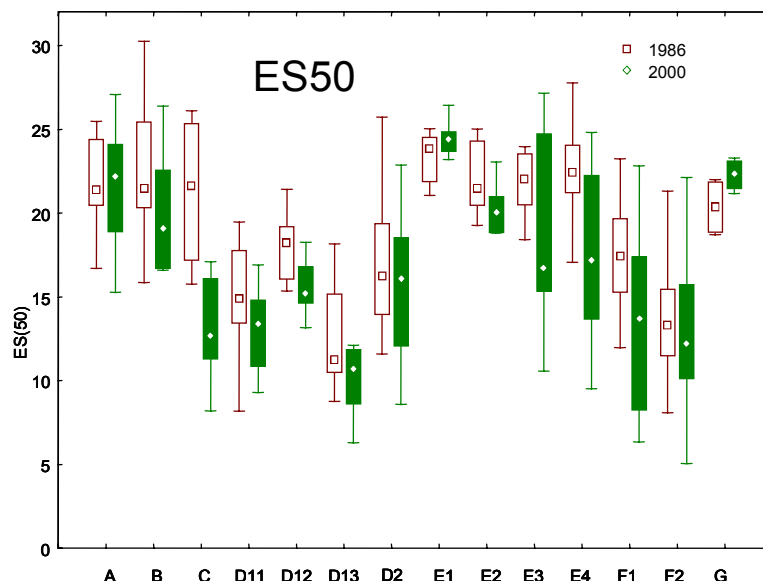


Figure 5.6.4. Box plots comparing ES(50) for 1986 (brown) and 2000 (green) across assemblage types identified in Section 5.2.

Biotic Coefficient (BC(AMBI))

In Figure 5.6.5, the different BC values for each assemblage are shown, and a scattered pattern of increases (more polluted) and decreases (less polluted) is observed, of which none is significant. There was no switch in status for any of the assemblages, and all could be classified as having a slightly polluted status (average $1.2 <BC > 3.3$) according to Borja *et al.* (2000).

The biotic coefficient increased in the northern North Sea assemblages (A, E1, E2, and G) similar to the assemblages of the >50 m depth line (E3 and E4). The assemblages of the Oyster Ground (D2) and the Dogger Bank (D12) showed increases in the BC, while the southern North Sea assemblages F1 and F2 showed a slight decrease.

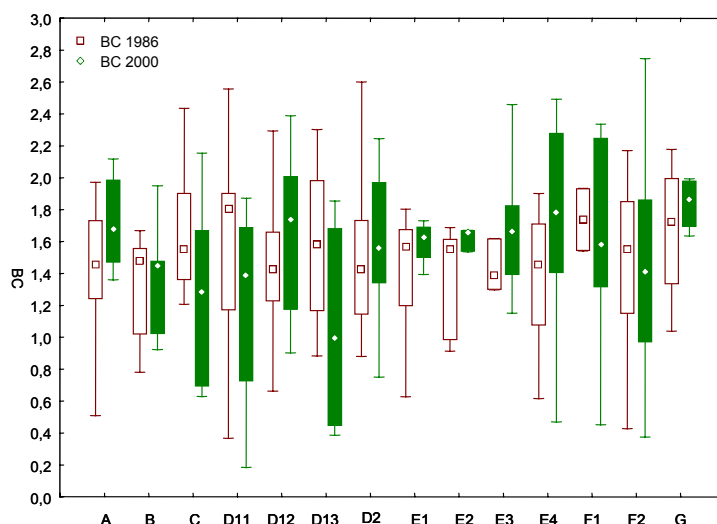


Figure 5.6.5. Box plots comparing the AMBI Biotic Coefficient for 1986 (brown) and 2000 (green) across assemblage types identified in Section 5.2.

m-AMBI, IQI, NQI, DKI

These multimetric indices are described together because most employ the same measures, and they are strongly correlated with each other (Borja *et al.*, 2007).

A comparison of the different multimetric indices between 1986 and 2000 highlighted mostly a decrease of the ecological quality (EcoQ) score in the central and southern North Sea, whereas the northern North Sea assemblages showed an increase in the EcoQ score (Figure 5.6.6). The NQI showed less variability compared with the others. Some of the observed changes in the assemblages between 1986 and 2000 were significant. The decrease in the Southern Bight assemblage F2 was significant for all indices except the IQI, which was the same for the Northern assemblages (A and E1). The decrease in the Dogger Bank assemblage D12 was only significant for the NQI and IQI. The increase in the English east coast assemblage B was significant for the DKI and m-AMBI. The m-AMBI also showed significant differences for assemblages D11 (decrease) and G (increase).

The status of the different assemblages according to the Danish methodology was high (boundary between high/good = 0.72), whereas according to the m-AMBI, the status was good for all assemblages ($0.55 < \text{good} < 0.85$). According to the IQI classification, the status of most assemblages was high (high/good = 0.8). The EcoQ values calculated with the NQI revealed that the status of the assemblages fluctuated around the high/good boundary (0.75). A difference in status between high and good between 1986 and 2000 was only observed for some assemblages with the NQI.

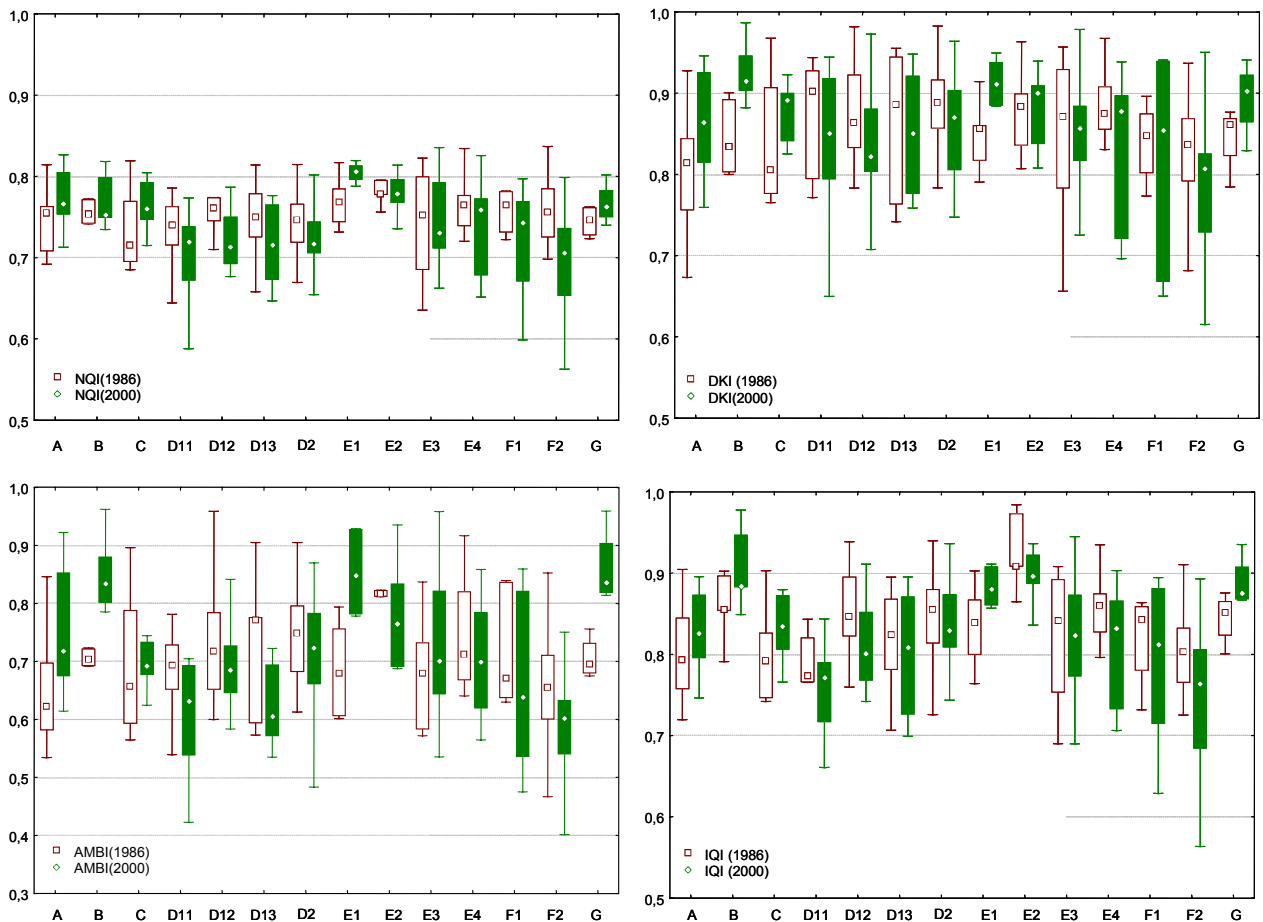


Figure 5.6.6. Box plots comparing m-AMBI, IQI, NQI, and DKI for 1986 (brown) and 2000 (green) across assemblage types identified in Section 5.2.

BQI

The Swedish index, which differs in formulation from the AMBI-related indices, showed a contrasting trend for some assemblages. In the Northern assemblages A and G and in the

English east coast assemblage B, the average BQI value decreased (Figure 5.6.7). The differences were significant for assemblages B, D11, D12, D2, and F2.

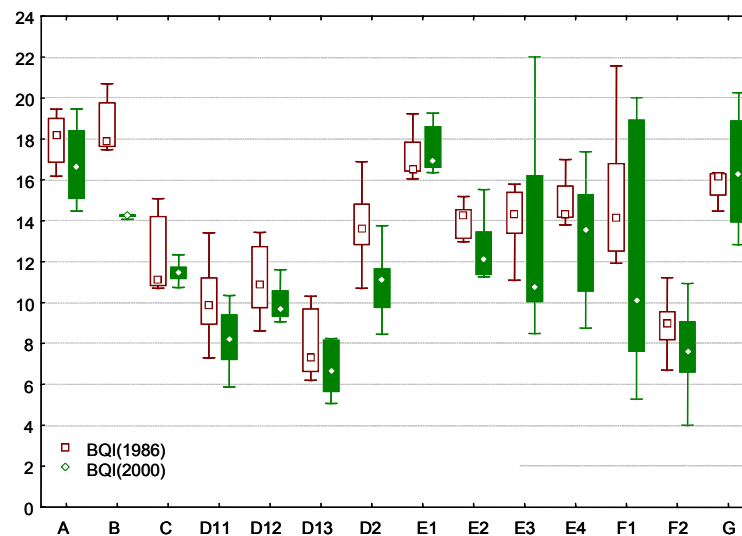


Figure 5.6.7. Box plots comparing the BQI of 1986 (brown) and 2000 (green) across the assemblage types identified in Section 5.2.

5.6.4 Discussion

The evaluation of changes between 1986 and 2000, based on a variety of indicator measures, shows that several factors can influence the observed patterns. For example, sampling effort, taxonomic precision, and variable distances between matched (1986/2000) stations could confound the identification of trends in quality status. We conclude that the observed changes in the northern North Sea were mainly caused by improved taxonomic sufficiency in 2000. For 1986, the available data for each station were pooled across variable numbers of replicates and/or variable surface areas sampled depending on the device used (see Section 3 and Künitzer *et al.*, 1992). Similar considerations with the potential to affect the interpretation of indicator values apply to the 2000 survey. For example, a 0.07 m² corer was used in Dutch waters, while a 0.25 m² corer was used by FRS (Scotland) for sampling in parts of the northern North Sea and at some offshore stations extending south to the German Bight. Differences in surface area (if not in efficiencies of the sampling gear) may be compensated for by pooling replicates and, for the 2000 dataset, a degree of parity was achieved in this way. However, it should be noted that the majority of the stations sampled in the southern North Sea using a large corer did not contribute to the reduced dataset in 1986 and 2000, as closer matches were found with those sampled by grab.

Despite the potentially confounding influences of sampling and analytical differences between 1986 and 2000, we consider that the present evaluation of selected indicator measures served a useful purpose, especially in light of the need by the developing European Marine Strategy for information on the relative utility of indicators of status and change, along with reference settings for the North Sea benthos, i.e. on the scale of whole sea areas. In this respect, the data from the North Sea Benthos surveys of 1986 and 2000 provide a valuable resource for testing.

Table 5.6.1. Summary of statistical comparisons between selected measures (1986 and 2000). Key: + indicates an increase in value; = indicates equal; – indicates a decrease in value. Significant differences (Mann–Whitney U-test) appear in parentheses. An increase in the value of the biotic coefficient (BC(AMBI)) signifies a decrease in status. This is in contrast to the other multimetric methodologies, where an increase in values signifies an increase in status.

| | UNIMETRIC | | | | | MULTIMETRIC | | | | | |
|-----|-----------|--------|-----|---------|---------|-------------|--------|-----|-----|-----|-----|
| | DENSITY | ES(50) | S | SHANNON | SIMPSON | BC(AMBI) | M-AMBI | IQI | NQI | DKI | BQI |
| A | – | + | (+) | (+) | (+) | + | (+) | + | (+) | (+) | – |
| B | (+) | – | + | (+) | + | = | (+) | + | = | (+) | (–) |
| C | + | (–) | + | = | – | – | + | + | + | + | + |
| D11 | + | – | – | – | – | – | (–) | = | – | – | (–) |
| D12 | + | (–) | = | – | – | + | – | (–) | (–) | – | (–) |
| D13 | – | – | – | – | – | – | – | – | – | – | – |
| D2 | (+) | = | – | – | (–) | + | – | – | – | – | (–) |
| E1 | + | + | (+) | (+) | (+) | + | (+) | + | (+) | (+) | + |
| E2 | – | – | – | + | + | + | – | – | = | + | – |
| E3 | + | – | = | + | = | + | + | – | – | – | – |
| E4 | + | (–) | = | + | + | + | – | – | – | = | – |
| F1 | + | – | – | – | – | – | – | – | – | = | – |
| F2 | = | – | (–) | – | – | – | (–) | (–) | (–) | – | (–) |
| G | (+) | + | (+) | + | + | + | (+) | + | + | + | = |

On a “global” scale (i.e. the whole North Sea), the different measures gave no clear pattern (only the increase of density and decrease of ES(50) and decreases of the multimetric indices NQI and BQI were significantly different), but it is recognized that such an approach may mask considerable regional or local variability. Therefore, in order to facilitate smaller scale evaluation, the benthic assemblages defined in Section 5.2 were employed and, at this level, trends were observed for some assemblages, depending on the measures employed (Table 5.6.1).

The Northern assemblages (A, E1, and G) showed mainly an increase in diversity. This was reflected in a variety of measures, including most of the multimetric indices. According to the classification schemes associated with the latter indices, this implies an improvement in quality status. However, we consider that this finding may be explained largely by sampling and analytical factors (see above).

The assemblages located between the 50 m and 100 m depth contours showed a variable pattern. For example, assemblage E2 in the north-central North Sea showed decreases in density, ES(50), and number of species and an increase in the Shannon–Wiener and Simpson diversity indices. This resulted in a decrease in the multimetric indices (except DKI). Assemblages B and C along the English east coast generally showed a marginally enhanced quality status according to values of the multimetric indices, which could be linked to increases of the diversity indices, except ES(50). (Note that the large FRS core samples did not contribute to the reduced 2000 data for the English east coast because all stations were exactly matched with 1986 stations and sampled by 0.1 m² Day or Hamon grabs). In the central North Sea (E3 and E4), the univariate indices gave a scattered pattern, whereas the multimetric indices mainly showed a decrease, although none was significant.

Assemblage D12 at the Dogger Bank showed a decrease in most measures, except density. Three of the five multimetric indices showed a significant decrease in values. This is consistent with other observations on changes at the Dogger Bank, which could be linked to changes in the hydroclimate under the influence of the North Atlantic Oscillation, resulting in enhanced current velocities, a limitation of organic input, and a more sandy environment in the vicinity (see Section 5.2 for more details). However, the magnitude of the observed

decreases in values was relatively small and did not signify a change of the ecological status according to the classification systems employed. These factors may also explain the observed changes in indices for assemblage D2 (Oyster Ground) and D13 (spatially scattered in the central North Sea), where a decrease in values was detected, although these were not significant.

Changes to the status of assemblages of the Southern Bight of the North Sea (F1 and F2) and the eastern North Sea (German–Danish coast, D11) were similarly linked to NAO-induced changes affecting the diversity and species composition in those areas (see Section 5.2 for more details). The multimetric values decreased, which might suggest a decline in the ecological quality of those areas, especially for assemblage F2 (four of five indices were significantly lower in 2000 than in 1986). However, the decreases were again relatively small and insufficient to indicate a switch in ecological status according to the classification systems employed.

We conclude that no spectacular differences in the status of the North Sea benthos were observed between 1986 and 2000, especially when evaluated on a wide geographical scale. However, differences on smaller scales (i.e. within certain assemblages) and of relatively small magnitude were detected between 1986 and 2000. Most of the existing ecological evaluation methodologies give an indication of changes, but they do not always react in the same way. The four multimetric approaches based on AMBI showed mostly the same pattern and were also strongly correlated ($R > 0.732$) with each other (Table 5.6.2). This confirms the findings of the intercalibration exercise in Borja *et al.* (2000). The BQI, which is based on a different approach of evaluating the sensitivity of species, was also significantly correlated, but with a much lower R value (0.233–0.406).

Table 5.6.2. Spearman rank correlation values between the different indices. The highlighted values were not significant ($p > 0.05$).

| | IQI | DKI | NQI | m-AMBI | BQI | BC | HI | SIMP | ES(50) |
|--------|--------|--------|--------|--------|-------|-------|-------|-------|--------|
| DKI | 0.835 | | | | | | | | |
| NQI | 0.860 | 0.787 | | | | | | | |
| m-AMBI | 0.817 | 0.821 | 0.732 | | | | | | |
| BQI | 0.406 | 0.233 | 0.402 | 0.391 | | | | | |
| BC | -0.179 | -0.140 | -0.172 | 0.099 | 0.078 | | | | |
| hi | 0.346 | 0.361 | 0.377 | 0.532 | 0.228 | 0.156 | | | |
| Simp | 0.284 | 0.345 | 0.308 | 0.447 | 0.187 | 0.078 | 0.939 | | |
| ES(50) | 0.184 | 0.041 | 0.182 | 0.155 | 0.597 | 0.052 | 0.497 | 0.484 | |
| S | 0.389 | 0.281 | 0.429 | 0.571 | 0.242 | 0.229 | 0.694 | 0.482 | 0.315 |

These multimetric indices were based on different combinations of univariate measures, and it is to be expected that they would be significantly correlated with these when tested. This is true for most indices (Table 5.6.2), but some curiosities require explanation. For instance, the m-AMBI showed no correlation with the Biotic Coefficient (BC(AMBI)), but was relatively strongly correlated with the Shannon–Wiener index and the number of species. This means that, for this dataset, the m-AMBI evaluation is mainly weighted by the changes in the diversity indices. Also, concerning the other multimetric indices, the correlation was strongest with the diversity indices and lowest with the Biotic Coefficient (BC(AMBI)). This is because most of the observed changes were not caused by changes in the occurrence of sensitive and tolerant species (BC changes were never significant), but rather by diversity changes. In Sections 5.2 and 5.4, clear shifts in the occurrence and dominance of species were detected in some areas and assemblages, but were not reflected by the AMBI. In the BQI, based on expected number of species (ES(50)), both measures correlated strongly, so shifts were better detected.

5.6.5 Conclusions

The results of an overall comparison between 1986 and 2000 (i.e. at the level of the entire North Sea) showed that:

- Density increased and ES(50) decreased;
- Two (of five) multimetric indices showed a significant decline;
- Other measures showed no significant difference;
- There was no indication of a change in quality status, according to the classification schemes accompanying the multimetric methods.

The results of a comparison between 1986 and 2000 at the assemblage level showed that:

- Northern assemblages (A, E1, and G1) showed a trend opposite to that of others for all measures, which could be explained largely by an increase in taxonomic sufficiency in 2000. For example, multimetric indices were generally higher, though not of a magnitude to indicate a change in quality status according to the accompanying classification schemes.
- Excluding Northern assemblages, the frequency of occurrence of negative changes in indicator measures between 1986 and 2000 was at least twice as high as for positive changes. However, only about 20% of the differences were significant (16 negative and five positive).
- On its own, the Biotic Coefficient (BC(AMBI)) detected no significant differences. There was no evidence of change in the dominance of the species groups employed in the derivation of this index between years.
- The selected multimetric indices generally showed the same trend, despite the different methodologies employed in their calculation.
- Two assemblages, D12 (Dogger Bank) and F2 (Southern Bight) showed a significant decrease in the Ecological Quality Ratio for most multimetric evaluation methods, but this did not signify a change in status and, overall, assemblages were classified as either “good” or “high”.

We conclude that there was no evidence of spectacular differences between years. From an appraisal of the combined North Sea-wide datasets for 1986 and 2000, there was evidence of a marginal though significant decrease in ES(50) values, accompanied by an increase in densities. The exercise demonstrated that it is important to evaluate the ecological status of the North Sea for each assemblage/habitat type separately to enhance insights into the nature and causes of any changes. The 1986 and 2000 North Sea benthos surveys provide a valuable source of data for comparisons of the utility of different measures in determining ecological quality status across different spatial scales and in providing a wider benchmark for the interpretation of the outcomes of local surveys.

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5.7 Benthic community studies over relevant timescales

H. L. Rees, E. Rachor, J. A. Craeymeersch, I. Kröncke, G. C. A. Duineveld, H. Reiss, and H. Rumohr

5.7.1 Introduction

In this compilation, we have selected studies of temporal trends covering all or most of the period between 1986 and 2000, especially those of a regular rather than intermittent nature. Collectively, these have the potential to throw light on broader scale influences on the macrobenthic communities of the North Sea and hence may contribute to explanations for any differences between the two ICES surveys.

5.7.2 Community studies

Scottish waters

No published studies on long-term annual trends in marine macrobenthic communities were located for the 1986–2000 period. However, an annual monitoring programme at alternating (summer/winter) sewage-sludge disposal sites off the River Forth, eastern Scotland, provided summary data on trends across 9–13 stations sampled with a 0.1 m² van Veen grab, employing a 0.5 mm mesh sieve to extract the fauna (Heaney *et al.*, 2000). Surveys were typically conducted in June/July each year. The stations, at depths of 50–70 m, were located at and peripheral to the disposal sites and only marginal effects arising from the activity were identified over the disposal period, which ended in 1998. Therefore, the overall trends may reasonably be expected to represent an integral of the effects of predominantly natural forces. These trends appear to indicate relative stability at both locations (Figure 5.7.1).

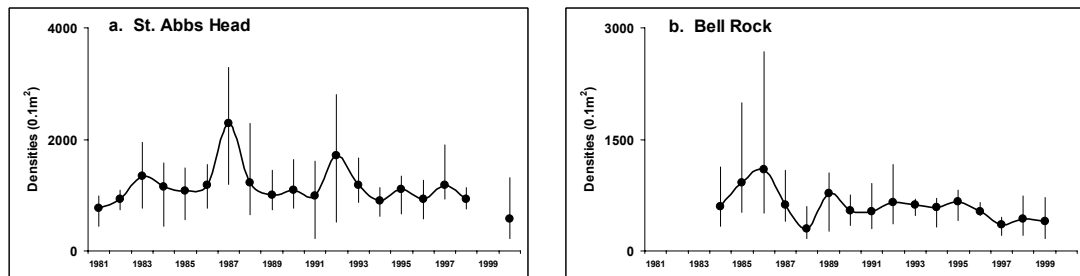


Figure 5.7.1. Annual trends in densities (means and ranges) at two locations off the River Forth, eastern Scotland (after Heaney *et al.*, 2000).

English waters

Rees *et al.* (2006) studied long-term changes in benthic communities off the River Tyne (northeast England). Three stations at approximately 50 m depth were sampled annually with a 0.1 m² Day grab in May/June, and a 0.5 mm mesh sieve was used to extract the fauna (Figure 5.7.2). Relationships with winter values of the NAO Index (year 1) indicated that the densities and variety of taxa tended to be lower in response to warmer winters characterized by westerly airflows, which were a common feature of weather patterns in the 1990s. This would appear to be logical for the responses of deeper water benthic assemblages comprising many taxa with a more northerly (“cold water”) distribution, in the absence of a compensatory increase in those with more southerly associations.

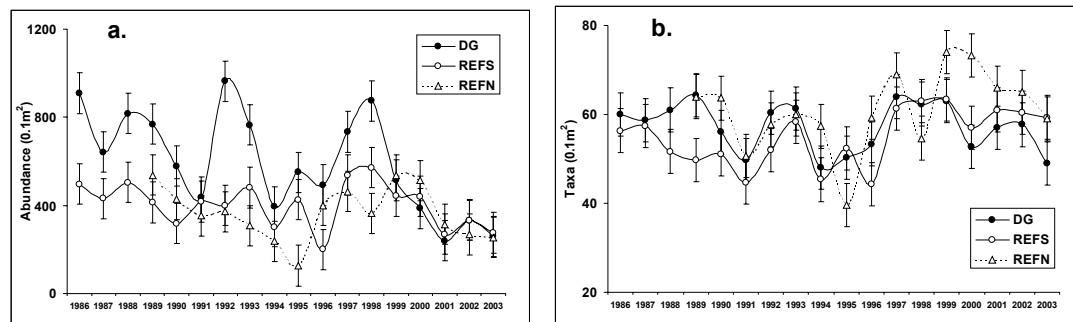


Figure 5.7.2. Changes in (a) densities and (b) numbers of taxa at muddy sand stations off the River Tyne, northeast England (means with 95% LSDs). Elevated densities at the DG station can be ascribed to the influence of sewage-sludge disposal, which ceased after 1998 (after Rees *et al.*, 2006).

Long-term temporal changes and their causes have been well documented by others in this area (e.g. Clark and Frid, 2001). Buchanan (1993) identified a significant positive relationship between temporal changes in the Phytoplankton Colour Index and the densities of the benthic macrofauna at a monitoring station off the English northeast coast, which was most plausibly expressed by offsetting values to the year prior to benthic sampling. This arose from a consideration both of the timing of food inputs from sedimenting phytoplankton and their influence on the survivorship or fecundity of benthic populations, and of the extended time interval leading to recruitment of juveniles to the (0.5 mm mesh) sieve.

Warwick *et al.* (2002) reported on long-term temporal changes in the benthos of soft sediments in Tees Bay (at ca. 20 m depth) and the Tees estuary, sampled annually or more frequently with a 0.1 m² Smith–McIntyre, then Day grab, between 1973 and 1996 (1999 for the estuary stations). A 1 mm mesh sieve was used to extract the fauna. Changes in densities, species numbers, and diversity are shown in Figure 5.7.3. Accompanying serial changes in community composition in Tees Bay over time, there was a major shift between 1986 and 1988, with generally greater interannual variability after 1987. This shift appeared to correlate with changes in other North Sea ecosystem components in this period, e.g. the zooplankton, which had been documented elsewhere (see also Section 4.1). In the River Tees, a major shift in community composition in 1994 coincided with the construction of a barrage. Subsequent increases in densities and numbers of species could be ascribed to local improvements in environmental quality or more saline conditions.

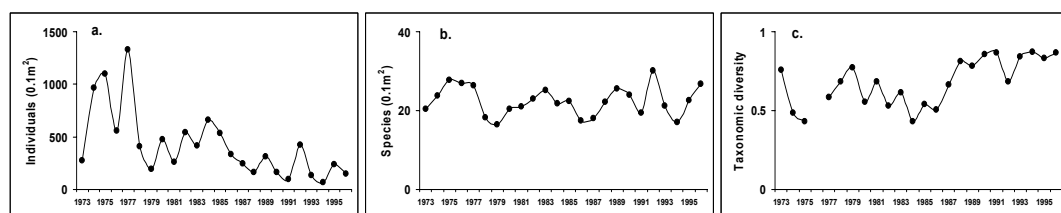


Figure 5.7.3. Trends in (a) macrofaunal densities, (b) numbers of species, and (c) taxonomic diversity averaged over six stations sampled annually in September in Tees Bay, northeast England (after Warwick *et al.*, 2002).

Central North Sea/Dogger Bank

Wieking and Kröncke (2001) revisited 28 stations at the Dogger Bank area in May 1996–1998, which were previously sampled in May 1985–1987, employing a 0.2 m² van Veen grab and a 1 mm mesh sieve to extract the fauna. Compared with the 1980s, abundances of “southern” and interface-feeding species increased in the 1990s on top and in the southern parts of the bank, whereas abundances of “northern” species decreased. Along the northern slope of the Dogger Bank, abundances and total number of species, which prefer coarser

sediment, increased in the 1990s as well as diversity of feeding types and total number of northern species, whereas abundances of species preferring fine sand and interface-feeding species decreased. The changes could be linked to changes in the NAO Index (see also Section 5.2).

French waters

Long-term monitoring has been conducted at seasonal intervals since the 1970s at coastal soft-sediment locations in the vicinity of a nuclear power plant at Gravelines, northern France (Ghertsov *et al.*, 2000). Replicate samples were collected with a 0.1 m² van Veen grab, and a 1 mm mesh sieve was used to extract the macrofauna. Strong interannual fluctuations in densities and biomass were accounted for by varying recruitment success, mainly of the structuring species *Janice conchilega* and *Abra alba* and, in 1991, the introduced American jackknife clam *Ensis directus*. These fluctuations could be partly explained by climatic influences, especially winter temperature regimes (Fromentin *et al.*, 1997). For example, the occurrence of high densities of *Abra alba* was associated with mild winters and low densities with cold winters (Fromentin and Ibanez, 1994).

Belgian waters

No published studies of long-term trends spanning the present period of interest were identified, though evaluations over shorter timescales have recently been reported, e.g. by Van Hoey *et al.* (2004, 2005). The spatial distribution of macrobenthic communities of the Belgian continental shelf have recently been described by Van Hoey *et al.* (2004) and Degraer *et al.* (2006).

Dutch waters

Daan and Mulder (2006) reported on the outcome of annual (spring) surveys of the Dutch continental shelf (DCS) conducted since 1986, employing a stratified, random-sampling design. The strata were defined as “coastal”, “offshore”, “Oyster Ground”, and “Dogger Bank”. Stations were sampled with a 0.068 m² boxcore, and a 1 mm mesh sieve was used for the extraction of the fauna. The data, therefore, provide a valuable perspective on the status of benthic communities inhabiting soft sediments in the southern North Sea in the period between the 1986 and 2000 surveys. Total densities, numbers of species, and AFDW biomass of the large-scale assemblages on the DCS have remained relatively stable during this period (exemplified in Figure 5.7.4 by trends at the “Oyster Ground” stratum). Within some assemblages, marked local changes of the species dominance have been observed. It should be noted that a more detailed examination of causal influences was beyond the scope of this annual monitoring report. Nevertheless, fishing effects and climate- (weather) related changes in sediment composition are considered as the most likely causes for the observed changes.

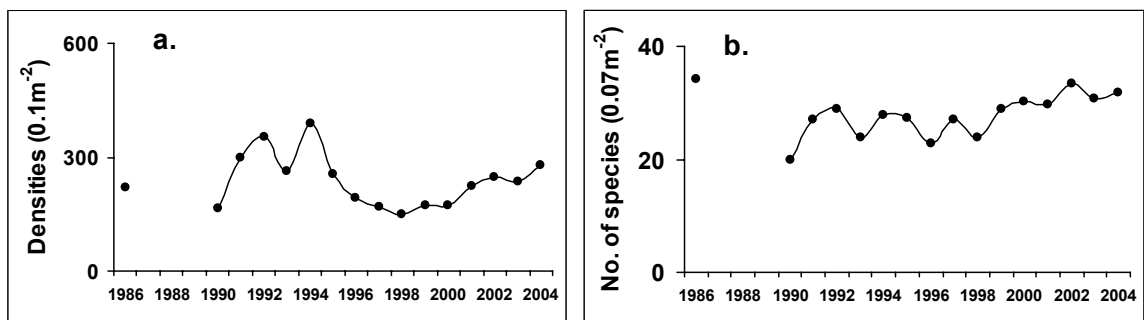


Figure 5.7.4. Temporal trends in mean (a) densities and (b) numbers of species for the “Oyster Ground” stratum, Dutch continental shelf (after Daan and Mulder, 2006).

A recent analysis by Wijnhoven *et al.* (2006) of long-term trends in the macrobenthos of soft sediments of the Dutch Voordelta sampled by boxcorer and van Veen grab, and employing a 1 mm mesh sieve, identified significant increases in densities and biomass (but not diversity), with minima encountered between 1995 and 1997 (Figure 5.7.5).

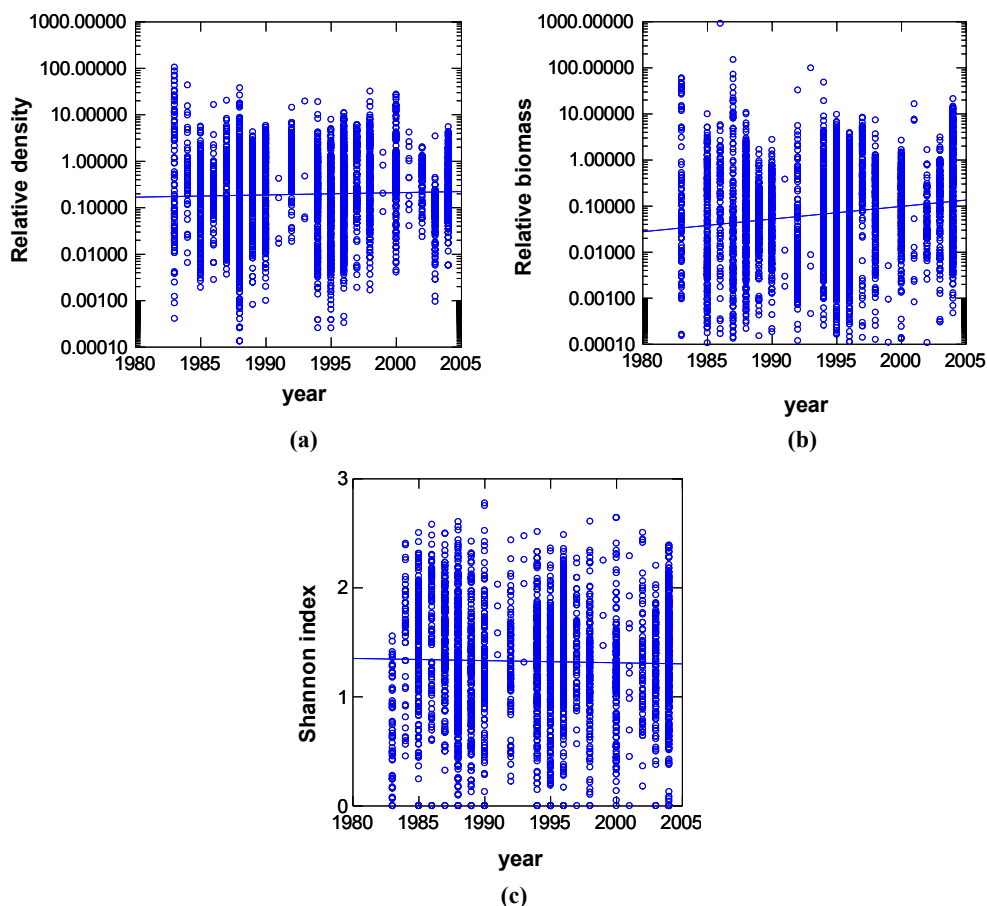


Figure 5.7.5. Long-term annual trends in (a) densities, (b) biomass, and (c) diversity of the subtidal macrofauna of the Voordelta, southwest Holland (from Wijnhoven *et al.*, 2006).

Wadden Sea

The Dutch, German, and Danish Wadden Sea areas have been intensively studied over many years, both in relation to commercial fisheries and the consequences of other human activities (e.g. Essink *et al.*, 2005). Because of regional variability in the nature and extent of these activities, it is difficult to identify trends in ecological data that might have wider interpretational value for the present North Sea benthos survey. Essink (2005) concluded that, in general, the status of the Wadden Sea ecosystem continues to reflect an early stage of eutrophication, though recent declines in nutrient inputs do not suggest a worsening trend. The system is also clearly responsive to climatic variability, but manifestations may differ regionally (see, e.g. Strasser *et al.* (2003) and Craeymeersch and Perdon (2006) for the bivalve *Macoma*). Since the 1970s, the biomass of intertidal polychaete worms has generally shown a rising trend, while the biomass of bivalve molluscs has fluctuated, with enhanced recruitment typically following cold winters (Essink *et al.*, 2006; see also Strasser *et al.*, 2003).

German Bight

In addition to natural influences, changes in the benthos of the German Bight have been related to eutrophication (Rachor, 1990) and the negative effects of bottom trawling (de Groot and Lindeboom, 1994; Lindeboom and de Groot, 1998). Long-term macro-zoobenthos variability has been studied by Rachor and Schroeder at four locations in different offshore

communities since 1969. Changes in densities and numbers of species are shown in Figure 5.7.6. Samples were collected in spring using a 0.1 m² van Veen grab supplemented in earlier years by a 0.017 m² Reineck boxcorer. A 0.5 mm mesh sieve was used to extract the macrofauna.

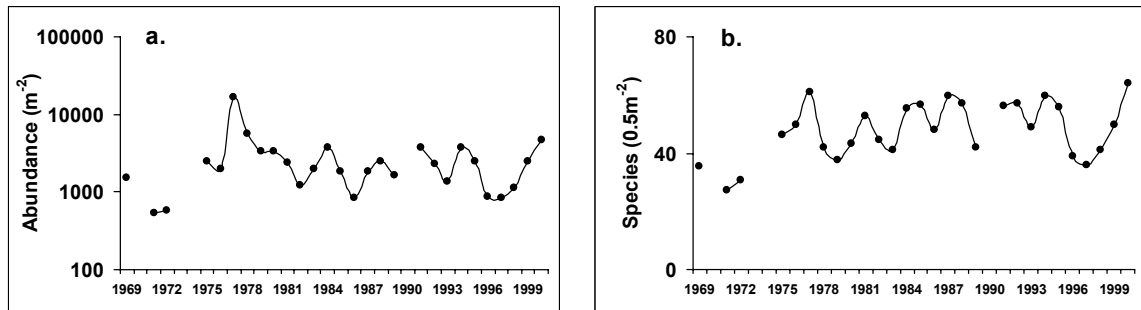


Figure 5.7.6. Long-term annual trends in (a) densities and (b) numbers of species of the macrofauna at a silty sand station at 36 m depth in the German Bight (after Schroeder, 2005).

Evaluations by Schroeder (2005) show clear correlations between faunal trends and climatic conditions, with dramatic changes seen mainly after extremely cold winters, especially in 1979, 1986, and 1996. For example, at the silty sand station in Figure 5.7.6, there was a significant positive correlation between the numbers of species present and the annual and winter NAO Index for the previous year, and a significant negative correlation with Elbe River run-off with a two-year time lag. Also, the relationship between nutrient concentrations (as an indicator of eutrophication) and zoobenthos dynamics is well established for the inner German Bight. Some shifts in the distribution patterns of species such as *Amphiura brachiata* and *Nucula nucleus*, as well as shifts in community boundaries (especially the mud-inhabiting *Nucula nitidosa* community) can be understood as consequences of warming and changes in circulation and eutrophication patterns.

Reiss *et al.* (2006) similarly identified significant negative responses of the benthos at two subtidal stations in the German Bight to the cold winter of 1995/1996, which was followed by recovery of most species after 1–2 years. However, a pronounced effect was not evident at two offshore stations on the Oyster Ground and Dogger Bank, respectively, which changed more gradually over time. The latter stations appeared to be less exposed to temperature extremes than those inshore, and may be responding to more subtle directional influences.

Franke and Gutow (2004) consider that a shift in the climate of the North Sea towards more oceanic conditions may be an important factor explaining long-term trends in the macrofauna of hard-bottom areas around Helgoland. Many of the recent records of new species occurrences in the area are of southern (oceanic) species, which may indicate a warming trend.

Kröncke *et al.* (1998, 2001) employed a 0.2 m² van Veen grab and a 0.63 mm mesh sieve to sample the fauna at shallow-water stations (12–20 m depth) off the island of Norderney (Figure 5.7.7). The macrofauna communities were severely affected by cold winters, but mild meteorological conditions during winter resulted in an increase in total biomass, as well as in abundance and species numbers since 1989. The results show that abundance, species number, and biomass in the second quarter of the year correlated with the NAO Index. The mediator between the NAO and the benthos was the sea surface temperature (SST) in late winter and early spring. This appears to be a result of the ecological preferences of certain species in this area, resulting in lower mortality but higher production and reproduction in mild winters, in combination with an earlier spring phytoplankton bloom and probable synergistic effects between climate and eutrophication.

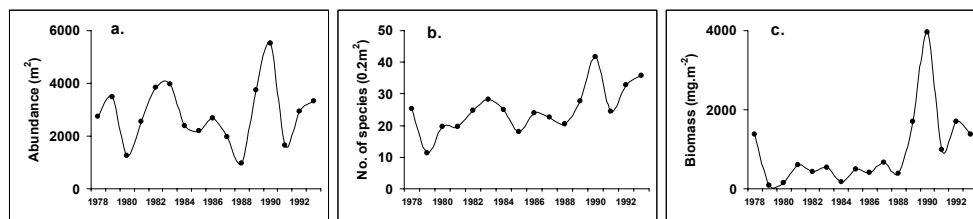


Figure 5.7.7. Annual (April–June) trends in (a) macrofaunal densities, (b) number of species, and (c) AFDW biomass off Norderney, German North Sea coast (after Kröncke *et al.*, 1998).

Danish waters

Josefson and Hansen (2003) identified bimodality in long-term annual trends in the major macrofaunal groups at three “open-sea” stations off the Danish coast (Kattegat/Sound/Belt; Figure 5.7.8). Sampling was typically conducted in May/June, and the depth range at the three stations was 17–55 m. Elevations around 1980 were mainly accounted for by crustaceans, while those around 1995 were mainly accounted for by polychaete worms. The dominant species contributing to changes in the major groups differed, both spatially and over time. However, overall, crustacean densities declined significantly over the years. Changes in biological variables were positively linked to those in the NAO Index and in freshwater run-off with a one- or two-year time lag. This may be partly explained by variation in winter nutrient inputs and the spring phytoplankton bloom. Reduced nutrient concentrations and reduced diatom abundance may have contributed to lower densities since 1997.

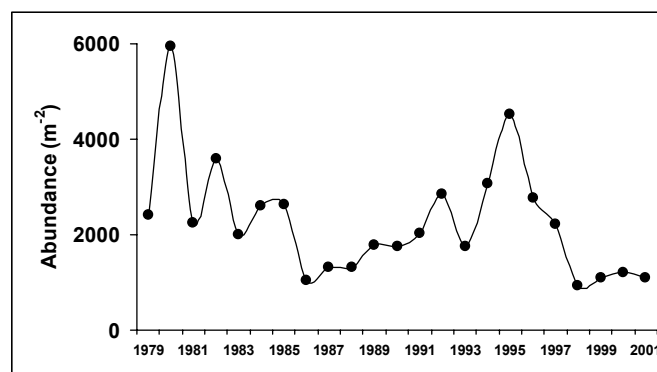


Figure 5.7.8. Annual trends in macrofaunal densities in open sea areas off Denmark (after Josefson and Hansen, 2003).

Swedish waters

Tunberg and Nelson (1998) identified correlations between changes in the winter NAO Index and related variables and the benthic fauna of Swedish (Skagerrak) waters, sampled with a Smith–McIntyre grab and using a 1 mm mesh sieve. Values of the index were offset in time to varying degrees to allow for possible delays in the manifestation of effects. They concluded that the influence of climatic variability operating on a regional scale may be a more important factor than eutrophication *per se* (mediated through enhanced settlement of plankton products), which had previously been considered as the main causative agent.

In the same study area, Hagberg *et al.* (2003) distinguished between local factors which determined differences among stations in species dominance and community composition, and broader scale climatic influences – best expressed through deep-water temperature variations – which explained changes in total densities across all stations (Figure 5.7.9).

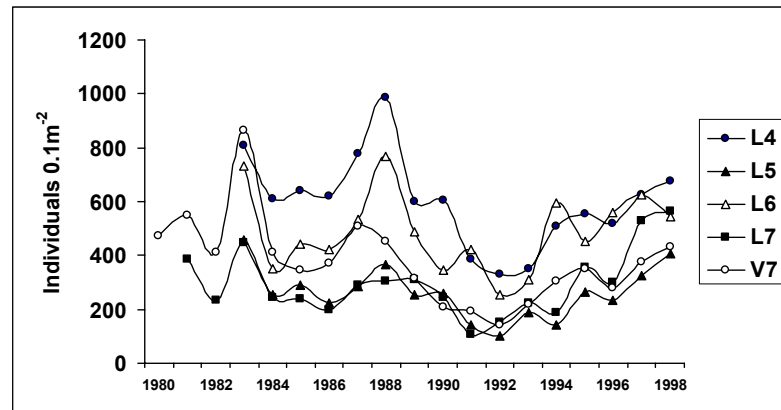


Figure 5.7.9. Total densities of the benthic macrofauna at five stations (40–100 m depth) off the Swedish west coast (after Hagberg *et al.*, 2003).

Norwegian waters

Pearson and Mannvik (1998) examined data on benthic communities at reference stations around offshore oil platforms in Norwegian waters (central North Sea). The stations were sampled at various intervals between 1988 and 1996, using a 0.1 m² van Veen grab and a 1 mm mesh sieve to extract the macrofauna. They identified climatic forces and the associated consequences for pelagic productivity as mediating factors in explaining broad-scale temporal and spatial variability across the sampling area.

Other relevant studies

Gröger and Rumohr (2006) modelled the relationship between annual changes in log(species) richness and climatic and hydrographic variables at five muddy stations sampled seasonally over a 30-year period in the western Baltic (Kiel Bight). Three samples were collected from each station with a 0.1 m² van Veen grab and the macrofauna were extracted over a 1 mm mesh sieve. They identified a significant positive relationship with changes in the winter NAO Index, noting that the immediacy of the community response was plausible in this relatively shallow (18–22 m) and physically-controlled environment. Explanations for a four-year lagged response to salinity were more speculative and may, for example, relate to circumstances that periodically promote the rapid influx of more saline waters from the North Sea to the western Baltic.

Oviatt (2004) described a variety of temperature-mediated changes in the biota of northwestern Atlantic waters associated with the occurrence of persistently positive values of the NAO Index in the 1980s and 1990s.

5.7.3 Intercomparison of trends (1986–2000)

Figure 5.7.10 is a compilation of data on annual macrofaunal densities from published studies, where these coincide with the majority (or all) of the period between 1986 and 2000. This is the only broadly comparable summary statistic that is readily available without further exploration of data sources and, clearly, is not meant to imply that other measures might not be equally or better suited to intercomparison. It should also be noted that four of the nine studies (Tees, Oyster Ground, Kattegat/Sound/Belt, and Skagerrak) employed a 1 mm mesh sieve to extract the macrofauna, while the others employed finer (0.5 or 0.63 mm) mesh sieves.

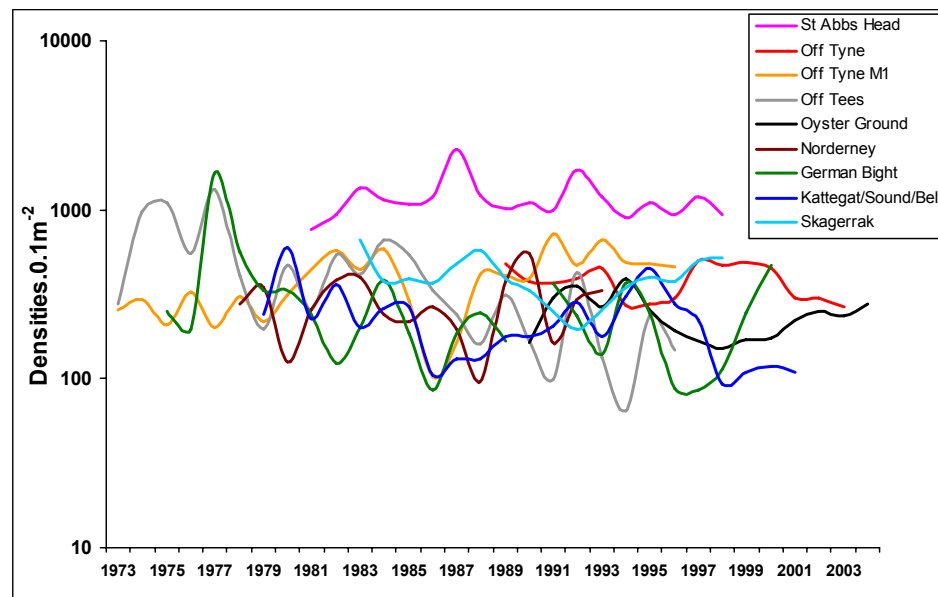


Figure 5.7.10. Annual trends in total densities of the macrofauna from various published studies.

There is little evidence of matching trends. Changes at the Tees and Kattegat locations appear to co-vary over some of this period, but are not significantly correlated. Indeed, the only significant positive relationship was between the Oyster Ground and Kattegat/Sound/Belt ($r = 0.57$, d.f. = 11, $p = 0.05-0.02$). Significant negative relationships were found for the Tyne series and the Kattegat/Sound/Belt ($r = -0.57$, d.f. = 11, $p = 0.05-0.02$), and for the Oyster Ground and Skagerrak ($r = -0.71$, d.f. = 8, $p = 0.05-0.02$). Offsetting surveys employing 1 mm mesh sieves (i.e. year+1), to allow for a possible delay in recruitment of juveniles to the larger mesh size, provided little additional insight. Neither is there evidence of an overall directional trend in densities between 1986 and 2000. Significant (negative) trends were identified only for the Tees ($p < 0.001$) and the Kattegat ($p = 0.05-0.02$).

For the more limited data on species richness, significant positive trends were identified off the Tyne (1989–2003: $p = 0.05-0.02$), off Norderney (1978–1993: $p = 0.01-0.001$), and in the German Bight (1969–2000: $p = 0.05-0.02$), while there was no significant trend off the Tees. However, in the last case, Warwick *et al.* (2002) identified enhanced taxonomic diversity since the mid-1980s (see also Figure 5.7.3).

5.7.4 Discussion

Ecological studies are typically conducted at the population or community level, and numerous measures are available that vary in their information content and sensitivity. Total density (Figure 5.7.10) can be a useful response variable but, without reference to its constituent parts, can provide little insight into the underlying mechanisms of change. Similarly, multivariate analysis (Section 5.2) revealed that the broad spatial pattern of communities is repeated in 1986 and 2000, as might be expected when taking into account the physical integrity of the North Sea environment as a whole, and the improbability of significant changes at this level over decadal timescales. However, at a more detailed level, appreciable changes were identified in species–abundance and functional relationships between 1986 and 2000 (Sections 5.3–5.5), and it was possible to posit causes for these changes, because they were more amenable to interpretation.

In this review, several studies identified links with climatic variability, some of which were reported as a lagged response of the macrobenthos on timescales of a year or more (see also Post, 2004). This may indicate a certain resilience of the affected cohort to environmental changes in the intervening period prior to its sampling. If, for example, the earlier effect acts

to promote the survivorship of larval recruits, perhaps as a result of enhanced food inputs to the seabed, then a cohort-specific response is plausible. The “lag” is then accounted for principally by the time taken for growth to the mesh size employed in sampling. If, on the other hand, the entire community is periodically vulnerable to extreme events such as exceptionally cold winters, then any year-*x* “lag” effect on the survivorship of recruits may be masked by an extreme event in the succeeding year. In general, shallow-water assemblages, therefore, may be better indicators of (near-)contemporary climatic influences, while deeper-water assemblages may integrate effects over longer timescales, as a result of the buffering capacity of the overlying water column (see e.g. Hagberg *et al.* (2003) and Reiss *et al.* (2006)).

Hallett *et al.* (2004) addressed the seemingly paradoxical finding that measures of large-scale climatic changes, such as the NAO Index, are often more effective correlates than locally measured variables (e.g. temperature) in biological studies. They noted that, in the absence of appropriate measures, the former can better integrate the complexities of interactions between local climate and ecological processes, including time-dependent variation in their relative importance, which may occur over periods of months or even years preceding sampling.

Genner *et al.* (2004) and Hagberg *et al.* (2004) identified the likelihood of regional differences in biological responses to climatic trends, which would be consistent with the outcome of studies of the North Sea benthos. A simple example would be the opposing effects of persistently strong westerly winds on the stability of shallow-water soft sediments along east-facing (“sheltered”) and west-facing (“exposed”) coasts of the North Sea. Recognizing both the diversity of possible ecosystem responses to changes in the NAO and the importance of location, Ottersen *et al.* (2004) proposed classifying effects as direct, indirect, or integrated.

Clark and Frid (2001) highlighted the importance of indirect influences that may complicate the elucidation of links between biological and climatic variability, citing as an example the observations of Reid *et al.* (1998) that recent negative changes in phytoplankton of the north-northeastern Atlantic might have been caused by cold-water influx arising from the increased melting of polar ice. Other influences may have loose or no association with climate-related variability, as was the case for changes at a benthic station (P) off the English northeast coast, which appeared to be confounded with the localized effects of enhanced commercial fishing activity at the seabed (Clark and Frid, 2001; Frid *et al.*, 2001).

There is evidence for the co-occurrence of changes in a variety of components of the North Sea ecosystem in the mid- to late 1980s, which has been ascribed to a “regime shift” (see e.g. Reid and Edwards (2001), Warwick *et al.* (2002), Kirby *et al.* (2007), and Section 4.1). In support of this, Alheit *et al.* (2005) identified synchronous changes in the North and Baltic seas associated with increases in the NAO Index and, linked to this, the influential role of water temperature. They noted that the processes determining population changes in commercial fish have different consequences, depending on the life-history strategies and location of individual species. Further support for the hypothesis of a regime shift in the 1980s is provided by Weijerman *et al.* (2005), who also found some evidence for another less well-defined shift in 1998.

Accepting such an occurrence in the mid-1980s, the 1986 and 2000 North Sea benthos surveys might conceivably represent “before” and “after” sampling occasions, although the hypothesized 1998 event adds a complicating layer. We found no evidence of a wholesale shift in structure or function between surveys (see e.g. Sections 5.2, 5.4, and 5.5). Changes at more localized levels are evident in these comparisons and in the outcome of this review, and commonly reveal a high sensitivity to climatic variability. However, these are generally not consistent with an immediate and synchronized response to a relatively abrupt “regime shift” (see also Lees *et al.* (2006) and van Nes *et al.* (2007)). The results of the above studies might

repay more detailed retrospective analyses for the existence of less pronounced signals of change, such as was evident in the findings of Warwick *et al.* (2002) off northeastern England.

5.7.5 Conclusions

The occurrence of change in benthic communities between 1986 and 2000 is consistent with what is known about the dynamics of the North Sea environment (Section 4.1). The lack of synchronicity in Figure 5.7.10 can be explained by regional differences in the nature of the responses to widely operating forces, rather than their absence. This is evident in most of the studies from which the data were derived, and from the observations of Hagberg *et al.* (2004) and the present report.

We conclude that, although the responses of the macrobenthos to climatic variability may differ spatially and may be locally confounded with other influences, they are nevertheless sensitive to such variability as expressed by the broader NAO Index or, more specifically, by winter temperatures, especially in shallower waters. The mechanism of action may also vary with locality. For example, climate-induced bottom-temperature variations in deeper waters have been considered a good proxy for the amount of food reaching the seabed (Hagberg *et al.*, 2003). In general, the responses of shallow-water benthic communities to extreme events are likely to be more immediate than for their counterparts in deeper waters, where any consequences may depend upon the responses of other ecosystem elements. Combined in some cases with cohort-specific responses and mesh selection, this may result in time lags of up to a year or more before the effects are detectable in samples.

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6 Ecosystem interactions: faunal components, fishing practices, and parallel studies

6.1 Links between infauna, epifauna, and demersal fish distributions

H. Reiss and H. L. Rees

6.1.1 Introduction

Until now, studies of North Sea faunal communities have focused mainly on the spatial structure of the infauna (e.g. Heip *et al.*, 1992; Künitzer *et al.*, 1992) and epifauna (Frauenheim *et al.*, 1989; Zühlke *et al.*, 2001; Callaway *et al.*, 2002), whereas less detailed information has been available for spatial patterns in fish communities (Daan *et al.*, 1990; Greenstreet and Hall, 1996).

Because of differences in the life-cycle traits and the mobility of the three faunal components, ranging from relatively sessile infaunal species to highly mobile fish species, the community structures as well as the responses to environmental parameters, are expected to differ among these faunal groups. Callaway *et al.* (2002) reported on a qualitative comparison of epifaunal and demersal fish communities in the North Sea and found contrary diversity patterns.

This section will analyse and compare the spatial community patterns of the infauna, epifauna, and demersal fish. Furthermore, preliminary analyses relating spatial patterns in the different faunal components to environmental parameters provide an insight into their functional similarities and differences.

6.1.2 Material and methods

The community structure of all three faunal components within a spatial range covering the entire North Sea was analysed. Therefore, different datasets had to be used and were provided by several sources.

INFAUNA. The NSBP 2000 infauna data were used. A detailed description of methods used for sampling and processing the infauna is given in Sections 3 and 5.1.

EPIFAUNA. The epifauna data were collected in summer 2000 as part of the EU project “Monitoring biodiversity of epibenthos and demersal fish in the North Sea and Skagerrak”. Samples were taken with a 2 m beam trawl with a chain mat attached. The mesh size of the net was 20 mm and a liner of 4 mm knotless mesh was fitted inside the codend. After contact with the seabed, the beam trawl was towed at approximately 1 knot for 5 minutes. Further details of the gear and the sampling procedure are given in Jennings *et al.* (1999), Zühlke *et al.* (2001), and Callaway *et al.* (2002). From the information on towing distances, all data were standardized to a sampled area of 500 m². Colonial (e.g. hydrozoans and bryozoans) organisms, infaunal species, and pelagic fish species were excluded from the quantitative analysis, whereas small demersal fish species such as solenette (*Buglossidium luteum*) or dragonets (*Callionymus* spp.), which can only be quantitatively sampled with a 2 m beam trawl, were included.

DEMERSAL FISH. The data for the demersal fish fauna were extracted from the ICES International Bottom Trawl Survey (IBTS) database. The main objective of IBTS is, *inter alia*, to monitor the distribution and relative abundance of all fish species in the North Sea (ICES, 2006). The standard gear used in IBTS is a Grande Ouverture Verticale (GOV). The height of the gear's vertical opening is approximately 4.5 to 5 m, with a wingspread of around 20 m depending on the water depth. The net is equipped with 20 cm diameter rubber disk groundgear in the bosom and 10 cm rubber disks in the net wings with iron disks fixed between them. The codend has a fine mesh liner of 20 mm mesh opening. The standard towing time is 30 minutes at a target speed of 4 knots over ground. Detailed characteristics of

the standard GOV and the sampling procedure are given in ICES (2006). Only data collected in summer 2000 (quarter 3) were used. Pelagic fish and invertebrate epibenthos were omitted prior to analyses.

ENVIRONMENTAL PARAMETERS. The environmental parameters were compiled from a variety of NSBP 2000 sources. Details can be found in Section 3.

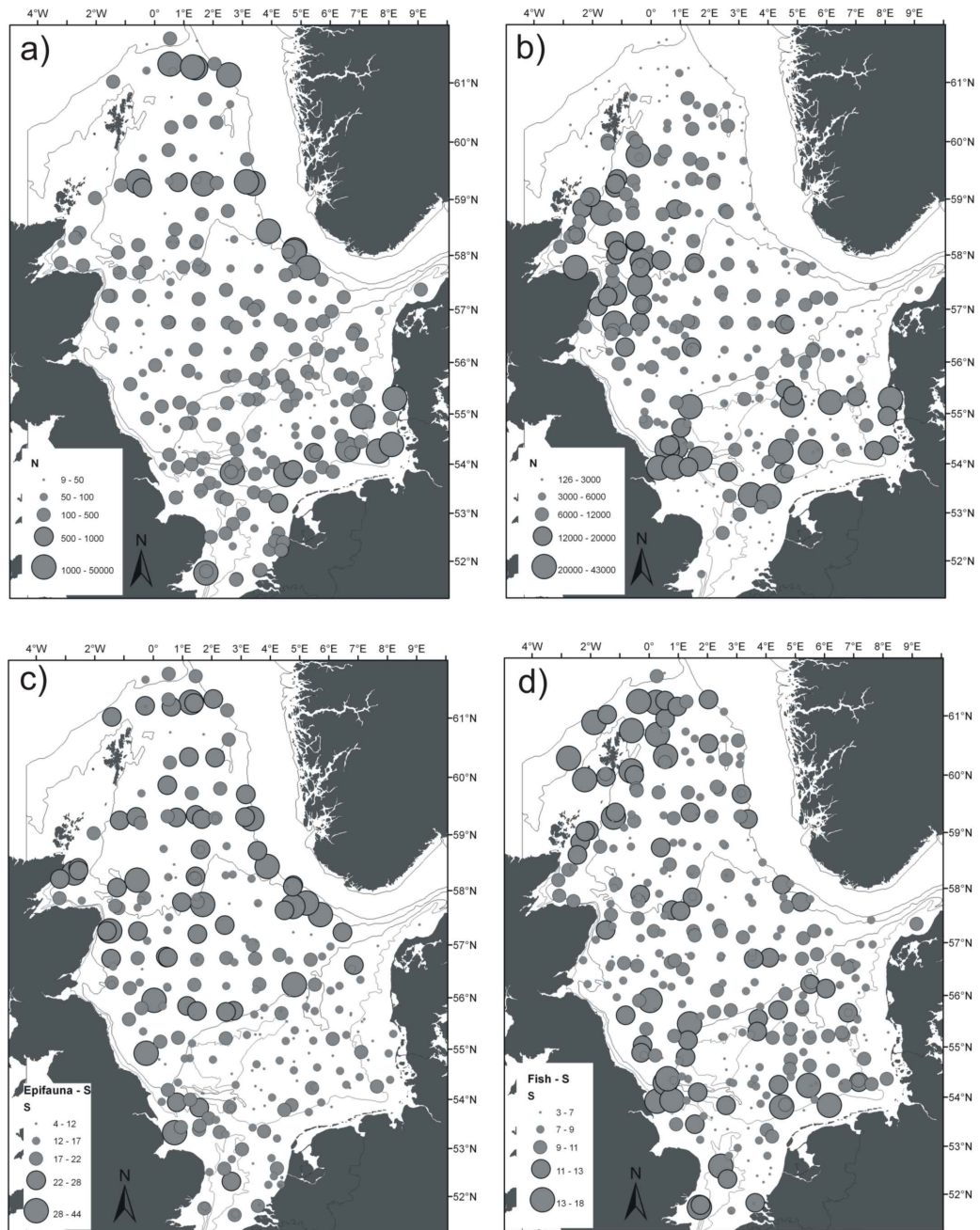


Figure 6.1.1. Abundance of (a) epifauna (ind. 500 m⁻²) and (b) demersal fish (cpue); and species number of (c) epifauna and (d) demersal fish (S/haul) in 2000.

Data analyses

Multivariate community analyses were carried out with the statistical package PRIMER 5 (Clarke and Warwick, 1994). Hierarchical cluster analysis was carried out using double square-root transformed abundance data and the Bray–Curtis similarity index.

For the community analyses of epifauna and fish, the complete datasets were used. Additionally, all datasets (infauna, epifauna, and fish) were reduced to stations close to each other, to compare the spatial patterns in univariate measures and multivariate outputs. The nearest stations were determined using GIS software (ArcView 3.1), and a dataset was created including only stations up to a maximum distance of 40 km apart (yielding a total of 130 matching stations; Figure 6.1.5).

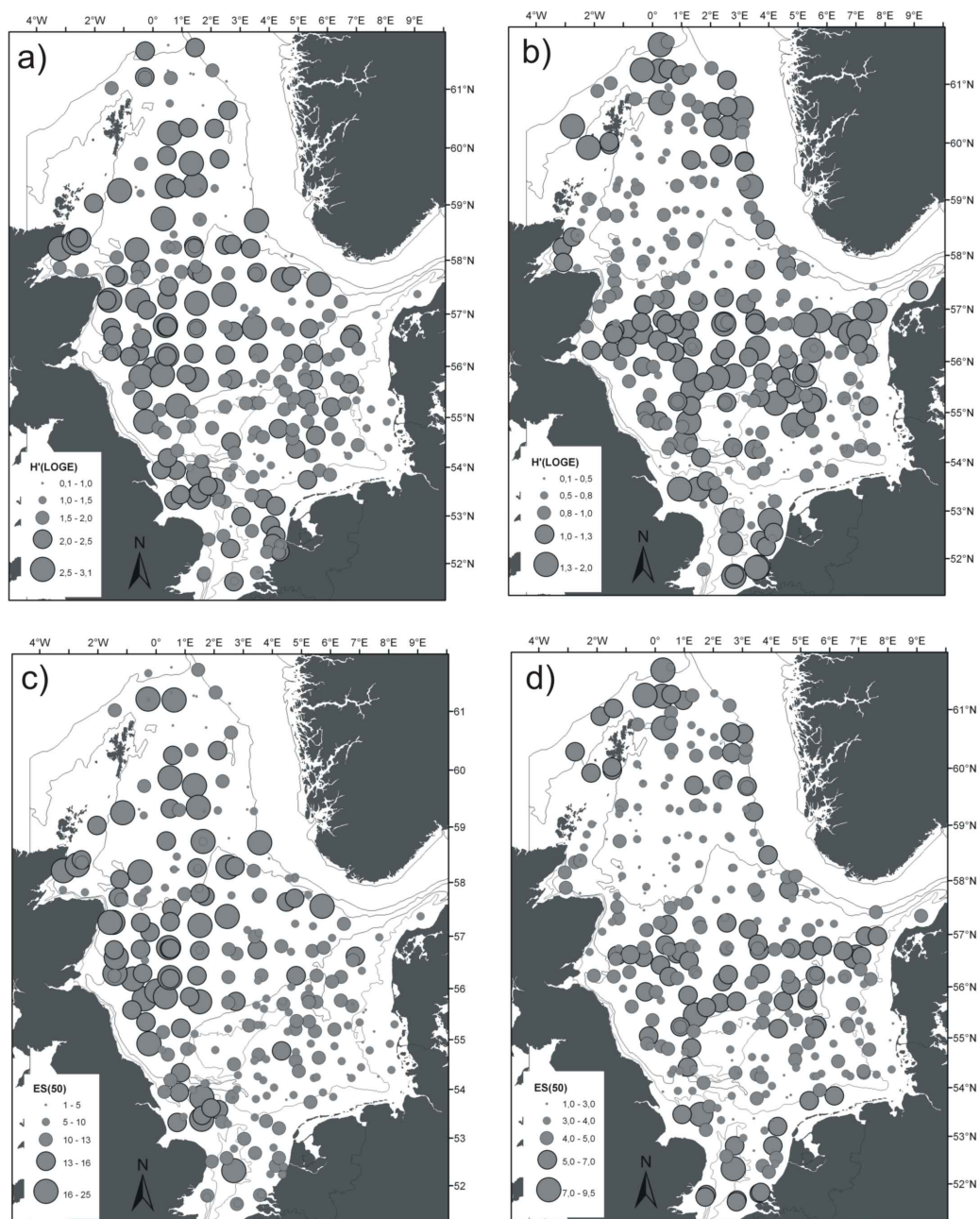


Figure 6.1.2. Shannon–Wiener index ($H'_{\log e}$) of (a) epifauna and (b) demersal fish; and the expected number of species per 50 individuals ($ES(50)$) of (c) epifauna and (d) demersal fish in 2000.

The relationship among the univariate faunal parameters and between environmental and univariate faunal parameters was determined by a Spearman rank correlation.

The relationship between environmental parameters and community structure was determined by calculating Spearman rank correlations between the similarity matrices using the RELATE and BIOENV routines of PRIMER. The similarity matrix for the environmental parameters was calculated using normalized Euclidean distance.

6.1.3 Results

The following analyses are divided into two main sections. In the first section, all available stations in each dataset are used in the analyses. Because the infaunal communities have already been described in detail in previous sections, only the epifauna and the fish fauna are analysed here. In the second part, infauna, epifauna, and fish are compared, using the matching stations.

6.1.3.1 Epifauna and fish communities

Abundance and diversity

The highest abundance of epifauna was found in the coastal areas of the southern North Sea and the northeastern North Sea especially along the Norwegian Trench (Figure 6.1.1a). A somewhat different pattern was found for fish abundances with the highest values in the northwestern North Sea and the area between the Dogger Bank and the English coast (Figure 6.1.1b). However, for the epifauna, high mean abundances of small demersal fish species were found in shallower parts of the southern North Sea.

Highest numbers of epifaunal species were found north of the 50 m depth contour, whereas the southeastern North Sea was characterized by low species numbers (4–17 species per haul; Figure 6.1.1c). Again, the pattern of species numbers of fish differed from the epifauna pattern. Highest values were found in the northern North Sea around the Shetlands and in the southern North Sea and the Dogger Bank area (Figure 6.1.1d). However, species numbers and species richness (Margalef d) were significantly correlated with latitude for epifauna and demersal fish, whereas no significant relationship with latitude was found for other univariate parameters except for evenness (J') of epifauna and latitude (Table 6.1.1).

Values of diversity indices such as the Shannon–Wiener index and the expected number of species per 50 individuals (ES(50)) for the epifauna were lower in the southern than in the northern North Sea (Figure 6.1.2a and c). In contrast, values of both measures for the demersal fish fauna show a maximum in the central North Sea between the 50 and 100 m depth contour and around the Shetlands (Figure 6.1.2b and d).

Table 6.1.1. Correlation coefficients between latitude and univariate measures for the epifauna and fish. Statistical significance is indicated ($p < 0.01$ and * $p < 0.05$).**

| | EPIFAUNA | FISH |
|-------------------------------|----------------|----------------|
| Abundance | 0.007 | -0.021 |
| Species number | 0.321** | 0.182** |
| Species richness (d) | 0.367** | 0.140* |
| Shannon–Wiener index (H') | -0.047 | 0.022 |
| ES(50) | 0.045 | 0.009 |
| Evenness (J') | -0.153* | -0.060 |

Community structure of the epifauna and fish

The cluster dendrograms and the distribution of the epifauna and demersal fish communities are shown in Figure 6.1.3 and Figure 6.1.4, respectively. For both faunal components, a clear separation of station clusters between the southern North Sea (<50 m), the central North Sea

(50–100 m), and the northern North Sea (100–200 m) was found (Figure 6.1.4). Within the southern cluster, a further separation between the eastern Channel area and the southeastern North Sea was obvious. In the northern North Sea, a distinct cluster was found for stations north of the Shetlands. In contrast to the epifauna communities, a distinct cluster of stations situated along the Norwegian Trench was additionally found for the demersal fish fauna.

The characteristics of the main clusters/communities are shown in Tables 6.1.2 and 6.1.3. Subclusters with a highly heterogeneous structure and low similarity values were marked with an “x” behind the main cluster indication and are not shown in the tables. Despite the clear distinction between the clusters of the demersal fish communities, there was a high degree of similarity between all the samples. This indicates that the distinctions between the clusters are mainly caused by differences in the abundance of the dominant species.

In contrast, the distinctions between the epifauna clusters were mainly caused by variation in the distribution and densities of a wide array of characterizing species.

6.1.3.2 Comparing infauna, epifauna, and fish communities

The station grid on which the comparison of infauna, epifauna, and fish was based is shown in Figure 6.1.5. In all, 130 stations were used for the comparison.

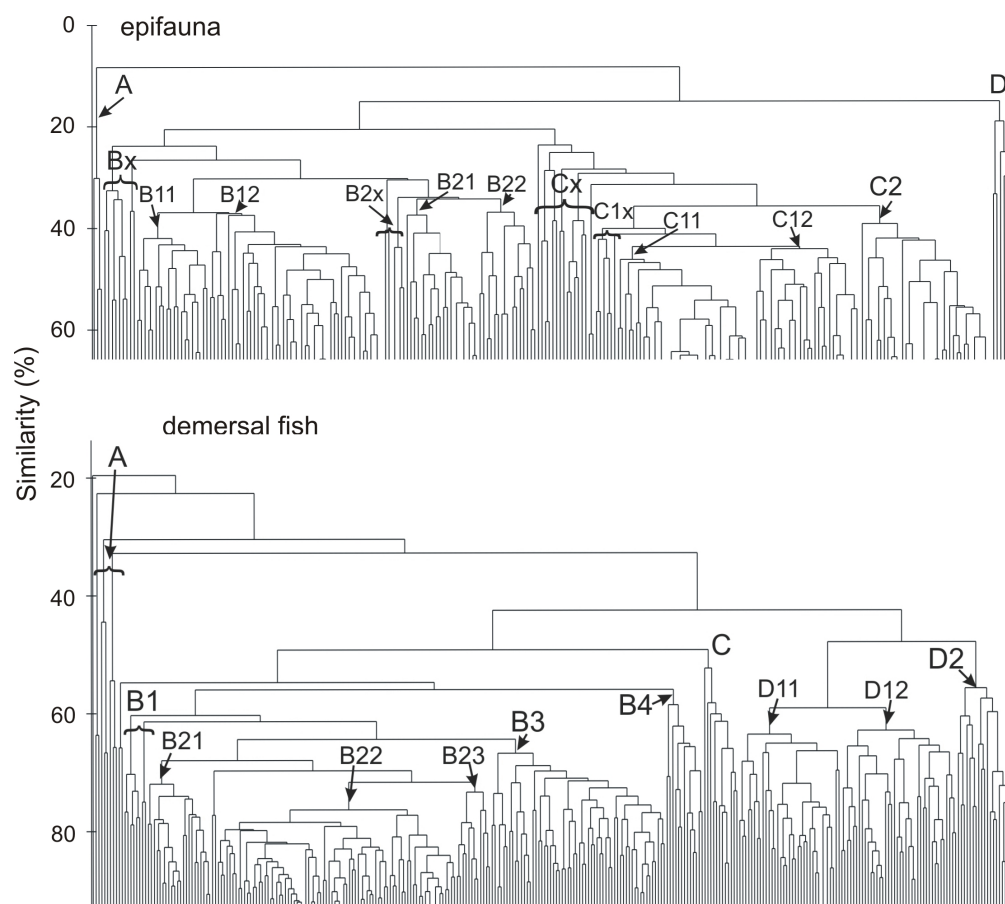


Figure 6.1.3. Dendrograms and groupings (shown in Figure 6.1.4) from cluster analysis of fourth-root transformed abundance data for the epifauna (top) and demersal fish (bottom).

Abundance and diversity

The comparison of the univariate measures of the different faunal components revealed a significant positive correlation for species number and species richness (d) as well as a negative correlation for evenness (J') between infauna and epifauna (Table 6.1.4). No significant relationship was found between the infauna and demersal fish. Between the

epifauna and fish, only the correlation of expected number of species per 50 individuals was significant.

The results of the comparison with univariate parameters should be interpreted with care, because of the species–area dependency of most diversity indices, species number, and species richness. However, the results indicate more similar patterns in diversity between infauna and epifauna compared with epifauna and fish or infauna and fish.

Community structure

In order to compare the spatial community patterns of the different faunal components in the North Sea, the similarity matrices of the infauna, epifauna, and fish datasets were compared by Spearman rank correlation within the RELATE routine of PRIMER. The patterns of all faunal components were significantly correlated with each other (Table 6.1.5). Surprisingly, the highest R value, as an indication of the magnitude of the similarity between the patterns, was found for fish and infauna communities.

In general, the lowest (but still significant) R values were found using untransformed abundance data, whereas the highest R values were found with fourth-root transformed abundance data, indicating the important influence of less abundant species for determining the similarity of the spatial patterns.

However, despite the significance of the relationships between the community patterns, scatterplots of the Bray–Curtis similarities revealed a rather high variability (not shown).

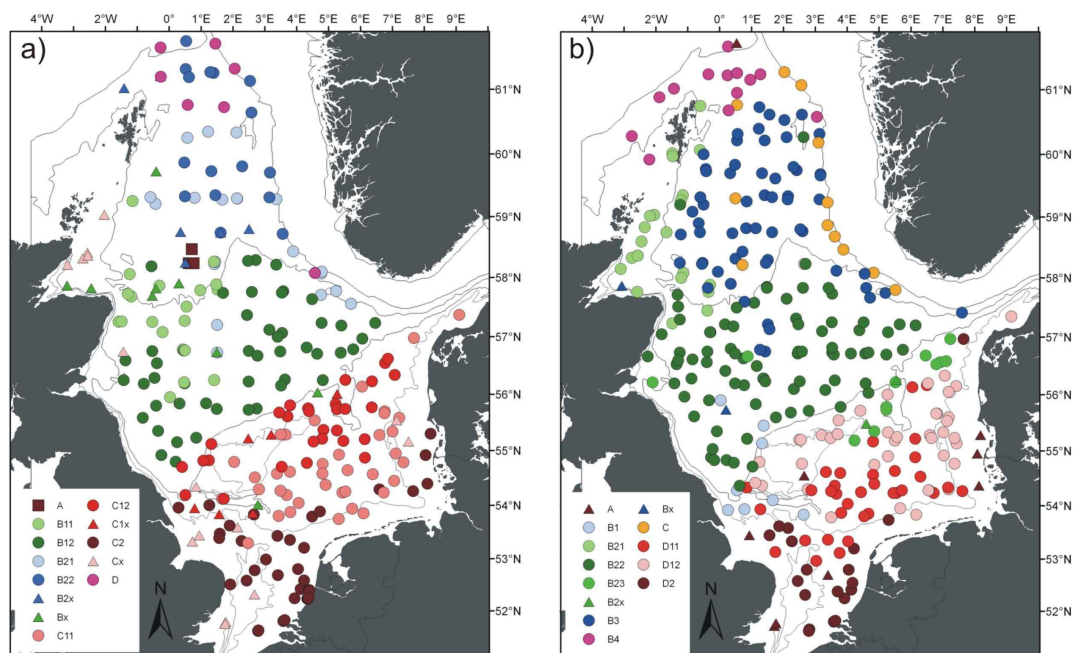


Figure 6.1.4. Distribution of (a) epifauna and (b) fish assemblages in the North Sea according to the outputs from cluster analyses of fourth-root transformed abundance data.

6.1.3.3 Relationship between faunal patterns and environmental parameters

The relationship between environmental parameters and the univariate faunal attributes is shown in Table 6.1.6. Significant correlations between the infaunal and epifaunal diversity measures and the environmental parameters were found in most cases except for mud content (epifauna) and median grain size (infauna and epifauna). In contrast, no significant correlations were found for the demersal fish. The relationship between abundance and

environmental parameters was somewhat less pronounced for the infauna and epifauna, as indicated by the comparatively low R values (Table 6.1.6). Only the infaunal attributes and fish abundances were significantly correlated with the mud content.

The significant relationships between the similarity matrices of all three faunal components (Table 6.1.5) suggested that the community patterns may be triggered by the same underlying environmental parameters. This is supported by the finding that the relationships between the similarity matrices and the environmental parameters were comparable for all three components. In general, highest R values were found for the main hydrographic parameters such as bottom water temperature and salinity and, in particular, summer bottom water temperature (Table 6.1.7), whereas the lowest R values were found for the relationship with sediment parameters (mud content). Differences between the faunal components included the relationship between tidal stress and community structure, with the second highest R value for the infauna (0.515) and much lower values for the epifauna (0.141) and fish fauna (0.381).

6.1.4 Discussion

The objective of this section was to compare the community structure of different faunal components of the North Sea ecosystem and to relate these patterns to the environmental parameters.

The multivariate analyses revealed the presence of large-scale patterns in the infaunal, epifaunal, and demersal fish data with major distinctions between a southern community (including the Oyster Ground and German Bight), an eastern Channel and southern coastal community, and at least two northern communities (50–100 m depth and >100 m depth) evident in all three components (see also Section 5.1). Similar results were found in previous studies of infaunal communities (Heip *et al.*, 1992; Künitzer *et al.*, 1992), epifaunal communities (Jennings *et al.*, 1999; Callaway *et al.*, 2002), and fish communities (Daan *et al.*, 1990; Callaway *et al.*, 2002).

Furthermore, the results of the direct (multivariate) comparison of the community structure in Table 6.1.5, showed a significant similarity between the infauna, epifauna, and demersal fish, suggesting that the same underlying environmental parameters may be influencing the community patterns. On a North Sea-wide scale, the most influential of these appear to be hydrographic parameters such as bottom water temperature, bottom water salinity, and tidal stress (in the case of the infauna). Sediment characteristics expressed as mud content appeared to be less influential, even for the infauna communities, which would be expected to be more closely dependant than the more mobile epifaunal and demersal fish fauna. However, this relationship seems to be valid on a North Sea-wide scale, but less so on a smaller spatial scale. Sediment characteristics were the most important parameter determining infaunal community structure in the southwestern North Sea (Schratzberger *et al.*, 2006) and epifaunal community structure in the southern North Sea (Rees *et al.*, 1999; Callaway *et al.*, 2002). Furthermore, in the southwestern North Sea, the influence of sediment characteristics on community structure was less pronounced or even absent for the epifauna and fish fauna, compared with the infauna (Schratzberger *et al.*, 2006).

Table 6.1.2. Main epifauna communities in the North Sea with information on the area, the mean and range of water depth, the average similarity of each cluster, characterizing species, and number of stations in the cluster.

| CLUSTER | AREA | WATER DEPTH (M) | AV. SIMILARITY (%) | CHARACTERISTIC SPECIES | STATIONS |
|---------|--|-----------------|--------------------|--|----------|
| A | Fladen Ground | 152 (149–158) | 37.40 | <i>N. norvegicus</i> , <i>P. borealis</i> , <i>M. glutinosa</i> | 3 |
| B11 | Northwestern NS | 91 (72–118) | 44.94 | <i>P. prideaux</i> , <i>P. bernhardus</i> , <i>A. laevis</i> , <i>A. rubens</i> , <i>H. tubicola</i> | 20 |
| B12 | Central NS | 72 (54–112) | 43.71 | <i>P. bernhardus</i> , <i>A. irregularis</i> , <i>A. rubens</i> , <i>B. undatum</i> , <i>C. gracilis</i> | 48 |
| B21 | Northern NS | 128 (93–165) | 45.88 | <i>A. irregularis</i> , <i>C. allmanni</i> , <i>Echinus</i> spp., <i>A. laevis</i> , <i>H. tubicola</i> | 20 |
| B22 | Northern NS | 145 (105–243) | 41.15 | <i>Echinus</i> , <i>A. irregularis</i> , <i>H. tubicola</i> , <i>L. sarsi</i> , <i>A. laevis</i> , <i>S. lignarius</i> | 16 |
| C11 | Oyster Ground | 44 (21–77) | 53.05 | <i>A. irregularis</i> , <i>A. rubens</i> , <i>B. luteum</i> , <i>P. bernhardus</i> | 28 |
| C12 | Dogger Bank and area around 50 m contour southern NS | 46 (34–69) | 47.44 | <i>A. irregularis</i> , <i>P. bernhardus</i> , <i>A. rubens</i> , <i>L. limanda</i> , <i>C. cassivelaunus</i> | 39 |
| C2 | Southwestern NS and eastern Channel | 30 (16–68) | 46.77 | <i>L. holsatus</i> , <i>O. ophiura</i> , <i>B. luteum</i> , <i>P. bernhardus</i> , <i>O. albida</i> | 36 |
| D | Northern NS north of Shetlands | 167 (112–205) | 25.22 | <i>Echinus</i> spp., <i>A. laevis</i> , <i>P. prideaux</i> , <i>P. bernhardus</i> , <i>C. gracilis</i> | 7 |

Table 6.1.3. Main demersal fish communities in the North Sea with information on the area, the mean and range of water depth, the average similarity of each cluster, characterizing species, and number of stations in the cluster.

| CLUSTER | AREA | WATER DEPTH (M) | AV. SIMILARITY (%) | CHARACTERISTIC SPECIES | STATIONS |
|---------|---|-----------------|--------------------|---|----------|
| B1 | Western central NS | 75 (51–94) | 66.61 | <i>M. merlangus</i> , <i>M. aeglefinus</i> , <i>L. limanda</i> , <i>E. gurnardus</i> | 8 |
| B21 | Northwestern NS | 92 (50–120) | 75.92 | <i>M. aeglefinus</i> , <i>M. merlangus</i> , <i>M. kitt</i> , <i>L. limanda</i> | 22 |
| B22 | Central NS | 75(43–111) | 87.86 | <i>M. aeglefinus</i> , <i>M. merlangus</i> , <i>L. limanda</i> , <i>H. platessoides</i> | 82 |
| B23 | East of Dogger Bank around 50 m contour | 45 (37–58) | 76.92 | <i>L. limanda</i> , <i>M. merlangus</i> , <i>M. aeglefinus</i> , <i>E. gurnardus</i> | 12 |
| B3 | Northern NS mainly >100 m | 122 (85–153) | 71.07 | <i>M. aeglefinus</i> , <i>M. merlangus</i> , <i>H. platessoides</i> , <i>G. morhua</i> | 60 |
| B4 | Northern NS, Shetlands | 150 (96–209) | 65.11 | <i>M. aeglefinus</i> , <i>H. platessoides</i> , <i>E. gurnardus</i> , <i>M. merlangus</i> | 13 |
| C | Mainly near Norwegian Trench | 157 (132–228) | 62.22 | <i>M. aeglefinus</i> , <i>P. virens</i> , <i>H. platessoides</i> , <i>M. merlangus</i> | 12 |
| D11 | Oyster Ground and southwestern NS | 42 (36–48) | 68.16 | <i>M. merlangus</i> , <i>L. limanda</i> , <i>E. gurnardus</i> , <i>P. platessa</i> | 35 |
| D12 | Dogger Bank and coastal southeastern NS | 35 (21–58) | 65.80 | <i>L. limanda</i> , <i>E. gurnardus</i> , <i>M. merlangus</i> , <i>P. platessa</i> | 40 |
| D2 | Southwestern NS and Channel | 32 (24–39) | 60.19 | <i>M. merlangus</i> , <i>L. limanda</i> , <i>T. vipera</i> , <i>P. platessa</i> | 19 |

Table 6.1.4. Correlation coefficients relating univariate measures for infauna, epifauna, and fish. Statistical significance is indicated (p <0.01 and *p <0.05).**

| | INFAUNA VS. EPIFAUNA | INFAUNA VS. FISH | EPIFAUNA VS. FISH |
|---------------------------|----------------------|------------------|-------------------|
| Abundance | -0.070 | -0.066 | 0.099 |
| Species number | 0.279** | 0.098 | 0.158 |
| Species richness (d) | 0.358** | 0.019 | 0.133 |
| Shannon–Wiener Index (H') | -0.099 | -0.141 | 0.159 |
| ES(50) | 0.049 | -0.11 | 0.179* |
| Evenness (J') | -0.177* | -0.097 | 0.159 |

Sediment type deduced from the same 0.1 m² grab sample used for collecting the infauna should provide an adequate habitat descriptor for the organisms in that sample. However, it must be cautioned that it may be wholly inadequate to describe the sedimentary environment along the entirety of epifaunal or fish trawl tows. Therefore, while it seems biologically plausible to expect a reduced dependency of motile epifaunal and fish species on substratum type, sediment descriptors from the NSBP 2000 survey alone are too narrowly defined to demonstrate this, other than in homogeneous areas. Also, other measures such as sorting coefficients may better describe the dynamic nature of the seabed environment, and hence may link more closely with measures such as tidal stress, which was an influential variable in our study (see also Rees *et al.*, 1999).

The intercomparison of univariate measures such as abundance and diversity for the different faunal components revealed no significant correlations in most cases. Only the patterns of species number and species richness between the infauna and epifauna were highly significantly correlated. However, because of the differences in the sampling procedures within the infaunal dataset (see Section 3), the low and partly unknown catch efficiency of the 2 m beam trawl and the GOV (Ehrich *et al.*, 2004; Reiss *et al.*, 2006) and the area dependency of diversity measures, a station-by-station comparison is expected to be relatively inaccurate. For example, the relationship between sampled area and epifaunal species number differs depending on the region within the North Sea (Reiss, unpublished data). Also, for the expected number of species (ES(50)), which is less dependent on sample size, no significant correlation for the comparison between the infauna and epifauna and the infauna and fish was found. Indeed, only a weak significant correlation between the epifauna and fish was found (Table 6.1.4). Thus, the processes influencing diversity patterns on one hand and community structure on the other might be different. This is also indicated by the results of the correlation between environmental parameters and univariate faunal parameters, which showed contrary results for infaunal and fish diversity (Table 6.1.6).

Because the data for the infauna, epifauna, and demersal fish were collected on different occasions and under separate programmes, no congruent station grid for all faunal components was available. Therefore, it was necessary to select a subset of matching stations to allow a direct quantitative comparison of faunal patterns, which further limited the scope of the analyses. Future research and development and monitoring programmes should aim at an integrated sampling of these faunal components to enable a comprehensive analysis of the faunal patterns and the underlying processes. These data are particularly important because future marine management strategies need to implement an ecosystem approach for the evaluation of anthropogenic impacts across all components.

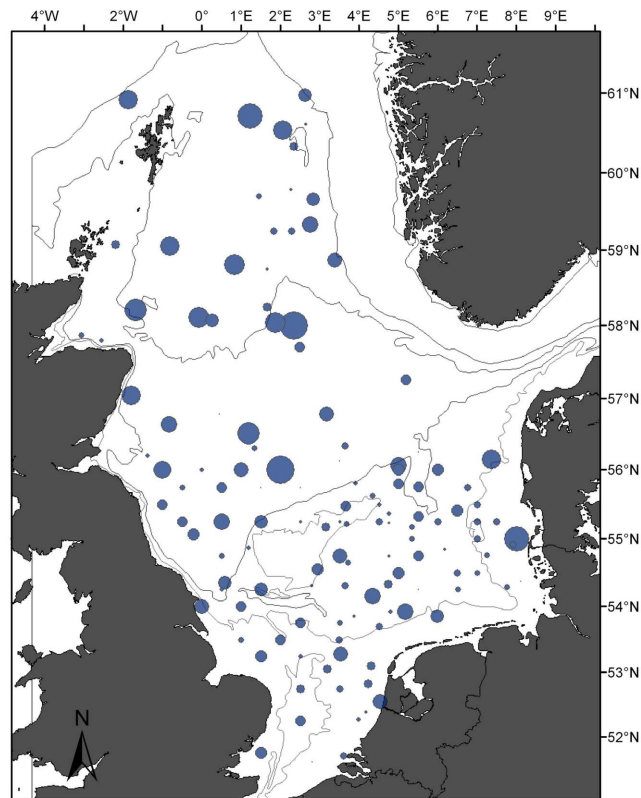


Figure 6.1.5. Positions of the nearest matching stations with distances to the nearest station superimposed (m).

Table 6.1.5. Correlation coefficients (Spearman rank) relating the similarity matrices of the infauna, epifauna, and demersal fish communities for different transformation types (RELATE). Statistical significance is indicated (** $p < 0.01$).

| | INFAUNA VS. EPIFAUNA | INFAUNA VS. FISH | EPIFAUNA VS. FISH |
|-------------------|----------------------|------------------|-------------------|
| Fourth root | 0.410** | 0.568** | 0.495** |
| Presence/absence | 0.386** | 0.502** | 0.369** |
| No transformation | 0.252** | 0.332** | 0.250** |

Table 6.1.6. Correlation coefficients relating univariate community attributes and environmental parameters. Number of stations compared is in parentheses. Statistical significance is indicated (** $p < 0.01$ and * $p < 0.05$).

| | SPECIES NUMBER | | | ABUNDANCE | | | ES(50) | | |
|------------------------------|-----------------|-----------------|--------|----------------|----------------|-----------------|-----------------|-----------------|--------|
| | INFAUNA | EPIFAUNA | FISH | INFAUNA | EPIFAUNA | FISH | INFAUNA | EPIFAUNA | FISH |
| Tidal stress (130) | -0.453** | 0.052 | -0.02 | 0.289** | 0.148 | -0.02 | 0.225** | 0.088 | -0.058 |
| Wave stress (130) | -0.464** | -0.419** | -0.09 | 0.202* | 0.150 | -0.08 | 0.442** | -0.349** | -0.093 |
| Bottom salinity winter (129) | 0.730** | 0.363** | 0.107 | 0.11 | -0.216* | 0.175* | 0.564** | 0.360** | 0.051 |
| Bottom salinity summer (129) | 0.697** | 0.373** | 0.135 | 0.12 | -0.212* | 0.17 | 0.526** | 0.373** | 0.081 |
| Bottom temp. winter (129) | 0.611** | 0.334** | 0.073 | 0.01 | -0.202* | 0.13 | 0.461** | 0.338** | 0.114 |
| Bottom temp. summer (129) | -0.754** | -0.339** | -0.154 | -0.13 | 0.248** | -0.237** | -0.589** | -0.347** | -0.042 |
| Mean grain size (72) | 0.122 | 0.143 | 0.144 | -0.050 | -0.109 | -0.117 | 0.132 | 0.135 | 0.184 |
| Mud content (96) | 0.516** | 0.113 | 0.00 | 0.238* | -0.04* | 0.248 | 0.434** | 0.030 | -0.152 |
| Chlorophyll (129) | -0.434** | -0.368** | -0.020 | 0.16 | 0.257** | -0.05 | -0.325** | -0.406** | -0.170 |

Table 6.1.7. Correlation coefficients (R) relating community structure (abundance data) and the environmental parameters (99 stations compared).

| | INFAUNA (R) | EPIFAUNA (R) | FISH (R) |
|------------------------|-------------|--------------|----------|
| Tidal stress | 0.515 | 0.141 | 0.381 |
| Wave stress | 0.352 | 0.290 | 0.431 |
| Chlorophyll | 0.290 | 0.358 | 0.361 |
| Bottom salinity winter | 0.470 | 0.424 | 0.531 |
| Bottom salinity summer | 0.434 | 0.416 | 0.487 |
| Bottom temp. winter | 0.405 | 0.462 | 0.481 |
| Bottom temp. summer | 0.526 | 0.582 | 0.631 |
| Mud content | 0.163 | 0.204 | 0.038 |

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6.2 Benthic foodweb studies

G. C. A. Duineveld

Benthic foodwebs in the North Sea have been relatively understudied compared with pelagic ones, despite decades of steadily increasing demersal fisheries. On one hand, intensive fishing releases predation pressure because of the depletion of fish stocks; on the other hand, selectively removes species and possibly whole feeding guilds. Furthermore, the large amounts of discards and dead benthos may have become a food source for scavenging organisms. All these effects can influence the benthic foodweb and the way and rates with which primary energy is stored, transferred, and recycled into nutrients.

Recently, Jennings and co-workers (e.g. Jennings *et al.*, 2001; Jennings and Warr, 2003) have begun to analyse benthic foodwebs in the North Sea, using stable nitrogen isotopes ($\delta^{15}\text{N}$). This powerful tool, which has been applied widely elsewhere, allows estimation of the trophic level of an organism or species, group of organisms, or size fraction given knowledge of the enrichment of ^{15}N per trophic level (usually assumed 3.4%). Information on $\delta^{15}\text{N}$ of organisms at the base and top of the foodweb makes it possible to make inferences about the food chain length.

An example of $\delta^{15}\text{N}$ signatures, and the relative trophic positions in a typical *Amphiura filiformis* community from the southern North Sea in 2000, is given in Figure 6.2.1. Here, the most important invertebrates (numerically or in terms of biomass) and fish have been plotted and ranked according to increasing $\delta^{15}\text{N}$. Species have been coloured in accordance with their supposed feeding guild. The ranking agrees to some extent with the accepted model of a benthic food chain, where fresh organic matter is assimilated by suspension-feeders – in this case bivalves. Surface-deposit feeders like the brittlestar *Ophiura albida*, the tubicolous polychaete *Owenia fusiformis*, and sipunculids assimilate a heavier (enriched) fraction of the organic material. Probably, this material has already been processed by other organisms e.g. bivalves and microbes. The suspension-feeder *Amphiura filiformis* also fits in this group, possibly owing to a selection of particles with a heavier $\delta^{15}\text{N}$ signature. Invertebrate predators and demersal fish rank highest in $\delta^{15}\text{N}$, consistent with the fact that they prey on other trophic levels (suspension-feeders, surface-deposit feeders). The range of $\delta^{15}\text{N}$ signatures among predators reflects the variation in prey items they take. Other conspicuous features of the species ranking in Figure 6.2.1 are: (a) large variation in $\delta^{15}\text{N}$ signatures of bivalves supposedly feeding on the same material, i.e. suspended matter (possibly this variation is explained by the different capacities of species to sort material on the gills); and (b) the relatively “light” $\delta^{15}\text{N}$ signatures of deep-burrowing mud shrimps (*Callinassa subterranea*, *Upogebia* spp.) which are reported as consumers of deep layers of sediment (Stamhuis *et al.*, 1998).

Although Figure 6.2.1 is far from complete, for example, because bacteria and meiofauna are missing, it nevertheless suggests that a linear food chain is probably a much too simple model for this community, notably at the base of the food chain, i.e. among suspension- and deposit-feeders. Many species classified in the same feeding guild can coexist because they are capable of sorting and assimilating different fractions of the same organic food pool. This capability also leads to similar trophic positions for organisms belonging to different feeding guilds.

shorter, and material is recycled at a higher rate. Conversely, a decrease in mud shrimps with increasing fishing pressure could indicate that more organic matter is available to interface-feeders, but whether this is true remains to be investigated.

Apart from inferring trophic levels and competition from $\delta^{15}\text{N}$ signatures, a more direct way to unravel foodweb relationships is to label whole communities with stable isotopes of C and N, as in intertidal habitats (van Oevelen *et al.*, 2006). Both in the deep sea (Moodley *et al.*, 2002; Witte *et al.*, 2003) and in the subtidal North Sea (e.g. Kamp and Witte, 2005), such experiments have been initiated, but the scale and duration still have technological limits, especially in relation to larger mobile species (crustaceans, fish). Other options for improved tracking of benthic food sources and foodweb relationships are using a combination of fatty acids and bulk stable isotopes (Ruess *et al.*, 2004) or stable isotope signatures in specific compounds such as lipids (Villinski *et al.*, 2004).

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6.3 Fishing practices

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6.3.1 Introduction

Since the first reports and alerts that bottom trawling and particularly beam trawling have a negative impact on benthic communities (see e.g. reviews by Collie *et al.* (2000) and Kaiser *et al.* (2002, 2006)) and possibly on demersal fish associated with these communities, efforts have been made to establish relations between fishing intensity (effort) and composition of the community. Attempts to resolve the long-term effects in this way, however, have been largely unsuccessful (Hall *et al.*, 1993; Bergman *et al.*, 1998; Craeymeersch *et al.*, 2000).

NSBP 2000 offers a new opportunity to identify long-term effects of fishing on the benthic communities on a North Sea-wide scale.

6.3.2 Material and methods

First, the species distribution data of 2000 (NSBP 2000 infauna data; see Section 3) were analysed in relation to effort data. 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 related directly to measured environmental variables: the first axes of the ordination are constructed in such a way as to explicitly optimize 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, because we are not interested in environmental variation, but want to focus on species responses to fishing disturbance.

Forward selection of the fishing effort variables (see below) was used to remove redundant variables, leaving only those that explained independently significant amounts of variation in the species data (identified using unrestricted Monte Carlo permutation tests; ter Braak and Smilauer, 1998). Variables were considered to be significant when $p < 0.05$ (199 permutations). Effort variables that did not add to the explanation of the species data were omitted from further analyses. The variance inflation factor (VIF) of the remaining effort variables was checked. High values of a particular variable indicate collinearity with other variables and should be excluded from the final canonical correspondence analysis (CCA). Possible effects of depth, sediment characteristics, temperature, salinity, wave stress, and tidal stress were factored in a partial CCA. The significance of all constrained axes of the final CCA was tested using Monte Carlo permutation tests (999 permutations). Data on species density, covariables, and fishing effort were available for 358 stations. Species that occurred in less than 1% of the samples were excluded, unless they had a density higher than 100 ind. m⁻² in a sample. Species data were square root transformed.

Second, we focused on whole-community changes between 1986 (North Sea Benthos Survey; Künitzer *et al.*, 1992; Craeymeersch *et al.*, 1997) and 2000. A nearest-neighbour comparison of stations sampled in 1986 and 2000 yielded a subset of 156 stations (see Section 5.2). At 123 of these stations, data on environmental variables were available. As in the first analysis, only species occurring in at least 1% of the stations were used, unless they had a density higher than 100 ind. m⁻².

There are no fishing effort data available for the first half of the 1980s and so a direct gradient analysis could not be done. Changes in species composition, therefore, were first described by an indirect gradient analysis, but with the same covariables as in the analysis of the 2000

dataset. We checked for changes in station scores on the first two unconstrained “residual” axes and the species involved. Next, a partial CCA ordination was conducted. The first axis was constrained to a time factor with two levels, in CANOCO represented by two sets of nominal variables (one for the year 1986 and one for the year 2000), i.e. maximizing the difference between 1986 and 2000. The significance of the first axis of the final CCA was tested using Monte Carlo permutation tests (999 permutations). Again, we checked for the largest changes in species scores and the contributing species.

All analyses were done with the program CANOCO, version 4 (ter Braak and Smilauer, 1998).

Environmental covariables at most of the stations were recorded at the time of sampling, and granulometry samples were taken (see Sections 3 and 4). Because all available sediment variables demonstrated a high correlation with each other (see Section 4), only one variable was used here: mud content (grain size <63 µm).

Tidal and wave (average and peak) stress data were derived from a model developed by John Aldridge (Cefas Lowestoft). Further details are given in Section 3.

Temperature and salinity data were retained from the HAMSOM model (Pohlmann, 1991): minimum and maximum values in February and June and the difference between February and June. Further details are given in Section 3.

Table 6.3.1. Species names used in figures.

| SPECIES NAME | TAXONCODE | SPECIES NAME | TAXONCODE |
|----------------------------------|-----------|-----------------------------------|-----------|
| <i>Abra nitida</i> | Abra niti | <i>Nothria conchylega</i> | Noth conc |
| <i>Acrocnida brachiata</i> | Acro brac | <i>Ophelina acuminata</i> | Ophe acum |
| <i>Ampelisca brevicornis</i> | Ampe brev | <i>Ophiodromus flexuosus</i> | Ophi flex |
| <i>Ampharete lindstroemi</i> | Amph lind | <i>Ophiothrix fragilis</i> | Ophi frag |
| <i>Aonides paucibranchiata</i> | Aoni pauc | <i>Ophiura albida</i> | Ophi albi |
| <i>Aricidea minuta</i> | Aric minu | <i>Ophiura ophiura</i> | Ophi ophi |
| <i>Bathyporeia tenuipes</i> | Bath tenu | <i>Paramphinome jeffreysii</i> | Para jeff |
| <i>Branchiostoma lanceolatum</i> | Bran lanc | <i>Pariambus typicus</i> | Pari typi |
| <i>Callianassa subterranea</i> | Call subt | <i>Pectinaria auricoma</i> | Pect auri |
| <i>Cerianthus lloydii</i> | Ceri lloy | <i>Pholoe pallida</i> | Phol pall |
| <i>Chone filicaudata</i> | Chon fili | <i>Phyllococe Anaitides</i> | Phyl Anai |
| <i>Cochlodesma praetenuae</i> | Coch prae | <i>Pisidia longicornis</i> | Pisi long |
| <i>Corbula gibba</i> | Corb gibb | <i>Pisione remota</i> | Pisi remo |
| <i>Diastylis bradyi</i> | Dias brad | <i>Podarkeopsis capensis</i> | Poda cape |
| <i>Edwardsia</i> | Edwa rdsi | <i>Polycirrus</i> | Poly cirr |
| <i>Eriopisa elongata</i> | Erio elon | <i>Polygordius</i> | Poly gord |
| <i>Exogone</i> | Exog one | <i>Protodorvillea kefersteini</i> | Prot kefe |
| <i>Gastrosaccus spinifer</i> | Gast spin | <i>Pseudocuma longicornis</i> | Pseu long |
| <i>Glycera alba</i> | Glyc alba | <i>Sabellaria spinulosa</i> | Sabe spin |
| <i>Goniadella</i> | Goni adel | <i>Scolecopsis bonnierii</i> | Scol bonn |
| <i>Goodallia triangularis</i> | Good tria | <i>Sphaerodorum gracilis</i> | Spha grac |
| <i>Heteromastus filiformis</i> | Hete fili | <i>Spio filicornis</i> | Spio fili |
| <i>Leucon nasica</i> | Leuc nasi | <i>Streptosyllis websteri</i> | Stre webs |
| <i>Leucothoe incisa</i> | Leuc inci | <i>Tellina tenuis</i> | Tell tenu |
| <i>Levisenia gracilis</i> | Levi grac | <i>Travisia forbesii</i> | Trav forb |
| <i>Mediomastus fragilis</i> | Medi frag | <i>Unciola planipes</i> | Unci plan |
| <i>Megaluropus agilis</i> | Mega agil | <i>Upogebia deltaura</i> | Upog delt |

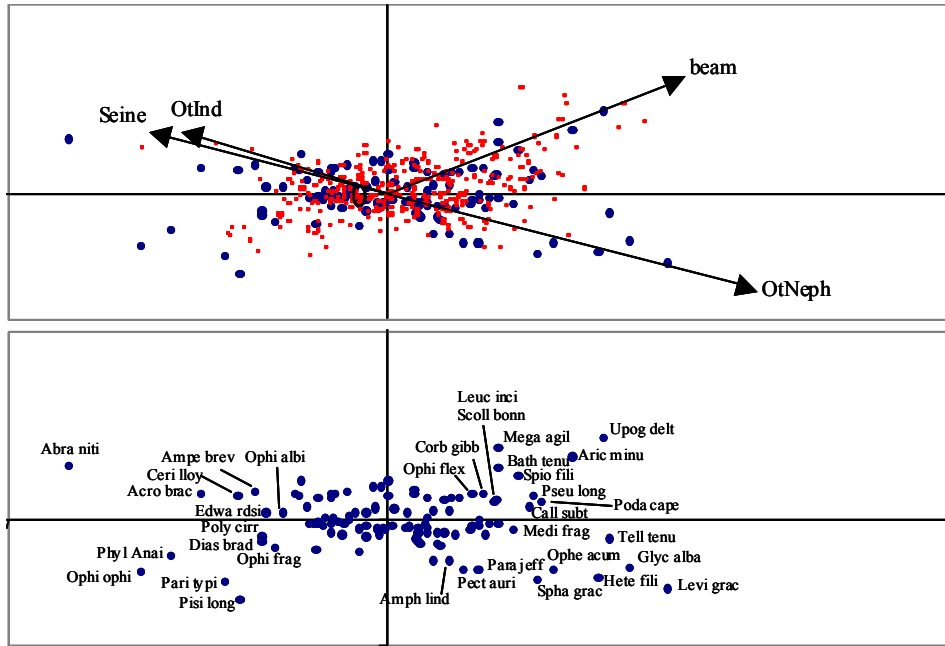


Figure 6.3.1. CCA ordination diagram based on the analysis of the 2000 data. The upper panel shows the distribution of samples (red) and species (blue) in relation to effort variables (arrows). The orthogonal projection of a species point onto an effort arrow represents the approximate centre of the species distribution along that particular gradient. The lower panel shows the species codes for selected species having their distribution centre situated at the ends of the fishing effort gradients (see Table 6.3.1 for species names).

Fishing effort

For components of the marine ecosystem beyond the targeted commercial species, measures of fishing effort provide the most appropriate means of quantifying levels of fishing activity (Greenstreet *et al.*, 2007b). Fishing effort statistics are available on the scale of the ICES rectangle, based on logbook data. It is known, however, that the effort is not distributed evenly within each rectangle (Rijnsdorp *et al.*, 1998). The most spatially detailed data on the distribution of the fishing fleets are the VMS data (European Community Satellite-based Vessel Monitoring System). Unfortunately, for most countries, access to the data is difficult or restricted. It was impossible, therefore, to get high-resolution effort data for the whole North Sea for the present study.

The MAFCONS project (www.mafcons.org) recently assembled the effort data as hours effort by gear per ICES rectangle (for the 215 rectangles in Area IV) per year (1997–2004) for UK, Dutch, Norwegian, and German vessels (Greenstreet *et al.*, 2007b). The major gears were assigned to six categories: otter trawl directed at fish for human consumption (OtFish), otter trawl directed at *Nephrops* (OtNeph), otter trawl directed at other invertebrates, e.g. shrimp, (OtInv), industrial otter trawling (OtInd), beam trawl (Beam), and seine gear (Seine). The data were kindly made available for this study. We used the sum of effort over the years 1997–2001.

6.3.3 Results

6.3.3.1 2000 data

The partial CCA did not reveal high VIF values for any of the effort variables (the maximum VIF was 2.6). Four effort variables were retained by the selection procedure among those initially considered in the CCA: effort by beam trawling, effort by otter trawling for *Nephrops*, industrial otter trawling, and seine gear. Otter trawling directed at fish and other invertebrates and total effort were not added to the model. Fishing effort only accounted for a small part of

the residual variance ($p = 0.001$, 2.8% of total variance of species data explained). The first axis explained 1.1% of the variance, the second 0.7%, the third 0.6%, and the fourth 0.4%. Thus, the first axis was not much more important than the second and third. The covariables (temperature, salinity, depth, sediment, shear stress) explained a significant part of the total variance in the species composition (test of all canonical axes: $p = 0.001$). The first three axes explained 15.7% of total variance of species data.

The position of the samples, species, and effort variables in the first ordination plane is given in Figure 6.3.1. Beam trawling and otter trawling for *Nephrops* are more strongly correlated with the ordination axes than the other two effort categories.

Figure 6.3.2 shows the ordination values on the first axis superimposed on the position of the samples. Apparently, stations on the left of the ordination diagram (shown green in Figure 6.3.2) are situated either in the northern North Sea or in a zone reaching from the Wash, south of the Dogger Bank, to its northeastern part and farther southeast to the Jade Bay.

6.3.3.2 Comparing 1986 and 2000

Figure 6.3.3 displays the partial CCA ordination diagram (first two axes); the magnitude of the change between the 1986 and 2000 surveys at each station is mapped in Figure 6.3.4. Most stations revealed a relatively small shift in their position from 1986 to 2000: see e.g. the two points farthest right in the upper panel of Figure 6.3.3, which are situated north of Borkum (ns695 = ra490). The largest (residual) differences apparently occurred at stations ns770 and ns741, both situated in Danish coastal waters. Species such as *Pisone remota*, *Branchiostoma lanceolatum*, and *Protodorvillea kefersteini* were more abundant in 2000 than in 1986, at least in one of these stations. Most of the other stations characterized by (relatively) large changes in species composition moved towards the upper left of the ordination diagram (see central panel of Figure 6.3.3). This shift is characterized by the presence and/or higher densities in 2000 of e.g. *Sabellaria spinolusa*, or the absence and/or lower densities of e.g. *Streptosyllis websteri* or *Travisia forbesi*. Most of these stations are situated along the UK coast and in the northern North Sea, except for station ns700 (= du27).

Figure 6.3.5 shows the shift in station scores along the first axis of the partial CCA, constrained by the year of sampling, while Figure 6.3.6 shows the species having the most negative and positive scores, and the centroids of the classes of the nominal variable “year”. The most striking difference with Figure 6.3.4 is the apparent relatively small difference at stations off Denmark. It further demonstrates relatively larger differences at several stations in the southern North Sea. *Echinocardium flavescens*, *Ophelia borealis*, *Ophiocten affinis*, and *Nothria conchylega* in particular were more abundant in 1986, *Lumbrineris gracilis*, *Mediomastus fragilis*, and *Ampharete lindstroemi* in 2000.

6.3.4 Discussion

The direct gradient analysis of the 2000 data (Figure 6.3.1) seems to point to a small but significant difference in species composition between areas experiencing different fisheries. Stations situated to the left in the ordination diagram are experiencing highest effort for seine gear and/or industrial otter trawling. Seine gear is most important in the northern North Sea, the German Bight, and on the Dogger Bank (Figure 6.3.7). Industrial otter trawling is most important in the Dogger Bank area and around the Shetland Islands. Stations situated to the right in the ordination diagram are associated with highest effort on beam trawling or *Nephrops* trawling. Effort associated with otter trawling for *Nephrops* is highest in UK waters off Northumberland and Scotland. Beam trawl effort is highest in the southern North Sea off the continental coast.

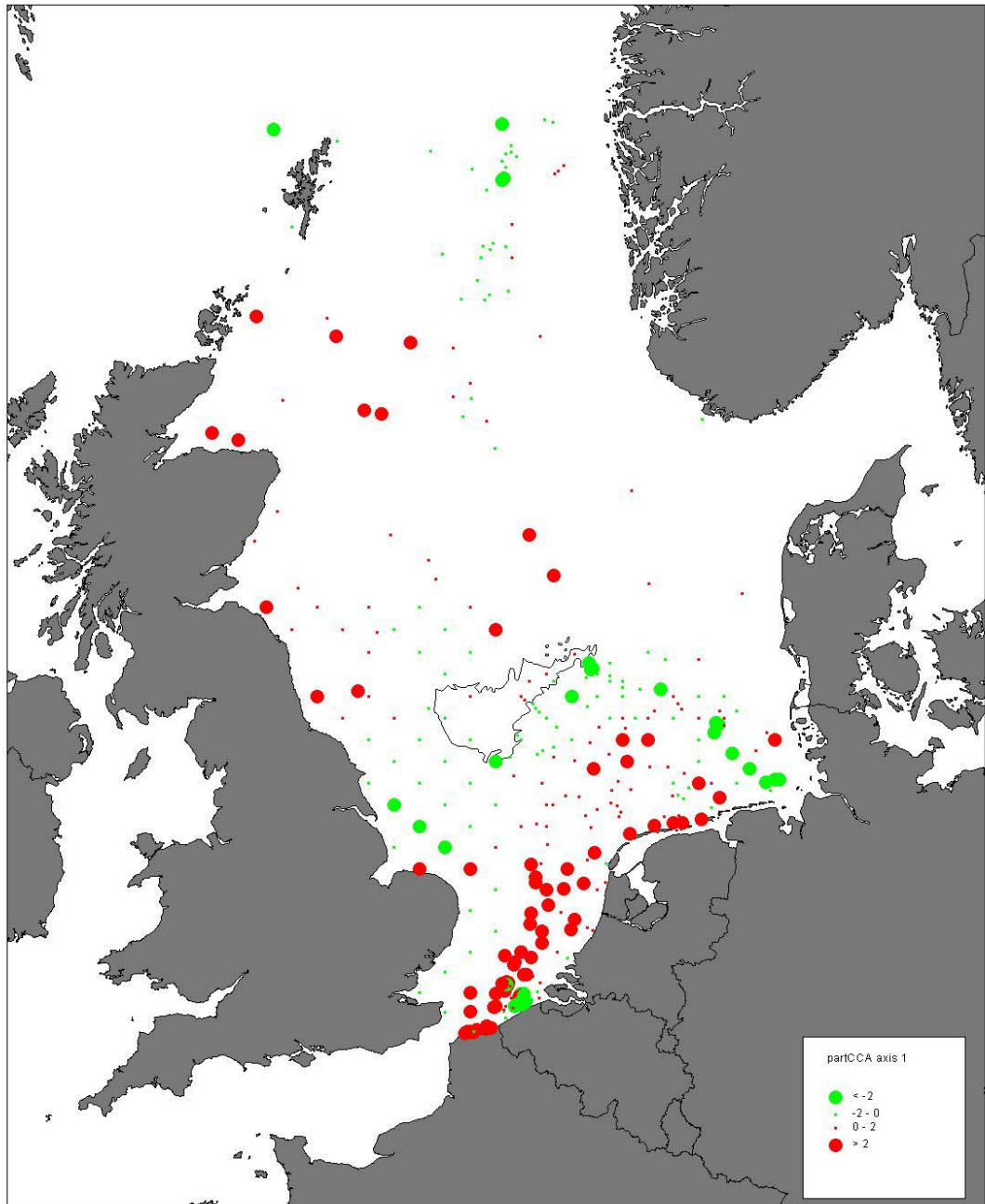


Figure 6.3.2. Position of the stations with the value on the first ordination axis superimposed (partial CCA of 2000 data).

Along the fishing effort gradients, the species composition differs between intensively fished locations and less heavily fished locations. The location of, for example, the spionid *Spio filicornis* in Figure 6.3.1 indicates a positive correlation with beam trawl pressure. Opportunistic species, among them many members of the spionids, are characterized by high growth rates, a short lifespan, a low reproductive age, and a large reproductive output. These characteristics permit them to adapt rapidly to environmental perturbation and quickly recolonize disturbed 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 variously as an effect of eutrophication, pollution, and/or fisheries (Gray *et al.*, 1990; Rachor, 1990; Kröncke, 1992).

Similar observations apply to the bivalve *Corbula gibba*. *C. gibba* is tolerant of a wide range of environmental disturbances. In soft bottom communities that are degraded or recovering from stress, the species appears to be highly abundant (Hrs-Brenko, 2006). *C. gibba* exhibited an increased density in areas dredged for blue mussels (Dolmer *et al.*, 2001).

The brittlestar *Ophiura ophiura* is situated in the lower left part of the ordination diagram of Figure 6.3.1, indicating higher densities in the areas less impacted by beam trawling. Mortality rates of this “discard” species, however, are low because of their relatively flexible exoskeleton and their ability to regenerate arms (Kaiser and Spencer, 1995; Kaiser, 1996). Nevertheless, a reduced biomass of ophiurid species has been recorded in trawled areas (Prena *et al.*, 1999).

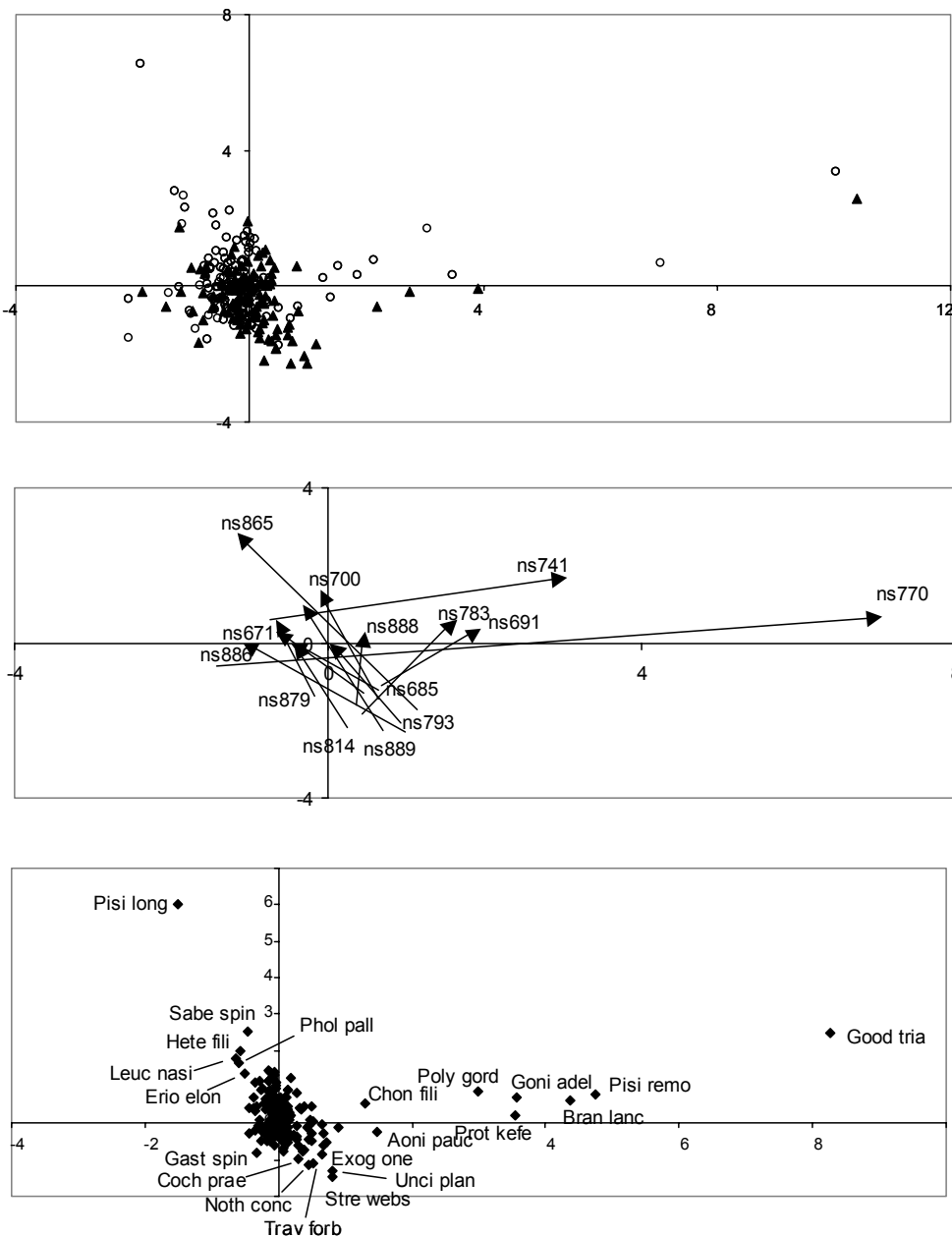


Figure 6.3.3. Ordination diagram of the partial CCA of the stations sampled in 1986 and 2000. Upper panel: samples (open circles: 1986; closed triangles: 2000). Central panel: most important shifts in the position of stations in the first ordination plane (station codes correspond with those used for the 1986 survey; see Figure 6.3.4 for their position). Lower panel: species (see Table 6.3.1 for species names).

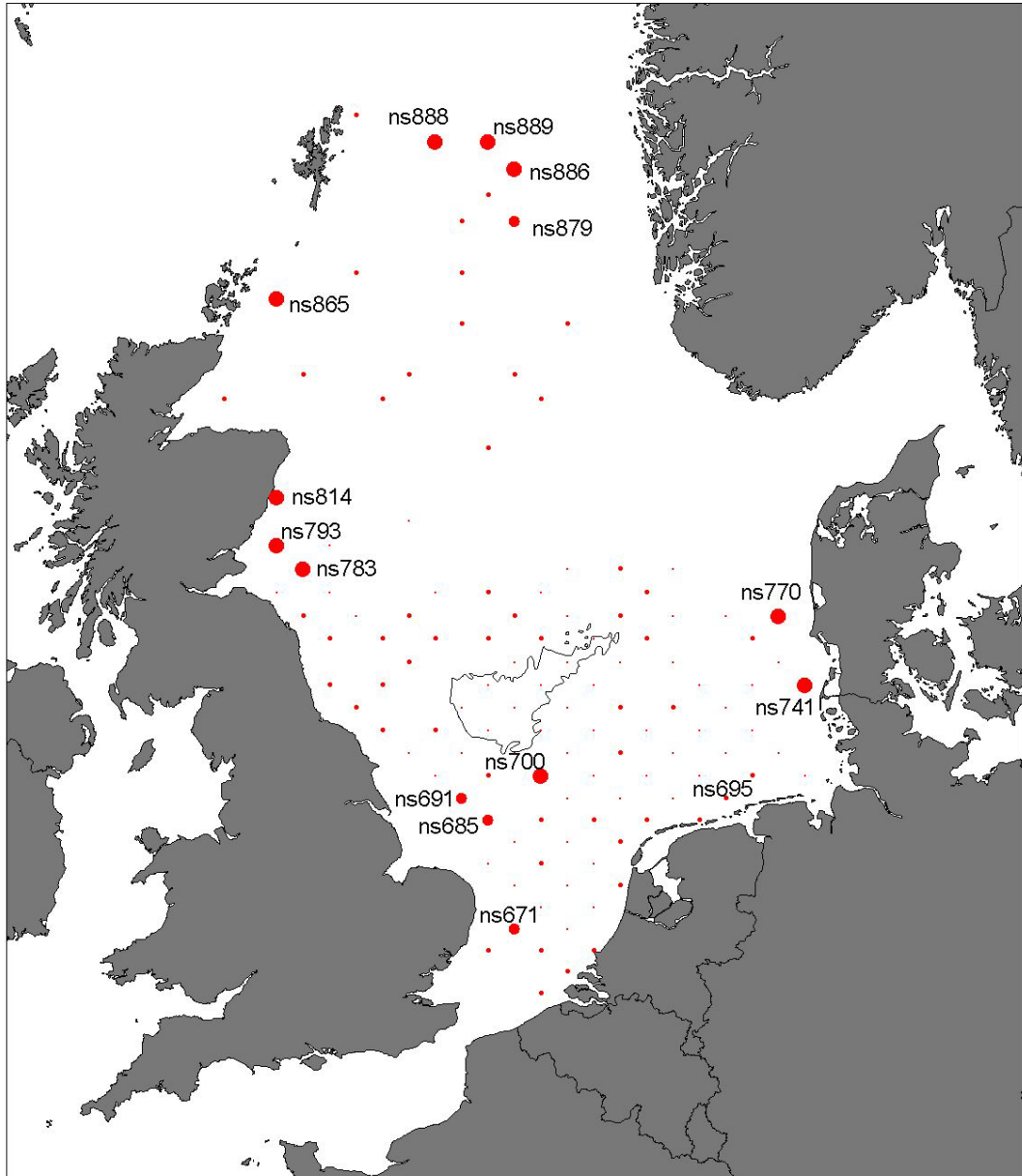


Figure 6.3.4. Position of the stations sampled in both 1986 and 2000 used for the partial correspondence analysis. The superimposed symbols represent the change in species composition: the larger the radius of the circles, the larger the change of the position on the first ordination plane.

Recently, Bergman *et al.* (2005) reported significantly larger numbers of deep-burrowing mud shrimps (thalassinids), which, through their mode of life, are not in direct contact with fishing gear. Mud shrimps strongly influence important ecosystem functions, such as nutrient recycling, microbial diversity, and sediment resuspension. If indeed fishing reduces such species, then the negative fishing effect will extend beyond what has been published so far. Our results, however, point to a positive effect of beam trawling and/or *Nephrops* trawling on the thalassinid species *Upogebia deltaura* and *Callinassa subterranea*.

For many species, a positive or negative relationship with fishing effort is hard to explain. Moreover, the apparent effect of seine gears and industrial otter trawling is surprising. Although seine gears catch considerable numbers of fish, they have a relatively low impact on benthic organisms (Greenstreet *et al.*, 2007b).

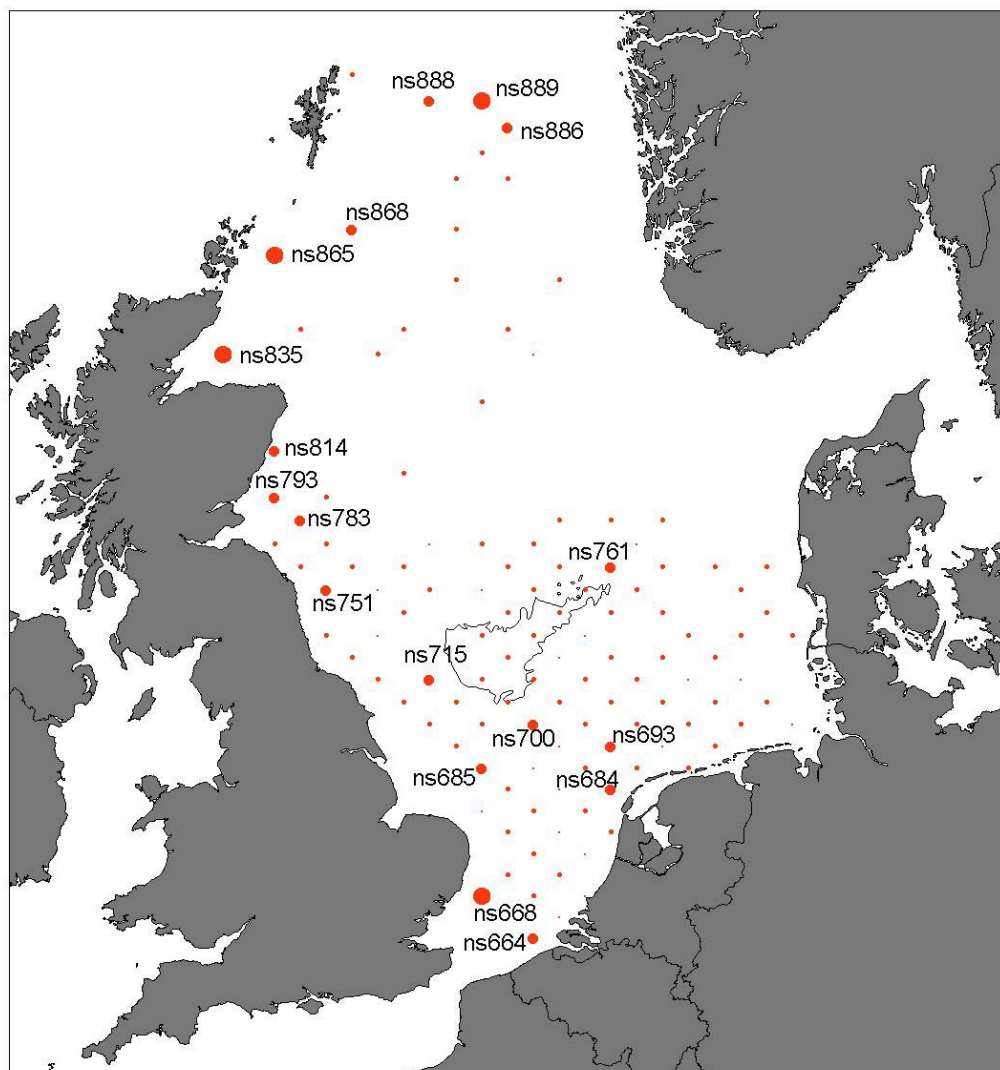


Figure 6.3.5. Position of the stations sampled in both 1986 and 2000 used for the partial CCA, constrained to the sampling year. The superimposed symbols represent the change in species composition: the larger the radius of the circles, the larger the change of the position on the first, constrained, ordination axis.

The relationship between fishing effort and community structure, therefore, is most probably largely correlative and not causal. The regional differences are not governed by the impact of fisheries, but most likely by environmental differences not factored out in our analysis. Distributions of benthos and fish in the southern North Sea are governed by the same strong natural gradients. The result is that certain types of communities are fished more frequently. The overlap of patterns in fishing effort and benthic communities hampers assessment of impacts because of the paucity of un- or less-disturbed reference sites within communities. A robust assessment of fishing impact, therefore, should be made within a community. It should be noted, however, that, even within benthic communities, patterns in species composition might exist related to differences in their environment. In that case too, a relationship between fishing effort and community structure might be correlative. This was the case in a study in two subareas in Dutch waters (Craeymeersch *et al.*, 2000). Although known differences in depth and sediment composition were factored out, the results pointed to a relationship with environmental variables not included in their study. Thus, the fact that unfished areas are usually unfished precisely because they differ from real fishing grounds further complicates the interpretation of such studies (Hall *et al.*, 1993). For investigations of the effects of fishing

gear, it would be preferable if part of a commercially fished area characterized by a relatively homogeneous environment could be closed, so that differences in fishing effort are not related to natural structural differences.

The differences in the community structure between 1986 and 2000 do not appear to be related to changes in fishing effort. Almost all species characterizing the most important shifts are not known to be particularly vulnerable to fishing disturbance.

The largest changes occurred in the northern North Sea and in the coastal areas. In the northern North Sea, the observed differences might be caused by different sampling methodology and better taxonomy (see Section 5.2). Moreover, the geographical position of many stations was not the same in both years, particularly in the northern North Sea.

Interannual changes of benthos might be caused either by successful recruitment of species modifying the species composition or by mortality of the adult stock (Reiss and Kröncke, 2006). Factors influencing the mortality of the adult stock will affect the interannual variability more than recruitment processes. The effect of severe winters, e.g. resulting in a reduction of cold-sensitive species and drastic changes in community structure, therefore, is more important in coastal areas than in offshore waters (Reiss *et al.*, 2006). In offshore waters, environmental changes in community structure are mainly caused by large-scale, long-term environmental changes, reflected in changes in species presence or absence. Hydroclimate change also affects nearshore communities, but mainly through effects on the abundance and biomass of common species, rather than species composition (Wieking and Kröncke, 2001; Reiss and Kröncke, 2006). Overall, the interannual variability is larger in coastal waters than in offshore waters (Reiss and Kröncke, 2006). Therefore, it is not surprising that, in our study too, the largest changes were found at stations in coastal waters.

In both analyses comparing 1986 and 2000, the community composition of station ns700 proved to be changed. Species such as *Arctica islandica*, *Echinocardium flavescens*, *Ophelia borealis*, and *Travisia forbesii* were not found in 2000; *Mediomastus fragilis* was not found in 1986. Station ns700 is one of the stations on the Dutch continental shelf sampled for macrobenthos since 1995 as part of the “biological monitoring programme of marine waters” (see e.g. Daan and Mulder (2005), station OYS20). In the period 1995–2005, *E. flavescens* and *T. forbesii* have never been found. Both species had very low densities in 1986 (only 3 ind. m⁻²). *Arctica islandica* was found up to 1999, always with densities higher than in 1986. *Mediomastus fragilis* was only recorded twice: in 2000 and in 2004. Nevertheless, the community composition at that station has changed, with a major shift in the mid-1990s (Figure 6.3.8). *Nephtys caeca*, *Glycera lapidum*, and *Echinocyamus pusillus* have not been recorded at this station from 1996 onwards. Higher densities of e.g. *Amphiura filiformis* and its commensal *Mysella bidentata* characterize the period 1996–2005.

The brittlestar *A. filiformis* is highly vulnerable to physical disturbance and experiences an increased predation owing to exposure after trawling (Kaiser and Ramsay, 1997; Queirós *et al.*, 2006). Indeed, Bergman *et al.* (2005) found higher densities of this brittlestar in the non-fished zone around an offshore platform compared with regular fished areas in the vicinity. Queirós *et al.* (2006) concluded that the effects of trawling were the most likely explanation for the observed relationship between the abundance of *A. filiformis* and fishing intensity in the Irish Sea. At the Frisian Front, annual monitoring (1982–2002) demonstrates a shift from a community dominated by *A. filiformis* to a community dominated by the mud shrimp *Callianassa subterranea* at the southernmost locations (Amaro, 2005). At the northern stations of the Frisian Front, *A. filiformis* increased in density, suggesting a distributional shift of the population to the north. The observed decline at southern locations took place over a period of five years (1992–1997). Because the Frisian Front has been fished for many years, Amaro (2005) concludes that fishing is, therefore, an unlikely reason for the observed shift. Station ns700 is situated at the same latitude as these northern stations. Thus, it is very likely that the

observed increase at station ns700 is caused by the same, as yet unrevealed factor as the shift at the Frisian Front and not related to fishing practices.

Not surprisingly, the analysis also demonstrates that relating whole-community changes between the two sampling occasions (1986 and 2000) with changes in fishing effort is very difficult because of the absence of information, especially on concurrent natural changes on a comparable scale in the intervening years.

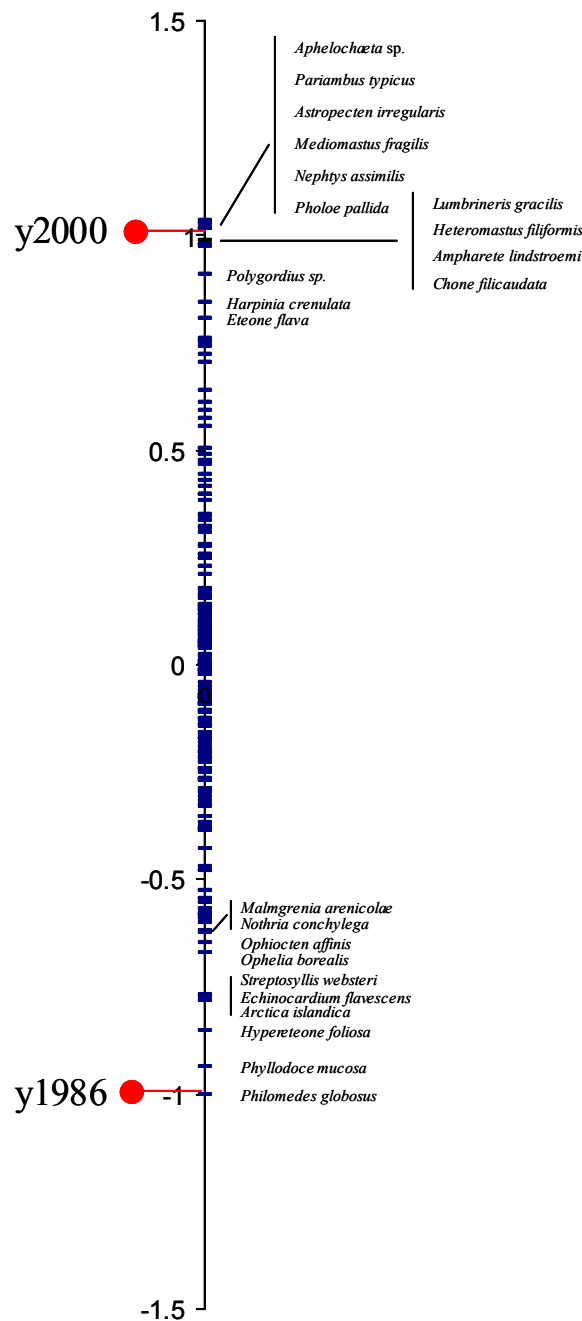


Figure 6.3.6. Position of the species (blue stripes) and the centroids of the two classes of the nominal variable “year” (red circles) along the constrained axis of a partial CCA (comparison 1986–2000). The species names for the ten most negative and positive scores are shown.

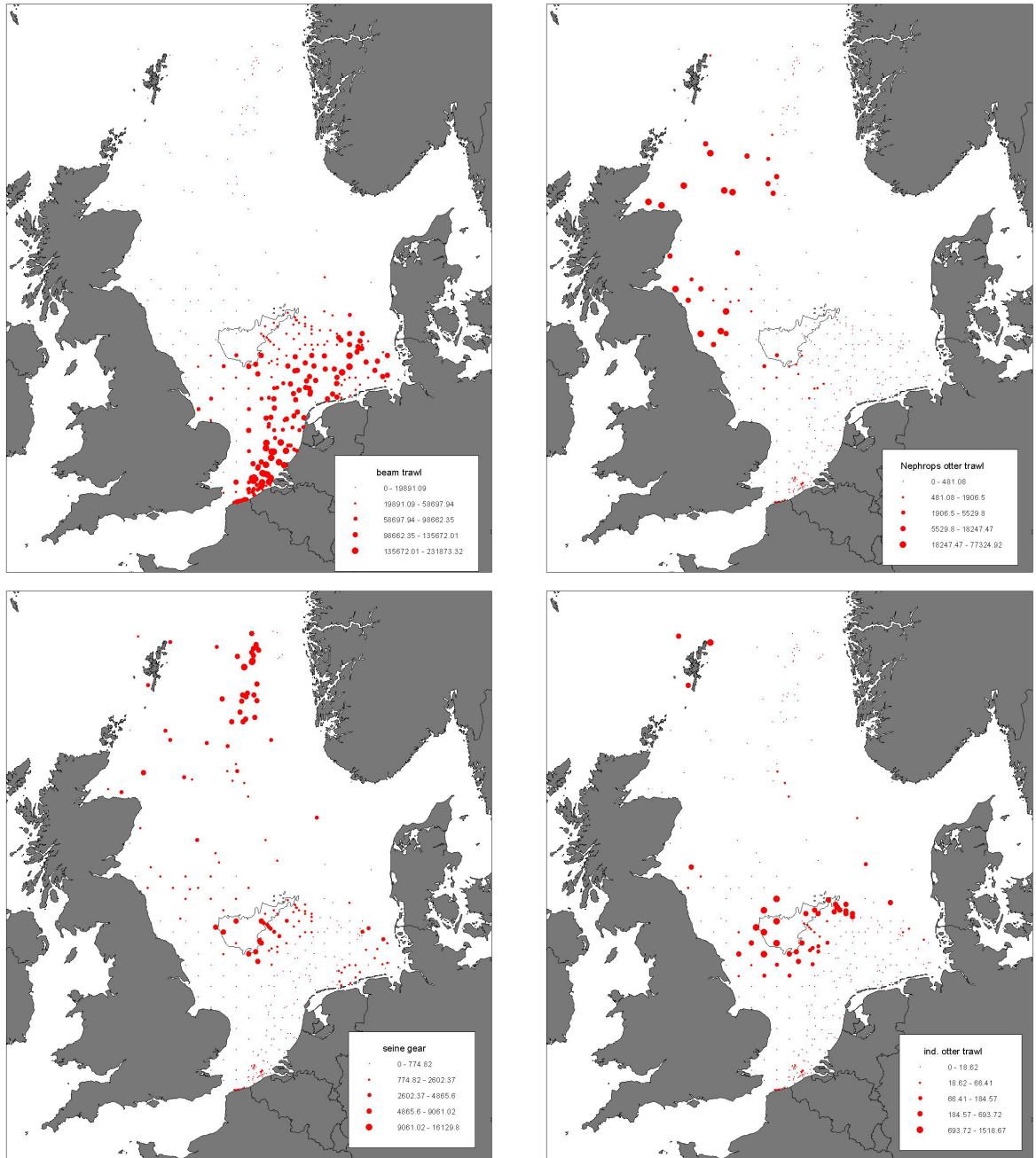


Figure 6.3.7. Spatial distributions of fishing effort (hours-fishing) using beam trawl, otter trawl for *Nephrops*, seine gear, and industrial otter trawl.

The results further demonstrate the existence of environmental gradients not factored out. In Figure 6.3.3, station ns695 (= ra490) is situated to the extreme right of the first ordination plane in both 1986 and 2000, and is characterized by the presence of *Goodallia triangularis*. The station is located at the Borkum Reef Ground, characterized by a specific and diverse fauna with mixed or coarse sediments. *Goodallia* was found by several studies in that area and also in the coarse sediments of the Amrum Bank (west of Sylt/Amrum). Both of these areas are relatively heterogeneous in sediment structure and habitat types. At least in the German EEZ, *G. triangularis* is only found on coarse sediments of the coastal areas (Rachor and Nehmer, 2003). Apparently, not all differences in sediment characteristics have been factored out.

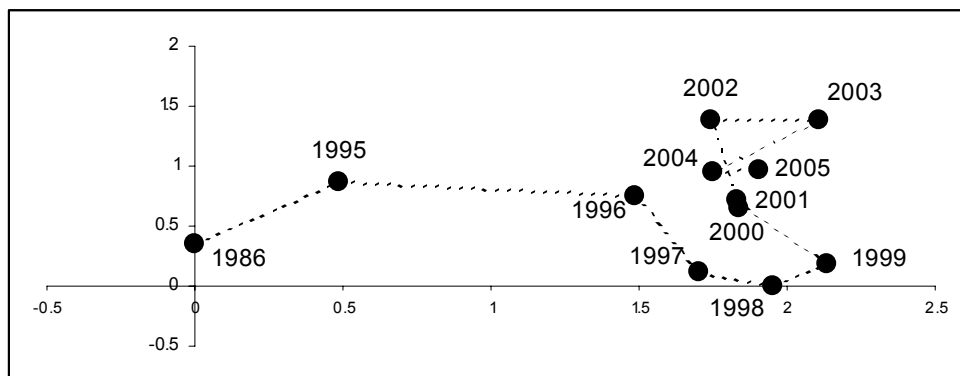


Figure 6.3.8. DCA ordination diagram of the macrobenthic infaunal community at station ns700 (data from the biological benthic monitoring of the Dutch continental shelf; see e.g. Daan and Mulder (2006)).

Lessons from other studies and future research directions

In this study, we focused on the whole macrobenthic infaunal community. As in previous studies, establishing a relationship between the distribution patterns of the benthic fauna and those of fishing intensity using ordination methods proved to be difficult. There is no means of establishing unequivocally that the disturbance of fishing is the only factor involved. One reason may be the lack of control areas, making it impossible to link observed changes directly with fishing (Frid *et al.*, 2000). This might also be caused by the fact that species not robust to fishing disturbance became rare many years ago. Studies on direct trawl path mortality indicated that large individuals of a species are generally more vulnerable than small ones (Bergman and van Santbrink, 2000). Moreover, the chance of being fished or destroyed increases with age. Because of the limited sample size, instruments such as boxcorers and van Veen grabs (both used in this study) are not suitable for sampling large species and/or species of low abundance (Bergman and van Santbrink, 1994), and certainly not for sampling epibenthic organisms.

Bergman *et al.* (1998) attempted to correlate fine-scale patterns of epi- and larger infauna with those of fishing effort in the Oyster Ground (southeastern North Sea). The area has gentle gradients of abiotic “nuisance” parameters, e.g. median grain size, mud percentage, and water depth and high invertebrate abundances. Data on species and fishing intensity in a total of 53 one-square-mile plots were used. Species were collected with a triple-D dredge while trawling effort was estimated from satellite tracking (APR system). Despite the relative homogeneity of the region in abiotic conditions, species composition was nevertheless clearly correlated with depth, grain size, and latitude. Trawling effort explained a significant but lower percentage of the variance in the fauna composition than each of the other variables. After correction for the relationship with abiotic variables, CCA ordination revealed a negative correlation between abundances of *Chamelea gallina*, *Acanthocardia echinata*, *Echinocardium cordatum*, and *Turritella communis* and trawling effort. For many species, abundances of larger (i.e. older) specimens were more negatively correlated with trawling effort than younger specimens.

The important fact that larger animals are more strongly affected by bottom trawling was confirmed in later studies by Kaiser *et al.* (2000) and Jennings *et al.* (2001). These authors compared production in two areas with a 10- to 27-fold difference in trawling intensity and found that, with the relative depletion of larger animals in the heavily fished area, total benthic production decreased accordingly. The enhanced production by smaller animals they observed in this area did not compensate for the loss in production by larger organisms. Remarkably, in the epifaunal community, no change in production was found.

Recently, Bergman *et al.* (2005) compared the composition, biomass, and production of small infauna (“boxcore fauna”) and larger in- and epifauna (“dredge fauna”) in an area closed to

fishing for 20 years with adjacent fished areas. Also in this study, larger in- and epifauna (dredge fauna) appeared significantly depleted in the fished areas in terms of the variety and densities of species, as well as biomass. Greater abundances of mud shrimps (*Callinassa subterranea*, *Upogebia deltaura*) and sensitive bivalves, both long-lived (*Arctica islandica*, *Thracia convexa*, *Cardium echinatum*) and shorter lived species (*Abra nitida*, *Cultellus pellucidus*), were evident near the platform. Species richness and evenness were greater as well. A similar analysis of the infauna collected with a boxcorer did not reveal a difference between the fauna in the closed platform subarea and that in the trawled reference areas. This is attributed to the large proportion of small, short-living species common to all boxcores and the relatively low abundances of sensitive larger species. The Triple-D dredge specifically targets these relatively less abundant, large, and long-living species such as bivalves. However, boxcore samples did confirm the greater abundance of mud shrimps (*C. subterranea*, *U. deltaura*) in some but not all non-fished platform subareas. There is no obvious explanation why not all subareas differ from the platform area, but is probably, at least partially, related to differences in beam trawl effort.

Thus, body size determines responses to mortality. Both the immediate mortality and the longer term ability of populations to cope with this mortality are functions of body size. Size-based models, therefore, are likely to provide a useful framework to examine the impact of trawling activities on the entire benthic community at the scale of a fishery (Duplisea *et al.*, 2002; Hiddink *et al.*, 2006). The model of Duplisea *et al.* (2002) provided a means of predicting the impact of trawling on biomass and production. Hiddink *et al.* (2006) extended the model to allow for the effects of habitat parameters on the dynamics of benthic communities. The initial and long-term impact of fishing depends on the fishing gear type and is habitat specific. A meta-analysis of 101 different fishing impact manipulations (Kaiser *et al.*, 2006) revealed that the most severe impact occurred in biogenic habitats, the smallest impact in naturally disturbed habitats (mobile sands). The extended model also allowed the prediction of the effects of trawling on species richness. The approach is based on general principles of allometry and a generalized body mass vs. species richness relationship. The model demonstrated that fishing disturbance in situations of high natural disturbance had a much smaller effect on the benthos than in situations of low natural disturbance. The model predicted that benthic community biomass was reduced by 56% and production by 21%. The model does not account e.g. for shifts in species composition that are not reflected in simple biomass or production estimates. A major part of the variation in biomass of epifauna remains unexplained, and the present model does not include predictions for biogenic habitats. The results indicate that size-based models can indeed be used effectively, but need further development.

This conclusion is further supported by the results of a recent EC-funded, North Sea-wide initiative to determine the ecosystem effects of bottom disturbance by fishing activities (MAFCONS). The primary aim of MAFCONS was to provide the tools to the scientific advisors of fisheries managers that would allow them to quantify the consequences to groundfish and benthic invertebrate species diversity of achieving particular fisheries objectives, supported by a sound theoretical basis. MAFCONS evaluated Huston's Dynamic Equilibrium Model, a species-based model. The model, however, failed to predict the response of species diversity to variation in productivity and disturbance and, therefore, could not provide the theoretical basis for a management protocol aimed at predicting the diversity consequences of specific disturbance regimes (Greenstreet *et al.*, 2007a).

In conclusion, future evaluations of the NSBP data should focus on the body-size structure of the benthic communities. Infaunal biomass data are now available for most of the stations (see Section 3). Epifauna data, unfortunately, are mostly not integrated in the ongoing monitoring programmes. Data are available from other programmes, but do not allow an accurate station-by-station comparison (see Section 6.1). Future projects and monitoring programmes should

aim at an integrated sampling of all benthic faunal components at all stations, to permit a comprehensive analysis of the faunal patterns and the underlying processes (Section 6.1) and disturbance pressures.

In the present study, fishing effort data were available on the scale of ICES rectangles. Even these data suffer from the lack of good coordination (Greenstreet *et al.*, 2007a). Finer-scale data, however, are necessary for precise modelling. Thus, we endorse the conclusion of the MAFCONS report that the spatial information provided by the Vessel Monitoring by Satellite scheme should be extended to include all fishing vessels, the monitoring frequency should be increased, and the data should be made readily available to scientists. This would also allow the continued observation of changes in the benthic communities in areas undergoing spatial changes in fishing effort.

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6.4 Patterns of nematode populations in the southwestern North Sea and their link to other components of the benthic fauna

Michaela Schratzberger

6.4.1 Background

During the past decade, considerable progress has been made in describing structural aspects of the biological communities of the offshore demersal ecosystem, and in particular the determinants of the distribution and abundance of larger, commercial species and the assemblages in which they occur (Dyer *et al.*, 1983; Frauenheim *et al.*, 1989; Rogers *et al.*, 1998; Jennings *et al.*, 1999; Rees *et al.*, 1999; Callaway *et al.*, 2002). There are fewer datasets available for smaller macrobenthic infauna and meiofauna, and no comparable assessments of community structure of these components on regional scales, despite the important contribution of these taxa to benthic biomass and productivity (Heip *et al.*, 1992; Huys *et al.*, 1992; Kunitzer *et al.*, 1992; Heip and Craeymeersch, 1995).

Numerically, the nematodes are the dominant animal group in most marine meiobenthic habitats. Their ubiquitous distribution, as well as their high abundance and diversity, often provides more robust datasets than can be obtained from most larger organisms. The ecological and practical advantages of using nematodes in benthic biological studies (summarized by Schratzberger *et al.*, 2000) provide good reasons to study nematode communities in the southwestern North Sea, where this important ecosystem component has not been previously studied in detail. The objective of this investigation, therefore, was to evaluate the contribution made by this group to the benthic community on a regional scale. Specific aims were:

- 1) To provide novel information on the species composition and abundance of North Sea meiobenthic nematode assemblages and identify the main environmental variables, biogeographical factors, and potential anthropogenic impacts that determine the distribution of community types;
- 2) To compare biotic data obtained from this survey with data from the study of other faunal groups in the study area (including macrobenthic infauna, invertebrate epifauna, and fish) to provide a more complete assessment of the ecology of the southwestern North Sea.

6.4.2 Methods

Nematode assemblages were collected at a subset of 19 stations in the southwestern North Sea (Figure 6.4.1), sampled under the auspices of NSBP 2000. To minimize the potential effect of anthropogenic activities on nematode communities, most stations studied were located away from point-source impacts. At each station, replicate sediment samples were collected from within a 100 m range ring by means of a 0.1 m² Day grab. From each Day grab, two subsamples, one for particle size and organic carbon content analysis and one for the study of meiofauna, were collected with a Perspex corer (7.1 cm² surface area) to a depth of 5 cm. The remainder of the sediment was retained for analysis of the macrobenthic infauna.

Meiofauna samples were washed onto a 63 µm sieve and processed following the extraction protocol described by Somerfield and Warwick (1996). All nematodes were counted and identified to genus or species level. Macrofauna samples were washed through a 1000 µm sieve, and retained individuals were counted and identified to family or species level.

Patterns observed for meiobenthic nematodes and macrobenthic infauna were compared with those from larger fauna, including invertebrate epifauna and fish. Invertebrate epifauna in the study area were collected in 2000 by means of a 2 m beam trawl, fitted with a chain mat. The trawl was towed for 5 minutes at approximately 1 knot. Sampling of fish communities

consisted of 30-minute tows at 4 knots with a Grande Ouverture Verticale (GOV) otter trawl (Figure 6.4.1). Trawl samples were washed through a 5 mm sieve, and fauna were identified to family or species level.

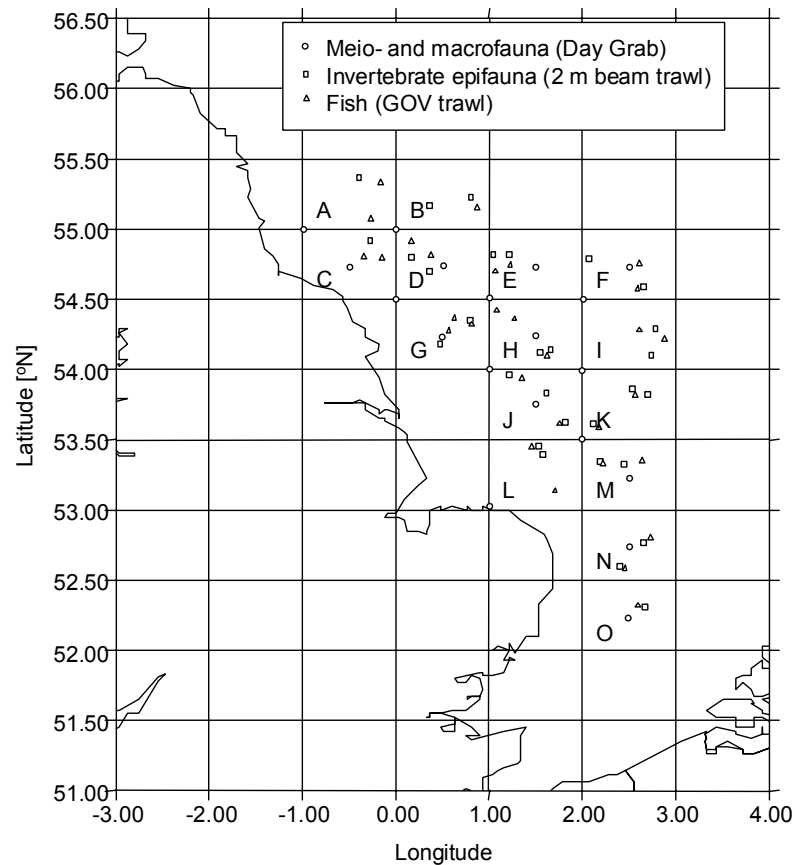


Figure 6.4.1. Location of stations in the southwestern North Sea sampled for meiobenthic nematodes, macrobenthic infauna, invertebrate epifauna, and fish in 2000/2001.

The comparison of nematode records with those of the above-mentioned faunal groups was based on a grid of ICES rectangles, because not all sampling positions coincided. Nematode and macrofauna sampling stations, located at the corner of a rectangle, were assigned to the rectangle to the northeast of the original sampling position (Figure 6.4.1, Areas A–O).

A combination of univariate and multivariate statistical analyses were performed, based on species abundance data. For each, appropriate statistical tests (e.g. one-way analysis of variance for univariate indices or one-way analysis of similarities for multivariate data) were applied to determine the significance of differences between replicated samples. The nature of the relationship between environmental variables and univariate community attributes was investigated using simple regression analyses. The relationship between environmental parameters and community structure was assessed by calculating rank correlations between similarity matrices derived from the biotic data and matrices derived from various environmental data (Clarke and Warwick, 1994).

6.4.3 Results

The study area comprised a temporally stable, sedimentary environment, decreasing significantly in depth towards the south ($F = 4.74$, $p = 0.04$) and the east ($F = 9.89$, $p = 0.01$). Comparatively lower tidal currents at higher latitudes resulted in increasingly finer sediments ($F = 23.00$, $p < 0.01$). Most of the sediment studied consisted of moderately to poorly sorted muddy sands with a generally low silt/clay fraction and low concentrations of trace metals.

Nematode density and species richness increased significantly with decreasing median particle diameter of the sediment. Species richness, diversity, and dominance of resident biota were significantly correlated with water depth. High diversity assemblages with a low degree of dominance were typical for deeper waters (>60 m) in the northern part of the study area. Spatial differences in environmental parameters and biogeographical factors were also highly influential in determining species distribution patterns. The most important environmental measures were water depth, median particle diameter, as well as the composition (% sand and silt fraction) and sorting of the substrate. The concentration of most trace metals and carbon content in the sediment bore little relation to univariate community attributes and observed species distribution patterns.

Nematode, macrofauna, epifauna, and fish datasets differed in terms of number of (sub)Phyla and species (Table 6.4.1).

Table 6.4.1. Number of (sub)Phyla, orders, and species in the datasets used.

| | SIZE RANGE (MM) | (SUB)PHYLA | ORDERS | SPECIES |
|-----------------------|-----------------|------------|--------|---------|
| Meiobenthic nematodes | >0.063 | 1 | 4 | 169 |
| Macrobenthic infauna | >1 | 10 | 33 | 179 |
| Invertebrate epifauna | >5 | 5 | 23 | 81 |
| Fish | >5 | 1 | 11 | 39 |

Results from the multivariate analyses, including all benthic components, showed the following characteristics in the multidimensional scaling (MDS) ordinations (Figure 6.4.2):

- 1) For all invertebrate datasets, a clear separation occurred for assemblages collected in the northern part of the study area (Areas A to I, positioned on the left side of the plots) and those sampled in the southern part (Areas J to O, located at the right side of the plots). Assemblages collected in the southern part of the study area displayed a more variable species composition compared with those sampled in the northern part.
- 2) Meiobenthic nematode, macrobenthic infauna, and invertebrate epifauna communities collected in Areas A and I, where the finest sediments with highest silt content were found, clustered separately from other more sandy stations in the northern part of the study area.
- 3) Fish assemblages sampled in Area F were separated from other communities at the 60% Bray–Curtis similarity level. This sampling area was shallower than other locations in the northern part of the study area.

Geographic location of the sampling area and associated differences in water depth were the main factors affecting assemblage structure. The influence of factors related to sediment granulometry (e.g. median particle diameter, silt content, etc.) decreased with increasing size and mobility of the faunal group.

6.4.4 Discussion

For the first time, extensive regional sampling of benthos in the North Sea has allowed a critical evaluation of the relationship between the nematode fauna and their sedimentary habitat and other larger faunal groups, including macrobenthic infauna, invertebrate epifauna, and fish.

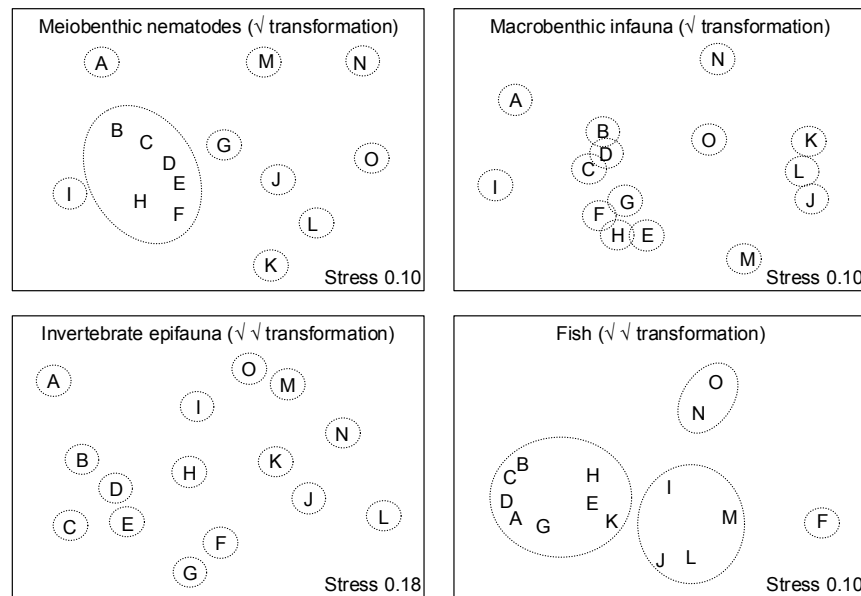


Figure 6.4.2. Non-parametric multidimensional scaling (MDS) ordination based on transformed mean abundance of meiobenthic nematodes, macrobenthic infauna, invertebrate epifauna, and fish. Lines indicate 60% Bray–Curtis similarity.

In terms of diversity and species composition, nematode communities encountered were similar to those occurring in comparable environments worldwide. Correlation analyses of nematode populations with the varied substrate occurring in the southwestern North Sea revealed that locations with similar sediment type and water depth were also most similar faunistically. This close association confirms previous studies showing that the median grain size and the silt content of the sediment are often dominant factors that explain a significant part of the variance in species abundance and diversity (review by Heip *et al.*, 1985). In addition, water depth was potentially important in affecting nematode assemblage structure, most likely because it determined other factors such as the amount and nature of phytoplankton-derived food reaching the seabed and the stability of physico-chemical factors.

Results from the combined analysis of different faunal groups in the southwestern North Sea revealed a notable similarity between species distribution patterns, partly based on common affinities for particular habitat conditions. The topography of the North Sea is an important factor in determining the pattern of water movements and thus the environmental conditions to which fauna and flora are subjected.

Of all faunal groups investigated, patterns in the assemblage structure of benthic invertebrates coincided most closely with sedimentary conditions at the sampling stations. This is partly because the morphology, physiology, and life history characteristics of the benthic infauna and epifauna are also strongly influenced by the substrate. In contrast to these smaller, less motile organisms, fish display a wider range of life histories. In addition to the sedimentary environment, factors related to habitat topography, water flow, proximity to source populations, and length of larval life are important in structuring these assemblages. Although benthic infauna and sediment samples were collected at comparable spatial scales, the trawl samples represented organisms from a wider range of substrates. Thus, in view of the relatively small surface area sampled for sediment analyses (i.e. 0.1 m² Day grab), results are not fully representative of the variety of habitats and environmental conditions prevailing in the trawled areas.

As evident from sediment, contaminant, and faunal analyses, acute effects of human activities on nematode populations seem unlikely, although an effect of fishing on the nematode fauna of the southwestern North Sea cannot be ruled out. The North Sea is one of the most

environmentally diverse regions in the Northeast Atlantic, and this generally precludes a separation of the combined influence of natural environmental parameters from artificial effects of human activities on a North Sea-wide scale. Assessing the relative roles of environmental variables and various anthropogenic activities, all operating on different spatial and temporal scales, in contributing to differences in biological diversity and the structure of benthic communities offers interesting and challenging avenues for future research.

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6.5 Spatial and temporal variation of microbial communities at selected sites in the North Sea

Michaela Schratzberger

There is an international trend towards an ecosystem approach to environmental management. As a result, the ability to predict the extent of man-made impacts on the composition, structure, and function of ecosystems depends on understanding and integrating the response of organisms at all levels of organization.

Benthic organisms are frequently used to monitor the biological effects of perturbations in the marine environment because, as a group, they are largely sedentary and so must withstand the extremes of their local environment or perish. Macrobenthos (multicellular organisms of >500 µm) have been the historical choice of workers in the field, but in recent years, there has been an increase in the use of smaller-sized organisms such as the meiofauna (multicellular organisms of 63–500 µm; see Section 6.4 and Schratzberger *et al.*, 2000, 2004, 2006). Microbiota (unicellular organisms including Archaea, Bacteria, Picoeucaryota) are excluded from most environmental assessments, although they are of fundamental importance to the functioning of benthic ecosystems (Figure 6.5.1). This is partly a result of unavailable technology, because only recently have a range of molecular techniques become sufficiently refined to be applied to environmental samples. Microbiota are characterized by short generation times and sensitivity to environmental disturbance, and have been shown to respond quickly to environmental changes and to provide accurate indications on specific types of impact (Cody *et al.*, 2000).

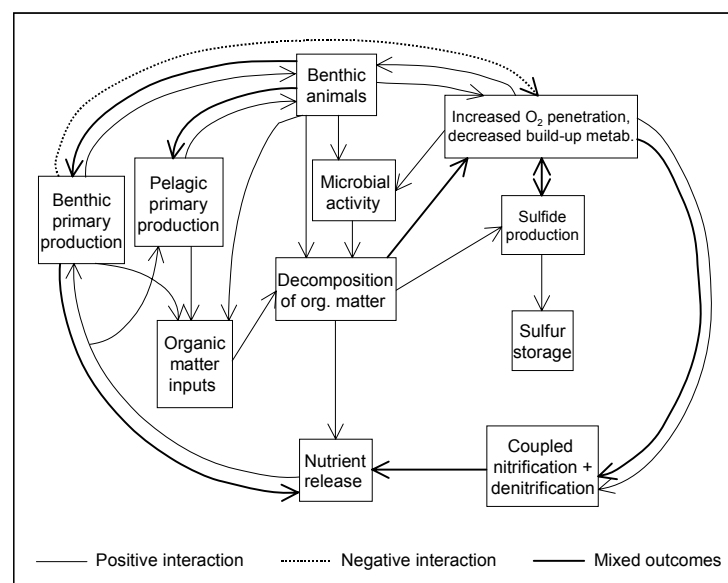


Figure 6.5.1. Model of the interactions between benthic organisms and biogeochemical processes in marine sediments (after Giblin *et al.*, 1995).

Between 2002 and 2004, a UK national collaborative research project between Cefas and the Universities of Essex and Sheffield focused on the development and application of molecular techniques to analyse microbial community structure, dynamics, and diversity in marine sediments. Specific aims of this research included:

- 1) The development of approaches to study both the total and active bacterial, archaeal, and picoeukaryal communities;
- 2) The investigation of spatio-temporal variability between microbial communities in UK offshore sediments (including two sites in the western North Sea).

Micro-organisms from the three domains of life showed different patterns and magnitudes of response to biogeographical variation, suggesting that functional flexibility, dynamic interaction between community members, and concerted evolution could all play a role in shaping biogeographical patterns of microbial communities. Total and active community structures for the three domains were remarkably different. This could be a result of sedimentation processes, bringing numerous foreign micro-organisms or detritus originating in the water column (Fevat *et al.*, 2005).

Bacterial communities showed the strongest pattern of spatial and temporal variation. This might reflect their ability to adapt to local conditions. Moreover, temporal variation was synchronized in distant bacterial communities, indicating a response to global ecological changes. Reduced Archaeal diversity was seen in coarse sediments, and this might indicate a general trend for Archaea to be confined to rare and specialized niches rather than to invade an extended environment. Spatial variation of total picoeukaryotic communities was evident from the community structure, but diversity was homogeneous across sites. Such fluctuations in community structure could reflect adaptations to local events, where one major species might replace another, while the equilibrium in diversity is maintained. Multivariate analyses showed that, similar to multicellular benthic invertebrates, microbial community composition was correlated with sediment granulometry (Fevat *et al.*, 2005).

This research has successfully shown that microbial studies at the population or community level have utility in both large-scale and localized investigations, are practical, and can be achieved after investment in molecular infrastructure. There is a strong case for the future use of molecular techniques in environmental impact assessment and wider applied research into microbial ecology.

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6.6 Habitat suitability modelling

Wouter Willems

6.6.1 Introduction

To underpin management decisions scientifically, there is a growing need to have detailed knowledge of the distribution of marine species. Predictive modelling is a time- and cost-effective method to produce detailed distribution maps. Predictive modelling objectively investigates the relationship between the occurrence of a species and the abiotic habitat. This habitat is quantified by a number of environmental variables, measured directly at the time of sampling (e.g. grain size), through remote sensing, or derived from other models (e.g. currents). These physical variables are often available for a much wider area and sometimes with full-scale coverage (e.g. depth rasters).

The most important goal of habitat suitability models (Guisan and Zimmerman, 2000) is to define the niche of a species quantitatively, in order to improve on the often vague assertions encountered in the literature, for example, that a species “prefers fine sand and shallow water depths”. Habitat suitability models can assign a probability of occurrence for each location, based on the local environmental variables. Additionally, the models can be applied to construct full-cover species distributions maps. These maps are generated by feeding full-cover maps of each environmental variable into the model. The model will predict the probability of occurrence for the species for each pixel of the raster (Figure 6.6.1). Species distribution maps are important in nature conservation and spatial planning in general for the North Sea (e.g. defining MPAs, fisheries closures, planning of wind farms).

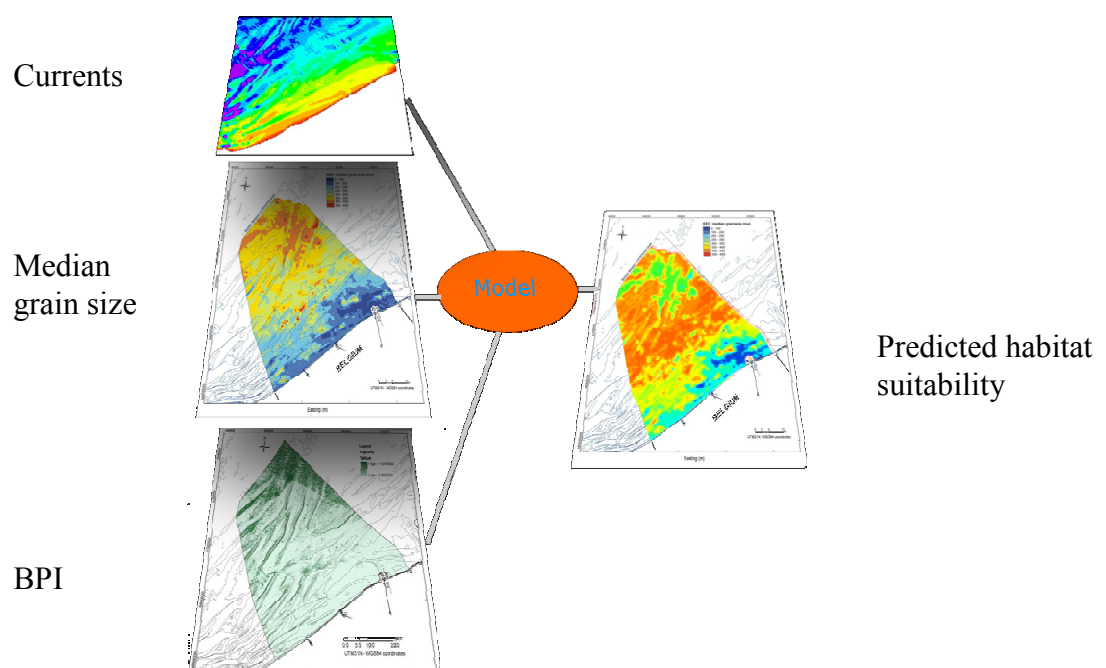


Figure 6.6.1. Application of a habitat suitability model to generate a full cover species distribution map: BPI = Benthic Position Index (Lundblad *et al.*, 2006).

This account will focus on *Ophiodromus flexuosus* (Chiaje, 1827), a free-living polychaete, as an example of the approach applied on a North Sea-wide scale. The aims of this research were (1) to identify the environmental variables determining the distribution of *O. flexuosus*; (2) to construct the optimal model predicting the presence of *O. flexuosus*.

6.6.2 Methodology

The methodology is explained in Figure 6.6.2. In the preparation phase, the dataset containing both the species observations and environmental variables is loaded. A first visualization is done by means of barplots that show the absolute and relative presence of the species along the range of a variable (Figure 6.6.3). Next, the dataset is split up in a training set and a test set. This process is repeated iteratively so that each sample has been in the training set or in the test set at one time. This technique is called cross validation and is used to construct replicas of the models. For each training/test set combination, a new model is created. From the available variables, a subset is selected. This variable selection removes variables for two reasons: (1) the variable is not relevant to the species; (2) there are redundant variables in the dataset. Variable selection will lead to simpler models with fewer parameters.

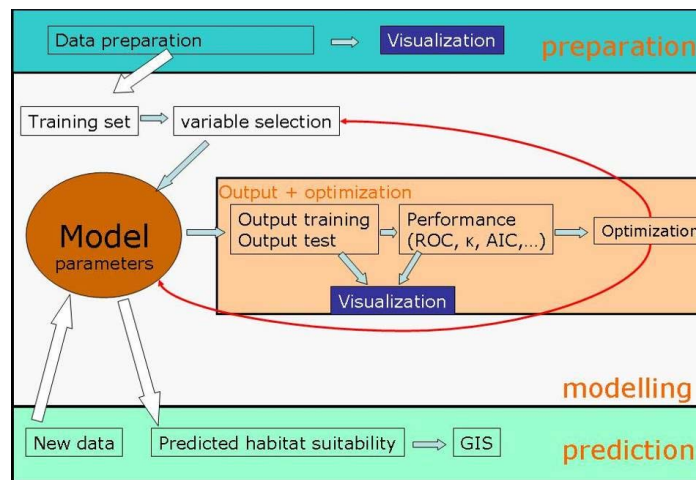


Figure 6.6.2. Overview of the Habitat Suitability Toolbox.

A model is then constructed that can predict the presence of a species in the training set from the environmental variables in the training set. Any modelling technique can be used (e.g. GLM, Neural Networks, fuzzy logic). In this account, the technique Artificial Neural Networks (ANN) is used. ANN is a technique from the field of artificial intelligence (Lek and Guégan, 1999). The networks have a structure similar to the human brain: a network of connected neurons. The neurons are the building blocks of ANN. Data enter a neuron from several other neurons, are summed, then fed into an activation function, which generates the output of the neuron. Neurons can pass on information because they are connected. The importance of a connection is expressed as an interconnection weight. The adjustment of these weights will influence the model output (Lek and Guégan, 1999). Through a learning algorithm, the weights will be adjusted iteratively, increasing the agreement between the observed and predicted presence of the species (Lek and Guégan, 1999). In this research, the neurons in the ANNs are organized in three layers: environmental variables are presented at the input layer, are passed on to the hidden layer (which processes the information), and finally the output layer generates the prediction of the probability of the presence of *O. flexuosus*.

ANN has several internal parameter settings (e.g. choice of number of interneurons, transfer functions). A series of models with different parameter settings was created. To identify the best model, performance indicators (Fielding and Bell, 1997) were used. These formulae allow the generation of a one-number summary of the predictive power of a model. The predictive power for the training set and the test set are stated separately. The test set is to be regarded as a set to test the predictive power for “unseen” samples. The relative contribution of each environmental variable in the prediction is also stated. This is done by calculating the

correlation between the model output with normal environmental variables and the same dataset with one variable ordered randomly. A low correlation between the model predictions means that the variable has a high correlation to the model output. The model predictions can then be visualized extensively. If full-scale rasters for the environmental variables are available, the model can be applied to generate full-scale species distribution maps.

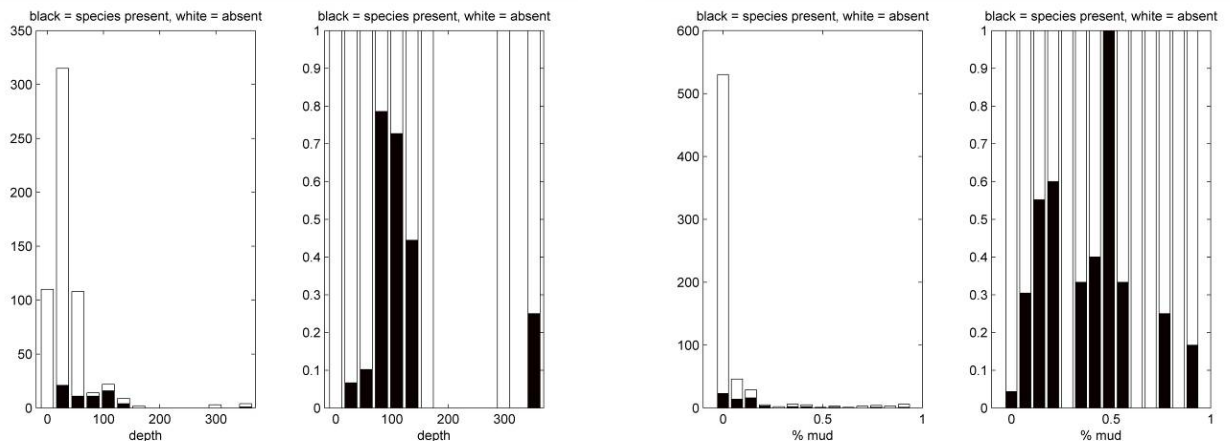
6.6.3 Results

Visualization and variable selection

An important visualization shows the presence of the species along the range of the variable. Additionally, it is important to show the distribution of samples along the range of the variable. The more samples that are available in a certain range, the more reliable the conclusions and models will be for that part of the range. In Figure 6.6.3, two graphs are plotted for each environmental variable. The left one shows the distribution of the samples along the range of the variable, and the right one shows the relative occurrence of the species.

Depth, maximum temperature in June, and percentage of mud show clear relationships with the presence of *O. flexuosus*. Depth shows a peak around 100 m, although few samples are available at such depths for the North Sea dataset. Although most samples were taken in low-mud environments, percentage of mud still shows a pattern with the occurrence of the species. *O. flexuosus* shows a relatively narrow environmental preference in response to variation in sorting, tidal stress, d10, and a high percentage of sand values.

Figure 6.6.3. Absolute and relative presence of *Ophiodromus flexuosus* along the range of the environmental variables in the final model. The left graphs show the number of samples in that range of the graph. The right graphs show the relative occurrence of the species (black bars). Continued on next page.



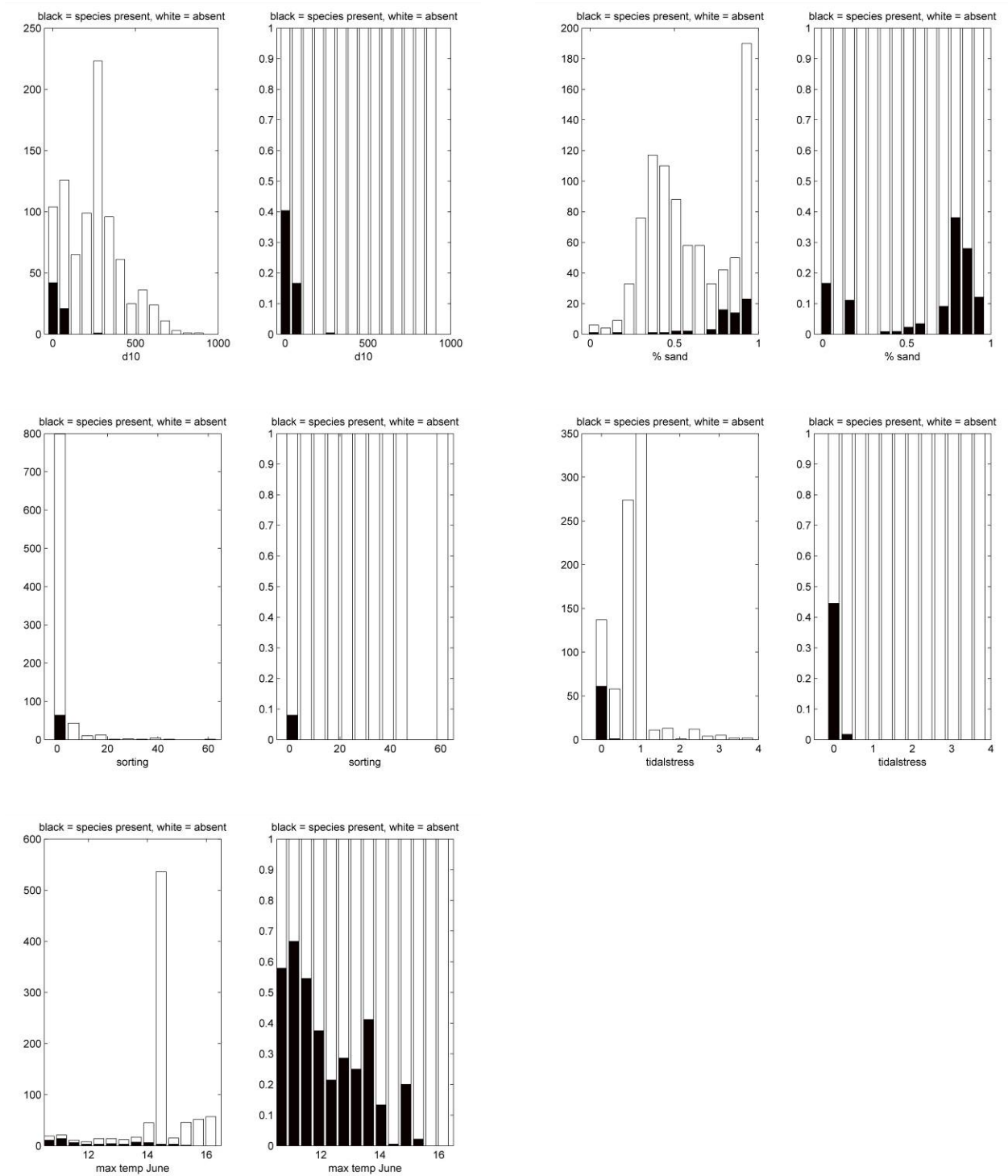


Figure 6.6.3 continued. Absolute and relative presence of *Ophiodromus flexuosus* along the range of the environmental variables in the final model. The left graphs show the number of samples in that range of the graph. The right graphs show the relative occurrence of the species (black bars).

Because related variables (e.g. maximum temperature in June and February) were expected to be highly correlated, and thus potentially redundant, principal components analysis (PCA) was used to examine the relationships between the variables for inclusion in the models. Based on the PCA, we could identify groups of highly correlated variables (see PCA in Section 5.3; Table 6.6.1).

Table 6.6.1. PCA components for the complete dataset.

| PC1 | PC2 |
|--|--------------------------|
| Variables positively correlated with the PCA axes. | |
| d10, d50, d90, ratio d10, d90, mode (mm), percentage of gravel | Average temperature June |
| Average temperature February | Tidal stress |
| Variables negatively correlated with the PCA axes. | |
| Percentage of sand | Depth |
| | Latitude |
| | Average salinity June |

Based on the plots (Figure 6.6.3) and the PCA, a subset of seven variables was retained (Table 6.6.2). This subset was iteratively split up in a training and test set, and models were constructed.

Table 6.6.2. Environmental variables in the final model for *Ophiodromus flexuosus*.

| | |
|--------------------|--------------------------|
| depth | sorting (geometric) |
| Percentage of mud | Tidal stress |
| d10 (mm) | Maximum temperature June |
| Percentage of sand | |

In Figure 6.6.4, a new PCA was plotted, based only on the seven environmental variables in the final model. The Channel samples are clearly delimited from the others, based only on these seven variables. The samples where the species is present are a distinct cloud in the PCA plot. Overall, the “species present” samples are well separated from the “species absent” and Channel samples, which indicates that the chosen environmental variables allow a distinction to be made between sites where the species will be present or absent.

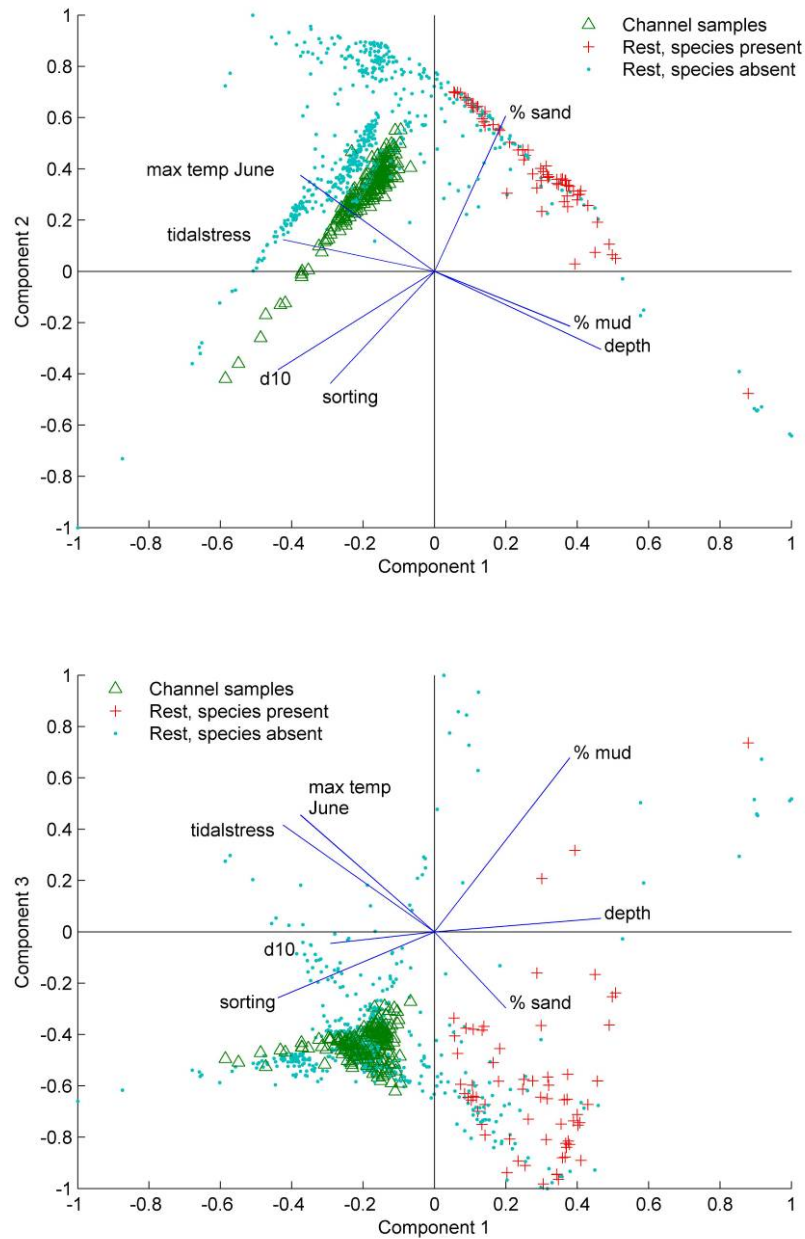


Figure 6.6.4. PCA ordination analysis. Only the environmental variables in the final model are plotted.

Model

By varying the number of interneurons (6–9) and the transfer functions of the interneuron and output neuron (logistic, pure linear and Gaussian transfer functions), 36 model parameter combinations were tested. The best overall model had six interneurons, logistic interneuron transfer functions, and Gaussian output neuron transfer functions. According to the performance statistic, the model performed well, and the performance of the unseen data in the test set was good (Table 6.6.3). The Kappa and NMI values were high. The AUC values close to 1 indicated a good balance between specificity and sensitivity. The CC_i indicated that 91.6% and 88.2% of the samples in the training and test set, respectively, were predicted correctly.

Table 6.6.3. Performance statistics of the best model for *Ophiodromus flexuosus*.

| | KAPPA | NMI | AUC | CCI |
|------------|----------|----------|----------|----------|
| training | 0.589529 | 0.338271 | 0.987066 | 91.59091 |
| validation | 0.489107 | 0.253546 | 0.962873 | 88.18182 |

The relative contribution of each environmental variable to the model output is shown in Figure 6.6.5. Depth and maximum temperature in June are very important. d10 and sorting make a moderate contribution, while tidal stress, percentage of sand, and percentage of mud make a very small contribution.

In the PCA based on the seven chosen variables (Figure 6.6.4), the importance of depth and maximum temperature in June is also clear. It is possible to delimit the cloud of samples where the species is present by drawing lines perpendicular to the vectors depth and maximum temperature in June.

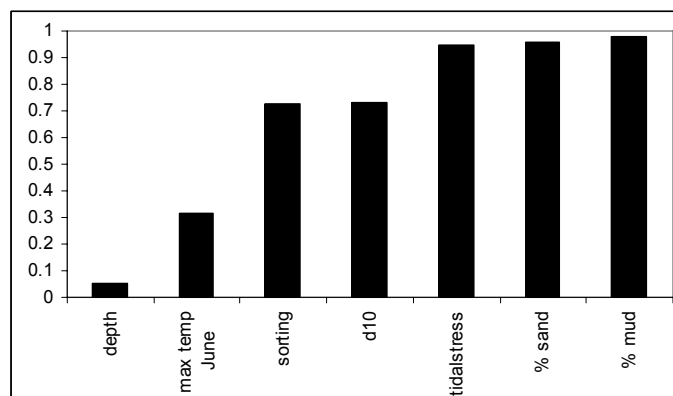


Figure 6.6.5. The relative contribution of each environmental variable to the model output.

Maps

Maps show the observed (Figure 6.6.6a) and predicted (Figure 6.6.6b) distribution of *O. flexuosus*. The overall pattern is very similar. That the model is a habitat suitability model (Guisan and Zimmerman, 2000) causes slight overestimation of the modelled species’ presence in some regions. It predicts the species’ presence, if the physical habitat is suitable. At some sites, the physical habitat is suitable, but the species can be absent for other reasons, e.g. sampling inefficiencies or biotic factors such as predation and patchy recruitment success. Thus, the model predicts the potential area where the species might be found; clearly, it cannot compensate for all circumstances (including sampling error) that determine the presence or absence of the species in field samples.

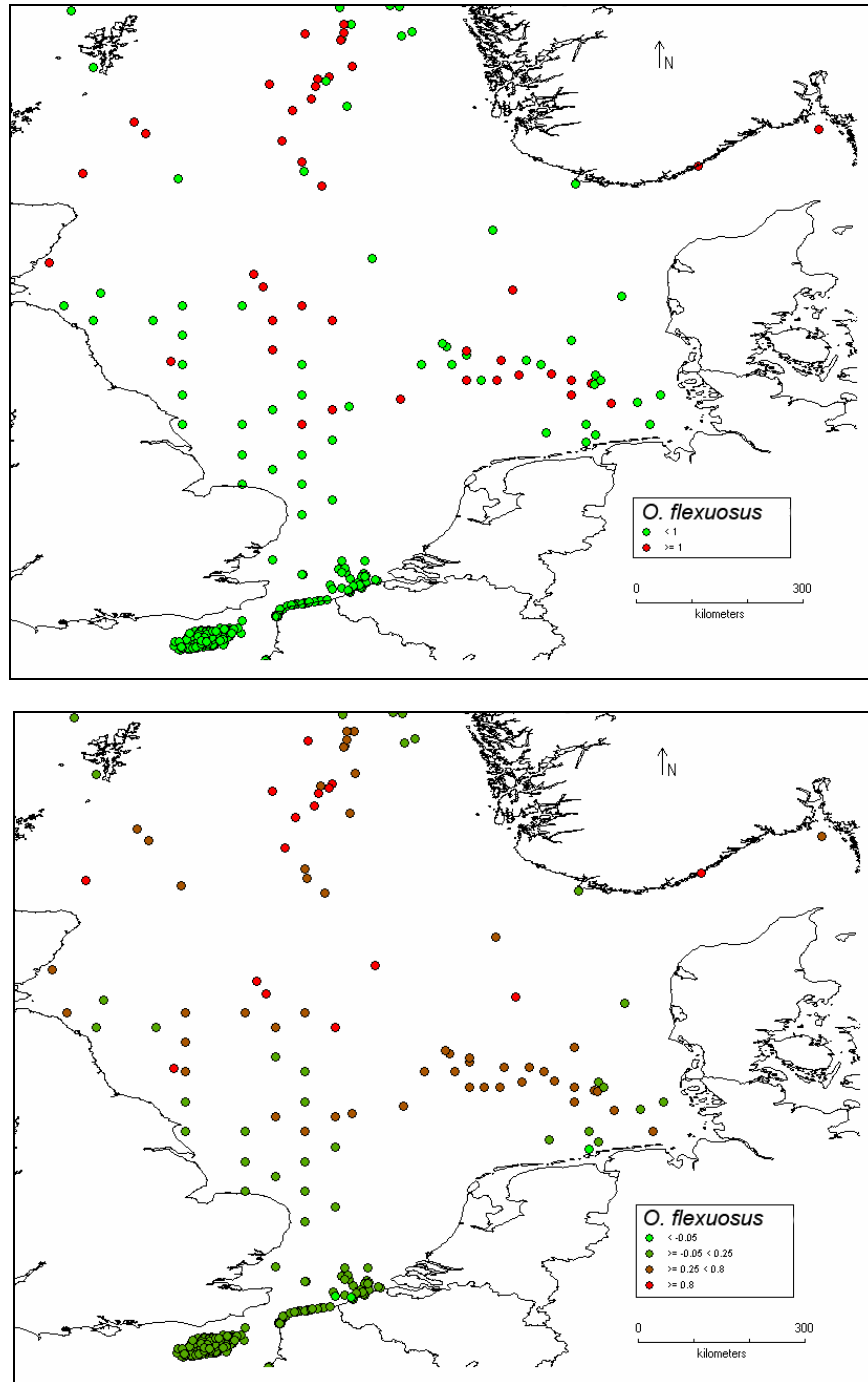


Figure 6.6.6a–b. Maps showing the distribution of *Ophiodromus flexuosus*. (Top) observed distribution, green = species absent, red = species present; (Bottom) predicted distribution, values indicated the habitat suitability, which is the probability of occurrence of the species.

6.6.4 Conclusions

This example of the application of a habitat suitability model demonstrates its utility in predicting species occurrence on the scale of the whole North Sea. It also demonstrates the importance of employing an array of relevant measures of environmental variability to identify a subset with the greatest predictive power. The model, applied to a wider range of species from NSBP 2000, should provide, *inter alia*, a useful tool for interpreting any changes evident in a repeated survey.

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6.7 The effect of the presence of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea

G. Van Hoey

6.7.1 Introduction

Biogenic habitat structures play a major role in determining the distribution pattern of benthic fauna by modifying the sediment (Eckman *et al.*, 1981; Carey, 1987) and hydrodynamic parameters (Eckman, 1983), or by changing interactions between species (Woodin, 1978). Some tube-building polychaetes provide considerable structures in the otherwise relatively unstructured soft-bottom sediments (Woodin, 1978; Zühlke *et al.*, 1998; Zühlke, 2001; Bolam and Fernandes, 2002; Rees *et al.*, 2005). An example of a structuring tube-forming polychaete is the sand mason *Lanice conchilega*, which lives in a tube of sand or shell breccia attached to an inner thin organic layer. The tube itself is crowned with a sand fringe, which protrudes 1–4 cm above the sediment surface (Ziegelmeier, 1952). This species can reach densities of several thousands of individuals per m² (Buhr and Winter, 1977; Ropert and Dauvin, 2000; Van Hoey *et al.*, 2006) and has the ability to influence the surrounding benthic populations (Zühlke *et al.*, 1998; Zühlke, 2001; Callaway, 2006). This ability is mainly the result of the following factors: (i) the tubes provide a settlement surface for larval and post-larval benthic organisms (Qian, 1999); (ii) there is an improved oxygen supply in the sediments surrounding *L. conchilega* tubes (Forster and Graf, 1995); (iii) the tubes affect the current velocities in the benthic boundary layer (Eckman *et al.*, 1981; Heuers *et al.*, 1998; Hild and Günther, 1999); (iv) the tubes have a stabilizing effect on the sediment; (v) the space between tubes can serve as a refuge from predation (Woodin, 1978). The presence of *L. conchilega* tube aggregations in an intertidal sandflat, for example, resulted in an increase in the species diversity and abundance compared with the surrounding sediment (Zühlke *et al.*, 1998; Zühlke, 2001; Callaway, 2003; Callaway 2006).

Lanice conchilega has an amphiboreal distribution, is found on all European coasts (see Figure 6.7.1), and colonizes a wide variety of intertidal and subtidal sediments down to about 1900 m (Hartmann-Schröder, 1996; Ropert and Dauvin, 2000). Despite its wide distribution and the formation of sometimes dense aggregations, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas.

The ICES NSBP 2000 dataset (see Section 3 and Rees *et al.* (2002)) forms the basis of the description of the impact of *L. conchilega* on the soft-bottom benthic ecosystem in the North Sea. More specifically, the present study aims to investigate the effects of the presence of *L. conchilega* on the abundance, species richness, diversity, and species composition of the North Sea benthos. These effects of *L. conchilega* will be investigated in relation to depth and sedimentology, and the results will be discussed in light of the potential environmental and biological effects that *L. conchilega* may cause.

6.7.2 Material and methods

6.7.2.1 Study area

The study area covers most of the eastern English Channel and the North Sea (delimited by Norway and Denmark in the east, the UK in the west, and Germany, the Netherlands, Belgium and northern France in the south). The North Sea (51° to 61°N, 3°W to 9°E) is divided into a number of loosely defined areas: a relatively shallow southern North Sea (Southern Bight and German Bight), the central North Sea (Dogger Bank, Oyster Ground), the northern North Sea, the Norwegian Trench, and the Skagerrak. The last two areas are not included in the present study.

6.7.2.2 Data origin

In all, 2227 macrobenthic samples (1405 stations) were gathered in the North Sea and English Channel in 1999–2001. These data originate from various projects, including national monitoring surveys (Rees *et al.*, 2002). Quantitative sampling of the infauna (and the smaller sedentary epifauna) was conducted with grabs of the van Veen type (generally at least two grabs of 0.1 m² at each station) and sieving alive over a 1 mm sieve. For coarser sediment types, some data contributors used other sampling devices, especially a Hamon grab. In the present study, only samples taken with a 0.1 m² van Veen or Day grab and sieved alive were included (except in the description of the distribution of *L. conchilega* in the North Sea as a whole). This resulted in a final dataset of 1098 samples (comprising 513 different stations).

All data were incorporated into a database, and taxonomic intercomparisons were performed (Rees *et al.*, 2002 and Section 3). These data modifications were executed during several workshops of the ICES Study Group on the North Sea Benthos Project 2000. After taxonomic clearance, a dataset consisting of 717 taxa (further referred to as species) was obtained. The density of *L. conchilega* in the present study is based on individual head counts rather than tube counts.

The sedimentological characteristics of the different samples were coded according to sediment classes: (a) mud, (b) muddy sand, (c) fine to medium sand, (d) medium to coarse sand, (e) sand and gravel, and (f) mixed sediments (ICES, 2004). Additionally, water depth at each sampling station was recorded. The different habitat types were distinguished by using the sediment classes. Based on the bathymetric information, each sediment class was divided into shallow (<70 m) and deep (>70 m; cf. Künitzer *et al.*, 1992).

6.7.2.3 Data analysis

The effects of *L. conchilega* on the macrobenthos were investigated for every habitat type in which the species was found and for which a sufficient number of samples (>100) was available (Figure 6.7.2). The following univariate indices were used to describe the macrobenthos (excluding *L. conchilega*) in each sample: (i) density N ; (ii) species richness S , expressed as number of species per sample (i.e. per 0.1 m²); (iii) the exponential form of the Shannon–Wiener index N_1 (Hill, 1973); (iv) expected number of species (ES(50)) (Hurlbert, 1971). All indices were calculated with the PRIMER 5.2.9 software package. The relations between density, species richness, expected number of species or N_1 -diversity, and the density of *L. conchilega* in the different habitats were observed and visualized based on different density classes of *L. conchilega*, and were statistically tested using Spearman rank correlations (Conover, 1971; Clarke and Warwick, 2001).

To identify species that are possibly associated with the presence of *L. conchilega*, three reductions and calculations of the species dataset were performed. First, only species present in more than five samples per habitat type were selected, thereby excluding rare species. Second, an association degree (the percentage of occurrence of a species in samples with *L. conchilega* relative to the total presence of that species in all samples) was calculated. Species with an association degree of more than 50% (>50% of all individuals were found in association with *L. conchilega*) were regarded as associated species. Third, the level of the significance of association was calculated using a Mann–Whitney U test comparing densities of a certain species between *L. conchilega* samples and samples without *L. conchilega*. Finally, species from which the densities showed a positive correlation (Spearman rank correlation) with the density of *L. conchilega* were retained. Non-parametric tests were used because the assumptions for parametric tests, even after transformation, were not fulfilled.

6.7.3 Results

6.7.3.1 Distribution pattern

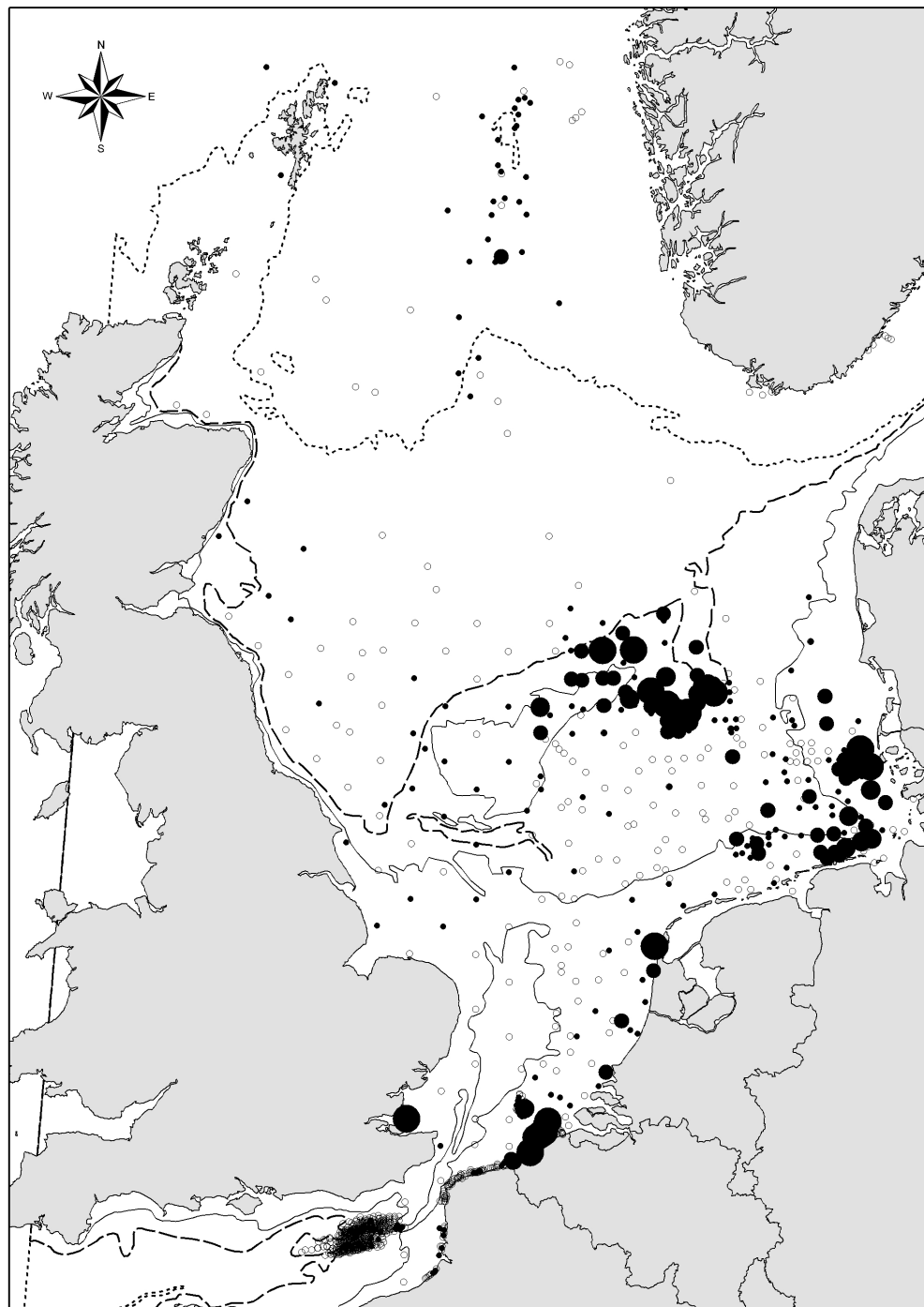
Lanice conchilega was found in the entire North Sea and English Channel (Figure 6.7.1; 25% of the stations). In the central English Channel, *L. conchilega* was seldomly found (<5% of the samples), whereas the species occurred frequently in the entire North Sea (42% of the samples). The areas with the highest frequency of occurrence and densities were the German Bight, the central part of the North Sea (Dogger Bank), and along the French, Belgian, and Dutch coasts. In the deeper northern part of the North Sea, *L. conchilega* was frequently found, but in low densities (<100 ind. m⁻²), whereas in the western North Sea, *L. conchilega* was seldom found.

6.7.3.2 Habitat preferences

L. conchilega was found in all soft-bottom sediment types in the North Sea, but with differences in frequency of occurrence and average density between the habitat types discerned (Figure 6.7.2). No evaluation of the occurrence of *L. conchilega* in shallow mud, deep muddy sands, and deep medium sands could be made, owing to the small number of samples in these habitat types (<30 samples). As for the other habitats, the highest percentages of occurrence (41–51%) and highest densities (138–419 ind. m⁻²) of *L. conchilega* in shallow areas were observed in muddy, fine, and mixed sediments. In shallow medium and coarse sediments, the frequencies of occurrence (24% and 30%, respectively) and average densities (17 and 12 ind. m⁻², respectively) were much lower. In deep muds and fine sands (>70 m), *L. conchilega* occurred frequently (53% and 45%, respectively), but in low average densities (32 and 14 ind. m⁻², respectively). Although *L. conchilega* was found in all habitat types, for reasons of representativeness further detailed analyses were only done for habitats containing more than 100 samples (deep fine sand, shallow muddy sand, shallow fine sand, and shallow medium sand).

6.7.3.3 Presence/absence of *L. conchilega*

A highly significant difference ($p < 0.0001$) in density and species richness (excluding *L. conchilega*) was found between *L. conchilega* samples and samples without *L. conchilega* in shallow muddy sands, fine sands, and medium sands (Table 6.7.1). Those differences in density and species richness were significant in deep fine sands ($p = 0.0115$ and $p = 0.0027$). The N_1 -diversity index in *L. conchilega* samples differed significantly in shallow fine sands ($p < 0.0001$), medium sands ($p = 0.0012$), and deep fine sands ($p = 0.0225$). Only in shallow muddy sands were no significant differences found ($p = 0.1299$). The ES(50) was only significantly different in shallow fine sands and medium sands.



- 0 ind. m⁻²
- 1–100 ind. m⁻²
- 100–500 ind. m⁻²
- 500–1000 ind. m⁻²
- >1000 ind. m⁻²

Figure 6.7.1. Density distribution of *L. conchilega* in the entire North Sea and English Channel.

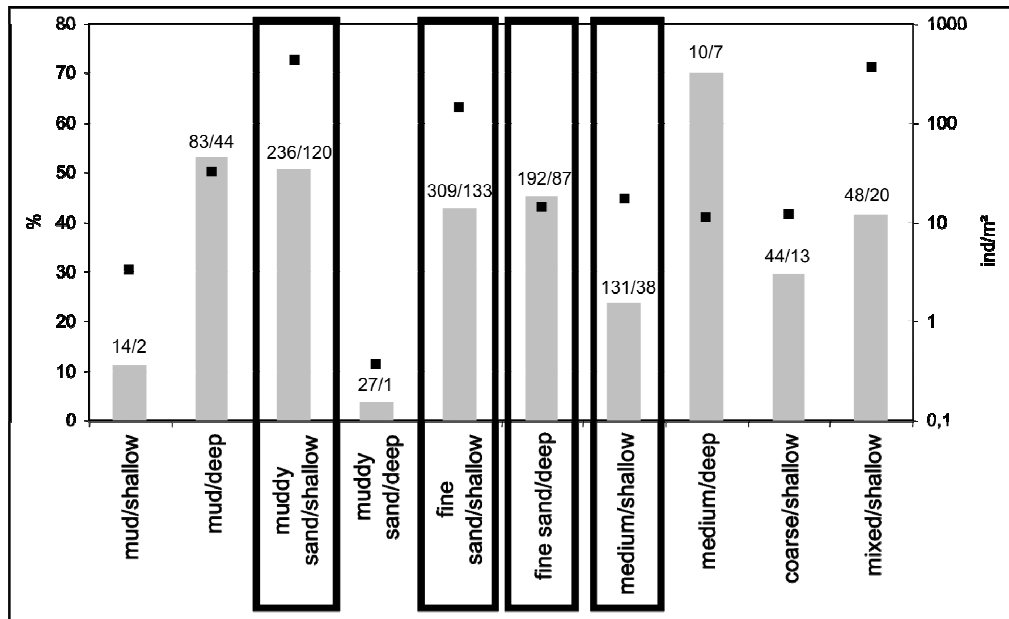


Figure 6.7.2. Percentage of occurrence (grey bars; values appear on the far left) and average density (ind. m⁻²; black squares; values appear on the far right) of *L. conchilega* in the different discerned habitat types, with indication of the total number of samples vs. samples with *L. conchilega*. The four habitats, which were represented by more than 100 samples in the database, are outlined in black.

6.7.3.4 Effect of *L. conchilega* on the benthic characteristics

Table 6.7.1. Difference in density, species richness, N₁-diversity, and ES(50) using the Mann-Whitney U test, between *L. conchilega* samples and samples without *L. conchilega* for the different habitats, and the Spearman rank correlation between the density, species richness, N₁-diversity, and ES(50) and the density of *L. conchilega* for the different habitats. The number of observations (n) within each habitat was 236 for shallow muddy sand, 309 for shallow fine sand, 192 for deep fine sand, and 131 for shallow medium sand.

| | HABITATS | MANN-WHITNEY U-TEST | SPEARMAN RANK CORRELATION | |
|------------------|---------------------|---------------------|---------------------------|------------|
| | | | R | P |
| Density | shallow muddy sand | p < 0.0001 | 0.45 | p < 0.0001 |
| | shallow fine sand | p < 0.0001 | 0.63 | p < 0.0001 |
| | deep fine sand | p = 0.0115 | 0.23 | p = 0.0013 |
| | shallow medium sand | p < 0.0001 | 0.39 | p < 0.0001 |
| Species richness | shallow muddy sand | p < 0.0001 | 0.4 | p < 0.0001 |
| | shallow fine sand | p < 0.0001 | 0.65 | p < 0.0001 |
| | deep fine sand | p = 0.0027 | 0.27 | p = 0.0001 |
| | shallow medium sand | p < 0.0001 | 0.5 | p < 0.0001 |
| N ₁ | shallow muddy sand | p = 0.1299 | 0.08 | p = 0.22 |
| | shallow fine sand | p < 0.0001 | 0.39 | p < 0.0001 |
| | deep fine sand | p = 0.0225 | 0.158 | p = 0.028 |
| | shallow medium sand | p = 0.0012 | 0.36 | p < 0.0001 |
| ES(50) | shallow muddy sand | p = 0.07 | 0.08 | p = 0.22 |
| | shallow fine sand | p < 0.0001 | 0.39 | p < 0.0001 |
| | deep fine sand | p = 0.16 | 0.17 | p = 0.17 |
| | shallow medium sand | p < 0.0001 | 0.34 | p < 0.0001 |

6.7.3.5 Correlation between benthic structure characteristics and density of *L. conchilega*

In the four habitats, the densities of the surrounding benthos increased with increasing density of *L. conchilega* (Figure 6.7.3). The increasing trend of the density was comparable in the four habitats. The correlation between densities of the benthic fauna and the densities of *L. conchilega* was positive and significant in all habitats, was strongest in shallow fine sands (Spearman R: 0.63), and was lowest in deep fine sands (Spearman R: 0.23; Table 6.7.1).

In shallow muddy sands, the species richness decreased when the density of *L. conchilega* exceeded 1000 ind. m⁻², while in shallow fine sands, the species richness levelled off at 500 ind. m⁻² of *L. conchilega* (Figure 6.7.3). Although species richness differed strongly between habitats, a significant correlation was found between species richness and the density of *L. conchilega* in all habitats, with the highest value in shallow fine sands (Spearman R: 0.65) and the lowest in deep fine sands (Spearman R: 0.27; Table 6.7.1). In shallow muddy sands, the correlation was atypical: the species richness decreased with higher densities of *L. conchilega*.

The N₁-diversity index and its relation with *L. conchilega* density differed between the habitats (Figure 6.7.3). In shallow muddy sands, the N₁-diversity index did not increase with the *L. conchilega* density and did not show a significant correlation (Spearman R: 0.07; p = 0.28; Table 6.7.1), whereas a minor, through significant to very highly significant correlation was observed in the other three habitats. The strongest correlation was found in shallow fine sands (Spearman R: 0.39; Table 6.7.1).

The trend in the ES(50) was comparable with that of the species richness (Figure 6.7.3), with some small differences: (1) in shallow muddy sands and deep fine sand no increase and no significant correlation in ES(50) with the *L. conchilega* density was observed; (2) in shallow fine and medium sands an increase and a significant correlation (Spearman R: 0.39–0.36, respectively) was found, but the curve levelled off at 100 ind. m⁻² in medium sands and slowly increased or even decreased in fine sands (Table 6.7.1).

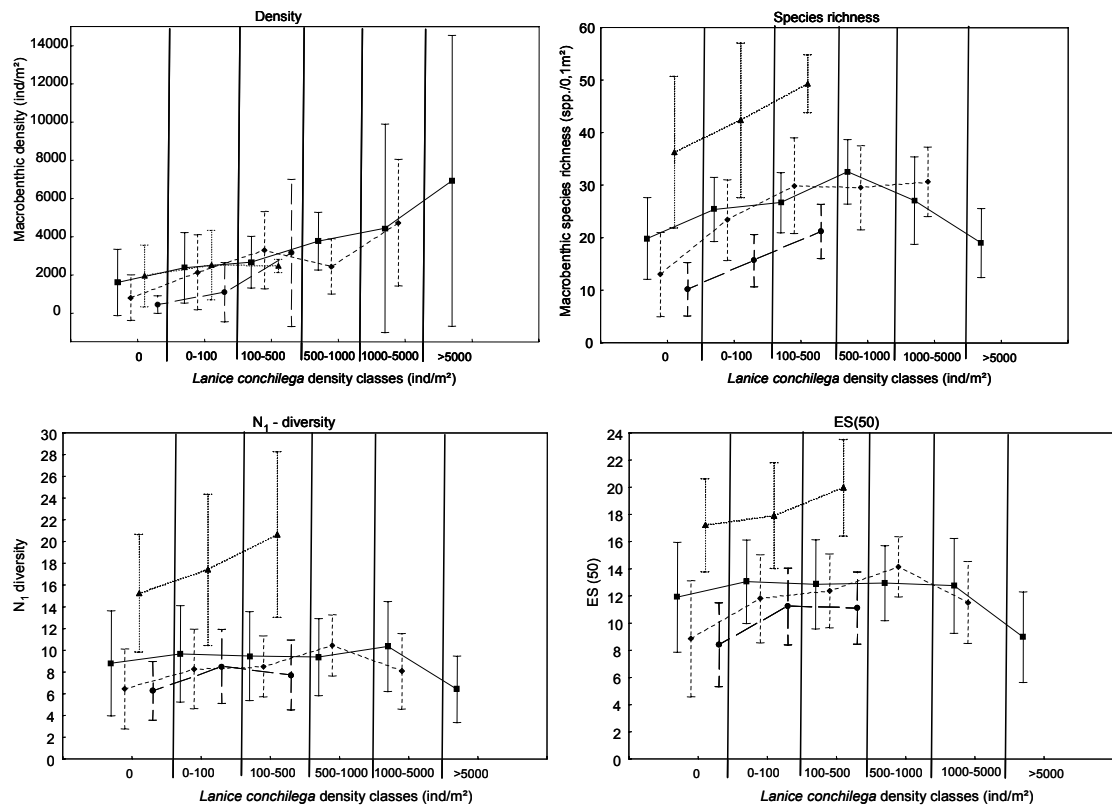


Figure 6.7.3a–d. Plot of (upper left) density, (upper right) species richness, (lower left) N₁ diversity, and (lower right) ES(50), of total benthic species (excluding *Lanice conchilega*) vs. different density classes of *L. conchilega* for four habitats (shallow muddy sand (square), shallow fine sand (rhombus), deep fine sand (triangle), and shallow medium sand (circle)). Bars indicate standard deviations.

6.7.3.6 Species associated with *L. conchilega*

A species was identified as being associated with *L. conchilega* if the association degree was more than 50%, if the species density significantly differed between the samples with and without *L. conchilega*, and if a positive correlation with the density of *L. conchilega* was found. An overview is presented in Table 6.7.2.

In shallow fine sands, 52% of the species were positively associated with *L. conchilega*, whereas only 23–25% of the species were associated in shallow muddy and medium sands. In deep fine sands, only 3 out of 202 species showed an association with *L. conchilega*. In the first three habitats, associated species were found within each higher taxon, except for the Echinodermata. The percentage of associated species within each higher taxon was highest (>40%) in shallow fine sands. Furthermore, most of the frequently occurring species within that habitat were associated with *L. conchilega* (85%). In shallow muddy sands, only 65% of those species were associated. In deep fine sands and shallow medium sands, the frequently occurring species were not associated with *L. conchilega*.

Differences in the relative abundance of each feeding type within a habitat were observed between samples containing *L. conchilega* and *L. conchilega*-free areas (Table 6.7.2). In the shallow habitat types, surface deposit feeding was the dominant feeding type and was more dominant in samples containing *L. conchilega*. The dominance of subsurface deposit feeders decreased in *L. conchilega* samples, especially in shallow muddy and medium sands. The percentage of omnivorous and predatory species did not change strongly, except in shallow medium sands, where their dominance was reduced.

Table 6.7.2. An overview of the percentage of the species associated with *L. conchilega* in relation to the total amount of frequently occurring species (>5 samples) is given for the most important higher taxa within each habitat type.

| HIGHER TAXA | SHALLOW MUDDY SANDS | | | SHALLOW FINE SANDS | | |
|---------------------------------|----------------------|-----------------|-----|----------------------|-----------------|-----|
| | # ASSOCIATED SPECIES | TOTAL # SPECIES | % | # ASSOCIATED SPECIES | TOTAL # SPECIES | % |
| Anthozoa | 1 | 1 | 100 | 1 | 1 | 100 |
| Polychaeta | 13 | 54 | 24 | 26 | 54 | 48 |
| Bivalvia | 6 | 22 | 27 | 10 | 19 | 53 |
| Gastropoda | 2 | 5 | 40 | 3 | 7 | 43 |
| Amphipoda | 4 | 16 | 25 | 12 | 20 | 60 |
| Cumacea | 2 | 9 | 22 | 3 | 8 | 38 |
| Decapoda | 1 | 5 | 20 | 5 | 6 | 83 |
| Echinodermata | 0 | 9 | 0 | 4 | 7 | 57 |
| Others | 1 | 8 | 13 | 5 | 11 | 45 |
| TOTAL | 30 | 129 | 23 | 69 | 133 | 52 |
| Most frequent occurring species | 13 | 20 | 65 | 17 | 20 | 85 |

| FEEDING TYPE | LANICE% | NO LANICE% | LANICE% | NO LANICE% |
|---|---------|------------|---------|------------|
| I: suspension feeding | 15 | 14 | 22 | 24 |
| II: surface deposit, facultative suspension and interface feeding | 64 | 54 | 64 | 56 |
| III: subsurface deposit feeding, grazing | 11 | 21 | 4 | 5 |
| IV: omnivore, predator, scavenger | 9 | 8 | 8 | 10 |
| V: unknown | 1 | 3 | 2 | 6 |

| HIGHER TAXA | DEEP FINE SANDS | | | SHALLOW MEDIUM SANDS | | |
|---------------------------------|----------------------|-----------------|-----|----------------------|-----------------|-----|
| | # ASSOCIATED SPECIES | TOTAL # SPECIES | % | # ASSOCIATED SPECIES | TOTAL # SPECIES | % |
| Anthozoa | 1 | 1 | 100 | 1 | 1 | 100 |
| Polychaeta | 1 | 107 | 1 | 7 | 32 | 22 |
| Bivalvia | 0 | 25 | 0 | 1 | 9 | 11 |
| Gastropoda | 0 | 7 | 0 | 0 | 1 | 0 |
| Amphipoda | 1 | 26 | 4 | 1 | 10 | 10 |
| Cumacea | 0 | 6 | 0 | 2 | 3 | 67 |
| Decapoda | 0 | 2 | 0 | 1 | 3 | 33 |
| Echinodermata | 0 | 6 | 0 | 0 | 3 | 0 |
| Others | 0 | 12 | 0 | 3 | 3 | 100 |
| TOTAL | 3 | 192 | 2 | 16 | 65 | 25 |
| Most frequent occurring species | 1 | 20 | 5 | 1 | 20 | 5 |

| FEEDING TYPE | LANICE% | NO LANICE% | LANICE% | NO LANICE% |
|---|---------|------------|---------|------------|
| I: suspension feeding | 9 | 8 | 5 | 6 |
| II: surface deposit, facultative suspension and interface feeding | 76 | 77 | 72 | 47 |
| III: subsurface deposit feeding, grazing | 4 | 5 | 6 | 12 |
| IV: omnivore, predator, scavenger | 9 | 8 | 15 | 33 |
| V: unknown | 2 | 2 | 2 | 2 |

6.7.4 Discussion

6.7.4.1 Distribution

Lanice conchilega has a cosmopolitan distribution, because it is found from the Arctic to the Mediterranean, in the Arabian Gulf and the Pacific, from the low water neap tide mark down to 1900 m (Hartmann-Schröder, 1996). In our survey, *L. conchilega* was found in the entire North Sea down to a depth of 180 m (the deepest record in the dataset was 380 m). This tube-building polychaete is known to live mainly in sandy sediments from mud to coarse sand (Hartmann-Schröder, 1996), as was confirmed by the present study. Yet, shallow muddy and fine sands were strongly preferred: *L. conchilega* showed its highest frequencies of occurrence and densities in these sediments (more than 1000 ind. m⁻² compared with maximally 575 ind. m⁻² in shallow medium sands). In the deeper habitats, *L. conchilega* was frequently encountered, but only in low abundance (maximally 170 ind. m⁻² in deep fine sand). Hence, it can be concluded that *L. conchilega* has a wide geographical distribution and a low habitat specialization (i.e. it is a eurytopic species).

From the distribution map of *L. conchilega* (Figure 6.7.1), it can be deduced that the highest densities and percentages of occurrence were observed in the coastal areas of the North Sea (German Bight, French, Belgian, and Dutch coasts), and in the central part of the North Sea (Dogger Bank). Those areas were already characterized as the zones with the highest primary production in the North Sea (McGlade, 2002; Peters *et al.*, 2005). Besides physical factors (sediment type, flow regime), which mainly determine the distribution of a benthic species, the availability of food might also have a positive influence on the abundance of *L. conchilega*. However, for modelling the habitat preferences of *L. conchilega* based on several types of environmental variables (granulometry, hydrodynamics, pigments, nutrients), only granulometric variables were selected in the final model (Willems *et al.*, in press).

6.7.4.2 Effect of *L. conchilega* on benthic characteristics

The results of the present study clearly show that *L. conchilega* has the potential to positively influence the benthos, as reflected in the significant and positive correlation between the density of other species and the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend, however, was not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* (>500 ind. m⁻²). The trend observed concerning the expected number of species indicates an enrichment of species in *L. conchilega* patches. The N₁-diversity index, which considers species abundance and richness, showed similar or slightly higher values in *L. conchilega* patches compared with patches without *L. conchilega*. This diversity pattern implies that species with mainly low abundance contribute to the higher species richness in samples containing *L. conchilega*. Owing to the higher density of many species in *L. conchilega* patches, the chance of sampling a certain species increases in those patches compared with the surroundings, which partly explains the increase of species richness in *L. conchilega* patches. The observed increases in species richness and abundances recorded in *L. conchilega* patches have also been observed around the tubes of other polychaetes (Woodin, 1978; Luckenbach, 1986), in *L. conchilega* patches in intertidal areas (Zühlke *et al.*, 1998; Zühlke, 2001; Callaway, 2006), and even around artificial tubes (Zühlke *et al.*, 1998; Dittmann, 1999).

The observed trends in density, species richness, and diversity were most pronounced in shallow fine sands and were less pronounced in deep fine sands. The strong effect of *L. conchilega* in shallow fine sands indicates that the habitat structuring capacity of *L. conchilega* has an optimal effect in shallow fine sands. In deep fine sands, which were already characterized by a high diversity and low densities of *L. conchilega*, the effect on benthic species was minimal. It is not known if the effect on the benthos increases with even higher

densities of *L. conchilega*. It can be hypothesized that the habitat structuring effect of *L. conchilega* in deeper environments has a less optimal result, owing to the lower environmental variability in such habitats; fewer species can profit from the improved conditions around *L. conchilega* tube aggregates. *L. conchilega* had an effect on the density of some benthic species in shallow muddy sands, but no real increases of the species richness and diversity were observed. On the contrary, very high densities of *L. conchilega* ($>1000 \text{ ind. m}^{-2}$) had a decreasing effect. In shallow medium sands, the effects of *L. conchilega* on density and diversity were not strongly pronounced, but were present owing to the lower maximal densities of *L. conchilega*.

The patterns in density and species richness observed in the present study agreed with the results of the species composition. In the habitat where the effect of *L. conchilega* was most pronounced (shallow fine sands), most associated species were found belonging to different higher taxa. These associated species mostly belonged to the overall species pool of a certain habitat, rather than being commensals of *L. conchilega*. Thus, it was demonstrated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own community (see also Zühlke *et al.*, 1998; Dittmann, 1999). It seems that the effect of *L. conchilega* tubes on the benthic fauna is highly dependent on the native species present in the surrounding sands at any moment and on their susceptibility to tube effects. Therefore, it is logical that species richness and diversity levelled off in some habitats: no new species for that habitat were attracted. Nevertheless, *L. conchilega* affected the habitat quality leading to increases of the densities of otherwise rare species in that habitat.

It can be argued that underlying factors (e.g. food availability) determine the densities of *L. conchilega* and therefore also the densities of other benthic species. However, the results of the present study clearly show that *L. conchilega* has the potential to affect the surrounding benthic species. The effects of *L. conchilega* on the surrounding benthos result from alterations of some habitat characteristics (cf. other studies on the effects of biogenic habitat structures). Changes in the following environmental and biological characteristics were induced by the presence of *L. conchilega*: (i) hydrodynamics (reduced current velocity leading to sedimentation of particles, detritus, and higher settlement of larvae); (ii) sediment modifications (increased habitat stability, oxygen supply); (iii) species interactions (species living attached or inside the tubes, prey–predator relations).

6.7.5 Conclusions

It can be concluded that *L. conchilega* influences the density and diversity of macrobenthos in soft-bottom sediments. This effect is most pronounced in shallow fine sand, which is the species' preferred habitat. Changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. Many benthic species can profit from the creation, modification, and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared with the surrounding soft-bottom sediments. It was further demonstrated that *L. conchilega* only has an effect on the benthos present in a particular habitat, rather than forming its own association. Consequently, *L. conchilega* beds can be considered as important habitat-structuring features in the soft-bottom sediments of the North Sea.

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7 Overall conclusions

Through the co-operation of a variety of existing data holders, and the conduct of additional sampling, the ICES NSBP 2000 initiative sought to evaluate the status of benthic communities on an international (North Sea-wide) scale and their relationship with other biotic and abiotic ecosystem elements. In addition to providing a contemporary description to update the findings of the ICES NSBS 1986, the exercise provided important lessons for the future coordination and resourcing of effort to facilitate such international assessments, including means to better exploit existing data from national sources. Elements of this collaborative initiative may also contribute usefully to the wider aim of developing an ecosystem approach to the assessment and management of the North Sea (e.g. Anon., 1998, 2001; OSPAR Commission, 2000; Commission of the European Communities, 2002).

7.1 Data quality, quantity, and management

Several issues had to be resolved during the management and analysis of the ICES NSBP 2000 data, mostly as a consequence of the opportunistic exploitation of available data sources. Many issues were similar to those encountered in NSBS 1986, but some were more acute. Uneven coverage of the area of interest was the most obvious one, with a concentration of stations in the southern North Sea (see Section 3 and below). Also, differences in the unit area sampled and in the level of replication necessitated the use of rarefaction to a standard sample size (we chose to calculate the numbers of species encountered in a random sample of 50 or 100 individuals), in order to allow a relative comparison of species richness across the majority of stations. A comparison of absolute numbers of species per unit area, of course, is still possible across a more restricted dataset comprising stations that were sampled using comparable gear types.

Sampling for NSBS 1986 was conducted on a regular grid of stations. For the NSBP 2000 survey, the locations of stations were largely dictated by national R and D or monitoring interests, and only a portion of the 1986 grid (in the southern North Sea) was systematically resampled. In order to facilitate a quantitative comparison between 1986 and 2000, a subset of “nearest neighbour” stations was identified, and this proved to be a very useful supporting tool for interpreting the data (see for example Sections 5.2 and 5.4). However, it is evident that the closeness of the matches is variable, especially to the north where geographical coverage in 2000 was more limited and, as a result, some caution was necessary in interpreting the outcomes of data analyses.

Significant effort was committed to the early resolution of taxonomic and nomenclatural issues. Spelling variations and synonymies were resolved at the data management level. Dealing with inconsistencies in identification that came to light during the process of combining the diverse array of existing data sources was more challenging. Some of these were resolved during laboratory workshop sessions of the ICES NSBP 2000 study group. As a general policy, taxonomic precision was sacrificed in favour of accuracy. For example, species counts were pooled to the level of the genus, if species identifications appeared to be inconsistent. However, in some cases, it was possible to improve taxonomic precision by allocating a taxon identified at a higher level by one laboratory to a lower one, in cases where this was strongly supported by the evidence from parallel datasets in the same area.

Although the integration of data from different sources presented significant challenges, the outcome certainly brought its rewards. Thus, the resulting dataset encompassed a wide geographical area with an intensity of coverage that would not be achievable by a single institute or country, without a disproportionately large resource commitment. Furthermore, North Sea-wide trends in the data are expected to be stronger than those typically encountered on more localized scales. Therefore, some loss of taxonomic precision, which was a necessary

expedient during the process of combining data from disparate sources (see above), should not obscure major signals of change encountered in space (2000) and over time (1986 vs. 2000).

The experience gained in the management of NSBP 2000 data was valuable in providing a framework for comparable activities under the EU MarBEF initiative, particularly under Theme 1 (“Global patterns of marine biodiversity across ecosystems”) through the provision of a common gazetteer (MarBEF, 2004) and register of taxonomic names as a starting point for further development. Also, contributions have been made to the European Register of Marine Species (Costello *et al.*, 2004), including new records and the provision of a strong incentive for its future updating.

Practical lessons for the conduct of future collaborative survey and data compilation exercises are similar to those identified by other national and international coordinating agencies engaged in comparable activity, but do no harm in their restating. These include harmonized survey and sampling methodologies, wider conduct of ring-testing and certification of taxonomic identification skills, better documentation of individual datasets, and improved incentives for the submission of data to repositories to avoid data loss.

The NSBP 2000 initiative provides an excellent example of the willingness of many data providers to cooperate under ICES auspices and reflects the changing attitude towards the sharing of data with others. The often underestimated resource need in relation to data management was overcome, in this case, by the support of the Flemish Government (see Section 7.4). Opportunistic exploitation of existing data is not a substitute for the commissioning of new and more targeted survey work. However, such exercises have the potential to increase the frequency of periodic assessments of environmental status on large (up to sea-wide) scales that are increasingly demanded to inform decision-makers on issues such as the consequences of global warming or ocean acidification.

7.2 Natural influences

The forces accounting for the major divisions in the habitats and communities of the North Sea appear to be little changed between 1986 and 2000. Variability within or at the boundaries of communities may be ascribed to more subtle local manifestations of these dominant forces or to other influences, and accounts for complexity in the biological data. For example, recent changes in the distributions of certain species have been identified (Sections 5.2 and 5.4; Wiekling and Kröncke, 2001), but clearly these have not occurred at the expense of evolutionary adaptations to substratum type. Therefore, influences which sustain the distribution (if not the stability) of the latter continue to be among the major determinants of North Sea-wide patterns in benthic communities. This partly accounts for the recurrence of broadly defined correlates, such as depth and tidal current velocity in the macroscale assessments of Table 7.2.1.

Table 7.2.1. Environmental correlates of benthic community structure in the North Sea identified from large-scale spatial assessments (“water masses” refer mainly to (extent of) Atlantic inflow).

| FAUNAL COMPONENT | PRINCIPAL CORRELATES | SOURCE |
|--|--|--|
| North Sea macro-infauna | Water temperature, stratification, sediment type, tidal current velocity | Glémarec, 1973 |
| North Sea macro-infauna | Latitude/longitude, sediment type, chlorophyll <i>a</i> in sediment, depth, water temperature, stratification, circulation patterns/water masses, food supply | Künitzer <i>et al.</i> , 1992; Heip <i>et al.</i> , 1992a; Heip and Craeymeersch, 1995 |
| North Sea macro-infauna | Depth, sediment type, plant pigments, certain trace metals in sediments | Basford <i>et al.</i> , 1993 |
| North Sea macro-infauna | Latitude, water temperature, salinity, depth, tidal current velocity, surface-water chlorophyll <i>a</i> , stratification, sediment type | Section 5.3; see also Section 5.1 |
| N North Sea macro-infauna | Depth, sediment type, organic carbon content of sediments, tidal current velocity | Eleftheriou and Basford, 1989 |
| S North Sea macro-infauna | Sediment type, depth, food supply, tidal current velocity, wave action | Duineveld <i>et al.</i> , 1991 |
| North Sea macro-infauna/epifauna | Tidal current velocity, wave action, salinity, water temperature, sediment type, surface-water chlorophyll <i>a</i> (infauna); wave action, salinity, water temperature, surface-water chlorophyll <i>a</i> (epifauna) | Section 6.1 |
| C North Sea macro-infauna/epifauna | Depth, sediment type, circulation patterns/water masses, food supply, latitude/longitude (infauna) Depth, circulation patterns/water masses, latitude/longitude (epifauna) | Künitzer, 1990 |
| S North Sea macro-epifauna; SW North Sea macro-infauna | Sediment type, depth, tidal current velocity, water temperature, latitude, water masses (epifauna) Tidal current velocity, sediment type (infauna) | Rees <i>et al.</i> , 1999 |
| North Sea macro-epifauna | Sediment type, circulation patterns/water masses, depth, water temperature, stratification, food supply | Dyer <i>et al.</i> , 1983 |
| North Sea macro-epifauna | Circulation patterns/water masses, season, depth, sediment type, latitude/longitude | Frauenheim <i>et al.</i> , 1989 |
| North Sea macro-epifauna | Depth, water temperature, stratification, latitude | Jennings <i>et al.</i> , 1999 |
| North Sea macro-epifauna | Stratification, depth, water temperature, sediment type, beam trawling | Callaway <i>et al.</i> , 2002 |
| N North Sea macro-epifauna | Depth, sediment type | Basford <i>et al.</i> , 1989 |
| S North Sea macro-epifauna | Latitude, depth, beam trawling | Duineveld and van Noort, 1990 |
| S North Sea meiofauna (mainly copepods) | Sediment type, latitude, depth, water masses | Huys <i>et al.</i> , 1992; Heip <i>et al.</i> , 1992b |
| SW North Sea meiofauna (nematodes) | Sediment type, latitude, depth | Schratzberger, Section 6.4 and Schratzberger <i>et al.</i> , 2006. |

Several studies in Table 7.2.1 report on the outcome of NSBS 1986, including evaluations of regional subsets of the data. Some reveal differences in influential variables or in their relative importance depending on location, the availability of supporting environmental data, and the analytical tools employed (see below). In summary, the correlates in Table 7.2.1 apply to:

- Sediments – sediment type, chlorophyll *a*/plant pigments, organic carbon, “food supply”, trace elements, trawl-induced disturbance;
- Water (and climate) – depth, water temperature, salinity, stratification, circulation patterns, water masses, season, tidal current velocity, wave action, surface-water chlorophyll *a*;
- Location – latitude, longitude.

The scope for interaction among these variables is readily apparent.

Most of the relationships in Table 7.2.1 were statistically significant, and the majority of these were identified from multivariate analyses; some (e.g. food supply to the seabed, circulation patterns) were based on inference. Many of the environmental variables measured over large geographical scales are intercorrelated, and the numbers examined differed appreciably between surveys. Some potentially important explanatory variables, such as carbon flux at the seabed or representative measures of sediment type along trawl tows, are costly to determine routinely, or are difficult to relate to infrequent spatial surveys (Sibuet *et al.*, 1989; Duineveld *et al.*, 1991; Section 6.1).

Measures of sediment type define the habitat within or on which benthic organisms live. As a result, they are widely determined, and historically have been the most commonly cited correlates of pattern in benthic communities (e.g. Petersen, 1918; Jones, 1950; Thorson, 1957). Although, in isolation, variables such as latitude and depth provide little insight other than revealing that they are linked in some way to patterns of occurrence, they may have value in deducing causes. For example, latitudinal correlations have allowed speculation on biogeographical trends in relation to the recent evolution of the North Sea basin (Heip *et al.*, 1992a). Similarly, while relationships between temporal changes in the benthos and the NAO Index (Section 5.7) reveal sensitivity to climatic influences, causal explanations require consideration of dependent oceanographic variables. These may affect the benthos directly, e.g. temperature extremes in shallower waters, or indirectly, e.g. via altered pelagic production. Further consideration of variability in food inputs to the seabed from pelagic processes is considered under “human influences” (Section 7.3) in the context of eutrophication.

Common to the outcome of all North Sea-wide assessments in Table 7.2.1 is a division between northern and southern assemblage types with a transition zone in the vicinity of the Dogger Bank. Although many species are widely distributed in the North Sea (Section 5.4), “cold water” species are generally not recorded south of the 50 m contour, i.e. the northern edge of the Dogger Bank, and “warm water” species generally do not extend north of the 100 m contour (Künitzer *et al.*, 1992; see also Kröncke and Bergfeld, 2003). Changes in the densities of such species in the vicinity of the Dogger Bank in the 1990s have been linked with NAO-mediated influences (Wieking and Kröncke, 2001; Section 5.2).

The outcomes of analyses of the NSBP 2000 data generally corroborate earlier findings (Table 7.2.1), rather than reveal hitherto unsuspected influences. The inclusion of a wider array of abiotic variables than in 1986 via modelled outputs aided data interpretation. For example, NSBP 2000 analyses highlighted the dynamic nature of the interaction between sediments and water movements and their role in structuring benthic communities (see e.g. Sections 5.3, 6.1, and Table 7.2.1). Combinations of variables that best explain patterns at a locality may change in their relative importance or differ at another, and additional variables may assume importance as the scale is enlarged to encompass the North Sea as a whole. Although

interpretational problems associated with autocorrelation and non-linearity in responses are likely to increase with the numbers employed, including more rate variables (Section 5.3), which may be cost-effectively sourced from validated ecosystem models, could enhance confidence in cause–effect deductions. At the same time, “stand-alone” biological assessments using appropriate interpretational tools continue to have utility (e.g. indicator applications: Section 5.6).

Similarities in the broader divisions between community types across the North Sea in 1986 and 2000 may be linked to well-established dependencies, such as depth and sediment type. As might be expected on this scale, the latter showed no significant compositional change (see Section 4.2). However, underlying these similarities, significant differences in structural and functional properties within communities were identified (e.g. Sections 5.2 and 5.5), i.e. there was evidence of local adaptation to environmental changes. This may also be deduced from comparisons of the distributions of individual species (see Section 5.4), but these did not, in combination, indicate a consistent directional trend. Although it is necessary to caution against undue reliance on the evidence from only two surveys, a number of sections (e.g. Sections 5.2 and 5.7) hint at why a uniform response to natural environmental changes is unlikely on the scale of the North Sea. For example, significant correlations between population fluctuations in the benthos and the NAO Index have been reported, but these may be either positive or negative, and lagged in time to varying degrees depending on locality.

Boesch and Rosenberg (1981) define resilience as “the ability to recover to some more or less persistent state”. The authors note that the concept is somewhat artificial when applied to communities, because the constituent species may show widely contrasting sensitivities to environmental change. Nonetheless, it appears to have some merit in accounting for the recurrence of major patterns in North Sea benthic communities, as episodic events (as well as longer term trends) with the potential to induce significant changes in the benthos have occurred over the 15-year interval between surveys. Thus, the evidence supports relative constancy, i.e. resilience, at the level of the North Sea, rather than the emergence of dramatically altered states and the breakdown of pattern. Of course, this is not to say that all North Sea communities are equally resilient (see e.g. van Nes *et al.*, 2007).

It is likely that the major divisions between community types in the North Sea will still be evident in a future synoptic survey conducted after an interval of 10–15 years, and this is easily testable (see Section 8). Predicting the path of population changes within communities is more difficult. For example, adaptations may be expected to accompany any directional climatic changes because there are known sensitivities, but these are not expected to follow the same trajectory throughout the North Sea. Thus, future observations in a North Sea-wide setting will be especially useful to identify the full range of any ecological consequences.

We conclude that North Sea benthic communities remain in equilibrium with natural environmental forces that account for most of the observed variability in space and time. Traits of resilience and adaptability may explain patterns and changes in the benthic communities at the level of the entire North Sea and more locally, respectively.

7.3 Human influences

The distribution of stations in 2000 is unsuitable to systematically addressing activities whose impacts are expected to be relatively localized in extent (see, e.g. Rees and Eleftheriou, 1989; Kröncke and Bergfeld, 2003 and below). However, general manifestations of the consequences of human inputs of persistent contaminants, especially via estuaries and the atmosphere, can be reflected in the status of seabed sediments that represent an eventual sink for most of those discharged to sea. For example, information on trace metal concentrations in sediments of the southwestern North Sea and German Bight (Section 4.3) provided evidence of an historical legacy of contamination, though there was no indication of adverse

consequences for the benthic fauna at the levels encountered. This is consistent with the North Sea-wide classification of “good to high” ecological status of faunal assemblages derived from biotic indices (Section 5.6).

Water-column eutrophication also has the potential to induce effects on seabed organisms on scales that might be detectable in a North Sea-wide survey. There is much historical evidence for the enrichment of sediments and modifications to the benthic fauna arising from the settled end products of enhanced primary production. This includes, in more serious cases, the induction of hypoxia or anoxia of bottom waters, resulting in widespread mortality of invertebrates and fish, especially in enclosed or periodically more quiescent waters of the eastern North Sea and the Skagerrak/Kattegat (see e.g. reviews by Heip (1995) and Kröncke and Bergfeld (2003)).

A recent evaluation of the status of the Wadden Sea ecosystem (see Essink (2005) and Section 5.7) concluded that it continued to reflect an early stage of eutrophication; a worsening future trend appeared to be unlikely, owing to declining nutrient inputs to the system (and to the North Sea generally: see OSPAR Commission, 2000). Coverage of the inshore environment by NSBP 2000 is too patchy to allow a systematic assessment, though the status of the benthic fauna at stations in parts of the German Bight has earlier been linked to the effects of eutrophication (Rachor, 1990). Certain compositional changes in the benthos of this locality between the 1986 and 2000 surveys may be linked to an NAO-induced increase in water-column productivity though these are not necessarily linked to human activities (Section 5.2).

On a wider scale, modelled outputs employed in the NSBP 2000 analyses indicated significantly higher chlorophyll *a* concentrations in surface waters in 2000 compared with 1986 (Section 5.3). There was no significant relationship with benthic biomass either within or between years, although this was not unexpected, given the complexity of the processes governing benthic–pelagic interactions. Heip *et al.* (1992a) found a significant positive correlation between benthic biomass and sediment chlorophyll *a* concentrations in 1986, noting that the distinction between stratified and mixed waters and its effect on food inputs to the seabed may be influential, i.e. there was no presumption of any link between the concentrations encountered and eutrophication. No measures of sediment chlorophyll *a* were made in 2000. Therefore, while we cannot dismiss a wider (offshore) influence on benthic assemblages arising from anthropogenically sourced nutrient inputs, we can conclude that there was no evidence of a regional or more localized legacy of an extreme event, or of a general trend towards the enrichment of benthic assemblages as a consequence of water-column eutrophication.

The activity with the greatest potential to influence benthic assemblages on a North Sea-wide scale is that of commercial fishing at the seabed. An assessment of the long-term consequences of selective predator removal for the benthic ecosystem was beyond the scope of this study. Our assessment (Section 6.3) was confined to a consideration of the consequences of the passage of commercial trawls across the seabed. These have been well documented, but the extrapolation of findings to larger sea areas can be problematic (e.g. Jennings and Kaiser, 1998). For example, the effect of a trawl tow across a shallow sandy area characterized by an infaunal assemblage that is adapted to frequent natural physical perturbations may be very different from that across mixed substrata at a more quiescent location, typically supporting a more diverse, structured, and long-lived fauna.

Moreover, the physical effects of trawling in less intensively fished areas may be localized to the immediate vicinity of each trawling event and, allowing for recovery processes, their detection will depend on the timing of coincident benthic sampling relative to the (earlier) occurrence of that event. An analogy may be drawn with environmental impact studies at aggregate extraction sites subject to varying intensities and histories of dredging. As a result of improved industrial practice in recent years, both are precisely known from “black box”

recorders of dredger activity in licensed areas (e.g. Boyd and Rees, 2003). Such precision is rarely feasible when investigating the effects of commercial fishing (but see Rijnsdorp *et al.*, 1998 and Mills *et al.*, 2007).

There was evidence (Section 6.3) of small but significant changes in species occurrences in areas of higher fishing intensity, but the broader scale relationship between the structure of benthic assemblages and the distribution of fishing effort was correlative rather than causative. Therefore, the evaluation was not immune from the difficulties of “scaling up”, encountered elsewhere. The analysis also indicated that structural changes in benthic assemblages between 1986 and 2000 were largely natural in origin rather than fishing-induced and, in agreement with the outcome of the recent EU MAFCONS project (Greenstreet *et al.*, 2007a), did not conform to classical ecological disturbance hypotheses. More emphasis on the measurement of functional traits was recommended (see e.g. Bremner *et al.*, 2003; Tillin *et al.*, 2006) for future studies, along with the targeting of the larger and rarer invertebrate species, which are inadequately sampled by grabs, and improved precision in the tracking of commercial trawling activity. A similar conclusion was reached from a review of foodweb studies (Section 6.2), which also noted that there was as yet no evidence of changes to the processes of energy flow through the benthic ecosystem as a result of fishing practices.

NSBP 2000 data coverage for the northern North Sea is too patchy to offer an overview of the consequences of offshore oil and gas developments. However, for the southwestern North Sea, where systematic sampling was similar to 1986, Smith *et al.* (2005) concluded that the ecological effects of anthropogenic influences arising from gas installations and aggregate extraction were not identifiable on the admittedly relatively coarse scale of the sampling grid. It followed that there was no evidence of a wider “footprint” associated with concentrations of these activities. This is also reflected in the outcome of the present wider scale assessment and confirms the findings of other more targeted studies, namely that effects are generally localized to scales of, at most, a few kilometres from installations (see e.g. OSPAR Commission, 2000). Even in combination, these are beyond the resolving power of the ICES grid.

The ICES North Sea benthos surveys in 1986 and 2000 are valuable for providing a wider context for the large numbers of ongoing environmental assessments typically conducted on much smaller spatial scales. A significant recent development is the commissioning of industrial-scale offshore wind farms. Although the 2000 dataset largely pre-dates these developments and hence cannot provide insights into any consequences for the seabed environment, coverage especially in the shallower waters of the southern North Sea may in future provide a useful international baseline for a combined assessment.

We conclude that, in general, the North Sea continues to support infaunal communities that are structured according to variations in predominantly natural forces, and that are sufficiently resilient to accommodate the consequences of contemporary anthropogenic influences operating over larger scales without significant degradation. We make no judgement about the degree to which climatic changes may be determined by human activities, an issue that is clearly beyond the scope of this study.

7.4 Lessons for sea-wide collaborative assessments

Some advantages and constraints associated with the conduct of periodic, sea-wide assessments of benthic communities, identified by the NSBP 2000 study group, are listed in Table 7.4.1. In 1999, German scientists took the initiative to commence a programme of resampling at a number of the NSBS 1986 stations. This stimulated new sampling effort and the provision of existing contemporary data by other countries, leading to the support of ICES for the creation of a study group to coordinate the activity. This followed a disappointing period in the 1990s when two bids for international funding promoted by the ICES Benthos

Ecology Working Group – one for a synoptic survey of the macro-infauna of the Irish and Celtic Seas, and another for a repeat of NSBS 1986 – were unsuccessful, principally because such exercises were deemed to be more appropriate for support at a national level. However, collaborative projects to evaluate epifaunal biodiversity and benthic responses to fishing pressures in the North Sea were successful in obtaining EU funding (Callaway *et al.*, 2002; Greenstreet *et al.*, 2007a, 2007b; www.mafcons.org). These had the merit of exploiting existing ship time committed to groundfish surveys. An incidental benefit of the field sampling of sediments under the EU MAFCONS project was the provision of material collected by Scotland for UK-funded taxonomic analyses as a contribution to NSBP 2000.

The proposed repeat of NSBS 1986 attracted the early interest of ICES; this was fortunate because, following the initiation of sampling in 1999, it was well placed to support an extended time frame for completion arising from the uneven resource commitment across countries. A similar challenge presented itself, albeit less acutely, in the aftermath of NSBS 1986. Additionally, a vital contribution to continuity of effort was provided by data management support at the Flanders Marine Institute (VLIZ). This included the construction of a database (Section 3) and the input of analytical expertise.

The wide respect that ICES commands across the marine science community had the important effect of assuaging the concerns of some contributors who were sensitive to the provision of expensively acquired data. As highlighted in Table 7.4.1, NSBP 2000 provided valuable opportunities for individual scientists to engage with others in international collaborative work, with lasting institutional benefits for the development of environmental assessment skills. Synergies arising from the contributions of research students affiliated with study group members were especially advantageous.

The exercise profited from the involvement of a number of experts engaged in parallel international initiatives, e.g. the EU MarBEF and MAFCONS projects. Though reporting through separate channels and to different deadlines, interaction was facilitated by the longer time frame of the ICES undertaking: a positive, if unintended, consequence of the absence of coordinated international funding for a synoptic survey. It resulted in improved integration with other North Sea-wide information sources, thereby contributing to the wider goal of promoting an ecosystem approach to environmental management.

The synthesis of products for the present ICES report was an important milestone for authors and data contributors, but this is not the end of the exercise. Further products will appear in the peer-reviewed literature and, as is now the case for the 1986 survey, the NSBP 2000 database will provide a well-structured and permanent repository for future exploitation by the wider scientific community.

The facility to report on wider spatial patterns and on changes occurring over long (10–20 year) timescales allows generic policy and scientific interests to be addressed, without substituting for the more detailed assessments that are also required. Thus, the insights gained from sea-wide synoptic surveys provide a valuable underpinning to more targeted R and D and monitoring programmes. The benefits for the latter, typically conducted on national or more localized levels, include the opportunity for individual countries to:

- Better understand large-scale changes that may be “hidden” in local datasets, e.g. in relation to the distribution of rare or endangered species.
- Evaluate the effectiveness of national monitoring designs (this applies particularly to checks on the continued validity of reference stations), and hence adapt programmes as necessary.
- Identify stations to facilitate routine cross-referencing against the outcome of other national programmes, to place survey outcomes into a wider geographical perspective.

- Use the results to assess the quality and comparability of sampling and analytical work.
- Improve the targeting of influential environmental variables, e.g. hydrodynamic properties, to underpin interpretations of biological data.

The lessons learned from NSBP 2000 and comparable initiatives are reflected in recommendations for follow-up work (Section 8). Finally, we conclude that, despite the challenges imposed by the lack of coordinated international funding, the outcome of NSBP 2000 has been successful and of a nature which amply demonstrates the capability of ICES to address the state of the marine environment across larger spatial scales and over longer periods than are feasible by most other organizations.

Table 7.4.1. The ICES North Sea Benthos Project: advantages/constraints associated with a repeated sea-wide assessment (synoptic resampling and/or data compilation).

| ADVANTAGES | CONSTRAINTS |
|--|--|
| Consistent sea-wide spatial coverage and quality of outputs through application of a uniform survey strategy and harmonized sampling and analytical methodologies. | Coordinated international surveys require a lot of work and hence adequate resources. |
| A fully resourced synoptic survey will provide the basis for a more formal hypothesis-testing framework and allow more specific scientific questions to be addressed. | “Opportunistic” exploitation of ship time and available personnel, or existing data sources, can lead to quality assurance (QA) problems and uneven coverage in the absence of adequate resources and planning at an international level. |
| The process (sampling, analysis, data management, etc.) will take less time in future, because much of the groundwork for a repeat survey has already been done. | Local and North Sea-wide methods have to be comparable. |
| The effects of local and regional developments can be compared with “global” benthic status. | |
| Evaluation of the success of actions, e.g. under the EU Habitats and Water Framework directives, Natura 2000, and OSPAR auspices. | |
| Evaluation of the success of fisheries and other resource management measures aimed at the protection of benthic ecosystem structure and function. | |
| Standard setting for monitoring activities in restricted areas (e.g. at wind farms, sand and gravel extraction areas, oil and gas platforms, marine nature reserves); incorporation of such data into a wider assessment framework. | Insufficient availability of such datasets, which may be restricted on the grounds of commercial confidentiality. |
| Support for ecosystem-level studies, including predictive modelling. | Lack of funding. |
| Keeps a well-trained and experienced group of scientists “alive” to the process of international collaboration, and the pursuit of excellence; provides an important training ground for young scientists. | If there is no longer term planning of a repetition, it will be difficult to find the (experienced) scientists to produce comparable data and interpretations on sea-wide scales. Currently, there is limited academic interest/commitment to the process, despite much interest in the outputs. |
| Generates a permanent archive of important sea-wide data on benthic biological status for historical comparisons (allowing the effects of, for example, climate change, eutrophication, fishing impacts, alien/invasive species, and conservation measures to be addressed). | Lack of public interest/resonance. |
| Strategically important benefit of integrating/amending national approaches for North Sea-wide ecosystem assessment and management. | |
| Sets a realistic (ten-year) timescale for sea-wide re-assessment. | |

| ADVANTAGES | CONSTRAINTS |
|--|--|
| Elaboration of North Sea-wide lists of rare and endangered species (e.g. for a “Red Book”) will be feasible. Sea-wide synoptic surveys also provide the means to identify the presence and/or range extensions of new or alien species. | Specific (national) lists may be inconsistent and therefore difficult or impossible to combine for international action. |
| Opportunity for identifying “representative” (habitat- or assemblage-based) stations for long-term monitoring. | |
| Fits with the international momentum towards holistic (sea-wide) ecosystem assessments, especially under OSPAR, ICES, and EU auspices. | |
| Achievable given good collaboration, international support, and adequate resources. | Earlier proposals for funding of collaborative sea-wide assessments of the benthos have tended to founder on the view that responsibilities and therefore funding rest with individual countries (leading to a circular argument). |
| New coordinated survey work would be an excellent opportunity to implement recent improvements in QA of benthic studies (sampling and analytical procedures; data management) and further exploit the high level of scientific skills of representatives from all North Sea countries. | Opportunistic data compilation can be a “hostage to fortune”, given limitations in spatial coverage and data quality at a given time (see above). |

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8 Recommendations

Several recommendations for future work were drafted by the ICES Study Group on the North Sea Benthos Project 2000, foremost among them being a proposal for a third synoptic survey. It is intended that, initially, these would be further developed by the ICES Benthos Ecology Working Group and approaches to implementing any new work will depend on the outcome of the planning phase.

- i) Plan for the conduct of a coordinated, interdisciplinary synoptic survey of the North Sea in 2010 under ICES auspices. In doing so, the following lines of inquiry should be pursued:
 - 1) Identify the circumstances which might in future attract international funding for periodic sampling and analytical effort on the scale of whole sea areas.
 - 2) Review the feasibility and costs, at a national level, of a periodic uplift in sampling effort to effect a sea-wide synoptic survey consistent with the needs of ongoing national assessments.
 - 3) Alternatively, seek the support of national agencies for a comparable ICES-sponsored international assessment using data from national monitoring programmes and other sources on an opportunistic basis.
 - 4) Appraise the advantages and limitations attached to widening the time interval (e.g. 2–3 years) for completion of a synoptic survey.
 - 5) Identify the scope for exploiting existing ship time for North Sea sampling.
- ii) Consider the feasibility of extending synoptic surveys into other sea areas using the North Sea benthos surveys as pilot schemes.
- iii) Conduct integrated assessments across sea areas employing the outcomes of targeted interdisciplinary effort and parallel information from other contemporary studies.
- iv) Ensure long-term support for the North Sea Benthos database and establish links with the ICES and EurOBIS* databases to facilitate access by the wider scientific community, subject to the requirements of data contributors as outlined in Section 3. (*European node of the Ocean Biogeographic Information System).
- v) Provide wider access to the NSBP 2000 database through initiatives such as the EU MarBEF network, subject to the requirements of data contributors as outlined in Section 3.
- vi) Further promote the benefits of annual monitoring at representative national locations, to facilitate the interpretation of infrequent, larger scale assessments.

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Annex 1: Trace metal concentrations, particle size statistics, and total organic carbon/nitrogen for NSBP samples completed at Cefas

| NSB STATION CODE | LATITUDE (DECIMAL DEGREES) | LONGITUDE (DECIMAL DEGREES) | AL (%) | AS (MG KG ⁻¹) | CD (MG KG ⁻¹) | CR (MG KG ⁻¹) | CU (MG KG ⁻¹) | FE (%) | HG (MG KG ⁻¹) | LI (MG KG ⁻¹) | MN (MG KG ⁻¹) | N (MG KG ⁻¹) | PB (MG KG ⁻¹) | RB (MG KG ⁻¹) | V (MG KG ⁻¹) | ZN (MG KG ⁻¹) | MEDIAN (PHI) | MEDIAN (OM) | MEAN (PHI) | MEAN (OM) | SORTING | SKENNESS | KURTOSIS | %GRAVEL | %SAND | %SILT/CLAY | %OC | %ON |
|------------------|----------------------------|-----------------------------|--------|---------------------------|---------------------------|---------------------------|---------------------------|--------|---------------------------|---------------------------|---------------------------|--------------------------|---------------------------|---------------------------|--------------------------|---------------------------|--------------|-------------|------------|-----------|---------|----------|----------|---------|-------|------------|------|------|
| 3 | 55.25 | 1.5 | 6.30 | 30 | 0.46 | 112 | 43 | 4.70 | 0.25 | 49 | 722 | 37 | 243 | 83 | 150 | 147 | 2.52 | 173.85 | 2.18 | 0.22 | 1.10 | -1.13 | 12.45 | 2.12 | 97.24 | 0.64 | ** | ** |
| 4 | 55 | -1 | 7.00 | 16 | 0.21 | 105 | 20 | 3.70 | 0.19 | 50 | 725 | 27 | 71 | 76 | 111 | 124 | 3.19 | 109.24 | 3.54 | 0.09 | 2.28 | 1.40 | 4.82 | 0.35 | 84.00 | 15.64 | 3.55 | 0.34 |
| 5 | 55 | 0 | 7.00 | 24 | 0.2 | 108 | 20 | 4.40 | 0.12 | 54 | 1502 | 34 | 112 | 88 | 135 | 142 | 2.44 | 184.77 | 2.79 | 0.14 | 1.82 | 2.46 | 9.57 | 0.05 | 92.60 | 7.35 | 2.96 | 0.35 |
| 7 | 55 | 2 | 2.80 | 70 | 0.34 | 93 | 18 | 3.03 | 0.08 | 19 | 472 | 30 | 27 | 30 | 91 | 88 | 2.52 | 174.58 | 2.48 | 0.18 | 0.64 | 3.91 | 50.37 | 0.03 | 99.44 | 0.53 | 1.60 | 0.25 |
| 8 | 54.75 | -0.5 | 9.71 | 48 | 0.19 | 137 | 27 | 5.33 | 0.2 | 80 | 3111 | 53 | 199 | 123 | 181 | 205 | 2.81 | 143.06 | 2.85 | 0.14 | 1.00 | 3.16 | 23.19 | 0.03 | 96.83 | 3.14 | 4.79 | 0.51 |
| 9 | 54.75 | 0.5 | 7.60 | 22 | 0.29 | 97 | 17 | 3.50 | 0.07 | 49 | 1138 | 27 | 90 | 92 | 143 | 139 | 3.03 | 122.41 | 3.17 | 0.11 | 1.05 | 4.65 | 29.81 | 0.00 | 97.19 | 2.81 | 3.54 | 0.43 |
| 10 | 54.75 | 1.5 | 5.40 | 18 | 0.26 | 86 | 27 | 3.50 | 0.08 | 48 | 494 | 34 | 51 | 75 | 110 | 92 | 2.58 | 167.67 | † | † | † | † | † | 0.08 | 98.83 | 1.09 | 3.71 | 0.59 |
| 11 | 54.5 | 0 | 8.52 | 72 | 0.2 | 136 | 26 | 6.06 | 0.19 | 82 | 9510 | 52 | 327 | 115 | 243 | 240 | 2.64 | 160.71 | 2.47 | 0.18 | 1.05 | 1.91 | 16.89 | 0.10 | 97.83 | 2.06 | 5.23 | 0.66 |
| 12 | 54.5 | 1 | 6.82 | 97 | <0.15 | 131 | 26 | 6.92 | 0.11 | 72 | 5331 | 48 | 232 | 111 | 265 | 217 | 2.24 | 211.43 | 2.26 | 0.21 | 1.01 | 1.70 | 32.19 | 1.43 | 97.29 | 1.28 | 4.92 | 0.71 |
| 13 | 54.5 | 2 | 3.63 | 20 | 0.32 | 58 | 15 | 3.10 | 0.09 | 37 | 574 | 7.8 | 66 | 60 | 109 | 85 | 2.53 | 173.62 | † | † | † | † | † | 0.42 | 98.59 | 0.99 | 3.84 | 0.62 |
| 14 | 54.25 | 0.5 | 7.54 | 59 | 0.18 | 139 | 29 | 5.79 | 0.18 | 86 | 5324 | 49 | 321 | 121 | 235 | 243 | 2.25 | 209.99 | 2.24 | 0.21 | 0.98 | 3.68 | 33.68 | 0.49 | 98.22 | 1.28 | 4.58 | 0.60 |
| 15 | 54.25 | 1.5 | 6.25 | 18 | 0.23 | 86 | 16 | 3.18 | 0.05 | 49 | 372 | 33 | 46 | 36 | 122 | 108 | 2.67 | 156.88 | 2.82 | 0.14 | 1.18 | 4.46 | 25.58 | 0.00 | 96.71 | 3.29 | 2.89 | 0.40 |
| 16 | 54 | 0 | 7.30 | 30 | 0.2 | 99 | 24 | 4.30 | 0.21 | 77 | 1957 | 35 | 106 | 78 | 139 | 143 | -2.44 | 5425.56 | -1.87 | 3.66 | 2.34 | 1.47 | 5.84 | 71.96 | 26.22 | 1.82 | 2.72 | 0.26 |
| 17 | 54 | 1 | 4.10 | 34 | 0.28 | 99 | 21 | 4.70 | 0.22 | 61 | 1143 | 27 | 119 | 66 | 192 | 169 | 2.79 | 144.49 | 2.95 | 0.13 | 0.98 | 5.43 | 36.72 | 0.08 | 97.40 | 2.52 | 3.48 | 0.49 |
| 18 | 54 | 2 | 5.95 | 14 | 0.16 | 103 | 15 | 3.83 | 0.06 | 34 | 514 | 32 | 57 | 79 | * | 98 | 3.09 | 117.37 | 3.66 | 0.08 | 1.70 | 2.50 | 8.64 | 0.00 | 85.52 | 14.48 | 1.90 | 0.19 |
| 19 | 53.75 | 0.5 | 7.73 | 33 | 0.16 | 99 | 22 | 4.24 | 0.12 | 82 | 842 | 48 | 61 | 96 | 125 | 110 | 1.04 | 486.09 | 0.39 | 0.76 | 2.84 | 0.22 | 3.31 | 31.19 | 63.68 | 5.13 | 2.26 | 0.18 |
| 20 | 53.75 | 1.5 | 8.34 | 53 | 0.15 | 101 | 20 | 4.36 | 0.07 | 77 | 926 | 45 | 55 | 57 | 154 | 117 | 1.42 | 373.43 | 1.25 | 0.42 | 1.38 | 0.44 | 12.88 | 7.76 | 91.41 | 0.82 | 2.25 | 0.21 |
| 21 | 53.5 | 2 | 8.84 | 36 | <0.14 | 86 | 28 | 3.66 | 0.19 | 55 | 957 | 34 | 80 | 85 | 114 | 109 | 1.66 | 315.64 | 1.67 | 0.31 | 0.71 | 2.82 | 34.16 | 0.37 | 98.94 | 0.69 | 3.35 | 0.51 |
| 22 | 53 | 1 | 5.43 | 68 | 0.41 | 98 | 43 | 2.95 | 0.23 | 53 | 948 | 39 | 190 | 66 | 102 | 155 | 1.93 | 263.30 | 2.01 | 0.25 | 0.96 | 4.91 | 42.32 | 0.70 | 97.81 | 1.49 | ‡ | ‡ |
| 23 | 53 | 2 | 2.57 | 78 | 0.12 | 55 | 27 | 3.99 | 0.12 | 32 | 1139 | 20 | 112 | 45 | 154 | 164 | 1.56 | 338.69 | 1.55 | 0.34 | 0.87 | 1.92 | 28.02 | 1.48 | 97.58 | 0.94 | 1.75 | 0.32 |
| 24 | 52.5 | 2 | 6.04 | 72 | 0.18 | 95 | 30 | 4.70 | 0.17 | 54 | 1182 | 41 | 58 | 73 | 172 | 150 | -1.94 | 3825.15 | -1.01 | 2.01 | 3.10 | 0.36 | 2.15 | 54.04 | 43.98 | 1.98 | 1.25 | 0.14 |
| 25 | 52 | 2 | 5.83 | 16 | 0.13 | 147 | 37 | 5.70 | 0.08 | 106 | 363 | 82 | 26 | 63 | 225 | 144 | 0.63 | 644.44 | 1.42 | 0.37 | 4.84 | 0.65 | 2.10 | 39.61 | 36.43 | 23.96 | 0.57 | 0.07 |
| 26 | 51.75 | 1.5 | 7.85 | 4.8 | 0.26 | 125 | 25 | 4.73 | 0.12 | 55 | 373 | 40 | 31 | 91 | 209 | 125 | -1.23 | 2347.32 | -0.26 | 1.20 | 3.52 | 0.65 | 2.56 | 51.15 | 40.01 | 8.83 | 0.71 | 0.08 |
| 27 | 51.5 | 1 | 4.36 | 19 | 0.32 | 119 | 22 | 3.47 | 0.23 | 46 | 427 | 19 | 42 | 69 | 122 | 110 | 1.40 | 379.71 | 0.99 | 0.50 | 2.60 | 0.16 | 3.96 | 23.08 | 72.14 | 4.77 | 0.87 | 0.09 |
| 28 | 51.5 | 2 | 2.40 | 14 | <0.13 | 40 | 14 | 1.47 | 0.07 | 26 | 190 | 17 | 12 | 32 | 67 | 50 | 1.30 | 405.33 | 1.31 | 0.40 | 0.49 | 3.61 | 79.57 | 0.43 | 99.41 | 0.15 | 1.00 | 0.15 |
| 29 | 51.25 | 1.5 | 4.07 | 41 | 0.33 | 68 | 11 | 3.07 | 0.08 | 33 | 663 | 24 | 26 | 48 | 90 | 78 | -0.29 | 1222.61 | -0.48 | 1.40 | 3.44 | 0.64 | 3.20 | 45.19 | 46.95 | 7.86 | 0.94 | 0.11 |
| 32 | 56 | -1 | 5.10 | 26 | 0.26 | 74 | 24 | 3.10 | <0.02 | 43 | 2791 | 40 | 113 | 70 | 117 | 112 | 2.03 | 245.19 | 1.84 | 0.28 | 1.47 | -0.57 | 10.00 | 6.16 | 91.98 | 1.86 | 3.59 | 0.50 |
| 33 | 56 | 0 | 5.40 | 16 | 0.24 | 77 | 15 | 3.10 | 0.08 | 43 | 793 | 30 | 77 | 73 | 98 | 98 | 2.53 | 172.69 | 2.58 | 0.17 | 1.13 | 2.66 | 17.48 | 0.02 | 96.18 | 3.80 | 3.41 | 0.43 |
| 34 | 56 | 1 | 5.59 | 6.2 | 0.46 | 92 | 14 | 1.56 | 0.1 | 36 | 434 | 31 | 53 | 72 | 91 | 105 | 2.59 | 166.43 | 2.63 | 0.16 | 0.69 | 5.21 | 47.40 | 0.02 | 98.14 | 1.83 | 3.89 | 0.50 |
| 35 | 56 | 2 | 5.64 | 9.3 | 0.42 | 111 | 16 | 3.14 | 0.44 | 43 | 439 | 33 | 59 | 75 | 103 | 104 | 3.07 | 119.41 | 3.22 | 0.11 | 1.19 | 2.41 | 12.20 | 0.04 | 91.55 | 8.40 | 3.26 | 0.37 |
| 36 | 55.75 | -1.5 | 6.50 | 17 | 0.23 | 89 | 19 | 3.70 | 0.15 | 52 | 834 | 38 | 68 | 82 | 112 | 109 | 1.47 | 361.40 | 1.28 | 0.41 | 2.14 | 1.01 | 6.78 | 14.06 | 81.68 | 4.26 | 2.76 | 0.33 |
| 37 | 55.75 | -0.5 | 6.80 | 36 | 0.23 | 98 | 17 | 4.80 | 0.07 | 58 | 1782 | 40 | 134 | 89 | 163 | 157 | 2.25 | 210.91 | 2.35 | 0.20 | 1.14 | 3.49 | 21.19 | 0.03 | 97.08 | 2.89 | 4.11 | 0.55 |
| 38 | 55.75 | 0.5 | 4.61 | 14 | 0.29 | 96 | 19 | 2.96 | 0.09 | 45 | 476 | 30 | 100 | 84 | 116 | 113 | 2.29 | 203.81 | 2.35 | 0.20 | 0.97 | 2.87 | 26.07 | 0.33 | 97.60 | 2.07 | 3.10 | 0.37 |
| 39 | 55.75 | 1.5 | 5.18 | 30 | 0.3 | 94 | 9.4 | 2.54 | 0.07 | 30 | 481 | 31 | 43 | 58 | 84 | 82 | 2.64 | 160.46 | 2.63 | 0.16 | 1.12 | -0.27 | 26.50 | 1.37 | 96.07 | 2.56 | 3.68 | 0.47 |
| 40 | 55.75 | 2.5 | 5.97 | 61 | 0.33 | 125 | 15 | 3.41 | 0.09 | 42 | 543 | 32 | 66 | 86 | 104 | 103 | 3.53 | 86.30 | 3.72 | 0.08 | 1.36 | 2.26 | 10.75 | 0.12 | 85.84 | 14.03 | 1.84 | 0.21 |
| 42 | 55.5 | 0 | 4.98 | 16 | 0.24 | 90 | 20 | 3.31 | 0.08 | 49 | 531 | 27 | 105 | 87 | 119 | 123 | 2.46 | 182.06 | 3.01 | 0.12 | 1.75 | 2.43 | 9.12 | 0.00 | 91.92 | 8.08 | 3.01 | 0.36 |
| 43 | 55.5 | 1 | 5.11 | 28 | 0.16 | 90 | 18 | 4.10 | 0.08 | 53 | 1089 | 28 | 117 | 94 | 146 | 145 | 2.40 | 189.58 | 2.69 | 0.16 | 1.25 | 4.21 | 21.68 | 0.00 | 95.74 | 4.26 | 3.58 | 0.45 |
| 44 | 55.5 | 2 | 7.16 | 11 | 0.56 | 111 | 19 | 4.02 | 0.14 | 57 | 447 | 42 | 94 | 114 | 145 | 146 | 2.76 | 147.15 | 2.89 | 0.14 | 0.93 | 4.92 | 36.76 | 0.11 | 97.47 | 2.43 | 1.97 | 0.25 |
| 46 | 54.75 | 2.5 | 5.84 | 22 | 0.32 | 94 | 19 | 4.56 | 0.09 | 58 | 545 | 26 | 52 | 88 | 162 | 130 | 2.98 | 126.33 | 3.15 | 0.11 | 1.25 | 3.94 | 22.45 | 0.23 | 96.25 | 3.53 | 2.75 | 0.34 |
| 48 | 53.75 | 2.5 | 5.96 | 28 | 0.17 | 88 | 27 | 4.21 | 0.11 | 66 | 820 | 31 | 33 | 77 | 145 | 111 | 1.63 | 323.64 | 1.51 | 0.35 | 0.84 | -0.31 | 14.07 | 1.40 | 98.24 | 0.36 | 2.57 | 0.31 |
| 49 | 53.5 | 1 | 5.80 | 20 | 0.21 | 70 | 16 | 3.40 | 0.11 | 57 | 775 | 34 | 56 | 59 | 108 | 109 | -0.88 | 1843.28 | -0.69 | 1.62 | 2.43 | 0.36 | 2.62 | 48.42 | 50.52 | 1.06 | 2.17 | 0.34 |
| 50 | 53.25 | 0.5 | 6.20 | 27 | 0.19 | 97 | 25 | 4.00 | 0.18 | 78 | 833 | 35 | 69 | 82 | 130 | 154 | 1.72 | 303.99 | 1.14 | 0.45 | 3.01 | 0.44 | 2.96 | 31.07 | 56.83 | 12.10 | 2.32 | 0.20 |
| 51 | 53.25 | 1.5 | 7.80 | 23 | 0.49 | 101 | 25 | 4.50 | 0.12 | 81 | 980 | 44 | 48 | 87 | 135 | 121 | 1.33 | 396.85 | 0.90 | 0.54 | 2.50 | 0.47 | 4.37 | 24.33 | 70.01 | 5.66 | 1.47 | 0.14 |
| 52 | 53.25 | 2.5 | 6.70 | 33 | 0.18 | 108 | 22 | 4.30 | 0.15 | 71 | 757 | 36 | 70 | 85 | 161 | 130 | 2.31 | 201.85 | 2.37 | 0.19 | 0.78 | 1.65 | 41.97 | 0.71 | 97.93 | 1.36 | 2.21 | 0.29 |
| 53 | 52.75 | 2.5 | 4.37 | 55 | <0.15 | 71 | 16 | 2.91 | 0.11 | 40 | 832 | 28 | 32 | 56 | 105 | 91 | 1.56 | 339.25 | † | † | † | † | † | 7.17 | 91.95 | 0.88 | 1.57 | 0.23 |
| 54 | 52.25 | 2.5 | 7.58 | 35 | <0.16 | 98 | 23 | 3.79 | 0.2 | 59 | 777 | 31 | 100 | 102 | 137 | 120 | 1.57 | 336.67 | † | † | † | † | † | 1.08 | 98.64 | 0.28 | 2.52 | 0.37 |

* not measured. † not calculated as insufficient material in the <63 µm fraction to complete laser diffraction. ‡ not completed.

Annex 2: Results of the SIMPER analysis from Section 5.2

Results of the SIMPER analysis based on fourth-root transformed abundance data. The 1986 clusters were compared with the corresponding stations in 2000.

Cluster A

Average dissimilarity = 72.50

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|--------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Thyasira</i> | 346.29 | 17.53 | 1.18 | 1.59 | 1.62 | 1.62 |
| <i>Lumbrineris latreilli</i> | 25.69 | 0.00 | 1.02 | 2.50 | 1.40 | 3.03 |
| <i>Myriochele</i> | 165.65 | 109.06 | 0.98 | 1.27 | 1.35 | 4.38 |
| <i>Paramphinome jeffreysii</i> | 29.88 | 97.03 | 0.95 | 1.45 | 1.31 | 5.69 |
| <i>Capitella</i> | 124.88 | 2.33 | 0.92 | 0.97 | 1.27 | 6.96 |
| <i>Pholoe baltica</i> | 74.35 | 4.56 | 0.90 | 1.40 | 1.25 | 8.21 |
| <i>Exogone</i> | 74.86 | 2.47 | 0.84 | 1.26 | 1.16 | 9.37 |
| <i>Aricidea catherinae</i> | 66.43 | 4.92 | 0.84 | 1.38 | 1.16 | 10.53 |
| <i>Cirrophorus lyra</i> | 67.41 | 1.42 | 0.83 | 1.22 | 1.14 | 11.67 |
| <i>Amphiura chiajei</i> | 2.50 | 55.75 | 0.83 | 1.32 | 1.14 | 12.81 |
| <i>Heteromastus filiformis</i> | 0.00 | 45.00 | 0.78 | 1.19 | 1.08 | 13.89 |
| <i>Pseudopolydora</i> | 39.85 | 2.11 | 0.76 | 1.27 | 1.05 | 14.94 |
| <i>Prionospio</i> | 50.95 | 15.00 | 0.76 | 1.22 | 1.05 | 15.99 |
| <i>Cautleriella</i> | 50.04 | 1.86 | 0.75 | 1.18 | 1.04 | 17.03 |
| <i>Eriopisa elongata</i> | 42.33 | 15.50 | 0.75 | 1.32 | 1.03 | 18.06 |
| <i>Mendicula ferruginosa</i> | 27.63 | 0.92 | 0.75 | 1.29 | 1.03 | 19.09 |
| <i>Leucon nasica</i> | 44.15 | 13.50 | 0.73 | 1.09 | 1.01 | 20.10 |
| <i>Diplocirrus glaucus</i> | 18.24 | 26.44 | 0.73 | 1.39 | 1.00 | 21.10 |
| <i>Levinsenia gracilis</i> | 99.36 | 37.28 | 0.71 | 1.34 | 0.98 | 22.08 |
| <i>Amphiura filiformis</i> | 30.06 | 30.17 | 0.69 | 1.31 | 0.95 | 23.03 |
| <i>Lumbrineris gracilis</i> | 0.00 | 7.69 | 0.68 | 1.66 | 0.94 | 23.96 |
| <i>Eudorella emarginata</i> | 21.05 | 16.92 | 0.68 | 1.20 | 0.93 | 24.90 |
| <i>Pectinaria</i> | 18.33 | 17.50 | 0.67 | 1.44 | 0.92 | 25.82 |
| <i>Glycera lapidum</i> | 57.56 | 2.78 | 0.66 | 1.05 | 0.91 | 26.73 |
| <i>Urothoe elegans</i> | 14.04 | 8.39 | 0.62 | 1.40 | 0.85 | 27.58 |
| <i>Spiophanes</i> | 91.23 | 62.69 | 0.61 | 1.08 | 0.84 | 28.43 |
| <i>Laonice sarsi</i> | 33.36 | 5.44 | 0.61 | 1.27 | 0.84 | 29.27 |
| <i>Notomastus</i> | 30.23 | 8.50 | 0.61 | 1.16 | 0.84 | 30.10 |
| <i>Owenia fusiformis</i> | 27.60 | 5.53 | 0.61 | 1.19 | 0.84 | 30.94 |
| <i>Goniada</i> | 19.68 | 9.03 | 0.60 | 1.24 | 0.83 | 31.77 |
| <i>Eclysippe vanelli</i> | 20.81 | 1.42 | 0.58 | 1.20 | 0.80 | 32.57 |
| <i>Nothria conchylega</i> | 28.25 | 0.75 | 0.58 | 1.05 | 0.80 | 33.37 |
| Aplacophora | 0.00 | 8.56 | 0.57 | 1.26 | 0.79 | 34.16 |
| <i>Eudorella truncatula</i> | 6.67 | 6.06 | 0.57 | 1.26 | 0.79 | 34.95 |

Cluster B

Average dissimilarity = 66.44

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|---------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Capitella</i> | 41.56 | 0.00 | 1.20 | 2.25 | 1.81 | 1.81 |
| <i>Ampharete lindstroemi</i> | 0.00 | 81.13 | 1.08 | 1.59 | 1.63 | 3.44 |
| <i>Praxillella</i> | 6.02 | 0.00 | 0.78 | 2.94 | 1.18 | 4.62 |
| <i>Paramphinome jeffreysii</i> | 0.66 | 25.10 | 0.77 | 1.47 | 1.16 | 5.78 |
| <i>Myriochele</i> | 178.86 | 261.83 | 0.76 | 1.60 | 1.15 | 6.93 |
| <i>Ampelisca spinipes</i> | 43.38 | 0.67 | 0.74 | 1.11 | 1.12 | 8.05 |
| <i>Anobothrus gracilis</i> | 8.64 | 2.00 | 0.72 | 2.05 | 1.08 | 9.13 |
| <i>Glycera rouxi</i> | 10.34 | 1.00 | 0.70 | 1.48 | 1.06 | 10.19 |
| <i>Thyasira</i> | 35.62 | 16.27 | 0.70 | 1.26 | 1.06 | 11.25 |
| <i>Levinsenia gracilis</i> | 38.88 | 16.03 | 0.69 | 1.25 | 1.04 | 12.29 |
| <i>Photis</i> | 6.72 | 0.00 | 0.63 | 1.60 | 0.95 | 13.24 |
| <i>Diplocirrus glaucus</i> | 7.94 | 19.63 | 0.63 | 1.41 | 0.94 | 14.18 |
| <i>Cirratulus</i> | 0.34 | 5.83 | 0.61 | 1.49 | 0.92 | 15.11 |
| <i>Heteromastus filiformis</i> | 0.00 | 17.40 | 0.61 | 0.98 | 0.92 | 16.03 |
| <i>Nephtys hombergii</i> | 12.40 | 5.33 | 0.61 | 1.58 | 0.92 | 16.94 |
| <i>Owenia fusiformis</i> | 5.36 | 26.53 | 0.60 | 2.03 | 0.91 | 17.85 |
| <i>Philomedes globosus</i> | 26.44 | 0.00 | 0.59 | 0.87 | 0.89 | 18.74 |
| <i>Echinocyamus pusillus</i> | 12.66 | 9.40 | 0.59 | 0.99 | 0.88 | 19.63 |
| <i>Malmgrenia arenicolae</i> | 2.68 | 0.00 | 0.57 | 1.80 | 0.86 | 20.48 |
| <i>Harpinia antennaria</i> | 6.66 | 23.13 | 0.57 | 1.53 | 0.85 | 21.34 |
| <i>Dipolydora flava</i> | 3.04 | 0.67 | 0.56 | 1.94 | 0.85 | 22.19 |
| <i>Urothoe elegans</i> | 4.00 | 10.50 | 0.56 | 1.14 | 0.84 | 23.03 |
| <i>Leucon nasica</i> | 1.66 | 17.47 | 0.56 | 1.07 | 0.84 | 23.87 |
| <i>Nuculoma tenuis</i> | 3.68 | 10.77 | 0.54 | 1.38 | 0.81 | 24.68 |
| <i>Scoloplos</i> | 7.70 | 1.33 | 0.53 | 1.15 | 0.80 | 25.48 |
| <i>Terebellides stroemi</i> | 8.38 | 3.83 | 0.52 | 1.04 | 0.78 | 26.26 |
| <i>Echinocardium flavescens</i> | 2.00 | 0.00 | 0.52 | 1.91 | 0.78 | 27.05 |
| <i>Diastylis lucifera</i> | 0.66 | 16.50 | 0.52 | 0.88 | 0.78 | 27.83 |
| <i>Cirrophorus lyra</i> | 11.00 | 7.47 | 0.52 | 0.86 | 0.78 | 28.61 |
| <i>Prionospio</i> | 3.34 | 7.83 | 0.52 | 1.24 | 0.78 | 29.39 |
| <i>Ampelisca macrocephala</i> | 1.00 | 6.13 | 0.52 | 1.41 | 0.78 | 30.16 |
| <i>Notomastus</i> | 2.68 | 11.30 | 0.51 | 1.37 | 0.77 | 30.94 |
| <i>Amphiura chiajei</i> | 0.00 | 15.50 | 0.51 | 0.79 | 0.77 | 31.71 |
| <i>Lucinoma borealis</i> | 6.42 | 2.00 | 0.50 | 1.32 | 0.76 | 32.47 |
| <i>Pectinaria</i> | 5.70 | 26.67 | 0.50 | 1.54 | 0.76 | 33.22 |
| <i>Scoletoma fragilis</i> | 3.66 | 0.00 | 0.50 | 1.14 | 0.76 | 33.98 |
| <i>Pholoe baltica</i> | 8.34 | 4.13 | 0.48 | 1.29 | 0.73 | 34.71 |

Cluster C

Average dissimilarity = 65.78

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|--------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Spiophanes</i> | 37.30 | 348.06 | 1.55 | 1.22 | 2.36 | 2.36 |
| <i>Phyllodoce groenlandica</i> | 0.00 | 9.72 | 1.41 | 3.89 | 2.14 | 4.50 |
| <i>Paramphinome jeffreysii</i> | 3.95 | 23.89 | 1.30 | 1.38 | 1.97 | 6.47 |
| <i>Myriochele</i> | 13.32 | 60.56 | 1.22 | 1.10 | 1.86 | 8.33 |
| <i>Ampharete lindstroemi</i> | 0.00 | 7.78 | 1.18 | 1.97 | 1.79 | 10.12 |
| <i>Mysella</i> | 27.82 | 18.06 | 1.16 | 1.43 | 1.77 | 11.89 |
| <i>Nucula nitidosa</i> | 0.00 | 15.28 | 1.14 | 1.88 | 1.74 | 13.62 |
| Nemertea | 5.27 | 16.67 | 1.14 | 1.57 | 1.73 | 15.35 |
| <i>Chaetozone</i> | 0.00 | 6.67 | 1.08 | 2.01 | 1.64 | 16.99 |
| <i>Pholoe baltica</i> | 7.90 | 6.39 | 1.03 | 1.55 | 1.56 | 18.55 |
| <i>Cirratulus</i> | 0.00 | 4.17 | 1.01 | 1.96 | 1.54 | 20.09 |
| <i>Harpinia antennaria</i> | 5.27 | 21.94 | 0.96 | 1.19 | 1.47 | 21.56 |
| <i>Abra prismatica</i> | 2.63 | 8.06 | 0.92 | 1.21 | 1.40 | 22.95 |
| <i>Bathyporeia</i> | 14.72 | 2.78 | 0.90 | 1.16 | 1.36 | 24.31 |
| <i>Eudorellopsis deformis</i> | 39.83 | 16.39 | 0.90 | 1.15 | 1.36 | 25.68 |
| <i>Polinices</i> | 0.00 | 4.44 | 0.88 | 1.30 | 1.34 | 27.01 |
| <i>Hippomedon</i> | 0.00 | 4.17 | 0.85 | 1.30 | 1.30 | 28.31 |
| <i>Goniada</i> | 14.67 | 15.56 | 0.84 | 1.03 | 1.28 | 29.58 |
| <i>Nuculoma tenuis</i> | 3.95 | 15.00 | 0.83 | 1.09 | 1.26 | 30.85 |
| <i>Ampelisca tenuicornis</i> | 3.95 | 4.44 | 0.82 | 1.25 | 1.25 | 32.10 |
| <i>Levinsenia gracilis</i> | 9.32 | 0.56 | 0.82 | 1.05 | 1.25 | 33.35 |
| <i>Nephtys hombergii</i> | 15.98 | 6.94 | 0.82 | 1.06 | 1.25 | 34.60 |

Cluster D11

Average dissimilarity = 63.22

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|----------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| Phoronida | 141.62 | 1053.33 | 2.47 | 1.09 | 3.91 | 3.91 |
| <i>Spiophanes</i> | 15.12 | 164.74 | 1.78 | 1.58 | 2.81 | 6.72 |
| <i>Chamelea gallina</i> | 92.47 | 10.56 | 1.64 | 1.19 | 2.60 | 9.32 |
| Hexacorallia | 57.51 | 6.11 | 1.56 | 1.20 | 2.46 | 11.78 |
| <i>Scoloplos</i> | 50.48 | 10.93 | 1.45 | 1.16 | 2.29 | 14.08 |
| <i>Bathyporeia</i> | 45.49 | 62.96 | 1.43 | 1.16 | 2.27 | 16.34 |
| <i>Pholoe baltica</i> | 19.12 | 5.00 | 1.40 | 1.50 | 2.21 | 18.56 |
| <i>Thracia</i> | 1.89 | 29.67 | 1.40 | 1.34 | 2.21 | 20.77 |
| <i>Tellina</i> | 24.37 | 82.26 | 1.39 | 1.23 | 2.20 | 22.97 |
| <i>Glycinde nordmanni</i> | 15.10 | 0.56 | 1.36 | 1.44 | 2.15 | 25.13 |
| <i>Magelona</i> | 161.19 | 221.70 | 1.29 | 0.90 | 2.04 | 27.16 |
| <i>Goniada</i> | 1.64 | 26.15 | 1.24 | 1.43 | 1.97 | 29.13 |
| <i>Urothoe poseidonis</i> | 5.89 | 59.78 | 1.22 | 0.95 | 1.94 | 31.06 |
| <i>Owenia fusiformis</i> | 7.10 | 18.89 | 1.20 | 1.32 | 1.89 | 32.96 |
| <i>Amphiura filiformis</i> | 18.22 | 3.89 | 1.14 | 1.00 | 1.80 | 34.75 |

Cluster D12

Average dissimilarity = 57.08

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|-------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Lanice conchilega</i> | 4.66 | 261.58 | 1.14 | 1.23 | 1.99 | 1.99 |
| <i>Bathyporeia</i> | 245.40 | 229.68 | 0.99 | 1.40 | 1.73 | 3.72 |
| <i>Amphiura filiformis</i> | 70.56 | 12.34 | 0.96 | 1.53 | 1.68 | 5.40 |
| <i>Mysella</i> | 101.64 | 24.97 | 0.95 | 1.20 | 1.66 | 7.07 |
| <i>Nephtys hombergii</i> | 32.94 | 3.16 | 0.94 | 1.59 | 1.65 | 8.72 |
| <i>Ophiura albida</i> | 53.31 | 4.75 | 0.91 | 1.42 | 1.59 | 10.31 |
| <i>Spiophanes</i> | 172.64 | 593.01 | 0.90 | 1.52 | 1.58 | 11.89 |
| <i>Urothoe poseidonis</i> | 32.27 | 52.60 | 0.89 | 1.36 | 1.56 | 13.45 |
| <i>Scoloplos</i> | 31.62 | 28.33 | 0.84 | 1.27 | 1.47 | 14.91 |
| <i>Ophelia borealis</i> | 28.16 | 4.01 | 0.81 | 1.48 | 1.43 | 16.34 |
| <i>Nephtys cirrosa</i> | 38.85 | 6.30 | 0.80 | 1.19 | 1.40 | 17.74 |
| <i>Abra prismatica</i> | 21.04 | 0.67 | 0.80 | 1.60 | 1.39 | 19.14 |
| <i>Echinocardium cordatum</i> | 15.75 | 14.36 | 0.79 | 1.42 | 1.39 | 20.53 |
| <i>Owenia fusiformis</i> | 7.86 | 11.33 | 0.75 | 1.72 | 1.31 | 21.84 |
| <i>Montacuta</i> | 21.39 | 10.15 | 0.72 | 1.21 | 1.26 | 23.10 |
| <i>Nephtys longosetosa</i> | 10.61 | 0.89 | 0.69 | 1.37 | 1.21 | 24.31 |
| <i>Acrocrida brachiata</i> | 13.51 | 23.65 | 0.69 | 1.32 | 1.21 | 25.53 |
| <i>Chamelea gallina</i> | 9.46 | 3.39 | 0.66 | 1.38 | 1.15 | 26.67 |
| <i>Arctica islandica</i> | 6.63 | 0.22 | 0.65 | 1.47 | 1.15 | 27.82 |
| <i>Pectinaria</i> | 3.66 | 23.69 | 0.65 | 1.11 | 1.15 | 28.97 |
| <i>Dosinia lupinus</i> | 6.81 | 1.71 | 0.65 | 1.38 | 1.14 | 30.11 |
| <i>Sigalion</i> | 11.28 | 9.39 | 0.65 | 1.26 | 1.14 | 31.25 |
| <i>Nucula nitidosa</i> | 13.99 | 10.50 | 0.64 | 0.94 | 1.11 | 32.36 |
| <i>Spio</i> | 18.08 | 11.18 | 0.62 | 1.24 | 1.09 | 33.46 |
| <i>Abra alba</i> | 0.94 | 84.05 | 0.62 | 0.67 | 1.08 | 34.54 |

Cluster D13

Average dissimilarity = 58.82

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|-------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Echinocardium cordatum</i> | 35.27 | 11.00 | 2.08 | 1.60 | 3.54 | 3.54 |
| <i>Urothoe poseidonis</i> | 47.64 | 82.17 | 1.90 | 1.47 | 3.24 | 6.78 |
| <i>Tellina</i> | 160.27 | 116.25 | 1.82 | 1.18 | 3.10 | 9.88 |
| <i>Magelona</i> | 112.96 | 296.88 | 1.70 | 1.17 | 2.90 | 12.78 |
| <i>Montacuta</i> | 18.24 | 0.91 | 1.65 | 1.61 | 2.81 | 15.58 |
| <i>Nephtys hombergii</i> | 12.63 | 1.39 | 1.63 | 1.86 | 2.77 | 18.36 |
| Nemertea | 59.36 | 22.14 | 1.50 | 1.15 | 2.55 | 20.91 |
| <i>Nephtys cirrosa</i> | 27.73 | 17.88 | 1.47 | 1.13 | 2.50 | 23.41 |
| <i>Spiophanes</i> | 38.80 | 146.17 | 1.45 | 1.33 | 2.46 | 25.87 |
| <i>Bathyporeia</i> | 325.09 | 114.73 | 1.39 | 1.23 | 2.36 | 28.24 |
| <i>Scoloplos</i> | 17.90 | 6.88 | 1.32 | 1.26 | 2.24 | 30.48 |
| <i>Donax vittatus</i> | 32.40 | 2.38 | 1.24 | 0.98 | 2.11 | 32.59 |
| <i>Spio</i> | 3.07 | 11.50 | 1.12 | 1.11 | 1.91 | 34.50 |

Cluster D2

Average dissimilarity = 59.70

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|--------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Amphiura filiformis</i> | 539.31 | 410.82 | 1.16 | 1.23 | 1.94 | 1.94 |
| <i>Mysella</i> | 215.87 | 106.71 | 1.08 | 1.21 | 1.80 | 3.74 |
| <i>Corbula gibba</i> | 4.40 | 103.17 | 1.01 | 1.19 | 1.70 | 5.44 |
| <i>Magelona</i> | 67.28 | 55.58 | 0.94 | 1.34 | 1.57 | 7.01 |
| <i>Myriochele</i> | 150.42 | 135.03 | 0.93 | 0.89 | 1.55 | 8.56 |
| <i>Ophiura albida</i> | 44.05 | 7.23 | 0.93 | 1.26 | 1.55 | 10.11 |
| <i>Scoloplos</i> | 35.52 | 14.31 | 0.88 | 1.28 | 1.48 | 11.59 |
| Phoronida | 74.74 | 64.26 | 0.84 | 1.20 | 1.41 | 12.99 |
| <i>Nuculoma tenuis</i> | 23.86 | 7.34 | 0.82 | 1.33 | 1.38 | 14.37 |
| <i>Chamelea gallina</i> | 32.31 | 4.99 | 0.82 | 1.23 | 1.37 | 15.74 |
| <i>Callianassa subterranea</i> | 19.62 | 15.71 | 0.80 | 1.34 | 1.34 | 17.08 |
| <i>Spiophanes</i> | 39.27 | 73.46 | 0.79 | 1.24 | 1.32 | 18.39 |
| <i>Pectinaria</i> | 25.85 | 13.40 | 0.76 | 1.25 | 1.28 | 19.67 |
| <i>Nucula nitidosa</i> | 36.79 | 47.63 | 0.73 | 1.11 | 1.23 | 20.90 |
| <i>Pholoe baltica</i> | 64.45 | 49.01 | 0.73 | 1.20 | 1.22 | 22.12 |
| <i>Montacuta</i> | 9.58 | 8.42 | 0.71 | 1.39 | 1.19 | 23.31 |
| <i>Eudorellopsis deformis</i> | 21.81 | 10.47 | 0.70 | 0.98 | 1.17 | 24.47 |
| <i>Gattyana cirrhosa</i> | 8.53 | 14.49 | 0.69 | 1.18 | 1.16 | 25.64 |
| <i>Chaetopterus</i> | 10.67 | 8.29 | 0.68 | 1.23 | 1.15 | 26.78 |
| <i>Abra alba</i> | 2.20 | 30.47 | 0.68 | 1.03 | 1.14 | 27.92 |
| <i>Polinices</i> | 13.61 | 10.70 | 0.68 | 1.26 | 1.14 | 29.06 |
| <i>Bathyporeia</i> | 10.08 | 9.12 | 0.67 | 1.25 | 1.13 | 30.18 |
| <i>Harpinia antennaria</i> | 32.79 | 41.90 | 0.67 | 1.19 | 1.12 | 31.30 |
| <i>Owenia fusiformis</i> | 9.28 | 5.59 | 0.66 | 1.19 | 1.10 | 32.41 |
| <i>Arctica islandica</i> | 7.96 | 0.00 | 0.65 | 1.27 | 1.09 | 33.50 |
| <i>Echinocardium cordatum</i> | 11.52 | 12.21 | 0.64 | 1.23 | 1.08 | 34.58 |

Cluster E1

Average dissimilarity = 65.54

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|---------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Paramphinome jeffreysii</i> | 8.37 | 127.67 | 0.98 | 2.06 | 1.50 | 1.50 |
| <i>Echinocardium flavescens</i> | 113.73 | 0.33 | 0.82 | 1.46 | 1.25 | 2.74 |
| <i>Exogone</i> | 59.85 | 1.67 | 0.80 | 1.89 | 1.22 | 3.97 |
| <i>Eudorellopsis deformis</i> | 105.42 | 2.67 | 0.78 | 1.35 | 1.20 | 5.16 |
| <i>Amphiura chiajei</i> | 0.00 | 39.50 | 0.76 | 1.66 | 1.15 | 6.32 |
| <i>Laonice sarsi</i> | 5.03 | 21.50 | 0.69 | 2.34 | 1.06 | 7.38 |
| <i>Thyasira</i> | 41.50 | 51.17 | 0.64 | 1.27 | 0.98 | 8.35 |
| <i>Lucinoma borealis</i> | 0.00 | 10.17 | 0.61 | 1.83 | 0.94 | 9.29 |
| <i>Philine</i> | 36.65 | 8.67 | 0.61 | 1.85 | 0.93 | 10.22 |
| <i>Glycera lapidum</i> | 23.20 | 17.17 | 0.61 | 1.66 | 0.93 | 11.15 |
| <i>Urothoe elegans</i> | 11.80 | 19.67 | 0.59 | 1.34 | 0.91 | 12.06 |
| <i>Abra prismatica</i> | 35.07 | 1.33 | 0.59 | 1.23 | 0.91 | 12.96 |
| <i>Lanice conchilega</i> | 0.00 | 15.17 | 0.59 | 1.88 | 0.90 | 13.86 |
| <i>Pholoe baltica</i> | 40.18 | 7.33 | 0.59 | 1.59 | 0.89 | 14.76 |
| <i>Pholoe pallida</i> | 0.00 | 12.17 | 0.57 | 1.80 | 0.87 | 15.63 |
| <i>Nothria conchylega</i> | 13.33 | 3.33 | 0.57 | 1.62 | 0.87 | 16.50 |
| <i>Aonides paucibranchiata</i> | 46.67 | 14.00 | 0.57 | 1.83 | 0.87 | 17.37 |
| <i>Terebellides stroemi</i> | 0.00 | 9.33 | 0.56 | 1.84 | 0.85 | 18.22 |
| Aplacophora | 0.00 | 14.83 | 0.55 | 1.21 | 0.84 | 19.07 |
| <i>Poecilochaetus serpens</i> | 20.17 | 24.83 | 0.55 | 1.12 | 0.84 | 19.91 |
| <i>Trichobranchus roseus</i> | 0.00 | 6.00 | 0.55 | 2.00 | 0.84 | 20.75 |
| <i>Phyllodoce mucosa</i> | 13.30 | 0.00 | 0.55 | 1.32 | 0.84 | 21.58 |
| <i>Ophiocten affinis</i> | 23.20 | 0.67 | 0.54 | 1.35 | 0.83 | 22.41 |
| <i>Pectinaria</i> | 26.77 | 51.67 | 0.54 | 1.42 | 0.82 | 23.24 |
| <i>Scolelepis</i> | 8.37 | 12.33 | 0.54 | 2.01 | 0.82 | 24.06 |
| <i>Anobothrus gracilis</i> | 8.30 | 11.67 | 0.54 | 1.78 | 0.82 | 24.89 |
| <i>Prionospio</i> | 126.92 | 25.67 | 0.54 | 1.52 | 0.82 | 25.71 |
| <i>Eudorella truncatula</i> | 28.32 | 8.00 | 0.53 | 1.19 | 0.81 | 26.52 |
| Hexacorallia | 26.80 | 21.67 | 0.53 | 1.47 | 0.80 | 27.32 |
| <i>Acidostoma</i> | 0.00 | 5.17 | 0.53 | 1.97 | 0.80 | 28.12 |
| <i>Aricidea catherinae</i> | 21.73 | 6.50 | 0.52 | 1.92 | 0.79 | 28.91 |
| <i>Chaetozone</i> | 28.30 | 12.50 | 0.51 | 1.28 | 0.78 | 29.69 |
| <i>Montacuta</i> | 1.67 | 4.33 | 0.51 | 2.78 | 0.77 | 30.46 |
| <i>Nephtys hombergii</i> | 6.67 | 11.00 | 0.50 | 1.45 | 0.77 | 31.24 |
| <i>Notomastus</i> | 8.37 | 10.00 | 0.50 | 1.58 | 0.77 | 32.00 |
| Phoronida | 10.00 | 23.33 | 0.50 | 1.39 | 0.77 | 32.77 |
| <i>Ampelisca tenuicornis</i> | 0.00 | 9.00 | 0.50 | 1.32 | 0.77 | 33.54 |
| <i>Sthenelais</i> | 16.72 | 3.33 | 0.50 | 1.19 | 0.76 | 34.30 |

Cluster E2

Average dissimilarity = 62.04

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|--------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Amphiura filiformis</i> | 37.74 | 113.20 | 1.45 | 1.54 | 2.34 | 2.34 |
| <i>Myriochele</i> | 3.02 | 232.80 | 1.16 | 0.99 | 1.88 | 4.22 |
| <i>Ophelia borealis</i> | 34.44 | 0.60 | 1.12 | 2.68 | 1.80 | 6.02 |
| <i>Mysella</i> | 34.56 | 18.40 | 1.00 | 1.71 | 1.62 | 7.64 |
| <i>Paramphinome jeffreysii</i> | 8.00 | 24.60 | 0.94 | 1.47 | 1.52 | 9.16 |
| Phoronida | 3.00 | 20.40 | 0.93 | 1.56 | 1.50 | 10.66 |
| <i>Unciola planipes</i> | 10.04 | 0.00 | 0.93 | 1.74 | 1.49 | 12.15 |
| <i>Bathyporeia</i> | 87.74 | 8.00 | 0.92 | 1.71 | 1.49 | 13.64 |
| <i>Anobothrus gracilis</i> | 0.00 | 4.40 | 0.87 | 5.37 | 1.40 | 15.04 |
| <i>Sthenelais</i> | 1.00 | 8.20 | 0.85 | 2.25 | 1.36 | 16.41 |
| <i>Tridonta montagui</i> | 24.36 | 0.80 | 0.82 | 1.22 | 1.32 | 17.73 |
| <i>Pectinaria</i> | 42.68 | 7.00 | 0.81 | 1.99 | 1.31 | 19.04 |
| <i>Timoclea ovata</i> | 10.04 | 0.20 | 0.81 | 1.68 | 1.31 | 20.35 |
| <i>Cylichna cylindracea</i> | 0.00 | 3.20 | 0.80 | 3.89 | 1.29 | 21.64 |
| <i>Diplocirrus glaucus</i> | 0.00 | 4.00 | 0.74 | 1.84 | 1.19 | 22.82 |
| <i>Magelona</i> | 1.00 | 6.20 | 0.73 | 1.41 | 1.17 | 23.99 |
| <i>Phyllodoce groenlandica</i> | 0.00 | 3.60 | 0.72 | 1.85 | 1.17 | 25.16 |
| <i>Chaetozone</i> | 34.42 | 3.60 | 0.72 | 1.34 | 1.16 | 26.32 |
| Scaphopoda | 7.94 | 6.40 | 0.71 | 1.47 | 1.15 | 27.47 |
| <i>Nephtys caeca</i> | 5.68 | 7.60 | 0.71 | 1.72 | 1.14 | 28.61 |
| <i>Travisia forbesii</i> | 14.62 | 0.40 | 0.70 | 1.21 | 1.12 | 29.74 |
| <i>Molgula</i> | 27.84 | 0.00 | 0.69 | 0.80 | 1.12 | 30.85 |
| Nemertea | 10.56 | 15.40 | 0.68 | 1.37 | 1.10 | 31.95 |
| Hexacorallia | 10.44 | 13.60 | 0.68 | 1.24 | 1.10 | 33.05 |
| <i>Philine</i> | 10.60 | 1.20 | 0.67 | 1.49 | 1.08 | 34.13 |

Cluster E3

Average dissimilarity = 68.78

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|---------------------------------|------------|------------|-----------|----------|------------|--------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB. % | CUM. % |
| <i>Ophelia borealis</i> | 54.80 | 4.18 | 1.37 | 2.08 | 1.99 | 1.99 |
| <i>Amphiura filiformis</i> | 48.75 | 65.91 | 0.93 | 1.31 | 1.35 | 3.34 |
| <i>Spiophanes</i> | 34.06 | 357.00 | 0.90 | 1.12 | 1.31 | 4.64 |
| <i>Echinocardium flavescens</i> | 5.63 | 0.00 | 0.85 | 3.21 | 1.24 | 5.88 |
| <i>Echinocyamus pusillus</i> | 40.98 | 17.48 | 0.84 | 1.49 | 1.22 | 7.10 |
| <i>Cochlodesma praetenuae</i> | 8.55 | 2.61 | 0.78 | 1.72 | 1.13 | 8.24 |
| <i>Exogone</i> | 29.87 | 0.91 | 0.78 | 1.21 | 1.13 | 9.37 |
| <i>Myriochele</i> | 7.20 | 116.36 | 0.77 | 1.15 | 1.11 | 10.48 |
| <i>Mysella</i> | 6.94 | 35.34 | 0.76 | 1.25 | 1.10 | 11.58 |
| <i>Ophiura albida</i> | 6.20 | 1.73 | 0.72 | 2.00 | 1.04 | 12.63 |
| <i>Owenia fusiformis</i> | 5.53 | 29.58 | 0.70 | 1.20 | 1.02 | 13.64 |
| <i>Bathyporeia</i> | 26.40 | 16.52 | 0.70 | 1.30 | 1.01 | 14.65 |
| Nemertea | 18.72 | 19.39 | 0.69 | 1.22 | 1.00 | 15.65 |
| <i>Amphiura chiajei</i> | 0.91 | 29.45 | 0.68 | 0.89 | 0.98 | 16.64 |
| Hexacorallia | 8.66 | 2.79 | 0.67 | 1.34 | 0.98 | 17.61 |
| Phoronida | 6.92 | 19.59 | 0.67 | 1.14 | 0.97 | 18.59 |
| <i>Tellina</i> | 17.63 | 2.06 | 0.66 | 1.14 | 0.96 | 19.54 |
| <i>Pholoe baltica</i> | 14.13 | 24.48 | 0.66 | 1.21 | 0.95 | 20.50 |
| <i>Notomastus</i> | 1.76 | 20.24 | 0.64 | 1.30 | 0.93 | 21.42 |
| <i>Thracia</i> | 14.84 | 4.36 | 0.61 | 0.95 | 0.89 | 22.31 |
| <i>Harpinia antennaria</i> | 1.82 | 15.70 | 0.60 | 1.02 | 0.87 | 23.19 |
| <i>Glycera lapidum</i> | 5.74 | 18.76 | 0.60 | 1.22 | 0.87 | 24.06 |
| <i>Nephtys caeca</i> | 2.34 | 7.88 | 0.58 | 1.18 | 0.85 | 24.91 |
| <i>Nephtys cirrosa</i> | 5.84 | 1.15 | 0.58 | 1.11 | 0.84 | 25.75 |
| <i>Chamelea gallina</i> | 0.45 | 13.43 | 0.58 | 1.09 | 0.84 | 26.59 |
| <i>Eudorellopsis deformis</i> | 4.90 | 5.09 | 0.57 | 1.08 | 0.83 | 27.42 |
| <i>Dosinia exoleta</i> | 4.96 | 2.00 | 0.56 | 1.19 | 0.82 | 28.24 |
| <i>Nephtys longosetosa</i> | 5.17 | 1.91 | 0.56 | 1.18 | 0.81 | 29.05 |
| <i>Polycirrus</i> | 2.12 | 7.94 | 0.55 | 1.00 | 0.80 | 29.85 |
| <i>Abra prismatica</i> | 6.15 | 5.15 | 0.55 | 1.16 | 0.80 | 30.65 |
| <i>Magelona</i> | 10.91 | 9.28 | 0.55 | 1.08 | 0.79 | 31.44 |
| <i>Nephtys hombergii</i> | 7.50 | 8.55 | 0.53 | 1.14 | 0.78 | 32.22 |
| <i>Aonides paucibranchiata</i> | 3.97 | 3.88 | 0.53 | 1.27 | 0.76 | 32.98 |
| <i>Lumbrineris gracilis</i> | 0.00 | 36.21 | 0.52 | 0.85 | 0.75 | 33.73 |
| <i>Sthenelais</i> | 2.34 | 4.04 | 0.51 | 1.11 | 0.75 | 34.48 |

Cluster E4

Average dissimilarity = 61.98

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|---------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Paramphinoe jeffreysii</i> | 1.97 | 61.28 | 1.18 | 1.50 | 1.90 | 1.90 |
| <i>Myriochele</i> | 132.73 | 357.13 | 1.03 | 1.21 | 1.67 | 3.57 |
| <i>Nephtys longosetosa</i> | 14.08 | 1.10 | 0.87 | 1.64 | 1.40 | 4.97 |
| <i>Spiophanes</i> | 46.10 | 242.87 | 0.86 | 1.07 | 1.39 | 6.35 |
| <i>Mysella</i> | 7.91 | 16.21 | 0.85 | 2.00 | 1.36 | 7.72 |
| <i>Echinocardium flavescens</i> | 4.65 | 1.92 | 0.79 | 2.28 | 1.28 | 9.00 |
| <i>Abra prismatica</i> | 8.06 | 6.67 | 0.78 | 1.70 | 1.25 | 10.25 |
| <i>Levinsenia gracilis</i> | 17.30 | 19.97 | 0.76 | 1.23 | 1.23 | 11.48 |
| <i>Polinices</i> | 4.02 | 5.00 | 0.74 | 1.83 | 1.20 | 12.67 |
| <i>Eudorellopsis deformis</i> | 16.10 | 16.82 | 0.74 | 1.21 | 1.19 | 13.86 |
| <i>Nephtys hombergii</i> | 8.55 | 1.33 | 0.72 | 1.61 | 1.16 | 15.02 |
| <i>Chaetozone</i> | 4.31 | 19.41 | 0.69 | 1.26 | 1.11 | 16.13 |
| <i>Pectinaria</i> | 9.18 | 13.44 | 0.67 | 1.17 | 1.09 | 17.21 |
| <i>Cirratulus</i> | 9.27 | 3.28 | 0.65 | 1.24 | 1.04 | 18.25 |
| <i>Hemilamprops rosea</i> | 4.13 | 2.46 | 0.65 | 1.66 | 1.04 | 19.29 |
| Aplacophora | 5.50 | 6.62 | 0.63 | 1.24 | 1.02 | 20.32 |
| <i>Montacuta</i> | 10.37 | 3.36 | 0.63 | 1.16 | 1.02 | 21.34 |
| <i>Ophiocten affinis</i> | 6.64 | 1.03 | 0.63 | 1.27 | 1.02 | 22.35 |
| Hexacorallia | 6.81 | 24.82 | 0.62 | 1.18 | 0.99 | 23.34 |
| <i>Prionospio</i> | 7.00 | 6.62 | 0.61 | 1.23 | 0.99 | 24.34 |
| <i>Phaxas pellucidus</i> | 5.80 | 5.82 | 0.61 | 1.22 | 0.99 | 25.32 |
| <i>Pholoe baltica</i> | 6.30 | 7.28 | 0.61 | 1.17 | 0.98 | 26.30 |
| <i>Ampelisca tenuicornis</i> | 9.39 | 5.59 | 0.61 | 1.15 | 0.98 | 27.28 |
| <i>Magelona</i> | 5.62 | 8.28 | 0.60 | 1.05 | 0.98 | 28.25 |
| <i>Owenia fusiformis</i> | 5.37 | 2.82 | 0.59 | 1.12 | 0.95 | 29.20 |
| <i>Westwoodilla caecula</i> | 4.45 | 0.87 | 0.58 | 1.26 | 0.94 | 30.14 |
| <i>Harpinia antennaria</i> | 2.66 | 6.97 | 0.57 | 1.19 | 0.91 | 31.05 |
| <i>Diplocirrus glaucus</i> | 3.43 | 5.64 | 0.55 | 1.15 | 0.89 | 31.94 |
| <i>Synchelidium</i> | 0.13 | 2.85 | 0.54 | 1.19 | 0.88 | 32.82 |
| <i>Trichobranchus roseus</i> | 0.88 | 5.33 | 0.54 | 1.12 | 0.87 | 33.69 |
| <i>Hippomedon</i> | 2.94 | 0.67 | 0.54 | 1.16 | 0.87 | 34.56 |

Cluster F1

Average dissimilarity = 78.73

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Pholoe baltica</i> | 53.42 | 16.67 | 1.29 | 1.23 | 1.64 | 1.64 |
| <i>Lanice conchilega</i> | 30.53 | 531.87 | 1.28 | 0.95 | 1.63 | 3.27 |
| <i>Capitella</i> | 31.17 | 0.00 | 1.26 | 1.82 | 1.60 | 4.87 |
| <i>Lumbrineris latreilli</i> | 26.71 | 0.00 | 1.23 | 1.18 | 1.56 | 6.42 |
| <i>Urothoe poseidonis</i> | 114.76 | 118.22 | 1.20 | 0.90 | 1.53 | 7.95 |
| <i>Mysella</i> | 111.51 | 39.24 | 1.16 | 0.99 | 1.48 | 9.43 |
| Nemertea | 54.67 | 27.96 | 1.14 | 1.07 | 1.45 | 10.88 |
| <i>Mya</i> | 22.24 | 7.14 | 1.11 | 1.37 | 1.41 | 12.29 |
| <i>Nicomache</i> | 122.94 | 1.90 | 1.06 | 1.05 | 1.35 | 13.64 |
| <i>Scoloplos</i> | 40.10 | 10.30 | 1.06 | 1.17 | 1.35 | 14.99 |
| <i>Spisula</i> | 1.12 | 739.56 | 1.05 | 0.56 | 1.34 | 16.33 |
| <i>Spiophanes</i> | 13.11 | 127.81 | 1.04 | 1.07 | 1.33 | 17.65 |
| <i>Pectinaria</i> | 10.09 | 226.12 | 1.04 | 0.89 | 1.33 | 18.98 |
| Hexacorallia | 3.46 | 73.81 | 0.99 | 0.95 | 1.26 | 20.23 |
| <i>Ophiura albida</i> | 19.77 | 1.90 | 0.98 | 1.53 | 1.24 | 21.48 |
| <i>Polycirrus</i> | 21.09 | 12.38 | 0.97 | 1.14 | 1.23 | 22.71 |
| <i>Ampelisca spinipes</i> | 18.39 | 1.90 | 0.94 | 1.03 | 1.20 | 23.90 |
| <i>Pomatoceros</i> | 10.36 | 77.62 | 0.93 | 1.10 | 1.18 | 25.09 |
| <i>Chaetozone</i> | 9.61 | 0.91 | 0.89 | 1.39 | 1.13 | 26.21 |
| <i>Scalibregma</i> | 6.76 | 18.10 | 0.88 | 1.16 | 1.11 | 27.33 |
| <i>Glycera lapidum</i> | 15.36 | 10.95 | 0.85 | 1.35 | 1.08 | 28.41 |
| <i>Urothoe brevicornis</i> | 25.36 | 20.16 | 0.82 | 0.93 | 1.04 | 29.45 |
| <i>Eusyllis blomstrandii</i> | 22.68 | 0.00 | 0.80 | 0.98 | 1.02 | 30.47 |
| <i>Eumida sanguinea</i> | 10.65 | 9.35 | 0.79 | 1.25 | 1.01 | 31.48 |
| <i>Malmgrenia arenicolae</i> | 10.52 | 0.00 | 0.78 | 0.91 | 0.99 | 32.46 |
| <i>Spio</i> | 13.95 | 6.63 | 0.77 | 1.10 | 0.98 | 33.44 |
| <i>Nephtys cirrosa</i> | 7.10 | 8.73 | 0.74 | 1.03 | 0.94 | 34.38 |

Cluster F2

Average dissimilarity = 72.82

| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|-------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Spiophanes</i> | 22.55 | 395.85 | 2.08 | 1.21 | 2.85 | 2.85 |
| <i>Ophelia borealis</i> | 44.78 | 4.28 | 2.07 | 1.24 | 2.84 | 5.69 |
| <i>Magelona</i> | 72.62 | 118.65 | 2.03 | 1.23 | 2.79 | 8.48 |
| <i>Scoloplos</i> | 46.41 | 54.78 | 1.98 | 1.29 | 2.72 | 11.20 |
| <i>Urothoe poseidonis</i> | 15.72 | 57.60 | 1.73 | 1.04 | 2.38 | 13.58 |
| <i>Tellina</i> | 22.01 | 54.40 | 1.67 | 1.05 | 2.29 | 15.87 |
| <i>Bathyporeia</i> | 47.77 | 38.10 | 1.62 | 1.22 | 2.23 | 18.10 |
| <i>Spio</i> | 18.85 | 32.54 | 1.56 | 1.12 | 2.14 | 20.24 |
| <i>Lanice conchilega</i> | 9.53 | 48.74 | 1.50 | 0.99 | 2.06 | 22.30 |
| Nemertea | 21.02 | 19.76 | 1.45 | 1.17 | 2.00 | 24.30 |
| <i>Urothoe brevicornis</i> | 24.78 | 4.72 | 1.37 | 0.94 | 1.88 | 26.18 |
| <i>Spisula</i> | 62.82 | 3.92 | 1.35 | 0.96 | 1.85 | 28.03 |
| <i>Nephtys cirrosa</i> | 21.94 | 19.71 | 1.31 | 1.11 | 1.80 | 29.83 |
| <i>Echinocardium cordatum</i> | 11.45 | 4.93 | 1.26 | 1.04 | 1.73 | 31.56 |
| <i>Gastrosaccus spinifer</i> | 3.15 | 27.68 | 1.26 | 0.76 | 1.72 | 33.28 |
| <i>Scolelepis</i> | 5.31 | 6.89 | 1.23 | 1.04 | 1.69 | 34.97 |

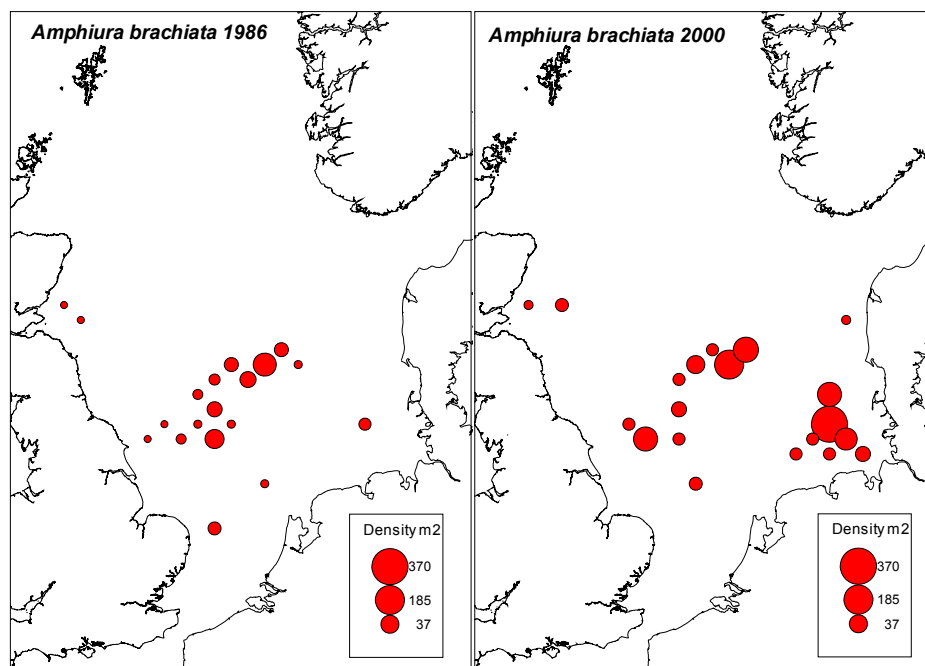
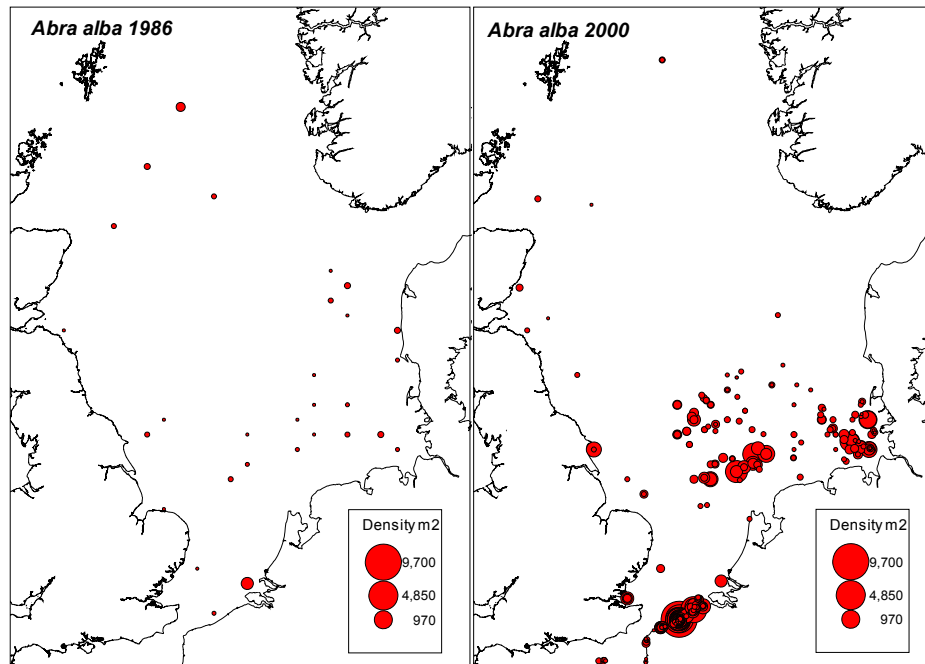
Cluster G

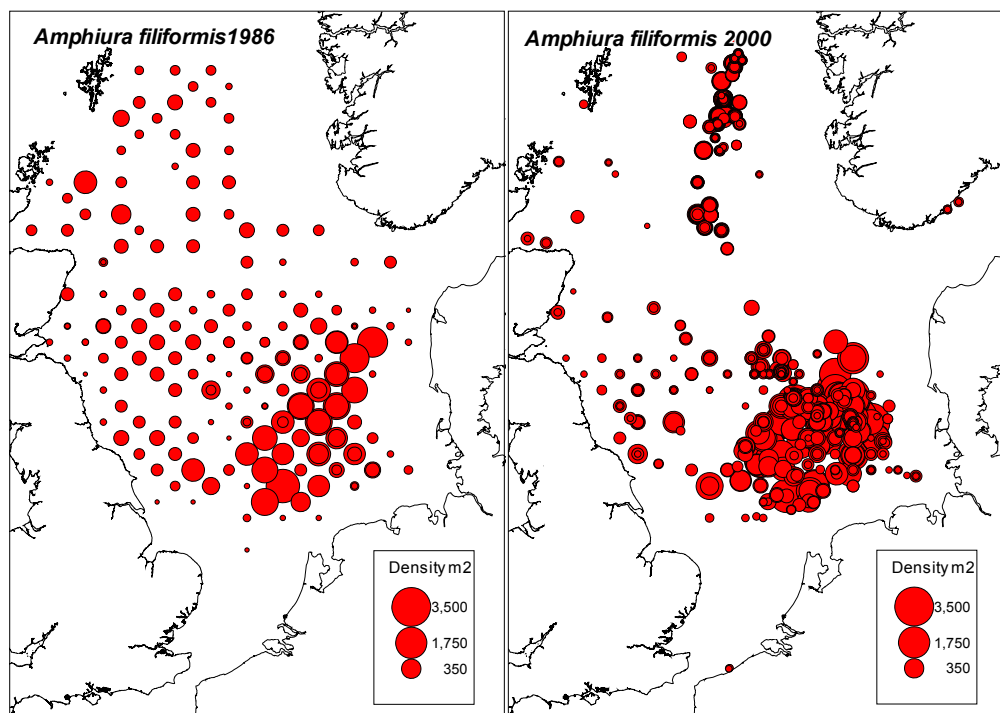
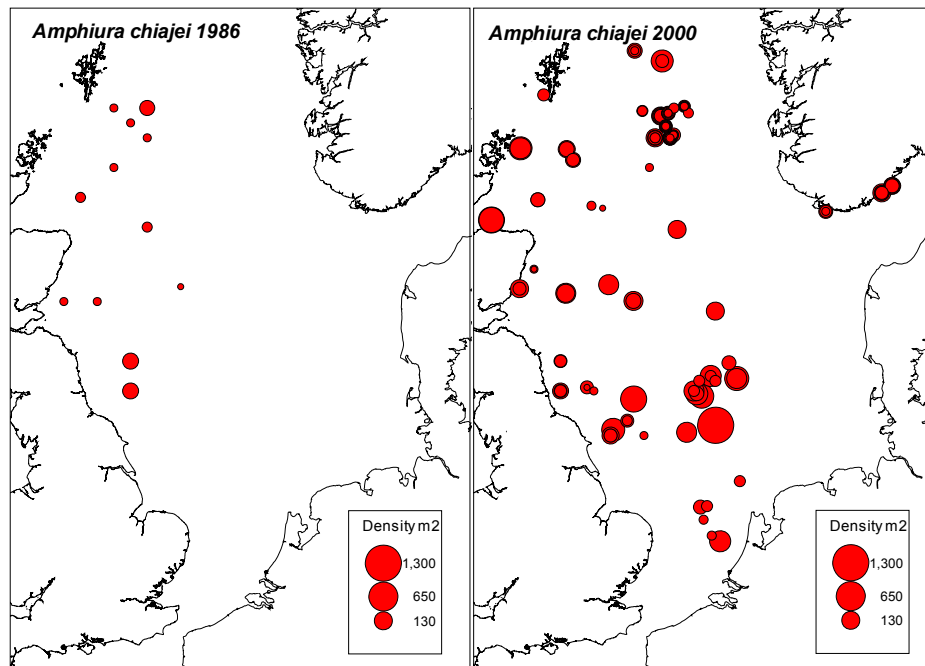
Average dissimilarity = 80.10

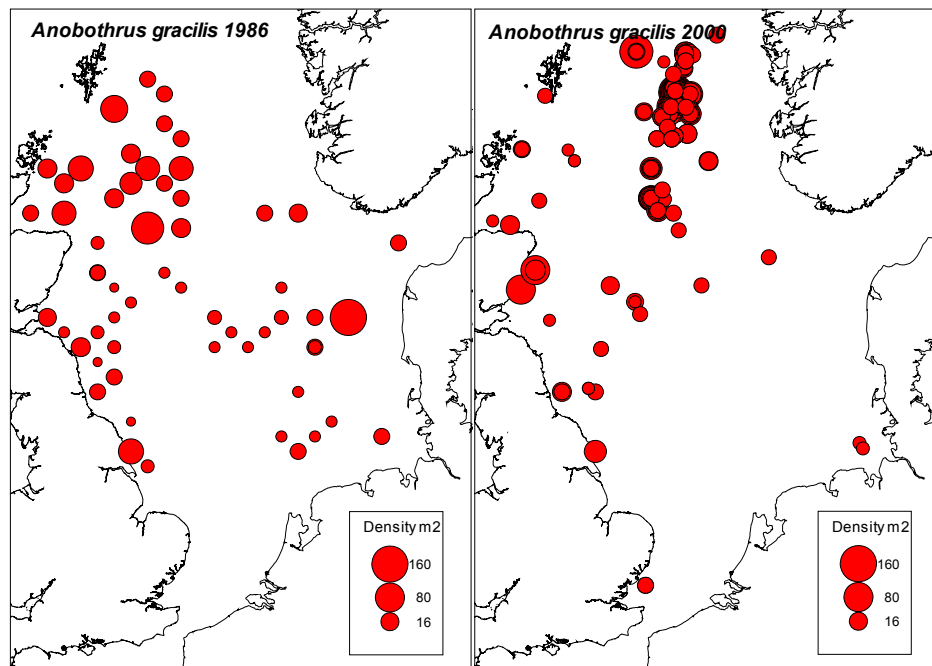
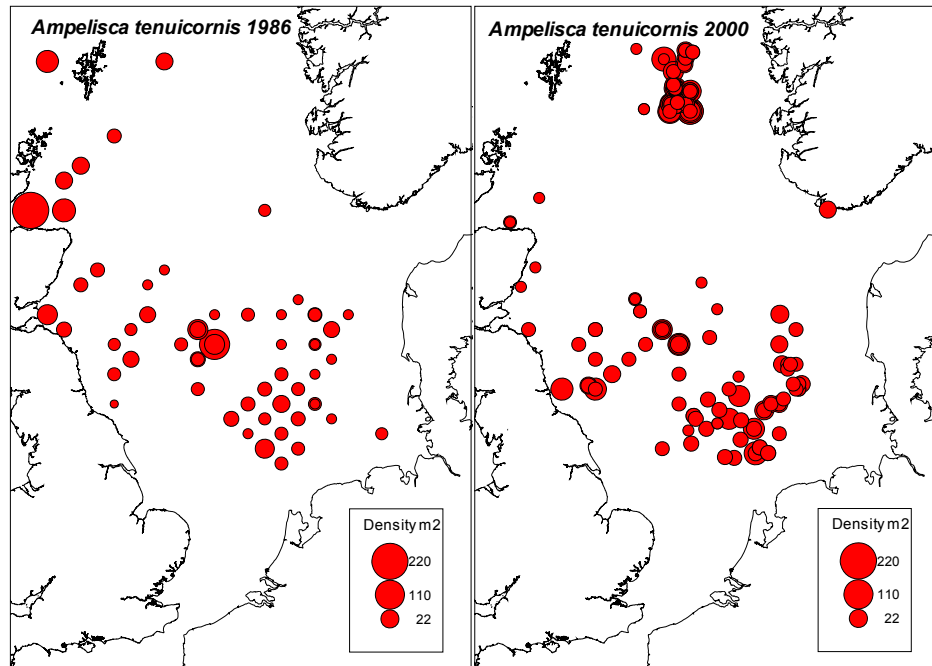
| SPECIES | GROUP 1986 | GROUP 2000 | | | | |
|--------------------------------|------------|------------|-----------|----------|-----------|-------|
| | AV. ABUND. | AV. ABUND. | AV. DISS. | DISS./SD | CONTRIB.% | CUM.% |
| <i>Spiophanes</i> | 14.26 | 53.30 | 1.18 | 1.43 | 1.47 | 1.47 |
| <i>Paramphinome jeffreysii</i> | 0.00 | 246.90 | 1.11 | 1.17 | 1.38 | 2.85 |
| <i>Aonides paucibranchiata</i> | 63.84 | 19.20 | 1.03 | 1.20 | 1.29 | 4.14 |
| <i>Magelona</i> | 0.00 | 86.67 | 1.03 | 0.65 | 1.28 | 5.42 |
| <i>Exogone</i> | 90.68 | 23.60 | 1.00 | 1.21 | 1.25 | 6.67 |
| <i>Glycera lapidum</i> | 76.78 | 24.90 | 0.99 | 1.16 | 1.24 | 7.91 |
| Phoronida | 0.00 | 22.90 | 0.97 | 0.94 | 1.21 | 9.12 |
| <i>Amphiura filiformis</i> | 3.42 | 64.47 | 0.93 | 1.12 | 1.16 | 10.28 |
| <i>Aricidea cerrutii</i> | 44.20 | 10.00 | 0.89 | 1.17 | 1.11 | 11.39 |
| <i>Myriochele</i> | 1.00 | 22.10 | 0.89 | 1.49 | 1.11 | 12.50 |
| <i>Unciola planipes</i> | 20.22 | 7.60 | 0.86 | 1.08 | 1.07 | 13.57 |
| <i>Harpinia antennaria</i> | 0.00 | 53.60 | 0.83 | 0.78 | 1.03 | 14.60 |
| Hexacorallia | 25.12 | 14.50 | 0.82 | 1.13 | 1.02 | 15.63 |
| <i>Scoloplos</i> | 14.68 | 12.33 | 0.82 | 1.32 | 1.02 | 16.64 |
| <i>Nephtys longosetosa</i> | 10.22 | 0.00 | 0.80 | 1.11 | 0.99 | 17.64 |
| <i>Scolelepis</i> | 12.08 | 18.10 | 0.77 | 1.17 | 0.97 | 18.61 |
| <i>Spio</i> | 2.00 | 23.30 | 0.77 | 1.14 | 0.96 | 19.56 |
| <i>Owenia fusiformis</i> | 18.88 | 14.60 | 0.76 | 1.16 | 0.95 | 20.51 |
| <i>Ophelia borealis</i> | 13.76 | 1.60 | 0.76 | 1.13 | 0.95 | 21.46 |
| <i>Corbula gibba</i> | 2.00 | 36.67 | 0.75 | 0.63 | 0.94 | 22.40 |
| <i>Echinocyamus pusillus</i> | 10.96 | 12.40 | 0.75 | 1.18 | 0.94 | 23.33 |
| <i>Bathyporeia</i> | 11.60 | 9.87 | 0.74 | 0.92 | 0.92 | 24.26 |
| <i>Goniada</i> | 41.22 | 21.03 | 0.74 | 1.29 | 0.92 | 25.18 |
| <i>Dipolydora socialis</i> | 11.96 | 0.00 | 0.73 | 1.13 | 0.92 | 26.10 |
| <i>Polinices</i> | 0.00 | 7.87 | 0.73 | 0.91 | 0.91 | 27.01 |
| <i>Pholoe baltica</i> | 0.00 | 9.07 | 0.72 | 1.12 | 0.89 | 27.90 |
| <i>Pisone remota</i> | 14.06 | 23.60 | 0.71 | 0.86 | 0.88 | 28.78 |
| Nemertea | 7.98 | 31.93 | 0.70 | 1.28 | 0.88 | 29.66 |
| <i>Chaetozone</i> | 9.46 | 17.47 | 0.70 | 1.15 | 0.87 | 30.53 |
| <i>Nephtys hombergii</i> | 0.00 | 5.30 | 0.69 | 1.06 | 0.86 | 31.39 |
| <i>Hesionura elongata</i> | 23.84 | 0.80 | 0.67 | 0.88 | 0.84 | 32.23 |
| <i>Spisula</i> | 6.42 | 0.40 | 0.67 | 1.08 | 0.84 | 33.07 |
| Oligochaeta | 0.00 | 26.00 | 0.66 | 0.79 | 0.82 | 33.89 |
| <i>Prionospio</i> | 2.00 | 14.10 | 0.65 | 1.17 | 0.81 | 34.70 |

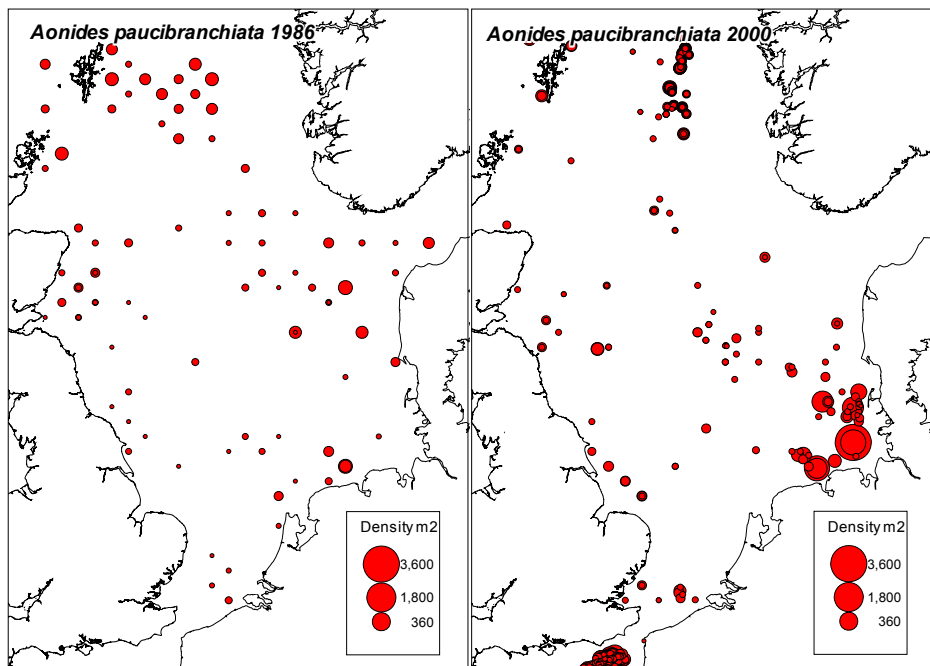
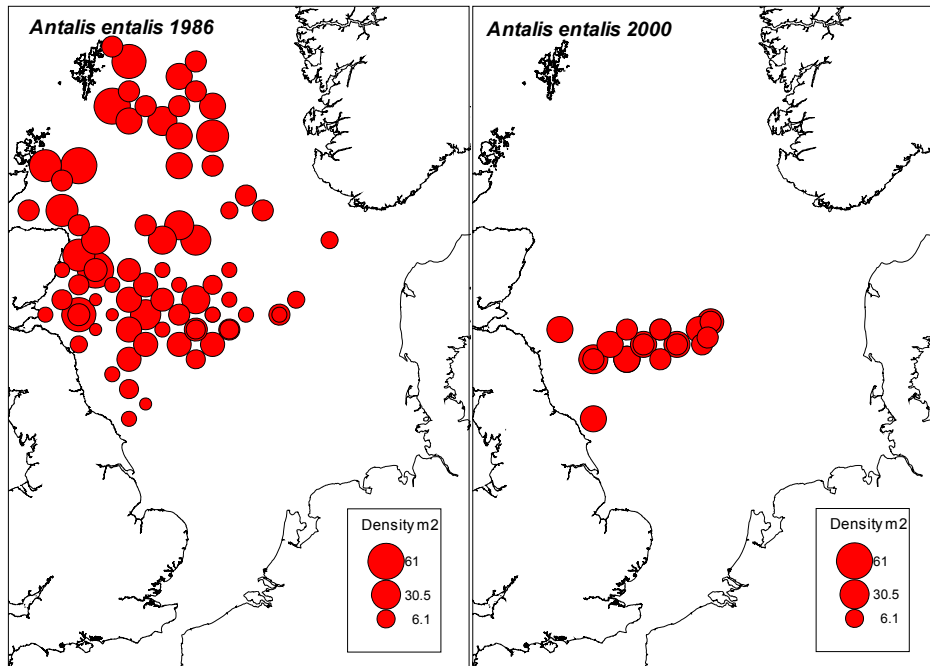
Annex 3: Maps of species distributions in 1986 and 2000

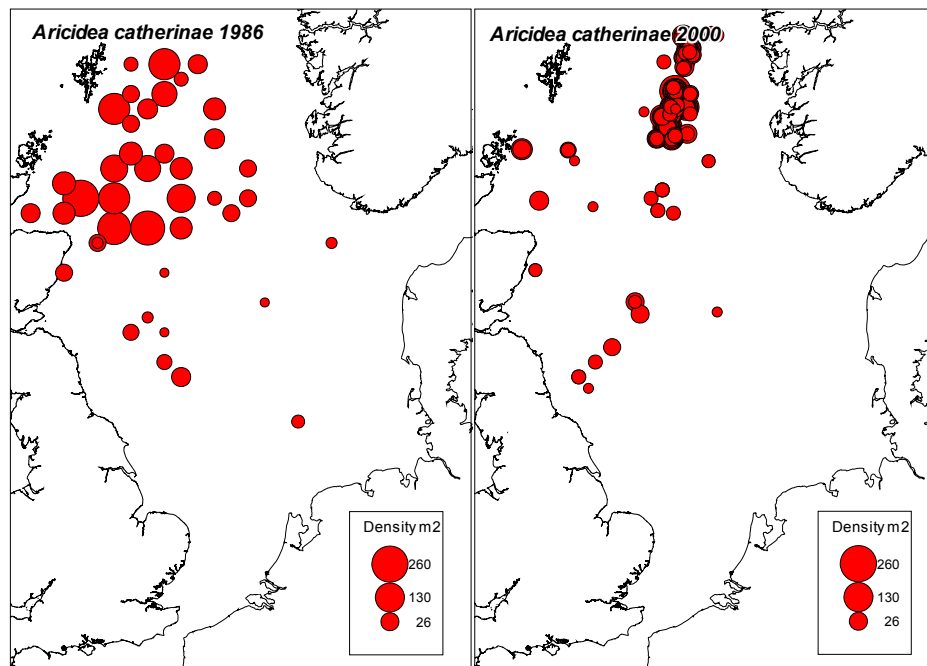
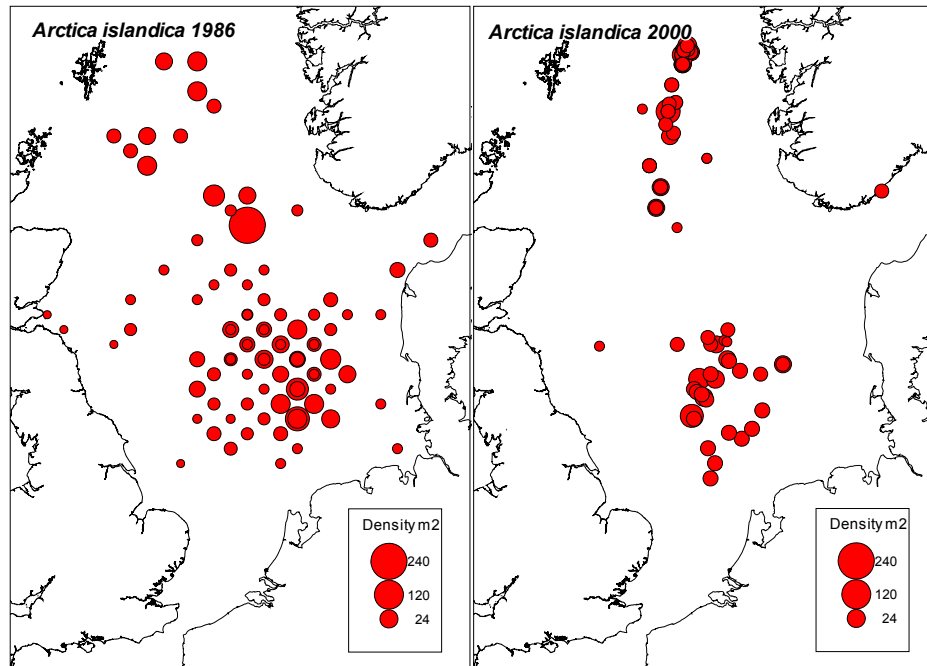
Distributions/densities are shown at all stations sampled for NSBS 1986 and NSBP 2000. Thus coverage was not the same, and reference should be made to the station grids for each year for detailed comparison (Section 5.4).

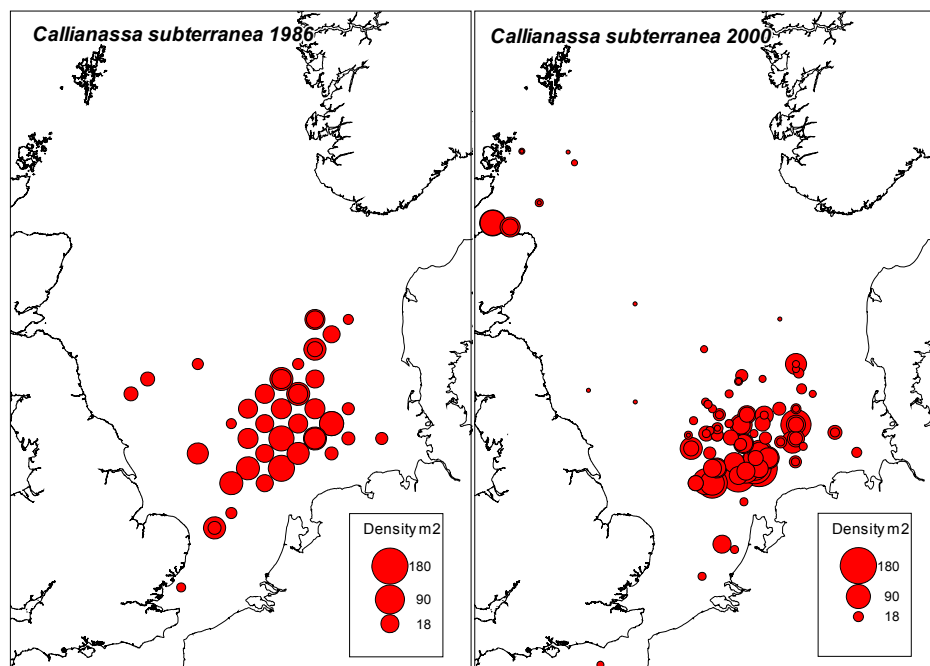
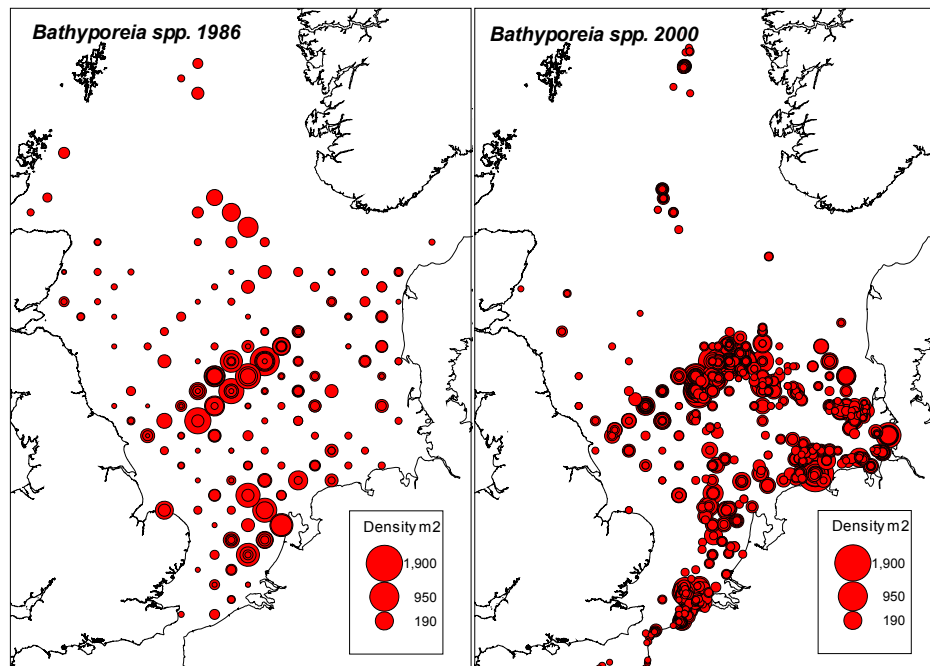


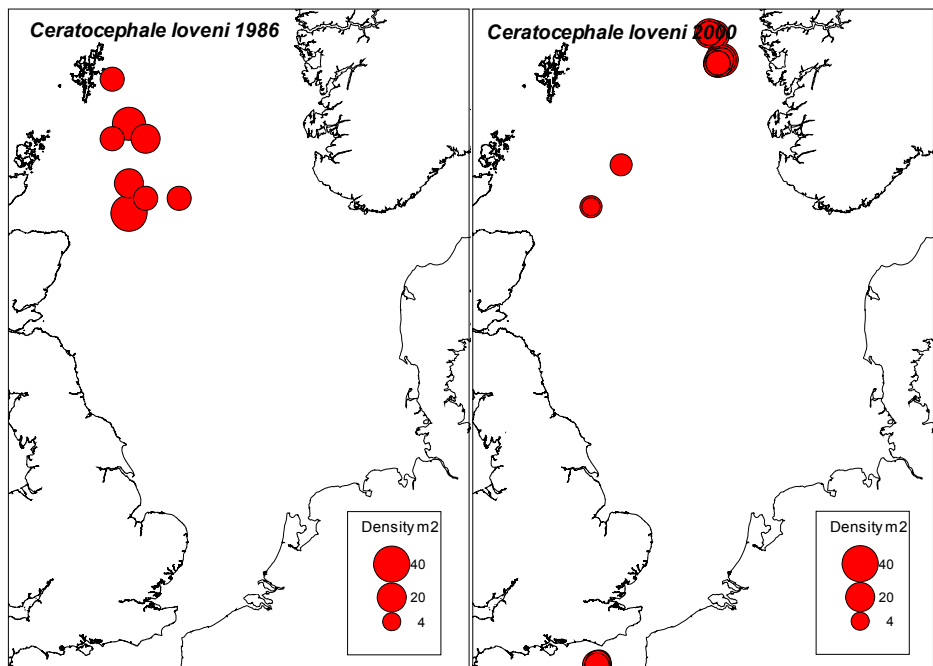
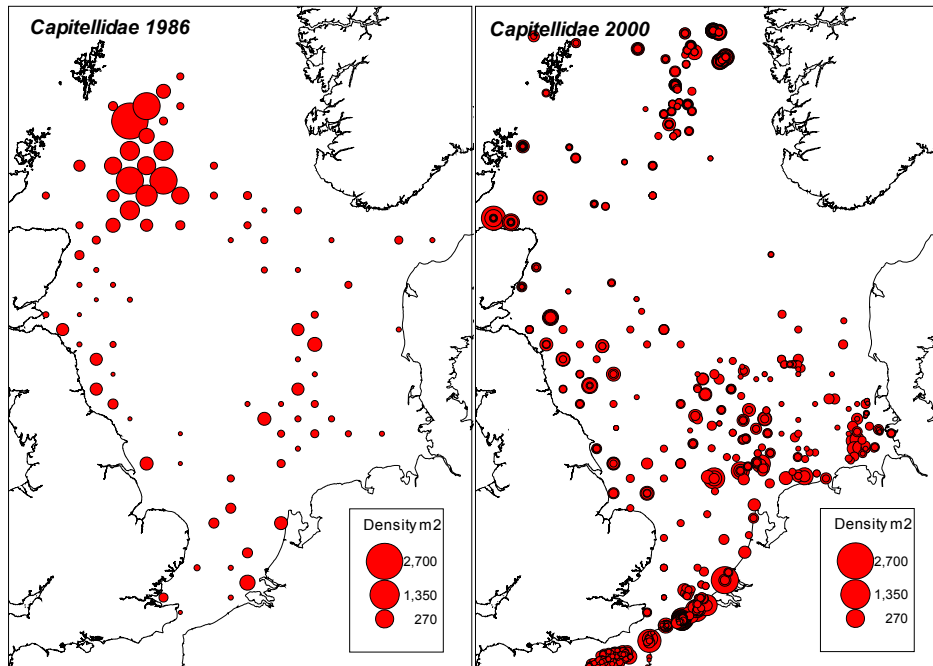


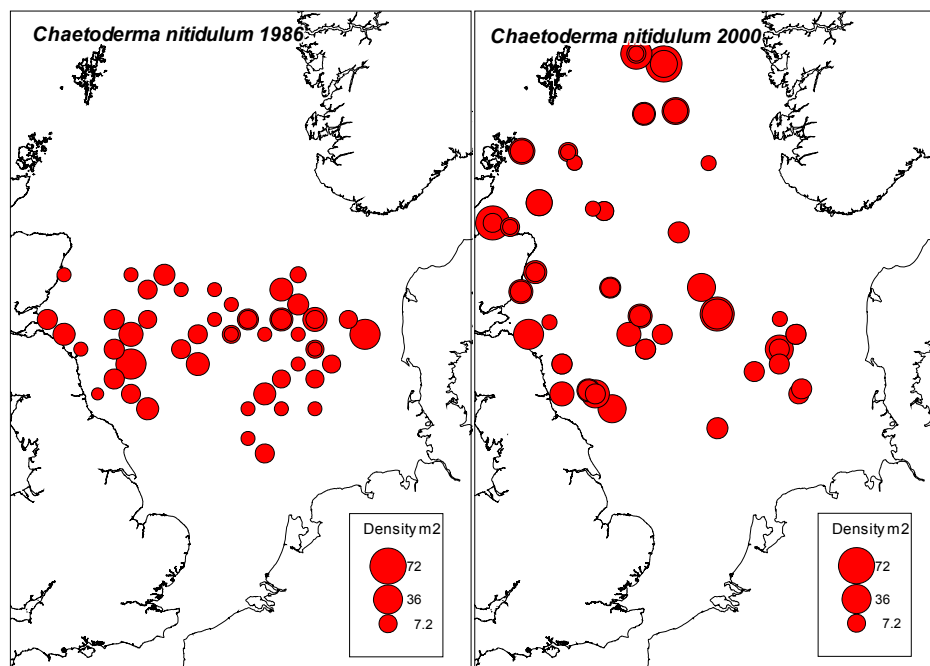
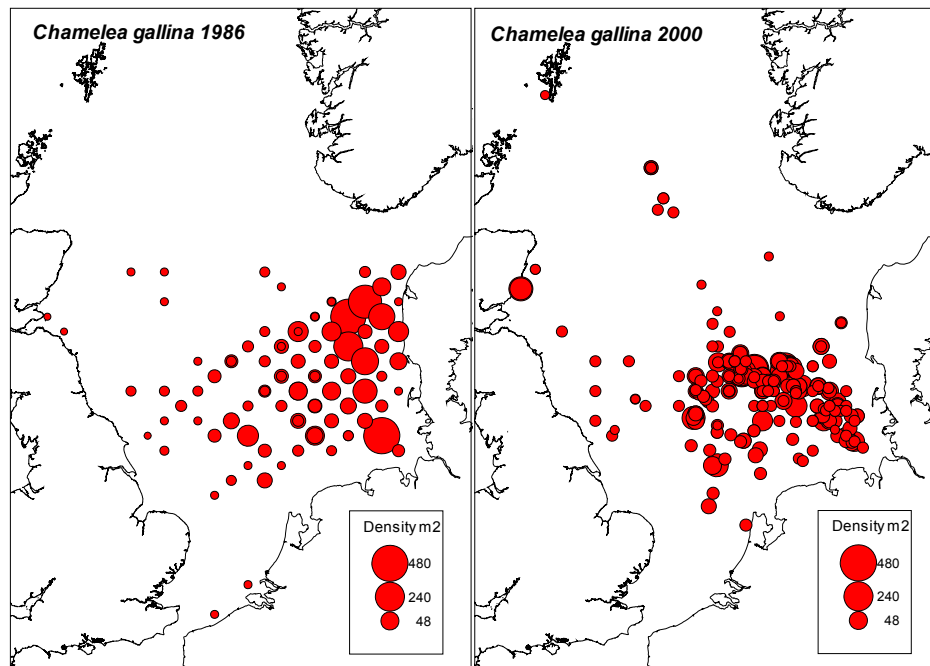


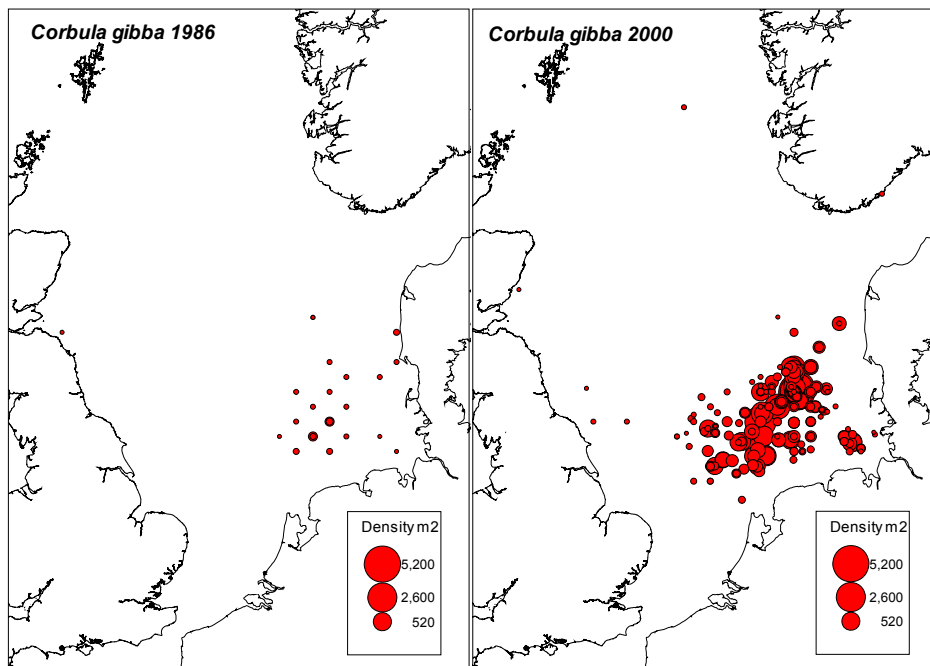
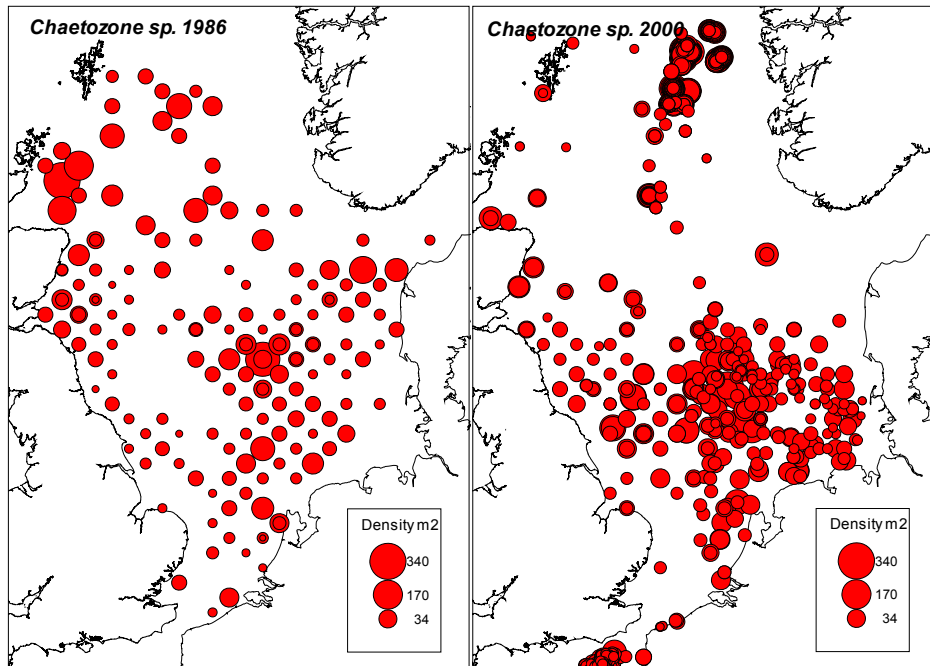


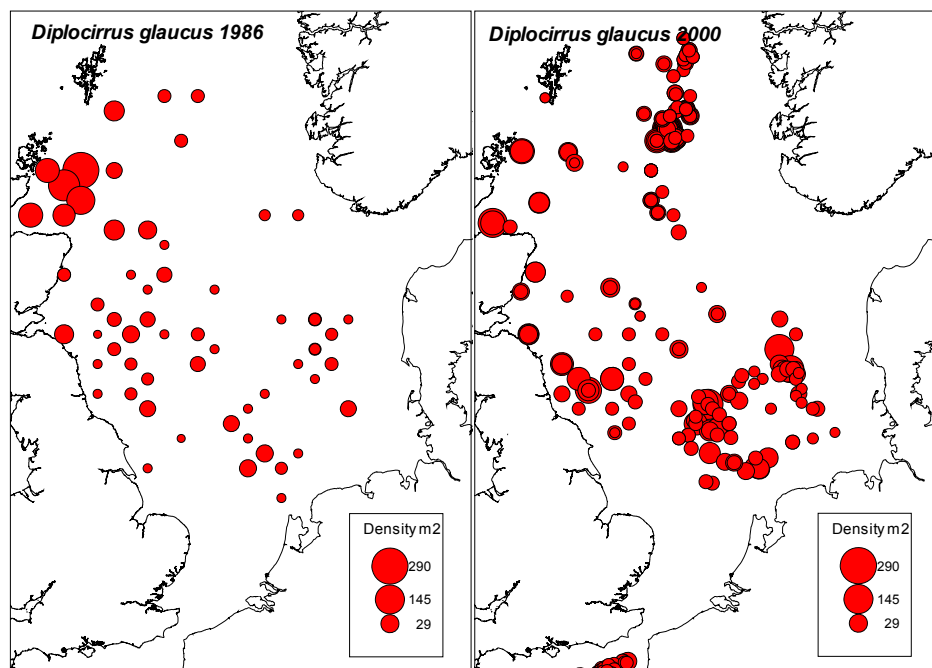
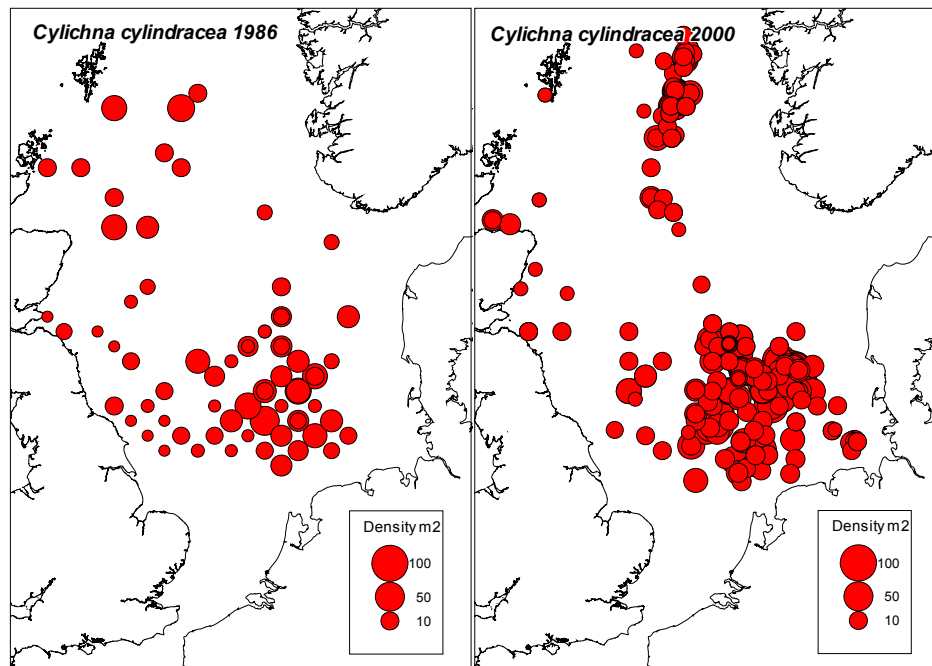


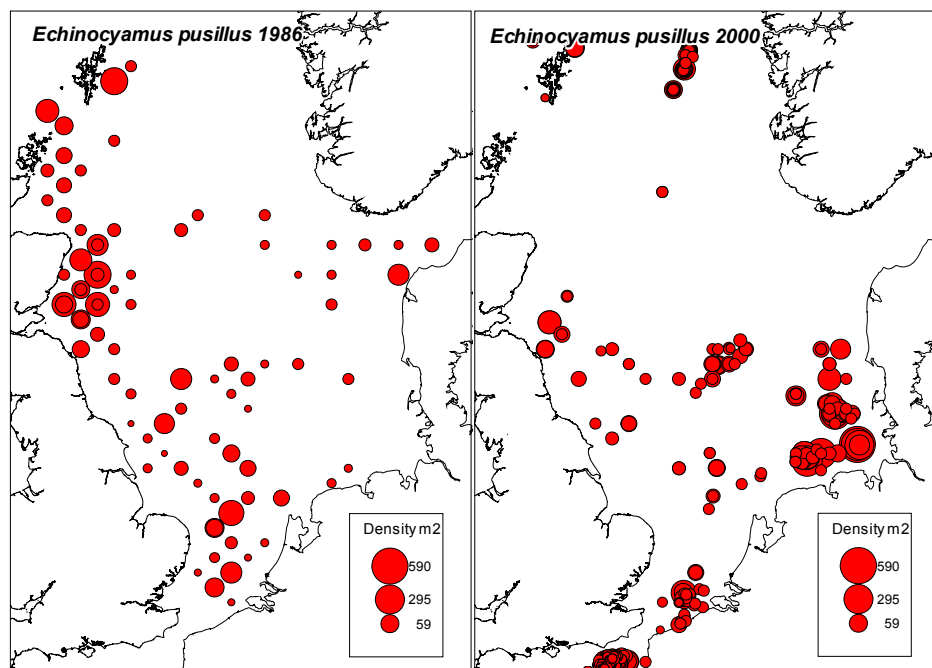
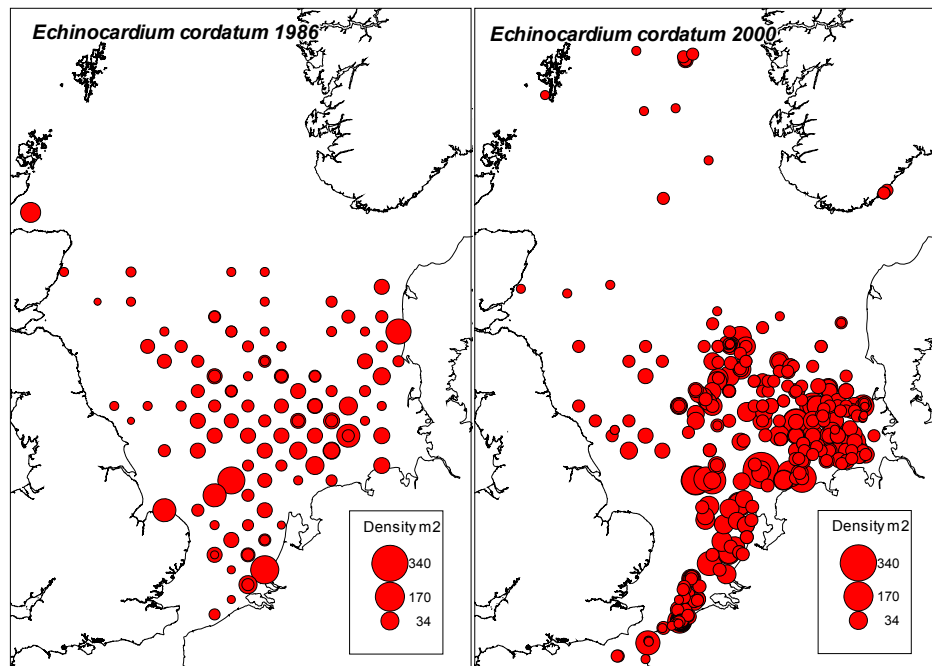


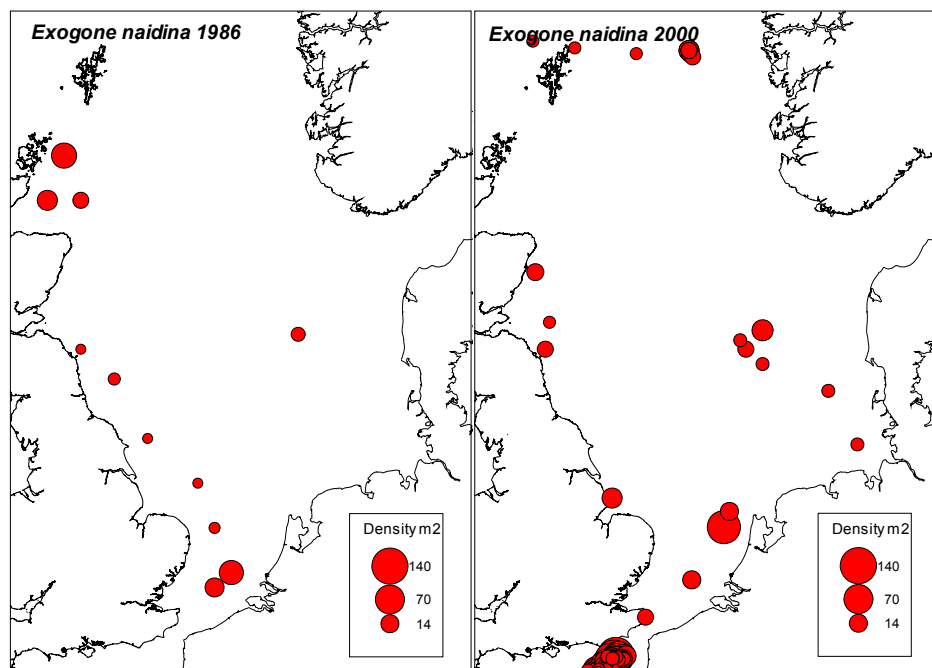
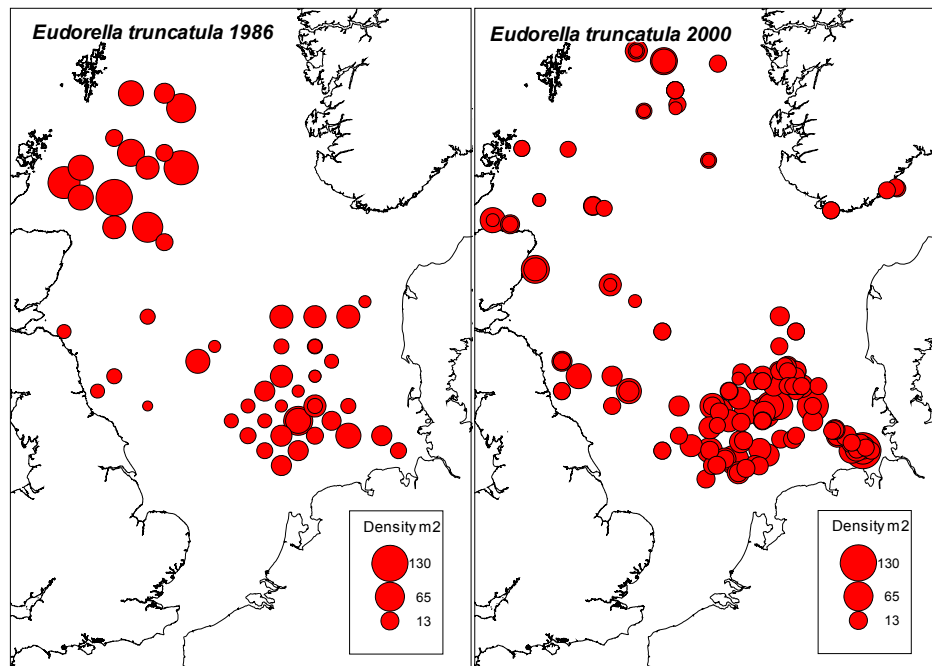


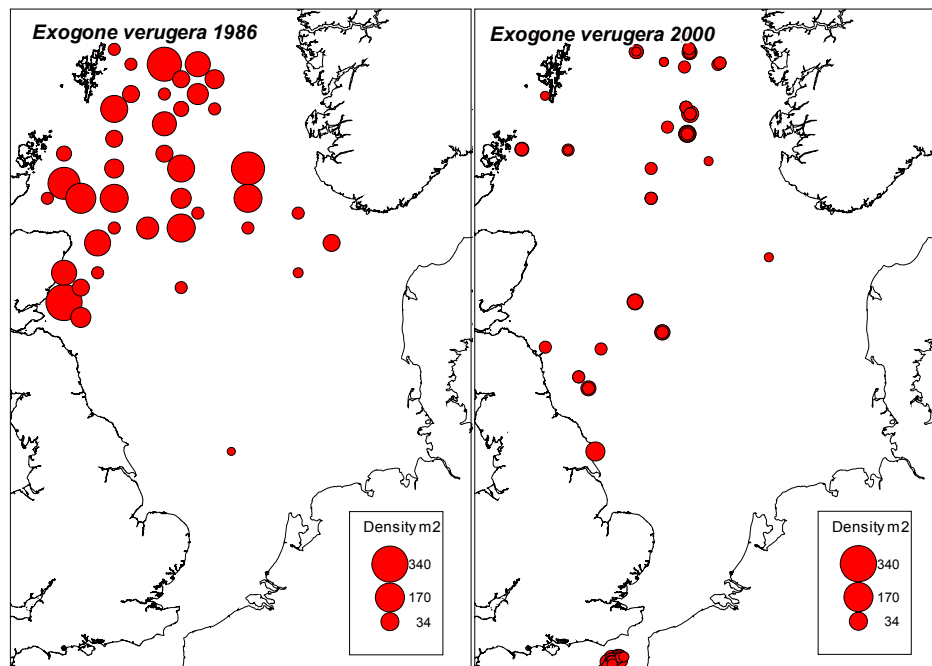
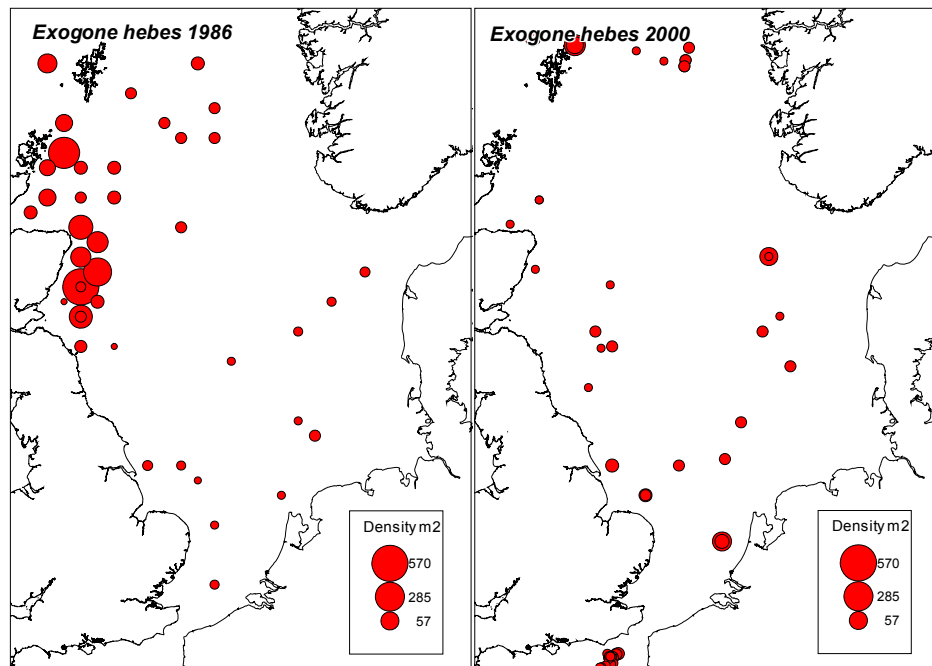


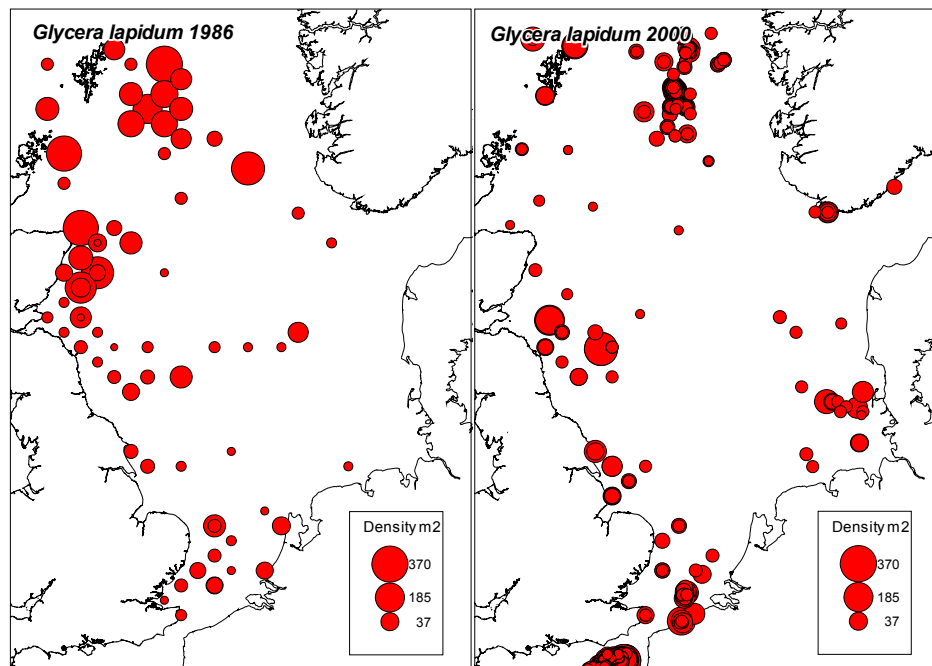
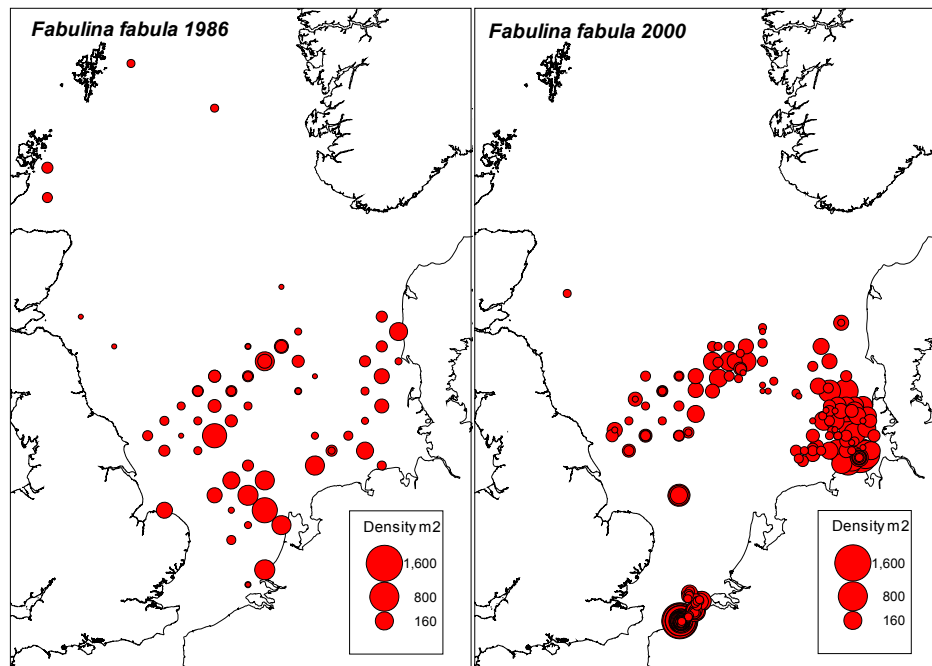


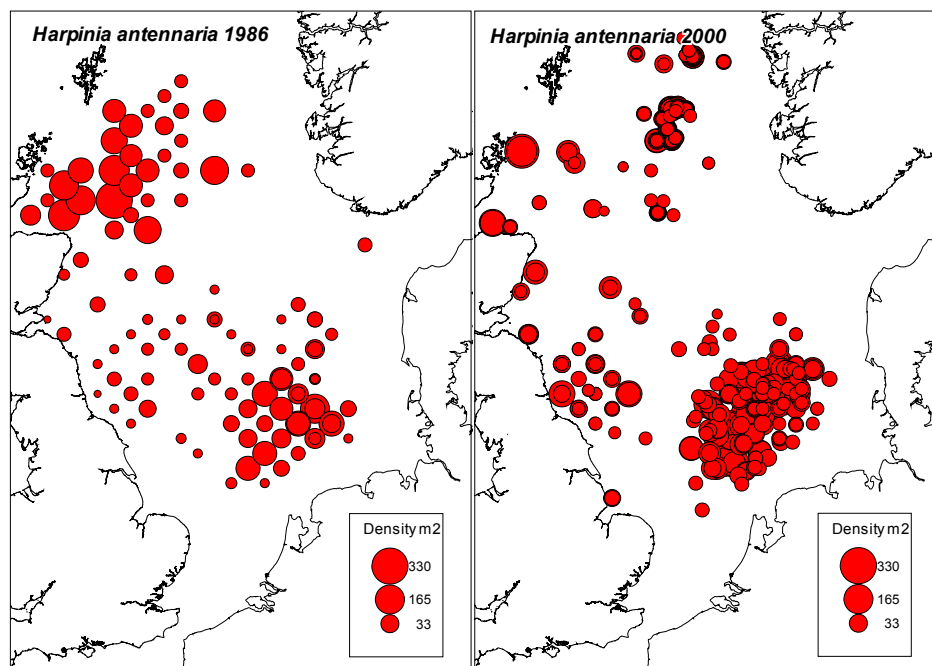
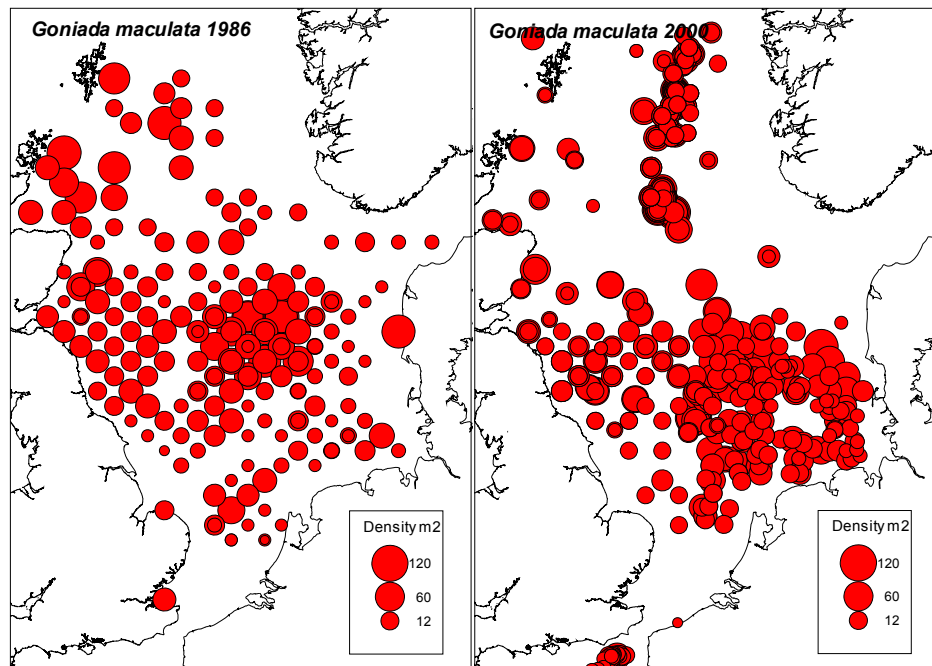


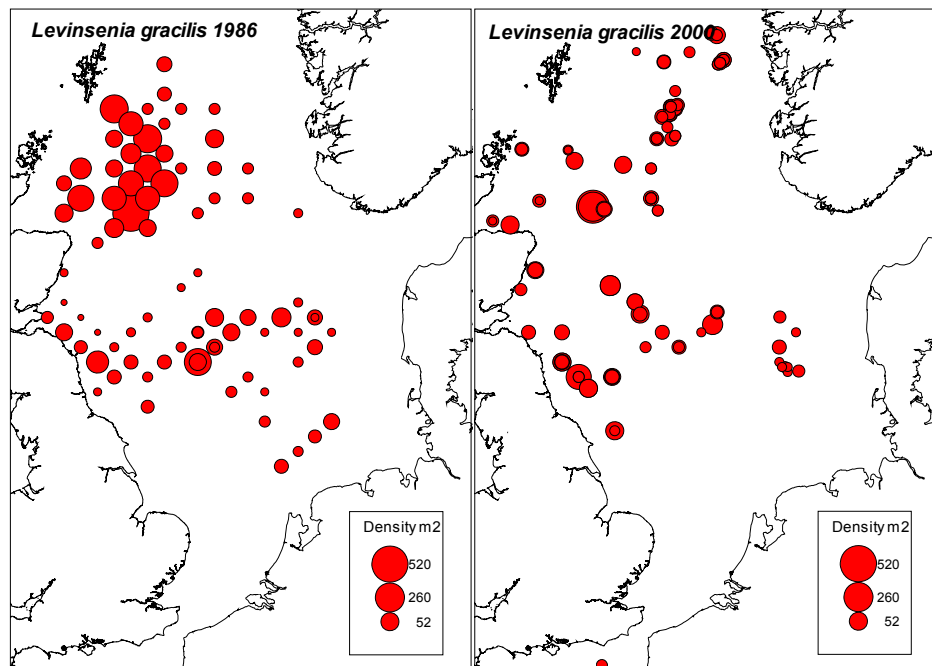
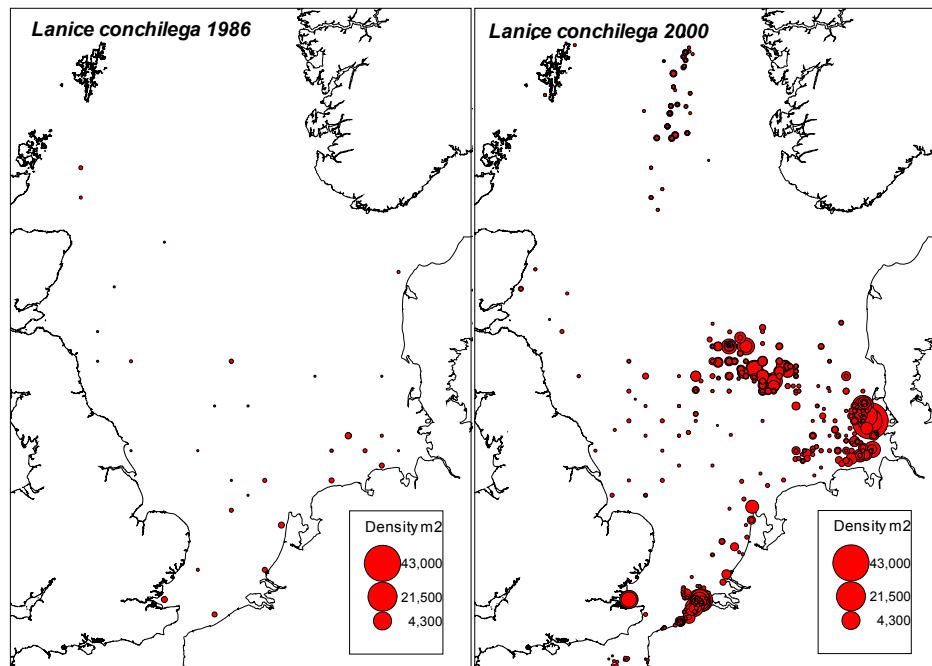


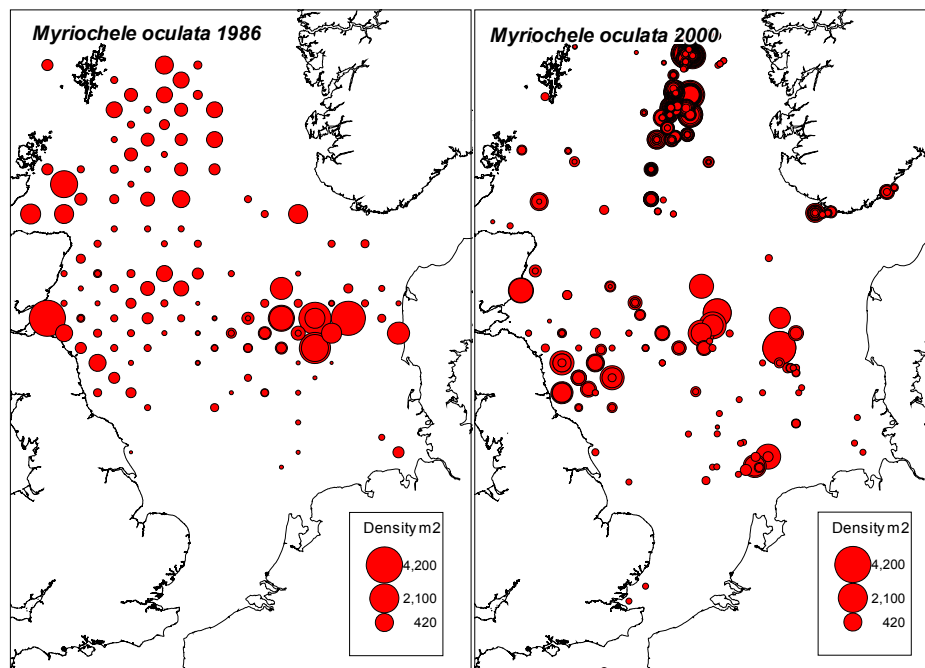
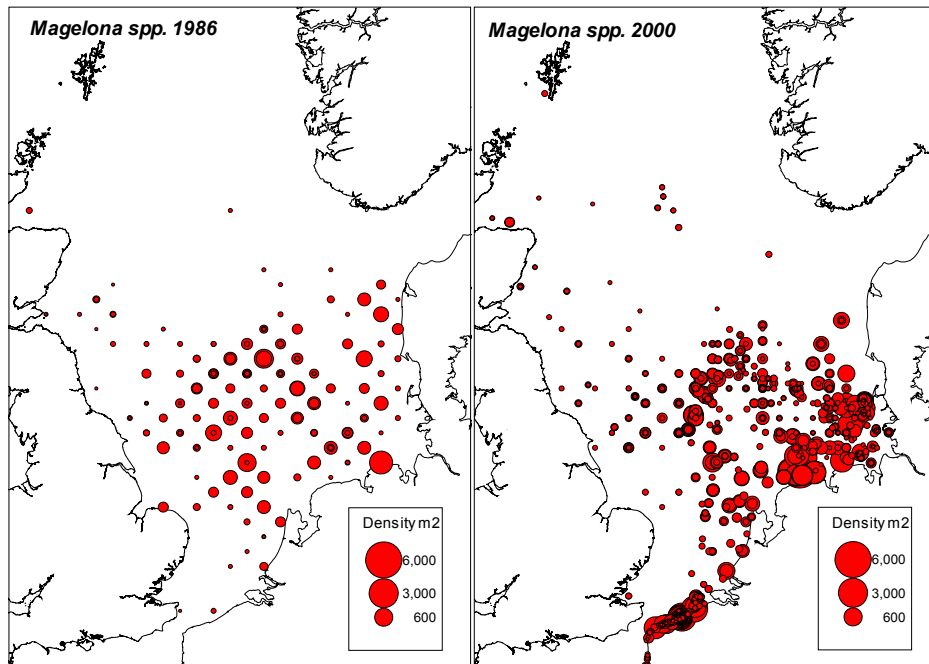


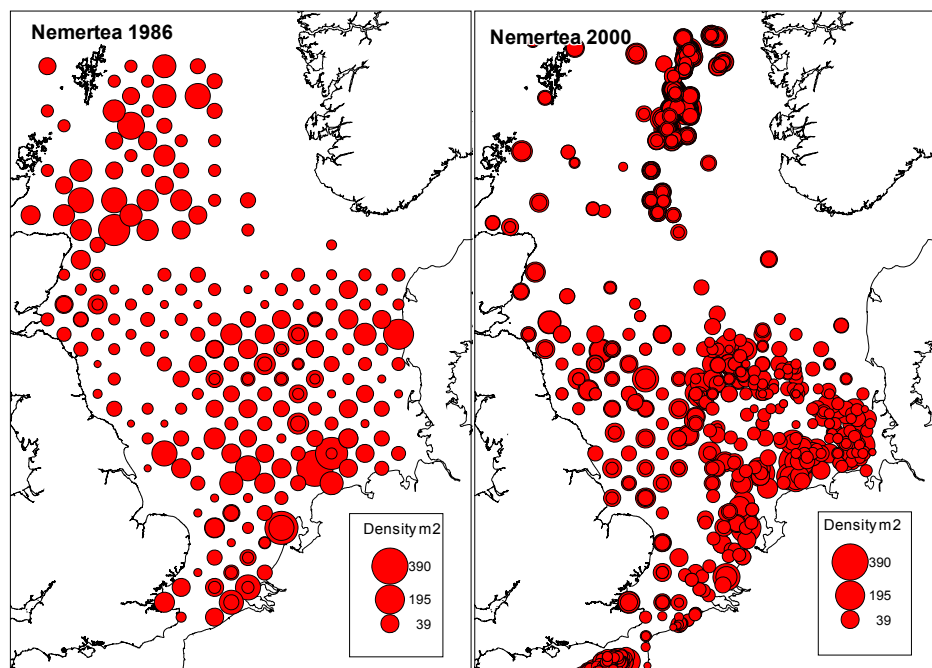
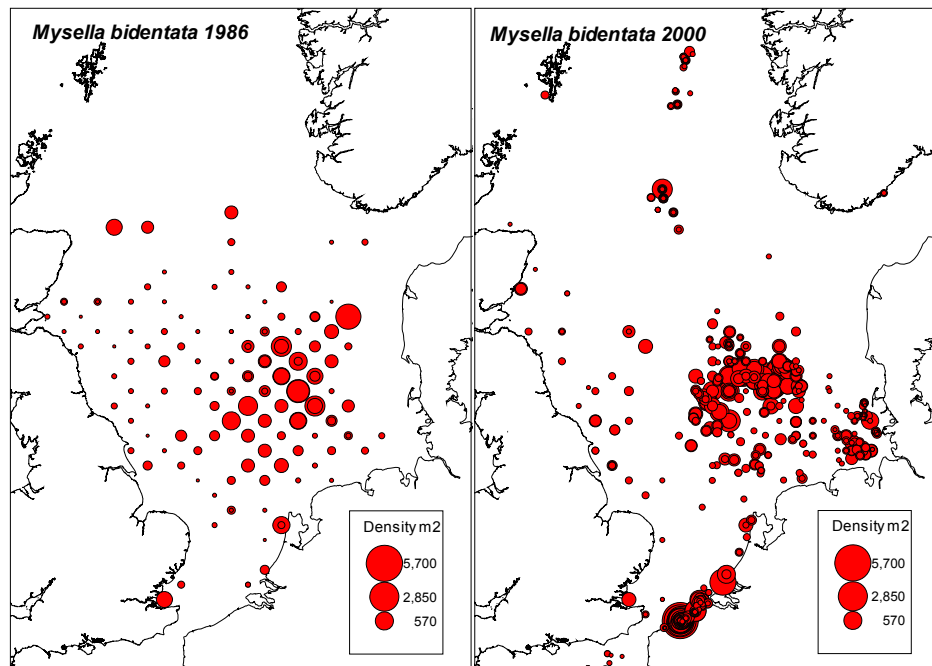


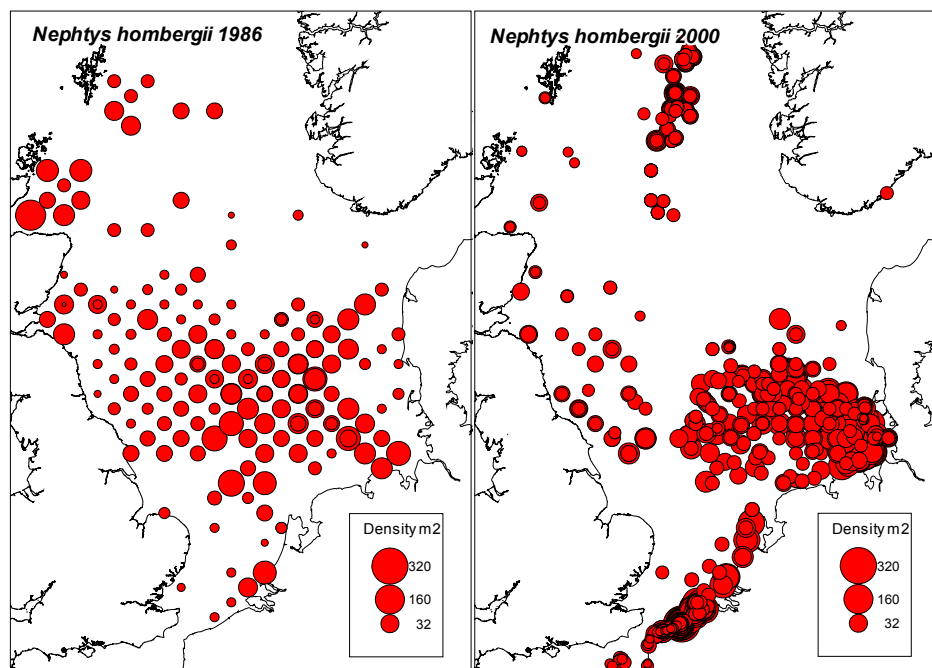
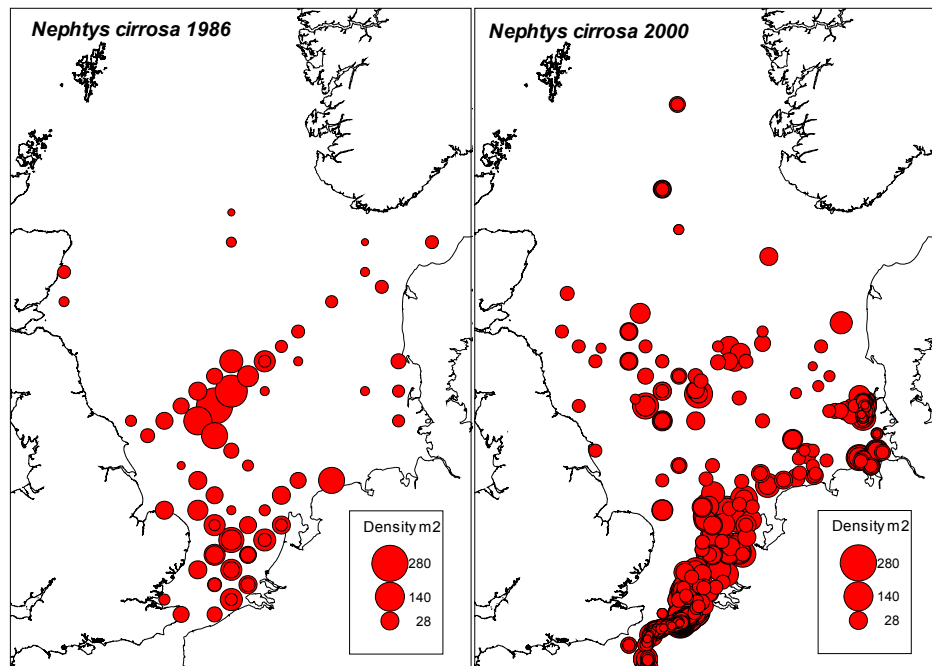


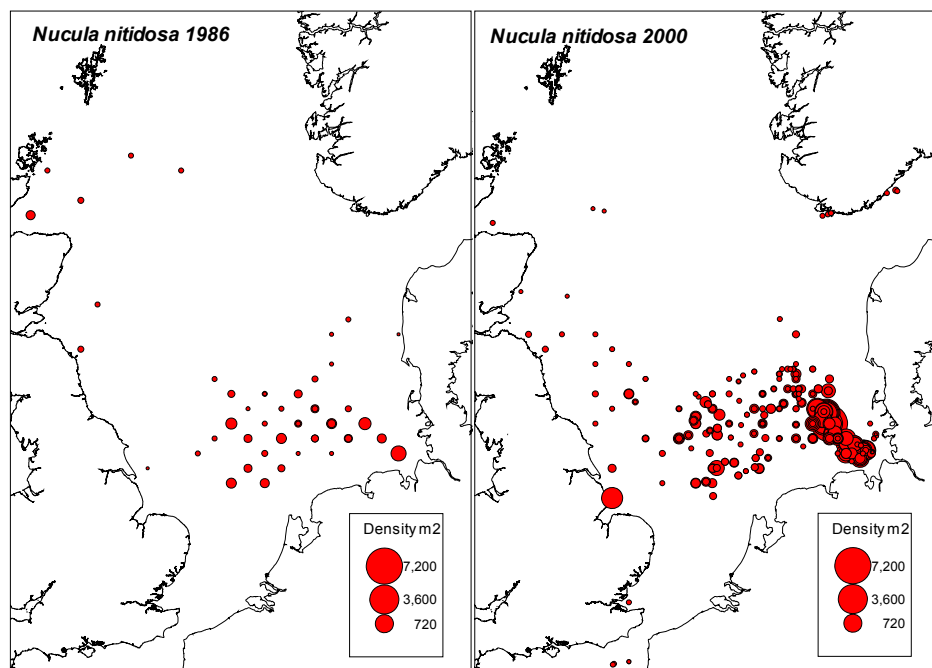
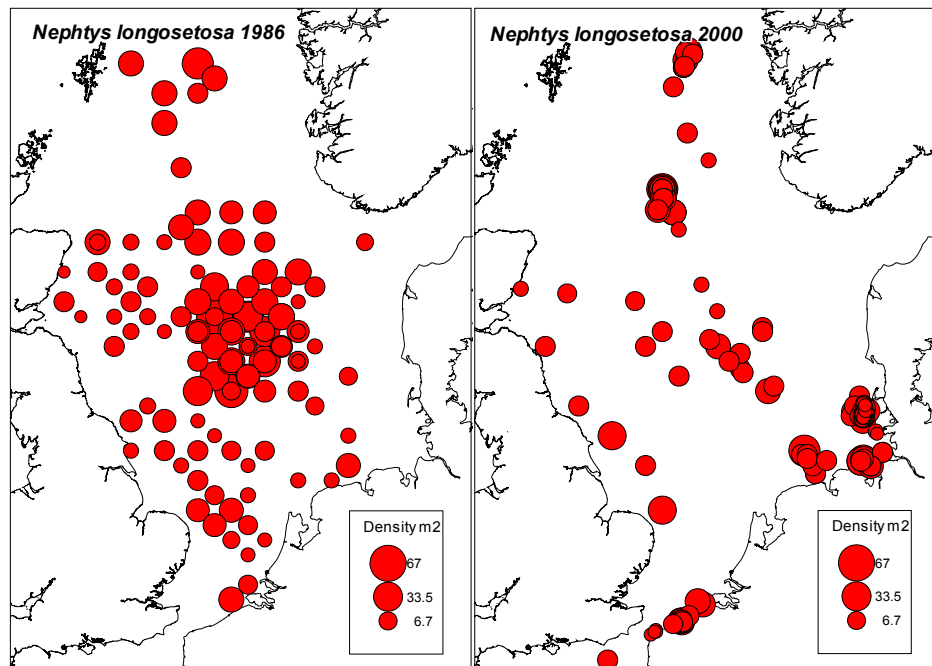


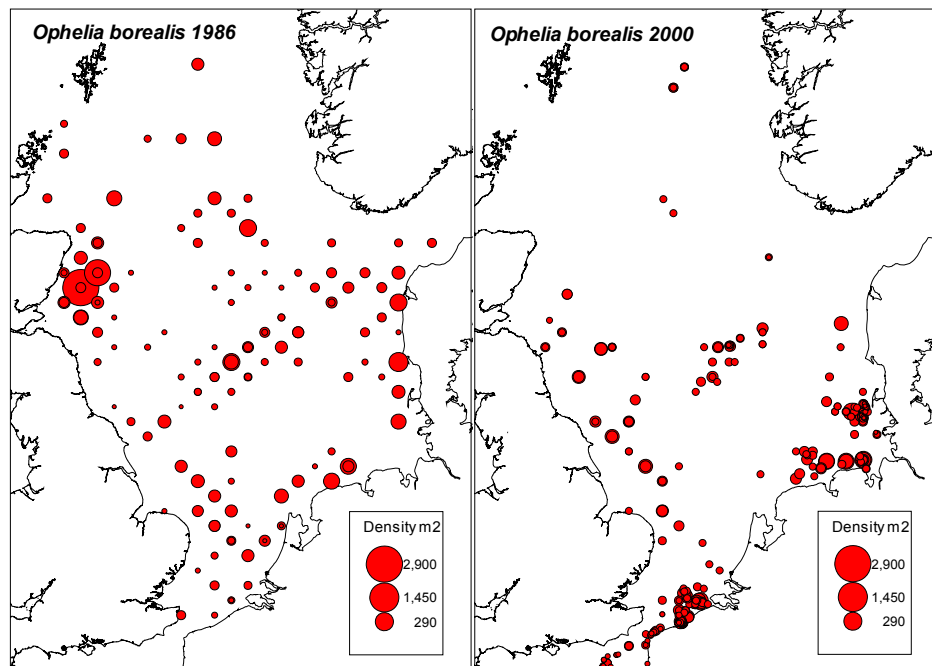
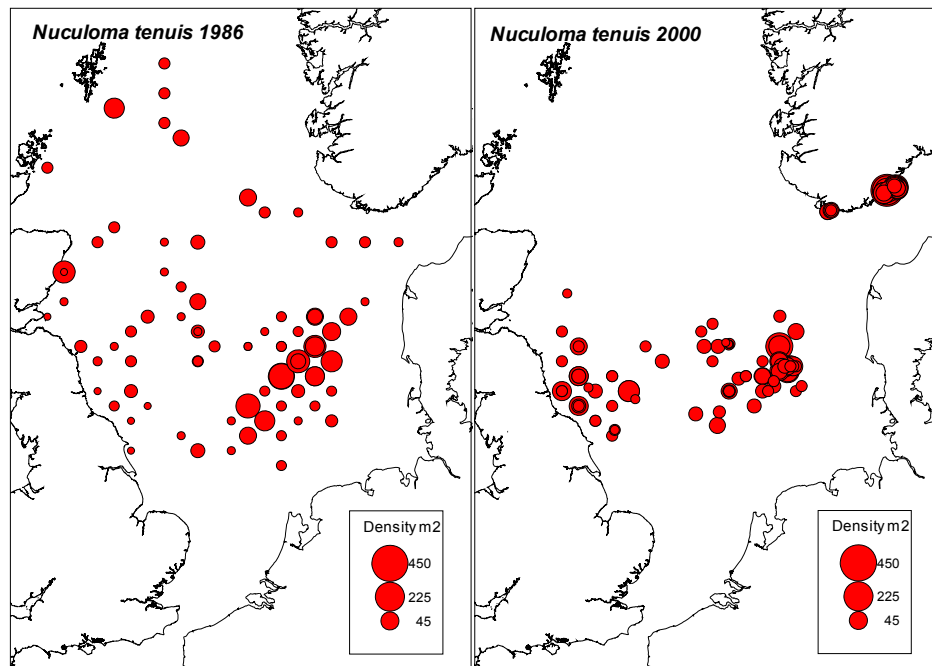


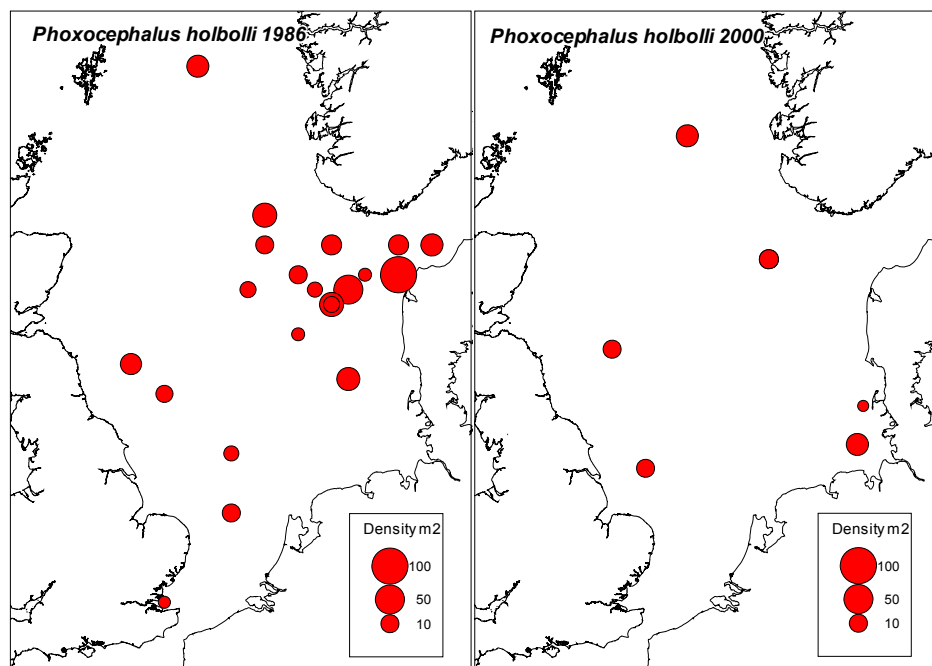
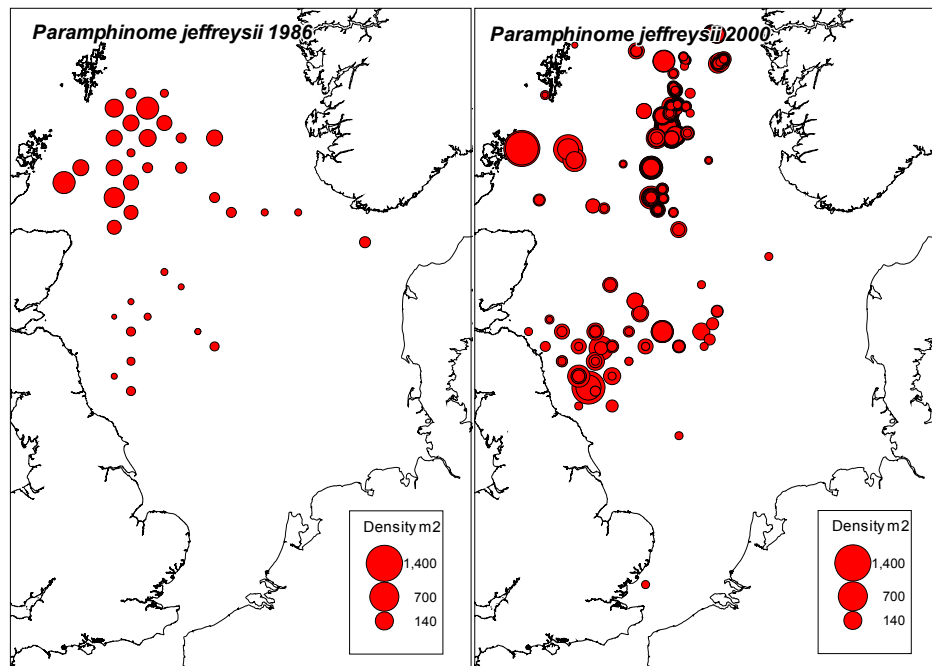


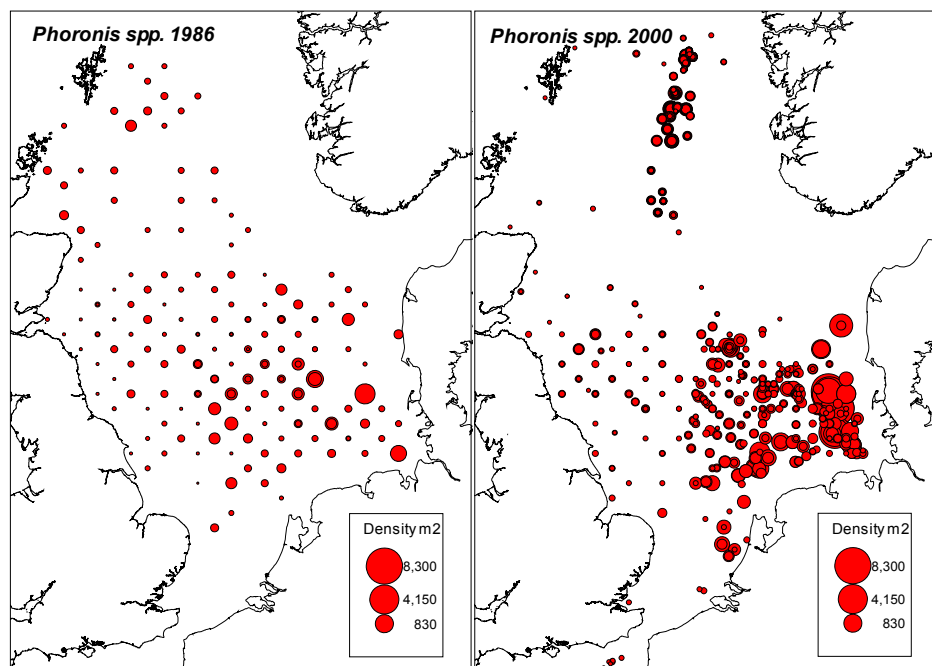
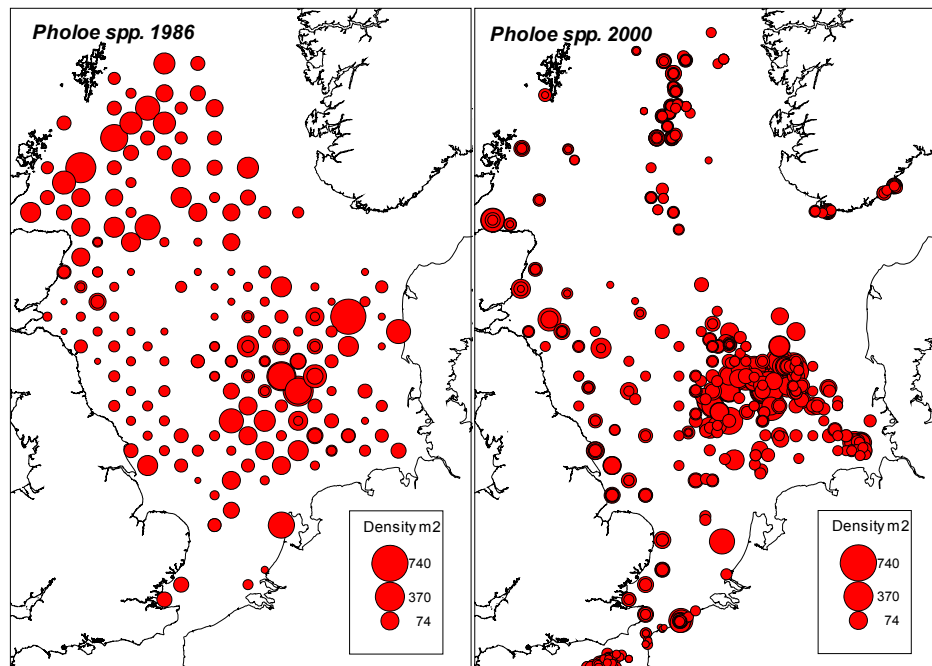


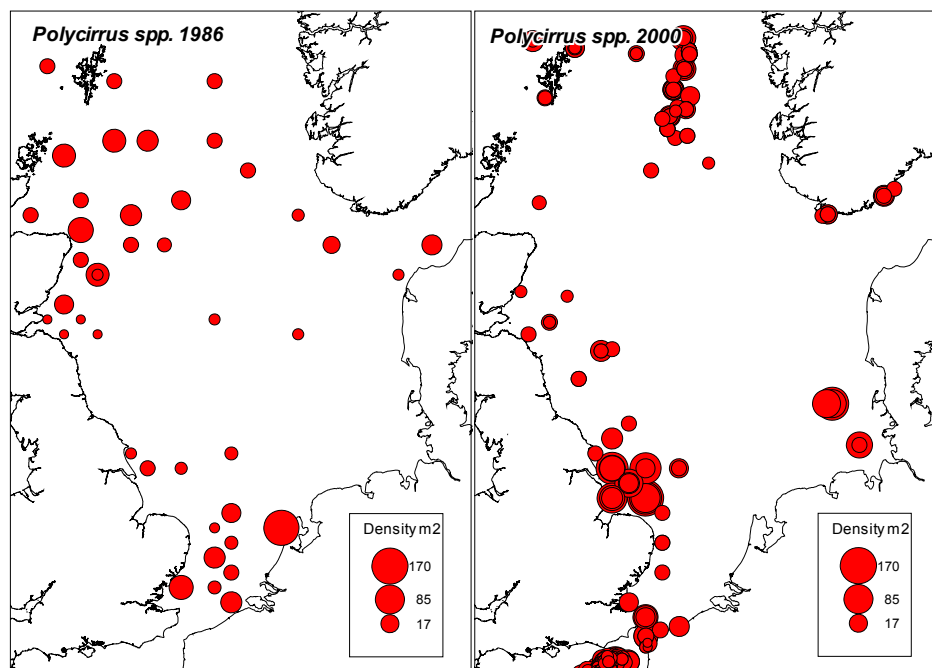
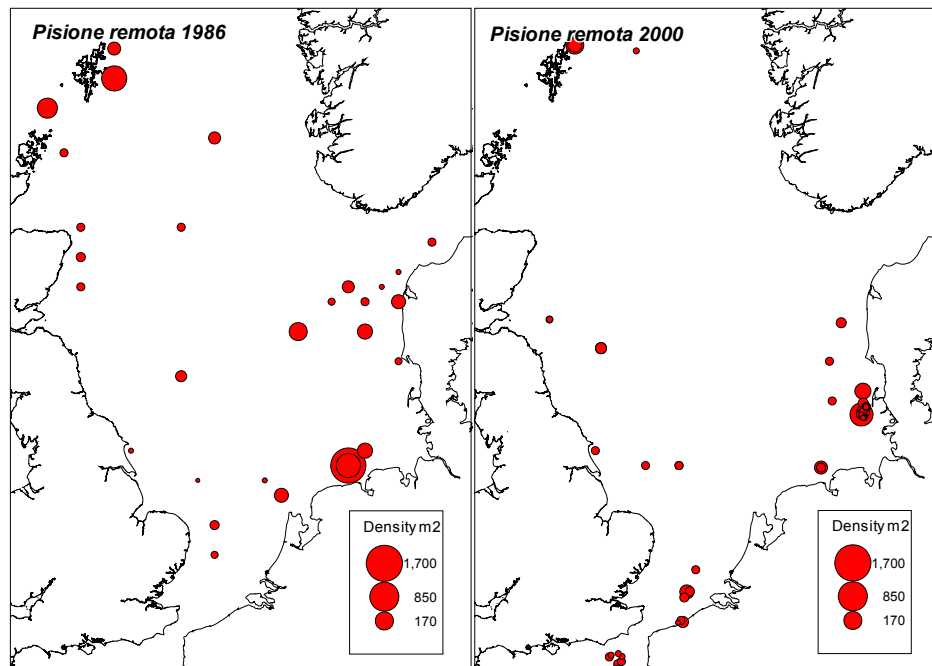


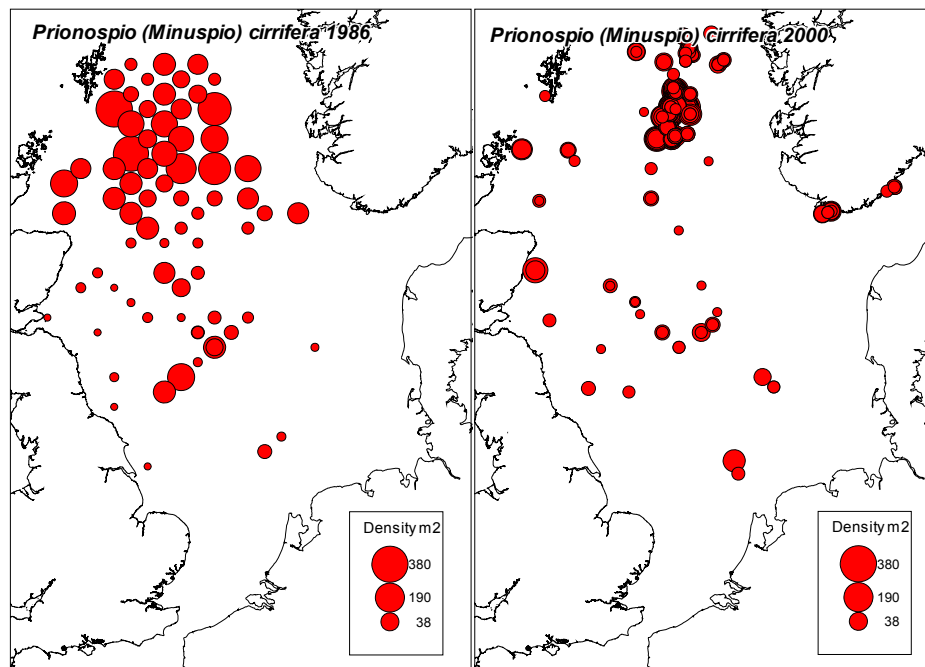
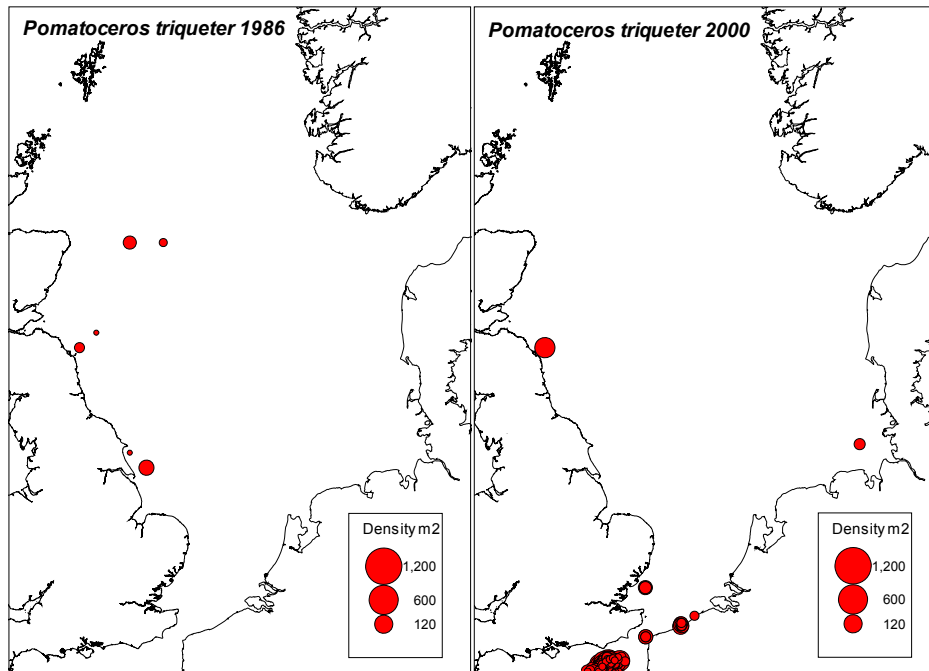


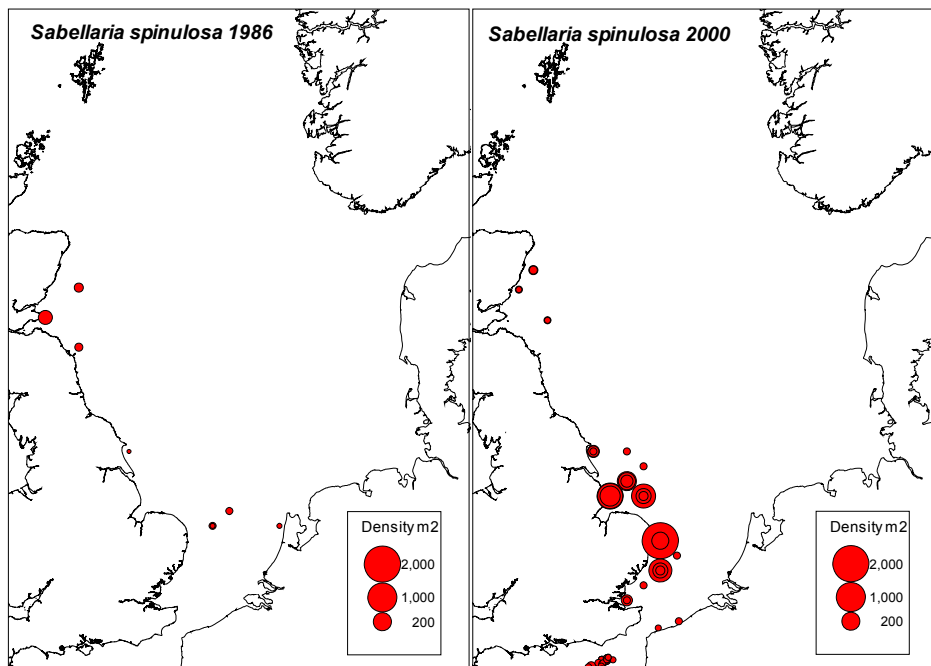
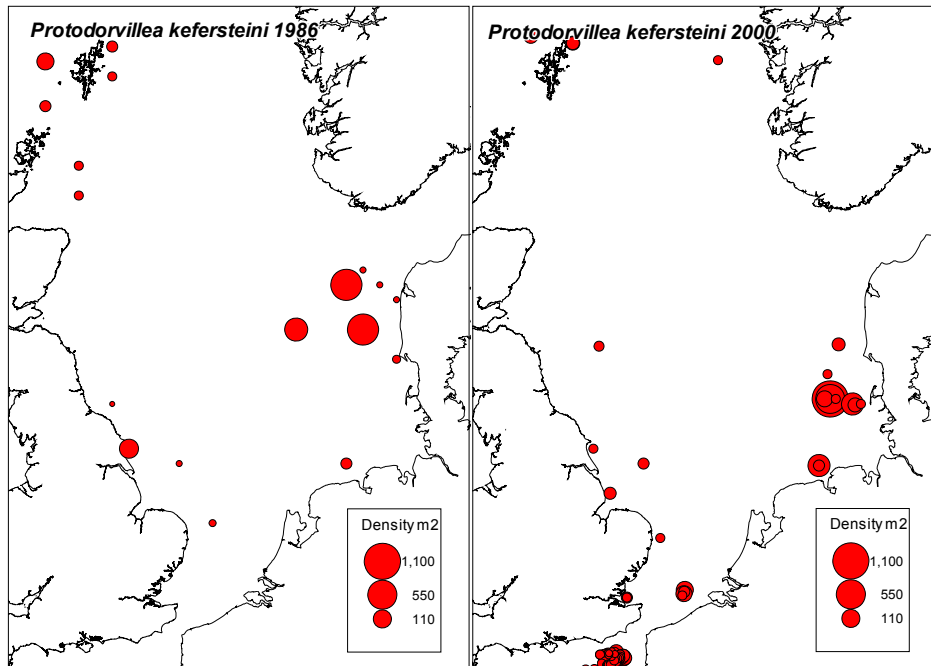


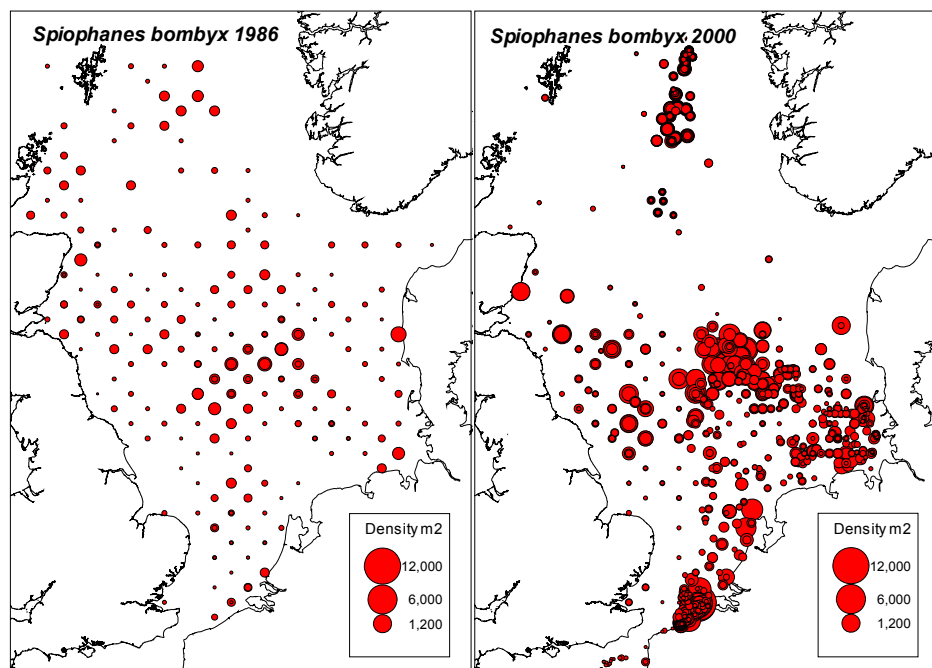
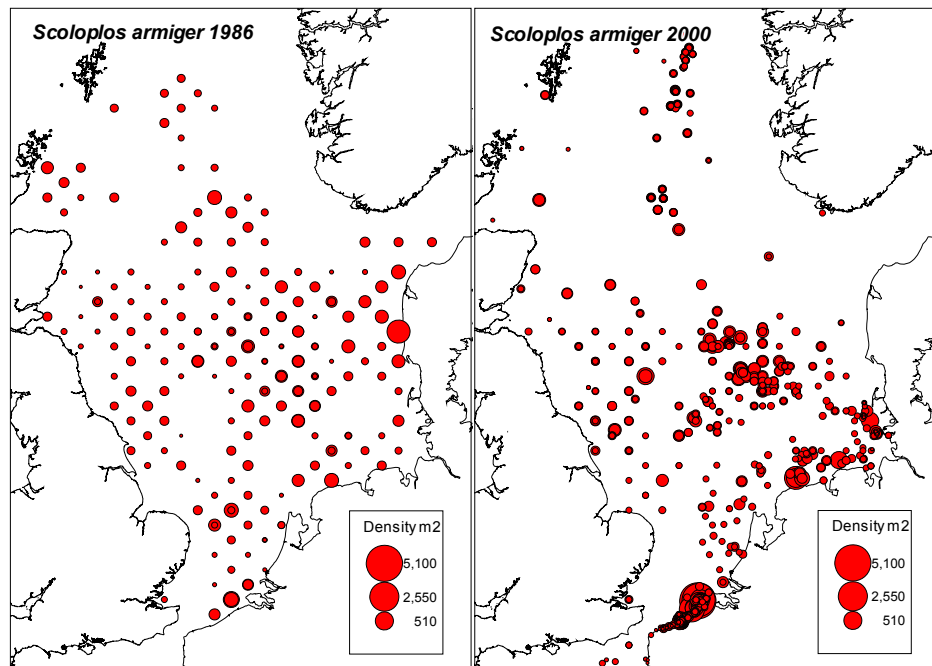


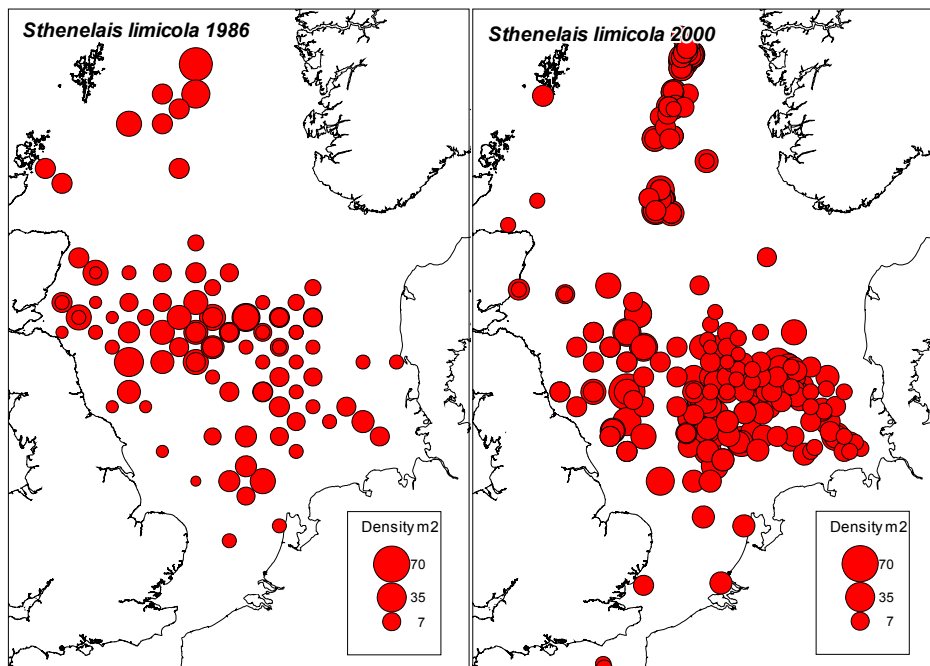
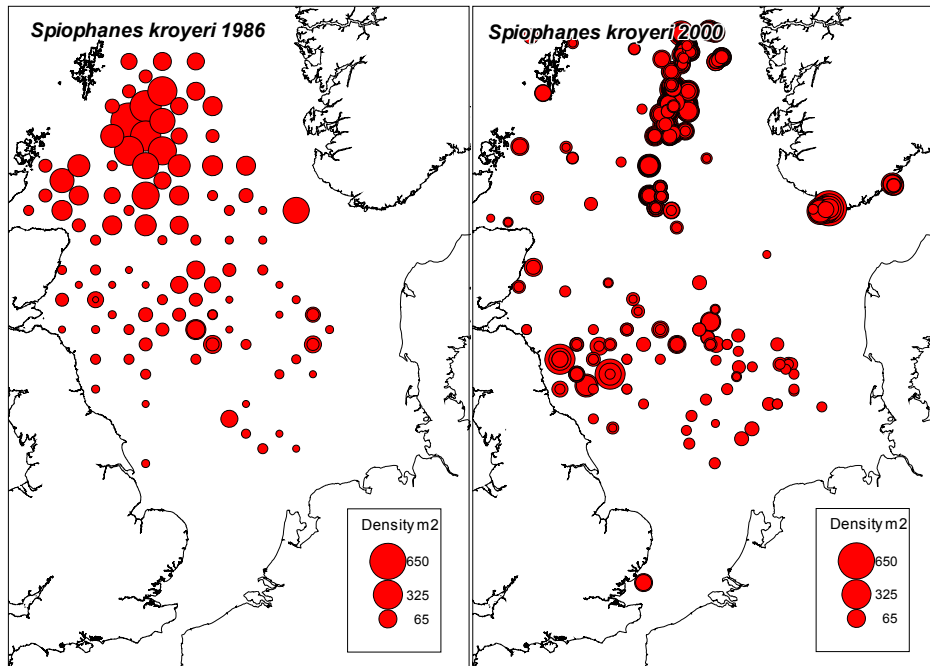


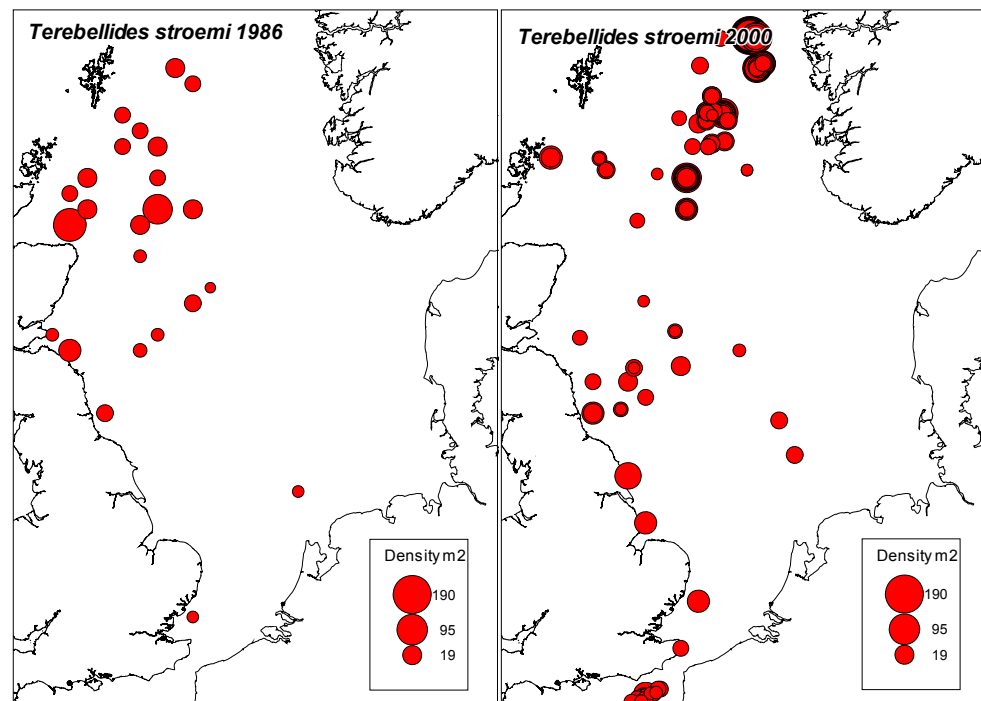
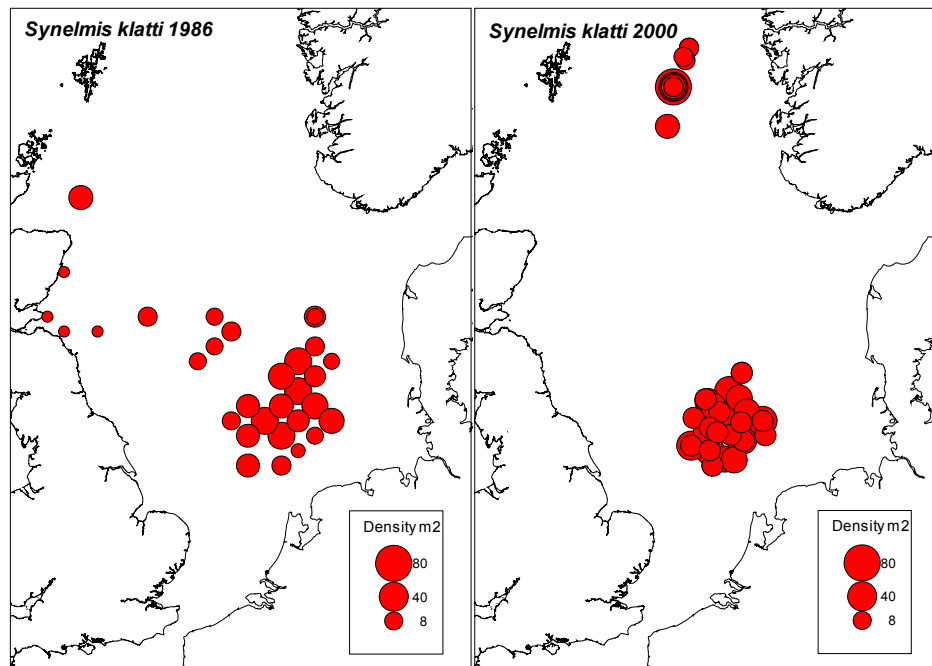


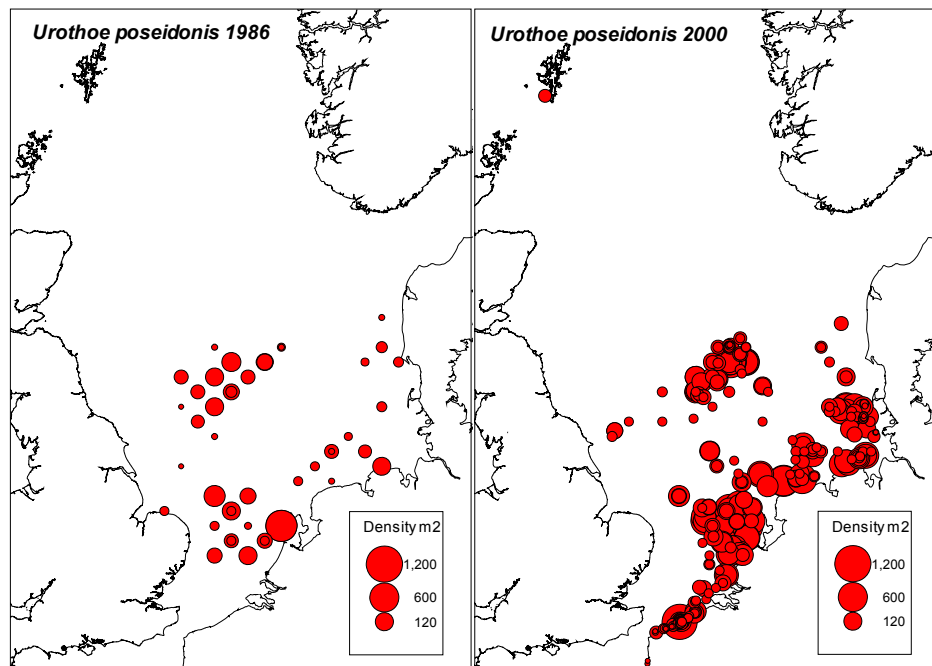
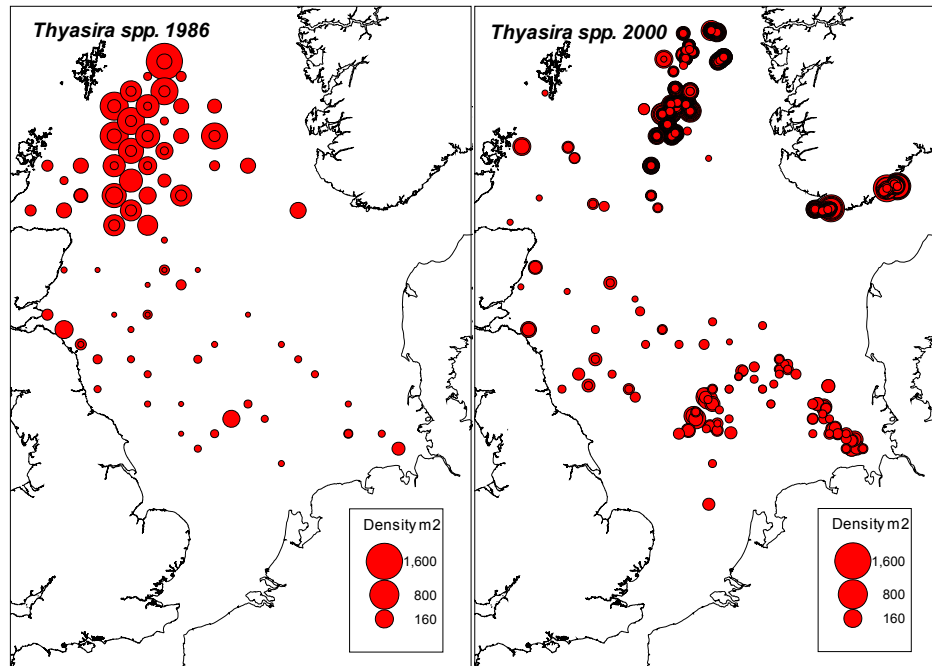












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