Rhyme and Reason:

Plankton community Changes in the North Sea

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Introduction

As a result of natural and human induced pressures, marine ecosystems exhibit continuous changes in production, biomass and species composition. A major challenge is to distinguish between natural or non-manageable drivers and anthropogenic or manageable drivers like fisheries or sand extraction. The first step towards this distinction involves understanding natural changes of marine ecosystems, the spatial scale at which they take place and their potential recurrent patterns in time. Large scale engineering initiatives like Building with Nature need to understand the current state of marine ecosystems which they will become part of in order to make the best use of their resources without deteriorating their resilience and responses to natural environmental changes. This deep understanding of the ecosystem is a prerequisite to balance the sustainable functioning of ecosystems with the demand for development and use.

SUDDEN ECOSYSTEM CHANGES AND STABLE STATES

During the last two decades marine ecological research has increasingly focused on sudden ecosystem changes which shift the whole ecosystem or some of its components into an alternative state. The idea of ecological systems changing suddenly between alternative stable states was developed at the beginning of the 1970s (Holling, 1973), but it was not until the 1990s that this idea was widely accepted and, since then, a whole theoretical background and practical experience on sudden changes in ecological systems has been developed (Scheffer & Carpenter, 2003). Scheffer (1990) described with minimal models the biotic-abiotic interactions in freshwater ecosystems, setting the ecological basis for these changes known today as regime shifts.

Scheffer's models described the equilibrium between turbidity and nutrient concentrations in freshwater lakes. At low nutrient concentrations the turbidity equilibrium is characterized by a "with vegetation" state of relatively low turbidity. As nutrient concentration increases so does turbidity, until a tipping point is reached (Fig. 1a). At this tipping point, the system shifts into a "without vegetation" equilibrium with much higher

turbidity. However, over a range of intermediate nutrient concentrations two alternative equilibria are possible. Therefore, two nutrient concentration thresholds exist; 1) to go from a "with vegetation" to a "without vegetation" equilibrium, 2) to go from a "without vegetation" to a "with vegetation" equilibrium (Fig. 1a). This phenomenon is known as hysteresis.

Hysteretic sudden change is just one of the possibilities in a continuum of changes in ecosystem dynamics (Fig. 1b). The term regime shift has been applied to any of these apparent shifts in oceanic and climatic conditions and marine community structure around the world. Collie et al. (2004) defined regime shifts as low-frequency, high-amplitude changes in oceanic conditions that may be specifically pronounced in biological variables and propagate through several trophic levels. They defined three types of regime shifts (Fig. 1b):

   • Smooth regime shifts are represented by a quasi-linear relationship between response and control variables.

   • Abrupt regime shifts exhibit a non-linear relationship between response and control variables, resulting in abrupt changes in the response variable as a consequence of gradual changes in the control variable crossing a threshold point.

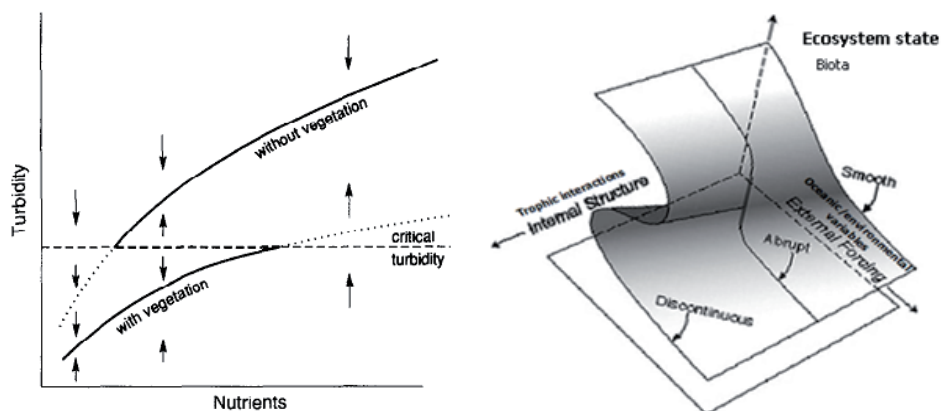   • Discontinuous regime shifts are characterized by a hysteretic process

Figure 1. Representation of regime shifts. (a) Response of turbidity to nutrient increase depending on the vegetation state. A hysteretic process happens when the system "jumps" from a vegetation to a no vegetation state. (b) Manifold representing the continuum of ecosystem responses to external forcing depending on its internal structure.

resulting in the occurrence of alternative "stable states" as the one described by Scheffer (1990).

The difference between the last two types is apparent when the driving force reverses.

Discontinuous regime shifts are hysteretic processes in which the driving force has to pass a second threshold in order to return to the original state, while abrupt regime shifts are characterised by just one threshold. As soon as the driving force returns to its values under the threshold the ecosystem would go back to its previous state.

MARINE ECOSYSTEMS

Various shifts between different regimes have been observed in the marine environment and, although the understanding of how these shifts work is not as developed as in the freshwater environments, it seems that the driving forces and mechanisms could be similar for both systems (Scheffer and Van Ness, 2004). Marine examples go from coral reefs (Hughes, 1994) and kelp forests (Stenneck et al. 2002) to basin-scale phenomena such as the North Pacific or the North Atlantic regime shifts (Hare & Mantua, 2000, Weijerman et al. 2005).

Caribbean coral reefs have undergone changes from dominance by hard coral to fleshy algae during the past three decades (Nystrom et al. 2000). This change has been a consequence of natural disturbances, such as hurricanes, and human impacts, such as eutrophication and overfishing. The past high resilience of the coral ecosystem was a result of the functional diversity of herbivorous species, fish and echinoids, which controlled the overgrowth of fleshy algae allowing the hard corals to recolonize open space after natural disturbances such as hurricanes. Overfishing of herbivorous fish reduced the resilience of the ecosystem, so the impact of a pathogen on the sea-urchin population in 1982-83 (Hughes, 1994) resulted in a shift from the coral dominated state to a macroalgae dominated state. In the past, the impact of the pathogen in the ecosystem would have been buffered by the higher herbivorous diversity.

Basin-scale regime shifts have been reported in the North Pacific (Hare & Mantua, 2000), the Central Baltic Sea (Mollman et al, 2009), and the North Sea (Weijerman et al. 2005). In all cases environmental and climatic

variables seemed to be drivers of the ecosystem change without them displaying sudden changes, pointing to a discontinuous regime shift. The detection of an ecosystem shift is based on the description of the ecosystem state as a multivariate set of biological indicators. The common patterns of change among these indices are then captured by multivariate ordinations, and these represent the ecosystem change. Similarly, the abiotic environment is represented by a suite of abiotic indicators, generally including global atmospheric patterns assumed to regulate the marine environment.

THE INDICATOR CHOICE

When characterising the state of an ecosystem, indicators are described to represent the functioning of an ecosystem. Ecosystem functioning (Hooper et al. 2005) is a broad term encompassing ecosystem properties (such as pools of materials and fluxes of these materials and energy through different compartments), ecosystem goods (properties with direct market value, such as food or construction materials) and services (properties of ecosystems that either directly or indirectly benefit human endeavours, such as maintaining hydrologic cycles, regulating climate, etc.). Ecosystem functioning is dependent on abiotic factors and on the biological species being part of the ecosystem. These species differ in the roles they play in the ecosystem processes and their relations with other species in the ecosystem (Sinclair and Byrom, 2006). Due to this diversity functional traits are defined as those species characteristics that influence ecosystem properties and/or species responses to environmental conditions (Hooper et al. 2005). Species that have similar effects on a specific ecosystem process or similar responses to environmental conditions are therefore grouped in functional types. It becomes obvious that the functional diversity (diversity of functional traits) of the ecosystem is a key factor in determining the ecosystem functioning and the resilience of ecological systems against change. In the example of Caribbean coral reefs presented before, the diversity of herbivores functional responses increased the system resilience, making it more "stable" against external forcing.

The importance of different functional traits is dependent on the ecosystem property under analysis, so functional types identified for a defined property may not be relevant to others. This makes it even more difficult to define relevant functional types from an overall perspective. Because of interactions among ecosystem functioning, abiotic and biotic factors,

defining ecosystem state and measuring ecosystem change can become very complicated.

PLANKTON COMMUNITIES

The North Sea planktonic system is one of the most studied cases of regime shifts in the marine environment. Continuous Plankton Recorder (CPR) data provided insight into the long-term trends and seasonal patterns of both phyto- and zooplankton and their relationships with hydrographical factors as well as climatological events. A cold episodic event (abrupt shift) in the late 1970s has been described and widely acknowledged (Reid et al. 2000, Reid & Edwards 2001, Edwards et al. 2002, Beaugrand 2004, Beaugrand & Ibanez 2004, Weijerman et al. 2005). These cold years were characterised by low sea surface temperature (SST) values in the North Sea (Becker & Pauly 1996), which were particularly harsh in the shallower southern North Sea. During this period (1) the phytoplankton bloom was smaller than average and occurred later in the year, (2) many early spring diatom species were absent from the spring bloom, and (3) *Chaetoceros* spp., one of the most abundant diatoms in the North Sea, were only present in small numbers (Edwards et al. 2002).

A second overall change in North Sea plankton occurred during the 1980s (Reid et al. 2001, Beaugrand & Ibanez 2004, Alheit et al. 2005, Weijerman et al. 2005, McQuatters-Gollop et al. 2007). During this period there was a strong biogeographic shift of warm-water copepod species (associated with a decrease in cold-water species) and warm-water fish species in the northeast Atlantic (Beaugrand & Reid 2003). This indicated a change in the pelagic ecosystem of the northeast Atlantic towards a warmer dynamic regime, which seemed to have been driven by climatic variables. In contrast with the late 1970s cold episodic event, the North Sea entered a warm-biological dynamic regime after the North Sea warm episodic event from 1988 to 1992 (Edwards et al. 2002). The new regime can be characterised by (1) higher Phytoplankton Colour Index (PCI) values in the central North Sea, particularly during winter and summer; (2) an extended phytoplankton season, and (3) a change in the zooplankton community structure (Reid et al. 2001).

All these changes have been related to different environmental factors, such as the increase in SST and changing Atlantic water inflow through the northern North Sea (Reid et al. 2003). Kirby & Beaugrand (2009) showed how the influence of SST propagates through the North Sea ecosystem

INTRODUCTION

Box 1. The continuous plankton recorder

The Continuous Plankton Recorder (CPR) has been routinely operated for 70 years, and for at least the 50 most recent years of sampling, the materials used and procedures applied have hardly varied. The CPR consists of two main parts, an outer body and an internal removable mechanism, which were fully described by Hardy (1939). The outer body has a rectangular cross-section, with a box-like central section that tapers to the front and rear (Fig. B1). A propeller linked to a gearbox is fitted in the roof of the box section at the rear of the body. The CPR is towed behind the volunteer operating vessel, usually a fast moving (~15–20 knots) merchant vessel. The length of the towing cable is designed to produce a towing depth of about 10 m at the operating speed of the vessel. Water enters through the front aperture in the nose cone of the CPR (Fig. B1-A). During the tow the filtering mesh (Fig. B1-B) is drawn steadily from the preloaded spools, through the internal mechanism and onto the storage spool.

The water is filtered through a continuously moving band of silk filtering mesh, which has a leno weave (a single thread in one direction and a double twisted thread in the other) and a mesh size of ~270 µm. A second band of silk covers the filtering layer forming a sandwich with the plankton trapped between the two layers of mesh. This sandwich is wound onto the storage spool in a tank that contains a dilute solution of borax-buffered formaldehyde (~4%) that fixes the plankton (Batten et al. 2003).

CPR data include a spatio-temporal bias due to the "opportunistic" character of sampling. In general, there is a trade-off between the precision of plankton estimates and their bias. For example, averaging over too small an area leads to fewer estimates of plankton abundance resulting in less confidence in mean monthly or annual values, as well as the increased likelihood of data gaps for particular months or years. By contrast, averaging over too large an area may combine disparate hydrographic regimes. CPR data are semi-quantitative estimates of plankton abundance and not absolute measures. Because of the relatively large mesh size of the CPR, it undoubtedly under-samples phytoplankton,

particularly the smaller species. Small zooplankton may also be under-sampled because of the relatively large mesh size compared with other standard nets for sampling mesozooplankton, and large zooplankton may be under-sampled because of active avoidance. Despite the semi-quantitative nature of CPR sampling, there is strong evidence that the CPR captures a roughly consistent fraction of each taxon and thus reflects real inter-annual and seasonal patterns (Richardson et al. 2006).
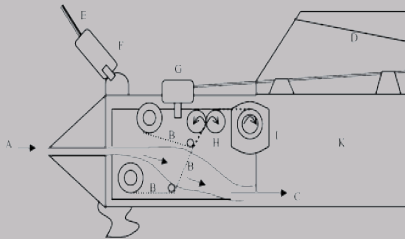
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affecting different trophic levels and resulting in a trophic amplification effect from phytoplankton primary production to the cod stock through changes in holozooplankton structure, jellyfish frequency, and decapod larvae. At the same time, other ecosystem properties, such as bivalve and echinoderm larvae, or sole and plaice spawning stock biomass were also affected by the changes in SST, indicating the importance of this driver in the changes in the North Sea ecosystem. A link has also been made to changes in the North Sea horse mackerel fishery (Reid et al. 2001).

A MATTER OF SCALE

Beaugrand (2004) pointed out that the shifts in the North Sea ecosystem could be better understood if changes in community structure at the level of, at least, the North-East Atlantic were taken into account. As stated by Beaugrand & Reid (2003) in their analysis of changes in the pelagic system in the North Atlantic Ocean, strong biogeographic shifts of copepod warm-water species (associated with a decrease in cold-water species), as well as of warm-water fish species, have taken place in the North East Atlantic during the last decades of the last century. This indicates a shift in the pelagic ecosystem of the North East Atlantic towards a warmer dynamic regime. This shift seems to be driven by climatic variables. Beaugrand & Reid (2003) proved that the North Atlantic Oscillation (NAO) is consistently positively correlated with the sea surface temperature (SST) in the North East Atlantic, while the correlation of the North Hemisphere Temperature (NHT) with North East Atlantic SST has changed from negative to positive during the end of the last century, increasing the effect of the NAO on SST thus leading to the shift towards a warm dynamic regime at the end of the 1980s decade. Widening our spatial perspective on the concept of ecosystem states could have deep repercussions on our ability to detect the causes behind all of these sudden changes. In some cases, it might be that what appears to be a sudden change is not so sudden when wider spatio-temporal scales are considered.

THESIS OUTLINE

In **Chapter 1** we analysed the plankton system in the North Sea looking for sudden changes during the last 40 years, testing our methodology by comparing our results with previously detected discontinuities such as the 1970s cold episodic event or the 1980s regime shift. We also looked for the environmental drivers that could be behind the detected changes.

Chapter 2 narrows down the analyses to the Dutch North Sea waters. In this study we looked at a widely used phytoplankton indicator, chlorophyll a, and investigate its relationship with another phytoplankton indicator, phytoplankton biomass. This relationship was analysed over time taking the phytoplankton community composition and environmental changes into account.

Chapter 3 connects the changes detected in plankton community in the first chapter with changes in population dynamics of higher trophic levels,

particularly the recruitment collapse of herring (*Clupea harengus*) in the North Sea.

In **Chapter 4** we broaden the view on ecosystem changes from the large marine ecosystem (LME) of the North Sea to the overall changes in LMEs across the northeastern Atlantic region. We also look for potential mechanisms that could lead to synchronous marine ecosystem changes across this large region.

In the **final chapter** we summarize the detected changes in plankton community composition, their relationship to higher trophic levels and environmental drivers. We discuss the importance of considering the scale at which ecological and environmental processes occur and the necessity of selecting biological and environmental indicators that allow to increase the understanding of ecological processes.

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> "*Come gather 'round people wherever you roam*
> *and admit that the waters around you have grown*
> *and accept it that soon you'll be drenched to the bone.*
> *If your time to you is worth saving*
> *Then you better start swimming or you'll sink like a stone*
> *For the times they are a-changin'.*"
>
> Bob Dylan

ABSTRACT: This paper analyses long-term and seasonal changes in the North Sea plankton community during the period 1970 to 2008. Based on Continuous Plankton Recorder (CPR) data covering 38 yr, major changes in both phytoplankton and zooplankton abundance and community structure were identified. Regime changes were detected around 1978, 1989 and 1998. The first 2 changes have been discussed in the literature and are defined as a cold episodic event (1978) and a regime shift towards a warm dynamic regime (1989). The effect of these 2 regime changes on plankton indicators was assessed and checked against previous studies. The 1998 change represents a shift in the abundance and seasonal patterns of dinoflagellates and the dominant zooplankton group, the neritic copepods. Furthermore, environmental factors such as air temperature, wind speed and the North Atlantic water inflow were identified as potential drivers of change in seasonal patterns, and the most-likely environmental causes for detected changes were assessed. We suggest that a change in the balance of dissolved nutrients driven by these environmental factors was the cause of the latest change in plankton community structure, which in turn could have affected the North Sea fish community.

1. Temporal changes in North Sea plankton:

Community changes and environmental drivers

INTRODUCTION

North Sea plankton changes

The North Sea planktonic system has been thoroughly studied during the past 6 decades (Colebrook 1979, Edwards et al. 2001, Reid et al. 2003, Beaugrand 2004b). Continuous Plankton Recorder (CPR) data provided insight into the long-term trends and seasonal patterns of both phyto- and zooplankton and their relationships with hydrographical factors as well as climatological events.

A cold episodic event in the North Sea in the late 1970s has been described and widely acknowledged (Reid et al. 2000, Reid & Edwards 2001, Edwards et al. 2002, Beaugrand 2004a, Beaugrand & Ibanez 2004, Weijerman et al. 2005). These cold years were characterised by low sea surface temperature (SST) values in the North Sea (Becker & Pauly 1996), which were particularly harsh in the shallower southern North Sea. Becker & Pauly (1996) related these low-SST years post-1977 to air–sea exchange processes, which in turn depended on the North Atlantic atmospheric circulation.

Edwards et al. (2002) described how during this period (1) the phytoplankton bloom was smaller than average and occurred later in the year, (2) many early spring diatom species were absent from the spring bloom, and (3) *Chaetoceros* spp., one of the most abundant diatoms in the North Sea, were only present in small numbers. Edwards et al. (2002) also described the crash of the *Ceratium macroceros* population, a very abundant dinoflagellate which may have lost its niche as a result of the late development of the spring bloom.

A second overall change in North Sea plankton occurred during the 1980s (Reid et al. 2001a, Beaugrand & Ibanez 2004, Alheit et al. 2005, Weijerman et al. 2005, McQuatters-Gollop et al. 2007). During this period there was a strong biogeographic shift of warm-water copepod species (associated with a decrease in cold-water species), as well as of warm-water fish species, in the northeast Atlantic (Beaugrand & Reid 2003). This indicated a change in the pelagic ecosystem of the northeast Atlantic towards a warmer dynamic regime, which seems to have been driven by climatic variables.

In contrast with the late 1970s cold episodic event, the North Sea entered a warm-biological dynamic regime after the North Sea warm episodic event from 1988 to 1992 (Edwards et al. 2002). This regime can be characterised by (1) higher Phytoplankton Colour Index (PCI) values in the central North Sea, particularly during winter and summer; (2) an extended phytoplankton season; and (3) a change in the zooplankton community structure (Reid et al. 2001a). All these changes have been related to different environmental factors, such as the increase in SST and changing Atlantic water inflow through the northern North Sea (Reid et al. 2003).

SST increase has also been related to changes in the meroplankton of the North Sea, particularly *Echinocardium cordatum*, decapod crustaceans, and bivalve larvae (Kirby et al. 2007, 2008). These changes in turn affect benthic-pelagic coupling in the North Sea, restructuring the trophic interactions (Kirby & Beaugrand 2009). Beaugrand et al. (2003) showed how fluctuations in plankton have resulted in long-term changes in cod recruitment in the North Sea, demonstrating the propagation of changes through different trophic levels. A link has also been made to changes in the North Sea horse mackerel fishery (Reid et al. 2001a).
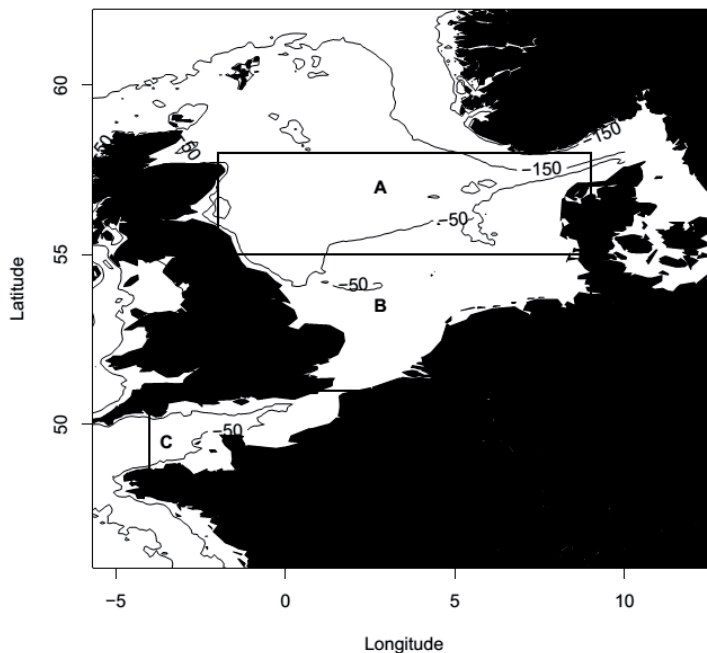
Regime shift considerations

Fig. 1. Study areas and their correspondence with Sir Alister Hardy Foundation for Ocean Science standard areas. The Royal Netherlands Meteorological Institute (KNMI) climatological station De Kooy is indicated (▫). A – Areas C1&2, B – Areas D1&2, and C – Area D3.

CHAPTER 1

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The transitions between the above-mentioned periods have been described in the literature as regime shifts. The term regime shift has been applied to apparent shifts in oceanic and climatic conditions and marine community structure around the world. Collie et al. (2004) defined regime shifts as low-frequency, high-amplitude changes in oceanic conditions that may be specifically pronounced in biological variables and propagate through several trophic levels.

Although all these transitions have been considered regime shifts in the past, not all long-term changes in time series should be considered regime shifts. A change could be contained and be exclusive to one part of a system, not transferred through different trophic levels, or not consistent over time.

The North Pacific (Hare & Mantua 2000) and the North Sea (Reid et al. 2001a, Weijerman et al. 2005) showed 2 regime shifts around 1977–79 and 1988–89, but the late 1980s shift did not return the system to the previous state. Weijerman et al. (2005) pointed out the possibility of another shift in the late 1990s, hinted at by their results. This late 1990s shift coincided with the second of the 2 pulses of oceanic incursion into the North Sea from the north around 1988 and 1998 that co-occurred with strong northward advection of anomalously warm water at the edge of the eastern British continental shelf (Reid et al. 2001b). Several studies relating to different trophic levels support the idea of a shift in the late 1990s, ranging from herring recruitment failure (Payne et al. 2009) to seabird breeding failure along the North Sea coast (Proffitt 2004, Wanless et al. 2005). Although there seemed to be a connection to changes in plankton dynamics after 1998, no in-depth study of the plankton system before and after this year has been carried out to our knowledge.

In the present study, a selection of plankton indicators taken from CPR survey data covering 1970 to 2008 were examined to investigate long-term changes in the planktonic system of the central North Sea, southern North Sea and English Channel. These indicators were ordinated by principal component analysis (PCA), and the resulting principal components (PCs) were tested for long-term and step changes using different techniques. Detected changes were assessed in relation to a range of local and global environmental variables, and the possibility for propagation to higher trophic levels.

MATERIALS AND METHODS

Study area

All data were aggregated into 3 different regions: central North Sea (55–58°N), southern North Sea (51–55°N), and the English Channel (Fig. 1).

These regions vary in bathymetry and hydrodynamic properties; e.g. the central North Sea is deeper than the southern part. This affects the mixing of the water, causing the central part to be stratified at times during warmer periods of the year (Richardson & Pedersen 1998).

Data collection

Plankton time series

CPR data were obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Plankton data were retrieved as monthly mean counts per sample per area from standard areas C1, C2, D1, D2 and D3 covering the North Sea region (Fig. 1). Each sample represents 10 nautical miles of tow and approximately 3 m^3 of filtered water (Warner & Hays 1994).

 The variables included in the analyses were:

PCI. PCI is a semi-quantitative estimation of algal biomass. It is based on a relative scale of greenness and is determined by reference to a standard colour chart (McQuatters-Gollop et al. 2007). Other studies have proven the validity of PCI as a representation of phytoplankton biomass (Batten et al. 2003, Raitsos et al. 2005).

Total copepods. This variable was log-transformed ($\log_{10}$ (Abundance + 1)) in order to homogenise the variance.

Dinoflagellates and diatoms. Because PCI does not give information about the phytoplankton community structure, data on total numbers of diatoms and dinoflagellates were also gathered for an in-depth analysis. Consequently, 6 new variables were added. Potential redundancy between variables was also assessed (see Table S1 in Supplement 1).

Copepod assemblages. Beaugrand (Beaugrand et al. 2002, Beaugrand

2004a) proposed different assemblages of plankton species to be used as indicators of changes in the ecosystem (Table 1). Abundances per area per month of 26 representative copepod species were retrieved from SAHFOS and aggregated according to their ecological preference. Once the abundance data were aggregated into the 3 regions, the ratio of warm-water species (assemblages A1 and A2), and cold-water species (assemblages A5, A6 and A7) to total copepods per region was calculated. These warm- and cold-water copepod species ratios serve as a representation of the copepod community structure and also give information about the other copepod assemblages, i.e. the warm-water copepods:total copepods ratio could change without changes in the original warm-water copepod abundances, but due to changes in shelf-sea species (assemblage A4). Subsequent analyses used these newly generated time series.

Environmental time series

Oceanographic variables. Monthly SST and sea surface salinity (SSS) data covering the study area were obtained from the International Council for the Exploration of the Sea (ICES). CPR coverage is scarce in coastal areas, so the plankton data set represents mainly

open-sea plankton. Because of the gradient from coastal to open sea in both SST and SSS, inclusion of coastal measurements would alter the average values significantly. For this reason, coastal measurements (up to 20 km from the coast) were removed to avoid the influence of riverine inputs in both temperature and salinity. Subsequently, monthly averages per region were calculated.

Monthly data on Atlantic water inflow to the North Sea was obtained from a numerical ocean model, NORWECOM, and it was represented as flow in and out of the North Sea through a section from Norway to the Orkneys along 59.17°N (Reid et al. 2003). Because we were interested in differences in North Sea regions, water flow was also obtained, from the same model, through a second section along 55°N from the UK to Germany. Water flow was represented by southward and northward transport (water moving south and north, respectively) and the difference between them as net transport.

Atmospheric variables. Monthly wind speed and direction, air temperature, sea-level pressure and humidity data series from De Kooy climatological

station (52.92°N, 4.78°E) were gathered from the Royal Netherlands Meteorological Institute (KNMI) for the period 1970 to 2008. This station was selected because of its time coverage, and it has been previously used in similar analyses (Weijerman et al. 2005).

Two more climate-related variables were included. The first, the Hurrell North Atlantic Oscillation (NAO) winter index (NAOi), a December–March index of the NAO (Hurrell & Deser 2009) based on the difference in normalised sea-level pressure (SLP) between Lisbon, Portugal and Stykkishólmur/Reykjavik, Iceland, was obtained from www.cgd.ucar.edu/cas/jhurrell/indices.html. The second, northern hemisphere surface temperature anomaly (NHTa) data, was obtained from the Hadley Centre for Climate Prediction and Research (www.metoffice.gov.uk/hadobs). These data are used as an index of temperature changes. The data set is based on regular measurements throughout the northern hemisphere of air temperature at a global network of long-term land stations and on SST measured from ships and buoys, and consists of annual differences from the 1951–80 monthly averages (Brohan et al. 2006).

Water nutrients. Total soluble nitrogen, total soluble phosphorus and silica data series were obtained from ICES. Data were calculated as $\mu mol\ l^{-1}$ monthly averages, representing surface concentrations (as collected by water bottle sampling <10 m depth), and covered a time span of 20 yr from 1988. As with SST and SSS, nearshore measurements were removed to avoid the influence of coastal nutrient dynamics, more related to riverine inputs. When available, data on different nitrogen compounds (i.e. NO_3, NO_2, NH_4) were also obtained from the same database, time period and depth.

Analyses

PCA

As a first step, 2 PCAs were run. Both PCAs used data covering 38 yr and, as monthly values were used, a total of 456 time steps (38 yr × 12 mo yr^{-1}) were analysed. The first PCA ordinated 12 plankton variables (PCI, total copepod abundance, warm- and cold-water copepod ratios; 456 × 12 matrix) based on correlations (Legendre & Legendre 1998, Oksanen et al. 2010); the second PCA included in addition diatom and dinoflagellate
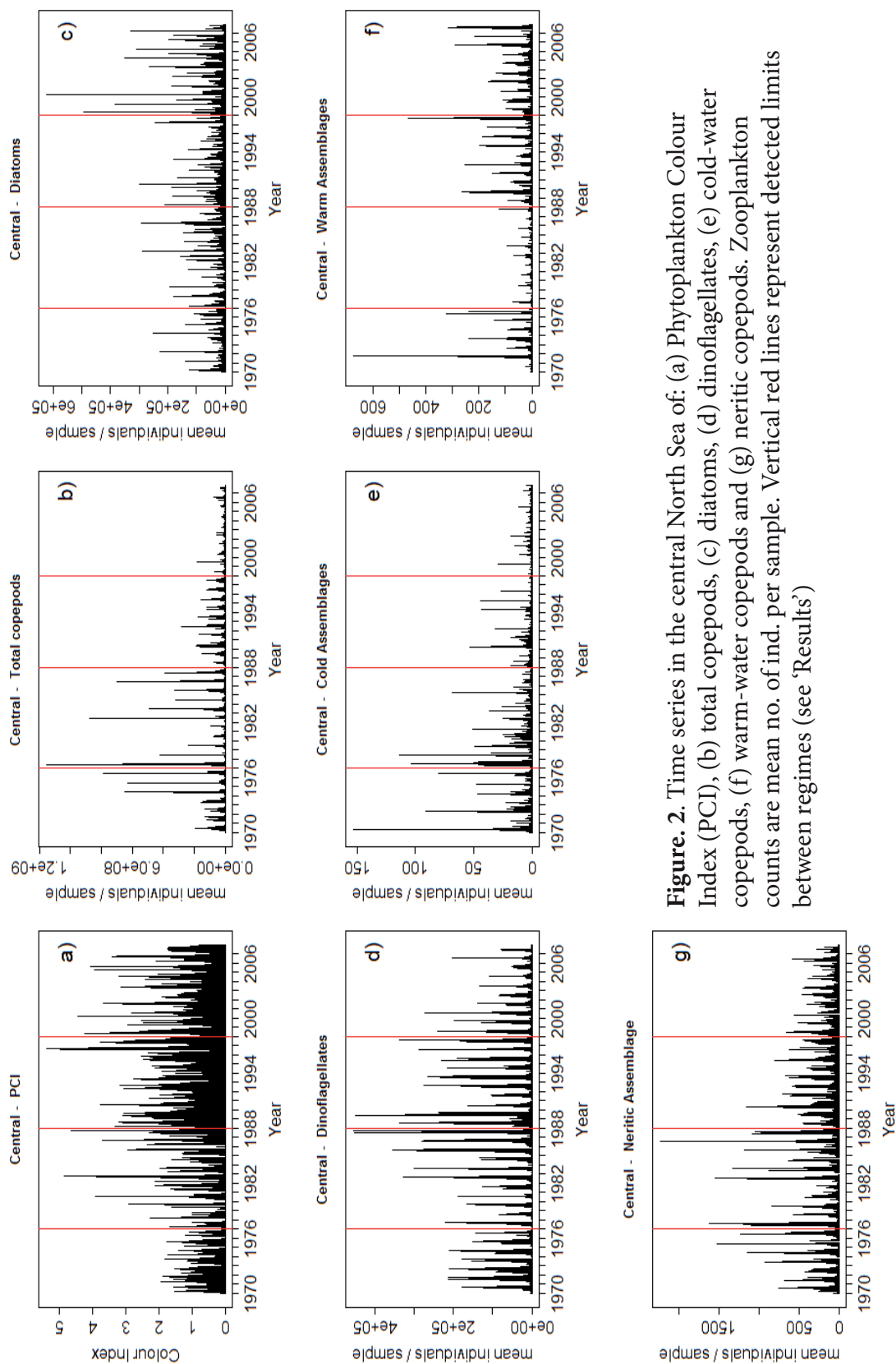
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Figure. 2. Time series in the central North Sea of: (a) Phytoplankton Colour Index (PCI), (b) total copepods, (c) diatoms, (d) dinoflagellates, (e) cold-water copepods, (f) warm-water copepods and (g) neritic copepods. Zooplankton counts are mean no. of ind. per sample. Vertical red lines represent detected limits between regimes (see 'Results')

abundances, giving a total of 18 plankton variables (456 × 18 matrix) based on correlations. These 2 PCAs were compared to identify the best representation of the system (see Figs. S1 & S2 and Table S2 in Supplement 2). The resulting PCs were used as indicators of the plankton ecosystem state, and the following analyses were carried out.

Regime detection analyses

Split-moving window boundary analysis (SMW). SMW (Beaugrand 2003) was used to detect regime changes in each of the PCs. For this analysis, each PC axis was converted from a linear vector into a 12 × 38 matrix (1 row mo^{-1} and 1 column yr^{-1}).

The calculation of SMW is realised in 4 steps: (1) A window of even-numbered size is introduced at the beginning of the time series matrix. (2) This window is then divided into 2 half-windows containing the data of all months for the same amount of years. (3) An association coefficient (Euclidean distance in this case) is used to evaluate the differences between the time periods contained in these 2 windows. A multiple response permutation procedure (Mielke et al. 1981) is applied to test the 2 periods on the basis of the information provided by all months. (4) The window is then moved from year to year, repeating steps 2 and 3 until the end of the time series is reached. This procedure provides a p-value for each year representing the statistical significance of a year being the limit between 2 different regimes.

Change point detection (CPD). A CPD method (Zeileis et al. 2003) as described by Quandt (1958) was applied as a hypothesis-testing method. To avoid the problem of inflation of p-values due to multiple testing, the supremum of F in the F-distribution(sup(F)) was used as proposed by Andersen et al. (2009). The R package 'strucchange' was used for this analysis (Zeileis et al. 2003).

Hierarchical clustering. Constrained hierarchical clustering was applied to the 38 × 12 matrix of each PC (Gordon & Birks 1972). In combination with the previous techniques, this allows us not only to see which years were more similar but also to detect sudden changes in the time series. The R package 'rioja' was used for this analysis (Juggins 2009).

Table 1. Zooplankton species-assemblage indicators and their ecological preferences (after Beaugrand 2004a). A1 and A2 are considered warm-water copepod species; A5, A6 and A7 are considered cold-water copepod species

Species assemblage	Assemblage indicator	Species composition	Ecological preference
A1	Warm-temperate pseudo-oceanic species	*Euchaeta gracilis*, *Euchaeta hebes*, *Ctenocalanus vanus*, *Calanoides carinatus*	Warm water along the European shelf
A2	Temperate pseudo-oceanic species	*Rhincalanus nasutus*, *Eucalanus crassus*, *Centropages typicus*, *Candacia armata*, *Calanus helgolandicus*	Oceanic and neritic waters
A3	Coastal species	*Isias clavipes*, *Anomalocera patersoni*, *Labidocera wollastoni*	Shallow and coastal habitat
A4	Shelf-sea species	*Centropages hamatus*, *Temora longicornis*, *Pseudocalanus* adult, *Para-Pseudocalanus* spp.	Neritic distribution
A5	Cold-temperate species	*Aetidus armatus*, *Pleuromamma robusta*, *Acartia* spp., *Metridia lucens*	Mixed water usually found at the boundary between warm and subarctic water
A6	Subarctic species	*Heterorhabdus norvegicus*, *Scolecithricella* spp., *Euchaeta norvegica*, *Calanus finmarchicus*	Subarctic water
A7	Arctic species	*Calanus hyperboreus*, *Metridia longa*, *Calanus glacialis*	Arctic water

Environmental drivers

In order to assess potential environmental drivers of the system, the correlation between environmental variables and the PCs was investigated, including lag periods of up to 3 mo. These correlations were investigated both with the original PCs and time series, and with detrended PCs and time series. Detrending was carried out by means of a general additive model (GAM) (Wood 2006), with 'Month' (1 to 12) as a smoothing function. The residuals of these models were considered the new detrended data series.

Variables showing a Pearson correlation value with a PC greater than 0.5 were pre-selected as possible explanatory variables in a GAM. In order to prevent problems caused by the presence of outliers and collinearity,

these variables were subjected to a data exploration and selection process as suggested by Zuur et al. (2010).

The variables that passed these data exploration protocols were included as smoothing functions in a generalised additive mixed model (GAMM) (Wood 2006), and a model selection process was performed using the Akaike information criterion (AIC) as a means of comparing the fit of different models.

Serial autocorrelation was accounted for by minimising autocorrelation in the model residuals. This was achieved by fitting an autoregressive-moving average correlation structure (ARMA) in a GAMM (Wood 2006, Pinheiro et al. 2009), using again the AIC to select the best model (Zuur et al. 2009).

In a parallel analysis, the yearly variables (i.e. NAOi and NHTa) were tested for regime changes via the CPD method. This analysis was run independently, as the frequency of the variables did not match the rest of variables considered.

All analyses were performed using the R free statistical software environment (R Development Core Team 2012)

RESULTS

A representation of the central North Sea data included in the PCA can be seen in Fig. 2. Temporal patterns previously described in the North Sea are visible. PCI was considerably higher after 1988 (Fig. 2a), which represented higher phytoplankton biomass. The practical disappearance of warm-water copepods (Fig. 2f) together with the increase in cold-water copepods (Fig. 2e) immediately post-1977 is in agreement with previous findings related to the late 1970s North Sea cold episodic event. The opposite situation post-1988, i.e. increase in warm-water copepods and decrease in cold-water copepods, was an indication of the warm regime in the North Sea since the late 1980s.

Principal components analyses

Plankton data were ordinated by 2 PCAs to create an index of the plankton ecosystem state through time. The output of both PCAs, one excluding diatom and dinoflagellate abundance data and the other including them, was

compared and PCs were selected by 1 of 2 criteria: (1) PCs that accumulate to at least 70% of the variation in the original data, (2) detection of a change point in a scree-plot of the eigenvalues, marking a separation between PCs with a large explanatory value and those with less explanatory value. This change point is commonly referred to as the 'elbow effect' (Zuur et al. 2007). The number of PCs selected for further analyses was defined by the first of these criteria reached.

For the first PCA, the elbow effect appeared after the second PC, while for the second PCA, where diatoms and dinoflagellates were included, it appeared after the third PC (Fig. S1 in Supplement 2). Hereinafter, all results and discussion will be addressing the second PCA, including diatom and dinoflagellate abundance data. A comparison of both PCAs can be found in Supplement 2.

Interestingly, the loadings for each variable in each of the studied PCs showed differences between groups, but are roughly consistent within each group, which indicated that no regional differences needed to be considered (Table 2).

Table 2. Loadings of the different variables for the first 3 principal components (PC) of the second principal component analysis including all biological variables. Explained variation was 28.8, 12.7 and 10.5% for PC axes 1, 2 and 3 respectively. PCI: Phytoplankton Colour Index.

|	PC1	PC2	PC3
Central North Sea warm-water copepods	0.217	−1.500	1.011
Central North Sea cold-water copepods	0.681	0.900	−0.209
Southern North Sea warm-water copepods	0.506	−1.407	0.947
Southern North Sea cold-water copepods	0.652	0.545	−0.212
English Channel warm-water copepods	−0.086	−1.203	0.796
English Channel cold-water copepods	0.669	−0.380	0.226
Central North Sea total copepods	−1.858	−0.281	−0.170
Southern North Sea total copepods	−1.845	−0.278	−0.304
English Channel total copepods	−1.786	0.025	−0.190
Central North Sea PCI	−1.424	−0.227	0.897
Southern North Sea PCI	−1.613	0.030	0.728
English Channel PCI	−1.574	0.453	0.172
Central North Sea diatoms	−0.708	0.950	1.360
Southern North Sea diatoms	−0.738	1.134	1.210
English Channel diatoms	−1.220	0.883	0.093
Central North Sea dinoflagellates	−1.468	−0.762	−0.727
Southern North Sea dinoflagellates	−1.182	−0.714	−0.921
English Channel dinoflagellates	−1.059	−0.275	−0.775
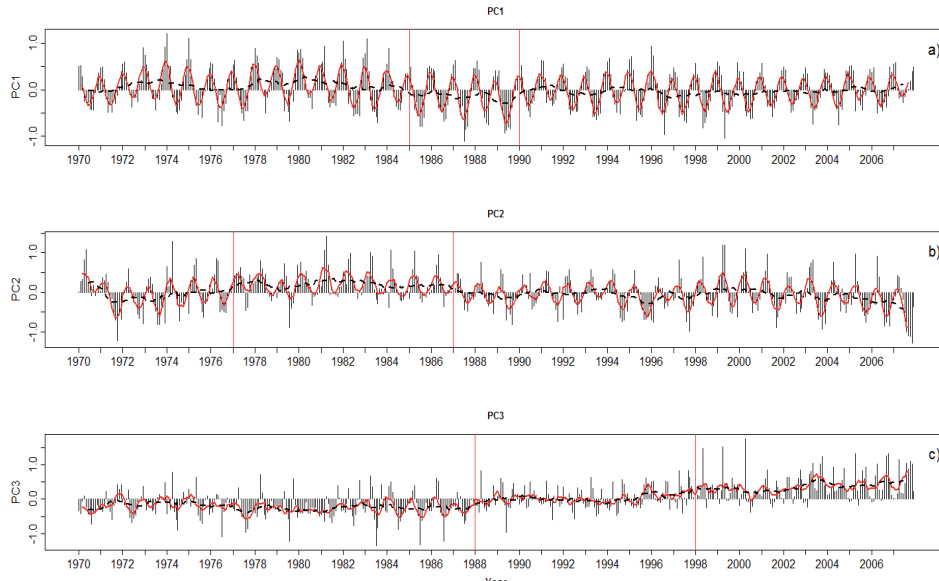
Figure 3. Representation of the 3 principal components (a: PC1, b: PC2, and c: PC3) of the principal component analysis that included all plankton data. Vertical red lines represent detected shifts. Two trend lines were added to the data: a 6-mo running mean representing the seasonal trend (solid red line) and a 12-mo running mean representing long-term patterns (dashed black line)

Table 3. Regime limits found by the different methods. SMW: split-moving window boundary analysis; CPD: change point detection method; CC: chronological clustering; PC: principal component. Numbers in brackets represent 95% confidence intervals, which were only available for CPD

Method	PC1	PC2	PC3
SMW	1984–85	1977–78	1987–88–89–90
	1990	1987	1998–99
CPD	1983 (1976–1990)	1977 (1975–1981)	1988 (1986–1990)
		1987 (1985–1989)	1997 (1996–1998)
CC	1985	1974	1988
	1990	1987	1998
		2005	

The first PC (PC1; 28.8% explained variance; Fig. 3a, Table 2) represents the seasonal patterns of total abundance of phytoplankton (PCI) and zooplankton (total number of copepods). It was also related to phytoplankton community composition (diatom and dinoflagellate abundances).

The second PC (PC2; 12.7% explained variance; Fig. 3b, Table 2) represents a temporal pattern, including a seasonal as well as a long-term signal, of the community composition of both phyto- and zooplankton in the 3 areas.

The third PC (PC3; 10.5% explained variance; Fig. 3c, Table 2) represents a different signal, with no apparent seasonal signal. It was highly related to community composition of both phyto- and zooplankton, and to phytoplankton abundance, particularly in areas C1&2 (central North Sea) and D1&2 (southern North Sea).

Regime change analyses

Three types of regime change analysis were applied to the PCs, which together represent 52% of the variation in the data set (Fig. 3).

All analyses found a regime change in PC1 around 1985 (Table 3). This change was better detected by the methods equipped to deal with seasonal variation. The period pre-1985 was characterised by a strong signal during winter months (positive values) and a weaker signal during summer months (negative values). The period 1985 to 1990 started with a strong signal during the summer months and weaker during the winter months (Fig. 3a). As all the highly related variables to this PC have a negative sign (Table 2),
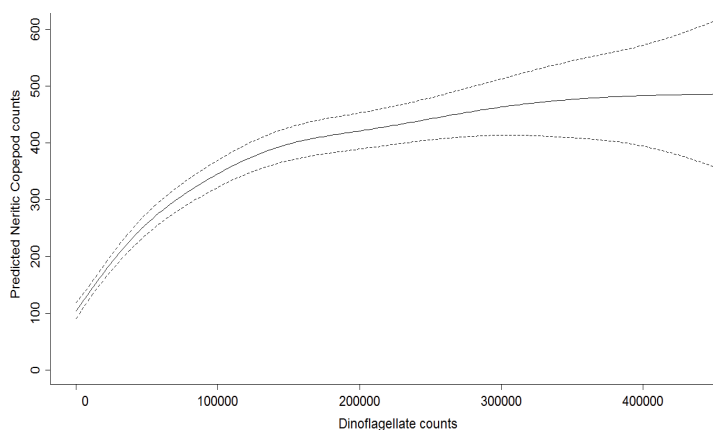

Figure 4. Predicted neritic copepod counts (mean no. of ind. per sample) as a smooth function of dinoflagellate counts. Dashed lines represent the approximate 95% confidence limits of the prediction
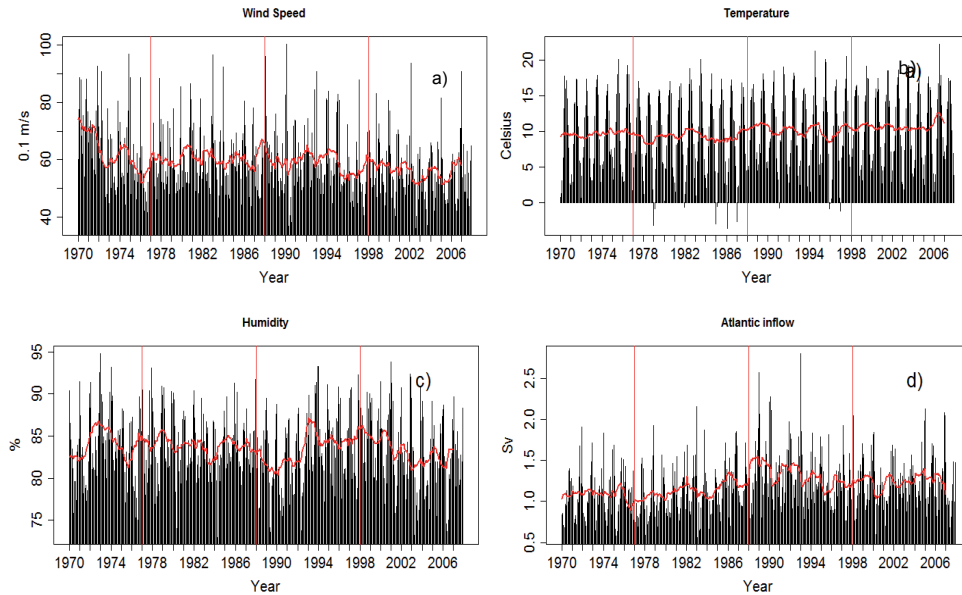
Figure 5. Trends of environmental drivers: (a) wind speed, (b) temperature, (c) humidity and (d) Atlantic water inflow. Red lines are a 12-mo running mean and represent the annual trend. Regime limits are indicated by vertical red lines.

the previous structure would translate as a period pre-1985 in which winter periods were characterised by very low abundances of both phyto- and zooplankton, followed by a second period from 1985 to 1990 where winter abundances were not as low and summer abundances were considerably higher. During the last period, post-1990, the seasonal oscillation is smaller, which is more apparent towards the end of the time series (Fig. 3a).

The different methods agree in the presence of 2 regime changes in PC2 around the years 1978 and 1987 (Fig. 3b, Table 3). These changes were more apparent in the long-term annual signal than in the seasonal signal. This PC showed a clear positive period from 1977 to 1988. Before and after that period, the PC oscillates around zero in a seasonal fashion, although the PC seems to approach a negative period post-2004 (Fig. 3b). This last period was only detected by chronological clustering (Table 3). This PC seems to be related to temperature changes, as warm- and cold-water copepods have an opposite loading sign (Table 2). Thus in the period 1976 to 1987, warm-water copepods would have lower abundances while cold-water copepods would be more abundant. After 1988, the opposite is occurring.
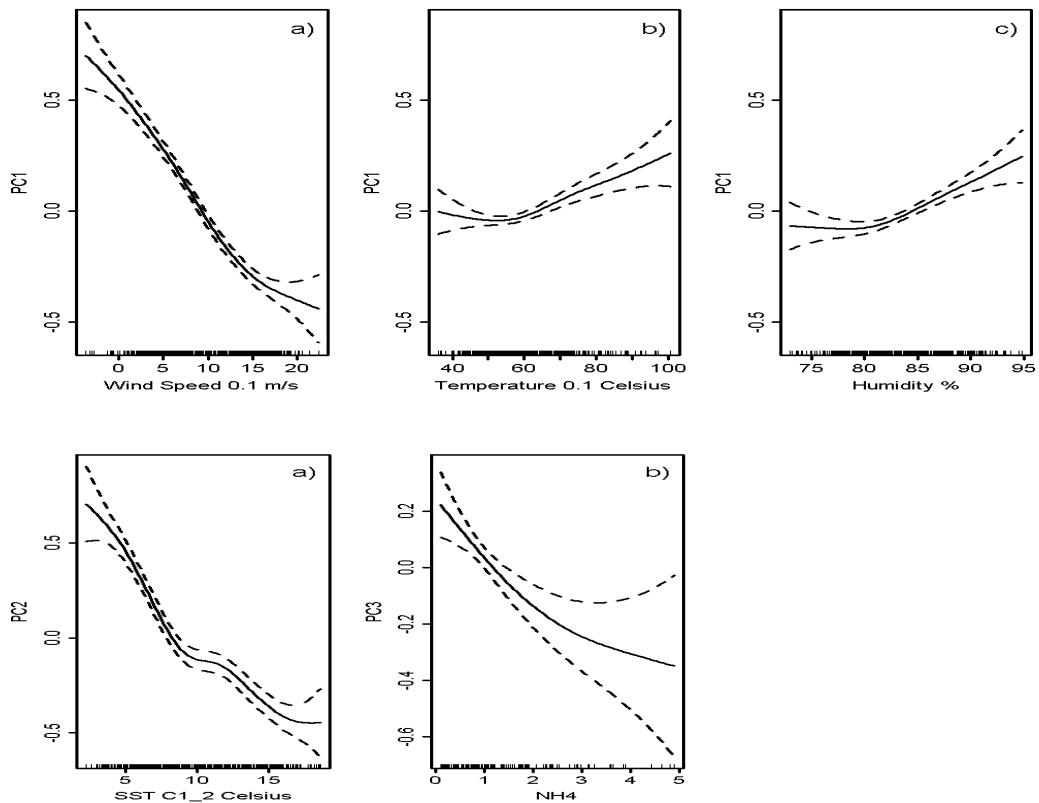
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Figure 6. Smoothing functions of generalised additive models predicting principal components (PCs). PC1 with (a) temperature, (b) wind speed, and (c) humidity; PC2 with (d) sea surface temperature (SST) in area C1&2; and PC3 with (e) ammonium concentration.

Three different regimes were detected in PC3 (Fig. 3c, Table 3): a negative period until 1988, a period of oscillation around zero from 1988 to 1998, and a third period from 1998 to 2007 characterised by positive values and an upward trend. Variable loadings for this PC are positive for all variables with absolute loadings over 0.7, except dinoflagellate abundance (Table 2). Therefore, PC3 expressed in terms of actual plankton variables represents an increase in warm-water copepod assemblages unrelated to any significant change in cold-water copepod assemblages; it also reflects an increase in phytoplankton biomass, as represented by PCI, a positive trend in the abundance of diatoms, plus a negative trend in dinoflagellate abundance.

The 95% confidence intervals resulting from the CPD method (Table 3) became smaller when there was no seasonal pattern in the time series. So, although this method is able to deal with seasonal time series, the accuracy of detection, as shown by the 95% confidence intervals, is higher with non-seasonal patterns.

PC1 and PC2 were subjected to seasonal decomposition in order to verify the shift in seasonal patterns suggested by the analyses (see Supplement 3 including Fig. S3).

Plankton changes

Post-1977. The years following 1977 had a lower phytoplankton biomass (PCI), and the growing season seemed to be shortened. Both diatoms and dinoflagellates also showed a period of lower total numbers. There was a prominent decrease in total numbers of copepods, and the number of individuals belonging to cold-water copepod assemblages increased, while the warm-water copepod assemblages decreased (Fig. 2b,e,f).

Post-1988. After 1988 there was a clear increase in phytoplankton biomass and there seemed to be a decrease in dinoflagellates from 1990 compared to the second half of the 1980s (Fig. 2d). There was a clear decrease in the annual maxima of total number of copepods (Fig. 2b) and an increase in the number of individuals of warm-water copepod assemblages (Fig. 2f). The number of neritic copepods (Assemblage A4 in Table 1) seemed

Table 4. Model selection for the general additive model of the first principal component. The model with the lowest, or most negative, Akaike information criterion (AIC) is considered the best (bold). Adjusted R^2, representing the fit of each model weighed by number of cases, is also included. SST: sea surface temperature

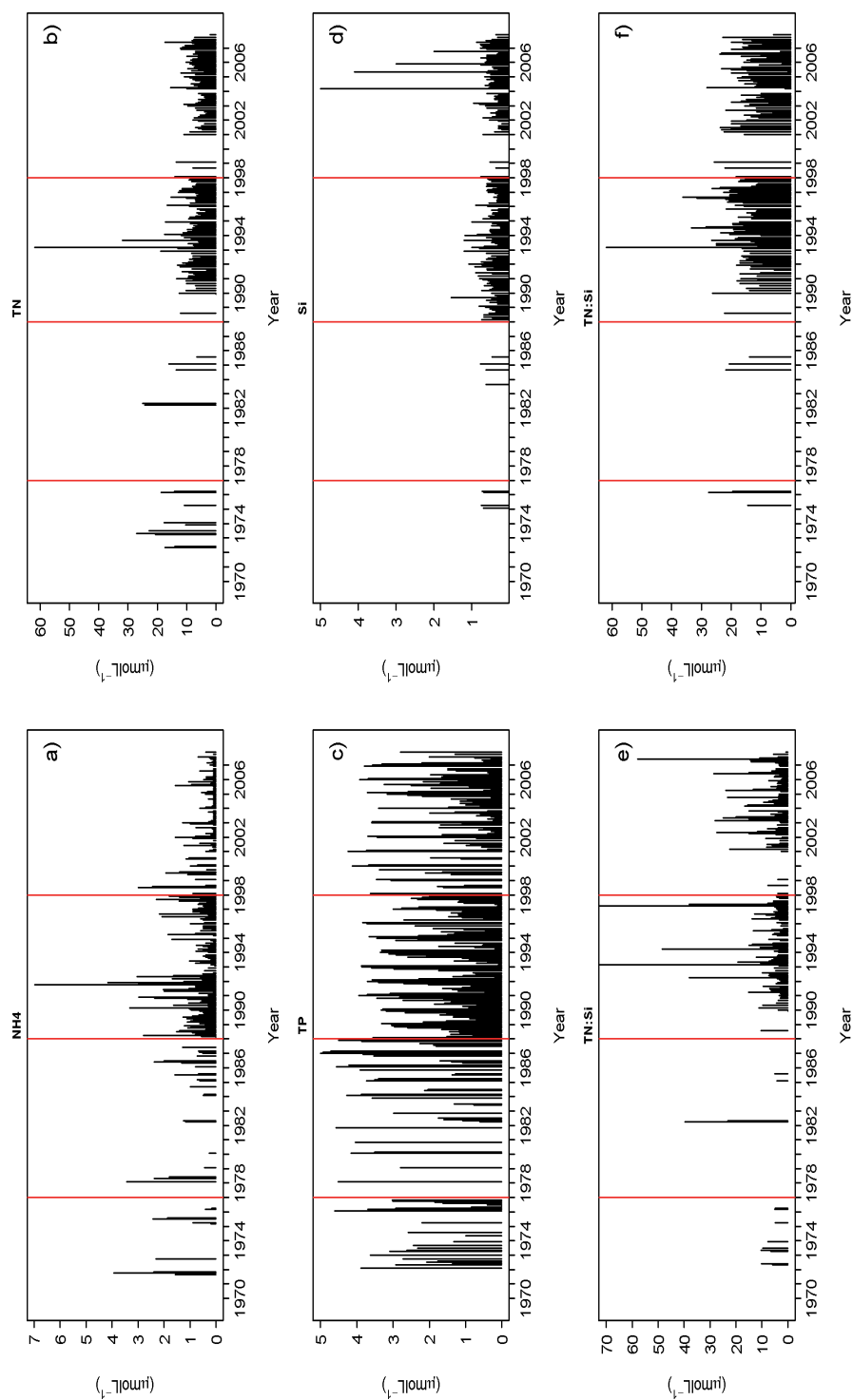| Smoothing functions	R² adj.	AIC
Wind speed, temperature, humidity, SST	0.755	−169.20
Temperature, humidity, SST	0.738	−142.77
Wind speed, humidity, SST	0.613	−15.49
Wind speed, temperature, SST	0.724	−149.78
Wind speed, temperature, humidity	0.751	−206.22
Wind speed, temperature, humidity, Atlantic water inflow		**−234.91**

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Fig.ure 7. Time series plot of: (a) ammonia (NH4), (b) total nitrogen (TN), (c) total phosphorus (TP), (d) silica (Si), (e) N:Si ratio and (f) TN:TP ratio. Vertical lines represent the regime limits detected in the plankton data
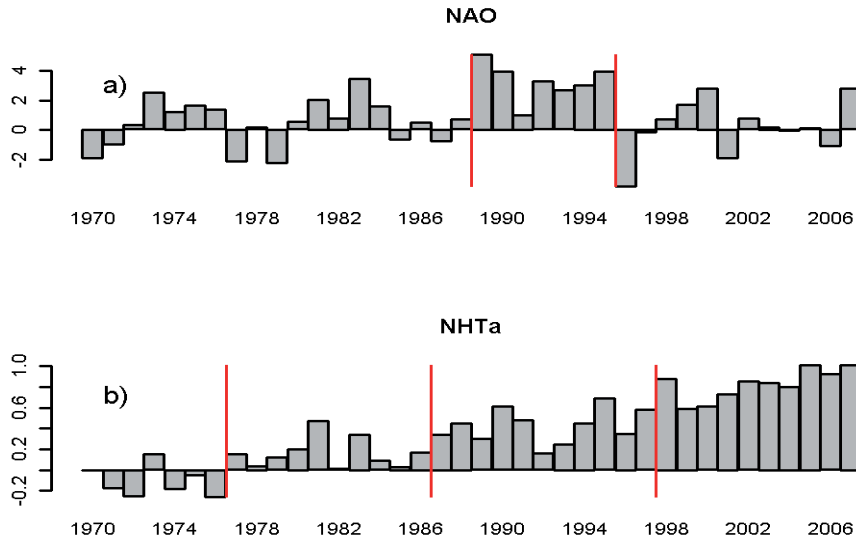
Figure 8. (a) North Atlantic Oscillation winter index (NAOi) and (b) northern hemisphere surface temperature anomaly (NHTa, °C). Vertical lines represent regime changes in these time series

to decrease from the previous years, but they were higher than the years immediately post-1977 (Fig. 2g).

Post-1998. PCI decreased post-1998, particularly in autumn and winter (Figs. 2a, see also Fig. 9b). The main change in the phytoplankton community is the pronounced decrease in dinoflagellates post-1999 (Fig. 2d) and the increase of the diatoms annual maxima (Fig. 2c).

After 1999 there was a further increase in the ratio of warm-water copepod species (data not shown), but this increase in the dominance of warm-water species was not particularly related to an increase in the number of individuals in this assemblage (Fig. 2f) but with a decrease in neritic copepods (Fig. 2g).

Counts of neritic copepods showed a high correlation (R = 0.57) with the number of dinoflagellates per sample (Fig. 4). In that period, 38.7% of the variation of neritic copepods was explained by a GAM using the mean counts of dinoflagellates. Including the mean counts of diatoms as a covariate only added another 0.6% of explained variation. The GAM showed a linear phase below 100000 dinoflagellates sample^{-1} and a stabilised phase above that number.

Environmental drivers

The best fit of models explaining the different PCs based on environmental drivers (Fig. 5) were those without a lag period between explanatory and response variables.

PC1. The pattern represented in the first PC showed high correlation (>0.5) with 6 environmental variables: wind speed, air temperature, solar radiation and humidity at De Kooy Station, and SST in areas C1&2 and D1&2.

SST in area D1&2 and solar radiation at De Kooy were not included in the GAM because of their high collinearity (>0.8) with SST in area C1&2 and temperature respectively. Variables that were collinear between 0.5 and 0.8 were included and evaluated during the model selection phase.

Autocorrelation in the model was accounted for using an $\mathrm{ARMA}_{(2,2)}$ autocorrelation structure, which showed the best fit (Table 4).

The best model (Table 4) included wind speed, temperature and humidity at De Kooy (Figs. 5 & 6). The residuals of this model were then compared with the remaining environmental variables to check for any missing covariate. A relationship with the Atlantic water inflow through the section Norway-Orkneys was found. Refitting the model with this variable as a linear covariate gave a significant improvement in the model AIC (Table 4).

PC2. The second PC only showed correlation values >0.5 with environmental variables related to temperature. The highest correlation value was with SST in area C1&2, so this variable was used as a smoother in a GAM. Temporal autocorrelation in the model residuals was accounted for via an $\mathrm{ARMA}_{(1,3)}$ structure and the best model included water temperature in area C1&2 with a lag of 1 mo (Fig. 6d).

PC3. The third PC only showed correlation values <0.5 with the environmental variables considered in this analysis. The only variables with values >0.25 were total nitrogen and ammonia in the central North Sea, and ammonia, total nitrogen and total phosphorus in the southern North Sea. Unfortunately, the nutrient data are not consistent in time, so only values after 1988 were available (see Fig. 7). Therefore only 159 data points were used for this model, as opposed to the previous 2 models, which were based on 455 and 456 data points, respectively; thus the results (Fig. 6e) should not be compared with the previous models (Fig. 6a-d).
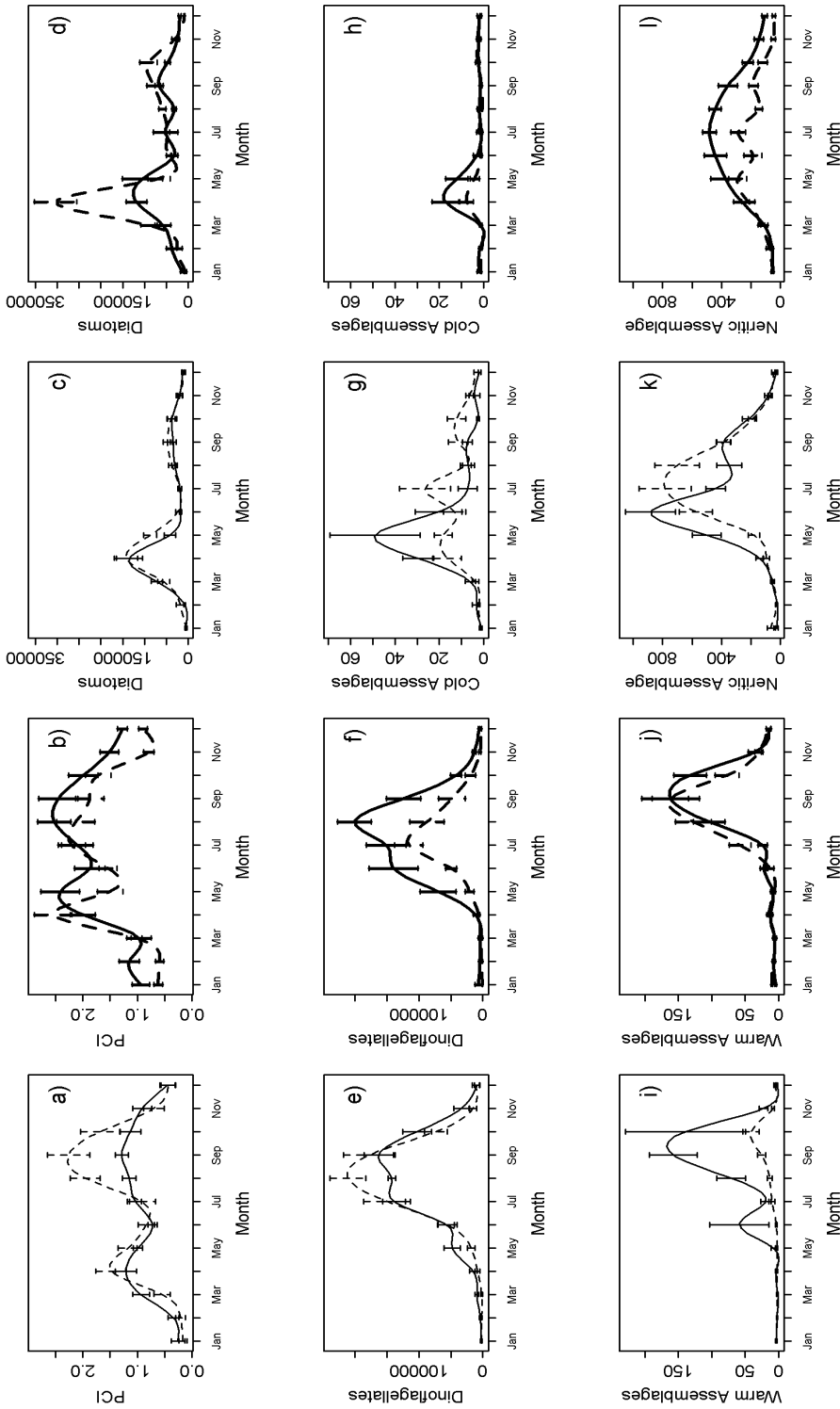
Figure 9. Seasonal patterns in the plankton variables: (a,b) Phytoplankton Colour Index (PCI), (c,d) coldwater copepods, (e,f) diatoms, (g,h) warm-water copepods, (i,j)dinoflagellates and (k,l) neritic copepods. Each line represents the seasonal trend for a specific period: (a,c,e,g,i,k) solid line is 1970–1977 and dashed line is 1978–1988; (b,d,f,h,j,l) solid line is 1988–1997 and dotted line is 1997–2007. Units are mean no. of ind. per sample for all variables, except CI, which is represented as mean colour index

Yearly variables. The analyses of NAOi and NHTa showed regime limits (CPD method) that coincided with the ones found in the PCs, with the exception of the late 1970s shift that was missing in the NAOi (Fig. 8a, Table 5), although 2 very low NAOi years occurred in 1977 and 1979. After a highly positive phase from the second half of the 1980s to the mid-1990s, the NAOi reached a neutral stage (Fig. 8a). Post-1997, NHTa showed several consecutive years with higher values, after a general positive phase with relatively lower values during the period 1977 to 1997 (Fig. 8b).

DISCUSSION

The results presented here suggest 3 regime changes in the North Sea plankton system around the year 1977 (PC2; Fig. 3), 1988 (PC2 and PC3; Fig. 3) and 1998 (PC3; Fig. 3), propagating from phytoplankton to zooplankton via food-limitation mechanisms. Another 2 changes were found in PC1 in 1985 and 1990 (Fig. 3, Table 3), which we interpret as a period of instability in seasonal patterns after the late 1970s cold episodic event previously identified (Beaugrand 2004b, Beaugrand et al. 2008). Wind speed, air temperature, humidity and Atlantic water inflow were identified as potential environmental drivers of the plankton seasonal dynamics (PC1) in the study area (Table 3).

Neither the PCA (see Supplement 2) nor the inspection of individual variables indicated big differences between the 3 regions. This suggests that our results and discussion are applicable to the whole study area.

Temporal changes and regime shifts

Post-1977

This regime change corresponds to the cold episodic event described previously (Reid & Edwards 2001, Edwards et al. 2002): phytoplankton biomass patterns clearly changed, the spring bloom was less apparent, and there was a higher biomass during the second part of the year (Fig. 9a). This period ended around 1984 (regime change detected in PC1), and gave way to a transition period during the late 1980s. Both the cold-water copepods and PCI returned to previous values during the mid-1980s (Fig. 2), which indicates the episodic character of this regime. Only the warm-water copepods seemed to stay in the cold event configuration throughout the 1980s (Fig. 2).
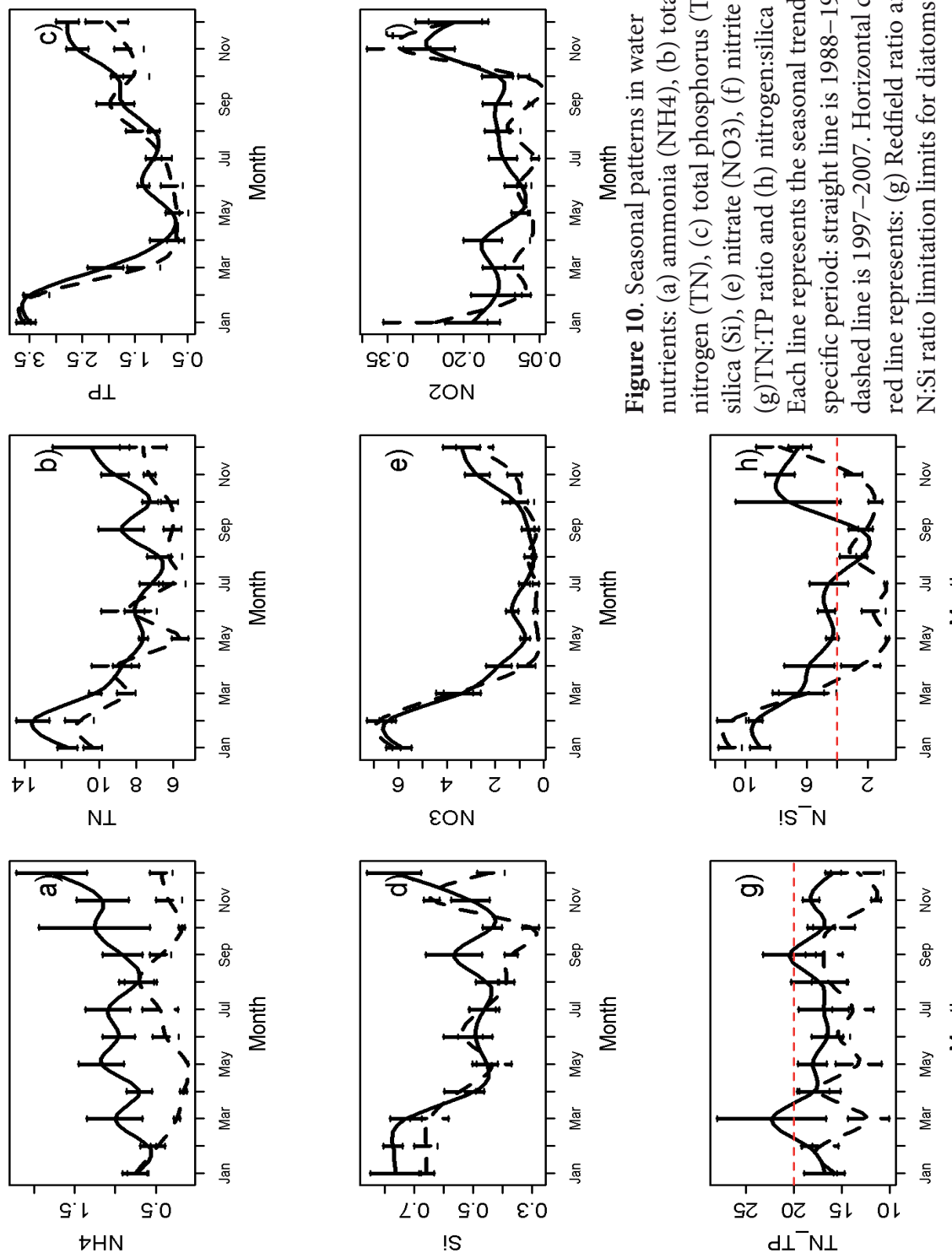
Figure 10. Seasonal patterns in water nutrients: (a) ammonia (NH4), (b) total nitrogen (TN), (c) total phosphorus (TP), (d) silica (Si), (e) nitrate (NO3), (f) nitrite (NO2), (g)TN:TP ratio and (h) nitrogen:silica ratio. Each line represents the seasonal trend for a specific period: straight line is 1988–1997 and dashed line is 1997–2007. Horizontal dashed red line represents: (g) Redfield ratio and (h) N:Si ratio limitation limits for diatoms

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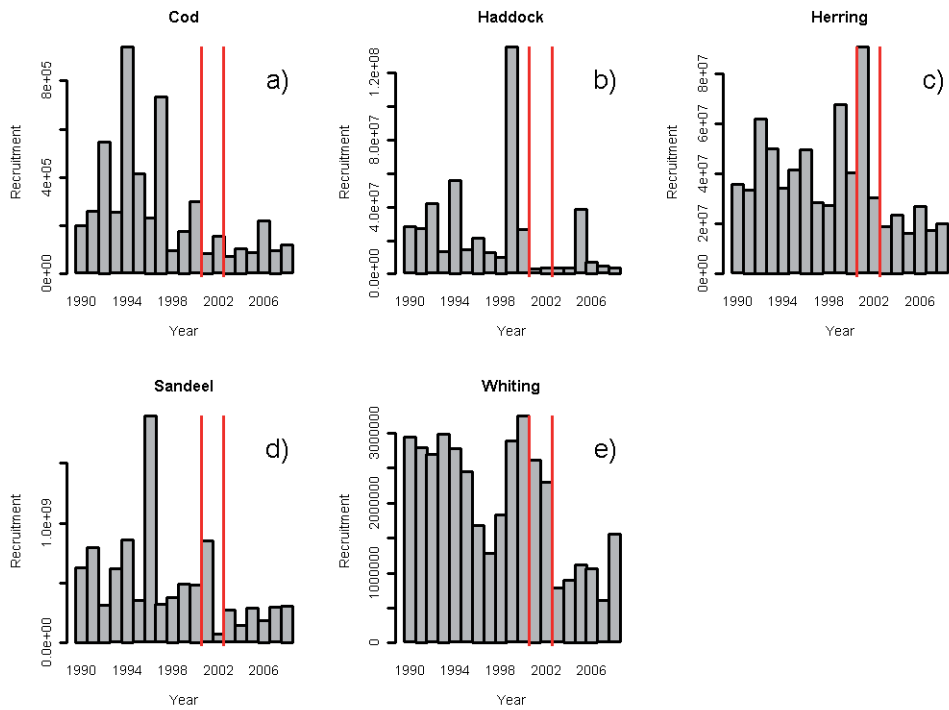
Figure 11. Recruitment for different fish species since 1990: (a) *Gadus morhua*,(b) *Melanogrammus aeglefinus*, (c)*Clupea harengus*, (d) *Ammodytes* spp.and (e) *Merlangius merlangus* in theNorth Sea. Vertical lines represent confidence intervals of regime limit detected in preliminary analyses. Note different scales of y-axes

Table 5. Regime limits found by the change point detection method for the North Atlantic Oscillation winter index (NAOi) and the northern hemisphere temperature anomaly (NHTa)

Indices	Regime limits (95% confidence intervals)		
NAOi		1988 (1986–1992)	1995 (1991–1997)
NHTa	1976 (1973–1979)	1986 (1982–1989)	1997 (1995–1999)

Post-1988

The late 1980s North Sea plankton regime shift was also clearly detected in PC2 and PC3, together representing a seasonal and a non-seasonal pattern in the phyto- and zooplankton community composition (Fig. 3, Table 2). There was a clear change from a cold-water copepod-dominated phase (dashed line in Fig. 9g,i) to a warm-type plankton system with higher phytoplankton biomass throughout the year (Fig. 9b,h,j).

Post-1998

A third regime change was detected at the end of the 1990s. After 1998 the relative contribution of warm-water copepod species increased considerably and the total number of copepods decreased (Fig. 2b).

Although the mean numbers of warm-water copepods per sample did not show a significant increase from the previous period (Fig. 9j), the copepod community showed a decrease in neritic species (Fig. 2g). This assemblage dominated in numbers per sample until 1998. After 1998 the neritic copepods contributed only half of the total copepods of the analysed assemblages from August onwards (Fig. 9l), when the warm-water copepods started growing in numbers (Fig. 9j). This drop in numbers of neritic copepods can be related to a decrease during the same period in dinoflagellates, a major food source for some of these copepods (Gentsch et al. 2009). Different studies have highlighted the importance of a high and constant food supply for the uccess of some neritic copepod species (Vidal 1980, Evans 1981, Tsuda 1994, Gentsch et al. 2009), so a decrease in prey, e.g. dinoflagellates, during part of the year could lead to limitation of population growth.

Although the number of diatoms showed an increase post-1998, particularly during the spring bloom (Fig. 9d), dinoflagellates showed an important decrease (Fig. 9f). The linear increase in neritic copepods shown by the GAM below 100000 dinoflagellates sample^{-1} and the stable phase above that number (Fig. 4) may indicate food limitation.

Moreover, Vidal (1980) showed how critical food concentration increased with increasing temperature for both growth and development of the most numerous copepod species, *Pseudocalanus*. This situation would also apply to the present study, as temperature was higher post-1998 (Fig. 5a).

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Environmental drivers

PC1

Wind speed and temperature were the main abiotic variables driving plankton biomass seasonal dynamics in the North Sea during this period (Table 4). Wind speed and temperature at De Kooy decreased and increased respectively after 1998, even though 1988 was the largest shift in temperature (Fig. 5a) and 1996 the sharpest decrease in wind speed (Fig. 5b). This was not the case for the Atlantic water inflow through the Orkneys-Norway transect (Fig. 5d), which showed a large decrease post-1996 after a period of high inflow in the early 1990s.

All of these variables are related to water mixing dynamics. In the 1998 case, lower wind speeds and higher temperatures would have led to a stronger and more permanent stratification.

PC2

There is a clear relationship between PC2 and temperature. This PC represents clearly the late 1970s cold episodic event and the late 1980s regime shift, which had a clear link with SST changes (Edwards et al. 2002, Beaugrand & Reid 2003).

The North Atlantic inflow to the North Sea has been previously linked to NAOi (Reid et al. 2003), while stratification patterns have additionally been linked with NHTa (Beaugrand 2004b).

Our analyses of these 2 indices agree with previous findings (Beaugrand 2004b), and point to the relationship between these indices and the ecosystem changes in the North Sea.

PC3

Because of the limited time coverage of the nutrient data, only relationships with the 1998 shift can be discussed. The decrease in dinoflagellates post-1998 might possibly be related to a change in nutrient balance in the North Sea post-1998 (Fig. 10). In this period, nitrogen values were considerably reduced (Fig. 10b), and consequently the total nitrogen:total phosphorus ratio dropped below 20, which would indicate nitrogen limitation

(Guildford & Hecky 2000) (our Fig. 10g). The most apparent change in dissolved nitrogen compounds was found in ammonia (Fig. 10a), which consistently showed lower mean values post-1998, although nitrate also showed lower levels after the spring bloom (Fig. 10e). In contrast, silica only showed a consistently significant decrease during the autumn period in the post-1998 period (Fig. 10d). The decrease in nitrogen could be the result of both the decrease in influx of nutrient-rich North Atlantic waters and a strong and more stable stratification that could promote the locking up of inorganic nutrients below the photic zone (Brockmann et al. 1990), and a subsequent shift in the nitrogen and phosphorus cycles. McQuatters-Gollop et al. (2007, 2009) suggested that nitrogen may be limiting in the open North Sea, and they discussed how, compared to coastal North Sea areas, changes in nutrient state are slower in open waters and less influenced by anthropogenic impacts.

In this new nitrogen-limited scenario, diatoms did not show any decrease in the second half of the year relative to the pre-1998 scenario because they would still be silica-limited, not nitrogen-limited as shown by the nitrogen:silica ratios, which were still around 4:1 during the late growing season, i.e. August and September (Fig. 10h). For diatoms, nitrogen:silica ratios of 4:1 have been shown to be an indication of silica limitation, not nitrogen limitation (Gilpin et al. 2004). The relative importance of temperature and nutrients affecting plankton dynamics is still under discussion (see Supplement 4), but it seems that both parameters are driving plankton dynamics.

In contrast, dinoflagellates showed a clear drop in abundance (Fig. 9f). This could be explained by phytoplankton becoming dominated by smaller species and bacteria because of their higher competitive ability for limiting factors (Riegman et al. 1993). In this case there would not be enough nitrogen in the system to sustain the high dinoflagellate abundances recorded pre-1998.

Further implications

The changes in plankton community structure presented in this paper may have knock-on effects on higher trophic levels. The copepod species that form the neritic assemblage (i.e. *Pseudocalanus* and *Paracalanus* spp., *Temora longicornis*) are the main prey items for larvae of several

important fish species in the North Sea, such as herring and sprat (Last 1989, Arrhenius 1996) and cod and whiting (Shaw et al. 2008). A significant drop in prey abundances (i.e. neritic copepods), caused by the decrease in dinoflagellate numbers, could potentially lead to more competition for prey, less larval survival and therefore lower recruitment for these species. For herring this has already been shown (Payne et al. 2009). The timing of the North Sea herring recruitment failure in the year 2000 (Payne et al. 2009) coincides with the shift detected in plankton community structure in 1998. Furthermore, a preliminary analysis of recruitment data in the period 1990 to 2008 for 5 North Sea fish species (cod *Gadus morhua*, whiting *Merlangius merlangus*, herring *Clupea harengus*, sandeel *Ammodytes* spp. and haddock *Melanogrammus aeglefinus*) showed a shift between 2000 and 2002 (95% confidence interval; Fig. 11). Recruitment values for these species for the 2000s are lower than in the previous period, although further analyses are required to weigh the exact relationship with larval prey (plankton) availability for each species and the reason behind different timings of recruitment failure for different species.

This fish recruitment failure could propagate to higher trophic levels. The sandeel recruitment collapse has already been related to seabird breeding failure on the North Sea coast (Proffitt 2004, Wanless et al. 2005). This propagation in time through different trophic levels would support the idea of a new regime shift in the late 1990s.

Further research is needed to assess the propagation of this shift and also the implication of changes in the nutrient balance for the plankton community and the different reactions of nitrogen, phosphorus and silica cycles to the environmental changes.

Although the results of our analyses seem to have a valid ecological interpretation, several considerations should be taken into account when working with CPR data: (1) the semi-quantitative nature of the PCI might make interpretation of total phytoplankton difficult; (2) the grouping of dinoflagellates and diatoms hampers the interpretation of food availability to the zooplankton community, i.e. a decrease in dinoflagellates could not be detrimental if it is caused by certain species that are not edible by the existing zooplankton, either because of their size or any other factors; and (3) diatoms and dinoflagellates, which are counted in CPR samples, are not the only major phytoplankton functional groups. For the sake of

discussion, we assumed here that the temporal patterns we found both in dinoflagellates and diatoms, although strictly being size classes collected in a 270 μm mesh, are a good representation of slightly smaller size classes.

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CHAPTER 1

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"*The season rubs me wrong*
The summer swells anon
So knock me down, tear me up,
I would bear it all broken just to fill my cup
Down by the water."
Colin Meloy

ABSTRACT: This study analyses long-term and seasonal changes of phytoplankton community Carbon : Chlorophyll a ratio (θ) during the period 1991 to 2010 in North Sea waters and its relationship to environmental drivers. Based on data from the Dutch water monitoring programme covering 20 yr, major trends in phytoplankton abundance, community structure and chlorophyll were identified. Overall C:Chla increased during the study period, particularly in coastal areas. This increase was related to an increase in average underwater photosynthetically active radiation (PAR) and a decrease in nutrient concentrations. A mismatch was detected between chlorophyll a and biomass carbon trends caused by both a decrease in chlorophyll a values and an increase in biomass. In coastal waters, physiological adaptation to higher light and lower nutrient levels may have enhanced the θ, increasing from yearly averages of 12 g C *g Chl a^{-1} in 1990 to 69 g C *g Chl a^{-1} in 2010. Offshore, the increased stratification coincided with a shift towards dinoflagellate dominance. This dominance of dinoflagellates co-occurred with an increase θ yearly averages from 62 g C *g Chl a^{-1} in 1991 to 119 g C *g Chl a^{-1} in 2010. Because of these changes detected in C:Chl a ratio of multispecies phytoplankton communities, we question the validity of chlorophyll a as a proxy for phytoplankton biomass and argue its possible misrepresentation of phytoplankton dynamics.

2. Chlorophyll a in North Sea coastal and offshore waters:

Missrepresentation of long term trends of phytoplankton biomass

INTRODUCTION

Phytoplankton are the base of the marine ecosystem. As primary producers of organic carbon, phytoplankton import carbon in the marine system making it available for secondary producers, sustaining the marine food webs. These primary producers are also very important for the regulation of biogeochemical cycles. Overall marine primary producers account for 50% of the planet's photosynthesis, extracting CO_2 from the atmosphere, and reducing its greenhouse effects (Falkowski, 1994).

Since the effects of nutrient enrichment in coastal waters due to anthropogenic land use have a clear impact on phytoplankton (Rabalais et al. 2009), monitoring programmes have been established in many coastal regions in which phytoplankton state was considered as a parameter of water quality. Since phytoplankton carbon is difficult to monitor (Lewellyn et al. 2005), optic methods have been developed to monitor the dynamics of primary producers. Detection of fluorescence, water colour and other methods have been used as proxies to infer the status of phytoplankton population. Chlorophyll has a centenary history as a phytoplankton biomass proxy (Buchanan, 1910, Harvey, 1934), and it is still the most common measure of phytoplankton in ecological studies (Boyce et al. 2010). Chlorophyll is often used as a proxy for phytoplankton biomass because it is both easy to measure in situ and from satellite measurements (Boyce et al. 2010). Furthermore, other proxies are related to chlorophyll to assess their validity as representation of phytoplankton dynamics. As an example, the Phytoplankton Colour Index (PCI) calculated in the Continuous Plankton Recorder survey (CPR) is generally accepted as a representation of phytoplankton biomass and productivity, but as discussed by Batten et al. (2003) PCI can be thought of as analogous to remotely sensed chlorophyll estimates. Similarly to remote sensing and in situ chlorophyll measurements, it is only by comparisons between the PCI and the taxonomic structure that a shift in the phytoplankton community composition might be revealed.

Even though chlorophyll is widely used as a proxy, the relationship between chlorophyll and phytoplankton biomass is not straight forward. C:Chl a ratio (θ) has been shown to be highly variable within and between algal species. In laboratory studies, Geider (1987) showed how θ is dependent on light and nutrient availability and temperature; it increases linearly with increased light level at constant temperature and decreases exponentially
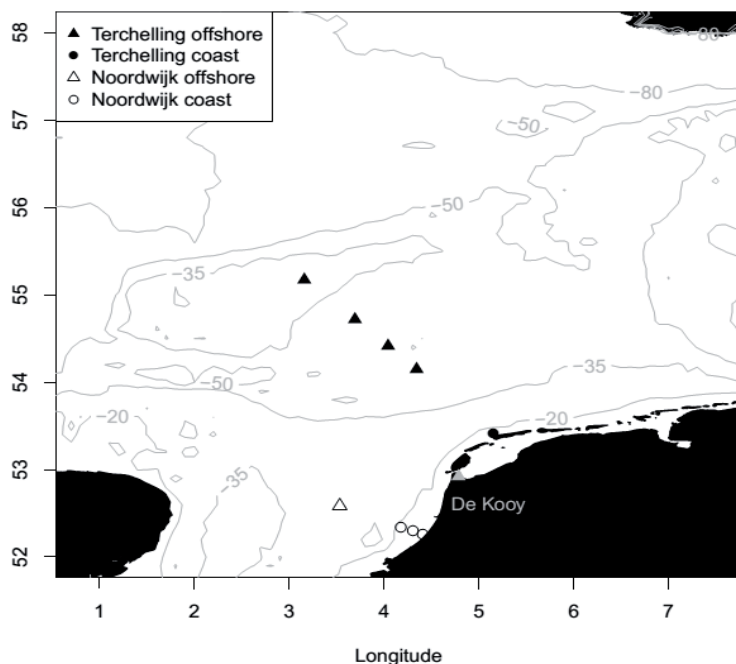
Figure 1 Area of study. Four different areas are distinguished. Noordwijk offshore (open triangle), Noordwijk coast (open circle), Terschelling offshore (triangle), Terschelling coast (circle).

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with increased temperature at constant light level. Other studies using mesocosm experiments have also shown the interspecific differences of θ, with differences of one order of magnitude (Kruskopf & Flynn, 2006). Geider (1987) also showed how dinoflagellates have higher θ values than diatoms both in natural blooms and axenic cultures.

In nature the determination of θ responses to environmental factors is more difficult. Regarding physiological responses of phytoplankton, light and temperature are generally correlated, and there is normally more than one growth rate limiting factor within multispecies communities. Moreover, depending on the species composition the overall community θ would change, as different phytoplankton species have different C:Chl a ratios. All these factors make the relationship between Chlorophyll and phytoplankton biomass theoretically variable, both seasonally and on an inter-annual basis. This raises the question of how well do chlorophyll measurements represent phytoplankton biomass.

For open ocean areas, Behrenfeld et al.(2005) already showed a mismatch between satellite estimations of phytoplankton carbon and chlorophyll, and advocated for carbon-based net primary production estimations. In

a similar way, Lionard et al. (2008) showed how for a short term field study in 2002 chlorophyll was a good estimation of overall phytoplankton biomass when diatoms were clearly dominant, but the performance of this proxy was poor for other phytoplankton groups and did not perform well when phytoplankton biomass was low.

In this study the long term trends of C:Chl ratio, taxonomic structure of phytoplankton and environmental factors are inspected in order to assess the validity of chlorophyll as a representation of phytoplankton biomass in the southern North Sea. To our knowledge this is the first study that addresses this issue based on long term field measurements (two decades) inspecting the C:Chl a behaviour both in the long term and seasonal scale. The inclusion of both coastal and offshore areas adds another important aspect to the analysis of performance of chlorophyll a as phytoplankton biomass proxy, as their intrinsic differences in limiting factors and physico-chemical parameters could be important for the C:Chl ratio.

MATERIALS AND METHODS

Study area

Dutch marine waters lie in the southern North Sea, a shallow shelf sea in the European continental shelf (Fig. 1). The water circulation in the North

Table 1. Models fitted to the data, allowing for different seasonal variation patterns. All model were fitted with an autocorrelation structure to avoid autocorrelation of the residuals

| Models	Smoothing functions	Variation patterns
M1	$f_{Area}(Year) + f_{Area}(DoY)$	Long term smoother per area
		Seasonal smoother per area
M2	$f_{Area}(Year) + f(DoY)$	Long term smoother per area
		Common seasonal smoother for all areas
M3	$f(Year) + f_{Area}(DoY)$	Common Long term smoother for all areas
		Seasonal smoother per area
M4	$f(Year) + f(DoY)$	Common long term and seasonal smoother
M5	$f_{Area}(Year, DoY)$	Bidimensional smoother per area, representing the change in seasonal patterns throughout the years.
M6	$f(Year, DoY)$	Common bidimensional smoother, representing the change in seasonal patterns throughout the years.
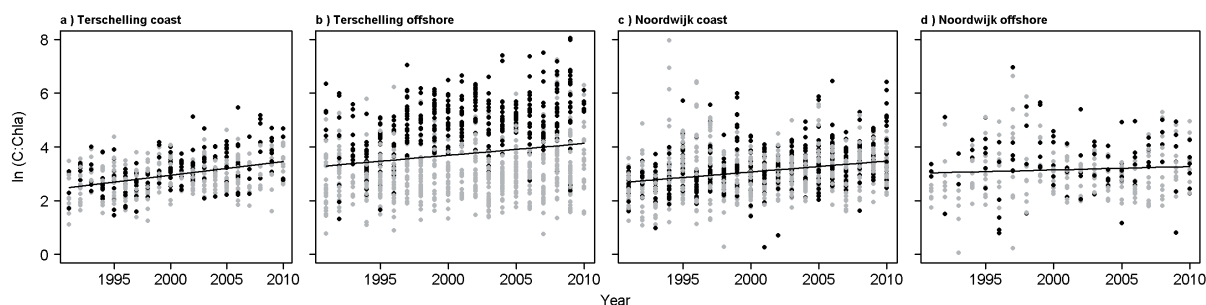
Figure 2 Top: Linear model of ln (C:Chl a ratio) per year for a)Terschelling coast, b) Terschelling offshore, c) Noordwijk coast, and d) Noordwijk offshore. Black circles represent summer values, and grey circles the rest of the year.

Sea is tidally driven, generally counter-clockwise, with water from the North Atlantic entering from the north-west, and flowing southward in the direction of the English channel, to flow from there together with Channel water along the Belgian and Dutch coast northward, leaving the North Sea with the Norwegian coastal current (Baretta-Bekker et al. 2009, Gieskes & Kraay, 1975).

Monitoring stations

Ten stations from two transects running perpendicular to the Dutch coast were selected for the study (Fig. 1). The Noordwijk transect is located off the west coast of The Netherlands, with four stations at 2, 10, 20 (coastal) and 70km (offshore) from the coast. Waters covered by this transect do not present a consistent thermo-haline stratification during the summer. The Terschelling transect lies north of The Netherlands, in front of the Wadden islands. In this study 6 stations were selected, at 4 and 10 (coastal) and at 100, 135, 175 and 235km off the coast (offshore). The offshore stations present thermal stratification during the summer (Baretta-Becker et al, 2009).

Data

Phytoplankton data from the selected stations were used for the analyses. Water samples were collected at 1 m below the water surface. One litre of phytoplankton samples was preserved with 4 ml acid Lugol's iodine and stored in brown glass bottles at 4 °C. Phytoplankton cells were identified and enumerated using inverted microscopy (Utermöhl sedimentation technique)(Prins et al. 2012). A minimum of 200 observations were collected per sample in such a way that the observations were evenly distributed

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Table 2. Statistical output of lineal regression analyses of ln (θ) against year

Area	N	R^2	Intercept	Slope	Slope CI	p-value
Terschelling coast	463	0.15	-98.59	0.05	0.01	< 0.05
Terschelling offshore	1024	0.03	-84.2	0.04	0.01	< 0.05
Noordwijk coast	1148	0.07	-78.8	0.04	0	< 0.05
Noordwijk offshore	307	0.001	-22.22	0.01	0.01	0.23

over the whole biovolume range (size classes 1-3, 3-10, 10-30 and >30 µm diameter). To optimize the counting process, the Lugol-preserved samples were checked for high densities of particles (phytoplankton or silt), and appropriate dilutions or concentrations were prepared for use with the 2 ml sedimentation chambers. In total, a volumeof 2–30 ml of the (undiluted) sample was investigated for analysis, depending on the amount of phytoplankton and/or silt in the sample(Prins et al. 2012). In practice the analysis was performed by counting in different subvolumes, whereby the smallest taxa were counted in few fields of view, and the largest taxa in the whole of the sedimentation chamber (Bijkerk et al. 2010). The detection limit in size lies around 1.5um, which excludes solitary cyanobacteria smaller than 2um. Generally, solitary cyanobacteria do not make a significant contribution to the biovolume, so they are safely neglected from the analyses.

Table 3. Models selected for time trend analysis of each variable by the Akaike Information Criterion

Variable	Best model	Variable	Best model
C:Chl a (θ)	f_{Area} (Year,DoY)	Im	f_{Area} (Year,DoY)
DIN	f_{Area} (Year) + f_{Area} (DoY)	Biomass	f_{Area} (Year,DoY)
DIP	f_{Area} (Year) + f_{Area} (DoY)	Chl a	f_{Area} (Year,DoY)
Si	f_{Area} (Year) + f_{Area} (DoY)	Temperature	f (Year) + f (DoY)

Table 4 Models selected for C:Chla in relation to environmental variables by the Akaike Information Criterion

Model	df	AIC
f (Im,Temp)+ f (DIN)+ f (P) + Si + Area	15	8413.333
f (Im,Temp)+ f (DIN)+ f (P) + f (Si)+ Area	16	8415.333
f (Im)+f (Temp) + f (DIN)+ f (P) + f (Si)+ Area	17	8424.601
f_{Area} (Im)+fArea (Temp) + f_{Area} (DIN)+ f_{Area} (P) + f_{Area} (Si) + Area	47	8436.288
f (Im)+f (Temp) + f (DIN)+ f (P) + f (Si)	16	8437.502
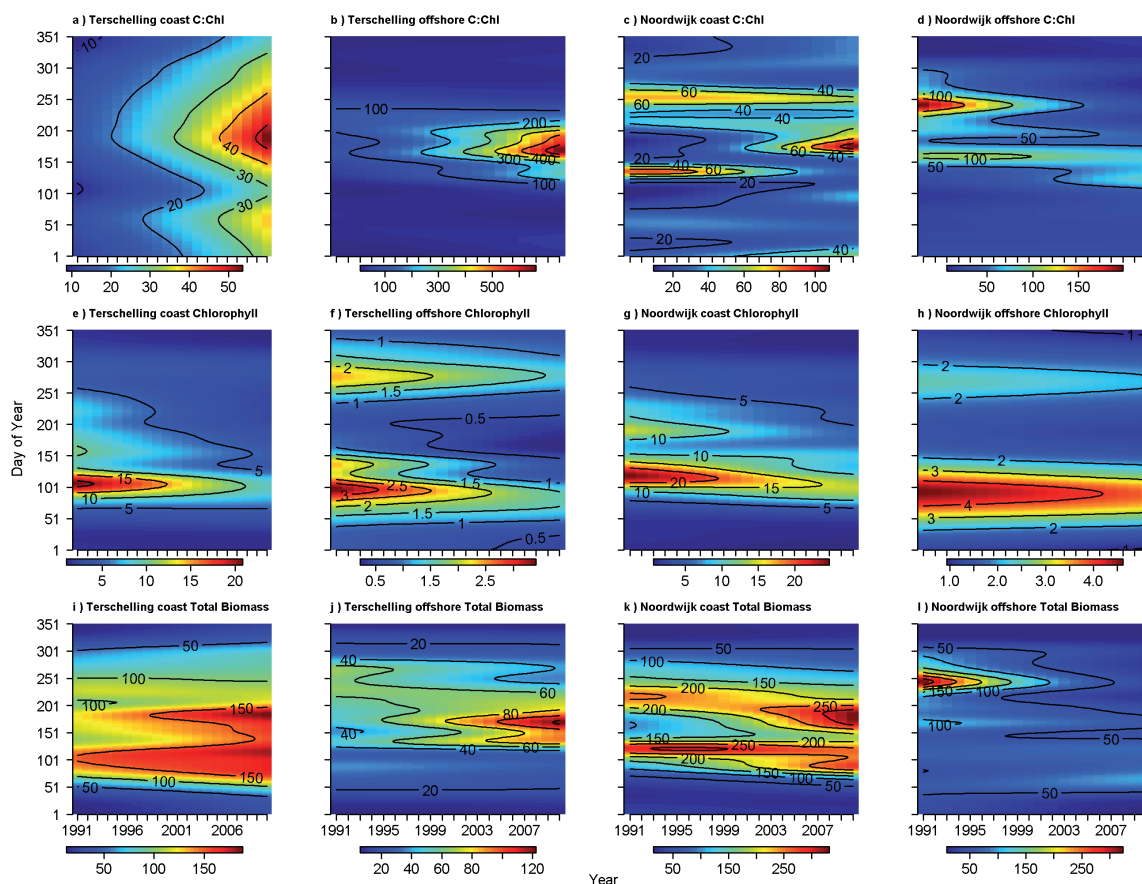
Figure 3 Modelled values of C:Chl-a (a-d), Chlorophyll (e-h), and phytoplankton biomass (i-l) in Terschelling coast (a,e,i), Terschelling offshore (b,f,j), Noordwijk coast (c,g,k), and Noordwijk offshore (d,h,l). The axis of these contour plots represent Year (x-axis) and Day of the Year(y-axis). The scale bar represents g C g^{-1}Chl-a (a-d) and µg L^{-1} (e-l)

Species counts of all non-heterotrophic phytoplankton species in water samples taken, at least once a month, from 1991 to 2010 were transformed into biomass values.The conversion from cell counts to carbon biomass was made taking into account species-specific cell volumes obtained from a table of average cell volumes calculated with geometric formulas by Koeman (2004). These geometric formulas, vary depending on the shape of each species, and are either linear, quadratic or third power equations. Average cell biovolumes per species (or higher taxonomic group) and size class were compared with literature values in Dutch waters in this report with satisfactory results (Koeman , 2004).

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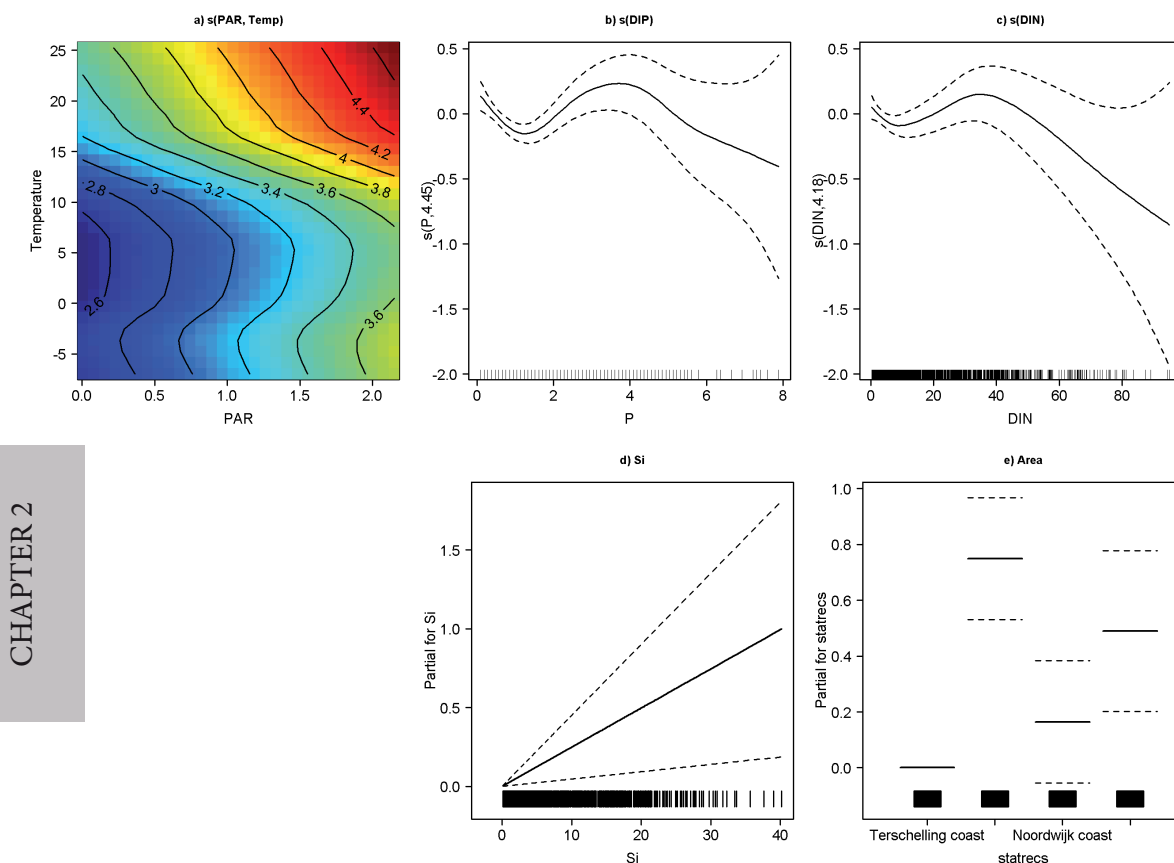
Figure 4 Results of the best model explaining C:Chl a ratio. a) Bidimensional smoother of underwater PAR and temperature, b) DIP smoother, c) DIN smoother, d) Si linear relationship, e) different intercepts based on Area.

After regression analyses of carbon content to biovolume of different species spanning across different taxa, Menden-Deuer and Lessard (2000) developed two formulas for converting cell counts volumes into carbon biomass. These equations are:

$$\text{Diatom pg/cell} = 0.288 \text{x cell volume}^{0.811}$$
$$\text{Other phytoplankton pg/cell} = 0.216 \times \text{cell volume}^{0.939}$$

The quantitative microscopical analyses were carried out by three different laboratories during that period, with laboratory changes occurring in 1994 and 2000. Unfortunately, comparisons between the three laboratories by counting identical samples as a way to check inter-laboratory variation

were not performed (Peperzak, 2010, Prins et al. 2012). After analysing this dataset, Zuur *et. al* (2009) concluded that, without data pre-processing, it was not possible to verify whether any community composition changes at the species level over time were due to a laboratory effect or whether they represented a real change.

In order to avoid the observer bias, species that were not detected in at least 15 years during the study period were not considered at the species level for biomass calculation, but grouped in a higher taxonomical unit, i.e. genus or family, for which an average cell biovolume was available. Koeman (2004) reported the average cell biovolume of higher taxonomical units for different size classes, increasing the accuracy of the estimation. For each sample, biomass was aggregated in three categories: diatom, dinoflagellate and other phytoplankton. Total biomass was also calculated. Total biomass values and the chlorophyll a values measured the same days in the same locations were used to calculate the C:Chl a ratio for each sample.

As discussed by Prins et al. (2012), with this aggregation in high and clearly distinct taxonomic groups the potential observer effect caused by a change in laboratories carrying out phytoplankton counts was avoided, at the cost of a reduction of taxonomic resolution. In a preliminary study, a comparison of C:Chla ratios calculated via species-specific biovolumes with ratios calculated via genus-specific biovolumes showed a an average 5% overestimation of C:Chl a per sample when only genus level was considered. In most cases the largest part of the difference was caused by species consistently identified during the study period. These species were identified by all laboratories therefore they would not affect our results. The deviation between datasets showed no trends in time or differences between areas, which supports the use of this method to avoid the potential observer effect in this dataset.

Data on Chlorophyll a, was determined by HPLC fluorescence method For HPLC analysis, samples of seawater were filtered onto Whatman GF/F filters and extracted in 85% acetone. Depending on the turbidity of the water between 100-1000 ml were filtered. Samples were analysed on an Alltech Absorbosphere C18 column (4.6 × 150 mm). After elution, chlorophyll fluorescence was detected with a Shimadzu RF-10AXL Fluorescence Detector, following calibration with chlorophyll a standard obtained from Sigma, samples were corrected for phaeophytin by means of acidification (Rijkswaterstaat, 2009).

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Salinity, nutrient concentrations and suspended particulate matter (SPM) for each station were obtained from the Rijkswaterstaat online database (live. waterbase.nl). Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate, nitrite and ammonia, while dissolved inorganic phosphate (DIP) represented orthophosphate concentrations in the water.

Climate data was obtained from the Royal Netherlands Meteorological Institute monitoring station at De Kooy (Fig. 1). Global irradiance values were converted to W h m^{-2}day^{-1}, and multiplied by 0.45 to obtain photosynthetically active radiation (I_0, PAR). Mean water column PAR (I_m) was calculated following Riley's formula (Riley, 1957):

$$I_m = I_0(1 - e^{-Kd*z}) / (K_d \times z),$$

where K_d is attenuation coefficient (m^{-1}) and z is water column depth (m). The depth of offshore Terschelling station was fixed at 18m during a fixed stratified period (June-September) for this calculation (OSPAR Commission, 2000)

The attenuation coefficient was calculated based on a formula used by Peperzak et al. (1998)

$$K_d = 2.404 - 0.058 \times salinity + 0.012 \times SPM + 0.020 \times Chl\ a$$
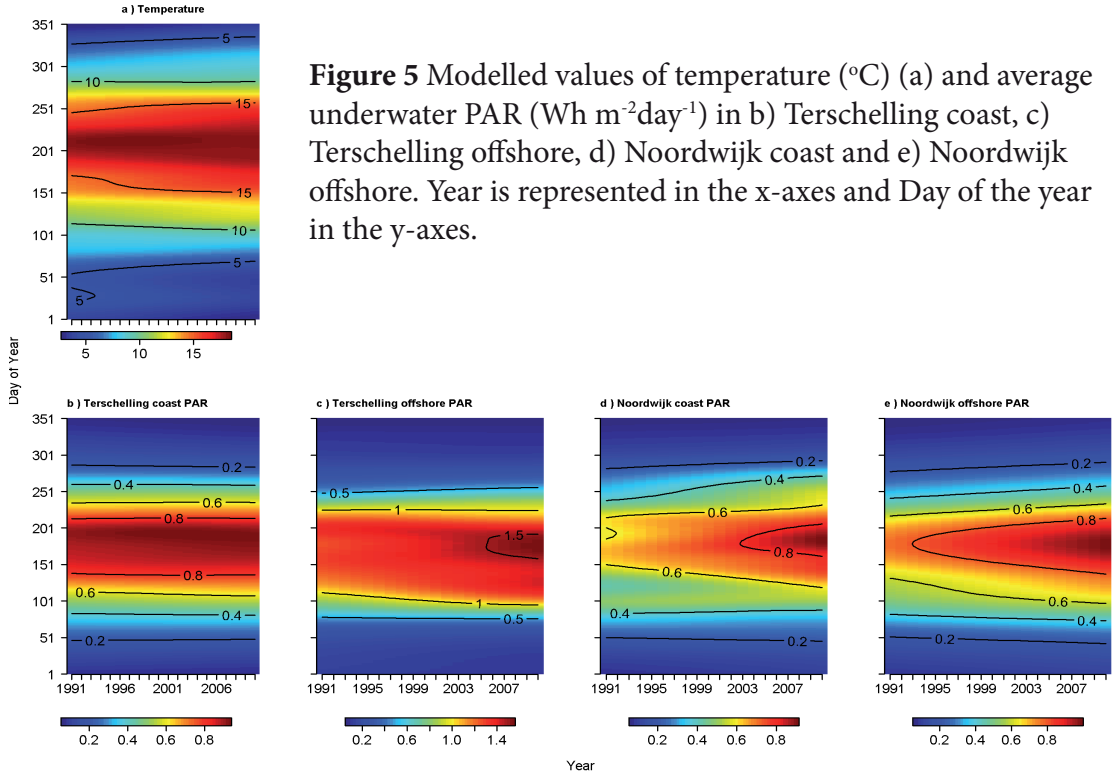
Figure 5 Modelled values of temperature (°C) (a) and average underwater PAR (Wh m^{-2}day^{-1}) in b) Terschelling coast, c) Terschelling offshore, d) Noordwijk coast and e) Noordwijk offshore. Year is represented in the x-axes and Day of the year in the y-axes.
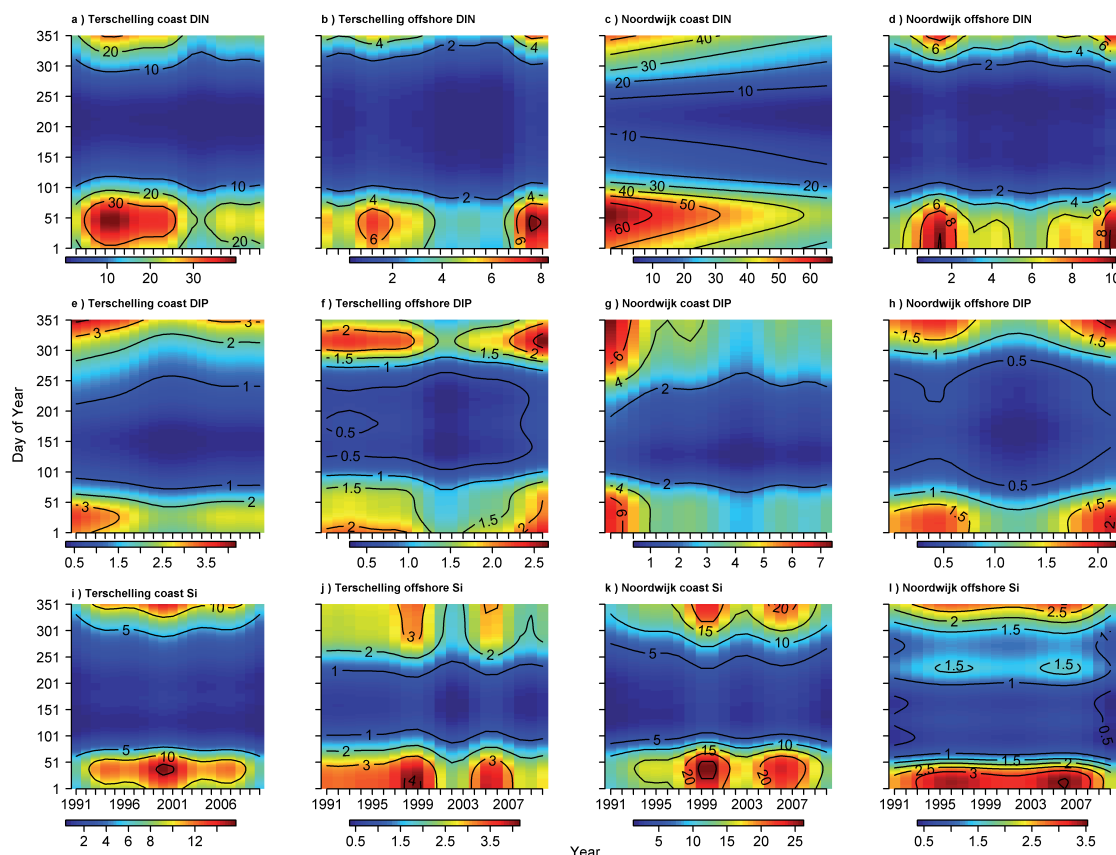
Figure 6 Modelled values in µM of: DIN (a-d), DIP (e-h) and Si (i-l) for the different areas. Terschelling coast (a,e,i), Terschelling offshore (b,f,j), Noordwijk coast (c,g,k), and Noordwijk offshore (d,h,l). Year is represented in the x-axes and Day of the year in the y-axes.

Analyses

Generalised additive (mixed) models (GA(M)Ms)(Wood, 2006, Zuur et al. 2009) were used to model C:Chl a variation based on environmental factors. Smoothers were allowed to vary in four different areas with shared hydrographical properties: Terschelling coast, Terschelling offshore, Noordwijk coast, and Noordwijk offshore (Fig. 1). An autocorrelation structure of order 1 was included in the model to account for temporal autocorrelation in the data, and the specific sampling location was used as a random intercept as the focus of this analysis was not the variation between sampling station (Zuur et al. 2009).

The trends in θ, chlorophyll a, carbon biomass, nutrient concentrations and

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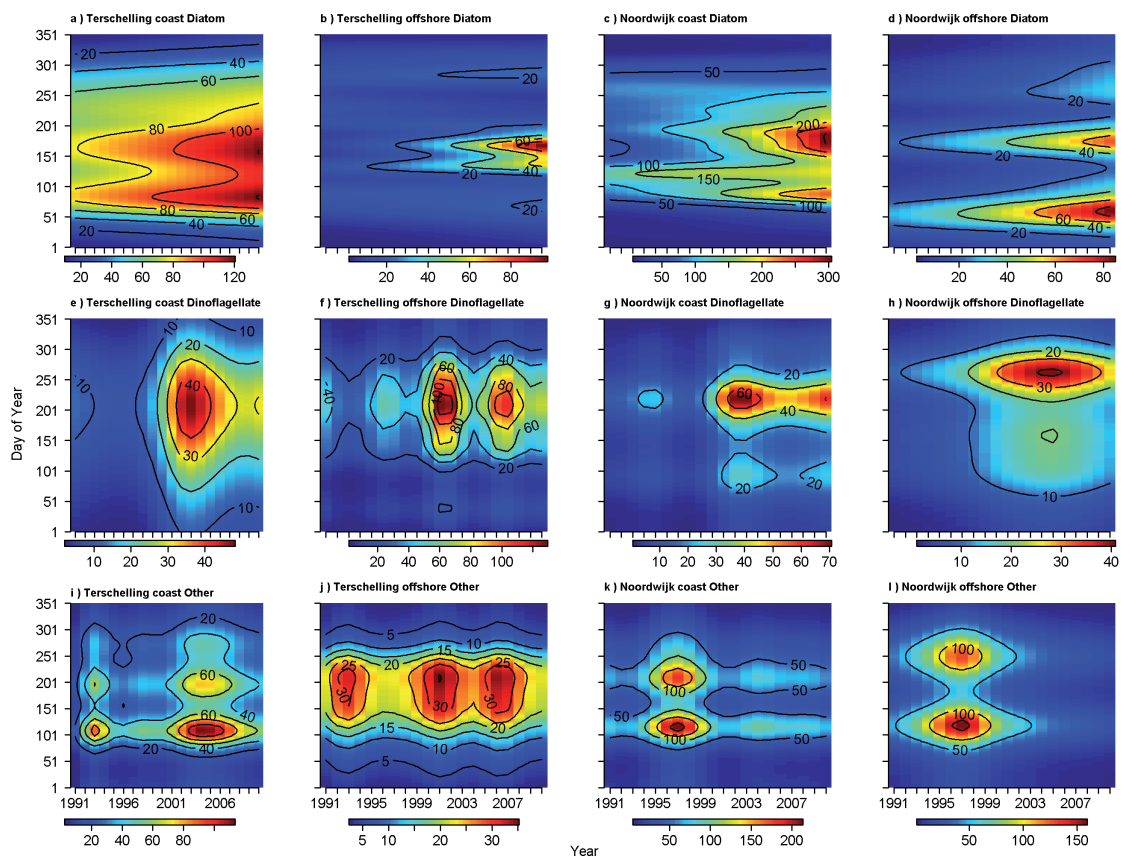
Figure 7 Modelled values in μg L⁻¹ of: Diatom carbon biomass(a-d), dinoflagellate carbon biomass (e-h), and other phytoplankton species carbon biomass (i-l) for the different areas. Terschelling coast (a, e, i), Terschelling offshore (b, f, j), Noordwijk coast (c, g, k), and Noordwijk offshore (d, h, l). Year is represented in the x-axes and Day of the year in the y-axes.

ratios, and climate forces were analysed by fitting Generalised additive (mixed) models (GA(M)Ms)(Wood, 2006, Zuur et al. 2009) with smoothers for Year, representing the long term trend, and day of the year (DoY), representing the seasonal patterns. Different models were fitted to the data and the best model was selected by means of the Akaike Information Criterion. The different models represented different patterns of variation in time (Table 1) allowing the seasonal patterns to either change in time or remain constant. An autocorrelation structure of order 1 was included in the model to account for temporal autocorrelation in the data.

RESULTS

Changes in C:Chla

Linear models of the ln-transformed θ against year showed an increasing trend in all areas but Noordwijk offshore (p-value < 0.05, Fig. 2, Table 2). It is interesting to notice that Terschelling offshore area has higher θ values than the rest (Fig. 2b) throughout the study period. In order to investigate the reliability of these regressions and the potential effect of different laboratories, supplementary regression analyses were carried out on split datasets for summer and rest of the year before and after 2000 (see Appendix). Results of these regressions strengthen the conclusion of an overall increase of C:Chl a ratios in all areas independently of the potential observer effect on the dataset.

The GAMM selection process showed bidimensional smoothers to be the best in representing θ variation in time (Table 3). This was mainly due to Terschelling offshore area, in which θ not only increased in time, but the seasonal patterns changed throughout the years, the summer values showing a sharper increase than the winter values (Fig. 3b). This apparent seasonality was not shown in the coastal areas until the second half of the time series (Fig. 3c).

Drivers of change

According to the AIC comparison, the environmental factors that best explained C:Chla variation were the averaged underwater PAR (I_m), temperature, and nutrient concentrations (Table 4, Fig. 4). C:Chla increased with temperature and I_m, (Fig.4a) and decreased under nutrient replete conditions (Fig.4b, and c), although excess of silica seemed to have a positive effect on C:Chla. These variations of C:Chla depending on the different environmental factors was shown to be independent of the area, although each area showed intrinsically different C:Chla ratios, being higher in offshore areas (Fig.4e). The model had an R^2 of 0.33.

Underwater PAR (Fig. 5b-e) showed different trends for each area, although an overall increase could be detected in all areas but Terschelling coast. It was also clear that Terschelling offshore area had the higher values of underwater PAR. Temperature (Fig. 5a) also increased throughout the time series, particularly during summer months.

GAMMs of nutrient data trends showed a long term smoother and a seasonal

smoother per area to best represent the data (Table 3, Fig. 6). This meant that the seasonal pattern did not change in time. Both DIN and DIP showed a clear decrease during the time series, particularly in coastal areas. For Si (Fig. 6i-l) a clear increasing trend in time was not found, but a very marked seasonal pattern was apparent, with high values at the beginning and the end of the year, and low values during the rest of the year.

Biomass and chlorophyll trends

In both coastal areas diatoms are dominant, with very high biomass values from March to October in Noordwijk and from March to April in Terschelling (Fig.7a and c). In the offshore areas dinoflagellates dominated in biomass, particularly in Terschelling, showing high values from May to October (Fig. 7f). In Noordwijk offshore, diatom biomass peaked in February (Fig. 7d), and its biomass went back to lower levels by April. Dinoflagellate biomass does not reach such high values as in Terschelling and reached their maximum in September. The third phytoplankton category was composed of other flagellates, chlorophytes, and cyanobacteria. All of these groups together accounted for less biomass than diatoms and reached similar levels to dinoflagellates just before the summer, apart from three incidents in the summer of 1997, 1998 and 2000 where a single day bloom of chrysophytes reached extremes values of biomass (Fig. 7k and l) .

Chlorophyll seasonal patterns seemed to follow diatom seasonality patterns in all areas , although they did not capture the second peak of biomass during the summer-autumn (Fig. 3e-h). Dinoflagellate biomass patterns were not captured by chlorophyll a values. This was particularly obvious in offshore Terschelling (Fig. 3f), where the summer concentrations of chlorophyll a were very low, while the phytoplankton biomass was highest during summer (Fig. 3j).

Similar chlorophyll a and biomass patterns were found in all areas. There was an overall decrease of chlorophyll (Fig. 3e-h) and an increase of biomass (Fig. 3i-l). When looking at the particular trends of taxonomic groups some differences could be found per area. On Noordwijk coast, the increase of diatoms was larger than on Terschelling (Fig. 7a). In the offshore areas there the biomass increase was more pronounced in dinoflagellates (Fig. 7f and h), although in Noordwijk, a slight increase of diatom biomass could be detected (Fig. 7d).

DISCUSSION

The present study shows a long term increase of θ in Dutch waters during the last 20 years, an apparent seasonal pattern, with higher values in the summer, was only found in the offshore areas (Fig. 3b, d). Analyses also showed C:Chla to be affected by the light environment, temperature, and nutrient concentrations in the whole study area during the study period (Fig. 4) . The results showed a clear θ increase with increased water column photosynthetically active irradiance (I_m) and a decrease with increasing nutrient concentrations (Fig. 4). This agrees with previous laboratory studies that showed C:Chl a ratio is affected by light environment, temperature and nutrients, being minimal at low irradiances under nutrient-replete conditions and increasing at high irradiances and under nutrient-limiting conditions (Geider et al. 1997, Geider, 1987).

Geider (1987) showed how the slope of a regression of θ against irradiance changes with temperature, being steeper at lower temperatures and showing a slower increase with higher irradiances at higher temperatures (Geider, 1987). This was corroborated in our model for temperatures over 10°C (Fig. 4a), but at lower temperatures there is a slower increase of θ with increased irradiance. On the other hand Goldman and Mann (1980) also showed a tight coupling between carbon and chlorophyll over a temperature range of 3-25°C under nutrient replete conditions, keeping θ relatively constant. This could explain why a clear seasonal pattern with low values in winter and high values in summer was not detected in coastal areas, due to the high nutrient concentrations along the coast.

On top of these changes in the phenotypic expression of algae, the effect of temperature, I_m, and nutrient concentrations could be the result of a progressive change in the phytoplankton community. Due to the large interspecific variation in θ, changes in the community composition would affect the overall θ. Dinoflagellates have been shown to have higher θ than diatoms both on natural blooms and axenic cultures (Geider, 1987), with dinoflagellates showing θ values three to four times higher than diatoms (Chan, 1980). This difference is the result of the cell structure of the different microalgae, diatoms having a large central vacuole not present in dinoflagellates; assuming that the amount of chloroplasts per cell is proportional to the cell surface area (Chan, 1980), for equal cell volume and shape a diatom would have lower θ. Additionally, the cell wall of diatoms mainly consists of silicate, not carbon, therefore comparatively

decreasing the carbon content of the cell. In our study, the two coastal areas showed similar patterns in phytoplankton taxonomic composition, with a clear dominance of diatoms over dinoflagellates, corresponding to lower values of θ. Offshore areas showed lower diatom biomass than coastal areas, higher biomass of dinoflagellates and the highest θ values.

From a seasonal perspective, in coastal areas diatoms are dominant throughout the year (Fig. 7), although in recent years, particularly in the Noordwijk area, dinoflagellates started to increase their summer biomass contribution to the community (Fig. 7g). In offshore areas dinoflagellates are abundant during the summer and autumn period (Fig. 7f and h). The contribution of the rest of species together was similar to that of dinoflagellates. This group was formed by flagellates, chlorophytes, and cyanobacteria. The contribution to biomass of this group was only considerable for the flagellate group, which remained at similar levels as dinoflagellates for most of the year. During the summer months dinoflagellates became more dominant, with the exception of three single dates in September 1997 and 1998 and October 2000, where a single species bloom of a chrysophyte algae caused extreme biomass values.

Predation pressure could also influence phytoplankton community composition, and size range, by generating selective pressure on the phytoplankton pool, therefore affecting the community θ. Zooplankton is known to control both the phytoplankton dynamics (Brussaard et al. 1995, Fuchs & Franks, 2010, Riegman et al. 1993) and the way primary production is transferred to higher trophic levels (Johannessen et al. 2012). Moreover, interactions between micro-, meso-, and macro-zooplankton have been shown to be important in shaping phytoplankton dynamics (Löder et al. 2011). In a recent study Alvarez-Fernandez et al. (2012) showed a decrease of several zooplankton species since 1998 in the North Sea which are known to prey upon dinoflagellates during the second half of the year. This result would agree with the detected increase in dinoflagellates in offshore stations in the present study. Unfortunately the lack of zooplankton monitoring in the Dutch waters monitoring programme makes it impossible to corroborate this effect.

Changes in nutrient concentrations.

The main trends in nutrient concentrations were a decrease in DIN, e.g. Noordwijk coast spring averages of 42.68 µM in 1991 to 27.83 µM in 2010 (Fig. 6a, c), and DIP, e.g. Noordwijk coast spring averages of 1.99 µM in

1991 to 0.48 µM in 2010 (Fig. 6e, g). An increase in Si was also detected. This Si increase seems more like an oscillation, having peaks around the years 2000 and 2006 (Fig. 6). It is well known that the major input of nutrients to Dutch coastal waters are riverine inputs, particularly from the rivers Rhine and Meuse (Prins et al. 2012). Since 1990, nitrogen and phosphorus riverine loads to the North Sea have decreased as a consequence of various sanitation measures (Colijn et al. 2002). On the Noordwijk coast, nutrient input from rivers kept the nutrient levels in coastal waters high throughout the year, although a clear decreasing long term trend can be detected in DIN and DIP (Fig. 6c, g).

Prins *et al* (2012) already pointed out the effect of increased riverine Si discharges on diatom blooms in the coastal zone. As postulated by Prins *et al* (2012) reduced retention of Si in the rivers due to the reduction of freshwater algal blooms following phosphate reduction due to anti-eutrophication measures in freshwater systems, led to increased silica loads to the coastal waters. This in turn allowed for an increase of diatom biomass in the coastal zone. The long term increase of diatom biomass (Fig. 7) detected in our study, could explain why the long term Si increase is not so obvious (Fig. 6i, k). In this scenario, dissolved Si would be consumed by the higher diatom biomass.

Change in climatic conditions.

The main changes detected in climate variables were an increase in average underwater PAR, and temperature (Fig. 5). These temperature changes could promote more permanent stratification in offshore areas such as Terschelling offshore. A long term data analyses by Beare et al. (2002), already identified an increasing trend in stratification in the North Sea, west of the 5°E meridian between 1958 and 1998. The relationship between these factors and long term trends of plankton dynamics in the overall North Sea has already been established in the past using Continuous Plankton Recorder data (Alvarez-Fernandez et al. 2012, Beaugrand, 2004, Reid et al. 2003). Stratification affects the competition between diatoms and dinoflagellates, improving the competitiveness of dinoflagellates because of their motility (Jones & Gowen, 1990). The inter-annual variation of stratification was not taken into account in this study for the calculation of average underwater PAR, due to the lack of data on stratification depth and timing in the locations studied. Despite this fact, the potential stratification effect would be in agreement with the data presented here for the Terschelling offshore, in which dinoflagellates showed a long term increase in biomass (Fig. 7f).

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Chl a as a proxy of phytoplankton biomass

Either of the aforementioned possibilities for explaining the variations in θ, i.e. phenotypic variation or differences in species composition, would ultimately be an effect of changes in environmental conditions. Considering the increase in available light represented by increased average underwater PAR particularly in coastal areas (Fig. 5d), the decrease in nutrient concentrations (Fig. 6a, c, e and g), and the increase of θ in the coastal area (Fig. 3a, c) it may seem that Dutch coastal waters are developing towards a nutrient limited environment. If this trend continues a θ seasonal pattern in coastal areas, similar to the one that appears in Terschelling offshore, could become a permanent feature in the Dutch coast. Because of this θ long term increase and clear seasonal variation, the use of Chl a measurements to represent phytoplankton biomass in the long term should be carefully considered.

Several decades ago Gieskes and Kraay (1975) already concluded that, in the southern North Sea, chlorophyll a concentrations at the surface usually correspond with surface primary production for a given incident radiation; but chlorophyll could not be used as an index of phytoplankton concentration measured as biovolume mm^3 * L^{-1}. Regardless, more recent studies on the plankton state in the North Sea (de Vries et al. 1998, Philippart et al. 2010, Weijerman et al. 2005) have assumed chlorophyll to represent phytoplankton biomass without further consideration of the taxonomic structure of the population or the environmental factors affecting the C:Chl ratio. In their thorough study of phytoplankton trends in the North Sea, McQuatters-Gollop et al. (2007) compare chlorophyll measurements from coastal and open waters. Even though they also used PCI measurements, and they correctly report the reduction of turbidity and nutrient concentrations in the North Sea, the possible effects of these factors in the relationship between chlorophyll and phytoplankton biomass were not considered. This approach hinders strong conclusions due to the differences between θ in nutrient depleted and nutrient-replete areas, and the inherent differences in limiting factors between open sea and coastal areas presented in our results.

In a similar way, other methods that use water characteristics dependant on chlorophyll, such as surface water colour do not necessarily reflect phytoplankton biomass trends without further consideration of factors like I$_m$ and nutrient limitation. Batten et al. (2003) already pointed out how PCI show a strong correlation to chlorophyll estimates, but this correlation is

weaker during summer months. As shown in the present study, summer months show the highest θ values. This seasonal uncoupling of Chl a, PCI and biomass deserves further attention and consideration in long term comparisons between all these factors.

On a global context, Boyce et al. (2010) concluded that there has been a global phytoplankton decline during the last century, after an extensive analyses of Chl a and Secchi depth data on 10 oceanic regions. Their conclusion related this phytoplankton decline to changes in the strength and depth of stratification, due to changes in associated atmospheric patterns. Although some criticism has already been risen because of the sampling strategy and statistical methods used (Rykaczewski, and Dunne, 2011), to our knowledge no one has disputed the implications of equating chlorophyll to phytoplankton biomass. As discussed in our study, changes in stratification patterns and all related physico-chemical factors could have an effect on θ, rendering any conclusions about the phytoplankton biomass based on Chl a invalid. Furthermore, comparison of trends amongst oceans(i.e. Atlantic vs. Pacific ocean) could also be misleading, due to the differences in nutrient dynamics found between these waters.

The issue of varying θ also extends to physical-biological modelling. Although most ecosystem models represent phytoplankton biomass in carbon units they deliver chlorophyll concentration as a proxy for phytoplankton biomass and validate the model against Chl a observations (Lenhart et al. 2010). These values are typically derived using fixed C:Chl a ratios, but as shown in this study the relation between carbon and chlorophyll is highly variable in natural assemblages, and inherently different between coastal and offshore areas.

Phytoplankton carbon, although more difficult to measure (Lewellyn et al. 2005), would be more efficient in assessing energy transfer or carrying capacity of ecosystems than chlorophyll a measurements. Carbon biomass conversions from microscopical counts, as the ones presented here, are also a possible solution, although a consistent sampling and identification are extremely important for this method in order to allow for long term comparisons at the species level.

The European Marine Strategy Framework Directive already recommends using phytoplankton composition and biomass as an assessment of phytoplankton state (European Commission, 2008). This will not substitute chlorophyll a monitoring but complement it, and it will hopefully improve our

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understanding of the relationship between chlorophyll a and phytoplankton biomass in different areas, helping to assess the shortcomings of inter-region comparisons of chlorophyll a trends.

In conclusion, this study shows that chlorophyll should not be used as an indication of phytoplankton biomass and dynamics without further consideration of limiting factors for algal growth, both when comparing different areas and in long term studies. Our results show there are clear deviations between the seasonal patterns and temporal trends of chlorophyll versus algal biomass, showing an overall decrease in chlorophyll and an overall increase in biomass (Fig. 3). Additionally, these deviations are not consistent amongst areas, as intrinsic spatial differences in limiting factors may result in different θ. The implications of θ trends in chlorophyll a measurements should be carefully assessed, considering the effect of environmental factors, particularly I_m and nutrient concentrations.

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CHAPTER 2

"*I'm slowly drifting away, drifting away*
Wave after wave, wave after wave
I'm slowly drifting, drifting away
And it feels like I'm drowning
Pulling against the stream"
Dennis Princewell Stehr

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ABSTRACT: During the last decade, North Sea autumn spawning herring (*Clupea harengus*) has gone through consecutive years of low recruitment despite high spawning stock biomass. Although several mechanisms, such as reduced larval growth and high early larvae mortality, have been identified as co-occurring during these years, the causes behind them have not been identified. In this study we analyse a long term dataset of larval distribution, obtained during the International bottom trawl survey (IBTS), in relation to environmental conditions during winter time and zooplankton abundances, obtained from the Continuous Plankton Recorder (CPR). These analyses assessed the potential influence of these factors on the reduced survival of larval stages. Generalized additive mixed models (GAMMs) on 30 years of data showed the abundance of Pseudocalanus sp. during winter to have a strong relationship with larval distribution and abundance, suggesting that predator-prey processes are behind the low recruitment in recent years. According to our models the direct effect of temperature on larval abundances was less than the effect of zooplankton abundances.

3. Effect of zooplankton on fish larval abundance and distribution:

A long term study on North Sea herring (*Clupea harengus*)

INTRODUCTION

Marine ecosystems in the northeastern Atlantic region have shown great variability on decadal and multidecadal scales (e.g. Hurrel and van Loon, 1997; Butler et al. 2013) which on a smaller scale significantly alter the hydrographic features like currents (Siegsmund and Schrum, 2001), salinity (Häkkinen et al. 2011) or temperature (Meyer et al. 2011). These hydrodynamic changes, at the bottom of the foodweb, cascade through all trophic layers leading to match-mismatch events, changes in growth, feeding and predator-prey interactions resulting in shifts in species distribution and productivity. Accordingly ecosystem changes seem to respond to global scale processes by displaying similar multidecadal variability(Alheit et al. 2014, Drinkwater et al. 2014, Goberville et al. 2014). This variability has been recorded across ecosystem components from phyto- and zooplankton (Edwards et al. 2001, McQuatters-Gollop et al. 2007, Beaugrand 2009,
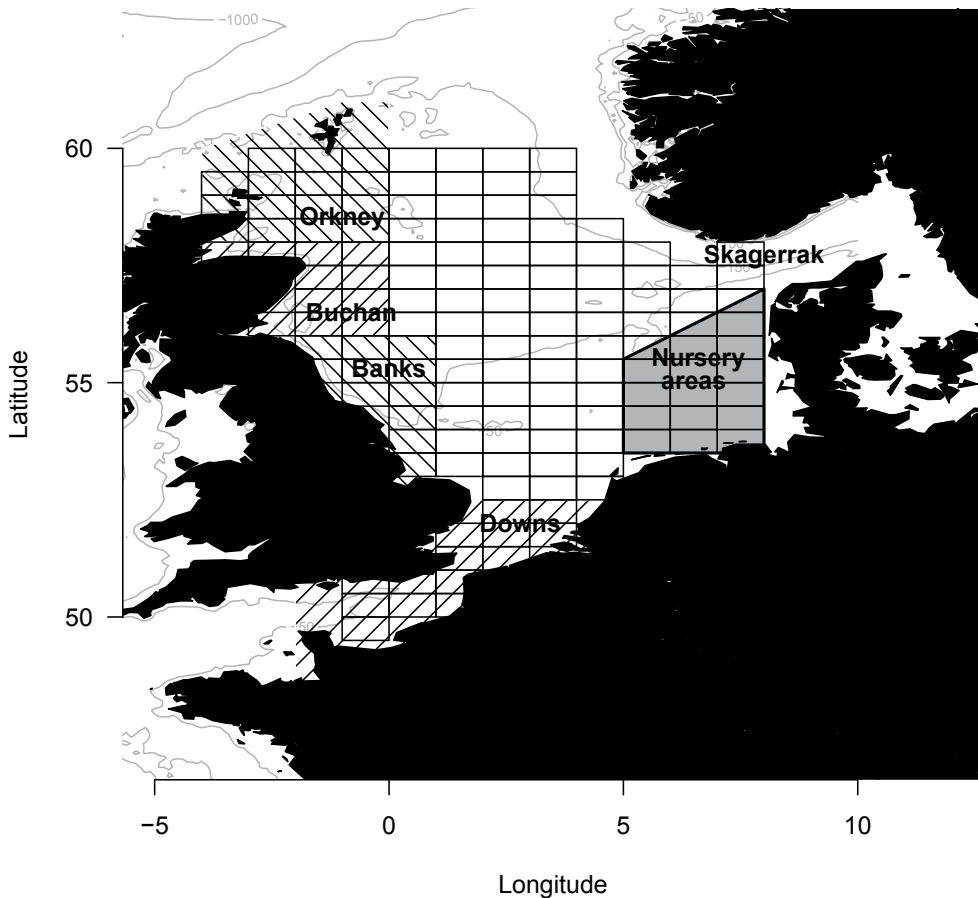
Figure 1 Study area showing spawning (striped) and nursery (shaded) areas. The grid represents ICES statistical rectangles

Alvarez-Fernandez et al. 2012), through planktivorous species (Hátún et al. 2009a, Óskarsson et al. 2009, Payne et al. 2009), all the way to top predators (Hátún et al. 2009b, Kirby & Beaugrand 2009). Fish populations showed synchronous changes in different areas such as the North Sea (Kirby et al. 2009), the Baltic Sea (Mollmann et al. 2008), and the northeastern Atlantic Ocean (Hátún et al. 2009a). Often these changes go along with antropogenic induced factors like increased or shifted fishing effort eutrophication etc. (Eero et al. 2011, Engelhard et al. 2014) altering whole population structures and distributions. Decreasing population size subsequently leads to decreasing numbers of recruits described by spawning stock biomass – recruitment relationships (Berverton and Holt, 1957). However, when time series are "cleaned" from these stock size and reproductive potential driven factors, still a significant amount of interannual and decadel variability remains. Although the exact processes behind such changes are not determined, the current paradigm embraces the idea that often a number of interacting processes affecting early life stages control the productivity of fish populations via starvation, predation, or unfavourable advection (Peck & Hufnagl 2012).

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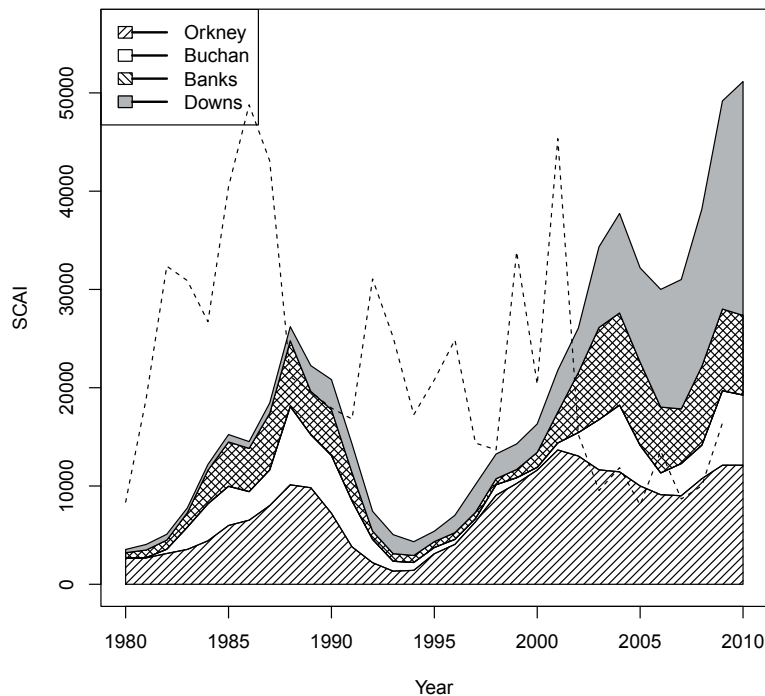
Figure 2 Contributions of each spawning component based on spawning component abundance index (SCAI) during the study period. The dashed line represents herring recruitment (different y-scale). After Payne (2010)

In the North Sea, Atlantic herring (*Clupea harengus*) plays a key ecological and economic role with ~0.3 to 0.4 million tons landed per year between 2007 to 2012 (ICES 2013). Herring exhibits a unique plasticity in temperate marine fish with a temperature tolerance ranging from -0.75 to 23°C and larvae capable of surviving relatively long time periods while displaying little or no somatic growth (Blaxter 1960, Johannessen et al. 2000). Hence, Atlantic herring inhabits environments across the North Atlantic with different water temperature, prey availability, and hydrography (Geffen 2009). Despite this plasticity, during the last decade herring in the North Sea, has produced successive weak year classes (ICES 2013, Payne et al. 2013) responding to detected changes in global hydro-climatic indices such as North Atlantic oscillation (NAO) and Atlantic multidecadal oscillation (AMO)(Gröger et al. 2010).

North Sea herring consists of four spawning stock components (Orkney, Buchan, Banks and Downs; Fig. 1) which can be differentiated by their spawning area and times. Spawning starts in the northern components in late August (autumn spawners) and continues southward to the Southern North Sea until January (winter spawners) (Gröger et al. 2010). Even though spawning stock biomass has been high during the last decade, recruitment of North Sea herring has decreased since 2002 (Fig. 2) (ICES 2013, Payne et al. 2013).

Despite the wealth of data available for all life stages of herring (Simmonds, 2009; Sinclair, 2009) the main mechanisms causing this low recruitment have not been definitely determined. There are indications that the early larval stage seems to be the critical point, with reduced survival and growth rates during the 2000s (Payne et al. 2009, Fässler et al. 2011). Larval survival is known to be affected by the quantity, suitability, and timing of planktonic prey (Durant et al. 2005, Payne et al. 2009). Therefore, the effect of atmospheric patterns on prey of herring larvae seems a logical mechanism affecting herring recruitment (Payne et al. 2009, Payne et al. 2013).

Plankton community changes have already been connected to the dynamics of other fish species in the North Sea, e.g. cod (Beaugrand et al. 2003) and horse-mackerel (Reid et al. 2001). In the case of herring larvae, known zooplankton prey such as *Temora sp*. and *Pseudocalanus sp,* (Blaxter 1965, Arrhenius 1996) have shown a sharp decline during the 2000s, halving

the abundances recorded during previous decades (Alvarez-Fernandez et al. 2012). Most recent combined approaches that either link survey data with hydrodynamic features and larval physiology (Hufnagl et al. 2014) or indirect larval feeding indices with growth and hydrodynamic features (Lusseau et al. 2014) also point towards a bottom up control of herring recruitment strength.

In this study the relationship between herring larvae and zooplankton prey has been assessed in space and time via generalized additive mixed modelling, considering the potential effect of different plankton regimes in the North Sea. With this analysis we try to discern the effect of food availability on the survival of herring larval stages.

MATERIALS AND METHODS

Datasets

Data on abundance of herring larvae were obtained from the MIK survey carried out during the International Bottom Trawl Survey (IBTS) in the first quarter of each year since 1977. Herring larvae are represented as the average number of larvae per length in each statistical rectangle (Fig. 1). The number of larvae between 25 and 55mm were considered as an index of pre-metamorphosis larvae (PML). These larvae come from the autumn spawning herring, therefore excluding the Downs component which spawns during winter. Only data since 1981 were used, as earlier years had several unsampled statistical rectangles.

The spawning-component abundance index (SCAI) was used to address the different contribution of each spawning component through time (Payne 2010). This index has been used in the herring stock assessment (ICES 2013) since 2011 and replaced the formerly used Larval Abundance Index (LAI). SCAI provides an index of the abundance of early larvae (less than 10-11mm) on the spawning grounds (ICES 2013). Because of the later spawning of the Downs component its dynamics are not represented by PML in February. Therefore, the SCAI of the Downs is not included in the analyses.

Data on zooplankton abundance were obtained from Continuous plankton recorder (CPR) data as provided by the Sir Allister Hardy foundation for Ocean Science (SAHFOS). Four different species considered prey of herring

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larvae, were included: *Temora longicornis*, *Oithona* sp., *Pseudocalanus elongates* and *Acartia* spp. Plankton data were fitted on a grid of 1x1 degrees (Fig. 3). At each node Inverse Distance Weighed averages (IDW, Isaaks & Srivastava 1989) with a search distance of one degree were calculated for each year per month (October, November, and December). These data provide information on herring larvae prey abundances post spawning.

Hydrographical backtracking

At each point, the gridded PML index was coupled to CPR prey-based prey index, as well as, temperatures likely experienced by the larvae along their larval drift phase. This temperature was obtained from the HAMburg Shelf Ocean Model (HAMSOM, Pohlmann 1996a, 1996b, 2006) and the drift path was obtained from an IBM-drift model (Hufnagl et al. 2014). In short: based on the herring larvae surveys five spawning hot spots were identified and in each area particles over a period of 10 days 1000 particles (in total 50000) were released following the main spawning periods in the respective area. For each statistical rectangle sampled in February thus the average temperature experienced was determined along with the percentage of time spent in any other rectangle at a given time before February. The latter allowed for an incorporation of prey abundance experienced by larvae sampled in one specific area in February. Thus by means of the drift results, the datasets (Temperature, *Temora longicornis*, *Oithona* sp., *Pseudocalanus elongates* and *Acartia spp.*) were paired spatially in 72 nodes covering the whole study area during the period 1981-2005, representing PML abundance in February and prey and environmental conditions per month that these larvae would have found during their drift across the North Sea.

For each datapoint, the absolute spawning contribution was calculated. The IBM-drift model provided the partial contribution of each spawning component to each spatial point in the study grid. An absolute spawning index was calculated as follows:

$$SAI_{x,j} = \sum_i SCAI_{i,j} \times SCAI\_f_{x,i,j}$$

Where $SAI_{x,j}$ represents the Spawning abundance index in gridpoint x and year j, $SCAI\_f$ the partial contribution of spawning component i (obtained from the model) to gridpoint x in year j. Only the northern spawning components were considered for this spawning index, as the PML larvae in February do not represent the dynamics of the Downs component.
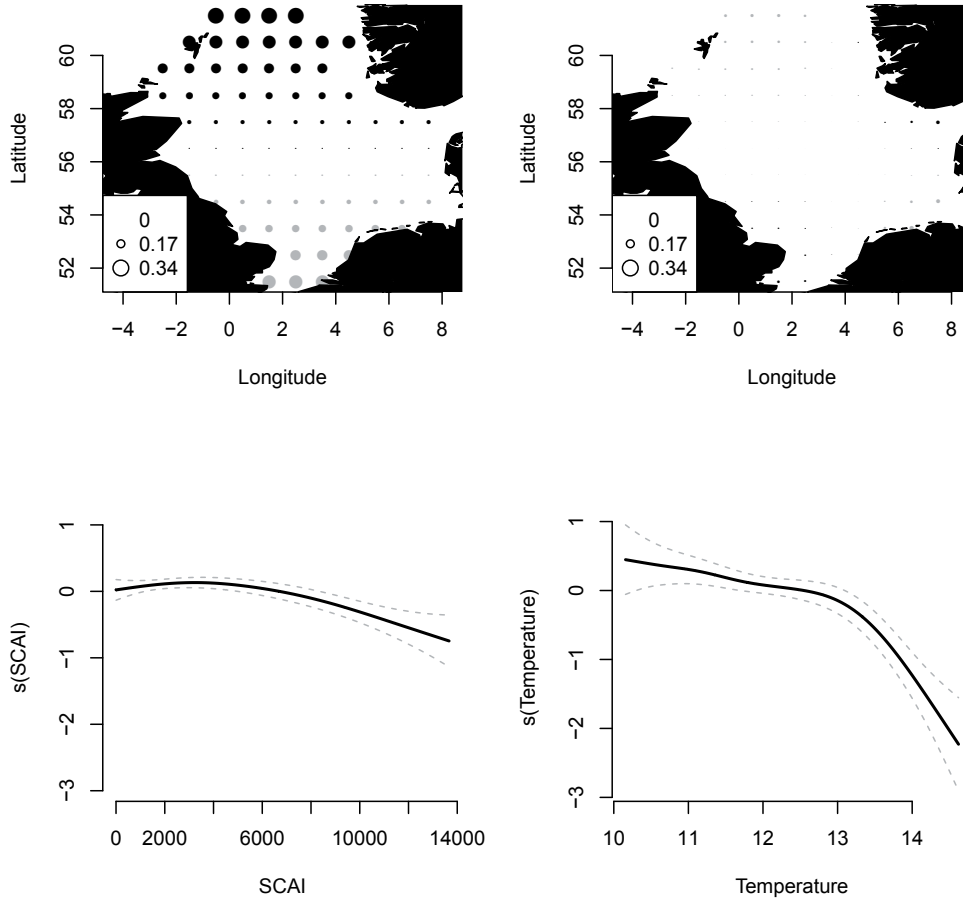
Figure 3 Contribution of each parameter to the predicted log(PML abundance) of: a) 10 ind/L increase in Pseudocalanus sp., b) 10ind/L increase in Acartia sp., c) SCAI, and d) Temperature. Grey indicates a decrease while black indicates an increase

Analyses

Split-moving window boundary analyses (SMW; Beaugrand, 2003) was performed on each variable by creating a matrix of its geographical location in time (72 rows by 24 columns). For each matrix, the calculation of SMW is realized in four steps: 1) A window of even-numbered size is introduced at the beginning of the time series matrix, 2) this window is then divided

into two half-windows, 3) an association coefficient (Euclidean distance in this case) is used to evaluate the differences between those time periods. A multiple response permutation procedure (Mielke et al. 1981) was applied to test the two periods on the basis of the information provided by all latitudinal/longitudinal points. Lastly, the window is then moved from year to year, repeating steps 2 and 3 until the end of the time series is reached. This procedure provides a p-value for each year representing the statistical significance of a year being the limit between two different periods. By repeating this procedure for different window sizes, the sharpness of change was also assessed. Changes also detected at small window sizes are considered to be sharper (more sudden) than those detected only at big window sizes.

Generalised additive mixed models (GAMMs) with Gamma distribution and a logarithmic link were used to analyse the relationship between herring larvae abundance, temperature, and its prey in space and time. Several models were fitted to assess all potential relationships between larvae and its prey. An overview of the models can be seen in Table 1. The full structure of the model was as follows:

$$\ln(\text{Larvae}_{(i,\theta)}) = f_0(\theta) + f_1(\text{SAI}_{(i,\theta)}) + f_2(T_{(i,\theta)}) + f_3(\text{Prey1}_{(i,\theta)}) + ... + f_n(\text{Prey-n}_{(i,\theta)}) + \varepsilon_{(i,\theta)},$$

Where i represents each year, θ the spatial location (longitude and latitude), SAI the spawning abundance index, T the temperature, Prey each different prey item, and ε is a residual term which is normally distributed with 0 mean and σ standard deviation related to noise in the data and not included paramters. The relationship of explanatory variables with larvae abundance (f_{0-n}) varies between models, being either equal for the whole spatial range, or being allowed to change in space (Table 1). All models were fitted with a spatial gaussian autocorrelation structure to account for spatial autocorrelation of the data.
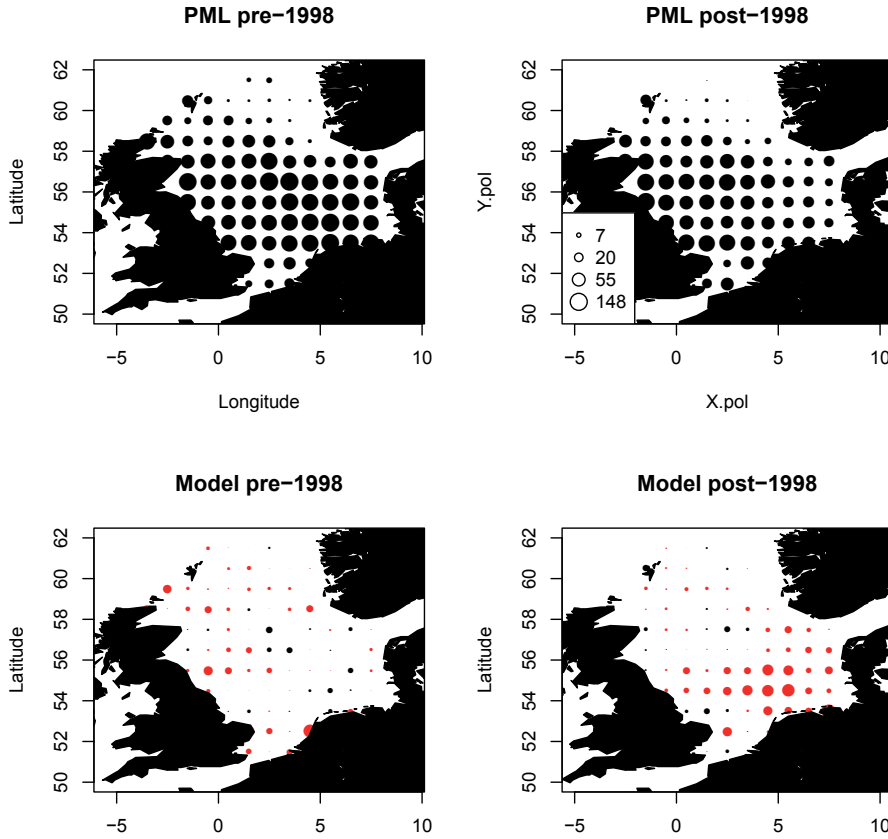
Figure 4 Average abundance per period of herring pre-metamorphosis larvae (top) in the study area and residuals of the best model (bottom). Red indicates negative values.

Table 1. Different relationship between explanatory variables and herring larvae abundance

Function type	Explanatory variables
f	Relationships modelled with a location-independent and period-independent smooth function.
f_P	Relationships modelled with a location-independent and period-dependent smooth function.
f_θ	Relationships modelled with a location-dependent tensor product, i.e. interaction between Longitude, Latitude tensor product (2D-smooth) and explanatory variables
$f_{(\theta,P)}$	Relationships modelled with a location-dependent tensor product. The interaction was allowed to be different in the different periods.

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Table 2. Best models as selected by the AIC index. Smaller AIC values mean better models; df represents the degrees of freedom of the model. The different functions representing relationship between explanatory variables and PML abundance are defined in Table 1. The subscript indicates the month at which larvae encounters the prey.

MODEL		df	AIC
M1	$f(SAI) + f(Temperature_{Oct}) + f_\theta(Acartia_{Oct}) + f_\theta(Pseudocalanus_{Oct})$	18	3362.108
M2	$f(Temperature_{Oct}) + f_\theta(Acartia_{Oct}) + f_\theta(Pseudocalanus_{Oct})$	16	3378.465
M3	$f(SAI) + f(Temperature_{Oct}) + f_\theta(Acartia_{Oct}) + f_\theta(Pseudocalanus_{Oct}) + Temora_{Nov}$	19	3385.252
M4	$f(SAI) + f(Temperature_{Oct}) + f_\theta(Pseudocalanus_{Oct})$	15	3395.912
M5	$f(SAI) + f(Temperature_{Oct}) + f_\theta(Acartia_{Oct})$	17	3404.479

Temperature

Pseudocalanus

Acartia
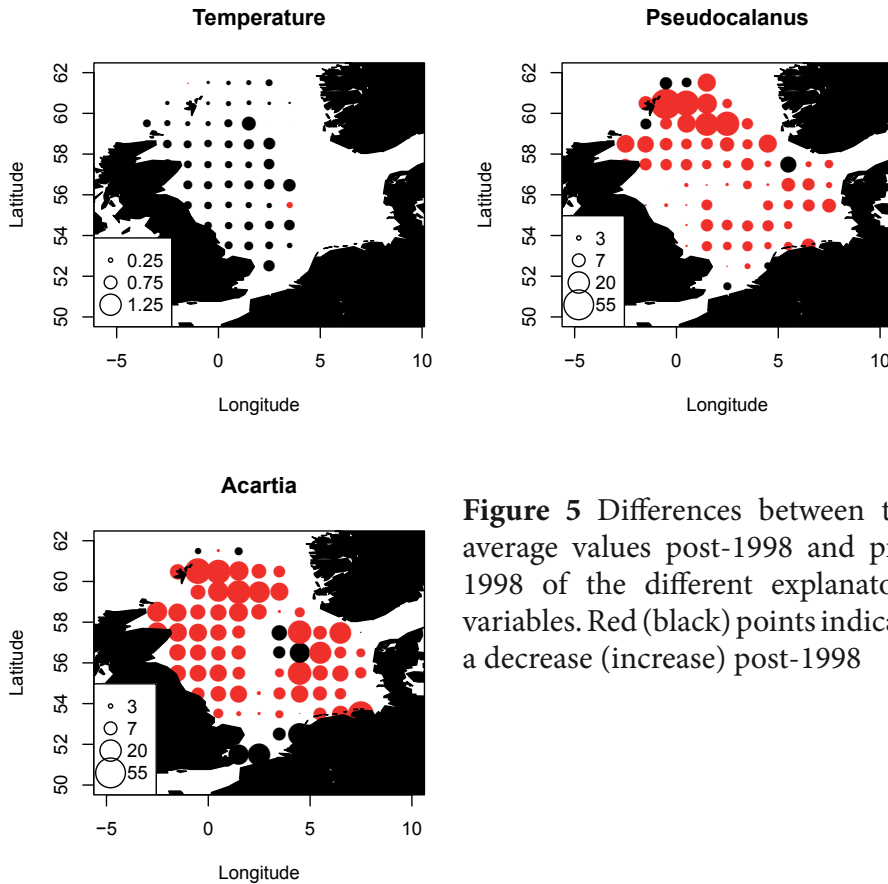
Figure 5 Differences between the average values post-1998 and pre-1998 of the different explanatory variables. Red (black) points indicate a decrease (increase) post-1998

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A backwards model selection process was carried out for each model type, starting with the most complex model including all explanatory variables. Smooth terms with p-values > 0.05 threshold were removed one by one until all terms were statistically significant. Smooth terms with estimated degrees of freedom close to one were replaced by their parametric counterparts. Models in which all smooth and parametric terms were significant were compared by means of the Akaike Information Criterion (AIC). AIC takes into account both the goodness of fit of the model and model complexity with lower values indicating better models. The model with the lowest AIC was considered the best suited to represent herring larvae distribution (Wood 2006).

RESULTS

Split moving window boundary analysis

Several variables showed statistically significant shifts in their geographical

distribution and abundances, i.e. temperature, *Pseudocalanus* and *Oithona* . The three variables showed a shift between 1996 and 1998, p-value<0.05; *Oithona* sp. (1996-1997), window size 20-24; temperature (1997-1999), window size 14-24; *Pseudocalanus sp.* (1997-1998), window size 20-24. The large window sizes indicate that the shift is not too sudden, it could even represent relatively gradual change. Nonetheless two different periods were detected, therefore a "period" variable was created to allow some of the modelled relationships to change before and after 1997 (Table 1).

Model selection

According to the AIC the best five models included zooplankton abundances in October as predictors (Table 2). The November abundance of *Temora* was significant in only one of the models (Table 2, M3). The best 5 models according to AIC also always included spatial interactions of zooplankton abundance effects (Table 2). Spawning abundance index and temperature were also significant explanatory variables.

The best model, according to AIC scores, included non-linear predictors for SAI and Temperature in October, and linear predictors for *Pseudocalanus* sp. and *Acartia* sp. also in October which vary in space (Table 2, Fig. 3). According to the AIC scores, the spatially defined smoothers are consistently a better fit than the period-defined smoothers, as none of the period-defined predictors were selected in the top-10 models. This indicates that the spatial variation of the responses of PML abundance is of greater importance than their change in different periods.

Pseudocalanus sp. showed a positive relationship with PML in the northern part of the North Sea, and a negative relationship in the southern part (Fig. 3a). *Acartia* sp. on the contrary only showed considerable negative relationship with PML in the southern nursery area and the Orkneys, and positive in the English Channel and the Skagerrak mouth (Fig. 3b). These relationships were always weaker than those of *Pseudocalanus*.

The spawning abundance index showed a non-linear relationship with PML abundance in the study area (Fig. 3c). This relationship was positive for the lower values of SAI and became negative for high values of SAI. There was also a negative relationship between temperature during October and PML abundance independently of location (Fig. 3d). This relationship was non-linear, becoming more negative as temperature increases.

DISCUSSION

The results presented here suggest that zooplankton abundances in October are an important predictor of post- winter PML abundance in the North Sea. Models with zooplankton as explanatory variables always performed better than their counterparts without zooplankton variables (Table 2). The different regimes detected in explanatory variables did not affect the relationship between larvae and zooplankton, as both zooplankton and temperature effect showed no difference before and after 1997, the year of sudden change in several explanatory variables. Even though temporal differentiation did not improve model performance, spatial differentiation of *Acartia* and *Pseudocalanus* effects were shown to improve it.

Pre-metamorphosis Larvae

Despite the abundant spawning in recent years (Fig. 2), PML abundance decreased in the second period, particularly in the eastern North Sea between 54-57º Latitude (Fig. 4a-b). This decrease is captured here as shown by the model errors (Fig. 4c-d), although there was some overestimation of PML by the model for the years after 1998 in this area (eastern North Sea). The decrease of PML while spawning values are high points in the direction of increased mortality or slower growth in early larval stages in recent years (Fässler et al. 2011, Payne et al. 2013) also reflected in a decrease in herring larvae size (Hufnagl et al. 2014).

The predictive value of this model is not very high, nor was it the intention of these analyses, but it serves the purpose of determining good explanatory variables for PML abundance and distribution and infer what processes may affect herring larvae dynamics. When interpreting the spatial effects of parameters on PML it has to be taken into account that these data represent a snapshot in time. The larvae collected between February and March each year, were coupled with the average zooplankton and temperature conditions they would encounter in the months after hatching, from October to December, along their larval drift. In the best model abundances of *Acartia* and *Pseudocalanus* in October were the best explanatory variables. This represents the conditions post-spawning which have been suggested to be of importance in the survival of larvae to juveniles by Fässler et al. (2011) and is also in line with recent findings by Lusseau et al. (2014).

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Temperature

Temperature post-spawning showed a negative relationship with abundance of PML. This relationship was consistent in space, and became more intense as temperature increased (Fig. 3d).

Average temperature in October has increased during the last decade (Fig. 5a), showing a warmer period during the 2000s. Even though temperature in different periods has been suggested to play an important role in larval survival (Payne et al. 2009, Fässler et al. 2011), it has been suggested that its direct role might be less important than previously thought (Payne et al. 2013). This would be in agreement with our results, which show temperature in October to have a weaker effect on PML than zooplankton abundances (Fig. 3c) until high temperatures are reached (>13°C). Blaxter (1960) showed autumn spawning larval herring to withstand a wide range of temperatures (-1.8°C – 23°C). However at $T > 14°C$ growth rates do not seem to increase further (Oeberst et al. 2009) indicating that an optimum is reached which is in line with laboratory investigations on survival (pers. com. Marta Moyano, university of Hamburg).Temperatures in the North Sea are in an appropriate range for larval survival, but the effect of temperature affecting metabolic rates and growth energetics is still in place within this range.

Spawning abundance

The Spawning abundance index (SAI) used here takes into account the proportional contribution of each autumn spawning component and represents the potential spawning abundance contributing to each grid-point (in space and time) in our analyses. This index showed a negative effect on the abundance of PML during the sampling period at high values, while showing a positive effect at low values (Fig. 3c). The positive phase of this effect can be interpreted as an increased post-winter larvae due to increased spawning output. The negative phase might represent increased cannibalistic pressure of adult herring on recently spawned larvae, particularly at very high values of SAI, decreasing the early larval survival. The possibility of higher abundance of adult herring in the spawning areas during the post-hatching period, should be further investigated to assess the validity of this interpretation. Another reason for this nonlinear shaped relation between SAI and PML could be habitat limitation factors which would be supported by the importance of zooplankton concentration

on PML. Thus especially in years with low dispersion and high larval concentrations a general decrease in survival can be expected.

Zooplankton

Zooplankton abundance and distribution in October have been shown here to have a relationship with the abundance and distribution of autumn spawning herring PML in February (Fig. 3a, b). *Pseudocalanus elongates* showed the strongest connection with PML abundance, and a latitudinal gradient was detected on this effect (Fig.3a). The relationship is positive in the northern North Sea, and negative in the southern North Sea. *Pseudocalanus* sp. is known to be a primary prey of recently hatched larvae (Blaxter 1965, Arrhenius 1996). In a compilation of previous studies, Blaxter (1965) showed that *Pseudocalanus* sp. was an important prey of herring larvae for smaller sizes (< 20mm), which could be expected to be abundant during winter period. In the last decade there has been a decrease in *Pseudocalanus* abundance across the North Sea (Fig. 5b), this change was particularly pronounced in the northern North Sea and becomes less going south along the east coast of the United Kingdom. This spatio-temporal trend can explain the latitudinal gradient on PML response. On the northern North Sea, where *Pseudocalanus* abundances were clearly reduced post-1998 there was a positive relationship between *Pseudocalanus* and PML. The weaker relationship in the southern North Sea (Fig.3a) was caused by the relatively constant abundances of *Pseudocalanus* in the Banks and Buchan spawning areas (Fig. 5). These results would suggest that the latitudinal shift on herring PML already detected by (Röckmann et al. 2011), can be explained by changes in abundance and distribution of *Pseudocalanus* in October and is in line with Hufnagl et al. (2014) who suggested prey quality and abundance to play an important role in larval survival and larval length in February.

Acartia sp. was also shown to influence PML abundance, although to a much lesser extent than *Pseudocalanus* (Fig.3b). Here, a negative relationship between *Acartia* sp. and PML in the nursery area (German bight) and the northwest of the study area was determined. Closer to the English Channel and the Skagerrak opening a positive relation was found. *Acartia* also displayed a decreasing abundance in the 2000s along the longitudinal margins of the North Sea, and an increase closer to the English Channel.

Results of the models including *Temora* sp. in November (M3 in Table

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2, not presented here) showed a positive linear relationship of *Temora* sp. in November with herring PML. This relationship was consistent in space. Even though the inclusion of T*emora* sp. improved the explanatory performance of the model, it also increased its complexity, and it was therefore not chosen as best model based on the AIC coefficient. Despite this, the fact that *Temora* was chosen as a good explanatory variable in November while *Acartia* and *Pseudocalanus* are the best explanatory variables in October, suggests that our model is capturing the influence of these species as prey of herring larvae. *Pseudocalanus* and *Acartia* spp. were already reported by Blaxter (1965) as prey for smaller herring larvae, while *Temora* is suitable prey for herring larvae of larger size. The influence of *Temora* abundances was less than that of *Acartia* and *Pseudocalanus*, and the increase in explanatory value of the model was low. This indicates that the first month of feeding is most important determining the winter survival of herring larvae, which would indicate a "critical period" following Hjorts hypothesis (Hjort 1914).

Together these results indicate the importance of the abundance of small copepod species, such as *Acartia* spp. and *Pseudocalanus* sp. on the winter survival of recently spawned herring larvae. The dynamics of other zooplankton species, such as *Temora longicornis*, also have an effect on the winter survival, but the results indicate the main bottle-neck before this prey becomes important. It has been shown that timing, abundance and distribution of prey affect the recruitment of the predator species (Durant et al. 2005), extending the classical view of the match-mismatch hypothesis (Cushing 1990) from a synchronicity problem to a timing and abundance interaction. Alvarez-Fernandez et al. (2012) showed that in the 2000s seasonal patterns of copepod assemblages in the North Sea have changed, whereby abundances of small copepod species decreased, particularly after the summer. These changes in plankton abundance are shown here not to be homogeneous in space (Fig. 5), therefore affecting differently the different spawning components of North Sea herring. This mismatch between herring larvae and potential prey should be further investigated at a finer spatial resolution in the spawning areas.

It should be noted that all results related to plankton in these analyses are based on CPR data, therefore some assumptions are implicitly made. The CPR dataset provides a long term view of the mesoplankton state ($> 270 \mu m$) in the North Sea and northeastern Atlantic area, but only in terms of catch

rates and species composition, and only in surface waters, without any information on the size spectra of the plankton community. We assumed here that the plankton trends detected in the CPR dataset also represent the dynamics of slightly smaller sized individuals of the same species.

Conclusion:

The results presented here give a new indication of the importance of zooplankton abundance, distribution and composition in explaining the low herring recruitment during the last decade. As expected our investigations indicated the importance of spawning abundance of autumn spawning components to be an important factor affecting post-winter pre-metamorphosis larvae (PML) abundances. However, even more important was the availability and distribution of prey organisms. Especially zooplankton abundance in October and the spatial distribution of suitable prey for early larval stages of herring (i.e. *Pseudocalanus elongates*, *Acartia* spp.) were the major factors affecting the abundance of PML. The spatial differentiation of the response of herring larvae to zooplankton abundances was shown to be important in the North Sea, and this should be taken into account in future investigations of herring larvae dynamics. The analyses were constrained by the spatial and temporal resolution of the data. Furthermore, size-structured data of the plankton community was not available for the analyses, and recent studies have highlighted the importance of microzooplankton for larval herring feeding ecology (de Figueiredo et al. 2007, Peck et al. 2012).

Further coordinated zooplankton and larvae sampling in addition to modelling efforts are needed to describe the zooplankton dynamics (micro- and mesoplankton) in spawning areas. Even more, the inclusion of size-structured plankton composition in these data collection efforts would greatly improve our understanding of the potential trophic relationships broadly represented in our model.

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ABSTRACT: Plankton communities have gone through changes in overall abundance and species composition during the mid-1990s in the northeastern Atlantic region. This study uses ordination techniques on a dataset representing phytoplankton, zooplankton and fish populations in different areas (North-east Atlantic, Iceland, Celtic Seas, Bay of Biscay, and North Sea) to characterise these changes during the period 1970-2008. An overall decrease in the most abundant zooplankton species was detected in all areas except around Iceland, and concomitant changes were observed in fish recruitment of several planktivorous stocks. Furthermore, correlation studies with the most common atmospheric and oceanic indices representing long term change in the northeastern Atlantic revealed rising temperature (Northern hemisphere temperature anomaly, NHTa) and changes in oceanic circulation (subpolar gyre index, SPG) as the most important driving forces behind these changes. We suggest that variability in the proportion of different water masses reaching the northeastern Atlantic region is a major factor affecting plankton dynamics. The results also point at changes in these proportions causing a bottom-up shift of the planktonic system in all areas during the mid-90s, which further affected fish populations.

4. Rhythm in the water:

Synchronous changes in north-eastern Atlantic plankton communities
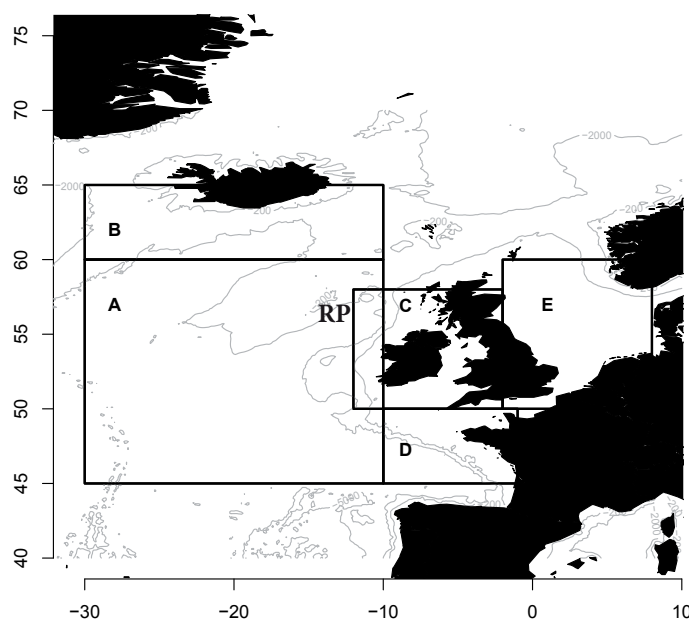
Figure 1 North-eastern Atlantic region with the areas differentiated in this study: A) North-east Atlantic, B) Iceland, C) Celtic Seas, D) Bay of Biscay, E) North Sea. RP indicates Rockall Plateau

INTRODUCTION

Marine ecosystems in the northeastern Atlantic region (Fig. 1) have shown great variability at decadal and multidecadal scales. This variability has been recorded across ecosystems from phyto- and zooplankton (Edwards et al. 2001, McQuatters-Gollop et al. 2007, Beaugrand et al. 2009, Alvarez-Fernandez et al. 2012), through planktivorous species (Hátún et al. 2009b, Óskarsson & Taggart 2009, Payne et al. 2009), all the way to top predators (Hátún et al. 2009a, Kirby & Beaugrand 2009). These large ecosystem changes or regime shifts happened in synchrony in different marine areas, leading to the idea that global scale processes, such as atmosphere-water interactions or large scale transport by oceanic currents were driving forces behind these changes (Alheit et al. 2014, Drinkwater et al. 2014, Goberville et al. 2014). The drivers of these regime shifts are also under debate. Investigating the late 1980s regime shifts reported in most European seas (Beaugrand et al. 2015), Conversi (2010) suggested that such apparent synchronicities might be by regional-, basin- or hemispheric-scale manifestations of large-scale climatic patterns. In particular, they proposed that the synergistic effects of changes in temperature and atmospheric pressure patterns could provide the means for transmitting the effects of atmospheric regime shifts and climate change to ecosystems in the pelagic realm.
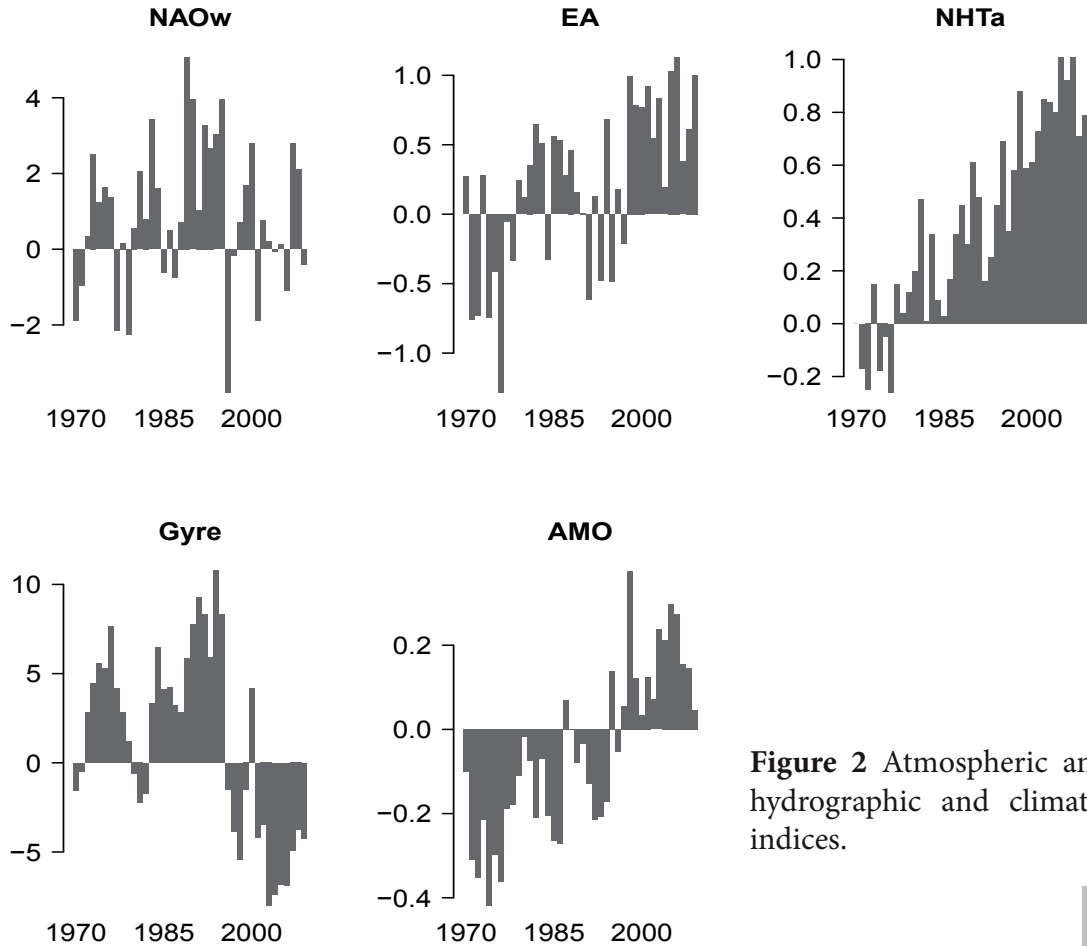
Figure 2 Atmospheric and hydrographic and climatic indices.

Several global change indices have been used in the search for correlations with marine ecosystem changes. The Northern Hemisphere temperature anomaly (NHTa), has been used as an index of global temperature rise, and associated with global trends in marine ecosystems (Goberville et al. 2014). The North Atlantic Oscillation index (NAO) (Hurrell 1995) is a leading pattern of weather and climate variability over the Northern Hemisphere. It affects the ocean primarily through air-sea heat fluxes and the action of wind stress curl, which in turn cause changes in the oceanic heat content, gyre circulations, mixed layer depth, salinity, high latitude deep water formation, and sea ice cover (Hurrell & Deser 2009). NAO has been widely investigated in the northeastern Atlantic region as a driver of biological change of phytoplankton, zooplankton, and other ecosystem components (Beaugrand et al. 2000, Edwards et al. 2001, Drinkwater et al. 2003).

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Table 1. Zooplankton species-assemblage indicators and their ecological preferences (after Beaugrand 2004a). A1 and A2 are considered warm-water copepod species; A5, A6 and A7 are considered cold-water copepod species

Species assemblage	Assemblage indicator	Species composition	Ecological preference
A1	Warm-temperate pseudo-oceanic species	*Euchaeta gracilis*, *Euchaeta hebes*, *Ctenocalanus vanus*, *Calanoides carinatus*	Warm water along the European shelf
A2	Temperate pseudo-oceanic species	*Rhincalanus nasutus*, *Eucalanus crassus*, *Centropages typicus*, *Candacia armata*, *Calanus helgolandicus*	Oceanic and neritic waters
A3	Coastal species	*Isias clavipes*, *Anomalocera patersoni*, *Labidocera wollastoni*	Shallow and coastal habitat
A4	Shelf-sea species	*Centropages hamatus*, *Temora longicornis*, *Pseudocalanus* adult, *Para-Pseudocalanus* spp.	Neritic distribution
A5	Cold-temperate species	*Aetidus armatus*, *Pleuromamma robusta*, *Acartia* spp., *Metridia lucens*	Mixed water usually found at the boundary between warm and subarctic water
A6	Subarctic species	*Heterorhabdus norvegicus*, *Scolecithricella* spp., *Euchaeta norvegica*, *Calanus finmarchicus*	Subarctic water
A7	Arctic species	*Calanus hyperboreus*, *Metridia longa*, *Calanus glacialis*	Arctic water

The Atlantic multidecadal oscillation (AMO, Kerr 2000) is another indicator of the environmental variability described in the northeastern Atlantic area. The AMO describes the slowly varying sea surface temperature (SST) anomalies that extend over most of the North Atlantic, with larger anomalies in the tropical Atlantic, the eastern portion of the entire basin, and over the subpolar gyre (from south of Greenland extending north-westward into the Labrador Sea). Similarly to the NAO, AMO has been investigated as a driver of change of all ecosystem components (Drinkwater et al. 2014), particularly in relation to sudden ecosystem changes(Alheit et al. 2014).

Finally, the subpolar gyre (SPG) dominates the physical oceanography on the North Atlantic. SPG is a large counter-clockwise rotating body of relatively cold and low-saline subarctic water in the central northern North Atlantic. SPG has also been mentioned as potential driver of change in the biology of ecosystems in the northeastern Atlantic (Alheit et al. 2014), but
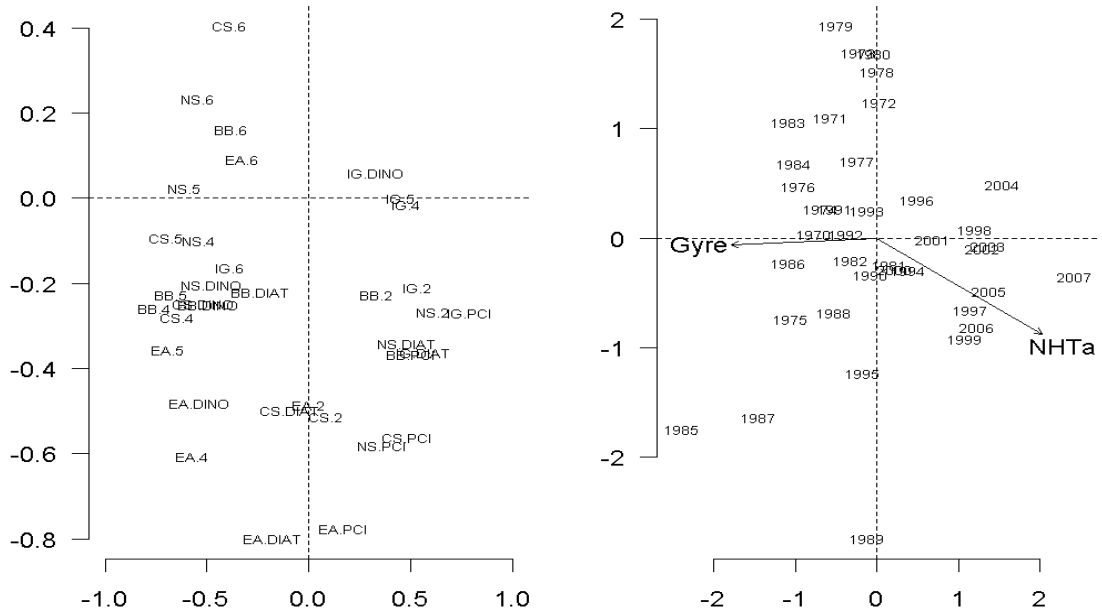
Figure 3 Ordination plot result of the plankton dataset principal component analysis (p-PCA). The influence of significant environmental variables is represented as vectors.

in few cases has its influence been studied in detail (Hátún et al. 2009a).

In this study we compiled phytoplankton, zooplankton, and fish recruitment data from different marine areas in the northeastern Atlantic region (Fig. 1) and described their major patterns of change in time looking for concurrent ecological changes. Furthermore, these patterns were compared to the most important hydro-climatic modes of variability in the area in order to assess the potential of these environmental drivers to cause changes across the northeastern Atlantic region.

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Table 2 Loadings of plankton variables for the principal components of p-PCA (plankton PCA)

	Bay of Biscay			Celtic Seas			Eastern Atlantic		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
Assemblage 2	0.33	-0.23	0.11	0.08	-0.51	0.20	0.00	-0.49	-0.26
Assemblage 4	-0.76	-0.26	0.25	-0.65	-0.28	0.14	-0.57	-0.61	0.04
Assemblage 5	-0.68	-0.23	0.42	-0.70	-0.09	0.16	-0.69	-0.36	0.34
Assemblage 6	-0.38	0.16	-0.07	-0.39	0.41	0.13	-0.33	0.09	-0.06
Total Diatoms	-0.23	-0.22	0.28	-0.10	-0.50	0.15	-0.17	-0.80	-0.07
Total Dinoflagellates	-0.49	-0.25	0.20	-0.52	-0.25	0.06	-0.54	-0.48	0
Phytoplankton colour index	0.50	-0.37	-0.29	0.48	-0.56	-0.21	0.17	-0.78	-0.20

	Iceland and Greenland			North Sea		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
Assemblage 2	0.53	-0.21	0.50	0.61	-0.27	0.21
Assemblage 4	0.47	-0.02	0.61	-0.54	-0.10	0.08
Assemblage 5	0.45	0.00	0.70	-0.61	0.02	0.23
Assemblage 6	-0.39	-0.16	0.28	-0.55	0.23	0.09
Total Diatoms	0.56	-0.36	0.49	0.48	-0.34	0.15
Total Dinoflagellates	0.33	0.06	0.35	-0.48	-0.20	-0.33
Phytoplankton colour index	0.79	-0.27	0.32	0.36	-0.58	-0.50
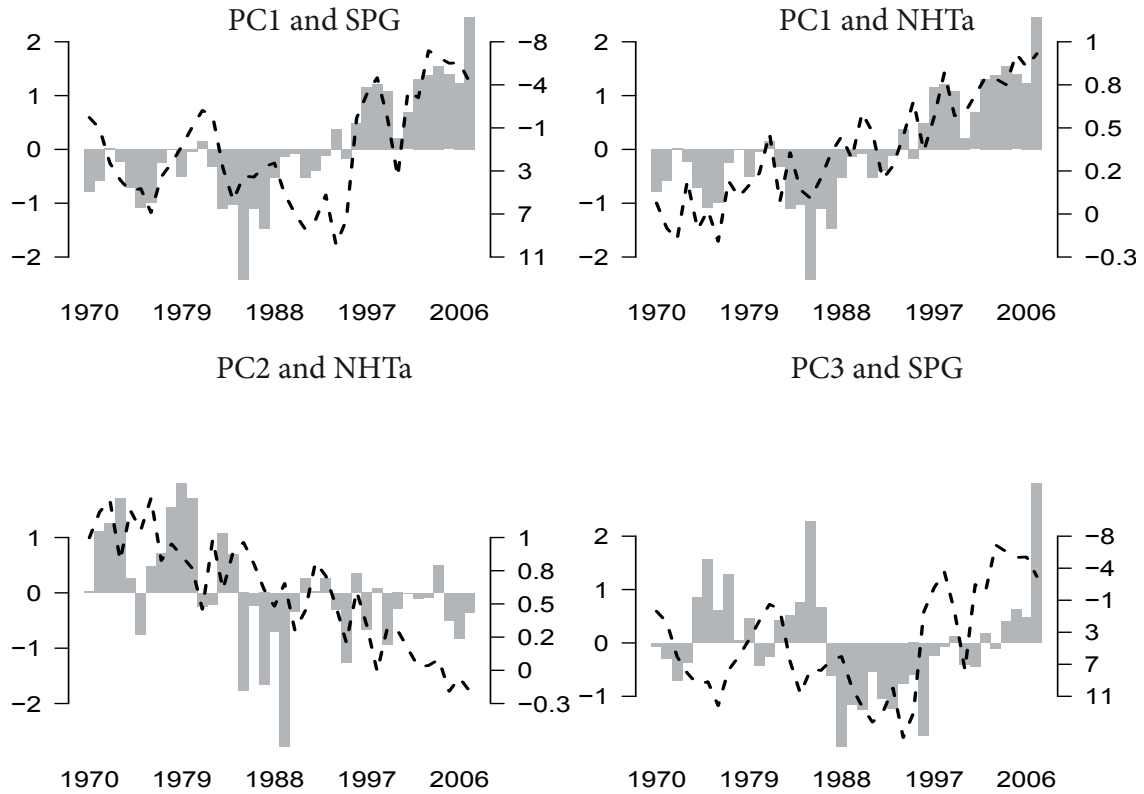
Figure 4 Trends of the different plankton principal components (bars) in time compared to environmental variables (dashed line)

MATERIALS AND METHODS

Data

Data on plankton abundance were obtained from Continuous Plankton Recorder (CPR) data as provided by the Sir Allister Hardy foundation for Ocean Science (SAHFOS) for 5 different areas representing Iceland, northeastern Atlantic, Celtic seas, Bay of Biscay and North Sea areas (Fig. 1). Three phytoplankton indices were used to represent the phytoplankton state: Phytoplankton colour index (PCI), total diatom, and total dinoflagellate numbers. PCI is a semi-quantitative estimation of algal biomass. It is based on a relative scale of greenness and is determined by reference to a standard colour chart (McQuatters-Gollop et al. 2007). Other studies have proven the validity of PCI as a representation of phytoplankton biomass (Batten et

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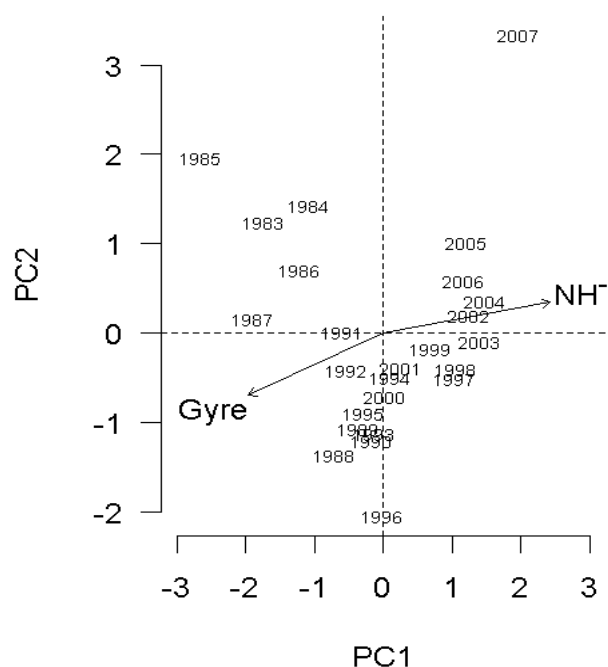
Figure 5 Ordination plot result of the plankton and fish dataset principal component analysis (pf-PCA). Each year is represented in a 2-dimensional space. The environmental variables are represented in the 2-dimensional space as vectors.

al. 2003, Raitsos et al. 2005). Because PCI does not give information about the phytoplankton community structure, data on total numbers of diatoms and dinoflagellates, also from CPR), were also included for a more in-depth analysis.

Zooplankton community was represented by the abundance of zooplankton assemblages based on biogeographic association (Beaugrand et al. 2002, Beaugrand 2004)(Table 1). The criteria used to classify species in these assemblages were based on spatial distribution of species, similarity in the seasonal variability of species and their diel variations.

Assemblages A1, A3 and A7 (Table 1) were not considered for the analyses

Table 3 Relations of environmental variables with the ordinations of both principal component analyses.

		PC 1	PC 2	PC 3	R^2	p-value
	NHTa	0.91	-0.40	-0.02	0.70	0.001
Plankton	SPG Index	-0.92	-0.07	-0.29	0.59	0.001
	AMO	0.92	-0.26	-0.07	0.54	0.001
	NHTa	0.98	0.14	-0.10	0.75	0.001
All	SPG Index	-0.93	-0.33	-0.11	0.56	0.001
	AMO	0.97	0.05	-0.19	0.43	0.003

Table 4 Loadings of plankton variables for the principal components of pf-PCA

	Bay of Biscay			Celtic Seas			Eastern Atlantic		
	PC1	PC2	PC 3	PC1	PC2	PC 3	PC1	PC2	PC 3
Assemblage 2	0.34	0.02	0.00	-0.08	0.33	-0.19	-0.13	-0.32	-0.04
Assemblage 4	-0.76	0.07	-0.07	-0.63	0.15	-0.08	-0.56	0.05	-0.40
Assemblage 5	-0.61	0.30	-0.20	-0.64	0.17	-0.14	-0.66	0.33	-0.20
Assemblage 6	-0.47	0.06	0.25	-0.53	0.22	0.04	-0.27	-0.12	0.22
Total Diatoms	-0.13	0.05	-0.05	-0.04	0.05	-0.43	-0.26	-0.18	-0.57
Total Dinoflagellates	-0.60	0.21	0.14	-0.50	-0.05	-0.36	-0.45	-0.08	-0.48
PCI	0.39	-0.38	-0.19	0.47	-0.27	-0.52	0.04	-0.36	-0.63

	Iceland and Greenland			North Sea		
	PC1	PC2	PC 3	PC1	PC2	PC 3
Assemblage 2	0.39	0.54	-0.17	0.54	0.22	-0.25
Assemblage 4	0.38	0.62	-0.01	-0.53	-0.14	-0.19
Assemblage 5	0.46	0.54	0.03	-0.56	0.14	-0.10
Assemblage 6	-0.38	0.19	0.10	-0.68	0.13	-0.17
Total Diatoms	0.53	0.37	-0.21	0.35	0.08	0.08
Total Dinoflagellates	0.37	0.15	0.12	-0.52	-0.13	-0.05
PCI	0.67	0.27	-0.12	0.17	-0.54	-0.23

Table 5 Loadings of fish variables for the principal components of pf-PCA

Area	Species	PC 1	PC 2	PC3
Celtic Sea	Celtic Sea herring	-0.36	0.19	-0.24
Celtic Sea	Herring in Division VIa (North)	-0.48	0.06	0.14
North Sea	Herring in North Sea (autumn-spawners)	-0.54	0.02	0.00
Iceland	Icelandic summer-spawning herring	0.32	0.43	0.00
Celtic Seas	Irish Sea herring	-0.13	0.62	-0.25
North Sea	Norway Pout in Fishing Area IV and IIIa	-0.26	-0.14	0.32
North Sea	Sandeel in the Central Eastern North Sea	-0.25	-0.34	0.29
North Sea	Sandeel in the Dogger Bank area	-0.36	0.07	0.40
North Sea	Sandeel in the South Eastern North Sea	-0.40	0.00	0.35
Iberian peninsula	Sardine	-0.42	0.08	0.34

CHAPTER 4

PC1 and NHTa

PC1 and SPG

PC2 and SPG
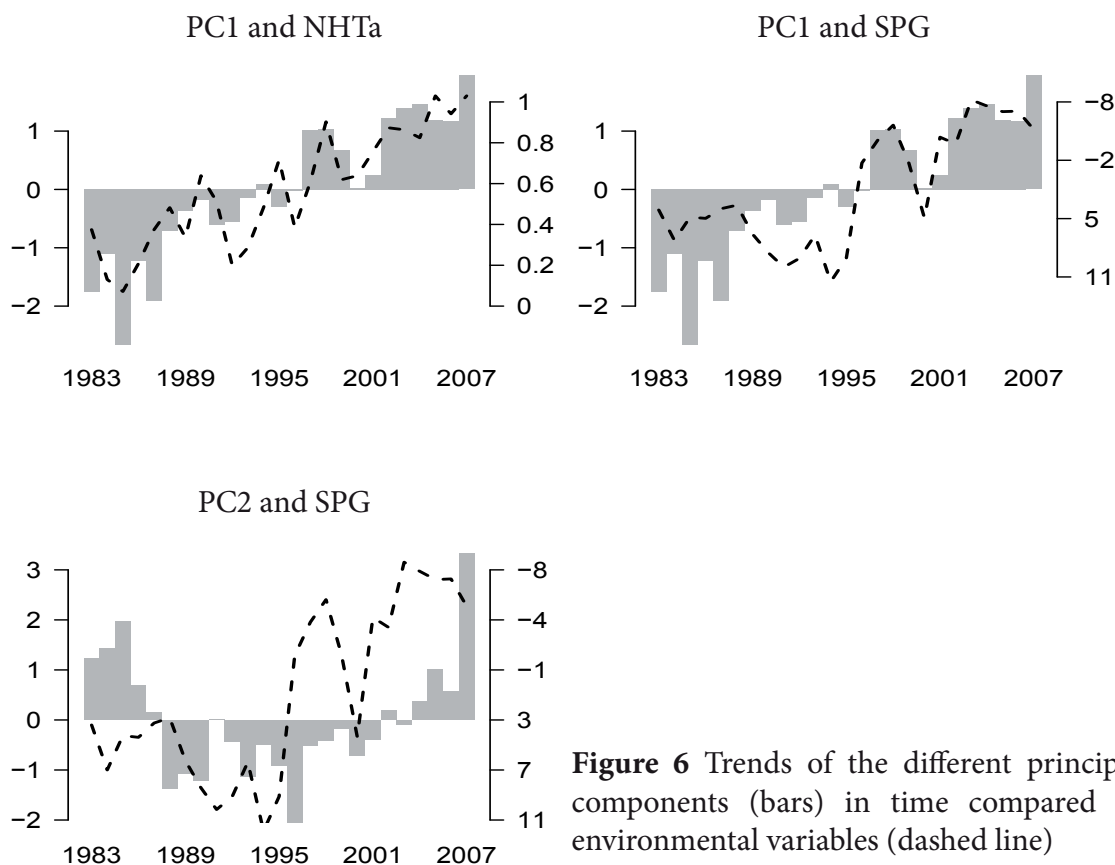
Figure 6 Trends of the different principal components (bars) in time compared to environmental variables (dashed line)

as they contributed to less than 1% of the total abundance in each area per year. Monthly averages of each of the remaining plankton variables were calculated for each area. After preliminary inspection of the data, yearly averages were calculated for the period between March and November, in order to avoid several missing values in some areas during the first two months of the year. Long term variation during the excluded months was low, due to the small plankton abundances during these months.

Fish recruitment data for several planktivorous species spanning across the study area were collected from the ICES database. These included: herring (*Clupea harengus*) in the Celtic seas, North Sea, Icelandic, and Irish sea; Norway pout (*Trisopterus esmarkii*) and sandeel (*Ammodytes sp.*) in the North Sea, and sardine (*Sardina pilchardus*) around the Iberian peninsula.

Time series of atmospheric, hydrological, and climate related indices suspected to regulate the marine system were gathered in order to assess their potential relationship with the biological state of the system:

Figure 7 Assemblage 4 abundances in average numbers per sample in a) North Sea, b) Bay of Biscay, c)Celtic seas, d) eastern Atlantic, and e) Iceland. The yearly average is shown by the white line (top axis) and SPG index showed by the red line. Bottom x-axis indicates the month

The NAO describes a basin-scale gradient of atmospheric pressures over the North Atlantic between the subtropical high pressures and the low pressures over Iceland. NAO was represented here by the Hurrell winter index (NAOw), a December-March index of the NAO (Hurrell & Deser 2009) based on the difference of normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkishólmur/Reykjavik, Iceland. The NAOw timeseries (Fig.2) was obtained from http://www.cgd.ucar.edu/cas/jhurrell/indices.html.

The NHTa was obtained from the NASA Goddard Institute for space studies (http://data.giss.nasa.gov/gistemp/). These data are used as an index of temperature changes. The dataset is based on regular measurements throughout the northern hemisphere of air temperature at a global network of long-term land stations and on sea-surface temperatures measured from ships and buoys, and consists of annual differences from the 1951-80
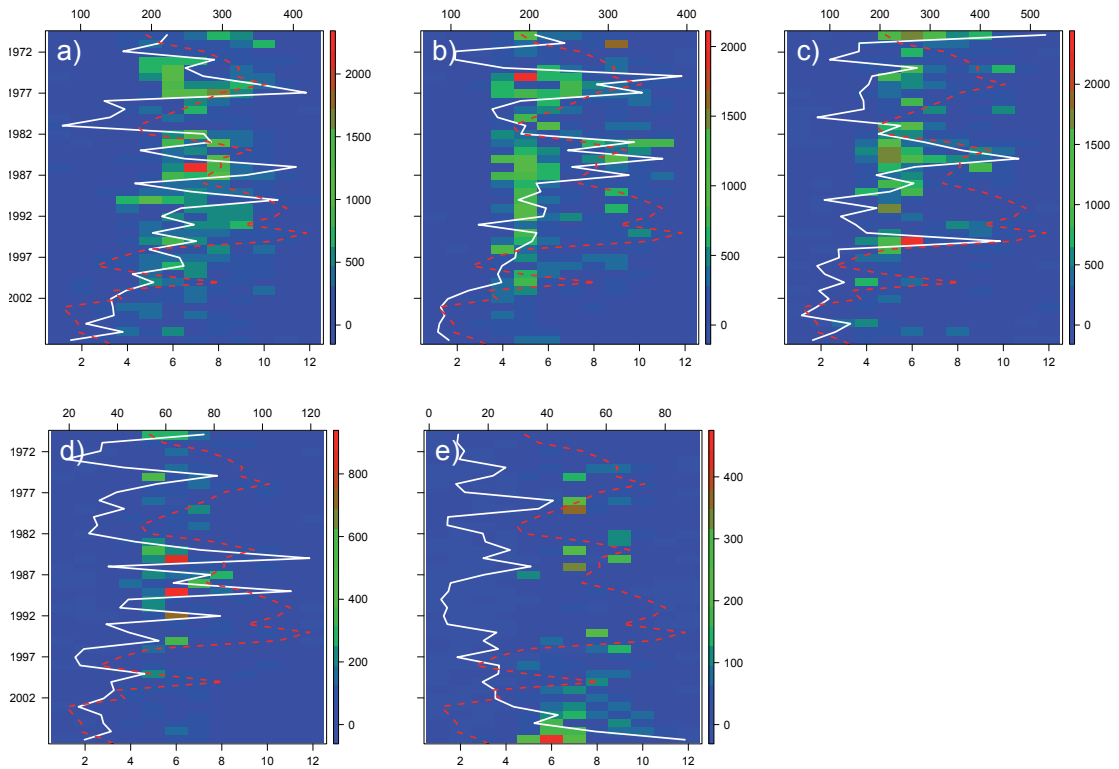
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Figure 8 Assemblage 5 abundances in average numbers per sample in a) North Sea, b) Bay of Biscay, c)Celtic seas, d) eastern Atlantic, and e) Iceland. The yearly averaged is shown by the white line (top axis) and SPG index showed by the red line. Bottom x-axis indicates the month

monthly averages (Fig. 2) (Hansen et al. 2010).

East Atlantic (EA) teleconnection pattern is the second prominent mode of low-frequency atmospheric variability over the North Atlantic and appears as a leading mode in all months (Barnston & Livezey 1987). The EA pattern is structurally similar to the NAO, and consists of a north-south sea-level pressure dipole of anomaly centres spanning the North Atlantic from east to west.

A measure of the strength of SPG (subpolar gyre index)(Hátún et al. 2005) can be obtained from the first principal component of sea surface height (SSH) over the subpolar North Atlantic. Since 1992 this has been derived from altimeter data (Häkkinen & Rhines 2004) and it shows a weakening trend between 1996 and the present day. A strong subpolar gyre results in strong influence of cold, subarctic water near the Rockall Plateau while a weak gyre results in a warm, subtropical anomaly near the Plateau (Hátún

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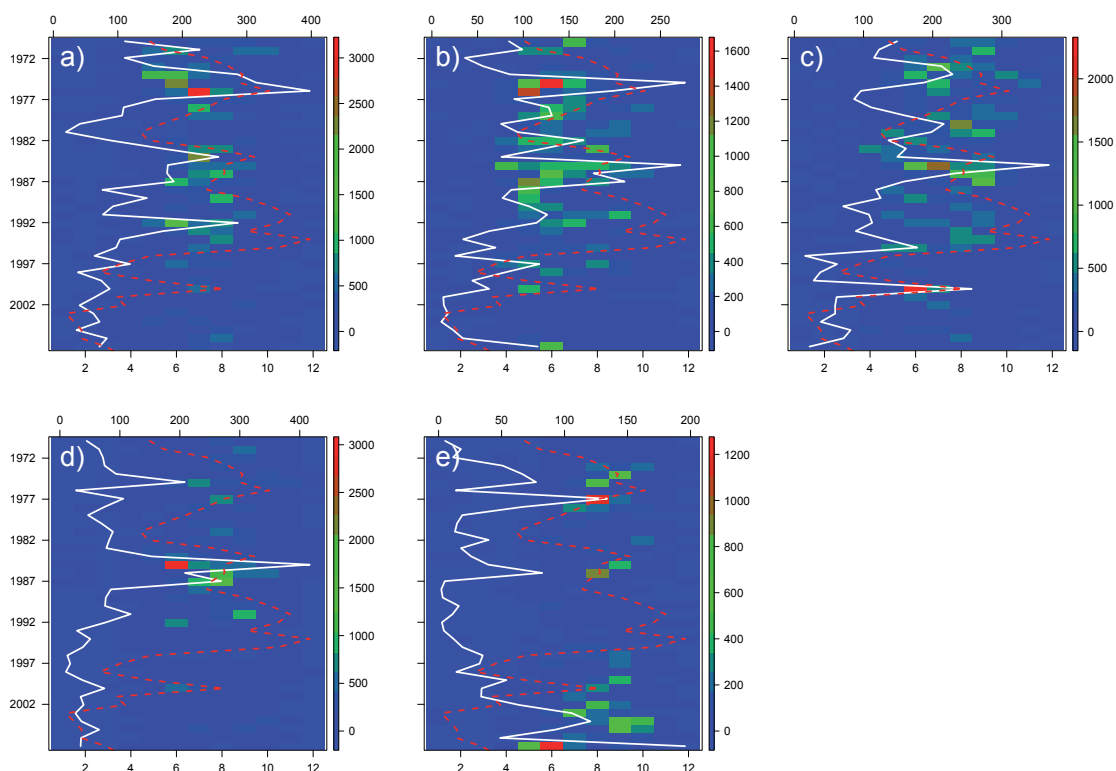**Figure 9** Dinoflagellates abundances in average numbers per sample in a) North Sea, b) Bay of Biscay, c) Celtic seas, d) eastern Atlantic, and e) Iceland. The yearly averaged is shown by the white line (top axis) and SPG index showed by the red line. Bottom x-axis indicates the month

et al. 2009a).

Atlantic multidecadal oscillation (AMO) AMO indices have been calculated using a number of different methods, but it has often been defined as the low-pass filtered SST anomaly averaged over the North Atlantic, representing SST anomalies not due to anthropogenic influences (Alexander et al. 2014). The AMO index (Fig. 2) was obtained from the U.S. National Oceanic and Atmospheric Administration (http://www.esrl.noaa.gov/psd/data/timeseries/AMO/) (Enfield et al. 2001)

Analyses:

Not all biological data series covered the same time-span. Therefore, in order to be able to extract the most information from the data two Principal Component Analyses (PCA) based on correlations (Legendre & Legendre 1998, Oksanen et al. 2010) were run to describe the most important common trends. Both PCAs used biological data, one including only the plankton
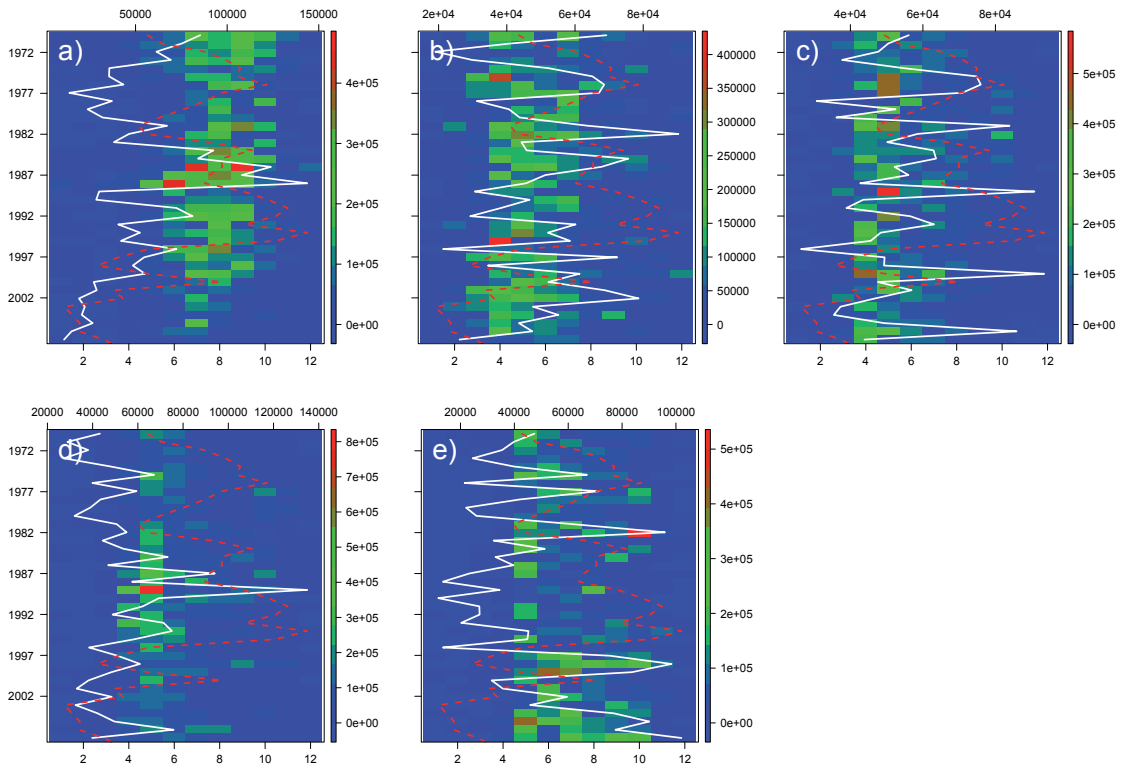
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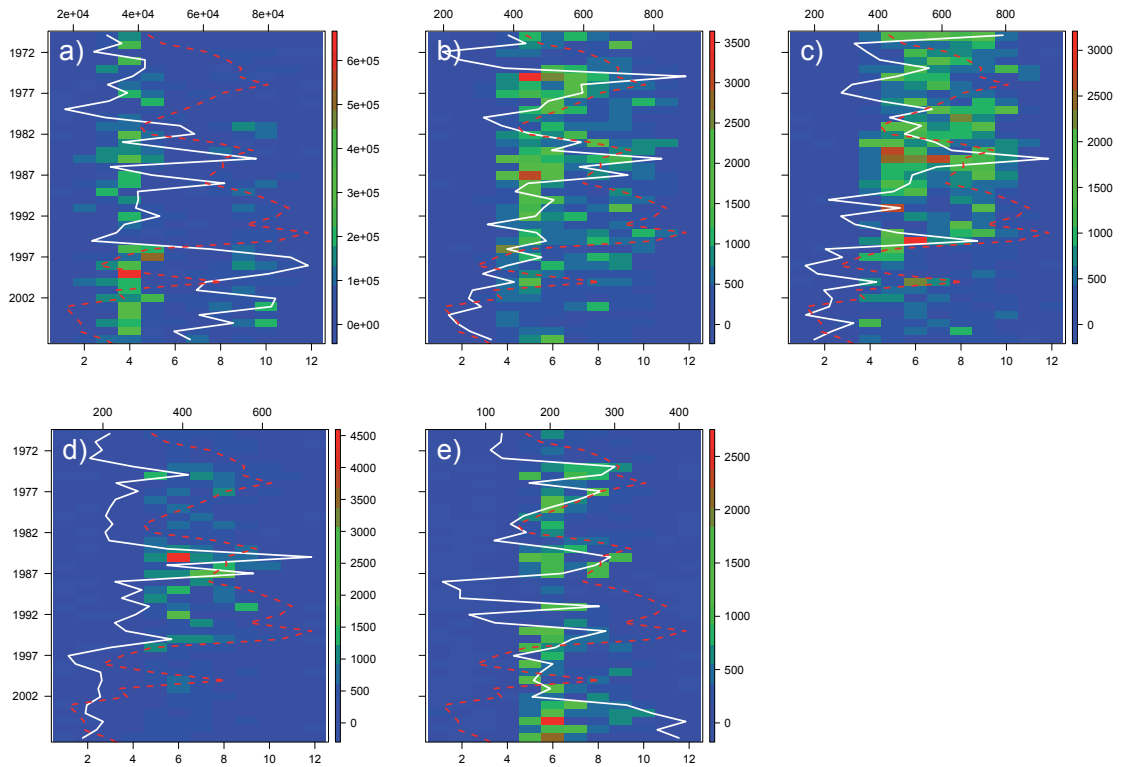
Figure 10 Diatoms abundances in average numbers per sample in a) North Sea, b) Bay of Biscay, c) Celtic seas, d) eastern Atlantic, and e) Iceland. The yearly averaged is shown by the white line (top axis) and SPG index showed by the red line. Bottom x-axis indicates the month

data (1970-2007) and the other collating fish and plankton data (1983-2007). The first PCA (p-PCA) ordinated 7 plankton variables (Zooplankton assemblages A2, A4, A5, and A6, PCI, total diatoms, total dinoflagellates) in each of the 5 areas of study (Bay of Biscay, Celtic Seas, Eastern Atlantic, Iceland/Greenland, and the North Sea), from 1970 to 2007 (35×38 matrix). The second PCA (pf-PCA) included in addition recruitment values for 6 planktivorous fish (herring in the Celtic Sea, North Sea, Iceland, and Irish sea; Norway Pout and Sandeel in the North Sea), giving a total of 41 variables from the period 1983 to 2007 (25×41 matrix). The resulting PCA axes (PCs) were used as indicators of the state of the biological system in time, and correlation analyses were carried out to compare the biological trends with atmospheric, hydrological, and climate related variables mentioned above Furthermore, the way in which biological variables are clustered in the ordination helped to identify similar trends per area or per variable.

RESULTS

Plankton PCA

The three first principal components ordinating the plankton matrix (p-PCA) explained over 45% of the dataset variation. The decade of the 2000s was clearly separated from the rest, clustered at the right side of the ordination plot (Fig. 3). After 1995 p-PC1 showed consecutive positive values, while before it was consistently negative, particularly strongly during the 80s decade (Fig.4a).

Plankton variables showed different relations to p-PC1, but these relations were consistent in the different areas (Fig. 3a, Table 2). Zooplankton assemblage A2 had a weak relationship with p-PC1, being only relatively stronger in the North Sea (0.61) and Iceland (0.53). A4 and A5 showed the strongest relationship with p-PC1 (average > .5), which was negative in all areas but Iceland (Table 2), while A6 showed a negative relationship with p-PC1 in all areas. Diatoms showed a weak relationship with p-PC1, but only positive and relatively stronger in the North Sea (0.48) and Iceland (0.56). Dinoflagellates showed a parallel relationship to A4 and A5, relatively strong and negative in all areas but in Iceland, where it was positive. Phytoplankton colour index showed the most variable relationship with p-PC1 although always positive, varying from very weak (0.17) in the eastern Atlantic to very strong (0.79) in Iceland.

p-PC2 relationship to plankton variables is weaker than p-PC1. The only areas with relationships stronger than 0.4 are Celtic seas, the Eastern Atlantic and the North Sea. In these areas all variables showed a negative relationship with p-PC2, apart from A6. Of these, the strongest relationships were those of phytoplankton variables, particularly of diatoms and phytoplankton colour index. p-PC3 only showed strong relationships in the Iceland area, which was stronger with zooplankton assemblages, particularly A4 and A5.

Out of all the environmental variables fitted to the plankton ordination, NTHa, SPG index, and the AMO showed significant correlations to the p-PCs (Table 3, Fig. 4). NHTa had a strong positive correlation with p-PC1 while SPG index showed a strong negative correlation. p-PC2 was negatively correlated with NHTa and p-PC3 was negatively correlated with SPG index.

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Fish Recruitment and plankton PCA

The three first principal components ordinating the complete dataset explained (pf-PCA) over 45% of the dataset variation. The decade of the 2000s was again separated from the rest, clustered at the right side of the ordination plot (Fig. 5). Since the second half of the 90s p-PC1 showed consecutive positive values. The start of the time series, until 1988, was clustered on the top-left side of the ordination plot (Fig. 5).

The plankton variables showed relations to pf-PC1 parallel to those of the plankton PCA (Table 4). Zooplankton assemblages A4 and A5 and dinoflagellates showed a strong relationship which was negative in all areas but Iceland. A6 showed negative relationship in all areas, and diatoms and PCI had a weaker correlation with pf-PC1, positive for PCI and negative for diatoms in all areas but Iceland and the North Sea. Relationships to pf-PC2 were only relatively strong, and positive in Iceland area, particularly A2, A4, and A5. The only variables strongly related to pf-PC3 were the phytoplankton variables in Celtic Sea and eastern Atlantic, all of these were negative relationships.

Recruitment of all planktivorous fish showed negative relationships with pf-PC1, except in the Icelandic area (Table 5). Relationships were stronger for herring, particularly autumn spawners in the North Sea. The strongest relationships of pf-PC2 were those related to Icelandic herring and herring in the Irish Sea, positively in both cases. Interestingly, the relationships of all these planktivorous fish recruitments are very similar to those of A4 and A5 in each area (Table 5).

Similarly to the plankton ordination, the NTHa, AMO, and SPG index showed significant correlations to the pf-PCA (Table 3, Fig. 6). NHTa had a strong positive correlation with pf-PC1 while SPG index showed a strong negative correlation. pf-PC2 was positively correlated with NHTa and negatively correlated with SPG index.

DISCUSSION

Hydro-climatic trends

The results presented here showed three hydro-climatic parameters to be closely related to biological changes in ecosystems of the northeastern

Atlantic region (Table 3). The NHTa, AMO, and SPG index, showed close relationships to the major pattern of change in both Principal Component Analyses, PC1, and at least one of the secondary variability modes (PC2 or PC3) (Table3, Fig. 4-6). In order to discuss the impact of external forcing on the biological systems, it is important to understand what each of these hydro-climatic indices represent, and how they are inter-related.

NHTa is an index of global temperature variability, and it is calculated as the departures from a historical (1951-1980) average of integrated temperatures accross land and ocean surfaces. The AMO describes slowly varying sea surface temperature anomalies that extend over most of the North Atlantic. Different ways of calculating AMO have been used in the literature, but their main characteristic is to remove the dominant increasing temperature trend, by detrending the global sea surface temperature timeseries (Enfield et al. 2001). Therefore, it is clear that the variability represented in AMO must be somehow represented in NHTa, although it is masked by the global temperature increasing trend.

Häkkinen et al. (2011) noted how atmospheric blocking over the northern North Atlantic influences the ocean circulation and upper ocean properties by affecting wind patterns, and this blocking showed variability trends similar to those of AMO. This blocking, which occurs between Greenland and Western Europe, prevents unimpeded westerly winds across the Atlantic leading to lowe NAO index (Woollings 2011), weaker ocean gyres and reduced heat loss from the ocean. They conluded that these changes in ocean dynamics are partly responsible for the temperature variability represented by AMO. A great part of this reduction in the ocean gyres is captured by SPG, represented by SPG index, which dominates the ocean dynamics in the Northern northeast Atlantic area. It can be seen that AMO and SPG index represent a very similar variablity pattern (Fig. 2), for low values of SPG index AMO showed positive values and viceversa.

Apart from influencing the temperature variability represented in AMO, SPG index also influences the salinity of the Atlantic Inflow to the Nordic Seas and the Arctic Ocean which feeds the North Atlantic thermohaline circulation (Hátún et al. 2005). It has also been shown how changes in SPG impact the strength of the meridional overturning circulation in the subtropical North Atlantic (Böning et al. 2006). By influencing both surface and deep currents, the intensity of SPG can influence water properties other than temperatures and salinity across the north Atlantic. Johnson et al. (2013) already showed how the strength of SPG affected the nutrient

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concentrations in an area of the northeastern Atlantic. When SPG is weak, waters become warmer, more saline and reduced in nitrate and phosphate. A strong silicate decline in the Atlantic waters flowing towards the Arctic has also been observed after the decline of the gyre (Rey 2012). This is probably caused by a lesser amount of nutrient rich subpolar waters and an increase in nutrient depleted southern waters. Because of its wider influence, we consider SPG index a better way of representing ocean variability. It provides an understanding of driving processes by capturing changes in water movements, salinity, temperature and nutrients, as opposed to AMO which represents just sea surface temperature variability.

Plankton

Both PCAs showed consistent temporal patterns in the plankton community in all areas (Tables 2 and 4), with very similar trends found in all areas apart from Iceland, that showed opposite trends.

Zooplankton assemblages A4, A5 and dinoflagellates showed strong negative relationships to PC1 in all areas apart from Iceland (Table 2 and 4), where a positive relationship was found. In both cases, PC1 showed a clear shift from a negative phase to a positive phase between 1995-1996 and was negatively related to SPG Index and positively related to both NHTa and AMO. A4 (Fig. 7) and A5 (Fig. 8) became less abundant in all areas apart from Iceland where their abundances increased (Fig. 7e, 8e). The seasonal patterns of these variables in each area (Figs. 7-9) changed after 1995. A4 showed a reduction of their seasonal presence, except in Iceland. Their high abundances spanning from April to October pre-1995 narrowed to only the spring period (Fig. 8a-d). This trend was particularly apparent in two taxa of the asssemblage 4, *Paracalanus* and *Pseudocalanus* in North Sea, Bay of Biscay and Celtic Sea (Fig. S6 a-c, g-h, Supplement 6). These species showed a bimodal distribution with maxima in spring and late summer before 1995 and shifted to a single maximum in spring post-1995. These temporal patterns in abundance are paralelled by similar dinoflagellate patterns (Fig. 9), particularly in the North Sea, eastern Atlantic and Iceland.

The decrease of small copepods like Pseudo- and Paracalanus at the end of the 90s has already been reported for the North Sea (Alvarez-Fernandez et al. 2012), and related to the decrease in dinoflagellate abundances. Different studies have highlighted the importance of a high and constant food supply for the success of some copepod species, such as *Temora* sp. and *Pseudocalanus* sp. (Vidal 1980, Evans 1981, Tsuda 1994, Gentsch et al.

2009). This would explain how a reduction of available phytoplankton prey in the second half of the year could lead to the apparent decrease of these copepods in all areas. Similarly, the reversed situation in Iceland (Fig. 8e, 9e) could be partly explained by the increased abundance of phytoplankton in the second half of the year (Fig. 9e and 10e).

Abundances of diatoms in the different areas also showed a change at the end of the 1990s (Fig. 10). The North Sea and Iceland region showed an increase in diatom abundance, particularly during spring months; while the other areas showed a clear decrease. In the case of the North Sea, it has been suggested that the increase in diatom abundance from the late 90s could be caused by changes in the nutrient environment both in coastal and open waters (McQuatters-Gollop et al. 2009, Alvarez-Fernandez et al. 2012, Alvarez-Fernandez & Riegman 2014). McQuatters-Gollop et. al (2007, 2009) suggested that nitrogen may be limiting in the open North Sea. Similarly, Alvarez-Fernandez and Riegman (2014) showed how in the last 20 years southern North Sea coastal waters are developing towards a nutrient limited environment, with both nitrogen and phosphate concentrations decreasing, while silica concentration remains stable due to riverine outputs (Prins et al. 2012). After the end of the 90s diatoms would still be silica-limited in the southern North Sea, as shown by the nitrogen:silica ratios, which were still around 4:1 during the late growing season (Alvarez-Fernandez et al. 2012). The detected decrease in diatom abundance should be considered in the context of CPR sampling. CPR only captures relatively large plankton species, due to its 270µm mesh size (Batten et al. 2003). Therefore, a potential shift to smaller species due to an increased nutrient/light limitation (Riegman et al. 1993) would not be detected by our methods. In any case, the trends in abundance of the larger sized diatoms can be definitely determined.

In the case of eastern Atlantic and Celtic seas, Goberville et al. (2014) reported a decrease in several diatom species and found a relationship between this reduction and other biological changes with NHTa and AMO. They also reported that climatic variables such as wind stress, precipitation and solar radiation remained relatively stable during the last 30 years, while nutrient concentrations increased and oxygen concentrations decreased in synchrony with the diatom changes. On the contrary, Johnson et al. (2013) on their thorough analyses of the Elett line time series found a decline of phosphate and nitrate concentrations since 1996. They concluded that the interannual chemical properties of waters in this northeastern Atlantic area are predominantly controlled by variations in the relative amount

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of different water masses in the basin, which in turn is controlled by the strength of SPG. Since the early-2000s the Subpolar Gyre has been the weakest since 1970. This caused the northeastern Atlantic waters to be warmer, saltier and more depleted in nitrate and phosphate than at any time in the last half century (Johnson et al. 2013). This reduction in nutrients seems more in accordance with our results, as lower nutrient concentrations would further limit the growth of phytoplankton populations in all areas but in Iceland, where the influence of nutrient rich subpolar waters would be sufficient even in weaker phases of SPG. This was also the interpretation of Hátún et al. (2009a), who identified increased mean primary production along the transition zone between subpolar and subtropical waters in the Rockal through. This transition zone offers favourable balance between nutrient and light limitation. They hypothesized that geographical shifts of this transition zone caused by weakening SPG would cause a shift in phytoplankton maxima towards the areas south of Iceland. Our results agree with this, showing an increase of phytoplankton abundance around Iceland in synchrony with decreasing abundances elsewhere.

Hátún et al. (2009a) discussed how a weak gyre circulation is characterised by reduced abundances of the subarctic copepod *Calanus finmarchicus* in waters south of Iceland, as changes in its biomass will reflect the highly variable volume of subarctic water in this basin. Our results also agree with this, as both SPG index and the copepod assemblage 6 showed negative relationships to PC1. As it could be expected, the warmer assemblage 2 showed opposite relationship in Iceland and the North Sea, probably representing the larger contribution of southern water masses, carrying warm (Lusitanian) species to the northern areas when SPG is weak.

NHTa showed strong correlation with PC1 in both PCAs and weaker correlation to one of the other two in each PCA. This shows the strong relationship between the biological system in all areas and temperature trends. As discussed by Goberville et al. (2014) it could be speculative to propose definitive mechanisms by which climate might affect northeast Atlantic ecosystems, but any of its influences could have a decisive effect on population dynamics, either affecting reproductive otput , metabolic rates (Mauchline 1998), growth (Huntley & Lopez 1992), or by determining the spatial distribution of organisms (Beaugrand et al. 2009). Moreover, Vidal (1980) showed how increasing temperature increased critical food concentration for both growth and development of the numerous copepod Pseudocalanus. This could lead to a synergic effect of lower food availability

caused by changes in water mass composition affecting primary production and increased food requirement due to global temperature increase.

Fish

Rijnsdorp et al. (2009) described how environmental effects may act in four, often interlinked, mechanisms affecting fish populations: (i) physiological responses to changes in temperature (Pörtner & Farrell 2008), (ii) behavioural responses, such as avoiding unfavourable conditions and moving into new suitable areas (Perry et al. 2005, Óskarsson & Taggart 2009), (iii) population dynamics, through changes in the balance between rates of mortality, growth, and reproduction in combination with dispersal (Hufnagl et al. *in press*, Heino et al. 2002, Fässler et al. 2011), and, (iv) ecosystem level changes in productivity and/or trophic interactions (Beaugrand et al. 2003, Hátún et al. 2009a, Kirby & Beaugrand 2009, Payne et al. 2013).

Alheit et al. (2014) study of historical time series showed how several populations of small pelagic clupeoid fish distributed in a large area between Senegal and Norway exhibit synchronous multidecadal changes in abundance and distribution, and hypothesized that these changes respond to the different phases of AMO. Nevertheless, Payne et al. (2013) studied the influence of changes in growth rate on herring recruitment in the North Sea, and concluded that inter-annually varying processes other than temperature are associated with greater variability, and are therefore more likely to be important. They hypothesized changes in the food supply as a candidate mechanism.

In our analyses, recruitment of planktivorous fish showed relationships with PC-1 (Table 5), except in the Icelandic area, where an opposite relationship was found, similarly to copepods

A4, A5 and dinoflagellates. This would also support the hypothesis of food supply being important for planktivorous fish recruitment in the northeastern Atlantic.

In the case of herring, recruitment is determined in the early larval stages post-hatching (Fässler et al. 2011). The distributions, behaviour and growth of herring larvae are influenced by water-mass features (Heath et al. 1991), as well as food concentrations and light intensity (Munk & Kiorboe 1985, Munk et al. 1989). Even in summer-spawning species, with relatively better food conditions, plankton increases have been shown to be profitable for fish

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larvae survival (Fiksen et al. 2002). In their analysis of the North Sea area Alvarez-Fernandez et al. (2012) already reported the decrease of copepod species (i.e. *Pseudocalanus* and *Paracalanus* spp., *Temora longicornis*, *Acartia* sp.), which are the main prey items for larvae of several important fish species such as herring and sprat (Last 1989, Arrhenius 1996) as well as cod and whiting (Shaw et al. 2008). Larval survival is known to be affected by the quantity, suitability, and timing of planktonic prey (Durant et al. 2005, Payne et al. 2009), so the parallel trends of larvae prey and fish recruitment seems logical. In the present analyses planktivorous fish in each area were clustered together with the plankton assemblages A4 and A5 (Fig. S2, Supplement 2).

For blue whiting, a synchronous shift of plankton and blue whiting has already been observed (Hátún et al. 2009a, Hátún et al. 2009b), and related to SPG. Having established a link between the spawning distribution and SPG, Hátún et al. (2009b) suggested that larval development in recent phases of SPG may be in closer synchrony with production cycles of key prey types than nearer the continental slope. Moreover, copepods *Pseudocalanus*, *Acartia* and *Oithona*, the most important larval prey items for blue whiting (Bailey 1982), also showed abundance increases related to the gyre index (Hátún et al. 2009a).

Conclusions

This study provides evidence that large plankton community changes occurred synchronically in different areas across the northeastern Atlantic region during the mid-1990s. These changes spanned from phytoplankton (e.g. total diatom and dinoflagellate abundances), to zooplankton (e.g. *Pseudocalanus*, *Paracalanus*, *Calanus finmarchicus*) and were also detected in the recruitment of planktivorous fish species in these areas (e.g. *Clupea harengus*).

The synchronicity of these changes, which were opposite in the Icelandic area compared to the rest of the northeastern Atlantic region, suggest a common driver behind the plankton dynamics. Furthermore, their coincidence with a shrinkage of the subpolar gyre initiated in 1995 suggests that variability of the water masses reaching the northeastern Atlantic region is a major factor affecting plankton dynamics.

The exact mechanisms behind the observed plankton changes could not be fully determined by the methods used, nor was it the intention of the

study, but the hypothesis of a bottom-up control of the zooplankton system seems to be supported. The decrease/increase of phytoplankton overall abundance and seasonal appearance was paralleled by same sign changes in zooplankton assemblages, possibly pointing to food limitation or a predator-prey mismatch process affecting zooplankton abundances. Physiological or population effects of temperature rise on phyto- and zooplankton and the change in water chemical properties on phytoplankton primary production could be behind the detected patterns. Either way a connection was found between water properties, determined by oceanic fluxes, phytoplankton, and zooplankton abundances.

Plankton community changes were also connected to temporal patterns in fish recruitment in the different areas, further stressing the importance of overall Atlantic water circulation for fish populations in each of the studied areas.

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CHAPTER 4

SYNTHESIS

Synthesis

SUMMARY

The research presented here was aimed to achieve a deeper understanding of long term plankton trends in the North Sea and the environmental drivers behind them. The approach taken throughout this research consisted on analyzing extensive long term monitoring data in the open North Sea (**Chapter 1 and 3**), the Dutch coastal area (**Chapter2**) and the whole northeastern Atlantic (**Chapter 4**). When doing this the shortcomings of some common indicators commonly used to describe both the biological and environmental dynamics were discovered (**Chapter 2 and 4**).

The methodology used throughout the thesis combined ordination techniques to reduce the dimension of multivariate datasets, sudden change detection methods in order to detect sudden changes in the planktonic system (**Chapters 1 and 4**), and generalised additive mixed modelling when trying to establish relationships between the biological system and environmental drivers (**Chapter 1, 2 and 4**) or between biological components of the system (**Chapter 3**). All these analyses are based on correlations, not necessarily implying causality. More precisely, not resolving a causal structure (Shipley 2002), i.e. when looking for a driver of change we cannot be sure statistically of which parameter is the cause, which the effect or if both are common effects of other parameter. Even though, based on previous ecological knowledge it is possible to infer the causal structure. As stated in previous chapters, further research, including experimental studies and monitoring surveys, would be required to prove the mechanisms proposed in this thesis.

The main results showed the North Sea planktonic system to have gone through a major change at the end of the 1990s (**Chapter 1**). This change could be detected as a shift in the abundance and seasonal patterns of dinoflagellates and the dominant zooplankton group, the shelf-sea copepods (i.e. *Temora longicornis*, *Pseudocalanus elongatus*, *Paracalanus* sp.). We suggest that the global temperature increase and a change in the balance of dissolved nutrients were behind the latest change in plankton community structure. Furthermore, wind speed and inflow of North-Atlantic water in the North Sea relate to the community changes. Although probably

involving different mechanisms, the 1990s community change is similar in magnitude to the one detected during the late 80s (Holliday & Reid 2001, Reid et al. 2001a, Beaugrand 2004), and has recently been confirmed by other authors (Beaugrand et al. 2014).

The North Sea plankton community change has not just affected the plankton system itself, but also spread through the North Sea trophic web. A previously detected change in the recruitment dynamics of North Sea herring (*Clupea harengus*), which suffered a collapse in the 2000s, could be related to shortage of prey for herring larvae (**Chapter 3**). Although it is not the only factor affecting herring recruitment, the importance of plankton community state for successful development of herring larvae is supported by our results.

Moreover, this newly detected change in the plankton community is not a self-contained event affecting the North Sea, but part of an overall change in the plankton community across different regions in the northeastern Atlantic (**Chapter 4**). A broad analysis of the plankton community across several regions in this area showed similar changes occurring synchronously. These synchronous changes point at a common driver behind these changes. Our analyses detected two potential factors as likely drivers: temperature increase and changes in water masses.

The results presented in this thesis also showed the importance of considering the North Sea, not only as a part of a bigger system in the northeastern Atlantic area, but to distinguish between its open sea areas and the southern North Sea coastal areas (**Chapter 2**). In the southern coastal areas both the community changes and the phytoplankton physiological adaptations to a changing environment are differentiated from those in offshore waters. Based on 20 yr of data from the Dutch water monitoring programme we identified an overall C:Chla increase. In coastal waters physiological adaptation to higher light and lower nutrient levels may have enhanced the C:Chla. In offshore waters, the increased stratification coincided with a shift towards dinoflagellate dominance. Dinoflagellates have a higher C:Chla ratio so their abundance increase could have caused the increase in C:Chla.

Furthermore, a mismatch was detected between chlorophyll a and phytoplankton biomass trends caused by both a decrease in chlorophyll a values and an increase in biomass. This made us question the validity of chlorophyll as a proxy for phytoplankton biomass and argue its possible

Box 2. The meandering path of research

As mentioned in the introduction, a deep understanding of ecosystems is a prerequisite to balance their sustainable functioning with the demand for development and use. Taking into account this prerequisite, Building with Nature incorporated in their research programme several fundamental research projects in order to build a knowledge base about ecosystems. The research presented in this thesis is the result of one of these projects.

The project had two original goals, understanding the ways in which the North Sea ecosystem develops in time, and disentangle the respective influence of environmental and anthropogenic factors on this change. It became evident relatively early in the project life that the second goal was not going to be feasible. The main reason for this was the lack of data properly describing the human activities of interest, particularly sand extraction and nourishment, in time and space. Drawing connections between biological changes and sand extraction needs of a detailed description of how much sand is being dredged where and when, and where is it going. Not knowing these parameters makes the task of inferring causation in the relationship anthropogenic factors-biological system nearly impossible, and more an exercise of guess-work than rational inference.

Once the lack of data was evident, the project design had to change, and focused on ecological relationships in the North Sea pelagic ecosystem, and their response to environmental external drivers. This flexible and adaptive approach to project design, in combination with a series of serendipitous encounters and surprises when analysing different datasets, allowed for several interesting and valuable findings. A clear example of this is Chapter 2 (this thesis). The first attempt to analyse the Dutch coastal water pelagos was aimed to assess how long-term changes in sand extraction and coastal nourishment would influence suspended particulate matter, and this in turn would affect the planktonic system. It became clear that the sand data did not have the required resolution (neither in space nor time) to draw sound conclusion. Furthermore, the governmental monitoring data on phytoplankton revealed an unexpected feature; the trends of chlorophyll a and phytoplankton biomass did not agree. This

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triggered a process of interest and curiosity driven research that resulted in the important findings showed in Chapter 2.

In a similar fashion, involvement in expert groups including researchers from different fields dealing with different aspects of the management of marine resources (i.e., International Council for the Exploration of the Sea working groups), triggered other paths of research that ended up shaping the results presented in Chapters 3 and 4. In my opinion the importance of these results is undisputable, as they deepen our understanding of long term changes in the marine ecosystem, but their inclusion in this thesis was a result of the impossibility to carry out other predetermined investigations.

This is why I think fundamental research, understood as research without a specifically conceived or immediately practical application, should be encouraged. Furthermore, as discussed by Scheffer (2014)curiosity driven research has an important role to play in the advancement of science, and maybe it should be encouraged and not frowned upon.

Scheffer M (2014) The forgotten half of scientific thinking. Proceedings of the National Academy of Sciences 111:6119
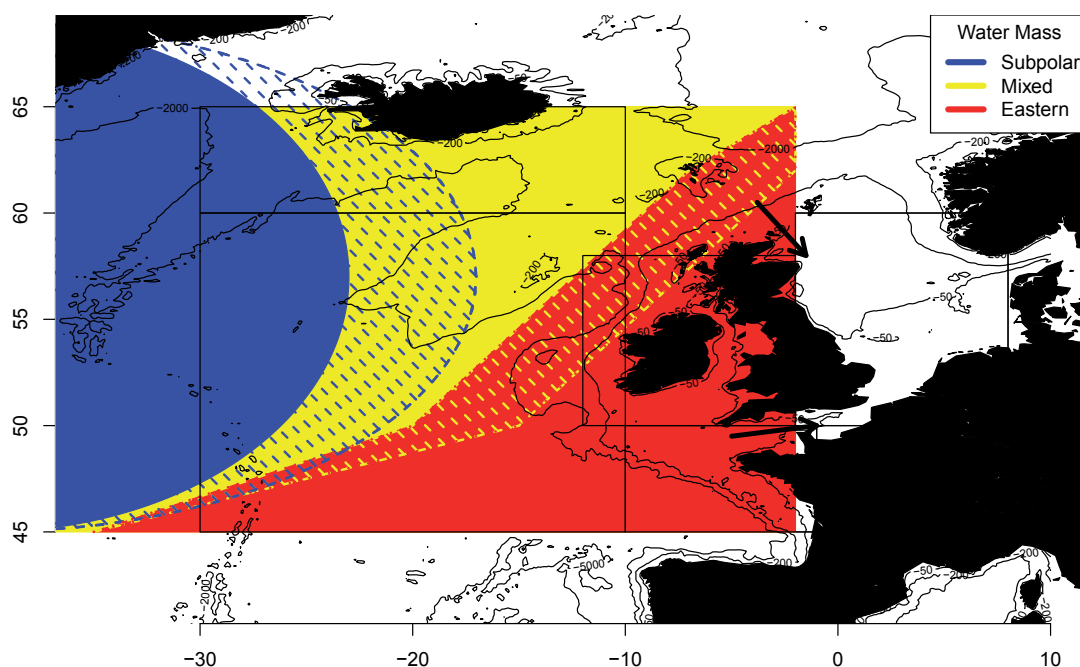
Figure 1. Representation of the different water masses affecting the northeastern North Atlantic. There is a cold and nutrient rich water mass (subpolar, blue), a warm and nutrient depleted water mass (easter North Atlantic, red) and a mixed water in between (yellow). The strength of the subpolar gyre defines where these water masses lay, i.e. Weak gyre (solid polygons), strong gyre (solid+dashed polygon).

misrepresentation of phytoplankton dynamics, particularly when comparing different areas, with potentially different environmental conditions, or time periods when the environmental parameters have changed considerably.

CHANGES IN THE NORTH SEA PLANKTON

Traditionally, the seasonal sequence of phytoplankton development in North Sea waters is of a spring bloom of diatoms followed by a later summer-autumn bloom generally dominated by other algal groups. Nonetheless, there may be considerable deviations from this standard pattern in different areas of the North Sea (Reid et al. 1990). As seen in **Chapter 2** there is a clear difference between coastal areas and open sea, even in the shallower waters of the southern North Sea. Along this coast, dense blooms of diatoms can occur as early as February, with smaller blooms as late as September. In northern coastal areas diatoms are growth limited, and the first bloom happens around the middle of April.

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Three big community changes have been detected in the North Sea plankton system during the last 40 years, roughly coinciding with the start of each decade (Table 1). A cold episodic event in the late 1970s (Reid et al. 2000, Reid & Edwards 2001, Edwards et al. 2002, Beaugrand & Ibanez 2004, Weijerman et al. 2005), a warm regime shift during the 1980s (Reid et al. 2001a, Beaugrand & Ibanez 2004, Alheit et al. 2005, Weijerman et al. 2005, McQuatters-Gollop et al. 2007) and finally a third sudden change at the end of the 1990s (Alvarez-Fernandez et al. 2012, Beaugrand et al. 2014).

During the cold episodic event the phytoplankton bloom was smaller than average, occurred later in the year, and many early spring diatom species were absent. Because of this late development of the spring bloom *Ceratium macroceros* population could have lost its niche (Edwards et al. 2002), and was only present in small numbers These cold years were characterised by low sea surface temperature (SST) values in the North Sea (Becker & Pauly 1996), which were particularly harsh in the shallower southern North Sea.

The 1980s warm regime shift can be characterised by higher Phytoplankton Colour Index (PCI) values in the central North Sea, an extended phytoplankton season, and a change in the zooplankton community structure (Reid et al. 2001a). All these changes have been related to different environmental factors, such as the increase in SST and changing Atlantic water inflow through the northern North Sea (Reid et al. 2003).

During the late 1990s community change there was a sudden drop of abundance of shelf-sea copepod species such as *Temora longicornis*, *Pseudocalanus elongatus*, and *Paracalanus spp.*, while the abundances of warm-affinity copepod species remained relatively stable. This abundance drop was paralleled by a decrease in dinoflagellate abundance, especially during autumn and winter.

In all cases the North Sea plankton community changes could be related to external hydro-climatic forcing. Reid et al. (2001b) related the 1980s regime shift to a pulse of unusually warm oceanic water from the shelf edge current entering the North Sea. At this time there was a strong biogeographic shift of warm-water copepod species, as well as of warm-water fish species, in the northeast Atlantic (Beaugrand & Reid 2003). The late 1990s change described in **Chapter 1** can also be related to oceanic waters, but the different response of North Sea plankton community indicates that other mechanisms might play a role.

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As shown in **Chapter 4** synchronous changes have taken place in different large marine ecosystems (LMEs) of the northeastern Atlantic region, indicating that common hydro-climatic forcing could be in place. A shrinkage of the subpolar gyre affecting variability of the water masses reaching the northeastern Atlantic region seems the most likely driver affecting plankton dynamics (Fig. 1). These changes affected mainly the dinoflagellate abundance and the contribution of shelf-sea species to the total copepod abundance with opposite trends in Iceland and the other areas. Moreover, a similar temporal trend could be detected in the recruitment of planktivorous fish (particularly *Clupea harengus*). Changes in the proportion of water masses contributing to the ocean waters in the northeastern Atlantic have already been shown to affect nutrient concentrations in the Rockall Trough (Johnson et al. 2013). This reduction of nutrients combined with a pulse of Atlantic water coming into the North Sea around 1998 (Reid et al. 2001b), could be responsible for the plankton community change detected in the North Sea at the end of the 1990s.

THE ZOOPLANKTON LINK

Changes in the plankton community such as the ones presented here will have repercussions on higher trophic levels. Traditionally, our view of the planktonic system could be summarized as primary producers (phytoplankton) that are consumed by primary consumers (zooplankton) which then serve as food for other zooplankton, pelagic fish and their larvae. Nowadays, the importance of reincorporation of dissolved organic carbon into the foodweb by microbial activity (microbial loop) has been acknowledged (Azam et al. 1983). Either way, the role of macrozooplankton as a link between biogeochemical cycles and fish dynamics is of clear importance and lately attention has shifted towards how to incorporate zooplankton in ecosystem studies (Mitra et al. 2014).

Rijnsdorp et al. (2009) discussed how the effect of climate change on fish population could take effect through ecosystem changes such as changes in zooplankton communities. This kind of effect has been identified in different ecosystems and fish populations during the last decade. Kirby and Beaugrand (2009) detected a trophic amplification of climate change in the North Sea ecosystem, causing the negative effect of temperature rise on cod (particularly on larval stages) to be accentuated by changes in the zooplankton community. Similarly, Möllmann et al. (2003) studied the importance of climate driven changes in *Pseudocalanus elongatus* as

drivers of change in diet and condition of herring in the Baltic Sea. In the North Atlantic, changes in spawning distribution of blue whiting have been related to hydro-climatic variability represented by the subpolar gyre index (Hátún et al. 2009b). Increased food availability for blue whiting caused by these hydroclimatic changes is one of the more plausible mechanisms for this change in spawning distribution (Hátún et al. 2009a).

In **Chapter 3** we studied the potential effect of hydro-climatically driven changes in zooplankton community composition on the abundance and distribution of herring larvae. Zooplankton abundance and distribution in October have been shown here to affect significantly the abundance and distribution of autumn spawning herring pre-metamorphosis larvae (PML) in February. *Pseudocalanus elongates* showed the strongest relation to PML abundance, and the spatial differentiation of this effect could explain the latitudinal shift in distribution detected in PML (Röckmann et al. 2011).

Due to the intrinsic limitations of the continuous plankton recorder survey (Box 1), this study was limited to abundance of species and therefore size spectra information was missing. Clearly the size distribution of plankton community has an important effect on how hydro-climatic variability affects higher trophic levels. As explained by Riegman et al. (1993) smaller phytoplankton species are expected to have a higher specific affinity for nutrients as well as light, and decreasing algae of smaller size fit into the size fraction which forms the optimal food for smaller plankton predators. These smaller predators have reproduction rates closer to those of their prey, therefore locking the energy transfer in smaller size classes which can not be accessed by larger predators such as fish.

Even when the productivity of the system reaches levels that allow larger plankton size classes to take part in the energy transfer, the size spectra of these plankton species (such as copepods) is important when considering predation by fish, particularly fish larvae. In this case, the match-mismatch mechanism potentially regulating fish recruitment would extend from a timing and abundance problem (Durant et al. 2005, Durant et al. 2013), to include also size spectra considerations.

IMPORTANCE OF MONITORING AND INDICATORS

After the agreement on a European Water Framework Directive in 2000 (WFD)(European Commission 2000), several pieces of European legislation were grouped in a single piece of framework legislation which would assure

the quality of European waters. A central requirement of the WFD was that the environment should be protected to a high level in its entirety. A list of quality elements to assess the ecological status of a coastal region is listed in the WFD, i.e. Composition, abundance and biomass of phytoplankton, other aquatic flora and benthic invertebrate fauna. With the introduction of the European Marine Strategy Framework Directive in 2008 (MSFD) (European Commission 2008), further protection is given to coastal waters, taking an ecosystem approach. MSFD aims to achieve Good Environmental Status (GES) of the EU's marine waters. The GES used in MSFD is much broader than in the WFD, and covers other elements of the ecosystem that also should be monitored and managed, such as zooplankton, fish, seabirds, and marine mammals (Borja et al. 2010). It also states that the distribution (spatial and seasonal) and the population dynamics of these parameters should be preserved. MSFD relies intensively on monitoring to obtain its goals, both for the definition and maintenance of GES.

Several monitoring shortcomings were identified during the studies presented in this thesis. Some of these complicated and, at some levels, prevented a good assessment of the temporal trends in the studied areas. Key problems, as stated in **Chapter 2**, were changes of laboratories analysing samples in the water monitoring programme, its unevenness in time with even whole years of missing data, and the methodology change reducing the number of stations monitored in both the water and benthos monitoring programmes. The strategies used here to avoid observer bias allowed us to carry out trend analyses and reach some valid conclusions, but greatly decreased the level of detail, e.g. plankton community composition analyses were severely weakened and a proper analysis of phytoplankton community dynamics was not possible.

Furthermore, the lack of zooplankton monitoring in Dutch waters hinders the ability to reach any strong conclusion about the ecosystem fluxes. Zooplankton is able to control phytoplankton dynamics (Riegman et al. 1993, Brussaard et al. 1995, Fuchs & Franks 2010), particularly through interactions between micro-, meso-, and macro-zooplankton (Löder et al. 2011). Zooplankton is also important in affecting the way primary production is transferred to higher trophic levels (Johannessen et al. 2012), and it has been proven to affect fish dynamics in the North Sea (Molinero & Flos 1992, Amara et al. 2001, Schückel et al. 2012).

In many areas of the northeastern Atlantic ecological studies rely heavily on

Continuous Plankton Recorder data when assessing zooplankton dynamics. The CPR dataset provides a long term view of the macroplankton state (> 270um) in the North Sea and northeastern Atlantic area (Box 1), but only in terms of catch rates and species composition and only in surface waters, without any information on the size spectra of the plankton community. Such view on plankton abundance is useful to assess long term trends and overall temporal patterns, but it makes very complicated to draw conclusions about the underlying mechanisms that would help increasing our understanding of processes involved in these changes.

Future zooplankton ecological research in this area should try to increase our understanding of such processes. Other zooplankton datasets from point sources are available in the North Sea area (e.g. Helgoland Roads, L4 English Channel observatory). These could be used to generate information about the size structure of zooplankton through modelling efforts, taking into consideration drift dynamics, vertical migrations and other environmental factors; using CPR data as corroborative data.

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SYNTHESIS

Supplements

Complementary information

SUPPLEMENT 1

Environmental variables

All the variables included in the analyses are presented in table S1. The source of the dataset and the timespan and area they cover are also mentioned

Table S1. Summary of environmental variables used in this work

Variable	Start	End	Area	Sub-Area	Source
Net Transport	1970	2008	North Sea	Central North Sea	IMR
Northward Transport	1970	2008	North Sea	Central North Sea	IMR
Salinity	1970	2008	North Sea	Central North Sea	ICES
Sea Surface Temperature	1970	2008	North Sea	Central North Sea	ICES
Southward Transport	1970	2008	North Sea	Central North Sea	IMR
Total Nitrogen	1988	2008	North Sea	Central North Sea	ICES
Total Phosphorus	1988	2008	North Sea	Central North Sea	ICES
Total Silica	1988	2008	North Sea	Central North Sea	ICES
Ammonium	1988	2008	North Sea	Central North Sea	ICES
Cloud Cover	1970	2008	Dutch Coast	De Kooy	KNMI
Humidity	1970	2008	Dutch Coast	De Kooy	KNMI
Precipitation	1970	2008	Dutch Coast	De Kooy	KNMI
Sea Level Pressure	1970	2008	Dutch Coast	De Kooy	KNMI
Solar Radiation	1970	2008	Dutch Coast	De Kooy	KNMI
Temperature	1970	2008	Dutch Coast	De Kooy	KNMI
Wind Speed	1970	2008	Dutch Coast	De Kooy	KNMI
Wind.Direction	1970	2008	Dutch Coast	De Kooy	KNMI
Den Helder Sea Level	1970	2008	Dutch Coast	Den Helder	KNMI
Solar.Irradiance	1970	2008	North Sea	Global	KNMI
Sunspots	1970	2008	North Sea	Global	ROB
Hurrel North Atlantic Oscillation winter index	1970	2008	Global	Global	CGD
Northern Hemisphere Temperature anomaly	1970	2008	Global	Global	HCCR
Net Transport	1970	2008	North Sea	Southern North Sea	IMR
Northward Transport	1970	2008	North Sea	Southern North Sea	IMR
Salinity	1970	2008	North Sea	Southern North Sea	ICES
Sea Surface Temperature	1970	2008	North Sea	Southern North Sea	ICES
Southward Transport	1970	2008	North Sea	Southern North Sea	IMR
Total Nitrogen	1988	2008	North Sea	Southern North Sea	ICES
Total Phosphorus	1988	2008	North Sea	Southern North Sea	ICES
Total Silica	1988	2008	North Sea	Southern North Sea	ICES
Ammonium	1988	2008	North Sea	Southern North Sea	ICES

Sources:

IMR – Norway's Institute Of Marine Research http://www.imr.no/en

ICES – International Council For The Exploration Of The Sea. http://www.ices.dk/indexfla.asp; http://www.ices.dk/datacentre/guidelines.asp

KNMI – Roya Netherlands Meteorological Institute. http://www.knmi.nl/index_en.html

ROB – Royal Observatory Of Belgium. http://www.observatory.be/

HCCR – Hadley Center For Climate And Research. http://www.metoffice.gov.uk/hadobs/

CGD – Climate Global Dynamics Division. http://www.cgd.ucar.edu/cas/jhurrell/indices.html

SUPPLEMENT 2

Principal Component Analyses comparison

In this Supplement, PCA1 refers to the Principal Component Analysis that excludes phytoplankton composition data, and PCA2 to the PCA that includes these data:

The patterns represented by the first two PCs are very similar in both analyses, as shown by the position of each variable in a two-dimensional space (Fig. S2). The different variables are clustered around the ordination space, and each different set of variables are clustered by area, which means that the patterns of same variables are similar in the different areas. The only clear exception is the assemblages of cold affinity copepods in the English Channel, which is clearly separated from the other two areas in both PCAs.

At a loading value of 0.7, commonly considered to indicate an important variable for a PC, the second PC of PCA1 would be clearly related to copepod community structure in the Central North Sea (Table S2), and also in the English Channel, while PC1 would be related with everything else.
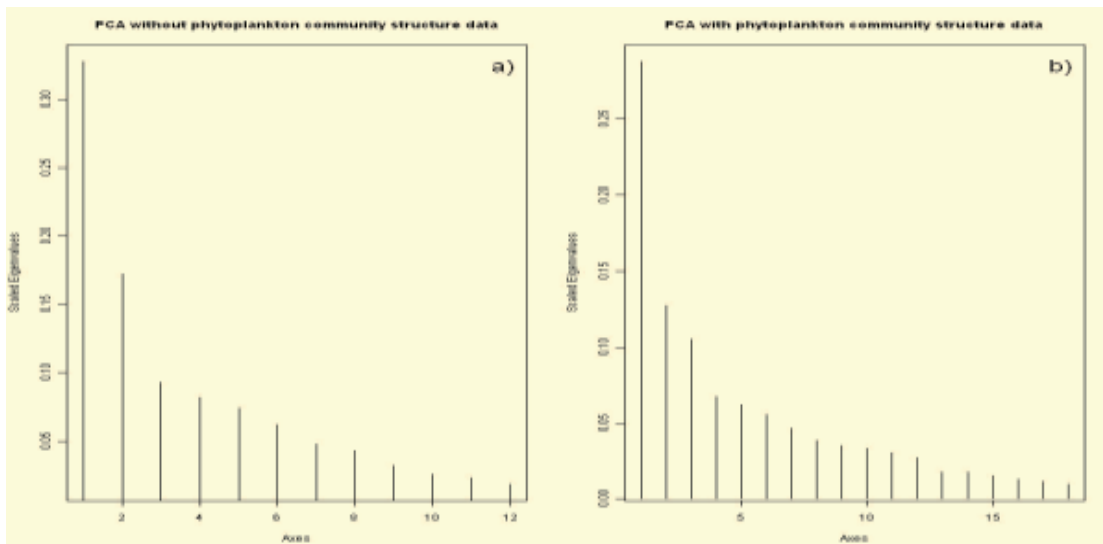

Figure S1. Scree plots for the two PCAs, showing the scaled eigenvalues for the different axes in both PCAs. See text

In PCA2 (Table S2), according to this criterion, the first PC represented the patterns of total abundance of phytoplankton (Phytoplankton Colour Index, PCI), zooplankton (total number of copepods), and phytoplankton community composition (diatoms and dinoflagellate abundances) in the three areas.

The second PC represented a trend of the community composition of both phyto- and zooplankton in the three areas; and the third PC represented a different trend that is highly related to community composition of both phyto- and zooplankton, and to phytoplankton abundance, particularly in areas C1_2 and D1_2.
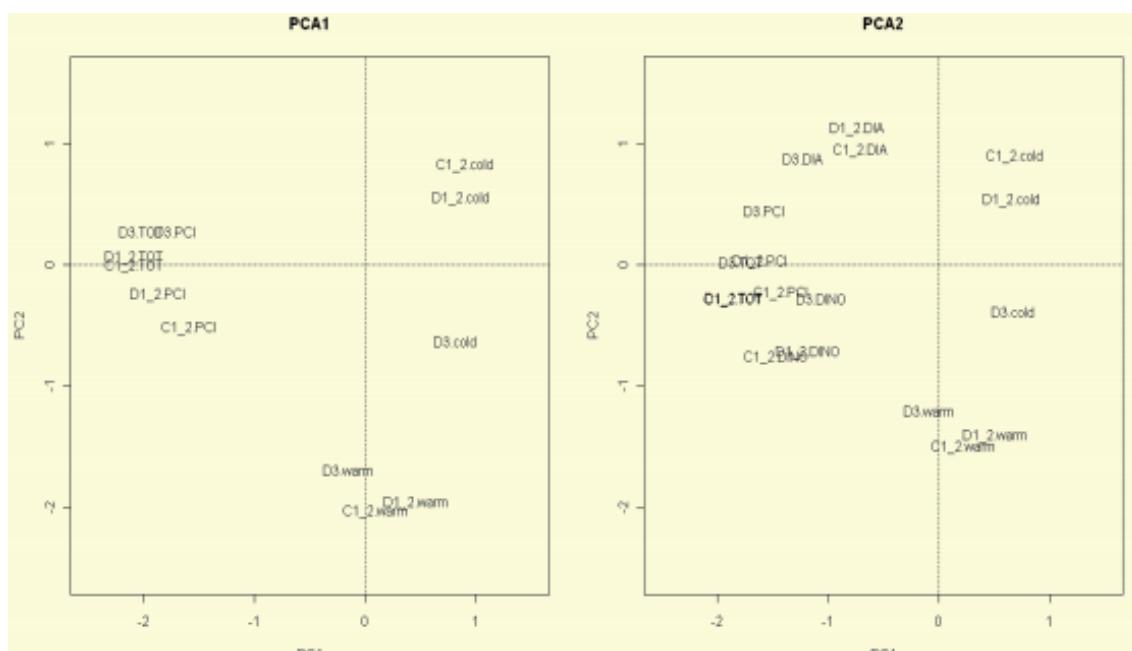

Figure S2. PCA plots of both PCAs, PCA1 excludes dinoflagellate and diatom abundances while PCA2 includes them

Table S2. Loadings of different variables on both PCAs. Values in italics indicate less important variables. Important variable in bold

SCORES	PCA1		PCA2		
	PC1	PC2	PC1	PC2	PC3
C1_2.warm	0.091	**-2.034**	0.217	**-1.500**	**1.011**
C1_2.cold	**0.896**	**0.830**	0.681	**0.900**	-0.209
D1_2.warm	**-1.962**	0.457	0.506	**-1.407**	**0.947**
D1_2.cold	**0.863**	0.559	0.652	0.545	-0.212
D3.warm	-0.153	**-1.691**	-0.086	**-1.203**	**0.796**
D3.cold	**0.812**	0.625	0.669	-0.380	0.226
C1_2.PCI	**1.593**	-0.516	**-1.858**	-0.281	-0.170
D1_2.PCI	**1.869**	-0.238	**-1.845**	-0.278	-0.304
D3.PCI	**1.713**	0.277	**-1.786**	0.025	-0.190
C1_2.TOT	**-2.088**	-0.008	**-1.424**	-0.227	**0.897**
D1_2.TOT	**2.083**	0.068	**-1.613**	0.030	**0.728**
D3.TOT	**-2.021**	0.277	**-1.574**	0.453	0.172
C1_2.DIA			**-0.708**	**0.950**	**1.360**
D1_2.DIA			**-0.738**	**1.134**	**1.210**
D3.DIA			**-1.220**	**0.883**	0.093
C1_2.DINO			**-1.468**	**-0.762**	**-0.727**
D1_2.DINO			**-1.182**	**-0.714**	**-0.921**
D3.DINO			**-1.059**	-0.275	**-0.775**

SUPPLEMENT 3

Post-hoc seasonal decomposition

PC1 and PC2 were subjected to seasonal decomposition in order to verify the shift in seasonal patterns suggested by the analyses.

This was done by means of a Generalized Additive Model (GAM) using Month in a smoothing function and comparing it with an alternative GAM using different Month smoothers for each detected regime.

PC1: The model accounting for different regimes fitted better the original data as the adjusted R^2 was higher for this model.

Unique Month smoother: $R^2adj = 0.791$
One Month smoother per regime : $R^2adj = 0.808$

The AIC method however did not select this model as the best because of the penalization caused by using more degrees of freedom (three smoothers instead of one) increased the AIC value which became less negative.

Unique Month smoother: AIC = -217.69   df= 9
One Month smoother per regime: AIC = -190.05   df= 5

As we are not looking to predict data, but for a better fit to the seasonal patterns, in this case we used the R^2 value to select the best model.

The seasonal patterns as seen in the model fit (Fig. S3) coincided with the ones seen in the raw data, the period 1985-1990 having a stronger signal during the summer months and weaker in the winter months than in the previous period. The last period, post-1990, the seasonal oscillation is clearly smaller (Fig. S3).

PC2: The model accounting for different regimes did not fit the original data better.

Unique Month smoother – $R^2adj = 0.576$
One month smoother per regime - $R^2adj = 0.575$

This indicates that the source of regime changes is contained in the long-term signal, not the seasonal pattern. If the seasonal pattern was the cause of the detected regimes a better fit would be shown by the seasonal smoother that considered regime changes. The adjusted R^2 is smaller for the model of the seasonal patterns of PC2. This may also indicate the importance of the long term signal in PC2, as opposed to PC1, in which most of the data variation is explained by the seasonal smoother.
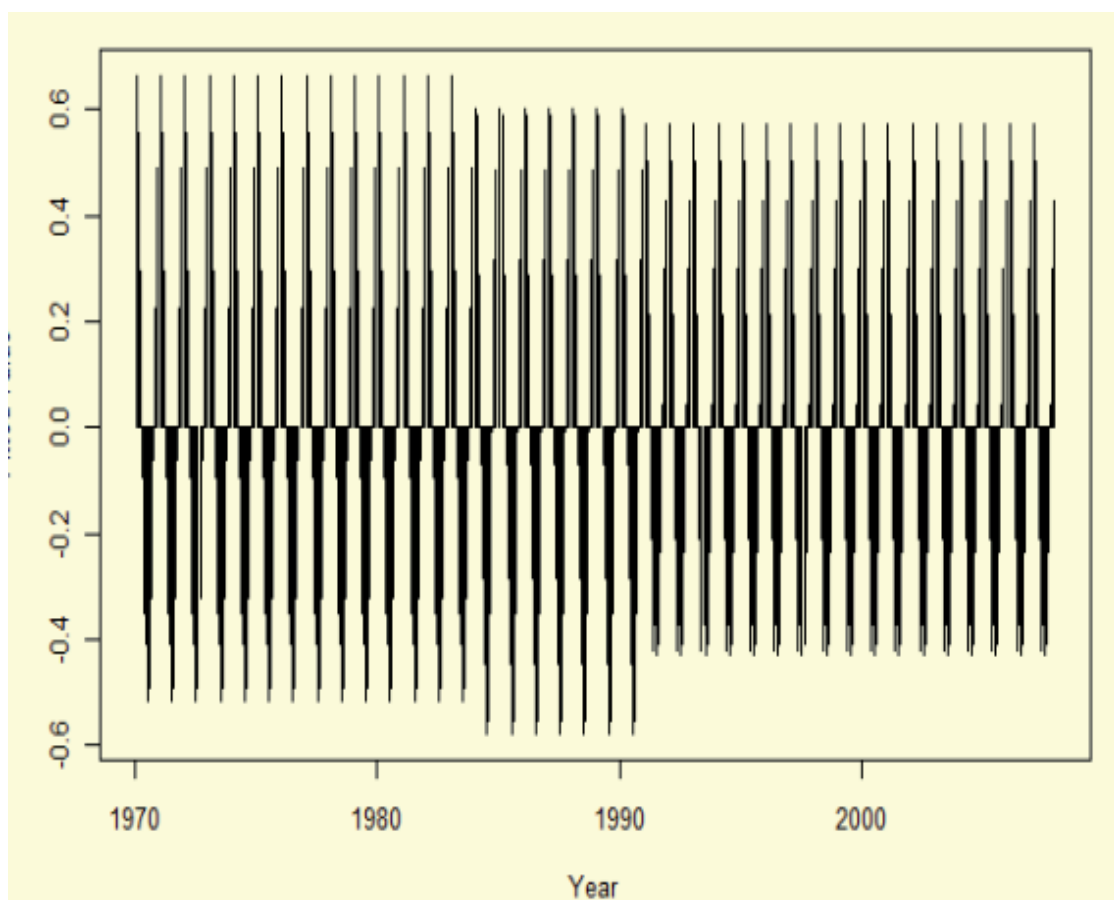

Figure S3. Result of the model using different seasonal smoothers per regime to explain PC1. See text for explanation.

SUPPLEMENT 4

Published as: Alvarez-Fernandez S (2014) The North Sea plankton regime shift in the late 1990s: Comment on Beaugrand et al. (2014). Mar Ecol Prog Ser 514:279-280

ABSTRACT:

In recent analyses Beaugrand et al. (2014), detected an abrupt plankton community change in the North Sea between 1996-2003, and reported it as a newly detected feature. Although the analyses they developed were used for the first time, this was not the first time this shift had been described. Alvarez-Fernandez et al. (2012) already described a regime shift in North Sea plankton community around 1998. Although the community changes found were parallel in both studies, the driving force behind these changes does not coincide in both studies.

COMMENT:

Beaugrand et al. (2014) analysed thoroughly and with an improved statistical technique (Multiscale split moving window boundary analyses) 5 plankton groups: diatoms, dinoflagellates, copepods, other holozooplankton, and meroplankton. As a result they detected 3 ecosystem shifts in the 1960s,1980s and between 1996-2003. They reported this last shift to be revealed for the first time in these analyses. We consider this new technique an improvement over previous methods, i.e. split moving window boundary analysis (SMW) (Webster 1973), and agree with their results. But this was not the first time this shift had been described. Alvarez-Fernandez et al. (2012), already described a regime shift in North Sea plankton community around 1998, using the same data sources, taking into consideration the seasonal patterns of the data, and using SMW amongst other detection methods. As reported in Alvarez-Fernandez et al. (2012), after 1998 the total number of copepods decreased considerably. The copepod community showed a decrease in characteristic shelf-sea species such as *Temora longicornis*, *Pseudocalanus* spp., and *Paracalanus* spp. These shelf-sea species contributed less to the total copepods during autumn and winter in the 2000s (Fig. S4c), when the warm-water copepods start increasing their abundances (Fig. S4d). Alvarez-Fernandez et al. (2012), related
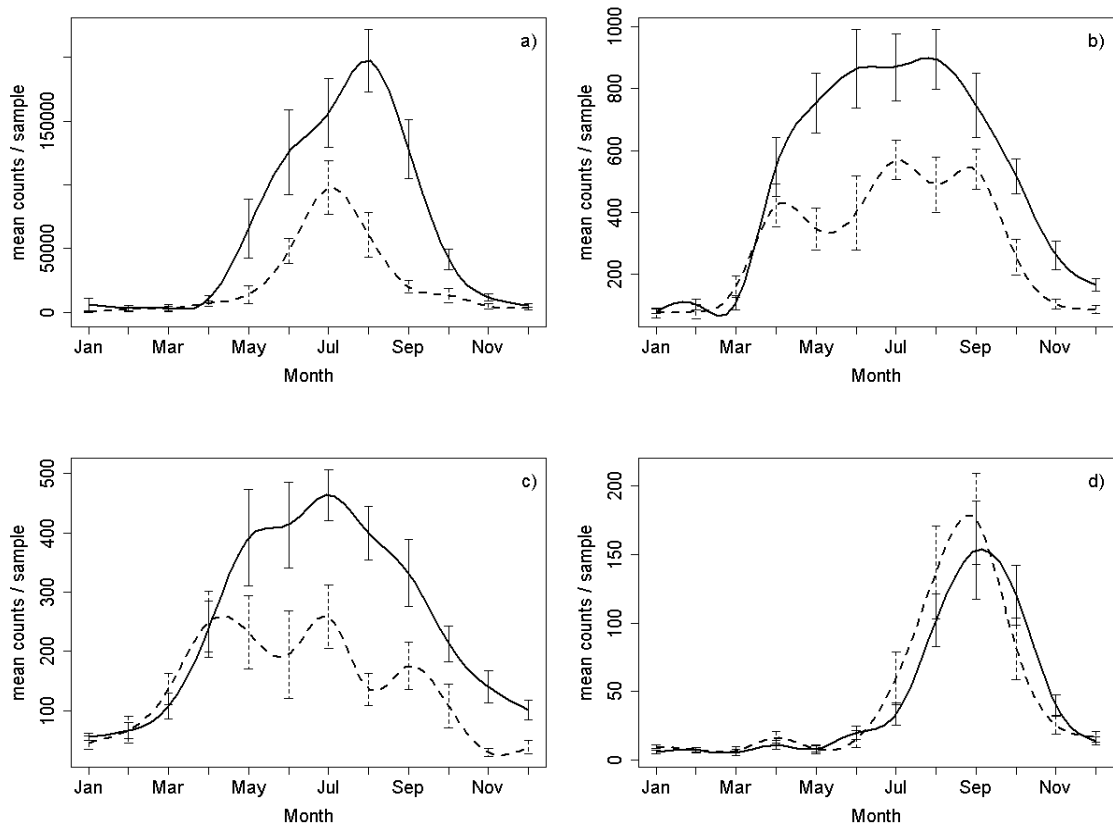
Figure S4. Seasonal patterns of plankton variables. a) Dinoflagellates, b) Total Copepods, c) Shelf-sea copepods, d) Warm water copepods. Each line represents the seasonal trend for a specific period of time: Solid line 1988-1998, dashed line 1999-2007. Units are number of individuals per sample for all variables. Modified from Alvarez-Fernandez et al. (2012).

this drop in numbers of shelf-sea species to a decrease during the same period in dinoflagellates (Fig. 1a), a major food source for some of these copepods (Gentsch et al. 2009). Different studies have highlighted the importance of a high and constant food supply for the success of some of these copepod species (Vidal 1980, Evans 1981, Tsuda 1994, Gentsch et al. 2009), so a decrease in prey, e.g. dinoflagellates, during part of the year could lead to limitation of population growth. We therefore also agree with the detected decrease in dinoflagellates by Beaugrand et al. (2014), also detected by Alvarez-Fernandez et al. (2012), but we do not fully agree with

rising temperature as driving force behind all these changes. Even though changes in temperature will clearly have an impact on plankton community, as showed by Alvarez-Fernandez et al. (2012), this last abrupt ecosystem change was more related to other water characteristics. They suggested changes in the nutrient dynamics in the North Sea as a potential driver. This interpretation might also connect the shift with changes reported in Atlantic waters for plankton community (Hátún et al. 2009), and nutrient dynamics (Johnson et al. 2013).

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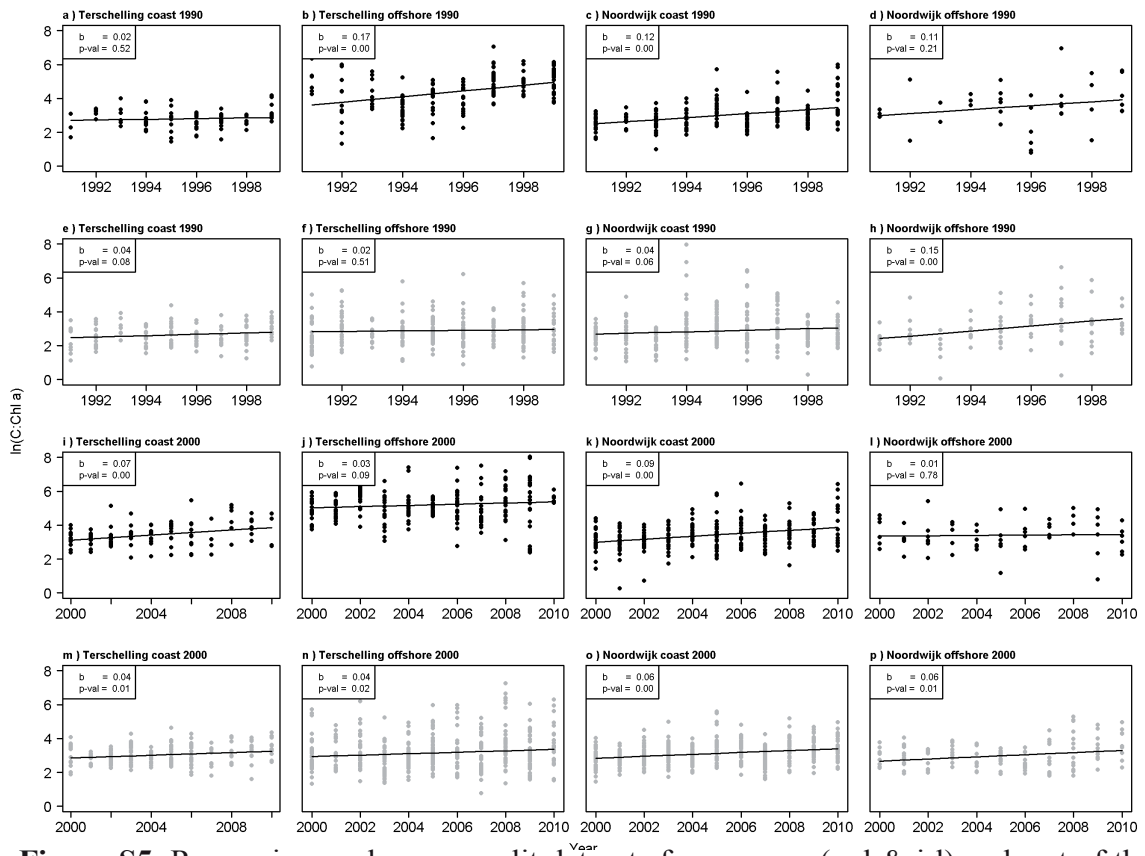APPENDICES

Figure S5. Regression analyses on split datasets for summer (a-d & i-l) and rest of the year (e-h & m-p) before (a-h) and after 2000 (i-p)

SUPPLEMENT 5

Regression analyses

In order to assess the validity of the original regression analyses on yearly C:Chl a values, supplementary regression analyses were carried out on split datasets for summer and rest of the year before and after 2000 (the year of laboratory change).

The results of these regression analyses showed significant increases of C:Chl a ratios in 15 out of 20 cases. Regressions were non-significant during the 90s summer period in Terschelling coast (Fig. S5a), 90s winter and 2000s summer in Terschelling offshore (Fig. S5f and j), and 90s and 2000s summer in Noordwijk offshore (Fig. S5d and l). All other periods showed statistically significant increasing trends. These results strengthen the conclusion of an overall increase of C:Chl a ratios in all areas independently of the potential observer effect on the dataset.

SUPPLEMENT 6

Abundances of shelf-sea copepods
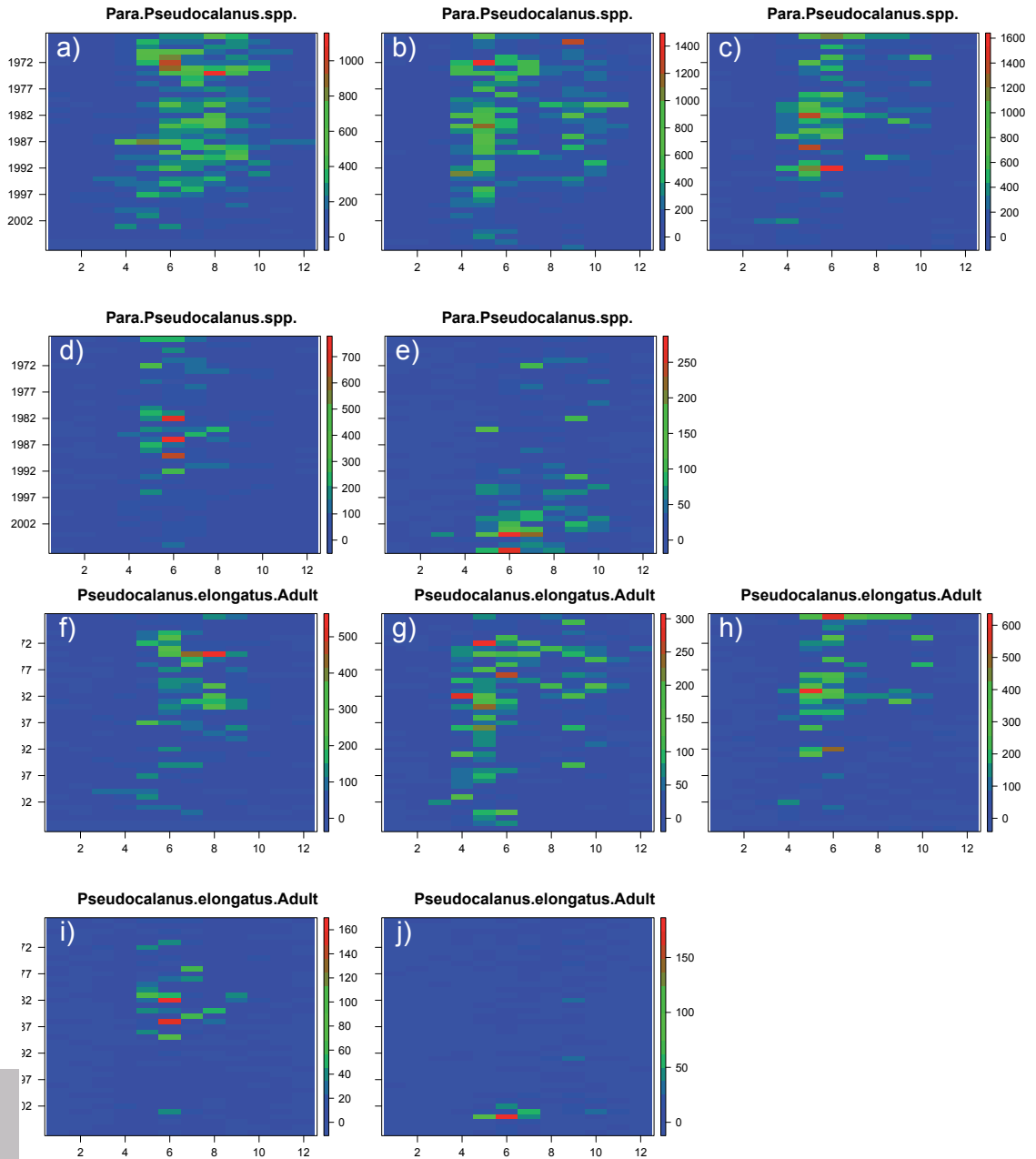

Figure S6. Abundances in mean numbers per sample of Para- Pseudocalanus (a-e) and Pseudocalanus elongatus (f-j) in different areas. a, f) North Sea; b, g)Bay of Biscay; c, h)Celtic Seas; d, i) Eastern Atlantic; e, j) Iceland

Samenvatting

De Noordzee planktongemeenschappen behoren tot de meest onderzochte systemen met betrekking tot plotselinge veranderingen of regiem verschuivingen. Data afkomstig uit het Continuous Plankton Recorder (CPR) programma gaven inzicht in seizoenveranderingen en lange-termijn trends in zowel de fytoplankton- als de zoöplanktongemeenschap en de relatie van deze veranderingen en trends met hydrografische en klimatologische gebeurtenissen gedurende de afgelopen 50 jaar. Zo werden de gevolgen van een plotselinge koude periode in de late jaren 70 en een verschuiving van een koudwater-planktongemeenschap naar een planktongemeenschap behorende bij een warmer milieu in de jaren 80 al uitgebreid beschreven in de literatuur. Beide gebeurtenissen werden gerelateerd aan veranderingen in verschillende omgevingsfactoren, zoals de temperatuur van het oppervlaktewater en de instroom van Atlantisch water via de noordelijke Noordzee. Dit proefschrift beoogt de al eerder beschreven lange-termijn trends in de Noordzee beter te begrijpen en eventuele recentere veranderingen in de planktongemeenschap te ontdekken, inclusief de omgevingsfactoren die die veranderingen in gang zetten. Hiervoor werden lange-termijn monitoring data die waren verzameld in de open Noordzee, de Nederlandse kustzone en de gehele noordoostelijke Atlantische oceaan, geanalyseerd.

In **hoofdstuk 1** wordt de verandering die zich voltrok in de planktongemeenschap in de Noordzee eind jaren negentig voor het eerst beschreven. Deze verandering kenmerkt zich door verschuivingen in aantallen en seizoenpatronen van dinoflagellaten en de meest dominante zoöplanktongroep; de neritische copepoden (roeipootkreeftjes) (Temora longicornis, Pseudocalanus elongatus, Paracalanus sp.). Veranderingen in temperatuur en samenstelling van de watermassa in de Noordzee lijken de meest aannemelijke sturende factoren.

Inzoomend op de planktontrends in het Nederlandse deel van de Noordzee, werd een toename in de koolstof: chlorofyl-a ratio waargenomen. In **hoofdstuk 2** wordt die toename onderzocht. In kustwateren kunnen aanpassingen van het fytoplankton aan meer licht en minder nutriënten

leiden tot een verhoogde C: chl ratio, terwijl in gebieden verder uit de kust andere factoren een rol spelen. De resultaten wijzen niet alleen op een snelle verandering van het milieu in de Noordzee, maar plaatsen ook grote vraagtekens bij het gebruik van chlorofyl-a als indicator van fytoplanktonbiomassa.

De gevonden veranderingen in de planktongemeenschap zijn niet de enige veranderingen in het pelagische systeem van de Noordzee. In **hoofdstuk 3** vergeleken we de veranderingen in aantallen en verspreiding van plankton met eerder gerapporteerde veranderingen in de rekrutering van haring. De rekrutering van Noordzeeharing neemt af sinds 2002, terwijl de biomassa van het paaibestand hoog is. Er waren al aanwijzingen dat door verminderde groei en overleving sinds 2000, de vroege larvale stadia van de haring wel eens de kritische ontwikkelingsfase zou kunnen zijn voor succesvolle rekrutering.. Onze analyses laten een sterke relatie zien tussen de hoeveelheid copepoden, Pseudocalanus sp., in de winter, de aantallen haringlarven in het pre-metamorfose stadium en de aantallen in latere haringstadia. Deze bevindingen suggereren dat predator-prooi relaties en mogelijke verhongering van larven op het moment dat ze beginnen met forageren de oorzaak zijn van de lage rekrutering in recente jaren.

De veranderingen in de Noordzee zoals hiervoor beschreven staan niet op zichzelf, maar zijn onderdeel van veranderingen in het gehele noordoostelijke Atlantische gebied. De resultaten gepresenteerd in **hoofdstuk 4** laten zien dat veranderingen zoals beschreven in hoofdstuk 1 en in zekere mate in hoofdstuk 3, synchroon liepen met veranderingen in verschillende regio's in de Atlantische oceaan. De gelijktijdigheid van de veranderingen suggereert dat er een gemeenschappelijke oorzaak achter de veranderingen zit die mariene ecosystemen op wereldschaal beïnvloedt. Wij suggereren dat deze synchronisatie wordt veroorzaakt door stijgende temperaturen en veranderingen in oceaancirculaties. Daarbij moduleren lokale omstandigheden of lokale atmosferische patronen zoals de Noord Atlantische Oscillatie in de Noordzee de reactie van het mariene ecosysteem.

In de synthese worden de belangrijkste conclusies uit de verschillende hoofdstukken samengebracht en wordt het belang van zoöplankton als schakel tussen primaire productie en consumenten uit hogere trofische niveaus bediscussieerd. Ten slotte wordt het belang van lange-termijn monitoring inclusief het selecteren van de juiste milieufactoren die gemeten moeten worden, benadrukt.

De kennis verkregen met dit proefschrift vergroot het begrip van de processen die de samenstelling van de planktongemeenschap reguleren in zowel de Noordzee (Hoofdstuk 1 &2) als de noordoost Atlantische oceaan (Hoofdstuk 4), van de mogelijke relatie van de planktongemeenschap met vroege vislarven stadia (Hoofdstuk 3) en hoe veranderingen in het mariene milieu de relevantie van bepaalde indicatoren die gebruikt worden om de status van het biologische systeem te bepalen, beïnvloeden (Hoofdstuk 2).

Summary

The North Sea planktonic system is one of the most studied cases of sudden community changes in the marine environment. Continuous Plankton Recorder (CPR) data provided insight into the long-term trends and seasonal patterns of both phytoplankton and zooplankton and their relationships with hydrographical factors as well as climatological events during the last 50 years. A cold episodic event in the late 1970s and a shift towards a warmer community in the late 1980s have been thoroughly described in the literature. Both events have been related to different environmental factors, such as changes in sea surface temperature and Atlantic water inflow through the northern North Sea. This thesis was aimed to achieve a deeper understanding of long term plankton trends in the North Sea, detect more recent changes in the plankton community, and the environmental drivers behind them. The approach taken throughout this research consisted of analyzing extensive long term monitoring data in the open North Sea, the Dutch coastal area and the whole north-eastern North Atlantic.

In **Chapter 1** we described for the first time a change in the plankton community of the North Sea at the end of the 1990s. This change particularly affected the abundance and seasonal patterns of dinoflgellates and the dominant zooplankton group, the shelf-sea copepods (i.e. *Temora longicornis*, *Pseudocalanus elongatus*, *Paracalanus* sp.). Temperature changes and different water mass composition of the North Sea are suggested as main drivers behind this change.

While looking more in detailed to the plankton trends in the Dutch North Sea waters, we identified an overall C:Chla increase, **Chapter 2** investigates this change. In coastal waters physiological adaptation to higher light and lower nutrient levels may have enhanced the C:Chlorophyll a, while different processes act in offshore waters. These findings not only indicate the rapidly changing environment in the Dutch coastal zone, but also about the validity of Chlorophyll a as an indicator of phytoplankton biomass trends.

The detected changes in the planktonic system are not the only pelagic

changes in the North Sea. In **Chapter 3** we related the changes in plankton abundance and distribution with reported changes in recruitment of North Sea herring, particularly through the predator-prey relationship of some plankton species with pre-metamorphosis larvae. Even though spawning stock biomass has been high during the last decade, recruitment of North Sea herring has decreased since 2002. There were already indications that the early larval stage could be the critical point of development, with reduced survival and growth rates during the 2000s. The analyses presented in Chapter 3 showed the abundance of *Pseudocalanus* sp. during winter to have a strong relationship with larval distribution and abundance later in herring life cycle, suggesting that predator-prey processes, and potentially starvation of first-feeding larvae, are behind the low recruitment in recent years.

These changes in the North Sea pelagic ecosystem are not self-contained, but part of an even larger scale process taking place all across the northeastern Atlantic region. The study presented in **Chapter 4** shows how the changes detected in Chapter 1 (and to some extent Chapter 3), occurred synchronously in different Atlantic regions. This synchronicity suggests common global trends affecting marine ecosystems. We suggest that rising temperature and changes in oceanic circulation are behind this synchronicity, and that local circumstances, or atmospheric patterns with more local influences, such as North Atlantic Oscillation in the North Sea, modulate the responses of marine ecosystems.

In the synthesis the main conclusions of each chapter are put in context together and the importance of zooplankton as a link between primary productivity and higher trophic level consumers is discussed. Furthermore, the importance of monitoring and the correct selection of biological and environmental indicators is also discussed

The knowledge provided by this doctoral thesis increase our understanding of the processes regulating the plankton community composition in the North Sea (**Chapter 1 & 2**) and the northeastern Atlantic region (**Chapter 4**), the potential relationship of plankton community with fish early-stage larvae (**Chapter 3**) and how environmental changes might affect the relevance of the indicators used to assess the state of the biological system (**Chapter 2**).

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The PhD journey is long, and can be desperating if there's no one to share it with. Luckily, I had plenty of colleagues and friends around to share it with. I need to start thanking my *paranymphs*: **Pascalle**, I'm not sure what I should do first, thanking you for all the time we spent discussing science, social interactions, random thoughts, and other worries; or apologise for all the moving around, tapping tables, humming songs, and several unintended noises that I generate while trying to remain quiet in the office. You've been the best office mate possible, and talking to you during the last years has kept me sane. I've learnt a lot from you professionally and personally! I hope we can keep working together one way or another, and if not we will have to look for another excuse to organise an equivalent to IMARES-PhD dinners. **Anja**, you've been my neighbour since the day I arrived to Texel, my smoking break buddy not long after that and my closest friend during the last five years. You've been there all the time, whether I was happy, sad, angry or simply losing my mind. You had the patience to share not just one, but two different houses with me! Seriously, what's wrong with you? Thanks for the laughs, the cries, the dancing, the drinking, trying to pick me up when I lost all strength - figuratively, and in some cases very literally. Also thank you for showing me the best sausages in the world, for all the bottles of Rotkäppchen, and specially for introducing me to the best pet ever existed: **Snoopy**, you are great!

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Texel is a great island, but sometimes you need a taste of home. Thanks to the "Spanish Committee" for providing that. Now is time to say *Gracias*: **Leo, Mireia**, **Natalia**, **Stefani**, **Anuar**, **Marta** (y **Ramon**). Gracias por cenar a horas razonables y disfrutar las sobremesas! Cuando ya me habia ido del Potvis me disteis ganas de volver a la charca! Sobre todo a los alcaldes **Andres** e **Irene**, y a mi compai **Jorge**, porque estais haciendo que me de penita irme de Texel. Se echarán de menos las tardes de cerves y tapas en el ayuntamiento. Asi que habra que verse por otras tierras, a ver por donde caemos cada uno...

A mis padres, sin más, porque os debo todo.

Gracias

Thank you