

Investigating environmental changes
in the southern North Sea:
a combined statistical assessment of
climatic and biogeochemical
long-term time series

Dissertation
zur Erlangung des Doktorgrades
der Naturwissenschaften im Fachbereich
Geowissenschaften
der Universität Hamburg

vorgelegt von

Merja Helena Schlüter

aus
Oulu/Finnland

Hamburg
2010

Als Dissertation angenommen vom Department Geowissenschaften der
Universität Hamburg

auf Grund der Gutachten von Prof. Dr. Hans von Storch
und Prof. Dr. Agostino Merico

Hamburg, den 8. Juni 2010

Prof. Dr. Jürgen Okenbrügge
(Leiter des Department Geowissenschaften)

To

my family

Abstract

The work presented in this thesis untangles the effects of changes in various physical and biogeochemical variables on the ecosystem of the southern North Sea with an emphasis on long-term variability. It is still a matter of debate how climate variations may affect the functioning of the ecosystem. Therefore, this study provided for the first time a detailed understanding of climate variability of the southeastern region of the North Sea, the German Bight, during the period 1975–2004, by combining a wide set of physical, biological and chemical data.

The first part of this work used Principal Component Analysis to examine the bulk variability of a diverse array of physical and biogeochemical long-term time series in order to understand the main mode of variability of the climate and the ecosystem of the coastal region. The outcomes motivated further investigations on the dynamic of the first trophic levels of the ecosystem. Therefore, in the second part of this work, the factors that drove the long-term seasonal variability of three most representative species of the diatom community (*Guinardia delicatula*, *Thalassionema nitzschioides* and *Odontella aurita*) were determined with multivariate linear regression analysis. Finally, in the third part, the results on the seasonal variability of the three phytoplankton species were put into the wider context of the German Bight ecosystem by studying the phenology of some important primary and secondary consumers. Hence, the long-term abundance dynamics of *Beroe gracilis*, *Pleurobrachia pileus* and their food calanoid copepods were analysed using Bayesian statistics.

Taken together, the results of this work revealed a more coherent picture of how and on what time scales biology responds to physical changes and the inherent consequences for the ecosystem. It was documented for the first time that the climate and the ecology of the German Bight experienced patterns of variability similar to the ones of the entire North Sea. The German Bight, however, is exposed to different natural and anthropogenic perturbations when compared to the whole of the North Sea, detailed investigations on some key organisms

have thus revealed the differential impacts of major driving factors on different species.

Although temperature variation was the major driver of changes in the abundance and seasonality of primary and secondary consumers (top down effect), evidence was provided suggesting the importance of bottom up processes. This work highlights the complex responses of a coastal ecosystem to climate change and the high nonlinearities in the atmosphere–ocean–biosphere system.

Acknowledgments

I am greatly indebted to Prof. Dr. Hans von Storch for giving me the opportunity to conduct this very interesting research and write this thesis at the GKSS Institute for Coastal Research in Geesthacht and for the appraisal of this work.

My gratitude is expressed to Prof. Dr. Agostino Merico for his advice and whose suggestions became part of this thesis.

Furthermore, I thank Prof. Dr. Inga Hense for examining this dissertation.

Special thanks to Dr. Eduardo Zorita to whom I was always welcome to discuss any scientific issues and who helped me with any scientific or technical request.

I thank Dr. Marcel Reginatto for his advice in Bayesian modelling.

Dr. Wulf Greve was helping me with his zooplankton data set and provided useful information about the “Wulf Greve collection of Helgoland Roads zooplankton.”

Prof. Dr. Karen H. Wiltshire allowed me to use material from the phytoplankton, nutrient and physical data at BSH.

Many thanks to several colleagues for their help and encouragement during my work at GKSS and for the great working environment at KOE.

The German Weather Service (DWD), the Bundesamt für Seeschifffahrt und Hydrographie (BSH), the International Council for the Exploration of the Sea (ICES) and the Biologische

Anstalt Helgoland (BAH) are appreciated for providing the data for this research.

Last but not least I am grateful for my family and parents supporting my decision morally and for my affiliate Dr. Jörn Tölle who supported me in any circumstance.

Contents

| | |
|---|------------|
| Acknowledgements | iii |
| List of Contents | v |
| List of Figures | x |
| List of Tables | xi |
| 1 Introduction | 1 |
| 1.1 Climate variability | 1 |
| 1.2 Regime shifts and their relation to climate variability | 3 |
| 1.2.1 Regime shifts in the North Pacific | 4 |
| 1.2.2 Regime shifts in the North Sea | 4 |
| 1.3 Impact of climate variability on the marine ecosystem | 5 |
| 1.3.1 Examples of changes in fish in the North Sea | 6 |
| 1.3.2 Examples of changes in phytoplankton in the NE Atlantic and North Sea | 6 |
| 1.3.3 Examples of changes in zooplankton in the NE Atlantic and North Sea . | 7 |
| 1.4 Requirements for climate models | 7 |
| 1.5 The German Bight | 8 |
| 1.6 Objective of the thesis | 8 |
| 1.7 Outline of the thesis | 11 |
| 2 Study area and data | 13 |
| 2.1 The German Bight | 13 |
| 2.2 Long-term time series | 13 |

| | | |
|----------|---|-----------|
| 3 | Climate variability and ecosystem response in the German Bight | 21 |
| 3.1 | Introduction | 21 |
| 3.2 | Methods | 23 |
| 3.3 | Results | 25 |
| 3.4 | Discussion | 33 |
| 3.5 | Summary | 37 |
| 4 | Seasonal long-term changes of three diatoms | 39 |
| 4.1 | Introduction | 39 |
| 4.2 | Methods | 41 |
| 4.2.1 | Data sets | 41 |
| 4.2.2 | Statistical analysis | 42 |
| 4.3 | Results | 44 |
| 4.4 | Discussion | 48 |
| 5 | Phenological shifts of three interacting zooplankton groups | 53 |
| 5.1 | Introduction | 53 |
| 5.2 | Methods | 56 |
| 5.2.1 | Data | 56 |
| 5.2.2 | Bayesian Approach | 58 |
| 5.2.3 | Model specification and comparison | 59 |
| 5.2.4 | Model selection | 61 |
| 5.2.5 | Correlation between forcing and SOGP | 62 |
| 5.2.6 | Testing predator–prey relationship hypotheses | 63 |
| 5.3 | Results | 63 |
| 5.3.1 | Model selection | 63 |
| 5.3.2 | Change point analysis | 66 |
| 5.3.3 | Correlation analysis | 70 |
| 5.3.4 | Changes in seasonal occurrence | 70 |
| 5.3.5 | Predator–prey relationships | 72 |
| 5.4 | Discussion and conclusions | 73 |
| 6 | Concluding remarks | 77 |
| A | Appendix | 83 |
| B | Abbreviations | 97 |

List of Figures

| | | |
|-----|--|----|
| 1.1 | Sea surface temperature at Helgoland Roads | 9 |
| 2.1 | Map of the German Bight | 14 |
| 3.1 | Scree plot of the first 10 eigenvalues | 26 |
| 3.2 | The first principal component (PC1) | 27 |
| 3.3 | Spectrum of loadings for the first principal component | 28 |
| 3.4 | Results from the regime shift analysis | 29 |
| 3.5 | The first principal component (PC1) of the separated data | 30 |
| 3.6 | Scatter plot of PC1s of biogeochemical against hydrophysical data | 31 |
| 3.7 | Time series of summer and winter SST for the period 1975–2004 | 32 |
| 4.1 | Biological temporal indices | 43 |
| 4.2 | Time series of the three diatoms from 1962–2008 | 45 |
| 4.3 | Annual mean abundances of the three diatoms | 46 |
| 4.4 | Categories of early, middle and late start of the bloom season | 47 |
| 5.1 | Diagram of two pathways of energy flow in an ecosystem | 55 |
| 5.2 | Weekly mean zooplankton abundances | 56 |
| 5.3 | Relations among the zooplankton organisms | 57 |
| 5.4 | Zooplankton SOGPs and SST together with the model evolution | 65 |
| 5.5 | PDFs for a change point of zooplankton SOGPs and SST | 67 |
| 5.6 | Change rate of winter SST versus zooplankton SOGP | 71 |
| 5.7 | Two seasonal mean abundances of <i>P. pileus</i> , <i>B. gracilis</i> and copepods | 72 |
| 5.8 | PDF of predator–prey relationships | 73 |

| | | |
|-----|---|----|
| A.1 | Time series of nutrients at Helgoland Roads | 87 |
| A.2 | Time series of diatoms at Helgoland Roads | 88 |
| A.3 | Time series of annual mean of zooplankton | 89 |
| A.4 | Time series of fish | 90 |
| A.5 | Time series of atmospheric indices | 91 |
| A.6 | Time series of GSI and NAOWI | 92 |
| A.7 | Time series of the annual mean of 9 atmospheric variables | 93 |
| A.8 | Time series of winter mean and annual mean SST of the German Bight | 94 |
| A.9 | Time series of salinity, SST and Secchi disk depth at Helgoland Roads | 95 |

List of Tables

| | | |
|-----|--|----|
| 2.1 | Variable description | 15 |
| 2.2 | Continued | 16 |
| 4.1 | Predictors for the end of the growth period of the three diatoms | 48 |
| 5.1 | Ranking of different models for SOGP using DIC | 64 |
| 5.2 | Ranking of different models for SST using DIC | 66 |
| 5.3 | Correlation coefficients between SST and SOGP | 68 |
| 5.4 | Correlation coefficients between the change rate of SOGP and SST | 69 |

Chapter 1

Introduction

The present work was undertaken at the Institute of Coastal Research of the GKSS Research Centre, in Geesthacht, Germany, as part of the topic "Coastal Change" in the Helmholtz research programme PACES (Programme Marine, Coastal and Polar Systems) – a series of interdisciplinary studies dealing with physical and biogeochemical processes in the coastal marine system. The aim of this work was to better understand the functioning of the marine ecosystem in the coastal area of the southeastern North Sea in a changing climate by focusing on the long-term variability of some key marine organisms and the environmental conditions in the region.

Marine ecosystems are sensitive to a variety of forcing factors. Of these factors, physical controls, such as thermal stratification, solar energy or temperature, and biological controls, such as predator–prey interactions (*Reynolds, 2006; Beninca et al., 2008*), are often the most prevalent. In addition, in many marine regions and particularly in coastal areas, the exploitation of the resources by humans constitute an important element of disturbance (*Lozan et al., 1994*).

1.1 Climate variability

Long-term changes in marine ecosystems are often assumed to be related to climate variations (*Cushing, 1988; Aebischer et al., 1990; Southward et al., 1995; Alheit and Hagen, 1997*). Although various other aspects can potentially explain the observed changes in the ecosystems (for example aspects related to physiological and ecological processes, e.g. autonomous changes in behaviour, changes in life-history traits, changes in nutrient stoichiometry or changes in population dynamics), the climate hypothesis is often the most obvious and most invoked one. Because it assumes that marine organisms respond to changes in the environment they live in, and because this response is to some extent proportional to the environmental change. It is also the most popular assumption because it can be easily tested, and it holds the hope for a better understanding of the biological variations in the system under

investigation, once the relationships with the environment have been identified and quantified.

A well-known example of a dominant mode of natural variability in western Europe is the North Atlantic Oscillation (NAO). The NAO consists of a long-term variation in the mean atmospheric pressure distribution over the North Atlantic in winter. It causes an alternation between periods of several years in which the winters in western Europe are generally mild, and periods in which winters tend to be cold. The NAO does not have a rigid periodicity, but oscillations tend to occur on a time scale of about 10 years (*Hurrell and Van Loon, 1997*). The NAO bears some resemblance to the El Niño Southern Oscillation (ENSO) in the Pacific. This is a shorter, more pronounced climate variation, which occurs on a time scale of 3–7 years (*Mann and Park, 1996*).

Long-term variations in atmospheric circulation and therefore air temperature will eventually have an impact on the sea. The relationship between atmospheric changes and hydrographic changes can be at times very direct, but often also rather complicated. An example of a direct relationship is the effect of atmospheric changes on water temperature in the North Sea during winter. When the NAO is in a positive phase, the increased westerly circulation will result in an increase in average air temperature during winter. This relatively high air temperature will reduce the winter cooling of the surface water. The increased cloud cover that accompanies this type of weather will further prevent heat loss through radiation. In addition to this direct effect, the NAO might influence the North Sea indirectly through changes in the circulation of the North Atlantic. These changes might start in remote parts of the North Atlantic (for example in the Gulf of Mexico or in the Labrador Sea) and influence the North Sea climate system after a time lag of several years.

In addition to natural variability, the climate is also affected by a strong anthropogenically-driven component generally expressed as global warming due to the accumulation of greenhouse gases in the atmosphere. The likely consequences of this climate change have been the subject of intensive studies, but much uncertainty still remains as to the ultimate effects on ecosystems. The main consequences expected on a global level during the present century are: 1) an increase in partial pressure of CO₂ from 380 μatm to 750 μatm , 2) and increase in mean temperature from 2° to 4.5°C, 3) a rise in mean sea level by 0.2 to 0.6 m, and 4) an increase in precipitations at high latitudes (*IPCC, 2007*). The increased fresh water input in the sub-polar areas (resulting from higher precipitation and melting of polar ice) may affect the thermohaline circulation (THC), and thereby the currents in the whole of the North

Atlantic.

While much uncertainty exists as to the effects of climate change at a global level, the effects on relatively small areas such as western Europe are even less quantifiable for example due to uncertainties in aerosol and radiative forcing (*IPCC*, 2007). In the last several decades a coastal region of the southern North Sea, the German Bight, exhibited an average temperature increase of about 1.2°C (*Wiltshire and Dürselen*, 2004). A rise of water temperature by 1°C is small in comparison to the variations of about 2°C caused by the NAO during pre-industrial times in the past. One can, therefore, expect that the changes in the biology of the region, resulting from such a temperature rise, would be smaller than those caused by natural variations.

However, even though the magnitude of the anthropogenic climate change may seem lower compared with the one of natural variability, the rate of today's changes are very rapid compared with previous natural changes. Consequently, the climate we may experience in the near future can be quite different than the one of the past if changes in NAO are amplified by the accumulation of greenhouse gases (*Gillett et al.*, 2003). Some model simulations indicate that rising greenhouse gas concentrations could lead to a change in the spatial patterns of the NAO, and to an increased storm activity over the eastern Atlantic and western Europe (*Ulbrich and Christoph*, 1999). If these climate changes in western Europe are confirmed, the increase in average water temperature of the North Sea in winter will be greater than the 1°C mentioned above. Extreme weather conditions could then become the rule instead of the exception (*IPCC*, 2007).

1.2 Regime shifts and their relation to climate variability

A regime shift is a feature of natural climate variability and can be due to a combination of local atmospheric and oceanic variability with forcing from more distant geographic areas (teleconnections). The processes causing a regime shift and the relationship between different regimes and anthropogenic climate change are not well understood. They are characterised by sudden and substantial changes in the state of an ecosystem and in the physical system, often with implications for resources vital to humans.

1.2.1 Regime shifts in the North Pacific

Investigations into the effects of climate change in the North Pacific have focussed strongly on regime shifts. The physical characteristics of these regime shifts and the biological consequences differ among five major regions of the North Pacific. One of the indices of ocean climate state for the North Pacific is the Pacific Decadal Oscillation (PDO) (*Mantua et al.*, 1997), which tracks the dominant spatial pattern of SST in the region. The alternate phases of the PDO represent cooling/warming in the central subarctic Pacific and warming/cooling along the North American continental shelf. This pattern represents changes along an east–west axis, but since 1989 a north–south pattern has also emerged. Other commonly used indices track the intensity of the winter Aleutian low pressure system and the sea level pressure over the Arctic (*Trenberth and Hurrell*, 1994). North Pacific regime shifts are reported to have occurred in 1925, 1947, 1977, 1989 and 1998 (*Mantua et al.*, 1997; *Hare and Mantua*, 2000; *Peterson and Schwing*, 2003) and palaeoecological records show many earlier ones (*Biondi et al.*, 2001). The duration of these regimes appears to have shortened from 50–70 years to around ten years, in particular for the two most recent (*Mann and Park*, 1996). Whether this apparent shortening in regime durations is real and how these are related to other aspects of climate change is a matter of current debate and concern. The El Niño - La Niña Southern Oscillation Index (SOI) also has a large impact on the North Pacific, adding an episodic overlay with a duration of one or two years to the decadal-scale regime behaviour. Impacts of regime shifts with their effects on pelagic fish species and the chlorophyll front located at the boundary between the low chlorophyll subtropical gyres and the high chlorophyll subarctic gyres on the five major regions of the North Pacific are well documented (*Mantua et al.*, 1997; *Hare and Mantua*, 2000; *Chavez et al.*, 2003).

1.2.2 Regime shifts in the North Sea

There are examples of ecological changes within the greater North Sea region which are in general agreement with a major shift in the late 1980s involving relatively abrupt changes in SST, in wind fields and in a number of biological indicators (*Reid and Borges*, 2001; *Beaugrand and Ibanez*, 2004). *Siegismund and Schrum* (2001) found an increase in wind speed and change in direction especially in February and March since the mid-1980s. The changed physical parameters can be related to a persistent change in the NAO (*Schrum*, 2001). Studies over the last forty years using General Circulation Models (GCM) concluded that the NAO is likely to remain high in response to enhanced greenhouse gases (*Gillett et al.*, 2003). The intensification of westerly winds brings with it an increased inflow of warm, high salinity North

Atlantic water into the northern North Sea. Cod recruitment, for example, appears negatively correlated with the increased temperature. *Beaugrand* (2004) and *Edwards and Richardson* (2004) proposed that a regime shift covering the period 1982–1988 in the North Sea may be connected to changes in large-scale hydrometeorological forcing. *Beaugrand et al.* (2002a) singled out large biogeographical shifts in all copepod assemblages in the eastern North Atlantic Ocean and European shelf seas in the early 1980s. *Reid and Borges* (2001) reported of an ecological regime shift in the North Sea around 1988 based on a compilation of plankton data derived from the Continuous Plankton Recorder (CPR) and fish catchment data. Such regime shift was clearly detected in the northern and central North Sea but not in the southern North Sea (*Beaugrand and Ibanez*, 2004). A critical question concerning also the management of coastal food resources is whether the ongoing anthropogenically induced changes in climate make it more or less likely that the present regime will eventually revert to its previous state, change to some other state, or remain in its current state.

1.3 Impact of climate variability on the marine ecosystem

There are many examples of changes in marine ecosystems throughout the world which are driven by shifts in climate (*Cushing*, 1995; *Beare et al.*, 2002; *Beaugrand et al.*, 2002a). Climate-associated impacts on species composition, seasonality and production of marine and freshwater organisms are accumulating (*Reid and Borges*, 2001; *Beaugrand and Ibanez*, 2004). Some examples from the large number of recent works analysing climate effects on a variety of taxa includes papers dealing with: phytoplankton (*Richardson and Schoeman*, 2004), global primary production (*Schmittner*, 2005), krill in the Southern Ocean (*Atkinson et al.*, 2004), plankton in the North Atlantic (*Edwards and Richardson*, 2004; *Richardson and Schoeman*, 2004), and fish species in North European shelf seas (*Perry et al.*, 2005). There are very few detailed studies of responses at individual level, however. Rising temperature may cause seasonal increases in growth of species, but may also have an impact on organisms living in areas where the magnitude of the temperature changes are close to their thermal tolerance (*Morgan et al.*, 2001). Changes in temperature sum up with other relevant changes, including increasing higher CO₂ levels, declining pH and increasing nitrogen and ammonia, to increase metabolic costs. The consequences of these interactions are very complex.

Survival of fish larvae during the planktonic stage is thought to depend strongly on the availability of sufficient quantities of suitable food. Since the production of plankton of a suitable size range and quality is seasonal and patchy, the match between larvae and

their food is by no means guaranteed. This “match/mismatch” mechanism (*Cushing*, 1990) remains the principal hypothesis used to explain variability in survival and consequent recruitment to fishable stocks. Climate induced changes in distribution and phenology of fish larvae, zooplankton and phytoplankton, could affect recruitment and production of fish stocks.

1.3.1 Examples of changes in fish in the North Sea

The stock of North Sea fish is subject to fishery-induced changes, to changes caused by variations in the environment and to predator–prey interactions. Fishing could affect the size composition of the exploited fish assemblage (*Rice and Gislason*, 1996). The entire North Sea was fished by 1900 (*Cushing*, 1988) and fishing efforts have increased consistently since that time. There were changes in the size and species composition of the North Sea fish community in the twentieth century with decreases in the abundance of primary target species such as cod (*Jennings et al.*, 2002). Gross changes in community structure are primarily due to the differential effects of fishing on species with contrasting life histories, although climate change has undoubtedly affected some species (*O’Brien et al.*, 2000). *Dippner* (1997b) put forward the possibility of recruitment failure in North Sea cod, North Sea whiting, and western mackerel in association with a warming climate. It was found by *Perry et al.* (2005) that the distributions of both exploited and non–exploited North Sea fishes have responded markedly to recent increases in sea temperature with northward shifts. Climate variations might influence distribution and abundance of fishes through changes in growth, survival, and reproduction, or through responses to changes at other trophic levels (*Beaugrand et al.*, 2002a, 2003).

1.3.2 Examples of changes in phytoplankton in the NE Atlantic and North Sea

A study based on over 100,000 plankton samples collected between 1958 and 2002 with the Continuous Plankton Recorder (CPR) (*Richardson and Schoeman*, 2004) showed an increase in phytoplankton abundance in the cool regions of the NE Atlantic (north of 55°N) and a decrease in warmer regions (south of 50°N). The likely explanation for this apparently contradictory result is that although both areas have undergone warming over this period, with a consequent reduction in vertical mixing, the nutrient supply in the cooler, more turbulent regions remains sufficient and plankton metabolic rates benefit from the increased

temperature.

Another study based on the CPR data attributed the observed decadal variability in phytoplankton biomass of the NE Atlantic to hydroclimatic forcing, as expressed by the NAO (*Edwards et al.*, 2001). In the North Sea this resulted in a shift in the seasonal timing of the peak in phytoplankton density from April to June which may have been accompanied by a taxonomic shift from diatoms to dinoflagellates, with consequent changes in the species composition of the grazing community.

1.3.3 Examples of changes in zooplankton in the NE Atlantic and North Sea

Calanus finmarchicus has declined throughout most of the North Atlantic since 1958 due to warming and due to changes of cold, deep water masses in which the species overwinters (*Beaugrand et al.*, 2002a). In the North Sea it has been largely replaced by a southern congener, *Calanus helgolandicus* (*Beare et al.*, 2002), but there have also been substantial changes in phenology, which affect trophic interactions, foodweb structure and ecosystem function (*Edwards and Richardson*, 2004).

1.4 Requirements for climate models

Changes in primary and secondary production will obviously have a major effect on fishery production, but it is not possible with the current state of knowledge to make quantitative predictions concerning the changes in the global marine primary production caused by climatic shifts. A comparative study (*Sarmiento et al.*, 2004), using six different atmosphere–ocean coupled general circulation models (AOGCM), indicates that production may increase by not more than 10% by 2050, but the level of confidence in this estimate is low and the baseline for the comparison is the “pre-industrial” state. By contrast, observations from satellite and large scale plankton sampling campaigns show declines in phytoplankton and chlorophyll over the past 20–50 years, which are consistent with the expected consequences of reduced nutrient supply due to strengthening of vertical density gradients. The understanding of the actual processes involved in ecosystem function is uncertain and the regional climate, which could be causing observed changes in production and ecosystem properties, may be substantially different from larger scale, global trends.

Although global marine primary production is not expected to change substantially over the next four or five decades, there is a stronger basis for predicting changes in production at regional level and also good observational evidence, particularly for the North Pacific and North Atlantic. The particular requirements for making projections of marine production at regional level are appropriate time scale resolution, better resolution of regional impacts, appropriate downscaling of global models and inclusion of relevant variables and processes. The temperature sensitivity of primary production has also been identified as a key issue for further investigations in plankton dynamics. Understanding the cause for large-scale synchrony in regime shifts, as well as the connections from global to regional processes, is a key to improve the necessary model parameterizations of the effects climate change will have on marine ecosystems.

1.5 The German Bight

Many of the biogeochemical and abiotic variables of the German Bight and the associated consequences on various organisms and on the ecosystem have been monitored over several decades (*Colijn, 1998*). The time series show both sudden or gradual regime changes. It is, however, still under debate whether and to what extent the marine ecosystem has responded to abiotic changes in the last few decades (*Philippart et al., 2000; Reid et al., 2003*). One of the challenges scientists have to face when studying the effects of climate change is the integration of existing monitoring information into statistical models in order to pinpoint shifts or long-term trends in the system. *Radach (1998)* performed a detailed statistical analysis investigating long-term trends at an ecosystem level in the southern North Sea. He found smooth changes during the 1960s and 1970s followed by an abrupt shift in phytoplankton biomass and nutrient concentrations at the end of the 1970s and suggested that this modification of phytoplankton succession might be due to eutrophication as well as alternating hydrographic regimes, possibly triggered by the NAO.

1.6 Objective of the thesis

Present climatic trends are expected to continue and are moving outside the bounds of previous climatic states (see Figure 1.1) (*Zorita et al., 2008*). The trend will not be smooth and will continue to have large interannual and decadal variability superimposed on it. Decadal variability in ocean climate is one of the major causes of regime shifts, when the biology of

large coastal regions changes quite rapidly to a different state (altered species dominance, production and seasonality). Previous studies have hypothesised the presence of regime shifts in observations extending over the entire North Sea. It is still unclear whether, on a smaller spatial scale, and closer to the coast, such regime shifts can be confirmed and what the consequences will be for the organisms of the region.

The first part of this study will concern the examination of the bulk variability of a diverse array of physical and biogeochemical long-term time series in the German Bight in order to understand the main mode of variability of the climate and the ecosystem of this coastal region. The physical time series represent atmospheric and marine (coastal) processes (derived from indices of atmospheric and sea level pressures, SST anomalies, etc.) while the biogeochemical time series (derived from the Helgoland Roads data set and from other databases) include inorganic nutrients, and will range from phytoplankton to fish.

The aim of this part is to determine whether a regime shift similar to the one previously identified in the North Sea can be detected also in observations restricted to the German Bight. Although the term “regime shift” is widely used in the literature, there is no universal definition for it. *Lees et al.* (2006) reviewed different criteria used to define a regime shift. Typically, common characteristics like speed and amplitude of the changes and the duration of quasi-stable states are used for defining climatic and ecological regime shifts. *Lees et al.* (2006) suggested that a standard definition should meet a number of conditions (like sudden,

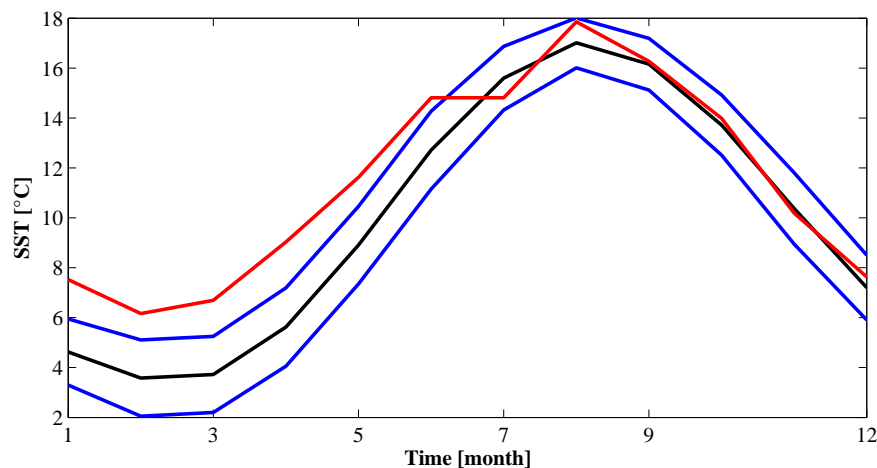


Figure 1.1: Seasonal sea surface temperature at Helgoland Roads in 2007 (red line), also showing 44-year mean (black solid line) of sea surface temperature and ± 1 standard deviation (blue line).

high-amplitude, infrequent events, number of trophic levels impacted by the shift and biophysical impacts) before a change in the data can be classified as a regime shift. Arguably, it is difficult to assess how useful these criteria are in universally characterising regime shifts.

This thesis is concerned with shifts that are not smooth or reversible within a short time period (a few years). Therefore, the following definitions are adopted:

Regime = Quasi-stationary state of a system persisting for several years and characterised by low frequency variability.

Regime Shift = Transition period between two regimes that occurs within a year or two.

Although detailed information on temperature changes are available, relatively little is known about how these changes affect the food webs of aquatic systems (*Cushing*, 1995; *Walther et al.*, 2002). The obvious next step was therefore to focus the second part of this study on the first trophic levels of the ecosystem because they are responsible for about half of the global primary production and represent the basis of the marine food web (*Rost et al.*, 2008). Thus, a good function of the whole food web depends on the first trophic levels. Three most representative species (in terms of relative abundance and annual presence) of the diatom community of the German Bight, which tend to co-occur throughout the time period under study, were investigated and the factors driving their long-term seasonal variability were determined.

Finally, a third part of this work was motivated by the need to put the results obtained by studying the variability in the three phytoplankton species into the wider context of the German Bight ecosystem. Emphasis was therefore placed on some important organisms representing trophic levels adjacent to primary producers, specifically herbivores and carnivores. Thus, the long-term abundance dynamics of two gelatinous zooplankton species, *Beroe gracilis* and *Pleurobrachia pileus*, and their main food calanoid copepods were analysed. Despite being of global relevance, only a few long-term records of gelatinous zooplankton abundance exist, and most of these records are semi-quantitative in nature. Therefore, the knowledge of the influence of environmental factors on their population development is limited. This part of the study focused on the response of the two ctenophores and their prey to climate warming. In particular, the phenological changes of these zooplankton were investigated together with the associated consequences on their predator-prey relationships.

This study is centred on the last 40 years of observation. The long-term variations on a time scale of more than 40 years are not considered. The specific objective of the present study is thus to identify the climatic factors that have driven the long-term changes in the coastal ecosystem of the southern North Sea during the last 40 years by exploring possible correlations between climatic and biogeochemical changes. To achieve this aim, a particular combination of advanced statistical methods is adopted.

1.7 Outline of the thesis

Chapter 2 introduces the geographical area of the study and the different biogeochemical and physical data sets used for the analysis.

Chapter 3 is concerned with the possibility that regime shifts have occurred in the German Bight and with the potential relations between the local changes in this region and the North Sea regime shifts observed in the 80s. The existence of common trends of variability within a group of selected physical and biogeochemical long-term time series is investigated by Principal Component Analysis (PCA), which allows to objectively isolate the most important modes of variability in the data. The PCA is a multivariate technique that identifies axes of maximum variability in a multi-dimensional space of data points. Each axis (or principal component) represents a variance that is independent of the variance measured by the other axes. The goal of the PCA is to concentrate most of the variance of a large data set into a small number of physically interpretable patterns of variability, and requires no *a priori* assumptions about specific regime years in the historical record. Variables that show similar variations over time have high weights on one or more of the principal components.

The decoupling of trophic interactions is one of the severe consequences of climate warming. Further, the timing of phytoplankton blooms affects competition within the plankton community and at higher trophic levels with consequences on the entire food web. Chapter 4 is therefore dedicated to improving the understanding of the controls of the long-term seasonal succession of three major phytoplankton species of the German Bight: the diatoms (*Guinardia delicatula*, *Thalassionema nitzschioides* and *Odontella aurita*). Both top-down and bottom-up processes are considered by analysing variables such as temperature, water transparency, nutrients and copepod data. The factors correlated with the variability in the three phytoplankton species' phenology related to the timing of events in the seasonal patterns of occurrence was explored with multivariate linear regression analysis.

This method is used to make quantitative estimates of the relationships between the variables.

The mechanism by which increasing temperatures affect the succession of the zooplankton community is considered in detail in Chapter 5. In this chapter, the changes in phenology of three interacting zooplankton groups are analysed with Bayesian statistics. With this technique, which is based on probability theory, observations are used to update the probability that a certain hypothesis describing for example the long-term trend in some observational data may be true. The approach allows one to uncover changes in time series of phenological data and to correlate these changes with potential driving factors. In addition, the analysis permits the quantitative expression of results in terms of probabilities. The study focuses on understanding the impact of climatic changes on the phenology of two gelatinous zooplankton populations and on a group of five most common crustacean zooplankton of the German Bight and aims at highlighting the associated consequences on their predator-prey interaction.

In Chapter 6 the overall results obtained with the three different statistical methods are summarized and the conclusions are presented together with an outlook.

The different variables used in this study and the details of the statistical methods adopted are described in each chapter and in Appendix A.

Chapter 2

Study area and data used in the analysis

This chapter introduces the study area and site for the analysis and the different biogeochemical and physical data sets used in this study.

2.1 The German Bight

The study area, the German Bight, (see Figure 2.1 for a map of the region) reaches from Hübnergat ($53^{\circ} 30' \text{ N}$, $6^{\circ} 30' \text{ E}$) to Sylt ($55^{\circ} 10' \text{ N}$, $9^{\circ} 10' \text{ E}$) in Germany. Several main rivers discharge into the southern North Sea, such as the river Elbe, the river Rhine, the river Weser and the river Ems. The position of the estuaries of these rivers, along with the counterclockwise residual current pattern which carries riverborne substances from west to east, favour the accumulation of eutrophying substances in the German Bight. Its coastal zone, i.e. the interface between land, ocean and atmosphere, plays a major role as a recipient of large amounts of nutrient from human activities, including effluents, agriculture runoff, and municipal sewage. In this coastal region the area around the offshore island Helgoland, about 60 km northwest of the Elbe river estuary, is a shallow (from 6 to 12 m) compared to the surrounding German Bight (depths of up to 30 m), year-round well-mixed and highly turbid ecosystem. Tidal currents and winds determine the circulation and vertical mixing.

2.2 Long-term time series

The analysis of this study included hydrophysical data sets comprising atmospheric, climate and hydrographic variables; and biogeochemical time series representing the most important levels of the ecosystem, from nutrients through phytoplankton and zooplankton to fish. The selected appropriate data sets were covering 40 years, at least 30 years, up to 100 or more samples per year and no obvious anthropogenic cause for sudden changes in a data set were detected. The variables are listed in Table 2.1 and 2.2.

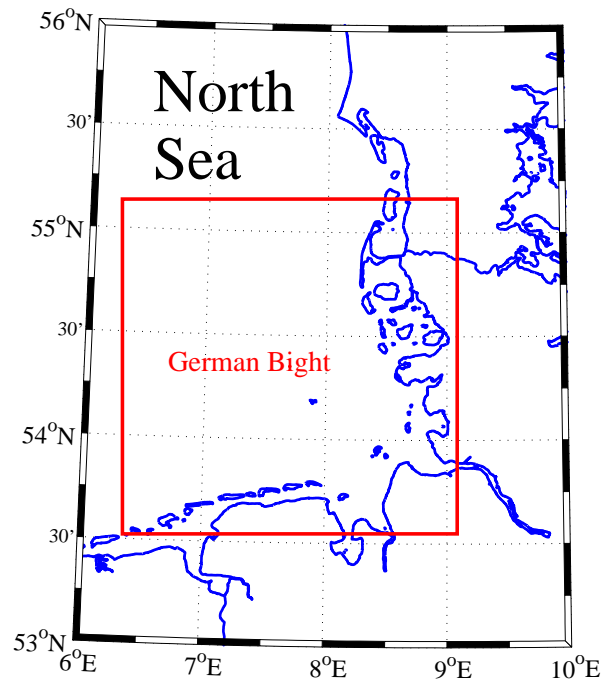


Figure 2.1: Map of the southeastern part of the North Sea and the area of the German Bight for analysis enclosed in the red box.

Changes in ecosystem variables were investigated as part of a few monitoring programmes such as the long-term time series at Helgoland Roads (HR) within the German Bight. In 1962, a long-term pelagic monitoring program observing dissolved inorganic nutrients, hydrographical parameters and plankton species composition at Helgoland Roads ($54^{\circ}11'3''$ N, $7^{\circ}54'0''$ E), a narrow channel between the offshore main island of Helgoland and a small, sandy island nearby, was initiated by the Biologische Anstalt Helgoland (BAH) (*Hickel et al.*, 1993; *Hickel*, 1998).

Table 2.1: Variable description: variable number, description, coordinates and period.

| Var.# | Description | Longitude | Latitude | Period |
|-------|--|-----------|-----------|-----------|
| 1 | NH4 at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 2 | NO2 at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 3 | NO3 at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 4 | PO4 at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 5 | SiO4 at Helgoland Roads | 7°54'E | 54°11.3'N | 1966–2008 |
| 6 | Annual mean salinity at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 7 | Mean Diatom Day of the spring bloom at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2004 |
| 8 | Annual mean of total cell counts of diatoms at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 9 | Spring mean (Mar, Apr, May) of total cell counts of diatoms at Helgoland Roads | 7°54'E | 54°11.3'N | 1962–2008 |
| 10 | Weekly mean <i>P. pileus</i> juvenile at Helgoland Roads | 7°54'E | 54°11.3'N | 1975–2005 |
| 11 | Weekly mean <i>P. pileus</i> adult at Helgoland Roads | 7°54'E | 54°11.3'N | 1975–2003 |
| 12 | Weekly mean <i>N. scintillans</i> at Helgoland Roads | 7°54'E | 54°11.3'N | 1975–2005 |
| 13 | Weekly mean <i>C. helgolandicus</i> NN at Helgoland Roads | 7°54'E | 54°11.3'N | 1975–2005 |
| 14 | Weekly mean <i>C. helgolandicus</i> CN at Helgoland Roads | 7°54'E | 54°11.3'N | 1975–2003 |
| 15 | Weekly mean of sum of 5 small calanoid copepods at Helgoland Roads | 7°54'E | 54°11.3'N | 1975–2005 |
| 16 | Spawning Stock Biomass of cod from ICES Quadrant IV | | | 1963–2006 |
| 17 | Spawning Stock Biomass of herring from ICES Quadrant IV | | | 1960–2006 |
| 18 | Spawning Stock Biomass of haddock from ICES Quadrant IV, IIIa | | | 1963–2007 |
| 19 | Spawning Stock Biomass sole from ICES Quadrant IV | | | 1957–2007 |
| 20 | Spawning Stock Biomass plaice from ICES Quadrant IV | | | 1957–2007 |
| 21 | Spawning Stock Biomass saithe from ICES Quadrant IV | | | 1967–2007 |
| 22 | North Atlantic Oscillation Winder Index (Dec, Jan, Feb) | | | 1864–2006 |

Table 2.2: Continued

| Var. # | Description | Longitude | Latitude | Period |
|--------|--|-------------------|---------------------|-----------|
| 23 | Gulf Stream Index | | | 1966–2005 |
| 24 | East Atlantic Pattern Index (Sep to Mar) | | | 1950–2005 |
| 25 | East Atlantic Jet Pattern Index (Apr to Aug) | | | 1950–2005 |
| 26 | Scandinavia Pattern Index (Aug to May) | | | 1950–2005 |
| 27 | Mean annual hor. wind speed of REMO | 6 °5'E – 9 °167'E | 53 °3'N – 55 °167'N | 1948–2006 |
| 28 | Annual mean air temperature at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 29 | Annual mean max. air temperature at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 30 | Annual mean min. air temperature at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 31 | Total annual sunshine duration at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 32 | Total annual precipitation amount at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 33 | Annual mean surface pressure at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 34 | Annual mean rel. humidity at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 35 | Total days with frost (min. temp. < 0°C) at List (Sylt) | 8 °25'E | 55 °1'N | 1965–2006 |
| 36 | Secchi disk depth at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1968–2008 |
| 37 | SST at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1962–2008 |
| 38 | Annual mean SST from BSH | 6 °5'E – 9 °10'E | 55 °5'N – 53 °3'N | 1969–2006 |
| 39 | Mean winter (Jan, Feb, Mar) SST from BSH | 6 °5'E – 9 °10'E | 55 °5'N – 53 °3'N | 1969–2006 |
| 40 | Cell counts of <i>Guinardia delicatula</i> at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1962–2008 |
| 42 | Cell counts of <i>Thalassionema nitzschioides</i> at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1962–2008 |
| 43 | Cell counts of <i>Odontella aurita</i> at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1962–2008 |
| 44 | Sunshine duration per day at Helgoland | 7 °54'E | 54 °11.3'N | 1962–2008 |
| 45 | Weekly mean <i>Paracalanus parvus</i> at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1975–2005 |
| 46 | Weekly mean <i>Pseudocalanus elongatus</i> at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1975–2005 |
| 47 | Weekly mean <i>Centropages</i> spp. at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1975–2005 |
| 48 | Weekly mean <i>Acartia</i> spp. at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1975–2005 |
| 49 | Weekly mean <i>Temora longicornis</i> at Helgoland Roads | 7 °54'E | 54 °11.3'N | 1975–2005 |

Normally in the morning hours, surface water samples were taken with a bucket from a research vessel. These samples were taken to be representative of the water column of 6 to 12 m depth, as strong tidal currents mix the water column. Salinity and temperature were determined every work day; nutrients and phytoplankton three times per week until 1974, and five times a week since 1975. Silicate has been measured since 1966 and secchi disc depth since 1967. Zooplankton samples were taken in oblique hauls from the surface to the bottom or towed behind the research vessel three times a week from 1975 to 2005 using a 150- μm -mesh Nansen net (NN) or a 500- μm -mesh CalCOFI net (CN), respectively, and counted in chambers using microscopes (*Greve et al.*, 2004). The microplankton was counted with an inverted microscope after fixation with neutralized Lugol's iodine solution and quality checked (*Wiltshire and Dürselen*, 2004). Zoo- and phytoplankton samples were distinguished at the species or genus level.

Secchi disk depth readings are affected by the sensitivity of the human eye which, in turn, may affect the visual contrast between the disk and the surrounding water in water bodies of varying spectral light transmission properties and between observers at the same water body. As argued by *Tilzer* (1998), these variations cannot be eliminated; however, comparative readings taken by inexperienced students in Lake Constance have shown a relatively narrow margin of subjective error (standard deviation of mean value $\pm 8\%$).

The nutrient data were quality checked (see *Raabe and Wiltshire* (2008)) for possible gaps, leaps and discontinuities with a variety of statistical and graphical plot procedures. Also, a direct correlation with data sampled in a "reference area" nearby Helgoland Stations and obtained by different sources was performed, in order to identify general divergences of the two independent data sets (*Raabe and Wiltshire*, 2008). No obvious anomalies suggesting strong inhomogeneity were reported in the data.

The Helgoland Roads time series can be regarded as one of the most extensive ecological data sets currently available, not only representative of the German Bight and the south-eastern edge of the North Sea, but also on a global scale. It is clear that despite the difficulties projected by *Hickel* (1998) and *Radach* (1998), the HR data set provides an invaluable source of quantitative information on ecosystem function. As *Greve et al.* (2004) argued, the distance to the coastline permits the plankton data to act as indicators of the surrounding German Bight plankton populations. The single spot high frequency, length and satisfactory data quality of the HR time series in principle allow the detection of even weak long-term overall trends.

Time series of the annual spawning stock biomass of various fish species in the southern North Sea were obtained from the International Council of Exploration of the Sea (ICES). ICES fish data are generally used to estimate the size of commercial fish populations. This work is coordinated internationally and independent review groups check the results. The North Sea is divided into a grid of rectangles which will be sampled a number of times with the same trawling gear. Mathematical models are then used to transform these records into population estimates.

The North Atlantic Oscillation (NAO) is one of the major modes of variability of the Northern Hemisphere atmosphere. The NAO influences the North Seas ecology through SST, wind direction and magnitude, and precipitation (*Ottersen et al.*, 2001) and is linked to oceanic inflow into the North Sea (*Reid et al.*, 2003). The NAO index is defined by the difference of normalized atmospheric sea level pressure (SLP) between Ponta Delgada/Azores, Portugal, and Stykkisholmur/Reykjavik, Iceland. The SLP anomalies at each station were normalized by division of each seasonal mean pressure by the long-term mean standard deviation. Normalization is used to avoid the series being dominated by the greater variability of the northern station. High values of the index indicate stronger-than-average westerlies over the middle latitudes because the subtropical high pressure center is stronger than normal and the Iceland low is deeper than normal. In the North Sea the dominant atmospheric circulation is cyclonic. If the atmospheric zonal mean flow is dominated by westerlies more continental coastal, channel and south North Sea water is advected into the German Bight west. The intensity of the NAO may also be correlated with the mean wave height which contributes to the mixing of water masses. The climate condition in the winter season has the greatest influence on biological processes, therefore the NAO winter index was considered in this study. Another factor, influencing the southern North Sea, is the Gulf Stream Index (GSI), which is an indicator of the North-South shifts in the latitude of the north wall of the Gulf Stream between 79°W and 55°W (*Taylor and Stephens*, 1980; *Taylor*, 1995, 1996). The GSI contributes to the heat and salinity transport into the North Sea. Three other low-frequency indices were obtained for this study which may influence the southern North Sea, namely the East Atlantic Pattern Index (EA pat. index), the East Atlantic Jet Pattern Index (EAjet) and the Scandinavia Pattern Index (Scan. pat. index). EA pat. index appears as a low-frequency variability over the North Atlantic from September to April. It is the second of three primary modes. The EAjet appears from April to August as the third primary mode of low-frequency variability over the North Atlantic. The Scan. pat. index appears from August to May as a primary mode of low-frequency variability over Scandinavia and western Russia.

The German Weather Service (DWD) monitors stations all over Germany. Most of the atmospheric variables are from the coastal station List on the island of Sylt in the German Bight. There were no site moves of the station during the selected time period. Wind measurements depend to a great extent on the details of the surroundings (e.g., exposition and obstacles) which influences the data homogeneity. Therefore the reconstructed horizontal wind speed data from the regional atmospheric climate model (SN-REMO) with Spectral Nudging with a horizontal resolution of 0.5° (see *Feser et al. (1988)*) were used instead because the output is dynamically consistent. Since 1968, the Bundesanstalt für Seeschifffahrt und Hydrographie (BSH) provided weekly quasi-synoptical charts of SST. The data were calculated from SST grids of 20 nm with the aim of obtaining an accurate insight into the spatio-temporal evolution (*Loewe and Becker, 2003*).

Chapter 3

Major mode of climate variability and ecosystem response in the German Bight

This Chapter 3 is structured as follows. First a brief introduction of the background of this study is given and the purpose for further analyses. The statistical methods are described, afterwards the results are presented and discussed.

3.1 Introduction

Global climate change is likely to affect the physical and biogeochemical characteristics of the oceanic and coastal environments with potentially profound impacts on ecosystems (*IPCC*, 2007). The analyses of long-term time series can help to understand how ecosystems respond to climate variability and to evaluate potential effects of anthropogenic perturbations.

In the North Sea, interannual and interdecadal variability has been observed in both hydrographical and biological variables. One of the strongest interdecadal signals, known as the Russell Cycle (*Russell*, 1973), was detected during the late 1920s and was characterised by a shift in the plankton community structure of the English Channel. The Russell cycle reversed during the late 1960s (*Russell*, 1973). Another important mode of variability in the 70s, consisting in a body of water with very low salinity and temperature entering the North Sea, was detected by *Dickson et al.* (1988) and was called the Great Salinity Anomaly (GSA). Although it was proposed by *Cushing* (1988) that the GSA event adversely affected the recruitment of a number of deep water fish stocks through a delay of the phytoplankton spring bloom, *Mertz and Myers* (1994) expressed doubts on the strength of such a climate food web coupling.

In data collected in the western North Sea by a Continuous Plankton Recorder (CPR), *Reid* (1975) observed a marked decrease in diatom abundance after 1965. Since the CPR data also suggested that at the same time the relative estimate of phytoplankton standing crop increased, Reid concluded that a shift in species composition must have been taking place in

this area in 1965 with a consequent impact on higher trophic levels.

Aebischer et al. (1990) reported of remarkable similarities in trends among abundances of phytoplankton, zooplankton and herring, kittiwake gull breeding performance, and variations in westerly weather. Although, as *Aebischer et al.* (1990) admitted, the reasons for these similarities remain unclear, it is tempting to call for a straight causal relationship between weather and ecosystem shifts.

More recently, *Dippner* (1997a) suggested that coastal areas of the North Sea could be very sensitive to climate change. The author supported the hypothesis that the coastal areas are mainly driven by direct atmospheric forcing rather than, for instance, by inflow of Atlantic water (*Cushing*, 1988, 1990).

More relevant to this study, *Heyen and Dippner* (1998) proposed that in the German Bight the interannual and interdecadal variability in surface salinity is correlated to river runoff rather than advection of Atlantic water. For the same area, *Kröncke et al.* (1998) found that the biomass, abundance and species number of macrozoobenthos is strongly affected by climate variability.

In addition to these signals two dynamic regimes in the North Sea plankton ecosystem were found: a cold–biological (1962–1982) regime and a warm–biological (1984–1999) regime (*Beaugrand and Ibanez*, 2004). Also, *Beaugrand* (2004) and *Edwards and Richardson* (2004) proposed that a regime shift covering the period 1982–1988 in the North Sea may be connected to changes in large–scale hydrometeorological forcing. A similar ecosystem response to climate variability has been previously detected in the Pacific Ocean by *Hare and Mantua* (2000). *Beaugrand et al.* (2002a) recognized large biogeographical shifts in all copepod assemblages in the eastern North Atlantic Ocean and European shelf seas in the early 1980s. *Beaugrand et al.* (2002b) demonstrated that warm–water North Atlantic species moved further towards north, in association with a decrease in the number of cold–water species, in relation to an increasing trend in the Northern Hemispheric temperature and North Atlantic Oscillation. *Reid and Borges* (2001) reported an ecological regime shift in the North Sea around 1988 based on a compilation of plankton data derived from the CPR and fish catchments. Such regime shift was clearly detected in the northern and central North Sea but not in the southern North Sea (*Beaugrand and Ibanez*, 2004). An important result of these studies is that with increasing temperature a shift occurs in the species composition from cold to warm

water adapted species.

Weijerman et al. (2005) investigated the possibility of a connection between physical changes and ecosystem state in the North and Wadden Seas. The authors suggested that regime shifts occurred in 1979, 1988 and 1998, although results were less clear-cut in the latter case. More recently, also *Kirby et al.* (2007) documented some climatic impacts on the North Sea ecosystem. *McQuatters-Gollop et al.* (2007) showed that chlorophyll *a* (Chl *a*) increased from the mid-1980s with a regime shift peak in 1989 to higher concentrations in both the open and the coastal North Sea. The authors suggested that the North Sea phytoplankton biomass is unconnected to nutrient trends but positively correlated with Secchi depth and SST.

In this study homogeneous long-term time series of data were compiled for a limited part of the southern North Sea: the German Bight. The resulting data set included 33 different variables and spanned over 30 years. By using Principal Component Analysis (PCA) the dominant modes of variability in the data set were investigated and the variables most accountable for those modes were identified. In particular, the following questions were addressed:

1. Can regime shifts in the German Bight be identified?
2. What is the time-scale of these events?
3. What are the variables dominating these events?
4. Can causes and effects be clearly identified?

Alternatively to many other studies of this kind, the focus was on a restricted location of the southern North Sea: the German Bight. For the first time a detailed understanding of climate variability in this region was provided, not based on physical and biological data only but also on chemical variables. However, the results were discussed also in the context of the overall North Sea variability.

3.2 Methods

In order to identify basic structures of variations, which reflect more clearly the influence of an external forcing, a diverse set of data including multiple trophic levels and several physical and chemical variables for the German Bight (6° 30' E to 9° 10' E and 53° 30' N to 55° 10' N, see Figure 2.1) were compiled.

Unbiased observations of nature are almost impossible, thus data were selected with the following criteria: 1) the time series had to be homogeneous, no obvious anthropogenic cause for sudden changes in the time series and no or few missing values in the data set, 2) long-term diverse set of variables including multiple trophic levels and different environmental indicators and 3) different sites representative of the German Bight. The resulting data set comprised a total of 33 variables spanning over 30 years and divided into three major categories: atmospheric and hydrophysical variables (13), biological variables (14) and chemical variables (6), see Chapter 2 and Appendix A for a full list of variables and descriptions. The biological variables were log-normalized and all time series were normalized by calculating the anomalies (deviations from the mean for each data point) and dividing these by the standard deviations. No smoothing or filtering techniques were applied to the data.

Following the approach of *Hare and Mantua* (2000), Principal Component Analysis (PCA) was used for investigation. PCA has been used in many studies to objectively identify coherent patterns of variability among a number of time series (*Mantua*, 2004). In brief, the PCA is an “ordination technique” that reduces the dimensionality and identifies the most important modes of joint variability in a multi-variable data set. Assuming that the data are linearly related, the PCA defines an orthogonal linear transformation that transforms the data to a new coordinate system such that the greatest variance by any projection comes to lie on the first coordinate (the first Principal Component), the second greatest variance on the second coordinate (the second Principal Component), and so on. This way one can capture the most important fluctuations in the data with a few components. A PCA generates three types of outputs: principal components (PCs), eigenvectors (or loadings) and eigenvalues. When plotted against time, PCs give the temporal variability of the most dominant patterns. Eigenvectors indicate which variable contributes most to the dominant patterns. Eigenvalues are used to determine the fraction of total data variance explained by each PC.

For a detailed review of the PCA method see von *Storch and Zwiers* (1999). Once the first Principal Component was computed, the overall step magnitude of the regime shift was quantified by using the method of *Ebbesmeyer et al.* (1991).

For investigating correlations between subsets of time series, Canonical Correlation Analysis (CCA) was used. As with PCA, there may be more than one significant dimension (more than one canonical correlation), each representing an orthogonally separate pattern of relationships between the two subsets of variables. The first canonical correlation is always the one that explains most of the relationship. The canonical correlations are interpreted the same as

Pearson's r .

To prove the robustness of the results, PCA with longer and shorter time series was performed. Because the zooplankton time series did not start before 1975, by excluding zooplankton PCA was conducted on longer time series starting from 1966 and up to 2004. Due to the expected regime shift in the late 1980s, PCA starting from 1983 was also performed so to examine this signal in more detail.

Whenever a regime shift was detected, the significance of the inequality of the means (before and after the shift) of the two identified regimes was tested with the Student's t test and the Mann–Whitney U test. To quantitatively ascertain that the two regimes (before and after the shift) were different a re-sampling bootstrap test on the means of the two regimes was used. This technique involves choosing random samples with replacement from the data set and analyzing each sample the same way with the PCA. An analysis of similarity test (ANOSIM) of the two regimes (before and after the shift) was performed.

3.3 Results

Principal component analysis was used to reduce the data set to new, fewer variables, called “Principal Components” (PCs), which account for the majority of the variability in the data. Eigenvalue analysis (see Figure 3.1) indicated that the first Principal Component (PC1) described the dominant mode of variability in the data set. The first and second principal components accounted for 23 % and 12 % of the total variance respectively (note that the percentage of variability explained by the first principal component was far above the equiprobability value = 3.03 % (1/33)). Since the interpretation of PCs higher than the first is problematic, because they are constrained to be orthogonal to each other and natural processes are not necessarily independent from each other (*Storch and Zwiers, 1999*), the focus of the study was on the first PC only.

Figure 3.2 shows the temporal variation of PC1. The loadings (correlation coefficients between each time series and PC1) are illustrated in Figure 3.3. According to the definition, the temporal evolution of PC1 showed a pattern with two regimes: negative until 1987 and then positive thereafter, with an abrupt shift in 1987/88 (Figure 3.2). The year 1996 appeared to be anomalous in that PC1 was temporarily reversed in sign. The PC1 showed a minimum in 1979 and a maximum in 2000. Among the environmental variables, air temperature, SST, winter SST and Gulf Stream Index showed the strongest positive correlation with

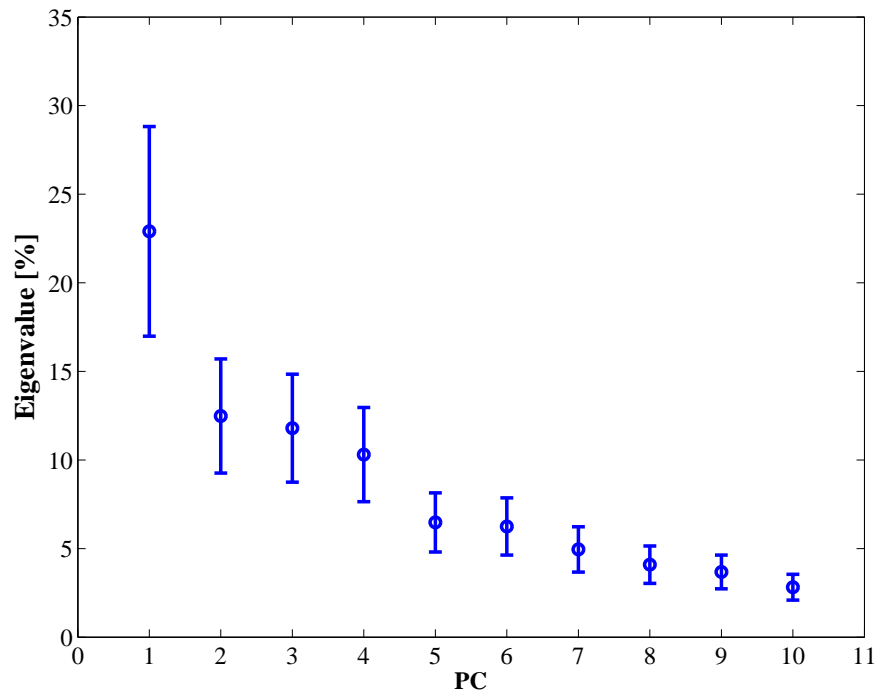


Figure 3.1: Scree plot of the first 10 eigenvalues for the principal component analysis of the full set of variables and their estimated standard errors.

PC1 (see Figure 3.3). Also Secchi disk depth was positive correlated with PC1. High negative loadings were found in nutrients like phosphate (PO₄) and ammonium (NH₄). Cod and saithe showed high negative correlation with PC1 while herring showed high positive correlation with PC1. In agreement with an increasing warming trend (*Edwards et al., 2002; Edwards and Richardson, 2004*), frost days showed high negative correlation with PC1. Temperature, through its influence on physiological processes, can potentially affect ecosystems (*Kirby et al., 2007*). However, not all biological/ecosystem variables showed pronounced shifts in the analyses. Diatoms and *Calanus helgolandicus*, for instance, did not show high correlation with the PC1, although other zooplankton species (sum of five small calanoid copepods, *Noctiluca scintillans* and *Pleurobrachia pileus*) showed slightly higher correlations (Figure 3.3).

Note that the way the PCA is used does not imply that the majority of the variables should show the same pattern as PC1. In other words, with the PCA a significant subspace (in terms of number of variables) was determined in which the change shown in PC1 is observed.

To quantify the overall step magnitude of the regime shift the method of *Ebbesmeyer et al. (1991)* was used. Therefore the normalised time series were separated into two regimes. That is

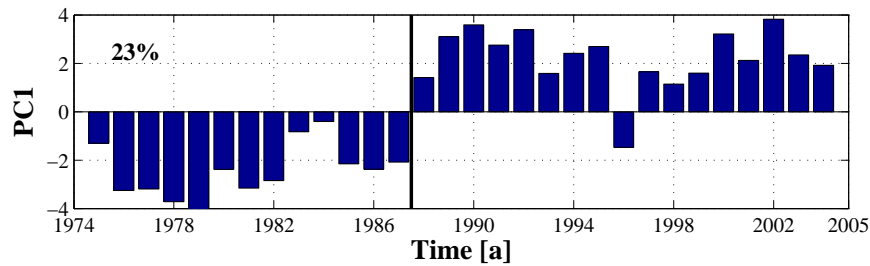


Figure 3.2: The first principal component (PC1) of the principal component analysis of the full set of variables for the time period from 1975 to 2004. The black vertical bar is shown before the data point 1988.

one regime before and one after the shift. The difference in the mean standard deviates of the two regimes was calculated. Figure 3.4 shows the step magnitude in the temporal evolution of PC1 as given by the difference between the two regimes (red dashed line in Figure 3.4). The marked step-wise increase in 1987 was about 1 standard deviation high. Figure 3.4 also shows that the two regimes are characterized by rather small inter-annual variations.

To statistically test the inequality of the means (before and after the shift) of the two identified regimes the two-tailed Student's t test was used. The null hypothesis is that the variables are normally distributed with the same variance and that the samples are randomly independent with equal means. The alternative hypothesis is that the means are not equal. The result suggests the rejection of the null hypothesis at the 5% significance level. However, some data violate the assumptions of the t test. Therefore, also the Mann-Whitney U test was used for testing the inequality of the two medians. Also in this alternative approach the result suggests the rejection of the null hypothesis of equal medians at the 5% significance level.

To quantitatively ascertain that the two regimes (before and after the shift) were different a re-sampling bootstrap test on the means of the two regimes was used. A confidence interval for the difference of the means of each regime was calculated from the constructed synthetic time series. This exercise was repeated 1,000 times. The null hypothesis was rejected at the 5% significance level indicating that the two populations were well separated.

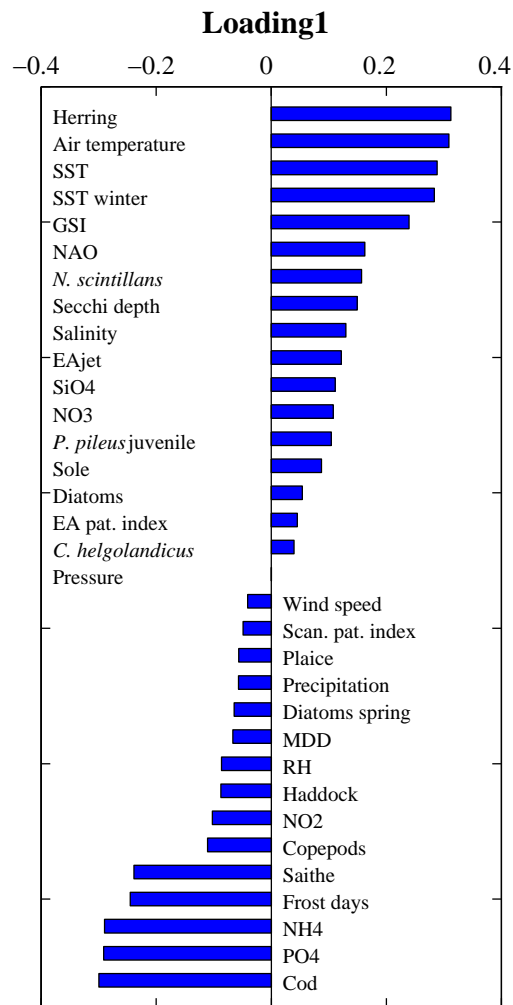


Figure 3.3: Spectrum of loadings for the first principal component from a principal component analysis of the full set of variables. The corresponding variable to each loading is written next to each bar.

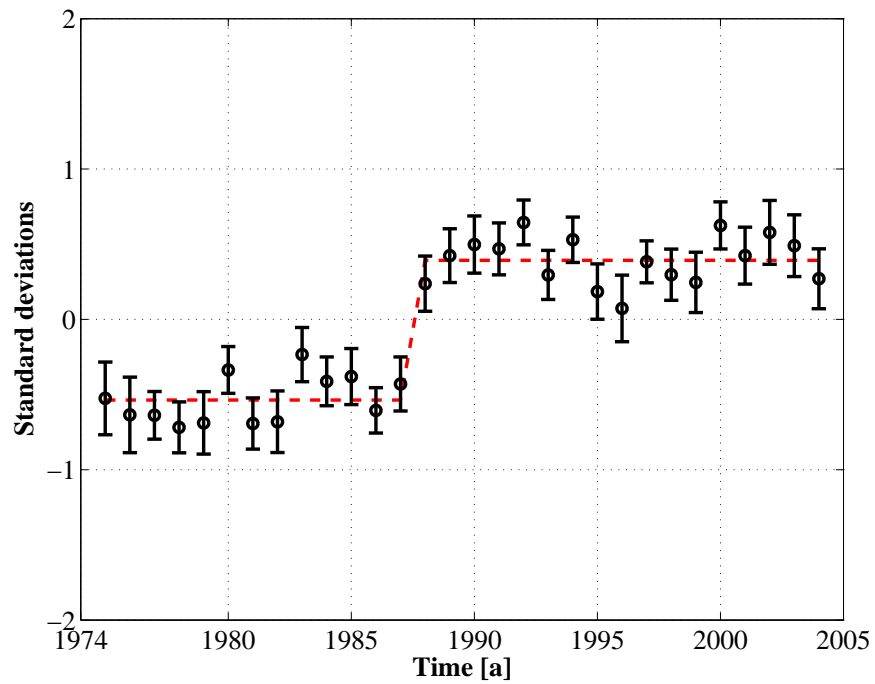


Figure 3.4: Results from the regime shift analysis of the full set of variables. The step (red) passes through the mean standard deviate within each regime. The standard error of the full set of variables is presented for each year and the circles show the annual means of the standardised time series.

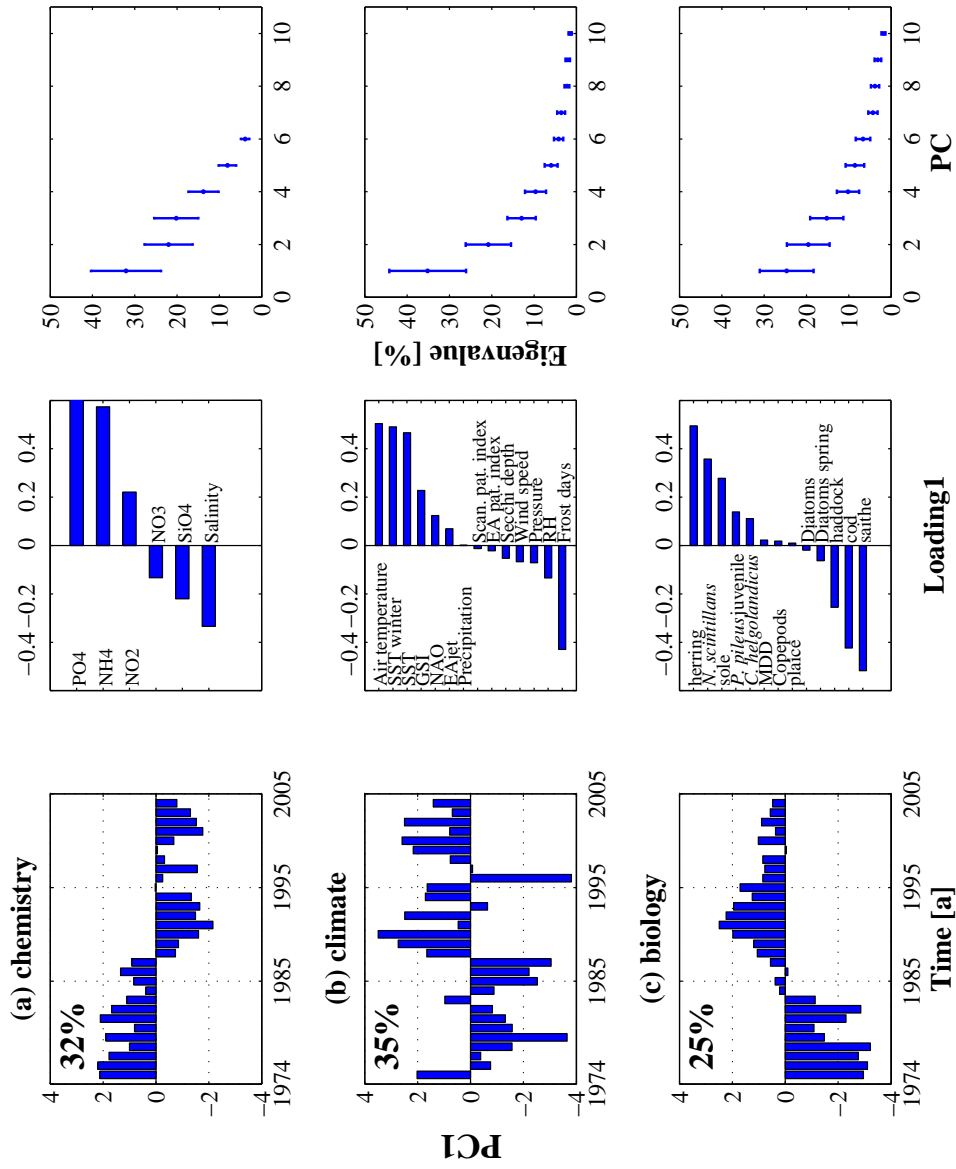


Figure 3.5: The first principal component (PC1) from the principal component analysis of the separated data for a) chemistry, b) climate and c) biology for the period 1975 to 2004 is shown in combination with each spectrum of loading and eigenvalue scree plot.

Following *Mantua* (2004), in order to identify dominant ecosystem state variables and to better isolate ecosystem behaviour from other influences (like environmental changes), the data were separated into three categories: 1) biological, 2) climatic, and 3) chemical. In Figure 3.5 the results of PCA performed on each of these groups are shown. The first PC of the chemical data, see Figure 3.5a, explains 32% of the total variance. Note that the second regime of the first PC for chemical data was not as smooth as the second regime in the PC1 obtained with the global data set (Figure 3.2). Ammonium (NH₄) and phosphate (PO₄) showed the strongest negative correlation with the first PC of chemical data, while salinity showed the strongest positive correlation with the first PC of chemical data. This may be connected to the fact that the German Bight waters changed over the last decade from a more coastal (fresher) dominated character to a more marine dominated character (clearer and saltier).

The first PC of climatic data (Figure 3.5b) showed pronounced interannual variability (likely reflecting the fact that physical variables respond faster to atmospheric changes and characterising the German Bight climate as highly dynamic) and had a distinct peak in 1996. The variance explained was 35%. The highest loadings were given by the temperature data

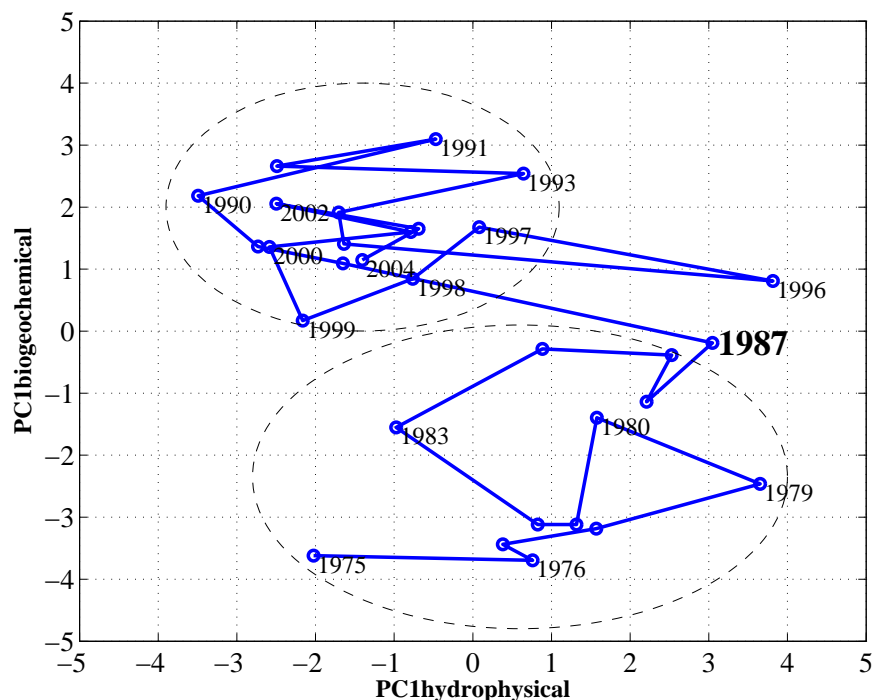


Figure 3.6: Scatter plot of the first principal component of all biogeochemical variables against the first principal component of all hydrophysical data. Circles indicate data from 1975 to 2004. The two identified regimes are surrounded with a black circle and the tipping point (1987) around the shift is highlighted. Lines between the circles indicate the variability.

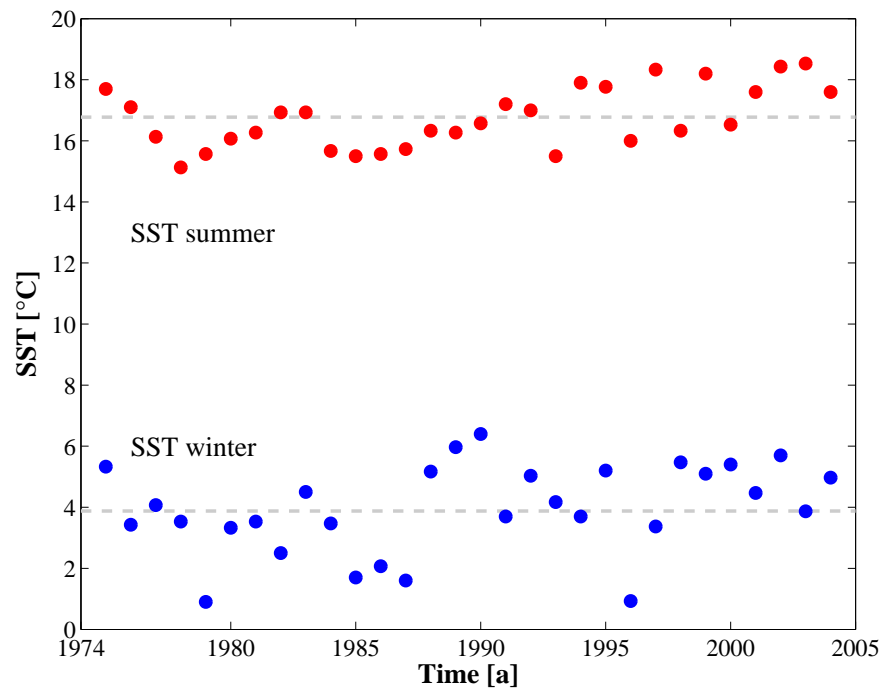


Figure 3.7: Time series of summer (red) and winter (blue) SSTs for the period from 1975 to 2004. The grey dashed lines represent summer and winter means.

similarly to the results obtained with the global data set (Figure 3.2) and, accordingly, the highest negative correlation with the first PC of climatic data was mainly given by frost days.

Figure 3.5c shows the results of the PCA performed on the biological data. The first PC of biological data explained 25 % of the total variance and was the smoothest among the three first PCs. Fish data such as saithe, cod and to a less extent haddock showed high negative correlation with the first PC of biological data and positive for herring similar to the results obtained with the entire data set. *N. scintillans* showed high correlation with the first PC of biological data as well as *P. pileus*.

In summary, the first PC obtained on the global data set showed a regime shift in 1987/88. The first PCs of chemical, climatic and biological time series were dissimilar from each other, highlighting the different modes of variability expressed by the three different categories of data and suggesting that the biological component of the German Bight system is rather resilient.

Regime shift analysis

An analysis of similarity test (ANOSIM) of the two regimes (before and after the shift) was

performed. The statistical significant difference obtained was $R = 0.82$, suggesting that the two regimes are indeed well separated and clearly distinct. The estimated probability that such a result could be generated by random chance is $p = 0.001$. 1,000 permutations were used for estimating the significance level R .

To further investigate the results, the first PC of all biogeochemical data against the first PC of all hydrophysical data (Figure 3.6) was plotted. Two clusters showed up with a separation in 1987. This year marks a tipping point around which the system shifts into a new state. The year 1996 was confirmed to be anomalous in that the changes occurred did not force the system to shift into a contrasting permanent regime. Canonical Correlation Analysis (CCA) was performed to study the relationship between biogeochemical and hydrophysical data. This statistical technique identifies the maximized correlation between two data sets. For both data sets the canonical correlation was $r = 0.9$.

3.4 Discussion

The impact of a changing climate on marine ecosystems is generating a wealth of new investigations. In this context, it was important to investigate whether the regime shifts suggested by various studies in the North Sea have also taken place locally, especially for highly populated coastal areas such as the German Bight.

In general, the results obtained by focusing on the German Bight and by including new time series confirmed those of earlier studies targeting the entire North Sea (*Reid and Borges*, 2001; *Beaugrand*, 2004; *Beaugrand and Ibanez*, 2004; *Weijerman et al.*, 2005): a regime shift took place in 1987/88 with important ecological consequences.

The underlying mechanisms for the shift can be inferred by analysing the SST data in more detail. Figure 3.7 shows the SST averaged over winter (Jan–Mar) and the SST averaged over summer (Jul–Sep). There were two exceptionally cold winter years (1979 and 1996) and an event of persistent cold winters from 1985 to 1987. The extreme cold anomaly of North Sea SSTs in 1996 is correlated with a persistent negative phase of the North Atlantic Oscillation (*Loewe*, 1996). The regime shift of 1987 is also preceded by persistent cold summers (from 1984). The repeated cold events observed in summer and winter SST might have been responsible for the shift shown in variables of higher trophic levels through the impact of persistent lower temperatures on physiological processes. The increasing warming

trend (Figure A.8), which has been attributed to global warming (*Edwards et al.*, 2002; *Edwards and Richardson*, 2004), might explain the persistence of the second regime shown by this analysis.

These analyses also suggested that temperature is an important player in the regime dynamic of the German Bight ecosystem. Plankton dynamics are indeed strongly influenced by temperature (*Beaugrand and Ibanez*, 2004; *Dippner*, 1997a; *Fromentin and Planque*, 1996; *Planque and Fromentin*, 1996; *Kröncke et al.*, 1998). Temperature may influence trophic interactions in several ways: (1) it determines the geographical distribution of many species, and (2) it affects physiological factors such as etching of eggs, respiration, growth, etc. Ecosystems may therefore be expected to show clear responses to a warming climate.

For instance, negative anomalies in North Sea cod SSB was obtained and this was correlated with a positive temperature anomaly. Two possible factors could account for a decrease in cod SSB: 1) a higher mortality in juvenile fish, resulting from a reduction in food supply (a bottom up effect proposed by *Russell* (1973)), or 2) a northward move of adult fish populations towards regions where temperatures are more favourable (*Svendsen et al.*, 1995). It is more likely that the decrease in the number of cods was due to this northward shift given that cods are adapted to colder temperatures (*Svendsen et al.*, 1995). *Dippner* (1997b) also put forward the possibility of recruitment failure in North Sea cod, North Sea whiting, and western mackerel in association with a warming climate. In this analysis negative anomalies in North Sea saithe SSB were correlated with positive temperature anomalies, suggesting that the recruitment success of this fish was connected with warm temperatures. This is in agreement with the study of *Svendsen et al.* (1995) indicating a positive response of North Sea saithe recruitment to warmer water. Positive anomalies were obtained in herring SSB. A possible explanation might be that herrings had an extended reproductive phase from 1990 to 1996, possibly due to the location of several sites within or near Helgoland exhibiting different spawning times (*Greve et al.*, 2005). Note that the SSB data cover year classes of 0–1 year thus excluding the possibility of lags between SSB data and hydrometeorological forcing (*Dippner and Ottersen*, 2001; *Sundby et al.*, 1989; *Helle et al.*, 2000).

Note that in the PC analysis no lag between GSI and other climatic variables was taken into account because of the contrasting results existing on these points (see for example *Frankignoul and de Coetlogon* (2001)). *Joyce et al.* (2000) found that the correlation with the NAO during winter was best at zero lag or Gulf Stream lagging by 1 year. They argued that

the un-lagged correlation may reflect a response of the NAO to the Gulf Stream shifts.

In the case of zooplankton, the results showed positive correlations of the abundance of *N. scintillans* and *P. pileus* with PC1. *Heyen and Dippner* (1998) detected that a warm North Sea (in late winter) coincided with high abundance of *N. scintillans*. They concluded that evidence exists that high water temperature in winter leads to an earlier start of the growth season of *P. pileus* and to earlier timing and high abundance of *N. scintillans*.

Beare et al. (2002) maintains that winters (January, February) have become considerably warmer than in the late 1960s. *Beare et al.* (2002) found that the *Calanus finmarchicus* population of the North Sea collapsed in the late 1950s, while abundance of temperate Atlantic species like *C. helgolandicus* and neritic species increased. The authors suggested that the fall in the population of *C. finmarchicus* coincided with long-term freshening and warming of the western North Sea, west of ca 4 to 5° E, and a long-term increase in the salinity of the eastern North Sea. *Fromentin and Planque* (1996) showed that the increase in temperature and alteration in the winter circulation pattern observed during the last decades of predominantly positive NAO index values have proved beneficial to *C. helgolandicus*, the abundance of which has increased. However, the result for *C. helgolandicus* differed from the findings just described and did not show high correlation with PC1. For this analysis time series of *C. helgolandicus* were collected at the Helgoland Roads (HR) station. A possible explanation for the discrepancy might be that *C. helgolandicus* at Helgoland Roads were subject to higher predation and lower water depths in contrast to the North Sea. At Helgoland Roads, *Greve* (2003) showed that the annual dynamics of *C. helgolandicus* changed in the 1990s compared to the 1980s due to the change in annual dynamics of *P. pileus*. *P. pileus* and *C. helgolandicus* prey on each other at appropriate developmental sizes. This interaction can thereby determine their relative dominance within the ecosystem (*Greve*, 1995). They are mutually exclusive, and higher abundances of *P. pileus* can be the driver of a later growth of *C. helgolandicus*.

Beaugrand et al. (2002a) demonstrated that clear biogeographical shifts in most of copepod assemblages have occurred with a northward extension of warm-water species associated with a decrease in the number of colder-water species. These biogeographical shifts were related both to the increasing trend in Northern Hemisphere temperature and to the North Atlantic Oscillation. In this case, small calanoid copepods were found to be negatively correlated with annual temperature. In other words, while the temperature anomaly was positive in the second regime (Figure A.9), the small calanoid copepods abundance was lower in this period

(Figure A.3). This suggests that phytoplankton–zooplankton mismatches might be responsible for this patterns through warmer winter temperature (Figure A.9) causing an earlier zooplankton development. However, one cannot rule out the possibility of a top–down control via predation. *Greve* (1994) documented an exceptional invasion of a population of *Mugilgiaea atlantica* in the German Bight in 1989 increasing the grazing pressure on small copepods.

The results in the case of diatoms showed weak correlation with the first PC. Diatoms are unicellular, short–lived phytoplankton and are subject to predation and to other processes affecting their physiology. Their population may increase exponentially and double within a few days. The low correlation with the increase of long–term SST might indicate that the long–term trend in SST is not a first–order influence on diatoms, rather other factors as the amount of incident light and temperature variability in the beginning of the year might determine their variability (*Wiltshire et al.*, 2008). One do not exclude the possibility that more than one mechanism may be responsible for the patterns observed thus leading to complex non–linear relationships between climate variability and diatom populations. Also after 1987/88 the regime shift the MDD did not change. This is in line with the recent work of *Wiltshire et al.* (2008) who found fairly stable spring bloom timings at Helgoland Roads.

The long–term trend of the Helgoland Roads (HR) ammonium time series reflected its overall “true” variability in the southern North Sea (see also *Raabe and Wiltshire* (2008)). For instance, ammonium concentration at HR shows a similar trend (a decrease) to the Dutch coastal waters (*Schaub and Gieskes*, 1991). Ammonium loads from the Elbe river have also been decreased since the 80s (*Hickel et al.*, 1993, 1995), consistently with observations at HR. A relation between Elbe river and nutrient concentrations at HR has been established since a long time now (*Lucht and Gillbricht*, 1978).

Generally speaking, a reliable Secchi disk depth data set should be positively correlated with salinity (*Hakanson and Bleckner*, 2008). The data reflected this relationship: the higher the salinity, the clearer the water. A recent study by *McQuatters-Gollop et al.* (2007) showed that water transparency, based on Secchi depth data, has been increasing in the coastal North Sea waters after a major decline during the early 1970s. The trend shown in the Secchi depth data was consistent with *McQuatters-Gollop et al.* (2007) work.

3.5 Summary

A diverse set of long-term time series for the German Bight was compiled. The resulting data set contained variables representing atmospheric, hydrophysical, biological and chemical observations. Principal Component Analysis (PCA) was used to identify the most important modes of variability in the data and determined the variables with highest correlation to these modes and used a number of tests for supporting the robustness of the results. This approach allowed to tackle some important scientific questions (as listed in Section 5.1). The answers are as follows:

1. This analysis indicated that the major mode of variability in the data was characterised by two regimes separated by an abrupt shift in 1987/88 (first PC).
2. The two regimes persisted for more than a decade (although evidence cannot be provided for the state of the system before 1975 and after 2004). The regime shift took place within a year and it was statistically significant.
3. SST, Air temperature, SST winter and herring showed the highest positive correlation to the major mode of variability (first PC), while phosphate, ammonium and some fish (cod and saithe) showed the highest negative correlation with the first PC. A pronounced positive correlation was also found for the Gulf Stream Index, Secchi depth and salinity. Consistently with an increasing warming trend, frost days showed high negative correlation with the first PC.
4. High positive loadings in SST, Gulf Stream Index and Secchi depth (and to some extent also in salinity) suggested that the regime shift of 1987/88 in the German Bight was likely caused by changes in hydroclimatic forcing. This conclusion was also supported by previous studies (*Beare et al.*, 2002; *Wiltshire and Manly*, 2004) maintaining that in the last decade the German Bight has been characterised by clearer and more marine waters. Changes in some ecosystem variables (plankton and fish) were associated to changes in the hydroclimatic forcing. However, not all biological variables showed pronounced shifts. Diatoms and *C. helgolandicus*, for instance, did not show high correlation with the major mode of variability (first PC) suggesting that the lower trophic levels of the German Bight ecosystem are remarkably resilient. In fact, specific analyses of the data divided into three different subsets (biological, climatic and chemical) characterised the climate of the German Bight as highly dynamic also on short time-scales (a few years) as compared to much smoother biological and chemical components.

This study documented for the first time that the German Bight was characterised by patterns of variability similar to the ones of the all North Sea (*Beaugrand*, 2004; *Weijerman et al.*,

2005). The German Bight, however, was characterised by a different exposure to natural and anthropogenic perturbations with respect to the North Sea as a whole. In this analysis various nutrients were included and it could be shown that phosphate and ammonium were characterised by stronger negative trends with respect to the weaker positive trends in silicate and nitrate concentrations. Although this coastal region appeared to be characterised by a quite dynamic climate regime, lower trophic levels of the ecosystem appeared to be rather resilient.

Given the complexity inherent to the studies of coastal ecosystem variability, it is crucial that long-term monitoring programmes are maintained in the future and that combined statistical analysis and ecosystem modelling approaches are undertaken.

Chapter 4

Top down versus bottom up factors determining the long-term changes in the seasonal succession of three diatom species

One conclusion in Chapter 3 is that the lower trophic levels are rather resilient. The possible decoupling of trophic interactions may be one of the consequences of climate warming. Further, the timing of phytoplankton blooms affects competition within the plankton community as well as food web interactions with zooplankton and fish. To improve our understanding with respect to climate warming effects on the phytoplankton successional patterns, this Chapter 4 is concerned with long-term records of three diatom species (*Guinardia delicatula*, *Thalassionema nitzschioides* and *Odontella aurita*), abiotic and copepod time series for the period 1975 to 2005 to study the effects top down versus bottom up control on the temporal bloom indices of these three diatoms. After a short introduction of the current, relevant literature, the statistical methods are described. Finally, the results of the analysis are presented and discussed.

4.1 Introduction

Global warming is unequivocal and the rate of this process has been far greater in the last decades than it has been for the last 10,000 years (*IPCC*, 2007). Despite the availability of detailed information on temperature changes, there is still only limited information on the effects of a warming climate on aquatic food webs (*Cushing*, 1995; *Walther et al.*, 2002).

Typical terrestrial plant responses to global warming included poleward and altitudinal extensions of geographic species ranges (*Thuiller*, 2007) and shifts in seasonal activity and growth patterns (*Cleland et al.*, 2007). Analogously to earlier blooming observed in terrestrial plants, various studies concerning marine phytoplankton reported of earlier seasonal succession of different species in connection to climate warming (*Edwards and Richardson*, 2004; *Schlüter et al.*, 2008). Also species replacements in zooplankton (*Möllmann et al.*, 2000; *Hays et al.*, 2005) and year-to-year variation in phytoplankton communities

(Müller-Navarra *et al.*, 1997; Jassby *et al.*, 1990) have been linked to climate change. However, (Wiltshire and Manly, 2004) found retarding or fairly constant diatom spring blooms in the German Bight of the last decades, in addition to large interannual variations in the timing of the spring bloom (Wiltshire *et al.*, 2008). Schlüter *et al.* (2008) found that diatoms based on average spring and annual abundances were rather resilient to step like shifts in temperature. Thus, resulting decoupling of trophic interactions from one another due to climate warming may have severe consequences for the entire food web (Cushing, 1990; Beaugrand *et al.*, 2003).

Most of the known factors determining phytoplankton succession relate to changes in nutrient concentrations, light (Reynolds, 2006), thermal stratification and predator–prey relationships (Reynolds, 1989; Sommer, 1989; Beninca *et al.*, 2008). In addition, plankton communities follow distinct seasonal succession patterns caused by changes in life–history traits (Sommer *et al.*, 1986; Litchman and Klausmeier, 2008) and nutrient stoichiometry (Philippart and Cadee, 2000). Responses to climate variability, and the effects of the conditions preceding the spring bloom in temperate shelf seas, have not been well characterized.

Phytoplankton succession may also be influenced by light in various ways. The light climate in the water column depends on turbulence. Specific conditions during winter may determine the inoculum of species in spring, and thus, may affect the succession patterns, e.g. Colijn and Cadee (2003). Only few studies have addressed the impact of climate change, i.e. changes in abiotic conditions such as temperature, light, nutrients, etc., on biotic interactions such as the long–term development of predator–prey relationships in natural marine pelagic systems so far e.g. Wiltshire *et al.* (2008). A recent modelling study by Gaedke *et al.* (2009) showed how changes in temperature may alter grazing thus delaying phytoplankton blooms. It is also still under debate to what extent and due to which processes the marine ecosystem has evolved in the second half of the 20th century (Philippart and Cadee, 2000).

The above examples of biological responses to global warming or periodic climate variability focused mainly on bulk biomass parameters, while neglecting biotic interactions. Because the timing of phytoplankton blooms has an impact on food web interactions with zooplankton and may ultimately affect fish, changes in the phenology of individual species and the factors determining such variations must be taken into account if we are to understand how marine ecosystems respond to increasing temperature. This emphasizes the need to analyse the responses of individual species including to seasonal changes in environmental conditions.

This study investigated how variations in environmental conditions and predation preceding the bloom affect the bloom timings of three common winter/spring and spring/summer diatom species observed at the Helgoland Roads time series station in the German Bight. Further, the factors which potentially affect the end of the succession pattern are determined. The Helgoland Roads time series were chosen because they are the most extensive ecological data sets currently available and represent an adequate data set to describe and evaluate changes in the phytoplankton species composition of the German Bight.

4.2 Methods

4.2.1 Data sets

Since 1962, dissolved inorganic nutrients (NO_2 , NO_3 , NH_4 and PO_4), plankton stocks and hydrographical parameters have been measured by the Biologische Anstalt Helgoland (BAH) at Helgoland Roads (HR) site ($54^\circ 11'3''$ N, $7^\circ 54'0''$ E) between the two islands at Helgoland. Measurements of silicate concentrations (SiO_4) started 1966. Temperature was determined every work day, nutrients and phytoplankton 3 times a week until 1974, and five times a week since 1975. Zooplankton samples were taken 3 times a week since 1975 to 2005 (*Greve et al.*, 2004). Secchi disc depth has been measured since 1968. The analysing methods and quality control of the water samples were described in detail in *Wiltshire and Dürselen* (2004); *Greve et al.* (2004); *Raabe and Wiltshire* (2008). The German Weather Service (DWD) provided concurrent measurements of sunshine duration per day from Helgoland since 1962.

The diatom data set used in the multivariate statistical analysis contained three representative (in terms of relative abundance and annual presence) winter/spring and spring/summer species, namely *Guinardia delicatula*, *Thalassionema nitzschioides* and *Odontella aurita*. *Odontella aurita* (Lyngbye) C.A. Agardh is a centric marine micro algae previously known as *Biddulphia aurita*. It is considered a neritic, littoral species by *Hendey* (1964), a tychoplegic diatom by *Drebes* (1974) and a cold meso–eurytherm, cosmopolitan species by *Baars* (1979). It is often found in long chains in the coastal region and provides an attachment site for other diatoms (*Tiffany and B.*, 2002). *Guinardia delicatula* (Cleve) Hasle is a centric diatom (*Drebes*, 1974), requires low Si:N ratios compared to other diatoms (*Rousseau et al.*, 2002), and, especially in summer, is one of the prominent primary producers in the phytoplankton of the German Bight. For the past 100 years the species was commonly known as *Rhizosolenia delicatula* (Cleve), but recently it has been transferred to the genus *Guinardia* by *Hasle and Syvertsen* (1996). The pennate diatom *Thalassionema nitzschioides* (Grunow)

Grunow ex Hustedt is a eurythermal species (*Karentz and Smayda, 1984*) and is a typical species for neritic waters and mostly associated with mid-latitude pelagic high temperature water. It is well adapted to water-mixing and high nutrient concentrations. *T.nitzschioides* has an elongate shape and a high surface-to-volume ratio which may explain its anomalously high Si:N biomass ratios (*Brzezinski, 2004*). The predator data consisted of the abundances of five small calanoid copepods (*Paracalanus parvus, Pseudocalanus elongatus, Centropages* spp., *Acartia* spp., *Temora longicornis*).

4.2.2 Statistical analysis

Data gaps and fluctuations due to changes in environmental conditions or measurement errors prevented a reliable determination of variable characteristics, hence, a Gaussian filter in time was applied to all raw data for subsequent analyses. Prior to statistical analyses, all plankton samples were log-transformed to normalize the distributions, while still preserving the relative differences in magnitude of occurrence.

To evaluate potential phenological changes among the diatom organisms, two biological temporal indices (similarly to the approach of *Greve et al. (2005)*) were defined: 1) the “Start Of Growth Period” (SOGP), i.e. the time at which organism populations began the build-up to a “bloom”, associated with the week of the year during which the population reached a level corresponding to 15% of the annual cumulative abundance, and 2) the “End Of Growth Period” (EOGP), associated with the week of the year during which the population reached a level corresponding to 85% of the annual cumulative abundance. The difference between EOGP and SOGP is defined as the growth duration (GD) (see [Figure 4.1](#) for the indices). Sensitivity analysis indicated that these threshold levels were insensitive to variations of up to 30% (results not shown). Only data from 1975 to 2005 were used for statistical analysis of the biological indices due to determination of predator data between 1975 to 2005. The biological indices were also assessed for linear temporal trends prior to use in statistical analysis by taking a least squares fit of the data against an index of time. Temporal trends were judged at the 5% significance level with a standard Student’s *t*-test of the estimated slope parameter.

In order to confine the analysis to the phenologically important bloom phase, observations were processed prior to the onset of the SOGP of *O. aurita, T. nitzschioides* and *G. delicatula*. In this procedure, nutrients were neglected as predictors in the regression model since severe nutrient depletion did not occur during that period and cells were far from being nutrient

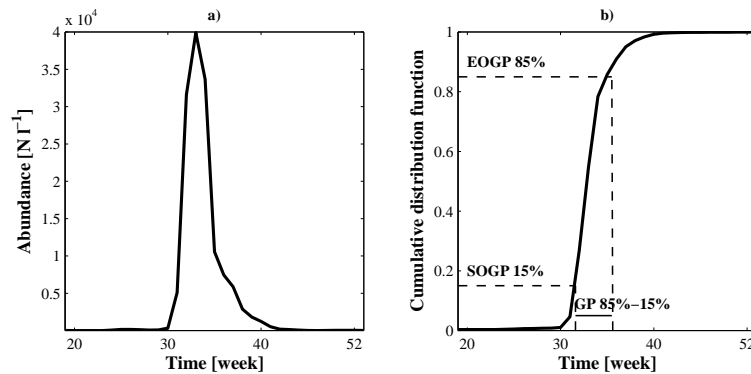


Figure 4.1: a) One annual weekly mean abundance of *Guinardia delicatula* and b) the cumulative distribution function of the annual weekly mean abundance with its “bloom” indices: Start Of Growth Period (SOGP), Growth Duration (GD), and End Of Growth Period (EOGP).

limited. For the EOGP nutrient depletion was relevant.

All time series were normalized prior to analysis by subtracting the yearly mean abundance from the values and then dividing by their standard deviation. To find the mean explaining factors following high, average, and low SOGP of the three diatoms, three values of their SOGP were defined: high values (> 1 above the deviation from the 1975–2005 mean value), average values (± 1 around the deviation from the 1975–2005 mean value) and low values (< 1 below the deviation from the 1975–2005 mean value).

In order to evaluate underlying factors for the temporal indices of the three diatoms *G. delicatula*, *T. nitzschoides* and *O. aurita* Pearson correlation and multivariate linear regression analysis were performed for possible relationships between the diatom indices and the environmental and grazing variables. The predicting variables for the EOGP were the mean values during the growth duration. For multiple regression modelling, data were first assessed for multicollinearity and normality (Kolmogorov-Smirnov test) and transformed if necessary. Then, a multiple regression on each diatom index was performed using all possible predictors and the best-fitting model was selected using a backward stepwise procedure. Parameters were assessed at the 5% significance level by a Student’s t -test. Robustness of the resulting models ($p < 0.05$) was assessed by testing the residuals for normality (Kolmogorov-Smirnov test) and homoscedasticity (scrutinizing plots of normalized residuals). The Durbin-Watson (DW) statistic was used to assess residuals for first-order autocorrelation. To quantitatively ascertain that the results were significant a re-sampling bootstrap test on the R^2 s of the results was used. This technique involves choosing random samples with replacement from the biological indices and regress each sample with the same predictors. All significant analyses

conformed to these regression assumptions. Normalized regression coefficients were used to infer the relative importance of model variables for explaining variations in the diatom indices.

4.3 Results

Among the three diatom species *G. delicatula* was numerically the most abundant species over the total time period considered (maximum about 15 log(cells per litre)). This species occurred at various times throughout the year (Figure 4.2a) with highest cell concentrations recorded in early summer and autumn and with lowest cell concentrations recorded during the period from December through February. From 1962 to 1978 *G. delicatula* was nearly absent during spring, it then appeared in April 1978, and reached its annual maximum during the months thereafter (Figure 4.2a). *G. delicatula*'s mean annual values were characterized by annual fluctuations (Figure 4.3a) and attained high mean annual population densities after 1997 with an exception in 2005 (Figure 4.3a). This species attained high population densities in 1980 (5.4 annual mean log(cells per litre)). The interval from 1982 to 1997 was a period of low abundance (2 – 4 annual mean log(cells per litre)), followed by another year of high population densities in 1999 (5.6 annual mean log(cells per litre)). From 1999 onwards, this species remained at relatively high yearly mean abundance levels (Figure 4.3a). A spectral analysis showed a marked 24-year cycle.

T. nitzschioides was the second most abundant species among the three and, with *O. aurita* representing the most important species of the winter and spring phytoplankton assemblages at Helgoland Roads (Figure 4.2b and c). Although *T. nitzschioides* and *O. aurita* occurred each year between January and April, their patterns of yearly abundance were dissimilar. *T. nitzschioides*' yearly pattern of maximal occurrence was bimodal; cell densities were highest during late winter–early spring and late summer–autumn, and lowest from June to including August (Figure 4.2b). *T. nitzschioides* exhibited wide annual fluctuations and peak levels (6 mean annual cells per litre log-transformed) occurred at 12-year intervals (Figure 4.3b), as inferred from spectral analysis. *T. nitzschioides* was absent from the phytoplankton assemblage in 1964. *O. aurita*, the least abundant species among the three, occurred each year between January and April (Figure 4.2c), showed a 6-year cell cycle and exhibited its highest annual mean abundances during the early 1960s (2.7 annual mean log(cells per litre)). From 1967 onwards, cell densities have been persistently lower than the preceding years (Figure 4.3c). *O. aurita* was absent in the phytoplankton assemblage in the years 1988, 1989 and 1995.

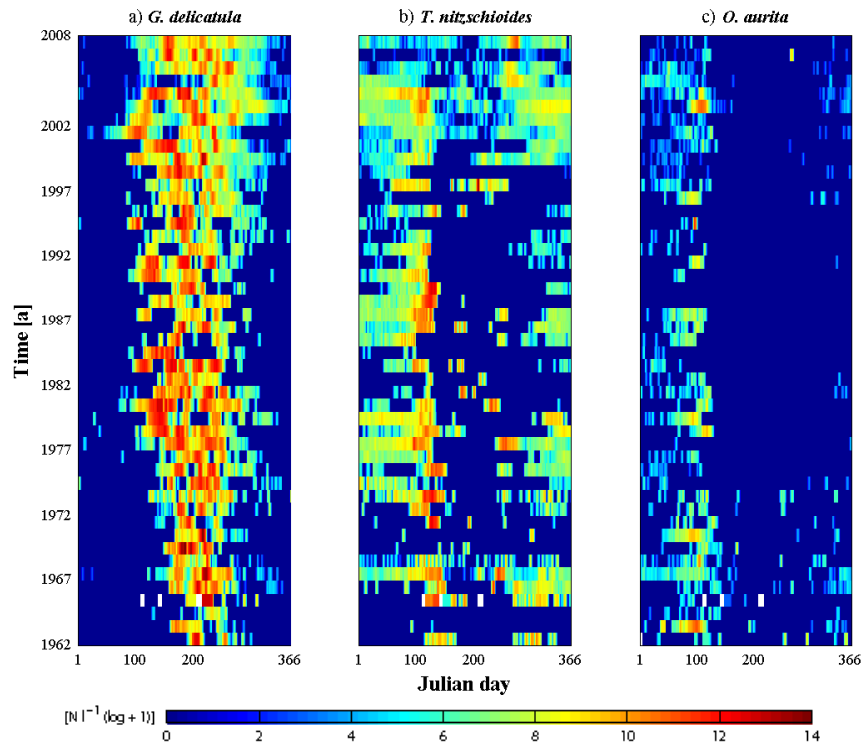


Figure 4.2: Filtered cell abundances (log transformed) at each julian day from 1962 to 2008 of a) *Guinardia delicatula*, b) *Thalassionema nitzschioides* and c) *Odontella aurita*. White boxes denote no observation.

Evidence of an increasing temporal trend was found in EOGP of *G. delicatula* ($R^2 = 14\%$, $p = 0.04$) at the 5% significance level. A decreasing linear trend was found for SOGP of *G. delicatula* at the 10% significance level. No significant ($p = 0.05$) linear temporal correlations were found in *T. nitzschioides*' or *O. aurita*'s indices.

The winter occurrences of *O. aurita* appeared to be associated with lower than average secchi disc depths and higher than average biomass during autumn (Figure 4.4) and did not appear to be affected by the grazer biomass of *Acartia* spp. The early spring occurrences of *G. delicatula* were instead associated with higher than average SST, lower than average grazing pressure and higher than average initial biomass during winter (Figure 4.4). Further, the later spring occurrences of *T. nitzschioides* were associated with lower than average secchi disc depths, higher than average grazing biomass and lower than average initial biomass during autumn (Figure 4.4). Lower than average secchi disc depth delayed *T. nitzschioides*' and *G. delicatula*'s bloom timings whereas *O. aurita*'s SOGP was advanced. Higher than average sunshine duration delayed *G. delicatula*'s spring bloom. In contrast to secchi disc depth, grazing biomass and initial phytoplankton biomass and to some extent SST,

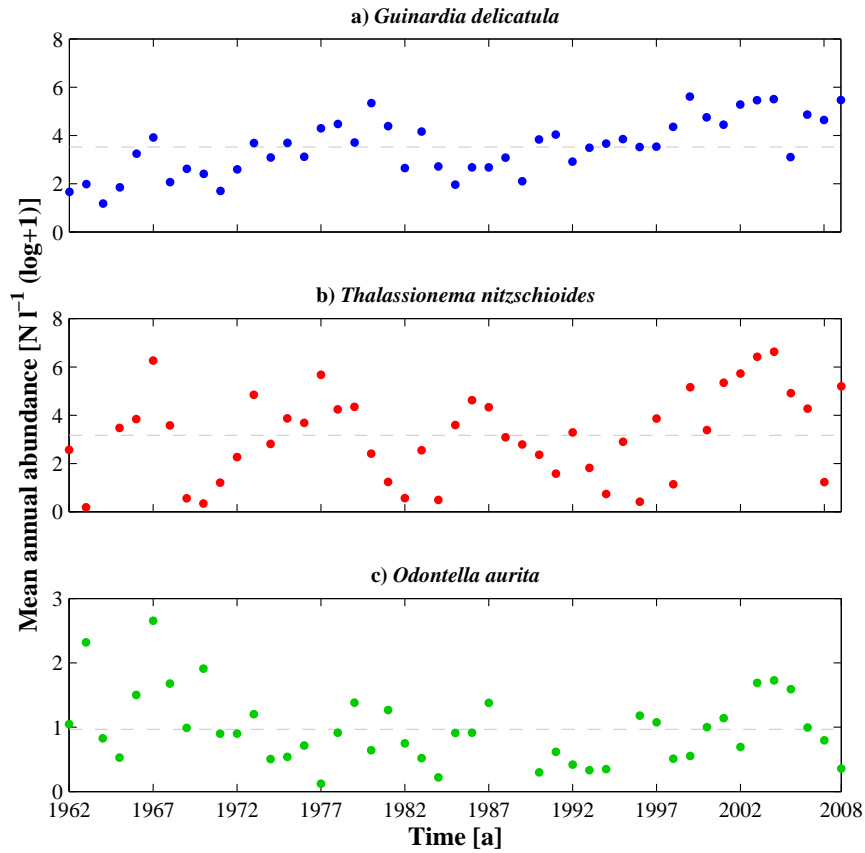


Figure 4.3: Annual mean abundances from 1962 to 2008 of a) *Guinardia delicatula*, *Thalassionema nitzschioides* and c) *Odontella aurita* and their 47 years mean (grey dashed line).

sunshine duration had apparently no big influence on the start of the blooms (Figure 4.4). The SOGP would therefore appear to be determined by a complex relation between secchi disc depth, grazing biomass and initial phytoplankton biomass (and to a lesser extent by SST).

The multivariate analysis of the EOGP of the three diatoms suggested that the mean values of sunshine hours during growth duration could explain most of the variation observed in the EOGP of the three diatom species (see Table 4.1). Higher mean sunshine hours delayed *T. nitzschioides*' and *O. aurita*'s EOGP. In contrast, *G. delicatula*'s EOGP was negatively correlated with sunshine duration and water transparency. Average SST during the bloom duration of *G. delicatula* and *T. nitzschioides* explained a remarkable part of the variability observed in their EOGP delaying their EOGP with warmer average SST. The magnitude of the mean grazing biomass during bloom duration was significantly correlated with *G. delicatula* and *O. aurita*. The positive correlation between silicate and *G. delicatula*'s EOGP indicated a delay of EOGP with higher silicate concentrations and ammonium's positive correlation with

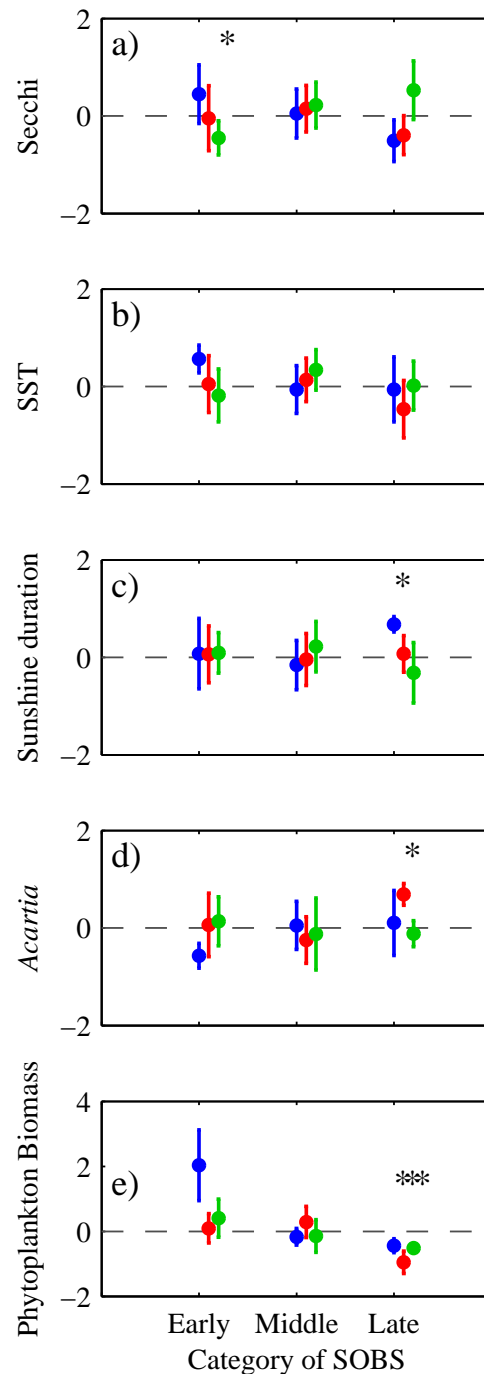


Figure 4.4: Normalized secchi disc depth, sea surface temperature, sunshine duration, acartia abundance and phytoplankton biomass with early, middle and late start of the bloom season of *Guinardia delicatula* (blue), *Thalassionema nitzschioides* (red) and *Odontella aurita* (green). The values of the physical variables were averaged over autumn (September – December) for *Thalassionema nitzschioides* and *Odontella aurita*, respectively, and winter (January – March) for *Guinardia delicatula* preceding the start of the bloom season. The three categories of early, middle and late start of the bloom season correspond to values > 1 above the deviation from the long-term mean value relative to 1975–2005, to values ± 1 around the deviation from the 1975–2005 mean value and to values < 1 below the deviation from the 1975–2005 long-term mean value, respectively. Error bars denote one standard error of the mean. Asterisks indicate time periods during which the anomalies differ significantly from zero. Note that the number of observations in the middle category is twice the number of observations in the other two categories, resulting in a higher statistical power for this category.

T. nitzschioides' EOGP indicated a delay of its EOGP with higher ammonium concentrations.

4.4 Discussion

The long-term abundances of *G. delicatula*, *T. nitzschioides* and *O. aurita* analysed in this study exhibited interannual variations in growth timings and dissimilar but regular cyclic annual abundance patterns during the period under study. It is rather unlikely that the same physical factor would determine most of the annual abundance patterns as the frequencies between the three diatom cycles were unequal. These dissimilar cycles might rather stem from differential grazing or internal variations in their reproduction or life cycle. Of these three diatoms, only the temporal biological indices (SOGP and EOGP) of *G. delicatula* showed significant linear decreasing and increasing trends with time during 1975 to 2005 and might be related to an increasing temperature trend. A recent study by *Wiltshire et al.* (2010) suggested a widening of the time period of occurrence of *G. delicatula*. The results of the statistical analysis in this study also suggested that the biological indices of the other two diatom species did not show a significant linear trend during this time period. The latter result confirms the view of fairly constant spring bloom timings in the central North Sea inferred from the Continuous Plankton Recorder (CPR) data by *Edwards and Richardson*

Table 4.1: Range of significant predictors for the end of the growth period of *G. delicatula*, *T. nitzschioides* and *O. aurita* are listed and the model diagnostics.

| p < 0.05 | Significant predictor | β | t-stat | F | R ² | Adj. R ² |
|------------------------------|---------------------------|---------|--------|-------|----------------|---------------------|
| EOGP <i>G. delicatula</i> | <i>Acartia</i> spp. | -0.56 | -5.1 | 14.8 | 0.75 | 0.69 |
| | Secchi disc depth | -0.32 | -2.8 | | | |
| | SiO ₄ | 0.24 | 2.15 | | | |
| | Sunshine duration | -0.66 | -5.67 | | | |
| | SST | 0.65 | 5.99 | | | |
| EOGP <i>T. nitzschioides</i> | NH ₄ | 0.31 | 2.1 | 8.34 | 0.48 | 0.40 |
| | Sunshine Duration | 0.41 | 2.5 | | | |
| | SST | 0.43 | 2.5 | | | |
| EOGP <i>O. aurita</i> | Sunshine duration | 0.71 | 4.92 | 12.25 | 0.47 | 0.41 |
| | <i>Temora longicornis</i> | -0.29 | -2.02 | | | |

(2004).

However, for interannual variations of the three diatoms different factors were responsible. *G. delicatula* showed a tendency of earlier bloom timings with higher than average water temperatures and lower than average grazing biomass. A strong vertical mixing, as indicated by lower secchi depths, had the most important role in the earlier appearances of *O. aurita*. One explanation could be that these species are tychopelagic (Drebes, 1974). Higher turbulence in the water through vertical mixing (e.g. strong tidal movements, storms, precipitation, run-off) preceding the bloom expressed in low secchi disc depth may seed the sea surface with *O. aurita* cells and favourable conditions in the surface water may then favour their growth. Lower water transparencies and higher grazing pressure, by contrast, delayed the bloom timings of *T. nitzschioides*. In this study, the copepod abundance showed considerable variation between years (with a decline in recent years) and may not be predictable from temperature conditions (Schlüter *et al.*, 2010). As the diatoms were affected by copepods abundance they showed also considerable variation in their SOGP between years. The timing of occurrences of each diatom species was affected by the magnitude of their preceding biomass which resulted in earlier bloom timings with higher than average preceding biomass and in later bloom timings with lower than average preceding biomass. Therefore, the magnitude of the biomass of the previous year resulting in an increased or decreased abundance of overwintering cells is important to determine the next years bloom timing. The differences in the factors responsible for the SOGP makes it unlikely that climate warming will result in the same temporal change in the onset of bloom season of all the three diatoms.

The SOGP of *T. nitzschioides* did not show an apparent correlation with SST. On the one hand, the reason for the lack of correlation might be that these species might have a wide temperature tolerance (Karentz and Smayda, 1984). On the other hand, as holoplanktonic species they must either maintain an indigenous population year-round, or depend on allochthonous seedings from contiguous waters. Allochthonous seedings vary in time, and therefore would be accompanied by variable incursion temperatures. It is suggested that the life history of individual species, i.e. those with and without known resting stages, will have an important impact on bloom dynamics.

As it could be expected, the end of the blooms were principally affected by different nutrient concentrations. Sunshine duration could prolong the duration of the bloom of *T. nitzschioides* and *O. aurita* provided that enough nutrients were available. In the case of *G. delicatula*, however, sunshine duration was negatively correlated with EOGP, suggesting the

possibility that *G. delicatula* might be photoinhibited under higher light intensities as gleaned by sunshine hours. Another explanation could be that *G. delicatula*'s photosynthesis and nutrient uptake rates were enhanced with higher light intensities leading to earlier nutrient deficiencies. *G. delicatula* and *T. nitzschioides* showed later declines in abundance with warmer water temperatures possibly via e.g. accelerated growth rates (*Harrison and Platt, 1980*) as photosynthetic carbon assimilation is enzymatically controlled and a temperature-dependent process (*Davison, 1991; Falkowski and Raven, 1997*). Since 1998/99 autumn SST is warmer compared to the previous years (results not shown) which may positively influence *G. delicatula*'s appearance in autumn. The occurrence of such a phenomenon may result in an increased abundance of overwintering *G. delicatula* cells, and thus may affect its next years spring succession. The observed differences in the variables affecting the three diatom species imply that changes in the responsible factors might influence the species assemblage and succession.

Previous studies concerning the biological responses to global warming or to periodic climate variability focused on bulk biomass or chlorophyll, while neglecting biotic interactions (e.g. *Edwards et al. (2001)*). Grazing pressure was identified as one of the major factors influencing the seasonal succession of all three diatoms. A higher grazing biomass delayed diatoms' first occurrence or advanced their EOGP. Grazing has been found to be important also in the fresh water ecosystem of Lake Constance (*Gaedke et al., 2009*).

In the late seventies, there was a considerable shift of *G. delicatula*'s bloom timings (not shown). However, these years were also characterized by changing silicate to nitrate ratios and nitrate in absolute values. There is ample evidence for an increase in nitrate inputs into coastal seas like the German Bight in the late seventies, but not so for silicate (*Anderson and Rydberg, 1988; Radach et al., 1990*). It is assumed that with decreasing silicate to nitrate ratios, more nitrate remains available for the growth of non-diatom biomass because silicate sets a limit only to diatoms growth. This hypothesis requires that diatoms be superior competitors for non-silicate nutrients under silicate sufficiency. *G. delicatula*, however, has lower silicate requirements compared to the other two species (*Rousseau et al., 2002*), does well under low silicate to nitrate ratios and may adapt to high nitrate demand for enhanced chlorophyll synthesis. It is suggested that nutrient changes could have triggered the shift in *G. delicatula*'s bloom timings rather than increasing temperatures. This is in line with *Radach (1998)* who found shifts in biomass and nutrient concentration levels at the end of the 1970s.

One unconsidered explanation for the advancement in the bloom period of *G. delicatula* could be the fact that *G. delicatula* might benefit from occurring during the same time as *Pheaocystis* spp. by producing transparent exopolymer particles which protect them from potential grazers as suggested by (Dutz *et al.*, 2005). The remaining variability of the three diatoms may stem from not considered factors like advected water masses with high plankton distribution into the German Bight from adjacent areas.

The left discrepancies in the predicted and observed values of EOGP could have many potential explanations. First, it is a fluctuating environment and hydrographic changes were not taken into account. Second, there were additional unidentified explanatory variables (a trace element, a vitamin) which were not considered. Third, one may deal with different genus types of the species. And fourth, other loss rates (e.g. sinking, parasitism) difficult to determine are other possible causes for changes as seasonal fluctuations in loss rate could lead to successional changes.

Increasing autumn and winter temperature is likely to exhibit complex indirect effects via changes in overwintering phytoplankton, zooplankton biomasses, grazing pressure and nutrient uptake rates by phytoplankton. It is expected that these variations also produce changes in phytoplankton species composition due to a differential impact of grazing. This study has shown that the three diatom species react unequally to different physical and predator variables. Due to this differential reaction changes in the entire ecosystem are to be expected.

Most of these relations have not been experimentally investigated yet. In particular, there is not yet any experimental or *in situ* evidence for the effects which trigger different life cycle stages in different species. This work provides a solid basis for further experimental investigations.

Chapter 5

Shifts in the phenology of three interacting zooplankton groups

Ctenophores such as *Beroe gracilis* and *Pleurobrachia pileus* could be particularly affected by temperature variations by changes in their own phenology and that of their prey (copepods), thus causing shifts in ecosystem function. Thus, in this Chapter 5 a new statistical methodology based on probability theory is processed to invest the successional patterns of these three zooplankton groups in relation to temperature. First a brief introduction of the background literature with the motivation is given. After the description of the data and methods the results are presented and discussed.

5.1 Introduction

General scientific consensus is that Earth's climate is warming at an accelerated rate (*IPCC*, 2007). Climate change is inevitably impacting habitats, ecosystems and biological resources. The seasonality of species in coastal waters could be particularly sensitive to warming (*Costello et al.*, 2006; *Sullivan et al.*, 2007).

A number of recently published works provide evidence for shifts in biotic variables in connection to climate change. For example, *Menzel et al.* (2001); *Sparks and Menzel* (2002); *Walther et al.* (2002); *Dose and Menzel* (2004, 2006); *Cleland et al.* (2007); *Schleip* (2008a); *Schleip* (2008b), reported phenological changes in terrestrial plants and animals in boreal and temperate zones of the Northern Hemisphere. A growing body of evidence also shows that northern marine ecosystems have experienced regime shifts related to climate change, including the North Sea (*Reid et al.*, 1998; *Beaugrand and Ibanez*, 2004; *Edwards and Richardson*, 2004; *Weijerman et al.*, 2005; *Schlüter et al.*, 2008), the Baltic Sea (*Möllmann et al.*, 2008), the Mediterranean Sea (*Molinero et al.*, 2008), the Black Sea (*Oguz and Gilbert*, 2007), the Bay of Biscay (*Hemery et al.*, 2008), the western North Atlantic and the Scotian Shelf (*Frank et al.*, 2006; *Choi et al.*, 2005; *Bailey et al.*, 2005; *Ciannelli et al.*, 2005; *Duffy-Anderson et al.*, 2005; *Belgrano et al.*, 2000), and the North Pacific (*Chiba et al.*, 2008; *Hare and Mantua*, 2000;

Belgrano et al., 2000; *Overland et al.*, 2008). Increases in the populations of gelatinous zooplankton have raised particular concern over the last decade, and their proliferations in coastal areas has been associated to warming trends (*Hay*, 2006; *Molinero et al.*, 2008; *Purcell*, 2009).

Predation of zooplankton by gelatinous zooplankton and prey escape mechanisms depend on many factors; these include the abundance of the predator, spatial and temporal predator-prey match/mismatch (*Cushing*, 1990), consumption rates (*Greve*, 1972), food preferences (*Baker and Reeve*, 1974; *Greene et al.*, 1986), and physical and chemical variations of the aquatic medium. These complex factors vary with the life histories of organisms. They determine the different energy flow in food webs, and could influence the function of the entire aquatic ecosystem.

Only two major pathways of energy flow, however, were relevant to this work: one that transfers resources to higher trophic levels linked to humans, in a presumably healthy ecosystem, and the other that moves resources to “waste” (in the sense of lost fish production) in the case of a system dominated by gelatinous organisms, see Figure 5.1. The relative dominance of these pathways determines the biogeochemical cycling of key elements, such as carbon. Important economical issues are at stake. For instance, blooms of ctenophore organisms, recently identified as the most basal known lineage of animals (*Dunn et al.*, 2008), have the potential to damage the fish industry by consuming fish eggs and larvae (*Purcell and Arai*, 2001).

The present study is on data of the marine holoplankton *Pleurobrachia pileus* (O. F. Müller, 1776), the most abundant gelatinous zooplankton in the German Bight and an important carnivore in coastal waters (*Bamstedt*, 1998). *P. pileus* has been found in many parts of the world ocean and is, therefore, of global relevance. This almost cosmopolitan organism shows marked seasonality, with peak abundances in the North Sea and adjacent areas appearing in early summer (*Veer and Sadee*, 1984; *Williams and Collins*, 1985) and autumn (*Fraser*, 1970).

The preferential preys of *P. pileus* are mesozooplankton, and calanoid copepods (*Greve and Reinert*, 1988; *Frid et al.*, 1994) in particular. Ctenophores are capable of regulating the abundance of their prey and thus can influence the dynamics of copepod populations (*Sullivan and Reeve*, 1982). *P. pileus* does not have many predators which are quantitatively important. In the coastal regions of the North Sea, only the ctenophore *Beroe gracilis* (C. Künne, 1939) can significantly graze down a *P. pileus* population. *Greve and Reinert* (1988) and *Bamstedt* (1998) proposed that *P. pileus* populations, observed in the North Sea, occur in cycles as they are restricted by the occurrence of *B. gracilis* as in

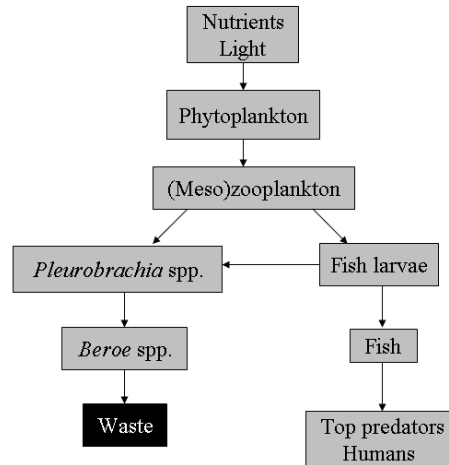


Figure 5.1: Schematic diagram of two possible developmental pathways of a simplified ecosystem in the German Bight.

a classical predator–prey relationship.

During the last three decades, the German Bight exhibited a warming trend (*Schlüter et al.*, 2008) with an average temperature increase of 1.7°C (*Wiltshire et al.*, 2008). The most substantial warming occurred during the winter and spring months. The present study focuses on understanding the impact of these climatic changes on the phenology of three interacting zooplankton groups (*B. gracilis*, *P. pileus* and *copepods*) at Helgoland Roads from 1975 to 2004 and on the possible consequences to their predator–prey interactions. The results could also clarify aspects connected to changes observed in the timing, duration and declining of the zooplankton growth phases.

The analyses were conducted using Bayesian statistics. An advantage of the Bayesian approach is that a coherent framework based on probability theory can be defined, allowing one to test multiple hypotheses concerning the characteristics of the time series under investigation. This analysis also provides estimates of uncertainties, because all calculations are performed using full probability distributions (*Gelman et al.*, 2004).

5.2 Methods

5.2.1 Data

The zooplankton data (which will be available under “Wulf Greve collection of Helgoland Roads zooplankton”) analysed in this study were from samples collected at Helgoland Roads ($54^{\circ} 11'3''$ N, $7^{\circ} 54'0''$ E) three times a week since 1975 (Greve *et al.*, 2004). Sea surface temperature (SST) data were sampled every working day (Wiltshire *et al.*, 2008). The weekly mean abundances of the zooplankton organisms together with the weekly mean SST as observed at Helgoland Roads are shown in Figure 5.2a–d during the period 1975 to 2004.

The selected data included adult *P. pileus*, juvenile *P. pileus*, juvenile *B. gracilis* (one of *P. pileus* most important predator), and a group of five small calanoid copepods (*Paracalanus parvus* (Claus, 1863), *Pseudocalanus elongatus* (Boeck, 1872), *Centropages* spp., *Acartia* spp.,

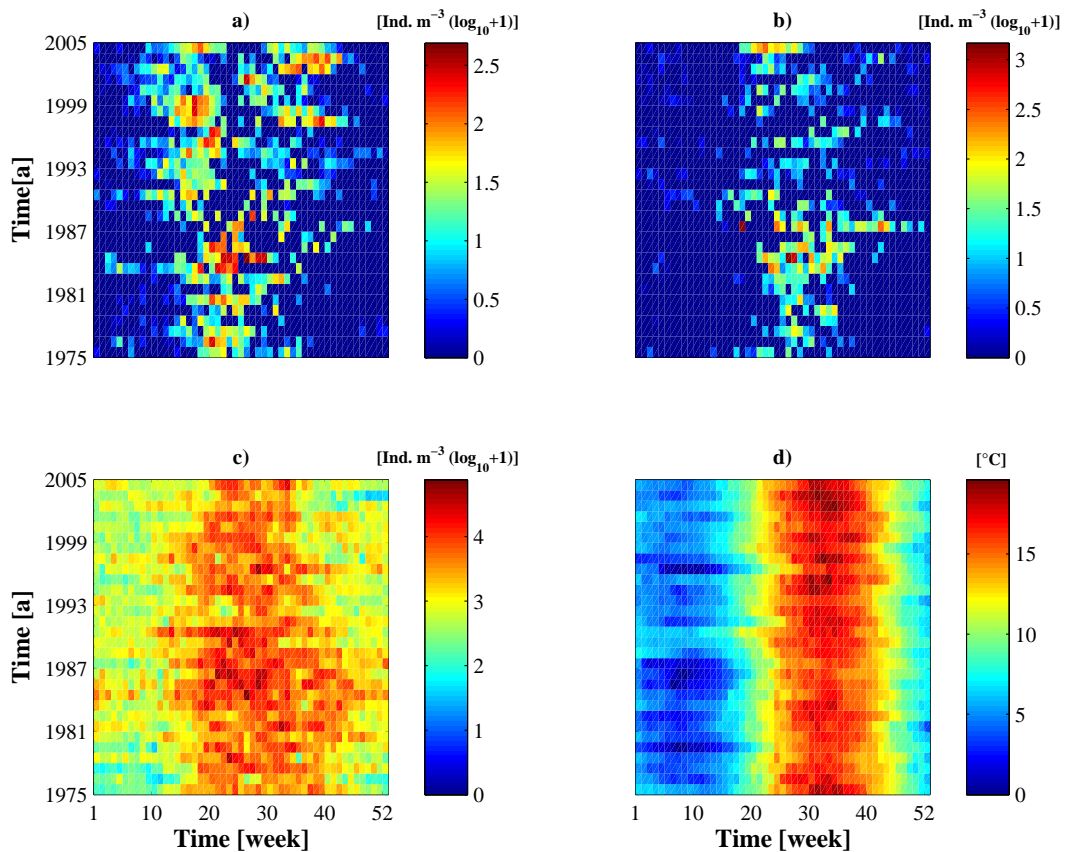


Figure 5.2: Weekly means during the period 1975 to 2004 of a) *Pleurobrachia pileus* abundances, b) *Beroe gracilis* abundances, c) copepod abundances, and of d) Sea Surface Temperature at Helgoland Roads.

Temora longicornis (O.F. Müller, 1785)), which are the most common copepods in the German Bight and represent the main food source for adult *P. pileus*. These copepods tended to co-occur each year, with some exceptional cases in which distinct succession patterns were noticeable. Periods of high *P. pileus* abundance tend to coincide with periods of high copepod abundance. Juvenile and adult *P. pileus* groups were analysed separately, although they are not independent from one another. From an ecological point of view, however, because of their size difference, they were decoupled into two distinct time series. The relations among these organisms are schematised in Figure 5.3.

To evaluate the potential phenological changes in all these groups, two indices as in Chapter 4 were defined: 1) the “Start Of Growth Period” (SOGP), i.e. the time at which organism populations began the build-up, associated with the week of the year during which the population reached a level corresponding to 15 % of the annual cumulative abundance, and 2) the “End Of Growth Period” (EOGP), associated with the week of the year during which the population reached a level corresponding to 85 % of the annual cumulative abundance. Sensitivity analysis indicated that these threshold levels were insensitive to variations of up to 30 % (results not shown). SST data were separated into multiple time series: one time series for each month, from January to June, over the period extending from 1975 to 2004. The monthly SSTs were also grouped into two main seasons, winter (from January to March) and spring (from April

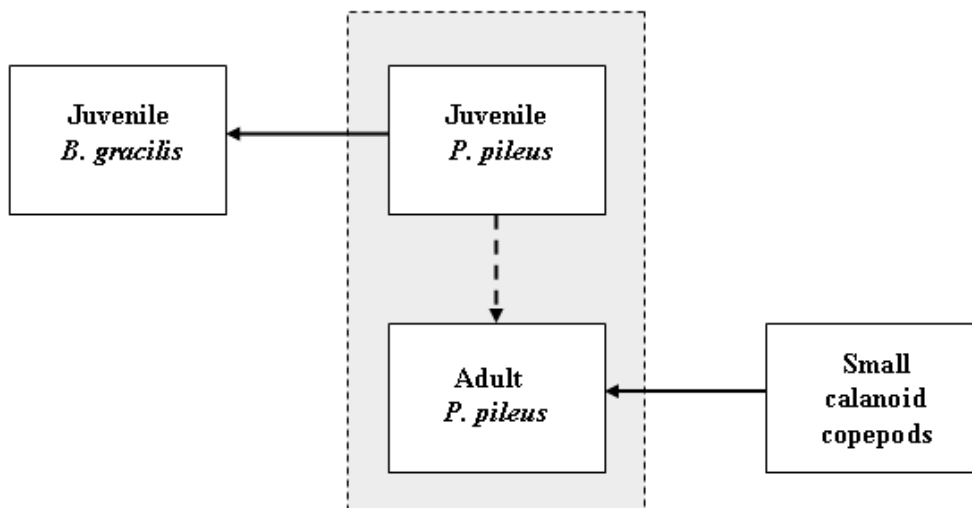


Figure 5.3: Relations among three zooplankton groups (*Beroe gracilis*, *Pleurobrachia pileus* and copepods) schematised in a diagram. The continuous arrow represents a feeding relationship and the dashed arrow shows coupling.

to June), to evaluate the different impacts of winter and spring temperatures on the organisms.

5.2.2 Bayesian Approach

Bayesian theory (*Gelman et al.*, 2004; *Sivia*, 2005) were used to characterize potential changes and correlations in the three zooplankton groups under study relative to temperature. Bayesian statistical methods use observations to update the probability that a hypothesis (model) is true. This approach was first used to detect phenological shifts in terrestrial systems by *Dose and Menzel* (2004), as it permitted the discovery of changes in the time series of phenological data and correlated these changes with potential driving factors, such as temperature (*Dose and Menzel*, 2006).

According to Bayesian statistics, a hypothesis H is evaluated by calculating the probability of the hypothesis given the observed data D and any background information I . In this respect, the Bayesian approach differs fundamentally from the frequentist view of orthodox statistics, which forbids assigning probabilities to hypotheses. Bayesian statistics is a straightforward application of the rules of probability theory to problems of data analysis. Two rules for manipulating conditional probabilities, the sum and the product rules, play an important role. The sum rule states that the probabilities of a proposition H and the proposition that H is false (signified by \bar{H}) add up to unity:

$$P(H|I) + P(\bar{H}|I) = 1. \quad (5.1)$$

Throughout this work, one will be concerned with exclusive and exhaustive hypotheses, so that if one particular hypothesis is true, all the others are false. For such hypotheses the normalization rule

$$\sum_i p(H_i|I) = 1 \quad (5.2)$$

holds. The product rule states that a joint probability or probability density function $P(H, D|I)$ can be factorized such that one of the propositions becomes part of the condition. Due to the symmetry with respect to H and D , this can be expressed as follows

$$P(H, D|I) = P(H|I) P(D|H, I) = P(D|I) P(H|D, I). \quad (5.3)$$

The second equality leads to Bayes' theorem

$$P(H|D, I) = \frac{P(H|I) P(D|H, I)}{P(D|I)}, \quad (5.4)$$

where H is the hypothesis, and D is the data. $P(H|D, I)$, known as the posterior, is the probability that the hypothesis H is true given the data D and any additional information I . $P(H|I)$, known as the prior, represents the initial state of knowledge; it is the probability that H is true before analyzing the data. $P(D|H, I)$, known as the likelihood, is the probability of measuring the data D when the hypothesis H is true. The remaining term, $P(D|I)$, is known as the evidence.

The posterior probability provides the full description of the state of knowledge about the hypothesis H . Since the denominator in equation (5.4) is a constant with respect to H , this equation is of the form

$$\textit{posterior probability} \propto \textit{prior probability} \times \textit{likelihood}. \quad (5.5)$$

This relation shows how the likelihood modifies the initial knowledge (as given by the prior) and produces an updated probability estimate that takes into account the new information provided by the data. The term $P(D|I)$ that appears in the denominator in equation (5.4) plays the role of a normalization factor, and it may be calculated from the requirement that $P(H|D, I)$ be normalized to one.

To carry out a Bayesian analysis, one needs to calculate the posterior and derive quantities of interest from it; e.g., marginal probabilities, best estimates of parameter values, etc. Such calculations can not be done analytically except for very special cases but, fortunately, there are good numerical techniques available for this (*Gelman et al.*, 2004).

5.2.3 Model specification and comparison

Three models were considered: 1) a constant model (M1), which assumed that the time series under investigation had no change, 2) a linear model (M2), which assumed that a linear trend was present (either increasing or decreasing), and 3) a change-point model (M3), which assumed that there were at least one and possibly more step-like shifts in the time series.

To model the spread in the data, one assumes that the observed values \mathbf{D} are normally distributed with unknown mean $\boldsymbol{\mu}$ and variance σ^2 . In terms of the precision τ , which is defined by $\tau = \sigma^{-2}$, one has

$$D_t \sim N(\mu_t, \tau), \quad (5.6)$$

where N indicates a normal distribution. While other distributions are possible, a normal distribution was chosen here because no additional information is existing that would suggest the need to introduce a more complex distribution to model the spread in the data.

The likelihood $P(\mathbf{D}|\boldsymbol{\mu}, \tau)$ for a sample of n data points (in this case $n = 30$ years, from 1975 to 2004) reads

$$P(\mathbf{D}|\boldsymbol{\mu}, \tau) = \left(\frac{1}{\sqrt{2\pi/\tau}} \right)^n \exp \left\{ -\frac{\tau}{2} \cdot \sum_{t=1}^n (D_t - \mu_t)^2 \right\}. \quad (5.7)$$

The functional form of μ_t is different for each of the three models. Note that the hypotheses H that are being addressed here are that μ_t and τ (or, correspondingly, σ) take particular values, which for μ_t may depend on time in the case of models M2 and M3.

For this analysis, standard, “noninformative” priors were chosen which reflect a lack of detailed prior knowledge regarding any trend in the data.

The main features of each model are discussed, now.

(1) The constant model M1 assumes that $\mu_t = a$ where a is a constant; i.e., a time independent μ . The parameters of the model are a and τ , and a prior $P(a, \tau|I) = P(a|I)P(\tau|I)$ with a uniform distribution for the prior of a and an appropriate gamma distribution for the prior of τ were chosen.

(2) The linear model M2 assumes a linear increase or decrease of the data with time, where μ_t is expressed as

$$\mu_t = a + bt. \quad (5.8)$$

The parameters of the model are a , b and τ , and a prior $P(a, b, \tau|I) = P(a|I)P(b|I)P(\tau|I)$ with uniform distributions for the priors of a and b and an appropriate gamma distribution for the prior of τ were chosen.

(3) The change point model M3 assumes that μ_t is constant everywhere except at one point in time, where it changes abruptly. Then,

$$\mu_t = \begin{cases} \mu_1, & \text{if } t < c \\ \mu_2, & \text{if } t \geq c \end{cases}, \quad (5.9)$$

where c is the change point and μ_1 and μ_2 are the values of μ before and after the change point. The parameters of the model are μ_1 , μ_2 , c and τ , and a prior $P(\mu_1, \mu_2, c, \tau|I) = P(\mu_1|I)P(\mu_2|I)P(c|I)P(\tau|I)$ with uniform distributions for the priors of μ_1 , μ_2 and c and an appropriate gamma distribution for the prior of τ were chosen.

These three models were also applied to the time series of various forcing variables.

All calculations were done using the software WinBUGS (*Lunn et al.*, 2000).

5.2.4 Model selection

To compare these three different models, a Bayesian model comparison method called Deviance Information Criterion (DIC) was used, (*Spiegelhalter et al.* (2002); *Gelman et al.* (2004)). The main idea behind DIC is to rank competing models based on a trade-off between the fit of the model to the data and the corresponding complexity of the model. The goodness of fit is measured via the deviance,

$$D(\theta) = -2 \log L(D|\theta). \quad (5.10)$$

where θ are the parameters of a model. The complexity is measured by estimating the number of effective parameters,

$$p_D = \bar{D} - D(\bar{\theta}); \quad (5.11)$$

i.e. posterior mean deviance minus deviance evaluated at the posterior mean of the parameters. The DIC is then defined as

$$DIC = D(\bar{\theta}) + 2p_D = \bar{D} + p_D. \quad (5.12)$$

Models with smaller DIC are better supported by the data. Differences of more than 10 might rule out the model with higher DIC, and differences above 5 are considered substantial.

5.2.5 Correlation between forcing and SOGP

In order to assess the strength of the linear relationship between an external forcing and the SOGPs of the zooplankton organisms the correlation structure from the two time series was estimated. The most commonly used index of correlation is the Pearson's product moment correlation coefficient, which will be considered here. This coefficient is equal to the covariance of the two variables divided by their standard deviations and is a measure of the strength of linear dependence between two variables. The correlation is +1 when there is an increasing linear relationship and -1 when there is a decreasing linear relationship. In other cases the correlation coefficient takes intermediate values, with a value of zero representing no correlation.

To carry out this calculation, a change point model like the one introduced before (model M3) was assumed, except that the likelihood of equation (5.7) by a bivariate normal distribution for the paired variables was replaced,

$$P(\mathbf{D}|\boldsymbol{\mu}, \Sigma) \propto |\Sigma|^{-1/2} \exp \left\{ -\frac{1}{2} \sum_{t=1}^n (\mathbf{D}_t - \boldsymbol{\mu}_t)^T \Sigma^{-1} (\mathbf{D}_t - \boldsymbol{\mu}_t) \right\} \quad (5.13)$$

where \mathbf{D}_t and $\boldsymbol{\mu}_t$ are now vectors of length 2 and Σ is a 2×2 variance matrix which is symmetric and positive definite. Standard, "noninformative" priors were chosen that generalized the ones selected for the analysis done with model M3; i.e., uniform distributions for the priors associated with $\boldsymbol{\mu}$ and the change point c , and an appropriate Wishart distribution for the priors associated with the matrix Σ^{-1} .

From the probabilities of the elements of the variance matrix it is straightforward to calculate the probability of the correlation coefficient. The advantage of this Bayesian approach relative to the usual frequentist procedure is that the former captures the joint uncertainty in the correlation induced by the data in all parameters, including variances and co-variances without the need of assuming a fixed and known correlation structure.

5.2.6 Testing predator–prey relationship hypotheses

At the position in the time series at which a step–like shift was detected, the strength of the predator–prey relationship between juvenile *P. pileus* and *B. gracilis* was characterised by calculating the Bayesian probability for observing the difference between the time series of the SOGP of *Beroe* and the time series of the EOGP of *P. pileus* ($\text{diff} = \text{SOGP}_{B.gracilis} - \text{EOGP}_{P.pileus}$), both during the period prior to the shift (the first regime, R1) and during the period after the shift (the second regime, R2). A high probability of small differences indicated a strong predator–prey relationship.

To test if a shift in abundance of *P. pileus* could have affected the abundance of the calanoid copepods, two time series were constructed: one for the copepod total spring abundances (from April to June) and another for the copepod total autumn abundances (from October to December). The probability of observing the difference between the two regimes in each time series was calculated.

For each hypothesis, independent samples from two normal distributions were considered and unknown variances were assumed. The formulation for $t = 1, \dots, n$ is as follows:

$$D_{at} \sim N(\mu_a, \tau_a) \text{ and } D_{bt} \sim N(\mu_b, \tau_b), \quad (5.14)$$

and the quantity of interest is the posterior distribution of

$$\delta = \mu_a - \mu_b. \quad (5.15)$$

5.3 Results

5.3.1 Model selection

As detailed in Section 5.2, three different models were tested: 1) no trend in the time series (model M1), 2) linear increasing or decreasing trend in the time series (model M2), and 3) change point like shift in the time series (model M3). The models were ranked using the Deviance Information Criterion (DIC).

The analyses based on the DIC indicated that the change–point model was best supported by the SOGP data for the *P. pileus* juvenile, *P. pileus* adult and *B. gracilis* juvenile (see

Table 5.1). The linear model was ranked second, and the constant model was ranked third in importance. The only exception was found in the copepod SOGP time series, for which the linear model was ranked first, followed by the change–point model, then by the constant model in importance. It is important to note that all models, M1, M2, and M3, exhibited a similar DIC for the copepods, suggesting that all models were equivalent (although not identical) in this case.

Figure 5.4 shows (in circles) the SOGP data for the *P. pileus* juvenile, *P. pileus* adult, *B. gracilis* juvenile and copepods, the average functional behaviour of the data calculated using the change–point model (continuous line), and the corresponding 95% credible intervals (dotted lines). The modelled evolution of the average SOGPs showed a step toward earlier weeks within the years 1987–1989, leading to permanent advances in the timings of their phenological occurrence in the following years. The shift was less pronounced in the SOGP data for copepods, for which a linear decreasing trend was determined to be most likely (see DIC values in Table 5.1). The step in the mean evolution of the SOGPs was sharpest in the adult *P. pileus* data.

For the period 1975–1987, the mean SOGP of *P. pileus* juvenile occurred around week 20 (Figure 5.4a), the mean SOGP of *P. pileus* adult occurred around week 21 (Figure 5.4b),

Table 5.1: Ranking of different models using DIC: comparison of the constant, linear, and change–point model for the SOGP of *Pleurobrachia pileus* juvenile, *Pleurobrachia pileus* adult, *Beroe gracilis* juvenile and copepods at Helgoland Roads.

| Species | Model | DIC | Best ranked model |
|--------------------------------|----------|--------|-------------------|
| <i>P. pileus</i> juvenile | Constant | 182.15 | Step |
| | Linear | 178.82 | |
| | Step | 171.82 | |
| <i>P. pileus</i> adult | Constant | 195.39 | Step |
| | Linear | 167.1 | |
| | Step | 143.71 | |
| <i>B. gracilis</i> juvenile | Constant | 189.1 | Step |
| | Linear | 183.53 | |
| | Step | 178.24 | |
| Copepods | Constant | 142.68 | Linear/step |
| | Linear | 138.92 | |
| | Step | 141.27 | |

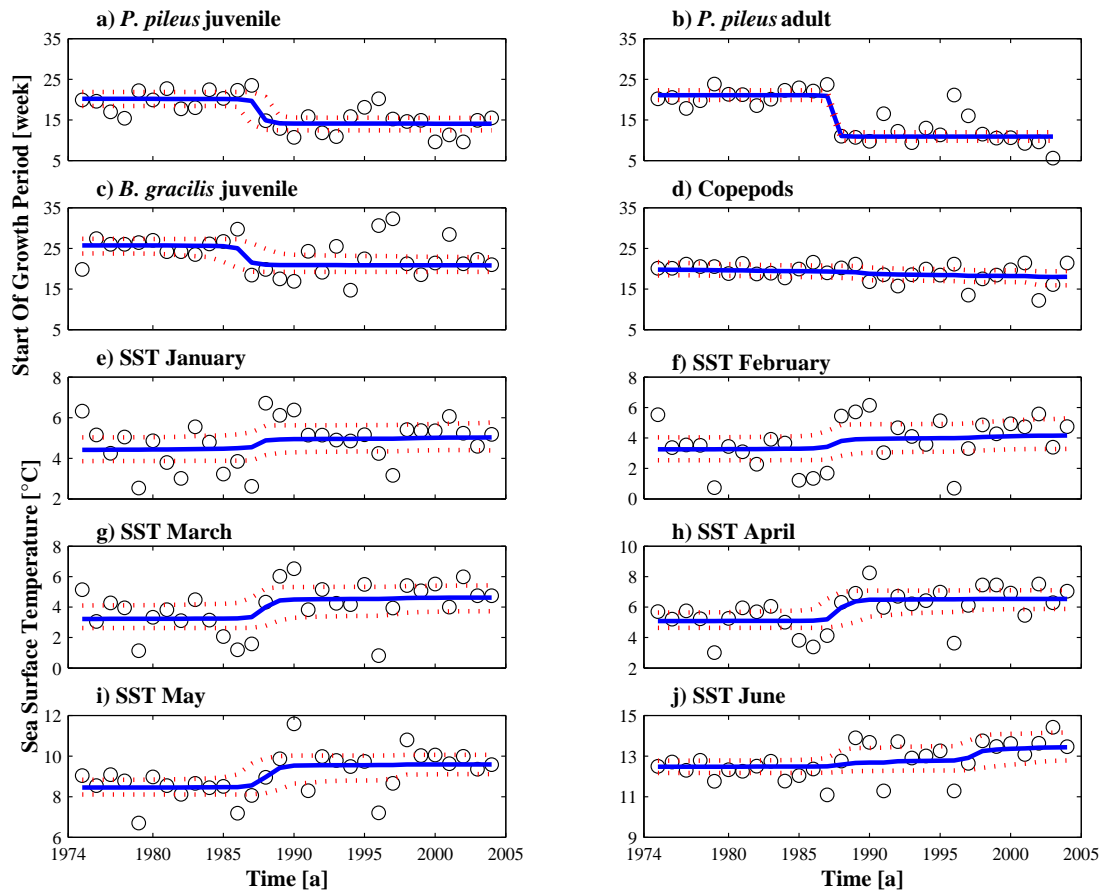


Figure 5.4: SOGP (in circles) of the respective zooplankton groups at Helgoland Roads in terms of weeks after the beginning of the year, together with the mean evolution of the phenological time series of the zooplankton data (line) calculated using the change–point model and the corresponding 95 % credible interval (dotted line) from 1975 to 2004: a) SOGP of *Pleurobrachia pileus* juvenile, b) SOGP of *Pleurobrachia pileus* adult, c) SOGP of *Beroe gracilis* juvenile, d) SOGP of copepods. Monthly mean SST at Helgoland Roads (open circles) from 1975 to 2004, together with the calculated evolution of the mean temperature using the change–point model (black line) and its 95 % credible interval (dotted line) for: e) SST of January, f) SST of February, g) SST of March, h) SST of April, i) SST of May, j) SST of June.

and the mean SOGP occurred around week 25 for *B. gracilis* juvenile (Figure 5.4c). For the period 1989–2004, the mean SOGP shifted forward to week 14 for *P. pileus* juvenile, to week 11 for *P. pileus* adult, and to week 21 for *B. gracilis* juvenile. In contrast, the SOGPs of the calanoid copepods were relatively stable (Figure 5.4d).

Based on the DIC the favoured model (see Table 5.2) appeared to be the change–point model in the monthly SST data as well. The linear model, however, was also supported by the data for January, March, April, and May. The constant model was ranked third. Figure 5.4

Table 5.2: Ranking of different models using DIC: comparison of the constant, linear, and change–point model for monthly mean SST at Helgoland Roads.

| Month | Model | DIC | Best ranked model |
|--------------|----------|--------|-------------------|
| SST January | Constant | 136.24 | Step |
| | Linear | 133.33 | |
| | Step | 130.22 | |
| SST February | Constant | 161.26 | Step |
| | Linear | 158.17 | |
| | Step | 153.18 | |
| SST March | Constant | 160.3 | Step |
| | Linear | 152.96 | |
| | Step | 149.17 | |
| SST April | Constant | 147.17 | Step |
| | Linear | 137.79 | |
| | Step | 134.75 | |
| SST May | Constant | 126.07 | Step |
| | Linear | 117.14 | |
| | Step | 113.69 | |
| SST June | Constant | 108.15 | Step |
| | Linear | 102.16 | |
| | Step | 95.28 | |

shows the modelled SST time series (from January to June, panels e–j), along with the corresponding 95 % credible intervals. Concomitant with the shift in the phenological data, a shift toward persisting higher mean temperatures occurred in the years between 1987 to 1989 in all time series, with the only exception being June annual SST, which showed a second step–like change in the year 1998. March and May annual values (Figures 5.4g and 5.4i) showed the steepest shifts.

5.3.2 Change point analysis

Figure 5.5 shows the probability distribution of a single change point in the phenophases of the three zooplankton types and in the winter and spring SSTs. The highest probability for a change point in the week representing the SOGP centred on the years 1988/89 both for *P. pileus* and *B. gracilis* (Figure 5.5a). The probability that the SOGP of copepods changed in a step–like fashion was considerably smaller than the probability for step–like SOGP changes in *P. pileus* and *B. gracilis* data and was centred around the years 1990/91. Low probabilities

of additional step-like changes in the SOGP time series of copepods were noticeable in the years 1997 and 2002.

The probability for a change point in SST winter and SST spring was highest in the years 1987–1989 (Figure 5.5b), which corresponded to a concomitant change in the phenological time series of the ctenophores.

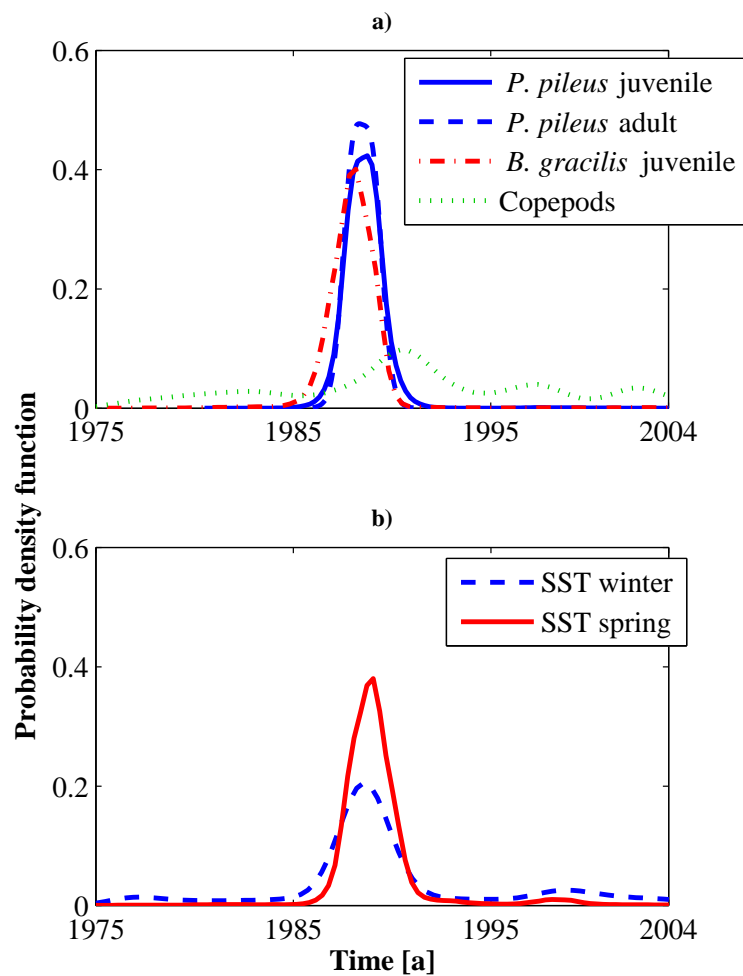


Figure 5.5: a) Probability for a change-point in the SOGP of *Pleurobrachia pileus* juvenile (continuous blue line), the SOGP of *Pleurobrachia pileus* adult (dashed blue line), the SOGP of *Beroe gracilis* juvenile (dashed dotted red line), the SOGP of copepods (dotted green line) from 1975 to 2004 and b) the probability for a change-point in the seasonal mean SST from 1975 to 2004: SST winter (dashed blue line) and SST spring (continuous red line).

Table 5.3: Median of the posterior distribution of the correlation coefficient for seasonal mean winter and spring SST and the SOGP of the zooplankton groups (*Pleurobrachia pileus* juvenile, *Pleurobrachia pileus* adult, *Beroe gracilis* juvenile and copepods), along with the 95 % credible interval.

| | <i>P. pileus</i> juvenile | <i>P. pileus</i> adult | <i>B. gracilis</i> juvenile | Copepods |
|------------|---------------------------|------------------------|-----------------------------|---------------------|
| SST winter | -0.59 (-0.79, -0.3) | -0.65 (-0.82, -0.37) | -0.53 (-0.75, -0.21) | -0.11 (-0.46, 0.25) |
| SST spring | -0.69 (-0.81, -0.36) | -0.77 (-0.89, -0.57) | -0.59 (-0.79, -0.27) | -0.2 (-0.53, 0.16) |

Table 5.4: Median of the posterior distribution of the correlation coefficient for the change rate of seasonal mean winter and spring SST and the change rate of the SOGP of the zooplankton groups (*Pleurobrachia pileus* juvenile, *Pleurobrachia pileus* adult, *Beroe gracilis* juvenile and copepods), along with the 95 % credible interval.

| | d <i>P. pileus</i> juvenile | d <i>P. pileus</i> adult | d <i>B. gracilis</i> juvenile | dCopepods |
|-------------|-----------------------------|--------------------------|-------------------------------|----------------------|
| dSST winter | -0.61 (-0.8, -0.3) | -0.74 (-0.87, -0.5) | -0.35 (-0.63, 0.02) | -0.26 (-0.58, 0.11) |
| dSST spring | -0.66 (-0.83, -0.4) | -0.76 (-0.88, -0.54) | -0.5 (-0.74, -0.17) | -0.38 (-0.66, -0.02) |

5.3.3 Correlation analysis

A Bayesian correlation (see Section 5.2 for details on the method used) between ctenophore abundance and SST winter indicated an advance in the timings of their phenological occurrence corresponding with a temperature rise ($r = -0.6$). This same correspondence pattern was especially strong for SST spring (Table 5.3). These analyses clearly indicated that changes in SST winter and SST spring are strongly correlated with the shifts to earlier times in the SOGPs of *P. pileus* and *B. gracilis*. The correlations between the SOGPs and SST spring were higher than the correlations between the SOGPs and SST winter, suggesting a strong sensitivity of the gelatinous zooplankton to temperatures at the beginning of the bloom season. Changes in temperature appeared to have a minor impact on the phenophase of copepods (correlation coefficient of about -0.2 , Table 5.3).

The importance of temperature as a determinant for the SOGP of gelatinous zooplankton was deduced by the relation between the year-to-year changes in the SOGPs (indicated by dSOGP) and the year-to-year changes in winter and spring temperatures (indicated by dSST winter and dSST spring, see Figure 5.6. For example, dSOGP of *P. pileus* could be advanced by up to eight weeks if dSST spring increased by approximately $1\text{--}2^\circ\text{C}$ (Figure 5.6a). The correlation analyses indicated that dSOGP and dSST spring time series yielded the best correlation (results are summarised in Table 5.4). This was also confirmed by a linear regression analysis using the Bayesian approach, shown in Figure 5.6.

5.3.4 Changes in seasonal occurrence

Following the results of the change-point analysis, the zooplankton abundances were averaged over two different periods (Figure 5.7): one period, regime 1 (R1), was defined from 1975 to 1987, and another period, regime 2 (R2), was defined from 1988 to 2004.

In R1, *P. pileus* phenology was characterised by a unimodal distribution with peak abundance at around weeks 23–25 (Figure 5.7a, dashed lines). In R2, the phenology of *P. pileus* was different, and was characterised by a bimodal distribution with a minimum abundance around weeks 23–25 (Figure 5.7b, dashed lines). The spring increase in abundance advanced in time from mid-late June in R1 to April–May in R2. Also, the total annual abundance increased from about $7,200$ individuals m^{-3} in R1 to about $9,800$ individuals m^{-3} in R2.

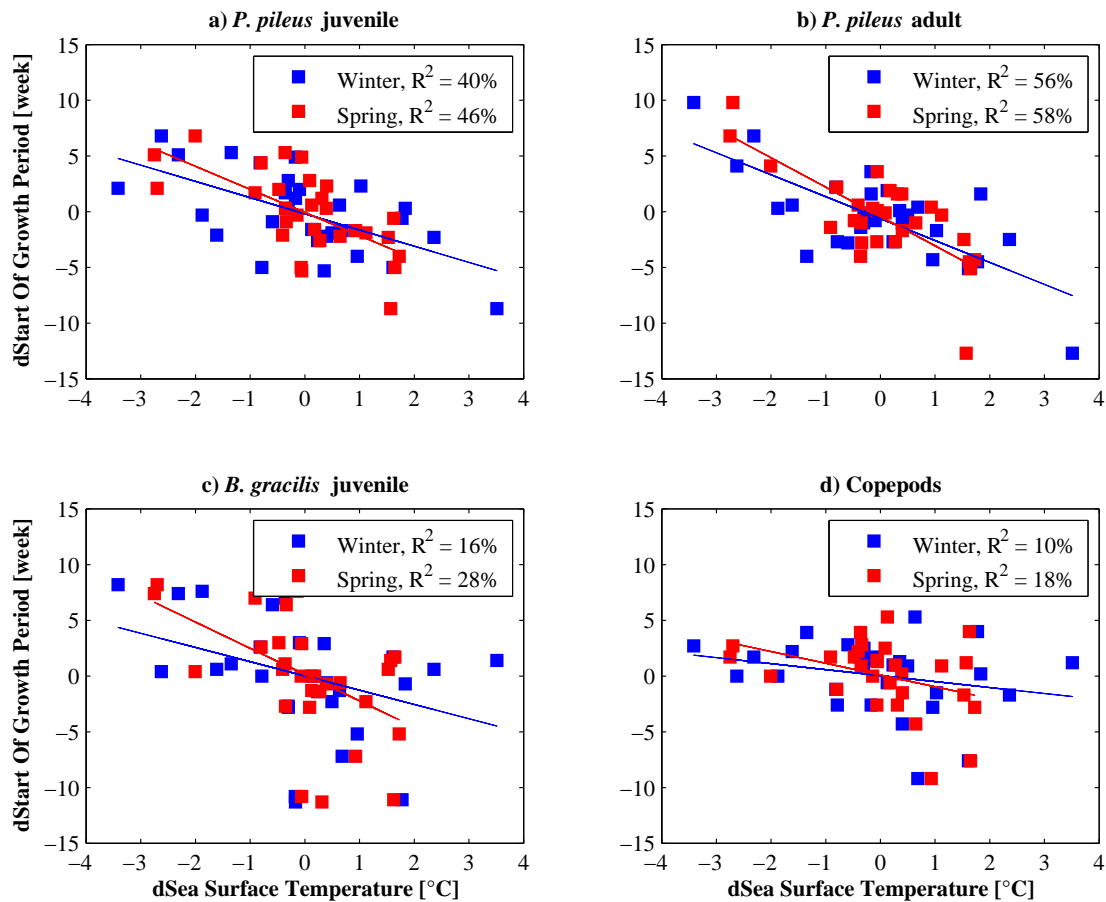


Figure 5.6: Annual change rate of seasonal mean winter SST versus annual change rate of SOGP (blue squares) of a) *Pleurobrachia pileus* juvenile, b) *Pleurobrachia pileus* adult, c) *Beroe gracilis* juvenile and d) copepods, and the slope of the relationship calculated using the Bayesian model (blue line) for the time period from 1975 to 2004. Annual change rate of seasonal mean spring SST versus the annual change rate of SOGP (red squares) of a) *Pleurobrachia pileus* juvenile, b) *Pleurobrachia pileus* adult, c) *Beroe gracilis* juvenile and d) copepods, and the slope of the relationship calculated using the Bayesian model (red line) for the time period from 1975 to 2004. The probability of R^2 was calculated for the best estimate of the parameters from the Bayesian analysis.

In contrast, *B. gracilis* exhibited a single population maximum in both periods (R1 and R2 in Figure 5.7a–b, dotted line). The phenologies of *B. gracilis* differed somewhat between the two regimes, but they differed to a far lesser extent than the phenologies of *P. pileus*. The total annual abundance in R1 (8,700 individual m^{-3}) was greater than in R2 (3,200 individual m^{-3}). The populations of *B. gracilis* and *P. pileus*, however, showed a predator–prey like pattern in both periods (R1 and R2). The copepod data showed a single maximum in the organism population between weeks 20–35 in both regimes (Figure 5.7a–b, grey lines). The distribution width was somewhat narrower in R2 compared to the distribution width in R1.

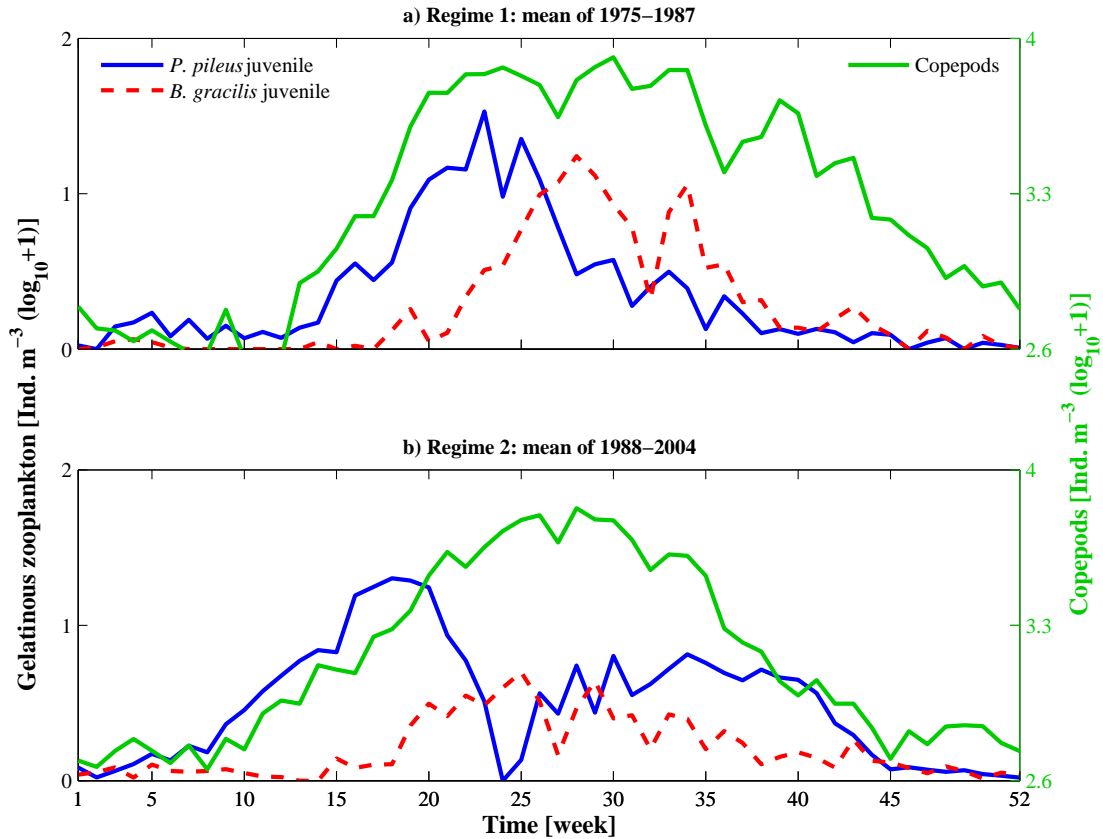


Figure 5.7: Two seasonal mean abundances of *Pleurobrachia pileus* juvenile (continuous blue line), *Beroe gracilis* juvenile (dashed red line) and copepods (green line), a) for regime 1 (R1; from 1975 to 1987) and b) for regime 2 (R2; from 1988 to 2004).

5.3.5 Predator–prey relationships

The strength of the predator–prey relationship between *P. pileus* and *B. gracilis* was investigated by calculating the probability of the difference between two phenophases, in this case the difference was between $EOGP_{P.pileusjuvenile}$ and $SOGP_{B.gracilisjuvenile}$ (the method is described in detail in Section 5.2). The time overlap of about four weeks between $SOGP_{B.gracilisjuvenile}$ and $EOGP_{P.pileusjuvenile}$ suggested a strong predator–prey relationship (see Figure 5.8a) in R1, whereas a probability maximum centred on positive values (two weeks) supported a weaker predator–prey relationship in R2 (Figure 5.8b).

To test if a shift in abundance of *P. pileus* could have affected the abundance of the calanoid copepods, the probability of observing the difference between the two regimes in the copepods' spring and autumn abundance time series was calculated using the Bayesian approach. The copepod spring abundance (from April to June) was reduced to about 500 individuals m⁻³

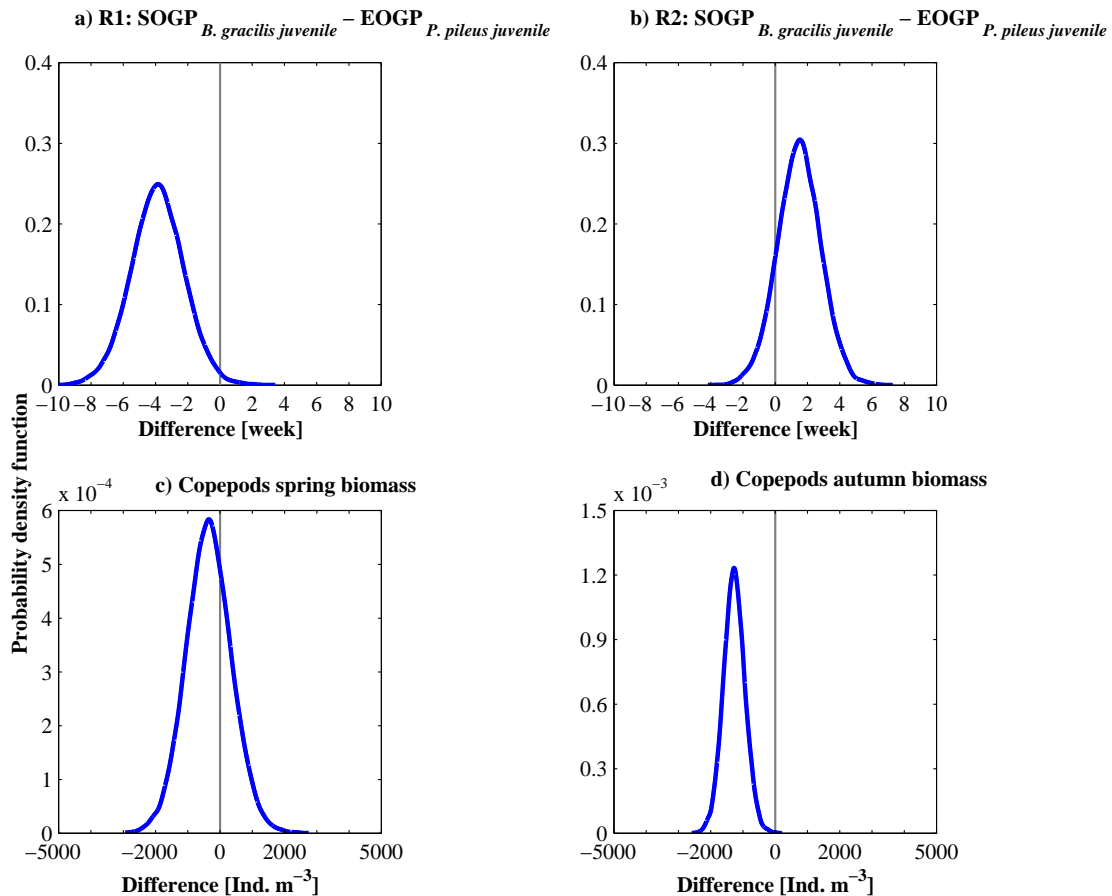


Figure 5.8: Probability density function of the difference between the SOGP in the annual abundance of *Beroe gracilis* juvenile and the EOGP of the first peak in the annual abundance of *Pleurobrachia pileus* juvenile for a) R1 (1975–1987) and b) R2 (1988–2004). Probability density function of c) the difference between the time series of copepods total spring abundance in R1 (1975–1987) and in R2 (1988–2004), and d) the difference between the time series of copepods total autumn abundance in R1 (1975–1987) and in R2 (1988–2004).

from R1 to R2. Note, however, that the evidence for such a change remained small because the 95 % credible interval (−1717.0 to +1066.0) included zero. The difference in abundance relative to the autumn period (from October to December) was more pronounced (see Figure 5.8b), with a reduction in R2 to about 1275 individuals m^{−3}.

5.4 Discussion and conclusions

The analysis of the timings of phenological occurrences of the three zooplankton groups provided an effective method for the detection of ecological changes in the populations of organisms related to climate change. Bayesian statistics provided a mathematically rigorous

framework for testing hypotheses (or models), and permitted the quantitative expression of results in terms of probabilities.

This study used the DIC criterion to evaluate three different models for the potential patterns in the phenological time series: 1) no change, 2) linear change, and 3) step-like change. In general, bloom timings of *P. pileus* (Figure 5.4a and 5.4b), *B. gracilis* (Figure 5.4c) and annual SSTs (Figure 5.4e–j) followed a similar pattern of change that, in general, was best represented by a step-like shift. A linear increasing or decreasing trend was found to be less likely, with the only exception being the phenological time series of copepods (Table 5.1). The constant model was ranked the least probable for all organisms, although for copepods the differences among the models were small (see Tables 5.1 and 5.2).

The highest probability for a step-like change in the SOGPs of *P. pileus* and *B. gracilis* was obtained in the year 1988/89 (Figure 5.5a) coincident with the step-like changes in SST winter and SST spring (Figure 5.5b). The timing of this step-change agreed with the timing of a regime shift, described by *Beaugrand and Ibanez* (2004) and *Schlüter et al.* (2008), in biological and hydrometeorological variables of the southern North Sea and German Bight. In line with previous findings (*Greve et al.*, 2004), the change-point analysis showed good correlation between the SOGP of *P. pileus* and SST winter. The correlation, however, improved when SST spring was considered, suggesting that the timing of the blooms were sensitive to the temperature conditions occurring in the bloom season.

The relatively high correlation between the spring bloom timings of ctenophores and SST winter (Table 5.3) and the higher winter densities of *P. pileus* of the second regime (Figure 5.7) support the hypothesis (*Purcell and Arai*, 2001; *Sullivan et al.*, 2001) of an effect of warm winter conditions on the survival and success of overwintering adults. The higher correlation found between the spring abundances and SST spring (Table 5.3) suggested a cause-effect relationship between warmer temperatures and the earlier ctenophore appearance during R2 via impacts on metabolic processes (*Molinero et al.*, 2008) and ovule production. In fact, the year-to-year changes in winter and spring temperatures were linearly related to the year-to-year changes in the SOGP of the ctenophores. The steeper slopes obtained from SST spring (Figure 5.6) confirmed that variations in spring bloom timings were more sensitive to spring SST than to winter SST.

This study also highlighted the differential impact of temperature on two different but adjacent trophic levels (copepods and their predator *P. pileus*), possibly through different

temperature tolerances. Only relatively modest changes in copepod phenology (Figure 5.4d and 5.5a) were detected, suggesting that a step-like shift toward warmer conditions had little influence on the whole group of these five copepods due to complex life history traits, e.g. diapause, larval development and dissimilarities in food requirements for the different life stages. When considered individually, these five copepods tended to co-occur each year, with some exceptional cases in which distinct succession patterns were noticeable. Generally, periods of high *P. pileus* abundances occurred during periods of high copepod abundance (see Figure 5.7). Ctenophores, nevertheless, are capable of causing marked decreases in copepods (Greve and Reiners, 1988; Kuipers et al., 1990; Purcell and Decker, 2005). The present study indicated a weak predator-prey like pattern between copepods and *P. pileus* in the spring (Figure 5.8c). The appearance of a second reproductive phase of *P. pileus* during R2, however, had an impact on the copepod group (Figure 5.8d), related to a reduction in the average autumn biomass (compare also Figure 5.7a with Figure 5.7b).

This study showed a remarkably robust predator-prey relationship between *B. gracilis* and *P. pileus*, during R1 (Figure 5.8a). Such a feature was less pronounced during R2 (Figure 5.8b), when *P. pileus* was characterised by two distinct reproductive phases. Although *B. gracilis* appeared to drive the decline of the first peak in *P. pileus* abundance, this seemed less likely for the decline of the second peak. The lower abundances of *B. gracilis* during R2 could be caused by a detrimental effect of warming conditions on this organism, an interpretation supported by the narrow thermal tolerance of *B. gracilis* (Purcell and Decker, 2005). The increase in mean temperature during the second regime made a second reproductive phase of *P. pileus* possible after *B. gracilis* had declined. This mismatch appeared responsible for the all-season presence of *P. pileus* in the plankton community of the German Bight.

However, the three interacting groups investigated in this study represented only a cross-section of the more complex ecosystem, and the importance of other factors cannot be excluded. Transport processes, for example, are among those aspects that contribute to the intricacies of the system (Williams and Collins, 1985; Greve and Reiners, 1988; Wang et al., 1995). Aggregation (Graham et al., 2001), complex life histories (Schneider, 1987; Greve et al., 1996) and adaptation are other processes that complicate the system, but these factors could not be considered here because of the difficulties associated with their quantification.

The fact that *P. pileus* extended its annual presence may lead to diverse consequences through various other top down (increased predation on fish eggs and larvae) and bottom up processes that could not be considered in this study but may ultimately cause ecosystem-wide disruption.

tions (Hay, 2006). North Sea fish stocks, for example, are presently in an alarming state of decline (ICES, 2008). Gelatinous zooplankton outbreaks could potentially exacerbate this situation and may lead to trophic dead ends by channelling the flow of energy to “waste” (in the sense of lost fish production).

Chapter 6

Concluding remarks

The work presented in this thesis contributed to untangling the effects of changes in various physical and biogeochemical variables on the ecosystem of the southern North Sea with an emphasis on long-term variability. A growing body of evidence shows that various marine ecosystems around the northern part of the globe, including the North Sea, have experienced regime shifts in relation to climate change. The main objectives of this study were: to explore the general mode of variability of the entire German Bight ecosystem, to single out the major environmental drivers of the long-term changes in the biogeochemistry and ecology of the region, and to investigate in detail the successional changes of key phytoplankton and zooplankton organisms and single out the associated consequences for their predator-prey relationships. As explained in the introduction of this thesis, it is still a matter of debate how climate change may affect the functioning of ecosystems. This study provided for the first time a detailed understanding of climate variability of the German Bight region, by combining a wide set of physical, biological and chemical data. A number of long-term changes of the biogeochemical variables were described and, with a combination of statistical methods, these changes were linked to environmental forcing.

A common assumption in climate variability studies is that long-term changes in the biogeochemistry are always related to changes in the physical environment. The results presented in Chapters 3, 4 and 5 showed that this assumption can be misleading. Only in a few cases the observed changes in the most representative plankton organisms of the German Bight could be linked to temperature (see Chapter 3). Temperature was strongly related to a persistent shift in 1987/88 to earlier annual appearance of two important gelatinous zooplankton species (see Chapter 5). Changes in the community of five of the most common copepods and in some common diatom species, however, were not well correlated with sea surface temperature (SST) (Chapter 4 and Chapter 5). The analysis of three common diatom species (Chapter 4) showed that changes in SST affected the starting of the growth period of only one species, namely *Guinardia delicatula*. Other factors like predation and water transparency could explain the variability in the start of the growth periods (SOGPs). The results presented in Chapter 5 also suggested that a predator-prey decoupling between *Pleurobrachia pileus*

and *Beroe gracilis* could be related to increased warming conditions causing an extended annual presence of *Pleurobrachia pileus*. A coincident decline in copepods abundance during autumn could have favoured the advancement of the EOGPs of *Guinardia delicatula*. These results untangled the complex long-term interactions among gelatinous zooplankton under a changing climate and highlighted those factors, such as temperature and water transparency, that combine to drive diatom and copepod dynamics.

Chapter 3 presented the investigations of common modes of variability, using Principal Component Analysis (PCA), in a wide array of time series representing the physical and biogeochemical condition of the German Bight. The results of the PCA indicated the occurrence of a step-like change in the year 1987/88. This change fitted into the definition of regime shift proposed in this thesis and was related to a series of hydroclimatic changes primarily represented by an increase in temperature. The consequent changes in the ecosystem included the decrease in the spawning stock biomass of some fish species and the increase in abundance of gelatinous carnivores. An increase in red-tide-forming species was noted as suggested by their weight for the first principal component (PC1). Minor connections could be detected between the long-term changes in abiotic forcing and the populations of *Calanus helgolandicus* and between abiotic forcing and the diatom community, as suggested by the loadings for the PC1 (Figure 3.3). PC1 explained only 23% of the total variance in the data. The lack of a strong common signal in the biological data set indicated either that sea surface temperature was not a dominant factor, or that different species might have been affected differently by temperature. The same holds for inorganic nutrients which are strongly affected by anthropogenic changes (Chapter 3). Specific analysis of three distinct subsets of data (biological, climatic and chemical) provided further insights into the functioning of the German Bight system. On short time-scales (a few years), for example, the climate of the region resulted to be highly dynamic while the biological and chemical variables showed a much smoother behaviour.

The PCA (Chapter 3) performed on the full data set indicated that diatoms were not much correlated with the major mode of variability of the entire system (as represented by the first principal component), thus characterising the first trophic levels of the ecosystem as rather resilient. This outcome motivated detailed research on the dynamic of this important phytoplankton group. Further work, presented in Chapter 4, was therefore concentrated on the successional patterns of the three most representative (in terms of relative abundance and annual presence) diatom species of the German Bight, namely *Guinardia delicatula*, *Thalassionema nitzschioides* and *Odontella aurita*. Specific biological indices, defined *ad*

hoc by the temporal occurrences of the three species, were analysed in combination with several physical and grazing factors. Of the three diatoms, only the start of the growth period (SOGP) and the timing of decline (EOGP) of *G. delicatula* showed significant linear decreasing and increasing trends with time. The bloom timings of *G. delicatula* occurred earlier with preceding higher temperatures, while the bloom timings of *O. aurita* were advanced by stronger than average vertical mixing right before the bloom seasons. Lower water transparencies, by contrast, delayed the bloom timings of *T. nitzschioides*. In addition, the SOGPs of the diatoms were delayed at higher zooplankton grazing pressure. Earlier bloom timings of each diatom species occurred when their winter concentrations were higher than average and later bloom timings occurred when winter concentrations were lower than average. The differences in the factors determining the SOGP suggested therefore that climate warming might affect the onset of the blooms of the three diatom species in different ways. Multivariate linear regression analysis showed that sunshine duration could prolong the duration of the blooms of *T. nitzschioides* and *O. aurita* provided that enough nutrients were available. In the case of *G. delicatula*, however, sunshine duration was negatively correlated with EOGP. Higher zooplankton grazing pressure advanced the timing of decline of *G. delicatula* and *O. aurita* as suggested by their regression coefficients. The observed differences in the variables affecting the three diatom species implied that changes in the responsible factors might influence species assemblage and succession. Since the statistical models adopted revealed that it was always a combination of different factors leading to a reasonable representation of the variability in the data, additional observational or *ad hoc* laboratory experiments could help to further narrow down the number of driving factors and therefore to improve the understanding of these processes. Factors other than the ones considered here, such as advection of water masses with high phytoplankton concentration into the German Bight, represents, however, an important source of uncertainty in these analyses.

Further work was motivated by the need to put the results obtained by studying the variability in the three phytoplankton species into the wider context of the German Bight ecosystem. The next step was therefore to investigate the variability of some important organisms representing trophic levels adjacent to the ones of primary producers, specifically herbivores and carnivores. Chapter 5 presented analyses, performed with Bayesian statistics, on the seasonality of three interacting zooplankton groups: *Beroe gracilis*, *Pleurobrachia pileus* and copepods. The approach allows one to highlight changes in time series of phenological data and to correlate these changes with potential driving factors such as temperature. The Bayesian analyses also provide estimates of uncertainties because the adopted models

(called hypotheses) are defined according to probability theory. Bayesian statistics therefore provided a mathematically rigorous framework for testing hypotheses, and the results were quantitatively expressed in terms of probabilities. Following this approach, it was found that the phenology of the two ctenophores, the predator *B. gracilis* and its prey *P. pileus*, shifted in a step-like mode in the year 1987/88 to permanent earlier appearances. More specifically, the timing of the seasonal increases in the populations of *P. pileus* and *B. gracilis* correlated with step-like increases in winter and spring sea surface temperatures. The correlation, however, improved when SST spring was considered, suggesting that the timing of the blooms were sensitive to the temperature conditions occurring in the bloom season. These gelatinous zooplankton were also observed to respond quickly to every short-term variation in SSTs. From the analysis, a predator-prey decoupling between *B. gracilis* and *P. pileus* was inferred and it was attributed to an extended appearance (almost year-round) of *P. pileus* occurring in the second regime (from 1987/88 onwards). The variations in SST, however, had no impact on the seasonal appearance of copepods. This leads to the conclusion that copepods represented an important food source for *P. pileus* also later during the year when, after the second regime, *P. pileus* showed a second peak in abundance.

In final conclusion, this study has focused on some major components of the marine ecosystem of the German Bight represented by several abiotic factors and trophic levels. Taken together, the results of this work revealed a more coherent picture of how and on what time scales biology responds to physical changes. Part of the complex interactions among phytoplankton, zooplankton and fish and their environment have been elucidated. The results suggested that there are sometimes very rapid changes in the physical properties (e.g. air temperature) over the German Bight which were reflected in the water properties (e.g. SST). Of particular importance were changes on decadal and longer time scales. It was documented for the first time that the German Bight climate and ecological system experienced patterns of variability similar to the ones of the entire North Sea. The marine ecosystem responded on similar time scales to the variations in the physical conditions. The limited evidence available for the German Bight suggested that responses occur at almost all trophic levels. However, this highly eutrophicated coastal region was exposed to different natural and anthropogenic perturbations when compared to the North Sea as a whole. Detailed investigations into key organisms of the German Bight have revealed the differential impacts of major driving factors on different key species. Due to this differential reaction changes in the entire ecosystem are to be expected. Although temperature variation was the major driver of changes in the abundance and seasonality of higher trophic levels (top down effect), evidence was provided suggesting the importance of bottom up processes. A case in point was the

relation of temperature with the diatom *Guinardia delicatula*. While the cases presented here demonstrated marine ecosystem response to climate forcing, they provided only hints of the mechanisms of interaction. There might be more than one important mode of variability in the German Bight, even at the decadal scale, to which the marine biology responds. It is still a long way to a model predicting ecosystem response to specified climate variation because of time mismatches and nonlinearities in the atmosphere–ocean–biosphere system. Even with an appropriate model, enhanced monitoring of physical forcing and ecosystem response will be required to provide the data necessary for useful operational predictions. Nevertheless, further investigating the potential synchrony in ecological changes between the North Sea and local coastal regions like the German Bight, thereby linking large– and small–scale processes and their influence on the regional ecological systems, will result in a better understanding of the mechanisms that influence coastal ecosystems.

Appendix A

Appendix

Long-term time series, sources and temporal patterns

Detailed information of each time series for the Principal Component Analysis (Chapter 3) is given below in the following format: the variable number as in Chapter 2 Table 2.1 and 2.2, followed by the series name and source of origin. The pattern of each time series is shown at the end of Appendix A standardized to zero mean and unit standard deviation.

Biogeochemical indices

Prior to data analysis, all biological time series were log-transformed to approximate linear distribution.

Chemistry

1: Long-term annual winter mean of ammonium concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

2: Long-term annual winter mean of nitrogen concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

3: Long-term annual winter mean of nitrate concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

4: Long-term annual winter mean of phosphate concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

5: Long-term annual winter mean of silicate concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

6: Long-term annual mean of salinity as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

Phytoplankton

7: Long-term annual Mean Diatom Day (MDD) of the algal spring bloom as calculated by Wiltshire and Manly (2004) from algal measurements every work day at Helgoland Roads. For $MDD = \sum f_i d_i / \sum f_i$, where f_i is the diatom count on day d_i of the quarter, and the sum is over the available samples in the quarter, see Wiltshire and Manly (2004) for more explanation.

Source: Wiltshire and Manly (2004)

8: Long-term annual mean of total cell counts of diatoms as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005) and Wiltshire and Dürselen (2004)

9: Long-term spring mean (Mar, Apr, May) of total cell counts of diatoms as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005) and Wiltshire and Dürselen (2004)

Zooplankton

10: Long-term annual mean of *Pleurobrachia pileus* juvenile NN in individuals m^{-3} as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpubl.)

11 Long-term annual mean of *Pleurobrachia pileus* adult CN in individuals m^{-3} as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpubl.)

12: Long-term annual mean of *Noctiluca scintillans* NN in individuals m^{-3} as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpubl.)

13: Long-term annual mean of *Calanus helgolandicus* NN in individuals m^{-3} as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany. (unpubl.)

14: Long-term annual mean of *Calanus helgolandicus* CN in individuals m^{-3} as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany. (unpubl.)

15: Long-term annual mean of the sum of the abundance of small calanoid copepods NN: *Paracalanus parvus*, *Pseudocalanus elongatus*, *Centropages* spp., *Acartia* spp. and *Temora longicornis* in individuals m^{-3} as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpubl.)

Fishes

- 16: SSB of North Sea cod from ICES Quadrant IV.
- 17: SSB of North Sea herring from ICES Quadrant IV.
- 18: SSB of North Sea haddock from ICES Quadrants IV and IIIa.
- 19: SSB of North Sea sole from ICES Quadrant IV.
- 20: SSB of North Sea plaice from ICES Quadrant IV.
- 21: SSB of North Sea saithe from ICES Quadrant IV.

Source: <http://www.ices.dk/committe/acfm/comwork/report/asp/advice.asp>.

Hydrophysical indices

Atmospheric indices

- 22: North Atlantic Oscillation Winter Index (Dec, Jan, Feb)
Source: <ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/>.
- 23: Gulf Stream Index
Source: <http://web.pml.ac.uk/gulfstream/data.htm>.
- 24: East Atlantic Pattern Index (Sep to Mar)
Source: <ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/>.
- 25: East Atlantic Jet Pattern Index (Apr to Aug)
Source: <ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/>.
- 26: Scandinavia Pattern Index (Aug to May)
Source: <http://www.cpc.noaa.gov/data/teledoc/scand.shtml>.

Climatic indices

- 27: Mean annual horizontal wind speed.
Source: <http://www.coastdat.de>, Feser et al. 2001.
- 28: Annual mean air temperature.
- 29: Annual mean maximum air temperature.
- 30: Annual mean minimum air temperature.
- 31: Total annual sunshine duration.
- 32: Total annual precipitation amount.
- 33: Annual mean surface pressure.
- 34: Annual mean relative humidity.
- 35: Total days with frost from November to March.

Source: DWD Offenbach, <http://www.dwd.de>.

Hydrographic indices

36: Long-term annual winter mean Secchi disk depth as measured every work day at Helgoland Roads.

Source: Karen H. Wiltshire, Biological Institute of Helgoland, Germany, (unpubl.)

37: Annual average sea surface temperature in $54^{\circ} 11' 3''$ N, $7^{\circ} 54' 0''$ E (Helgoland Roads) measured every work day.

Source: Wirtz and Wiltshire (2005)

38: Annual average sea surface temperature in $^{\circ}$ C for the German Bight ($6^{\circ} 5' E$ to $9^{\circ} 10' E$ and $55^{\circ} 5' N$ to $53^{\circ} 3' N$) from the Bundesamt für Seeschifffahrt und Hydrographie (BSH).

Source: Peter Loewe, BSH, Hamburg, Germany.

39: Annual mean winter (January, February, March) sea surface temperature in $^{\circ}$ C for the German Bight ($6^{\circ} 5' E$ to $9^{\circ} 10' E$ and $55^{\circ} 5' N$ to $53^{\circ} 3' N$) from the Bundesamt für Seeschifffahrt und Hydrographie (BSH).

Source: Peter Loewe, BSH, Hamburg, Germany.

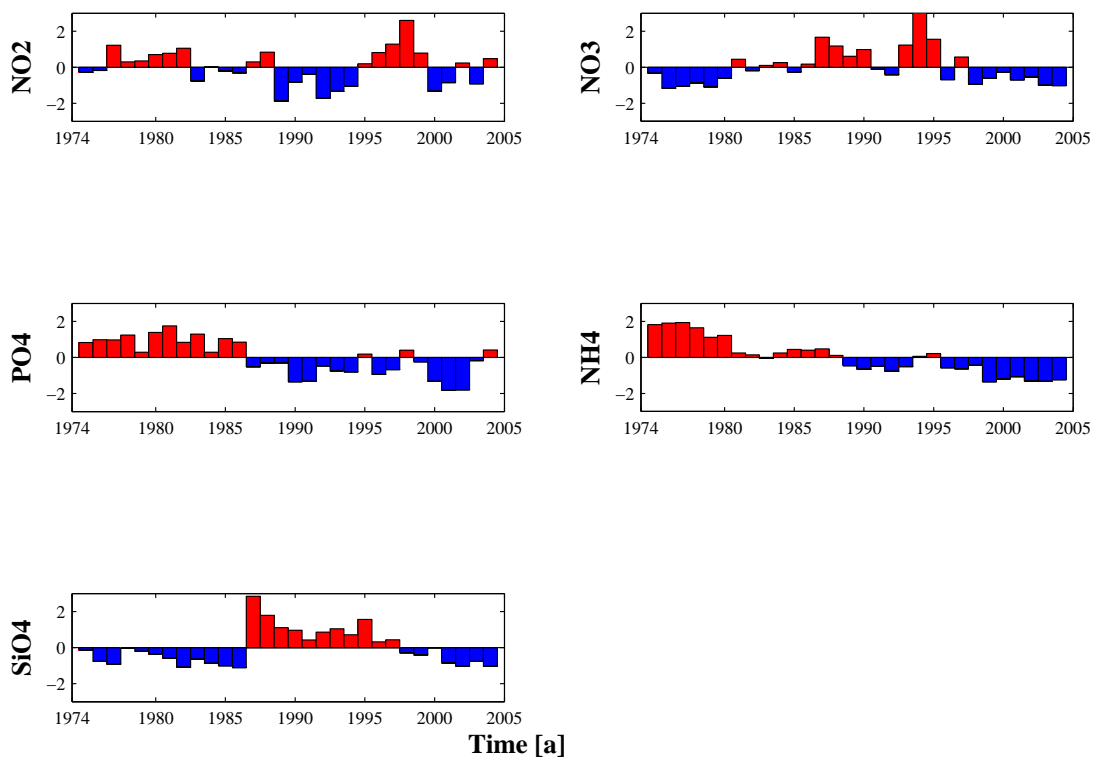


Figure A.1: Time series of annual winter mean of NO₂, NO₃, PO₄, NH₄ and SiO₄ at Helgoland Roads standardized to zero mean \pm 1 SD for the period 1975 to 2004.

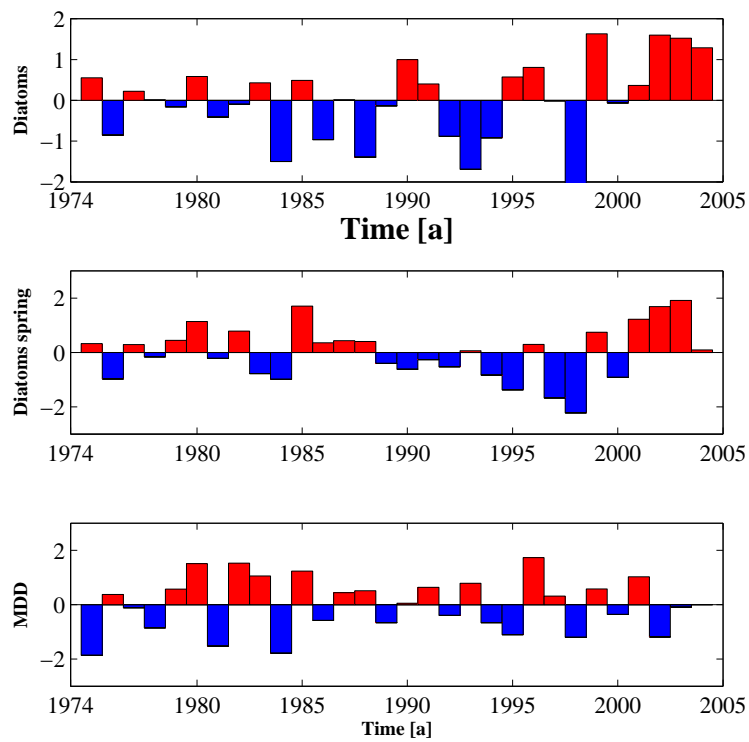


Figure A.2: Time series of annual mean of diatoms, mean of spring diatoms and MDD of the diatom spring bloom at Helgoland Roads standardized to zero mean \pm 1 SD for the period 1975 to 2004.

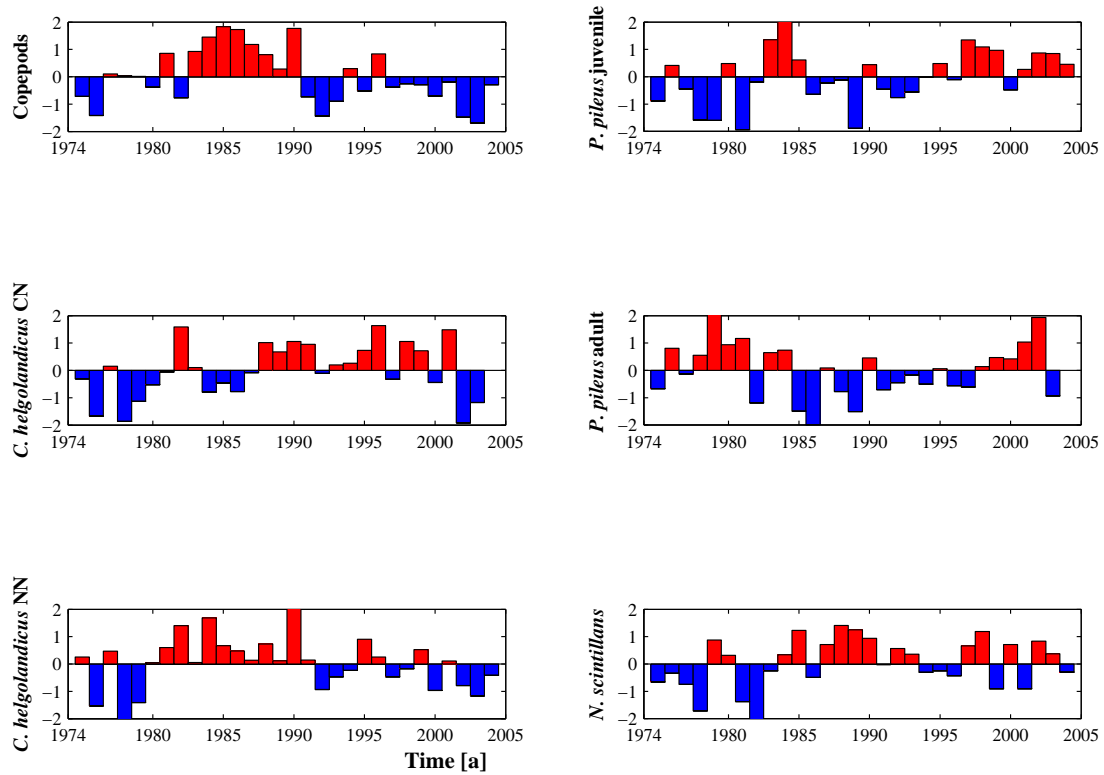


Figure A.3: Time series of annual mean of the sum of the abundance of five small calanoid copepods and of *Pleurobrachia pileus* juveniles, *Calanus helgolandicus* CN, *Pleurobrachia pileus* adults, *Calanus helgolandicus* NN and *Noctiluca scintillans* at Helgoland Roads with zero mean ± 1 SD.

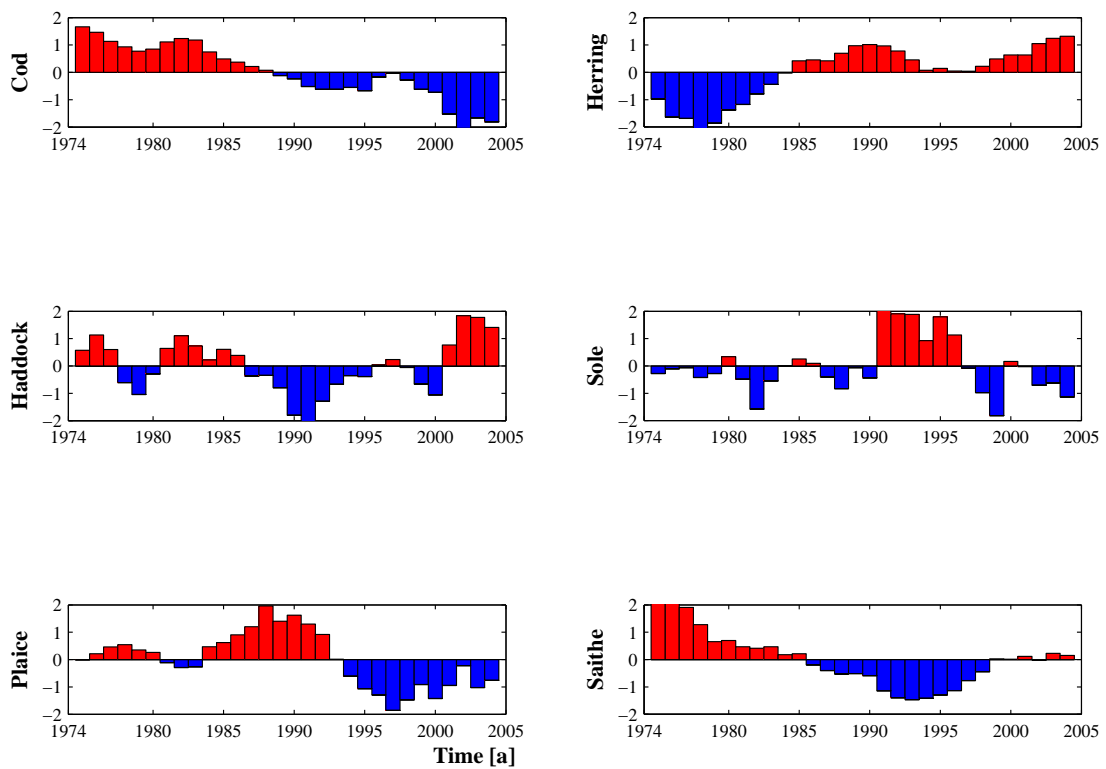


Figure A.4: Time series of SSB of cod, herring, haddock, sole, plaice and saithe in the North Sea standardised to zero mean \pm 1 SD for the period 1975 to 2004.

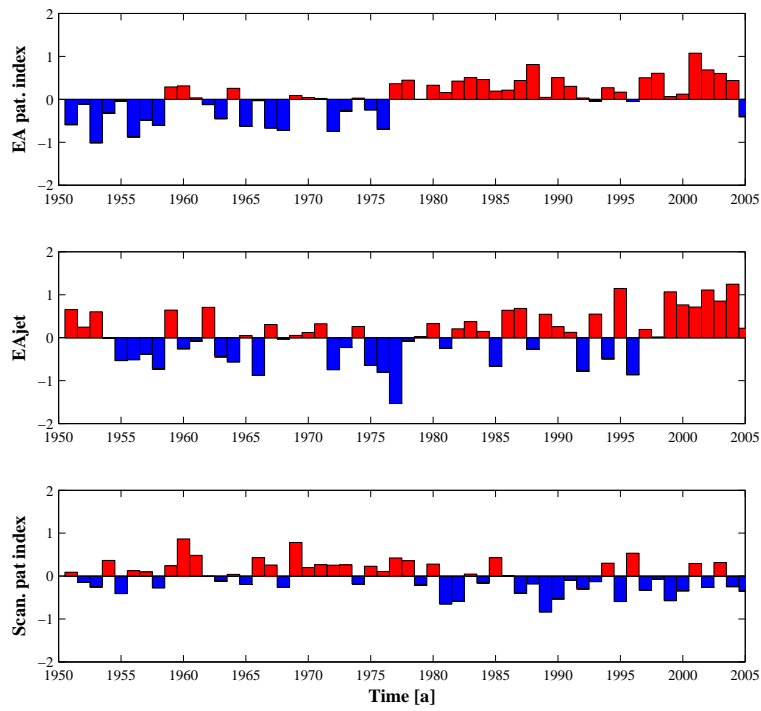


Figure A.5: Time series of East Atlantic Pattern Index (EAI), East Atlantic Jet Pattern Index (EAjet) and Scandinavian pattern Index (ScanI) with zero mean \pm 1 SD for the period 1950 to 2005.

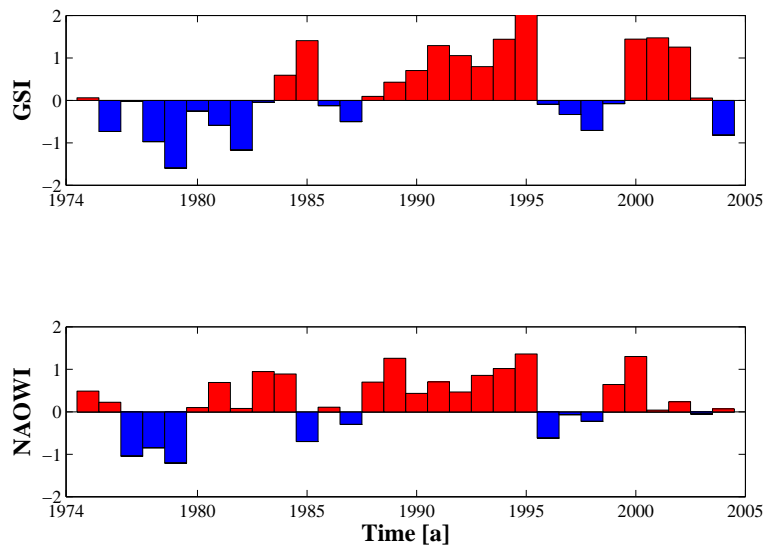


Figure A.6: Time series of the Gulf Stream Index (GSI) and North Atlantic Oscillation Winter Index (NAOWI) with zero mean ± 1 SD for 1975 to 2004.

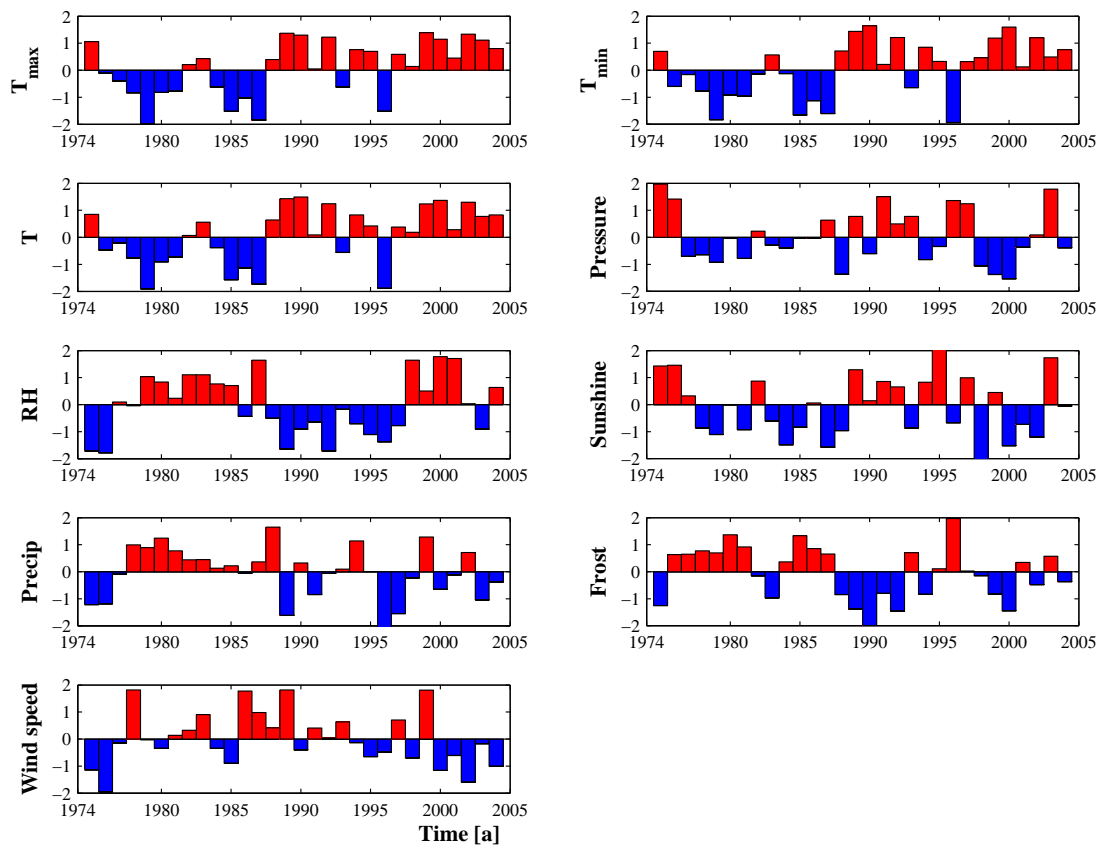


Figure A.7: Time series of the annual mean of 9 atmospheric variables: maximum air temperature, minimum air temperature, air temperature, pressure, relative humidity, total sunshine duration, precipitation amount, frost days at List/Sylt and wind speed for the German Bight with zero mean ± 1 SD from 1975 to 2004.

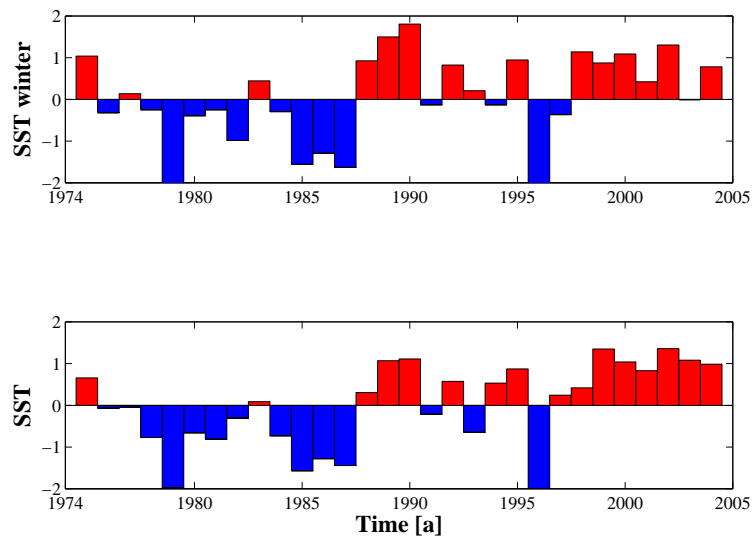


Figure A.8: Time series of winter mean and annual mean sea surface temperature for the German Bight with zero mean ± 1 SD for 1975 to 2004.

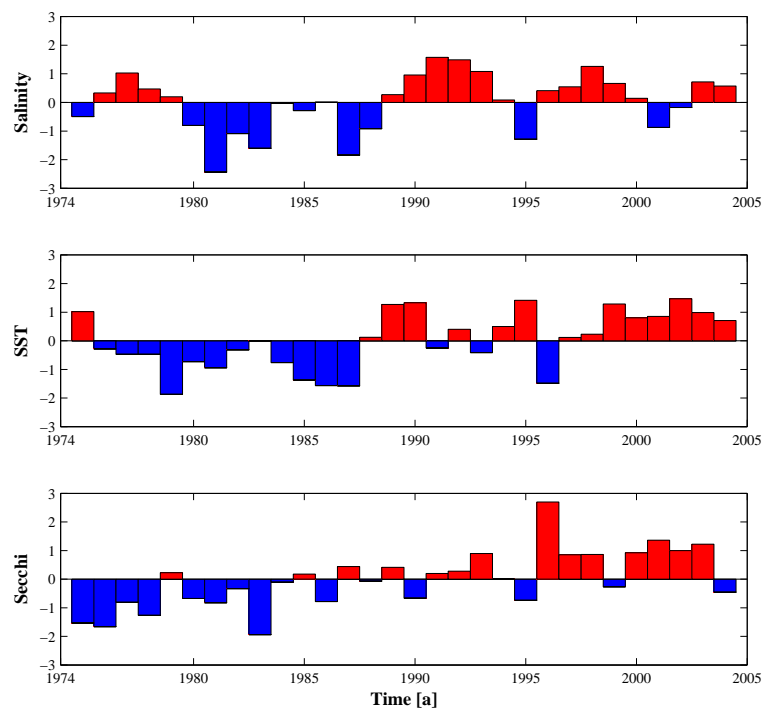


Figure A.9: Time series of annual mean of salinity, sea surface temperature and Secchi disk depth at Helgoland Roads with zero mean ± 1 SD for 1975 to 2004.

Appendix B

List of Abbreviations

| Abbreviation | Explanation |
|-------------------------|--|
| ANOSIM | Analysis of similarity |
| AOGCM | Atmosphere-ocean coupled general circulation model |
| Apr | April |
| Aug | August |
| BAH | Biologische Anstalt Helgoland |
| <i>B. gracilis</i> | <i>Beroe gracilis</i> |
| BSH | Bundesamt für Seeschifffahrt und Hydrographie |
| <i>C. helgolandicus</i> | <i>Calanus helgolandicus</i> |
| CN | CalCOFI Net |
| CPR | Continuous Plankton Recorder |
| Diatoms | Annual mean diatom cell abundances |
| Diatoms spring | Annual spring mean diatom cell abundances |
| DWD | Deutscher Wetterdienst |
| EA pat. index | East Atlantic Pattern Index |
| EAjet | East Atlantic Jet Pattern Index |
| ENSO | El Niño Southern Oscillation |
| EOGP | End of growth period |
| Feb | February |
| Frost | Frost Days |
| GCM | General Circulation Model |
| GP | Growth period |
| GSI | Gulf stream index |
| HR | Helgoland Roads |
| ICES | International Council for the Exploration of the Sea |
| IPPC | Intergovernmental Panel on Climate Change |
| Jan | January |
| Jul | July |

Continued

| | |
|-----------------------|---|
| Mar | March |
| MDD | Mean Diatom Day |
| NAO | North Atlantic Oscillation |
| NAOWI | North Atlantic Oscillation Winter Index |
| NE Atlantic | North East Atlantic |
| NH ₄ | Ammonium |
| NN | Nansen Net |
| NO ₂ | Nitrit |
| NO ₃ | Nitrat |
| <i>N. scintillans</i> | <i>Noctiluca scintillans</i> |
| PACES | Programme Marine, Coastal and Polar Systems |
| PCA | Principal Component Analysis |
| PC1 | First Principal Component |
| PDO | Pacific Decadal Oscillation |
| <i>P. pileus</i> | <i>Pleurobrachia</i> |
| PO ₄ | Phosphate |
| Precip | Precipitation |
| R1 | Regime 1 (1975–1987) |
| R2 | Regime 2 (1988–2004) |
| RH | Relative Humidity |
| Scan. pat. index | Scandinavian pattern Index |
| Secchi | Secchi disc depth |
| SiO ₄ | Silicate |
| Sep | September |
| SST | Sea Surface Temperature |
| SST winter | Annual mean winter Sea Surface Temperature |
| SST spring | Annual mean spring Sea Surface Temperature |
| SST summer | Annual mean summer Sea Surface Temperature |
| SLP | Sea level pressure |
| SOGP | Start of growth period |
| SOI | Southern Oscillation Index |
| SSB | Spawning Stock Biomass |
| Sunshine | Sunshine duration |
| T | Air temperature |
| T _{max} | Maximum air temperature |
| T _{min} | Minimum air temperature |
| THC | Thermohaline circulation |

Bibliography

- Aebischer, N. J., J. C. Coulson, and J. M. Coolebrook, Parallel long-term trends across four marine trophic levels and weather, *Nature*, *347*, 753–755, 1990.
- Alheit, J., and E. Hagen, Long-term climate forcing of european herring and sardine populations, *Fisheries Oceanography*, *6*(2), 130–139, 1997.
- Anderson, L., and L. Rydberg, Trends in nutrient and oxygen conditions within the kattegat: Effects of local nutrient supply, *Estuarine, Coastal and Shelf Science*, *26*, 559–579, 1988.
- Atkinson, A., V. Siegel, E. Pakhomov, and P. Rothery, Long-term decline in krill stock and increase in salps within the southern ocean., *Nature*, *432*, 100–103, 2004.
- Baars, J. W. M., Autoecological investigations on marine diatoms 1: Experimental results in biogeographical studies, *Hydrobiological Bulletin*, *13*, 123–137, 1979.
- Bailey, K. M., L. Ciannelli, N. A. Bond, A. Belgrano, and N. C. Stenseth, Recruitment of walleye pollock in a physically and biologically complex system: A new perspective, *Progress in Oceanography*, *67*, 24–42, 2005.
- Baker, L. D., and M. R. Reeve, Laboratory culture of the lobate ctenophore *mnemiopsis mccradyi* with notes on feeding and fecundity, *Marine Biology*, *26*, 57–62, 1974.
- Bamstedt, U., Trophodynamicx of *pleurobrachia pileus* (ctenophora, cydippida) and ctenophore summer occurrence of the norwegian north-west coast, *Sarsia*, *83*, 169–181, 1998.
- Beare, D. J., S. Batten, M. Edwards, and D. G. Reid, Prevalence of boreal atlantic, temperate atlantic and neritic zooplankton in the north sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and atlantic inflow, *Journal of Sea Research*, *48*, 29–49, 2002.
- Beaugrand, G., The north sea regime shift: evidence, causes, mechanisms and consequences, *Progress in Oceanography*, *60*, 245–262, 2004.
- Beaugrand, G., and F. Ibanez, Monitoring marine plankton ecosystems. ii: Long-term changes in north sea calanoid copepods in relation to hydro-climatic variability, *Marine Ecology Progress Series*, *284*, 35–47, 2004.
- Beaugrand, G., F. Ibanez, J. A. Lindley, and P. C. Reid, Diversity of calanoid copepods in the north atlantic and adjacent seas: species associations and biogeography, *Marine Ecology Progress Series*, *232*, 179–195, 2002a.

- Beaugrand, G., P. C. Reid, F. Ibanez, J. A. Lindley, and M. Edwards, Reorganization of north atlantic marine copepod biodiversity and climate, *Science*, 296, 1692–1694, 2002b.
- Beaugrand, G., K. Brander, A. Lindley, S. Souissi, and P. C. Reid, Plankton effect on cod recruitment in the north sea, *Nature*, 426, 661–664, 2003.
- Belgrano, A., S. D. Batten, and P. C. Reid, *Encyclopedia of Biodiversity*, chap. Pelagic Ecosystems, pp. 497–508, 4, Princeton University Academic Press, 2000.
- Beninca, E., J. Huisman, R. Heerkloss, K. D. Jöhnk, P. Branco, E. H. Van Nes, M. Scheffer, and S. P. Ellner, Chaos in a long-term experiment with a plankton community, *Nature*, 451, 822–825, doi:10.1038/nature06512, 2008.
- Biondi, F., A. Gershunov, and D. R. Cayan, North pacific decadal climate variability since 1661, *Journal of Climate*, 14, 5–10, 2001.
- Brzezinski, M. A., The si:c:n ratio of marine diatoms: interspecific variability and the effect of some environmental variables, *Journal of Phycology*, 21(3), 347–357, 2004.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. Niquen, From anchovies to sardines and back: Multidecadal change in the pacific ocean, *Science*, 299, 217–221, 2003.
- Chiba, S., M. N. Aita, K. Tadokoro, T. Saino, H. Sugisaki, and K. Nakata, From climate regime shifts to lower-trophic level phenology: Synthesis of recent progress in retrospective studies of the western north pacific, *Progress in Oceanography*, 77, 112–126, 2008.
- Choi, J. S., K. T. Frank, B. D. Petrie, and W. C. Legget, Integrated assessment of a large marine ecosystem: A case study of the devolution of the eastern scotian shelf, *Canada. - Oceanography and Marine Biology: An Annual Review*, 43, 47–67, 2005.
- Ciannelli, L., K. M. Bailey, K. S. Chan, A. Belgrano, and N. C. Stenseth, Climate change causing phase transitions of walleye pollock (*theragra chalcogramma*) recruitment dynamics, pp. 1735–1743, 2005.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and S. M. D, Shifting plant phenology in response to global change, *Trends in Ecology and Evolution*, 22(7), 357–365, 2007.
- Colijn, F., The temporal variability of plankton and their physico-chemical environment, *ICES Journal of Marine Science*, 55, 557–561, 1998.
- Colijn, F., and G. C. Cadee, Is phytoplankton growth in the wadden sea light or nitrogen limited?, *Journal of Sea Research*, 49, 83–93, 2003.

- Costello, J. H., B. K. Sullivan, and D. J. Gifford, A physical-biological interaction underlying variable phenological responses to climate change by coastal zooplankton, *Journal of Plankton Research*, 28(11), 1099–1105, 2006.
- Cushing, D. H., *Towards a theory on biological–physical interactions in the world ocean*, chap. The northerly wind, pp. 234–244, Kluwer Academic Publishers, Dordrecht, 1988.
- Cushing, D. H., Plankton production and year–class strength in fish populations: an update of the match/mismatch hypothesis, *Advances in Marine Biology*, 26, 1–122, 1990.
- Cushing, D. H., The long–term relationship between zooplankton and fish, *ICES Journal of Marine Science*, 52, 611–626, 1995.
- Davison, I. R., Environmental effects of algal photosynthesis: Temperature, *Journal of Phycology*, 27(1), 2–8, 1991.
- Dickson, R. R., J. Meincke, J.-A. Malmber, and A. J. Lee, The "great salinity anomaly" in the northern north atlantic 1968-1982, *Progress in Oceanography*, 20, 103–151, 1988.
- Dippner, J., and G. Ottersen, Cod and climate variability in the barents sea, *Climate Research*, 17, 73–82, 2001.
- Dippner, J. W., 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, 1997a.
- Dippner, J. W., Recruitment success of different fish stocks in the north sea in relation to climate variability, *German Journal of Hydrography*, 49, 277–293, 1997b.
- Dose, V., and A. Menzel, Bayesian analysis of climate change impacts in phenology, *Global Change Biology*, 10, 259–272, doi:10.1111/j.1365-2486.2006.01160.x, 2004.
- Dose, V., and A. Menzel, Bayesian correlation between temperature and blossom onset data, *Global Change Biology*, 12, 1451–1459, 2006.
- Drebes, *Marine Phytoplankton, eine Auswahl der Helgoländer Planktonalgen (Diatomeen, Peridinee)*, Georg Thieme Verlag, Stuttgart, 1974.
- Duffy-Anderson, J. T., K. Bailey, L. Ciannelli, P. Cury, A. Belgrano, and N. C. Stenseth, Phase transitions in marine fish recruitment processes, *Ecological Complexity*, 2, 205–218, 2005.

- Dunn, C. W., A. Hejnol, and D. Q. *et al.*. Matus, "broad phylogenomic sampling improves resolution of the animal tree of life", *Nature*, *452*, 745–749, doi:10.1038/nature06614, 2008.
- Dutz, J., W. C. M. Klein Breteler, and G. Kramer, Inhibition of copepod feeding by exudates and transparent exopolymer particles (tep) derived from *phaeocystis globosa* dominated phytoplankton community, *Harmful Algae*, *4*, 929–940, 2005.
- Ebbesmeyer, C., C. Cayan, D. McLain, F. Nicols, D. Peterson, and K. Redmond, 1976 step in the pacific climate: forty environmental changes between 1968 and 1975 and 1977 and 1984, in *Proceedings of the Seventh Annual Climate (PACLIM) Workshop*, edited by J. Betancourt and V. Tharp, no. 26 in Interagency Ecol Studies Prog Tech Rep, pp. 115–126, California Department of Water Resources, Sacramento, CA, USA, 1991.
- Edwards, M., and A. J. Richardson, Impact of climate change on marine pelagic phenology and trophic mismatch, *Nature*, *430*, 881–884, 2004.
- Edwards, M., P. C. Reid, and B. Planque, Long-term and regional variability of phytoplankton biomass in the northeast atlantic (1960-1995), *ICES Journal of Marine Science*, *58*, 39–49, 2001.
- Edwards, M., G. Beaugrand, P. C. Reid, A. A. Rowden, and J. M. B, Ocean climate anomalies and the ecology of the north sea, *Marine Ecological Progress Series*, *239*, 1–10, 2002.
- Falkowski, P. G., and J. A. Raven, *Aquatic Photosynthesis*, 375 p pp., Blackwell Science, Massachusetts USA, 1997.
- Feser, F., F. Weisse, and H. von Storch, Multi-decadal atmospheric modeling for europe yields multit-purpose data, *EOS*, *82*(28), 305, 1988.
- Frank, K. T., B. Petrie, N. L. Shackell, and J. S. Choi, Reconciling differences in trophic control in mid-latitude marine ecosystems, *Ecological Letters*, *9*, 1096–1105, 2006.
- Frankignoul, C., and G. de Coetlogon, Gulf stream variability and ocean atmosphere interactions, *Journal of physical Oceanography*, *31*, 3516–3529, 2001.
- Fraser, J. H., The ecology of the ctenophore *pleurobrachia pileus* in scottish waters, *Journal du Conseil International pour l'Exploration de la Mer*, *33*, 149–168, 1970.
- Frid, C. L. J., L. C. Newton, and J. A. Williams, The feeding rates of *pleurobrachia* (ctenophora) and *sagitta* (chaetognatha), with notes on the potential seasonal role of planktonic predators in the dynamics of north sea zooplankton communities., *Netherlands Journal of Aquatic Ecology*, *28*, 181–191, 1994.

- Fromentin, J.-M., and B. Planque, *Calanus* and environment in the eastern north atlantic. ii. influence of the north atlantic oscillation on *C. finmarchicus* and *C. helgolandicus*, *Marine Ecological Progress Series*, 134, 111–118, 1996.
- Gaedke, U., M. Ruhlenstroth-Bauer, I. Wiegand, K. Tirok, N. Aberle, P. Breithaupt, K. Lengfellner, J. Wohlers, and U. Sommer, *Global Change Biology*, doi:10.1111/j.1365-2486.2009.02009.x, 2009.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin, *Bayesian Data Analysis*, 2nd ed., Chapman & Hall, London, 2004.
- Gillett, N. P., H. F. Graf, and T. Osborn, *The North Atlantic Oscillation: climatic significance and environmental impact*, chap. Climate change and the North Atlantic Oscillation, pp. 193–209, American Geophysical Union, 2003.
- Graham, W. M., F. Pagès, and W. M. Hammer, A physical context for gelatinous zooplankton aggregations: a review, *Hydrobiologia*, 451, 199–212, 2001.
- Greene, C. H., M. R. Landry, and B. C. Monger, Foraging behavior and prey selection by the ambush entangling predator *pleurobrachia bachei*, *Ecology*, 67(6), 1493–1501, 1986.
- Greve, W., ökologische untersuchungen an *pleurobrachia pileus*, *Helgoländer wissenschaftliche Meeresuntersuchungen*, 23, 141–164, 1972.
- Greve, W., The 1989 german bight invasion of *muggiaea atlantica*, *ICES Journal of Marine Science*, 51, 355–358, 1994.
- Greve, W., Mutual predation causes bifurcations in pelagic ecosystems: the simulation model plitch (planktonic switch), experimental tests and theory, *ICES Journal of Marine Science*, 52, 505–510, 1995.
- Greve, W., *Phenology: An integrative environmental science*, chap. Aquatic plants and animals, pp. 385–403, Kluwer Academic Publishers, Netherlands, 2003.
- Greve, W., and F. Reiners, Plankton time - space dynamics in german bight - a systems approach, *Oecologia*, 77, 487–496, 1988.
- Greve, W., F. Reiners, and J. Nast, Biocoenotic changes of the zooplankton in german bight: the possible effects of eutrophication and climate, *ICES Journal of Marine Science*, 53, 1951–1956, 1996.

- Greve, W., F. Reiners, J. Nast, and H. S, Helgoland roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the north sea, *Helgoland Marine Research*, *58*, 274–288, 2004.
- Greve, W., S. Prinage, H. Zidowitz, J. Nast, and F. Reiners, On the phenology of north sea ichthyoplankton, *ICES Journal of Marine Science*, *62*, 1216–1223, doi:10.1016/j.icesjms.2005.03.011, 2005.
- Hakanson, L., and T. Bleckner, A review on operational bioindicators for sustainable coastal management—criteria, motives and relationships, *Ocean & Coastal Management*, *51*, 43–72, 2008.
- Hare, S. R., and N. J. Mantua, Empirical evidence for the north pacific regime shifts in 1977 and 1989, *Progress in Oceanography*, *47*, 103–145, 2000.
- Harrison, W. G., and T. Platt, Variations in assimilation number of coastal marine phytoplankton: Effects of environmental co-variates, *Journal of Plankton Research*, *2*, 249–260, 1980.
- Hasle, G. R., and E. E. Syvertsen, *Identifying Marine Phytoplankton*, chap. Marine diatoms, pp. 5–385, Academic Press, Florida, 1996.
- Hay, S., Marine ecology: Gelatinous bells may ring change in marine ecosystems, *Current Biology*, *16*, 679–682, doi:10.1016/j.cub.2006.08.010, 2006.
- Hays, G. C., A. J. Richardson, and C. Robinson, Climate change and marine plankton, *Trends in Ecology & Evolution*, *20*, 337–344, 2005.
- Helle, K., B. Bogstad, C. T. Marshall, K. Michalsen, G. Ottersen, and M. Pennington, An evaluation of recruitment indices for arcto-norwegian cod (*gadus morhua* l.), *Fishery Research*, *993*, 1–13, 2000.
- Hemery, G., F. d’Amico, and I. e. a. Castege, Detecting the impact of oceano-climatic changes on marine ecosystems using a multivariate index: The case of the bay of biscay (north atlantic–european ocean), *Global Change Biology*, *14*, 27–38, 2008.
- Hendey, N., An introductory account of the smaller algae of british coastal waters. 5. bacillariophyceae (diatoms), Fishery Investigations, london, 1964.
- Heyen, H., and J. Dippner, Salinity variability in the german bight in relation to climate variability, *Tellus*, *50A*, 545–556, 1998.

- Hickel, W., Temporal variability of micro- and nanplankton in the german bight, *ICES Journal of Marine Science*, 55, 600–609, 1998.
- Hickel, W., P. Mangelsdorf, and J. Berg, The human impact on the german bight: eutrophication during three decades 1962-1991, *Helgoland Marine Research*, 47, 243–263, 1993.
- Hickel, W., M. Eickhoff, and H. Spindler, Langzeit-untersuchungen von nährstoffen und phytoplankton in der deutschen bucht, aktuelle probleme der meeresumwelt: Vorträge des 5. internationalen wissenschaftliches symposiums, hamburg, *Deutsche Hydrographische Zeitschrift, Supplement 5*, 197–211, 1995.
- Hurrell, J. W., and H. Van Loon, Decadal variations in climate associated with the north atlantic oscillation, *Climatic Change*, 36, 301–326, 1997.
- ICES, Report of the ices advisory committee on fishery management, advisory committee on the marine environment and advisory committee on ecosystems, ICES Advice, 2008.
- IPCC, *Climate change 2007, the Fourth Assessment Report (AR4)*, Cambridge University Press, Cambridge, UK, 2007.
- Jassby, A. D., T. M. Powell, and C. R. Goldman, Interannual fluctuations in primary production: direct physical effects and trophic cascade at castle lake, california, *Limnology and Oceanography*, 35, 1021–1038, 1990.
- Jennings, S., S. P. R. Greenstreet, L. Hill, G. J. Piet, J. K. Pinnegar, and K. J. Warr, Long-term trends in the trophic structure of the north sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics, *Marine Biology*, 141, 1085–1097, 2002.
- Joyce, T. M., C. Deser, and M. A. Spall, The relation between decadal variability of subtropical mode water and the north atlantic oscillation, *Journal of Climate*, 13, 2550–2569, 2000.
- Karentz, D., and T. J. Smayda, Temperature and seasonal occurrence patterns of 30 dominant phytoplankton species in narragansett bay over a 22-year period (1959-1980), *Marine Ecology Progress Series*, 18, 277–293, 1984.
- Kirby, R. R., G. Beaugrand, J. A. Lindley, A. J. Richardson, M. Edwards, and P. C. Reid, Climate effects and benthic-pelagic coupling in the north sea, *Marine Ecological Progress Series*, 330, 31–38, 2007.
- Kröncke, I., J. W. Dippner, H. Heyen, and B. Zeiss, Long-term changes in macrofaunal communities off norderney (east frisia, germany) in relation to climate variability, *Marine Ecological Progress Series*, 167, 25–36, 1998.

- Kuipers, B. R., U. Gaedke, L. Enserink, and H. Witte, Effect of ctenophore predation on mesozooplankton during a spring outburst of *pleurobrachi pileus*, *Netherlands Journal of Sea Research*, *26*, 111–124, 1990.
- Lees, K., S. Pitois, C. Scott, C. Frid, and S. Mackinson, Characterizing regime shifts in the marine environment, *Fish and Fisheries*, *7*, 104–127, 2006.
- Litchman, E., and C. A. Klausmeier, Trait-based community ecology of phytoplankton, *Annu. Rev. Ecol. Evol. Syst.*, *39*, 615–639, 2008.
- Loewe, P., Surface temperatures of the north sea in 1996, *German Journal of Hydrography*, *48*, 175–184, 1996.
- Loewe, P., and G. Becker, North sea sst since 1968: some gross statistics contribution to 2003 report of the ices working group on oceanic hydrography (wgoh), Bundesamt für Seeschifffahrt und Hydrographie, Hamburg, 2003.
- Lozan, J. L., E. Rachor, K. Reise, v. H. Westernhagen, and W. Lenz, *Warnsignale aus der Nordsee*, Blackwell Wissenschaftsverlag, Berlin, 1994.
- Lucht, F., and M. Gillbricht, Long-term observations on nutrient contents near helgoland in relation to nutrient input of the elbe river, *Rapports et Procès-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer*, *172*, 358–360, 1978.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter, Winbugs – a bayesian modelling framework: concepts, structure, and extensibility, *Statistics and Computing*, *10*, 325–337, 2000.
- Mann, M. E., and J. Park, Joint spatiotemporal modes of surface temperature and sea level pressure variability in the northern hemisphere during the last century, *Journals of Climate*, *9*, 2137–2162, 1996.
- Mantua, N., Methods for detecting regime shifts in large marine ecosystems: a review with approaches applied to north pacific data, *Progress in Oceanography*, *60*, 165–182, doi:10.1016/j.pocean.2004.02.016, 2004.
- Mantua, N., S. Hare, Y. Zhand, J. Wallace, and R. Francis, A pacific interdecadal climate oscillation with impacts on salmon production, *Bulletin of the American Meteorological Society*, *78*, 1069–1079, 1997.

- McQuatters-Gollop, A., D. E. Raitsons, M. Edwards, Y. Pradhan, L. D. Mee, S. J. Lavender, and M. Attrill, A long-term chlorophyll data set reveals regime shift in north sea phytoplankton biomass unconnected to nutrient trends, *Limnology and Oceanography*, 52(3), 635–648, 2007.
- Menzel, A., N. Estrella, and P. Fabian, Spatial and temporal variability of the phenological seasons in germany from 1951 to 1996, *Global Change Biology*, 7(6), 657–666, 2001.
- Mertz, G., and R. A. Myers, The ecological impact of the great salinity anomaly in the northern north-west atlantic, *Fishery and Oceanography*, 3(1), 1–14, 1994.
- Molinero, J. C., M. Casini, and E. Buecher, The influence of the atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern mediterranean, *Limnology and Oceanography*, 53(4), 1456–1467, 2008.
- Möllmann, C., G. Kornilovs, and L. Sidrevics, Long-term dynamics of main mesozooplankton species in the central baltic sea, *Journal of Plankton Research*, 22, 2015–2038, 2000.
- Möllmann, C., R. Diekmann, B. Müller-Karulis, G. Kornilovs, M. Plikshs, and P. Axe, The reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure - a discontinuous regime shift in the central baltic sea, *Global Change Biology*, doi:10.1111/j.1365-2486.2008.01814.x, 2008.
- Morgan, I., D. G. McDonald, and C. M. Wood, The cost of living for freshwater fish in a warmer, more polluted world., *Global Change Biology*, 7, 345–355, 2001.
- Müller-Navarra, D. C., S. Güss, and H. von Storch, Interannual variability of seasonal succession events in a temperate lake and its relation to temperature variability, *Global Change Biology*, 3, 429–438, 1997.
- O'Brien, C. M., C. J. Fox, B. Planque, and J. Casey, Climate variability and north sea cod, *Nature*, 404, 142, 2000.
- Oguz, T., and D. Gilbert, Abrupt transitions of the top-down controlled black sea pelagic ecosystem during 1960-2000: Evidence for regime-shifts under strong fishery exploitation and nutrient enrichment and modulated by climate-induced variations., *Deep-sea research I*, 54, 220–242, 2007.
- Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, and N. C. Stenseth, Ecological effects of the north atlantic oscillation, *Oecologia*, 128, 1–14, doi:10.1007/s004420100655, 2001.

- Overland, J., S. Rodionov, S. Minobe, and N. Bond, North pacific regime shifts: Definitions, issues and recent transitions, *Progress in Oceanography*, 77, 92–102, 2008.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds, Climate change and distribution shifts in marine fishes., *Science*, 308, 1912–1915, 2005.
- Peterson, W. T., and F. B. Schwing, A new climate regime in northeast pacific ecosystems, *Geophysical Research Letters*, 30(17), 1–4, 2003.
- Philippart, C. J., and G. C. Cadee, Was total primary production in the western wadden sea stimulated by nitrogen loading?, *Helgoland Marine Research*, 54, 55–62, 2000.
- Philippart, C. J. M., G. C. Cadee, W. Van Raaphorst, and R. Riegman, Long-term phytoplankton–nutrient interactions in a shallow coastal sea: algal community structure, nutrient budgets, and denitrification potential, *Limnology and Oceanography*, 45, 131–144, 2000.
- Planque, B., and J.-M. Fromentin, *Calanus* and environment in the eastern north atlantic. i. spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*, *Marine Ecology Progress Series*, 134, 101–109, 1996.
- Purcell, J. E., Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research, *Hydrobiologia*, 616, 23–50, doi:10.1007/s10750-008-9585-8, 2009.
- Purcell, J. E., and M. N. Arai, Interactions of pelagic cnidarians and ctenophores with fishes: A review., *Hydrobiologia*, 451, 27–44, 2001.
- Purcell, J. E., and M. B. Decker, Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in chesapeake bay during 1987–2000, *Limnology and Oceanography*, 50, 376–387, 2005.
- Raabe, T., and K. H. Wiltshire, Quality control and analyses of the long-term nutrient data from helgoland roads, north sea, *Journal of Sea Research*, 3, 3–16, doi:10.1016/j.seares.2008.07.004, 2008.
- Radach, G., Quantification of long-term changes in the german bight using an ecological development index, *ICES Journal of Marine Science*, 55, 587–599, 1998.
- Radach, G., J. Berg, and E. Hagmeier, Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at helgoland and at lv elbe 1 in the german bight, *Continental Shelf Research*, 10(4), 305–328, doi:10.1016/0278-4343(90)90054-P, 1990.

- Reid, P. C., Large scale changes in north sea phytoplankton, *Nature*, 257, 217–219, 1975.
- Reid, P. C., and S. E. Borges, MdeF, A regime shift in the north sea circa 1988 linked to changes in the north sea horse mackerel fishery, *Fisheries Research*, 50, 163–171, 2001.
- Reid, P. C., B. Planque, and M. Edwards, Is observed variability in the long-term results of the continuous plankton recorder survey a response to climate change?, *Fisheries Oceanographie*, 7(3-4), 282–288, 1998.
- Reid, P. C., M. Edwards, G. Beaugrand, M. Skogen, and S. D, Periodic changes in zooplankton of the north sea during the twentieth century linked to oceanic inflow, *Fisheries Oceanographie*, 12, 260–269, 2003.
- Reynolds, C. S., *Plankton Ecology*, chap. Physical determinants of phytoplankton succession, pp. 9–56, Springer-Verlag, Berlin, 1989.
- Reynolds, C. S., *Ecology of phytoplankton*, Cambridge University Press, 2006.
- Rice, J., and H. Gislason, Patterns of change in the size spectra of numbers and diversity of the north sea fish assemblage, as reflected in surveys and models, *ICES Journal of Marine Science*, 53, 1214–1225, 1996.
- Richardson, A. J., and D. S. Schoeman, Climate impact on plankton ecosystems in the north-east atlantic., *Science*, 305, 1609–1612, 2004.
- Rost, B., I. Zondervan, and D. Wolf-Gladrow, Sensitivity of phytoplankton to future changes in ocean carbonate chemistry: current knowledge, contradictions and research directions, *Marine Ecology Progress Series*, 373, 227–237, 2008.
- Rousseau, V., A. Leynaert, N. Daoud, and C. Lancelot, Diatom succession, silicification and silicic acid availability in belgian coastal waters (southern north sea), *Marine Ecology Progress Series*, 236, 61–73, 2002.
- Russell, F. S., A summary of the observations on the occurrence of planktonic stages of fish off plymouth 1924-1972, *Journal of the Marine Biological Association of the United Kingdom*, 53, 347–355, 1973.
- Sarmiento, J. L., et al., Response of ocean ecosystems to climate warming, *Global Biogeochemical Cycles*, 18(3), doi:10.1029/2003GB002134, 2004.
- Schaub, B. E. M., and W. W. C. Gieskes, *Estuaries and coasts: temporal and spatial intercomparisons*, chap. Eutrophication of the North Sea: the relation between Rhine river

- discharge and chlorophyll-a concentration in Dutch coastal waters, pp. 85–90, Olsen and Olsen, Fredensborg, 1991.
- Schlüter, M. H., A. Merico, K. H. Wiltshire, W. Greve, and v. H. Storch, A statistical analysis of climate variability and ecosystem response in the german bight, *Ocean Dynamics*, 58(3-4), 169–186, 2008.
- Schlüter, M. H., A. Merico, M. Reginatto, M. Boersma, K. H. Wiltshire, and W. Greve, Phenological shifts of three interacting zooplankton groups in relation to climate change, *Global Change Biology*, 2010.
- Schmittner, A., Decline of the marine ecosystem caused by a reduction in the atlantic overturning circulation., *Nature*, 434, 628–633, 2005.
- Schneider, G., Role of advection in the distribution and abundance of *pleurobrachia pileus* in kiel bight, *Marine Ecology Progress Series*, 41, 99–102, 1987.
- Schrum, C., Regionalization of climate change for the north sea and baltic sea., *Climate Research*, 18, 31–37, 2001.
- Siegismund, F., and C. Schrum, Decadal changes in the wind forcing over the north sea., *Climate Research*, 18, 39–45, 2001.
- Sivia, D. S., *Data Analysis-A Bayesian Tutorial*, Clarendon, Oxford, 2005.
- Sommer, U., *Plankton Ecology*, chap. The role of competition for resources in phytoplankton succession, pp. 57–106, Springer-Verlag, Berlin, 1989.
- Sommer, U., Z. M. Gliwicz, W. Lampert, and A. Duncan, The peg-model of seasonal succession of planktonic events in fresh waters, *Archi für Hydrobiologie*, 106, 433–471, 1986.
- Southward, A. J., S. J. Hawkins, and M. T. Burrows, 70 years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western english channel in relation to rising sea temperature, *Journal of Thermal Biology*, 1-2, 127–155, 1995.
- Sparks, T. H., and A. Menzel, Observed changes in seasons: An overview, *International Journal of Climatology*, 22, 1715–1725, 2002.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van der Linde, Bayesian measures of model complexity and fit (with discussion), *Journal of the Royal Statistical Society*, 64(4), 583–616, series B, 2002.

- Storch, v. H., and F. W. Zwiers, *Statistical analysis in climate research*, Cambridge University Press, Cambridge, 1999.
- Sullivan, B. K., and M. R. Reeve, Comparison of estimates of the predatory impact of ctenophores by two independent techniques, *Marine Biology*, *68*, 61–65, 1982.
- Sullivan, B. K., D. Van Keuren, and M. Clancy, Timing and size of blooms of the ctenophore *mnemiopsis leidyi* in relation to temperature in narragansett bay, ri, *Hydrobiologia*, *451*, 113–120, 2001.
- Sullivan, B. K., J. H. Costello, and D. Van Keuren, Seasonality of the copepods *acartia hudsonica* and *acartia tonsa* in narragansett bay, ri, usa during a period of climate change, *Estuarine, Coastal and Shelf Science*, *73*, 259–267, 2007.
- Sundby, S., H. Bjorke, A. V. Soldal, and S. Olsen, Mortality rates during the early life stages and year-class strength of northeast arctic cod (*gadus morhua* l.), *Rapp P-V Reun Cons Int Explor Mer*, *191*, 351–358, 1989.
- Svendsen, S., A. Algen, S. A. Iversen, D. W. Skagen, and O. Smestad, Influence of climate on recruitment and migration of fish stocks in the north sea, *Can Spec Publ Fish Aquat Sci*, *121*, 641–653, 1995.
- Taylor, A. H., North-south shifts of the gulf stream and their climatic connection with the abundance of zooplankton in the uk and its surrounding seas, *ICES Journal of Marine Science*, *52*, 711–721, 1995.
- Taylor, A. H., North-south shifts of the gulf stream: ocean-atmosphere interactions in the north atlantic, *International Journal of Climatology*, *16*, 559–583, 1996.
- Taylor, A. H., and J. A. Stephens, Latitudinal displacements of the gulf stream (1966 to 1977) and their relation to changes in temperature and zooplankton abundance in the n.e. atlantic, *Oceanologica Acta*, *3*, 145–149, 1980.
- Thuiller, W., Climate change and the ecologist, *Nature*, *448*, 550–542, 2007.
- Tiffany, M. A., and L. C. B., Diatoms provide attachment sites for other diatoms: a natural history of epiphytism form southern california, *Phycologia*, *41*(2), 116–124, 2002.
- Tilzer, M., Secchi disk - chlorophyll relationships in a lake with highly variable phytoplankton biomass, *Hydrobiologia*, *162*, 163–171, 1998.
- Trenberth, K. E., and J. W. Hurrell, Decadal atmospheric–ocean variations in the pacific, *Climate Dynamics*, *9*, 303–319, 1994.

- Ulbrich, U., and M. Christoph, A shift of the nao and increasing storm track activity over europe due to anthropogenic greenhouse gas forcing., *Climate Dynamics*, *15*, 551–559, 1999.
- Veer, v. d. H. W., and C. F. M. Sadee, Impact of coelenterate predation on larval plaice *pleuronectes platessa* and the flounder *platichthys flesus* stock in the western wadden sea, *Marine Ecology Progress Series*, *25*, 229–238, 1984.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein, Ecological responses to recent climate change, *Nature*, *416*, 389–395, doi:10.1038/416389a, 2002.
- Wang, Z., E. Thierreaut, and J. C. Dauvin, Spring abundance and distribution of the ctenophore *pleurobrachia pileus* in the seine estuary: advective transport and diel vertical migration, *Marine Biology*, *124*, 313–324, 1995.
- Weijerman, M., H. Lindeboom, and A. F. Zuur, Regime shifts in marine ecosystems of the north sea and wadden sea, *Marine Ecology Progress Series*, *298*, 21–39, 2005.
- Williams, R., and N. R. Collins, Chaetognaths and ctenophores in the holoplankton of the british channel, *Marine Biology*, *85*, 97–107, 1985.
- Wiltshire, K. H., and C. D. Dürselen, Revision and quality analyses of the helgoland reede long-term phytoplankton data archive, *Helgoland Marine Research*, *58*, 252–268, doi:10.1007/s10152-004-0196-0, 2004.
- Wiltshire, K. H., and B. F. J. Manly, The warming trend at helgoland roads, north sea: phytoplankton response, *Helgoland Marine Research*, *58*, 269–273, doi:10.1007/s10152-004-0196-0, 2004.
- Wiltshire, K. H., A. M. Mahlzahl, K. Wirtz, W. Greve, S. Janisch, P. Mangelsdorf, B. F. J. Manly, and M. Boersma, Resilience of north sea phytoplankton spring bloom dynamics: An analysis of long term data at helgoland roads, *Limnology and Oceanography*, *53*(4), 1294–1302, 2008.
- Wiltshire, K. H., et al., Helgoland roads, north sea: 45 years of change, *Estuaries and Coasts*, *33*, 295–310, doi:10.1007/s12237-009-9228-y, 2010.
- Zorita, E., T. F. Stocker, and H. von Storch, How unusual is the recent series of warm years?, *Geophysical Research Letters*, *35*, L24,706, doi:10.1029/GL036228, 2008.