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VARIABILITY WITHIN MARINE ECOSYSTEMS OF NORTHWESTERN EUROPE

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EXECUTIVE SUMMARY

1 OBJECTIVES

Physical and biological factors governing marine ecosystems are far from constant. Currents, tides and wind mix the ingredients of these waters, which originate from the ocean and rivers. In Western Europe, the water temperatures may vary between ice-covered –2 °C during winter and almost 20 °C in warm summers. Within this ever-changing world, marine plants and animals survive and reproduce. During their lifetime, the marine organisms must not only deal with variations in their physical environment but also with variable densities of other organisms such as prey, competitors, predators and parasites. Furthermore, the marine systems are additionally influenced by human activities such as fishing, land reclamation, eutrophication and pollution.

The processes that underline the observed variability in time and space within the marine communities are still hardly captured. The main objective of the DYNAMO (DYnamics through Natural and Anthropogenic causes of Marine Organisms) project is to improve our understanding of the natural dynamics of marine ecosystems by analyzing long-term data sets on environmental and ecological variables. The analysis of variations in the abundance and life history parameters (e.g. mortality, recruitment) of marine plants and animals may reveal key-factors that govern these systems. More insight in the dynamics of the structuring factors and processes within marine ecosystems is not only necessary for a better understanding of the variability within these communities, but can also be considered as base-line studies for prediction of effects of management of these communities. The research focussed on marine ecoystems of northwestern Europe, viz. the Baltic Sea, the North Sea (in particular the German Bight and the shallow areas along the northwestern coasts) and the Wadden Sea.

2 RESULTS

2.1 STATISTICAL ANALYSIS TECHNIQUES

2.1.1 Multivariate statistical tools

For the analysis of the climatic, biological and environmental data several multivariate statistical tools were used. Mainly conventional methods based on eigentechniques such as Principal Components Analysis, PCA (also known as Empirical Orthogonal Function analysis, EOF) or Canonical Correlation Analysis (CCorA).

Various new dimension reduction techniques were developed such as Restricted Gaussian Regression (RGR) or Restricted Generalised Additive Model (RGAM).These techniques are applied on ecological data sets containing observed abundances of species, sampled at different sites, and monitored over time. Information is available on spatial and temporal environmental variables. The newly developed statistical techniques can be used as aids to answer the following questions. First, we examined the relationships between species abundances and spatial environmental variables, and the relationships between species. Second, we analysed how these species-environmental relations and species interactions change from year-to-year, and what were the effect of global environmental variables on these year-to-year variations.

2.1.2 Statistical downscaling

The identification and explanation of the influence of climatic factors on the North Sea and Baltic Sea has proven to be a quite difficult task. In the most simple case of those shown in this report, namely salinity in the Baltic Sea, where biology can be assumed to play a very minor role, the mechanism by which the atmospheric forcing is active is still unclear, although there are solid candidates (rainfall-runoff). However, there is discrepancy with other authors on the question if runoff represent a fresh water flux or an obstacle for water inflows from the North Sea. In the case of the relationship between oxygen in the Baltic Sea and large-scale circulation, the mechanisms are not so clear and there are several competing hypothesis.

This difficulties apply perhaps in a stronger fashion to biological populations. There seems to be statistical links between biology and the atmospheric circulation (North Atlantic Oscillation index), or sea-surface-temperatures, but the mechanisms by which climate affects biology is obscured by the complicated non-linear interactions between climate and biology and among different actors in the ecosystems. As a consequence the influence of climate is more clear for some species and in some regions, but it cannot be taken as a general rule. The estimation of possible consequences of climate change due to increasing concentrations of atmospheric greenhouse gases on the biological ecosystems considered in this project seems to us to be in general problematic.

2.2 LONG-TERM VARIABILITY IN NORTHWESTERN EUROPEAN MARINE ECOSYSTEMS

2.2.1 Hydrography

North Sea – A relationship between observed variability in large-scale climate and salinity in the German Bight is sought using a multivariate statistical approach. It is found that on an annual timescale, 90% of the observed salinity variability is in-phase and correlated with a lag of several months to large-scale air pressure. The statistical model is used to estimate annual mean salinity anomalies from large-scale air pressure back to 1900. The correlations between estimated and observed salinities range from r=0.4 to r=0.7, depending on the position. It is shown that advective precipitation is the mechanism that links air pressure and salinity anomalies. Advection of Atlantic Water has only a minor impact on the annual mean in the examined coastal zone. If air pressure data from a climate change experiment is used as predictor, a slight drop of the mean salinity level in the range of 0.2 to 0.3 psu is predicted under the IPCC scenario A of greenhouse gas concentrations.

Baltic Sea – The relationship between the low-frequency (annually averaged) salinity and oxygen concentrations in the last 30 years in the Baltic Sea and the large-scale atmospheric circulation has been statistically analyzed. It has been found that at these time scales the evolution of salinity and oxygen is quite homogeneous in depth, i.e. deviations from the long-term mean tend to be of the same sign in the upper and deeper layers simultaneously. Moreover, the evolution of the salinity and oxygen concentrations are negatively correlated within each layer: lower than normal salinities tend to be observed simultaneously with higher than normal oxygen concentrations, and vice versa.

The statistical analysis seems to indicate that the forcing by the atmospheric circulation may be responsible for this anticorrelation between salinity and oxygen. Stronger meridional sea-level-pressure gradient over the North Atlantic, and therefore stronger westerly winds, cause positive rainfall anomalies in the Baltic Sea catchment area and increase run-off giving rise to decreased salinities at all depths. The mechanisms by which a stronger zonal atmospheric circulation enhances the oxygen concentrations may be related either to a weakened stratification through the reduced salinity (at long time scales), or by stronger or more frequent inflows of North Sea waters (at short time scales). The influence of the atmospheric circulation may explain at these time scales of the order of 60 % and 40 % of the variability of these hydrographic variables, respectively.

The question has also been addressed of how salinity and oxygen in the Baltic Sea may respond to changes of the atmospheric circulation in a global climate change scenario. For these purpose the intensities of the relevant atmospheric circulation patterns in a transient experiment with a coupled atmosphere-ocean General Circulation Model forced with increasing anthropogenic greenhouse gases concentrations between the years 1860 and 2099 have been estimated. In this integration the change of the atmospheric circulation most relevant for salinity and oxygen in the Baltic Sea seems to be an enhancement of the meridional sea-level-pressure (SLP) gradient in the North Atlantic. Thus, under the assumption that the statistical relationship between SLP and the hydrographic variables also holds in the future, this trend in the atmospheric circulation would lead to decreased salinity and improved oxygen conditions in the Baltic Sea.

2.2.2 Phytoplankton and zooplankton

Wadden Sea – In the eutrophic Marsdiep, the westernmost tidal inlet of the Wadden Sea, phytoplankton biomass and production almost doubled at the end of the 1970s and remained high ever since. Principal component analysis of 20-year (1974-1994) high-resolution time series of the 32 most numerous marine algal species revealed that the phytoplankton community changed drastically both between 1976 and 1978 and again between 1987 and 1988, and that it was relatively stable in-between (1974-1976, 1978-1987) and hereafter (1988-1994). These major changes in phytoplankton biomass and species composition coincided with changes in absolute and relative (TN:TP) nutrient concentrations. During the summer of 1977, the Marsdiep shifted from a rich, but phosphorus-controlled system to an even more eutrophic but nitrogen-controlled environment. The system re-shifted towards P-control between 1987 and 1988. The coincidence of the shifts in relative nutrient concentrations and phytoplankton species composition implies a strong causal relationship between TN:TP ratio's and phytoplankton community structure. Amongst diatoms, the observed increase in phytoplankton biomass under eutrophic N-controlled conditions was particularly due to an increase of the abundance of larger algae. Our results indicate that the N-budget of the area is correlated with the community structure, suggesting enhanced loss of nitrogen to the sediment through increased deposition of larger algal cells.

Additional comparison between estimates (based on a relationship with external nitrogen loadings) and actually observed primary production rates of autotrophic components (phytoplankton, microphytobenthos, macroalgae and seagrasses) revealed that primary production is not invariably stimulated by nitrogen loading from land. If other factors (i.e. additional nutrient sources, N:P ratio's, internal nutrient dynamics and co-limiting effects of nutrients and light) are not taken into account, management regulations that target at diminishing the effects of eutrophication hold the risk of seriously under- or overestimating nutrient reductions that are thought necessary to obtain their goals.

North Sea – A multivariate statistical approach is presented that allows a systematic search for potential relationships between the variability in ecological time series and climate records. In this study, interannual variability in large- and mesoscale climate variables in the North Sea region is compared with variability in local zooplankton observations from Helgoland. The species *Noctiluca scintillans* (Protozoa), *Temora longicornis* and *Acartia* sp. (Copepoda), and spionid larvae (Polychaeta) are examined. The multivariate model detected several high correlations between zooplankton abundance and winter climate. Based on these correlations, complementary hypotheses about the causal relationships are discussed using available local data.

2.2.3 Macrofauna

North Sea – Macrofaunal samples were collected seasonally from 1978 to 1995 in the subtidal zone off Norderney, one ofthe East Frisian barrier islands. Samples were taken with a 0.2 m2 van-Veen grab at five sites with water depths of 10-20m. Interannual variation of biomass, abundance and species number of the biota were related to interannual variations in climate using multivariate regression models and by identifying congruent changes in the time series. Changes in the biota were described in relation to human impact, seasonal and long-term meteorological variability. Our analysis suggest that macrofauna communities were severely effected by cold winters, whereas storms and hot summers have a minor impact. It appears that mild meteorological conditions, probably acting in conjunction with eutrophication, resulted in an increase in total biomass since 1989.

Indeed, the multivariate model found a strong relationship between the species number and environmental conditions, especially the sea surface temperature in spring. On the basis of our results, we suggest most of the interannual variance in macrozoobenthos can be explained by climate variability.

The ecosystem in the south-eastern North Sea is affected considerably by various sources of both natural and anthropogenic origin. The effect of a reduced beamtrawling effort on the benthic invertebrate assemblage could be studied from changes in the assemblage following the establishment of a protected area, the "plaice box". This area was established in 1989 and closed for all vessels with an engine power over 300 Hp, which constitutes the main part of the beamtrawling fleet. At first it was only effective part of the year but since 1995 the box was closed during the whole year. In order to be able to distinguish between this effect and that of potentially confounding influences from natural origin, two relevant environmental variables, seawater bottom temperature and depth, were incorporated in the analyses. Multivariate analysis revealed not only a significant effect of bottom seawater temperature and depth but also a significant effect of the closure of the box. Remarkable was that the partial closing of the box caused an increase in abundance of several species followed by a decline when the box was closed year-round. A possible explanation is that the most abundant species were scavengers and predators for which the deleterious effect of additional mortality was overruled by a decreased competition for food and risk of predation.

Wadden Sea – Multivariate analysis (RGR) of annual data of macrobenthos abundances in March of each year during the period 1974-95 indicated that the environmental gradient during different years is mainly determined by the distance to tidal inlet. Using one underlying gradient based mainly on this variable, changes in the ecological parameters (maximum, optimum and tolerance (distribution) of species abundance) were estimated. The results for species fitted well in the model indicated an increase of the maxima of *Scoloplos armiger* and *Heteromastus filiformis* from late 1970s to the mid 1980s, followed by a minimum 1990 and an increase again. For the estimated maxima of *Cerastoderma edule* 0-year class a 4-year cyclical pattern was evident. Cross-correlations between the ecological parameters for different species showed correlations between the maxima and optima of *Nephtys diversicolor*, *S. armiger* and *H. filiformis* which could indicate interactions between the species. Only low correlations were found between ecological and temporal environmental parameters with this approach.

In the approach of Dynamic GAM, a smoothing function, describing the average, over time, species-environmental relationship and a stochastistic trend, representing deviations from the previous relationship, were estimated for each species. Based on cross-correlations between species trends, various groups could be identified. Within these groups, estimated trends were highly correlated with a time lags between –2 and 2 years. Considering cross-correlations between species trends and temporal environmental variables, most trends were significantly ($p<0.05$) correlated to water temperature with time lags of 0, 1 and 2 years.

Baltic Sea – An analysis of spatial distribution of macrozoobenthos (1996-97) using MDS demonstrated different assemblages characterising different subareas and depth zones of the Baltic Sea. Only five species (*Harmothoe sarsi*, *Saduria entomon*, *Monoporeia affinis*, *Pontoporeia femorata* and *Macoma balthica*) dominated the communities in most of the study area. Low total biomass and diversity was found in the northernmost areas and in the deep central Baltic Sea. The deepest central basin was devoid of macrofauna due to anoxia. The species distribution and community structure correlated with salinity and oxygen conditions.

However, a study of long-term changes (1965-94) of macrofauna in the subhalocline Baltic Proper and Gulf of Finland area showed major changes in species abundance, community structure and depth distribution. The highest variability was found at intermediate depths (70-100 m) corresponding to changes in hydrography. The major inflows of North Sea water in 1975-76 led to rapid benthic recolonization of even deeper areas due to improved oxygen conditions. The subsequent, prolonged stagnation period in 1977-93 caused first a deterioration of macrozoobenthos as a consequence of anoxia and hydrogen sulphide formation in subhalocline (70-250 m) areas. However, later a recovery was observed in the 70-100 m depth zone when vertical stratification weakened and intensified vertical mixing resulted in improved oxygen conditions at these depths. The effect of this process was most pronounced in the Gulf of Finland. An expansion of macrofauna was observed in the late 1980s and early 1990s, leading to abundant amphipod dominated communities, followed by a sudden collapse of the communities in 1996-97. The statistical analysis indicated that these changes were best explained by a combined effect of annual observed minimum oxygen concentration (with a 1 year time lag) and salinity, the poor oxygen conditions being obviously the critical factor for most of the study period. The analysis based on structural time series models further demonstrated the importance of the oxygen conditions in the Baltic Proper and Gulf of Finland area. The trends of the five common species were most correlated to trends in near-bottom oxygen concentration.

In the Gulf of Bothnia area an increase of abundance and biomass of the macrobenthic communities was observed during the study period (1965-97). This is probably caused by the general eutrophication, increasing the sedimentation and the amount of food available for the benthic communities. In addition, cyclical variability was found in the abundance of the dominant amphipod species. Density dependent regulation of populations in connection to food availability is suggested to cause the cyclical pattern. In contrast to other areas in the Baltic Sea, changes in hydrography did not have a major impact on the succession of the communities but affected only the occurrence of some marine species.

2.2.4 Fish

North Sea – The North Sea fish community was studied using data from three surveys as well as data based on Virtual Population Analysis. In general the patterns observed in the different surveys were consistent and the minor differences can probably be attributed to the differences between the surveys in terms of gear used, area covered and time of year the surveys were conducted.

Three aspects of the fish community were studied: species composition, size-structure and total biomass. The overriding pattern in each of the surveys is that of the total biomass There is a strong increase during the eighties until a maximum is reached in the early nineties after which it remains high (offshore North Sea proper) or decreases (inshore southeastern North Sea). The offshore survey also shows a period of increased biomass in the late seventies linking the changes in the fish community to those of other biota but this was not observed in the inshore survey.

The size-selective mortality induced by fishing activities probably affected the size-structure of the fish community as well as the species composition. The size-structure showed a progressive decrease of the average weight of the fish. The species composition showed a gradual shift from K-strategists toward r-strategists. Part of the variation in size-structure, species composition and total biomass could be attributed to factors from natural origin such as sea surface temperature or atmospheric circulation. No distinct relationships were found that could explain the variation in recruitment succes.

The patterns of variation in recruit numbers of fish in the northwestern North Sea did not correspond with the expectations (i.e. low variation in recruit numbers near the geographical centre, high variation at the northern edge and intermediate variation near the southern edge of the distribution range). The sign of the correlation between recruit variation in plaice and dab and latitude and temperature was opposite to the prediction. All species examined showed no significant variation in recruit numbers in relation to the variables considered. We accept nor reject the hypothesis, however, because the expected relationships between CVR and latitude may have been overruled by other sources of variation such as sampling methods, average age of the catch, inshore-offshore gradients and possibly northward shifts of species' ranges.

2.2.5 Sediment cores

The suitability of the sediment core as an archive of long-term variations within a particular area strongly depends on the presence of undisturbed accumulation of material that represents environmental conditions at the moment of sedimentation. The core, therefore, should not have been contaminated by material that was in fact produced years ago such as old resuspended material from other surrounding areas, nor should the material have been reworked after sedimentation as the result of bioturbation or local resuspension. Many soft-sediment benthic species do not live at the sediment surface but burry themselves in the sediment, e.g. ostracods either crawl on the sediment surface or burrow to a depth of a few centimeters. Densities of such burrowing and bioturbating animals found at a particular depth should therefore in fact be "updated" to a more recent period. The timing and actual values of environmental variables that are retrieved from sediment cores of the German Bight and the western wadden Sea have to be interpreted with much caution, due to (i) uncertainties and methodological difficulties in dating of the sediment core, (ii) mixing of relatively old and fresh material throughout the core by bioturbation and resuspension mechanisms, and (iii) burrowing behaviour of marine benthic organisms.

North Sea – The pistoncore sampled in the German Bight (ranging from ca. –312 to 1996 AD), contained a suite of faunal remnants. However, remnants of several species were considered not to be representative for actual densities due to the low number, e.g. fish remnants and large bivalve shells. Therefore, we focussed on the annual deposition of three species of ostracods, viz. *Elofsonella concinna*, *Palmoconcha guttata* and *P. laevata*. Based on the ratios of the left and right halves of the shells in the sediment core sampled in the German Bight the origin of the remains of the ostracod *Palmoconcha guttata* is most probably more autochtonous than those of *P. laevata*. For *P. guttata*, there is no relationship between the right:left shell halve ratio and shell deposition rate at rates higher than 500 shells m^{-2} y^{-1}. At lower rates, this ratio declines, which may indicate a higher proportion of allochtonous material during periods of low deposition rates. No such indications were found for the shell-deposition rate and the age-class structure of *P. guttata*, nor for both relationships of *P. laevata*. We concluded, therefore, that the shell deposition rates of *P. guttata* appear to be related with mortality rates of the local stock, whilst those of *P. laevata* most probably reflect a combination of rates of mortality and transport of specimen from a wider area. Furthermore, the gradual increase in the juvenile:adult ratio of *P. laevata* since 1500 AD cannot be attributed to changes in transport rate, because the left:right shell-halve ratio of this species remained more or less constant during this period.

Wadden Sea – The sediment core sampled in the former Vlieter channel (ranging from 1932 to 1997 AD) contained a suite of faunal remnants. However, remnants of several species were considered not to be representative for actual densities due to the low number, e.g. fish vertebra and large bivalve shells. Therefore, we focussed on the annual deposition of mudsnails and small bivalves (i.e. < 2 mm) which are considered to be the spat (= first-year juveniles). Most of the mudsnails retrieved from the sedimentcore belonged to the smallest sizeclass (250-400 μm), which are very young animals, or the one-but-largest sizeclass (1400-2000 μm), which are most probably animals of 1 year and older. The high shell-deposition rate of adult mudsnails around 1945 might have been caused by anoxia event during the summer of 1947 and/or be the result of high overall densities of this species in the western Wadden Sea. Trends in shell-deposition rates of bivalve spat are most probably strongly influenced by changes in hydrodynamics due to gradual shallowing of the Vlieter channel. High shell-deposition rates of bivalve spat around 1945 and 1952 are most probably part of the very high spatfall phenomenen of marine fauna all along the west European marine waters during the summers of 1947 and 1952. High deposition of large Cockles around 1964 was most probably the result of mass mortality, a phenomenen observed for a suite of marine faunal species in west European waters during the very cold winter of 1962/'63 or due to a phytoplankton bloom causing anoxia in 1964.

3 DISCUSSION & CONCLUSIONS

The aim of this project was to examine possible relationships between environmental factors and time series of different characteristics (e.g. abundance, species composition, production) of marine living resources. Hereby, we assumed that the effects of environmental factors on the marine ecoystem were that strong and direct that they would result in clear signal in the characteristic studied. This assumption proved to be only true under particular circumstances (see above). In most cases, however, we found that if there was even an effect of the environmental factor its signal was probably lost in the signals of a suite of other external and internal factors or not detected due to limitations in the techniques and in the data. We distinguished the following complicating factors that interfere with correlation analysis of time series on enviromental factors and biological variables:

- **Spurious correlations** – Caution is needed when correlating different time series for analysis of causality. If the data consist of factors related to each other by complex mechanisms the interpretation may be difficult even if strong correlation would exist. For instance, in the Baltic Sea changes in the winter nutrient reserves potentially causes changes in the input of organic material to benthic communities but this relationship is obviously modified by weather during the spring bloom period, affecting the duration and probably also the species composition of phytoplankton. Thus the sedimentation may alter in quality and quantity despite increasing nutrient concentrations. Obviously, long-term data on sedimentation or pelagic production should be used but do not exist or are too scarce to be used.
- **Non-linear relationships** – The climate variables, such as circulation indices, e.g. the NAO index are often normally distributed, whereas biological variables, such as zooplankton populations, follow logarithmic-type distributions. Linear statistical models cannot describe a relationship between both types of variables. Therefore, a nonlinear transformation of the biological time series is often mandatory. The nature of this transformation is empirical, and the danger of falsifying observed data and increasing the error of the parameter estimation may be high.
- **Extreme values** – The influence of climate on the ecosystem level became most clear or even just detectable when studying episodes of extreme climatic events, in particular in the case of non-linear responses of stocks to environmental factors. For example, enhanced mortality may only occur at temperatures lower or higher than lethal thresholds. In general, west European marine ecosystems appear to be strongly influenced by severe winters. Zooplankton, zoobenthos and even fish may die off, supplying the opportunity for others (recruits of the same species or other individuals of other species) to take over. Under such circumstances, e.g. the very low temperatures at the end of the 1970's, this influence appears to overrule other (internal) factors in the ecosystem. The analysis of such effects is hampered by the low frequency of appearance of the extreme events themselves, e.g. during the entire study period (1965-1997) only a few strong inflows into the Baltic Sea occurred, leading to a low representativity of the data available.
- **Coinciding and synergistic effects** – All time series that we studied were derived from actual marine ecosystems and not produced under experimental conditions. This implies that several environmental factors may have changed at the same time, i.e. coinciding effects. For instance, the same climatic forcing may have competing effects on the environmental variables and at the ecosystem level. For instance, it was found that the strength of the NAO index (westerly winds) may cause stronger inflow from the North Sea water into the Baltic Sea, but at the same time salinity is reduced due to increased rainfall in the Baltic Sea catchment area. Which mechanism is more important depends in this case on the time-scale considered. At the ecosystem level, milder winter water temperatures associated to a stronger NAO may support a stronger growth of certain zooplankton species, but may also favour a predator species, giving rise to a decrease of the prey species. In the North Sea, similar increasing trends in temperature and fishing effort were observed over the past thirty years during which the biota were sampled. Even at a much smaller spatial scale different but coinciding temporal patterns of temperature and fishing effort were observed in the areas in- versus outside the plaice box which considerably complicated the formal distinction of the relative contribution of each factor to the observed changes. In addition, the total effect of coinciding factors may even be more than the sum of the single effects. In other words, the combination of the effects may give an additional effect too (statistically examined by testing the significance of an interaction effect).
- **Spatial-temporal interactions** – The significant interaction effects of space (roundfish areas) and time (year) on the biomass of North Sea fish may point at synergistic effects, i.e. seasonal variation in environmental conditions has significantly more effect on fish biomass under some (local) conditions than under others. At first it was concluded that the existence of a spatial-temporal interaction indicates that before and after the closing of the plaice box the composition of the (fish or benthic) community in- and outside the box area changed differently

and this was originally attributed to reflect an effect of fisheries. However, the existence of significant space-time interactions within non-protected areas of the North Sea (roundfish areas) confirms that small-scale spatial differences exist irrespective of any of our known external forces.

- **Limits to data series** – Length of data series is crucial, especially for studying the relationship between climate and variability in biological communities. Changes in the communites can take place as slowly progressing trends or sudden changes, switching in function of the communities. For the Gulf of Finland, a rapid collapse of the communities was observed by including 1996-97 in the data which well demonstrated the effects of the stratification changes. Otherwise the recent development would have been concurrent with the trends in nutrients, indicating the eutrophication of the area. Also the initial conclusion (based on a 1985-1994 dataset) that the introduction of the plaice box affected the fish community in a rather straightforward manner with an increase of abundance of the larger fish in the box area where fishing effort decreased was refuted when a longer dataset (1985-1998) became available.
- **Limits to biological knowledge** – Examined relationships between environmental factors and ecosystem dynamics describe at best what happened during the study period. Making predictions based on these relationships assumes that the behavior and population dynamics of the species involved is fully understood and that these characteristics do not change in the future. Both assumptions are not true. First, we hardly understand the complexity within marine ecosystems. Second, species evolve and subsequently changing their characteristics continuously.

We, therefore, conclude that marine organisms show complex responses to external factors such as climatic events, which has proven to make correlation analysis often very difficult or even impossible. We found that at the one hand, external factors may affect the state of the ecosystem, whilst at the other hand it is the state of the system which determines the actual effect of the particular factor. This is probably one of the main reasons that we often observed significant spatial-temporal interactions when examining the covariance within time series of different locations throughout north-western European marine ecosystems.

ABSTRACTS

ENGLISH SUMMARY

The variability of marine ecosystems in the North and Baltic Sea is driven by internal and external factors, which in turn may be natural (e.g. climatic) or anthropogenic (e.g. eutrophication, anthropogenic climate change). The analysis of variations in the abundance and life history parameters (e.g. mortality, recruitment) of marine plants and animals may reveal key-factors that govern these systems. More insight in the dynamics of the structuring factors and processes within marine ecosystems is not only necessary for a better understanding of the variability within these communities, but can also be considered as base-line studies for prediction of effects of management of these communities. The research focussed on long-term dynamics of environmental factors (salinity, oxygen and nutrients) and organisms (phytoplankton, zooplankton, macrozoobenthos and fish) within marine ecoystems of northwestern Europe, viz. the Baltic Sea, the North Sea (in particular the German Bight and the shallow areas along the northwestern coasts) and the Wadden Sea. Different methods of research have been used. We applied statistical analysis of cross-correlationships in the existing time series of the last decades. We designed and tested several statistical models, describing the observed relationships between the atmospheric circulation and hydrographic variables and analyzed the output of climate change simulations with global climate models. We performed new measuring field campaigns to raise data in the last years and we retrieved historical data describing past variations from sediment cores and analysis of large-scale field experiments.

Several relationships between the external climatic forces and the biota could be established. The climate was observed to affect the hydrography, which in turn affected the macrofauna in the Baltic and North Sea and the fish community in the North Sea. The link between climate forcing and salinity was established in the German Bight and in the Baltic Sea. In both cases the atmospheric circulation drives changes in precipitation that affect salitinity. In the case of oxygen there exists also a statistical link to climate forcing but the ultimate physical mechanism could not be identified. Probably, biological and chemical process may play also an important role in the case of oxygen. The relationships between the North Atlantic Oscillation and zooplankton species in the North Sea seems to be statistically clear. In some cases, such as *Noctiluca scintillians*, the explained variance is high, but the mechanisms responsible probably involve the interaction with phytoplankton. For other species, such as *Temora longicornis*, the link is also detectable but the explained variance is low and the mechanisms for such a link could not be cleared up.

For macrozoobenthos in the coastal areas of the North Sea, including the tidal Wadden Sea, an increase in communities was observed in late 1970's, peaking in the middle 1980's. In addition a secondary maxima is obvious in the 1990's. Similar succession is evident for communities in the subhalocline areas of the Baltic Sea with only a slight difference in timing, a clear peak in the late 1970's and a more gradual increase again in the early 1990's, followed by a collapse after the middle of the 1990's in some areas. The observed increase in the North Sea benthic communities could be related to climatic factors causing stronger than normal westerly winds and mild winters with higher temperatures in the surface layer. In the Baltic Proper and Gulf of Finland area the variability in subhalocline macrozoobenthos was much related to the oxygen and salinity changes, setting limits for the species distribution and roughly half of the variability in these factors could be explained by a westerly climate pattern. Thus climate can at least partly explain the contemporaneous changes in the Baltic Sea. The rapid and temporary increase which in the late 1970's was caused by inflowing North Sea waters while in the 1990's it was a consequence of positive anomalies in the fresh water input with its positive effects on oxygen conditions. Both of these events can be connected to the same weather patterns (high NAO with westerly winds) which has affected also the North Sea area and thus give an example of a common forcing of the ecosystems by climate.

The water temperature affected the species composition of the North Sea fish community with regard to their bio-geographic origin. After a warm autumn the Lusitianian (southerly) species increased whereas the Boreal (northerly) species decreased. Also, the period of elevated fish biomass in the seventies that was observed in the North Sea coincides with observed changes in climatic, abiotic and biotic variables of the North Sea ecosystem (see Introduction). This confirms that in that period large-scale changes at various levels of the North Sea ecosystem were taking place, possibly triggered by a shift in the basic state of the atmosphere-ocean climate system. However, to what extent the subsequent decline in fish biomass in the early eighties followed by an increase towards a maximum in the nineties coincides with such variables remains unsolved.

Likewise anthropogenic factors such as eutrophication or fisheries were observed to have an impact on respectively plankton in the Wadden Sea or the fish community in the North Sea. In the western Wadden Sea, the coincidence of the shifts in relative nutrient concentrations and phytoplankton species composition implies a strong causal relationship between TN:TP ratio's and phytoplankton community structure. Amongst diatoms, the observed increase in phytoplankton biomass under eutrophic N-controlled conditions was particularly due to an increase of the abundance of larger algae. Our results indicate that the N-budget of the area is correlated with the community structure, suggesting enhanced loss of nitrogen to the sediment through increased deposition of larger algal cells, which may have affected the biomass and species composition of the macrozoobenthos in the western Wadden Sea.

The human impact on the fish community was revealed by two progressive trends in the fish community that can be attributed to the effect of fisheries. First a progressive decrease in the biomass of large fish was observed that was caused by the size-selective mortality induced by fisheries. This in turn affected the species composition through differences in the species' life-history characteristics. The trend observed was towards a community with less K-strategists (species adapted to stable environments) and more r-strategists (species adapted to unpredictable, disturbed environments).

Summarized, the results of these lines of research show a broad spectrum. In general, it could be said that the source of variability could be better identified at the physical or chemical level at large-spatial scales. The relationships between climate forcing and hydrography, or between eutrophication and nutrient in the Wadden Sea proved reasonably. But the analysis gets increasingly more complicated at the biological and ecosystem level. The amount of variance explained by factors external to the system also decreases with the internal complexity and reducing spatial scale. The explanation of observed past variability in plankton or fish populations in terms of simple external forcing becomes only possible for very large external influence (e.g. climate extreme events), whereas in normal situations the internal ecosystems dynamics and local environmental factors have to be invoked. In some cases the reaction of the ecosystem to external forcing is fairly different to what it could have been expected (e.g. fishing effort reduction and fish populations).

In conclusion, marine organisms show complex responses to external factors such as climatic events, which has proven to make correlation analysis often very difficult or even impossible. We found that at the one hand, external factors may affect the state of the ecosystem, whilst at the other hand it is the state of the system which determines the actual effect of the particular factor. This is probably one of the main reasons that we often observed significant spatial-temporal interactions when examining the covariance within time series of different locations throughout northwestern European marine ecosystems.

DEUTSCHE ZUSAMMENFASSUNG

Die Variabilität des marinen Ökosystems in der Nord- und Ostsee wird von internen und externen Faktoren getrieben, die entweder natürliche (z.B. klimatische) oder anthropogene (z.B. Eutrophokation, anthropogene Klimaänderungen) Ursachen haben können. Die Analyse von Variationen der Häufigkeit sowie lebengeschichtlicher Parameter (z.B. Mortalität, Rekrutment) mariner Pflanzen und Tiere kann Aufschluß über die wesentlichen Prozesse geben, die diese Systeme bestimmen und steuern. Verbesserte Einsicht in die Dynamik strukturierender Faktoren und Prozesse innerhalb des marinen Ökosystems ist nicht nur für das bessere Verständnis der internen Variabilität innerhalb der Gemeinschaften wichtig, sondern kann auch als Grundlagenstudie für die Vorhersage von Effekten des Managements dieser Gemeinschaften betrachtet werden.
Die Forschung konzentrierte sich auf die langzeitliche Dynamik von Umweltfaktoren (Salzgehalt, Sauerstoff, Nährstoffe) und Organismen (Phytoplankton, Zooplankton, Macrozoobenthos und Fisch) innerhalb der marinen Ökosysteme Nordwesteuropas — der Ostsee, der Nordsee (hier insbesondere die Deutsche Bucht und die Flachwassergebiete entlang der nordfriesischen Küste sowie des Wattenmeeres. Verschiedene Forschungsansätze wurden verwendet. Kreuzkorrelationen in existierenden Zeitreihen der letzten Dekaden wurden untersucht. Verschiedene statistische Modelle, die die beobachteten Zusammenhänge zwischen atmosphärischer Zirkulation und hydrographischen Variablen sowie Ergebnissen von Klimaänderungssimulationen mit globalen Klimamodellen beschreiben, wurden entwickelt und getestet. Es wurden neue Feldmeßkampagnen zur Vergrößerung des Datenbestands der letzten Jahre, sowie eine Analyse der Daten durchgeführt. Historische Daten, die die vergangenen Variationen anhand von Sedimentbohrkernen beschreiben wurden reanalysiert.

Eine Reihe von Zusammenhängen zwischen klimatischen Faktoren und der Biota konnte gefunden werden. Es wurde beobachtet, daß das Klima die hydrographischen Bedingungen beeinflußt, welche wiederum die Macrofauna in der Nord- und Ostsee sowie die Fischpopulationen in der Nordsee beeinflussen. Ein Zusammenhang zwischen klimatischem Antrieb und Salzgehalt konnte für die Deutschen Bucht sowie für die Ostsee hergestellt werden. In beiden Fällen gehen Veränderungen der atmosphärischen Zirkulation mit Veränderungen im Niederschlag einher, die ihrerseits den Salzgehalt beeinflussen. Auch für Sauerstoff wurde ein statischer Zusammenhang mit der atmosphärischen Zirkulation gefunden. Der zugrunde liegende physikalische Mechanismus konnte jedoch nicht identifiziert werden. Für Sauerstoff spielen wahrscheinlich auch biologische und chemische Prozesse eine entscheiden Rolle. Dagegen scheint die statistische Beziehung zwischen der Nordatlantischen Oszillation und Zooplanktonspezien in der Nordsee klar zu sein. In einigen Fällen wie für *Noctiluca scintillians* ist die erklärte Varianz hoch, aber der zugrunde liegende Mechanismus involviert wahrscheinlich Wechselwirkungen mit dem Phytoplankton. Für andere Spezies wie *Temora longicornis* ist ebenfalls ein Zusammenhang auffindbar, jedoch ist die erklärte Varianz gering und die zugrundeliegenden Mechanismen für einen solchen Zusammenhang konnten nicht geklärt werden.

Für Macrozoobenthos in den Küstengebieten der Nordsee einschließlich der tidebeeinflußten Wattengebiete wurde ein Anstieg der Gemeinschaften in den späten siebziger Jahren beobachtet, der seinen Höhepunkt Mitte der achtziger Jahre fand. Außerdem ist in den neunziger Jahren ein sekundäres Maximum ersichtlich. Mit einem nur geringen Unterschied der genauen Zeitpunkte wird eine ähnliche Abfolge für Gemeinschaften in der Ostsee unterhalb der Halokline beobachtet, es existieren ein deutlicher Peak in den späten siebziger Jahren und ein allmählicher Anstieg wiederum in den neunziger Jahren gefolgt von einem plötzlichen Zusammenbruch in einigen Gebieten nach Mitte der neunziger Jahre. Der beobachtete Anstieg benthischer Gemeinschaften in der Nordsee konnte mit klimatischen Faktoren in Verbindung gebracht werden, die ein strengeres Westwindregime und mildere Winter mit höheren Temperaturen in den oberen Meeresschichten beschreiben. Im "Baltic Proper" und im Finnischen Meerbusen war die beobachtete Variabilität im subhaloklinen Macrozoobenthos größtenteils mit Veränderungen im Sauerstoff- und Salzgehalt verbunden, die Limitierungen für die Spezienverteilung darstellen. Ungefähr die Hälfte der Variabilität dieser Faktoren wird durch ein westliches Klimamuster erklärt. Folglich können klimatische Faktoren zumindest teilweise die gleichzeitigen Änderungen in der Ostsee beschreiben. In den späten siebziger Jahren wurde der schnelle Anstieg durch einströmendes Nordseewasser verursacht, während er in den neunziger Jahren das Resultat positiver Anomalien des Süßwasser Eintrags mit entsprechendem Einfluß auf das Sauerstoffregime war. Beide Ereignisse können mit demselben atmosphärischen Zirkulationsregime (hoher NAO Index mit westlichen Winden) in Zusammenhang gebracht werden. Dieses Zirkulationsregime hat ebenfalls die Nordsee beeinflußt und liefert somit ein Beispiel für einen gemeinsamen Antrieb beider ökosysteme durch klimatische Faktoren.

Die Wassertemperaturen der Nordsee wirkten sich auf die Spezienzusammensetzung der Fischgemeinschaft in der Nordsee bezüglich ihrer bio-geografischen Herkunft aus. Nach einem milden Herbst sank die Anzahl der borealen (nördlichen) Spezien wogegen die Anzahl der südlichen (Lusitianian) Spezien anstieg. Die Periode erhöhter Fischbiomasse in der Nordsee, die in den siebziger Jahren beobachtet wurde, fällt ebenfalls mit beobachteten änderungen in klimatischen, abiotischen und biotischen Variablen im Ökosystem der Nordsee zusammen (s. Einleitung). Das bestätigt, daß in diesen Perioden grosskalige Änderungen in verschiedenen Bereichen im Ökosystem Nordsee stattgefunden haben, die möglicherweise durch eine Änderung des Grundzustandes des atmosphärisch ozeanischen Systems ausgelöst wurden. Jedoch bleibt ungelöst, in welchem Umfang der anschließende Rückgang der Fischbiomasse in den frühen Achtzigern gefolgt von einem Maximum in den Neunzigern mit änderungen solcher Variablen zusammenfällt.

Es wurde beobachtet, daß anthropogene Faktoren wie Eutrophication oder Fischerei ebenfalls Auswirkungen auf das Plankton im Wattenmeer bzw. die Fischgemeinschaft in der Nordsee haben. Die Koinzidenz von Änderungen der relativen Nährstoffkonzentrationen im westlichen Wattenmeer und der Spezienzusammensetzung des Phytoplankton impliziert einen starken ursächlichen Zusammenhang zwischen TN:TP Verhältnissen und der Struktur der Phytoplanktongemeinschaft. Für die der Diatomeen rührt der beobachtete Anstieg der Phytoplanktonbiomasse unter N-kontrollierten Bedingungen teilweise von einem Anstieg der Häufigkeit größerer Algen her. Unsere Ergebnisse zeigen an, daß das Stickstoffbudget des Gebietes mit der Struktur der Gemeinschaft korreliert ist, was einen nahelegt. Letzteres könnte die Biomasse und Spezieszusammensetzung des Macrozoobenthos im westlichen Wattenmeer beeinflußt haben.

Der menschliche Einfluß auf die Fischbestände wurde durch zwei Trends der Fischbestände offenbart, die einen Effekt der Fischerei darstellen. Als erstes wurde eine fortschreitende Abnahme der Biomasse großer Fische beobachtet, die durch eine durch die Fischerei induzierte größenselektive Mortalität verursacht wurde. Dieses wiederum beeinflußte durch Unterschiede in den Charakteristika der Lebensgeschichten die Zusammensetzungen der Spezien. Der beobachtete Trend ging in Richtung einer Gemeinschaft mit weniger K- (Spezien, die an stabile Umweltbedingungen angepaßt sind) und mehr r-Strategen (Spezien, die an gestörte unvorhersagbare Umweltbedingungen angepaßt sind).

Zusammenfassend zeigen die Resultate dieser Forschungsrichtungen ein breites Spektrum. Allgemein kann gesagt werden, daß die Quelle der Variabilität auf physikalischem oder chemischem Niveau besser auf größeren räumlichen Skalen identifiziert werden kann. Die Zusammenhänge zwischen klimatischem Antrieb und Hydrographie oder zwischen Eutrophication und Nährstoffen im Wattenmeer erwiesen sich als sinnvoll. Auf biologischem oder ökosystem-Niveau jedoch erwies sich die Analyse als zunehmend kompliziert. Der Anteil der durch externe Faktoren erklärten Varianz sank mit zunehmender interner Komplexität und abnehmender räumlicher Skala. Die Erklärung beobachteter vergangener Variabilität in Fisch- oder Planktonpopulationen mittels einfacher Zusammenhänge mit dem externen Antrieb ist nur für extreme Ereignisse im Antrieb (z.B. klimatische Extremereignisse) möglich. Unter normalen Bedingungen müssen ebenfalls die interne Dynamik des Ökosystems und lokale Umweltfaktoren berüksichtigt werden. In einigen Fällen ist die Reaktion des Ökosystems auf externen Antrieb ziemlich verschieden von den erwarteten Reaktionen (z.B. zwischen der Milderung des Fangdrucks und Fischpopulationen).

Schlußfolgernd kann gesagt werden, daß marine Organismen komplexe Reaktionen auf externe Faktoren wie klimatische Ereignisse zeigen, wodurch sich gezeigt hat, daß die Korrelationsanalyse sich oftmals sehr schwierig gestaltet oder gar unmöglich ist. Wir fanden heraus, daß auf der einen Seite externe Faktoren den Zustand des Ökosystems beeinflussen können, während auf der anderen Seite es der Zustand des Systems ist, der den aktuellen Effekt oder einen speziellen Faktor bestimmt. Dieses ist wahrscheinlich einer der Hauptgründe dafür, daß oftmals signifikante zeitlich-räumliche Wechselwirkungen bei der Untersuchung der Kovarianz innerhalb von Zeitserien oder an verschiedenen Orten innerhalb des nordwestlichen europäischen marinen Ökosystems gefunden werden.

SUOMENKIELINEN YHTEENVETO

Meriekosysteemin vaihtelua Pohjanmerellä ja Itämerellä ohjaavat sisäiset ja ulkoiset tekijät, jotka ovat joko luonnollista alkuperää (esim. ilmastoon liittyviä) tai ihmisen aikaansaamia (esim. rehevöityminen ja ilmastonmuutos). Meriekosysteemiä sääteleviä avaintekijöitä voidaan selvittää analysoimalla merieliöiden runsauden vaihtelua ja elinkiertoon liittyviä tekijöitä (esim. kuolleisuus, lisääntyminen). Tarkempaa meriekosysteemin rakennetta muokkaavien tekijöiden ja prosessien tuntemusta tarvitaan paitsi havaitun vaihtelun ymmärtämiseksi myös perustaksi yhteisöjen hallintaan liittyville toimille. Tutkimuksessa keskityttiin sekä ympäristötekijöiden (meriveden suola- ja happipitoisuus, ravinteet) että eliöiden (kasvi- ja eläinplankton, makroskooppinen pohjaeläimistö ja kalat) pitkäaikaisdynamiikkaan luoteisen Euroopan meriekosysteemeissä. Tutkimusalueet sijaitsivat Itämerellä, Pohjanmerellä (erityisesti Saksanlahti ja matalat luoteisrannikon alueet) ja Wattimerellä. Tutkimuksessa analysoitiin sekä olemassa olevaa aineistoa että uutta, hankkeen aikana kerättyä materiaalia. Olemassa olevia viime vuosikymmenet kattavia aikasarjoja analysoitiin vertaamalla niitä keskenään tilastollisin menetelmini. Lisäksi kehitettiin ja testattiin useita tilastollisia malleja, jotka kuvaavat havaittuja ilmakehän ja hydrografiamuuttujien välisiä yhteyksiä. Globaalisten ilmastomallien avulla analysoitiin ilmastonmuutosta kuvaavien simulaatioiden tulosta. Havaintosarjoja täydennettin viime vuosien osalta kenttänäytteenotolla ja lisäksi otettiin sedimenttinäytteitä, joista tutkittiin historiallista vaihtelua. Myös laaja-alaisten kenttäkokeiden materiaalia käytettiin.

Tutkimuksessa havaittiin useita yhteyksiä eliöstön ja ilmastotekijöiden välillä. Ilmasto heijastui hydrografiaan, joka puolestaan vaikutti Itämeren ja Pohjanmeren makrofaunaan ja Pohjanmeren kalastoon. Ilmaston ja suolapitoisuuden välinen yhteys kyettiin osoittamaan Saksanlahdella ja Itämerellä. Kummassakin tapauksessa ilmasto vaikutti sadannan kautta suolaisuuteen. Happipitoisuuden ja ilmaston välillä havaittiin myös tilastollinen yhteys mutta fysikaalista mekanismia näiden kahden tekijän välillä ei kyetty varmentamaan. Biologisilla ja kemiallisilla prosesseilla on ilmeisesti myös merkittävä vaikutus happipitoisuuteen. Pohjoisen Atlantin oskillaation (NAO) ja Pohjanmeren planktonin välillä näyttää tilastollisesti olevan selvä yhteys. Eräissä tapauksissa, kuten *Noctiluca scintillans* –panssarisiimalevällä, ilmastotekijöillä selittyvän vaihtelun määrä on suuri, mutta mekanismiin liittynee myös vuorovaikutusta kasviplanktonin kanssa. Toisilla lajeilla (esim. *Temora longicornis* –hankajalkainen) yhteys ilmastotekijöihin oli havaittava mutta selittyvän vaihtelun määrä jäi alhaiseksi eikä varsinaista vaikutusmekanismia kyetty selvittämään.

Makroskooppisen pohjaläimistön havaitiin runsastuneen 1970-luvun lopulla ja olleen huipussaan 1980-luvun puolivälissä Pohjanmeren rannikkoalueilla, mukaanlukien Wattimeren vuorovesialue. Toinen maksimi on ilmeinen 1990-luvulla. Samantyyppinen kehitys tapahtui Itämeren halokliinin alapuolisissa pohjaeläinyhteisöissä, joskin ajoitus eroaa hieman: selvä huippu havaittiin 1970-luvun lopulla ja vähittäinen runsastuminen alkoi jälleen 1990-luvun alussa. Tätä seurasi kuitenkin eräillä alueilla romahdus vuosikymmenen puolivälissä. Pohjanmerellä tapahtunut pohjayhteisöjen runsastuminen voitiin liittää ilmastotekijöihin, jotka aiheuttivat normaalia voimakkaampia länsituulia ja lauhoja talvia. Tällöin pintavedet olivat lämpimämpiä kuin normaalisti. Varsinaisen Itämeren ja Suomenlahden halokliinin alapuolisten pohjaeläinyhteisöjen vaihtelu oli paljolti yhteydessä happipitoisuuden ja suolaisuuden muutoksiin, joka rajoittivat lajien levinneisyyttä ja runsautta. Noin puolet happi- ja suolapitoisuuden vaihtelusta voitiin selittää läntisellä säätyypillä. Siten ilmastolliset tekijät ainakin osittain selittävät Itämeren pohjaeläimistössä tapahtuneita samanaikaisia muutoksia. 1970-luvun puolivälin nopea mutta lyhytaikainen pohjaeläimistön runsastuminen Itämerellä johtui voimakkaiden suolavesipulssien vaikutuksista, kun taas 1990-luvulla se oli seurausta normaalia suuremmasta makean veden tulosta Itämereen ja sen positiivisesta vaikutuksesta veden happitilanteeseen. Molemmat taphtumat voidaan liittää samaan ilmastotyyppiin, voimakkaaseen pohjoisen Atlantin oskillaatioon ja länsituuliin, joilla on ollut vaikutuksia myös Pohjanmeren alueella. Tämä toimii siten esimerkkinä ekosysteemien yhteisestä ilmastollisesta säätelymekanismista.

Meriveden lämpötila vaikutti Pohjanmeren kalaston lajikoostumukseen eri lajien eliömaantieteellisen alkuperän kautta. Lämpimän syksyn jälkeen eteläistä (lusitaanista) alkuperää olevat lajit runsastuivat ja samalla pohjoiset (boreaaliset) lajit taantuivat. Pohjanmerellä 1970-luvulla havaittu kohonnut kalojen biomassa osui lisäksi yksiin ilmaston ja Pohjanmeren ekosysteemin muiden abioottisten sekä bioottisten tekijöiden muutoksen kanssa. Kyseiset laaja-alaiset muutokset Pohjanmeren ekosysteemin useilla eri tasoilla laukaisi mahdollisesti muutos ilmakehä-valtameri -vuorovaikutussysteemin perustilassa. On kuitenkin selvittämättä, missä määrin kalojen biomassan lasku 1980-luvulla ja kasvu jälleen huippuunsa 1990-luvulla liittyvät em. tekijöihin.

Myös ihmisen toiminnasta johtuvia seurauksia havaittiin, sekä rehevöitymisen vaikutuksina Wattimeren plantonyhteisöihin että kalastuksen vaikutuksina Pohjanmeren kalastoon. Yhtäaikaiset muutokset läntisellä Wattimerellä osoittavat voimakasta yhteyttä ravinnesuhteiden (TN:TP) ja kasviplanktonyhteisön lajikoostumuksen välillä. Havaittu kasviplanktonbiomassan kasvu rehevöityneessä, typpikontrolloidussa tilanteessa johtui piilevien osalta erityisesti suurikokoisten levien määrän lisääntymisestä. Tulokset indikoivat alueen typpibudjetin korreloivan yhteisöjen rakenteen kanssa sekä mahdollisesti kasvanutta typen poistumaa sedimenttiin suurikokoisten levien runsastumisen vuoksi. Tämä on edelleen saattanut vaikuttaa pohjaeläimistön biomassaan ja lajikoostumukseen Wattimerellä.

Ihmisen vaikutusta kalastoon osoitti kaksi trendiä, jotka voidaan liittää kalastuksen vaikutuksiin. Ensin havaittu

vähittäinen isokokoisten kalojen biomassan lasku johtui kalastuksen aiheuttamasta yksilökoosta riippuvasta kuolleisuudesta. Tämä vaikutti edelleen lajikoostumukseen lajien erilaisen elinkierron ja –tapojen kautta. K-strategistien (vakaaseen ympäristöön sopeutuneet lajit) osuus väheni ja r-strategistien (ennustamattomaan ja häiriytyneeseen ympäristöön sopeutuneet lajit) osuus kasvoi kalastossa.
Eri osatutkimusten tulosten kirjo oli varsin laaja. Yleisesti voidaan todeta, että havaitun vaihtelun lähteet oli helpompi määritellä fysikaalisella tai kemiallisella tasolla ja laajassa alueellisessa mittakaavassa. Ilmastollisen säätelyn ja hydrografian välinen suhde sekä Wattimeren rehevöitymisen ja ravinteiden yhteys kyettiin osoittamaan melko hyvin. Analyysi mutkistuu kuitenkin huomattavasti siirryttäessä biologiselle ja ekosysteemitasolle. Ulkoisten tekijöiden systeemin vaihtelusta selittämä osuus laskee myös sisäisen monimutkaisuuden myötä ja tilaskaalan pienetessä. Plankton- tai kalapopulaatioissa tapahtuneen vaihtelun selittäminen yksinkertaisen ulkoisen tekijän avulla on mahdollista vain hyvin voimakkaan vaikutuksen tapauksessa (esim. äärimmäiset ilmasto-olot). Normaalitilanteissa myös ekosysteemin sisäinen dynamiikka ja paikalliset ympäristötekijät on otettava huomioon. Eräissä tapauksissa ekosysteemin vaste ulkoiseen pakotteeseen voi olla jokseenkin erilainen kuin mitä on odotettu (esim. kalastuspaineen väheneminen ja kalapopulaatiot).

Yhteenvedettynä, merielöiden vasteet ulkoisille tekijöille (kuten ilmastollisille tapahtumille) ovat monimutkaisia, minkä vuoksi korrelaatioihin perustuva analyysi osoittautuu usein hyvin vaikeaksi, jollei mahdottomaksi. Tulosten perusteella voidaan todeta, että ulkoiset tekijät voivat vaikuttaa ekosysteemin tilaan, mutta toisaalta itse ekosysteemin tila saattaa määrätä millaiseksi jonkin ulkoisen tekijän vaikutus muodostuu. Tämä on luultavasti yksi pääsyistä siihen, miksi havaitsimme usein merkittäviä vuorovaikuksia ajan ja paikan suhteen tarkastellessamme eri alueiden aikasarjojen yhteisvaihtelua Luoteis-Euroopan meriekosysteemeissä.

NEDERLANDSE SAMENVATTING

Variatie in mariene ecoystemen zoals die van de Noordzee, de Waddenzee en de Oostzee wordt aangestuurd door interne en externe factoren, die zowel een natuurlijke (b.v. klimaat) als een menselijke (b.v. eutrofiëring en door de mens veroorzaakte veranderingen in het klimaat) oorsprong kunnen hebben. De analyse van de variaties in aantallen en "life-history" parameters (b.v. sterfte en reproductie) van mariene planten en dieren kunnen mogelijk de sleutelfactoren onthullen waardoor dit type systemen gestuurd worden. Meer inzicht in de dynamiek van deze structurerende factoren en processen draagt niet alleen bij tot een beter begrip van mariene systemen, maar kan ook beschouwd worden als basis informatie voor overheidsbeleid. Het onderzoek richtte zich met name op de lange-termijn dynamiek in omgevingsfactoren (zoutgehalte, zuurstof en nutriënten) en organismen (fytoplankton, zooplankton, macrozoobenthos en vis) van mariene systemen van noordwest Europa, d.w.z. de Oostzee, de Noordzee (met name de Duitse Bocht en de ondiepe kustgebieden ten noordwesten van het vasteland van Europa) en de Waddenzee. Voor het onderzoek naar de variatie in deze systemen zijn verschillende onderzoeksmethoden gehanteerd. Ten eerste is de aanwezigheid van kruiskorrelaties in bestaande tijdseries met een tijdspanne van decaden geanalyseerd. Verder zijn een aantal statistische modellen ontworpen en getest, welke de waargenomen relaties tussen de atmosferische circulatie en hydrografische variabelen beschrijven. Daarnaast is met behulp van klimaatmodellen gekeken naar de mogelijke gevolgen van klimaatsveranderingen. Naast de verwerking van de beschikbare tijdseries zijn een aantal aanvullende meetcampagnes uitgevoerd, historische gegevens verzameld en verwerkt, en de resultaten van grootschalige veldexperimenten geanalyseerd.

Uit dit onderzoek bleek dat in sommige gevallen de waargenomen veranderingen in de onderzochte systemen kunnen worden verklaard aan de hand van externe climatologische factoren. Zo kunnen veranderingen in het klimaat tot veranderingen in de hydrografie leiden, waardoor vervolgens verschuivingen in de zoobenthos- en visgemeenschappen van de Oostzee en Noordzee zijn opgetreden. Zowel in de Duitse Bocht als in de Oostzee bleek er een verband tussen het klimaat en het zoutgehalte van deze wateren te bestaan, veroorzaakt door veranderingen in de neerslag in deze gebieden. Ook de waargenomen schommelingen in het zuurstofgehalte bleken gecorreleerd te zijn met die in het klimaat, maar het verklarend mechanisme voor deze samenhang is vooralsnog onduidelijk. Waarschijnlijk liggen hier allerlei biologische en chemische processen in de gebieden zelf aan ten grondslag. Ook bleek er een statistisch verband te bestaan tussen de wisselingen in de NoordAtlantische Oscillatie index en het voorkomen van een aantal zooplankton soorten in de Noordzee. In sommige gevallen, zoals bij de soort *Noctiluca scintillians*, is de verklaarde variantie hoog en worden de aantalsfluctuaties waarschijnlijk veroorzaakt door klimaatgestuurde veranderingen in het fytoplankton. Voor andere soorten, zoals bij *Temora longicornis*, lijkt er wel een statisch verband te bestaan maar is de verklaarde variantie laag en kon het verklarend mechanisme niet gedetecteerd worden.

Zowel de aantallen als de biomassa van de macrozoobenthos gemeenschappen in de kustgebieden van de Noordzee, inclusief het intergetijdegebied van de Waddenzee, namen aan het eind van de zeventiger jaren toe en vertoonden pieken in de mid-tachtiger en in de negentiger jaren. Soortgelijke veranderingen werden waargenomen voor macrozoobenthos gemeenschappen in de Oostzee. Ook hier werd een piek in aantallen en biomassa aan het eind van de zeventiger jaren waargenomen, gevolgd door een geleidelijke toename in het begin van de negentiger jaren en, in sommige gebieden, een sterke achteruitgang in de mid-negentiger jaren. De waargenomen toename in Noordzee gemeenschappen zou mogelijk kunnnen samenhangen met bepaalde klimaatsomstandigheden zoals sterkere westelijke winden en zachte winters met hogere watertemperaturen. De veranderingen in het zoobenthos van de centrale Oostzee en de Golf van Finland staan onder sterke invloed van schommelingen in zuurstof- en zoutgehalten, welke op hun beurt weer bepaald worden door het klimaat. De snelle en tijdelijke toename in macrozoobenthos aan het eind van de zeventiger jaren werd veroorzaakt door een sterke aanvoer van Noordzee water, terwijl de de toename in de negentiger jaren het gevolg was van een bovengemiddelde zoetwater toevoer. Beide veranderingen leidden tot verbeterde zuurstofcondities in het water. Net als voor de Noordzee, vielen deze gebeurtenissen samen met eenzelfde weerspatroon, gekarakteriseerd door een hoge NAO index met overwegend westelijke winden. De veranderingen in soortensamenstelling van de visgemeenschap in de Noordzee bleken samen te hangen met schommelingen in de watertemperatuur. Een warme herfst leidde in het algemeen tot een toename van de zuidelijke (Lusitiane) en een afname van de noordelijke (Boreale) soorten. Tevens werd een periode met hoge visbiomassa aan het eind van de zeventiger jaren waargenomen, welke samenviel met waargenomen veranderingen in de andere onderzochte ecosystemen. Zulke gelijktijdige en grootschalige veranderingen lijken te wijzen op sterke sturing van mariene ecosystemen door het klimaat.

Naast de invloed van het klimaat op de mariene ecosystemen van west-Europa, zijn er sterke aanwijzingen dat deze systemen ook onder invloed staan van menselijke ingrijpen zoals eutrofiëring en visserij. In de westelijke Waddenzee konden de verschuivingen in de fytoplanktongemeenschap verklaard worden aan de hand van veranderingen in de TN:TP ratio's. De fytoplankton biomassa nam met name toe onder geëutrofieerde stikstof-gelimiteerde omstandigheden. Deze omstandigheden bleken met name gunstig voor de ontwikkeling van de grotere soorten diatomeeën. Tijdseries van nutriëntenbudgetten lieten zien dat de fluctuaties in het N-budget gecorreleerd waren met de ontwikkelingen in het fytoplankton, mogelijk als gevolg van een verhoogde sedimentatie en denitrificatie van de grotere algencellen.

Een aantal waargenomen veranderingen binnen de visgemeenschap van de Noordzee konden aan de visserij worden toegeschreven. De geleidelijke afname van de biomassa van de grotere vissen is waarschijn-

lijk veroorzaakt door de verhoogde mortaliteit van grotere vissen als gevolg van de visserij. Naast veranderingen in de grootte samenstelling leidde dit ook tot veranderingen in de "life-history" karakteristieken van de visgemeenschap. Met de verschuiving naar meer kleine vis, vond er tevens een verschuiving van vissen met een K-strategie (aangepast aan onveranderlijke systemen) naar soorten met een r-strategie (aangepast aan sterk veranderende en onvoorspelbare systemen) plaats.

Samengevat lieten de resultaten een breed spectrum van mogelijk sturende factoren van mariene ecosystemen zien. In het algemeen leidde het onderzoek tot de identificatie van een aantal externe sleutelfactoren op het gebied grootschalige veranderingen in de fysische en chemische eigenschappen van deze wateren. Zo konden een aantal duidelijke relaties tussen het klimaat en de hydrografie en tussen eutrofiëring en nutrientendynamiek beschreven worden. Maar de identificatie werd meer complex als het de biologische veranderingen betrof en naarmate de veranderingen op een kleinere ruimteschaal hadden plaatsgevonden. Externe sleutelfactoren kunnen alleen geïdentificeerd worden voor grootschalige veranderingen in plankton, zoobenthos en visgemeenschappen zoals extreme weersomstandigheden. Onder meer normale (weers-) omstandigheden spelen de interne dynamiek en de locale omstandigheden een grote rol bij de structurering van de levensgemeenschappen in mariene eosystemen. In sommige gevallen bleek de reactie van het systeem op externe aansturing ook geheel anders dan oorspronkelijk verwacht (b.v. in het geval van het effect van verlaging van de visserijdruk op vispopulaties).

Geconcludeerd wordt dat mariene organismen complexe reacties vertonen op veranderingen in hun omgeving zoals klimaatsveranderingen, waardoor correlatie analyse moeilijk zo niet onmogelijk is. Bovendien werd gevonden als een externe factor een invloed heeft op de toestand van het ecosysteem, dat met een verandering in de toestand van het systeem daarmee ook de gevoeligheid voor de invloed van een dergelijke factor verandert. Deze complicerende factor verklaart waarschijnlijk het feit dat we bij veel statistische analyses van tijdseries van verschillende locaties in de noordwest Europese mariene wateren significante ruimte-tijd interacties hebben gevonden.

1. INTRODUCTION

1.1 AIM OF THE RESEARCH

Physical and biological factors governing marine ecosystems are far from constant. Currents, tides and wind mix the ingredients of these waters, which originate from the ocean and rivers. In Western Europe, the water temperatures may vary between ice-covered –2°C during winter and more than 20 °C in warm summers. Within this ever-changing world, marine plants and animals survive and reproduce. During their lifetime, the marine organisms must not only deal with variations in their physical environment but also with variable densities of other organisms such as prey, competitors, predators and parasites. Furthermore, the marine systems are additionally influenced by human activities such as fishing, land reclamation, eutrophication and pollution, as well as other activities possibly resulting in climate change.

The processes that underline the observed variability in time and space within the marine communities are still hardly captured. The main objective of the DYNAMO (DYnamics through Natural and Anthropogenic causes of Marine Organisms) project was to improve our understanding of the observed dynamics of marine ecosystems by analyzing long-term data sets on environmental and ecological variables. The analysis of variations in the abundance and life history parameters (e.g. mortality, recruitment) of marine plants and animals may reveal key-factors that govern these systems. More insight in the dynamics of the structuring factors and processes within marine ecosystems is not only necessary for a better understanding of the variability within these communities, but can also be considered as base-line studies for prediction of effects of management measures of these communities. The research focussed on marine ecoystems of northwestern Europe, viz. the Baltic Sea, the North Sea proper and the Wadden Sea (Fig. 1.1.1).

In many cases, we wanted to unravel the nature and magnitude of ecosystem processes from available time series of marine organisms in space and time, even though the data were not collected for this purpose. This reasons for caution. Sampling procedures may not have been consistent or not optimally suited for estimating the total population size, organisms may have been misidentified, sampling locations may have been changed and analysis techniques may have been improved. We, therefore, spend much effort on the quality checks of the data applied. We hope that we succeeded in restricting ourselves to those scientific questions, which are thought that could be answered within the boundaries set by the data.

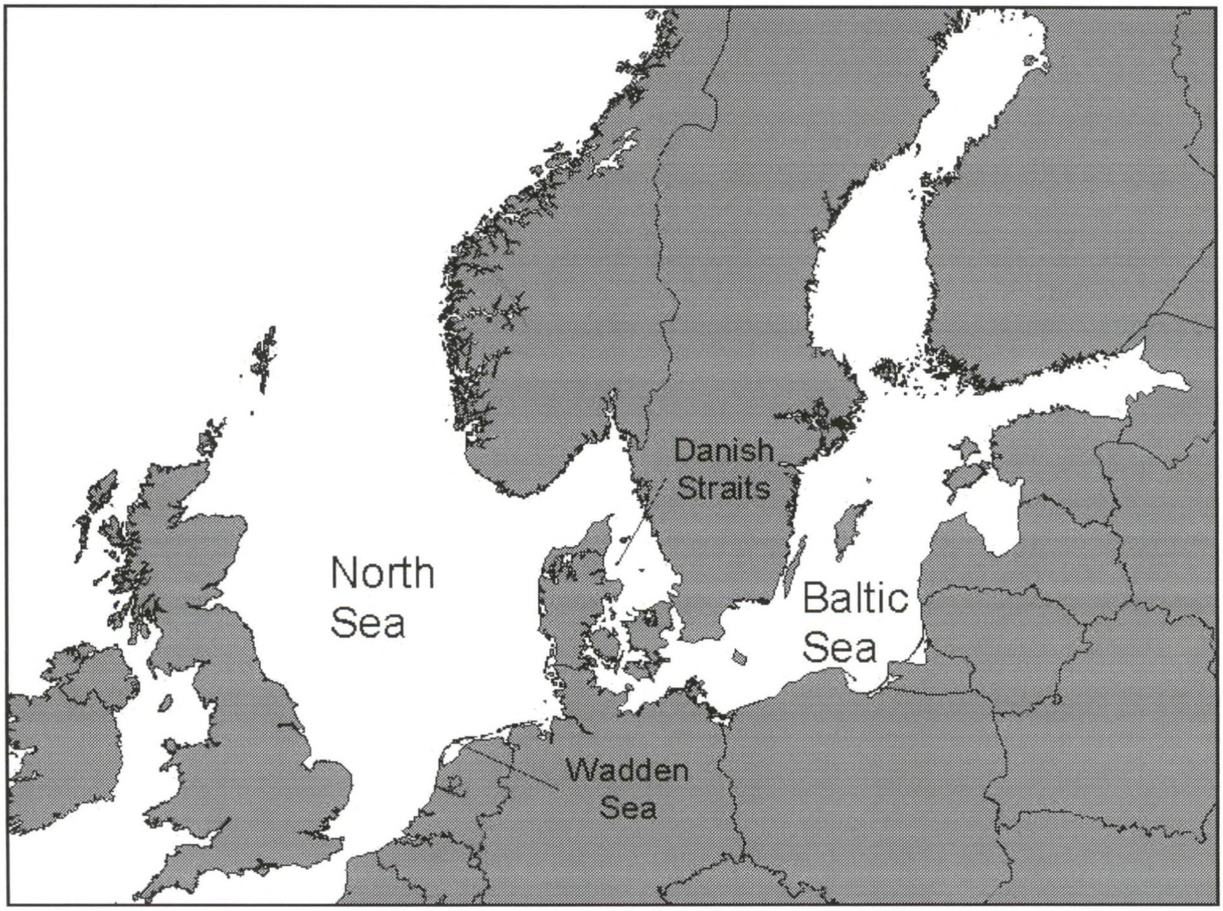

Fig. 1.1.1. Main long-term sampling locations of environmental variables (salinity, oxygen and nutrients) and marine organisms (phytoplankton, zooplankton, macrozoobenthos and fish) in northwestern European marine ecosystems as discussed in this report.

1.2 VARIABILITY WITHIN MARINE ECOSYSTEMS

1.2.1 HYDROGRAPHY

The North Sea (surface area 575,300 km^2) receives an input of oceanic water of about 55,000 km3 per year (Otto et al. 1990). Reid et al. (1992) hypothesized that the actual influx of oceanic water into the North Sea depends on acceleration of the circulation by north/south movement of the tracks of dominant weather systems. The residual currents of the North Sea are anti-clockwise and may be reinforced by dominant westerly winds when depressions have a northerly track. In years when depression tracks are further south, the general circulation and oceanic influx to the North Sea is likely to be reduced.

Wind stress is considered to influence the nutrient supply to North Sea waters by determining the influx of relatively nutrient-rich Atlantic water (Turrell 1992), and by resuspension of nutrients from the bottom (Harris et al. 1991). The influx of water from the Atlantic Ocean may have a severe impact on the North Sea food webs due to its varying amount and varying composition, in respect to nutrients, phytoplankton and zooplankton (Reid et al. 1992, Lindeboom et al. 1995). Aebischer et al. (1990) found parallel trends in westerly weather and four trophic levels of marine organisms. Since the residual current is responsible for the transport of material, its strength may determine the recruitment of fish species of which the larvae must be transported by this current from the spawning grounds to the nurseries (Corten 1990).

The strongest interdecadal change in Atlantic inflow was the entrance of a large cold water body with low salinity in the North Sea, the so-called Great Salinity Anomaly (GSA), between 1977 and 1978 (Dickson et al. 1988). This inflow more or less coincided with changes in abundance in phytoplankton, zooplankton, fish and breeding success of birds in the northern North Sea (Colebrook 1986, Daan et al. 1990), the southern North Sea (Hickel et al. 1994), and the Wadden Sea (Beukema 1991a, Cadée & Hegeman 1991, Swennen 1991).

Concerning more especifically the German Bight, hydrografical studies by Schott (1966) and Dickson (1971) revealed a connection between salinity variations in the North Sea and the atmospheric circulation. Though, both authors disagreed on the mechanism. Wile Schott (1966) found evidence that the surface salinities in the entire North Sea are dominated by large-scale atmospheric advection via precipitation, Dickson (1971) believes that advection of haline Atlantic waters is the main cause. Despite the fact that the German Bight is a coastal region with several estuaries, salinities 34.8 psu are observed occasionally, clearly indicating an inflow of Atlantic water through the English Channel (Kalle 1937, Deutsches Hydrographisches Institut 1984, Becker et al. 1992, Becker & Dooley 1995). Atlantic water entering the North Sea from the north mainly recirculates in the Dooley Current of north of the Doggerbank (e.g. Svendse et al. 1995) and therefore does not influence the German Bight.

The Baltic Sea is one of the worlds largest brackish water basin (surface area 373 000 km^2), which is characterized by low salinity and consequently a low number of species at all ecosystem levels when compared with oceanic or limnic environments. The Baltic Sea is a relatively cold sea, the northern parts being subarctic with a long ice season but the climate of the southern Baltic resembles more the North Sea area. The Baltic Sea is a semi-enclosed sea, which is connected to the North Sea by the shallow Danish Straits. The annual inflows of salt and fresh water are more or less balanced, and are estimated at 446-470 km3 (Voipio 1981, Kullenberg 1983). The fresh water input and the inflow of highly saline North Sea water into the Baltic Sea regulate salinity and the vertical stratification. Both the inflow of fresh and oceanic water is governed by meteorological factors, the latter being also affected by oceanography (Matthäus & Schinke 1994).

The inflow of North Sea water is irregular and major inflows classified as very strong and affecting the entire area in this century have taken place in 1913, 1921, 1951, 1969, 1976 and 1993 (Matthäus & Franck 1992, Matthäus & Schinke 1999). The stagnation between the major inflows causes oxygen depletion and formation of hydrogen sulfide in the deep basins and consequently deterioration of macrozoobenthos in the subhalocline area in the Baltic Proper and Gulf of Finland. The macrofauna rapidly recovers after the renewal of the bottom waters and increase of the oxygen content. The community structure of macrofauna exhibits long-term changes in respect to changes in hydrographical regime (Andersin et al. 1978a, Andersin & Sandler 1991, Laine et al. 1997).

Salinity and oxygen conditions in the Baltic Sea affects species distribution and biological productivity up to the fisheries level (e.g. Segerstråle 1969, Elmgren 1984, Nissling & Westin 1997, Flinkman et al. 1998). The conditions depend quite strongly on the water balance of the Baltic Sea, which is mainly regulated by the salt water inflow from the North Sea and by the fresh water run-off from the catchment area. The frequency of major inflows from the North Sea seems to have been decreasing in the last decades and some concerns have been raised that these changes may be associated to anthropogenic global climate change. If these concerns happen to be verified, the life conditions for biota in the Baltic Sea under a continued or increased intensity of global climate change may be altered by modifications in the hydrological regime.

The study within this project was focused on the relationship between the large-scale atmospheric circulation and salinity and oxygen in the Baltic Sea at multiyear and longer time scales. We tried to contribute to the understanding of the influence of the naturally occurring low-frequency changes of the atmospheric circulations on these two hydrographic variables, by trying to identify which are the first-order processes of atmospheric origin (e.g. major North Sea inflows, runoff, etc.) that may play a role. It has to be noted that other processes, specially for oxygen, may be also locally important. Once the relationships between environmental factors and biota are described, it becomes possible to estimate the effects of future environmental change on these biota.

Basic questions on hydrography were:

- *Is there a link between salinity in the German Bight and the large-scale atmospheric circulation?*
- *Is there a link between salinity and oxygen concentrations in the Baltic Sea and the large-scale atmospheric circulation?*

1.2.2 PLANKTON

In shallow coastal marine waters, the total primary production and biomass of phytoplankton is generally assumed to be hyperbolically related to nutrient loadings from land and subsequent availability of these nutrients in the water column (e.g. Borum & Sand-Jensen 1996). Understanding the effect of nutrient enrichment on living resources requires, however, detailed knowledge of how nutrients enter and leave these waters. Dissolved and particulate materials as well as living organisms are exchanged between the coastal waters and the open sea, and net material fluxes appear to depend on physical and biological responses within these systems to changes in nutrient loadings from land (e.g. Dame & Allen 1996).

Phytoplankton species obviously respond in different ways to nutrient enrichment, most probably depending on their specific life-history characteristics such as growth curves and storage capacities (Grover 1997, Roelke et al. 1997). Current theories on plankton ecology predict that a eutrophic and nitrogen-controlled environment gives rise to a dominance of large phytoplankton species (Stolte & Riegman 1995). Due to their larger storage capacity they are better competitors under high and fluctuating nutrient regimes (Sommer 1984, Stolte et al. 1994, Grover 1997), while the biomass of smaller algae is controlled by microzooplankton (Thingstad & Sakshaug 1990, Riegman et al. 1993). This will subsequently result in an enhanced flux of large phytoplankton species to benthic communities via sedimentation (Thingstad & Sakshaug 1990, Riegman et al. 1993), where part of the associated nutrients is buried or denitrified.

The fundamentals of eutrophication phenomena in coastal waters are best understood by including the effects of nutrient enrichment on all autotrophic components, i.e. phytoplankton, microphytobenthos, macroalgae and seagrasses. Nutrient enrichment in coastal waters is often accompanied by a shift from large slow-growing macrophytes to small fast-growing microalgae (Borum 1996; de Vries et al. 1996). Both in the field and the laboratory, eutrophication usually results in an increase in biomass of phytoplankton (Doering et al. 1989, Keller et al. 1990, Sullivan & Banzon 1990, Carlsson & Granéli 1993, Hofmann & Höfle 1993), microphytobenthos (Nilsson et al. 1991) and ephemeral macroalgae (Nilsson et al. 1991, Sfriso et al. 1989). Concurrent with these changes, the abundance of seagrasses and perennial macroalgae has been observed to decline (Borum 1983, Kautsky et al. 1986, Cambridge et al. 1986). The eutrophication-induced shift towards more phytoplankton biomass often coincides with an increase in pelagic primary production (Oviatt et al. 1986, Sampou and Oviatt 1991, Borum & Sand-Jensen 1996). However, although eutrophication may change the species composition of a marine vegetation drastically, the summed primary production by all autotrophic components was stated not to be affected (Borum & Sand-Jensen 1996). In many shallow coastal marine waters (mean depths of less than 40m), either phytoplankton or macrobenthic primary production (perennial macrophytes such as kelps and seagrasses) is high. Combined primary production rates, averaged across the entire ecosystem, appears to remain more or less constant within a broad range of nitrogen loadings (Borum & Sand-Jensen 1996).

In addition to nutrients, the interannual variability in marine plankton is often associated with climate variability. Aebischer et al. (1990) found parallels between the trends of "westerly weather" (Lamb 1972) and the abundance of phyto- and zooplankton. Taylor (1995) showed that a correlation exists between the Gulf Stream Index (GSI) and the abundance of zooplankton in the eastern Atlantic. Since the time lag is less than 1 month, the connection must be via the atmosphere. Fromentin & Planque (1996) correlated the abundance of 2 Calanus species to the North-Atlantic Oscillation Index (NAOI), which influences wind stress and temperature in Western Europe. Frid & Huliselan (1996) found high correlations between highly aggregated taxa (i.e. total copepods, plankton species composition, and total zooplankton) and the GSI. These correlations are hypothesized to be weather-induced effects on biological processes such as (i) alterations in the stratification of the surface layer that modify the spring phytoplankton bloom, (ii) variations in sea surface temperature, and (iii) changes in interspecific competition (Fromentin & Planque 1996). However, no clear knowledge about the driving climatic factor exists.

Basic questions on plankton dynamics were:

- *What was the impact of changes in nutrient loadings from land on other fluxes to and from the western Wadden Sea, i.e. exchange with the open sea, burial and denitrification?*
- *Was the shift towards eutrophic conditions accompanied by a shift in phytoplankton species composition, in particular towards larger species with relatively large storage capacity?*
- *How did different plant components (i.e. phytoplankton, microphytobenthos, macroalgae and seagrasses) respond to the nutrient enrichment?*
- *How can a relationship between interannual variability in plankton and climate be detected if the mechanism is not known?*

1.2.3 MACROBENTHOS

Marine soft-sediment community structures are the result of continuous selection pressures due to a combination of physical and chemical factors (e.g. temperature, salinity, oxygen, sediment characteristics, exposure and inundation) and biological factors (e.g. predation, parasites and competition). The selection pressures operate at different scales in time and space.

In the Baltic Sea, the low salinity values limit the distribution of both marine and limnic species and thus strongly reduce the number of species. Because of the characteristic water circulation mechanisms, approximately 100 000 km^2 of the Baltic Sea bed periodically have unfavorable oxygen conditions (< 2 ml l^{-1}) and are therefore temporarily devoid of macrobenthic organisms (e.g. Andersin 1978, Zmudzinski 1989, Olenin 1994, Laine et al. 1997). In general, much of the sub-halocline macrobenthos variability in the Baltic Sea can be related to the alteration between oxic and anoxic conditions in deep water. In areas where or during such periods when the physico-chemical environment is not strictly limiting, biological interactions are possible. Despite the low species number the interactions within the benthic communities can be complicated (Ankar 1977, Uitto & Sarvala 1990, Bonsdorff & Blomqvist 1993) and both inter- and intraspecific interactions has been demonstrated for many of the key-species (e.g. Leonardsson 1991, Hill 1992, Bonsdorff et al. 1995, Ejdung & Elmgren 1998). Food supply is obviously also controlling the communities (e.g. Lehtonen & Andersin 1998) and the general eutrophication is suggested to be responsible for the long-term increase of benthic biomass (Cederwall & Elmgren 1980).

Observed changes in North Sea and Wadden Sea macrobenthos were discussed in relation to environmental factors. For a suite of marine organisms, low temperatures were found to cause high mortality and/or enhanced recruitment (Ziegelmeier 1970, Beukema 1979, 1989, 1992, Dörjes et al. 1986). Sessile animals may be displaced by storm events (Rachor & Gerlach 1978). Eutrophication is considered to have an impact on both total biomass and benthic species composition (Beukema & Cadée 1986, Rosenberg et al. 1987, Rachor 1990). Pollution (Borchardt et al. 1988, Kersten & Krönke 1991) and fisheries (Lindeboom & de Groot 1998) may increase mortality or reduce reproduction. In addition, several studies have emphasized that the environmental effects may be synergistic (Rees & Eleftheriou 1989, Krönke 1995).

The main target species of beam trawl fishery in the North Sea are plaice and sole (Piet et al. 1998). Beam trawls are fitted with heavy tickler chains, which cause the target flatfish species to leave the bottom and be caught. Consequently, beam trawlers catch demersal fish as well as epifaunal and infaunal invertebrates (Creutzberg et al. 1987), i.e. those animals that live within the upper-layer of the sediment (approx. 5 cm). Investigations by means of experimental trawling showed that bottom fisheries increase the mortality of both target and by-catch species (Duineveld et al. 1987, Kaiser & Spencer 1996a). Benthic species that are not caught in the nets may still be damaged by the passing fishing gear (Bergman & Hup 1992, Eleftheriou & Robertson 1992, Bergman & Van Santbrink 1994, Thrush et al. 1995, Currie & Parry 1996). In 1989 a protected area in the south-eastern North Sea was established: "the "plaice box", resulting in a marked decrease of fishing effort.

Basic questions on macrobenthic dynamics were:

- *What is the connection between the long-term development of macrobenthic communities and the hydrographical events in the Baltic Sea?*
- *How much of the observed variation in the macrobenthic communities off Norderney can be attributed to the interannual variability of atmospheric pressure fields and the variability of the sea-surface temperature in the southern North Sea?*
- *Did the establishement of a protected area in the North Sea result in changes in the benthic invertebrate assemblage?*

1.2.4 FISH

Traditionally information of the ecology of fish stems from fisheries research focussing mainly on single species of few commercially exploited taxa. Only recently relatively long-term datasets from research vessel surveys became available allowing studies from a wider community perspective (Overholtz & Tyler 1985, Gabriel 1992, Solow 1994, Greenstreet & Hall 1996) and of specific non-target species (Heessen & Daan 1996, Heessen 1996). Three important community properties are the species composition, the size structure and the total biomass. In a fish community these properties are determined by variation in recruitment, mortality or distribution which can be affected by factors of natural (climate) or anthropogenic origin (fisheries, eutrophication, pollution, greenhouse effects).

Interannual variation in recruits may result from varying egg production (i.e. related to abundance and fecundity of adults as well as quality of spawning products) or from mortality induced by changes in biotic (food availability, predators) or abiotic variables (temperature, salinity) (e.g. Cushing 1995). Both aspects can vary from year to year and within the zoogeographic range of distribution, e.g. along a latitudinal gradient (Houde 1989, Miller et al. 1991). Temperature has been shown to have the potential to influence recruitment (Pauly 1994, Pauly & Pullin, 1988; Chambers et al. 1988, Victor 1986) and in temperate seas average water temperatures are lower at high latitudes. This results typically in longer development times for eggs and larvae which have been hypothesized to result in a greater dispersion and an incresed cumulative mortality (Chambers & Legget 1987). This could cause variation in recruit numbers to increase with increasing latitude (Miller et al. 1991, Van der Veer et. al. 1998). Also, for species for which a stock-recruitment relationship exists it can be hypothesized that recruitment variation increases in any direction away from the geographical centre of the species range. The combination of these two potential sources of variation, if active, is likely to result in low variation in recruit numbers near the geographical centre, high variation at the northern limits and intermediate variation near the southern limits of species distributions.

An important source of mortality in the fish community is that caused by fisheries. Fishing mortality of the most important commercial species in the North Sea was estimated at about 33% for plaice, 39% for sole and 45% for cod (Anonymous 1999a). Although the fishery only targets the large specimen of a relatively few commercial species there is a considerable by-catch of non-target species. An estimated 44% of the total fish catch consists of non-target species or undersized commercial species which are discarded (Van

Beek 1998). The effect of this additional mortality can be assessed by comparing areas that differ in fishing effort or, even better, areas where sudden changes in fishing effort have occurred. In the North Sea such changes were caused by the establishment in 1989 of a (semi) closed area: the "plaice box". At first it was only effective during the 2nd and 3rd quarter but in 1994 the box was extended to the 4th quarter and since 1995 the box was closed during the whole year. Although an exemption fleet of smaller beam trawl vessels ("Eurocutters" ≤ 300 Hp) was still allowed to fish in the box and fishing activities by the larger beam trawlers (>300 Hp) in notably the fourth quarter continued during the period 1989-1994 this resulted in a marked decrease of trawling intensity in the box area. Because most of the surplus effort was redirected to the area just outside the plaice box, fishing intensity probably increased in that area. This reallocation of fishing effort provided the opportunity to study the effect of fishing activities on the fish community.

Basic questions on fish dynamics were:

- *Did long-term changes in the species composition, size-structure or total biomass of the fish community occur and, if so, to what extent can these changes be attributed to human activities (i.e. fisheries) or natural causes (i.e. climate)?*
- *Does the interannual variation in fish recruit numbers increase with latitude or with distance from the centre of distribution?*
- *How much of the observed variation of the SST can be attributed to the interannual variability of the atmospheric pressure fields, and what can be the influence on the theoretical spawning time of fish?*

1.2.5 SEDIMENT CORES

Although many time series exist and were analysed during this project, a problem is that only a few of these series extend beyond two to three decades. This time span is too short to determine long-term variations of the marine ecosystem. Unravelling of the sedimentary record of faunal remnants may offer the possibility to create longer data series on the occurrence of different species. Hereto, the sediment cores have to be sampled at sites with high sedimentation rates of material (> 1 cm y^{-1}) in combination with only modest bioturbation phenomena.

The Vlieter channel, situated in the western part of the Dutch Wadden Sea, used to be one of the main drainage channels of the former Zuiderzee, a subtidal embayment nowadays called Lake IJsselmeer. The Zuiderzee was closed by the completion of the 'Afsluitdijk' barrier dam on May 28, 1932. The building of this dam resulted in the abandonment of the Vlieter channel. An abrupt change from an active channel into a hydraulically quiet area occurred, and current velocities dropped. As a result the rates and patterns of sedimentation in the area changed; a steady infill with fine-grained sediment came on top of coarser grained sand deposition in the active channel (Midderham & De Boer 1983, Berger et al. 1987). Nowadays the infill of the channel is completed and the Vlieter acts as part of the surrounding tidal flats. Faunal abundances in the sediment core may be indices of the abundance of those particular species for the entire study period, i.e. from 1932 to 1997.

The German Bight, a south-eastern part of the North Sea, is a relatively shallow area (19 m), with water temperatures varying between 4 °C in winter and more than 18 °C in summer (Lohse et al. 1995). The water column is generally well mixed throughout the year due to tidal stirring, and bottom water oxygen concentrations are close to saturation values (Slomp et al. 1997). Salinity stratification, however, occurs regurlarly due to large freshwater inputs from the Elbe/Weser river (Lohse et al. 1995). The average sedimentation rate in the inner German Bight is 0.5-1 cm y^{-1} (Eisma & Kalf 1987). In summer, large amounts of locally produced fresh organic matter are deposited (Joint & Pomroy 1993).

Basic questions related to the sediment cores were:

- *How much of the observed long-term variation of deposition of faunal remnants as derived from the sediment cores can be attributed to the interannual variability of faunal densities, thus reconstructing past changes in the commmunities?*

1.3 AUTHORS

This report, being the final report to the European Commission, is written as a joint effort by the subcontractors in the project "DYNAMO" (FAIR CT95.710). The writing was organized in such a way that one representative of each institute drafted chapters which were then read by the others. The information in the chapters is mainly based on the scientific publications that were written within the project by all members of the participating institutes.In this report, we included only those papers, reports and theses of which at least one of the authors was financed by the DYNAMO project (see Appendix).

Ari Laine (FIMR) drafted the chapters on macrobenthos. Katja Philippart (NIOZ) compiled the introduction and the chapters on plankton and sediment cores. Gerjan Piet (RIVO) drafted the chapters on fish and multivariate statistical tools. Eduardo Zorita (GKSS) drafted the chapters on climate and statistical downscaling. Several hypotheses that are addressed in these papers were postulated during the annual and special meetings of the project group during the last four years. The executive summary containing the main conclusions was drafted after discussing the results during the last final meeting of the project group in December 1999.

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2 MATERIAL AND METHODS

2.1 STATISTICAL ANALYSIS

2.1.1 MULTIVARIATE STATISTICAL TOOLS

For the analysis of the climatic, biological and environmental data several multivariate statistical tools were used. Mainly conventional methods based on eigentechniques such as (1) Principal Components Analysis (PCA), also known as Empirical Orthogonal Function (EOF) analysis or (2) Canonical Correlation Analysis (CCorA). But also new techniques were developed such as Restricted Gaussian Regression (RGR) or Restricted Generalised Additive Model (RGAM).

Principal Components Analysis (PCA)
PCA is widely used as a method to reduce the dimensionality of data sets, retaining only the variables or combination of variables that explain most part of the variability, but also as a method to identify the most important processes that are taking place in a data set, provided that these processes can be represented as linear relationships between the different variables. This technique has been mostly used in this project to identify basic structures of variations in, for instance, data sets of different fish species in the North Sea, zooplankton in the North Sea or salinity variations in the Baltic Sea. One of these basic structures can in principle reflect more clearly the influence of an external forcing, such as climatic factors, than the individual time series for each species which can be more strongly affected either by factors related to that particular species (reproduction dynamics, food availability, etc.).

Canonical Correlation Analysis (CCorA)
CCorA is also a linear multivariate method that identifies patterns or structures that tend to appear simultaneously in two different data sets. This techniques is suitable for analyzing the possible relationship that may exist between climatic factors and fish populations directly or between climate and hydrographic variables that may in turn affect the biological ecosystems, such as water temperature, salinity and dissolved oxygen.

Technically both methods are based on the linear assumption that the anomalies of a k-dimensional field, i.e. deviations from a normal state which is usually taken as the long-term mean, can be expanded by a sum of the type:

$$f(i,t) = \sum_{k-1}^{n} p^k(i) a^k(t)$$

where the *p*'s represent time-independent structures or loadings and a's denote the evolution of the amplitude of these structures. In the PC or EOF analysis these structures are defined in such a way that only a few of them can describe most part of the variability of the whole field, i.e. the residual term epsilon is as small as possible, and the information content present in the original data set can be compressed to a certain approximation by a few key indices. In observational data sets as the ones analyzed in this project the usual situation is that just five or less of these structures can describe of the order of 80% of the total variability. The advantage of such an expansion is obvious by considering that in that case just five time series convey almost all the information contained in a field that may consist of hundreds of measuring stations, or 20-30 different species. Furthermore, the structures p themselves indicate the variables (stations or species) that are more important for the dominant structures and the relationships among them.
Numerically the structures p are the result of an eigenvalue problem, in which the covariance or correlation matrix of the data sets is diagonalized, i.e. the leading PC's or EOF's are simply the eigenvectors of the covariance or correlation matrix corresponding to the highest eigenvalues.

Example of PCA or EOF – An example of a PCA or EOF analysis of a data set comprising time series of annual new recruits measured in October of 12 species in the North Sea (herring, twaite shad, cod, whiting, pollock, lumpsucker, scad, grey mullet, turbot, place, flounder and sole) from 1972 until 1992 is shown in Figure 2.1.1.1. It can been seen in figure 2.1.1.1 that about one third of the total variability can be described by a structure where species 1,3,6,7,11,12 evolve all of them in-phase, with species 2 (twaite shad) and 8 (grey mullet) evolving out-of-phase. The time evolution of the intensity of this structure (thick line in right panel of figure 2.1.1.1) shows a slow increase from the year 1972 to 1984 with rapid variations thereafter.

Biplot – A useful technique for representing the PCA results is the biplot. This was introduced by Gabriel (1971) and visualises and approximates elements of a matrix by representing its rows and columns in a low (two or three) dimensional space. The elements of the matrix can be inferred by using the inner product rule on the a's and p's (see Jolliffe (1986), Krzanowski (1988) and Ter Braak (1983) for examples).

The methodology for the Canonical Correlation Analysis (CCorA)is somewhat similar to that of PCA. The anomalies of two fields are decomposed in a sum:

$$f(i,t) = \sum_{k-1}^{n} p^k(i) a^k(t)$$

$$\theta(i,t) = \sum_{k-1}^{n} q^k(j) b^k(t)$$

where p_i and q_i are time independent patterns and a_i and b_i are time series that can be defined to have standard deviation equal to 1. The result of CCorA are time series $a_1(t)$ and $b_1(t)$ which show the highest correlation. The following pair $a_2(t)$ and $b_2(t)$ shows the highest correlation with the additional constraint that they are uncorrelated with $a_1(t)$ and $b_1(t)$, respectively. The patterns p_i and q_i are called the canonical patterns, the associated time series a_i (t) and $b_i(t)$ are the canonical

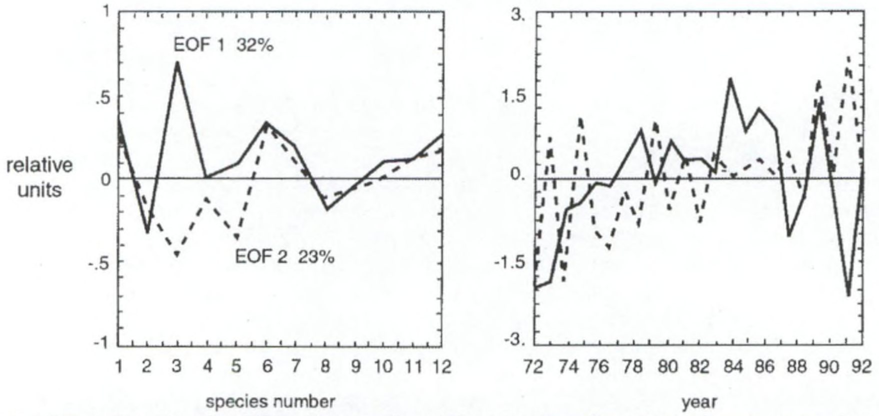


Fig. 2.1.1.1 The first two leading EOFs (left panel) and the corresponding principal components (right panel) of new annual recruits of 12 species in the North Sea in the period 1972-1992.

time series, and the correlation between them are called the canonical correlations. Therefore, in a linear approximation, the canonical patterns are the structures in both fields that are optimally coupled, in the sense that they are the ones that tend to appear either more strongly or more frequently at the same time.

Example of CCorA – An example of Canonical Correlation Analysis is shown in Chapter 2.1.2 and describes the relationship between sea-surface- temperature in the North Atlantic and annual juvenile abundance of fish species from different bio-geographic regions.

Innovative techniques – Various new dimension reduction techniques were developed in Zuur (1999). These techniques are applied on ecological data sets containing observed abundances of species, sampled at different sites, and monitored over time. Information is available on spatial and temporal environmental variables. The newly developed statistical techniques can be used as aids to answer the following questions:

- What are relationships between species abundances and spatial environmental variables?
- What are relationships between species?
- How do these species-environmental relations and species interactions change from year-to-year? What is the effect of global environmental variables on these year-to-year variations?

These questions dealt with in two separate ways. First, the time aspects were ignored and we focussed on the first question introducing techniques to analyse spatial data. Second, models were developed to analyse spatio-temporal data.

Spatial data

Data sets which are used to analyse spatio data are Balgzand data measured in 1995 (14 selected zoobenthic species monitored at 24 sites in an intertidal area), Baltic Sea data measured in 1996 (5 selected zoobenthic species monitored at 25 sites), DCS data of 1996 (14 selected zoobenthic species monitored at 25 sites in the Dutch Continental Shelf), and hunting spider data (12 wolfspider species captured in 28 pitfall traps in a dune area).

General characteristics of these data sets are: (i) there is no detailed prior knowledge of the ecological systems, (ii) the data contain many zero observations, and (iii) data are counts. Traditionally, ordination techniques such as principal component analysis (Jolliffe 1986), correspondence analysis (Gauch 1982), and canonical correspondence analysis (Ter Braak 1986) have been associated with such (spatial) data. See Birks et. al. (1994) for numerous references. Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) can be considered as state-of-the-art techniques in community ecology in the 80's respectively the 90's. The reason for this is that CA and CCA have an ecological rationale. This ecological rationale is based on the so-called Gaussian response model. This is a very simple model, used by Whitaker (1978), Gauche (1982) and many other authors, to describe unimodal behaviour of a single species along a gradient. Ter Braak (1985, 1986) showed that under certain conditions, results of CA and CCA, and estimated parameters of the Gaussian response model are approximately equal.

Two disadvantages of CCA are: (i) its ecological rationale is based on rather strong assumptions which are unlikely to hold for our data sets, and (ii) it is not designed to analyse spatio-temporal data. To deal with the first disadvantage, we introduce a new technique, called Restricted Gaussian Regression (RGR). RGR is a parametric equivalent of CCA. RGR uses the Gaussian response model with the additional restriction that the covariates in the model are restricted to be linear combinations of spatial environmental variables. The motivation for using such a dimension reduction on the environmental variables, is to reduce the number of parameters. Although formulation of RGR is not new by itself, the present solution of it is.

Example of RGR - A RGR model could have the following form:

$$\textit{abundance of species k at site i} = f_k\,(z_i)$$

where the function $f_k(z_i)$ describes the species-environmental relations (via the Gaussian response model) for species k containing unknown parameters, and z_i is a linear combination of the q environmental variables. In formula:

$$z_i = a_1 * X_1 \textit{ at site } i + \ldots. + a_5 X_q \textit{ at site } i$$

where X_1, .., X_q are explanatory variables and a_1,.. ,a_5 are unknown coefficients. Note that these coefficients have the same value for all species (Zuur 1999).

Because RGR is a regression problem, more tools are available for a model validation compared to the ordination technique CCA. Model validations for various data sets in Zuur (1999) indicate that the Gaussian response model is too simple for some of the species in the data sets. For that reason, we use Generalised Additive Modelling (GAM). GAM is a smoothing technique in which the observed abundances are modelled as a function of smoothing terms of the environmental variables. One disadvantage of GAM is that it results in a smoothing curve for each species and each environmental variable. All these smoothing curves have to be interpreted. In order to reduce the number of smoothing functions, a dimension reduction is applied on the environmental variables. Hence, we obtain a GAM model in which the argument of the smoothing terms are restricted to be linear combinations of environmental variables. We denote this new approach by restricted GAM, abbreviated as RGAM. The advantage of this approach is that we end up with less smoothing curves to interpret.

Example of GAM & RGAM – A GAM model could have the following form:

$$\textit{Abundance of species } k \textit{ at site } i = f_{k1}\ (X_1 \textit{ at site } i) + \ldots + f_{k5}\ (X_q \textit{ at site } i)$$

for all species k and sites i. The smoothing functions $f_{k1}, \ldots, f_{k5}$ are to be estimated from the data and can have any shape. A RGAM model for these data could have the following form:

$$\textit{Abundance of species } k \textit{ at site } i = f_k\ (z_i)$$

where z_i is a linear combination of the q environmental variables. In formula:

$$z_i = a_1 * X_1 \textit{ at site } i + \ldots + a_5 * X_q \textit{ at site } i$$

and $a_1, \ldots, a_q$ are unknown coefficients. Note that these coefficients have the same value for all species. The difference between RGR and RGAM is that in the first method the function f_k represents a regression model for each species k, while in RGAM it is a smoothing function.

The ordination, regression and smoothing techniques CA, CCA, RGR, GAM and RGAM analyse relations between species abundances and environmental variables. In all these techniques it is assumed that species behave independently of each other. This may not be the case due to for example prey-predator relations of species or competition for space (Beukema & Flach 1995). Violation of the independence assumption in regression models may result in estimated parameters which are unbiased but do not have minimum variance. To overcome this, feasible generalised least squares (Greene 1997) can be used. In feasible generalised least squares, the regression model is extended by modelling the covariance structure of the error term as well. This results in unbiased estimators with minimum variance Zuur (1999). Liang & Zeger (1986) extended FGLS to generalised linear models. The resulting technique is called generalised estimated equations (GEE). Because the Gaussian response model is basically a generalised linear model, we can easily combine the Gaussian response model and GEE. The advantage of doing this is that the parameters of the Gaussian response model estimated in a GEE context, are unbiased and have minimum variance. Additionally, a correlation matrix representing species interactions is estimated as well.

We combined RGR and GEE. Because model validations indicated that nonparametric models are better for some species in the data sets, we extend the GEE techniques to smoothing models. Wild & Yee (1996) combined GEE with GAM. They called it vector GAM. We follow the approach of Wild & Yee (1996), and model species abundances as a nonparametric function of environmental variables, and at the same time a correlation matrix representing species interactions is derived. Instead of vector GAM, we call the combination of GAM and GEE nonparametric GEE. We also combine RGAM and GEE. It results in a technique in which species-environmental relations are modelled by smoothing functions along a gradient. This gradient is a linear combination of spatial environmental variables. Additionally, a correlation matrix representing species interactions is estimated. This technique is called restricted nonparametric GEE.

Spatio-temporal data

When analyzing the spatial-temporal data, we follow two approaches. In the first approach, various ordination, regression and smoothing techniques used in when analyzing the spatial data are applied on observed abundances of each year of the two data sets. Changes over time in estimated gradients, parameters and smoothing curves are analysed. The disadvantage of this approach is that in estimating parameters or smoothing functions of data of year s, no information is used of data of year s-1 or s+1. To overcome this limitation, a dynamic GAM model was developed by Zuur (1999). In this technique, the average (over time) species-environmental relations are modelled by using a smoothing curve. Additionally, a trend over time is estimated. This trend represents the yearly deviations from the average species-environmental relations. This is done for each species. In Zuur (1999), a formulation for a stochastic trend model is presented. Estimation of this smoothing function, trend and unknown parameters is carried out within the framework of GAM, Kalman Filtering, Kalman Smoothing (Harvey 1989), and the EM-algorithm. One of the underlying assumptions of linear Kalman filtering and smoothing is normality of the data. Because we use count data, which are always equal or greater than zero, this assumption is inappropriate. For this reason, an extended form of Kalman filtering and smoothing is used. Technically, we developed a dynamic GAM model by combining GAM and Iteratively Reweighted Kalman Filtering and Smoothing (Fahrmeir & Tutz 1994). Finally, a dimension reduction on the spatial covariates in the dynamic GAM model was carried out as well.

2.1.2 STATISTICAL DOWNSCALING

General Circulation Models (GCMs)

GCMs are important tools in the study of climate variability and climate change. These models are state-of-the art numerical coupled models that represent several subsystems of the earth's climate (atmosphere, oceans, sea-ice, land surface processes, etc.) that are thought to be capable of simulating the large scale state of the climate. At global scales, GCMs are able to simulate reliably the most important mean features of the global climate, for instance the Intertropical Convergence Zones, the three dimensional atmospheric circulation cells, the jet streams, etc. With some limitations, they also simulate reasonably well essential features of the ocean circulation like the western boundary ocean currents and the conveyor belt driven by the thermohaline circulation. Some of the latest GCMs also produce atmosphere-ocean coupled variability in the Pacific basin similar to that linked to the El Niño -Southern Oscillation phenomenon.

With respect to the interannual variability, it has been found that some GCMs also reproduce satisfactorily the most important patterns of variability of the atmospheric flow and of the sea surface temperature at mid-latitudes. However, at finer spatial resolutions, with scales of a few grid distances, General Circulation Models have much smaller skill and their output cannot be directly used for climate impact studies. There are several reasons for the low skill of climate models at the regional and local scales. The spatial resolution provides an inadequate description of the structure of the earth's surface. The land-sea distribution is heavily smeared out and the mountains appear as broad flat hills, factors that can be very important for the right simulation of climate aspects in the North Sea and Baltic Sea.

Downscaling - The term downscaling denotes the methods that try to make use of the information provided by the climate models at large-scales to estimate climate changes at regional scales. The general strategy is to set-up transfer functions that link climate features at both scales. These functions may be very complicated, such as regional climate models nested in global climate models, or based in observed empirical relationships: essentially the idea of the statistical downscaling consists in using the observed relationships between the large-scale circulation and the local climates to set up statistical models that could translate anomalies of the large-scale flow into anomalies of some local climate variable.

An example of statistical downscaling can be found in Fig. 2.1.2.1. Time series of annual juveniles abundance of "warm" and "cold" species and sea-surface-temperature in the North Atlantic in summer were subject to Canonical Correspondence Analysis. The results indicate that colder than normal water temperatures are associated to a greater abundance of both types of group species. The reason for such a link is discussed in chapter 3.

Of course, an important assumption that underlies the statistical approach to climate impact assessment is that the link between the large-scale circulation and the local climate remains unchanged in an altered climate, which is by no means guaranteed. However, if the time series used to tune the statistical model are long enough (ideally of the order of several decades) it is reasonable to assume that they contain many different situations, including those that will be stronger or more probable in an altered climate. If these situations are important for the local climate, the statistical model should be able to identify them in the historical observations and estimate with some skill the probable impact on the local climate.

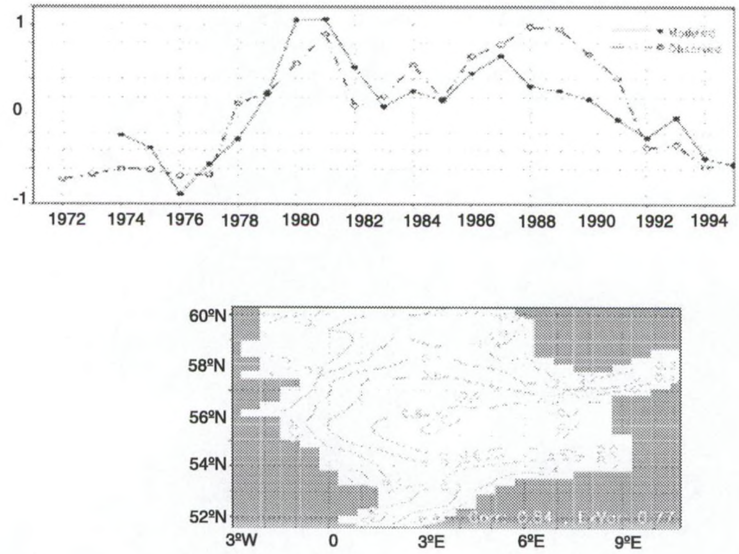


Fig. 2.1.2.1 The canonical time series (upper panel) between sea-surface-temperature in July and annual abundance of fish in the North Sea. The lower panel shows the canonical temperature structure. The fish time series describe the abundance of "southerly", "northerly" and neutral fish species. The canonical fish structure is positive for all three groups, indicating that cold North Sea water temperatures are associated with an increased abundance of all three groups of species.

This assertion is only valid if the range of variations of the large-scale variable in the new climate lies roughly within the natural variability of the present climate, which is the information used by the statistical model. However, the fact that the statistical model is able to reproduce reasonably the variability in the past increases the level of confidence in the model but does not strictly imply that it can be used for future conditions, since the statistical relationship may not hold any more. If the range of variations in the new climate is larger than the observed natural variability of the observed climate the estimation via statistical downscaling may still be useful but it should be considered with care.

Marine ecosystems

The statistical downscaling strategy has been applied to oceanic variables, such as sea-level in the Baltic Sea (Heyen et al. 1996), sea level along the Japanese coast (Cui et al. 1995) and Chinese coast (Cui & Zorita 1998), and salinity in the German Bight (Heyen et al. 1998). The general assumptions, problems and strategies of the statistical downscaling approach can be found, for instance, in Wilbey & Wigley (1997). In this project this strategy has been extended to biological variables, like fish population and zooplankton populations, bearing a priori in mind that such application is much more difficult, since ecosystems do not only react passively to external forcing (like the local climate to a very good approximation), but contain non-linear interactions that may mask the signal of the external forcing to a great extent. However, the application of downscaling methods to biology may give a first-order estimation of the possible impact of climate changes on the biological population. These problems are discussed in more detail in the following sections.

Linear models

Although there are several families of statistical downscaling methods, ranging from the linear models trough classification models, up to neural networks, in this project we have almost exclusively have made use of linear models. The identification of relationships between the large-scale climate and biology or even hydrographic variables that are affected by biochemical processes is already hindered by the complicated nature of the biological systems, so that the use of a technically obscure non-linear method could have been potentially more skillful in the mathematical representation of these relationships, but much more difficult to interpret conceptually. Even in the relatively simple case of the link between the North Atlantic Oscillation and salinity and oxygen concentration in the Baltic Sea (see section 3.1) there exists several interpretation of the results of linear methods.

2.2 VARIABILITY WITHIN MARINE ECOSYSTEMS

2.2.1 HYDROGRAPHY

Long-term data on salinity and oxygen concentration in the Baltic Sea have been compiled from data bases at the Finnish Institute of Marine Research and the Swedish Metereological and Hydrological Institute. At each station measurements were taken typically every 10 meters in the upper 100 meters and every 25 meters below 100 meters. The measurements are not uniformly distributed in time and the sampling frequency is about one measurement per month in the summer half year and less or no measurements in the winter months. Concentrations of hydrogen sulphide H_2S were not considered as equivalent negative oxygen concentrations, i.e. the minimum oxygen concentration is zero.

The data set previous to 1962 is considered to be too sparse for the statistical analysis, and therefore mainly data from 1962 to 1996 have been used in the present study. Due to the scarcity of the measurements and the focus of this study the salinity and oxygen data were annually averaged, so that only the low frequency relationships between both variables and with the atmospheric circulation has been considered.

Since the levels of variability of the salinity and oxygen time series varies horizontally and vertically the time series were normalized to unit standard deviation to avoid that the statistical analysis (Empirical Orthogonal Functions or Canonical Correlation Analysis, see following sections) are dominated by a few stations or levels with high variability.

Monthly mean surface values from 9 light vessels and the island of Helgoland are used (data from Bundesanstalt für Seeschifffahrt und Hydrographie, BSH, Hamburg). Salinity was measured with interruptions between 1908 and 1995. During this period, most light vessels were relocated several times, leading to inconsistencies in the records. A homogenization is difficult, since the relocations were often only a few months apart, making it impossible to check whether they led to changes in the observed mean or standard deviation.

To find a statistical relationship between climate and salinity in te German Bight, only the light vessels LV Borkumriff, LV Weser, LV Elbe1 and LV P11/P8 were used. The first three were selected because they possess the longest observational records, the latter was included to obtain a more regular spatial distribution of stations. The records of these 4 vessels contain the following obvious inhomogeneities:

- Pre-war salinity observations at LV Borkumriff are about 0.5psu (which corresponds to aprox. 1 standard deviation at that station) higher than post-war observations. The reason is the relocation in March 1954, 20km eastward from its pre-war position.
- In 1972 the observed mean salinity at LV P11/P8 increases by about 0.9psu (1.2 standard deviations) while the standard deviation itself decreases by about 25 %. Simultaneously LV P11/P8 was moved 50km westward.
- At LV Elbe1 the observed pre-war salinity mean is about 0.5psu (0.5 standard deviation) lower than the post-war one. LV Elbe1 was withdawn in August 1939 and reestablished in August 1945 3km southwest from its pre-war position. Relocations within the same distance took place 7 times between 1924 and 1988, but the discrepancy between pre- and post-war salinity levels is the only obvious inhomogeneity in the time series of LV Elbe1.

2.2.2 PLANKTON

Western Wadden Sea

Phytoplankton dynamics

Bucket water samples were collected at high water from the so-called NIOZ jetty, which is located at the northern shore of the Marsdiep,the western most tidal inlet of the Wadden Sea (Fig. 2.2.2.1), between 1974 and 1994. Sampling frequency varied from once to twice a month in winter up to twice a week during phytoplankton spring blooms. For biomass (expressed as chlorophyll-a) measurements, 0.5 to 1 l water samples were filtered over $MgCO_3$ coated filters (Whatman GF/C); acetone extracts were measured following Lorenzen (1967). Chlorophyll-a concentrations (mg m^{-3}) were averaged for every month from 1974 to 1994 (Philippart et al. 2000). Most algae were identified to the species level; the others were clustered into larger groups. G.C. Cadée performed all identifications and counts of the algae during the entire study period, based on Drebes (1974) and Tomas & Hasle (1997). Statistical analysis of changes in the phytoplankton covered the 32 most numerous marine algal taxa (Table 2.2.2.1), which together contributed more than 99.9% to the total numbers of marine algae in the Marsdiep between 1974 and 1994.

In order to account for the seasonality in limiting resources, viz. light during winter and nutrients during summer, multivariate analyses of phytoplankton species composition were performed separately for six different two-monthly periods. The average interannual covariability between algal species (i.e. coexistence) was examined by means of Principal Component Analysis (PCA) that was performed on the correlation matrices of species abundances by means of SYSTAT (Wilkinson 1988). Data on algae densities were logarithmically transformed and standardised to mean 0 and variance 1 for each species before analysis. As the result of standardisation, all algal species had a similar weight. The results of the PCA were visualised in biplots showing the correlations between each pair of species (Gabriel 1971).

The total cell volume (biovolume) of the phytoplankton community was then calculated as the sum of individual cell volumes of all species present. The species-specific cell volumes were derived from lists supplied by Urban Tillmann (Research and Technology Centre Westcoast, University of Kiel, Germany), that were based on taxa-specific allometric formulae derived and adjusted from Rick (1990) and Edler (1979). Total vacuole volume is considered to be an index of the ability of diatoms to store inorganic nitrogen (Dortch et al. 1985, Stolte et al. 1994). This volume was calculated as the sum of individual vacuole volumes of all diatoms present derived from their total cell volume according to Stolte & Riegman (1996). To compensate for coinciding changes in total phytoplankton biomass, we divided the total vacuole volume by ambient chlorophyll concentrations. Since we have no actual data on the intracellular nitrate pools for the western Wadden Sea, we assesed their magnitude on the basis of available data from other coastal marine waters (Dortch et al. 1985, Petterson 1991).

Primary production

Production estimates – Estimates of total, pelagic and benthic primary production rates (gC m^{-2} y^{-1}) were based on nitrogen loadings (mol N m^{-2} y^{-1}) according to the empirical relationships described by Borum and Sand-Jensen (1996) for shallow marine coastal waters. The nutrient loadings were calculated by multiplying water-transport rates with corresponding nutrient concentrations. Data on transport rates and concentrations were taken from the water-quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public

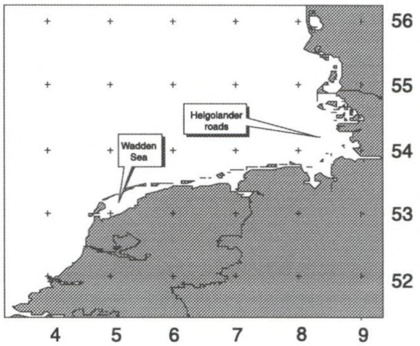


Fig. 2.2.2.1. Location of sampling areas of phytoplankton (Marsdiep tidal inlet) and zooplankton (Helgolander Roads).

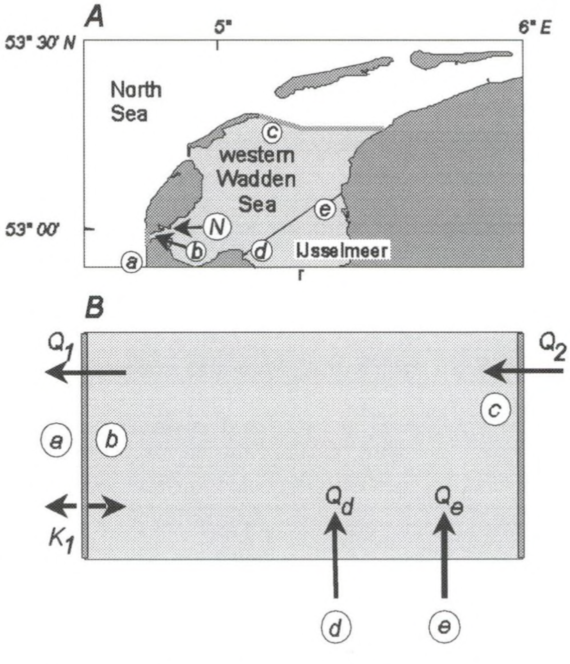


Fig. 2.2.2.2. **A** Geographical map of the Western Wadden Sea with locations of the phytoplankton sampling station in the Marsdiep tidal inlet (Station N) and the nutrient sampling stations in the North Sea (Station *a*), the western Wadden Sea **B** (Stations *b* & *c*) and near the sluices in the dam that closes off the man-made freshwater-lake IJsselmeer from the Wadden Sea (Stations *d* & *e*). One-compartment representation of the western Wadden Sea. Solid arrows represent tidally-averaged advective water transport (Q_1,Q_2) and bi-monthly averaged major freshwater inputs (Q_d,Q_e), the dashed arrow (K_1) represents the dispersive exchange with the North Sea (Ridderinkhof et al. 1990).

TABLE 2.2.2.1

Taxon code as used in biplots and scientific name of the 32 most numerous marine phytoplankton species or groups of species in the Marsdiep tidal inlet between 1974 and 1994 (Philippart et al. 2000)

Code	Taxon
	FLAGELLATES
FLAGL	large Flagellates spp.
FLAGS	small Flagellates spp.
GYROS	*Gyrodinium* spp.
PHAES	*Phaeocystis* spp. (mainly *P. globosa*)
RHODS	*Rhodomonas* spp.
	DIATOMS
ASTEG	*Asterionellopsis glacialis*
ASTEK	*Asterionella kariana*
BROCB	*Brockmanniella brockmannii*
CERAP	*Cerataulina pelagica*
CERAPE	*Cerataulina pelagica* var. *elongata* [b]
CHAEL	large *Chaetoceros* spp.
CHAES	small *Chaetoceros* spp. (mainly *C. socialis*)
CYLIC	*Cylindrotheca closterium*
CYMAB	*Cymatosira belgica*
DYTIB	*Ditylum brightwellii*
EUCAZ	*Eucampia zodiacus*
GAILS	*Gaillonella sulcata*
GUIND	*Guinardia delicatula*
LAUDA	*Lauderia annulata*
LEPTD	*Leptocylindrus danicus*
LEPTM	*Leptocylindrus minimus*
NITZL	*Nitzschia longissima*
ODONA	*Odontella aurita*
PSEUS	*Pseudo-nitzschia* spp. (incl. *P. seriata, delicatissima, pungens*)
PENND	Pennate diatoms
PLAGV	*Plagiogrammopsis vanheurckii*
RHIZI	*Rhizosolenia imbricata*
RHIZS	*Rhizosolenia hebetata* & *R. setigera*
SKELC	*Skeletonema costatum*
THALL	large *Thalassiosira* spp.
THALN	*Thalassionema nitzschioides*
THALS	small *Thalassiosira* spp.

[a] In most cases, the main species in this group (*Chaetoceros socialis*) has appeared in colonies.

[b] A very slender growth form of *Cerataulina pelagica* without taxonomic status (distinguished from common growth form because of its difference in biovolume).

Works. Loadings of the western Wadden Sea were determined as the summed outputs by the two sluices from the fresh-water lake IJsselmeer divided by the surface area of the western part of the Dutch Wadden Sea (Ridderinkhof et al. 1990).

Production measurements – Most field data on phytoplankton production in the western Wadden Sea (Fig. 2.2.2.2) were derived from a long-term sampling program in the Marsdiep tidal inlet during high tide (Cadée & Hegeman 1974a, Cadée 1986, 1992). Considering the geomorphologic properties of the western Wadden Sea (Hoppema 1991), we calculated the pelagic primary production rate of the western Wadden Sea from the production measured at the Marsdiep tidal inlet (Philippart & Cadée 2000). Corrected for the geomorphologic properties of this particular area (Hoppema 1991) in a similar way as for pelagic production, the average primary production by benthic microflora in the western Wadden Sea was approximately 27% of the rates measured at the monitoring station (Cadée & Hegeman 1974b, Cadée 1980, Cadée 1984). Although on sheltered tidal flats macroalgae (mainly *Ulva* and *Enteromorpha*) may form a dense vegetation during summer in some years, their average contribution to the total Wadden Sea primary production is considered to be relatively small (Philippart & Cadée 2000). At present, intertidal seagrass stands (mainly *Zostera noltii*) cover less than 1 km^2 in the western Wadden Sea (Philippart & Dijkema 1995). Average primary production of seagrasses in the western Wadden Sea was based on a species-specific productivity range of dense seagrass stands (Hillman et al. 1989) and other estimates (Philippart & Cadée 2000).

Nutrient dynamics

Time series on nutrient loadings and concentrations were taken from the water quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public Works. Total phosphorus (TP) includes phosphate (PO_4^{3-}), dissolved organic phosphorus (DOP) and particulate compounds of phosphorus; total nitrogen (TN) is the sum of ammonium (NH_4^+), nitrate plus nitrite (NO_x), dissolved organic nitrogen (DON) and particulate compounds of nitrogen.

To determine the nutrient fluxes to and from the western Wadden Sea (Fig. 2.2.2.2), we have compiled the phosphorus and nitrogen budgets for this system for every two month period from Jan-Feb 1975 to Nov-Dec 1993. The nutrient budgets were based on a hydrodynamical model by Ridderinkhof et al. (1990). Nutrient mass fluxes were calculated by multiplying the advective water transport rates with corresponding nutrient concentrations, and the tidal exchange rate with the corresponding nutrient gradient (Van Raaphorst & Van der Veer 1990). The atmospheric nitrogen input was based on values estimated for the southern North Sea by Rendell et al. (1993).

Each bi-monthly phosphorus budget was closed with a residual TP-flux, which included the accumulation of particulate matter originating from the open sea, a process described for the Wadden Sea (Postma 1961) and several other coastal areas (Postma 1980). Subsequently, the inward transport rates of nitrogen were calculated from coinciding phosphorus fluxes using ambient nutrient ratios (mol mol^{-1}). Finally, the nitrogen budget was closed with a residual N-specific flux which comprises net inputs (+) or outputs (-) not accounted for in the TP budget.

Missing values

Missing values within the data sets (phytoplankton species, chlorophyll-a and nutrients) were filled in under the assumption that the expected monthly averaged density of each species was a product of a 'year effect' and a 'month effect'. These effects were estimated by a linear Poisson regression (McCullagh & Nelder 1989). Years were excluded from further analysis if the proportion of missing values was relatively high (> 25%). The method for filling in the missing data assumes that the differences among years were the same for all months, and the seasonal trends were the same for all years. These assumptions are probably unrealistic because they do not include year-to-year differences in the seasonality within the variables. However, the biases in the final results of this technique are thought to be small due to more or less random distribution and the low proportion of missing values in most data sets.

Helgoland Roads

Zooplankton dynamics

Since 1974, mesozooplankton (150 μm net series) has been sampled at Helgoland Roads (Fig. 2.2.2.1) approximately three times per week (Greve & Reiners 1995). In this study, *Noctiluca scintillans,* the metatrochophora larvae of spionids (Polychaeta) and the calanoid copepods *Temora longicornis and Acartia* sp. are examined. The main criteria for this choice were that these (groups of) species represent different trophic levels and generally exhibit high abundances at Helgoland Roads, and that nearly complete records with weekly resolution exist from 1974 to 1995.

Of the selected species, the dinoflagellate *N. scintillans* is of special importance to the ecosystem. It is known as a voracious feeder that swallows small items without differentiating between food and non-food. It exhibits a pronounced trophic relationship with copepods and fish since it feeds on their eggs (Kimor 1981). Its explosion-like growth in certain years is manifested in the "red-tide"-phenomenon (Uhlig & Sahling 1990). This phenomenen has a significant impact on the ecosystem due to the mass release of NH_4 and the oxygen reduction by the decaying material, which can result in high fish mortality (Wulf Greve, Heino Fock & Uwe Lange, pers. comm., Ho & Hodgliss 1992).

We examined four indices of these zooplankton species or groups, *viz.* log-transformed mean abundances (A_i), net change in log-transformed abundances (calculated as the difference in mean abundances between several two-month periods), integrated log-transformed abundance (A_{sum}I) over time periods of 1 month, and the relative change in abundance (Da_l). The latter index varied from -1 (extreme decrease around week i) to 0 (no change) to 1 (extreme increase) (Heyen et al. 1998).

In a first step it was tested whether any correlations between the abundances of *N. scintillans*, the group of copepods and the group of spionid larvae exist. Such correlations could indicate a common forcing by climate, a predator-prey relationship or competition for food. Also, it was tested whether the two copepods *T. longicornis* and *Acartia sp.* are correlated with each other.

Climate dynamics

As potential predictors for plankton dynamics at the Helgoland Roads, we applied:

- sea surface temperature estimated for a 2° x 2° grid (Comprehensive Ocean Atmospheric Data Set)
- monthly differences in sea surface temperature (SST)
- air temperature measured at 2 m height on a 5° x 5° grid (Climate Research Unit, Jones 1994)
- sea level air pressure estimated for a 5° x 5° grid (National Centre for Atmospheric Research, Trenberth & Paolino 1980)
- monthly differences in sea level pressure (SLP)
- freshwater discharge from the river Elbe (Arbeitsgemeinschaft Elbe) correlating with salinity in the German Bight (Heyen & Dippner 1998)
- Gulf Stream Index (Taylor 1995)
- the North Atlantic Oscillation (NAO) index correlating with westerly winds and mild winters in Europe (Hurrell 1995).

Validation of these climate indices was performed using:

- SLP variance calculated as a proxy for storm activity (Blackmon 1976)
- SST from the North Sea on a 20 x 20 n.m. grid (Bundesanstalt für Seeschiffart und Hydrographie, Becker & Pauly 1996)
- local surface salinity, sea surface temperature (Greve & Reiners 1995)
- wind strength and direction (GMS). Wind strength was supplied in Beaufort and wind directions were classified according to the wind induced circulation patterns after Backhaus (1993) into type 1 (directions S, SW, W), type 2 (NW), type 3 (N, NE, E) and type 4 (SE). Weekly means for the wind effect for each wind type were calculated as the duration of each wind type multiplied by its strength (Heyen et al. 1998).

Before predictors and predictands were linked to each other by means of downscaling analysis (see 2.1.2), the time series were processed under the following aspects (Heyen et al. 1998). First, we considered the possibility that the relationship between climate and zooplankton may only occur at a specific time scale only, e.g. for low-frequency variability. Therefore, we calculated l-, 3- and 6-mo running averages of the climate data, and 1-2-1-weighted, 8-wk and 26-wk running averages of log-abundance and relative increase of the zooplankton groups. Second, since our main interest was in interannual variability, the seasonal cycle was subtracted from all predictands and predictors. Third, we computed statistical models for each season seperately. Fourth, we examined the possibility of the existence of time lags between the climate signal and its impact on the zooplankton within our analysis.

2.2.3 MACROBENTHOS

Western Wadden Sea

Macrozoobenthos sampling – The Balgzand data set has been used to analyse and develop statistical methods for studying the relationship between variability in biota and environmental factors (Zuur 1999). The Balgzand is a 50 km^2 tidal flat area in the western part of the Wadden Sea. In this area, twelve randomly selected permanent sampling stations (transects) have been sampled in a uniform way at least annually since 1969. At each transect, 50 cores of 0.018 m^2 each, along a line, at 20 m intervals, were taken. Twenty five consecutive cores, covering 500 m of the transects, were pooled. Hence, each of the 1 km long transect is represented by 2 samples, covering 500 m. A sample will be denoted by site. The geographical locations of the 24 sites, located on 12 transects are illustrated in Figure 2.2.3.1. The cores were sieved with a 1 mm mesh, and numbers of macrozoobenthic species were counted. Further details of the sampling are given in Beukema (1974, 1988). In the analysis we have concentrated on annual data monitored in March of each year during the period 1974-95.

In each year, approximately 40 different zoobenthic species were monitored. Some of these species appeared only at a few sites, in a few years. To avoid numerical problems we have selected 9 species which are believed to be important (Beukema, personal communication). Two of the species were divided in age and year classes. These species are given in Table 2.2.3.1. Because species abundances vary substantially, we have applied a square root transformation on the data.

Spatial environmental variables – At each of the 24 sites, the values of silt content, median grain size, and mean tidal level are known. Furthermore, the distance of each site to the nearby dike (SW boundary of Balgzand), and to the tidal stream (North of Balgzand) were calculated. The first distance can be considered as a measure of shelter to the prevailing south westerly winds, while the second distance represents the exposure to waves and tidal currents (it can also be seen as a measure of water-transported food). The five environmental variables were standardised to zero mean and unit variance. Unfortunately, these spatial environmental variables have been monitored only once or twice. But it is believed that these spatial environmental variables did not change much over time (Beukema & Cadée 1997). For that reason, we use the same values for all years.

Temporal environmental variables – Available temporal environmental variables are water temperature and salinity (measured daily at the NIOZ-pier in the Marsdiep), wind speed and insolation (continuously measured at airport De Kooy), and chlorophyll-a measurements (measured every week in spring at the NIOZ-pier). Yearly means (based on winter measurements) of each of these variables were calculated in Philippart et al. (1996).

Statistical analysis – Various multivariate techniques (CA, CCA, RGR, GAM) based mainly on unimodal response of species on environmental factors were used and further developed to analyse the data. For details see 2.1.1 and Zuur (1999).

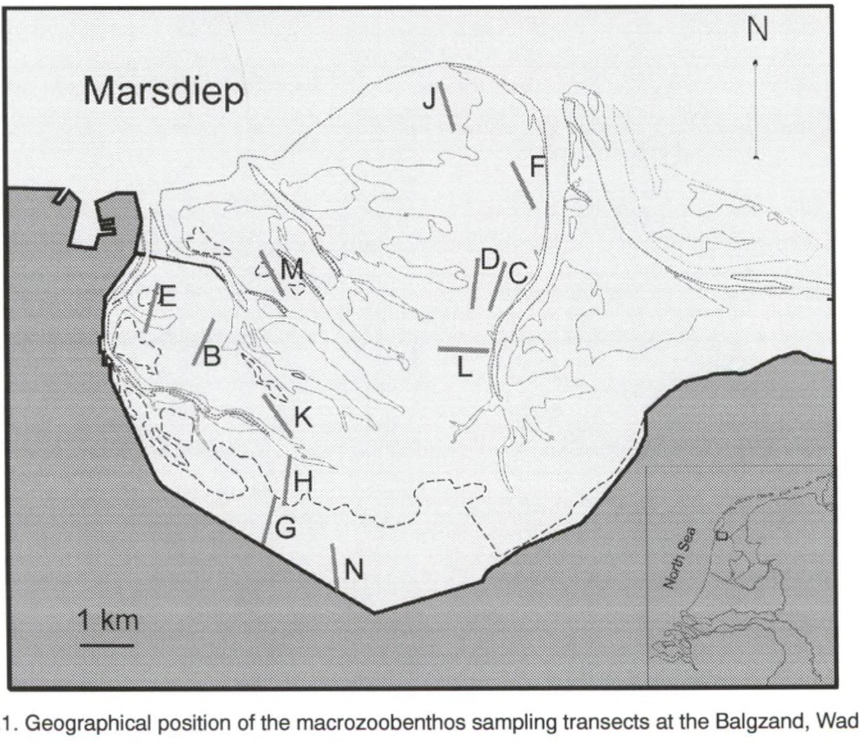


Fig. 2.2.3.1. Geographical position of the macrozoobenthos sampling transects at the Balgzand, Wadden Sea.

TABLE 2.2.3.1

Occurrence of selected zoobenthic species in the Balgzand, Dutch Continental Shelf (DCS) and Baltic Sea data sets. The numbers indicate the year-classes included in the analysis

Class	Species	Balgzand	DCS	Baltic Sea
Polychaeta	*Harmothoe sarsi*			X
	Nereis diversicolor	X		
	Nephtys hombergii	X	X	
	Nephtys cirrosa		X	
	Scoloplos armiger	X	X	
	Spiophanes bombyx		X	
	Magelona papillicornis		X	
	Heteromastus filiformis	X		
	Arenicola marina	X		
	Lanice conchilega	X	X	
Crustacea	*Saduria entomon*			X
	Bathyporeia elegans		X	
	Monoporeia affinis			X
	Pontoporeia femorata			X
	Urothoe poseidonis		X	
	Callianassa subterranea		X	
Gastropoda	*Mysella bidentata*		X	
Bivalvia	*Cerastoderma edule*	0, 1, 2		
	Spisula subtruncata		X	
	Tellina fabula		X	
	Macoma balthica	0, 1, 2, 3		X
	Mya arenaria	X		
Ophiuroidea	*Amphiura filiformis*		X	
Echinoidea	*Echinocyamus pusillus*		X	

North Sea

Dutch Continental Shelf monitoring data

Data from the Dutch Continental Shelf (DCS) long-term monitoring program for the period 1991-1996 has been used on an annual basis. In 1996, the sampling design changed considerably. We have only used those sites that were monitored in all years. These 25 sites are located on four transects perpendicular, and one transect parallel, to the Dutch coast. The sites cover four subareas, namely the south of the Dogger Bank, the Oyster grounds, and coastal and offshore areas. We used observed abundances of 14 selected zoobenthic species (Van der Meer, pers. comm.). The selected species are presented in Table 2.2.3.1. Because observed abundances varied substantially, square root transformed data are analysed. At each site, the following variables are available: longitude, latitude, depth, median grain size and mud content. Details of the monitoring program can be found in Holtmann et al. (1996). The geographical positions of the sites are given in Fig. 2.2.3.2.

North Sea trawling by-catch data

Sampling – In two surveys, sole net survey (SNS) and beam trawl survey (BTS) the invertebrate by-catch has been recorded (Piet et al. in prep.). The SNS was initiated in 1969 and is a national survey carried out in September/October by the Netherlands. It aims at obtaining pre-recruit indices for 1- and 2-group plaice and

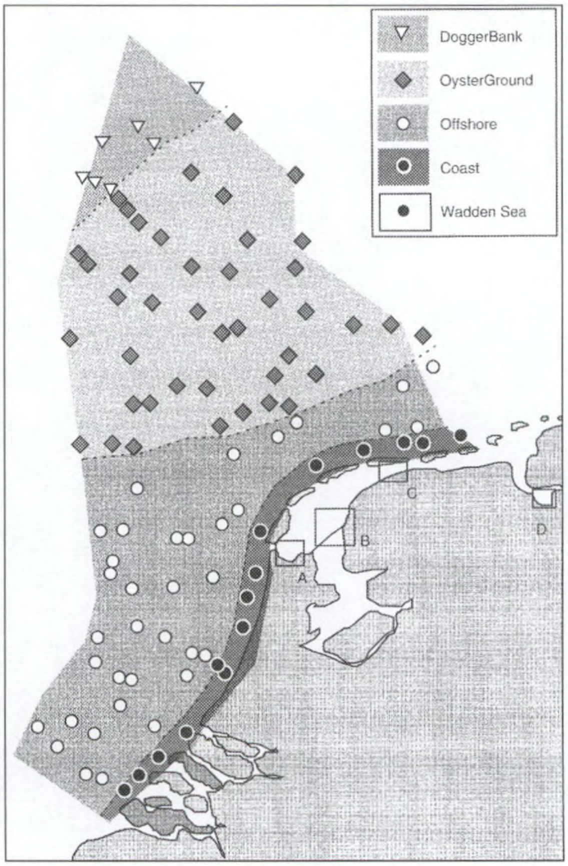


Fig. 2.2.3.2 Geographical position of the sites in Dutch continental shelf (DCS) data.

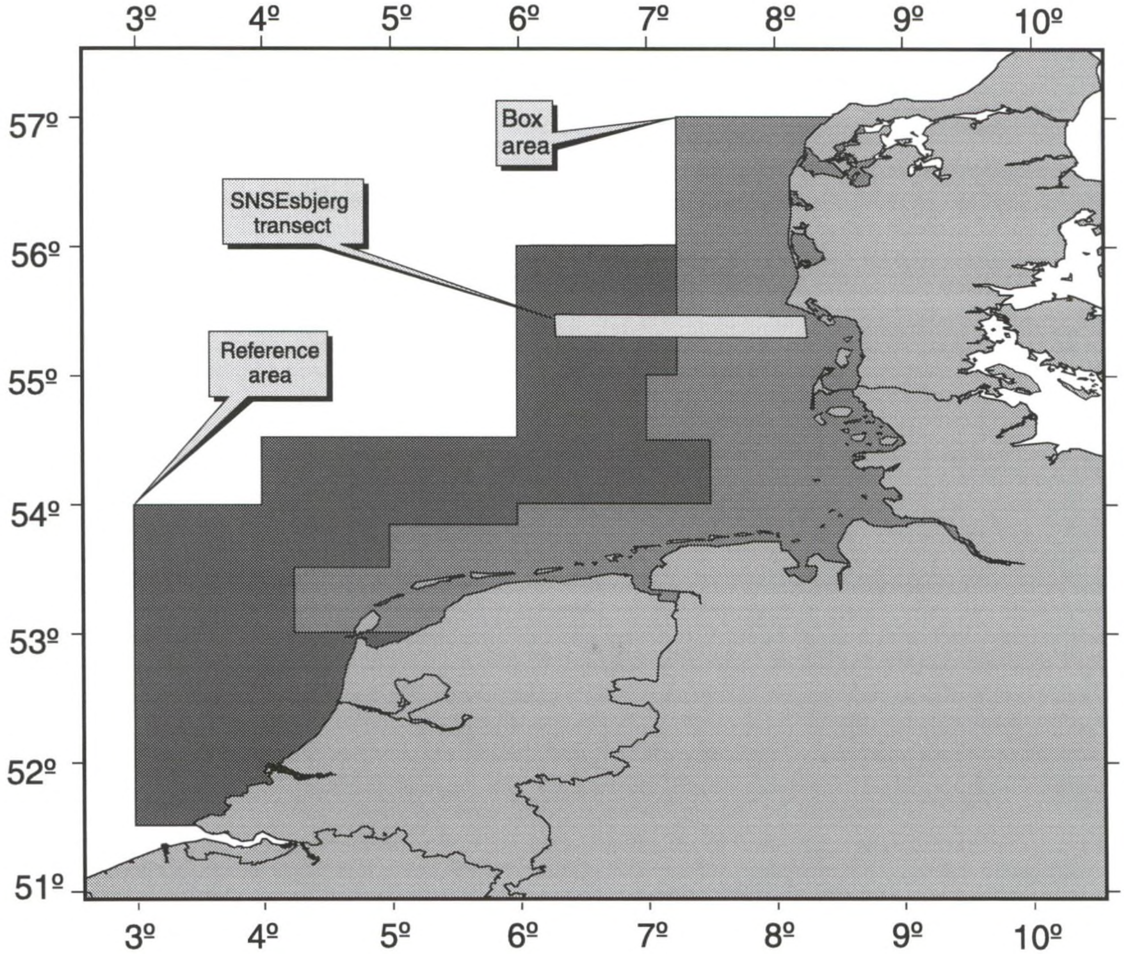


Fig. 2.2.3.3 Map of the trawling areas. Indicated are the plaice box, the reference area and the transect covered by the SNS study.

sole. The survey is carried out along the coast of the Netherlands, Germany and Denmark, which is the major distribution area of these age groups. For details of the sampling methods see 2.2.4. For this study only the transect perpendicular to the coast at Esbjerg in Denmark was used because the hauls of this transect represent a cross section from the coast straight through the box area into the area outside the box (Fig. 2.2.3.3). The transect was divided into four sectors differing in their distance from the shore: (1) 0-25 km, contains the 12 miles zone; (2) 25-50 km, inside the box; (3) 50-80 km, contains the boundary of the box; (4) > 80 km, outside the box.

The internationally coordinated BTS survey was initiated in 1985 and aims at obtaining abundance estimates of the dominant age groups of plaice and sole including pre-recruits. The survey is carried out in August/ September and covers both inshore and offshore areas throughout the North Sea, Channel and western waters of the UK. For sampling methods and strategies, see 2.2.4. Two different areas were distinguished in this study: the box area and a reference area (Fig. 2.2.3.3).

The data sets were divided in three time periods reflecting changes in the fishing effort: period before closure of the box (SNS:1980-1988, BTS: 1985-1988), period when the box was closed part of the year (1989-1994) and when the box was closed year-round (1995-1997).

Environmental data – The environmental data consist of time series of the North Atlantic Oscillation (NAO, Hurrell 1995; monthly averages obtained from http://www. cru.uea.ac.uk/ftpdata/nao.dat) and recordings during the surveys of depth at each sampling station and seawater temperature, measured at the bottom (only BTS) and the surface. By selecting the hauls in the box and reference areas the average temperature in each of the areas could be determined.

Statistical analysis – The relationship between the NAO and seawater temperature was determined using linear regression. The effects of environmental and anthropogenic factors on the benthic invertebrate assemblage were analysed using several multivariate techniques. For these analyses a selection of species was made that consisted of more than 99% of the specimen in the catch of both surveys. Of this selection the number caught per haul was logarithmically transformed. Analysis of variance (ANOVA) and multiple analysis of variance (MANOVA) were used to determine the effect of the closure of the box on the benthic invertebrate assemblage. Bottom temperature and depth were used as covariates for the analyses of BTS data, while only depth was used as a covariate for the analyses on the SNS data. Principal component analysis (PCA) was used to show how the environmental (bottom temperature and depth) and anthropogenic factors (fishing effort) affected the composition of the benthic invertebrate assemblage.

Norderney benthos monitoring data

Sampling – The area of investigation was situated north of the island Norderney in the Wadden Sea. Five stations were located in waterdepths between 12 and 20 meters (Kröncke et al. 1998). Samples were taken with a 0.2 m^2 Van Veen grab and sieved with a 0.63mm mesh screen. Samples were taken monthly from 1978 to 1991, but since 1982 sampling has been restricted to late winter and late summer. Prior to statistical analysis all samples were revised taxonomically. Species number, abundance and biomass (ash-free dry weight) were calculated as means per 0.2 m^2 or of 5 stations and were given as values per yearly quarter. The data set is characterized by a high number of species, a total of 196 taxa were found in 351 samples. However, in data divided to seasons, typically 20-40 species are observed annually.

Environmental variables – As environmental predictors in this study were used several climatic variables and sea surface temperature (SST, retrieved from Bundesanstal für Seeschiffart und Hydrografie, Germany). The variables decribing climatic conditions included the NAO index (from NCAR, Boulder, CO, USA; Hurrell 1995), monthly means of sea-level air pressure (SLP) fields (from NCAR), monthly means of storm activity (derived from previous), monthly means of air temperature (Jones 1994), monthly means of Gulf Stream Index (GSI, Taylor 1995), discharge from the River Elbe (from the Arbeitsgemeinschaft Elbe, ARGE) and monthly means of high and low tide at Helgoland (from the Biologische Anstalt Helgoland).

Statistical analysis – Variability in species numbers, total abundance and biomass were related to patterns in climatic variables and sea surface temperature by means of statistical downscaling (Von Storch et al. 1993, Kröncke et al. 1998).

Baltic Sea

Macrozoobenthos sampling – The basis for the Baltic Sea macrozoobenthos analysis is formed by monitoring data which has been collected by the Finnish Institute of Marine Research (FIMR) since 1965 (Andersin et al 1978a, Laine et al. 1997). The monitoring network is based on fixed sites which cover most of the Baltic Sea. The sampling sites are in general arranged in transects crossing the main basins (Fig. 2.2.3.4). These sites represent muddy soft bottom habitats generally deeper than 60 meters. Sediments are characterized by fine material in surface layer, in some areas covering harder, mainly clayed substrates. Sandy sediments are rare but in some areas Fe/Mn concretes are present. For more sediment characteristics, see Laine (in prep.).

In this project we have concentrated on 30 to 65 most frequently sampled sites (Andersin et al. submitted, Laine et al. 1997, Laine, submitted). Sampling has been done annually and data since 1965 has been used in the analysis. Major gaps in the data exist in 1976 (no sampling) and 1983-85 (restricted sampling network). Sampling coverage in the central Baltic was improved considerably in 1978-79 when three new transects crossing the Eastern Gotland Basin were established (Laine et al. 1997). For the temporal sampling coverage see e.g. Laine et al. (1997) or Laine & Zuur (in prep.). The existing data on macrozoobenthos was completed by field sampling in 1996-97, on four research cruises onboard RV Aranda.

Sampling has been done with a standard 0.1 m^2 van Veen grab, taking generally 3 replicate samples per station and sampling occasion. The main change in the grab during the study period has been the enlargement of the flow-through windows which could have increased the sampling efficiency (Andersin & Sandler 1981). This change took place in 1977-78. The annual sampling occasion has been in May-July, except for 1977-78, 1983 and 1989, when sampling in the Gulf of Finland was carried out in August-September. The samples were sieved through a sieve with a mesh size of 1.0 mm following the guidelines by Dybern et al. (1976) and Baltic Marine Environment Protection Commission (1988). In the laboratory the samples were sorted to species level and enumerated. After a storage of at least 3 months, the biomass was determined as wet weight, including the bivalve shells. In the study of *Monoporeia affinis* population structure the length of the specimens were measured with 1/6-mm accuracy under a stereo microscope.

The macrozoobenthos data is characterized by a low number of species, only five species being dominant in most of the data (Table 2.2.3.1). Only in- and epifaunal species have been included, thus rejecting nektobentic species which are not sampled quantitatively by the methods used.

Environmental variables – The data on hydrography includes salinity, temperature and dissolved oxygen/hydrogen sulphide concentration. The salinity and temperature data prior to 1976 originate from water samples taken at standard depths and is after 1976 complemented by CTD-casts. The oxygen and hydrogen sulphide data originate from water samples at standard depths. The near-bottom water values have been recorded from water samples, taken approx. 1 m above the seabed. Data on nutrients consist of phosphate, nitrate and silica concentration measured in the surface layer (0-10 m) during winter months (December-March).

The main source for hydrographical and nutrient data has been the FIMR database. Records have been completed with data retrieved from SMHI database (Swedish Meteorological and Hydrological Institute, Göteborg, Sweden).

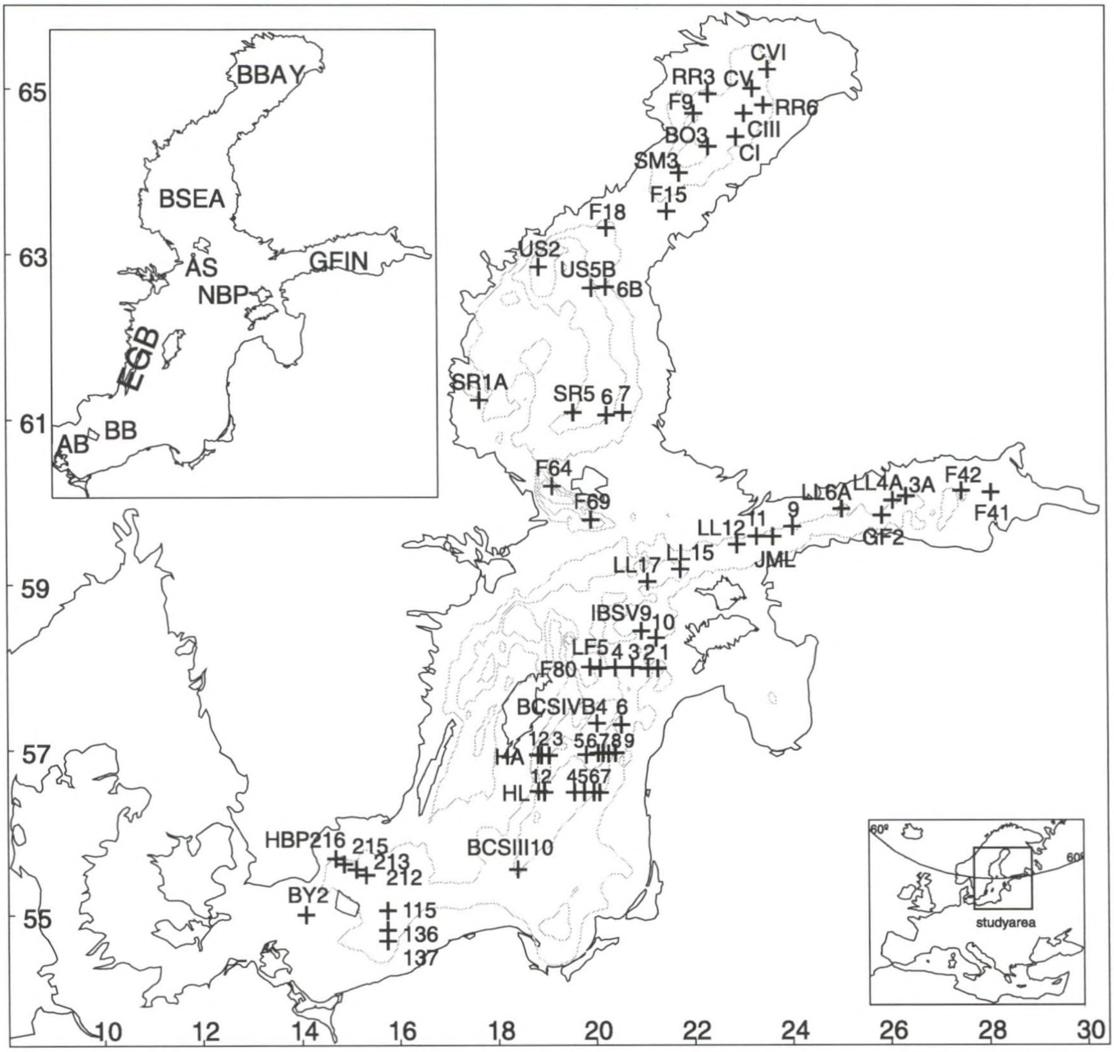


Fig. 2.2.3.4 Bathymetric map of the Baltic Sea including locations of the sampling sites. Sea areas in the upper right map: AB=Arkona Basin, BB=Bornholm Basin, EGB=Eastern Gotland Basin, NBP=Northern Baltic Proper, GFIN=Gulf of Finland, BSEA=Bothnian Sea and BBAY=Bothnian Bay.

Field sampling on sediments was carried out during the r/v Aranda cruises in 1996-97 (Laine, submitted). Sampling was done with a Gemini twin corer (tube diameter 8 cm). The cores were sliced to 1 cm and dated using Cs-137 method, which utilises the 1986 fallout from the Chernobyl accident as a reference level (Kyzyurov et al. 1994, Kankaanpää et al. 1997, Ilus et al. 1999). The sediment slices were further analysed for dry and ash weight and total carbon and nitrogen content. The sediment data base consist of (i) sedimentation rate (recent dry matter accumulation), (ii) C/N ratio in surface sediment (0-1 cm) and total carbon and nitrogen content of the sediment, measured as (iii) the percentage of dry matter in sediment surface (0-1 cm), and (iv) as total amount in 0-5 cm upper sediment layer.

Statistical analysis – In the statistical analysis of long-term data we have used mainly abundance values. Biomass (wet weight) has been used only in the spatial analysis of macrofauna distribution (Laine in prep.). The general approach in analysing Baltic Sea data has been to study first the relationship between biota and water column characteristics or sediments and then try to relate the latter variables to climatic variability by using downscaling methods (Zorita & Laine 2000). In the analysis of species data we have applied multivariate ordination techniques like Canonical Correspondence Analysis (Ter Braak 1986) and non-metric Multi Dimensional Scaling (MDS, Clarke & Warwick 1994). Species were related to environmental variables by using weighted Spearman rank correlation between the (dis)similarity matrices (Clarke & Ainsworth 1993), Restricted Gaussian Regression Techniques (RGR, Zuur 1999), Restricted Generalized Additive Modelling (RGAM, Zuur 1999) and structural time series models (Harvey 1990, Laine & Zuur in prep.).

2.2.4 FISH

North Sea

Long-term variation in fish communities

Fish community data – Information on the demersal fish assemblage in the North Sea comes mainly from two sources: (1) fishery independent data from yearly research vessel surveys assessing the entire fish community and (2) data on the age-class abundance per year for a limited number of commercial species based on Virtual Population Analysis (VPA).

The fishery–independent data used in this project came from various (inter)national surveys using different type of gear or sampling technique, each covering specific areas (Table 2.2.4.1, Figure 2.2.4.1). The International Bottom Trawl Survey (IBTS), Beam trawl survey (BTS) and Sole Net Survey (SNS) are described below, other surveys are described in Henderson (1989), Philippart et al. (1996) and Rogers & Millner (1996).

Virtual population analysis (VPA) data for plaice, sole cod, haddock, saithe, and whiting for the North Sea can be obtained from Anonymous (1999a). The data are time series of stock biomass or stock numbers per age group and year.

The International Bottom Trawl Survey (IBTS) is a follow-up of the International Young Fish Survey (IYFS) that was conducted in the North Sea and Skagerrak/Kattegat in February of each year starting in the late 1960's. Over the years the survey has changed from a survey on young herring into one for demersal fish and herring of all ages and sizes. At the same time the area surveyed has expanded until from 1974 onwards the whole North Sea proper, Skagerrak and Kattegat were covered. The IBTS was conducted in international collaboration with different research vessels covering specific areas. Over time standardization in gear type, rigging specifications and sampling strategy was persued among participating countries (Anonymous 1999b). During the early years of the survey a 78-foot Dutch herring trawl was recommended as the standard gear but in 1977 it was decided to use the GOV-trawl (Grande Ouverture Verticale) as standard gear. From then onward most vessels used GOV but it took several years before it was adopted by all vessels. The GOV has a high vertical net opening of 5 to 6 m. The horizontal opening of the net is approximately 20 m. Standard fishing speed is 4 knots measured as trawl speed over the ground. Each haul lasts 30 minutes. For the present study only quarter 1 data from North Sea proper (excluding Kattegat and Skagerrak) were used for the years 1974 until present. Each year only those hauls were used where all species caught were recorded.

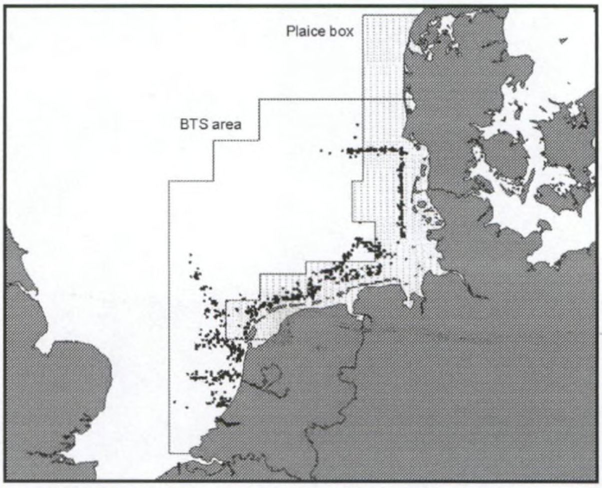


Fig. 2.2.4.1 Area covered by the surveys SNS (dots) and BTS. Indicated is the 'Plaice box".

The BTS survey was initiated in 1985 and aims at obtaining abundance estimates of the dominant age groups of plaice and sole including pre-recruits. The survey is carried out in international cooperation and covers both inshore and offshore areas throughout the North Sea, Channel and western waters of the UK. The fishing gear used is a pair of 8 m beam trawls rigged with nets of 120 mm and 80 mm stretched mesh in the body and 40 mm stretched mesh cod-ends. A total of 8 tickler chains are used, 4 mounted between the shoes and 4 from the groundrope. The survey was designed to take between 1 and three hauls per ICES rectangle depending on the rectangle. The stations are allocated over the fishable area of the rectangle on a "pseudo-random" basis to ensure that there is a reasonable spread within each rectangle. No attempt is made to return to the same tow positions each year. Towing speed is 4 knots for a tow duration of 30 min-

TABLE 2.2.4.1

Characteristics of the surveys. Mesh size in mm stretched mesh. Haul duration in minutes and towing speed in knots

	IBTS	BTS	SNS
Area	North Sea proper	SE North Sea In-/Offshore	Coastal zone Inshore
Gear	GOV	8m beam trawl	6m sole net
Tickler chains	none	8	4
Mesh size	20	40	45
Haul duration	30	30	15
Towing speed (knots)	4	4	4
Months	Jan.-Feb.	Aug.-Sept.	Sept.-Oct.

utes and fishing occurs during daylight only. From the start of BTS in 1985 until present the same research vessel (RV "Isis") was used.

The SNS was initiated in 1969 and is a national survey carried out by the Netherlands only. It aims at obtaining pre-recruit indices for 1- and 2-group plaice and sole. The survey is carried out along the coast of the Netherlands, Germany and Denmark, which is the major distribution area of these age groups. The SNS used one 6 m beam trawl, rigged with 4 tickler chains and a sole net with a stretched mesh size of 40 mm in the cod-end. The standard station grid of the SNS exists of 10 transects parallel or perpendicular on the continental North Sea coast between the Dutch/Belgian border and Esbjerg in Denmark. The gear is fished with a fishing speed of 3.5 knots and the haul duration is 15 minutes. For the SNS survey three research vessels were used: RV "Tridens" (old, 1969-1989), RV "Tridens" (new, 1990-1995) and RV "Isis" (1996-present).

Although for each of the surveys changes have occurred over time, it was assumed that for the time period considered for each of the selected surveys the methodology and equipment used were sufficiently consistent not to induce a marked bias. For each survey the number and length of each fish species were recorded per haul.

Environmental variables – The following data of factors from both natural and anthropogenic origin were avail-

TABLE 2.2.4.2

Characteristics of the fish species used in this study. Proportion biomass in three surveys, life-history parameters, length-weight parameters of the allometric relationship $W=a*L^b$, characterisation as demersal (D) or pelagic (P) and according to biogeographic origin (B=Boreal, L=Lusitanian, A=Atlantic).

Taxon	Abb.	Surveys			Life-history		Length-Weight		Characterization	
		IBTS %	BTS %	SNS %	Max. size	Size at maturity	a	b	Biogeographic	Pelagic/ Demersal
Agonus cataphractus	ACAT		0.7	0.8	17	8	0.0196	2.6139	B	D
Anarhichas lupus	ALUP	0.1					0.0033	3.2491		
Buglossidium luteum	BLUT		0.6	0.3	18	8	0.0039	3.4134	L	D
Callionymidae	CAL		1.7	2.2	25	13	0.0162	2.5781	L	D
Clupea harengus	CHAR	27.0				25	0.0060	3.0904	B	P
Cyclopterus lumpus	CLUM	0.3			50	20	0.0587	2.9390	B	D
Eutrigla gurnardus	EGUR	1.6	1.5	0.6	38	19	0.0062	3.1003	L	D
Gadus morhua	GMOR	9.2	0.9	2.6	113	66	0.0049	3.1966	B	D
Gasterosteus aculeatus	GACU			0.3		6	9.9444	1.7915	B	D
Hippoglossoides platessoides	HPLA	0.6	0.3		34	18	0.0044	3.2039	B	D
Limanda limanda	LLIM	5.3	37.6	34.5	38	13	0.0074	3.1128	B	D
Lophius piscatorius	LPIS	0.2			120	53	0.0153	2.9979	L	D
Melanogrammus aeglefinus	MAEG	21.6		0.2		32	0.0182	2.8268	B	D
Merlangius merlangus	MMER	14.6	2.1	2.9	46	21	0.0042	3.0565	L	D
Microstomus kitt	MKIT	0.3	0.4	0.4	39	24	0.0265	2.7643	B	D
Molva molva	MMOL	0.3			155	70	0.0010	3.4362	B	D
Myoxocephalus scorpius	MSCO		0.7	0.6	34	15	0.0126	3.1235	B	D
Platichthys flesus	PFLE	0.6	1.6	2.3	44	30	0.0087	3.0978	L	D
Pleuronectes platessa	PPLA	1.0	42.9	44.9	60	30	0.0082	3.0260	L	D
Pollachius pollachius	PPOL	0.3			90	36	0.0283	2.7374	L	D
Pollachius virens	PVIR	2.0			115	45	0.0283	2.7374	B	D
Raja clavata	RCLA	0.2	0.1		100	86	0.0025	3.2489	L	D
Scomber scombrus	SSCO	0.3			40	30	0.0030	3.2900	A	P
Scophthalmus maximus	SMAX		1.0	0.8		38	0.0044	3.3862	L	D
Scophthalmus rhombus	SRHO		0.4	0.3	48	32	0.0055	3.3047	L	D
Solea solea	SSOL		5.4	4.4	70	29	0.0036	3.3133	L	D
Sprattus sprattus	SSPR	3.7			15	10	0.0021	3.4746	L	P
Squalus acanthias	SACA	0.4			110	75	0.0049	2.9269	A	D
Trachinus vipera	TVIP		0.2	0.2	19	7	0.0018	3.4099	L	D
Trigla lucerna	TLUC		0.8	0.6	75	25	0.0080	3.0610	L	D
Trisopterus esmarki	TESM	9.7			20	16	0.0073	3.1228	B	P
Trisopterus luscus	TLUS		0.4	0.7	38	18	0.0038	3.3665	L	D
Trisopterus minutus	TMIN	0.1	0.1		24	13	0.0092	3.0265	L	D

able to explain the observed patterns in the fish community:

- Measurements of salinity and seawater temperature collected during the research vessel surveys (ICES Hydrographic data, http://www.ices.dk/ocean/project/data /iyfs.htm).
- Monthly data of sea surface temperature at a 2 by 2 degree resolution (Comprehensive Ocean Atmosphere Data Set) until 1992 provided by GKSS,
- Monthly data of the North Atlantic Oscillation (NAO) until present were available from the internet (http://www.cru.uea.ac.uk /ftpdata/nao.dat),
- Estimates of fishing effort at a temporal scale (per year) based on logbook data of the Dutch beam-trawl fleet provided by LEI-DLO
- Estimates of fishing effort at a spatial scale (30*30 Nm ICES rectangles) of the international fleet (Lindeboom & De Groot 1998)
- Weekly data with a resolution of about 20x20 miles of Sea surface temperature data (provided by the German Bundesanstalt für Seeschiffahrt und Hydrographie)
- Time series of mixed layer depth (MLD). Based on a simulation of the North Sea with the ocean isopycnic model (OPYC). The data are a reconstruction of the North Sea three dimensional circulation for the period 1979-1993.

Data analysis - Several approaches have been used to study the long-term changes in the North Sea fish community and their causes. For each of these approaches log-transformed biomass at the species level was used except for the Callionymidae where species were grouped at a higher taxonomic level. Biomass was calculated using the length-weight relationship of the species from literature (Table 2.2.4.2). For the higher taxonomic levels the available length-weight relationship of the most common species was used. For each survey taxonomic groups were excluded for which no length-weight relationship was available or that contributed less than 0.01 % of the total biomass.

From the beamtrawl surveys only demersal species (Table 2.2.4.2) were used for the analyses. For one analysis based on IBTS, pelagic and demersal species were distinguished, otherwise both pelagic and demersal species were used. For analyses of the changes in size-structure twelve 5-cm size-classes were distinguished: < 10, 10-15, 15-20.....> 60 cm.

Several multivariate techniques were used e.g. Principal Component Analysis (PCA), Canonical Correlation Analysis (CCorA) and Generalised Linear Models (GLM). Three indices were developed that were assumed to represent part of the changes in respectively the size-structure and species composition of the fish community: a size index and two life-history indices. The size index was represented by the average weight per haul which was determined for each year by multiplying the biomass per haul of a 1-cm-class with the length of that cm-class and dividing it by the total biomass per haul. The life-history indices were represented by multiplying the log-transformed biomass per haul of each species with the value of specific life-history characteristics and dividing it by the log-transformed total fish biomass per haul. Two life-history characteristics were used: maximum size and size at maturity. These data were also derived from literature (Table 2.2.4.2) and treated similar to the parameters of the length-weight relationship. Linear regression and GLM were used on IBTS and SNS data to examine whether a progressive trend in these indices could be observed and to what extent this trend could be attributed to fishing activities. For the IBTS data two areas differing in fishing intensity were distinguished separated by 56° latitude (Polet et al. 1998; Jennings et al. 1999).

Effect of fisheries

Another possibility to determine the effect of fishing activities on the fish community arose from a management measure reducing fishing effort in a specific area. In 1989 a closed area, the "plaice box", was established. At first it was only effective during the 2nd and 3rd quarter but in 1994 the box was extended to the 4th quarter and since 1995 the box was closed during the whole year. Although an exemption fleet of smaller beam trawl vessels ("Eurocutters" < 300 Hp) was still allowed to fish in the box and fishing activities by the larger beam trawlers (> 300 Hp) in notably the fourth quarter continued during the period 1989-1994 this resulted in a decrease of trawling intensity in the box area (Figure 2.2.4.2). Because most of the surplus effort was redirected to the area just outside the plaice box, fishing intensity increased in that area. This reallocation of fishing effort provided the opportunity to study the effect of fishing activities on the fish community. This study was based on BTS, a survey that covers both the plaice box and the area outside of it. Principal Component Analysis (PCA), Analysis of Variance (ANOVA) and Multiple Analysis of Variance (MANOVA) were used to determine the effect of the closure of the box on the fish community. Any effect of the closure of the box follows from a significant interaction between the temporal and the spatial factor. For both surveys three temporal units were distinguished: period before closure of the box (1985-1988), period when the box was closed part of the year (1989-1994) and when the box was closed year-round (1995-1998). Two spatial

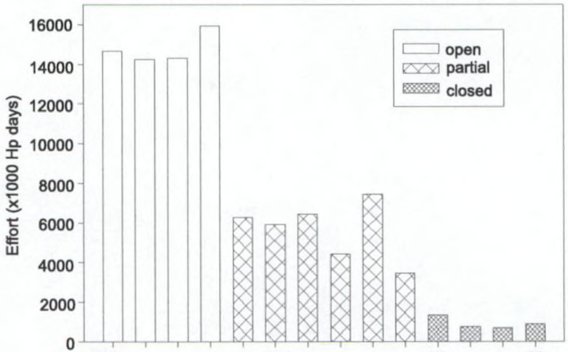


Fig. 2.2.4.2 Effort (*1000 Hp days) of the Dutch beamtrawl fleet inside the box area.

units were distinguished i.e. respectively the areas in- and outside the "plaice box".

Fish and climate

Several CCA were performed studying the relationship between the species composition and size-structure of the IBTS catches and two of the major factors from natural origin: NAO and SST. For these analyses the species were characterised as either demersal or pelagic or according to their biogeographic origin (Table 2.2.4.2). The NAO data were monthly indices of the year prior to sampling. The SST data were monthly averages per roundfish area of the year prior to sampling as derived from the Comprehensive Ocean Atmosphere Data Set.

Because of the lack of observational data the Mixed Layer Depth (MLD) was investigated in a reconstruction of the North Sea three dimensional circulation with the ocean model OPYC. In this simulation the OPYC model was forced with the ECMWF re-analyses for the period 1979-1993. The model area consists of the North Sea and large parts of the North Atlantic. In the inner domain (North Sea) the horizontal resolution is in the order of 10 x10 km^2. The OPYC model was forced with re-analyses (pseudo-observations) from the European Centre for Medium-Range Forecast and was verified against existing observations. It was found that the model reproduces the observed circulation and the variability in the North Sea reasonably well.

The onset of the spawning season was calculated from the SST according to Lange and Greve (1997). As a measure of the recruitment success stock biomasses and stock numbers were used in age group 1 or 0 for cod, haddock, saithe, and whiting.

Additionally, the hypothesis was tested that the recruitment success of plaice and sole was related to the length of the spawning season, i.e. the longer the season the higher the recruitment success. The time of the year and the temperature range at which spawning occurs was estimated from Muus (1991). We assumed that for plaice spawning occurs from January to June at temperatures around 6 °C. For sole a temperature range from 6-12 °C between March and July was assumed. Using these assumptions the length of the spawning season (LSS) was estimated for both species from the SST data. As a measure of the recruitment success the stock biomasses in age group one were used.

Recruitment and latitude

Time series on recruit numbers were obtained from fishery-independent surveys conducted at stations ranging from Southwest England in the south, i.e. latitude 50.9 °N, to the Skagerrak in the north, i.e. latitude 58.5 °N. The independent time series had different lengths but overlapped for a 14 year period, i.e. from 1981 to 1994. Abundance values were logarithmically transformed to approximate normality: $\log_e$ (numbers +1) prior to analysis. The coefficient of year-to-year variability in recruitment in each species (CVR) was defined as the standard deviation expressed as a percentage of the mean of the log-transformed time series (Sokal & Rohlf 1981, McArdle 1995). For the roundfish species under consideration, the analysis of the time series could be restricted to mainly 0-group fish. We had to include older age groups for the flatfish species (Philippart et al. 1998).

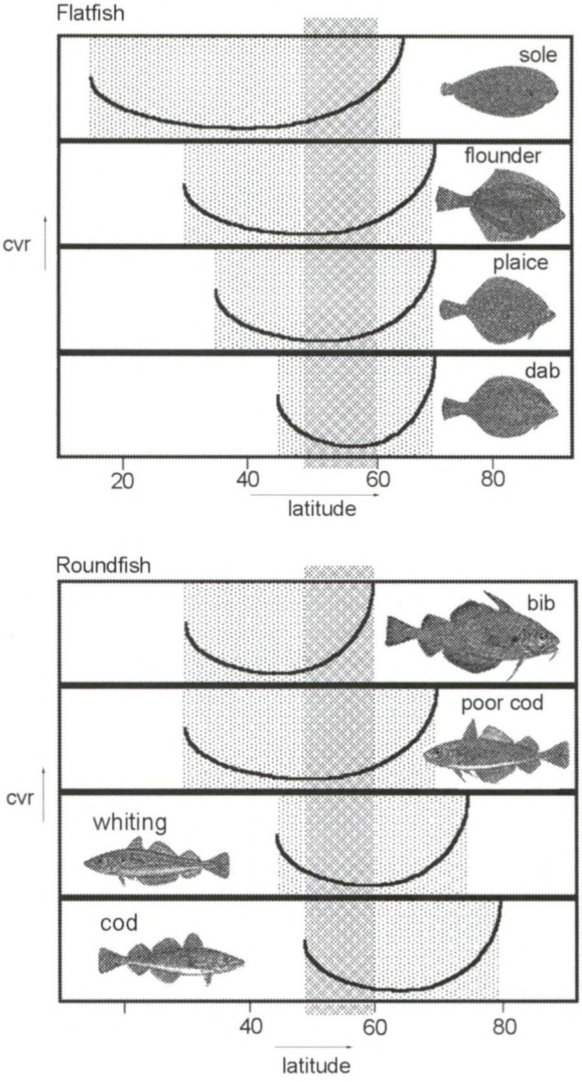


Fig. 2.2.4.3 Range of distribution and hypothesised variation in recruit numbers of (a) selected flatfish (sole, flounder, plaice and dab), and (b) roundfish species (bib, poor cod, whiting and cod). The species ranges were derived from Whithead et al. (1986).

If variation in recruit number is influenced by both latitude and species range, the realised variation in fish recruits along the Northwest European coastlines should be related to the geographic location of the stock within the species range. Given the range of latitudes over which observations were drawn and the geographical range of the species in question (Fig. 2.2.4.3), the interannual variation of recruits of several species we studied (i.e. sole, flounder, plaice, bib and poor cod) is hypothesised to exhibit an increase in variance with latitude, for other fish species the variance is hypothesised to decrease from south to north.

For Northwest European waters, water temperature is not directly correlated with latitude (Otto et al. 1990). For example, German Bight waters are much warmer in summer and much colder in winter than coastal waters of east England at the same latitude, i.e. around 54 °N. Long-term temperature series for the sampling stations were used to asses the relationships between the coefficient of variation in recruits (CVR) and temperature in both summer and winter.

In our analysis we assumed that the CVR for all species exhibited no temporal trends. This was verified by assessing the mean CVR over short intervals (3 years). In this analysis we used only the Skagerrak time series which was the longest one available.

2.2.5 SEDIMENT CORES

German Bight

Sampling, magnetic susceptibility & selection

Sampling – Using the NIOZ research vessel "Pelagia", 12m long piston cores were sampled at eleven sites in the North Sea between May 28 and June 5, 1996. The sampling locations were selected for their high to very high sedimentation rates (up to 1 cm/yr) of material relatively rich in organic carbon, in combination with only modest bioturbation phenomena, i.e. in the Skagerrak, the Norwegian Trench and the Helgoland Deep. In the pistoncorer 90mm PVC liners were applied. Onboard, these liners were cut into 1m long sections and stored upright.

Magnetic susceptibility – Immediately after collection the *in situ* magnetic susceptibility (MS) of the sediments in the pistoncore liners was measured onboard using a Barlington MS2 magnetic susceptibility meter. Segments of the core were moved incrementally (in 5 cm intervals) through a sensor loop (coil diameter 12 cm) in which a magnetic field is generated which magnetizes the sediments susceptible substances (i.e. Fe-bearing minerals). Susceptibility is thus quantified by the single unitless parameter *k* (expressed in CGS units). Original data were corrected for methodical errors (gradual shift of the background values of the equipment) by substracting reference values (blanks) taken at the beginning and end of each segment, assuming a linear course over time.

Selection – Piston core GB17 showed no apparent signs of bioturbation and disturbance during core taking and were therefore considered suitable for further treatment (Fig. 2.2.5.1).

Dating

^{210}Pb – The element ^{210}Pb (resulting from the decay of atmospheric ^{222}Rn) has a short residence time in the atmosphere and after being transported into the marine environment is absorbed onto particles in the water column. After sedimentation of these particles, ^{210}Pb concentrations rapidly decline (half life is 22.3 years) and can therefore be used as a tool to determine the age of a sediment layer (to a maximum of 110 years). The inner diameter of the sampling tube was 16 mm (outer: 17 mm). Each sample consisted of 4 to 6 ml of wet sediment. The total ^{210}Pb activity is a combination of activity originating from decay of ^{222}Rn in the atmosphere (i.e. the so-called "excess ^{210}Pb") and of activity originating from decay of ^{226}Ra in the sediment (i.e. the so-called "supported ^{210}Pb"). Total ^{210}Pb was determined by means of a-spectrometric analyses (see Berger et al. 1987 for detailed description of methods). Because ^{210}Pb dating is grainsize-dependent the samples were only taken from clay layers in the sediment core. To correct for the (still remaining) difference in grainsize, additional samples were taken at the same depths as the ^{210}Pb samples, and analysed by means of a laser-particle sizer (Coulter LS230) for specific area of the sediment. Each sample was taken by means of a small sample spade (width: 7 mm), and consisted of approximately 1 ml wet sediment.

^{14}C – To come to an accurate dating of the deeper sediment layers in the German Bight core, external ^{14}C measurements of organic material were carried out at the Faculty of Physics and Astronomy at the University of Utrecht in the Netherlands.

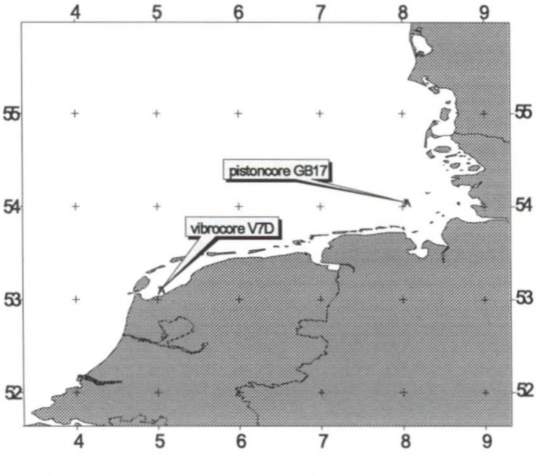


Fig. 2.2.5.1 Locations of pistoncore GB17 (sampled on June 4, 1996) and vibrocore V7D (sampled on May 20, 1997) that were analysed for the presence of biological remnants.

Western Wadden Sea

Sampling, magnetic susceptibility, X-ray fluorescence & selection

Sampling – Before the cruise, seven sampling stations were selected along two transects, one crosswise and one lengthwise the former Vlieter channel. On June 20, 1997, in total nine 6 meter cores were obtained from these locations using an electrical vibrocorer (provided by the NITG) suitable for unconsolidated, heterogenous sediments. In the vibrocorer 70mm PVC liners were applied. Onboard, these liners were cut into 1m long sections and stored upright, after small holes were made in the bottom cap to let excess water pore out.

Magnetic Susceptibility – Immediately after collection the *in situ* magnetic susceptibility (MS) of the sediments in the vibrocore liners was measured onboard in 5 cm intervals. The MS curves demonstrated which of the cores hit the course sands that mark the bed of the former channel.

Both vibrocores 7D and 8A showed no apparent signs of bioturbation and disturbance during core taking and were therefore considered suitable for further treatment. The known geological history of the Vlieter area offers a valuable recognition point in the cores where the bed of the former channel was hit. The interface between the former bed of the active channel, marked by course sand, and the finer grained deposits after the closure of the 'Afsluitdijk' indicates the early 1930s. Because this transition zone was only present in vibrocore 7D, we decided to focus on this particular sample (Fig. 2.2.5.1).

XRF – Both originally selected vibrocores were scanned with an X-ray fluorescence core scanner, which scans elements with an atomic number of 13 and higher. The scans were done with a tube voltage of 20 kV and a current of 0.04 mA. The count time per step amounted 30 seconds. Before XRF measurements, the core was subdivided into parts of approximately 40 cm (which fit into the X-ray apparatus). Top and down end of the core segments gave low values as a result of the lower sediment concentrations, and these data have to be ignored during analysis of the XRF curves. The X-rayed halves of these core segements were sliced into subsamples of variable thickness (approximately 1 cm) leaving the visible lamination in tact as much as possible.

Dating

Emperical infill – The emperical infill of the former channel was based on sedimentation processes as described for the infill of dredging holes (Albert Oost, pers. comm). The value of t was derived from an emperical relationship (Galavazi 1998) between the depth of different parts the former Vlieter channel and the coinciding response time. In addition, we fitted the value of t in such a way that the former Vlieter channel at the location of core 7D was filled in totaly between 1932 and 1997 (161.8 cm in 65 years).

Echo soundings – From the early 1930s onwards, the Dutch Department of Water Transport (Rijkswaterstaat) regurlarly determines waterdepth by means of echo soundings. Based on these soundings, Midderham and de Boer (1983) determined sedimentation rates in an area of 1 km^2 (centered around 53°-00',4 N; 05°-04',00 E) located within the Vlieter channel. Berger et al. (1987) stated that the infill stopped and sedimentation had decreased to background sedimentation rates from the 1973 onwards. We subsequently estimated the sedimentation rates at our sampling location by correcting for the difference in total infill of the RWS area (434 cm) compared to the total infill at our sampling site (161.8 cm). Furthermore, we assumed that sedimentation was neglectible from 1980 onwards.

^{210}Pb – See above.

PCBs and PAHs – In order to supply additional dating information, contaminant profiles were produced (Booij & Lewis 1999), which were matched to the profiles found by Beurskens (1995) in sediments from the Ketelmeer (Lake IJsselmeer). It was hoped to match contaminant profiles to the profiles found by Beurskens (1995) in sediments from the Ketelmeer (Lake IJssel, Netherlands). The latter sediments were deposited at the same time as in the Vlieter. Subsamples were selected on the basis of comparable grain size to the trained eye. A layer of 2 mm from cutting surface was scraped off. The width of the samples layer was about 1-1.5 cm, except for V_0, for which a 3cm thick layer was sampled. PAHs in downcore samples of comparable grainsize were analyzed using a HP5890 gas chromatograph, PCBs using a Carlo-Erba 5160 gas chromatograph.

Biological Remnants

Extraction – After wet sieving the subsamples into <63 mm, 63-250 mm, 250-500 mm, 500-1000 mm, and > 1000 mm fractions, all faunal remnants were collected from subsamples of over 250 mm using a Wild stereo microscope. Faunal remnants were determined up to species level as much as possible, and the number of undamaged specimen and undamaged halves of specimen (such as bivalve and ostracod shells) was counted. Abundance of these "bivalve" type of species was calculated for each subsample as the number of undamaged specimen + the number of halve shells/2. All abundances were expressed as the number of specimen per volume (n cm^{-3}), and subsequently multiplied by the sedimentation rate (cm y^{-1}) to get a sedimentation rate of the particular species at a particular time (n cm^{-2} y^{-1}).

Sources of variation – Faunal remnants in the sediment core can be autotochtonous or allochtonous, viz. material originating from animals that lived at the spot or from animals of which the remnants were transported from the original habitat to the German Bight or Vlieter channel. Variation in these remnants throughout the core may result from at least three different processes, namely variation in mortality, variation in spatfall and variation in transport rates.

Other time series – The proxy for spatfall of bivalves were compared with actual time series as determined for the Balgzand, the westernmost tidal flat of the Wadden Sea, between 1973 and 1997. Here, 15 permanent stations are marked by iron poles (i.e. 12 1-km transects and three 900-m^2 plots). These stations cover almost the full range of intertidal levels and sediment types in the westernmost part of the Wadden Sea (a.o. Beukema & Cadée 1997). Sampling is performed twice a year (in early spring and in late summer) applying a 1-mm sieve (Beukema 1974). For comparison of the bivalve densities, we only used the late summer data. Since the juveniles of bivalves generally settle during summer, it is considered that the abundance in late summer results in the most reliable index of spatfall for that particular year. Furthermore, we selected for each bivalves the stations at which late-summer density of juveniles of that particular species was high, i.e. on average > 100 m^{-2} between 1973 and 1997. We used spring data of Balgzand for comparison of the mudsnail densities. Furthermore, we compared our indirect mudsnail abundance data with sublittoral densities as determined in the western part of the Wadden Sea. Sampling is performed twice a year (in early spring and in late summer) applying a 1-mm sieve (Dekker 1998).

3 RESULTS

3.1 HYDROGRAPHY

Baltic Sea

We have analysed long-term data on salinity and oxygen concentration in the Baltic Sea. Due to the scarcity of the measurements and the focus of this study the salinity and oxygen data were annually averaged, so that only the low frequency relationships between both variables and with the atmospheric circulation has been considered. Also, essentially two depth levels in the Baltic were considered, an upper level, which represents average values of the upper 50 meters of the water column and a lower level including the average in waters deeper than 100 m.

Perhaps one of the most important results in this study was that salinity and oxygen concentrations in the Baltic Sea are negatively correlated at both levels, which is somewhat surprising, since oxygen is a non-conservative variable whereas salinity is. This fact (Fig. 3.1.1) suggests that the low-frequency evolution of both variables have a common forcing. We have therefore analysed the statistical relationships between salinity, oxygen and the atmospheric circulation by means of Canonical Correlation Analysis.

We have chosen the Sea Level Pressure (SLP) field as representative of the atmospheric circulation to perform the correlation analysis with the salinity and oxygen concentration. Long monthly time series of this variable covering the Northern Hemisphere are available, and at these time scales, different averagings in different seasons have been tried in this correlation analysis. It turned out that the atmospheric signal is essentially dominated by the winter (December-February) anomalies. Inclusion of other seasons or even averaging over the whole year did not significantly improve the results nor yielded different information. In the following only the results concerning the SLP winter averages are shown. The analysis therefore correlates the winter SLP (December of year y-1 to February in year y) with the salinity and oxygen concentrations averaged between January to December of year y. the SLP is directly related to the surface wind through the geostrophic relation. Figure 3.1.2 shows the two leading canonical pair of patterns of the winter mean SLP and the annually averaged salinity in the first 50 m.

The first canonical SLP pattern represents a region of higher SLP centred over the Gulf of Biscay, with anomalous geostrophic wind blowing from the northwest in the Baltic Sea. This pattern will be denoted hereafter as the Eastern Atlantic High. The associated salinity pattern shows in general positive values in the Gulf of Bothnia and central Baltic and negative values in the south-west and Gulf of Finland areas. The variance described by this salinity pattern is relatively small, only 12% of the total variance. The second SLP canonical pattern shows high pressure over the whole central North Atlantic and negative SLP anomalies over Greenland and Iceland. This second pattern is very similar to the well-known pattern of the North Atlantic Oscillation (NAO) (Lamb & Peppler 1987). The SLP describes the strength of westerly wind anomalies over the North Atlantic and in particular over the region connecting the North and the Baltic Seas. This pattern will be denoted as the North Atlantic zonal circulation pattern. The associated salinity pattern is negative in all stations in the Baltic Sea and describes a great part (61%) of the salinity variability. Since CCA is a linear method this pair of patterns also describes the relationship when both pairs belonging to a canonical pair have the opposite sign to the ones in Fig. 3.1.2.

The structure of the first canonical salinity pattern, associated with the Eastern Atlantic High, resembles the long-term horizontal salinity gradient in the Baltic Sea with lower salinity waters concentrated along the Swedish coast and higher salinity along the eastern coasts. This long-term salinity gradient is related to the mean weak cyclonic circulation, with more saline water inflowing from the North Sea being driven along the eastern coast. Although the inflow of more saline water masses occurs primarily at deeper levels, this long-term effect is also apparent at the surface (Kullenberg 1981). A plausible explanation for the association between the Eastern Atlantic High and the above mentioned salinity gradient may be that the anomalous anticyclonic (cyclonic) wind forcing associated with the SLP pattern slows the mean cyclonic circulation and weakens (strengthens) the horizontal salinity gradient. The second canonical pair represents a relationship between SLP and salinity. This relationship is not consistent with the hypothesis that higher than normal salinity in the Baltic is caused by direct wind-driven inflow of more saline waters from the North Sea, as has been documented to be the case for major episodes of North Sea water inflows (Matthäus & Schinke 1994, Lass & Matthäus 1996). Actually, the relationship described by this second pair is the opposite: stronger than normal westerly winds are associated in general with lower than normal salinities.

Figure 3.1.3 shows the results of the canonical correlation between SLP and oxygen in the upper levels. In this case only one canonical pair can be identified. The SLP pattern resembles the one obtained in the correlation with salinity, supporting the hypothesis that the coherent evolution of salinity and oxygen may have their origin in a common atmospheric forcing. The canonical SLP pattern is similar to the NAO pattern. Stronger than normal westerlies are associated in general with positive oxygen concentrations anomalies in the upper layer in all areas with the exception of the south-western Baltic, Arkona and Bornholm basins. The variance described by the oxygen pattern is however low, namely 21% of the total variability. It is not completely clear how to interpret this result. One possibility may be that stronger than normal zonal winds may cause increased water mixing in the upper layer and thus positive oxygen anomalies. Other possible explanation may involve water inflows from the North Sea in periods when the zonal circulation is stronger. However, the influence on the inflowing North Sea waters should not be obvious for the surface layer because being denser they should penetrate as deep current and the surface waters in the Baltic Sea are probably in the mean not much less oxygenated than in the North Sea, since both oxygen concentrations will tend to be in equilibrium with the atmosphere.

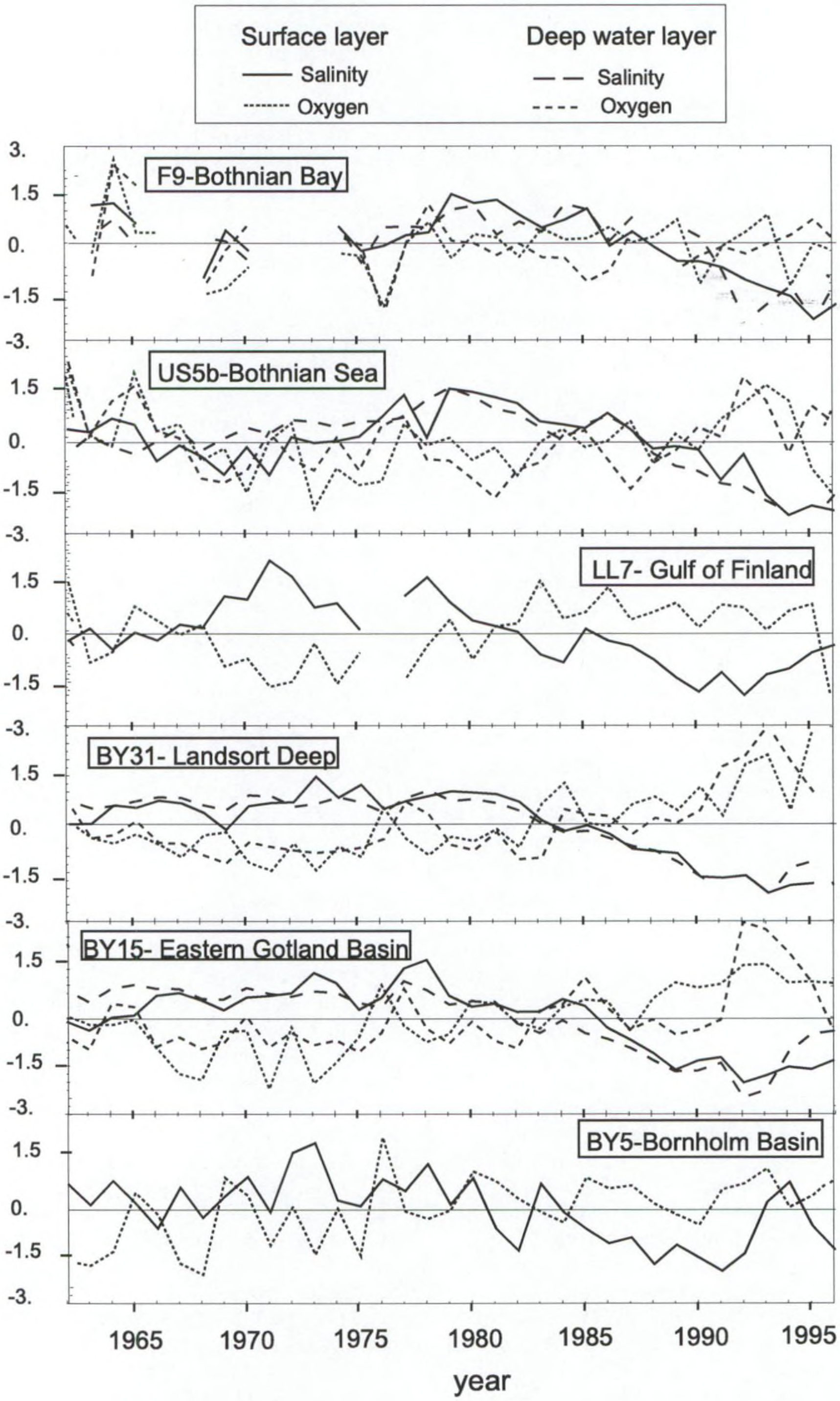


Fig. 3.1.1 Time series of annually averaged salinity and oxygen concentrations at some stations in the Baltic Sea. Surface values have been averaged in the upper 50 meters; deep-water values have been averaged below 100m depth.

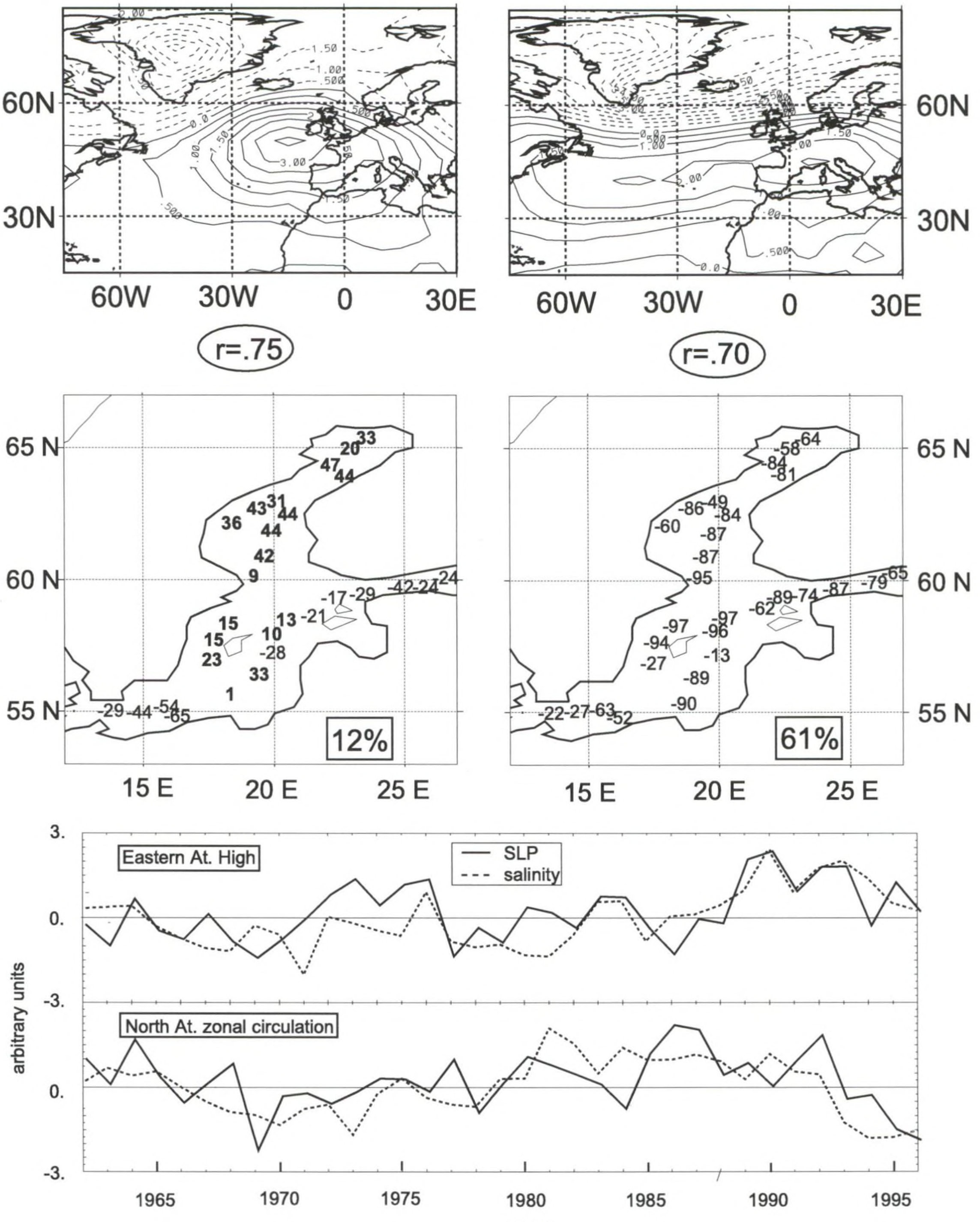


Fig. 3.1.2 The two leading canonical pair of patterns between sea-level-pressure (mb) in wintertime and annual salinity (normalised to unit variance, 100 in the figure) in the upper 50 meters in the Baltic Sea. The canonical correlation is encircled. The explained variances are also indicated.

We have used the output of a long integration with the state-of-the-art climate model ECHAM4-OPYC3. The ECHAM4 atmosphere spectral model was used with a horizontal resolution of T42 (about 2.8^{o}). The technical details of the integration as well a summary of the most important results can be found in Roeckner et al. (1998). In this experiment the model was forced with historical greenhouse gas concentrations starting in 1860 until 1990 and after this point the concentrations were assumed to evolve according to the projections envisaged by the Intergovernmental Panel on Climate Change (IPCC) in the Scenario A (IPCC 1992). Figure 3.1.4 shows the time series describing the evolution of the relevant atmospheric circulation patterns in this climate simulation.

The westerly zonal circulation becomes more intense in the last decades of the climate simulation. The associated canonical patterns of salinity (negative at almost all stations) and oxygen (positive) describe a great part of the total variability. Therefore, it can be expected that such atmospheric circulation changes will be related to decreased salinity (due to increased precipitation and run-off in the Baltic Sea catchment area) and increased levels of oxygen concentration. In addition to these atmospheric changes, the Eastern Atlantic High pattern tends to become weaker in the simulation. Since this pattern is related to an anomalous horizontal salinity gradient in the upper layers this atmospheric trend could cause a decrease of the horizontal salinity gradient in the west-east direction. However, the variances described by the upper salinity and upper oxygen canonical patterns are smaller and the trends should be smaller.

North Sea

Concerning the German Bight, an statistical model was built with 4 air pressure EOFs and 1 salinity EOF. We selected a 12-month average of salinity, centered around August, and a 9-month average of air pressure, centered around the previous November. The structure of the obtained results can be seen in Fig. 3.1.5. A salinity mean centered around the summer months is correlated to an air pressure mean about 6 to 18 months earlier.

The canonical correlation pattern (Fig. 3.1.5) show a positive pressure anomaly of typically 2hPa over Europe that is correlated with a positive salinity anomaly of typically 0.5 psu in the German Bight. Using this model the salinity time series can be reconstructed based on the simultaneous SLP observations (Fig. 3.1.6). The model reproduces the interannual variability fairly well. The correlation between estimated salinity and observation data from other stations indicated that the major part of the variability is in-phase across the entire German Bight and, hence, that the estimated time series is valid for the entire region.

The associated pattern of storm activity explains only 10% of variance over Europe and the North Atlantic. This means that the overwhelming portion of storm activity is not correlation to the occurrence of the CCorA air pressure is r=0.2. It can be concluded that neither variability in storm activity, nor variability in the NAO can explain the found relationship between air pressure and salinity.

The associated pattern of precipitation shows that a round 50% of the variability is associated with the canonical air pressure pattern. The depicted anticyclone over northern Europe coincides with low precipitation and high salinities. The associated pattern of for the west-east component of the wind stress explains 50% of variance over the English Channel, a westerly wind stress coincides with low salinities. The associated pattern for the north-south component explains 70% of variance over the northern North Sea, a northerly wind stress coincides with low salinities.

The statistical model has been applied to the output of a climate change simulation with the ECHAM climate model. The model estimates a slight increase of the intensity of the SLP pattern in the future, and thus an increase of rainfall over the catchment area, giving rise to slightly reduced salinities for the next decades.

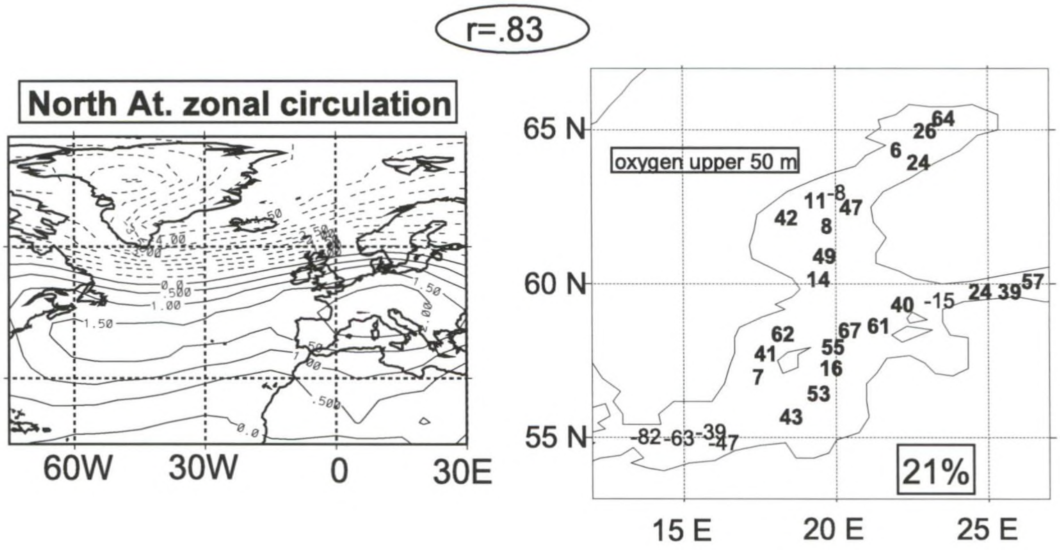


Fig. 3.1.3 Leading canonical correlation pair between sea-level-pressure (mb) in wintertime and annual oxygen concentration in the upper 50 meters. The canonical correlation is encircled and the variance explained by the oxygen pattern is also indicated.

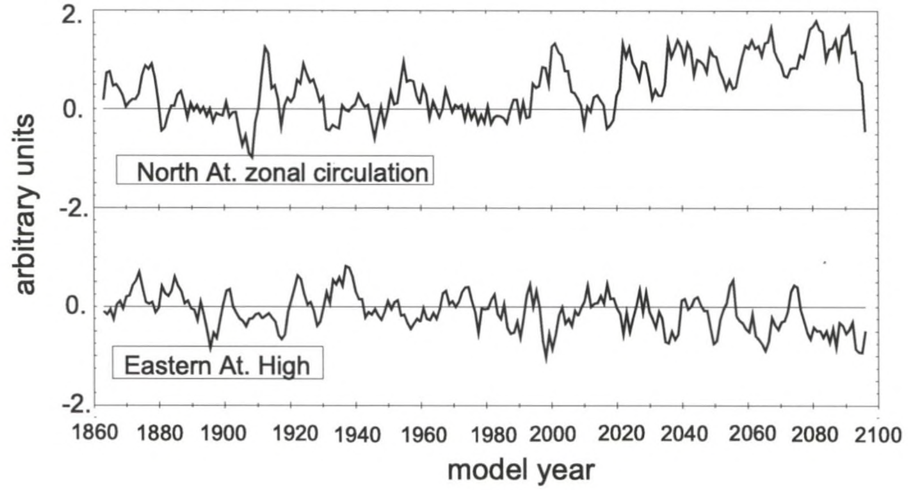


Fig. 3.1.4 Future evolution of the atmospheric circulation patterns relevant for the hydrographic variables in the North Sea, simulated by the ECHAM4-OPYC3 climate model driven by the greenhouse-gases concentrations envisaged by the IPCC in their scenario A.

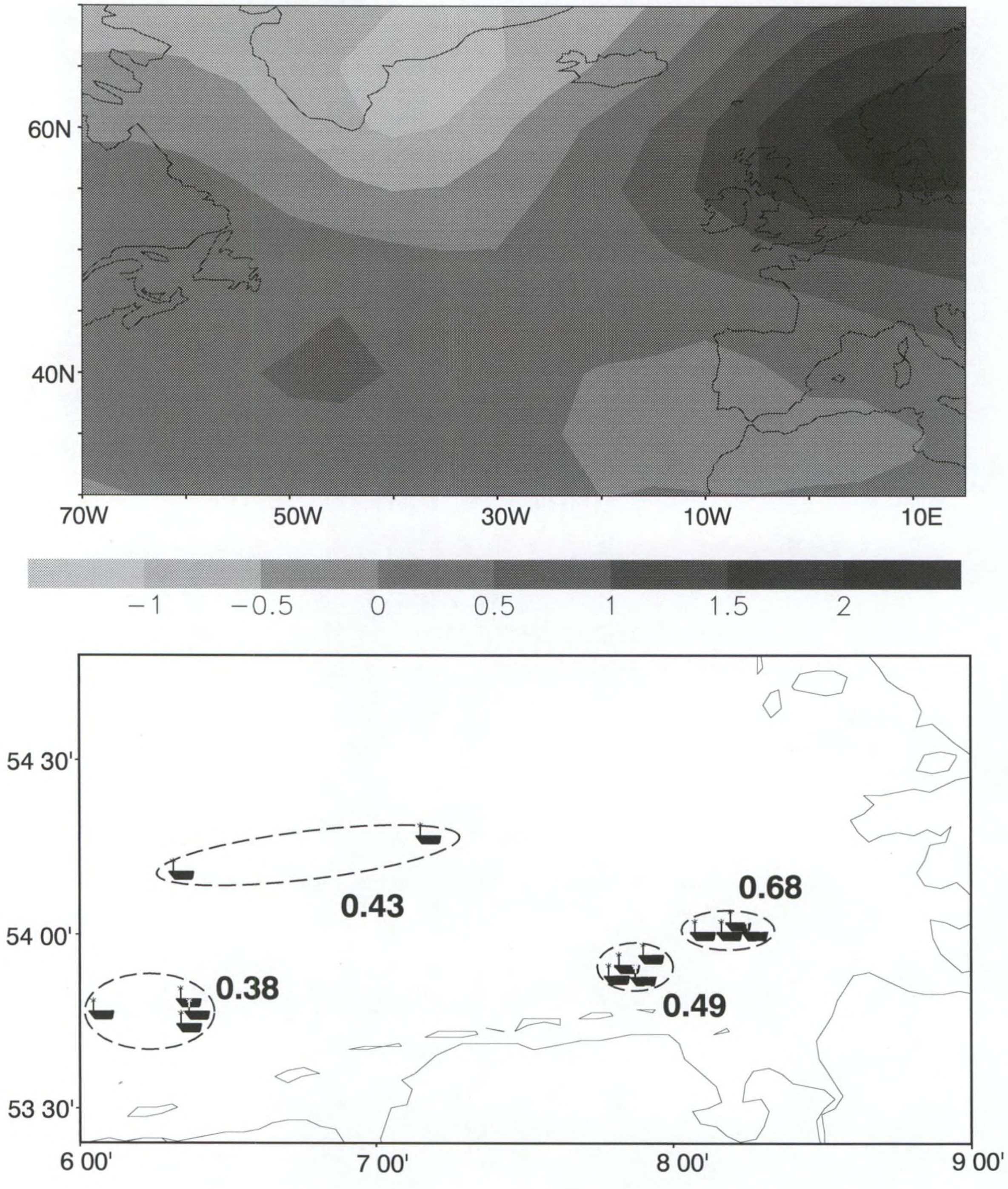


Fig. 3.1.5 Leading canonical correlation patterns between sea-level-pressure in the North Atlantic (12-month-running-mean centered in November) and salinity in the German Bight (9-month-running-mean centered in the following August).

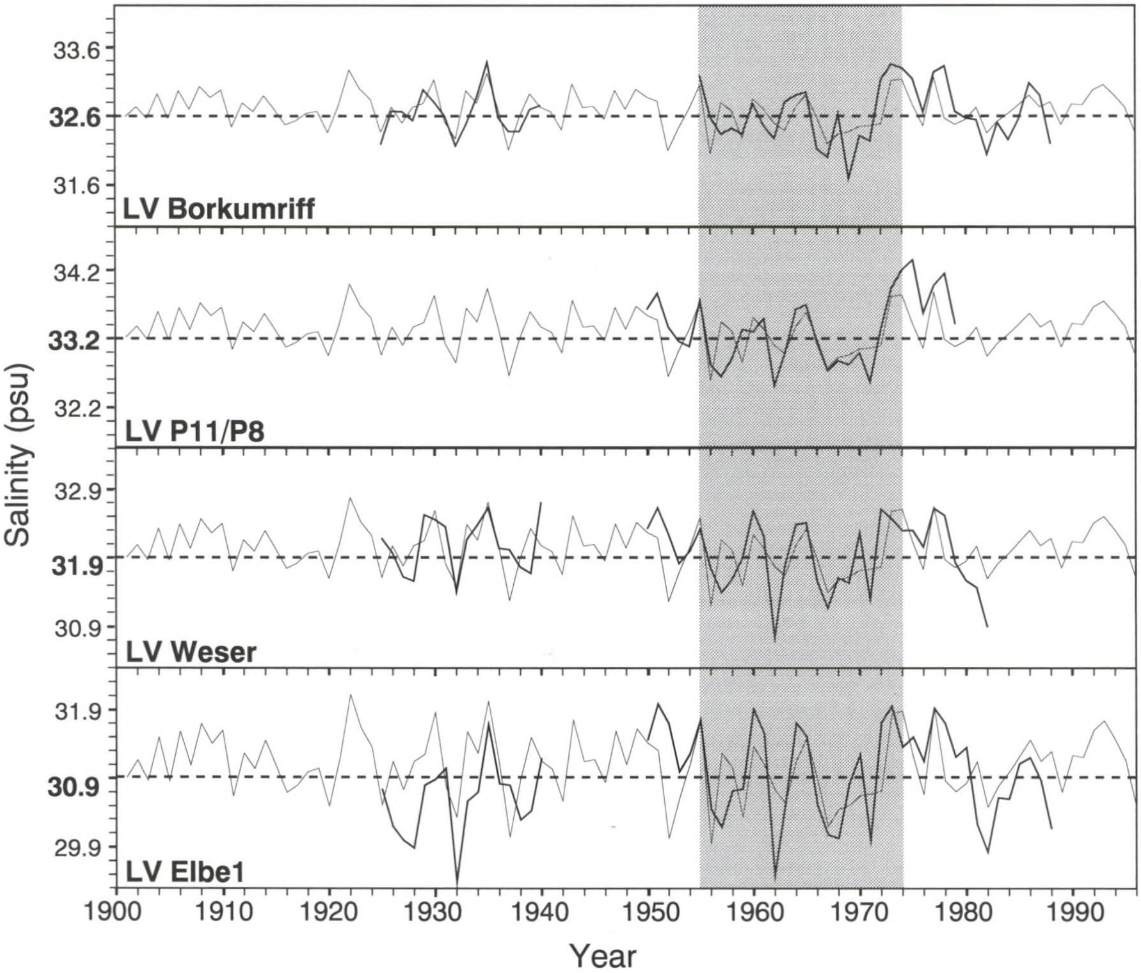


Fig. 3.1.6 Observed and reconstructed (based on the sea-level-pressure) time series in the German Bight.

3.2 PLANKTON

Western Wadden Sea

Phytoplankton dynamics

The first two principal components (PCs) of the PCA of the abundance of algal species accounted for 34% to 39% of the total variance of the $\log_e$-transformed and standardized annual averages (Philippart et al. 2000). Covariability between species was relatively high considering that the explained variance by the first two PCs is approximately six times higher than it would have been if the time series of the 32 algal species were not correlated at all (i.e. 2/32 ·100% » 6%). Thus more than one-third of the year-to-year variation in 32 algal species is accounted for in just two dimensions.

Based on the biplot of July-Aug, the study period can be divided into three successive periods, i.e. 1974-1976, 1978-1987 and 1988-1994 (Philippart et al. 2000). As was observed for March-April, the first three years (1974-1976) were characterized by relatively low abundances of most algal species considered. The following period was characterized by (i) an increase in most algae in particular *Rhodomonas* and other (small and large) flagellates, and (ii) an alternation of two different groups of dominant algal species. Between 1978 and 1987, the algae community was characterized by relatively high abundances of small *Chaetoceros* species and Pennate diatoms. In the following years (1988-1994), *Leptocylindrus minimus* appeared in relatively high abundances.

Changes in species compositions as described above were accompanied by changes in chlorophyll-a concentrations (Fig. 3.2.1A). Annual mean values ranged from 4.6 mg m^{-3} in period A (1974-1976) to more than 9 mg m^{-3} hereafter (periods B1 and B2). During the entire study period, monthly averaged chlorophyll concentrations were more or less similarly low during the beginning of the year, *viz.* from January to March. The magnitude of the spring bloom, however, doubled between 1974-1976 (period A) and 1978-1994 (periods B1 and B2). After 1988 (period B2), the timing of the peak of the spring bloom appeared to have shifted one month forward, *viz.* from May to April (Philippart et al. 2000).

The interannual changes in phytoplankton biomass and species compositions were accompanied by changes in size distribution. The increase after 1978 was mainly due to species with large individual cell volumes, particularly when going from period A (1974-1976) to period B1 (1978-1987). The additional biomass of the algae community during the nutrient-controlled period of the year (July-Aug) then was characterized by a high proportion (> 65%) of diatom species with an individual cell size of more than 1000 μm^3 (Fig. 5) such as large *Thalassiosira* sp. (8%), *Erataulina pelagica* (8%), *Rhizosolenia imbricata* (14%), *R. hebetata* and *R. setigera* (together 20%), and by smaller diatoms that are able to form colonies, i.e. *Chaeotoceros socialis* (30%).

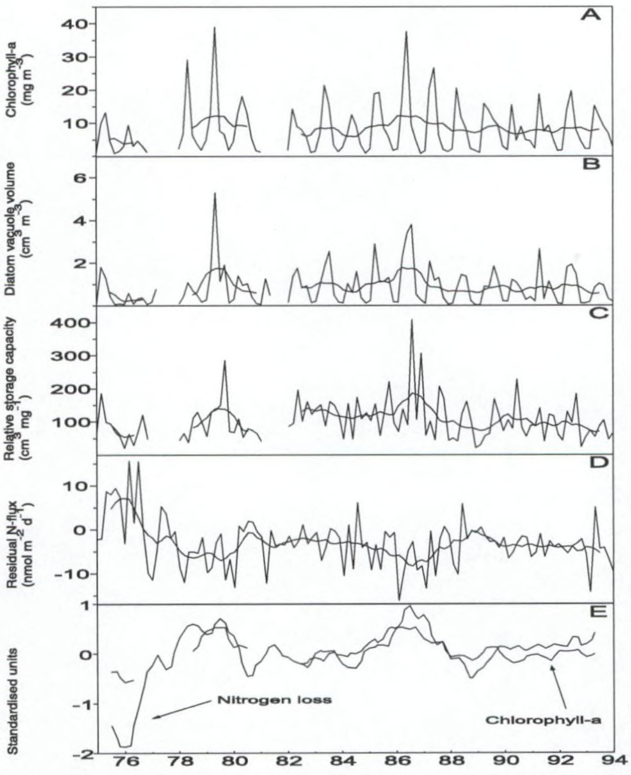


Fig. 3.2.1 Bi-monthly averaged time-series and 12-month running means in the western Wadden Sea from 1975 to 1993. A. Chlorophyll-a concentrations (mg m^{-3}). B. Total vacuole volume of diatoms (cm^3 m^{-3}). C. Relative storage capacity (total diatom vacuole volume per unit of chlorophyll-a; cm^3 mg^{-1}). D. Residual nitrogen fluxes (mmol m^{-2} d^{-1}) as estimated by means of nitrogen budgeting. E. Running means of standardised (zero mean, unit variance) chlorophyll-a concentrations (thickest line) and nitrogen loss (Philippart et al. 2000).

The annual mean of the total diatom vacuole volume increased from less than 0.4 cm^3 m^{-3} during the mid-1970s (period A) to more than 1.5 cm^3 m^{-3} until the mid-1980s (period B1), and decreased hereafter to less than 1.3 cm^3 m^{-3} (Fig. 3.2.1B). Relative storage capacity (total diatom vacuole volume per unit of chlorophyll-a; Fig. 3.2.1C) increased from more than 80 cm^3 mg^{-1} to almost 170 cm^3 mg^{-1} from period A to period B1, and decreased to less than 140 cm^3 mg^{-1} during the last years of the study period (1988-1994). Relative storage capacity followed a similar trend as chlorophyll for the entire study period. Applying the empirical relationship from other coastal marine waters to ambient chlorophyll data, the annual mean intracellular pool of nitrate in the water column was 0.2 mmol m^{-3} after 1978, corresponding to an intracellular nitrate concentration of about 200 mM. Such an accumulation of nitrate by phytoplankton is high compared to the range reported for marine diatoms between 20 and 150 mM (Dortch et al. 1985, Stolte & Riegman 1995, Villareal & Lipschultz 1995).

Primary production

Production estimates – Applying the empirical relationships on local nitrogen loadings, the total primary production in the western Wadden Sea was estimated to have been approximately 410 gC m^{-2} y^{-1} between 1974 and 1994 (Fig. 3.2.2A). Pelagic production rates would have been approximately 310 gC m^{-2} y^{-1} in the

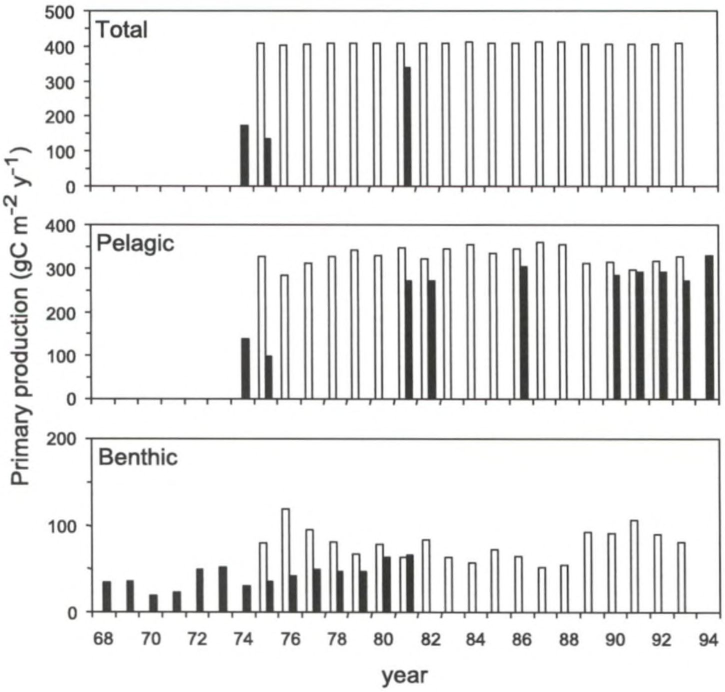
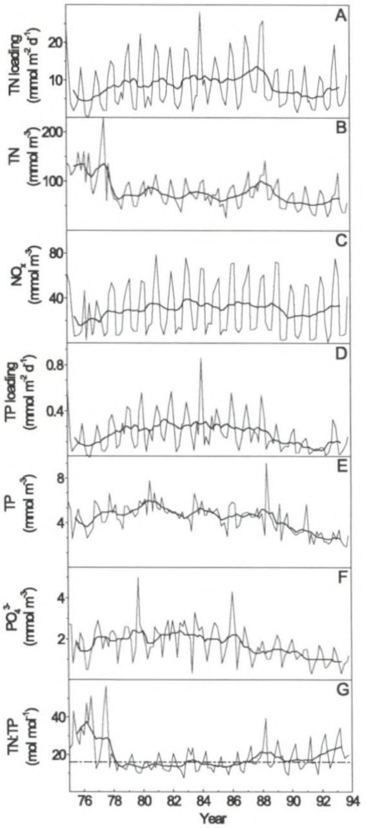


Fig. 3.2.2 Total (A), pelagic (B) and benthic (C) primary production (gC m^{-2} y^{-1}) in the western Wadden Sea between 1968 and 1994. White bars indicate the production estimates as derived from N loadings from the freshwater lake IJsselmeer according to empirical relationships for shallow marine coastal areas supplied by Borum & Sand-Jensen (1996); solid bars show actual production values as measured in the study area (Philippart & Cadée 2000).



mid-1970s, 340 gC m^{-2} y^{-1} around the 1980s and roughly 320 gC m^{-2} y^{-1} during the early 1990s (Fig. 3.2.2B). Consequently, coinciding benthic production must have been almost 100 gC m^{-2} y^{-1}, 70 gC m^{-2} y^{-1} and around 90 gC m^{-2} y^{-1}, respectively (Fig. 3.2.2C).

Production measurements – In the Marsdiep tidal inlet, pelagic production was approximately 150 gC m^{-2} y^{-1} during the 1970s, and more than 300 gC m^{-2} y^{-1} in the 1980-1990s (Cadée 1986, 1992). During the 1970s, phytoplankton production near the Marsdiep tidal inlet was approximately 150 gC m^{-2} y^{-1} (Cadée & Hegeman 1974a) and in the water column over the tidal flats around 20 gC m^{-2} y^{-1} (Cadée & Hegeman 1974b). Applying the geomorphologic ratio (Hoppema 1991) to Marsdiep measurements, resulted in pelagic production rates for the western Wadden Sea of less than 100 gC m^{-2} y^{-1} in the mid-1970s, and more than 280 gC m^{-2} y^{-1} hereafter (Fig. 3.2.2B). Rates of primary production of microphytobenthos increased between 1968

Fig. 3.2.3 Bimonthly averaged time-series and 12-month running means in the western Wadden Sea from 1975 to 1993 (Philippart et al. 2000). A. Total nitrogen loadings (mmol m^{-2} d^{-1}). B. Total nitrogen concentrations (mmol m^{-3}). C. Summed nitrate and nitrite concentrations (mmol m^{-3}). D. Total phosphorus loadings (mmol m^{-2} d^{-1}). E. Total phosphorus concentrations (mmol m^{-3}). F. Phosphate concentrations (mmol m^{-3}). G. Ratios between total nitrogen and total phosphorus concentrations (mol mol^{-1}). The dotted line represents the Redfield ratio (TN: TP=16 mol mol^{-1}). Time series on nutrient loadings and concentrations were taken from the water quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public Works.

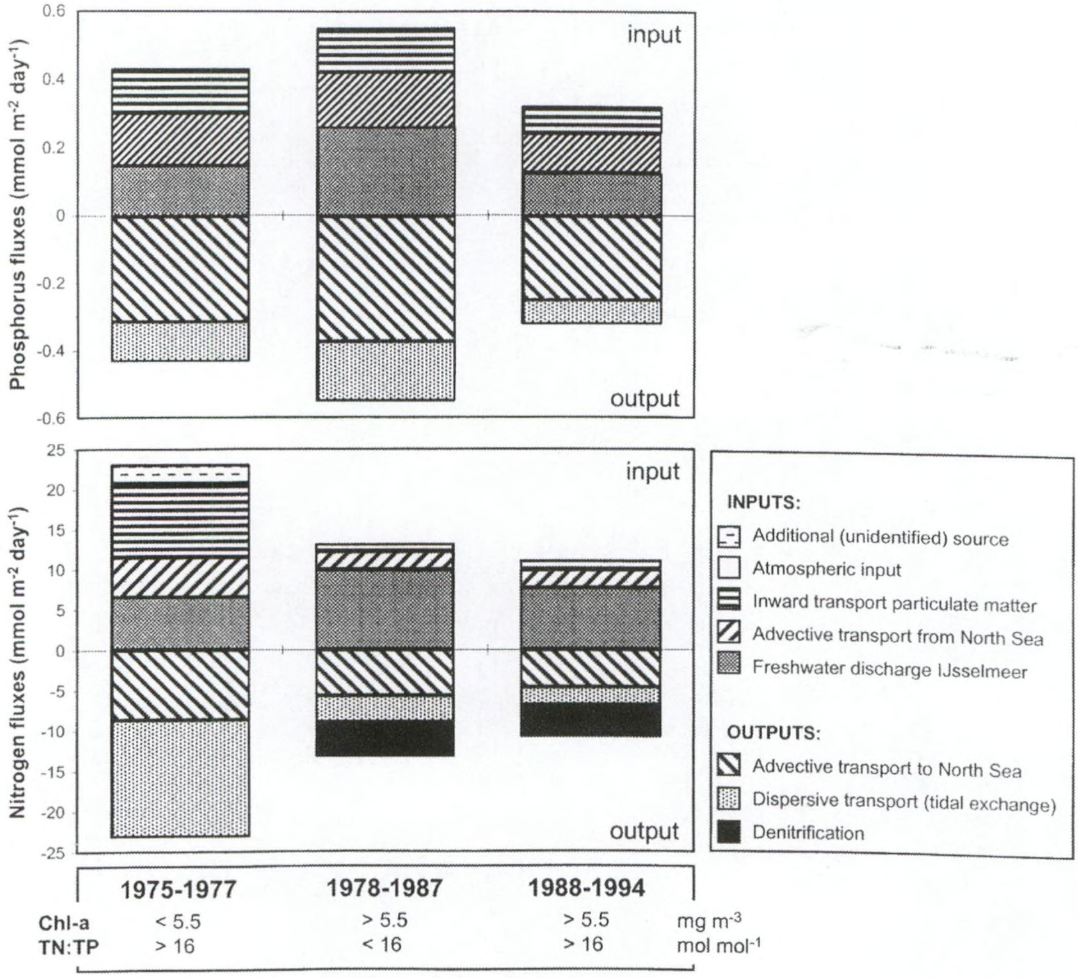


Fig. 3.2.4 Annual averages of phosphorus and nitrogen mass fluxes (mmol m^{-2} day^{-1}) of the western Wadden Sea between 1975 and 1993 (Philippart et al. 2000). The nutrient budget calculations were based on the hydrodynamic model by Ridderinkhof et al. (1990), and data on freshwater inputs and nutrient concentrations (114 bimonthly averages) were taken from the water quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public Works. The division into three different periods was based on indices for trophic state (indicated by annual averaged chlorophyll-a concentrations) and TN: TP ratio.

TABLE 3.2.1

Correlation coefficients (r) of time series on indices of zooplankton abundance at Helgoland Roads (predictands) and climate in northwestern Europe (predictors) from 1974 to 1995

Zooplankton taxon	Predictand	Predictor	EOFs	r
Noctiluca scintillans	Log-abundance (summer)	SST (winter)	3	0.72
	Integrated log-abundance (winter→summer)	SST (winter)	3	0.75
	Net increase log-abundance (winter→summer)	SST (winter)	3	0.75
Spionid larvae	Log-abundance (winter)	SLP (winter)	2	0.91
Temora longicornis	Log-abundance (winter)	NAOI (winter)	1	0.62

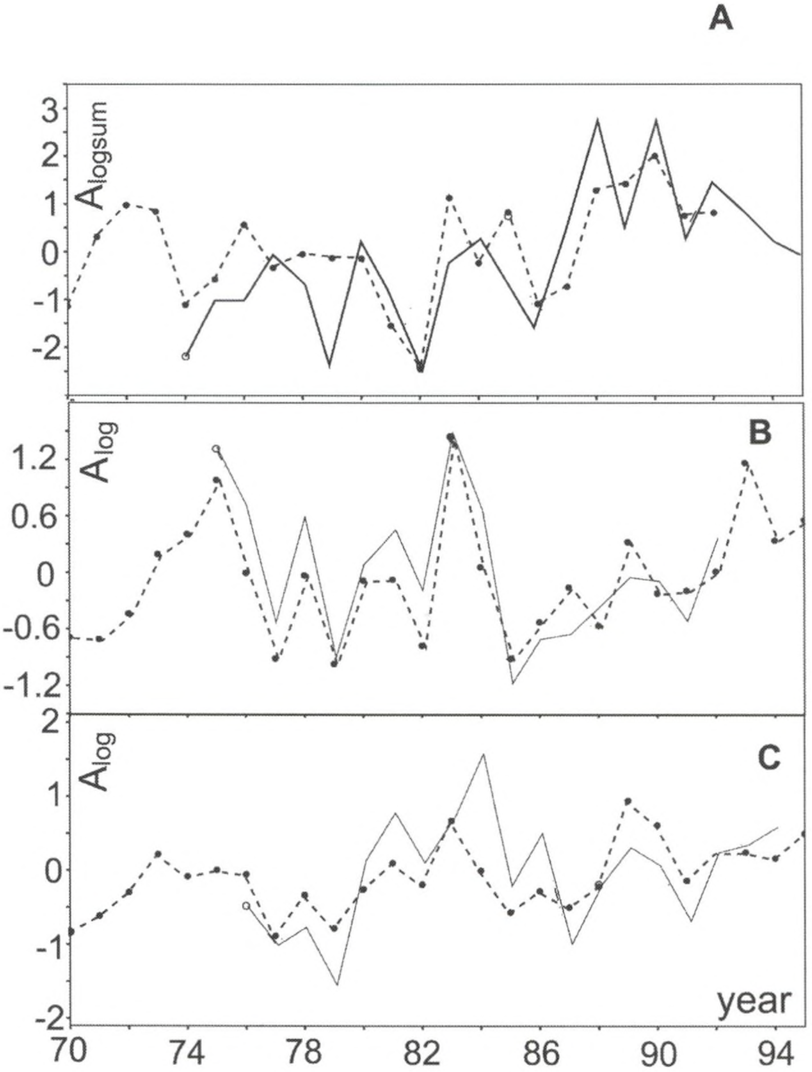


Fig. 3.2.5 A. Observed (solid) and estimated (dot-dashed) anomalies of *Noctiluca scintillans* (integrated log-abundance; Jan-July) at Helgoland Roads between 1970 and 1995. The estimations on zooplankton abundance were derived from the three leading EOFs of Sea Surface Temperature (°C; Nov-Jan). B. Observed (solid) and estimated (dot-dashed) anomalies of Spionid larvae (log-abundance; Jan-Feb) at Helgoland Roads between 1970 and 1995. The estimations on larvae abundance was derived two leading EOFs of Sea Level Pressure (hPa; Dec-Feb). C. Observed (solid) and estimated (dot-dashed) anomalies of *Temora longicornis* (log-abundance; Jan-Feb) at Helgoland Roads between 1970 and 1995. The estimations on zooplankton abundance were derived from the North Atlantic Oscillation Index (Heyen et al. 1998).

and 1981 from 100 gC m^{-2} y^{-1} to more than 200 gC m^{-2} y^{-1} (Cadée 1984). For the early 1970s, production by microphytobenthos was found to be 100 gC m^{-2} y^{-1} at tidal flats, 10 gC m^{-2} y^{-1} in relatively shallow and close to 0 gC m^{-2} y^{-1} in relatively deep subtidal areas (Cadée & Hegeman 1974b, Cadée 1980). Corrected for the geomorphologic properties of this particular area (Hoppema 1991) microphytobenthos production rates for the western Wadden Sea were more than 40 gC m^{-2} y^{-1} in the mid-1970s, and almost 60 gC m^{-2} y^{-1} during the early 1980s. The average contribution of macroalgae to the total Wadden Sea primary production is considered to be relatively small, approximately 5 gC m^{-2} y^{-1} during the mid-1970s (Goedheer 1977, van den Hoek et al. 1979, Cadée 1980) and remained more or less constant during the entire study period (J.J. Beukema, pers. comm.). Average primary production of seagrasses in the western Wadden Sea was close to 0 gC m^{-2} y^{-1} during the entire study period.

Comparison of production estimates and measurements – During the 1980s and 1990s, both the pelagic and total production estimates were in good agreement

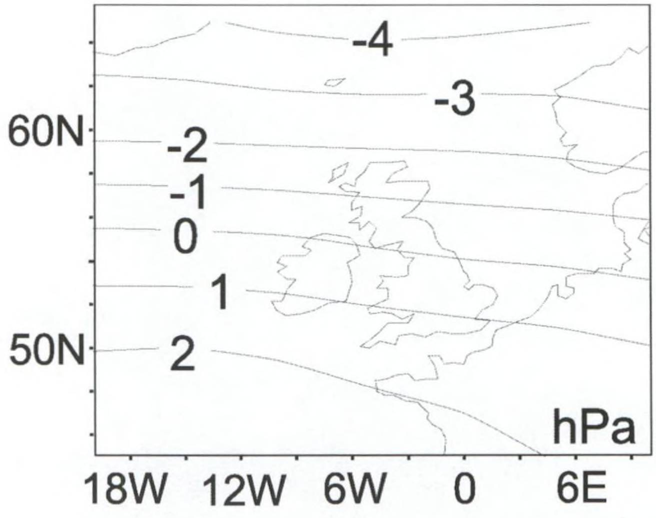


Fig. 3.2.6 Main geographical pattern of Sea Level Pressure (hPa; Dec-Feb) of Northwestern Europe, explaining 40% of SLP variance between 1970 and 1995. The pattern shows a latitude gradient with negative pressure anomalies in the north and positive anomalies in the south (Heyen et al. 1998).

with the actual field data on primary production in the western Wadden Sea (Fig. 3.2.2). In general, the phytoplankton production estimates of on average 330 gC m^{-2} y^{-1} were higher (by ca. 15%) than the actual measurements (actual mean value 280 gC m^{-2} y^{-1}). In 1981, the estimate of the total production was approximately 20% higher than the sum of the actual production rates of phytoplankton, microphytobenthos and macroalgae (Fig. 3.2.2A). During the 1970s, however, the estimated pelagic production of more than 300 gC m^{-2} y^{-1} was much higher than actually measured production for phytoplankton during this period, i.e. less than 100 gC m^{-2} y^{-1} (Fig. 3.2.2B). Because pelagic production represented the main part of total production (> 75%), similar differences between estimated (400 gC m^{-2} y^{-1}) and measured (150 gC m^{-2} y^{-1}) rates of total production were observed. The measured values of pelagic production in the 1960s and early 1970s were more or less constant (ca. 150 gC m^{-2} y^{-1} for the Marsdiep tidal inlet) and consistent with chlorophyll and algae density data (Cadée 1986, 1992). We believe, therefore, that the model strongly overestimated the pelagic as well as the total production in the western Wadden Sea during the beginning of the study period.

Nutrient dynamics

The increases of N and P inputs from land from the mid-1970s until the end of the 1980s were followed by distinct decreases (Fig. 3.2.3). Concentrations of nitrate plus nitrite (NO_x), total phosphorus (TP) and phosphate (PO_4^{3-}) in the Marsdiep reflected these changes in the loadings. In contrast, mean total nitrogen concentrations (TN) dropped sharply from 100-150 to 50-100 mmol m^{-3} between 1977 and 1978 and remained at this lower level ever since. Up to mid-1977, the mean TN: TP ratio during the growing season from March to August was mostly much higher (40 ± 6) than the Redfield ratio (Redfield et al. 1963). This suggests that, on average, phosphorus rather than nitrogen was controlling net annual community phytoplankton production. Between 1978 and 1987 with relatively low TN: TP ratios (15 ± 2), nitrogen was probably more often controlling than phosphorus. During this period, nitrate was the main nitrogen source (Riegman et al. 1992) with NO_x concentrations significantly higher than 1 mmol m^{-3} even in summer, which may point at other limiting factors than N or P. Growth conditions re-shifted towards P-limitation after 1987, as shown by the increase of TN: TP ratios (21 ± 3) in most recent years (Philippart et al. 2000).

For the phosphorus budget (Fig. 3.2.4), both the summed inputs and outputs were higher during period B1 (1978-1987) than during period A (1974-1977) and period B2 (1988-1993). The residual flux of the phosphorus budget calculations was, however, more or less constant during the entire study period. The average flux of 0.11 mmol TP m^{-2} d^{-1} between 1975 and 1993 is similar to the inward transport of particulate matter retaining 2400 kg P per tide as estimated by Postma (1961) for the early 1950s. For the nitrogen budget (Fig. 3.2.4), both the summed inputs and outputs declined from the period between 1974 and 1977 to period B1 (1978-1987) and period B2 (1988-1993), despite the increase in nitrogen loadings from land. From 1975 to 1977, the exchange flux to the North Sea was more than four times the magnitude of this flux hereafter. Budget calculations imply that the high TN concentrations in the western Wadden Sea during period A were accomplished by a high rate of accumulation of particulate matter originating from the open sea or trapped in the Wadden Sea basin and a relatively small gain from an unknown source. After 1978 (periods B1 and B2)

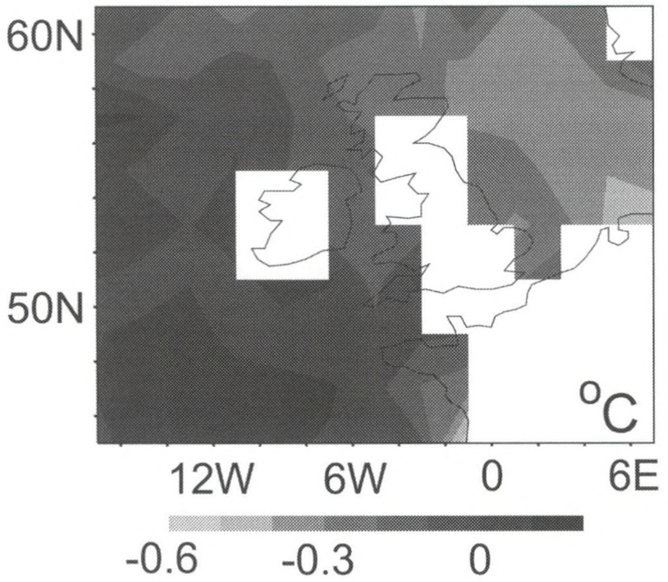


Fig. 3.2.7 Anomalous geographical pattern of Sea Surface Temperature (°C; Nov-Jan) of Northwestern Europe. This pattern shows an anomalously cold winter, corresponding with anomalously low abundances of *Noctiluca scintillans* (Heyen et al. 1998).

the inward transport of particulate nitrogen from the open sea decreased. At the same time, the residual nitrogen flux shifted from net gain into net loss (Fig. 3.2.4).

German Bight

Interspecific comparison of the time series revealed that only the two copepods *Temora longicornis* and *Acartia sp*. are related to each other. Hence, in addition to relating the two species separately to climate, the 1st EOF of a compound vector of these species was related to climate, too (the EOFs of the compound vector were calculated from the correlation matrix to avoid the dominance of the species with the higher variability).

<u>*Noctiluca scintillans*</u>
Three different correlations were detected between sea surface temperature (SST) and *Noctiluca scintillans* (Table 3.2.1). However, since the highest abundances of *N. scintillans* occur in summer, the variables 'log-abundance in summer', 'integrated log-abundance from winter to summer' and 'net increase of log-abundance between winter and summer' all depend on the height of abundance in summer. Hence, the three detected correlations in Table 3.2.1 all represent similar information. The leading three EOFs of the November to January SST field are used to estimate the integrated log-abundance of *N. scintillans* from January to July. The skill of the model is r = 0.75 and ß = 0.56, which is significantly higher than the 99% confidence level (r_{99} = 0.6, $ß_{99}$ = 0.3).

The SST CCA-pattern shows the entire North Sea to be cold (Figure 3.2.5A). If this is the signal that influences *N. scintillans*, it can be expected that a relationship between *N. scintillans* and the 1st EOF of the finely resolved North Sea SST data exists as well. The reason is that - on the monthly time scale - about 80% of SST variance in the North Sea is in phase and therefore represented by the 1st EOF (Figure 3.2.6). This figure compares the time series of the integrated log-abundance of *N. scintillans* from January to July with the time series of the 1st EOF of the finely resolved North Sea SST from November to January (r=0.63). The conclusion is that the detected correlation is based on the simple signal 'warm North Sea in winter' or 'cold North Sea in winter' and that spatial details play only a minor role.

<u>Spionid larvae</u>
A high correlation exists between the log-abundance of Spionid larvae in winter and the three leading EOFs of the winter SLP (Table 3.2.1). The skill is highest between the January to February mean of log-abundance and the November to January mean of SLP (r = 0.91, P = 0.76), and this is clearly above the 99% confidence level obtained for 10000 Monte-Carlo simulations (r_{99} = 0,6, $ß_{99}$ = 0.3).

The information in the SLP is contained in the two leading EOFS, which explain 45% and 37% of SLP variance, respectively. Hence, the important information is large scale. Fig. 3.26B shows the comparison of the observed and estimated log-abundance of Spionid larvae, if two SLP EOFs are used as predictors. The skill of the model is r = 0.86 and b = 0.71. The SLP

CCA pattern (Fig. 3.2.7) shows a gradient with low-pressure anomalies in north and high-pressure anomalies in the south. This gradient coincides with an anomalously high number of Spionid larvae.

Temora longicornis
A correlation maximum exists between the log-abundance of *Temora longicornis in* winter and the North Atlantic Oscullation (NAO) index in the same period (Table 3.2.1), with the highest skill between the NAOI and the January to February mean of log-abundance. This combination is shown in Fig. 3.2.5C. The obtained skill is $r = 0.62$ and $ß = 0.38$, which is slightly higher than the 99% confidence level ($r_{99} = 0.6$ and $ß_{99} = 0.2$). An anomalously high NAO index coincides with an anomalously high abundance of *T. longicornis* and, in the same way, a weak NAO index coincided with low abundances of this zooplankton species.

The NAO index is closely related to the North Sea SST in late winter and spring (Becker & Pauly 1996, Dippner 1998, Kröncke et al. 1998). Fromentin & Planque (1996) describe a relationship between the NAO index, winter SST and two copepod species. However, only about 20% of the December to February SST in the south-eastern North Sea are associated with the January to February log-abundance of *T. longicornis (*Heyen et al. 1998). This low percentage might indicate that SST is not a first-order influence on *T. longicornis.* Furthermore, an influence of storm activity is not likely, since its associated pattern does not explain more than 5% of the variance at any point in the North Sea. Within the study period, no correlation was found between abundance indices of this species and the run-off of the river Elbe.

3.3 MACROBENTHOS

Western Wadden Sea

The Wadden Sea data was used to develop statistical tools and several multivariate methods were applied on this data set, exploring both spatial distribution and temporal development in the macrobenthic communities and their relation to environmental variability. For a general description of species distribution in the area and variability of environmental factors included in the analysis, see Zuur 1999.

All the different multivariate methods (Correspondence Analysis (CA), Canonical Correspondence Analysis (CCA), Restricted Gaussian Regression (RGR) and Restricted Generalized Additive Modelling (RGAM)) applied on 1996 data showed very similar results and both CA and CCA indicated that relevant environmental variables had been included, no latent variable could explain better the variability. By using CCA a gradient from northern/north-eastern transects to south and south-western areas was detected. The first area was characterized by *Nephtys hombergii*, *Scoloplos armiger*, *Lanice conchilega* and *Cerastoderma edule* 0 year-class and the latter by *Nereis diversicolor* and *Macoma balthica* of year-classes 0, 2 and 3. This gradient is mainly determined by the median grain size of the sediment and distance to tidal stream. Other methods related the variability to the distance to dike as well.

Analysis of the long-term data (1974-1995) with RGR applied on each year separately indicated that the environmental gradient during different years is mainly determined by the distance to tidal inlet. Using one underlying gradient based mainly on this variable, changes in the ecological parameters (maximum, optimum and tolerance (distribution) of species abundance) were estimated. The results for species fitted well in the model indicated an increase of the maxima of *S. armiger and Heteromastus filiformis* from late 1970s to the mid 1980s, followed by a minimum 1990 and an increase again (Fig. 3.3.1). For the estimated maxima of *C. edule* 0-year class a 4-year cyclical pattern was evident. Cross-correlations between the ecological parameters for different species showed correlations between the maxima and optima of *N. diversicolor, S. armiger* and *H. filiformis* which could indicate interactions between the species or similar response to external factors. However, only low correlations were found between ecological and temporal environmental parameters with this approach.

In the approach of Dynamic GAM, a smoothing function, describing the average, over time, species-environmental relationship and a stochastic trend, representing deviations from the previous relationship, were estimated for each species. Based on cross-correlations between species trends, various groups could be identified, (1) *N. diversicolor, S. armiger*, *H. filiformis*, *N. hombergii* and *Mya arenaria*, (2) *C. edule* year classes 0, 1, 2, (3) *M. balthica* year classes 0, 1, 2 and (4) *M. balthica* year class 3 and *Arenicola marina*. Within these groups, estimated trends were highly correlated with a time lag of –2 and 2 years. Considering cross-correlations between species trends and temporal environmental variables, most trends were significantly ($p < 0.05$) correlated to water temperature with time lags of 0, 1 and 2 years (Table 3.3.1). The estimated GAM curves, describing the average species-environment relationship, could also be divided in groups of similar response, namely (1), *S. armiger* and *N. hombergii* (2) *N. diversicolor*, *H. filiformis*, *A. marina*, *M. balthica* year classes 0, 1, 2 and 3, and *M. arenaria* (3) *L. conchilega* and *C. edule* year classes 0, 1 and 2.

North Sea

Dutch continental shelf monitoring data

Spatial analysis of 1996 data demonstrated different communities in different areas (Zuur 1999). Both CA and CCA indicated that the Oyster ground area is characterized by *Mysella bidentata* and *Nephtys hombergii* and high mud content while *Bathyporeia elegans* and *Nephtys cirrosa* are abundant in the offshore sites with coarse sediments and at one coastal site. At two of the coastal sites *Spisula subtruncata* was abundant. However, these environmental variables could explain only minor part of the variability in zoobenthos, indicating that evidently other, unmeasured variables could be more important. When analysing the development during the period 1991-1996, no obvious changes were detected in the communities (Zuur 1999).

Norderney benthos monitoring data

Long-term changes of macrozoobenthos (1978-1995) were studied at five subtidal locations in south-eastern coast of North Sea (Norderney, East Frisian Islands) in relation to climatic variability (Kröncke et al. 1998). The quarterly divided data of species numbers showed

TABLE 3.3.1

Significant (at the 5% level) estimated cross-correlation coefficients between temporal environmental variables and trends of species (including year-classes). Indices refer to the time lag in years (from Zuur 1999).

Species	temp.	salinity	Chl-a
Nephtys hombergii	0.74_0	0.55_0	
Lanice conchilega	0.73_0	0.47_0	
Cerastoderma edule 0	-0.51_{-1}		
Macoma balthica 0	-0.57_{-1}		
Macoma balthica 1	-0.45_{-2}		0.52_0
Macoma balthica 2			0.51_{-1}
Mya arenaria	-0.70_{-1}		0.48_0

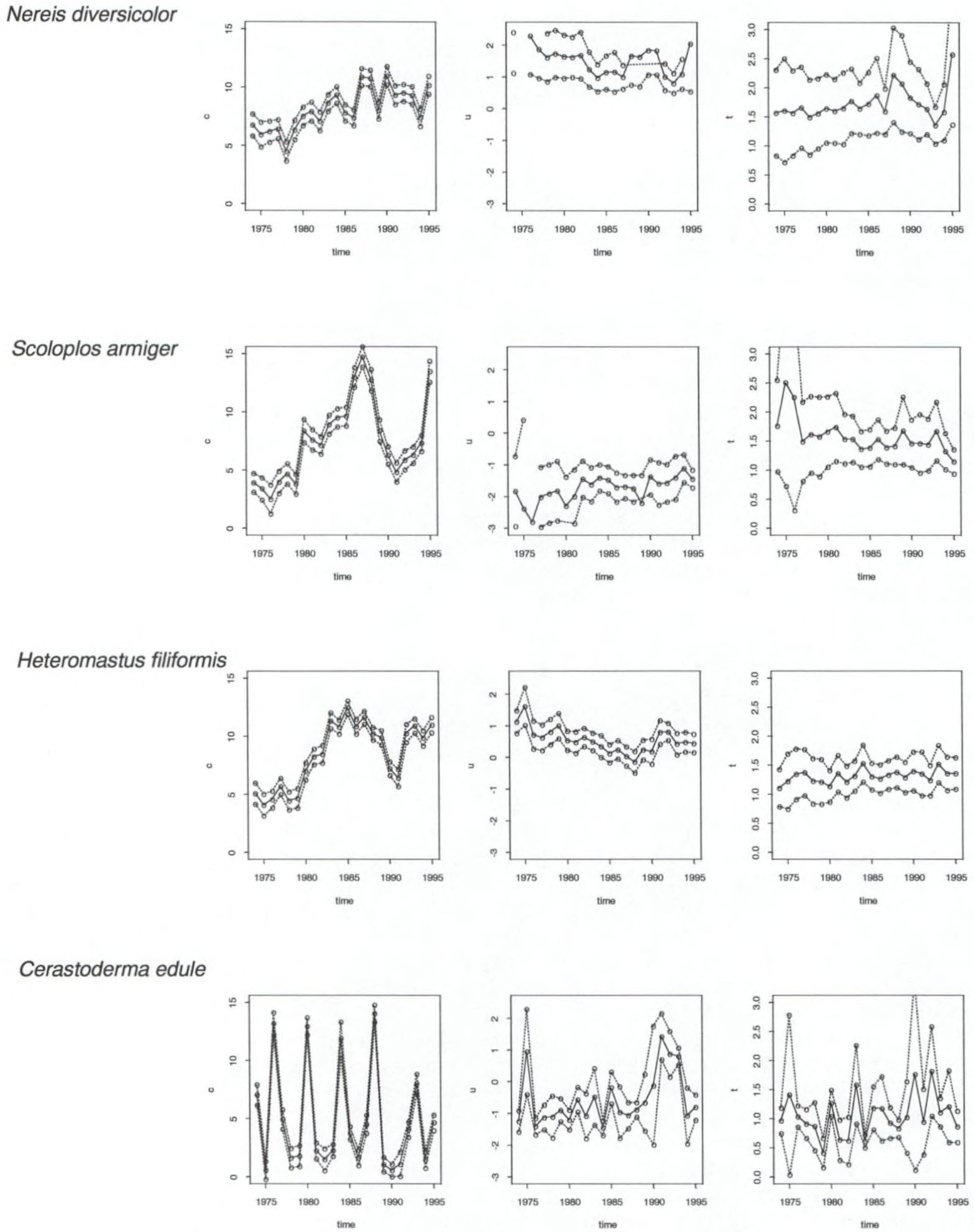


Fig. 3.3.1 Changes in the estimated parameters maximum (c), optimum (u) and tolerance (t) for *Nereis diversicolor*, *Scoloplos armiger*, *Heteromastus filiformis* and *Cerastoderma edule* (0-year class). For more details, see Zuur (1999).

generally highest values during the third quarter. A common pattern for most seasons was that lowest species numbers were observed in 1979, with a secondary minimum in late 1980s, followed by the highest species numbers in the beginning of the 1990s. For abundance, high numbers were also typical for the third quarter series. As for species number, low abundance was observed in late 1970s and 80s but the highest abundances occurred in early 1980s and 1990s. In total biomass a distinct increase can be seen in all series starting in 1988-89.

When relating these changes to climatic varibility, highest correlations were found between the second quarter benthos data (abundance and biomass log transformed) and climate data from winter or early spring. Climatic variability was best described by sea surface temperature (SST), sea level pressure (SLP) and NAO index. The highest correlations between benthos and climate data are shown in Table 3.3.2.

Abundance was found to be correlated with SLP and NAO index. Higher than normal abundance was connected to low pressure anomalies in the north and high pressure anomalies in the south, producing strong westerly winds, and vice versa. This air pressure pattern also decribes NAO index and it can be concluded that the two climatic variables represent the same mechanism.

TABLE 3.3.2

The best of the detected combinations between macrozoobenthos and climatic parameters. All combinations possess a maximum of skill within a narrow range of time lags and clearly lower skills for any other time lags. In addition, the significance of the skill is > 99%. A subscripted p to a predictor month indicates a month in the preceding year. All combinations contained the benthos observations in the second quarter. Anomalously high log abundances and species numbers in the second quarter seem to depend on anomalously mild 'westerly' climate conditions in winter or early spring. The left column contains reference model numbers that are used in Kröncke *et al.* (1998)

Model				Skill	
	Predictor (months)		Predictant (season)	r	β
1	SLP (12_p-3): westerly winds	and	high log-abundance (second)	0.73	0.52
2	NAO index (12_p-3): westerly winds	and	high log-abundance (second)	0.73	0.52
3	SST (1-3): warm North Sea	and	high species number (second)	0.74	0.52
4	SLP (11_p-4): westerly winds	and	high species number (second)	0.66	0.38
5	NAO index (12_p-3): westerly winds	and	high species number (second)	0.67	0.44

Species number was correlated to SST, SLP an NAO index. High species numbers occurred in connection to anomalously warm southeastern North Sea. This pattern in SST is closely related to the climatic variables (r=0.71 for NAO index, Kröncke et al. 1998) and they all describe the same relationship. SST might actually be the mediating mechanism between SLP or NAO index and abundance in the previous models.

In Fig. 3.3.2 the relationship between species number, total abundance and biomass and the NAO index in the preceeding winter is shown. It is evident that all important information on climate can be reduced to NAO index (Kröncke et al. 1998). Although the correlation between biomass is less clear than for species number and abundance, high biomass coincides with a high NAO index and seems thus also be related to the atmospheric circulation.

North Sea trawling by-catch data

Two beam trawl surveys (SNS: 1980-1997 and BTS:1985-1997) conducted in the south-eastern North Sea were used to evaluate the effects of restricting bottom trawling (establishment of the "plaice box") on the benthic invertebrate assemblages. In order to be able to distinguish between the effect of a reduction of beam trawling effort and potentially confounding influences from natural origin, two relevant environmental variables, bottom seawater temperature and depth, were incorporated in the analyses (Piet et al. in prep.)

MANOVA showed for both surveys significant ($p < 0.01$) environmental, temporal and spatial effects as well as a significant temporal*spatial interaction, indicating a significant effect on the assemblage of the closure of the box in spite of the co-occurring changes in temperature and differences in depth distribution between the box and reference area. For many of the species separately, however, the interaction term was not significant ($p \leq 0.05$) and no effect of the closure of the box was observed. Exceptions for both surveys were brittle star *Ophiura* spp., trough shell *Spisula* spp. and shore crab *Carcinus maenas*.

The main changes in the benthic invertebrate assemblage caused by depth and temperature as characterized by PCA indicate that only the first Principal component (PC) showed a distinct trend. This PC, explaining 18% of the variation related to depth, had high positive loadings of masked crab *Corystes cassivelaunus*, starfish *Astropecten irregularis* and seamouse *Aphrodita aculeata*. For temperature, the first PC, explaining 24% of the variation, had high loadings of

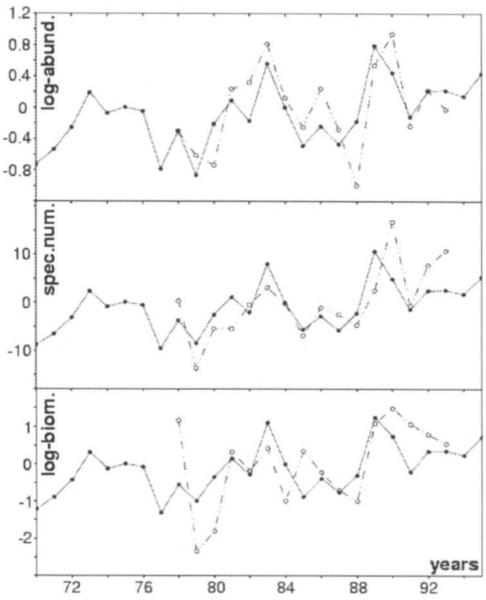


Fig 3.3.2 Estimated and observed anomalies of (a) log abundance, (b) species number and (c) log biomass of macrozoobenthos in the second quarter. The estimations were derived from the NAO index in the preceeding winter. An anomalous NAO index of +1 is correlated with an anomalous log abundance of +0.3, species number of +3.8 and log biomass of +0.6 (the same is also true for the reverse situation). Estimations and observations are corrected with r=0.73, β=0.52 (log abundance), r=0.67, β=0.44 (species number) and r=0.56, β=0.31 (log biomass). From Kröncke et al. (1998).

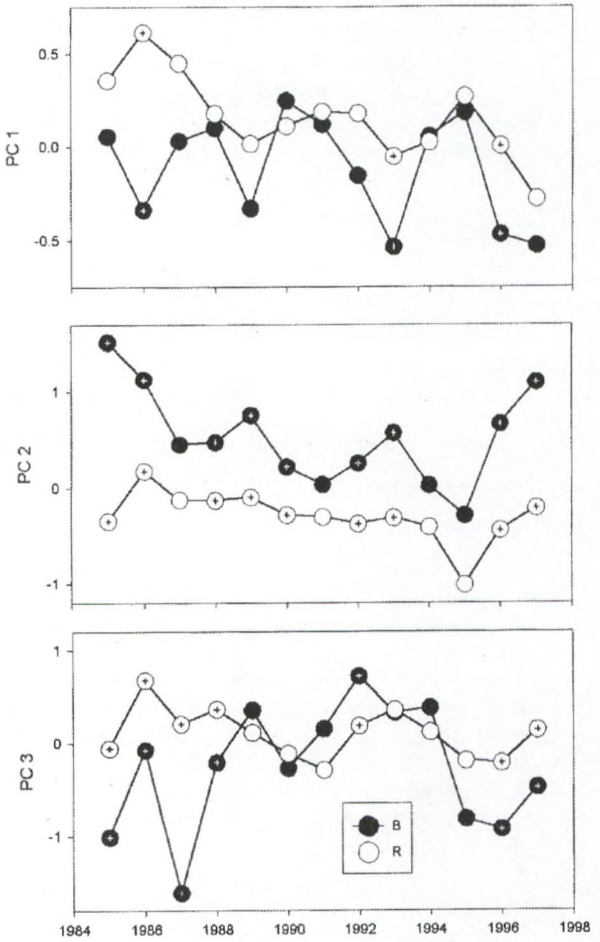


Fig. 3.3.3 Temporal changes in the box (B) and reference (R) area expressed by the first three principal components (PC) for the BTS survey. Significant diffrences are indicated with (+).

masked crab *Corystes cassivelaunus* (+) and starfishes *A. irregularis* (+) and *Asterias rubens* (-).

For the species that were significantly affected by the establishment of the box, the first three principal components explain 39% and 55% of the variation in the BTS and SNS survey catches, respectively. For BTS, the species with the highest loadings were masked crab *C. cassivelaunus* (+), starfishes *A. irregularis* (+) and *A. rubens* (-) for PC1, beadler anemone *Actiniaria* spp. (+), whelk *Buccinum undatum* (+) and edible crab *Cancer pagurus* (+) for PC2 and common starfish *A. rubens* (+), sea urchin *Echinocardium* spp. (+) and swimming crab *Liocarcinus holsatus* (+) for PC3. The temporal changes in the box and reference area, corrected for the effects of the environmental variables are shown for the first three PC's (Fig. 3.3.3). All show relatively little variation around a slowly decreasing trend in the reference area. In the box area, year-to-year variation was markedly stronger and a decreasing trend was only observed for the first PC. Remarkably, significant differences between the box and reference area were observed during all periods, but were least frequent during the period 1989-1994 when the box was closed only part of the year.

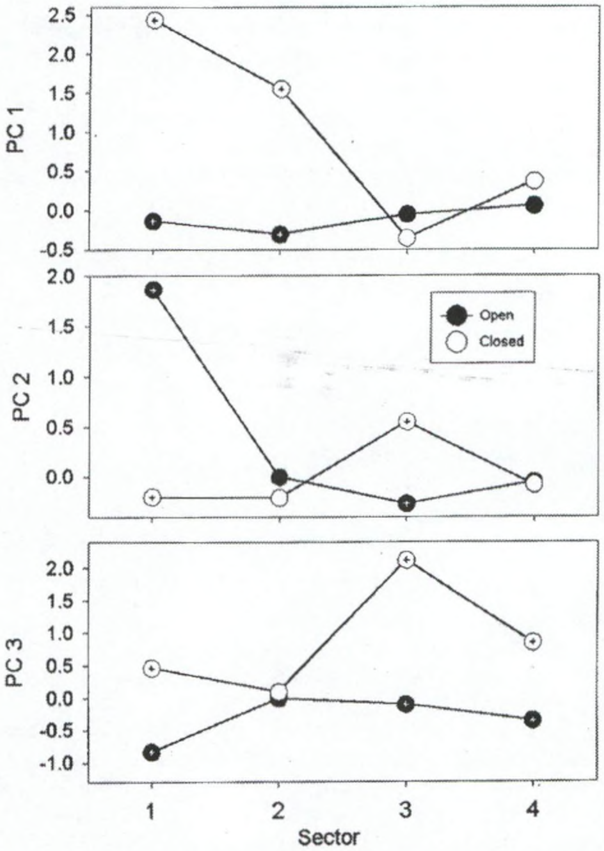


Fig. 3.3.4 Values for the three principal components for the sectors of the SNS for the period before the closure (1980-1988) and after year-round closure (1995-97) of the box. Sector (1) 12 miles zone, (2) 25-50 km, inside the box, (3) 50-80 km, boundary area and (4) over 80 km, outside the box. Significant differences between the two periods are indicated by (+).

For SNS, the species with the highest loadings were shrimp *Crangon crangon* (+) and brittle star *Ophiura* spp. (+) for PC1, shore crab *Carcinus maenas* (+) and *Alcyonium digitatum* (-) for PC2 and trough shell *Spisula* spp. (+) and shore crab *C. maenas* (-) for PC3. The first three PC's, corrected for the effect of depth show a significant increase in the two transects within the box area after year-round closure of the box for the first PC and a decrease in the first sector and an increase in the third sector after closure of the box for the second PC. The third PC shows an increase for all but the second sector (Fig. 3.3.4).

Baltic Sea

Factors affecting spatial distribution of species – A total of 22 infaunal or epifaunal species/groups were recorded at the 65 sites sampled in 1996-97 and included in the analysis of the spatial distribution of the communities (Laine in prep.). Five species are clearly more common, occurring at more than 20 sites. Those are the polychaete *Harmothoe (Antinoella) sarsi*, isopod *Saduria entomon*, amphipods *Monoporeia affinis* and *Pontoporeia femorata* and the bivalve *Macoma balthi-*

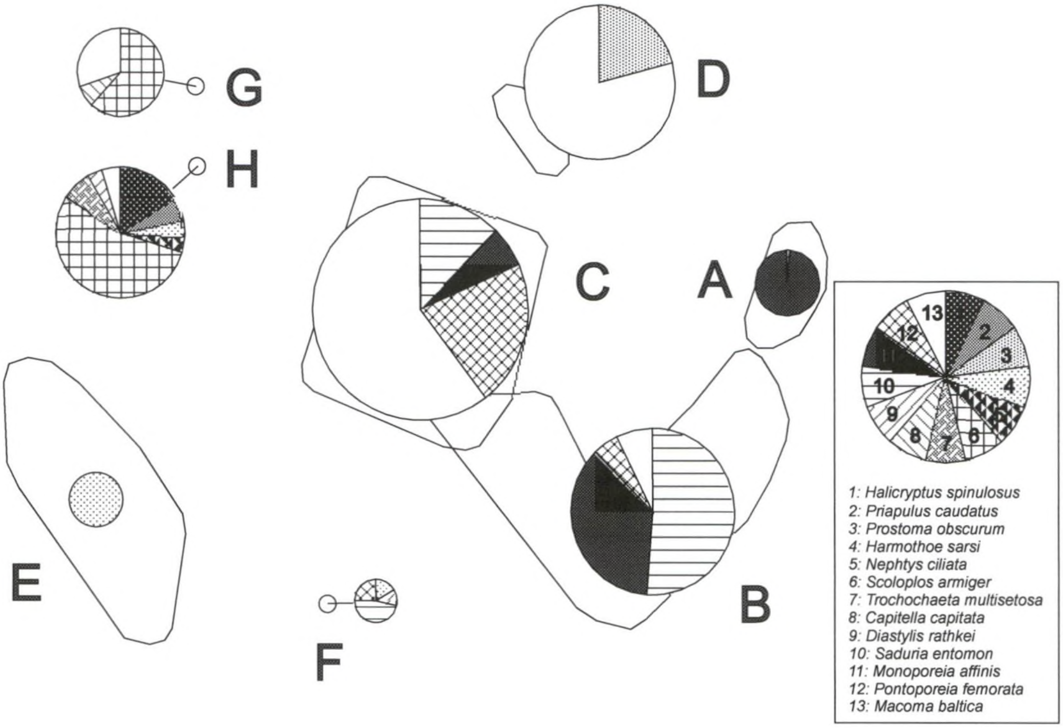


Fig 3.3.5 Two dimensional MDS ordination showing the generalised community structure of the identified groups. The groups (subsets of sites) are separated by the broken line, based on the 40% Bray-Curtis similarity level. The pie graphs illustrate the average species composition of the groups (A-H), overlaid on the MDS ordination. The pie diameter is relative to the total biomass. Only species forming 95% of total biomass has been included.

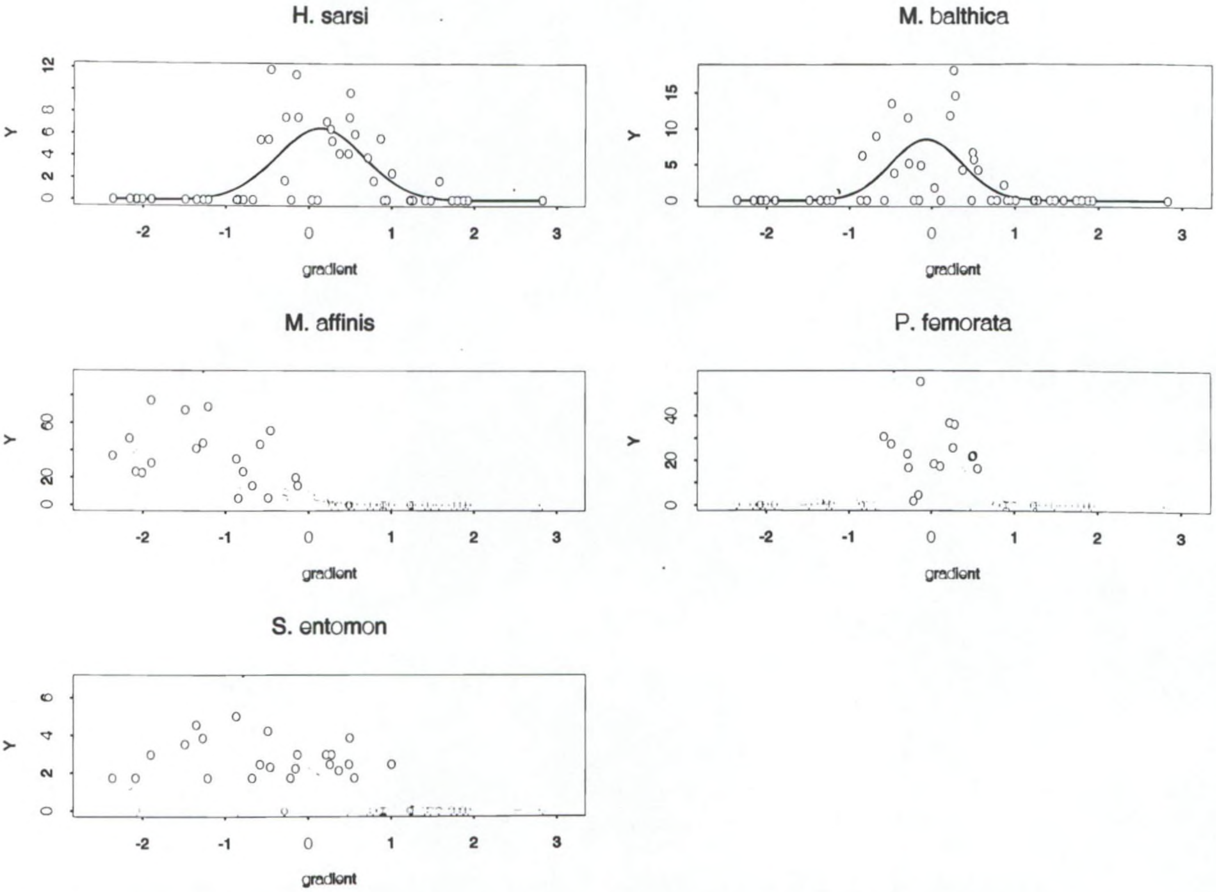
ca. These species, with the exception of *H. sarsi*, are also dominating in terms of biomass.

Multidimensional scaling (MDS) of square-root transformed macrozoobenthos biomass showed distinct assemblages that represent different sea areas and depth zones. In the MDS-ordination groups A and B form a gradient from a number of sites in the Bothnian Bay to Bothnian Sea and to some sites in the Gulf of Finland and Åland Sea (Fig 3.3.5). The latter areas are transitory and slightly overlapped with group C sites which represent the intermediate depth zone in the Gulf of Finland, northern Baltic Proper and Eastern Gotland Basin area. The deep, clearly subhalocline areas in the Eastern Gotland and Bornholm basins are located in the group E. Group D consist of only two, relatively shallow and near coastal sites in the Gulf of Bothnia. The single sites F, G and H are located in the central and SW Baltic Sea.

Along the above described spatial gradients the total benthic biomass increases from group A to C (Fig 3.3.5). Based on the group averages the dominant species change from *M. affinis* (in group A) to *S. entomon / M. affinis* (in B) and to *M. balthica / P. femorata / S. entomon* (in C). Group E is characterised by low biomass of only one species, *H. sarsi*. Site F is formed by low biomass of a species composition intermediate to groups C and E.The group D in the Gulf of Bothnia is characterised by high biomass of M. balthica or the nemertinean *Prostoma obscurum*. The sites G and H in the Arkona and Bornholm basins, respectively, represent areas dominated by marine polychaetes, mainly *Scoloplos armiger*, and bivalve M. balthica or the priapulid *Halicryptus spinulosus*.

Community structure was related to environmental variability by searching for a combination of environmental factors that produces a maximal correlation between the two multivariate similarity matrices. The results indicated the importance of salinity or the combined effect of salinity, dissolved oxygen saturation and sediment organic carbon content. However, the absolute correlations found were relatively low (r=0.56-0.52, weighted Spearman rank correlation). One reason for this could be the momentary nature of the hydrographical records. They represent only the conditions of the sampling time and may contain noice caused by short-term variability or be representative only for the sampling season, thus not giving the right information on average conditions or the extremes of the variability.

Very similar results were obtained by applying different multivariate methods on the five most important species in Zuur (1999). In both CA and CCA most of the variability was explained by the first axis and the high total inertia explained by the two axes indicated that all important environmental variables affecting the species distribution were included in the analysis. The above described differences in the geographical distribution were distinguished. *H. sarsi* and *P. femorata*



H. sarsi

M. balthica

M. affinis

P. femorata

S. entomon

Fig. 3.3.6 Fitted RGEE curves and observed abundances along the gradient for the Baltic Sea data sampled in 1996 (from Zuur 1999).

showed similar behaviour and apperad at sites with low oxygen concentaration, high salinity, high sediment organic matter content, high temperature and high winter PO_4 concentrations. *M. balthica* was more typical at sites with high temperature, high sediment organic matter content and low winter NO_3 concentration. *M. affinis* distribution was characterised by good oxygen conditions. High correlations were found between the following environmental variables: (i) PO_4, sediment carbon content, salinity and temperature, (ii) NO_3, depth and longitude, and (iii) latitude and oxygen concentration.

Application of RGR, RGAM and RGEE models further demonstrated the importance of the above mentioned factors (Zuur 1999). It should be noted that the winter nutrient concentrations also played a role in these models. RGEE also showed association between the species *H. sarsi* and *P.femorata* and between *M. balthica* and *P. femorata*. As an example of the results, fitted RGEE curves for the five species is given in Fig. 3.3.6. The gradient is determined by:

TABLE 3.3.3

Correlations of estimated common trends between species and hydrographical variables in the Baltic Proper and Gulf of Finland area during the period 1965-97. When correlating smoothed curves, higher correlations tend to exist compared to analysing raw data. Therefore only correlations exceeding 0.70 are considered important here and indicated in bold

Species	Oxygen concentration	Salinity	Temperature
Harmothoe sarsi	**0.87**	**-0.71**	-0.43
Saduria entomon	**0.87**	-0.63	-0.28
Monoporeia affinis	**0.76**	-0.56	-0.45
Pontoporeia femorata	**0.83**	-0.56	-0.38
Macoma balthica	**0.88**	-0.66	-0.30

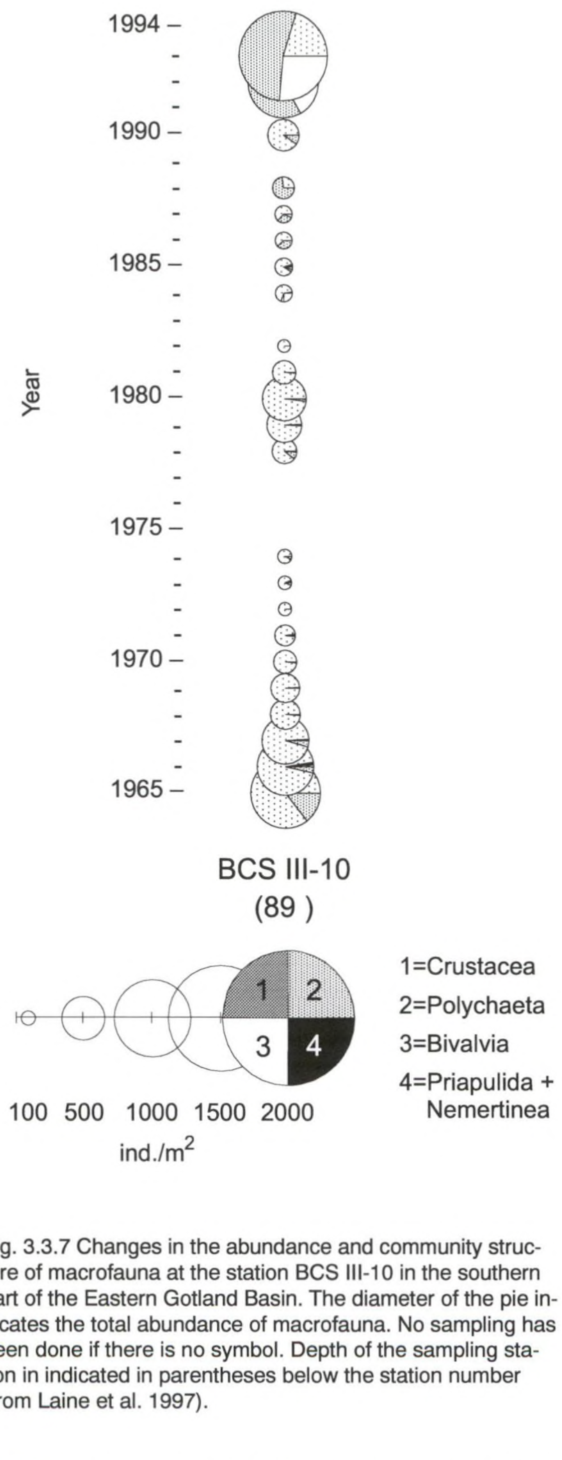


Fig. 3.3.7 Changes in the abundance and community structure of macrofauna at the station BCS III-10 in the southern part of the Eastern Gotland Basin. The diameter of the pie indicates the total abundance of macrofauna. No sampling has been done if there is no symbol. Depth of the sampling station in indicated in parentheses below the station number (from Laine et al. 1997).

$$z_i = -0.31\ \text{salinity}_i + 0.59\ \text{sediment surface C content}_i + 0.39\ PO_{4i} - 0.48\ NO_{3i}$$

The distribution of the Baltic macrofauna species in relation to salinity and oxygen combinations was studied by using all records for the period 1965-97 (Laine & Seppänen, in prep.). The results showed clear differences between species in tolerance limits for these factors, resulting in different geographical distribution due to sea area specific differences in the salinity-oxygen concentration relationship. *H. sarsi* occurred over the widest salinity and oxygen range while the distribution of *M. affinis* is obviously limited by the combination of salinity and oxygen. For many species the critical oxygen concentration is below 2 ml l^{-1} based on their occurrence in field data.

Long-term changes of the communities in relation to environmental variability

Baltic Proper and Gulf of Finland area

In Laine et al. (1997), changes in the macrofauna of the subhalocline areas in the Eastern Gotland Basin, northern Baltic Proper and the Gulf of Finland during 1965-1994 were described in relation to the salinity and oxygen regimes. During the study period, covering several significant major inflows of North Sea water, as well as the recent long stagnation period, major changes in the abundance, community structure and depth distribution of the macrobenthic assemblages were observed. At the beginning of the study period vast areas below the halocline were devoid of benthic macrofauna. The major inflows of North Sea water in 1975-76 led to rapid benthic recolonization down to approximately 150m depth in the Eastern Gotland Basin where the oxygen conditions had improved, but had no effect on the macrobenthic communities in the Gulf of Finland. The subsequent, prolonged stagnation period in 1977-93 caused first a deterioration of macrozoobenthos as a concequence of anoxia and hydrogen sulphide formation in subhalocline (70-250 m) areas. However, later a recovery was observed in the 70-100 m depth zone when vertical stratification weakened and intensified vertical mixing resulted in improved oxygen conditions at these intermediate depths (Fig. 3.3.7). The effect of this process was most pronounced in the Gulf of Finland. Parallel to this development, major changes in community structure took place in the Easten Gotland Basin area. The marine polychaete dominated communities were replaced by assemblages of *Harmothoe sarsi*, *Pontoporeia femorata* and *Macoma balthica*, resulting in higher similarity of the communities over the study area compared to the beginning of the study period (Laine et al. 1997).

The long-term development (1965-1997) in the Gulf of Finland was further studied in Laine et al. (in prep.). For most of the 1970s and 1980s scarce communities, with variable species composition or dominated by the polychaete *H. sarsi* have been prevailing. An expansion of macrofauna was observed in the late 1980s and early 1990s, leading to abundant amphipod (*P. femorata* and *Monoporeia affinis*) dominated communities, followed by a sudden collapse of the communities in 1996-'97. These changes were best explained by a combined effect of annual observed minimum oxygen concentration (with a 1 year time lag) and salinity, the poor oxygen conditions being obviously the crital factor for most of the study period. The main reason for changes in these two environmental factors can be attributed to alterations of stratification in the area (Fig 3.3.8). Simultaneously with previous development, we observed increasing winter nitrate concentrations describing eutrophication of the area and changes in the NO_3/PO_4 ratio with a peak in the early 1990s.

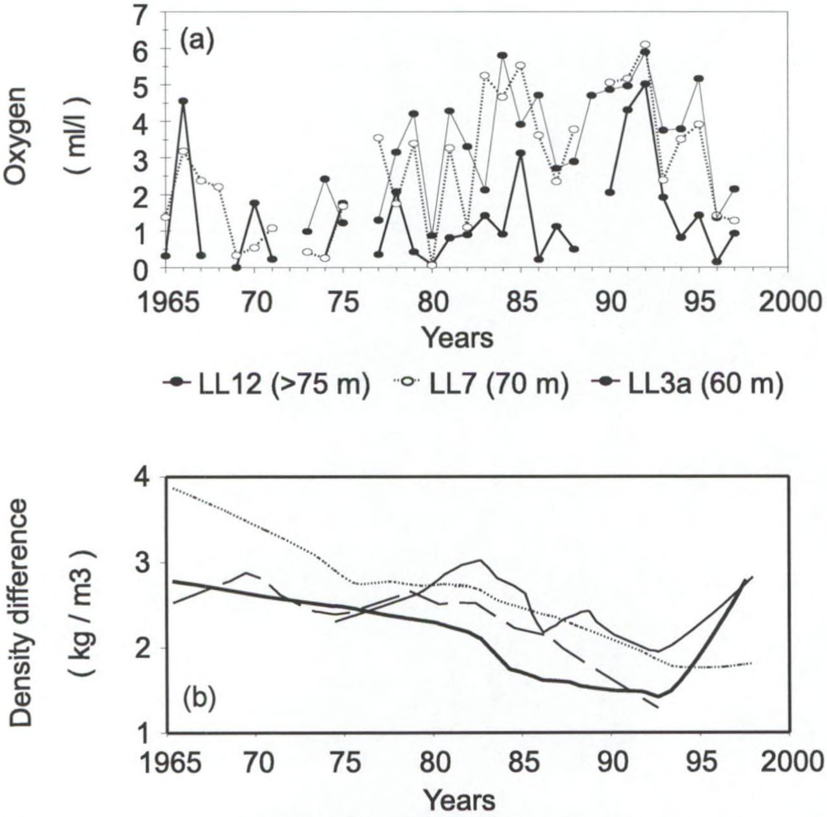


Fig. 3.3.8 (a) The annual recorded minimum of dissolved oxygen concentration of near-bottom water in different parts of the Gulf of Finland, (b) long-term changes in the strength of stratification, expressed as a density difference between surface layer and near-bottom water. Smoothed lines by locally weighted regression.

Structural time series models were applied to detect common trends in species data and hydrographical variables in the Baltic Proper and Gulf of Finland area (Laine & Zuur, in prep.). Most of the species had a constant trend for the first half of the study period, corresponding to low abundance but since 1985-90 increasing trends were observed. An exception was made by *H. sarsi* which peaked also in the middle of the 1970s (Fig. 3.3.9). Trends in species were correlated with the common trends in hydrography. For all species high positive correlations were found for oxygen concentrations (Table 3.3.3). *H. sarsi* was also negatively correlated with trends in salinity. This is somewhat contradictory but can be explained by the negative correlation in oxygen and salinity conditions. In this case salinity should fluctuate in such range that it does not limit the occurrence of *H. sarsi*.

Gulf of Bothnia

In the Gulf of Bothnia the long-term changes in the communities are caused by fluctuations in the few dominating species, in abundance by the amphipod *M. affinis* and in biomass also by the isopod *S. entomon*. During 1965-97 an increase in the total abundance and biomass of the communities was observed. When comparing different periods (1965-68, 1984-87 and 1994-97) a significant increase of abundance was found between the first and second period, but not between second and third ones. For biomass a statistically significant increase was found only between second and third period. The total abundance, highly dominated by *M. affinis*, showed 6-7 years periodicity prior to 1976 in the Bothnian Sea (cf. Andersin et al. 1978) but from the early 1980s onwards some sites showed out-of-phase behaviour (Fig. 3.3.10). However, most of the sites peaked again in 1993-94. In the Bothnian Bay, characterized in general by lower abundance and biomass, no corresponding perodicity can be observed but strong year to year variability in the total abundance seems to exist.

No significant correlation between trends in species and salinity, temperature or oxygen concentration could be detected when analysing the data for common trends (Laine & Zuur, in prep.). However, analysis of long-term changes in the *M. affinis* population structure offered some explanation for the observed fluctuations (Laakkonen et al., in prep.). High abundance values were connected to low condition of younger year-classes, which probably affects later recruitment by reducing the number of reproducing individuals and their fecundity, also postponing the propagation. Correspondingly, good condition of the animals at low densities levels could lead to rising abundance. Thus a density-dependent mechanism could explain the variability.

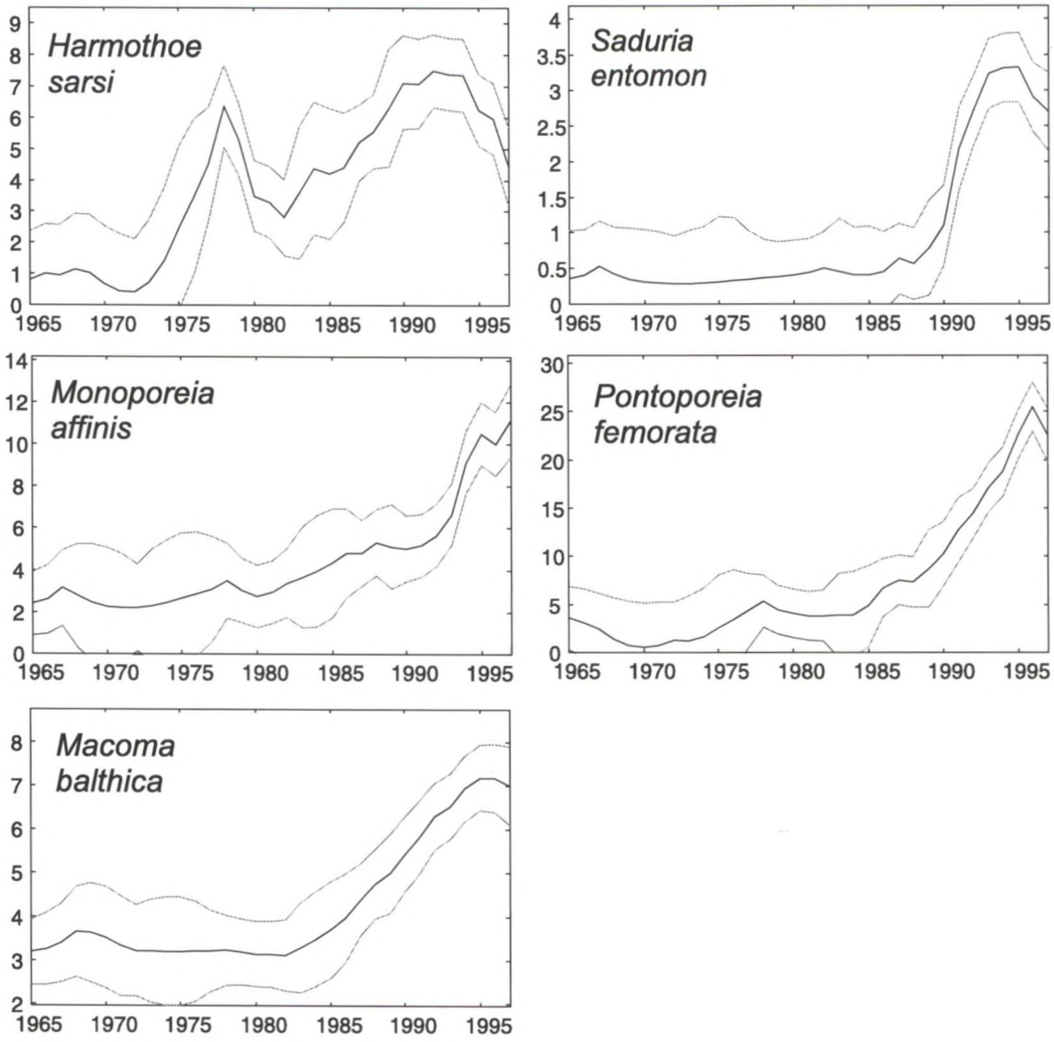


Fig. 3.3.9 Estimated common trends (with confidence intervals) for macrofauna species in the Baltic Proper and the Gulf of Finland area.

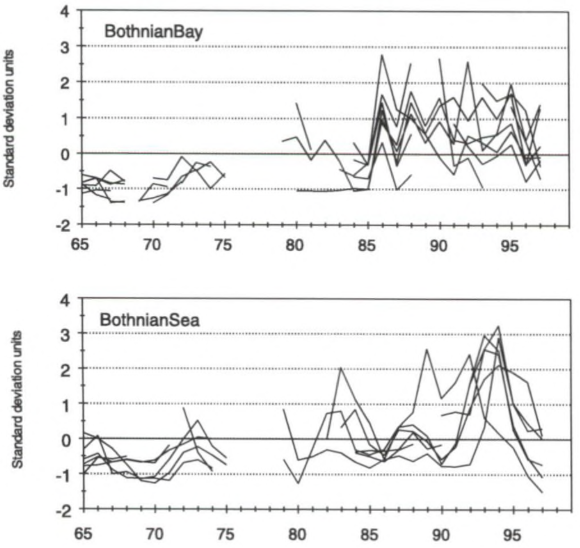


Fig. 3.3.10 Fluctuations of the total macrobenthic abundance in the northern (Bothnian Bay) and southern (Bothnian Sea) parts of the Gulf of Bothnia in 1965-1997, expressed as standardized values for the different sites.

3.4 FISH

North Sea

The long-term changes in the species composition as reflected in the catches of two demersal surveys are shown per survey in a PCA biplot. These biplots explain a considerable part of the variation (52% for IBTS and 46% for SNS) and show a remarkable consistency (Fig. 3.4.1). Many species are characterised similarly in the PCA biplots of the two surveys and the observed patterns show a strong resemblance. From the seventies to the eighties IBTS and SNS show a shift in the community structure caused by a decrease in biomass of species such as cod (*Gadus morhua*), spurdog (*Squalus acanthias*), pollack (*Pollachius pollachius*) and an increase in biomass of whiting (*Merlangius merlangius*), plaice (Pleuronectes platessa) and lemon sole (*Microstomus kitt*). The three surveys show a shift in community structure from the eighties to the nineties caused by decreasing biomasses of plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), whiting (*Merlangius merlangius*) while biomasses of solenette (*Buglossidium luteum*), bullrout (*Myoxocephalus scorpius*) and lesser weever (*Trachinus vipera*) increased.

The size-structure of the fish community is also reflected in two PCA biplots (Fig. 3.4.1). These biplots show the same trend in both surveys: a shift from larger fish toward smaller fish. The threshold boundary, however, differs between surveys: 30- 35 cm for IBTS, 25 cm for SNS.

The dominant pattern in all biplots is that of total biomass caused by simultaneous changes in most of the fish species involved: low in the seventies, increasing in the eighties until a maximum was reached in the early nineties and biomass decreased (Fig. 3.4.2). Although both surveys show more or less consistent patterns in total biomass it should be realised that considerable spatial differences may exist. When for the IBTS catches a number of smaller management areas, the so called roundfish areas (Fig. 3.4.3), were distinguished, marked and often significant differences in biomass patterns over time were observed in these areas (Table 3.4.1+3.4.2).

Effect of factors from anthropogenic origin

The effect of the closure of the "plaice box" and resulting reallocation of fishing effort on the size-structure and species composition of the BTS catches are shown in two PCA biplots (Fig. 3.4.4). Although changes in both size-structure and species composition are apparent the overriding pattern is governed by the total biomass in the catches. Biomass per haul in the box area is markedly higher than in the reference area but the patterns in these areas are similar. From the start of the BTS in 1985 a strong increase in biomass per haul was observed. The first year after (partial) closure of the box there is a slight increase in biomass followed by a decrease until the minimum is reached in 1995 when the box was closed year-round. After that biomass increased. The major difference between the areas occurs in the period 1995-1998 when the box was closed year-round. In the reference area a markedly stronger increase of biomass was observed than in the box area.

The species composition mainly shows a difference between the box and reference area. The box area is preferred by species like spurdog (*Squalus acanthias*), bullrout (*Myoxocephalus scorpius*), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in contrast to the reference area which is preferred by species like cod (*Gadus morhua*), long rough dab (*Hippoglossoides platessoides*) and grey gurnard (*Eutrigla gurnardus*). The most conspicuous change in both the box and reference area is that of an increase of what can be considered typical "box" species.

In the display of the spatial and temporal variation in the size-structure a distinct boundary is made between fish smaller than 25 cm and those larger than 25 cm. Like the species composition, the size-structure mainly displays a difference between a box area with relatively small species and a reference area with relatively large species. The most remarkable change after the year-round closure of the box is that small fish have increased in the reference area after 1995 resulting in a size-structure more similar to that in the box area.

Effect of factors from natural origin

Here results are presented that aim at explaining the patterns in the fish community that occurred in the North Sea using factors of natural origin. Unfortunately, part of the work is not yet finished, but is still ongoing. First a relationship between the fish community and two important factors, sea-surface-temperature (SST) and NAO index, was studied. The next step would be to try to further explain the observed patterns of the

TABLE 3.4.1

Level of significance of the interaction between spatial (roundfish areas) and temporal (year) components of total biomass IBTS. Significant interactions (p<0.01) are in bold. Roundfish areas are shown in Figure 3.4.3

Roundfish area	1	2	3	4	5	6	7
1		0.25	**0.00**	**0.00**	0.81	**0.00**	0.20
2			**0.00**	**0.01**	0.71	**0.01**	0.32
3				**0.00**	0.20	**0.00**	**0.00**
4					0.11	**0.00**	**0.00**
5						0.20	0.32
6							0.08
7							

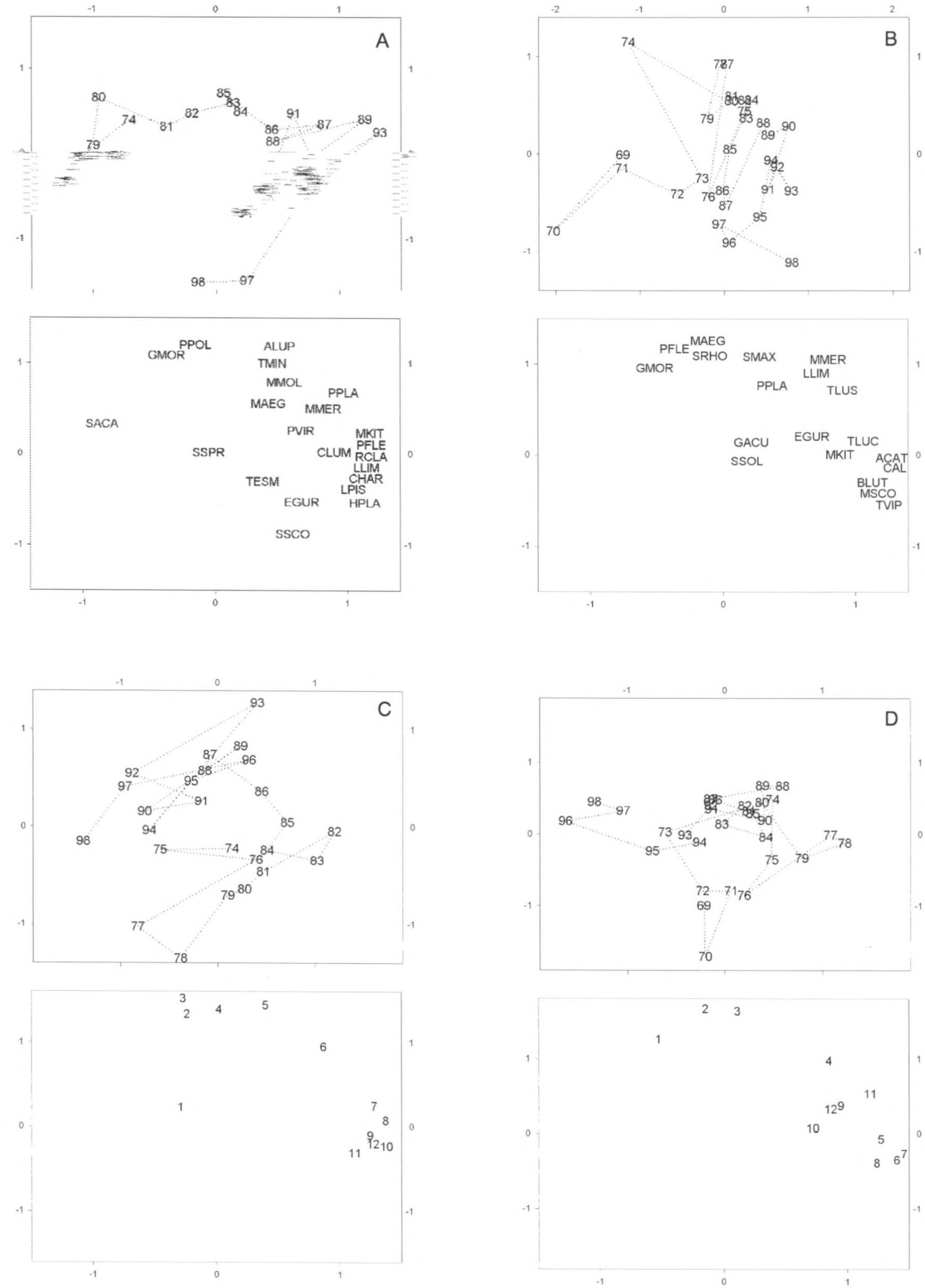


Fig. 3.4.1 Biplots of species composition over time of IBTS (a) and SNS (b) catches and size-structure over time of IBTS (c) and SNS (d) catches. The principal component values per year are shown above, the loadings below. For species abbreviations see Table 2.2.4.2. Size-classes are 5-cm-classes starting from 1 (≤10 cm) untill 12 (>60cm)).

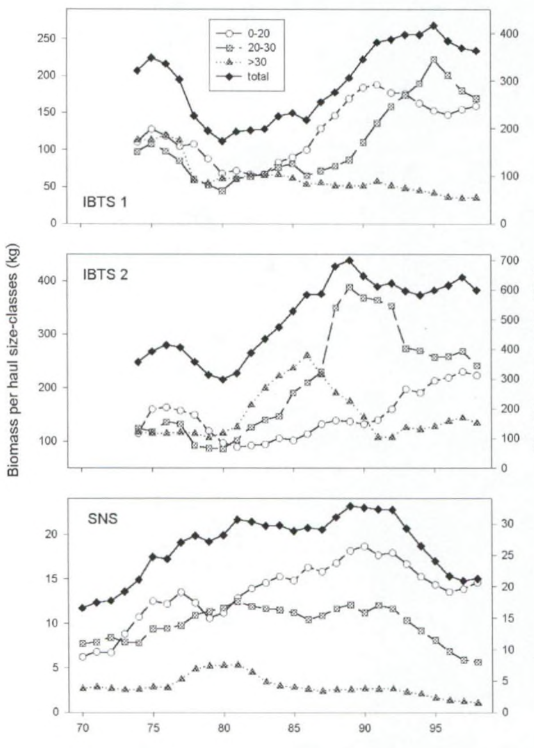


Fig. 3.4.2 Long-term changes in fish biomass from two surveys. For IBTS two areas were distinguished: one below 56 latitude with high fishing effort (IBTS 1), the other above 56 latitude with low fishing effort (IBTS 2). Both total biomass and biomass of three size-classes are shown.

fish community by the interaction between SST and nutrient availability via the mixed layer depth (MLD).

The total biomass of the pelagic species in the IBTS catches in the easterly North Sea is significantly correlated (p£0.05) with the NAO index (Table 3.4.3). Biomass of pelagic species was high after years with high NAO indices. This did not apply for the demersal species. In the roundfish areas where a significant effect was observed between 15% and 20% of the variation in the pelagic species' biomass was explained.

With Canonical Correlation Analysis (CCorA) the relationship between Sea Surface Temperature (SST) and the composition of the fish community (in terms of size or bio-geographic association) was studied. For the analyses of size-structure and species composition based on IBTS a significant relationship was detected. The first two canonical variables describing the relationship between the size-structure of the IBTS and the SST are significant ($p< 0.01$) and explain together more than 79% of the variation (Table 3.4.4). The first canonical variable shows that warm winters in the previous year result in an increased biomass of notably fish between 25-40 cm but a decrease of fish smaller than that. The second canonical variable shows that a warm winter/autumn and/or cold summer/spring results in an increased biomass of fish smaller than 30 cm and a decreased biomass of larger fish.

CCorA also reveals a significant relationship between the monthly SST and overall fish biomass as well as the species composition in terms of their bio-geographic association (Table 3.4.5). The first canonical variable explaining 67% of the variation, shows that a warm winter results in an overall higher biomass without any major effects on the composition. The second canonical variable addresses the composition in terms of bio-geographic associations explaining 29% of the variation. This variable indicates that a warm autumn (Sept., Oct.) results in an increased biomass of Lusitanian species and a decreased biomass of Boreal species in the first quarter of the next year.

The mixed layer depth (MLD) in the model is characterised by two different areas: In the southern part of the North Sea mixing of the entire water column usually occurs throughout the year; in the northern part thermal stratification is present from spring to autumn and mixing does not reach the bottom at this time of the year. In the transition zone between these two areas two different regimes in the MLD could be identified.

TABLE 3.4.2

Results of linear regression on three indices in two surveys IBTS and SNS. For IBTS two areas were distinguished, one with high fishing effort (IBTS1) the other with low fishing effort (IBTS2)

Survey	R^2	Intercept (g)	Slope ($g.yr^{-1}$)	p	Mean Weight (g)	$T_{1/2}$ (yr)
			Average weight			
SNS	0.55	33.25	-0.15	0.00	20.9	111
IBTS1	0.45	69.39	-0.48	0.00	28.0	72
IBTS2	0.27	51.69	-0.26	0.00	29.3	99
			Size at maturity			
SNS	0.46	44.84	-0.21	0.00	26.9	107
IBTS1	0.74	51.54	-0.23	0.00	48.3	112
IBTS2	0.32	47.16	-0.12	0.00	59.6	197
			Maximum size			
SNS	0.50	79.65	-0.33	0.00	51.9	121
IBTS1	0.58	73.94	-0.30	0.00	31.9	123
IBTS2	0.00	61.02	-0.02	0.88	36.6	1526

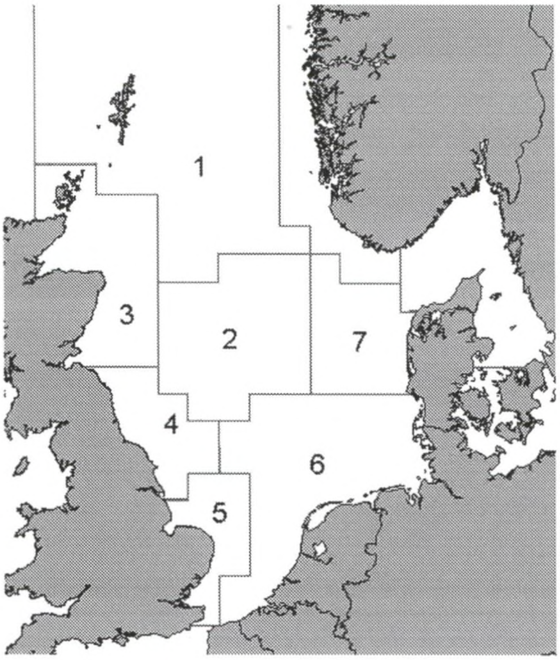


Fig 3.4.3 ICES roundfish areas in the North Sea proper.

Until 1988 usually a very shallow MLD was observed, whereas from 1988 on the MLD in summer was always deeper than normal in all years (Fig. 3.4.5).

Three hypotheses on the variation in recruit numbers were tested: (1) Length of the spawning season determines recruitment succes, (2) onset of the spawning season determines recruitment succes and (3) variation in recruitment increases with increasing latitude.

TABLE 3.4.3.
Correlation between the biomass of pelagic and demersal species in the IBTS catches per roundfish area and the average of the NAO indices of two years prior to sampling

Roundfish area	p-value	R^2
	Demersal fish	
1	0.73	0.01
2	0.11	0.11
3	0.28	0.05
4	0.21	0.07
5	0.43	0.03
6	0.11	0.10
7	0.12	0.10
	Pelagic fish	
1	0.95	0.00
2	0.03	0.19
3	0.93	0.00
4	0.08	0.12
5	0.15	0.09
6	0.05	0.15
7	0.05	0.15

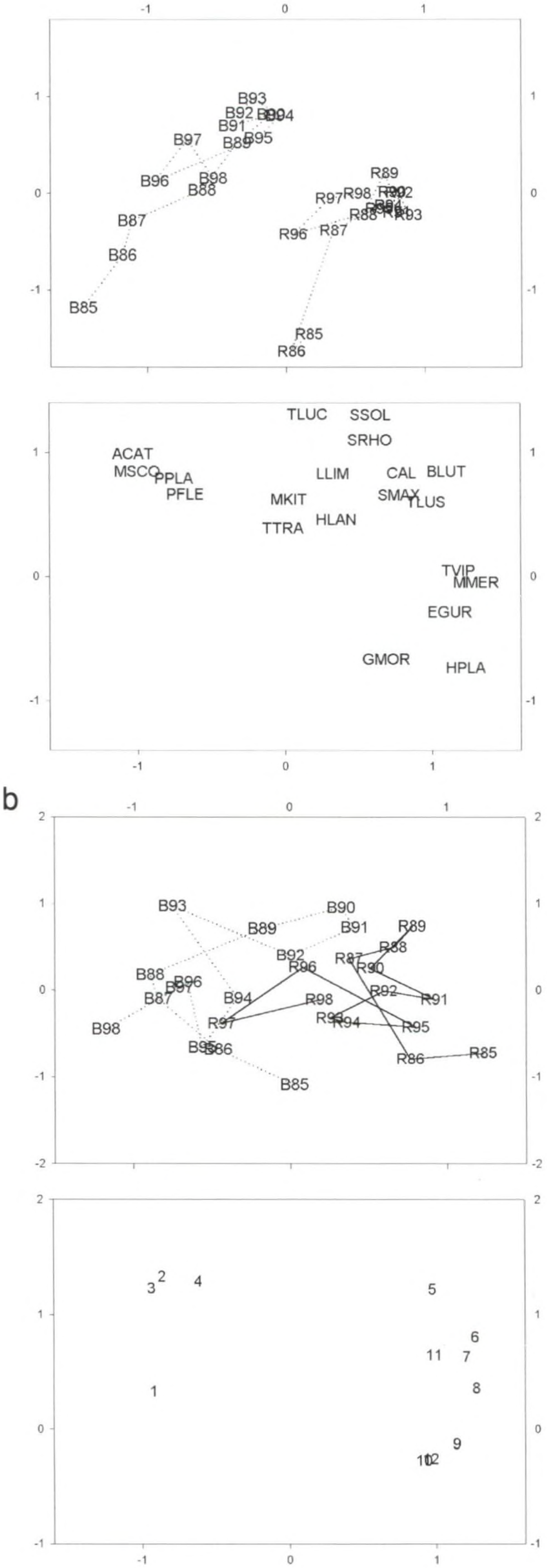


Fig. 3.4.4 Biplots of species composition (a) and size-structure (b) over time of the BTS. The "B" prefix indicates the box area, the "R" prefix the reference area. The principal component values are shown above, the loadings below.

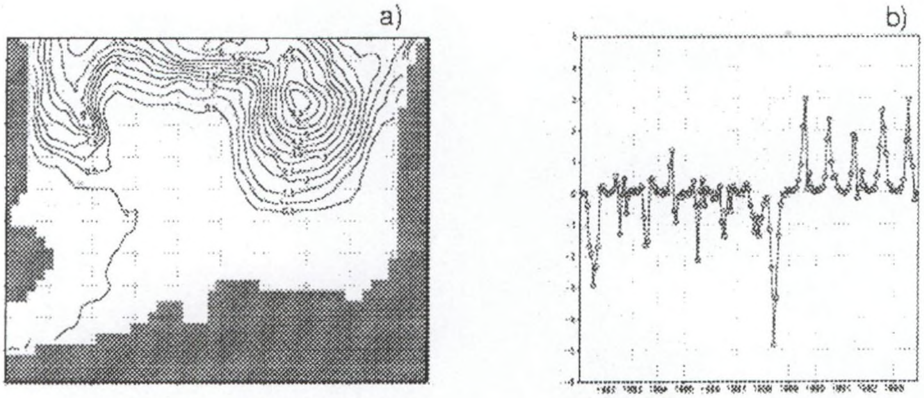


Fig. 3.4.5 First EOF and associated time series of the mixed-layer-depth in the North Sea simulated by the OPYC model driven by the observed fluxes of heat, fresh water and momentum between 1979 and 1993.

TABLE 3.4.4

Results canonical correlation monthly SST one year prior to sampling the fish community and size-structure of that community

Size-class (cm)	Canonical variables	
	1	2
≤10	-0.30	0.25
10-15	0.28	0.11
15-20	-0.16	-0.01
20-25	-0.27	0.76
25-30	0.57	0.38
30-35	0.26	-0.31
35-40	0.53	0.11
40-45	-0.08	-1.24
45-50	0.01	0.58
>50	-0.13	-0.04
	Canonical variables	
Month	1	2
1	-0.10	0.37
2	0.45	0.34
3	0.48	-0.64
4	-0.51	0.56
5	-0.12	0.02
6	0.00	-0.01
7	0.02	0.01
8	-0.20	-0.78
9	0.07	0.29
10	-0.27	1.19
11	-0.21	-0.47
12	0.21	0.49
Canonical R^2	0.68	0.46
Proportion	0.56	0.23
p	0.00	0.00

The first two hypotheses were tested for plaice and sole only using VPA data. The difference in the Length of the spawning season (LSS) between the four years with the highest and the three years with the lowest stock biomass in age group one for sole seems to indicate that recruitment success of sole and the LSS are indeed positively correlated. For plaice, it was found that the results are very sensitive to the exact definition

TABLE 3.4.5

Results canonical correlation monthly SST one year prior to sampling the fish community and composition in terms of bio-geographic association of that community

	Canonical variables	
Association	1	2
Atlantic	0.35	-0.02
Boreal	0.51	-1.06
Lusitanian	0.47	1.10
	Canonical variables	
Month	1	2
1	0.28	0.14
2	0.18	0.17
3	0.21	-0.06
4	-0.08	0.46
5	-0.09	0.08
6	-0.06	-0.38
7	0.03	-0.32
8	-0.68	-0.22
9	0.36	0.52
10	0.33	1.06
11	-0.44	-0.02
12	0.44	-0.10
Correlation	0.50	0.30
Proportion	0.67	0.29
p	0.00	0.00

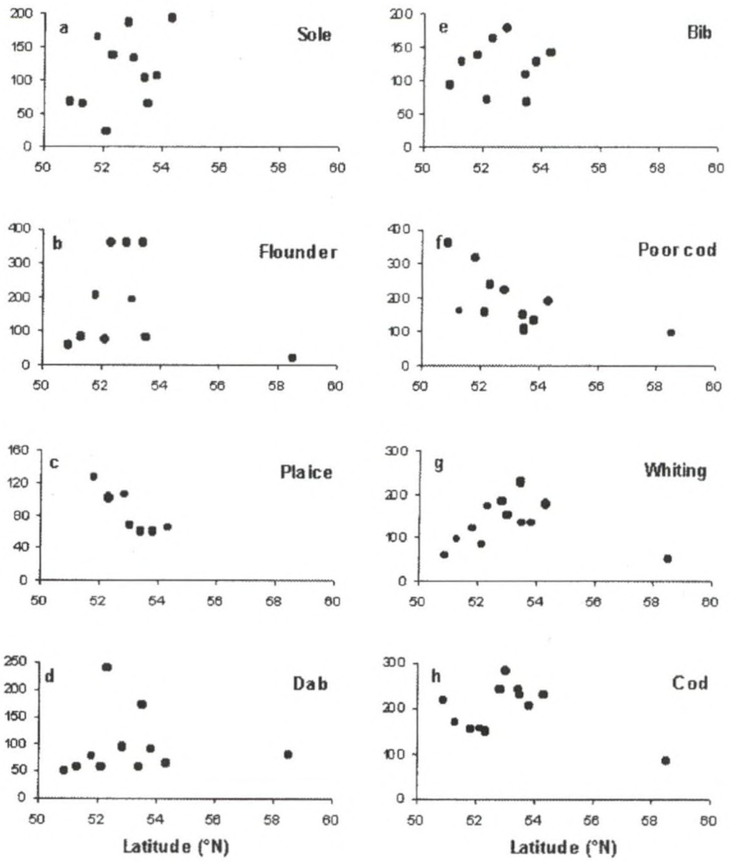


Fig. 3.4.6 Relationships between latitude and variation in recruit numbers (CVR) of selected flatfish (sole, flounder, plaice and dab) and roundfish species (bib, poor cod, whiting and cod) along the Northwest European coastlines.

of the temperature range at which spawning occurs and are therefore not very reliable.

The second hypothesis was based on the assumption that on average the onset of the spawning season of several fish species is correlated with a temperature integral over a certain time period. Consequently the onset of the spawning season may vary due to the interannual temperature fluctuations. Because food availability is known to vary throughout the year these variations may eventually result in variations of the recruitment success. However, a large scatter within the data and the very short time series obscured any possible signal.

The effect of latitude on the variation in recruit numbers was studied for four flatfish species: sole, flounder, plaice and dab and four roundfish species: bib, poor cod, whiting and cod differing in their range of distribution. In contrast to expectations only for two species for which the study area lay near the centre of their distribution range, plaice and poor cod, a significant relationship between latitude and variation in recruit numbers was observed (Figure 3.4.6)

3.5 SEDIMENT CORES

German Bight

Dating

Different methods (^{210}Pb and ^{14}C) gave similar results, i.e. an average sedimentation rate of 6.9 cm $100y^{-1}$. Based on this rate, we estimated the age of the subsamples of the pistoncore.

Faunal remnants

The pistoncore sampled in the German Bight contained a suite of faunal remnants (Table 3.5.1). However, remnants of several species were considered not to be representative for actual densities due to the low number, e.g. fish remnants and large bivalve shells. Therefore, we focussed on the annual deposition of three species of ostracods, viz. *Elofsonella concinna*, *Palmoconcha guttata*, and *P. laevata*. These species are found mainly on sedimentary substrates such as sand and mud, where they either crawl on the sediment surface or burrow to a depth of a few centimeters (Athersuch et al. 1989). Water temperature is probably the main control on the geographical distribution of ostracods, just as salinity is the main control of their environmental distribution.

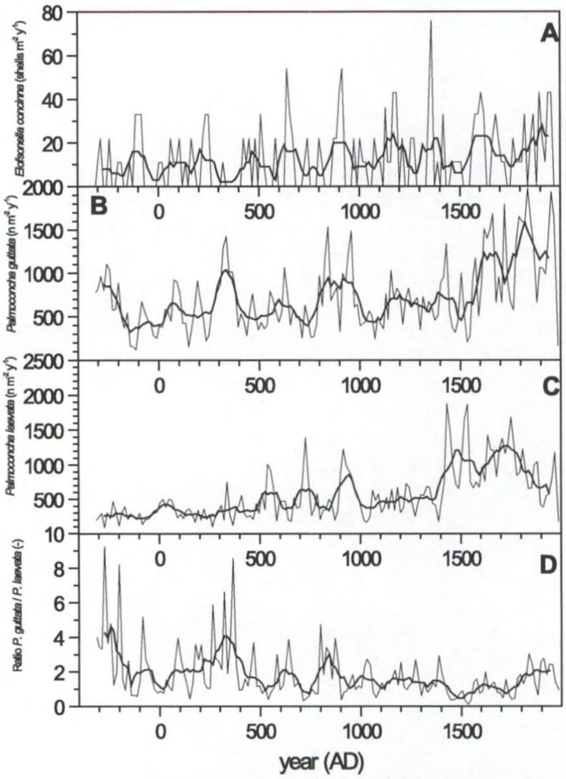


Fig. 3.5.1 Absolute and relative shell-deposition rates of ostracods (n m^{-2} y^{-1}) in the German Bight between -312 and 1996 AD as derived from a pistoncore taken on June 4, 1996. A. Shell-deposition rate of of *Palmoconcha guttata* (shells m^{-2} y^{-1}). B. Shell-deposition rate of *Palmoconcha laevata* (shells m^{-2} y^{-1}). C. Ratio of shell-deposition rates of *Palmoconcha guttata* and *Palmoconcha laevata* (-).

Elofsonella concinna – A marine sublittoral species, found at depths between 2 and 250m (most commonly in the deeper part of this range) on silt and sandy substrates. It lives in the northern British waters where it is at the southern limit of its distribution; its geographical range extends from Scandinavia to Spitsbergen, Iceland and northeastern North America (Athersuch et al. 1989).

Compared to *Palmoconcha* species, the shell-deposition rate of this species was low, approximately 10 specimen m^{-2} y^{-1} (Fig. 3.5.1A).

Palmoconcha guttata – A marine species frequently recorded from Northwest European coastal waters, particularly around the British Isles and Scandinavia, at depths of 10 to 90m (Athersuch et al. 1989).

The shell deposition rate varied between 100 to almost 2000 specimen m^{-2} y^{-1} (Fig. 3.5.1B), with relatively high values between 300 and 400 AD, 800 and 1000 AD, and from 1500 AD onwards. The ratio of left and right shell halves was on average > 1 indicating that the material was not entirely autochtonous (Fig. 3.5.2A). High ratios (> 2) were observed around 1000 and around 1100 AD. The ratio between phase-8 and adult specimen was approximately 2 within the studied period, with highest values (> 5) around 0 and 1500 AD (Fig. 3.5.2C).

Palmoconcha laevata – A common marine species around the coasts of Britain and Ireland, Scandinavia and the Atlantic coasts of northwestern Europe, at depths of 0 to 90m. It has been found amongst littoral algae in rock pools, but most records are from sublitoral waters and on sediment substrates (Athersuch et al. 1989).

The shell deposition rate varied between 100 to almost 2000 specimen m^{-2} y^{-1} (Fig. 3.5.1C), with relatively high values from 1400 AD onwards. The ratio of left and right shell halves was on average approximately 1 indicating that the material was mainly autochtonous (Fig. 3.5.2B). High ratios (> 2) were observed around 0, 500 and 1300-1500 AD. The ratio between phase-8 and adult specimen was approximately 2 during most of the studied period, with increasing values from 1500 AD onwards (Fig. 3.5.2D).

The ratio between *Palmoconcha guttata* and *P. laevata* was on average 1.8, with relatively high densities of P. guttata at the beginning of the studied period, and around 300-400 AD (Fig. 3.5.1D).

Western Wadden Sea

Dating

Different dating methods gave different results (Fig. 3.5.3). The curve based on the formula of infill of dredging holes indicated that the channel was already mostly filled in at the mid-1940s, whilst the other curves indicated a more gradual infill. We decided to base the final dating of vibrocore Vlieter 7D on the measurements performed on this core itself (and not on the curves that were more indirectly estimated).

Since we had no way to discriminate between the reliability of the ^{210}Pb-based curve and the PCBPAH-

TABLE 3.5.1

Type and total number (N) of faunal remnants found in pistoncore GB17, sampled in the German Bight on June 4, 1996.

PHYLUM	Family	Scientific name	Type	N
CRUSTACEA				
	Ostracoda	*Cytheropteron latissimum*	Shells	1
		Elofsonella concinna	Shells	8
		Loxoconcha elliptica	Shells	4
		Palmoconcha guttata	Shells	5329
		Palmoconcha laevata	Shells	4079
	Paguridae	*Pagurus bernhardus*	Propodus & dactylus	10
	Portunidae	*Liocarcinus* spp.	Propodus & dactylus	4
MOLLUSCA				
	Lamellibranchia	*Corbula gibba*	Shells	186
		Mya arenaria	Shells	546
		Nucula nitidosa	Shells	371
ECHINODERMATA				
	Ophiuroidae		Dorsal arm plates	2165
	Spatangidae	*Echinocardium cordatum*	Spines	11668
CLUPEIFORMES				
	Clupeidae	*Clupea harengus*	Vertebra	19
			Scales	56
			Otoliths	1
		Sprattus sprattus	Vertebra	9
			Scales	40
PLEURONECTIFORMES				
	Pleuronectidae	*Pleuronectes platessa*	Vertebra	7
		and/or Platichthys flesus	Scales	60
GADIFORMES		*Gadus morhua*	Vertebra	1
			Scales	24
		Merlangius merlangus	Vertebra	2
			Scales	18
			Otoliths	2

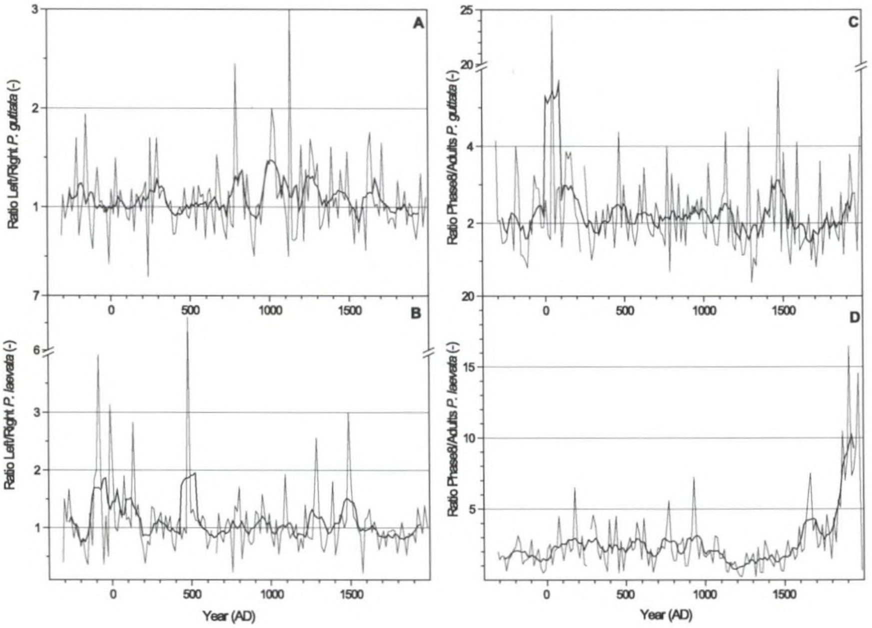


Fig. 3.5.2 Relative shell-deposition rates of ostracods (n m^{-2} y^{-1}) in the German Bight between -312 and 1996 AD as derived from a pistoncore taken on June 4, 1996. A. Ratio of left and right shell-halves of *Palmoconcha guttata* (-). B. Ratio of left and right shell-halves of *Palmoconcha laevata* (-). C. Ratio of phase8 and adult specimen of *Palmoconcha guttata* (-). D. Ratio of phase8 and adult specimen of *Palmoconcha laevata* (-).

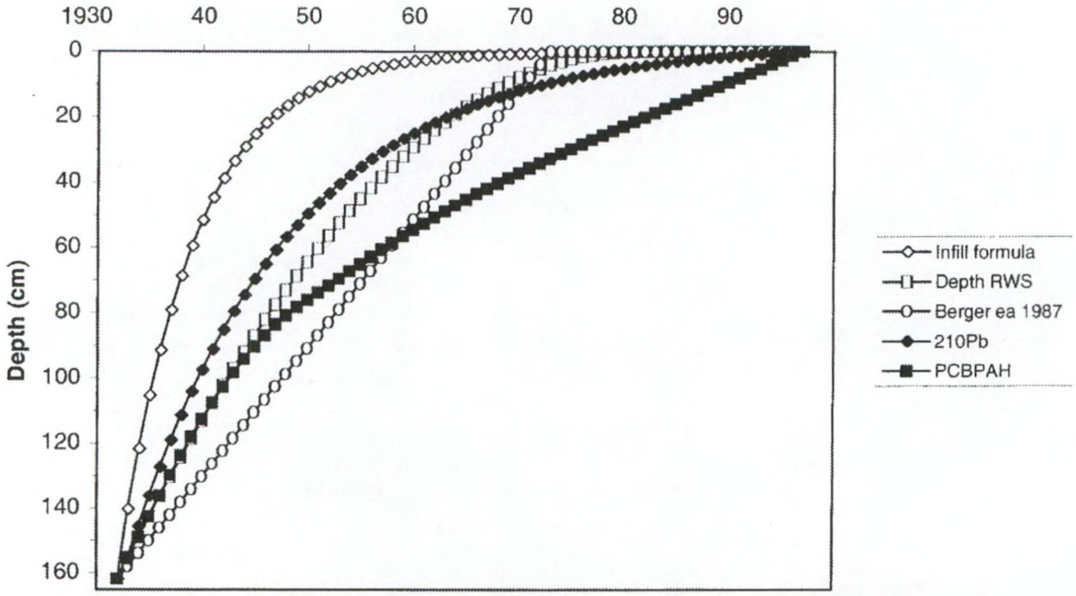


Fig. 3.5.3 Infill of the former Vlieter channel at different times as derived from different aging methods, i.e. based on an emperical infill formula (A. Oost, pers. comm), echo soundings performed by Rijkswaterstaat in the Vlieter channel (Midderham & De Boer 1983), ^{210}Pb activity of a sediment core sampled and analysed by Berger et al. (1987), ^{210}Pb activity of vibrocore Vlieter 7D (analysed by Wim De Boer), and PCB and PAH levels (analysed by Kees Booij & Wilma Lewis) in vibrocore Vlieter 7D.

based curve, we assumed the truth to be in the middle. We took, therefore, the average values of these two curves as an index for the infill of the Vlieter channel at the location where vibrocore 7D was sampled (Fig. 3.5.3). This curve suggests that sedimentation gradually declined from more than 8 cm y^{-1} just after the closure of the former Zuiderzee down to less than 1 cm y^{-1} in the mid-1990s. Based on this average curve, we estimated the age of the subsamples of the sediment core.

Lithology

In the cores taken, the shift in hydraulic regime due to the closure of the Afsluitdijk can clearly be seen in the sediments (Galavazi 1998). In all cores opened thus far there was an abrupt change from high-angle fine-sand megaripple laminations to horizontal laminae-like clayey silt deposits alternating with very fine sand (Fig. 3.5.4). At this shift in sedimentation, all cores showed a thick layer of Cockle shells (*Cerastoderma edule*; thickness 5-15 cm) embedded in the mud. The Cockles are of different age classes, viz. 1, 2 and 3 years old. The

TABLE 3.5.2

Type and total number (N) of faunal remnants found in vibrocore 7D, sampled in the former Vlieter channel on June 20, 1997.

PHYLUM	**Family**	**Scientific name**	**Common Name**	**Type**	**N**
PORIFERA			Sponges	Spicules	241
MOLLUSCA					
	Gastropoda	*Hydrobia ulvae*	Mudsnail	Shells	27776[a]
	Lamellibranchia	*Cerastoderma edule*	Cockle	Shells	131[b] 29[c]
		Macoma balthica	Baltic tellin	Shells	336[b] 0[c]
		Mya arenaria	Gaper	Shells	286[b] 2[c]
		Mytilus edulis	Mussel	Shells	1535[b] 3[c]
		Spisula subtruncata	Soft clam	Shells	377[b] 0[c]
ARTHROPODA					
	Ostracoda			Shells	514[d]
CLUPEIFORMES					
	Clupeidae	*Clupea harengus and/or*	Herring	Vertebra	7
		Sprattus sprattus	Sprat	Scales	6
PLEURONECTIFORMES					
	Pleuronectidae	*Pleuronectes platessa*	Plaice	Vertebra	8
		and/or *Platichthys flesus*	Flounder	Scales	33

a total number of specimen (damaged and undamaged; all size-classes combined)
b only juveniles, i.e. shell width < 2 mm; sum = number of complete shells + number of shell halves/2
c shell halves of adult specimen, i.e. shell width > 2 mm
d sediment core only contained shell halves of juvenile specimen

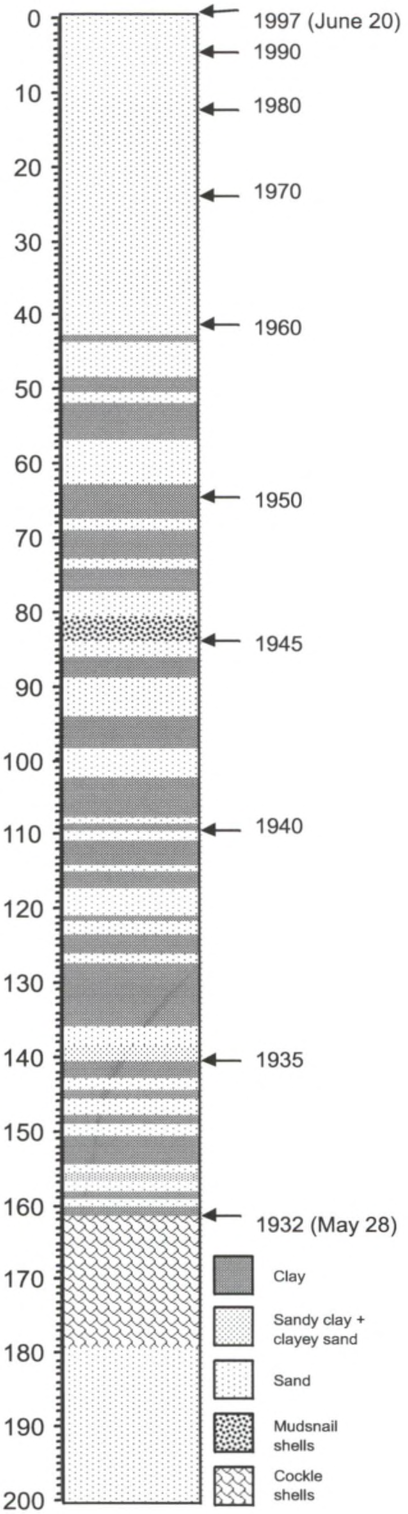


Fig. 3.5.4 Lithography of vibrocore V7D sampled in the former Vlieter channel on June 20, 1997. Only layers wider than 5 mm are shown.

layer contains shell fragments as well as single and double shell halves, but none of all were in life position.

The shell layer is followed by an alternation of mostly horizontally thinly laminated very fine sand and silt with clay. Sometimes sand lenses are found, resembling ripples but no foresets can be noticed. Also there are some clay drapes, formed in ripple throughs, present. This indirectly points to the formation of some ripples during sedimentation. Just above the shell layer the clayey silt-sand laminations are dominated by clayey bands with little sand but gradually the amount and thickness of the sand bands increases towards the top. So the sand layers are thickening up, and the general trend is coarsening up.

Throughout the core, high densities of Mudsnails shells (*Hydrobia ulvae*) were present. Highest densities of these marine snails were found at a depth between 80.5 and 83.5cm. All the top 30 cm of the cores are mostly deposits with very fine sand and only a minor amount of clay present (Galavazi 1998).

Faunal remnants

The sediment core sampled in the former Vlieter channel contained a suite of faunal remnants (Table 3.5.2). However, remnants of several species were considered not to be representative for actual densities due to the low number, e.g. fish vertebra and large bivalve shells. Therefore, we focussed on the annual deposition of small bivalves (i.e. < 2 mm) which are considered to be the spat (= first-year juveniles) and the mudsnails.

Bivalves (Mollusca) – Most of the bivalves found in the sediment core were so small that they could be considered to be spat, viz. first-year juveniles. Juveniles of bivalve species generally spend the first weeks of their life in the water column as planktonic larvae and subsequently settle on to the sediment surface. Spawning generally takes place in spring, but the exact timing differs for different species. Larvae of *Macoma balthica* are generally produced in April-May, followed by larvae of *Mya arenaria* in May-June and larvae of *Mytilus edulis* in May-August. The larvae of *Cerastoderma edule* appear in June and those of *Spisula subtruncata* in August-September (R. Dekker, pers. comm.).

Most of the adult stocks of the bivalve species found in the sediment core occur at both the intertidal and the subtidal areas of the western Wadden Sea. Only the distribution of the adult stocks of *Spisula subtruncata* are restricted to locations outside the Wadden Sea, viz. the shallow coastal zone of the North Sea such as areas north of the Wadden Sea islands. Additional sources of juvenile mussels most probably were the artificial mussel plots in close surrounding of the Vlieter channel, where fishermen grow mussels from seed (young mussels older than spat) that they collected from other areas of the Wadden Sea.

Shell-deposition rates of *Cerastoderma edule* spat were higher during the first 15 years of the study period (i.e. 1932-1947) than hereafter (Fig. 3.5.5A). Highest rates (> 6000 $m^{-2}\ y^{-1}$) occurred around 1934, 1935, 1944 and 1945. Shells of adult specimen were mainly found (n=9) at a depth that corresponded with the year 1964. As for Cockles, the shell-deposition

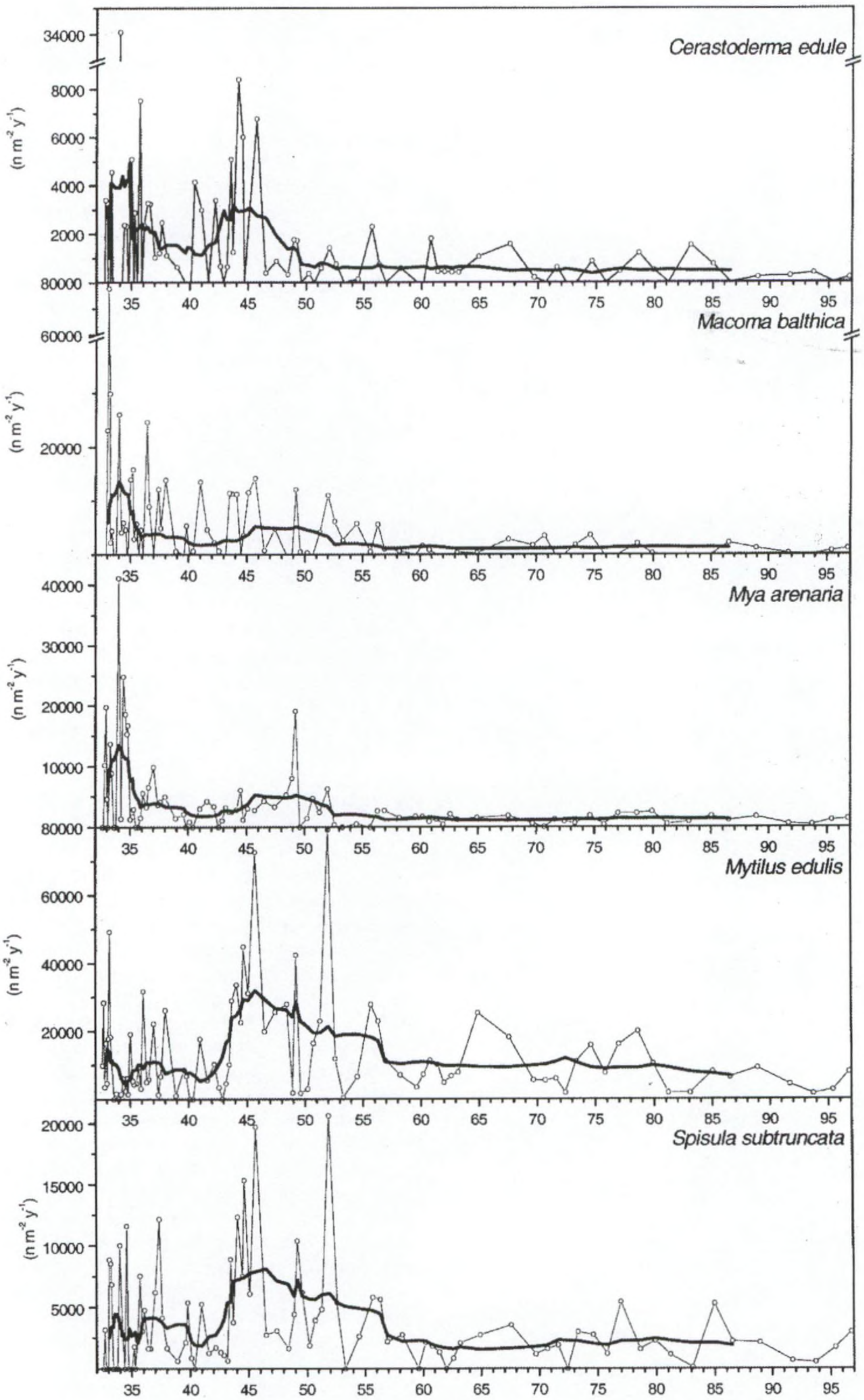


Fig. 3.5.5 Shell-deposition rates of bivalve spat (juveniles < 2 mm) in the western Wadden Sea between 1932 and 1997 as derived from a vibrocore taken in the former Vlieter channel on June 20, 1997.

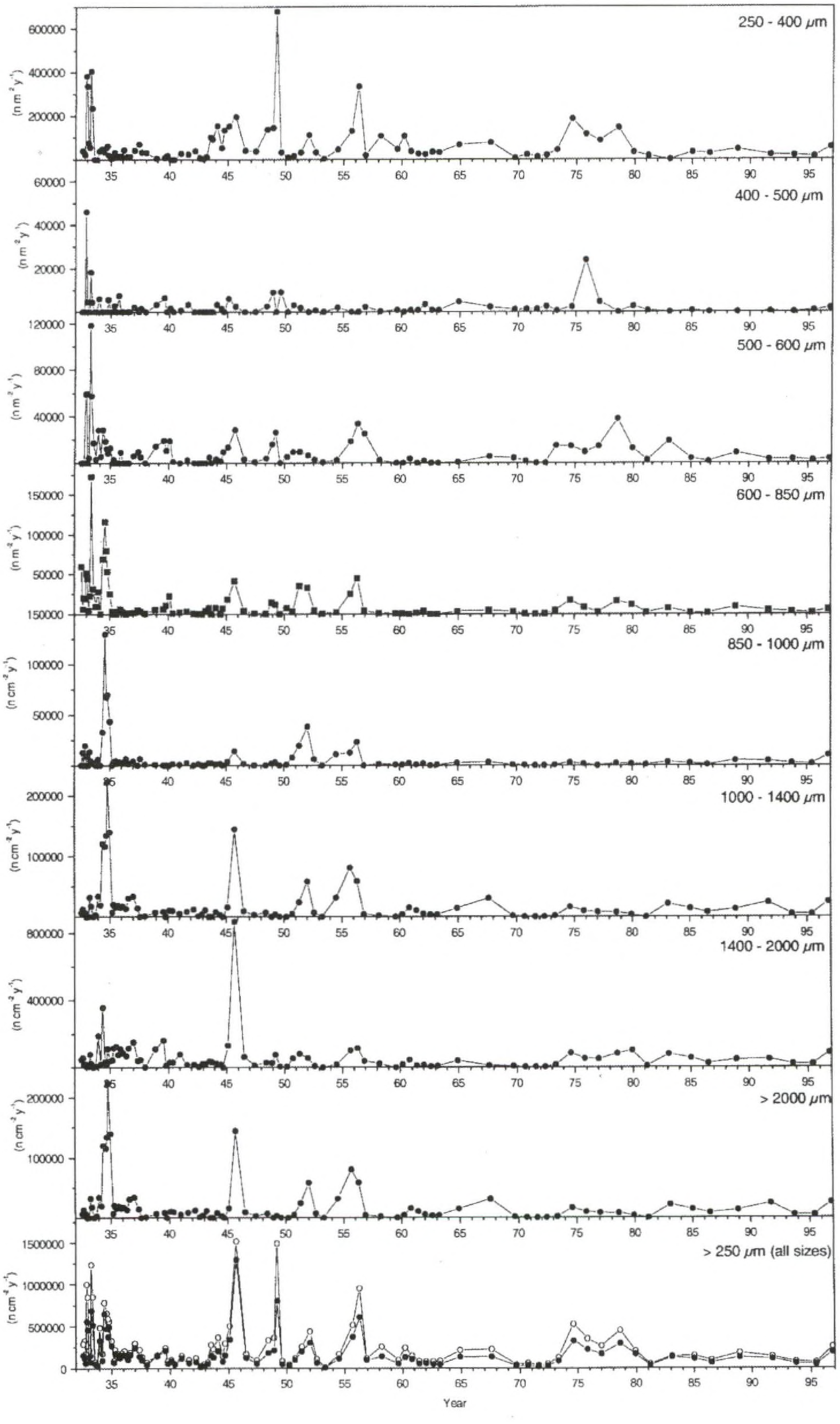


Fig. 3.5.6 Shell-deposition rates of different size-classes of mudsnails (*Hydrobia ulvae*) in the western Wadden Sea between 1932 and 1997 as derived from a vibrocore taken in the former Vlieter channel on June 20, 1997 (black symbols: undamaged shells only; white symbols: sum of damaged and undamaged shells).

rates of *Macoma balthica* spat were highest during the beginning of the study period with highest values (> 20 000 m^{-2} y^{-1}) occurring around 1933, 1934 and 1936 (Fig. 3.5.5B). Shell-deposition rates of *Mya arenaria* spat were higher during the 1930s-1940s than hereafter with highest rates (> 18.000 m^{-2} y^{-1}) occurring around 1932, 1934 and 1949 (Fig. 3.5.5C). Shell-deposition rates of *Mytilus edulis* spat were relatively high from the early 1940s to the late 1950s compared to other years within the study period (Fig. 3.5.5D). Highest rates (> 20.000 m^{-2} y^{-1}) occurred around 1945 and 1952. As for mussels, the shell-deposition rates of *Spisula subtruncata* spat were relatively high from the early 1940s to the late 1950s compared to other years within the study period (Fig. 3.5.5E). Highest rates (> 20.000 m^{-2} y^{-1}) occurred around 1944, 1945 and 1952.

The first two principal components (PCs) of the PCA of the shell-deposition rates of bivalve spat accounted for 43% and 27% of the total variance of the standardised values. Covariability between species was not that high considering that the explained variance by the first two PCs (70%) is less than two times higher than it would have been if the time series of the 5 species were not correlated at all (i.e. $2/5 \cdot 100\% = 40\%$). Based on PCA and correlation analysis (Philippart & Winter 2000), the species can be divided into two groups with more or less similar behaviour, *viz.* the species *Mytilus edulis*, *Spisula subtruncata* and *Macoma balthica*, and the species *Cerastoderma edule* and *Mya arenaria*. Note, however, that within the first group the time series of *Macoma* was not significantly correlated with that of *Mytilus*.

On average, the total number of bivalve spat shells that was deposited within a year had the same order of magnitude as actual spat densities measured at Balgzand during spring, i.e. the time of the year when highest densities are found (Philippart & Winter 2000). Only deposition rates of *Mytilus* spat as derived from the sediment core were approximately ten times as high as actual spat densities observed for the Balgzand tidal flat. This difference may be due to the contribution of spat originating from the culture plots to the total spat deposited in the Vlieter channel. Although there appears to be some similarity in the time series originating from that sediment core and those from the Balgzand, such as low densities in 1980-1981 for *Cerastoderma*, *Mya* and *Mytilus*, the correlation is non-significant for all four species examined.

Mudsnails (Gastropoda) – Most of the mudsnails retrieved from the sedimentcore belonged to the smallest sizeclass (250-400 μm), which are very young animals, or the one-but-largest size-class (1400-2000 μm), which are most probably animals of 1 year and older. The snails within these size-classes contribute together more than 75% to the total numbers of undamaged shells and more than 50% to the total number of individuals retrieved from the core. On average, only densities in adjoining size-classes were significantly correlated (Philippart & Winter 2000).

Highest shell-deposition rates (> 250.000 m^{-2} y^{-1}) of the small mudsnails (250-400 μm) occurred around 1932, 1933, 1949 and 1956. Annual deposition of larger mudsnails (1400-2000 μm) was high (> 300.000 m^{-2} y^{-1}) around 1934 and 1945 (Fig. 3.5.6). The mudsnail layer as described earlier consisted mostly of animals within this size-class (approximately 67%).

On average, the total number of mudsnails that were deposited within a year had the same order of magnitude as the actual mudsnail densities measured at in a sublitoral area of the western Wadden Sea (Philippart & Winter 2000). However, densities in the sediment were much higher than occurred at the Balgzand intertidal flats.

4 DISCUSSION

4.1 HYDROGRAPHY

Baltic Sea

Two main conclusions arise from the analysis of the low-frequency variability of salinity and oxygen concentration in the Baltic Sea. First, the evolution of salinity seems to be coherent at all depths; i.e. the salinity tends to be higher or lower than normal simultaneously (at the interannual time scales) at all depths. This feature is less marked for the evolution of oxygen, but it is still remarkably high. The second conclusion is that although oxygen concentrations are affected by additional biological and chemical processes that do not influence salinity, the evolution of both variables seems to be related. Obviously, common forcing factors exist. The low-frequency evolution of salinity and oxygen is such that higher than normal salinities tend to occur simultaneously with lower than normal oxygen concentrations and vice versa. This relationship is more marked in the upper than in the lower layers, probably because of the stronger relative influence of processes which deplete oxygen from the deep water. This coherent evolution of salinity and oxygen is also linked to the atmospheric circulation. Stronger than normal westerly winds are related to lower than normal salinities in the upper and lower layers in all areas of the Baltic sea and with higher that normal oxygen concentrations in the upper layers (with the exception of the Arkona and the Bornholm Basin at the Baltic Sea entrance) and in the lower layers (with the exception of the Bothnian Bay).

The analysis of this link between the large-scale atmospheric circulation and annual salinity and oxygen concentration reveals that roughly one half of the salinity and oxygen variability is correlated to the meridional atmospheric pressure gradient over the North Atlantic, and thus to the strength of the westerly zonal winds. However, the nature of this relationship is not consistent with the hypothesis that salinity variability is on the long-term caused by major water inflows from the North Sea, as it is well known at shorter time scales (e.g. Matthäus & Schinke 1994). These major inflows cause strong ventilation of most of the deep central Baltic, increasing the salinity and improving the oxygen conditions. Stronger westerly winds not related to major inflow events probably also cause enhanced inflow from the North Sea and positive oxygen anomalies in the deepest layers (North Sea water entering the deep basins of the central Baltic Sea being well oxygenated compared to the stagnant waters in these deep layers), but at the same time the zonal winds are also linked with decreased salinity.

Our analysis seems to indicate that these negative salinity anomalies may be caused by increased precipitation in the Baltic Sea catchment area and this process may be more important in longer time scales than the inflow of saltier North Sea waters. Run-off is linked to salinities in the Baltic Sea at time scales of several months and longer (Launiainen & Vihma 1990, Samuelsson 1996, Schinke & Matthäus 1998). Therefore for the determination of the low-evolving mean salinity in the Baltic the low-frequency variability of the atmosphere seems to be more important than the extreme wind-related events.

The physical link between oxygen and the atmospheric circulation does not come out as clear from this statistical analysis alone. In the upper layer the oxygen concentrations may be influenced positively by vertical mixing, being more intense in periods with stronger zonal circulation. In the deeper layers short term variability in the central Baltic area is evidently caused by the inflows from the North Sea. However, for the long term and low frequency evolution of oxygen other mechanism may be more important. The analysis revealed that similar patterns of the atmospheric circulation are simultaneously connected to the variability of salinity and oxygen variability but causing opposite anomalies.

One explanation could be that the increased oxygen concentrations are a consequence of the decreased salinities and weakened stratification resulting in enhanced vertical mixing affecting also the deeper layers, as it has been observed during the recent prolonged stagnation period (Matthäus 1990, Elken 1996, Matthäus & Schinke 1999). The increased precipitation and run-off associated to intense zonal circulation would also tend to reduce the inflows of oxygen-rich water, as has been suggested by Stigebrandt (1983), Samuelsson (1996), Schinke and Matthäus (1998) and Matthäus and Schinke (1999). Another possibility is that rainfall waters contribute improving the oxygen conditions, although their influence is probably minor. Obviously more work trying to model the oxygen cycle in the Baltic is needed to clarify this question. It was also found that at the interannual time scales salinity in upper levels is highly positively correlated with salinity in the deeper layers.

This phenomenon is also clear, albeit somewhat in a weaker form, for oxygen. It seems that at the multiyear time scale there must be strong enough vertical water exchange or vertical turbulent transport. This is contradictory with the idea of the vertical stratification effectively preventing vertical mixing at longer time scales in the Baltic Sea. Previous modelling studies (Kouts & Omstedt 1993) seem to indicate that the waters entering the Baltic from the North Sea are distributed in much of the deep Baltic in a time scale of six months to one year (excluding the deepest subbasins). This could offer some explanation for the horizontal coherence of the salinity and oxygen anomalies. However, the typical time scale for salinity anomalies entering the deepest layers from the North Sea to be upwelled to the surface layers seems to be of the order of 30 years in other model (Omstedt & Axell 1998). This could indicate that the observed statistical connection between the deep and surface layers is not caused by slow filling-up from the bottom layers. The fact that the position of the halocline also shows a seasonal cycle (Kouts & Omstedt 1993) offers some support to the idea that the mixing between the upper and deeper layers at interannual time scales may be strong enough. However, the statistical analysis alone cannot yield any definite answers to those two problems, but may point to subjects for future research in Baltic Sea modelling.

In the German Bight it is concluded that the canonical SLP pattern describing an anticyclonic circulation leads to easterly winds over western Europe that hinder a large-scale advection of marine air to Europe and cause reduced precipitation (or vice versa). This connection is strongest in the southern North Sea region.

Reduced precipitation leads to higher salinity levels (or vice versa). The time lag between the occurrence of the air pressure pattern and changes in the salinity leads to the conclusion that the impact of precipitation is indirect, i.e. via runoff.

This hypothesis can be proved when 12-month averages of river transport are correlated with the salinity observations. The closer the river estuaries are situated to the German Bight, the higher the correlation and the shorter the lag.

Global warming

A transient experiment with a global General Circulation Model is under scenario. Greenhouse gas emissions shows a strengthening of the zonal circulation in the North Atlantic in the next 100 years, so that to first approximation it could be expected that in this scenario salinities would tend to decrease and oxygen concentrations to increase in the Baltic Sea. However, a cautious researcher believes that precipitation cannot increase indefinitely with the intensity of the zonal circulation and that perhaps if the zonal circulation gets considerably stronger some saturation effects would appear. In addition, a stronger mean zonal circulation may cause more frequent water inflows from the North Sea and in this case the effect of major water inflows could become more important than run-off.

The intensity and frequency of the weather situations giving rise today to major water inflows could in principle be investigated in the GCM integration. In spite of considerable progress in recent times (Hack et al. 1998), however, simulation of regional rainfall by General Circulation Models and Regional Climate Models is far from optimal (Machenauer et al. 1996, Noguer et al. 1998). Subsequently, the question of how these competing effects may evolve in the future remains unanswered. Another source of uncertainty is related to the behaviour of evaporation under climate change. If surface temperatures tend to become warmer due to the new radiation balance, surface salinity will tend to increase due to increased evaporation from the surface. Similarly, increased temperatures may speed up chemical and biological processes and affect oxygen concentrations. In summary, the results of this statistical downscaling should be seen as an estimation of the contribution of the changes of the atmospheric circulation on salinity and oxygen conditions, bearing in mind that other factors might potentially become more important in a changed climate.

North Sea

Conclusions

In summary, the following conclusions can be made:

- A relationship between climate forcing and hydrography in the Baltic Sea and the German Bight existst and has been identified, although the physical mechanisms that operate are not completely clear in all cases.
- In the most simple case of those shown in this report, namely salinity in the German Bight, the mechanism invloves precipitation and runoff . For the Baltic Sea, the mechanism by which the atmospheric forcing is active, there are solid candidates (rainfall-runoff). However, there is discrepancy with other authors on the question if runoff represent a fresh water flux or an obstacle for water inflows from the North Sea. For oxygen in the Baltic Sea the hypothesis are weaker, and the mechanisms may involve the stratification or North Sea water inflows.

More concretely:

1 Salinity and oxygen tend to be higher or lower than normal simultaneously in the entire area at all depths.
2 There is, at all depths a negative correlation between salinity and oxygen, indicating that there exist a common forcing factor.
3 Roughly one half of the salinity and oxygen variability is correlated to the meridional atmospheric pressure gradient over the North Atlantic.

4.2 PLANKTON

Western Wadden Sea

Phytoplankton dynamics

Phytoplankton species composition – Based on the observed changes in species composition, particularly during the nutrient-controlled months of the growing season (July-August), we conclude that the phytoplankton community structure in the western Wadden Sea changed drastically between 1977 and 1978 and between 1987 and 1988. The community structure was relatively stable during the periods between these shifts, *viz.* from 1974 to 1976 (period A), from 1978 to 1987 (period B1) and 1988 to 1994 (period B2). The major changes in phytoplankton biomass and species composition coincided with changes in absolute and relative (TN: TP) nutrient concentrations. A combination of the time series on trophic state (using chlorophyll-a as a proxy) and limiting resources (TN: TP ratio) shows the same distinctive periods as phytoplankton community structure (Fig. 4.2.1C). The increase in phytoplankton abundance between 1976 and 1978 (Fig. 4.2.1A) corresponded with a decrease in TN: TP ratio (Fig. 4.2.1B). Hereafter, the phytoplankton biomass remained high, but the community structure changed again between 1987 and 1988 upon the re-shift to phosphorus-controlled conditions.

Co-limitation effects – It may be questioned whether nutrient control is relevant at all in the Marsdiep since summer values of nutrients showed minimum thresholds of 1 mmol m^{-3} for nitrate plus nitrite (Fig. 3.2.3C) and 0.2 mmol m^{-3} for phosphate (Fig. 3.2.3F). The strong correlation between phytoplankton community structure and TN: TP ratios strongly suggest that, despite the relatively high concentrations of these nutrients, they do have a regulatory effect with respect to species composition. This apparent contradiction can be explained on the basis of phytoplankton ecophysiology. During nutrient-limited growth at non-saturating irradiance levels, algae enhance their nutrient quota and growth is sustained at higher substrate concentrations. In coastal areas where sub-optimal light conditions prevail during summer periods due to high suspended matter levels, nutrients can still be limiting the specific growth rate at higher concentrations compared to waters with lower turbidity, as a consequence of co-limitation effects (Cloern et al. 1995, Hegarty & Villareal 1998). Indeed, physiological studies (only occasionally performed) on summer phytoplankton in the Marsdiep area, do indicate the occurrence of N- or P-limitation despite elevated dissolved inorganic nutrient concentrations (Riegman et al. 1990).

Size structure – Our results further imply that a shift towards a eutrophic environment particularly favored flagellates such as colony-forming *Phaeocystis* spp. (Cadée & Hegeman 1986, Riegman et al. 1992), and diatoms > 1000 μm^3 such as *Rhizosolenia* and *Thalassiosira* spp.. This latter development confirms the theoretical forecast by Stolte & Riegman (1995) stating that eutrophication results in a dominance of large phytoplankton species. Theory further predicts an extensive overflow of these large phytoplankton species via sedimentation to benthic communities (Thingstad & Sakshaug 1990, Riegman et al. 1993). Most of the large diatom species that increased in the Marsdiep inlet does not appear as single cells but form chains. High densities of chain-forming diatoms rapidly coagulate (Jackson 1990), which may have further intensified the downward flux of these species (Smetacek 1985, Logan & Alldredge 1989, Kiørboe 1993), and thus the deposition of phytoplankton cells at the sediment after 1978. Although the phytoplankton composition shifted between 1987 and 1988, the total biovolume and the proportion of large diatoms remained high.

Nutrient budgets and denitrification – We applied budget calculations to better understand the response of the western Wadden Sea to changing nutrient supply. Whilst trends in TP loadings from land were reflected in phosphate and TP concentrations, the gradual increase in TN loadings from 1975 to 1988 was reflected in NO_x concentrations but not in those of TN. This disparity suggests a non-linear system response to enhanced nutrient inputs, thus questioning the often-assumed one-to-one relationship between loadings and availability of nutrients. The drop in TN concentrations after 1978 can be explained by first a decreased input of particulate N from the open sea, and second an increased removal of nitrogen in the basin itself. Apparently, the trapping efficiency of particulate N decreased upon increased N loading and decreasing TN: TP ratios.

The residual flux of the nitrogen budget was negative after 1978. Because this flux is N-specific, i.e. not accounted for in the P-budget, the most plausible explanation for this loss is denitrification, the reduction of nitrate to dinitrogen-gas. Nitrogen loss in coastal marine systems has been considered proportional to the TN input (25-75%; Seitzinger 1988, Borum 1996) or concentration (Borum 1996). Our calculations indicate that nitrogen removal in the western Wadden Sea was 35% of the total nitrogen inputs and 45% of the input from land from 1978 onwards, corresponding well to the budgets reviewed by Borum (1996).

The calculated annual mean residual losses of approximately 4 mmol N m^{-2} d^{-1} are high, but still within the range of directly measured denitrification rates reported for a suite of coastal marine sediments (Seitzinger 1988, Christensen 1994, Borum 1996). Additionally, this rate agrees well with the relationships described for two Danish fjords at an average TN concentration of about 70 mmol m^{-3} (Borum 1996). Recently published mean denitrification rates measured in sediments in the German Wadden Sea (Jensen et al. 1996) and Danish coastal waters (Nielsen et al. 1994) with the ^{15}N isotope pairing technique, however, point at values of about 0.4 mmol N m^{-2} d^{-1}. Winter measurements with acetylene-blockage techniques at high nitrate concentrations indicated similarly low rates for the western Wadden Sea (Kieskamp et al. 1991). The discrepancy between budget estimates and experimental data of different origin cannot easily be explained. Enhanced sediment-water exchange due to wave action in the actual field situation compared to the different experimental set-ups may play a role, in particular for permeable sandy Wadden Sea tidal flats (Rutgers van der Loeff 1981, Shum 1993, Hüttel et al. 1998).

Denitrification and phytoplankton – Rates of benthic denitrification are related to water column concentrations of nitrate and to fluxes of labile organic matter to the sediment following phytoplankton blooms (Jensen et al. 1988, Middelburg et al. 1996). Subsequently, the increase in nutrient loadings and coinciding higher phytoplankton biomass probably explains the major part of the increase in denitrification in the western Wadden Sea after 1978. Standardised time series of chlorophyll and denitrification rates showed indeed very similar patterns in the long-term trends between 1978 and 1993 (Fig. 3.2.1E). This resemblance in trends strongly suggests phytoplankton biomass to be an important factor determining the interannual variation in nitrogen loss of the western Wadden Sea.

As for the phytoplankton biomass, major changes in phytoplankton community structure occurred around 1977 such as the observed increase of larger cells and the suggested increase in nitrate storage capacity (Fig. 3.2.1D). These additional responses of the phytoplankton community to changes in nutrient resources may have contributed to the observed increase in denitrification. Assuming that the annual average specific growth rate of phytoplankton is about 0.5 day^{-1} (Parsons et al. 1977), and that 25-50% of the phytoplankton production sinks out to the sediment with the nitrate pools still intact (Lomstein et al. 1990) and is subsequently mineralised by the denitrifying community (Jørgensen 1996), the maximum denitrification of the pools may have been 0.1-0.2 mmol N m^{-2} day^{-1}. This implies that even if such a mechanism existed, its contribution to the total estimated residual fluxes of the nitrogen budget would have been very small (< 5%).

Conclusions

The major conclusions of our long-term field observations on phytoplankton dynamics in the western Wadden Sea were that:

- The phytoplankton community changed drastically both between 1976 and 1978 and again between 1987 and 1988, and was relatively stable in-between (1974-1976, 1978-1987) and hereafter (1988-1994).
- Shifts in TN: TP ratios have had a strong effect on the species composition of the marine phytoplankton community in the western Wadden Sea.
- Eutrophic and nitrogen-controlled conditions result in a disproportional increase of large diatom species (individual cell size > 1000 μm^3).
- Long-term trends in chlorophyll-a concentrations were positively correlated with those in nitrogen-loss rates, suggesting enhanced benthic denitrification through increased deposition of phytoplankton biomass.

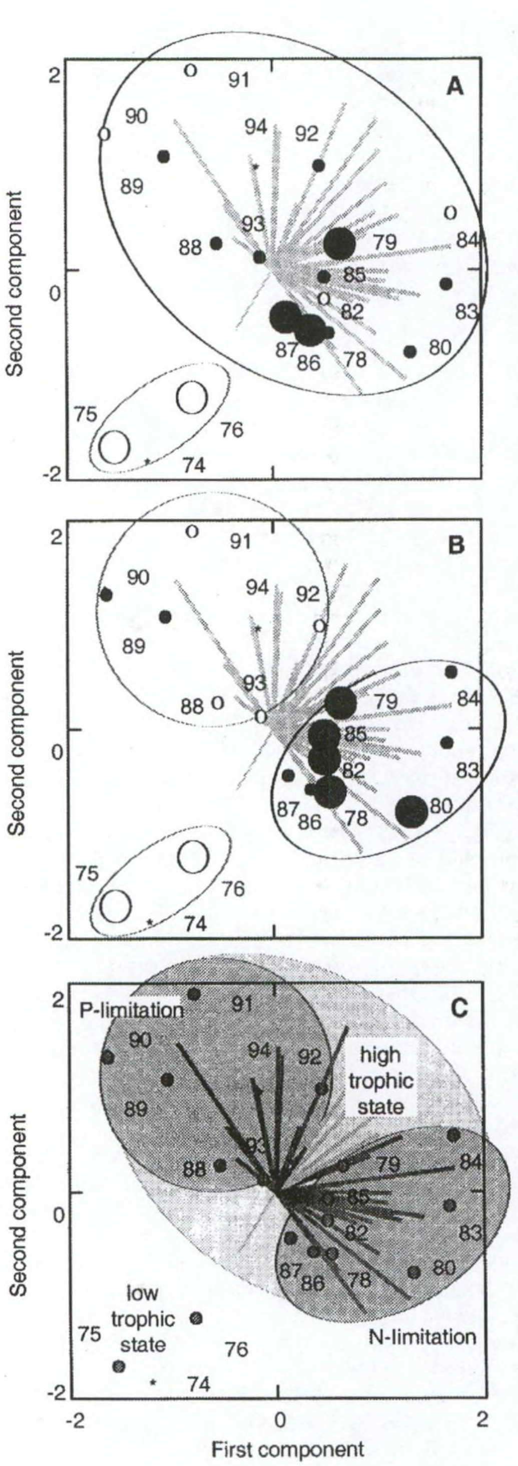


Fig. 4.2.1 Covariance biplots (1st and 2nd axis) based on Principal Component Analysis of the species composition of the phytoplankton community during the nutrient-controlled periods of the growing season (July-Aug) between 1974 and 1994. Grey vectors and years represent relative phytoplankton species abundances by numbered dots. A. Trophic state (indexed as the average annual chlorophyll-a concentrations: large white dots < 5.5 mg m^{-3}, small white dots 5.5-7.5 mg m^{-3}, small black dots 7.5-9.5 mg m^{-3}, large black dots > 9.5 mg m^{-3}). B. Average TN:TP ratios during the growing season from March to August are indicated for each year (large white dots < 16 mol mol^{-1}, small white dots 16-20 mol mol^{-1}, small black dots 20-30 mol mol^{-1}, large black dots > 30 mol mol^{-1}). C. Indications of different growing circumstances for phytoplankton during the study period as derived from the trophic state and the ambient nutrient ratios. The indications of annual trophic state and TN: TP ratio are restricted to the period for which the nutrient budgets could be estimated (1975-1993), the remaining years (1974 and 1994) are indicated with asterisks (Philippart et al. 2000).

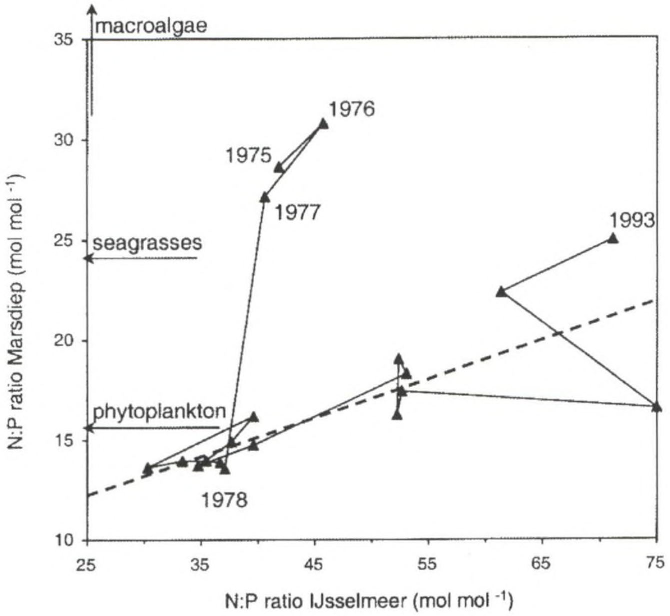


Fig. 4.2.2 Relationship between total N: P ratio of the nutrient loadings from the freshwater lake IJsselmeer and that of the concentrations in the Marsdiep tidal inlet from 1975 to 1993 (Philippart & Cadée 2000). The stippled line indicates the linear relationship between these ratios for the period from 1978 to 1993 ($N:P_{conc.} = 7.5 + 0.19\ N:P_{loading}$; $p < 0.001$; $n = 16$).

Primary production

Growth-limiting nutrients for phytoplankton – During the 1980-1990s, the total and pelagic production estimates based on annual nitrogen loadings appear to be in good agreement with actually observed production rates in the western Wadden Sea (Fig. 3.2.2) and lie well within the range as found for other shallow coastal marine waters (Borum & Sand-Jensen 1996). During the 1960-1970s, however, the total- and pelagic-production estimates based on local nitrogen loadings were much too high compared with actual field values. This difference suggests that (i) primary production was probably not related to the supply of this particular nutrient but to another factor during the beginning of the study period, and (b) the Borum and Sand-Jensen model was not applicable to this situation, e.g. because primary production was not stimulated by N-loading from land.

Loadings and concentrations – The TN: TP ratios of the discharged freshwater from IJsselmeer into the western Wadden Sea always exceeded the Redfield ratio of 16 (Fig. 4.2.2). However, this does not imply that phosphorus rather than nitrogen was the limiting factor for algal growth in these shallow marine waters (*contra* De Jonge et al. 1996). Due to mixing with other water masses and denitrification, the N:P ratios of ambient nutrient concentrations ($ratio_{Marsdiep}$) were generally lower than those of the loadings from land ($ratio_{IJsselmeer}$) between 1978 and 1993 (Fig. 4.2.2). Only between 1975 and 1977, the TN: TP ratios of the ambient nutrient concentrations were almost as high as those of the loadings. Furthermore, nutrient budget calculations of the western Wadden Sea implied that before 1978 the nutrient loadings originating from the freshwater lake IJsselmeer comprised only a relatively small portion of the total nutrient input into the system, i.e. 35% for phosphorus and 28% for nitrogen (Philippart et al. 2000). At that time, the inward transport of organic matter from the North Sea was an important additional source of nutrients, i.e. more than 30% of total P inputs and almost 40% of total N inputs (Fig. 3.2.4). This flux remained more or less stable for phosphorus, but its importance was drastically declined for nitrogen from 1978 onwards. From 1978 onwards, nutrient loadings from IJsselmeer represented 45% of the total P and 75% of the total N inputs.

Growth-limiting nutrients – The nutrient that limits primary production in a particular area is generally identified by a comparison of the ratio of the concentrations of the local nutrients in the water column with the contents of these nutrients in the specific autotrophic component. By comparing the ambient nutrient ratios and the Redfield ratio (TN: TP = 16) which is generally considered to approximate phytoplankton composition (Redfield et al. 1963), it appears that phytoplankton growth in the western Wadden Sea was probably more limited by ambient P than N concentrations before 1978 and after 1987 (Riegman et al. 1992; Philippart et al. 2000).

When examining growth-limiting nutrients for the other autotrophic components, it has to be considered that nutrient contents of marine macroalgae and seagrasses may deviate markedly from those of phytoplankton. Assuming that the N: P ratio of the nutrient contents of phytoplankton is 16 (Redfield et al. 1963), of macroalgae is 49 (Duarte 1992) and of seagrass 24 (Duarte 1990), the limiting nutrient in the western Wadden Sea differed between years and between autotrophic components throughout the study period (Fig. 4.2.2). It has to be contemplated that even relatively

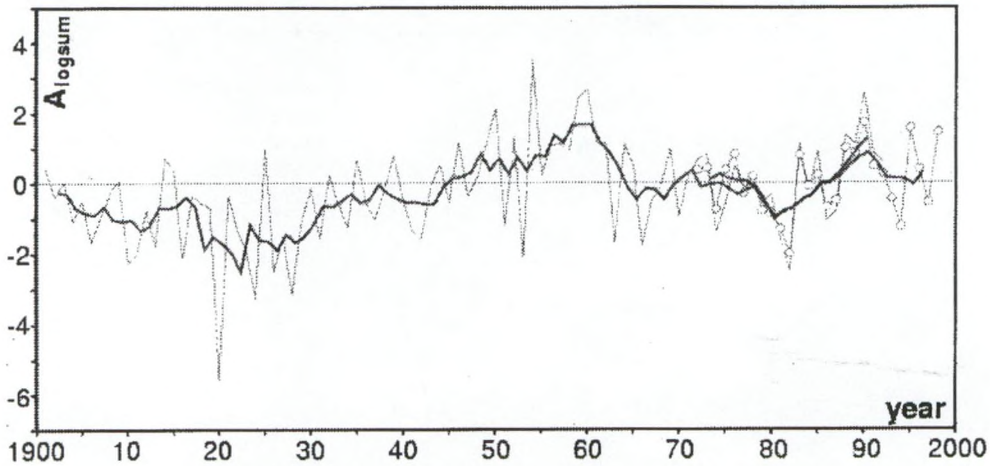


Fig. 4.2.3 Estimated integrated log-abundance from January to July for *Noctiluca scintillans*, which is a proxy for the total abundance of this species. The estimations were derived from the November to January SST. The two leading EOFs of the coarsely resolved SST (1900 to 1992, solid line) and the 1st EOF of the finely resolved SST (1971 to 1998, solid line with circles) were used by the model. The thick lines represent 5 year running averages.

small differences in the taxonomic outcome of resource competition for nutrients may be followed by secondary and tertiary effects which enhance the shift within autotrophic components. For example, elevated phytoplankton biomass decreases the photosynthetic activity of seagrasses and thereby affects its ability to reduce the toxic sulfide in the sediment (Hemminga 1998).

Co-limitation effects – Total primary production will not only depend on ambient nutrient concentrations but also on other properties of the study area such as morphometry, light climate and hydraulics (Nienhuis 1992, De Vries et al. 1996, Colijn 1982). Changes in these assets may therefore result in changes of the total primary production. In 1932, the former Zuiderzee was closed off from the western Wadden Sea by means of the Afsluitdijk. Because this engineering work had a severe effect on several properties such as the morphodynamics and hydraulics of the study area (Dijkema et al. 1980), we have to be cautious to extrapolate present production values to the period before 1932. From the 1930s onwards, however, no such major modifications were made and, as far as we know, neither were significant changes observed in freshwater discharges, salinity and water temperatures (e.g. Van der Hoeven 1982, Cadée 1984, De Jonge 1997).

Possible changes in turbidity of Dutch Wadden Sea waters since the 1930s are still under discussion. Monitoring results at several sampling stations from the 1970s to the 1990s suggest an increase in suspended-matter concentrations to the beginning of the 1980s followed by a decrease (De Jonge & De Jong 1992; de Jonge et al. 1996). However, part of these observed trends can be satisfactorily explained by systematical changes in sampling procedures (Maiwald & Verhagen 1991). Moreover, the Secchi-disk readings, which were consistently taken at high tide in the Marsdiep tidal inlet between 1974 and 1990, did not indicate such changes in turbidity (Cadée & Hegeman 1991).

Furthermore it has to be noted that in coastal areas where sub-optimal light conditions prevail during summer periods due to high suspended matter levels, nutrients can still be limiting the specific growth rate at higher concentrations compared to waters with lower turbidity, as a consequence of co-limitation effects (Riegman pers. comm.). Some indication for this mechanism is already there: during the past decade the P-discharge into the area has been gradually reduced with 50%, but a significant reduction in the average chlorophyll-a during summer periods has not been observed until now (Cadée & Hegeman 1993, De Jonge 1997, Riegman pers. comm.).

Conclusions

Our results strongly suggest that the empirical relationships as described by Borum & Sand-Jensen (1996) cannot be applied for the estimation of primary production in those coastal environments

- in which other factors than the ambient N concentrations limit primary production,
- where availability of the actual limiting resource is not reflected in the N loadings from land.

German Bight

Noctiluca scintillans – Since the overwhelming portion of *N. scintillans* is observed during the summer months, the integrated log-abundance from January to July can be used as a proxy for the total yearly abundance of *N. scintillans* or for the height of the summer bloom. For example, it is correlated with the integrated log-abundance from January to December, i.e. the sum of the yearly log-abundance, with r=0.90, and to the May to June log- abundance with r=0.83. The suitability as a proxy for the total abundance and the simplicity of the identified SST pattern (i.e. an anomalously warm or cold North Sea) make it possible (i) to use coarsely resolved SST data to reconstruct historical abundances of *N. scintillans* and (ii) to validate the found relationship with data of *N. scintillans* from other sites in the North Sea. Since winter SST is the predictor, (iii) an estimation of the expected bloom in the following year is possible.

Figure 4.2.3 shows the estimation of the integrated log-abundance from January to July for the twentieth century. The estimations were derived from the two leading EOFs of the coarsely resolved SST (1900 to 1992) and the 1st EOF of the finely resolved SST (1971 to 1998). The dominating signal is a continuous increase from 1930 to 1960, a steep drop after 1960, and a recovery after 1980. It is interesting that this curve bears similarities with observations by the Plankton Recorder Network from the North Sea and northeastern Atlantic, which shows a drop around 1960 and a recovery after 1980 for several zooplankton species (Cushing 1996). Another interesting point is that the start of the increase around 1930 coincides with the beginning of the warm period of the so-called Russell Cycle (Cushing 1982). The end of that period at around 1970 is not recognisable.

Since the lifetime of the unicellular *N. scintillans* is short, the spring or summer population cannot be directly linked to winter temperatures. One possible explanation is that mild temperatures lead to an earlier start of the blooming season and thus to a longer period of productivity, as has been observed for some plankton time series (Uwe Lange, pers. comm.). As a simple test of this hypothesis, the "start of the blooming season" was defined as the week in which (i) more than ca. 3000 animals per week were counted in 2 successive weeks or (ii) more than ca. 1000 animals per week were counted in three successive weeks. The comparison between the resulting time series with the time series of the first SST EOF for the months November to April shows an agreement as to the lowest value (high SST, early bloom), occurring between 1988 and 1992, but apart from this extreme, no correlations exist. However, the high SST anomalies in the period 1988 to 1992 represent the strongest signal in the time series and therefore the agreement in this extreme indicates that the hypothesis "mild winter leads to early start of bloom" is worth further investigation.

In addition, other holoplanktonic species like ctenophores are known to have a negative influence on the development of *N. scintillans*. An early bloom of the ctenophore *Pleurobrachia pileus* is correlated with r=0.63 to high temperatures in the 1st quarter of the year and with r=0.45 to a high abundance of *N. scintillans*. Thus, another possible explanation is that high summer maxima for *N. scintillans* are reached when the development of interacting populations occurs earlier in the year than usual (Heino Fock, pers. comm.).

Zooplankton dynamics and climate – The model identified 3 clusters of high correlations. It is likely that at least 2 of these correlations represent causal relationships to winter SST. No correlations were found between zooplankton and climate parameters in other seasons. This could indicate that abiotic factors are of high importance in winter and of lower importance later in the year, a result that is widely accepted for limnic plankton communities (PEG model; Sommer et al. 1986).

Since zooplankton feeds on phytoplankton, another important determinant for marine zooplankton could be light, which determines the growth of phytoplankton. Low light availability may be caused by clouds, by storms (that increase the depth of the mixing layer) or by SST (low stratification increases the mixing layer).

In the present study, no correlation between the proxy variable storm activity and zooplankton was found. This could mean that this variable is not suited for this purpose, but it is also reasonable that the relationships are too complex. Low light conditions may lead to low primary production and thus to a low zooplankton abundance, but they could also lead to a delay in primary production and thus cause changes in the species composition (match/mismatch hypothesis, e.g. Cushing, 1990). If possible, the topic light should be examined more closely in future studies.

In the previous case study, data from a climate simulation were used to estimate the development of the mean salinity level under climate change conditions. In the present study, it would be of interest to estimate the development of *Noctiluca scintillans*, since this species is of high ecological importance. Unfortunately, such an estimation is problematic, since in the firs place the predictor "North Sea SST'" is represented by only a few grid points in GCMs, and information derived from single grid points is not reliable (Robinson & Finkelstein 1991). Secondly, it was discussed that the relationship between SST and *N. scintillans* might be indirect via interacting species, making the relationship complex and, therefore, less robust. Hence, the idea of estimating the abundance of *N. scintillans* for a climate scenario was abandoned.

Conclusions

The major conclusions with regard to climatic indices and zooplankton dynamics in the Helgoland Roads are that

- the relationships between the North Atlantic Oscillation and zooplankton species in the North Sea seems to be statistically clear.
- In some cases, such as *Noctiluca scintillians*, the explained variance is high, but the mechanisms responsible probably involve the interaction with phytoplankton.
- For other species, such as *Temora longicornis*, the link is also detectable but the explained variance is low and the mechanisms for such a link could not be cleared up.
- It was possible to design a statistical strategy to search systematically for relationships between climatic time series and plankton abundances. Some relationships of this king were found for plankton populations in the German Bight.
- The interpretation of the these relationships in terms of physical or/and biological mechanisms proved not to be straight forward. In some cases the internal interactions between planktonic species probably play a more important role than external climate forcing.

4.3 MACROBENTHOS

Western Wadden Sea

In the spatial analysis of the Wadden Sea tidal macrobenthic communities a gradation in the species distribution was observed. Different species characterized the different ends of the study area along a gradient which was mostly determined by distance to tidal stream and changes in the sediment structure. Distance to dike was also found important in some cases. The distances to tidal stream and dike represent variables that are related to the exposure of the area, to waves and currents and to prevailing southwesterly winds, respectively. Thus, it is obvious that the sediment characteristics, here measured as grain size and silt content, will also change along the gradient due to the exposure related factors evidently modifying sediment structure of the shallow area. It is apparent that all these variables describe the exposure gradient of the area in a slightly different ways and indicate the role of the physical processes in structuring the tidal communities. The importance of sediment structure and physical factors in structuring the North Sea benthic communities was also pointed out by Basford et al. (1990) and Duineveld et al. (1991). The distance to the tidal inlet could also be a measure of food transport to the benthic communities. Heip et al. (1992) also suggested primary production variability to affect the distribution of North Sea communities.

When analysing the temporal development (1974-1995) of the communities, distinct changes in abundance were observed and some of the species could be grouped based on similar trends and on similar response on the estimated environmental gradients (see 3.3.1). The polychaetes (*Nereis diversicolor, Scoloplos armiger, Heteromastus filiformis*), showed increasing trends in abundance since the middle of 1970s, the two latter species also in the 1990s. For the bivalves cyclical behaviour was typical, obviously related to the recruitment success. However, in most of the analysis none of the temporal variables describing salinity, temperature, wind and insolation conditions or phytoplankton biomass could explain these changes. The environmental gradients related to species distribution was year after year determined mostly by the above mentioned exposure-related factors. Only in DGAM high correlation were found between temperature and the polychaetes *Nephtys hombergii* and *Lanice conchilega* (positively affected) and the bivalve *Mya arenaria* (negatively affected). Thus climatic variability potentially affects the succession of the benthic communities by causing changes in the temperature regimes (see discussion later).

Conclusions

- Sediment structure and exposure to physical factors obviously modify locally the macrobenthic communities in the tidal areas.
- Long-term changes in abundance of a group of species were correlated to temperature, which indicates that climate potentially structures the communities. However, the analysis did not reveal the mechanisms causing the concurrent trends.

North Sea

Aebisher et al. (1990) and Lindeboom et al. (1995) have demonstrated distinct changes in several trophic levels coinciding in late 1970s in the North Sea area and concluded that climatic and oceanic factors could be a common cause for the changes. The changes in benthic communities of the area has been attributed to winter climate conditions and alternation between cold and mild periods (Evans & Edwards 1993, Fromentin & Ibanez 1994, Beukema et al. 1996, Fromentin et al. 1997). Eutrophication and its consequences to food supply to benthos and other anthropogenic effects were pointed out by Austen et al. (1991), Josefson et al. (1993), Kröncke (1995), Beukema et al. (1996). A high amount of the variability in benthic communities could be related to changes in phytoplankton abundance or biomass, indicating the significance of benthic-pelagic coupling (Heip et al. 1992, Buchanan 1993). Introduction of non-indigenuous species may also alter the communities as demonstrated by Essink et al. (1998). Cyclical behaviour of communities is discussed in Gray & Christie (1983) and Beukema et al. (1996).

In studies conducted here changes in the benthic communities related both to climatic factors and fisheries effects could be demonstrated. In Nordeney material a common feature was a minimum in species number in the late 1970s/ turn of the decades, followed by an increase. In addition, clearly higher values were observed in the first half of the 1990s. A great part of this variability could be connected sea surface temperature and climatic factors similar to conditions described by NAO index (Kröncke et al. 1998). Especially the winter and early spring conditons showed to be important for the development of the communities. Cold winters affect negatively the communities and mild winters in connection to eutrophication effects obviously explain the observed increase in biomass in the 1990s. Positive anomalies in the NAO will cause increase of benthic biomass by introducing mild winters. The consequences in water termperature are expected to be most profound along the southeastern coasts. However, it is obvious that several other factors, extremes in climatic events and eutrophication and its consequences to oxygen conditions may also structure the communities (e.g. Von Westerhagen et al. 1986, Beukema 1992, Kröncke et al. 1997). Synergistic effects between these environmental factors are also likely to exist.

In the Dutch continental shelf areas characterized by different benthic community structure and sediment characteristics (grain size and mud content) were identified but these factors could not explain the temporal variability. However, the period studied in the 1990s was comparatively short and it is unlikely that major changes could have taken place in these variables in such a short time.

The negative effects of bottom trawling has gained much attention lately and is considered to be one of the major impacts on benthic communities in intensively fished areas like the North Sea (Bergman & Hup 1992, Lindeboom & de Groot 1998). Two surveys were

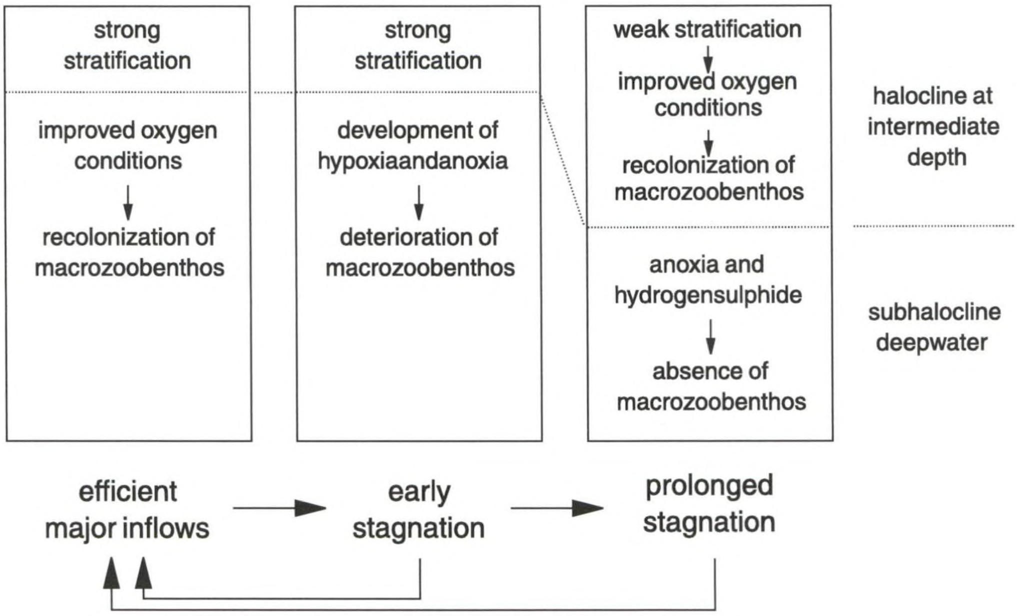


Fig. 4.3.1 A schematic diagram of the effects of the major inflows and stagnation periods on the macrozoobenthos in halocline and subhalocline depths in the Baltic Sea (Laine et al.1997).

conducted to study the effects of fishing restrictions in the southeastern coastal North Sea (Piet et al. in prep.). The stepwise implementation of an area closed for fisheries evidently moved the fishing pressure to the borders of the plaice box area (Rijnsdorp et al. 1998). Of the two surveys the BTS is more likely to show temporal changes due to its higher intensity and larger area covered. The representativeness of the by-catch material for detecting changes in communities is obviously reasonable (De Vooys & Van der Meer 1998). The bottom temperature has to be taken into account when interpreting the results presented here as the reference and box areas represent different temperature regimes, the first one being located below the thermocline.

However, an effect on the communities due to fisheries activity could be observed but the sign of the change was in some cases contradictory. We assume that, with the (partial) closing of the box, fishing effort in the box area decreased while it increased in the reference area. Therefore, the strongest evidence that a population was affected by fishing activities is that both surveys show inverse changes in density in the two areas. A general pattern in the structure of the benthic invertebrate assemblage in the box area was a change toward a composition more similar to that in the reference area when the box was closed part of the year, but returned to its original composition when the box was closed year-round. This pattern was observed for species such as *Ophiura* spp., *Cancer pagurus*, *Corystes cassivelaunus*, *Echinocardium* spp., *Actiniaria* spp. and *Liocarcinus holsatus*. A possible explanation may be that the assemblage was dominated by scavengers and predators (Kaiser & Spencer 1994, 1996, Holtmann et al. 1996, Lindeboom & De Groot 1998). For such species the expected effect of fishing activities on abundance are somewhat ambivalent. Although fishing activities will cause additional mortality, the fishery produces a large amount of potential food material in terms of discarded by-catch while removing fish species that are potential predators of all benthic species or competitors of the benthic predators. Possibly, the relationship between abundance of these species and fishing intensity may show an optimum curve because the deleterious effect of additional mortality is counteracted by decreased competition for food and risk of predation. This effect may even have been enhanced by the timing of the survey in relation to the activities of the fleet. Just after the sampling period there was a period with high fishing intensity followed by a period of about half a year prior to the sampling period with relatively low fishing intensity. Whereas fishing mortality decreases at the time when fishing activities stop, it can be expected that the effect of increased food availability and decreased predation may continue to affect the assemblage.

Conclusions

- In the coastal Norderney area, roughly half of the variability in macrobenthic communities could be related to large-scale climatic variability. The mediating factor between NAO and benthos is probably the sea surface temperature in late winter and early spring.
- Cold winters were found to affect negatively the communities while the increase in biomass is probably connected to mild conditions in conjuction with eutrophication.
- Benthic communities in the North Sea showed a response to changes in fishing effort, demonstrating the structuring effects of bottom trawling. The affected communities were evidently dominated by

scavengers and predators which benefit of the discarded by-catch and decreased predation by fish at intermediate disturbance.

Baltic Sea

In the analysis of the distribution of the macrozoobenthic species different assemblages were identified that were related to different subareas and depth zones in the Baltic Sea. The variation of the community structure is evidently connected to the large scale horizontal and vertical gradients of salinity and oxygen which are often correlated due to the hydrological regime. Sediment organic matter content may determine the community structure but is in Baltic Proper area at least partly related to depth which also describes the vertical salinity-oxygen gradient. These results are in agreement with the studies of Rumohr et al. (1996), Olenin (1994) and Bonsdorff & Pearson (1999).

The spatial distribution and structure of these communities is modified by major changes observed in the species distribution and abundance during 33 year long study period (Andersin et al. 1978, Laine et al. 1997). A basic differentiation of the Baltic Sea into two different areas showing different dynamics can be done. This division also coincides with the main differences in salinity stratification and oxygen conditions between the Baltic Proper area and the Gulf of Bothnia. In the Baltic Proper and the Gulf of Finland the temporal variability of the subhalocline zoobenthic communities is evidently related mainly to the limiting oxygen conditions. Salinity is more important for the marine component of fauna. The major changes include a decline of marine species, leading to increseased similarity of the communities in an area extending from southwestern Baltic to the Gulf of Finland. The other one is a peak in abundance in the late 1970's and a more gradual increase again since the end of the 1980's. These changes are obviously caused by the consequences of the alternation between major inflows of North Sea water and the effects of the stagnation on the stratification and vertical mixing properties modifying the salinity and oxygen conditions (Matthäus 1990, Elken 1996, Matthäus & Schinke 1999) (Fig. 4.3.1). The depth zone most affected by this variability is 70-100 m, representing the halocline area and corresponding to about 19% of the total area included in the study (Laine et al. 1997). This depth interval is of even higher importance in the relatively shallow Gulf of Finland area. The changes in the factors which control the water balance and hydrological regime, fresh water runoff and occurrence of salt water inflows, are evidently regulated by climatic varibility. Of this the meridional pressure gradient, resembling conditions of NAO and causing westerly winds seems to be most important (Matthäus & Schinke 1999, Zorita & Laine 1999).

One further factor obviously affecting the benthic communities is the eutrophication of the Baltic Sea, evidenced by the increasing nutrient trends and its consequences on pelagic production (Grönlund & Leppänen 1990, Nehring & Matthäus 1991, Wulff et al. 1994, Perttilä et al. 1995), increasing turbidity (Sandén & Håkansson 1996) and changes in littoral algal zonation (Kautsky et al. 1986). The increased load of organic matter to the deeper layers (Jonsson & Carman 1994) accelerates the oxygen depletion but also increases the input of food to the benthic communities. Cederwall & Elmgren (1980) suggested the latter mechanism to explain the observed increase of benthic biomass in above halocline areas where the oxygen conditions is not a limiting factor. It can be assumed that biotic interactions which have been demonstrated for many of the species play only a minor role when the physical or chemical environment is limiting the communities.

For the Gulf of Bothnia the most prononced long-term change is the fluctuation of the highly dominant amphipod *Monoporeia affinis*. This species has shown cyclical behaviour in abundance which has been suggested to be related to fluctuations in available food and the density of the population (Andersin et al. 1978, Lehtonen & Andersin 1998, Laakkonen et al., in prep.). None of the hydrographical variables used in the analysis could explain the species trends in the Gulf of Bothnia. Despite this we assume that the occurrence of marine species in this area (*Pontoporeia femorata* and *Harmothoe sarsi*) is affected by salinity since they occur at their lower tolerance limits. For the dominant species however, other factors than hydrography, related mainly to variability in food resources are evidently more important but more research is needed to resolve the underlying mechanisms of the variability. Of special interest would be how the climate modifies the onset, duration and species composition of the spring bloom and consequently the sedimentation but this approach is impeded by the scarcity of data.

Conclusions

- In the Baltic Proper and Gulf of Finland area the long-term changes in the communities could be related to hydrographical factors. Oxygen concentration is the main factor affecting the succession of the communities in intermediate depths but the distribution of species is evidently also affected by salinity.
- Changes in hydrography are caused both by salt water inflows and stagnation periods. These factors are highly regulated by climate, especially conditions described by NAO.
- In the Gulf of Bothnia area however, the long-term development of macrozoobenthos could not be explained by factors related to hydrography. In this area food availability in connection to population density probably controls the succession of the dominant amphipod species.

4.4 FISH

North Sea

The long-term patterns in three aspects of the fish community: size-structure, species composition and overall biomass revealed both strong variability as well as progressive trends. In general the progressive trends appear to be caused by anthropogenic factors whereas much of the variability was caused by factors from natural origin.

Fish and fisheries

The most conspicuous progressive trend is that of a change in size-structure of the fish community. The nature of this change together with circumstantial evidence from a comparison of two areas that differ in fishing intensity strongly suggests that it is caused by fishing activities. The size-selective fishing mortality causes a decrease in the biomass of large fish which in turn is reflected in a decrease of the average weight of the fish community as reflected in the catches of all surveys.

Size-selective mortality may also impact the species composition through differences in life-history characteristics of the various species. Theoretically two extremes in life-history strategies can be distinguished: K- and r-strategists. K-strategists usually live in stable and predictable environments and because their fitness mainly depends on their ability to exploit the limited resources efficiently, they generally have longer life-spans and reproduce at a later life stage. They usually produce fewer young but often exhibit parental care. Finally, they usually have a larger body size and greater competitive ability. In contrast, r-strategists live in variable, unpredictable, disturbed or temporary environments. Because their mortality is often sudden and catastrophic, their fitness is heavily dependent on producing as many young as rapidly as possible, under conditions where competition is minimal. They have characteristically evolved high intrinsic rates of increase at the expense of lesser ability to compete under crowded conditions when resources are limited. They are generally small, with brief life-spans and early reproduction. It should be realised, however, that these differences between K- and r-strategists are not absolute but relative. All gradations between the two extreme types are possible, depending on the relative mix of density-dependent and density-independent limitations to which a population is subjected. So instead of trying to position each fish species on a scale ranging from K- to r-strategist the whole community was positioned on this scale by weighting the abundance of each species with quantified life-history characteristics. This resulted in two life-history indices: one based on the maximum size, another on the size at maturity of the species. These two indices showed a trend over time towards a community with less K-strategists and more r-strategists. Like the trend in average weight this trend was stronger in an area where fishing pressure was high thereby providing more circumstancial evidence that this trend is caused by fisheries.

To what extent the fish community was affected by sudden changes in fishing activities such as those induced by management measures could be studied after a large area in the southeastern North Sea, the "plaice box", was closed for the main part of the fishing fleet thereby causing a major reallocation of fishing effort. During the period 1989-1994 when the box was closed during the second and third quarter only a reduction in fishing effort of more than 50% was realized. For the period 1995-1998 when the box was closed year-round, fishing effort in the box area was about 6% of that before (partial) closure of the box.

The BTS catches in the southeastern North Sea show a distinct difference between the box and reference area which is hardly, if at all, affected by the reallocation of fishing effort. This difference between areas can be attributed to a combination of various environmental characteristics such as depth or temperature. However, major changes were also observed in the area. Piet & Rijnsdorp (1998) studied the effect of the introduction of the "plaice box" for the period 1985-1994. The main effect of the partial closure of the box was a change in size-structure caused in particular by an increase in the number of fish within the size-range 25-40 cm. This was assumed to be the result of the effort reduction in the box area. More recent analyses over a longer period (1985-1998) that also incorporates the period when the box was closed year-round do not support this conclusion. Although there was a temporary increase in biomass just after the box became effective, the overall trend over a longer period shows a decrease in biomass of all size-classes. Thus, considering that after the box was established biomass per haul has decreased with 54% in the box area and 14% in the reference area it seems that the overriding effect of the introduction of the plaice box is a reduction in fish biomass which is strongest in the closed area and less so in the surrounding area. However, the conclusion that a reduction in fishing effort results in a decrease in biomass would contradict the observation that in the heavily fished IBTS area biomass is markedly lower than in the lesser fished area. Also, this does not explain the increase in biomass after the box was closed year-round. But possibly another factor was involved here: in recent years and notably from 1994 onwards water temperature near the bottom in the box area was markedly higher than that in the reference area. Since fish are known to adjust their distribution according to their temperature preferences (Bridges 1993) this has probably caused a migration of fish from the box area to the cooler reference area. The sudden change after 1995 in size-structure and species composition of the reference area toward a more "box-like" community together with the increase in biomass would confirm this hypothesis. However, this does not explain why the biomass in the box area also, but to a lesser extent, increased.

The analyses on the effect of the establishment of the "plaice box" were based on BTS, a survey conducted in a relatively small part of the North Sea. To put the observed changes in a bigger perspective the IBTS catches were studied. The area below 56º latitude comprises the area covered by BTS. The IBTS catches in this area confirm the high biomass around 1990 and the subsequent decrease that was observed in BTS but also shows a period of exceptionally high biomass in the early seventies. Moreover, the period of high biomass in the seventies puts the biomass changes which were allegedly initiated by the combination of the closing of the "plaice box" and exceptional high water temperatures, into perspective. Also, the significant interaction between the spatial component (area) and the temporal component (year) which was supposed to indicate an effect of the closure of the box was also observed between various roundfish areas which were not affected by any major changes in fishing activities. This indicates that throughout the North Sea relatively small-scale environmental conditions are affecting the fish community, causing variation that is difficult to distinguish from that caused by large-scale management measures affecting fishing activities such as the introduction of the "plaice box".

Fish and climate

Comparison of the patterns in total biomass of IBTS (two areas separated by 56º latitude: 1 below with high fishing effort and 2 above with low fishing effort) and SNS shows both similarities as well as differences. For IBTS both areas show a period of elevated biomass of all size-classes in the late seventies, decreasing until a minimum is reached in the early eighties, followed by an increase towards a more or less stable maximum level of biomass. This level however, is reached earlier in area 2 and is markedly higher than in area 1. The period of elevated biomass in the seventies that was observed all over the North Sea coincides with observed changes in climatic (Trenberth 1990, Miller et al. 1994), abiotic (Turrell 1992) and biotic variables (Aebisher et al. 1990) of the North Sea ecosystem. This confirms that in that period large-scale changes at various levels of the North Sea ecosystem were taking place, possibly triggered by a shift in the basic state of the atmosphere-ocean climate system. Although in both areas an increase in total biomass was observed during the eighties different mechanisms appear to be responsible. In area 2 there is a subsequent rise and fall in biomass of large fish (mainly gadoids: cod, haddock and saithe), fish of intermediate size (mainly herring and norway pout) and small fish. In contrast in area 1 biomass of large fish is markedly lower and steadily decreasing (probably due to fishing activities) and the increase in biomass was caused by an increase in small fish (< 20 cm) followed by an increase of intermediately sized fish which possibly causes the decline of the smaller fish. Hence, it appears as if the fish community in the area with low fishing effort was top-down regulated whereas the area with high fishing effort was bottom-up regulated. Considering that from the early eighties onwards the biomass of large fish in area 2 is between three to five times that of area 1 this is not unlikely. Theoretically the consequence of an area becoming bottom-up regulated with a decreasing biomass of large fish is that the lower level of predation will cause the biomass of small fish to increase until it reaches carrying capacity. As the small fish feed at a lower trophic level an increase in total biomass can be expected as less of the primary production is lost in the transfer of energy to a higher trophic level. This increase will continue until carrying capacity is reached and small fish remain at the level determined by the carrying capacity of the environment. Hence, the total biomass will show a pattern determined by biomass of relatively small fish that depends on the carrying capacity and the biomass of large fish that shows a progressive decrease due to fishing activities. Carrying capacity of an environment may be affected by local conditions (light, temperature, nutrient availability, mixed layer depth) which in turn may be affected by climate or fishing activities. The observed patterns in area 1 would support this theory but the fact that the same pattern is also observed for area 2 at a much higher level of total biomass is reason for caution on the applicability of this theory. The sudden increase in mixed layer depth in area 2 after 1988 may explain the relatively high level of biomass but does not explain the increase before 1988.

The SNS catches show a slightly different pattern. Here an increase in total biomass was observed from the start of the survey in 1969 until 1989. Then biomass remained high for four years after which it declined. The difference between the two surveys is not surprising since SNS covers a relatively small inshore area and uses a different gear thereby targeting a different part of the fish community. The SNS pattern is comparable to that of the BTS which is more comparable to the SNS in terms of gear used and area covered. Because both the SNS and BTS cover an area inside or close to the "plaice box" it is not unlikely that some of the observed changes are related to the changes in fishing activities induced by the (partial) closing of this area but in this study no causal relationship could be established.

Thus, it is difficult to attribute any of the relatively short-term changes in the fish community directly to fishing activities. The study of the changes occurring after the establishment of the "plaice box" in the south-eastern North Sea and comparison with variation observed in other parts of the North Sea merely exemplifies the difficulty to interpret observations and disentangle the effects the various factors of natural origin have on the fish community from those of anthropogenic origin (e.g. fisheries).

In contrast to the progressive trends the observed variability appears to be mainly from natural origin. In this variability the year-to-year variation should be separated from the variation on a longer time-scale. The year-to-year variation is mainly caused by variation in recruitment, which depends to a large extent on relatively small-scale environmental conditions (Philippart et al. 1997). One environmental factor that was studied was Sea Surface Temperature (SST). Dippner (1997) and Lange & Greve (1997) have computed the theoretical onset of the spawning season from the monthly mean bottom water temperature assuming that gonadal maturation requires a specific growth time at favourable temperature so that the product of both could be identified as the crucial quantity. The theoretical onset of the spawning season in the North Sea was computed by Dippner (1997) for a high NAO index composite and a low NAO index composite. The computed extremes were in good agreement with the observed band-width of the onset of spawning of dab in the English Channel and the southern North Sea (Deniel & Tassel, 1986) and of lemon sole in front of the Scottish coastline (Rae 1965). During low NAO index and strong cooling of SST due to the connected influx of cold continental air masses, the spawning time has a lag of about eight weeks in the German Bight. If the "match/mismatch" hypothesis of Cushing & Dickson (1976) is correct this implies that recruitment succes may be (partly) controlled by the effect of atmospheric circulation on SST. However, no correlation was observed between recruitment succes and onset of the spawning season for cod, haddock, saithe and whiting.

The variability at longer scales may be caused by various environmental factors that show interannual or decadal variation. For example: the fluctuations in overall biomass, size structure and species composition in the IBTS catches in the first quarter are highly correlated with the monthly SST during the previous year. A warm winter results in an overall high fish biomass due to an increase of notably the larger (25-40 cm) fish. Species composition was also affected by SST. It was observed that after a warm autumn the biomass of Lusitanian species increased whereas that of Boreal species decreased. Further, biomass of pelagic species in the eastern North Sea was higher during years with high NAO index. This was not observed for the demersal species.

So far the attempts to explain the variation in recruitment of plaice and sole from the variation in SST have not been very succesfull. This is not surprising considering that recruitment succes depends on a multitude of processes involving eggs, larvae and young juveniles. The time of year and geographical position at which each of these processes take place are often interrelated and may depend on different factors (for review see for example Bakun et al. 1982, Shepherd et. al. 1984, Legget 1986, Wooster &Bailey 1989, Legget & DeBlois 1994). The complexity of this system makes it difficult to select one process or environmental factor that determines the succes of recruitment of a particular species. This was also concluded by Philippart et. al. (1996) for the variation in fish recruit abundance in the Wadden Sea.

Conclusions

- Summarizing it can be concluded that changes over time are continuously taking place in the North Sea fish community. When studying these changes it is important to incorporate the spatial component because many processes act on a relatively small spatial scale thereby creating markedly different temporal patterns between spatial entities. A further understanding of the factors that determine the changes in the fish community can only be achieved if not only longer time-series and data on other factors become available but also if the spatial component can be incorporated at a sufficiently high resolution.

4.5 SEDIMENT CORES

Suitability of a core as an archive

The suitability of the sediment core as an archive of long-term variations within a particular area strongly depends on the presence of undisturbed accumulation of material that represents environmental conditions at the moment of sedimentation. The core, therefore, should not have been contaminated by material that was in fact produced years ago such as old resuspended material from other surrounding areas, nor should the material have been reworked after sedimentation as the result of bioturbation or local resuspension.

Many soft-sediment benthic species do not live at the sediment surface but burry themselves in the sediment, e.g. ostracods either crawl on the sediment surface or burrow to a depth of a few centimeters (Athersuch et al. 1989). Densities of such burrowing and bioturbating animals found at a particular depth should therefore in fact be "updated" to a more recent period.

The Vlieter core V7D showed no obvious signs of bioturbation such as the presence of bioturbating animals or remnants of their sediment-reworking behavior such as tunnels and funnels. Although there were also no indications of local resuspension of material within the former Vlieter channel, we can not exclude the probability of this process due to the shallowness of the sampling location. Unfortunately, we do have indications that the relatively fresh material in the sediment core has been contaminated by older material. The variation in ^{210}Pb profiles of this vibrocore was high even after correction for grainsize. Furthermore, a boxcore sampled in close surrounding of the vibrocore contained remnants of the eelgrass *Zostera marina* (Van Dongen et al. 2000), a seagrass species that virtually died out in the Wadden Sea in 1932. The seagrass material can be eroded from older deposits, but some minor *Zostera* beds were still present after 1932.

Conclusions

Timing and the actual values of environmental variables that are retrieved from sediment cores have to be interpreted with much caution, because:

- Uncertainties and methodological diffulties in dating of the sediment core
- Mixing of relatively old and fresh material throughout the core by bioturbation and resuspension mechanisms
- Burrowing behaviour of marine benthic organisms.

German Bight

Based on the ratios of the left and right halves of the shells, the origin of the remains of the ostracod *Palmoconcha guttata* is most probably more autochtonous than those of *P. laevata*. For *P. guttata*, there is no relationship between the right:left shell halve ratio and shell deposition rate at rates higher than 500 shells m^{-2} y^{-1} (Fig. 4.5.1A). At lower rates, this ratio declines, which may indicate a higher proportion of allochtonous material during periods of low deposition rates. No such indications were found for the shell-deposition rate and the age-class structure of *P. guttata* (Fig. 4.5.1B), nor for both relationships of *P. laevata* (Fig. 4.5.1CD).

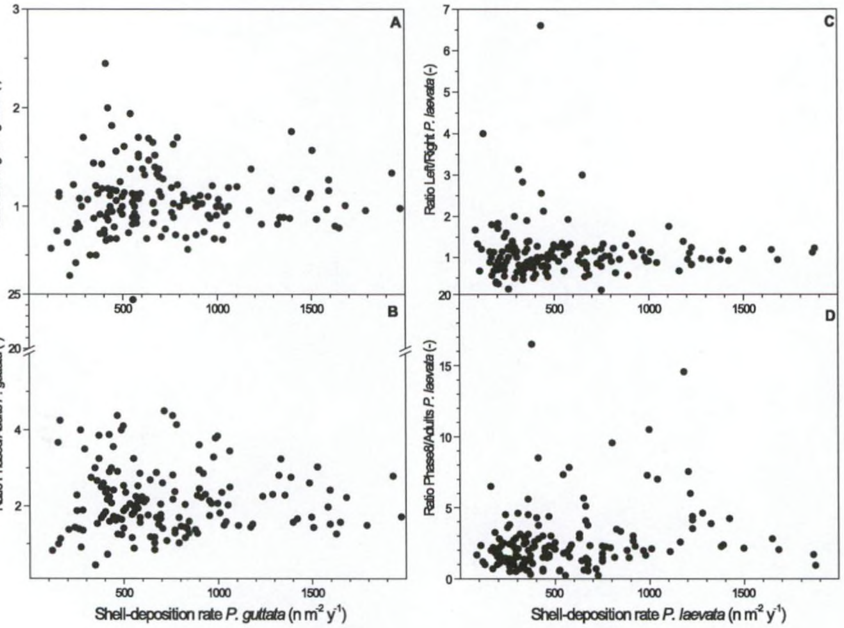


Fig. 4.5.1 Relationship between shell-deposition rates (n m^{-2} y^{-1}) of the ostracods *Palmoconcha guttata* (A, B) and *P. laevata* (C, D) and the ratios of left:right shell halves (A, C) and phase8:adults (B, D), respectively, as derived from a pistoncore sampled in the German Bight on June 4, 1996.

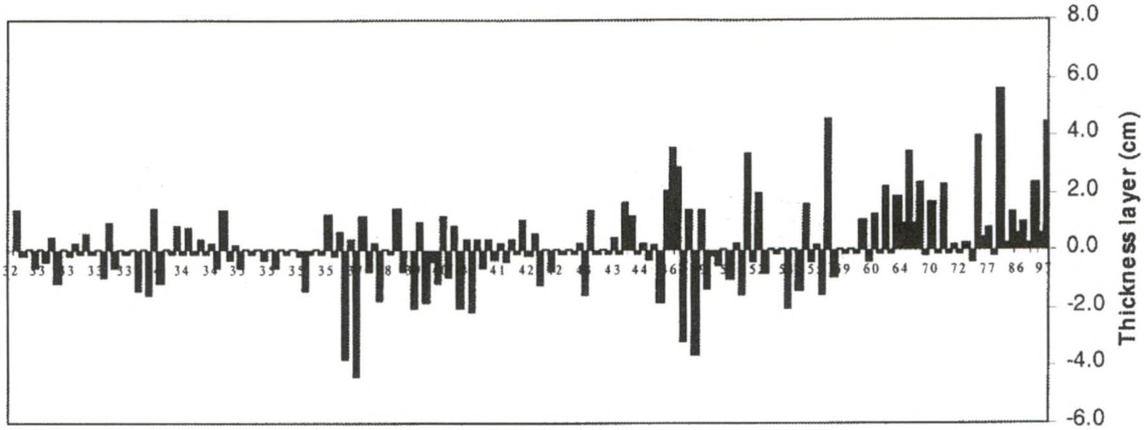


Fig. 4.5.2 Lithology of vibrocore V7D taken in the former Vlieter channel on June 20, 1997. The positive values refer to the thickness of the sandy layers over depth (from left to right is from bottom to top, viz. from May 1932 to June 1997), the negative values to those of the non-sandy layers (mainly containing clay, but also clayey sand or sandy clay).

Conclusions

Variations in ostracod densities in the German Bight core suggest that during the past 2000 years:

- Based on left:right shell-halve ratios, the shell deposition rates of P. guttata appear to be related with mortality rates of the local stock, whilst those of *P. laevata* most probably reflect a combination of rates of mortality and transport of specimen from a wider area.
- The gradual increase in the juvenile:adult ratio of *P. laevata* since 1500 AD cannot be attributed to changes in transport rate, because the left:right shell-halve ratio of this species remained more or less constant during this period.

Western Wadden Sea

Lithology

Vibrocore V7D showed a similar course as the other vibrocores taken during the same cruise, suggesting the following processes during the infill:

1 From bottom to top, there were firstly the sand high-angle foresets that were megaripples deposits formed in the Vlieter channel just before the closure of the Afsluitdijk. When this dike was almost closed and only a small gap remained, current velocities went up to 3.9m s-1 (Candt & Vandenbossche 1975).

2 On top of this sandy layer, all cores contained a thick layer of shells of Cockles that consist of doublets as well as single halves, suggesting that this material washed in within a relatively short period of time. When the dike was fully closed the current velocities dropped low enough to enable clay deposition. The clay that deposited first settled in between the shells of Cockles what made them embedded in mud (Galavazi in prep.).

3 The shell layer is covered by a clay-sand alternation deposited in the low-energy environment of the abandoned channel (Fig. 4.5.2). Towards the top, the amount and thickness of the sandy layers increases and the amount and thickness of the clay layers decreases. It is suggested that this alternation is most likely the result of individual storms (Galavazi in prep.) importing sandy sediments from locations in the direction from where the wind blows.

4 As for the material in the boxcores, the top of all vibrocores hardly contained clay (Fig. 4.5.2). This transgression towards more sandy sediment over time suggests that with increased shallowing of the former Vlieter channel, the system became too energetic (i.e. under greater influence of waves, and wave- and tide-generated currents) to allow the deposition of clay (Galavazi in prep).

5 The lithology of vibrocore V7D specifically shows deposition of mud around 1936, and deposition of sandy layers around 1945, the mid-1960s and from the mid-1970s onwards.

Mudsnails

The origin of the mudsnail remains in the sediment core is most probably autotochtonous as well as allochtonous. First, these animals are known to live in high densities in areas like the Vlieter channel (R. Dekker 1985-1999). Second, alive and dead specimen may have been transported towards the Vlieter channel.

Small individuals must be buried quickly after sedimentation in order to “survive” the scouring effects of sand-grains at the sediment surface (R. Dekker, pers. comm.). We established an index of mechanical wear (locally or transport-induced) by means of dividing the number of damaged shells by the total number of shells (Fig. 4.5.3), which reveals that wear was not at all constant over time. Fragmentation of shells in marine sediments may be due to biological (predation by crustaceans, fish and birds) or physical processes (Cadée 1994). Interpretation of deposition rates of fragile remnants must be done cautious because these rates may not only reflect population dynamics and transport mechanisms, but also detoriation of the material after sedimentation has taken place.

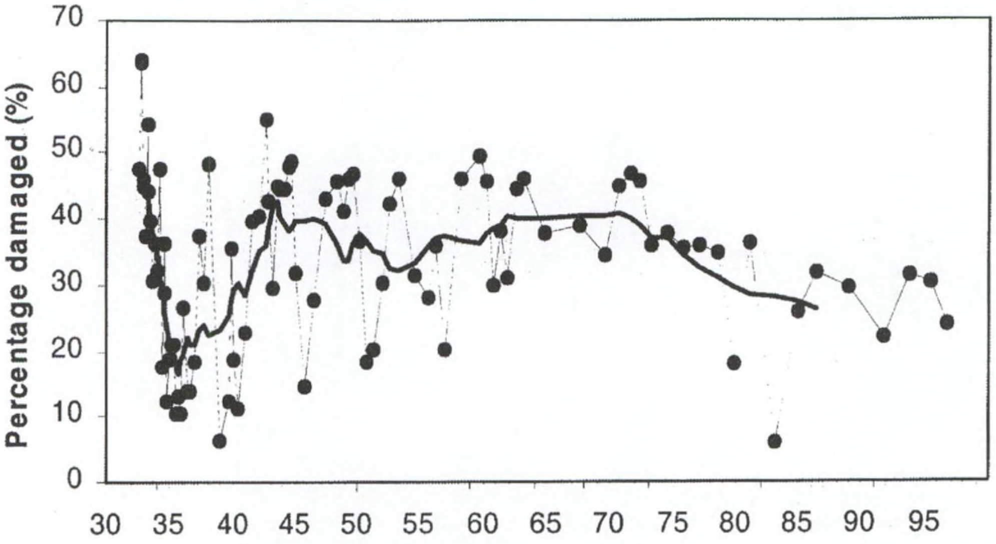


Fig. 4.5.3 Percentage of damaged mudsnails (all sizes combined) in subsamples of a sediment core taken in the former Vlieter channel on June 20, 1997. Thick line represents running mean.

We, therefore, focussed on the shell-deposition rates of adult specimens. Their high deposition rate around 1945 could have been the result of an enhanced spatfall one or two years earlier or of a mass mortality event. Coinciding high MS levels, however, strongly suggest the occurrence of anoxia and/or enhanced sedimentation at that time, which is expected to result in mass mortality of local stocks. In 1947, mudsnails were so abundant that they washed ashore and formed high banks on the saltmarshes and dikes throughout the western Wadden Sea (Cees Swennen, pers. comm.).

Bivalves

In general, the shell-depositon rate of all bivalve species was lower from 1960 onwards than during the first decades of the studied period (Fig. 4.5.4). Trends in shell-deposition rates were most probably strongly influenced by changes in the local hydrodynamics in the Vlieter channel. Baggerman (1953) observed that spat of Cockles of 600-1800 μm (*viz.* of at least 4 weeks old) are being transported regularly by currents in large quantities in the western Wadden Sea. These young animals, whose deposition rates can be compared with those of sandgrains of 100-250 μm (*viz.* fine sand), are deposited especially on places where cur-

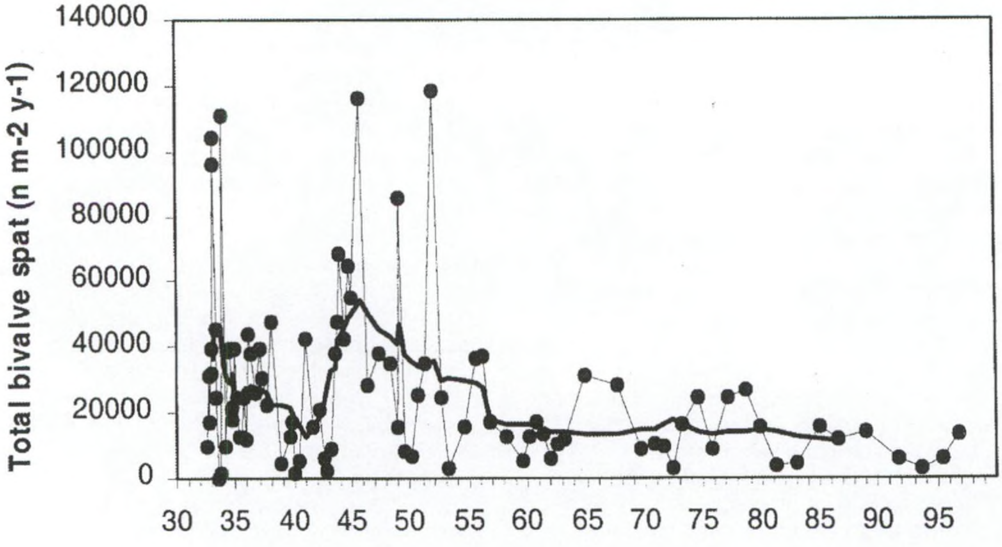


Fig. 4.5.4 Shell-deposition rate of bivalve spat (all species combined) between 1932 and 1997 as derived from a sediment core sampled in the Vlieter channel on June 20, 1997. Thick line represents running mean.

rents are weak and where winds get little hold. Most bivalve spat in the sediment core (75-95%) belonged to the size-class 250-400 μm. According to the measurements performed on *Cerastoderma* (Baggerman 1953), such a shell-size would result in sinking rates comparable to those of sediments with a median grain-size of less than 60 μm (*viz.* silt and possibly clay). If spat behaves like silt, we may expect to find a decline in spat deposition over time as the result of the observed decrease in clay deposition.

Shell-deposition rates of bivalve spat were particularly high around 1934 (*Cerastoderma*, *Macoma* and *Mya*), 1945 (*Cerastoderma*, *Mytilus* and *Spisula*) and 1952 (*Mytilus* and *Spisula*). The high spatfall as observed for 1934 may have actually occurred in the summer of 1939, which showed a rich settlement of may species along the Dutch coast (Kristensen 1959), but this would mean a shift in dating of the core 5 years.

High deposition rates around 1945 may have been the result of an enhanced spatfall following the very cold winter of 1947. During this winter, many animals were frozen to death such as Cockles (*Cerastoderma edule*), shore crabs (*Carcinus maenas*) and barnacles (Cees Swennen, pers. comm.). Not all species were wiped out, the musselbeds were damaged but did not disappear, and periwinkles (*Littorina littorea*) could still be found. The severe winter was followed by high spatfall of Wadden Sea species such as Periwinkles, Cockles and Gapers (*Mya arenaria*), in addition to spat originating from North Sea stocks such as Tellina's and Petricola's. On average, the bivalve spat showed a very high survival rate (Cees Swennen, pers. comm.). Beukema and co-authors (1993) found a positive relationship between the coldness of a winter and the bivalve spatfall during the following summer. According to Baggerman (1947) and Kristensen (1959), the warm weather of the summer of 1947, combined with highly saline waters during the pelagic state of the young, favoured the development of a new population. During the autumn of that year the whole area abounded in animals of one single yearclass. According to Kristensen (1959), a second summer rich of spat was 1952 and a third was 1957, both years with a hot summer. The high spatfall as observed for 1952 coincides with the high deposition rates as observed in the sediment core.

Although spatfall was most probably also high in other years such as after the very cold winters of 1963 (Cees Swennen, pers. comm.) and 1979, no high depostion rates were found in the following years. This might be due to the fact that, from bottom to top, a sample contains material deposited during one season or even one storm event to material deposited during a range of years. High spatfall during the summer of 1979 may then be already averaged down to biased-low levels.

Highest densities of relatively large Cockles (> 2 mm shell-size) were found at a depth corresponding to 1964. The winter of 1962-1963 was the coldest one within the study period, resulting in high mortality of marine benthos and fish all over western Europe (Crisp 1964, Woodhead 1964, Ziegelmeier 1964). In addition, Cockles may also have been affected by a phytoplankton bloom, which occurred in the summer of 1964 (Cees Swennen pers. comm.). Dying or dead Cockles emerge to the sediment surface. Once lying on the tidal flat, they are easily transported by means of water currents (Cadée 1990).

Conclusions:

Variations within the lithology, mudsnail and bivalve spat densities in the western Wadden Sea core suggest that between 1932 and 1997:

- General trend towards deposition of more sandy material over time, most probably related to decrease in depth of sedimentation area.
- Deposition of relative muddy material around 1936, and deposition of relative sandy material around 1945, during the mid-1960s and from the mid-1970s onwards.
- Deposition of fragile elements can be underestimated as the result of wear.
- High shell-deposition rate of adult mudsnails around 1945 might have been caused by anoxia event during the summer of 1947 and/or be the result of high overall densities of this species in the western Wadden Sea.
- Trends in shell-deposition rates of bivalve spat are most probably strongly influenced by changes in hydrodynamics due to gradual shallowing of the Vlieter channel.
- High shell-deposition rates of bivalve spat around 1945 and 1952 are most probably part of the very high spatfall phenomenen of marine fauna all along the west European marine waters during the summers of 1947 and 1952.
- High deposition of large Cockles around 1964 was most probably the result of mass mortality, a phenomenen observed for a suite of marine faunal species in west European waters during the very cold winter of 1962/'63 or due to a phytoplankton bloom causing anoxia in 1964.

5 CONCLUSIONS

5.1 GENERAL APPROACH

The aim of this project was to examine possible relationships between environmental factors and time series of different characteristics (e.g. abundance, species composition, production) of marine living resources (Fig. 5.1). Hereby, we assumed that the effects of environmental factors on the marine ecoystem were that strong and direct that they would result in clear signal in the characteristic studied. This assumption proved to be only true under particular circumstances (see §5.2). In most cases, however, we found that if there was even an effect of the environmental factor its signal was probably lost in the signals of a suite of other external and internal factors or not detected due to limitations in the techniques and in the data (see §5.3).

5.2 LONG-TERM RELATIONSHIPS WITHIN NORTHWESTERN EUROPEAN MARINE ECOSYSTEMS

Several relationships between the external forces and the biota could be established. The climate was observed to affect the hydrography, which in turn affected the macrofauna in the Baltic and North Sea or the fish community in the North Sea. Likewise anthropogenic factors such as eutrophication or fisheries were observed to have an impact on respectively plankton in the Wadden Sea or the fish community in the North Sea.

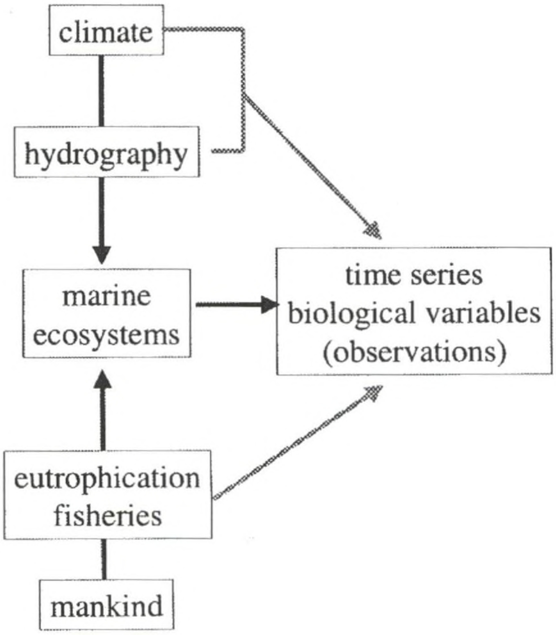


Fig. 5.1 Actual (black arrows) and examined (grey arrows) relationships between external factors and biological parameters of marine ecosystems as examined during the DYNAMO project.

When studying long-term changes in the ecosysystems, both the spatial and temporal scales affect the interpretation of the results. At geographically small scales the succession of the biological communities may be a result of local and large-scale factors and distinguishing the different factors involved can be complicated if they point in the same direction. At larger scales however, common trends for different areas may indicate a common forcing, such as widely distributed eutrophication or climatic impacts.

Within each of the study areas, trends indicating at least the impact of local factors were observed. In addition, concurrent trends over the relatively wide Baltic Sea area and coinciding changes in both North Sea and Baltic Sea areas may indicate common forcing of the ecosystems.

The link between climate forcing and salinity was established in the German Bight and in the Baltic Sea. In both cases the atmospheric circulation drives changes in precipitation that affect salitinity. In the case of oxygen there exists also a statistical link to climate forcing but the ultimate physical mechanism could not be identified. Probably, biological and chemical process may play also an important role in the case of oxygen.

The relationships between the North Atlantic Oscillation and zooplankton species in the North Sea seems to be statistically clear. In some cases, such as *Noctiluca scintillians*, the explained variance is high, but the mechanisms responsible probably involve the interaction with phytoplankton. For other species, such as *Temora longicornis*, the link is also detectable but the explained variance is low and the mechanisms for such a link could not be cleared up.

In the western Wadden Sea, major changes in phytoplankton biomass and species composition coincided with changes in absolute and relative (TN:TP) nutrient concentrations. During the summer of 1977, the Marsdiep shifted from a rich, but phosphorus-controlled system to an even more eutrophic but nitrogen-controlled environment. The system re-shifted towards P-control between 1987 and 1988. The coincidence of the shifts in relative nutrient concentrations and phytoplankton species composition implies a strong causal relationship between TN:TP ratio's and phytoplankton community structure. Amongst diatoms, the observed increase in phytoplankton biomass under eutrophic N-controlled conditions was particularly due to an increase of the abundance of larger algae. Our results indicate that the N-budget of the area is correlated with the community structure, suggesting enhanced loss of nitrogen to the sediment through increased deposition of larger algal cells.

For macrozoobenthos in the coastal areas of the North Sea, including the tidal Wadden Sea, an increase in communities was observed in late 1970's, peaking in the middle 1980's. In addition a secondary maxima is obvious in the 1990's. Similar succession is evident for communities in the subhalocline areas of the Baltic Sea with only a slight difference in timing, a clear peak in the late 1970's and a more gradual increase again in the early 1990's, followed by a collapse after the middle of the 1990's in some areas. The observed increase in the North Sea benthic communities could be related to climatic factors causing stronger than normal westerly winds and mild winters with higher temperatures in the surface layer. In the Baltic Proper and Gulf of Finland area the variability in subhalocline macrozoobenthos was much related to the oxygen and salinity changes, setting limits for the species distribution and roughly half of the variability in these factors could be explained by a westerly climate pattern. Thus climate can at least partly explain the contemporaneous changes in the Baltic Sea showing a rapid and temporary increase which in the late 1970's was caused by inflowing North Sea waters while in the 1990's it was a consequence of positive anomalies in the fresh water input with its positive effects on oxygen conditions. Both of these events can be connected to the same weather patterns (high NAO with westerly winds) which has affected also the North Sea area and thus give an example of a common forcing of the ecosystems by climate.

The species composition of the North Sea fish community in terms of their bio-geographic region was affected by the water temperature. After a warm autumn the Lusitianian (southerly) species increased whereas the Boreal (northerly) species decreased. Also, the period of elevated fish biomass in the seventies that was observed in the North Sea coincides with observed changes in climatic, abiotic and biotic variables of the North Sea ecosystem (see Introduction). This confirms that in that period large-scale changes at various levels of the North Sea ecosystem were taking place, possibly triggered by a shift in the basic state of the atmosphere-ocean climate system. However, to what extent the subsequent decline in fish biomass in the early eighties followed by an increase towards a maximum in the nineties coincides with such variables remains unsolved.

The human impact on the fish community was revealed by two progressive trends in the fish community that can be attributed to the effect of fisheries. First a progressive decrease in the biomass of large fish was observed that was caused by the size-selective mortality induced by fisheries. This in turn affected the species composition through differences in the species' life-history characteristics. The trend observed was towards a community with less K-strategists (species adapted to stable environments) and more r-strategists (species adapted to unpredictable, disturbed environments).

5.3 COMPLICATING FACTORS

Spurious correlations – Caution is needed when correlating different time series for analysis of causality. If the data consist of factors related to each other by complex mechanisms the interpretation may be difficult even if strong correlation would exist. For instance, in the Baltic Sea changes in the winter nutrient reserves potentially causes changes in the input of organic material to benthic communities but this relationship is obviously modified by weather during the spring bloom period, affecting the duration and probably also the species composition of phytoplankton. Thus the sedimentation may alter in quality and quantity despite increasing nutrient concentrations. Obviously, long-term data on sedimentation or pelagic production should be used but do not exist or are too scarce to be used.

Non-linear relationships – The climate variables, such as circulation indices, e.g. the NAO index are often normally distributed, whereas biological variables, such as zooplankton populations, follow logarithmic-type distributions. Linear statistical models cannot describe a relationship between both types of variables. Therefore, a nonlinear transformation of the biological time series is often mandatory. The nature of this transformation is empirical, and the danger of falsifying observed data and increasing the error of the parameter estimation may be high.

Extremes – The influence of climate on the ecosystem level became most clear or even just detectable when studying episodes of extreme climatic events, in particular in the case of non-linear responses of stocks to environmental factors. For example, enhanced mortality may only occur at temperatures lower or higher than lethal thresholds. In general, west European marine ecosystems appear to be strongly influenced by severe winters. Zooplankton, zoobenthos and even fish may die off, supplying the opportunity for others (recruits of the same species or other individuals of other species) to take over. Under such circumstances, e.g. the very low temperatures at the end of the 1970's, this influence appears to overrule other (internal) factors in the ecosystem. The analysis of such effects is hampered by the low frequency of appearance of the extreme events themselves, e.g. during the entire study period (1965-1997) only a few strong inflows into the Baltic Sea occurred, leading to a low representativity of the data available.

Coinciding and synergistic effects – All time series that we studied were derived from actual marine ecosystems and not produced under experimental conditions. This implies that several environmental factors may have changed at the same time, i.e. coinciding effects.

For instance, the same climatic forcing may have competing effects on the environmental variables and at the ecosystem level. For instance, it was found that the strength of the NAO index (westerly winds) may cause stronger inflow from the North Sea water into the Baltic Sea, but at the same time salinity is reduced due to increased rainfall in the Baltic Sea catchment area. Which mechanism is more important depends in this case on the time-scale considered. At the ecosystem level, milder winter water temperatures associated to a stronger NAO may support a stronger growth of certain zooplankton species, but may also favour a predator species, giving rise to a decrease of the prey species.

In the North Sea, similar increasing trends in temperature and fishing effort were observed over the past thirty years during which the biota were sampled. Even at a much smaller spatial scale different but coinciding temporal patterns of temperature and fishing effort were observed in the areas in- versus outside the plaice box which considerably complicated the formal distinction of the relative contribution of each factor to the observed changes.

In addition, the total effect of coinciding factors may even be more than the sum of the single effects. In other words, the combination of the effects may give an additional effect too (statistically examined by testing the significance of an interaction effect).

Spatial-temporal interactions – The significant interaction effects of space (roundfish areas) and time (year) on the biomass of North Sea fish may point at synergistic effects, i.e. seasonal variation in environmental conditions has significantly more effect on fish biomass under some (local) conditions than under others. At first it was concluded that the existence of a spatial-temporal interaction indicates that before and after the closing of the plaice box the composition of the (fish or benthic) community in- and outside the box area changed differently and this was originally attributed to reflect an effect of fisheries. However, the existence of significant space-time interactions within non-protected areas of the North Sea (roundfish areas) confirms that small-scale spatial differences exist irrespective of any of our known external forces.

Limits to data series – Length of data series is crucial, especially for studying the relationship between climate and variability in biological communities. Changes in the communites can take place as slowly progressing trends or sudden changes, switching in function of the communities. For the Gulf of Finland, a rapid collapse of the communities was observed by including 1996-97 in the data which well demonstrated the effects of the stratification changes. Otherwise the recent development would have been concurrent with the trends in nutrients, indicating the eutrophication of the area. Also the initial conclusion (based on a 1985-1994 dataset) that the introduction of the plaice box affected the fish community in a rather straightforward manner with an increase of abundance of the larger fish in the box area where fishing effort decreased was refuted when a longer dataset (1985-1998) became available.

Limits to biological knowledge – Examined relationships between environmental factors and ecosystem dynamics describe at best what happened during the study period. Making predictions based on these relationships assumes that the behavior and population dynamics of the species involved is fully understood and that these characteristics do not change in the future. Both assumptions are not true. First, we hardly understand the complexity within marine ecosystems. Second, species evolve and subsequently changing their characteristics continuously.

5.4 CONCLUSION

Marine organisms show complex responses to external factors such as climatic events, which has proven to make correlation analysis often very difficult or even impossible. We found that at the one hand, external factors may affect the state of the ecosystem, whilst at the other hand it is the state of the system which determines the actual effect of the particular factor. This is probably one of the main reasons that we often observed significant spatial-temporal interactions when examining the covariance within time series of different locations throughout northwestern European marine ecosystems.

REFERENCES

Aebischer, N.J., J.C. Coulsen & J.M. Colebrook, 1990. Parallel long-term trends across four marine trophic levels and weather. Nature 347: 753-755.

Andersin, A.-B & H. Sandler, 1991. Macrobenthic fauna and oxygen deficiency in the Gulf of Finland. Memoranda Soc. Fauna Flora Fennica 67: 3-10.

Andersin, A.-B, J. Lassig, L. Parkkonen & H. Sandler, 1978b. Long-term fluctuations of the soft bottom macrofauna in the deep areas of the Gulf of Bothnia 1954-1974; with special reference to *Pontoporeia affinis* Lindstroem (Amphipoda). Finnish Mar.Res. 244: 137-144.

Andersin, A.-B. & H. Sandler, 1981. Comparision of the sampling efficiency of two van Veen grabs. Finnish Mar. Res. 248: 137-142.

Andersin, A.-B., J. Lassig, L. Parkkonen & H. Sandler, 1978a. The decline of macrofauna in the deeper parts of the Baltic proper and the Gulf of Finland. Kieler Meeresforsch. 4:23-52.

Andersin, A.B., J. Lassig, L. Parkkonen, H. Sandler, J. Lenz, G. Siedler & H. Theede, 1978. The decline of macrofauna in the deeper parts of the Baltic proper and the Gulf of Finland. Kiel. Meeresforsch. 4: 23-52.

Anderson, J.T., 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. Journal of Northwest Atlantic Fisheries Science 8: 55-66.

Ankar, S., 1977. The soft bottom ecosystem of the northern Baltic Proper with special reference to the macrofauna. Contr. Askö Lab. Univ. Stockholm 19: 1-62.

Anonymous, 1995. Report of the study group on ecosystem effects of fishing activities. ICES Cooperative Research Report 200.

Anonymous, 1999a. Final report EU contract no. 95/69: "Input of historic IBTS data". RIVO report C014/99.

Anonymous, 1999b. Working group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 1999/ACFM:8.

Athersuch, J, D.J. Horne, J.E. Whittaker, 1989. Marine and brackish water ostracods (superfamilies Cypridacea and Cytheracea). Keys and notes for the identification of the species. Synopses of the British fauna., E.J. Brill, Leiden (netherlands) no. 43, 365 pp.

Austen, M.C., J.B. Buchanan, H.G. Hunt, A.B. Josefsson & M.A. Kendall, 1991. Comparison of long-term trends in benthic and pelagic communities of the North Sea. J. mar. biol. Ass. U.K. 71: 179-190.

Baggerman, B., 1953. Spatfall and transport of *Cardium edule* L.. Archives Néerlandaises de Zoologie, Tome X, Livr. 3: 315-342.

Bakun, A., J. Beyer, D. Pauly, G. Pope & G.D. Sharp, 1982. Ocean sciences in relation to living resources. Can. J. Fish. Aquat. Sci. 39: 1059-1070.

Baltic Marine Environment Protection Commission - Helsinki Commission, 1988. Guidelines for the Baltic Monitoring Programme for the Third Stage, Part D. Biological Determinands. Baltic Sea Environment Proceedings 27 D: 161 pp.

Basford, D., A. Eleftheriou & D. Raffaelli, 1990. The infauna and epifauna of the northern North Sea. Neth. J. Sea Res. 25: 165-173.

Becker, G. & H. Dooley, 1995. The 1989/91 high salinity anaomaly in the North Sea and adjacent areas. Ocean Challenge 6: 52-57.

Becker, G.A. & M. Pauly, 1996. Sea surface temperature changes in the North Sea and their causes. ICES J. Mar. Sc. 53.

Becker, G.A., S. Dick & J.W. Dippner, 1992. Hydrography of the German Bight. Mar. Ecol. Progr. Ser.

Berger, G.W., D. Eisma & A.J. Van Bennekom, 1987. ^{210}Pb-derived sedimentation rate in the Vlieter, a recently filled-in tidal channel in the Wadden Sea. Neth. J. Sea Res. 21: 287-294.

Bergman, M.J.N. & J.W. Van Santbrink, 1994. Direct effects of beam trawling on macrofauna in sandy areas off the Dutch coast. In: S.J. De Groot & H.J. Lindeboom. Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea, p. 179-208. NIOZ Report 1994-11, RIVO-DLO Report C026/94: 257 pp.

Bergman, M.J.N. & M. Hup, 1992. Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. ICES J. Mar. Sci. 49: 5-11.

Beukema, J.J. & E.C. Flach, 1995. Factors controlling the upper and lower limits of the intertidal distribution of two *Corophium* species in the Wadden Sea. Mar. Ecol. Prog. Ser. 125: 117-126.

Beukema, J.J. & G.C. Cadée, 1986. Zoobenthic responses to eutrophication in the Dutch Wadden Sea. Ophelia 26: 55-64.

Beukema, J.J. & G.C. Cadée, 1997. Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only a limiting factor. Limnol. Oceanogr. 42: 1424-1435.

Beukema, J.J., 1974. Seasonal changes in the biomass of the macro√benthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 94-107.

Beukema, J.J., 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. Neth. J. Sea Res. 13: 203-223.

Beukema, J.J., 1988. An evaluation of the ABC√method abundance/biomass comparison) as applied to macrozoobenthic communities living on tidal flats in the Dutch Wadden Sea. Mar. Biol. 99: 425-433.

Beukema, J.J., 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. Helgoländer Meeresunters. 43: 405-415.

Beukema, J.J., 1991a. Changes in the composition of bottom fauna of a tidal-flat area during a period of eutrophication. Mar. Biol. 111: 293-301.

Beukema, J.J., 1991b. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. J. exp. Mar. Biol. Ecol. 153: 97-113.

Beukema, J.J., 1992. Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. Neth. J. Sea Res. 30: 73-79.

Beukema, J.J., K. Essink & H. Michaelis, 1996. The geographic scale of synchronized fluctuation patterns in zoobenthic populations as a key to underlying factors: climatic or man-induced. ICES J. Mar. Sci. 53: 964-971.

Beukema, J.J., K. Essink, H. Michaelis & L. Zwarts, 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Neth. J. Sea Res. 31: 319-330.

Beurskens, J.E.M., 1995. Microbial transformation of chlorinated aromatics in sediments. PhD Thesis, Wageningen Agricultural University, 173 pp.

Beverton, R.J.H., 1995. Spatial limitation of population size; the concentration hypothesis. Neth. J. Sea Res. 34: 1-6.

Birks, H.J.B., S.M. Peglar & H.A. Austin, 1994. An Annotated Bibliography of Canonical Correspondence Analysis and Related Constrained Ordination Methods 1986-1993, Botanical Institute, Bergen, Norway.

Blackmon, M.L., 1976. A climatological spectral study of the 500 mbar geopotential height of the northern hemisphere. J. Atmos. Sci. 33: 1607-1623.

Bonsdorff, E. & E.A. Blomqvist, 1993: Biotic couplings on shallow water soft bottoms – examples from the northern Baltic Sea. Oceanogr. Mar. Biol. Ann. Rev. 31: 153-176.

Bonsdorff, E. & T.H. Pearson, 1999. Variation in sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. Austr. J. Ecol. 24: 312-326.

Bonsdorff, E., A. Norkko & E. Sandberg, 1995. Structuring zoobenthos: the importance of predation, siphon cropping and physical disturbance. J. Exp. Mar. Biol. Ecol. 192: 125-144.

Booij, K. & W. Lewis, 1999. PCB and PAH levels in a core from the Vlieter (Wadden Sea). Internal Note NIOZ, 3pp.

Borchardt, T, S. Burchert, L. Karbe & R. Zeitner, 1989. Enhanced heavy metal concentrations in *Mytilus edulis* from the central North Sea. Sci. Mar. (Barc.) 53: 725-728.

Borum, J. & K. Sand-Jensen, 1996. Is total primary production in shallow marine waters stimulated by nitrogen loading? Oikos 76: 406-410.

Borum, J., 1983. The quantitative role of macrophytes, epiphytes, and phytoplankton under different nutrient conditions in Roskjilde Fjord, Denmark. Proc. Intern. Symp. Aquat. Macrophytes, Nijmegen: 35-40.

Borum, J., 1996. Shallow waters and land/sea boundaries. In: Jørgensen, B.B. & K. Richardson (eds.) Eutrophication in coastal marine ecosystems: coastal and estuarine studies. American Geophysical Union: 179-203.

Brander, K., 1981. Disappearance of common skate *Raia batis* from Irish Sea. Nature 290: 48-49.

Bridges, C.R., 1993. Ecophysiology of intertidal fish. In: J.C. Rankin & F.B. Jensen. Fish ecophysiology, Chapman & Hall: 375-396.

Brockwell, P.J. & R.A. Davis, 1987. Time series: theory and methods. Springer, New York.

Buchanan, J.B., 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. J. exp. mar. Biol. Ecol. 172: 1-10.

Cadée, G.C., 1980. Reappraisal of the production and import of organic carbon in the western Wadden Sea. Neth. J. Sea Res. 14: 305-322

Cadée, G.C., 1984. Has input of organic matter increased during the last decades? In: Laane, R.W.P.M. & W.J. Wolff (eds) The role of organic matter in the Wadden Sea. Neth. Inst. Sea Res. Publ. Ser. 10: 71-82.

Cadée, G.C., 1986. Recurrent and seasonal changing seasonal patterns in phytoplankton of the westernmost tidal inlet of the Dutch Wadden Sea from 1969 to 1985. Mar. Biol. 93: 281-289.

Cadee, G.C., 1990. Feeding traces and bioturbation by birds on a tidal flat, Dutch Wadden Sea. Ichnos 1: 23-30.

Cadée, G.C., 1992. Phytoplankton variability in the Marsdiep, The Netherlands. ICES Mar. Sc. Symp. 195: 213-222.

Cadée, G.C., 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea: Palaeoecological implications. Palaeontology 37: 181-202.

Cadée, G.C., J.P. Boon, C.V. Fischer, B.P. Mensink & C.C. ten Hallers-Tjabbes, 1995. Why the whelk (*Buccinum undatum*) has become extinct in the Dutch Wadden Sea. Neth. J. Sea Res. 34: 337-339.

Cadée, G.C. & J. Hegeman, 1974a. Primary production of phytoplankton in the Dutch Wadden Sea. Neth. J. Sea Res. 31: 147-152.

Cadée, G.C. & J. Hegeman, 1974b. Primary production of benthic microflora living on the tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 260-291.

Cadée, G.C. & J. Hegeman, 1986. Seasonal and annual variation in *Phaeocystis pouchetii* (Haptophycea) in the westernmost inlet of the Wadden Sea during the 1973 to 1985 period. Neth. J. Sea Res. 20: 29-36.

Cadée, G.C. & J. Hegeman, 1991. Phytoplankton composition, primary production, and chlorophyll: organic carbon, and turbidity in the Marsdiep in 1990 compared with earlier years. Hydrobiol. Bull. 25: 29-35.

Cadée, G.C. & J. Hegeman, 1993. Persisting high levels of primary production at declining phosphate concentration in the Dutch coastal area (Marsdiep). Neth. J. Sea Res. 31: 147-152.

Cambridge, M.L., A.W. Chiffings, C. Brittan, L. Moore, A.J. McComb, 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. Aquat. Bot. 24: 269-285.

Camphuysen, C.J., 1990. Fish stocks, fisheries and seabirds in the North Sea. Techn. Rapp. Vogelbescherming 5: 122 pp.

Carlsson, P. & E. Granéli, 1993. Availability of humic bound nitrogen for coastal phytoplankton. Est. Coast. Shelf Sci. 36: 433-447.

Cederwall, H. & R. Elmgren, 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. Ophelia 1: 287-304.

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

Chambers, R.C. & W.C. Leggett, 1987. Size and age at metamorphosis marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can. J. Fish. Aquat. Sci. 44: 1936-1947.

Chambers, R.C., W.C. Leggett & J.A. Brown, 1988. Variation in *Pseudopleuronectes americanus*. Mar. Ecol. Prog. Ser. 47: 1-15.

Christensen, J.P., 1994. Carbon export from continental shelves, denitrification and atmosphere carbon dioxide. Cont. Shelf Res. 14: 547-576.

Clarke, K.R. & M. Ainsworth, 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92: 205-219.

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

Cloern, J.E., C. Grenz & L. Vidergar-Lucas, 1995. An emperical model of the phytoplankton chlorophyll: carbon ratio – the conversion factor between productivity and growth rate. Limnol. Oceanogr. 40: 1313-1321.

Colebrook, J.M., 1985. Continuous plankton records: Overwintering and annual fluctuations in the abundance of zooplankton. Mar. Biol. 84: 261-265.

Colijn, F., 1982. Light absorption in the waters of the Ems-Dollard estuary and its consequences for the growth of phytoplankton and microphytobenthos. Neth. J. Sea Res. 15: 196-216.

Colijn, F., J.F.P. Malschaert, H.T. Kloosterhuis & G.C. Cadée, 1990. Assessment of growth rate limiting nutrients in the North Sea by the use of nutrient-uptake kinetics. Neth. J. Sea Res. 26: 53-60.

Corten, A. & G. van der Kamp, 1992. Natural changes in pelagic fish stocks of the North Sea in the 1980s. ICES Mar. Sc. Symp. 195: 402-417.

Corten, A., 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. Neth. J. Sea Res. 25: 227-235.

Creutzberg, F., G.C.A. Duineveld & G.J. van Noort, 1987. The effect of different numbers of tickler chains on beam trawl catches. J. Cons. Inter. Explor. Mer 43: 159-168.

Crisp, D.J., 1964. The effects of the winter of 1962/63 on the British marine fauna. Helgol. Meeresunters. 10: 313-327.

Cui, M., H. von Storch & E. Zorita, 1994. Coastal sea level and the large-scale climate state: A downscaling exercise for Japanese Islands. Tellus 46: 1-13.

Cui, M., H. von Storch & E. Zorita, 1995. Coastal Sea level and the large-scale climate state: a downscaling exercise for the Japanese Islands. Tellus 47A: 132-144.

Cui, M. & E. Zorita, 1998. Analysis of the sea-level variability along the Chinese coast and estimation of the impact of a CO_2-perturbed atmospheric circulation. Tellus 50A: 333-347.

Currie, D.R. & G.D. Parry, 1996. Effects of scallop dredging on a soft sediment community: a large-scale experimental study. Mar. Ecol. Progr. Ser. 134: 131-150.

Cushing, D.H., 1982. Climate and fisheries. Academic Press, London and New York.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv. Mar. Biol. 26: 249-294.

Cushing, D.H., 1995. Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, Cambridge.

Cushing, D.H. 1996. Towards a science of recruitment in fish populations. Excellence in Ecology. Ecology Institute, Oldendorf Luhe, Germany.

Cushing, D.H. & R.R. Dickson, 1976. The biological response in the sea to climatic changes. Adv. Mar. Biol. 14: 2-122.

Daan, N., P.J. Bromley, J.R.G. Hislop, & N.A. Nielsen, 1990. Ecology of North Sea fish. Neth. J. Sea Res. 26: 343-386.

Dame, R.F. & D.M. Allen, 1996. Between estuaries and the sea. J. exp. mar. Biol. Ecol. 200: 169-185.

Davis, A.J., L.S. Jenkinson, J.H. Lawton, B. Shorrocks & S. Wood, 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391: 783.

Dayton, P.K., S.F. Thrush, M.T. Agardy & R.J. Hofman, 1995. Environmental effects of marine fishing. Aquat. Conserv. 5: 205-232.

De Candt, P. & M. Vandenbossche, 1975. De afsluiting van de Zuierzee en z'n gevolgen op het Waddengebied. Publication of the University of Gent.

De Groot, S.J. 1984. The impact of bottom trawling on benthic fauna in the North Sea. Ocean Management 9: 177-190.

De Jonge, V.N., 1997. High remaining productivity in the Dutch western Wadden Sea despite decreasing nutrient inputs from riverine sources. Mar. Poll. Bull. 34: 427-436.

De Jonge, V.N., J.F. Bakker & M. Van Stralen, 1996. Recent changes in the contributions of the river Rhine and North Sea to the eutrophication of the western Dutch Wadden Sea. Neth. J. Aquat. Ecol. 30: 27-39.

De Jonge, V.N. & D.J. De Jong, 1992. Role of tide, light and fisheries in the decline of *Zostera marina*. Neth. Inst. Sea Res. Publ. Ser. 20: 161-176.

De Vooys, C.G.N. & J. Van der Meer, 1998. Changes between 1931 and 1990 in by-cathes of 27 animal species from the southern North Sea. J. Sea Res. 39: 291-298.

De Vooys, C.G.N., J.IJ. Witte, R. Dapper, J. Van der Meer & H.W. Van der Veer, 1991. Lange termijn veranderingen in zeldzame vissoorten op het Nederlands Continentaal Plat van de Noordzee [Long-term changes in uncommon fish species in the south-eastern North Sea]. NIOZ Report 1991-6: 81 pp.

De Vooys, C.G.N., J.IJ. Witte, R. Dapper, J. Van der Meer & H.W. Van der Veer, 1993. Lange termijn veranderingen op het Nederlands Continentaal Plat van de Noordzee: trends in evertebraten van 1931-1990 [Long-term changes in the south-eastern North Sea: trends in invertebrates between 1931 and 1990]. NIOZ Report 1993-17: 68 pp.

De Vries, I., C.J.M. Philippart, E.G. DeGroodt & M.W.M. Van der Tol, 1996. Coastal eutrophication and marine benthic vegetation: a model analysis. In: Schramm, W. & P.H. Nienhuis (eds) Marine benthic vegetation: recent changes and the effects of eutrophication. Springer, Berlin: 79-113.

Dekker, R. & W. De Bruin, 1998. Het macrozoobenthos op twaalf raaien in de Waddenzee en de Eems-Dollard. NIOZ-Report 1998-3.

Deniel, C. & M. Tassel, 1986. Reproduction et croissance de la limande (*Limanda limanda*) (Linnaeus, 1758) (Téléostéen, Pleuronectidae) in Manche Orientale et Baie de Dournanez. Cybium 10: 155-176.

Deutsches Hydrographisch Instiut, 1984. Deutsche Bucht, Hydrographie. Meereskundliche Beobachtungen und Ergebnisse 57: 1-166.

Dickson, R.R. & K.M. Brander, 1993. Effects of a changing windfield on cod stocks of the North Atlantic. Fisheries Oceanography 2: 124-153

Dickson, R.R., 1971. A recurrent and persisten pressure anomaly pattern as the principle cause of intermediate-scale hydrographic variation in the european shelf seas. Dt. Hydrogr. Zt. 24: 97-119.

Dickson, R.R., P.M. Kelly, J.M. Colebrook, W.S. Wooster & D.H. Cushing, 1988. North winds and production in the eastern North Atlantic. J. Plankton Res. 10: 151-169.

Diggle, P.J., 1990. Time series: a biostatistical introduction. Clarendon Press, Oxford.

Dijkema, K.S., H.-E. Reineck & W.J. Wolff, 1980. Geomorphology of the Wadden Sea area: final report of the section 'Geomorphology' of the Wadden Sea Working Group. Reports of the Wadden Sea Working Group 1.

Dippner, J.W., 1997. SST Anomalies in the North Sea in relation to the North Atlantic Oscillation and the influence on the theoretical spawning time of fish. German Journal of Hydrography 49: 267-275.

Doering, P.H., C.A. Oviatt, L.L. Beatty, V.F. Banzon, R. Rice, S.P. Kelly, B.K. Sullivan & J.B. Fritshen, 1989. Structure and function in a model coastal ecosystem: silicon, the benthos and eutrophication. Mar. Ecol. Prog. Ser. 52: 287-299.

Dörjes, J. 1992. Langfristige Veränderungen des Artenbestandes der Makroendo fauna im Vorstrand der Düneninsel Norderney in der Zeit von 1976 bis 1988. Senckenbergia Marit. 22: 11-19.

Dörjes, J., 1976. Primärgefüge, Bioturbation und Makrofauna als Indikatoren des Sandversatzes im Seegebiet vor Norderney (Nordsee). II. Zonierung und Verteilun g der Makrofauna. Senckenbergia Marit. 8: 171-188.

Dörjes, J., H. Michaelis & B. Rhode, 1986. Long-term studies on macrozoobenthos in the intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). Hydrobiologia 142: 217- 232.

Dortch, Q., J.R. Clayton Jr., S.S. Thoresen, J.S. Cleveland, S.L. Bressler & S.I. Ahmed, 1985. Nitrogen storage and use of biochemical indices to asses nitrogen deficiency and growth rate in natural plankton populations. J. mar. Res. 43: 437-464.

Drebes, G., 1974. Marines Phytoplankton. Eine Auswahl der Helgoländer Planktonalgen (Diatomeen, Peridineen). Georg Thieme Verlag.

Duarte, C.M., 1990. Seagrass nutrient content. Mar. Ecol. Prog. Ser. 67: 201-207.

Duarte, C.M., 1992. Nutrient concentration of aquatic plants: patterns across species. Limnol. Oceanogr. 37: 882-889.

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

Duineveld, G.C.A., A. Künitzer, U. Niermann, P.A.W.J. de Wilde, & J.S. Gray, 1991. The macrobenthos of the North Sea. Neth. J. Sea Res. 28: 53-65.

Dybern, B.I., H. Ackefors & R. Elmgren, 1976. Recommendations on methods for marine biological studies in the Baltic Sea. The Baltic Marine Biologists Publ. 1: 98 pp.

Ebbesmeyer, C.C., D.R. Cayan, D.R. McLain, F.H. Nichols, D.H. Peterson & K.T. Redmond, 1991. 1976 step in the Pacific climate: Forty environmental changes between 1968-1975 and 1977-1984. In: Proc. 7th Ann. Pacific Climate Workshop. Calif. Dept. Water Res., Interagency Ecol. Stud. Prog. Rep. 26.

Edler, L., 1979. Recommendation on methods for marine biological studies in the Baltic Sea. The Baltic Marine Biologists, Publication Nr. 5.

Eisma, D. & J. Kalf, 1987. Suspended matter between Norway and Shetland and in the Sognefjord. Int. Rep. Neth. Inst. Sea Res., Texel, 1978-13: 28 pp.

Ejdung, G. & Elmgren, R. 1998: Predation on newly settled bivalves by deposit-feeding amphipods: a Baltic Sea case study. Mar. Ecol. Prog. Ser. 168: 87-94.

Eleftheriou, A. & M.R. Robertson, 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. Neth. J. Sea Res. 30: 289-299.

Elken, J., 1996. Stratification changes in 1975-1995. In: J. Elken. Deep water overflow, circulation and the vertical exchange in the Baltic Proper. Estonian Marine Institute, Report Series 6: 9-17.

Elmgren, R., 1984: Trophic dynamics in the enclosed, brackish Baltic Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 183:152-169.

Essink, K., J. Eppinga & R. Dekker, 1998: Long-term changes (1977-1994) in the intertidal macrozoobenthos of Dollard (Ems estuary) and effects of introduction of the North American polychaete *Marenzelleria cf. wireni*. Senckenbergiana Marit. 28: 211-225.

Evans, F. & A. Edwards, 1993. Changes in the zooplankton community off the coast of Northumberland between 1969 and 1988, with notes on changes in the phytoplankton and benthos. J. exp. mar. Biol. Ecol., 172: 11-29.

Fahrmeier, L. & G. Tutz, 1994. Multivariate statistical modelling based on generalized linear models. Springer-Verlag, New York.

Flinkman, J., E. Aro, I. Vuorinen & M. Viitasalo, 1998. Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. Mar. Ecol. Prog. Ser. 165: 127-136.

Fonds, M. & S. Groenewold, 1996. The production of food for opportunistic scavenging species by beamtrawl fishery in the southern North Sea. In: Quality Status Report North Sea.

Fonds, M., 1994. Mortality of fish and invertebrates in beam trawl catches and the survival changes of discards. In: De Groot, S.J. & H.J. Lindeboom. Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea, NIOZ Report 1994-11, RIVO-DLO Report C026/94: 131-146.

Frid, C.L.J. & N.V. Huliselan, 1996. Far-field control of long-term changes in Northhumberland (NW North Sea) coastal zooplankton. ICES J. Mar. Sci. 53: 972-977.

Fromentin, J.-M. & F. Ibanez, 1994: Year-to-year changes in meteorological features of the French coast area during the last half-century. Examples of two biological responses. Oceanol. Acta 17: 285-296.

Fromentin, J.-M. and B. Planque, 1996. Calanus and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser. 134: 111-118.

Fromentin, J.-M., F. Ibanez, J.C. Dauvin, J.M. Dewarumez & B. Elkaim, 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. J. mar. biol. Ass. U.K. 77: 287-310.

Gabriel, K.R. 1971. The biplot graphic display of matrices with application to principal component analysis. Biometrika 58: 453-467.

Gabriel, W.L., 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. J. Northw. Atl. Fish. Sci. 14: 29-46.

Gaemers, P.A.M., 1977. Recente en jong-kwartaire visresten van het Long Forties gebied, noordelijke Noordzee. (Recent and Late Quaternary fish remains from the Long Forties area, northern North Sea). Meded. Werkgr. Tert. Kwart. Geol. 14: 21-40.

Galavazi, M., 1998. Study on the abandonment of the Vlieter-channel in the Dutch Wadden Sea as a result of the closure of the "Zuiderzee". MSc Report University of Utrecht (in press).

Gauch, H.G., 1982. Multivariate Analysis in Community Ecology, Cambridge University Press, Cambridge.

Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth. J. Sea Res. 32: 191-206.

Goedheer, P.F., 1977. Biomassa en produktie van macro-algen. Internal Report Netherlands Institute for Sea Research 1977-11.

Gray, J.S. & H. Christie, 1983. Predicting long-term changes in marine benthic communities. Mar. Ecol. Prog. Ser. 13: 87-94.

Greene, W.H., 1997. Econometric Analysis, 3 edn. Prentice-Hall, Inc.

Greenstreet, S.P.R. & S.J. Hall, 1996. Fishing and the groundfish assemblage structure in the northwestern North Sea: an analysis of long-term and spatial trends. J. Animal Ecol. 65: 577-598.

Greve, W. & F. Reiners, 1995. Biocoenotic process patterns in the German Bight. In: Biology and ecology of shallow coastal waters. Olsen & Olsen, Fredensborg (Denmark): 67-72.

Grönlund, L. & J.-M. Leppänen, 1990. Long-term changes in the nutrient reserves and pelagic production in the western Gulf of Finland. Finnish Mar. Res. 257: 15-27.

Grover, J.P., 1997. Resource competition. Chapman & Hall.

Gyalitras, D., H. von Storch, A. Fischlin & M. Beniston, 1994. Linking GCM-simulated climate changes to ecosystem models. Case studies of statistical downscaling in the Alps. Climate Res. 4: 167-189.

Hack, J, J.T. Kiehl & J.W. Hurrell, 1998. The hydrological and thermodynamic characteristics of the NCAR CCM3. J. of Climate 11: 1179-1206.

Hagendorff, R., 1993. Untersuchungen zur räumlichen und zeitlichen Variabilität des Makrozoobenthos im Vorstrandbereich von Norderney in den Jahren 1990 und 1991. Diploma thesis, Universität Oldenburg.

Hall, S. J. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogr. Mar. Biol. Ann. Rev. 32: 179-239.

Harris, G.P., F.B. Griffiths, L.A. Clementson, V. Lyne & H. van der Doe, 1991. Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. J. Plankton Res. 13: 109-131.

Harvey, A.C., 1989. Forecasting, structural time series models and the Kalman filter. Cambridge University Press, Cambridge.

Harvey, A.C., 1990. The Econometric Analysis of Time Series. 2 edn., Philip Allan.

Heessen, H.J.L. & N. Daan, 1996. Long-term trends in ten non-target North Sea fish species. ICES J. Mar. Sci. 53: 1063-1078.

Heessen, H.J.L., 1996. Time-series data for a selection of forty fish species caught during the International Bottom Trawl Survey. ICES J. Mar. Sci. 53: 1079-1084.

Hegarty, S.G. & T.A. Villareal, 1998. Effects of light level and N:P supply ratio on the competition between *Phaeocystis* cf. *pouchetii* (Hariot) Lagerheim (Prymnesiophyceae) and five diatom species. J. exp. mar. Biol. Ecol. 226: 241-258.

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

Hemminga, M.A., 1998. The root/rhizome system of seagrasses: an asset and a burden. J. Sea Res. 39: 183-196.

Henderson, P.A., 1989. On the structure of the inshore fish community of England and Wales. J. mar. biol. Ass. UK, 69: 145-163.

Hewitson, B.C. & R.G.L. Crane, 1992a. Regional-scale climate prediction from GISS GCM. Palaeography, Palaeoclimate, Palaeocology 97:249-267.

Hewitson, B.C. & R.G.L. Crane, 1992b. Large-scale atmospheric controls on local precipitation in tropical Mexico. Geophys. Res. Letters 19: 1835-1838.

Heyen, H. & J.W. Dippner, 1998. Salinity variability in the German Bight in relation to climate variability. Tellus 50A: 545-556.

Heyen, H., H. Fock & W. Greve, 1998. Detecting relationships between the interannual variability in ecological time series and climate using a multivariate statistical approach – a case study on Helgoland Roads zooplankton. Clim. Res. 10: 179-191.

Heyen, H., E. Zorita & H. Von Storch, 1994. Statistical Downscaling of winter monthly mean North Atlantic sea-level pressure to sea level variations in the Baltic Sea. Max-Planck-Institut für Meteorologie, Report No. 150, Hamburg: 13 pp.

Heyen, H., E. Zorita & H. von Storch, 1996. Statistical downscaling of monthly mean North Atlantic air-pressure to sea-level anomalies in the Baltic Sea. Tellus 48A: 312-323.

Hickel, W., M. Eickhoff & H. Spindler, 1994. Changes in the German Bight pelagic environment during three decades. ICES Annual Science Conference, Marine Environmental Quality Committee E:18, Ref. C.L.

Hill, C., 1992. Interactions between year classes in the benthic amphipod *Monoporeia affinis*: effects on juvenile survival and growth. Oecologia 91: 157-162.

Hillman, K., D.I. Walker, A.W.D. Larkum, A.J. McComb, 1989. Productivity and nutrient limitation. In: Larkum, A.W.D., A.J. McComb & S.A. Shepherd (eds) Biology of seagrasses. Aquatic Studies 2. Elsevier, Amsterdam: 635-685.

Ho, K.C. & I.J. Hodgliss, 1992. Severe fishkill in Hong Kong caused by *Noctiluca scintillans*. Red Tide Newsletter 5: 1-2.

Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82: 898-903.

Hofmann, W. & M.G. Höfle, 1993. Rotifer population dynamics in response to increased bacterial biomass and nutrients: a mesocosm experiment. Hydrobiol. 255/256: 171-175.

Holden, M., 1977. Elasmobranchs. In: J. Gulland. Fish population dynamics, John Wiley and Sons, London, UK: 187-215.

Holtmann, S.E., A. Groenewold, K.H.M. Schrader, J. Asjes, J.A. Craeymeersch, G.C.A. Duineveld, A.J. Van Bostelen & J. Van der Meer, 1996. Atlas of the zoobenthos of the Dutch continental shelf. Ministry of transport, public works and water management, North Sea Directorate, Rijswijk.

Hoppema, J.M.J., 1991. The oxygen budget of the western Wadden Sea, the Netherlands. Est. Coast. Shelf Sci. 32: 483-502.

Houde, E.D., 1989. Comparative growth, mortality and energetics of marine fish larvae; Temperature and implied latitudinal effects. Fish. Bull. 87: 471-495.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676-679.

Hüttel, M., W. Ziebis, S. Forster & G.W. Luther, 1998. Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. Geochim. Cosmochim. Acta 62: 613-631.

Ilus, E., J. Mattila, H. Kankaanpää & A. Laine, 1999. Caesium-137 in Baltic Sea sediments since the Chernobyl accident. In: Marine Pollution Proceedings of a symposium held in Monaco, 5-9 October 1998. International Atomic Energy Agency. IAEA-TECDOC-1094: , p. 379-380.

IPCC (Intergovernmental Panel on Climate Change), 1992. Climate Change: the supplementary report to the IPCC scientific assessment. J. Houghton, B.A. Callander, S.K. Varney (eds). Cambridge University Press.

Jackson, G.A., 1990. A model of the formation of marine algal flocs by physical coagulation processes. Deep Sea Res. 37: 1197-1211.

Jennings, S, J. Lancaster, A. Woolmer & J. Cotter, 1999. Distribution, diversity and abundance of epibenthic fauna in the North Sea. J. mar. Biol. Assoc. U.K. 79: 385-399.

Jensen, M.H., T.K. Andersen & J. Sørensen, 1988. Denitrification in coastal bay sediment: regional and seasonal variation in Aarhus Bight, Denmark. Mar. Ecol. Prog. Ser. 48: 155-162.

Jensen, K.M., M.H. Jensen & E. Kristensen, 1996. Nitrification and denitrification in Wadden Sea sediments (Königshafen, Island of Sylt, Germany) as measured by nitrogen isotope pairing and isotope dilution. Aquat. Microb. Ecol. 11: 181-191.

Joint, I. & A. Pomry, 1993. Phytoplankton biomass and production in the southern North Sea. Mar. Ecol. Prog. Ser. 21: 283-287.

Jolliffe, I.T., 1986. Principal Component Analysis. Springer-Verlag, Berlin.

Jones, J., 1992. Environmental impact of trawling on the seabed: a review. New Zealand J. Mar. Freshw. Res. 26: 59-67.

Jones, P.D., 1994: Hemispheric surface air temperature variations: a reanalysis an update to 1993. J. Clim. 7: 1794-1802.

Jonsson, P. & R. Carman, 1994. Changes in deposition of organic matter and nutrients in the Baltic sea during the twentieth century. Mar. Poll. Bull. 28: 417-426.

Jørgensen, B.B., 1996. Material flux in the sediment. In: Jørgensen, B.B. & K. Richardson (eds.) Eutrophication in coastal marine ecosystems: coastal and estuarine studies. American Geophysical Union: 115-135.

Josefson, A.B., J.N. Jensen & G. Ærtebjerg, 1993. The benthos community structure anomaly in the late 1970s and early 1980s - a result of a major food pulse? J. exp. mar. Biol. Ecol. 172: 31-46.

Kaiser, M.J. & B.E. Spencer, 1994. Fish scavenging behaviour in recently trawled areas. Mar. Ecol. Prog. Ser. 112: 41-49.

Kaiser, M.J. & B.E. Spencer, 1996a. The effects of beam-trawl disturbance on infaunal communities in different habitats. J. Anim. Ecol. 65: 348-358.

Kaiser, M.J. & B.E. Spencer, 1996b. The behavioural response of scavengers to beam-trawl disturbance. In: S.P.R. Greenstreet & M.L. Tasker. Aquatic predators and their prey, Blackwell Scientific Publications, Oxford, UK: p.116-123.

Kalle, K., 1937. Nährstoff-Untersuchungen als Hydrographisches Hilfsmittel zur Unterscheidung von Wasserkörpern. Annalen der Hydrographie und Maritiemen Meteorologie 65: 1-18.

Kankaanpää, H., H. Vallius, O. Sandman & L. Niemistö, 1997. Determination of recent sedimentation in the Gulf of Finland using 137Cs. Oceanol. Acta 20: 823-836.

Karbe, L., J. Gonzalez-Valero, T. Borchardt, M. Debinski, A. Duch, H. Hablizel & R. Zeitner, 1988. Heavy metals in fish and benthic organisms from the northestern, central and southern North Sea: regional patterns comparing dab, blue mussel and hermit crab. ICES CM E:22: 14 pp.

Kautsky, N., H. Kautsky, U. Kautsky & M. Waern, 1986. Decreased depth penetration of *Fucus vesiculosus* L. since the 1940s indicates eutrophication of the Baltic Sea. Mar. Ecol. Prog. Ser. 28: 1-8.

Keller, A.A., P.H. Doering, S.P. Kelly & B.K. Sullivan, 1990. Growth of juvenile Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae) in MERL mesocosms: effects of eutrophication. Limnol. Oceanogr. 35: 109-122.

Kersten, M. & I. Kröncke, 1991. Bioavailability of lead in North Sea sediments. Helgoländer Wiss. Meeresunters. 45: 403-409.

Kieskamp, W.M., L. Lohse, E. Epping & W. Helder, 1991. Seasonal variation in denitrification rates and nitrous oxide fluxes in intertidal sediments of the western Wadden Sea. Mar. Ecol. Prog. Ser. 72: 145-151.

Kimor, B., 1981. The role of phagotrophic dinoflagellates in marine ecosystems. Kieler Meeresforsch. 5: 164-173.

Kiørboe, T., 1993. Turbulence, phytoplankton cell size and the structure of pelagic food webs. Adv. mar. Biol. 29: 1-72.

Koroleff, F., 1979. Meriveden yleisimmät kemialliset analyysimenetelmät (In Finnish). Meri 7: 1-60.

Koslowski, G. & P. Loewe, 1993. The western Baltic Sea ice season in terms of a mass-related severity index 1879-1992. Part I: Temporal variability and association with the North Atlantic Oscillation. BSH Sea Ice Branch, Rep. No. 1.

Kouts, T. & A. Omstedt, 1993. Deep water exchange in the Baltic proper. Tellus 45A: 311-324.

Kristensen, I., 1959. The coastal waters of the Netherlands as an environment of molluscan life. Basteria 23, Suppl.: 18-55.

Kröncke, I., 1995. Long-term changes in North Sea benthos. Senckenbergiana Marit. 26: 73-80.

Kröncke, I., J.W. Dippner, H. Heyen & B. Zeiss, 1998. Long-term changes in macrofaunal communities off Nordeney (East Frisia, Germany) in relation to climate varibility. Mar. Ecol. Prog. Ser. 167: 25-36.

Kröncke, I., B. Zeiss & S. Dahms, 1997. Makrofauna-Langzeitreihe im Inselverfeld von Nordeney. Umveltbundesamt Berlin Final Rep. 98-021: 1-139.

Krzanowski, W.J., 1988. Principles of Multivariate Analysis: A Users's Perpective. Clarendon Press, Oxford.

Kullenberg, G., 1981. Physical Oceanography. In: A. Voipio (ed.). The Baltic Sea, Elsevier: 135-145.

Kyzyurov, V., Y. Mikheev, L. Niemistö, B. Winterhalter, E. Häsänen & E. Ilus, E. 1994. Shipboard determination of deposition rates of recent sediments based on Chernobyl derived Cesium-137. Baltica 8: 64-67.

Laine, A.O., Sandler, H., Andersin, A.-B. & Stigzelius, J. 1997. Long-term changes of macrozoobenthos in the Eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. J. Sea Res. 38: 135-159.

Lamb, H.H., 1972. British Isles weather types and a register of daily sequence of circulation patterns, 1861-1971. Geophys. Mem. 116, HMSO, London.

Lamb, P.J. & R.A. Peppler, 1987. North Atlantic Oscillation: Concept and an application. Bull. Am. Met. Soc. 68: 1218-1225.

Lange, U. & W. Greve, 1997. Does temperature influence spawning time, recruitment and distribution of flatfish via its influence on the rate of gonadal maturation? German J. Hydrogr. 49: 251-263.

Lass, H.U. & W. Matthäus, 1996. On temporal wind variations forcing salt water inflows into the Baltic Sea. Tellus 48A: 663-671.

Launiainen, J. & T. Vihma, 1990. Metereological, ice and water exchange conditions. In HELCOM. Second perdiodic assessment of the state of the marine environment of the Baltic Sea, 1984-1988; background document. Baltic Sea Environment Proceedings 35 B: 22-33.

Leggett, W.C., 1986. The dependence of fish larval survival on food and predator densities. In: E. Skreslet (ed.). The role of freshwater outflow in coastal ecosystems, NATO ASI Series, Series G, Ecological Sciences, 7. Springer-Verlag, Berlin: 117-137.

Leggett, W.C. & E. DeBlois, 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. 32: 119-134.

Lehtonen, K.K. & A.-B. Andersin, 1998. Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. Mar. Ecol. Prog. Ser. 168: 71-85.

Leonardsson, K., 1991. Effects of cannibalism and alternative prey on population dynamics of *Saduria entomon* (Crustacea, Isopoda). Ecology 72: 1273-1285.

Liang, K.-Y. & S.L. Zeger, 1986. Longitudinal data analysis using generalized linear models. Biometrika 73: 13-22.

Lindeboom, H.J. & S.J. De Groot (eds.), 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. NIOZ-rapport 1998-1/RIVO-DLO report C003/98: 404 pp.

Lindeboom, H.J., W. Van Raaphorst, J.J. Beukema, G.C. Cadée & C. Swennen, 1994. (Sudden) changes in the North Sea and Wadden Sea: Oceanic influences underestimated? Quality Status Report North Sea Symp, Ebeltoft, Denmark.

Lindeboom, H.J., W. van Raaphorst, J.J. Beukema, G.C. Cadée & C. Swennen, 1995. (Sudden) changes in the North Sea and Wadden Sea: Oceanic influences underestimated? Dt. Hydrogr. Zt. 2: 87-100.

Logan, B.E. & A.L. Alldredge, 1989. Potential for increased nutrient uptake by flocculating diatoms. Mar. Biol. 101: 443-450.

Lohse, L., J.F.P. Malschaert, C.P. Slomp, W. Helder & W Van Raaphorst, 1995. Sediment-water fluxes of inorganic nitrogen compounds along the transport route of organic matter in the North Sea. Ophelia 41: 173-197.

Lomstein, E., M.H. Jensen & J. Sørensen, 1990. Intracellular NH_4^+ and NO_3^- pools associated with deposited phytoplankton in a marine sediment (Aarhus Bight, Denmark). Mar. Ecol. Prog. Ser. 61: 97-105.

Lorenzen, C.J., 1967. Determination of chlorophyll and pheo-pigments: Spectrophotometric equations. Limnol. Oceanogr. 12: 343-346.

Machenhauer, B., M. Windelband, M. Bozet & M. Deque, 1996. Validation of present-day regional climate simulations over Europe: nested LAM and variable resolution global model simulations with observed or mixed ocean boundary conditions. Max-Planck-Institut für Meteorologie Report No 191.

Maiwald, K.D. & J.H.G. Verhagen, 1991. Trendanalyse van zwevende stof gegevens van de Waddenzee. Report Delft Hydraulics T 753.

Mann, K.H. & K.F. Drinkwater, 1994. Environmental influences on fish and shellfish production in the Northwest Atlantic. Environ. Rev. 2: 16-32.

Mann, K.H. & J.R.N. Lazier, 1991. Dynamics of marine ecosystems. Biological-physical interactions in the oceans. Blackwell Scientific Publ. Oxford.

Matthäus, W., 1990. Mixing across the primary Baltic halocline. Beitr. Meereskd. 61: 21-31.

Matthäus, W. & H. Franck, 1992. Characteristics of major Baltic inflows - a statistical analysis. Cont. Shelf Res. 12: 1375-1400.

Matthäus, W. & H. Schinke, 1994. Mean atmospheric circulation patterns associated with major inflows. Dt. Hydrogr. Zt. 46: 321- 339.

Matthäus, W. & H. Schinke, 1999. The influence of river runoff on deep water conditions of the Baltic Sea. Hydrobiologia 393: 1-10.

McArdle, B.H., 1995. The temporal variability of densities: back to basics. Oikos 74: 165-171.

McCullagh, P. & J.A. Nelder, 1989. Generalized linear models. 2nd ed. Chapmann and Hall, London.

McHugh, J.L., 1967. Estuarine nekton. In: G.H. Lauff. Estuaries, Publication of the American Association for the Advancement of Science 83: 581-619.

Middelburg, J.J., K. Soetaert, P.M.J. Herman & C.H.R. Heip, 1996. Denitrification in marine sediments: a model study. Global biogeochem. Cycles 10: 661-673.

Midderham, H. & M. De Boer, 1983. Sedimentatie-onderzoek detailgebied de Vlieter. Rapport Rijkswaterstaat, Directie Waterhuishouding en Waterbeweging, District Kust en Zee, Adviesdienst Hoorn. Notitie WWKZ-83.H217.

Miller, J.M., J.S. Burke & G.R. Fitzhugh, 1991. Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. Neth. J. Sea Res. 27: 261-275.

Miller, A.J., D.R. Cayan, T.P. Barnett, N.E. Graham & J.M. Oberhuber, 1994. The 1976-77 climate shift of the Pacific Ocean. Oceanography 7: 21-26.

Murawski, S.A., 1993. Climate change and marine fish distributions: forecasting from historical analogy. Transact. Americ. Fish. Soc. 122: 647-658.

Muus, B.J., 1991. Zeevissengids. Elsevier,Amsterdam.

Myers, R.A., J.A. Hutchings & N.J. Barrowman, 1996. Hypotheses for the decline of cod in the North Atlantic. Mar. Ecol. Prog. Ser. 138: 293-308.

Mysak, L.A., W.W. Hsiehand & T.R. Parsons, 1982. On the relationship between interannual baroclinic waves and fish populations in the Northeast Pacific. Biol. Oceanogr. 2: 63-103.

Nehring, D. & W. Matthäus, 1991. Current trends in hydrographic and chenical parameter and eutrophication in the Baltic Sea. Int. Revue ges. Hydrobiol. 76: 297-316.

Nielsen, L.P., P.B. Christensen & S. Rysgaard, 1994. Denitrification in fjords and coastal waters. Havforsking fra Miljøtyrelsen 50, Danish Environmental Protection Agency, Copenhagen.

Nienhuis, P.H., 1992. Eutrophication, water management, and the functioning of Dutch estuaries and coastal lagoons. Estuaries 15: 538-548.

Nijssen, H. & S.J. de Groot, 1987. De Vissen van Nederland. Stichting Uitgeverij KNNV, Utrecht.

Nilsson, P., B. Jönsson B, I. Lindström Swanberg & K. Sundbäck, 1991. Response of a marine shallow-water sediment system to an increased load of inorganic nutrients. Mar. Ecol. Prog. Ser. 71: 275-290.

Nissling, A. & L. Westin, 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and potential for cod stock interactions in the Baltic Sea. Mar. Ecol. Prog. Ser. 152: 261-271.

Noguer, M. R. Jones & J. Murphy, 1998. Systematic errors in the climatology of a regional climate model over Europe. Climate Dynamics 14: 691-712.

O'Brien, J.J., D. Cayan, R. Dickson, R.H. Godin, N. Graham, L.A. Mysak, T. Nitta, G. Reverdin, D. Salmon, K. Trenberth & T. Yamagata, 1992. Oceanic Climatic Variability. UNESCO IOC Techn. Ser. 40.

Olenin, S., 1994. Some biological consequenses of deep water stagnation in the Eastern Gotland Basin, Baltic Sea in 1980s. In: R.V. Thurston (ed.). Environmental studies in the Nemunas River Basin, Lithuania. Montana State University, Fisheries Bioassay Laboratory. Technical Report 94-1. Bozeman, Montana: 147-156.

Omstedt, A. & L. Axell, 1998. Modelling the seasonal, interannual and long-term variations of salinity and temperature in the Baltic Proper. Tellus 50A: 637- 652.

Oosterbaan, A.F.F., 1989. Veranderingen in de Hollandse kustfauna [Changes in the Dutch coastal fauna]. Wetenschappelijke Mededeling KNNV 193. Stichting Uitgeverij KNNV, Utrecht.

Otto, L., J.F.T. Zimmerman, G.K. Furnes, M. Mork, R. Sætre & G. Becker, 1990. Review of the physical oceanography of the North Sea. Neth. J. Sea Res. 26: 161-238.

Overholtz, W.J. & A.V. Tyler, 1985. Long-term responses of the demersal fish assemblages of Georges Bank. Fish. Bull. 83: 507-520.

Oviatt, C.A., A.A. Keller, P.A. Sampou & L.L. Beatty, 1986. Patterns of productivity during eutrophication: a mesocosm experiment. Mar. Ecol. Progr. Ser. 28: 69-80.

Parsons, T.R., M. Takahashi & B. Hargrave, 1977. Biological oceanographic processes. 2nd ed., Pergamon.

Pauly, D. & R.S.V. Pullin, 1988. Hatching time in spherical, pelagic fish eggs in response to temperature and egg size. Environ. Biol. Fish. 21: 261-271.

Pauly, D., 1994. A framework for latitudinal comparisons of flatfish recruitment. Neth. J. Sea Res. 32: 107-118.

Perttilä, M., L. Niemistö & K. Mäkelä, 1995. Distribution, development and total amonts of nutrients in the Gulf of Finland. Est. Coast. Shelf Sci. 41: 345-360.

Petterson, K., 1991. Seasonal uptake of carbon and nitrogen and intracellular storage of nitrate in planktonic organisms in the Skagerrak. J. exp. mar. Biol. Ecol. 151: 121-137.

Philippart, C.J.M. & G.C. Cadée, 2000. Was primary production in the western Wadden Sea stimulated by nitrogen? Helgoland Mar. Res. 54: 55-62.

Philippart, C.J.M., G.C. Cadée, W. Van Raaphorst & R. Riegman, 2000. Long-term phytoplankton-nutrient interactions in a shallow coastal sea: Algal community structure, nutrient budgets, and denitrification potential. Limnol. Oceanogr. 45: 131-144.

Philippart, C.J.M. & K.S. Dijkema, 1995. Wax and wane of *Zostera noltii* Hornem. in the Dutch Wadden Sea. Aquat. Bot. 49: 255-268.

Philippart, C.J.M., P.A. Henderson, T. Johannessen, A.D. Rijnsdorp & S.I. Rogers, 1998. Latitudinal variation in fish recruits in Northwest Europe. J. Sea Res. 39: 69-77.

Philippart, C.J.M., H.J. Lindeboom, J. Van der Meer, H.W. Van der Veer & J.IJ. Witte, 1996. Long-term fluctuations in fish recruit abundance in the western Wadden Sea in relation to variation in the marine environment. ICES J. mar. Sci. 53: 1120-1129.

Philippart, C.J.M., H.J. Lindeboom, J. Van der Veer, J.IJ. Witte, 1996. Long-term fluctuations in fish recruit abundance in the western Wadden Sea in relation to variation in the marine environment. ICES J. Mar. Sci. 53: 1120-1129.

Philippart, C.J.M. & C.J.N. Winter, 2000. Long-term variations within the western Wadden Sea ecosystem as derived from a sediment core. Internal NIOZ-Report: 65 pp.

Piet, G.J. J. Craeymeersch, J. Buijs & A.D. Rijnsdorp, 1998. Changes in the benthic invertebrate assemblage following the establishment of a protected area, the "plaice box". International Counc. for the Exploration of the Sea Copenhagen (Denmark) Theme Sess. on Recovery and Protection of Marine Habitats. ICES, Copenhagen (Denmark).

Piet, G.J. & A.D. Rijnsdorp, 1998. Changes in the demersal fish assemblage in the south-eastern North Sea following the establishment of a protected area ("plaice box"). ICES J. Mar. Sci. 55: 420-429.

Pihl, L., 1989. Year class strength regulation in plaice *Pleuronectes platessa* L. on the Swedish west coast. Hydrobiologia 195: 79-88.

Polet, H., B. Ball, W. Blom, S. Ehrich, K. Ramsay & I. Tuck, 1998. Fishing gears used by different fishing fleets. In: Lindeboom, H.J. & S.J. De Groot (Eds) IMPACT II: The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. NIOZ-Report 1998-1.

Postma, H., 1961. Transport and accumulation of suspended matter in the Dutch Wadden Sea. Neth. J. Sea Res. 1: 148-190.

Postma, H., 1980. Sediment transport and sedimentation. In: Olausson E. & I. Cato (eds.) Chemistry and biogeochemistry of estuaries. John Wiley & Sons: 153-186.

Priestly, M.B., 1981. Spectral analysis and time series. Academic Press, London.

Priestly, M.B., 1988. Non-lineary and non-stationary time series analysis. Academic Press, London.

Rachor, E., 1990. Changes in sublittoral zoobenthos in the German Bight with regard to eutrophication.

Rachor, E. & S.A. Gerlach, 1978. Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 172: 418-431.

Rae, B.B., 1965. The lemon sole. Fishing News (Books) Ltd.

Ramsay, K., M.J. Kaiser & R.N. Hughes, 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. Mar. Ecol. Prog. Ser. 144: 63-72.

Redfield, A.C., B.A. Ketchum & F.A. Richards, 1963. The influence of organisms on the composition of sea-water. In: Hill, M.N. (ed.) The sea. Wiley: 26-77.

Rees, H.L. & A. Eleftheriou, 1989. North Sea benthos: a review of field investigations into biological effects of man's activiteis. J. Cons. Int. Expl. Mer 172: 418-431.

Reid, P.C., S.C. Surey-Gent, H.G. Hunt & A.E. Durrant, 1992. *Thalasiothrix longissima*, a possible oceanic indicator species in the North Sea. ICES Mar. Sci. Symp. 195: 268-277.

Reise, K., 1993. Die verschwommene Zukunft der Nordseewatten. In: H.-J. Schellnhuber & H. Sterr. Klimaänderung und Küste, Springer Verlag: 223-232.

ReMeDy,1990. Simulation Tool for Easy Modelling. Manual, V(2). Enschede.

Rendell, A.R., C.J. Ottley, T.D. Jickells & R.M. Harrison, 1993. The atmospheric input of nitrogen species to the North Sea. Tellus 45B: 53-63.

Rick, H. -J., 1990. Ein Beitrag zur Abschätzung der Wechselbeziehung zwischen planktischen Primärproduzenten des Nordseegebietes und der Schwermetallen Kupfer, Zink, Cadmium und Blei auf Grundlage von Untersuchungen an natürlichen Planktongemeinschaften und Laborexperimenten mit bestandsbildenden Arten. Dissertation, RWTH Aachen, Germany.

Ridderinkhof, H., J.F.T. Zimmerman & M.E. Philippart, 1990. Tidal exchange between the North Sea and Dutch Wadden Sea and mixing time scales of the tidal basins. Neth. J. Sea Res. 25: 331-350.

Riegman, R., F. Colijn, J.F.P. Malschaert, H.T. Kloosterhuis & G.C. Cadée, 1990. Assessment of growth rate limiting nutrients in the North Sea by the use of nutrient-uptake kinetics. Neth. J. Sea Res. 26: 53-60.

Riegman, R., B.R. Kuipers, A.A.M. Noordeloos & H.J. Witte, 1993. Size differential control of phytoplankton and the structure of pelagic communities. Neth. J. Sea Res. 31: 255-265.

Riegman, R., A.A.M. Noordeloos & G.C. Cadée, 1992. *Phaeocystis* blooms and eutrophication of the continental coastal zones of the North Sea. Mar. Biol. 112: 479-484.

Rijnsdorp, A.D., A.M. Buijs, F. Storbeck & E. Visser, 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to trawling frequency of the sea bed and the impact on benthic organisms. ICES J. mar. Sci. 55: 403-419.

Rijnsdorp, A.D., F.A. Van Beek, S. Flatman, R.M. Millner, J.D. Riley, J.M. Giret & R. De Clerck, 1992. Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. Neth. J. Sea Res. 29: 173-192.

Rijnsdorp, A.D. & P.I. Van Leeuwen, 1994. Changes in growth of North Sea plaice and its relation to density, eutrophication, beam trawl effort and temperature. ICES C.M. 1994/G:9.

Rijnsdorp, A.D., P.I. Van Leeuwen, N. Daan & H.J.L. Heessen, 1996. Changes of demersal fish species in the North Sea between 1906-1909 and 1990-1995. ICES J. Mar. Sci. 53: 1054-1062.

Robinson, P.J. & P.L. Finkelstein, 1991. The development of impact-oriented scenarios. Bull. Amer. Met. Soc. 4: 481-490.

Roeckner, E., L. Bengtsson, J. Feichter, J. Lelieveld & H. Rodhe, 1998. Transient climate change simulations with a coupled atmosphere-ocean GCM including the tropospheric sulphur cycle. Max-Planck-Institut für Meteorologie Report No. 266.

Roelke, D.L., L.A. Cifuentes & P.M. Eldridge, 1997. Nutrient and phytoplankton dynamics in a sewage-impacted Gulf Coast estuary: a field test of the PEG-model and Equilibrium Resource Competition theory. Estuaries 20: 725-742.

Rogers, S.I. & R.S. Millner, 1996. Annual abundance and regional distribution of English inshore demersal fish populations: 1973-1994. ICES J. Mar. Sci. 53: 1094-1112.

Rosenberg, R., J.S. Gray, A.B. Josefson & T.H. Pearson, 1987. Petersen's benthic stations revisited. 2. Is the Oslofjord and eastern Skagerrak enriched? J. exp. mar. Biol. Ecol. 105: 219-251.

Rumohr, H., E. Bonsdorff & T. Pearson, 1996. Zoobenthic succession in Baltic sedimentary habitats. Arch. Fish. Mar. Res. 44:19-214.

Russell, F.S., 1973. A summary of the observations on the occurrence of planktonic stages of fish off Plymouth 1924-1952. J. mar. biol. Ass. U.K. 53: 347-3 56.

Rutgers van der Loeff, M.M., 1981. Wave effects on sediment water exchange in a submerged sand bed. Neth. J. Sea Res. 15: 100-112.

Sampou, P. & C.A. Oviatt, 1991. Seasonal patterns of sedimentary carbon and anaerobic respiration along a simulated eutrophication gradient. Mar. Ecol. Progr. Ser. 72: 271-282.

Samuelsson, M., 1996. Interannual salinity variations in the Baltic during the period 1954-1990. Cont. Shelf Res. 16: 1463-1477.

Sanden, P. & B. Håkansson, 1996. Long-term trends in Secchi depth in the Baltic Sea. Limnol. Oceanogr. 41: 346-351.

Schinke, H. & W. Matthäus, 1998. On the causes of major Baltic inflows - an analysis of long time series. Cont. Shelf Res. 18: 67-97.

Schott, F., 1966. Der Oberflächensalzgehalt in der Nordsee. Dt. Hydrogr. Zt. (Suppl. 9A): 1-58.

Segerstråle, S.G., 1969: Biological fluctuations in the Baltic Sea. In: M. Sears (ed.). Prog. Oceanog. 5: 196-184.

Seitzinger, S.P., 1988. Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. Limnol. Oceanogr. 33: 702-724.

Sfriso, A., B. Pavoni & A. Marcomini, 1989. Macroalgae and phytoplankton standing crops in the central Venice Lagoon: primary production and nutrient balance. Sci. Total Environm. 80: 139-159.

Shepherd, J.G., J.G. Pope & R.D. Cousens, 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 185: 255-267.

Shum, K.T., 1993. The effects of wave-induced pore water circulation on the transport of reactive solutes below a rippled sediment bed. J. Geophys. Res. 98: 10289-10301.

Slomp, C.P., J.F.P. Malschaert, L. Lohse & W. Van Raaphorst, 1997. Iron and manganese cycling in different sedimentarry environments on the North Sea continental margin. Cont. Shelf Res. 17: 1083-1117.

Smetacek, V.S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Mar. Biol. 84: 239-251.

Sokal, R.R. & F.J. Rohlf, 1981. Biometry: the principles and practice of statistics in biological research (2nd ed) Freeman, San Francisco.

Solow, A.R., 1994. Detecting change in the composition of a multispecies community. Biometrics 50: 556-565.

Sommer, U., 1984. The paradox of the plankton: fluctuations of phosphorus availability maintain diversity in flow-through cultures. Limnol. Oceanogr. 29: 633-636.

Sommer, U., Z.M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106: 433-471.

Stigebrandt, A., 1983. A model for the exchange of water and salt between the Baltic and the Skagerrak. J. Phys. Oceanog. 13: 411-427.

Stolte, W., T. McCollin, A.A.M. Noordeloos & R. Riegman, 1994. Effect of nitrogen source on the size distribution within marine phytoplankton populations. J. exp. mar. Biol. Ecol. 184: 83-97.

Stolte, W., & R. Riegman, 1995. Effect of phytoplankton cell size on transient-state nitrate and ammonium uptake kinetics. Microbiol. 141: 1221-1229.

Stolte, W., & R. Riegman, 1996. A model approach for size selective competition of marine phytoplankton for fluctuating nitrate and ammonium. J. Phycol. 32: 732-740.

Sullivan, B.K. & P.V. Banzon, 1990. Food limitation and benthic regulation of populations of the copepod *Acartia hudsonica* Pinhey in nutrient-limited and nutrient-enriched systems. Limnol. Oceanogr. 35: 1618-1631.

Svendsen, E., A. Aglen, S.A. Iversen, D.W. Skagen & O. Smestad, 1995. Influence of climate on recruitment and migration of fish stocks in the North Sea. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121: 641-653.

Swennen, C., 1991. Fledgling production of Eiders *Somateria mollissima* in The Netherlands. J. Orn. 132: 427-437.

Taylor, A.H., 1995. North-south shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. ICES J. Mar. Sc. 52: 711-721.

Ten Hallers-Tjabbes, C.G., J.M. Kemp & J.P.Boon, 1994. Imposex in whelks (Buccinum undatum) from the open North Sea: relation to shipping traffic intensities. Mar. Poll. Bull. 28: 311-313.

Ter Braak, C.J.F., 1983. Principal component biplots and alpha and beta diversity. Ecology 64: 454-462.

Ter Braak, C.J.F., 1985. Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. Biometrics 4: 859-873.

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

Thingstad, T.F. & E. Sakshaug, 1990. Control of phytoplankton growth in nutrient recycling ecosystems. Mar. Ecol. Prog. Ser. 63: 261-272.

Thrush, S.F., J.E. Hewitt, V.J. Cummings & P.K. Dayton, 1995. The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? Mar. Ecol. Prog. Ser. 129: 141-150.

Tomas, C.R. & G.R. Hasle, 1997. Identifying marine plankton. Academic Press.

Tong, H., 1990. Non-linear Time Series. A Dynamical System Approach. Oxford University Press, Oxford.

Trenberth, K.E., 1990. Recent observed interdecadal climate changes in the northern hemisphere. Bull. Am. Meteor. Soc. 71: 988-993.

Trenberth, K.E. & D.A. Paolino Jr., 1980. The northern hemisphere SLP-dataset: trends, errors and discontinuities. Mon. Wea. Rev. 112: 1999-2015.

Turrell, W.R., 1992. The East Atlantic inflow. ICES Mar. Sci. Symp. 195: 127-143.

Uhlig, G. & G. Sahlig, 1990. Long term studies on *Noctiluca scintillans* in the German Bight. Population dynamics and red-tide phenomena 1968-1988. Neth. J. Sea Res. 25: 101-112.

Uitto, A. & J. Sarvala, 1990. Perspectives on the ecological factors regulating *Pontoporeia* populations in the northern Baltic Sea. Ann. Zool. Fennici 27: 297-301.

Van Beek, F.A., 1998. Discarding in the Dutch beamtrawl fishery. ICES CM 1998/BB:5.

Van Beek, F.A., A.D. Rijnsdorp & R. De Clerck, 1989. Monitoring juvenile stocks of flatfish in the Wadden Sea and the coastal areas of the southeastern North Sea. Helgoländer Meeresunters. 43: 461-477.

Van den Hoek, C., W. Admiraal, F. Colijn & V.N. De Jonge, 1979. The role of algae and seagrasses in the ecosystem of the Wadden Sea: a review. In: Wolff, W.J. (ed) Flora and vegetation of the Wadden Sea. Reports of the Wadden Sea Working Group 3: 9-118.

Van der Hoeven, P.C.T., 1982. Observations of surface water temperature and salinity, State Office of Fishery Research (RIVO): 1860-1981. KNMI Scientific Report WR 82-8. KNMI, De Bilt.

Van der Meer, J., J.IJ. Witte & H.W. van der Veer, 1995. The suitability of a single intertidal fish trap for the assessment of long-term trends in fish and epibenthic invertebrate populations. Environm. Monit. Assessm. 36: 139-148.

Van der Veer, H.W., 1986. Immigration, settlement and density-dependent mortality of a larval and early post-larval)-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29: 223-236.

Van der Veer, H.W. & M.J.N. Bergman, 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 35: 203-215.

Van der Veer, H.W., M.J.N. Bergman, R. Dapper & J.IJ. Witte, 1991. Population dynamics of an intertidal 0-group flounder *Platichthys flesus* population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 73: 141-148.

Van der Veer, H.W., L. Pihl & M.J.N. Bergman, 1990. Recruitment mechanisms in North Sea plaice Pleuronectes platessa. Mar. Ecol. Prog. Ser. 64: 1-12.

Van der Veer, H.W., P. Ruardij, A.J. van den Berg & H. Ridderinkhef, 1998. Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice *Pleuronectes platessa* L. in the southern North Sea. J. Sea Res. 39: 29-40.

Van Dongen, B.E., W.I.C. Rijpstra, C.J.M. Philippart, J.W. de Leeuw & J.S. Sinninghe Damsté, 2000. Biomarkers in upper Holocene Eastern North Sea and Wadden Sea sediments. Org. Geochem. 31:1533-1543.

Van Leeuwen, P.I., A.D. Rijnsdorp & B. Vingerhoed, 1994. Variations in abundance and distribution of demersal fish species in the coastal zone of the south-eastern North Sea between 1980 and 1993. ICES Paper Demersal Fish Committee C.M. 1994/G:10.

Van Raaphorst, W. & H.W. Van der Veer, 1990. The phosphorus budget of the Marsdiep tidal basin (Dutch Wadden Sea) in the period 1950-1985: importance of the exchange with the North Sea. Hydrobiologia 195: 21-38.

Veldhuis, M.J.W., 1987. The ecophysiology of the colonial alga *Phaeocystis pouchetii*. PhD. thesis, Groningen: 127 pp.

Venrick, E.L., J.A. McGowan, D.A. Cayan & T.L. Hayward, 1987. Climate and chlorophyll a: long-term trends in the central Pacific Ocean. Science 238: 70-72.

Victor, B.C., 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Can. J. Fish. Aquat. Sci. 43: 1208-1213.

Villareal, T.A. & F. Lipschultz, 1995. Internal nitrate concentrations in single cells of large phytoplankton from the Sargasso Sea. J. Phycol. 31: 689-696.

Voipio, A., 1981. The Baltic Sea. Elsevier Oceanogr. Ser. 30. Elsevier, Rotterdam.

Von Storch, H., E. Zorita, & U. Cubasch, 1993. Downscaling of global climate change estimates to regional scales: An application to Iberian rainfall in wintertime. J. Climate 6: 1161-1171.

Von Westerhagen, H., W. Hickel, E. Bauerfeind, U. Niermann & I. Kröncke, 1986: Sources and effects of oxygen deficiencies in the southeastern North Sea. Ophelia 26: 457-473.

Walker, P.A. & H.J.L. Heessen, 1996. Long-term changes in ray populations in the North Sea. ICES J. Mar. Sc. 53: 1085-1093.

Whitaker, R.H., 1978. Classification of Plant Communities. Junk, The Hague.

Whitehead, P.J.P., M.-L. Bauchot, J.-C. Hureau, J. Nielsen & E. Tortonese, 1986. Fishes of the north-eastern Atlantic and the Mediterranean. Part II and III. UNESCO, Paris.

Wilby, R.L. & T.M.L. Wigley, 1997. Downscaling general circulation model output: a review of methods and limitations. Prog. Phys. Geogr. 21:b530- 548.

Wild, C.J. & T.W. Yee, 1996. Additive Extensions to Generalized Estimation Equation Methods. J. R. Statist. Soc. B. 58: 711-725.

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

Woodhead, P.M.J., 1964. The death of North Sea fish during the winter of 1962/63, particularly with reference to the sole, *Solea vulgaris*. Helgol. Meeresunters. 10: 283-312.

Wooster, W.S. & K.M. Bailey, 1989. Recruitment of marine fishes revisted. In: R.J. Beamish & G.A.

McFarlane (eds). Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, Can. Spec. Publ. Fish. Aquat. Sci. 108: 153-159.

Wulf, F., L. Rahm & M. Rodriguez-Medina, 1994. Long-term and regional variations of nutrients in the Baltic Sea. Finnish Mar. Res. 262: 35-50.

Yee, T.W., 1993. The Analysis of Binary Data in Quantitative Plant Ecology. Unpublished PhD-Thesis, Department of Mathematics and Statistics, University of Auckland.

Zeiss, B. & I. Kröncke, 1997. Macrofauna long-term studies in a subtidal habit at off Norderney (East Frisia, Germany) from 1978 until 1994. Oceanol. Acta 20: 311-318.

Zevenboom, W., G.J. de Groot & L.R. Mur, 1980. Effects of light on nitrate-limited *Oscillatoria agardhii* in chemostat cultures. Arch. Microbiol. 125: 59-65.

Ziegelmeier, E., 1964. Einwirkungen des kalten Winters 1962/63 auf das Makrobenthos im Ostteil der Deutschen Bucht. Helgol. Meeresunters. 10: 276-282.

Zijlstra, J.J., 1978. The function of the Wadden Sea for the members of the fish fauna. In: N. Dankers, W.J. Wolff & J.J. Zijlstra. Fishes and fisheries of the Wadden Sea. Balkema Press, Rotterdam: 20-25.

Zijlstra, J.J. & J.IJ. Witte, 1985. On the recruitment of 0-group plaice in the North Sea. Neth. J. Zool. 35: 360-376.

Zmudzinski, L., 1989. Long-term changes in deepwater macrozoobenthos of the Baltic Sea. In: Klekowski, R. E. Styczynska & L. Falkwski (Eds) Proc. 21st Europ. Mar. Biol. Symp. Polish Academy of Sciences, Wroclaw: 509-517.

Zorita, E. & A.O. Laine, 2000: Dependence of salinity and oxygen concentration in the Baltic Sea on the large-scale atmospheric circulation. Climate Res. (accepted).

Zuur, A.F., 1999. Dimension reduction techniques in community ecology, with applications to marine ecological data. PhD-thesis, Department of Mathematical Sciences, University of Aberdeen, Aberdeen.

APPENDIX

ABSTRACTS OF MAIN PUBLICATIONS

Andersin A.-B., A.O. Laine & S. Seppänen (in prep.) Long-term changes of macrozoobenthos in the open Gulf of Bothnia. 1. Trends and fluctuations of the communities

The Gulf of Bothnia, the northernmost part of the Baltic Sea differs markedly from the Baltic Proper area due to its subarctic climate, low salinity level and benthic communities characterised by only a couple of species. This study is a description of the changes in the macrobenthic communities in 1965-1997 in relation to the general fluctuations in the near-bottom hydrography. The number of days with ice coverage is included as a general description of climatological variability.

No marked changes were observed in the community structure. Throughout the period the communities has been numerically dominated by the amphipod *Monoporeia affinis*. The effect of the increased salinity in the 1980s is seen in temporal occurrence of the marine species *Pontoporeia femorata* in the southern part of the area. One non-indigenous species, the polychaete *Marenzelleria viridis* was for the first time observed in the Gulf of Bothnia in 1996.

The total macrobenthic abundance and biomass increased during the study period, both in the northern and southern part of the area. Comparisons between different periods showed that the *M. affinis* abundance values increased significantly between the periods 1965-68 and 1984-1987. Between the periods 1984-87 and 1994-97 no significant difference could be stated. As regards the biomass values the increase was statistically significant only between the two latter periods. *M. affinis* abundance and biomass was significantly greater in the southern part of the Gulf despite the greater increase in the northern areas during the study period.

Abundance of *M. affinis* showed 6-7 years periodicity in the Bothnian Sea prior to 1976, but from the early 1980s onwards out-of-phase behaviour was observed at some sites. However, most of the sites in the Bothnian Sea peaked again in 1993-94. In the Bothnian Bay the variability is more irregular. The observed changes in the macrobenthic communities depend most probably on changes in the food availability, i.e. fluctuations in the amount and quality of the sedimenting material.

Bergman M.J.N. & H.J. Lindeboom (1999) Natural variability and the effects of fisheries in the North Sea. In: J.S. Gray, W. Ambrose Jr, A. Szaniawska (Eds) Biogeochemical cycling and sediment ecology. NATO ASI Series 59: 173-184.

Marine ecosystems are not in steady state, but exhibit continuous changes in production and species composition of different trophic levels. Sudden changes in biomasses or species composition, a reversal of trends, increased seasonal variation and cyclic behaviour all seem to contribute to the interannual and decadal variability of the North Sea ecosystem. An array of possible causes is introduced and the need for more long-term data sets is stressed. From this highly variable ecosystem men tries to extract a maximum quantum of fish using more and more efficient fishing methods, resulting in an overexploitation of fish stocks and notable effects on other species. In this paper an estimate is given for the fishing mortality, *i.e.* the total direct mortality, in the populations of non-target invertebrate species generated by the trawl fisheries in the Dutch sector of the North Sea in 1994. For the species studied the fishing mortality appeared to range from 7 to 48%. Long term observations indicate that stocks of several species declined and some species disappeared from the southern North Sea.

So far, attempts to control overfishing failed. Measures to regulate fisheries should be integrated into a general policy for the ecosystem. A sustainable North Sea ecosystem has to be a common objective for fisheries and nature management, also taking into account the high natural variability of the ecosystem. In this paper, several measures are proposed: an overall reduction in fishing effort leading to a moratorium in case of steep declines in fish stocks, stimulation of new designs of more selective and less damaging gears, and designation of areas closed for fishing activities to protect species and habitats that can not be protected sufficiently otherwise.

Dippner J.W. (1997) SST anomalies in the North Sea in relation to the North Atlantic Oscillation and the influence on the theoretical spawning time of fish. German Journal of Hydrography 49: 267-275.

The weekly sea surface temperature (SST) of the whole North Sea and selected areas are analyzed using empirical orthogonal functions (EOF's) and related to the North Atlantic Oscillation (NAO) index. With the exception of the inflow area of the Fair Isle current, the SST anomalies of the whole North Sea and the selected areas show a good correlation with the NAO index, which indicates that the North Sea SST is mainly controlled by direct atmospheric forcing. In the Fair Isle current or the Fladenground area the SST seems to be influenced by advection. The strong anomalies of the EOF pattern in shallow water close to the continental coast, especially in the German Bight, and the strong seasonality during winter time suggest that these areas could be very sensitive with respect to climate change. A theoretical computation shows that climate variability influences the spawning time of fish up to two month in the nmear coastal area.

Heyen H (1998) Detecting relationships between the interannual variability in climate records and ecological time series using a multivariate statistical approach – four case studies for the North Sea region. PhD Thesis, University of Hamburg & GKSS-Forschungszentrum Geesthacht GmbH. External GKSS report 98/E/32 78 pp.

A multivariate statistical approach is presented that allows a systematic search for relationships between the interannual variability in climate records and ecological time series. Statistical models are built between climatological predictor fields and the variables of interest. Relationships are sought on different temporal scales and for different seasons and time lags. The possibilities and limitations of this approach are discussed in four case studies dealing with salinity in the German Bight, abundance of zooplankton at Helgoland Roads, macrofauna communities off Norderney and the arrival of migratory birds on Helgoland.

Heyen H. & J.W. Dippner (1998) Salinity variability in the German Bight in relation to climate variability. Tellus 50A: 545-556.

A relationship between observed variability in large-scale climate and salinity in the German Bight is sought using a multivariate statistical approach. It is found that on an annual timescale, 90% of the observed salinity variability is in-phase and correlated with a lag of several months to large-scale air pressure. The statistical model is used to estimate annual mean salinity anomalies from large-scale air pressure back to 1900. The correlations betweenestimated and observed salinities range from r=0.4 to r=0.7, depending on the position. It is shown that advective precipitation is the mechanism that links air pressure and salinity anomalies. Advection of Atlantic Water has only a minor impact on the annual mean in the examined coastal zone. If air pressure data from a climate change experiment is used as predictor, a slight drop of the mean salinity level in the range of 0.2 to 0.3 psu is predicted for the near future.

Heyen H., H. Fock & W. Greve (1998) Detecting relationships between the interannual variability in ecological timeseries and climate using a multivariate statistical approach - a case study for Helgoland Roads zooplankton. Clim.Res. 10: 179-191.

A multivariate statistical approach is presented that allows a systematic search for potential relationships between the variability in ecological time series and climate records. In this study, interannual variability in large- and mesoscale climate variables in the North Sea region is compared with variability in local zooplankton observations from Helgoland. The species *Noctiluca scintillans* (Protozoa), *Temora longicornis* and *Acartia sp.* (Copepoda), and spionid larvae (Polychaeta) are examined. The multivariate model detected several high correlations between zooplankton abundance and winter climate. Based on these correlations, complementary hypotheses about the causal relationships are discussed using available local data.

Kröncke I., J.W. Dippner, H. Heyen & B. Zeiss (1998) Long-term changes in macrofauna communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar. Ecol. Prog. Ser. 167: 25-36.

Macrofaunal samples were collected seasonally from 1978 to 1995 in the subtidal zone off Norderney, one ofthe East Frisian barrier islands. Samples were taken with a $0.2m^2$ van-Veen grab at five sites with water depths of 10-20m. Interannual variation of biomass, abundance and species number of the biota were related to interannualvariations in climate using multivariate regression models and by identifying congruent changes in the time series. Changes in the biota were described in relation to human impact, seasonal and long-term meteorological variability.

Our analysis suggest that macrofauna communities were severely effected by cold winters, whereas storms and hot summers have a minor impact. It appears that mild meteorological conditions, probably acting in conjunction with eutrophication, resulted in an increase in total biomass since 1989. Indeed, the multivariate model found a strong relationship between the species number and environmental conditions, especially the sea surface temperature in spring. On the basis of our results, we suggest most of the interannual variance in macrozoobenthos can be explained by climate variability.

Laakkonen T., A.-B. Andersin & A.O. Laine (in prep.) Long-term changes of macrozoobenthos in the open Gulf of Bothnia. 2. Population dynamics of *Monoporeia affinis* (Amphipoda)

The amphipod *Monoporeia affinis* strongly dominates the soft-bottom fauna in the open sea areas of the northern and southern Gulf of Bothnia. Both abundance and biomass values at the investigated localities showed cyclical fluctuations, with a length of about 7 years when the period 1965-1974 was studied. The cycles during this period seemed to be quite well synchronised between the different sites. However, adding the period 1975-1998 to the data makes the pattern more confusing, resulting in variable length of cycles both between and within localities.

Based on size distributions the population dynamics of *M. affinis* in 1980-1998 was studied at three localities in different parts of the Gulf of Bothnia. At all stations there was an alternation between periods with a 3-year and a 4-year life cycle. Low abundance values tended to be connected to high condition values (length/weight relationship), and a three-year life cycle. This phase lead to increasing abundance values. The high abundance values were on the other hand connected to lower condition and leading to a 4-year life cycle. Good condition of the reproducing third year-class results in high reproduction capacity. An abundant reproducing year-class affects negatively the condition of the next generation, causing that only a part of this year class maturates the next autumn, the rest living for one year more before propagation. The driving force for this internal population regulating mechanisms is obviously food limitation at high densities.

A general increase in abundance was observed at all localities investigated, taking place in the beginning of the 1990s. The development of the population structure was similar at the two northernmost localities, while the locality in the southern part of the area differed, showing stronger variations in abundance values of the different stages in the cycles. The elevation of the abundance level may be coupled to changes in the food supply, caused by increase in nutrients leading to an increase in the sedimenting material. Concluding, the reasons for the observed population fluctuations are suggested to be internal population regulation mechanisms connected to fluctuations in the food supply.

Laine A.O. (in prep.) Distribution of soft-bottom macrofauna in the open Baltic Sea in relation to environmental variability

In order to analyse the present distribution of macrofauna, material on species abundance and biomass has been collected in 1996-97, supplemented by multiple environmental variables describing the sediment and near-bottom water characteristics. The benthic community structure is used to classify and describe different assemblages and the observed distribution of communities is related to environmental factors by means of statistical multivariate methods. The results show distinct benthic assemblages that can be related to different subareas and/or depth zones of the Baltic Sea, characterized by a combination of environmental factors. Salinity or the combined effects of salinity, dissolved oxygen saturation and sediment organic matter content explained best the patterns in community distribution, indicating the importance of hydrography and sediment quality as structuring factors of the macrozoobenthos communities. The present distribution of species and assemblages is discussed in relation to the observed long-term changes in the Baltic soft bottom communities and the changing environment, evidently affecting the community structures and distribution presented here.

Laine A.O., H. Sandler, A.-B. Andersin & J. Stigzelius (1997) Long-term changes of macrozoobenthos in the Eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. J. Sea Res. 38: 135-160.

Changes in the macrofauna of the subhalocline bottoms of the Eastern Gotland Basin and the Gulf of Finland during 1965-94 have been studied in relation to the salinity and oxygen regimes. The study period covers several significant major inflows of North Sea water, as well as the longest stagnation period during the last one hundred years with semi-permanent anoxia affecting the distribution and community structure of the macrozoobenthos. At the beginning of the study period vast areas below the halocline were devoid of benthic macrofauna. The major inflows of North Sea water in 1975-76 led to rapid benthic recolonization down to approximately 150 m depth in the Eastern Gotland Basin where the oxygen conditions had improved, but had no effect on the macrozoobenthos communities in the Gulf of Finland. The subsequent, prolonged, stagnation period in 1977-93 caused a deterioration of macrozoobenthos as a concequence of anoxia and hydrogen sulphide formation in subhalocline (70-250 m) areas. Later, a recovery was observed in the 70-100 m depth zone when vertical stratification weakened and intensified vertical mixing resulted in improved oxygen conditions at these intermediate depths. The effect of this process was most pronounced in the Gulf of Finland. The 1993-94 inflows led to the highest oxygen levels in the Gotland Deep since the 1930s. Consequently, in 1994 polychaetes were found at 243 m depth indicating a recolonization of even the deepest part of the basin. The fluctuations in salinity have also affected the distribution of marine species. The biological significance of the hydrographical regime, potential impact of eutrophication on the oxygen balance of the deep waters, and the consistency of long-term data sets are discussed.

Laine, A.O. & S. Seppänen (in prep.) Salinity and oxygen limits of Baltic Sea soft bottom macrofauna based on field observations

The distribution of the Baltic macrofauna species in relation to salinity and oxygen conditions was studied by using long-term data. The data set covers the open Baltic Sea area for the period 1965-97 and represents soft bottom habitats generally deeper than 60 m. Near-bottom water salinity and oxygen concentration have been measured simultaneously with macrofauna sampling, resulting in more than 1600 observations for the study period. The results showed clear differences between species in tolerance limits for salinity and oxygen. Of the seven main macrofauna species, the amphipods *Monoporeia affinis* and *Pontoporeia femorata* seemed to be most sensitive to low oxygen concentrations and also showed clear salinity limits. For the marine species *P. femorata* the lower salinity limit lies between 6-7 psu. The oxygen limit is slightly less than 2 ml/l. *M. affinis* prefers low salinity and high oxygen content. The abundance of the species decreases strongly when the salinity rises over 8 psu. Lower oxygen limit seems to be between 2-3ml/l. The distribution of *M. affinis* may also be affected by the combined effect of salinity and oxygen limitation due to correlation between these factors in our data. The third common species, the euryhaline isopod *Saduria entomon* exists all salinities as expected, but is almost absent at oxygen concentration below 1 ml/l. The occurrence of the species may be further influenced by the distribution of its prey species, i.e. *M. affinis* and *P. femorata*. The bivalve *Macoma balthica* has a wide tolerance both as regards to oxygen and salinity. The lower salinity limit is about 4 psu and this species is found also in oxygen concentrations less than 1ml/l. Highest hypoxia tolerance was observed for two euryhaline marine species, the polychaete *Harmothoe sarsi* and the priapulid

Halicryptus spinulosus which were found at oxygen concentrations less than 0.5 ml/l. The lower salinity limit of both species is, according to field data, about 6 psu. The distribution of the marine polychaete *Scoloplos armiger* in the deep soft bottom habitats of the Baltic Sea is evidently limited by both salinity and oxygen conditions. This species was found only when the salinity was more than 9 psu and the oxygen concentration at least 1 ml/l.

Laine, A.O., S. Seppänen, S. & A.-B. Andersin (in prep.) Stratification induced hypoxia as a structuring factor of macrozoobenthic communities in the open Gulf of Finland (Baltic Sea)

This study describes the long-term development (1965-97) of macrozoobenthos communities on a longitudinal transect in the Gulf of Finland and analyses the changes in relation to variability in oxygen conditions, salinity, temperature and winter nutrient concentrations. Gulf of Finland is a shallow extension of the brackish Baltic Proper, affected both by the run-off from the Neva estuary and the inflow dynamics of the North Sea water, causing long-term changes in the stratification of the water column. Subhalocline areas in the Baltic Sea are affected by semi-permanent hypoxia and the oxygen conditions exhibit periodicity alternating with the inflow - stagnation dynamics. For most of the study period deteriorated communities have been prevailing until an expansion of macrofauna was observed in the late 1980s, coinciding with the late phase of the 17 year long stagnation period. As a consequence of the long stagnation, a general freshening and weakening of the stratification has been observed in intermediate depths, leading to improved oxygen conditions in the open parts of the Gulf of Finland. However, a strengthening of the stratification and deteriorated oxygen conditions have been observed recently, most probably caused by the strong inflows of salt water into the Baltic Sea in 1993-94. A sudden collapse of the abundant macrobenthic communities took place in 1996 when severe hypoxia occurred again. The changes in the community were best explained by a combined effect of annual observed minimum oxygen concentration (with a 1 year time lag) and salinity indicating that the primary factor causing the recolonisation in the late 1980s and early 1990s is the absence of hypoxia, critical to the development of benthic communities. Changes in hydrography have obviously played a key role in regulating the long-term succession of macrozoobenthos in the deep areas of the Gulf of Finland.

Laine, A.O. & A.F. Zuur (in prep.) Multivariate time series analysis to detect long-term trends of macrozoobenthos and hydrography in the Baltic Sea.

Structural time series models have been used to used to estimate long-term trends (1965-1997) in five macrozoobenthos species and near-bottom salinity, temperature and oxygen concentration in the Baltic Sea. Three different models with increasing complexity have been developed and applied on data to describe the succession and relate the variability in benthic communities to changes in hydrography. The results indicated that one common trend for each of the variables, covering the entire study area is too general and includes too much variability. However, for most species a basic division into two subsets could be done, resulting in trends describing the general pattern related to two different areas, the Baltic Proper area (including the Gulf of Finland) and the Gulf of Bothnia. In the Baltic Proper area four of the analysed species (*Saduria entomon, Monoporeia affinis, Pontoporeia femorata and Macoma balthica*) showed very similar trends, with no change in abundance prior to the middle of the 1980s, followed by a rapid increase. One species (*Harmothoe sarsi*) peaked also in the middle of the 1970s. The trends in species had highest correlations with oxygen concentration, indicating the limiting effects of hypoxia for the development of the communities. In the Gulf of Bothnia area however, different trends were found and correlations between species and the hydrographical variables were in general weak. Low oxygen concentrations did not occur and obviously other factors have influenced the long-term development in this area. Biotic interactions may be involved, as exemplified by the high correlation between *M. affinis* and the predatory *S. entomon*. The results thus suggest different structuring factors of the benthic communities in the two sea areas, representing different hydrographical regimes.

Leopold M.F., C. van Damme, C.J.M. Philippart & C.J.N. Winter (in press) Otoliths and other hard parts of fishes of the North Sea and adjacent fresh waters. CD-ROM, ETI Biodiversity Center, Amsterdam & Springer Verlag, New York

Fish that have died and disintegrated can often still be identified by specific hard parts that dissolve only slowly. In bony fish, the 'ear-stones' or otoliths are particularly useful in this respect. Otoliths are made out of a very hard, calcareous material, are species-specific in their shape and have an allometric relation with fish size. Thus, from an otolith, the species of fish and its size can be reconstructed if a good reference collection of otoliths of fish of the region can be consulted.

Otoliths may be retrieved from sediments, to reconstruct past fish fauna's, or from present-day fish predators (from stomachs or guts, regurgitates or faeces) to reconstruct their diets. For both lines of work, a referenced collection is now presented on CD-ROM. The work contains electron microscopic photographs of otoliths of over 10,000 fish, comprising 90 species, collected in the North and Wadden Seas, as well as in some adjoining fresh waters. Data on some other hard parts, such as pharyngeal bones and chewing pads are also provided. Linked to the photographs are written accounts on identification, including special characters of the described items and pitfalls from similar species and wear of otoliths that have passed through a predator's gut; a database of regression equations relating otolith size to fish size and fish mass; and a database on known predators of that particular species of fish. Line drawings of the different fish species, as well as from 'standard' fish, fish otoliths, pharyngeal bones and chewing pads, showing how measurements were taken, are included.

The CD-ROM allows identification of a large number of the common fish species from the North and Wadden Sea and their adjoining fresh water systems. After specific identification, it makes possible back-calculations of fish size and mass. The database on known predators puts identifications into a wider context of existing knowledge and will enhance confidence in identification or, in the case that the current predator was not earlier known as predator of the fish in question, form a check on the identification and add to the dissemination of new knowledge.

Philippart C.J.M. & G.C. Cadée (2000) Was total primary production in the western Wadden Sea stimulated by nitrogen loading? Helgol. Mar. Res. 54: 55-62.

Borum and Sand-Jensen (1996) described empirical relationships between nitrogen loadings from land and total (benthic plus pelagic) primary production rates in shallow coastal marine waters. We applied these relationships to nitrogen loadings of the western Wadden Sea system, and compared the production estimates with actually observed primary production rates of autotrophic components (phytoplankton, microphytobenthos, macroalgae and seagrasses) for those years for which field data were available. During the 1980s and early 1990s, primary production values appear in good agreement with those derived from the empirical relationships. During the 1960s and early 1970s, however, these relationships substantially overestimated the total primary production in the western Wadden Sea. Based on ambient nutrient concentrations and the Redfield ratio, production in that period was considered not to be limited by N but by P during most of the time. It is concluded that primary production is not invariably stimulated by nitrogen loading from land. If other factors (i.e. additional nutrient sources, N:P ratio's, internal nutrient dynamics and co-limiting effects of nutrients and light) are not taken into account, management regulations that target at diminishing the effects of eutrophication hold the risk of seriously under- or overestimating nutrient reductions that are thought necessary to obtain their goals.

Philippart C.J.M., G.C. Cadée, W. van Raaphorst & R. Riegman (2000) Long-term phytoplankton-nutrient interactions in a shallow coastal sea: algal community structure, nutrient budgets and denitrification potential. Limnol. Oceanogr. 45: 131-144.

In the eutrophic Marsdiep, the westernmost tidal inlet of the Wadden Sea, phytoplankton biomass and production almost doubled at the end of the 1970s and remained high ever since. Principal component analysis of 20-year (1974-1994) high-resolution time series of the 32 most numerous marine algal species revealed that the phytoplankton community changed drastically both between 1976 and 1978 and again between 1987 and 1988, and that it was relatively stable in-between (1974-1976, 1978-1987) and hereafter (1988-1994). These major changes in phytoplankton biomass and species composition coincided with changes in absolute and relative (TN:TP) nutrient concentrations. During the summer of 1977, the Marsdiep shifted from a rich, but phosphorus-controlled system to an even more eutrophic but nitrogen-controlled environment. The system re-shifted towards P-control between 1987 and 1988. The coincidence of the shifts in relative nutrient concentrations and phytoplankton species composition implies a strong causal relationship between TN:TP ratio's and phytoplankton community structure. Amongst diatoms, the observed increase in phytoplankton biomass under eutrophic N-controlled conditions was particularly due to an increase of the abundance of larger algae. Our results indicate that the N-budget of the area is correlated with the community structure, suggesting enhanced loss of nitrogen to the sediment through increased deposition of larger algal cells.

Philippart C.J.M., P.A. Henderson, T. Johannessen, A.D. Rijnsdorp & S.I. Rogers (1998) Latitudinal variation in fish recruits in Northwest Europe. J. Sea Res 39: 69-77.

In many fish species, ambient temperature is known to govern larval duration and, therefore, interannual variation in temperature can act to induce variation in recruit numbers. In general, interannual variation in water temperature increases with latitude. It may be expected, therefore, that variation in fish recruit numbers will increase with latitude along the coastlines of Northwest Europe. Variation in stock and subsequently in egg numbers is also believed to increase from the geographical centre of the species range of distribution towards the borders. It has been hypothesised that the combination of these two sources of variation will yield low variation in recruit numbers near the geographical centre, high variation at the northern edge and intermediate variation near the southern edge of the distribution range.

We tested the predicted patterns in recruit variation by examining the relationships between latitude, temperature and the variation in recruit numbers in 4 flatfish (dab, flounder, plaice and sole) and 4 roundfish species (cod, bib, poor cod, whiting) time series. Data on interannual variation in recruit numbers were obtained for sampling sites ranging from Hinkley Point and the English Channel in south England to the continental coast of the southern North Sea, the Marsdiep tidal inlet, and the Skagerrak in the north. The data were analysed for (1) correlations between interannual variation and latitude, (2) interannual variation in recruits in relation to distance of the sampling site from the geographical centre of the species' distribution, and (3) variation in interannual recruit numbers in response to the combination of these two sources of variation.

The patterns of variation observed did not correspond with the expectations. The sign of the correlation between recruit variation in plaice and dab and latitude and temperature was opposite to the prediction. All species examined showed no significant variation in recruit numbers in relation to the variables considered. We accept nor reject the hypothesis, however, because the expected relationships between CVR and latitude may have been overruled by other sources of variation such as sampling methods, average age of the catch, inshore-offshore gradients and possibly northward shifts of species' ranges.

Philippart C.J.M. & C.J.N.Winter (2000) Long-term variations within the western Wadden Sea ecosystem as derived from a sediment core. Internal NIOZ report.

The main objective of the DYNAMO project is to improve our understanding of the natural dynamics of marine ecosystems by collecting, creating and analysing long-term datasets on environmental and ecological parameters. In particular changes in the stocks of marine species of commercial interest, and the relationship of these changes with changes in climate, physical conditions, nutrient cycles and primary production will be studied. Although many time series exist and were analysed during this project, a problem is that only a few of these series extend beyond two to three decades. This time span is too short to determine long-term variations of the marine ecosystem. Unravelling of the sedimentary record of faunal remnants may offer the possibility to create longer data series on the occurrence of different species. Hereto, the sediment cores have to be sampled at sites with high sedimentation rates of material (> 1 cm y^{-1}) in combination with only modest bioturbation phenomena.

The Vlieter channel, situated in the western part of the Dutch Wadden Sea, used to be one of the main drainage channels of the former Zuiderzee, a subtidal embayment nowadays called Lake Ijsselmeer. The Zuiderzee was closed by the completion of the 'Afsluitdijk' barrier dam on May 28, 1932. The building of this dam resulted in the abandonment of the Vlieter channel. An abrupt change from an active channel into a hydraulically quiet area occurred, and current velocities dropped. As a result the rates and patterns of sedimentation in the area changed; a steady infill with fine-grained sediment came on top of coarser grained sand deposition in the active channel (Midderham & De Boer 1983; Berger *et al.* 1987). Nowadays the infill of the channel is completed and the Vlieter acts as part of the surrounding tidal flats.

In this report, we present 60-year (1932-1997) time series of different animal species (a.o. mudsnails, bivalves, ostracods) as derived from a sediment core taken at the former Vlieter channel. First, we discuss the results of the different dating techniques applied to this sediment core. Second, we present the trends and variations in the sediment-based indices of abundance of different species of which remnants occurred in sufficient numbers. Third, we compare those indirectly determined time series with available directly determined faunal densities in close surroundings of the sampling area for the last few decades. Fourth, we discuss which faunal abundances in the sediment core may be considered as indices of the abundance of that particular species for the entire study period, i.e. from 1932 to 1997.

Piet G.J., J. Craeymeersch, J. Buijs & A.D. Rijnsdorp (submitted) Changes in the benthic invertebrate assemblage in the south-eastern North Sea following the establishment of a protected area (plaice box).

The ecosystem in the south-eastern North Sea is affected considerably by various sources of both natural and anthropogenic origin. The effect of a reduced beamtrawling effort on the benthic invertebrate assemblage could be studied from changes in the assemblage following the establishment of a protected area, the "plaice box". This area was established in 1989 and closed for all vessels with an engine power over 300 Hp, which constitutes the main part of the beamtrawling fleet. At first it was only effective part of the year but since 1995 the box was closed during the whole year. In order to be able to distinguish between this effect and that of potentially confounding influences from natural origin, two relevant environmental variables, seawater bottom temperature and depth, were incorporated in the analyses.

Multivariate analysis revealed not only a significant effect of bottom seawater temperature and depth but also a significant effect of the closure of the box. Remarkable was that the partial closing of the box caused an increase in abundance of several species followed by a decline when the box was closed year-round. A possible explanation is that the most abundant species were scavengers and predators for which the deleterious effect of additional mortality was overruled by a decreased competition for food and risk of predation.

Piet G.J. & A.D. Rijnsdorp (1998) Changes in the demersal fish assemblage in the south-eastern North Sea following the establishment of a protected area (plaice box). ICES J. Mar. Sci. 55: 420-429.

This paper studies the effect of the reduction in the trawling effort of large beam trawlers (> 300 hp) in the coastal waters of the south-eastern North Sea following the establishment in 1989 of a protected area, the "plaice box", using data from annual beam trawl surveys carried out since 1985. Two different aspects of the demersal fish assemblage were analysed: 1) the size distribution using multiple analysis of variance and 2) the species composition using multivariate techniques such as principal component analysis, multidimensional scaling and multiple analysis of variance.

It is shown that the overall size structure of the commercially exploited fish species was affected by the change in trawling effort whereas that of the non-target species was not. Particularly the abundance of commercial fish within the marketable size-range of 25-40 cm increased when fishing effort was reduced.

Multiple analysis of variance showed that in contrast to the size structure of the fish assemblage, the species composition was not significantly affected by the change in fishing effort. However, principal component analysis does indicate that a considerable proportion of the variation in the abundance of the large fish (Δ 25 cm) over the years can be explained by a higher abundance in the box area than in the reference area, of most fish species, including the two main commercial species plaice and sole, after the closure of the "plaice box". Other trends that were observed during the study period both within and outside the closed area: 1) a decrease of the relative abundance of plaice and 2) a general increase of species richness due to the influx of southerly species.

Van Dongen B.E., W.I.C. Rijpstra, C.J.M. Philippart, J.W. de Leeuw & J.S. Sinninghe Damsté (2000) Biomarkers in the upper Holocene Eastern North Sea and Wadden Sea sediments. Org. Geochem. 31:1533-1543.

Total extracts of sediment cores from fice different stations in the North Sea and wadden Sea were analysed for their biomarker composition. Only sediments of the Skagerrak contained significant amounts of marine biomarkers (mainly alkones), other sites contained predominatly terrestrial markers. Bioturbation in the Skagerrak is, however, far too high to determine sea surface temperature (SST) within short time intervals. Thes e results indicate that biomarkers contained in these sediments are not useful to recontruct climatic fluctuations during the upper Holocene. High amounts of a-, b- and w-hydroxy fatty acids as well as small amounts of a, b- dihydroxy fatty acids were released from the insoluble organic material of the Wadden Sea station, indicating a significant input of the eelgrass *Zostera marina*. This was confirmed by microscopic observations. This is the first time that the of a, b- dihydroxy fatty acids are found in a sediment core and they have proven to be potential biomarkers for this seagrass species.

Zorita E. & A.O. Laine (in press) Dependence of salinity and oxygen concentrations in the Baltic Sea on the large-scale atmospheric circulation. Clim. Res.

The relationship between the low-frequency (annually averaged) salinity and oxygen concentrations in the last 30 years in the Baltic Sea and the large-scale atmospheric circulation has been statistically analyzed. It has been found that at these time scales the evolution of salinity and oxygen is quite homogeneous in depth, i.e. deviations from the long-term mean tend to be of the same sign in the upper and deeper layers simultaneously. Moreover, the evolution of the salinity and oxygen concentrations are negatively correlated within each layer: lower than normal salinities tend to be observed simultaneously with higher than normal oxygen concentrations, and vice versa.

The statistical analysis seems to indicate that the forcing by the atmospheric circulation may be responsible for this anticorrelation between salinity and oxygen. Stronger meridional sea-level-pressure gradient over the North Atlantic, and therefore stronger westerly winds, cause positive rainfall anomalies in the Baltic Sea catchment area and incr ease run-off giving rise to decreased salinities at all depths. The mechanisms by which a stronger zonal atmospheric circulation enhances the oxygen concentrations may be related either to a weakened stratification through the reduced salinity (at long time scales), or by stronger or more frequent inflows of North Sea waters (at short time scales). The influence of the atmospheric circulation may explain at these time scales of the order of 60% and 40% of the variability of these hydrographic variables, respectively.

The question has also been addressed of how salinity and oxygen in the Baltic Sea may respond to changes of the atmospheric circulation in a global climate change scenario. For these purpose the intensities of the relevant atmospheric circulation patterns in a transient experiment with a coupled atmosphere-ocean General Circulation Model forced with increasing anthropogenic greenhouse gases concentrations between the years 1860 and 2099 have been estimated. In this integration the change of the atmospheric circulation most relevant for salinity and oxygen in the Baltic Sea seems to be an enhancement of the meridional sea-level-pressure (SLP) gradient in the North Atlantic. Thus, under the assumption that the statistical relationship between SLP and the hydrographic variables also holds in the future, this trend in the atmospheric circulation would lead to decreased salinity and improved oxygen conditions in the Baltic Sea.

Zuur, A.F. (1999) Dimension reduction techniques in community ecology with applications to spatio-temporal marine ecological data. PhD Thesis, University of Aberdeen, UK. 299 pp.

The aim of the PhD-thesis is to develop techniques, which can be used to analyse spatial-temporal ecological datasets. Central questions are (1) What are the relationships between species abundances and spatial environmental variables in a particular year? What are the relationships between species? (2) How do these species-environmental relations and species interactions change from year-to-year? What is the effect of global environmental variables on these year-to-year variations? Based on these questions, the thesis is divided into two parts.

In Part I, we concentrate on the first question. We discuss the state-of-the-art technique canonical correspondence analysis (CCA). Using assumptions, which are unlikely to hold in practice, Ter Braak (1986) showed that CCA estimates certain parameters of the 'restricted Gaussian response (RGR) model'. This model describes species abundances as a unimodal, symmetric function along a gradient. The key feature in CCA and RGR is that the gradient is a linear combination of environmental variables. Using numerical optimisation routines, we show that the parameters of the RGR model can be easily estimated. This has considerable advantages over CCA, because all parameters are estimated in a regression context, without making doubtful assumptions.

RGR is applied on various datasets. A model validation indicates that for some species the model is inappropriate. For this reason, we develop a smoothing model in which the covariate is a linear combination of environmental variables. It is called restricted generalised additive modelling (RGAM). The motivation for the dimension reduction is that it reduces the number of parameters and smoothing functions to be estimated and interpreted. Both RGR and RGAM are extended to analyse species interactions as well. This is done in the context of generalised estimation equations.

In Part II, we concentrate on the second question. We develop a new technique, called dynamic generalised additive modelling. For each species a smoothing function and a stochastic trend are estimated. The smoothing function describes species-environmental relations. The stochastic trend represents deviations over time -from these species-environmental relations.

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CONTENTS

Names and addresses of participants