University of Southampton

Faculty Of Ocean and Earth Science

Marine Biogeochemistry

Long-Term Trends and Variability of North Atlantic Phytoplankton Populations

by

Stephanie Rose Allen

Thesis for the degree of Doctor of Philosophy

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ORCID ID: https://orcid.org/0000-0001-5414-1931

University of Southampton

Abstract

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Marine phytoplankton are microscopic in size, but have substantial roles in the marine environment, structuring the base of the marine food web and facilitating marine biogeochemical cycles. Changes to their community therefore have important consequences on the functioning of marine ecosystem services. This thesis, describes long-term variability in the phytoplankton community at a taxonomic scale resolution over the North Atlantic region, using in-situ data from the Continuous Plankton Recorder (CPR) survey and output from the MIT Integrated Global Systems Model (IGSM).

An innovative approach assesses the stability and disorder of the phytoplankton community in the North-East Atlantic using the CPR survey. Phytoplankton were found to return to its original structure after a period dominated by two diatom species, indicating its resilience to perturbation. Changes were not significantly linked to the physical environment, however, the results from novel approach emphasise that a rigid community structure may make the plankton population more prone to collapse under the extreme changes of a future climate.

Generalised additive models (GAMS) were employed in a unique attempt to demonstrate the importance of multiple driving mechanisms. While phytoplankton continued to show very few links to the physical environment, zooplankton had a positive relationship with phytoplankton throughout the North Atlantic and had a strong negative response to deeper mixed layers and colder temperatures. It was concluded that a traditional bottom-up approach is an over simplification at inter-annual scales and future analysis should reflect this.

In a final analysis, the MIT IGSM is used to explore the variability of phytoplankton in the 21st century under the pressures of increasing CO_2 and global climate change. Analysis demonstrated a regional decline in biomass, with 94% of the North Atlantic demonstrating significant change. Change-point analysis shows abrupt shifts in biomass and richness occurred earlier in the sub-tropical regions (2030s) than the higher latitudes (2050s) and functional analysis showed these changes would result in a shift to smaller phytoplankton types in the higher latitudes.

This study highlights the importance of maintaining spatially and temporally extensive datasets in the assessment of marine phytoplankton ecology. It highlights the potential impact of future changes to the marine environment, and the consequences this will have on the phytoplankton communities while reflecting on the broader implications this may have on the wider marine ecosystem.

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Research Thesis: Declaration of Authorship

Print name: **Stephanie Rose Allen**

Title of thesis: **Long-Term Trends and Variability of North Atlantic Phytoplankton Populations**

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. None of this work has been published before submission

Signature:

Date:

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Definitions and Abbreviations

AIC	Akaike Information Criterion
AMO	Atlantic Multidecadal Oscillation
AMOC	Atlantic Meridional Overturning Current
ANOSIM	Analysis of Similarities
ANOVA	Analysis of Variance
ARCT	Atlantic Arctic
Chl-a	Chlorophyll-a
CPR	Continuous Plankton Recorder
ENSO	El Niño-Southern Oscillation
EnvCPT	Environmental Time-series Change-point
EOF	Empirical Orthogonal Function
GAMs	Generalised Additive Models
IGSM	Integrated Global System Model
IOCCG	International Ocean-Colour Coordinating Group
IPCC	Intergovernmental Panel on Climate Change
MBA	The Marine Biological Association
MIT	Massachusetts Institute of Technology
MLD	Mixed Layer Depth
NADR	North Atlantic Drift
NAO	North Atlantic Oscillation
NASE	North-East Atlantic Subtropical Gyre
NASW	North-West Atlantic Subtropical Gyre

NATR	North Atlantic Tropical Gyre
nMDS	Non-metric Multidimensional Scaling
NO3	Nitrate
NOAA	National Oceanic and Atmospheric Administration
PC	Principle Component
PCI	Phytoplankton Colour Index
SAHFOS	Sir Alister Hardy Foundation for Ocean Science
SeaWiFS	Sea-Viewing Wide Field-of-View Sensor
SEM	Structural Equation Modelling
SST	Sea Surface Temperature
UCAR	University Corporation for Atmospheric Research

"the knowledge that all things are one thing and that one thing is all things—plankton, a shimmering phosphorescence on the sea and the spinning planets and an expanding universe, all bound together by the elastic string of time. It is advisable to look from the tide pool to the stars and then back to the tide pool again."

— John Steinbeck, The Log from the Sea of Cortez

Chapter 1 Thesis Structure and contributions

The thesis begins with a review of phytoplankton types, distribution, diversity, ecological theory and an overview of the abiotic and biotic variables driving abundance and community structure **(Chapter 2**). Chapter 3 provides an overview of the in-situ and model datasets for the biological and physical parameters used in this thesis.

Author contributions: SA wrote the introduction and methodology as it appears in this thesis, text from these is used as text in each of the results chapters for submission to publication, but was removed from Chapter 4 to Chapter 6 to prevent duplication of text.

Chapter 4 uses data from the Continuous Plankton Recorder (CPR) survey to examine the inter-annual stability of phytoplankton across the North-East Atlantic and relates any changes in community to the physical environment. This chapter is in preparation for submission for publication as:

Allen, S. R., Henson, S. A., Hickman, A., Beaulieu, C., Doncaster, C. P., Johns, D. G. (2018). "Long-term stability of phytoplankton community composition in the North-East Atlantic." ***in preparation for submission.***

Author contributions: SA, SH, AH and CB conceived the project. DJ provided data from the CPR survey and PD provided the methodology for bio-disorder analysis. The manuscript was produced by SA and all authors provided editorial advice.

Chapter 5 uses data from the CPR survey to assess the control of phytoplankton across the North-East and West Atlantic from 'bottom-up' drivers, such as the physical environment, and 'top-down' drivers, such as the zooplankton community. This is examined using generalised additive models to assess for non-linear relationships. This chapter is in preparation for submission for publication as:

Allen, S. R., Henson, S. A., Hickman, A., Beaulieu, C., Johns, D. G. (2018). "Inferring the inter-annual control of plankton communities across the North Atlantic." ***in preparation for submission.***

Author contributions: SA, SH, AH and CB conceived the project. DJ provided data from the CPR survey. The manuscript was produced by SA and all authors provided editorial advice.

Chapter 6 uses data from the MIT Integrated Global System model (IGSM) to examine changes to the phytoplankton community structure from 1990 to 2100 across the North Atlantic basin under the pressures of a changing climate. This chapter is in preparation for submission for publication as:

Allen, S. R., Henson, S. A., Hickman, A., Barton, A. D., Beaulieu, C., Dutkiewicz, S. (2018). "Future shifts of North Atlantic phytoplankton community structures." ***in preparation for submission.***

Author contributions: SA, SH, AH, AB and SD conceived the project. SD provided data from the MIT IGSM. The manuscript was produced by SA and all authors provided editorial advice.

Chapter 7 briefly summarises the findings of Chapter 4 to Chapter 6 and discusses the results of combining the perspectives of the CPR survey and MIT IGSM. This section also discusses the limitations of the techniques used and the scope for future work.

Chapter 2 Introduction

2.1 Marine phytoplankton: types and distribution

Marine phytoplankton are a group of single celled, largely photoautotrophic, photosynthetic organisms that live in the sunlight layers of the ocean (Acevedo-Trejos et al., 2015). Phytoplankton are present throughout the world's oceans and with a life span of a few days, given the right environmental conditions, are able to rapidly reproduce forming vast blooms that can be seen from space.

Although microscopic in size and accounting for less than 1% of the Earth's photosynthetic biomass, marine phytoplankton are responsible for just under half the global primary productivity, producing 48 Pg C yr^{-1} (Field et al., 1998, Falkowski et al., 2004, Graham et al., 2009). Phytoplankton have an essential role at the base of the marine food web transferring energy to higher trophic levels through predation by marine zooplankton and as such are considered the main structural component of marine ecosystems. The transfer of energy is continually fed up the food chain fuelling the production of ~240 million metric tonnes of fish, around one third of which is harvested annually in commercial fishing activities, highlighting phytoplankton as an important aspect of ocean goods and services (Field et al., 1998, Worm et al., 2006).

Phytoplankton also have an important interaction with our climatic system and the regulation of atmospheric CO_2 concentrations. Through their actions during photosynthesis, phytoplankton fix dissolved inorganic carbon, assimilating it into their cells. Detritus from these phytoplankton result in the export of carbon from the surface layers to the deep ocean, enabling the ocean to act as a global sink for atmospheric CO_2 (Richardson and Schoeman, 2004, Hays et al., 2005, McQuatters-Gollop et al., 2007a, Henson et al., 2012)·

The oceans host an extensive variety of phytoplankton species, which are frequently classified into broader functional groups including diatoms, dinoflagellates, haptophytes and cyanobacteria (Mutshinda et al., 2016, Hood et al., 2006). These functional groups are an assortment of species that share defining morphological, physiological or biogeochemical characteristics or traits and perform similar ecosystem services (Mutshinda et al., 2016, Peña, 2003, Le Quéré et al., 2005, IOCCG, 2014).

One major functional group are diatoms, which produce unique external structures called frustules from silica that help protect them from predation and result in an important role within the cycling of marine nutrients (Tréguer et al., 2017). Diatoms are thought to export ~40% of particulate carbon to the seafloor as part of the biological pump and provide a critical food source for considerable marine life including zooplankton and fisheries at the ocean surface and filter feeders at the sea floor (Graham et al., 2009, Tréguer et al., 2017). Diatoms are typically dominant in turbulent, nutrient-rich waters as suggested in the canonical theory of phytoplankton ecological niches (Margalef, 1978). The theory suggests that diatoms are able to outnumber other functional groups in terms of abundance in high turbulent conditions due to their quick reproduction times, causing them to bloom usually before any other group and beat grazing pressures (Margalef, 1978). Some observations have also shown them to thrive in meso- and sub-mesoscale structures such as ocean fronts and deep chlorophyll maxima (Lévy et al., 2014, Tréguer et al., 2017).

Another major functional group is the dinoflagellates, defined by the presence of two dissimilar flagella within their life cycle. This form of motility allows the dinoflagellates to thrive and persist in regions with low nutrients, and less turbulent conditions (Margalef, 1978). The dinoflagellates have a major role in transferring energy into the marine food web through predation. Roughly half of dinoflagellates are photosynthetic, the second most productive primary producers to the diatoms, however the other half are heterotrophic, feeding via osmotrophy or phagotrophy (Gaines and Elbrächter, 1987). With this role as phagotrophic organisms, dinoflagellates are also important components of the microbial loop in the oceans, channelling significant amounts of energy into planktonic food webs. Several species also have important roles as toxin producers that control the populations of other trophic levels through harmful algal blooms (Graham et al., 2009).

There are several other functional groups that may include nitrogen fixers (e.g. *Trichodesmium*), calcifiers (coccolithophores) and Dimethyl sulphide producers (e.g. *Phaeocystis*), all playing specific roles and importance in the marine ecosystem. Phytoplankton are not evenly distributed across the globe, with functional groups tracking their optimal environmental conditions. Biomass is greatest in the high latitudes where the oceans are nutrient rich from winter mixing compared to the tropical regions, enabling the coexistence of multiple individuals. In the tropics where nutrients are scarce, smaller functional types such as Prochlorococcus prevail, their small cell size enabling them to uptake nutrients efficiently. In the sub-polar region of the North Atlantic, larger functional groups such as the diatoms dominate, outcompeting many other functional groups in the lower-light, cold and nutrient richer conditions due to their ability to rapidly reproduce.

Biogeochemical studies of ecological communities require knowledge of the range of tolerances a species has to external conditions, known as its realised niche (Figure 2.1)

(Hutchinson, 1961, Helaouët and Beaugrand, 2009). This niche is an important concept as it helps researchers assess the potential effects of global climate change, including changes to species distributions (Helaouët and Beaugrand, 2009, Helaouet et al., 2013). Figure 2.1 demonstrates the fundamental niche in which a species responds to external environmental conditions (Helaouët and Beaugrand, 2009). Only in optimal conditions can a species thrive and produce high abundances, at its extremes a species may even effect its chance of survival. The mechanisms influencing phytoplankton, that would have a role in their realised niche, are described in section 2.2.

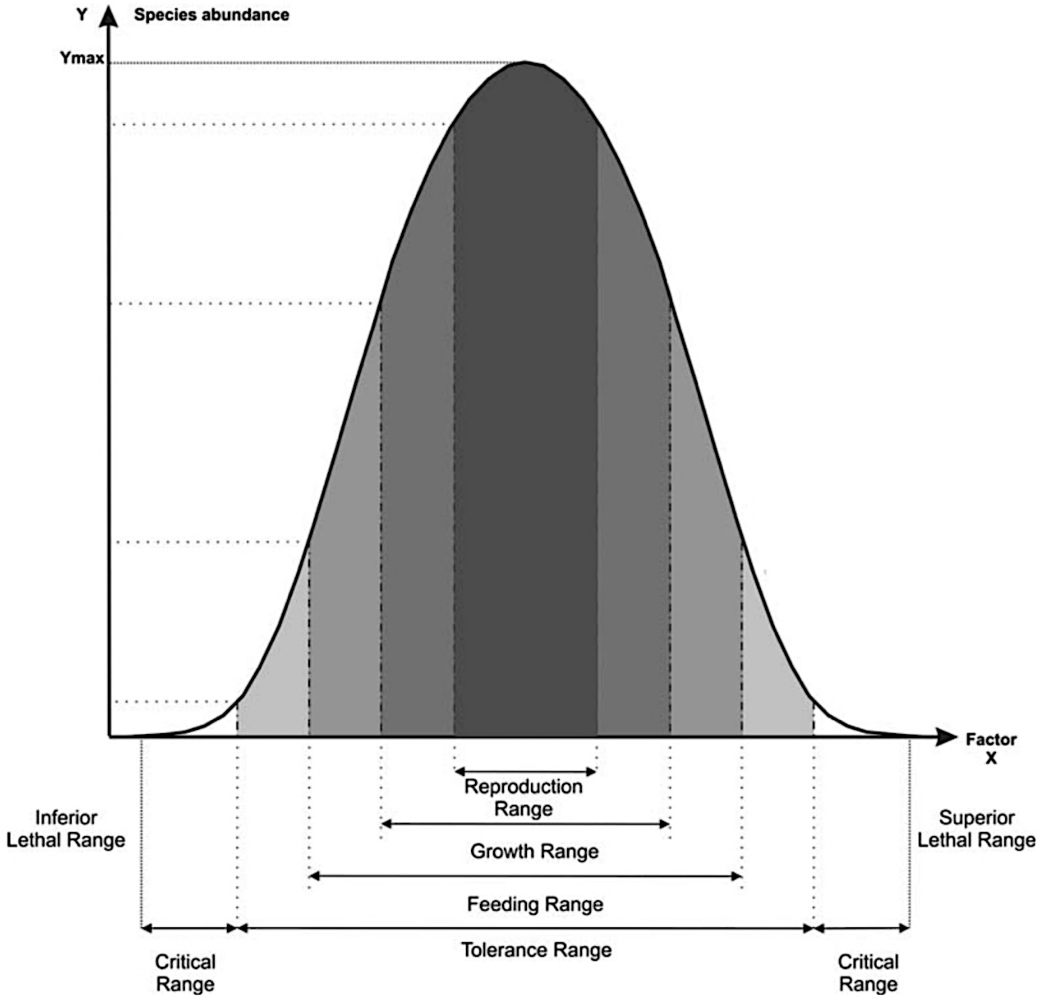

Figure 2.1: Response curve, illustrating a species ecological niche through the response of a species abundance (Y) to an external environmental factor (X). Optimal conditions occur at the middles of factor X, however as the extreme values are reached physiological functions such as reproduction, growth and feeding decrease. Figure from Helaouët and Beaugrand (2009).

2.2 Mechanisms controlling phytoplankton populations

The structure of the phytoplankton community largely depends on the response of individual species to external forcing, biotic or abiotic. As such phytoplankton have large spatio-temporal variability in abundance and diversity (Beaugrand et al., 2002, Edwards and Richardson, 2004, Legendre and Legendre, 2012). Mechanisms that structure phytoplankton communities over inter-annual and multidecadal timescales, especially in open ocean regions, remain poorly understood. The literature that is available primarily centres on bulk phytoplankton properties, such as total biomass and productivity (Edwards, 2001, Beaugrand et al., 2008, Platt et al., 1990) or examines changes in community structure at the functional group level (Litchman et al., 2006, Boyd et al., 2010, Barton et al., 2016). Species specific phenological responses and short generation times of phytoplankton mean that they are able to track different environmental conditions (Irwin et al., 2012). We have a great requirement to understand these mechanisms as, due to phytoplankton's important roles in the ocean, changes in the structure and abundance of communities may have a profound impact on future ocean functioning.

Biological populations fundamentally depend on food, and due to the direct contact with their environment and small size range (less than 2µm for picoplankton, 2–20µm for nanoplankton, and up to 20–200µm for microplankton), much focus has been placed upon examining the bottom-up control of a community (Acevedo-Trejos et al., 2015). The most fundamental of these bottom-up processes are the physical processes which control the availability of light and nutrient supply that is required for photosynthesis. The availability of nutrients also has the direct impact of determining which species are able to grow in the environment. Diatoms require silica to produce their external structures and in regions of low silica availability other phytoplankton functional groups may become dominant. Sea surface temperature (SST) also directly impacts phytoplankton growth and metabolic rates (Eppley, 1972) and, through subsequent changes to ocean stratification, indirectly affects phytoplankton abundance by altering the light and nutrient availability of the local environment through impacting the strength of stratification (Edwards and Richardson, 2004, Bopp et al., 2013).

Seasonal changes in phytoplankton, especially in the North Atlantic region due to the spring bloom phenomena, have been thoroughly documented. Consistently in the complied literature, a large fraction of variability in the abundance, biomass and functional groups has been attributed to changes in the physical environment particularly changes in nutrients, SST and mixed layer depth (MLD) (Follows and Dutkiewicz, 2002, Dandonneau et al., 2004, McQuatters-Gollop et al., 2007a). A basin wide study of the North Atlantic by Barton et al.

(2014) found a strong relationship between physical variables and phytoplankton at seasonal scales, but highlighted that these relationships can vary spatially. For example, diatoms in the study were found to increase in abundance in the sub-polar gyre region of the North Atlantic when oceanic conditions consisted of deep mixed layers, strong turbulence and weak stratification, however, a decrease of diatoms was recorded for these same conditions in the sub-tropical gyre (Barton et al., 2014, Martinez et al., 2016). This spatial variability was attributed to the changes in light and nutrient availability between low and high latitude environments. Changes in the physical forces have been demonstrated to influence the timing of phytoplankton blooms, the length of the stratification period as well as the dominance of functional groups, and will consequently impact the annual averages of community abundance and diversity.

The control of phytoplankton over inter-annual and decadal scales remains less studied. Phytoplankton biomass across the North Atlantic basin has been associated with increased SST on interannual scales, particularly in the sub-polar gyre region (Colebrook, 1982, Beaugrand and Reid, 2003, Beaugrand et al., 2008, Barton et al., 2014, Martinez et al., 2016). Warmer temperatures have also been shown to result in increased dominance by dinoflagellates instead of diatoms between years (Boyd et al., 2010, Henson et al., 2012, Zhai et al., 2013). Changes in temperatures have also been documented as the primary mechanism for altering species distributions on interannual scales (Beaugrand et al., 2009).

Temporal variability in the mixed-layer depth (MLD) has also been shown to influence abundance and presence of species in the phytoplankton community. Diatoms have the ability to survive in lower light conditions than other phytoplankton (Graham et al., 2009), and can successfully out compete other phytoplankton types in conditions with deeper mixed layers. In areas with increased stratification haptophytes are outcompeted by smaller, Protista, species. These patterns have been described in model (Litchman et al., 2006) and observational data (van de Poll et al., 2013, Brun et al., 2015). The transition from a turbulent, well mixed state through to a stable stratified environment is found in the seasonal succession of phytoplankton types from diatoms, through to dinoflagellates.

In this thesis, the geographical focus is the North Atlantic basin. This region hosts an extensive phytoplankton spring bloom in the higher latitudes, where phytoplankton rapidly reproduce in response to seasonally warming temperatures, stratified, nutrient rich waters from winter mixing and reduced light limitation. The North Atlantic is divided by the presence of the Gulf Stream, which itself creates a ‘drift’ or ‘transitional’ region in which the diversity of phytoplankton is enhanced (Longhurst, 2007). South of the gulf stream the North Atlantic is a largely stratified oligotrophic gyre which is lower in biomass but higher in diversity than towards the poles (Barton et al., 2010, Boyce et al., 2017). With rising atmospheric CO_2, climate models forecast the North Atlantic region will experience large environmental changes including increased temperatures, intensification of stratification, increased ocean acidification and weakening of the Atlantic Meridional Overturning Current (AMOC) (IPCC, 2013, Doney, 2006). These conditions would increase stress on the phytoplankton community by increasing thermal stress that can effect biological processes and reduce the nutrient availability in the surface layers of the ocean, leading to a likely decline in phytoplankton biomass (Boyce et al., 2010). The prominence of phytoplankton in the North Atlantic make it an important area for carbon sequestration and fishing activities, as such the mechanisms, variability and consequences of changes to this region are being increasingly examined.

Inter-annual and multidecadal variability in the phytoplankton community in the North Atlantic has also been linked to the basin-wide climatic oscillation, the North Atlantic Oscillation (NAO). The NAO index is a measure of the difference in sea level pressure between the Azores and Iceland, which produces shifts to atmospheric circulation that cause broad changes to the physical ocean environment (Hurrell, 1995). The phase of the NAO index is correlated with changes in the relative abundance of diatoms, which increased in the North-East Atlantic during positive NAO phases, typical of cooler conditions that lead to stronger winders, increased mixed, cooler SST, and consequently deeper mixed layers (Henson et al., 2012). Dinoflagellates dominated in warmer conditions during negative NAO periods in the sub-polar region of the North Atlantic (Edwards, 2001, Henson et al., 2012). Long-term positive trends in phytoplankton biomass have also been associated with long-term trends in the NAO index, suggesting that the NAO may be a key driving factor in phytoplankton variability on inter-annual to decadal timescales (Edwards, 2001, Henson et al., 2012, Zhai et al., 2013). In addition to the cycles of the NAO, the Northern hemisphere also experiences variability with the Atlantic Multidecadal Oscillation (AMO) cycling the environment through cool and warm phases at a low frequency of ~60-80 years (Edwards et al., 2013b). While the AMO is believed to influence SST across the North Atlantic, it is heavily weighted to the sub-polar gyre region in the North West Atlantic (Harris et al., 2014).

The preference of phytoplankton types for different environmental states demonstrates how changes in the marine environment, with global climate change, may be reflected in the phytoplankton community composition. The physical environment has been suggested as the dominant factor driving population fluctuations over inter-annual timescales (Beaugrand and Reid, 2003, Leterme et al., 2005, Platt et al., 2005).

While the changes in the physical environment are consistently linked to seasonal changes in the phytoplankton community, the relationship over inter-annual timescales is less clear, studies such as Barton et al. (2014) demonstrate that when using inter-annual averages the relationships between variables appear less significant. This may be due to year-to-year variability in the phytoplankton community being greater than the variability in the physical environment or due to chaotic ecological relationships. Model studies have demonstrated that inter-annual variability can arise without external forcing forming a natural property of plankton communities (Dakos et al., 2009, Barton et al., 2014).

While much of the literature on seasonal and inter-annual timescales has focused on the traditional bottom-up forcing of the physical environment, biological forcing in a top-down approach can also be used to describe changes, in which pressure is applied from higher trophic levels through predation. The match-mismatch hypothesis describes the effects of predator-prey populations. It states that components of a population are controlled by the availability of prey during vital reproductive stages of their life-history, for example if there is a mismatch between food requirement and prey availability, successful recruitment of the predator will be reduced (Durant et al., 2013, Durant et al., 2007). The mismatch hypothesis can be used to describe climate effects on ecological patterns and processes, as climate changes may alter the reproductive timings of prey or change distribution patterns increasing the mismatch between predator-prey (Durant et al., 2007, Durant et al., 2013). The influence of predator interactions has been suggested in several studies as a key driver of phytoplankton community biomass and competition as pressure is placed upon preferred prey groups (Dakos et al., 2009, Barton et al., 2014).

In-situ, it is the combination of these bottom-up and top-down processes that shape the abundance and structure of the phytoplankton community, with species competing for available resources (such as light, nitrate and iron) while experiencing pressure from predators in the water column. The continued examination of these controlling mechanisms is required if we are to understand the consequences of a changing climate for phytoplankton populations (Tilman, 1981, Beaugrand and Reid, 2003, Barton et al., 2014).

2.3 Phytoplankton diversity

The principle of *competitive exclusion* dictates that in homogenous, well-mixed environments, species that compete for the same resources are unable to coexist due to direct competition, as the species can survive at the lowest resource supply will outcompete the others by drawing down available resources (Hardin, 1960, Armstrong and McGehee, 1980). This competition should theoretically form an equilibrium state of very low biodiversity for regions with limiting resources and suggests that the number of species able to coexist should not exceed the number of limiting nutrients, unless further mechanisms are involved (Hardin, 1960, Armstrong and McGehee, 1980).

The vast diversity of phytoplankton species across the open ocean environment, when there are such limited resources, results in Hutchinson's theory of "*The Paradox of the Plankton*" (Hutchinson, 1961). Hutchinson's original theory suggests that in the open ocean environment, the equilibrium state assumed in the principle of *competitive exclusion* is never truly achieved, and that a high diversity of phytoplankton communities can occur because of the natural spatio-temporal variability (Hutchinson, 1961).

Several studies have been dedicated to exploring the mechanisms enforcing this paradoxical state that have included mesoscale turbulence of the water column, natural chaos, self-generated segregation and compensation dynamics under temperature fluctuations (Roy and Chattopadhyay, 2007). In general, a community consisting of species with similar resource needs can be maintained through trade-offs between intrinsic population growth capacity and competitive impact (Dakos et al., 2009, Doncaster et al., 2016).

Due to the vast diversity of phytoplankton species and their important roles in important biogeochemical processes, changes to the community composition may cause crucial alteration to ecosystem functioning and structure including food web dynamics, primary production rates and biogeochemical cycling (Karl et al., 2001, Hays et al., 2005, Eggers et al., 2014). The identification and quantification of variability in the community composition has therefore become of increasing interest within marine ecology (Margalef, 1978, Beaugrand and Ibanez, 2002).

2.4 Long-term datasets

While several studies have examined changes in the phytoplankton community, ecosystem dynamics may not be easily characterised on short timescales; long-term datasets can allow the differentiation between natural oscillations in communities and changes that are forced by anthropogenic climate change (Irwin et al., 2012). Due to the scale of many physical processes like the North Atlantic Oscillation, datasets longer than 40 years have been suggested as a minimum requirement in order to distinguish anthropogenic change from natural variability (Henson et al., 2010, McQuatters-Gollop et al., 2015). Long-term datasets also allow for the detection of significant shifts and non-linear responses in the abundance, distribution and composition of phytoplankton which may have subsequent effects on food web dynamics, primary production rates and biogeochemical cycling (Bates et al., 2014, Killick et al., 2016, Giron-Nava et al., 2017, Legendre and Legendre, 2012).

The commercial fishing industry has provided some of the longest records of biodiversity (number of species and the evenness of their presence) for the marine environment through the monitoring of fish stocks, however, their long life spans and commercial exploitation mean that detection of anthropogenic change from natural variability can be unclear (Planque and Taylor, 1998). Phytoplankton however have short life cycles (1-2 days) and quick successional response rates to changing conditions, rapidly outcompeting each other in more favoured conditions, which allows them to be used as indicators to assess changing ocean conditions and ecosystem health (Widdicombe et al., 2010, McQuatters-Gollop et al., 2015).

The lengths of inter-annual phytoplankton studies vary dramatically. Many shipboard programs are relatively short (5-10 years), however there are some extensive long-term studies such as the sampling program at the Biologische Anstalt Helgoland station, in the North Sea, that has sampled phytoplankton, zooplankton, temperature and nutrients since 1962 (Wiltshire et al., 2008). Such inter-annual studies have detected declines in total phytoplankton biomass and shifts in composition to smaller functional groups such as cyanobacteria (Sommer and Lengfellner, 2008, Morán et al., 2010).

Remote sensing techniques provide a comprehensive source for spatially and temporally accessible datasets. Since 1998, the Sea-Viewing Wide Field-of-View Sensor (SeaWIFS) satellite has provided relatively consistent temporal information on ocean colour, including the pigment Chlorophyll-a (Chl-a), an index of phytoplankton biomass, found in phytoplankton that may be used to assess their biomass (Beaugrand et al., 2008, Henson et al., 2010). Such studies have revealed declines in phytoplankton biomass and primary productivity in the sub-tropical regions, but increases in the North Atlantic sub-polar gyre driven by changes in MLD, wind speed and SST (Barton et al., 2014, Martinez et al., 2016).

Phytoplankton functional types can also be derived from ocean-colour remote sensing techniques (Brewin et al., 2011). This can be determined through direct effects, where changes in phytoplankton composition can lead to changes in the absorption and backscattering coefficients, as well as indirect effects in which changes in the phytoplankton composition are accompanied by changes in the ensemble of particles and dissolved substances. Both these effects lead to changes in the reflectance spectra enabling us to estimate functional composition from space (IOCCG, 2014, Bracher et al., 2017). Satellites provide the ability to assess change at a global scale, enhancing the information received from in-situ studies by providing a wider context.

The fossil record has also been used to assess spatio-temporal change of plankton communities, and demonstrates that phytoplankton community structure, in particular the diatom functional group, has historically responded rapidly to changes in the physical environment, whilst remaining largely robust to alteration over long geological time scales (Cermeño et al., 2010).

2.4.1 The Continuous Plankton Recorder survey

One of the few data sets that is temporally and spatially extensive enough to examine ecological changes is the Continuous Plankton Recorder (CPR) survey. Since the CPR survey began in 1931 it has routinely identified >400 planktonic taxa at monthly intervals across the North Atlantic and North Sea region, and to date remains the largest multi-decadal plankton monitoring programme in the world with >250,000 samples (Figure 2.2) (Richardson et al., 2006, SAHFOS, 2018).

The survey was founded in 1931 by Alister Hardy, who designed the CPR device as a simplistic way to routinely sample plankton in-situ over vast spatial regions. The survey is maintained by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in Plymouth (now the Marine Biological Association (MBA)). Publication output from the CPR survey has increased dramatically, enhancing our understanding of plankton dynamics, particularly in the North sea and North Atlantic region, becoming an invaluable source of information (Beaugrand and Edwards, 2001, Richardson et al., 2006). Data from the survey has been increasingly used for forming a baseline to assess the impacts of global climate change on the pelagic system (Edwards and Richardson, 2004, Richardson and Schoeman, 2004, Richardson et al., 2006).

The survey has also helped assess regional to international concerns of biodiversity loss, climate change, eutrophication and harmful algal blooms (Brander, Dickson, & Edwards, 2003). Much of the output from the survey has concentrated on the North Sea and North-East Atlantic, due to the high sampling effort, but has primarily focused on changes to the abundance of the total phytoplankton or zooplankton community or the abundance of functional groups (Colebrook, 1982, Beaugrand, 2003, Henson et al., 2012, Beaugrand and Reid, 2003). However, the survey provides information at finer taxonomic resolution that has generally not been as extensively analysed.

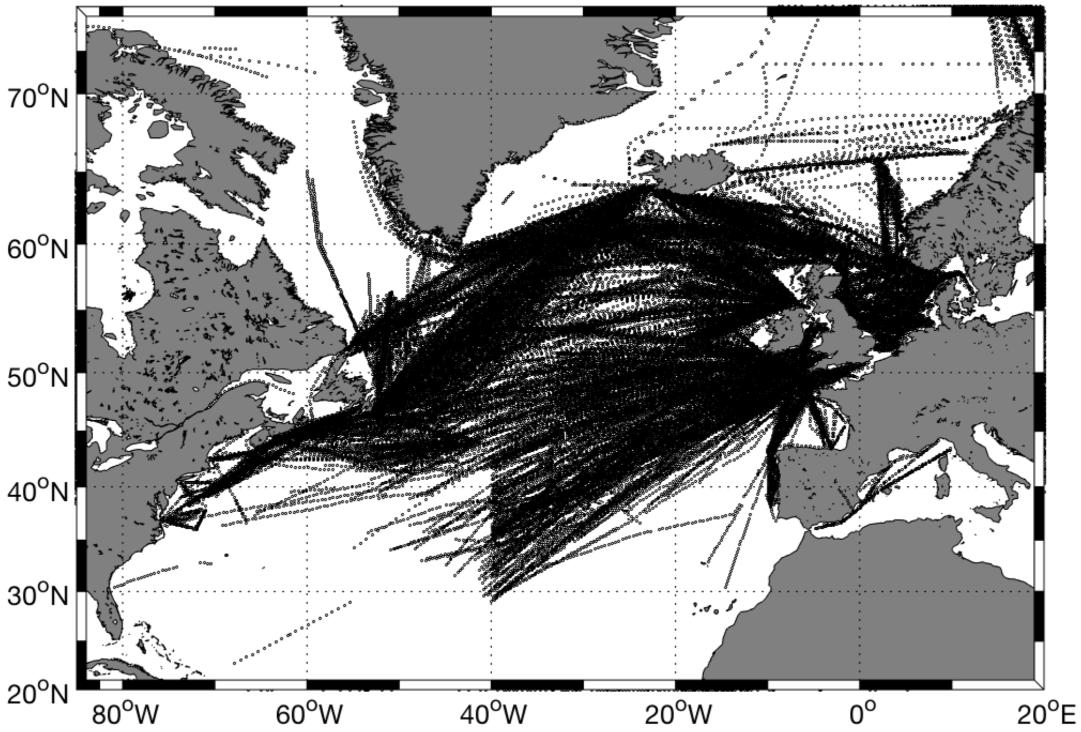

Figure 2.2: Map of Continuous Plankton Recorder samples from 1946 to 2017 across the North Atlantic, collected and analysed by the Sir Alister Hardy Foundation for Ocean Science with a total of 262,761 samples (SAHFOS, 2018).

Literature using the survey is primarily focused on the North Sea basin, likely due to the concentration of CPR samples in that region (Williams et al., 1993, Beare et al., 2013, Wouters et al., 2015). This thesis, however, focuses on the data from the North Atlantic which while less saturated with samples than the North Sea, the phytoplankton variability and community dynamics are less understood and in such an open ocean area may response very different to changes described in the North Sea.

2.4.2 Ecosystem models

With focus rising around the impact of a changing climate, global models have become an increasingly popular data source due to their extensive spatiotemporal, biogeochemical and ecosystem coverage compared to in-situ data, and the flexibility of extending timeseries with forecasting techniques. Ocean models are forced by physics and circulation, as well as atmospheric forcing, and are coupled to ocean biogeochemistry. Model simulations have recreated the decline of phytoplankton diversity and abundance, and are also able to reconstruct the distributional patterns seen in-situ such as diversity hot-spots in regions of energetic ocean circulation (Barton et al., 2010). Model studies have demonstrated that ocean processes have a key role in shaping the abundance and distribution of global phytoplankton populations, consistent with many in-situ programs (Barton et al., 2010, Adjou et al., 2012).

Some models are also able to represent functional groups within the community, simulating phytoplankton types that have specific thermal and nutrient requirements allowing them to respond to environmental forcing and reflect in-situ adaptations to the abiotic and biotic conditions through trade-offs (Acevedo-Trejos et al., 2015, Adjou et al., 2012, Denman, 2003, Dutkiewicz et al., 2009).

The major advantage of model studies is the spatiotemporal extent of the information available. As warming of the ocean environment has become unambiguous, the ability to predict future changes has become paramount (Beaugrand et al., 2009, IPCC, 2013). Studies have demonstrated that changes will impact the biodiversity, structure and functioning of marine ecosystems as we continue into the 21st century and the quantification of these changes through modelling will be vital to future mitigation efforts (Beaugrand et al., 2002, Edwards and Richardson, 2004, Drinkwater et al., 2003, Beaugrand et al., 2008).

2.5 Thesis goals and overview

The research presented in this thesis aims to advance the field of phytoplankton community ecology by improving the understanding of community structure variability and the potential driving mechanisms of such change in in-situ and model datasets. There has been extensive research into the seasonal variability of phytoplankton composition, however, the examination of inter-annual and multi-decadal trends are less so. This has led to the specific aims of this thesis, which are to:

- Quantify the variability of the North Atlantic phytoplankton community structure using taxonomic data from the CPR survey
- Demonstrate the relationship between the phytoplankton community composition, the physical environment and zooplankton community composition in top-down and bottom-up forcing
- Infer the importance of the above driving forces, to assess whether the community demonstrates a traditional top-down or bottom-up approach, in different regions of the North Atlantic
- Investigate the future change in the phytoplankton community composition using model output from the MIT, Integrated Global Systems Model
- Identify and estimate the timing of abrupt shifts in the phytoplankton abundance and diversity in the 21st century

Chapter 3 Data collection and processing

This thesis uses in-situ data from the CPR survey and model output from the Massachusetts Institute of Technology (MIT) Integrated Global Systems Model (IGSM). The collection and processing of the in-situ data from the CPR survey are described in section 3.1. Environmental data that were used alongside data from the CPR survey in Chapter 4 and Chapter 5 are detailed in section 3.2. Details of the IGSM used in Chapter 6 are given in section 3.3 and processing of the model output for use here is given in section 3.3.4.

3.1 The Continuous Plankton Recorder Survey

In-situ information on the phytoplankton and zooplankton community was obtained from the CPR survey, operated by SAHFOS, Plymouth UK. The CPR device, shown in Figure 2.2, is towed behind 'ships of opportunity', usually at speeds of 15-20 knots at a depth of ~7 m (Richardson et al., 2006). As the device is towed, water enters the CPR through a square aperture, 1.61 cm^2, flows down an expanding tunnel to help minimise damage to entrained plankton, and exits through the rear of the device (Figure 2.2). The movement of the CPR through the water also turns an external propeller at the rear of the device, which, through gears, operates an internal filtering system (Figure 2.2). Plankton entrained in the flow of water become trapped on a moving silk mesh, filtering them from the water. The filtering silk mesh is then met by a second band of 'covering silk' which together are wound onto a spool in a storage tank containing 4% formalin (Richardson et al., 2006). The filtering silk has a mesh size of 270μm allowing an adequate representation of the zooplankton community and larger phytoplankton species, while reducing clogging by small phytoplankton cells (Richardson et al., 2006, Hardy, 1936). Despite the relatively large mesh size of the filtering silk, smaller phytoplankton are regularly retained and recorded in the survey, for example Coccolithophores have had their presence recorded since 1969 and counted since 1993 (Richardson et al., 2006, Raitsos et al., 2005). Each CPR sample consists of a 15cm by 10.5cm section of silk, representing 10 nautical miles of tow, regulated by the speed of the rear propeller driving the internal filtering system (Richardson et al., 2006). This methodology has been rigorously maintained since 1946.

3.1.1 CPR sample processing

Alternate 10 nautical mile samples are allocated to SAHFOS analysists in a semi-random manner, to prevent the same analysist from analysing two successive samples on a route. There are four stages of analysis carried out on each CPR sample: (1) qualitative assessment of phytoplankton abundance through the phytoplankton colour index (PCI), (2) phytoplankton species count (phytoplankton traverse), (3) smaller zooplankton species count (zooplankton traverse) and (4) larger zooplankton species count (zooplankton count by eye). The phytoplankton and zooplankton traverse counting methods are an ‘on-silk’ counting procedure, whereas specimens are removed from the silk for zooplankton eye count (Richardson et al., 2006).

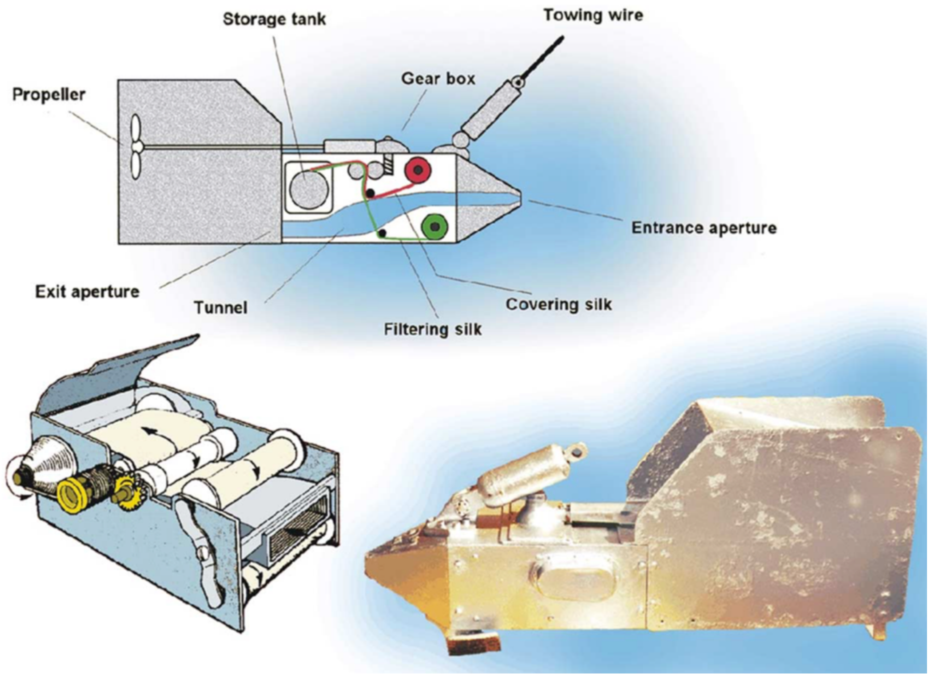

Figure 3.1: The cross-section (top), internal mechanisms (bottom left) and external housing (bottom right) of the Continuous Plankton Recorder device (Richardson et al., 2006).

3.1.1.1 The Phytoplankton Colour Index

Each sample from the survey is visually assessed and assigned a greenness index, referred to as the PCI, by the comparison of standardised colour charts (Robinson and Hiby, 1978, Richardson et al., 2006). PCI is classified into the following categories: “no colour”, “very pale green”, “pale green”, and “green” (Robinson and Hiby, 1978). This is subsequently assigned numerical values based on acetone extracts using spectrophotometric methods (Richardson et al., 2006). The PCI is used as a semi-quantitative assessment of total community biomass, which accounts for the biomass of diatoms and dinoflagellates, as well as other micro- and nanoflagellates that were destroyed or too damaged for species identification while nevertheless contributing to the retained pigments (Richardson et al., 2006). PCI is one of the largest ocean colour datasets and has been widely used in the literature and the quantitative validity of the PCI categories were tested in a recent study by Raitsos et al. (2013).

3.1.1.2 Phytoplankton counts

Due to the scale and spatial coverage of the CPR survey, phytoplankton cells are recorded as present or absent across 20 microscopic fields of view, at 450x magnification, amounting to 1/10,000 of the area of the filtering silk (Richardson et al., 2006). These fields of view provide 20 abundance categories in which a taxon has been seen, which have an assigned total abundance per sample (Richardson et al., 2006). Due to historical data storage limitations, these 20 values are averaged into 10 for the final abundance per sample (Table 3.1) (Richardson et al., 2006). Due to this, phytoplankton abundance values are classified as semi-quantitative estimates.

Due to the large mesh size of the CPR device, smaller phytoplankton species are likely under-sampled, although organisms as small as coccolithophores are regularly recorded as they get trapped in the strands of the silk, or with clogging of the silk by larger species (Rivero-Calle et al., 2015). Larger phytoplankton, including armoured dinoflagellates and chain-forming diatoms are better sampled (Edwards et al., 2013a).

Table 3.1: Phytoplankton analysis from the Continuous Plankton Recorder survey. Calculating the abundance of a particular taxon to an entire CPR sample from total fields of view. Replicated from Richardson et al. (2006).

Total number of fields	Accepted value	Abundance per sample	Recorded abundance per sample
1	1	10000	15000
2	2	20000	15000
3	3	30000	35000
4	4	40000	35000
5	6	60000	65000
6	7	70000	65000
7	9	90000	95000
8	10	100000	95000
9	12	120000	130000
10	14	140000	130000
11	16	160000	170000
12	18	180000	170000
13	21	210000	225000
14	24	240000	225000
15	28	280000	300000
16	32	320000	300000
17	38	380000	420000
18	46	460000	420000
19	60	600000	750000
20	90	900000	750000

3.1.2 Zooplankton counts

A stepped traverse of the CPR filtering silk and covering silk, at 54x magnification (field of view is 2.06 mm), is used to count all zooplankton organisms <2mm total length. Organisms are assumed to be uniformly distributed on the silk, however, the design of the analysis ensures that all areas of the silk receive equal weighting (Richardson et al., 2006). The zooplankton traverse surveys around 1/50th of the silk. Zooplankton >2mm are counted and removed from the silk for identification. In general, all individuals are counted, but if a particularly dense sample occurs a sub-sample may be taken (Richardson et al., 2006).

As for phytoplankton, due to the large number of samples a category counting system is used for the zooplankton abundances. This results in abundances being semi-quantitative but still reflects changes in abundance through time (Richardson et al., 2006). The individual counts of zooplankton are recorded as logarithmic categories. These have an associated accepted value and if the count was sub-sampled a total abundance for the whole sample is estimated (Table 3.2) (Richardson et al., 2006).

While this categorical counting system reduces the precision of the abundance estimates for sampling, it does allow for large numbers to be sampled every year, thus supporting the large spatio-temporal coverage of the CPR survey.

Table 3.2: Zooplankton analysis (traverse and eye count) from the Continuous Plankton Recorder survey. Calculating the abundance of a particular taxon to an entire CPR sample. Replicated from Richardson et al. (2006).

Number counter	Category	Accepted Value	Abundance per sample for zooplankton
1	1	1	50
2	2	2	100
3	3	3	150
4-11	4	6	300
12-25	5	17	850
26-50	6	35	1750
51-125	7	75	3750
126-250	8	160	8000
251-500	9	310	15500
501-1000	10	640	32000
1001-2000	11	1300	65000
2001-4000	12	2690	134500

3.1.3 CPR standard areas and calculation of annual averages

Due to the survey collecting samples by using ‘Ships of Opportunity’ that are restricted to commercial shipping routes, large areas of the North Atlantic are under sampled (Richardson et al., 2006). As such, data from the survey was spatially averaged into defined CPR standard areas as described in Figure 3.2. These standard areas have been widely used in the assessment of the CPR data in examining seasonal, inter-annual and environmental forcing of the plankton community across the North Atlantic (Helaouet et al., 2013, Barton et al., 2014, Edwards, 2001).

Monthly data from the CPR survey were used to calculate annual averages, used for analysis in Chapter 4 and Chapter 5. While the CPR survey data provide extensive temporal coverage compared to other in-situ datasets, there can be multiple months where data is insufficient. To account for this a method developed by Colebrook (1975) is used to calculate annual averages. This method is only applied to years that contain 8 or more months of data and if two or more consecutive years contained missing data they were also removed from the study.

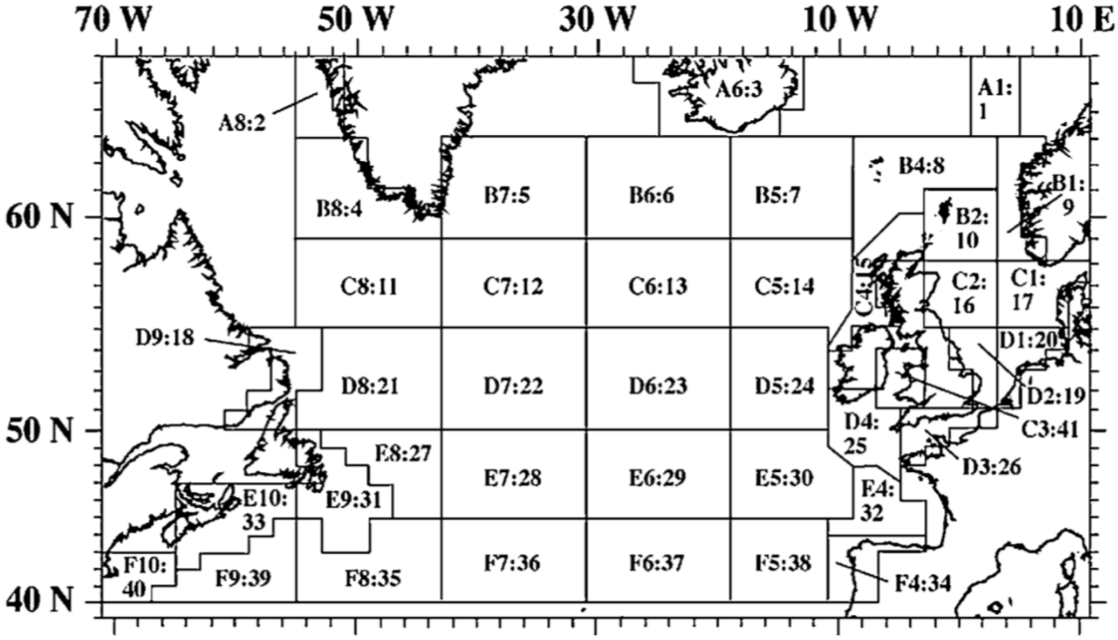

Figure 3.2: Map of the CPR standard areas (SAHFOS area code: area numbers) (Barton et al., 2003).

3.1.4 CPR sampling bias

The large mesh size of the CPR survey (270 μm) introduces a sampling bias favouring larger plankton types and underestimates the total community diversity in the in-situ environment. While this is a widely known sampling bias of the CPR survey, and should be taken into account when assessing the data, it must also be highlighted that as the CPR survey has had an unchanged methodology for phytoplankton since 1958 and zooplankton since 1948, these biases are consistent throughout the history of the survey and therefore do not prevent comparison through space-time (Beaugrand and Edwards, 2001).

There are also temporal breaks in the CPR survey. This may occur due to maintenance of CPR devices or longer breaks in the time series due to shipping companies no longer towing certain routes or insufficient funding for deployment (Richardson et al., 2006). These biases in the data are not consistent through space-time, and the employment of averaging as described in section 3.1.3 is used to address such concerns (Colebrook, 1975, Richardson et al., 2006).

3.2 Environmental data

Chapter 4 and Chapter 5 that utilise data from the CPR survey also assess the physical environment. Sources and processing of environmental data used throughout this thesis are described in this section.

3.2.1 Sea surface temperature and mixed layer depth

Information on subsurface ocean temperature and salinity was obtained from the Hadley Centre’s EN4 quality-controlled dataset (at 1° resolution, downloaded from http://www.metoffice.gov.uk/hadobs/en4/) (Ingleby and Huddleston, 2007, Good et al., 2013). Data for the EN4 is obtained from a number of ocean profiling sources, checked for duplicates and then subjected to a series of quality control checks which are used to produce a monthly objective analysis of ocean temperature and salinity (Good et al., 2013). Details of the Hadley Centre’s EN4 dataset can be found in depth in Good et al. (2013) and Ingleby and Huddleston (2007).

For this thesis, the EN4 dataset was used to obtain sea surface temperature (SST) and to calculate mixed layer depth (MLD). Density was calculated from monthly temperature and salinity values and MLD was defined as the depth at which a density difference of >0.125 kg m^{-3} from the surface was observed (Chiswell, 2011, Chiswell et al., 2013). Annual averages were calculated for both SST and MLD values to correspond with the data from the CPR survey.

3.2.2 North Atlantic Oscillation index

The North Atlantic Oscillation (NAO) index time series was obtained from the University Corporation for Atmospheric Research (UCAR) Climate Analysis Section (Hurrell et al., 2003) (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based). The principal component (PC)-based index of the NAO were used in this thesis. This is a time series of the Empirical Orthogonal Function (EOF) of surface level pressure anomalies over the Atlantic sector, 20°-80°N, 90°W-40°E, between the Azores and Iceland (Hurrell, 1995). This index quantifies the phase of the NAO throughout the year, with positive values associated with stronger westerly winds that may result in deeper mixed layers and negative values having the opposite effect. The PC-based index of the NAO provides a better representation of the spatial patterns and is less noisy than the station-based index (Hurrell, 1995). For this thesis, I used a normalised average of the NAO index across the months of December to March of each year, referred to as the winter-mean.

3.2.3 Atlantic Multi-decadal Oscillation index

The monthly, unsmoothed Atlantic Multi-decadal Oscillation (AMO) index since 1948 was provided by the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory (Enfield et al., 2001). The AMO is a climate cycle that affects the SST of the North Atlantic ocean basin. Here, the timeseries is derived from the Kaplan SST dataset, a gridded global dataset of SST from the UK Met Office SST data which has then been interpolated and had statistical smoothing techniques applied to fill gaps. The AMO index is the area-weighted average of temperatures over the North Atlantic, 0°N-70°N (Enfield et al., 2001) (https://www.esrl.noaa.gov/psd/data/timeseries/AMO).

3.3 The MIT Global integrated model

In Chapter 6 I utilise model output from the MIT Integrated Global Systems Model (IGSM). This section provides an overview of the model components and experiments used in this thesis. I also describe any processing of the IGSM output.

3.3.1 Earth System Model

The IGSM is an earth system model of intermediate complexity formed of a high resolution, three-dimensional (latitude, longitude and depth) ocean module that is coupled to a coarse resolution, two-dimensional (latitude and height) atmospheric module with physical and chemical components and finally with a terrestrial module (summarised in Figure 3.3) (Dutkiewicz et al., 2013).

The ocean model has horizontal resolution of 2º x 2.5º and 22 vertical levels from 10 to 500m depth. The coarse resolution horizontal resolution means that mixing by eddy motions is not clearly defined (Dutkiewicz et al., 2005). However, boundary layer physics and mesoscale eddies are parameterized following Gent and McWilliams (1990) and Large et al. (1994).

The coupled system was spun up for 2000 years using 1860 ‘pre-industrial’ conditions before simulating changes from 1990 to 2100. For the 21st century, anthropogenic emissions follow a ‘business as usual’ scenario that simulates a future climate on the assumption that trends follow past signals with no change to development or policy. This was predicted from an economics module that is similar to the IPCC AR5 RCP8.5 scenario (Dutkiewicz et al., 2015).

In the spin-up, the three-dimensional ocean was forced by winds that were repeated in the model, whose variability was provided by the National Centre for Environmental Prediction (NCEP) in which detrended winds over the period of 1948 to 2007 are applied and ‘recycle’ for other years to drive the interannual variability (Dutkiewicz et al., 2013). This allowed, for example, an El Niño-Southern Oscillation (ENSO) type signal to occur.

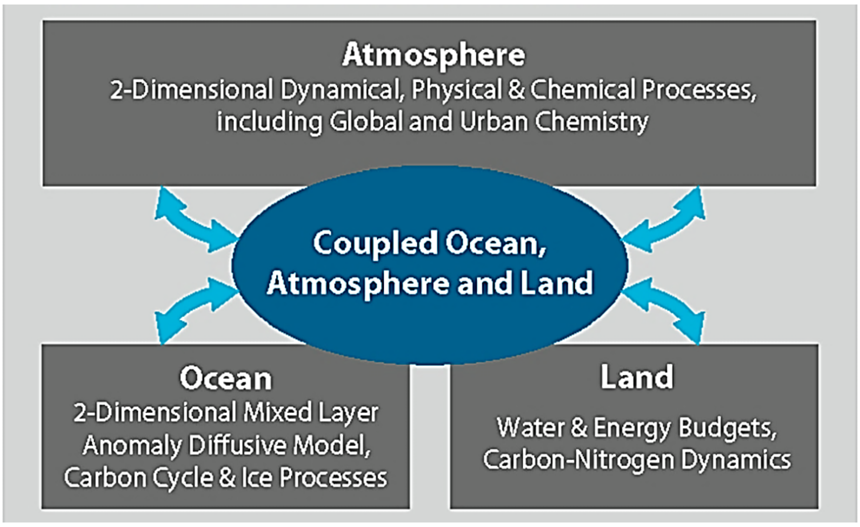

Figure 3.3: Visual representation of the MIT IGSM, Earth component adapted from (Sokolov et al., 2018). Diagram demonstrates the three components of the Earth System Model: Ocean, Atmosphere and Land.

3.3.2 Marine Ecosystem Model

The oceans’ physical fields (temperature, mixing and velocities) from the earth system model were used to drive changes in a modified marine ecosystem model. Within the marine ecosystem model, inorganic and organic carbon, nitrogen, phosphorus, iron and silica and phytoplankton types were transported (Dutkiewicz et al., 2015, Dutkiewicz et al., 2013, Dutkiewicz et al., 2005).

The model simulates 96 types of phytoplankton divided into 6 functional groups, loosely defined by their roles in nutrient cycling: Diatom, Other Large, Other Small, Prochlorococcus, Diazotroph and Coccolithophore (Dutkiewicz et al., 2015) . Each phytoplankton type had its own temperature range and optima (Dutkiewicz et al., 2015) and each of the 6 functional groups had different values of maximum photosynthesis, nutrient half-saturation constant, and potentially nutrient requirements as in previous studies (Dutkiewicz et al., 2015). These differences allowed each functional group to have a distinct spatio-temporal niche within the model (Dutkiewicz et al., 2015).

The change in biomass for each phytoplankton type is determined in terms of growth, sinking, grazing, other mortality, and transport by the fluid flow. Phytoplankton growth is a function of light, temperature and nutrient availability. The growth rate for each type j (where j = 1 to 96) is determined by:

$$\mu_j = \mu_{max_j}\, {\gamma_j}^T {\gamma_j}^I {\gamma_j}^R$$

In which, μ_{max_j} is the maximum growth rate of phytoplankton type j, and ${\gamma_j}^T {\gamma_j}^I {\gamma_j}^R$ are the functions modulating growth due to temperature, light and nutrient resource availability (Dutkiewicz et al., 2013).

Within the model the phytoplankton growth rates were parameterized as functions of maximal photosynthesis rate, light, nutrients and temperature, as in previous studies (Dutkiewicz et al., 2015, Dutkiewicz et al., 2013). Nutrient limitation for growth was determined by the most limiting resource:

$$\gamma_{j^N} = \min\,({N_1}^{lim},\ {N_2}^{lim},\ {N_3}^{lim}\ \ldots)$$

In which the nutrients (N_i) are phosphate, iron, silicic acid, and dissolved inorganic nitrogen and j represents the phytoplankton type (Dutkiewicz et al., 2015). The effect of phytoplankton growth rate on the ambient concentrations of these nutrients is determined by a Michaelis–Menten function given by:

$${N_1}^{lim} = \frac{N_i}{N_i + k_{ij}}$$

where k_{ij} are half-saturation constants for phytoplankton type j for the remaining concentration of nutrient i (Dutkiewicz et al., 2015). The model resolves three potential sources of inorganic nitrogen (ammonia, nitrite and nitrate) (Dutkiewicz et al., 2015, Dutkiewicz et al., 2005).

This parameterisation implements a series of trade-offs for each phytoplankton type allowing the development of spatial and temporal niches for functional groups. For example larger phytoplankton types, such as the Diatoms, distinguished by higher intrinsic maximum growth rates, faster sinking speeds, and higher half-saturation constants, means that these types suit highly seasonal, high nutrient regions (Dutkiewicz et al., 2013, Dutkiewicz et al., 2015). Smaller phytoplankton types are adapted to low nutrient, stable waters, such as in the tropical regions of the ocean. *Prochlorococcus* has the lowest growth rate and the lowest half-saturation of nutrients (Dutkiewicz et al., 2015, Dutkiewicz et al., 2013).

Temperature regulation of phytoplankton growth was represented by a non-dimensional factor, that was a function of ambient temperature, given by:

$$\gamma_{jT} = \tau_T \, exp\left(A_T\left(\frac{1}{T} - \frac{1}{T_N}\right)\right) \exp\left(-B_T|T - T_{oj}|^b\right)$$

In which the coefficient τ_T normalized the maximum value of temperature for growth, whereas A_T, B_T, T_N and b regulate the sensitivity envelope. T_{oj} sets the optimum temperature specific to each of the 16 types, j, in each functional group. Zooplankton in the model were also regulated by this temperature function, but without the second exponential function (Dutkiewicz et al., 2015).

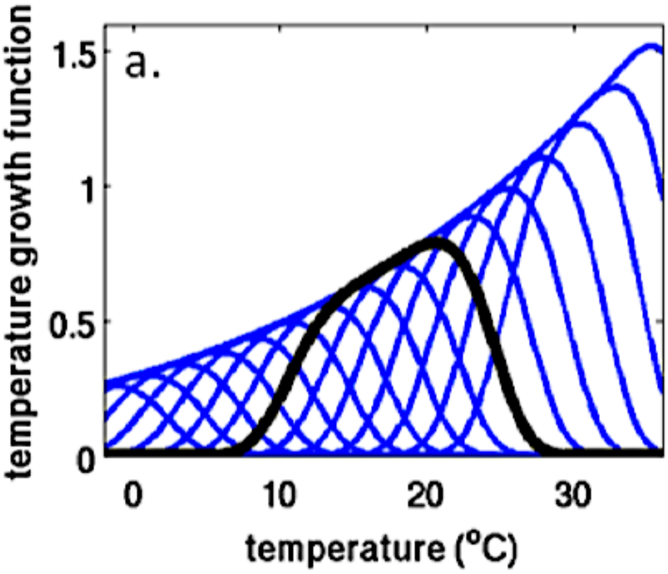

Figure 3.4: The MIT IGSM experiments used in this thesis contain 16 phytoplankton types within 6 functional groups (totalling 96 phytoplankton types) that have a temperature range and optima for growth (Dutkiewicz et al., 2013). The black line highlights an individual phytoplankton type to demonstrate the shape of the temperature function. All other phytoplankton types are represented in blue. The function is unitless as actual growth rates are also dependant on maximum growth rates, nutrient use and light limitation for each functional type. This figure is taken from Dutkiewicz et al. (2015).

Parameters that regulate the effects of temperature and light on phytoplankton growth are drawn from laboratory and field studies, with each phytoplankton type being randomly assigned an optimal growth temperature, in which there was an increase in maximum growth rates for types with higher optimum temperatures, and was only viable over a specified temperature range (Thomas et al., 2012, Boyd et al., 2013, Eppley, 1972, Bissinger and Montagnes, 2008, Dutkiewicz et al., 2013, Dutkiewicz et al., 2015).

3.3.3 Model Experiments

The ecosystem was forced with the physical fields from the earth system model for the pre-industrial control and run for 50 years to allow the phytoplankton community and the upper ocean biogeochemistry to establish a quasi-equilibrium.

From this quasi-equilibrium state, two experiments from this model were used in this thesis. The first was the 'Control' in which the pre-industrial temperature, circulation, mixing and sea-ice fields and p_{CO2} were used. The control run starts from the 1860 year spin up and run for another 240 years (Dutkiewicz et al., 2015). The 'Control' provides a measure of the biogeochemical and community drift, and therefore provides a baseline from which a climate signal can be compared. The second experiment is the 'All-Other' run in which the Earth system is allowed to change over the same period in response to increasing CO_2 and other greenhouse gas levels (Dutkiewicz et al., 2015). Temperature, mixing, circulation and sea-ice are allowed to change in the model, after starting at the same initialization point as the above control run, while p_{CO2} fields remain unchanged therefore do not have a role influencing phytoplankton populations (Dutkiewicz et al., 2015).

It must be highlighted that ecosystem models are simplifications of reality and as such they focus upon the main mechanisms that influence the community and their physical environment (Dutkiewicz et al., 2005). As such the assumptions behind the model must be considered when analysing the results of this study.

3.3.4 Notes on model output

The model output used in this thesis is provided in 5-year averaged time periods between 1990 and 2100, resulting in 22 time 'blocks'. Only phytoplankton that contributed to more than 1% of the total biomass of the community were used in the analysis, as phytoplankton are never truly removed from the model allowing them to return if suitable conditions emerge.

Chapter 4 Inter-annual stability of phytoplankton community composition in the North-East Atlantic

4.1 Abstract

As primary producers, phytoplankton play a pivotal role in the marine environment and are central to many biogeochemical processes. Changes to phytoplankton community composition could have major consequences for wider ecosystem functioning and may occur in response to climate change. Here I describe multi-decadal variability in phytoplankton community structure using taxonomic data from the Continuous Plankton Recorder collected in the North-East Atlantic from 1969 to 2013, using a total of 42 diatom and dinoflagellate taxa. I consider a range of characteristics of community structure, including taxonomic diversity and community stability and disorder, and how these characteristics change in response to sea surface temperature, mixed layer depth and the North Atlantic Oscillation.

A community stability analysis finds that the studied phytoplankton composition was largely stable on inter-annual timescales. There was a change in the community composition between 1985 and 1995 due an increased dominance of two diatom species, however, after this period the community returned to its previous composition. Further, a community disorder analysis found that phytoplankton compositional structure became more rigid in recent years, which may lead to an eventual community shift in the future.

In contrast to previous studies that reveal relationships between total phytoplankton abundance or biomass and environmental forcing, I find that the community structure has, at most, a very weak relationship with the environmental parameters tested. Changes to the physical environment may therefore have less influence at inter-annual timescales on phytoplankton community structure than previously thought.

4.2 Introduction

The stability of a community's taxonomic composition largely depends on the capacity for individual species to withstand perturbation, with external forcing capable of altering a community over multiple spatio-temporal scales (Beaugrand and Ibanez, 2002, Edwards and Richardson, 2004, Beaugrand et al., 2008). Due to phytoplankton having many ecological and biogeochemical functions, the alteration of species within a community in response to global climate change may have the potential to alter global biogeochemical cycles, ecosystem functioning and predator-prey relationships, causing trophic mismatch (Edwards and Richardson, 2004, Beaugrand et al., 2008, Eggers et al., 2014).

In a community of species with similar resource needs, the community composition can be maintained through trade-offs between intrinsic population growth capacity and competitive impact through growth rates and nutrient affinity (Dakos et al., 2009, Doncaster et al., 2016). During periods of exogenous forcing, ecological theory predicts an early replacement of weakly competitive and slow replicating species, referred to as 'canary species', by species that have a higher competitive fitness (Doncaster et al., 2016). Strong competitors may take a 'keystone' role, in which case their rising prevalence enforces structural rigidity on the community. Ongoing exogenous forcing eventually disadvantages all species with intrinsically slow population growth capacity, including the strong competitors. The loss of keystones then allows species that were previously out competed, 'weedy species', to quickly replicate and flourish, allowing the community to transition to an entirely different composition (Doncaster et al., 2016). Analysis of temporal variations in community composition may thus provide an early warning signal of exogenous forcing affecting the community (Beaugrand and Reid, 2003, Edwards and Richardson, 2004, Beaugrand et al., 2008, Doncaster et al., 2016).

Due to the diverse role that phytoplankton play in the marine environment much research has been devoted to fluctuations in the abundance, biomass and community composition of these organisms (Dutkiewicz et al., 2001, Beaugrand and Reid, 2003, Sommer and Lengfellner, 2008). Current work concerning long-term variability in phytoplankton populations has predominantly focused on the abundance and biomass of the entire phytoplankton population or large functional groups within it, such as the diatoms and dinoflagellates (Edwards, 2001, Henson et al., 2009, Barton et al., 2014). For example, seasonal changes in North Atlantic phytoplankton have been thoroughly documented and a significant fraction of the variability in functional groups has been attributed to fluctuations in the physical environment (Follows and Dutkiewicz, 2002, Dandonneau et al., 2004, McQuatters-Gollop et al., 2007a). The physical environment has also been implicated as the dominant factor driving population fluctuations over inter-annual timescales (Beaugrand and Reid, 2003, Leterme et al., 2005), however this remains under debate with some studies concluding that predator-prey and other ecological interactions cause natural chaos and this dominates the variability (Benincà et al., 2008, Boeing, 2016, Dakos et al., 2009). The variability of phytoplankton on longer timescales (multi-decadal, geological) is less well known, especially in regard to shifts in species composition.

SST directly impacts phytoplankton growth and metabolic rates (Eppley, 1972) and indirectly impacts phytoplankton abundance through altering stratification and thus light and nutrient availability (Edwards and Richardson, 2004). Inter-annual variability in bulk phytoplankton biomass across the North Atlantic basin has been associated with increased SST, particularly in the sub-polar gyre region (Colebrook, 1982, Beaugrand and Reid, 2003, Beaugrand et al., 2008, Barton et al., 2014). Further, dinoflagellates have been shown to outcompete diatoms (on average) in warmer years (Boyd et al., 2010, Henson et al., 2012, Zhai et al., 2013). Temporal variability in the MLD has also been shown to influence the magnitude and composition of phytoplankton communities. In a model study, longer periods of stratification and shallower mixed layers increased diatom, coccolithophore and prasinophyte biomass compared with years of frequent deep mixing (Litchman et al., 2006) and observational studies have linked shallower mixed layers to the dominance of smaller protista species over haptophytes (van de Poll et al., 2013, Brun et al., 2015).

Multi-decadal variability in North Atlantic phytoplankton abundances has also been linked to the basin-wide climatic oscillation, the NAO. The NAO index is a measure of the difference in sea level pressure between the Azores and Iceland, which results in shifts to atmospheric circulation causing broad changes to the physical ocean environment (Hurrell, 1995). The phase of the NAO index is correlated with changes in the relative abundance of diatoms, which increased in the North-East Atlantic during positive NAO phases, typical of cooler conditions with deeper mixed layers (Henson et al., 2012). Conversely, dinoflagellates dominated in warmer conditions during negative NAO periods in the sub-polar region of the North Atlantic (Edwards, 2001, Henson et al., 2012). Long-term positive trends in phytoplankton biomass have also been associated with long-term trends in the NAO index, suggesting that the NAO may be a key driving factor in phytoplankton variability on inter-annual to decadal timescales (Barton et al., 2003, Henson et al., 2012, Zhai et al., 2013).

Investigations into multi-decadal scale variability in North Atlantic phytoplankton using in-situ observations have tended to focus on bulk phytoplankton properties such as total biomass or productivity (Edwards, 2001, Beaugrand et al., 2008), while studies exploring community composition generally focus on functional groups (Litchman et al., 2006, Boyd et al., 2010, Barton et al., 2016). There remains limited knowledge on the long-term variability in phytoplankton species composition at the taxon-specific level across the North Atlantic as observational studies are generally hampered by a lack of long-term data. However, changes in the community structure and relative abundances of species constituting functional groups may subsequently result in impacts to the wider marine food web and biogeochemical cycles.

In this chapter, I analyse multi-decadal variability in the North Atlantic diatom and dinoflagellate community composition using data from the CPR survey from 1969-2013. The CPR survey provides a unique multi-decadal view of plankton across the North Atlantic basin that resolves individual taxa and has followed a consistent sampling methodology since 1948 for phytoplankton and 1958 for zooplankton. I consider several ecological metrics describing the phytoplankton community and relate the temporal variability in these metrics to three environmental drivers; SST, MLD and the NAO index. The aim of this paper is to evaluate the stability of phytoplankton species composition in the North-East Atlantic, an environment that has changed substantially over the past half century, by testing the following hypotheses:

- There is no change in the diversity and structure of the phytoplankton community in the North-East Atlantic between 1969 and 2013
- The phytoplankton community can be considered stable over the study period using bio-disorder analysis
- There is no relationship between phytoplankton community structure and SST, MLD or NAO index in the North-East Atlantic

4.3 Methods

4.3.1 Phytoplankton community composition

The area of study is defined by four CPR Standard Areas (B5, C5, D5 and E5, Figure 4.1). This region encompasses sections of the temporal and sub-polar regions of the North Atlantic.

Information on phytoplankton species abundance was obtained from the CPR survey, whose methods are described in detail in section 3.1. Due to the mesh size and processing methodology employed by the survey I focus on dinoflagellate and diatom species composition on this temporal scale.

A total of 30,281 samples were collected between 1969 and 2013 across four standard CPR areas of the North-East Atlantic (Figure 4.1; Table 4.1). The time period 1969 to 2013 was chosen because the sampling effort was sufficient for annual interpolation of the data. Within these years, if a year contained less than 8 months of data it was removed from further analysis (resulting in the timeseries containing 43 years in region B5, 29 in C5, 22 in D5, 36 in E5). Data within the remaining years were linearly interpolated to create an annual mean of abundance for each phytoplankton species (Colebrook, 1975) unless 2 or more consecutive years were missing data. Phytoplankton abundances were then 4th root transformed to reduce the influence of the most dominant species (Clarke et al., 2008), and all species with a frequency of less than 1% for all CPR samples were removed from the dataset. By removing species that contributed to less than 1% of the community, smaller and poorly-sampled species such as coccolithophores were removed from the CPR dataset. Our statistical analysis of community composition therefore focuses on diatoms and dinoflagellates, organised in a community matrix of up to 45 years by 42 taxa for each region.

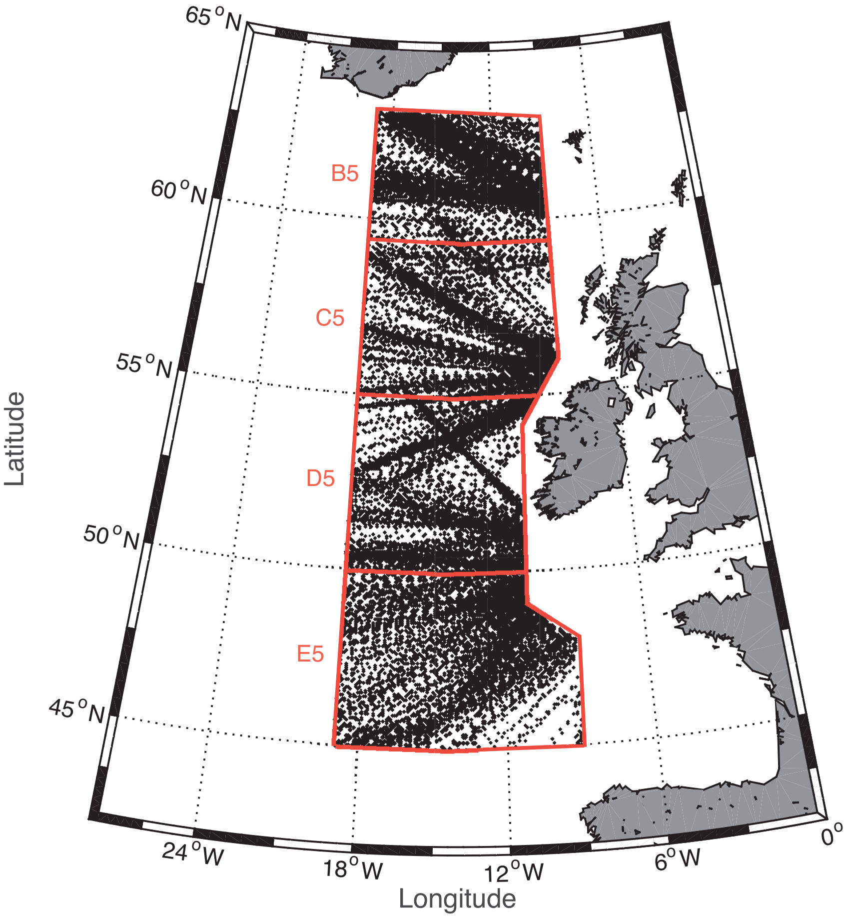

Figure 4.1: Map of the study site in the North-East Atlantic (45ºN to 63ºN, 10ºW to 20ºW). The CPR standard areas are highlighted in red and the individual samples collected by the CPR survey are represented by black dots.

PCI data from the CPR survey were also included in our analysis, detailed in section 3.1.1.1. The PCI is used as a semi-quantitative assessment of total community biomass, which accounts for the biomass of diatoms and dinoflagellates, as well as other micro- and nano-flagellates that were destroyed or too damaged for species identification while nevertheless contributing to the retained pigments (Richardson et al., 2006).

Table 4.1: Number of data points and percentage of missing months over the study period of 1969 to 2013 for each CPR standard area.

	Number of data points	Percentage of missing months
B5	10,076	13.1
C5	7,196	30
D5	6,440	42
E5	6,569	23.1

4.3.2 Environmental Data

In this study, the physical variables of SST, MLD and the NAO index were used to assess the controls of the phytoplankton community in North-East Atlantic. The methodology of these variables were described in section 3.2.

4.3.3 Statistical Analysis

Different statistical analyses were used to explore changes in community composition, relationships to environmental forcing, and the stability and potential for change within the phytoplankton community over time.

4.3.3.1 Characterizing long-term changes

To determine the presence of temporal changes in the SST and PCI time series and characterize their patterns, Environmental Change-Point Analysis was used. The R package ‘EnvCpt’ (Killick et al., 2016) automates selection between 8 models that are commonly used to represent environmental time-series: 1) a constant mean (no change), 2) a constant mean with background autocorrelation, 3) a long-term trend, 4) a long-term trend and background autocorrelation, 5) change points in the mean, 6) change points in the mean and background autocorrelation, 7) change points in the slope of the trend, and 8) change points in the slope of the trend with background autocorrelation. To select the best model to characterize a time-series, the Akaike Information Criterion (AIC) was used. The smallest AIC value indicates the best model fit, and the AIC difference between models is a measure of how significant the differences are (Killick et al., 2016, Killick et al., 2012). Results of EnvCPT analysis were used to identify breakpoints and trends in the physical environment that may be linked to changes in the phytoplankton community.

4.3.3.2 Analysis of community composition

To evaluate changes in community composition over time, Bray-Curtis dissimilarity coefficients (C_n) were calculated for each of the four CPR regions of the North Atlantic (Bray and Curtis, 1957, Legendre and Legendre, 2012, Anderson et al., 2011). This technique calculates a diversity measure that accounts for both the presence and abundance of species:

$$C_n = \left(\frac{2w}{n_a + n_b}\right)$$

where n_a is the total number of individuals in year *a*, n_b is the total number of individuals in year *b*, and $2w$ is the sum of the lowest value of abundances for species found in both year *a* and year *b* (Bray and Curtis, 1957). Bray-Curtis analysis matches abundances at a taxon-by-taxon level, comparing each year to all other years in pairwise testing. Resulting values of C_n range between 0 (two identical communities) and 1 (two entirely different communities) and take account of both the presence and abundance of taxon within a sample.

4.3.3.3 Relationship between phytoplankton composition and the physical environment

For each environmental variable a dissimilarity matrix was produced in order to apply a Mantel test (Mantel, 1967) to evaluate the relationship between the phytoplankton community structure and the environment. The Mantel test is a pairwise correlation that tests the null hypothesis that there is no relationship between two dissimilarity matrices (i.e. community data and an environmental parameter).

$$Z_M = \sum_{a=1}^{N-1} \sum_{b=a+1}^{N} {C_{n1}}_{ab} {C_{n2}}_{ab}$$

Where C_{n1} and C_{n2} are two dissimilarity matrices with *N* samples, in which *a* and *b* are row and column indices, the first being the community dissimilarity matrix and the second an environmental parameter. The resulting correlation coefficient, Z_M, ranges between -1 (a strong negative correlation) and 1 (a strong positive correlation), with 0 as no correlation and a *p* value indicating the significance of the relationship.

4.3.3.4 Analysis of taxon dominance

To further examine the structure of the phytoplankton community, the dominance of each species was calculated as the percentage contribution of an individual species to the total abundance. Species dominance allows for examination of inter-annual changes in specific taxa, as opposed to the whole community quantified in Bray-Curtis analysis.

4.3.3.5 Analysis of community stability

To assess the stability and potential for change within the phytoplankton community, two metrics were applied to each of the four standard areas of the North-East Atlantic. The first metric is a measure of resilience defined as the rate of return of a community to its mean state after a disturbance (Pimm, 1984). Communities with a high resilience to change demonstrate fast return times, whereas communities with lower resilience take longer to return to their mean state (Dakos et al., 2012, De Keersmaecker et al., 2014). In this study, the temporal relationship between the observed years is used as a measure of resilience and is expressed through the first-order autocorrelation. For the taxonomic time series, ts_A, with N observations from time t_1 to t_N, the resilience of a community is calculated as:

$$1 - \rho_1 = \frac{\sum_{i=2}^{N}(ts_A(i) - \overline{ts_A})(ts_A(i_{-1}) - \overline{ts_A})}{\sum_{i=1}^{N}(ts_A(i) - \overline{ts_A})^2}$$

where ts_A is the ecological time series (here the abundance of each diatom and dinoflagellate) and $ts_A(t_i)$ is the time series at time i (adapted from (Dakos et al., 2012, De Keersmaecker et al., 2014)). The resilience metric ranges between a value of 0 and 1. The lower the value of p_1, the more resilient a community is to disturbance and the faster it will return to its mean state after a disturbance.

The second test of resilience is a test of ecological variance used to assess the stability of a community. Ecological variance is defined as the total variability of a community and provides a more general measure of ecological stability than measures such as resilience (De Keersmaecker et al., 2014). The coefficient of variance (V) is calculated as:

$$V = \frac{S(ts_A)}{\overline{ts_A}}$$

where ts_A is the ecological time series and S is its standard deviation. Variance was normalised to the average of the time series ($\overline{ts_A}$) in order to aid comparison between sampled regions. Communities were deemed to have a relatively large sensitivity to change in the environment if they take a longer time to return to equilibrium after a disturbance and demonstrate a higher variance than less sensitive communities.

4.3.3.6 Analysis of community disorder

Community disorder (D_0) provides a method of evaluating changes in functional composition (Doncaster et al., 2016, Thébault and Fontaine, 2010). When a community's composition is disordered the structure of the community is determined by species turnover and has no relation to species richness, resulting in an altered composition when compared to other years. I analysed disorder following methods detailed in Doncaster et al. (2016), using the R function 'nestedtemp' in the 'vegan' library (Team, 2016, Oksanen and Carvalho, 2013).

Each disorder value was calculated from a community incidence matrix encompassing 10 consecutive years with *x* total species present during the 10-year period. The matrix was shuffled to order the years (in rows) by descending abundance from top to bottom and the species (in columns) by descending prevalence from left to right. A perfectly ordered matrix would have all presences in the top left, and all absences in the bottom right. Dividing these two extremes is the threshold of perfect fill calculated as:

$$y = (1 - [1 - x]^c)^{1/c}$$

for matrix coordinates (x, y) with c selected to create a curve that integrates to the same area as the proportion of presences (Oksanen and Carvalho, 2013). Any presence to the right of the threshold, or absence to the left, is classed as an anomalous observation, and disorder is quantified as a function of the sum across all surprise observations of squared deviations from the threshold. Values of disorder range between 0 for a perfectly ordered community to 100 for a completely disordered community (Rodriguez-Girones and Santamaria, 2006). A perfectly ordered community at 0 means that the year in the bottom row of the matrix has a species composition that is a perfectly ordered subset of the composition in the year above it in the matrix, and so on through all of the years, i.e. community composition in any year is determined by ordered accumulation and/or attrition of species from previous years. In contrast, complete disorder with a value of 100 means that the species composition in one year provides no information about composition in the year for the row above.

For each year of available data, disorder values were tested to examine if they were correlated with species richness, defined as the number of species present. Disorder was also tested for correlation with the Hills N_2 biodiversity parameter that considers the richness and evenness of the community (Hill, 1973), calculated as:

$$N_2 = \frac{1}{\sum_{\alpha=1}^{n} {A_\alpha}^2}$$

where A_i is the proportional abundance of species α in a community of n species, with abundance given by the square-root percentage presence (using R package 'vegan', Oksanen and Carvalho (2013)). Both species richness (R) and biodiversity (N_2) were calculated at the last time point in the matrix used for each 10 year period disorder calculation. Correlations were calculated using Pearson's product moment correlation on paired first differences in biodiversity (or species richness) and disorder values in consecutive years over the time series. This analysis required an unbroken time series. Consequently, in region B5 data from 45 consecutive years (1969 to 2013) were used, in region C5 32 years (1969 to 2000), for region D5 20 years (1969 to 1988) and region E5 45 years (1969 to 2013) of data were used. Other years from C5, D5 and E5 that could not be interpolated were discarded.

The sequential correlation coefficients between richness (R) and disorder (D_0) provide information on the relative occurrence of different types of species. A prolonged period of negative coefficients indicates a dominance of more persistent species over ephemeral species, as upward fluctuations in biodiversity are associated with an ordered species accumulation and downward fluctuations with disordered turnover. In communities of species that compete for similar resources, the most persistent species are likely to function as keystones, which shape community composition through strong inter-specific interactions that may exclude more weakly competitive 'canary' species (Doncaster et al., 2016). A switch from negative coefficients to a period of positive coefficients indicates a change to dominance of faster replicating weedy species (Doncaster et al., 2016).

4.4 Results

4.4.1 Temporal change in the physical environment and PCI

Fluctuations to the physical parameters showed variability in temperature, displaying a cooler and warmer period, but not in mixed-layer depth or NAO (Figure 4.2). All regions displayed an eventual change to a warmer regime (Figure 4.2a), whilst MLD remained between 35 and 65m (Figure 4.2b) and the NAO varied widely spanning from its lowest value in 1969 and 2010 of -2.5 to its largest value in 1990 of +2.5 (Figure 4.2c). The EnvCpt analysis conducted on the SST timeseries indicated that region B5 had an overall increasing trend with a change point in 1978, whereas regions C5, D5 and E5 all showed a change point in the mean during 1994 that shifted the environment to a warmer regime.

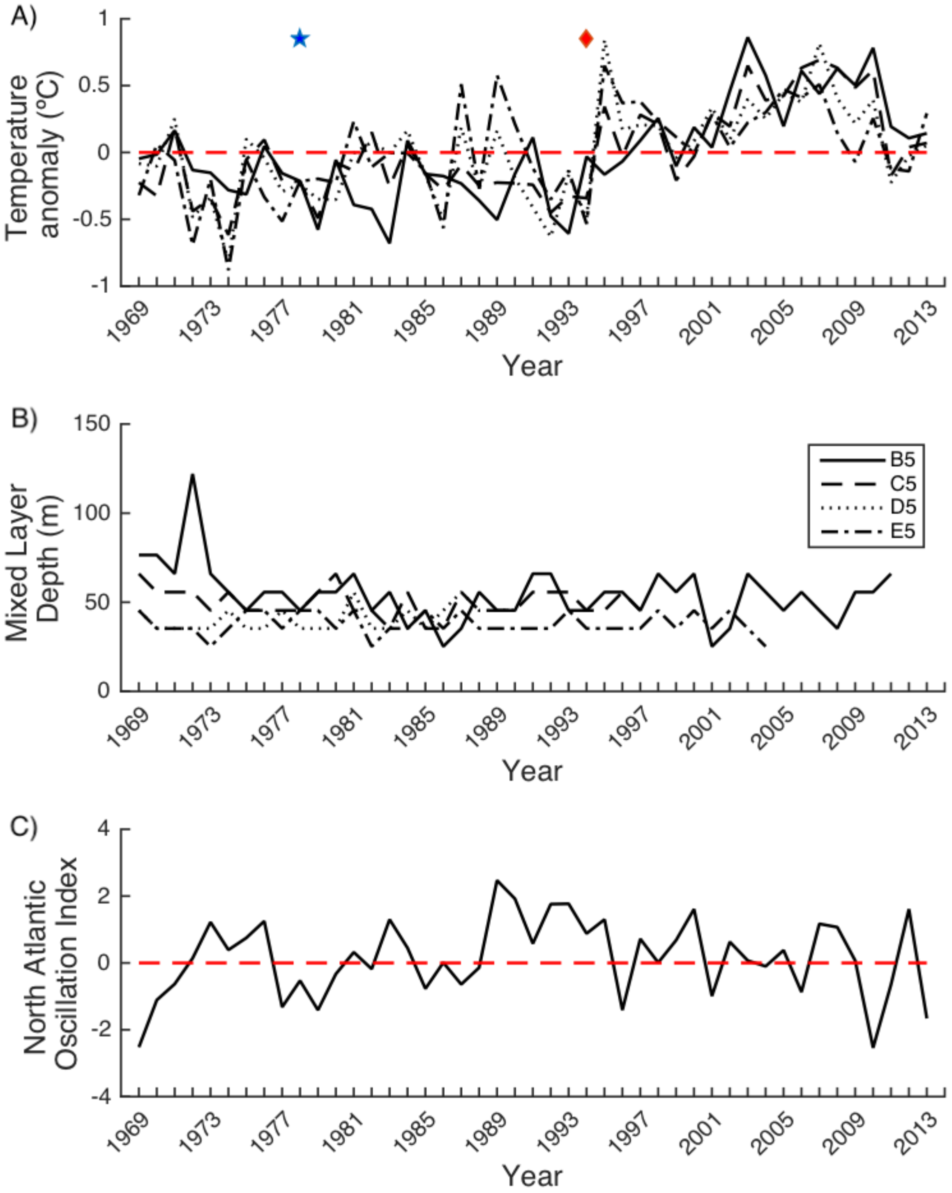

Figure 4.2: Variability in the physical environment for each CPR region over the study period of 1969 to 2013 (a) Sea surface temperature (ºC) anomalies, (b) Mixed Layer Depth (m) and (c) principle component-based North Atlantic Oscillation index (Ingleby and Huddleston, 2007, Hurrell et al., 2003). The blue star marks a change point in 1978 for region B5 and the red diamond for a change point in 1994 for regions C5, D5 and E5.

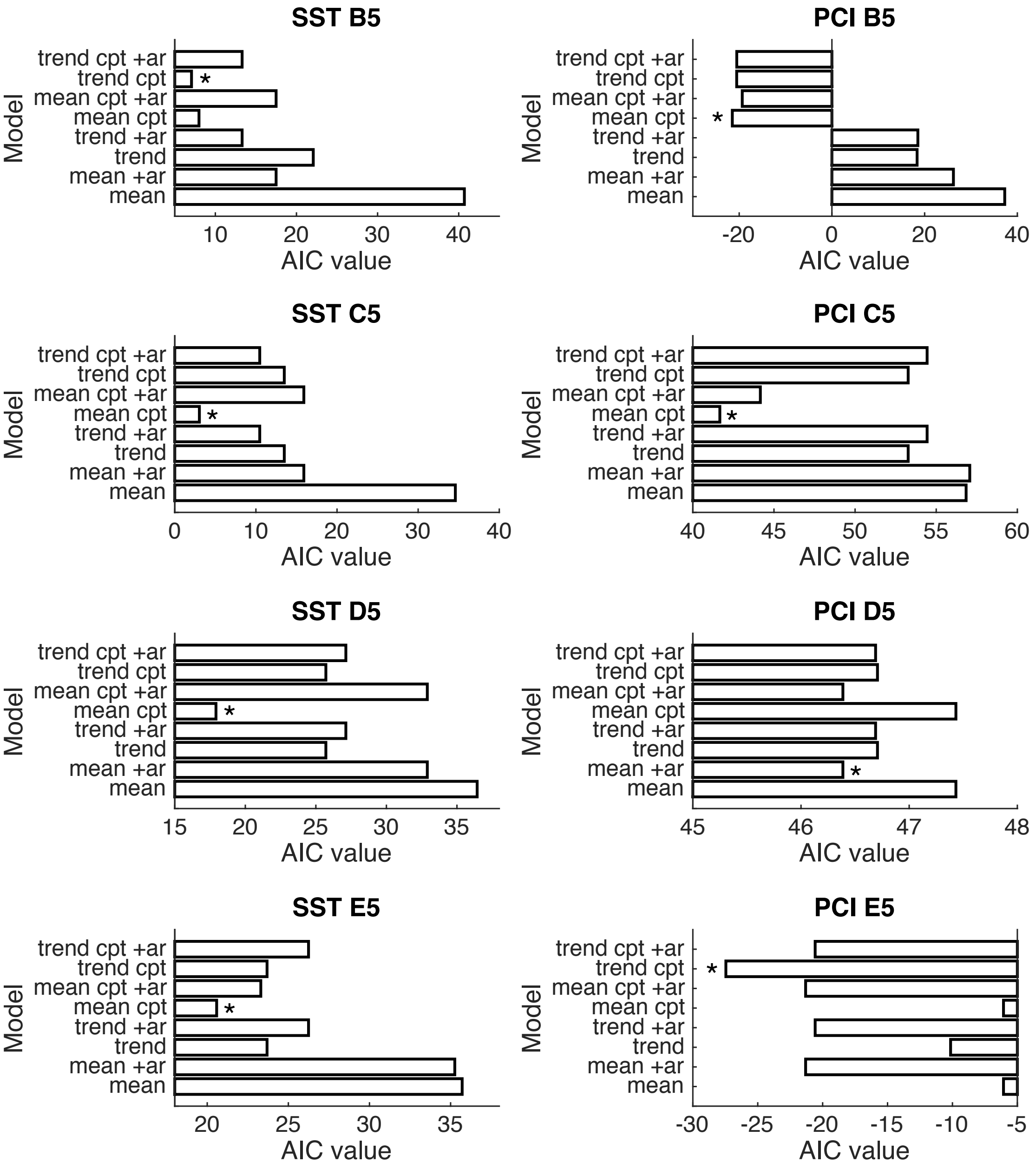

*Figure 4.3: Akaike Information Criterion from EnvCpt analysis for both SST and PCI in all regions of the North-East Atlantic. The model of best fit is indicated by * and the significance of the result is indicated by the difference in model AIC values. The abbreviation 'cpt' refers to change point and 'ar' refers to autocorrelation, for more details on each model see methods section of main text.*

Analysis of the PCI time series using the 8 models tested via the EnvCpt framework revealed structural changes for each region throughout the time series. The best fit model for the PCI timeseries within Region B5 and C5 was model 5, which indicated a positive change in the mean of the time series with change points in 1997 for region B5 and 1984 for region C5 (Figure 4.4). Small AIC values for this model compared to the other models suggest a good fit in the model choice (Figure 4.3). The region D5 time series was best modelled as mean with autocorrelation (model 2, constant mean with autocorrelation), however, the AIC value for this region was similar to model 6 which indicated a change point. The most robust model for the time series in region E5 was Model 7, which indicated an increasing trend with a change point in 1978 (Figure 4.3).

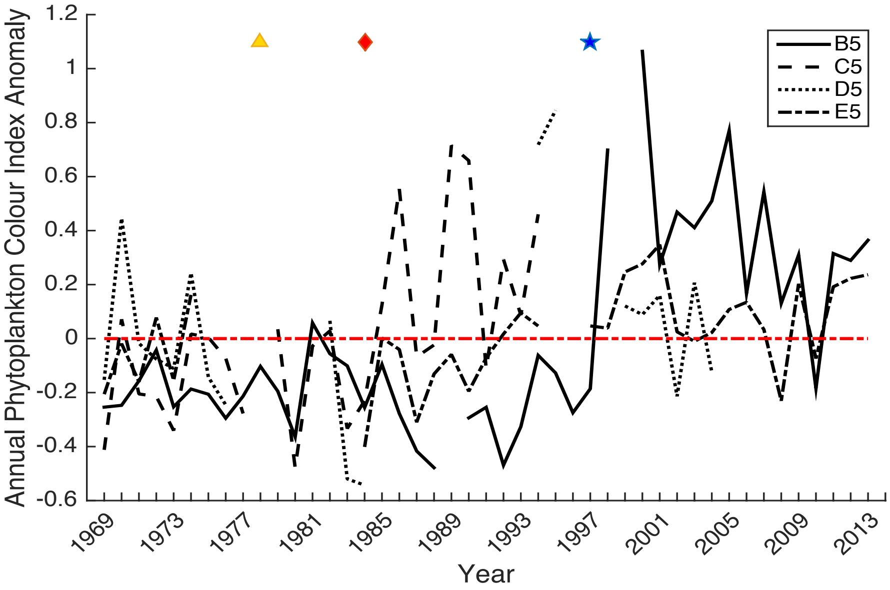

Figure 4.4: Phytoplankton Colour Index (PCI) anomalies for each CPR region over the study period of 1969 to 2013. The yellow triangle marks a change point in the trend for region E5 in 1978, the red diamond marks a change point in the mean for region C5 in 1984 and the blue star marks a change point in the mean for region B5 in 1997.

4.4.2 Temporal change in community composition

Bray-Curtis dissimilarity coefficients described variability in the phytoplankton community structure, accounting for changes in species presence and abundance through time. The Bray-Curtis analysis revealed clear inter-annual variability in the phytoplankton community composition between 1969 and 2013 for all four regions of the North-East Atlantic (Figure 4.5). The greatest changes in community composition occurred in region B5 during 1988, and region C5 in 1993. Taxon level examination of the data revealed that temporal changes in these two regions were caused by a large increase in the abundance of two diatom species: *Rhizosolenia styliformis* in region B5 and *Thalassiosira spp.* in region C5. Although there were peaks in the Bray-Curtis dissimilarity coefficient, all regions after 1994 returned to a level of inter-annual variability no greater than 0.05, representing only relatively small fluctuations in the community's composition over time (Figure 4.5).

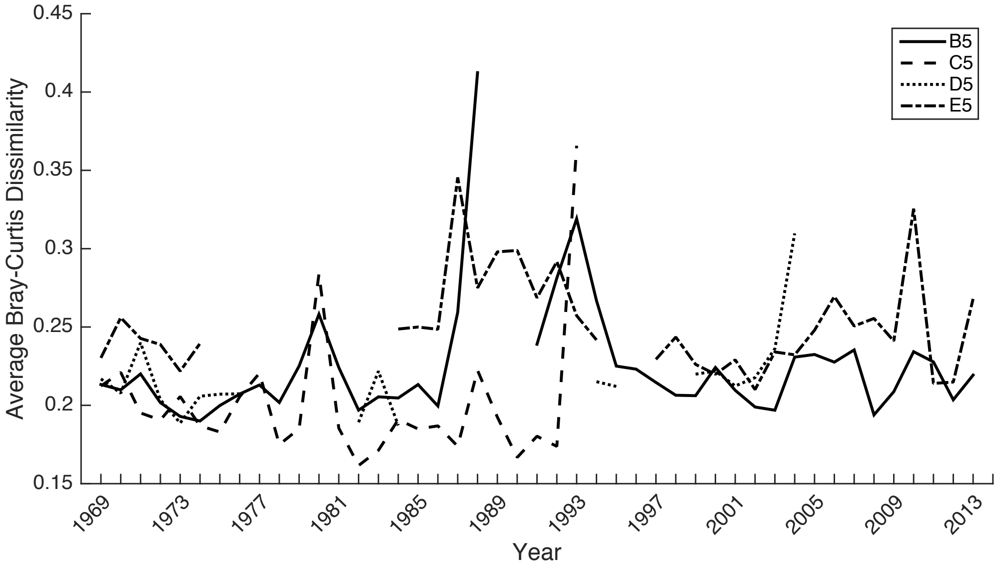

Figure 4.5: Community composition, represented by Bray-Curtis dissimilarity coefficients for each CPR region over the study period of 1969 to 2013. Bray-Curtis values range from 0 a community identical to other years, to 1 a community entirely different to other years.

Mantel tests revealed very little correlation between phytoplankton community composition, PCI and the physical parameters over the study period. Only three instances resulted in correlations that were statistically significant at the 95% level (p <0.05). The strongest correlation was between the Bray-Curtis dissimilarity coefficients and PCI, which was to be expected between two associated biological datasets (r = 0.31). This result demonstrates that PCI, used as a proxy for phytoplankton biomass, correlates weakly with the taxonomic information used in this study, reflecting the likely influence of smaller phytoplankton species in determining PCI (Batten et al., 2003). The only significant correlations between biological and physical parameters were between PCI and SST for region B5 (r = 0.18) and C5 (r = -0.18), and for phytoplankton community composition and MLD in region B5 (r = -0.14). Although statistically significant links were found in these few instances the correlation coefficients were relatively low and showed no consistent response of PCI to environmental forcing. Overall, the Mantel tests revealed weak to no relationship between the three physical parameters (SST, MLD and NAO) and the inter-annual variability of the biological datasets.

Examination of the contributions of different species to the community throughout the study period revealed few temporal changes, with the clear exceptions of the dominance of *Rhizosolenia styliformis* in region B5 during 1988, and *Thalassiosira spp.* in region C5 during

1993. The dinoflagellate assemblage across all four study regions was dominated by the *Ceratium* genus, particularly *Ceratium fusus* and *Ceratium furca*, while the diatom assemblage was dominated by the *Thalassiosira* genus. The low inter-annual variability in composition between 1969 and 2013 suggests that the phytoplankton community composition in the North-East Atlantic remained largely stable with the timeseries having a change in the key dominant species occurring between 1985 and 1995 before returning to its original state.

Ecological resilience (1-p_1) and variance metrics (V) applied to the biological data represent the stability of the phytoplankton community in the North-East Atlantic and its ability to return to community equilibrium after perturbation. Ecological resilience values (1-p_1) were predominantly close to zero for all four regions indicating a capacity for communities to return quickly to equilibrium following a disturbance in composition (Table 2). The phytoplankton community composition of region B5 was found to be the most stable, with a resilience value of only 0.0001 (

Table 4.2). The resilience value for region D5 however was exceptionally high compared to all other regions (0.4618) and may be the slowest to return to equilibrium following a perturbation. The ecological variability experienced across the North-East Atlantic was very similar in all regions.

The most abrupt change in disorder (D_o) occurred in region B5 around 1995, with a greater than two fold increase in disorder at a time of rising biodiversity (N_2) (Figure 4.6) and species richness (R, not shown here). Region E5 had two increases in disorder, the first in 1977 with return to low values of disorder before a second increase in 1997 (Figure 4.6). The decline of disorder values after each dramatic increase demonstrates that the community consistently returns towards a stable state (Figure 4.6). Such return further supports the results of the ecological resilience test that demonstrated the ability of phytoplankton to return quickly to equilibrium following perturbation (

Table 4.2). The timing of changes to the phytoplankton community were different between the Bray-Curtis and disorder analysis, reflecting how different signals and ecological characteristics can be detected by these techniques.

Table 4.2: Results of Ecological Resilience (1-p_1) and Ecological Variance (V) for averaged Bray-Curtis values, across each region of the North-East Atlantic.

	Ecological Resilience	**Ecological Variance**
	(1-p_1)	**(V)**
B5	0.0001	0.1817
C5	0.0165	0.1947
D5	0.4618	0.1604
E5	0.0026	0.1705

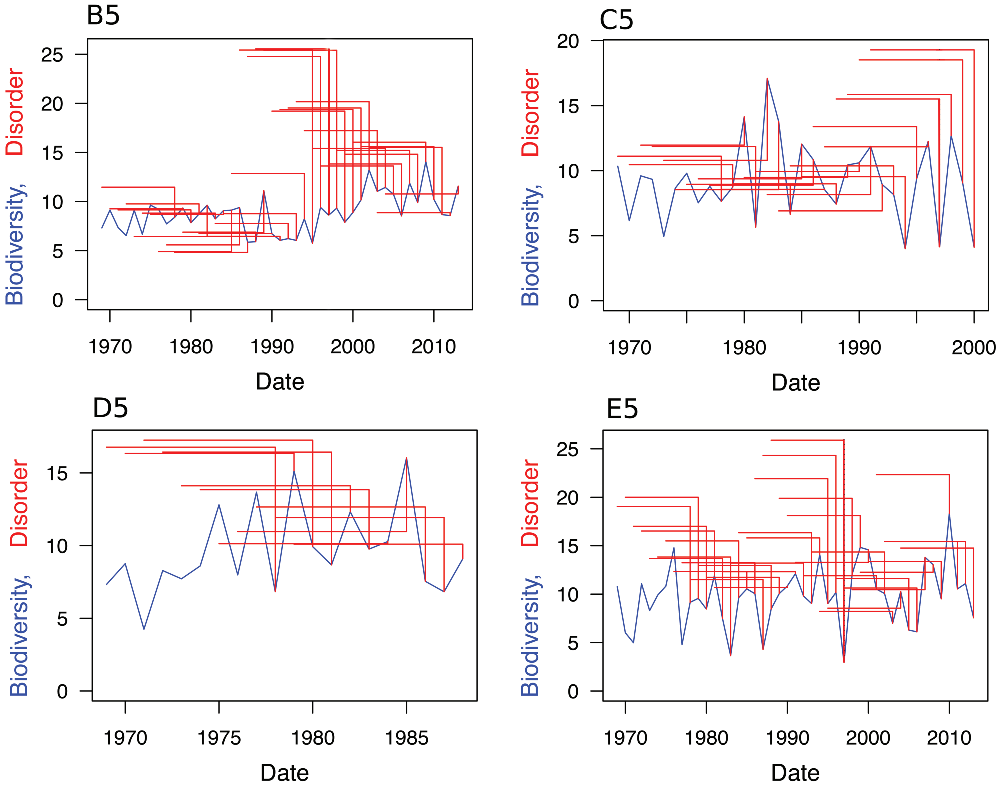

Figure 4.6: Results of disorder analysis for regions B5, C5, D5 and E5. Each plot displays the time series of disorder (D_0, red) and biodiversity (N_2, blue). Each red line joins the disorder value to its corresponding biodiversity value (vertical part), and stretches back through the 10 time steps used for calculation of disorder (horizontal part). Note the different scales on each y-axis.

Sequential correlations were calculated on the first differences of each time series to provide insight into the population dynamics of different types of taxa (Figure 4.7). Regions B5 and E5 showed a switch in the sign of sequential coefficients of correlation on first differences from

1997 onwards, to a more positive correlation between disorder and biodiversity, and a more negative correlation between disorder and species richness (as indicated by the difference in the green and orange traces in Figure 4.7). These switches were consistent with recent samples having species influxes, with an increasing prevalence of frequently-present (potentially competitively-dominant) species. Species out-fluxes in contrast would result in a more even spread of abundances, with turnover and loss principally of ephemeral (potentially canary) species. Sequential correlation of first differences for regions C5 and D5 find both biodiversity and species richness switch to a more negative correlation (as indicated by the difference in the green and orange traces in Figure 4.7), implying greater disorder from the early 1990s (Figure 4.7).

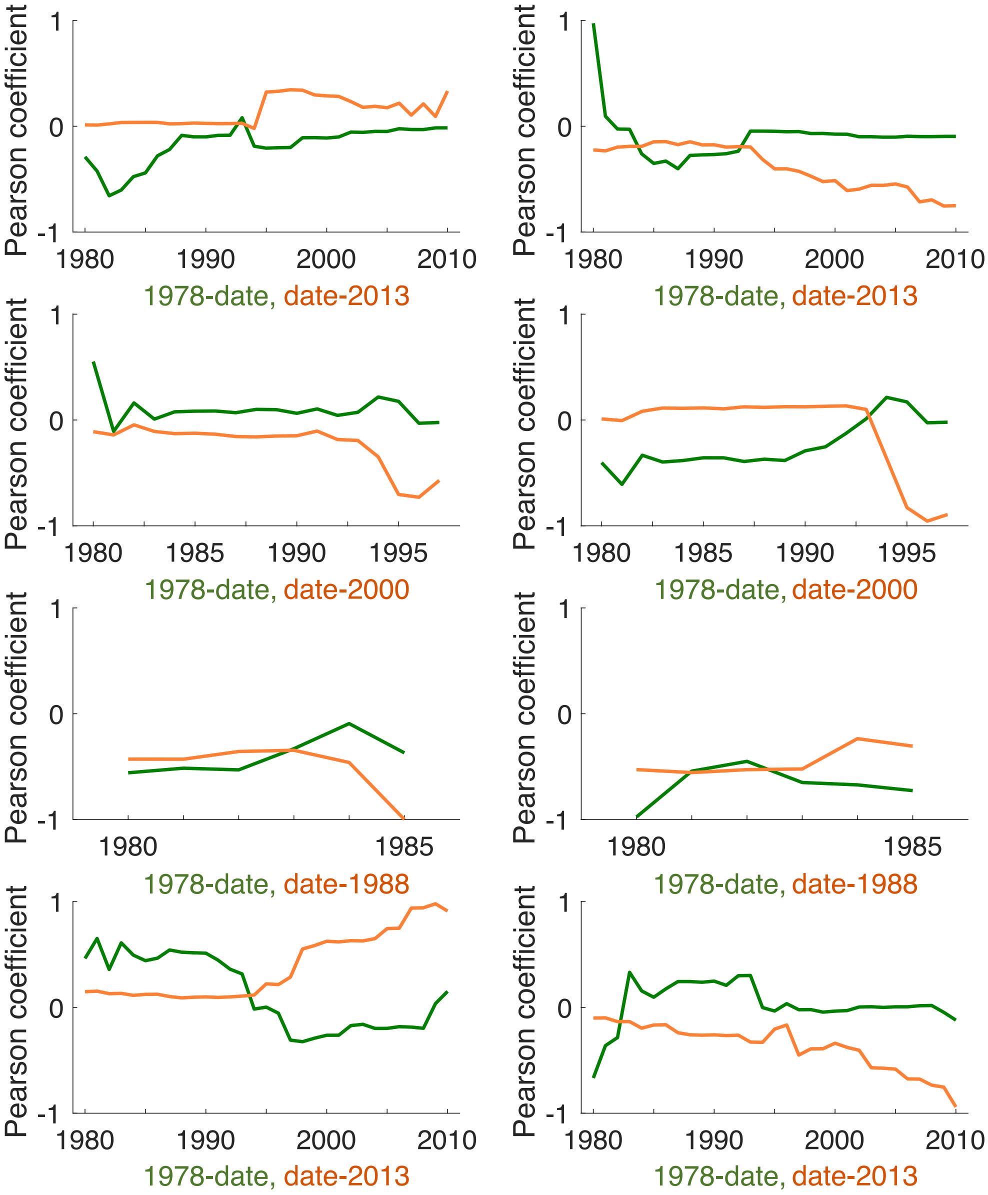

Figure 4.7: Sequential product-moment correlations calculated on first differences of disorder (D_o) with biodiversity (N_2) and species richness (R) for each CPR standard area. Green trace calculates correlations backwards from the x-axis date to 1978; orange trace calculates correlations forward from the x-axis date to 2013. Switches in correlation from between the green and orange trace indicate changes to the community composition.

4.5 Discussion

4.5.1 Inter-annual variability of phytoplankton community structure

This study provides new insight into the consequences of changes to the physical environment for phytoplankton community structure in the North-East Atlantic at a taxa level. Bray-Curtis analysis demonstrated that the community remained relatively stable between 1969 and 2013, regardless of the variability in the physical environment (Figure 4.3 and Figure 4.4). In region B5 during 1988, and region C5 in 1993 the community composition temporarily positively veered away from its equilibrium due to a substantial increase in abundance of two centric diatom species, *Rhizosolenia styliformis* in region B5 and the *Thalassiosira* genus in region C5 (Figure 4.5). However, no links with the physical environment were found to explain these years of dramatic community change.

The lack of long-term variability in the species composition despite the observed increase in SST could potentially be explained by the fact that the majority of the species in this region have large thermal ranges, many of which span the annual average SST for each region as well as the inter-annual variability (Irwin et al., 2012, Barton et al., 2013). The community could thus be well adapted to withstand the changes in annual mean SST observed in the North Atlantic, leading to a weak coupling between community structure and the physical environment over inter-annual time scales.

The dominant community members were found to have cosmopolitan distributions spanning large areas of the North Atlantic beyond the studied CPR regions and thus are expected to have a large thermal range, which is further evidence that broad temperature tolerance is important for the observed phytoplankton community stability (Barton et al., 2016, Barnard et al., 2004). For example, the dinoflagellate composition proved to be highly stable in terms of species dominance, with *C. fusus* dominant amongst our observed taxa throughout the time series for areas B5, C5 and D5. *C. fusus* has a wide biogeographic distribution (Beaugrand, 2004, Barnard et al., 2004) and thermal niche (Irwin et al., 2012, Barton et al., 2013) that potentially allows this species to remain dominant under changing SST conditions through inter-specific competition with other species (Barnard et al., 2004). Similarly, the observed diatoms were dominated by the *Thalassiosira* genus, which also has a broad bio-geographical range (Beaugrand, 2004, Richardson et al., 2006, Barnard et al., 2004).

The disorder analysis provided a unique assessment of phytoplankton community composition in terms of structural rigidity and unpredictability over the study period. Changes in disorder demonstrated fluctuations in the relative dominance of persistent species over ephemeral species in the community, with the most abrupt change occurring in region B5 around 1995, with an increase in disorder at a time of rising biodiversity (Figure 4.6). Supporting prior dominance analysis, *C. fusus* and the *Thalassiosira* genus may be considered as 'keystone' species to the community structure, i.e. species that dominate the community regardless of the physical environment by occupying wide niches. Sequential correlations suggested a high turnover of ephemeral species in more recent years, in favour of more persistent and potentially competitively dominant species. Although this variability in the structure of the community was detected in disorder analysis, the magnitude of disorder never exceeded 25 indicating that no more than a quarter of the community changed in any given year, as also reflected in the magnitude of the Bray-Curtis analysis. Although no large or persistent shifts were detected in the community over the studied time period, ecological theory suggests that an increase in the strength of interactions between species will raise the structural rigidity of the community and render it more prone to collapse from external forcing (Doncaster et al., 2016).

The analysis of PCI across the North-East Atlantic demonstrates an increase in the mean that contrasts with the stability suggested by the Bray-Curtis community analysis (Figure 4.4 and Figure 4.5). Previous studies have linked changes in phytoplankton community biomass, through the use of the PCI from the CPR survey and satellite derived Chl-a measurements, to changes in the physical environment over inter-annual timescales (Raitsos et al., 2005, Martinez et al., 2016, McQuatters-Gollop et al., 2007a). As a proxy for biomass, PCI allows insight into a greater proportion of the 'true' in-situ phytoplankton community that was not fully taxonomically resolved in this study. The initial data manipulations conducted, as well as the mesh size of the CPR device and counting procedure by the analysts, exclude many smaller and potentially less cosmopolitan species. Previous studies have reported a general decline in PCI until the late 1980s and then an increase beyond the 1990s, which tend to agree with the findings of our study (Figure 4.4) (Edwards, 2001, Beaugrand and Reid, 2003, Martinez et al., 2016, Raitsos et al., 2014). Future work should examine a larger proportion of the in-situ community for species based population changes, including species smaller than those captured by the CPR and species outside the diatom and dinoflagellate functional groups and consider larger geographical regions.

4.5.2 Implications for the bottom-up control of community structure

The relationship between phytoplankton and the physical environment on inter-annual timescales has been widely debated (Barton et al., 2014, Dakos et al., 2009, Prowe et al., 2012), however, the weak correlations between the physical environment and community composition in this study were unexpected and largely contrasted with the outcomes of prior studies. Beaugrand and Reid (2003) suggested that an increase in global temperatures would lead to a marked change in the organisation of phytoplankton communities within the North Atlantic and such links have been demonstrated in studies showing dinoflagellates dominate over diatoms in warmer SST regimes (Leterme et al., 2005, Henson et al., 2012, van de Poll et al., 2013). The influence of the NAO on the marine environment across the North Atlantic has also been well documented (Drinkwater et al., 2003, Barton et al., 2003, Henson et al., 2012). The effect on phytoplankton is suggested to be that diatoms dominate in positive NAO years when conditions create a cooler climate with stronger wind stress and deeper mixed layers, whereas during negative NAO periods (where the reverse conditions occur) dinoflagellates dominate (Edwards, 2001, Henson et al., 2009, Henson et al., 2012). Increased temperatures were suggested to also cause a reduction in the overall cell size of the phytoplankton community and reduce the ecological diversity in warmer regions (Edwards et al., 2013a). Our Mantel test results, however, found that for this region of the North-East Atlantic between 1969 and 2013, the phytoplankton community remained relatively stable with little change in composition. Furthermore, when changes did occur, such as in region B5 during 1988 and region C5 in 1993, the community soon returned to its original state (Figure 4.5).

Our analysis of the PCI time series revealed structural changes for each region throughout the studied time series, in agreement with the inter-annual analysis of Barton et al. (2014). In their study, Barton et al. suggested that physical changes in the environment in the North-East Atlantic (surface wind speed, heat flux, SST, mixed layer depth, stratification and turbulent kinetic energy) were strongly related to phytoplankton on seasonal timescales but had little influence on the long-term (inter-annual) structure of phytoplankton communities.

As inter-annual fluctuations in community structure were not statistically linked to changes in the physical environment, I speculate that the variability of phytoplankton populations on interannual timescales may be driven by other factors, e.g. chaotic variability or zooplankton grazing (Dakos et al., 2009, Barton et al., 2014). Dakos et al. (2009) utilised a model to describe variability of phytoplankton over seasonal and inter-annual timescales without the requirement for external forcing. Inter-annual variability within the phytoplankton population was found to be a naturally occurring property of multi-species communities, with chaotic fluctuations occurring frequently without environmental perturbation (Dakos et al., 2009). Population chaos has also been demonstrated in mesocosm experiments in which community fluctuations occurs without external forcing (Benincà et al., 2008).The results of the Mantel test determined that there was no relationship between the phytoplankton community structure and changes to the physical environment. However, variability in the community may have resulted from the chaotic nature of a multi-species phytoplankton community, as described by Dakos et al. (2009), and that this could be the driver of community fluctuations on inter-annual scales.

4.5.3 Stability of phytoplankton in the North-East Atlantic

The apparent stability of the phytoplankton community in the North-East Atlantic identified by our analysis, suggested that the community is well suited to the environmental perturbations within the study period. When multiple species are well adapted to withstand environmental perturbations, I can expect a community to remain stable throughout time as demonstrated by the North Atlantic community examined here (Colebrook, 1982, Leterme et al., 2005, Beaugrand et al., 2008). Observed changes in SST, MLD and NAO index demonstrate variability in the physical environment in the North-East Atlantic (Figure 4.2). Investigation of species thermal ranges and biogeographical distributions reported in the literature show that the majority of species enumerated in the CPR survey have a large thermal tolerance that spans across the total SST variability from region B5 to E5 likely reducing their susceptibility to population change due to variable SST (Irwin et al., 2012, Barton et al., 2013). Coupled with this, the prevalence of other inter-annual variability, including the NAO, may contribute to the cosmopolitan distribution of species and the resilience of the community to environmental change. The robustness of the phytoplankton community to long-term change in the physical environment has also been demonstrated in the fossil record, assessed also with Bray-Curtis analysis (Cermeño et al., 2010), where the biodiversity and community structure of marine diatoms were found to recover after significant environmental perturbations. Cermeño et al. (2010) suggested that the high dispersal of marine phytoplankton, resulting in large bio-geographical distributions, ensured the survival and recovery of the community (Cermeño et al., 2010, Cermeño and Falkowski, 2009).

The observed stability and predictability of the community contrasts with the results from some model studies which predict that continued global warming will alter the phytoplankton community composition (Barton et al., 2010, Bopp et al., 2013, Dutkiewicz et al., 2015). For example, Barton et al. (2016) demonstrated that phytoplankton communities appear poised for a bio-geographical shift and community re-shuffle in the dominance of key members in the second half of the 21st century. The shift was predicted to result in decreased species richness in sub-tropical regions and an increase in sub-polar regions, as only approximately 35% of local species survive in future environmental conditions (Barton et al., 2016). The Bray-Curtis analysis and stability metrics shown here demonstrate that even with changes to the physical environment the community was able to return to its original state after perturbation, when a change to the dominance of key species occurred between 1985 and 1995, suggesting that larger temporal and spatial studies may be required to observe the changes demonstrated in Barton et al. (2016).

The findings here also contrast with results from the North Sea region, where a regime shift in the 1980s resulted in an increase in PCI values which was linked to increased SST (McQuatters-Gollop et al., 2007b, Raitsos et al., 2014). The North Sea a relatively closed basin and shallower than the North-East Atlantic, which may increase the impact of changes to the physical environment compared to a more open ocean basin. The regime shift described in the North Sea was also detected in PCI which encompasses information from a greater proportion of the in-situ community. Changes in the phytoplankton community may therefore be occurring in the smaller size fraction not captured in this study (McQuatters-Gollop et al., 2007b, Raitsos et al., 2014). While a regime shift was not detected in the North-East Atlantic here, the results of the disorder analysis highlighted that the community structure remained similar towards the end of the timeseries, which may make future communities more susceptible to collapse if a negative external pressure was apparent (Doncaster et al., 2016).

4.6 Conclusion

The findings presented here suggest that the mechanisms driving long-term ecological change in phytoplankton community composition within the North-East Atlantic are highly complex and perhaps more uncertain than previously described. The temporal and spatial extent of the CPR survey allows for a unique insight into the long-term variability of phytoplankton communities in the North-East Atlantic due to its unchanged methodology and consistent taxonomic detail. I found little or no correlation between diatom and dinoflagellate community composition and SST, MLD or the NAO index.

There was a change in the community composition between 1985 and 1995 from its initial state due to an increased dominance of two diatom species, however after this period the community returned to its previous composition. As such the diversity of the community remained relatively unchanged over the time series despite a shift to increased SST in the mid 1990s. This stability was confirmed by tests of ecological resilience, which revealed high resilience of community composition over the time series. The resilience may be explained by the fact that the majority of species identified by the CPR have thermal tolerances greater than the environmental variability experienced. This study examined changes in the diatom and dinoflagellate fraction of the phytoplankton community captured by the CPR survey. I recognised however that the community assessed here does not contain the smaller sized fraction of the in-situ phytoplankton community, which may manifest different patterns of variability than the larger size fraction captured by the CPR survey.

To conclude, our analysis demonstrates the ability of the phytoplankton community to return quickly to equilibrium composition after environmental perturbation, with a relatively stable community composition between 1969 and 2013 in the North-East Atlantic. With no clear relationship with the physical environment, I suggest that interannual variability in phytoplankton community composition may be driven by other factors, including internal community forcing such as chaos (Dakos et al., 2009).

Chapter 5 Inferring the inter-annual control of plankton communities across the North Atlantic.

5.1 Abstract

The oceanic environment is changing rapidly in response to global climate change, especially in higher latitudes with increased pressure from rising temperatures. Marine plankton are highly sensitive indicators of oceanic change due to their size and dependence on the physical environment but also hold important roles in the marine ecosystem, such as forming the base of the marine food web.

Relationships between phytoplankton and the physical environment have been frequently examined over a variety of spatial and temporal scales. However, our understanding of the influence of zooplankton communities acting as a top-down pressure on phytoplankton remains relatively understudied over inter-annual timescales. While the environment may change through time, so may predator and prey relationships, and has the potential to alter the relative balance of top-down and bottom-up regulation of phytoplankton assemblages.

In this study, community abundance and richness from the CPR survey was used to examine relationships between phytoplankton, zooplankton and physical environment across the East and West North Atlantic using generalised additive models (GAMs). Results demonstrate a strong largely linear relationship between phytoplankton and zooplankton across the North Atlantic, however, there was little evidence of a relationship between phytoplankton and the physical environment on these interannual timescales. Zooplankton however, demonstrated a range of largely nonlinear response to the physical environment, that generally demonstrated a reduced response in colder temperatures with deeper mixed layers. While the general response of zooplankton to the physical variables was consistent across the North Atlantic, the strength and shape of the relationship varied greatly between the East and West sections of the Atlantic.

The variability in the response of plankton communities to environmental drivers suggested that on interannual timescales, traditional top-down or bottom-up concepts may be a simplification of reality and a combination of factors should be considered.

5.2 Introduction

The relationship between phytoplankton and the physical environment has been studied intensively across a variety of spatial and temporal scales. Over short timescales (~days to weeks), abiotic factors may affect phytoplankton both directly, such as SST altering metabolic rates (Eppley, 1972), or indirectly, such as through changes in stratification of the water column altering available light and nutrients (Edwards and Richardson, 2004, Adjou et al., 2012). Both pathways have the ability to affect the growth and metabolism of individuals in the community (Follows and Dutkiewicz, 2002, Dandonneau et al., 2004, McQuatters-Gollop et al., 2007a).

The influence of the physical environment as a bottom-up driving force has also been documented over inter-annual timescales with particular interest in the link between increasing SST, following reports from several climate models (IPCC, 2013), and phytoplankton biomass (Colebrook, 1982, Beaugrand and Reid, 2003, Beaugrand et al., 2008, Barton et al., 2014). Mixing and large scale advection processes in the open ocean have a potential impact on the distribution of phytoplankton species and have also been shown to enhance the diversity of the community (Adjou et al., 2012). Other environmental indicators, such as the North Atlantic Oscillation (NAO) index have also been suggested to be a key driving force over inter-annual to decadal timescales (Barton et al., 2003, Henson et al., 2012, Zhai et al., 2013) and the role of ocean dynamics in determining the distributions, abundance and diversity of phytoplankton has been demonstrated in model simulations (Barton et al., 2010, Adjou et al., 2012).

All biological populations are fundamentally dependent on a supply of nutrients, so it is expected that regulation will principally occur by bottom-up control, in which, higher trophic levels are regulated by lower trophic levels (Durant et al., 2013). However, as studies turn to examine the longer timescale implications of global climate change, the scope of relationships may need to change to include not only abiotic, but also biotic factors.

In comparison to physical studies, there are relatively few considering the top-down control of phytoplankton by zooplankton on inter-annual timescales, and even fewer that assess the importance of both bottom-up and top-down controls on phytoplankton simultaneously (Beaugrand and Reid, 2003, Adjou et al., 2012, Kerimoglu et al., 2013, Dakos et al., 2009, Barton et al., 2014). Studies that have examined the inter-annual relationship of phyto- and zooplankton have been primarily focused in the Eastern North Atlantic. Outcomes have consistently documented the importance of top-down mechanisms in determining phytoplankton abundance and diversity, with zooplankton tracking changes in the phytoplankton population (Beaugrand and Reid, 2003, Prowe et al., 2012).

Ecological theory tends to focus on the unidirectional approach of bottom-up and top-down controls on a community, however, in a dynamic system such as the ocean, these concept's may not be so straight forward. As the environment changes through time, predator and prey relationships may also change, having the potential to alter the relative balance of top-down and bottom-up regulation of plankton assemblages (Martinez et al., 2016, Boyce et al., 2010, Beaugrand et al., 2002, Behrenfeld, 2010, Edwards and Richardson, 2004, Barton et al., 2014). For example, changes to the timing of overwintering in copepods or dormant phases in dinoflagellates could alter species relationships through mismatches in predation and competition for nutrient resources (Rose and Caron, 2007, Kiørboe and Hirst, 2008, Kerimoglu et al., 2013).

The majority of studies focus on the Eastern North Atlantic and adjacent coastal seas (Beaugrand and Reid, 2003, Leterme et al., 2005). However, the Western North Atlantic is also of great importance, with the subpolar gyre hosting some of the most widespread phytoplankton blooms globally (Sabine et al., 2004).

In order to examine the relationships between plankton groups and the physical environment a spatially and temporally extensive dataset is required, as these complex ecological interactions are likely non-linear and require a longer timeseries to be studied (Giron-Nava et al., 2017). One such dataset is compiled by the CPR survey. Although the CPR does have limitations (see section 5.55.5), when previously compared with other studies it has been found that the CPR generally provides reliable and consistent semi-quantitative index of phytoplankton and zooplankton abundance, capturing real seasonal and inter-annual changes (Richardson et al., 2006, Barton et al., 2003).

5.2.1 This study: Aims

In this study, GAMs were used to assess the relationship of both phytoplankton and zooplankton abundance and richness to each other and the physical environment across seven regions of the North Atlantic basin, defined by CPR standard areas (Figure 5.1). Over inter-annual timescales, the response of the community abundance and richness was used to investigate whether there is a clear top-down or bottom-up control on the plankton community by assessing the following questions:

- Are the Eastern and Western Atlantic communities of plankton different?

- Does the response of phytoplankton abundance and richness, on inter-annual timescales, relate to the physical environment and/or the copepod community?
- Does the response of zooplankton abundance and richness, on inter-annual timescales, relate to the physical environment?
- Is it possible to infer top-down or bottom up relationships on inter-annual time scales?

While I recognise that significant correlations do not imply causality, the presence of consistent relations that support our hypothesis under question, are considered significant relationships.

5.3 Methods

5.3.1 The Continuous Plankton Recorder survey

Abundance indices and richness for a representation of the phytoplankton and zooplankton community was provided by the CPR survey, as detailed in section 3.1. Due to the sampling methodologies employed by the CPR survey, the phytoplankton community is represented by the diatom and dinoflagellate functional groups and the zooplankton community is represented by the copepods.

A total of 48,586 samples were collected between 1958 and 2013 across seven standard CPR areas of the North-East and North West Atlantic (Figure 5.1). If a year contained less than 8 months of data it was removed from analysis, and the remaining years were linearly interpolated to create an annual mean (Colebrook, 1975).

Abundances were 4th root transformed to reduce the influence of the most dominant species (Clarke et al., 2006), and all species with a frequency of <1% for all CPR samples were removed from the dataset. By removing species that contributed to less than 1% of the community, smaller and poorly-sampled species such as coccolithophores were removed from the CPR dataset.

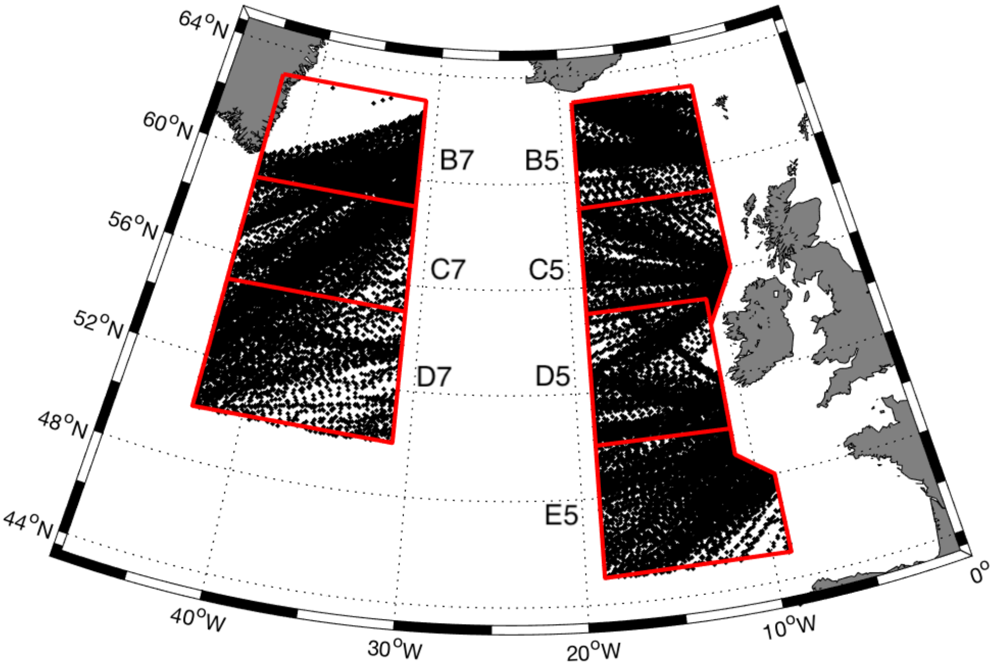

Figure 5.1: Map of the North Atlantic Eastern and Western regions and CPR areas. Each CPR standard areas are highlighted in red and the individual samples collected by the CPR survey are represented by black dots.

5.3.2 The Physical Environment

In this study, the physical environment is represented using SST, MLD, NAO and AMO variables, which are detailed in section 3.2.

5.3.3 Principle Component Analysis

Physical oceanographic variables are serially correlated temporally and spatially, and often have high covariation between variables. To account for this and provide a broader picture of the physical environment in the North Atlantic, principle component analysis (PCA) was applied to the 4 oceanographic variables (SST, MLD, NAO and AMO). PCA was calculated across the mean of the East (B5, C5, D5 and E5) and West (B7, C7 and D7) regions first and then for each individual CPR region. Only principle components (PCs) with eigenvalues >1 were retained and used in the following analysis, as the bottom-up forcing factor, resulting in two PCs per test.

5.3.4 Statistical Analysis

To assess changes to the plankton community, the following statistical analysis were performed on the phytoplankton and zooplankton data.

5.3.4.1 nMDS and ANOSIM:

Non-metric Multidimensional Scaling (nMDS) is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin, 1987) and was used here to examine whether the North Atlantic should be assessed as a whole or divided into Eastern (B5, C5, D5 and E5) and Western (B7, C7 and D7) regions. Analysis of similarities (ANOSIM) provided a way to test whether there was a significant difference between the two groups of sampling units, East and West.

5.3.4.2 Generalised Additive Models (GAMs)

I applied GAMs to assess the year to year response of phytoplankton and zooplankton to each other, as well as the physical environment between 1958 and 2013. GAMs are an extension of Generalised Linear Models that allow for the exploration of nonlinear relationships without requiring a priori knowledge and due to their flexibility for data types, are becoming increasingly popular to explore complex interactions in marine ecology (Chen et al., 2012).

Here, GAMs were applied to the CPR data in two stages. First, the North Atlantic was assessed for 2 regions, the East (B5, C5, D5 and E5) and West (B7, C7 and D7), within which each of the CPR standard areas were included as a categorical factor. Secondly, a new model was performed for each CPR area to assess the response of plankton to the biotic and abiotic factors of that specific CPR region. As there are multiple CPR areas to be used as categorical factor, an ANOVA can be applied to the final model to provide a compact assessment of whether the CPR area has a significant effect on the response variable (Zuur et al., 2009).

For each GAM, the response of phytoplankton abundance and richness was tested against the predictor variables of zooplankton and PC1 and PC2 for the physical environment, and then the response of zooplankton abundance and richness was tested against the PCs for the physical environment. By performing the GAM analysis on both the studied phytoplankton and zooplankton communities I can aim to infer whether the control of plankton is a simple, top-down or bottom up relationship on inter-annual scales.

In all GAMs, ‘Year’ was added as a linear un-smoothed variable to account for long-term changes through time. Autocorrelation between sequential observations was tested for using, ACF and variograms. Further to this a continuous autoregressive correlation structure (CAR-1) was added to the model that was then tested against the original model using an ANOVA (Zuur et al., 2009). For all tests, an autocorrelation structure was not required, likely due to the temporal scale the plankton populations are assessed at in this study (i.e. annual means).

The Gaussian family with Identity Link were the best fit for abundance data and negative binomial family with log link were used for community richness (Zuur et al., 2009, Wood, 2017). A forward and backward fitting procedure was used to remove insignificant predictor variables for each model in order to improve model fit and the deviance explained, I retained variables considered highly significant ($p= <0.05$). Best fit 'final' models were selected using Analysis of variance (ANOVA) and the Akaike's information criterion (AIC). It must be noted that AIC rewards goodness of fit of model output to raw data, however, this does not reflect the quality of the model itself and only its goodness in reference to other tested models.

For all models, checks were made to assure the validity of the model. Homogeneity was checked by examining the residual values versus the fitted values, normality was assessed using QQ-plots and histograms and the model fit was also visually examined, this is demonstrated in appendix B (Zuur et al., 2009). A comparison of initial GAMs using all predictor variables, and final GAMs with only the significant variables retained, are also demonstrated in appendix B.

Analysis was performed using the mgcv package (Wood, 2017) in the software R (Team, 2016).

5.4 Results

5.4.1 Results of nMDS and ANOSIM

MDS plots for phytoplankton and zooplankton (not shown here) displayed clustering of the Eastern and Western sites to form two separate groups. The stress results for phytoplankton (0.091) and zooplankton (0.081) indicate this was an accurate representation of the data.

ANOSIM analysis was then performed with the four Eastern sites clustered into one group and the three Western sites clustered into another. For both phytoplankton ($R = 0.63$, $p = 0.02$) and zooplankton ($R = 0.39$, $p = 0.05$) results indicate there was greater between group variance than within group, and as such the East and Western regions were treated independently to each other in further statistical analysis.

5.4.2 Results of PCA

Only PCs with an eigenvalue greater than one were retained for use to represent the physical envirnonment in the GAM analysis. This resulted in two principle components being retained for each of the seven regions of the North Atlantic. The selected PCs cumulatively accounted for 70% or more of the variability in the four original physical variables (SST, MLD, NAO and AMO).

The resultant loading for each PC in the East and West GAM test are displayed in Table 5.1. As we can see, PC1 across the Atlantic largely represents variability in the SST and MLD, while PC2 largely represents the NAO and AMO signals. Note that the sign of the loadings differs between the East and West regions (Table 5.1).

Table 5.1: Results of PCA. Rotation loadings of PC1 and PC2 for the East and West Atlantic. Bold values represent a >0.5 or <-0.5 loading.

	West		***East***	
	PC1	**PC2**	**PC1**	**PC2**
SST	**-0.653**	-0.004	**0.594**	-0.226
NAO	0.008	**0.793**	-0.038	**-0.797**
MLD	**0.574**	-0.406	**-0.643**	0.225
AMO	-0.493	-0.454	0.483	**0.513**

5.4.3 Results of GAMs

GAMs were used to analyse the response of phytoplankton to zooplankton and the physical environment across the North Atlantic. Forward and backward fitting procedures and the use of AIC values were used to find the best model to demonstrate the response of the phytoplankton community.

For the Eastern Atlantic abundance and richness and Western Atlantic richness values, this resulted in Zooplankton was the only statistically significant predictor variable (Table 5.2). For Western phytoplankton richness both Zooplankton and PC2 (increased NAO index) of the environment were statistically significant (Table 5.2). In all models, zooplankton abundance/richness was a significant (p = <0.05) predictor variable with a positive correlation to phytoplankton abundance/richness (Figure 5.2, A-C and E). In the case of abundance responses in the Western Atlantic and richness responses in the Eastern Atlantic, the final model was best fit as a linear response (Figure 5.2, A and E) as reflected in the estimated degrees of freedom (edf) being equal to 1.

The only phytoplankton model that also had a significant (p = <0.05) response to the physical environment was richness in the Western Atlantic (Table 5.2; Figure 5.2, C and D). Here, phytoplankton richness had a non-linear response to PC2 (predominantly representing the NAO index (Table 5.1)), increasing in response to a peak at PC2=0.5 and thereafter decreasing in response to when PC2>0.5 (Figure 5.2, D).

Table 5.2: Summary of final Generalised Additive Models for the East and West Atlantic. Final model equations are given as well as the t- and f- values for the Gaussian Abundance tests and the z- and chi squared values for the Negative Binomial richness tests. Bold values for year indicate statistically significant values (p = <0.05). For the f- and chi squared values only significant values are presented, '-' indicates the predictor was removed from the final model and 'x' indicates it was not included at all. The final column indicates the adjusted R^2 value of the final model fit.

	Model Response	Final Model	*t-value*	*f-value*			Adjusted
			Year	Zoo	PC1	PC2	R2
East	Phytoplankton Abundance	*Phyto ~ s(Zoo) + (Year) + factor(Station)*	-1.76	16.24	-	-	50.80%
	Zooplankton Abundance	*Zoo ~ s(PC1) + (Year) + factor(Station)*	**-3.90**	x	4.24	-	62.70%
West	Phytoplankton Abundance	*Phyto ~ s(Zoo) + (Year) + factor(Station)*	1.63	42.35	-	-	40.30%
	Zooplankton Abundance	*Zoo ~ s(PC1) + (Year) + factor(Station)*	0.67	x	4.56	-	78.40%

	Model Response	Final Model	*z-value*	*Chi squared*			Adjusted
			Year	Zoo	PC1	PC2	R2
East	Phytoplankton Richness	*Phyto ~ s(Zoo) + (Year) + factor(Station)*	0.43	12.44	-	-	29%
	Zooplankton Richness	*Zoo ~ (Year) + factor(Station)*	-0.95	x	-	-	67.80%
West	Phytoplankton Richness	*Phyto ~ s(Zoo) + s(PC2) + (Year) + factor(Station)*	**3.76**	37.81	-	12.56	44.60%
	Zooplankton Richness	*Zoo ~ s(PC1) + s(PC2) + (Year) + factor(Station)*	0.15	x	7.03	5.23	47.80%

The second sequence of GAMs were run to analyse the response of zooplankton to the physical environment without the inclusion of phytoplankton. These results demonstrated that unlike the phytoplankton, zooplankton had a clear response to the physical environment (Table 5.2; Figure 5.2 F-I). The Western Atlantic demonstrated a declining zooplankton abundance and richness in response to PC1 (Figure 5.2, F and H) which is a result of decreasing SST and increased MLD values (Table 5.1). Zooplankton richness in the West also had a decreasing response to PC2 (Figure 5.2 I) which reflected changes to the NAO index (Table 5.1).

In the Eastern Atlantic, zooplankton richness had no significant response (*p* = <0.05) to either of the principle components (Table 5.2). However, zooplankton abundance in the east, had a positive response to increasing PC1 to a peak of PC1=1.5 (Figure 5.2, G), which reflect changes to SST and MLD. However, for this model run at values of PC1>1.5, this positive response changes to a negative response of zooplankton abundance (Figure 5.2, G).

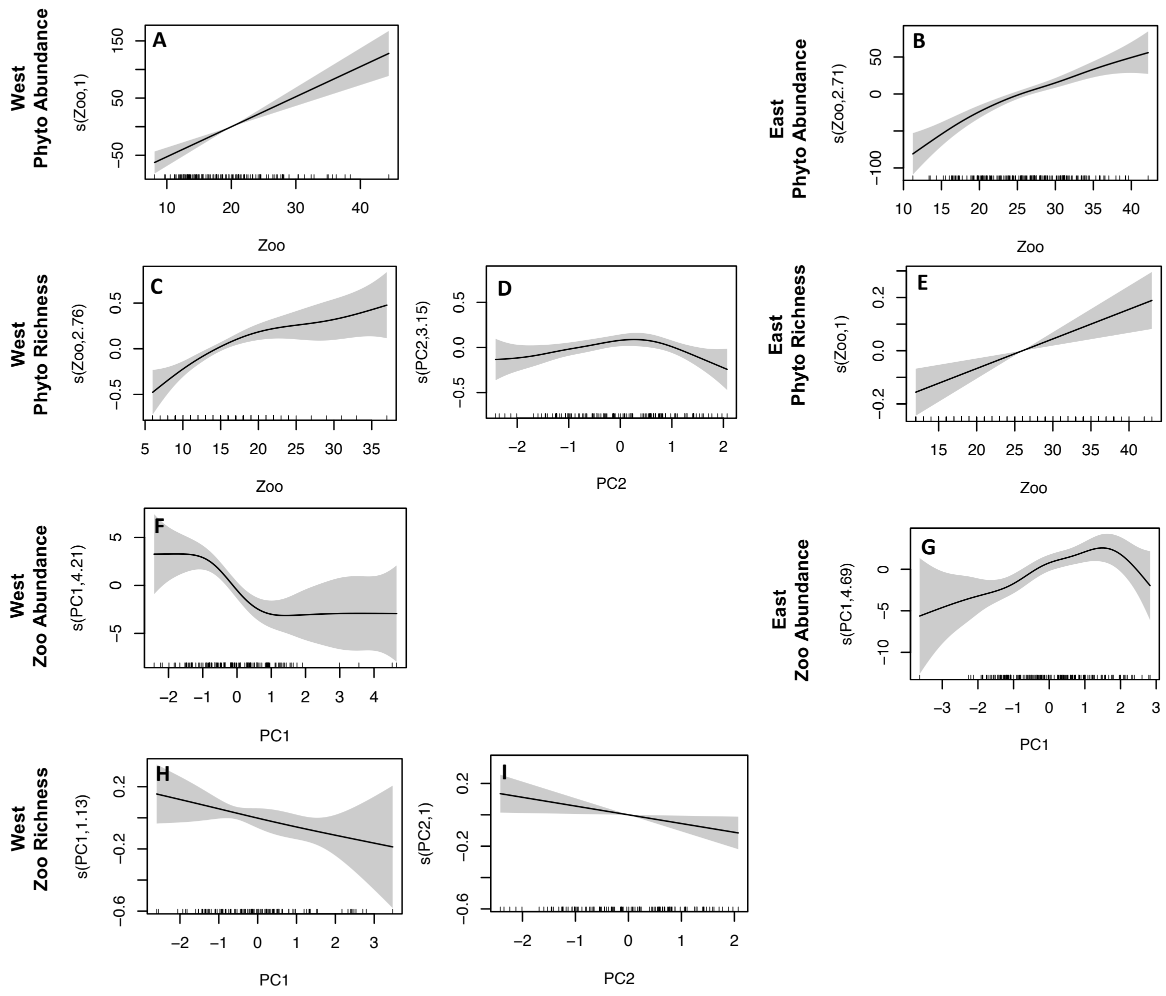

Figure 5.2: Significant (p = <0.05) estimated smoothed terms retained from the final models described in Table 2 for the East and West Atlantic. The solid line is the smoother of the overall relationship between predictor and response (across CPR areas) and the grey area denotes the 95% confidence bands. The x-axis shows the value of the predictor variable and the y-axis shows the contribution of the smoother to the fitted values. The y-label denotes smoothed predictor variable and the estimated degrees of freedom (edf) for that variable. An edf of 1, signifies a linear relationship and an edf >1 indicates an increasingly non-linear relationship. The vertical lines along the x-axis indicate the predictor variables values of observations.

5.4.3.1 Two predictor variables

For most models, only one predictor variable was retained in the final model run (Table 2, Figure 5.2, A, B, E, F and G). However, in the case of phytoplankton richness in the West and zooplankton richness in the East, two predictor variables were retained (Table 5.2, Figure 5.2 C, D, H and I). The combined effect of the two predictor variables on the response can be summarised using a heat-map which is shown in Figure 5.3. This demonstrates the non-linear feedback of the response variable to the applied predictor variables.

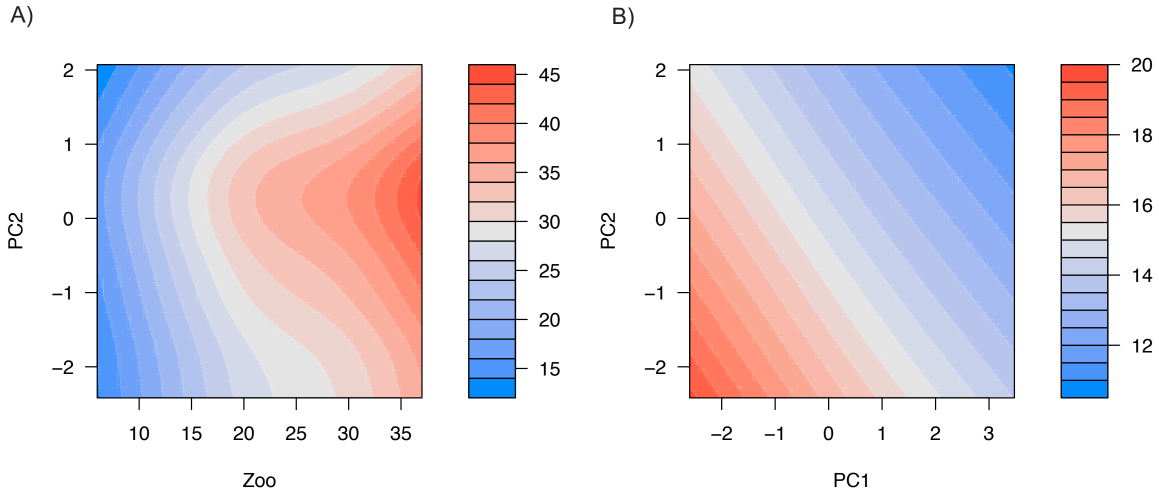

Figure 5.3: Heat maps showing the influence of two predictor variables (x and y axis) to the response variable (colour reflects response variable value). Plot A) is the response of phytoplankton richness in the western Atlantic to zooplankton (Zoo) and principle component 2 (PC2) of the physical environment. Plot B) is the response of zooplankton richness in the eastern Atlantic to principle component 1 (PC1) and principle component 2 (PC2) of the physical environment

In the case of phytoplankton richness in the West Atlantic, at high values of zooplankton richness I see a response with phytoplankton richness increasing (Figure 5.3). However, at strong positive or negative PC2 values (reflecting a positive or negative NAO index, Table 5.1) this response is reduced and lower phytoplankton richness values occur (Figure 5.3).

For zooplankton richness in the East Atlantic, increasing negative values for PC1 (reflecting increased SST and decreased MLD, Table 5.1) and PC2 (reflecting decreased NAO and increased AMO indices, Table 5.1) result in an increased response of zooplankton richness. The opposite is true at increasing positive values of PC1 and PC2, resulting in a reduced zooplankton richness response (Figure 5.3).

5.4.3.2 Individual CPR areas

Across the phytoplankton models, ANOVA tests show that the CPR standard areas were found to be a significant factor in predicting the response variable for abundance in the East (F = 18.03, *p*-value = 4.42e-10), abundance in the West (F = 25.71, *p*-value = 7.86e-10) and richness in the West (Chi.sq = 41.55, *p*-value = 9.52e-10). However, this was not the case for richness in the East (Chi.sq = 5.982, *p*-value = 0.112).

Stations were added as a factor to the models in order to account for spatial variation in the response variable. The response of phytoplankton abundance in the East Atlantic had significant differences between stations, with area C5 responding 16.17 units higher than B5 and area E5 responding 39.62 units lower than area B5. However, the response of phytoplankton richness in the East had no significant difference in response between CPR areas.

Phytoplankton abundance in the West Atlantic also had a significant difference in the response between CPR areas. There were no clear latitudinal patterns, however, as area C7 had a response 91.26 units higher than area B7. To the south in CPR area D7, phytoplankton abundance had responded 54.02 units lower than the most northern site in the West Atlantic. Phytoplankton richness in the West Atlantic demonstrated a latitudinal change in response across the CPR areas. The response of phytoplankton decreased with latitude with the most southern area, D7, having a response 0.47 units lower than area B7.

For all zooplankton models, the CPR standard areas were found to be a significant factor in predicting the response variable for abundance in the East (F = 35.24, *p*-value = 0.000), abundance in the West (F = 155.04, *p*-value = 0.000) richness in the East (Chi.sq = 252.02, *p*-value = 0.000) and richness in the West (Chi.sq = 74.295, *p*-value 0.000).

For all zooplankton models, latitude had a significant effect on the tested response variable. The response of zooplankton abundance and richness to the predictor variables in the East Atlantic increased with decreasing latitude. Abundance had an increased response 8.85 units higher at area E5 and richness responded 0.65 units higher in E5 than B5.

In the West Atlantic, area had a significant effect on zooplankton abundance but there was no clear latitudinal response. Area C7 had a response 13.77 units higher and area D7 had a response only 1.52 units higher. Zooplankton richness increased with decreasing latitude with area D7 responding 0.52 units higher than area B7 to the North.

5.5 Discussion

Over inter-annual timescales, our study highlights the complexity of bottom-up and top-down controls on marine phytoplankton in the North Atlantic region. Results demonstrated a clear difference between the response of plankton communities in the East and West Atlantic (Figure 5.1). This likely reflects the different hydrographical regimes of the subpolar West

Atlantic and transitional conditions of the East Atlantic, whilst being further imitated in differences between the response from each GAM model.

For the East Atlantic, phytoplankton had a positive relationship to zooplankton in all models but failed to demonstrate a significant relationship with the physical environment. Many studies have focused on the Eastern Atlantic and have demonstrated a mix of driving forces for the phytoplankton community (Edwards, 2001, Hátún et al., 2009, Lauria et al., 2013).

Edwards (2001) found a decrease in phytoplankton biomass associated with increasing SST that was influenced by the NAO index in the most northern most Eastern CPR region B5, as covered in our study. Other studies have related the response of phytoplankton to both top-down control and changes in SST, however, our study found no such response to the physical environment on inter-annual timescales (Beaugrand et al., 2002, Barton et al., 2003, Beaugrand and Reid, 2003).

For the West Atlantic a significant driver of phytoplankton abundance was zooplankton abundance, again demonstrating a positive relationship, however, for phytoplankton richness there was both a significant positive relationship with zooplankton richness and non-linear relationship to the physical environment (PC2), contrasting the responses in the East. Higher values of PC2 represent a negative NAO index and positive AMO index, implying warmer SST and shallower mixed layers. The non-linear response of phytoplankton to PC2 in Figure 5.2 shows that the highest values of phytoplankton richness occurred around a PC2 value of zero, when the NAO and AMO were not in the extremes of a positive or negative phase likely favouring a more diverse group of phytoplankton than at the extremes.

The mixed response of phytoplankton to top-down and bottom-up controls has been previously demonstrated by Martinez et al. (2016) in the North-West Atlantic, who found that positive NAO conditions resulted in bottom up control with deeper MLD leading to a decoupling between phytoplankton and grazers resulting in enhanced phytoplankton biomass. Further to this, the AMO regime also resulted in unfavourable top-down controls with cold SST conditions leading to higher copepod abundance (Martinez et al., 2016).

The lack of significant correlations between phytoplankton and the physical environment are however supported by the findings of Barton et al. (2003), who also demonstrated that the across the North Atlantic phytoplankton had mostly a nominally significant ($p = <0.20$) relationship with the physical environment, a significance that would have been discarded in this GAM analysis.

At seasonal timescales, the phytoplankton community has been shown to be coupled with the physical environment, however, I demonstrate that this relationship weakens when examined at inter-annual timescales (Barton et al., 2003, Barton et al., 2014). This may suggest that at this temporal resolution the variability in the phytoplankton community may be greater than the bottom-up physical drivers, or as established in a model study it may be a natural property of multi-species communities where interannual variability can arise without the variability in the external environment occuring (Barton et al., 2014, Dakos et al., 2009).

Our study does however clearly demonstrate the importance of zooplankton to the phytoplankton assemblage with significant positive relationships across all tested areas. This suggests at interannual timescales, zooplankton may be the primary driving mechanism of phytoplankton community abundance and richness. Previous in-situ (Beaugrand and Reid, 2003, Barton et al., 2014) and ecosystem model studies (Prowe et al., 2012) for inter-annual timescales have also demonstrated the importance of top-down mechanisms to phytoplankton as a driving mechanism.

This coupling to zooplankton however does not appear to be a uniform response across different regions, as a global study by Irigoien et al. (2004) concluded no relationship between phytoplankton and zooplankton diversity, clearly contradicting our linear relationship in the East (Figure 5.2E) and a non-linear relationship in the West (Figure 5.2C). This may however highlight the uniqueness of the North Atlantic compared to other study sites and suggests that grazing may be more regulated by specific prey-preferences than other regions (Irigoien et al., 2004).

Compared to phytoplankton, zooplankton demonstrated a much stronger relationship with the physical environment with significant negative responses in the West and positive responses in the East Atlantic (Table 5.2). In the western Atlantic zooplankton abundance and richness had a negative response to PC1, representative of deeper mixed layers and colder SST, while zooplankton richness also had a negative response to PC2, representative of a positive NAO phase typified by with stronger winds, deeper MLD and colder SST (Figure 5.2, Table 5.1). This demonstrates that in these cooler conditions, detected through the direct variables and indirect indexes (Table 5.1), the zooplankton population is reduced. In the East Atlantic zooplankton abundance responded positively to PC1, representative of shallower mixed layers and increased SST (Figure 5.2, Table 5.1). The only instance where zooplankton showed no significant response to the physical variables was richness in the East Atlantic (Table 5.2). Overall, these results reveal that zooplankton has a higher response value to increased SST and shallower MLDs, typical of negative NAO and positive AMO conditions, but that this analysis represents this response is different between the East and West Atlantic.

The response of zooplankton abundance and diversity to changes in SST, MLD, NAO and AMO has been widely reported across the North Atlantic and it has been suggested that the response to the physical environment is amplified in zooplankton due to the dependency of certain biological events, such as the overwintering of particular copepod species (Beaugrand and Reid, 2003, Behrenfeld et al., 2013, Harris et al., 2014, Martinez et al., 2016). Zooplankton also have much longer regeneration times and go through multiple development stages which are dependent on different temperatures, which may attribute to their dependence on the physical environment over longer timescales (Rose and Caron, 2007, Kiørboe and Hirst, 2008).

While there was no significant modelled correlation between the phytoplankton and the physical environment on interannual timescales, the significant negative response of zooplankton to colder temperatures and deeper mixed layers in the North-West Atlantic may be a reflection of stress in the phytoplankton community, whose strong positive relationship with zooplankton is shown in Figure 5.2a and 5.2c. On a seasonal timescales, colder temperatures and deeper mixed layers have been shown to reduce nutrient and light availability reducing phytoplankton success; on the interannual timescales examined here, it may also negatively impact the zooplankton community.

Environmental drivers, however, differ through time and space. At a short time scale of hours phytoplankton populations have been shown to follow the small-scale variability of turbulent mixing however at inter-annual and decadal timescales such patterns can be lost, even though they remain a strong mechanisms for the zooplankton community as demonstrated in this study (Blauw et al., 2018, Richardson and Schoeman, 2004, Barton et al., 2003, Barton et al., 2014).

Not only do the results demonstrate a difference in the response of communities between the East and West Atlantic, I also demonstrate that for some models a clear latitudinal pattern was found in the response variable. In the West, there was a latitudinal gradient in phytoplankton richness that demonstrates decreasing diversity with increasing latitude. This finding is supported by observations across marine and terrestrial taxa as well as in model studies (Yasuhara et al., 2012, Barton et al., 2010). However, this pattern was not so clear for phytoplankton abundance in the East or West Atlantic.

Our results highlight that the simplistic ecological view of bottom-up or top-down control on a community may not be as straight forward over inter-annual timescales. I suggest that the interannual variability in the physical environment has the ability to influence species interactions, which in turn have the capability to alter the relative importance of bottom-up and top-down control on a community (Kerimoglu et al., 2013). I therefore hypothesise that the physical environment may be important in determining phytoplankton communities on inter-annual scales but principally through the control of marine zooplankton and the tight predator-prey coupling.

I also must acknowledge that variability may arise internally within a plankton community, even in the absence of external forcing (Kerimoglu et al., 2013, Dakos et al., 2009), which may account for some portion of the variability not explained by our response variables.

5.5.1 Data limitations

The CPR survey is spatially and temporally extensive and because of this it has been used to address an extensive range of ecological questions and has captured perspectives of change up to a scale of decades (Giron-Nava et al., 2017, Barton et al., 2003). It is well documented that the CPR analysis does not generate absolute population abundance however as a semi-quantitative index of phytoplankton and zooplankton abundance it has been found to be a reliable and comparable dataset (Frederiksen et al., 2006, Richardson and Schoeman, 2004, Raitsos et al., 2005, Richardson et al., 2006). In this study phytoplankton are represented by the dinoflagellate and diatom species captured by the large mesh size of the CPR survey (270μm) and the zooplankton community by marine copepods. However, it must be recognised that this represents only a proportion of the total in-situ community. The results of this study may be specific to these functional groups and without sampling the response of other groups, such as coccolithophores in phytoplankton and cnidarians in zooplankton, I can only comment on the specific response of the studied groups.

Despite these limitations, this study and others have demonstrated the importance of long-term ecological datasets such as the CPR survey for continuing to understand the trends and relationships of ecological communities as well as to be able to improve future models and forecasts in order to support environmental management actions (Martinez et al., 2016, Giron-Nava et al., 2017).

5.6 Conclusion

The CPR survey is a prime example of how long timeseries can provide new perspectives in ecology. The use of generalised additive models in this study indicates that the traditional top-down or bottom-up view of plankton ecology may not be so straight forward over extended time periods and demonstrates the importance of including both types of driver in future studies and models.

Across the North Atlantic, phytoplankton had significant positive and largely linear relationships with the zooplankton community however in 3 out of 4 models relationships with the physical environment were insignificant and removed from the final model format. The only phytoplankton response that had a significant correlation to the physical environment was non-linear and demonstrated that richness in the North-West Atlantic was highest when the indexes of the NAO and AMO were in a neutral phase.

Zooplankton showed significant relationships to the physical environment in the East and West Atlantic, with abundance and richness in the West declining with colder SST, deeper MLDs and positive NAO values, also typical of strong winds and cooler conditions, and abundance in the East increasing with warmer SST and shallower MLDs. While the response of zooplankton in the East and West act in opposite and therefore reflect the same patterns.

The response of the plankton community also demonstrated latitudinal gradients with decreased diversity with increasing latitude, which are consistent with well documented trends across both marine and terrestrial taxa. This study highlights the importance of spatial and temporal considerations and recommends that future studies should not treat the North Atlantic as a whole and maintain higher resolutions when addressing complex ecological questions.

Chapter 6 Future shifts of North Atlantic phytoplankton community structures

6.1 Abstract

The ocean environment has undergone physical changes as a response to human-induced global change, including variation in sea surface temperature, mixing and nutrient availability. These changes have the potential to impact the fitness of marine phytoplankton effecting their growth, productivity and distribution. To better understand the impacts to ocean ecosystems I examine changes to the phytoplankton abundance and diversity using model output from the MIT IGSM from 1990 to 2100 across the North Atlantic basin.

A range of techniques are applied to assess the phytoplankton community, and the application of change-point analysis is used to evaluate the timeseries for abrupt ecological shifts. Results demonstrate that as changes to the marine environment continue, including increased SST and shoaling of the MLD, declines in the abundance and shifts composition of the phytoplankton community should be expected, with smaller species migrating towards the poles. Changes to phytoplankton were recorded in 94% of the North Atlantic basin with declines in biomass occurring in all regions except for an increasing biomass in the sub-polar gyre. Results also demonstrate that different regions of the North Atlantic will respond to changes at different times with abrupt changes occurring later in the higher latitudes (2050s) than the subtropical regions (2030s) and the higher latitudes will also be affected by the restructuring of the phytoplankton community to a smaller functional size.

6.2 Introduction

Phytoplankton are highly diverse, with species that vary in shape, size and biogeochemical function. These individual species can be clustered into functional groups that play different roles in the marine ecosystem. For example, diatoms are relatively heavy and have a sinking efficiency which allows efficient export of carbon to the deep ocean, whereas, through the production of calcium carbonate plates, the coccolithophore group can reduce seawater alkalinity (d'Ovidio et al., 2010). The relative contribution of different species and functional groups to the total biomass of a community will thus determine its function within the ecosystem.

Over multidecadal timescales, climate change has the potential to alter environmental conditions that impact the fitness of marine phytoplankton including changes to their growth, productivity and distribution. The ocean environment has undergone physical changes as a response to human-induced global change, including warming of sea surface temperature, increase in sea level and a decrease in ocean pH levels (Gleckler et al., 2012, IPCC, 2013, Barnett et al., 2005). Earth system models predict changes will continue and result in further increases in ocean stratification, reduction of nutrient supply by mixing and reduced ventilation, while a response to increased uptake of anthropogenic carbon by the ocean results in decreased seawater pH (Doney et al., 2009, Doney, 2010, Bopp et al., 2013, Barton et al., 2016). Such variability within the environment can shape ecosystems by controlling the spatial distribution of species, promoting biological competition, fitness and extinction that ultimately has the ability to drive the structure and evolution of communities through time (Cermeño et al., 2010). As changes to the marine environment continue, marine organisms are expected to respond through changes in abundance and community composition including pronounced regional changes as species suited to warmer climates expand their distributions at the expense of cold-water species (Bopp et al., 2013, Hallegraeff, 2010).

With rising temperatures, some organisms may be able to acclimate, while other organisms may experience a poleward shift following their thermal niches or result in an decline in diversity (Thomas et al., 2012). Climate models have demonstrated the potential for a poleward movement of phytoplankton types, and for a prominent loss of cold-water species, particularly in stratified waters, has also been reflected in some in-situ studies (Barton et al., 2016, Beaugrand et al., 2015). Reports by the IPCC have concluded that warming under the RCP2.6 scenario may only have a minor influence on marine pelagic biodiversity, however, moderate warming under the RCP4.5 scenario may result in physical changes far greater than those observed over the past 50 years, and it is widely acknowledged there may be a resulting internal reorganization or shuffle in community structure (Beaugrand et al., 2015, IPCC, 2013, Barton et al., 2016). However, with emissions currently following the “business as usual” RCP8.5 scenario, the impact on the future state of the marine ecosystem is likely to be high (IPCC, 2013).

If enough pressure is applied to the phytoplankton community by its external environment, a sudden shift in the structure and biomass of the community may occur that may have a much greater impact on ecosystem services and biogeochemical cycles than a gradual change in the community (Beaugrand et al., 2009, Barton et al., 2016). This change in state of an ecosystem is a phenomena referred to as a regime or stepwise shift (Beaulieu et al., 2012, Killick et al., 2016). It is predicted that climate change will intensify and increase the frequency with which these regime shifts occur in the marine environment (Beaugrand and Reid, 2003, Beaugrand et al., 2008, Reid et al., 2016).

Regardless of how changes to the community are driven, pronounced declines to phytoplankton biomass, productivity and community structure are likely to have profound effects on the marine food chain, decreasing energy flows from plankton to fish stocks, and ecosystem services, including a reduction in the particulate carbon sinking flux (Bopp et al., 2013, Barton et al., 2016).

There has been much debate as to whether the length of current observational records are sufficient to distinguish a global warming trend in phytoplankton biomass from natural variability (Bopp et al., 2013, Henson et al., 2018). The use of model output can help us better understand how these changes may develop across the rest of the 21st century. For example, models suggest that future ocean conditions will have increased nutrient-depletion in the surface waters that will favour smaller phytoplankton at the expense of larger diatoms which are important contributors to the ocean biological carbon pump leading to reduction in its efficiency and may form a feedback loop between climate change and the ocean carbon cycle (Bopp et al., 2005).

6.2.1 Aim of this study

In this study I seek to assess the changes to abundance, richness and structure of North Atlantic phytoplankton communities driven by changes to the environment over the 21st century. This was achieved using a marine ecosystem model, coupled to an Earth system model of intermediate complexity from the MIT IGSM framework (Dutkiewicz et al., 2015). The model has a diverse range of phytoplankton consisting of 96 phytoplankton types in 6 functional groups with output extending from 1990 to 2100, allowing an examination of a century of change in North Atlantic phytoplankton populations. The hypotheses of this study are as follows:

- There were no significant temporal or spatial changes to phytoplankton biomass or richness across the North Atlantic from 1990 to 2100
- There was no change to the structure of the phytoplankton community over the study period at the functional group level
- There was not greater change in the smaller sized fraction of the phytoplankton community than in the larger sized fraction from 1990 to 2100
- There was no relationship between decadal changes in sea surface temperature, mixed layer depth, nitrate or zooplankton and phytoplankton biomass or richness

6.3 Methods

6.3.1 Integrated Global Systems Model

In this study, the MIT IGSM framework (Dutkiewicz et al., 2015) was used to assess changes to the phytoplankton community in the North Atlantic region, defined here as 78°N to 0°N and 1°W to 99°W. The MIT IGSM is detailed in section 3.3.

This model has several experimental runs available. The control run of the model in which the pre-industrial temperature, circulation, mixing, sea-ice fields and pCO_2 were used, started from the year 1860 after spin up and ran for another 240 years, to provide a baseline that the climate run could be compared to (Dutkiewicz et al., 2013, Dutkiewicz et al., 2015).

In this study, the ALL-OTHER experiment of the model was used to examine changes across the 21st century, referred to here after as the climate run. In the climate run, the Earth system is allowed to change over the period 1990-2100, after starting at the same initialization point as the control run. In the Climate experiment, pCO_2 was held at pre-industrial conditions while all other fields impacting growth, temperature affecting biological rates, circulation, mixing and sea-ice, were allowed to change (Dutkiewicz et al., 2013, Dutkiewicz et al., 2015). The Climate run used in this study contains natural variability, as described by a control run, and changes driven by alterations to the environment with climatic forcing (Dutkiewicz et al., 2013, Dutkiewicz et al., 2015). The difference between the Climate and Control experiments of the model differ substantially by 2100, (Supplementary Figure 0.9).

I emphasise that ecosystem models are simplifications of reality and as such they focus upon the principal mechanisms that influence the studied community and their environment. As such the assumptions behind the model must be considered when analysing the results of this study. For in depth model details refer to the following references (Dutkiewicz et al., 2013, Dutkiewicz et al., 2015).

6.3.2 Model Analysis

Only phytoplankton with biomass, measured in mmol P m^{-3}, contributing to more than 0.1% of the total biomass, was used in the analysis. This threshold was applied to model output as phytoplankton types within the model cannot 'die off' if conditions become unfavourable, instead their abundance drops to zero, allowing them to reoccur if conditions become favourable. It is also used to remove any numerical errors, such as negative values.

To quantify the diversity of the community, richness was calculated as the number of phytoplankton types that contribute to >0.1% of the total community biomass. By applying a richness index to the analysis I can assess whether changes to the community are purely a result of changes to the total biomass, or to the structuring of the community.

6.3.3 Change-point analysis

Change-point detection was used to investigate the presence and timing of abrupt changes to the biomass and richness of the modelled phytoplankton community. Here, I used the environmental time-series change-point detection approach 'EnvCpt' (Killick et al., 2016). EnvCpt change-point analysis allows for 'regime shifts' to be distinguished from any long-term trends and red noise (driven by stochastic atmospheric forcing of the ocean). I use it here to detect abrupt changes in total phytoplankton biomass and richness.

The EnvCpt method assumes that the timeseries behaves as a combination of a constant mean or a long-term trend, with a background of white-noise or a first-order autocorrelation process (AR(1)), with the possibility of abrupt changes in all possible model configurations.

The EnvCPT method computes 8 model fits with (1) a constant mean and variance, (2) a constant mean and variance with a change-point, (3) a constant mean and variance with AR(1), (4) a constant mean and variance with a change-point and AR(1), (5) a linear trend, (6) a linear trend with a change-point in, (7) a linear trend with AR(1), and (8) a linear trend with change-point and AR(1). The different model fits attempt to distinguish patterns in long-term trends, regime shifts and internal variability. The best model is selected using the Akaike Information Criterion (AIC). It is noted here that AIC selection only provides 'goodness of fit' relative to other models tests and not to the model quality.

All 8 change point models were applied to the data, but here the results of models 2, 4, 6 and 8 are presented as these included information on the timing of change-points. The EnvCpt package for R is available at (Killick et al., 2016) (https://cran.r-project.org/web/packages/EnvCpt/index.html) and includes further details on the approach.

6.3.4 Testing for a change: T-test

To assess spatial and temporal changes in the phytoplankton community between 1990 and 2100, the difference between the first and last 20 years of the model data was calculated at each pixel. To calculate the percentage change, this difference was divided by the last 20 years and multiplied by 100.

A t-test was used to assess the null hypothesis that there was no difference between the two periods of data. The t-test results in a 1 if the null hypothesis is rejected and a 0 if it is accepted. A *p*-value in the range of 0 to 1 is also given to the probability of observing a test statistic as extreme, or more extreme than, the observed value under the null hypothesis. I consider the periods to be statistically different if the p-value is < 0.05.

6.3.5 Changes to Functional Groups

To assess changes to the functional group structure, the difference between the first and last 20 years of the modelled biomass for each functional group was calculated. A t-test was used to assess if the change between the first and the last 20 years was significantly different.

Polar plots were also produced to visually demonstrate the change in the percentage contribution of each functional group to the total community structure between the first and last 20 years of the modelled data. Polar plots were produced for five regions of the North Atlantic as defined by Longhurst (2007): the Atlantic Arctic (ARCT), the North Atlantic Drift (NADR), the North-East Atlantic subtropical gyre (NASE), the North-West Atlantic subtropical gyre (NASW) and the North Atlantic tropical gyre (NATR). The regions are shown in Figure 6.4a.

6.3.6 Drivers of phytoplankton variability

To attempt to understand the forces controlling the phytoplankton community structure four predictor variables of phytoplankton biomass and richness were extracted from the model and tested for significant relationships using Spearman’s correlation coefficient.

Here I tested sea surface temperature (°C), mixed layer depth (m), nitrate (mmol N m^{-3}) and zooplankton biomass (mmol P m^{-3}). The significance of this relationship was given by a *p*-value (statistically significant if $p<0.05$).

6.4 Results

6.4.1 Temporal and spatial changes to phytoplankton biomass and richness

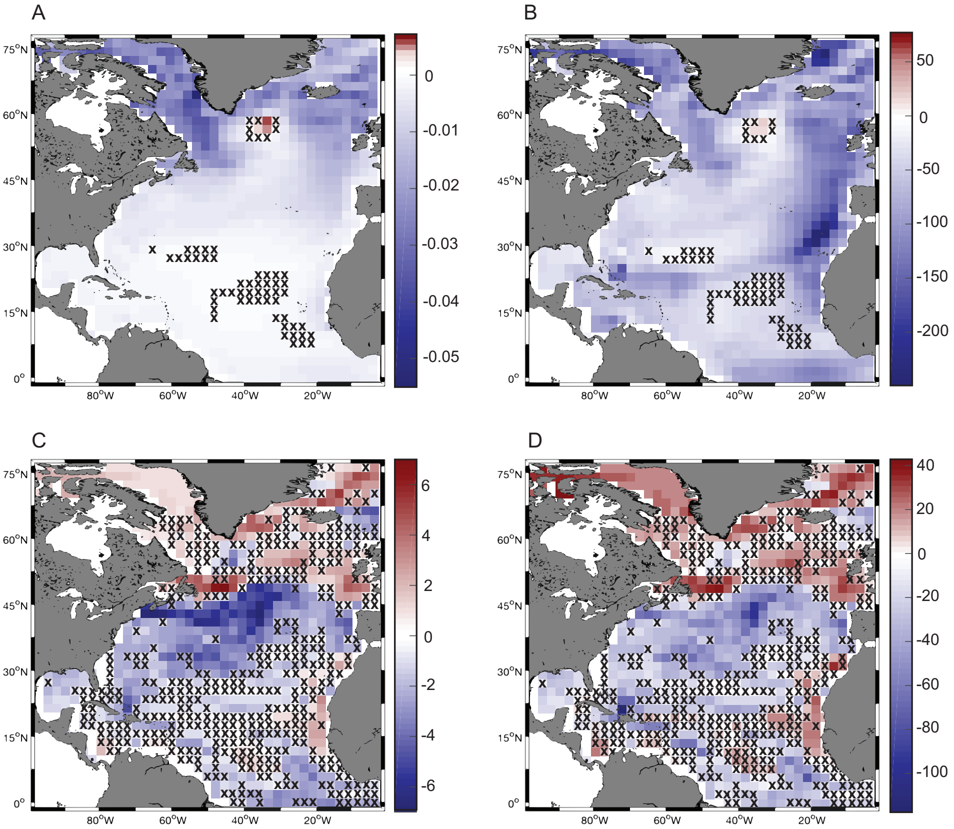

Figure 6.1: Difference in the biomass (A) and richness (B) of modelled phytoplankton community between the first and last 20 years of the model. Percentage change for biomass (C) and richness (D) is also shown. A t-test was performed between the first and last 20 years of the model, if it was not significant (p>0.05) an 'x' was overlaid on the map.

In the model, phytoplankton demonstrate a decline in biomass with increasing latitude across the North Atlantic between 1990 and 2100 (Figure 6.1a-b). This spatial pattern is however reversed in the sub-polar gyre of the North West Atlantic, which has an increase of ~25% in phytoplankton biomass over the 21st century (Figure 6.1a-b). The decline of biomass across the North Atlantic between the first and last 20 years of the model run varies from 25% to over 200% loss off the coast of Africa and in the high latitudes off Greenland (Figure 6.1a-b). Approximately 94% of the pixels in the North Atlantic show this change to be statistically significant (Figure 6.1a-b). In the sub-tropical gyre region of the North Atlantic there was a significant decrease in phytoplankton richness (up to 60% loss of species richness than the original community) and a few regions of increased richness in the high latitudes of the North Atlantic (Figure 6.1c-d). However, ~43% of the changes to North Atlantic richness were found to be insignificant in the results of the t-test (Figure 6.1c-d).

6.4.2 Results of change point analysis

The application of change point analysis to the modelled phytoplankton time series allows for an insight into the types of changes predicted to occur in the biomass and richness over the period 1990 to 2100. The time series of phytoplankton biomass in the subtropical gyre was best described by model 2 (lowest AIC) in which the community had a constant mean and variance with a change-point to a decreased mean from 2030, and model 5 that had a decreasing linear trend (Figure 6.2a and b). To the North in the sub-polar, North Atlantic drift and sub-arctic regions, model 5 (a decreasing linear trend) and 6 (a decreasing linear trend with a change-point) had the lowest AIC values (Figure 6.2b). The year of the first change-point with a decreasing linear trend was later in the sub-arctic than the sub-tropical gyre, occurring from 2050 onward (Figure 6.2a).

The response of the modelled phytoplankton richness was much more varied, with less coherent regional patterns than the modelled biomass (Figure 6.2). The sub-tropical region still showed model 2 (a constant mean and variance with a change-point to a decreased state) to have the lowest AIC value and the change points began to occur in the region from the early 2000s (Figure 6.2c-d). In the higher latitudes the variability can be described by a mixture of models including model 2 (a constant mean and variance with a change-point to a decreased state), 6 (a decreasing linear trend with a change-point) and 8 (a decreasing linear trend with change-point and AR(1)), again displaying a slightly later time for the change point (Figure 6.2c-d).

Results of the change point analysis demonstrate that the mean timing of abrupt shifts in the richness of the phytoplankton community occur earlier than for biomass (Figure 6.2,Supplementary Figure 0.10).

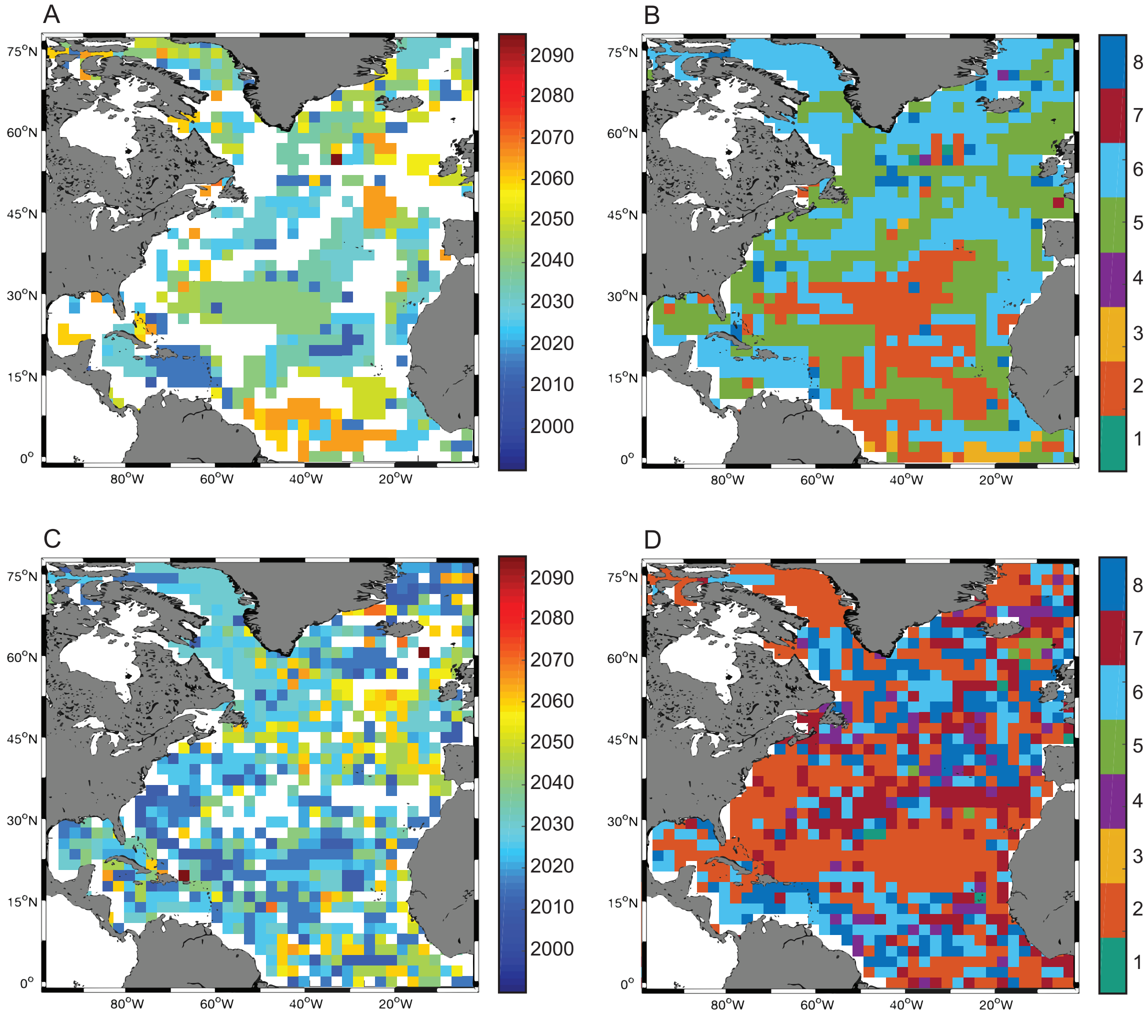

Figure 6.2: Results of change point analysis on total phytoplankton biomass (row 1) and total phytoplankton richness (row 2). The year of the first change point, for the model with the lowest AIC, is shown for biomass (A) and richness (C). White space is used when the model with the lowest AIC does not have a change point. The model with the lowest AIC for biomass (B) and richness (D) is shown, where models 1 to 8 represent changes as follows: (1) a constant mean and variance, (2) a constant mean and variance with a change-point, (3) a constant mean and variance with AR(1), (4) a constant mean and variance with a change-point and AR(1), (5) a linear trend, (6) a linear trend with a change-point in, (7) a linear trend with AR(1), and (8) a linear trend with change-point and AR(1).

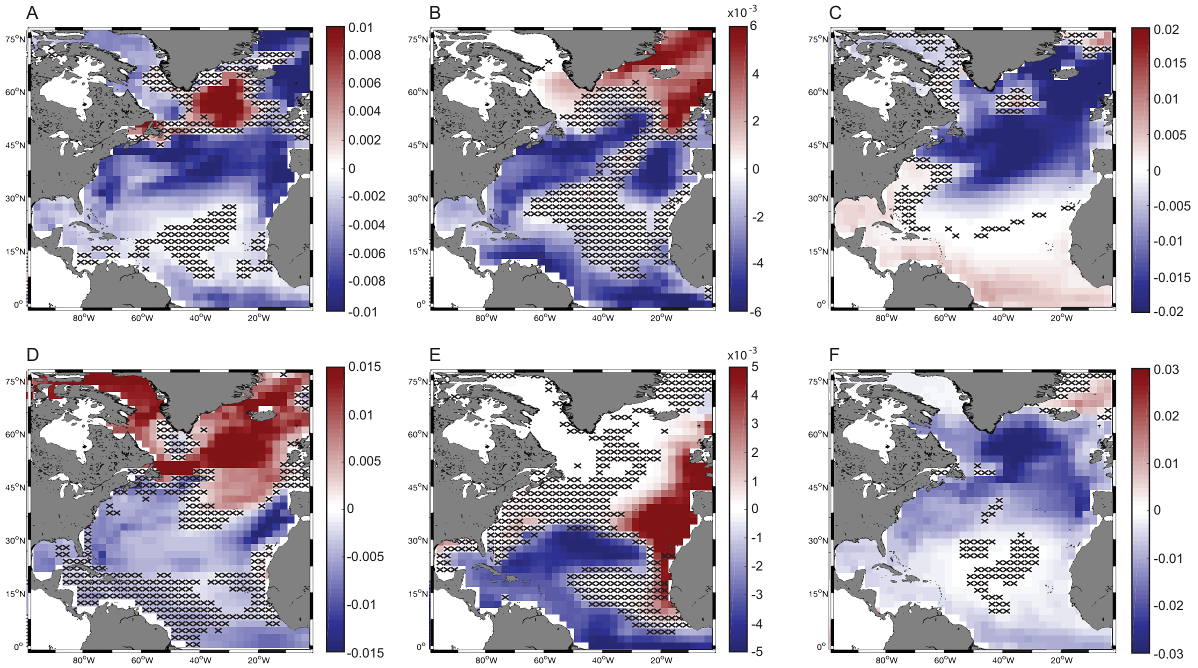

Figure 6.3: Differences between the first and last 20 years of each of the modelled functional groups: Diatoms (A), Diazatrophs (B), Other Large (C), Other Small (D), Prochloroccus (E) and Coccolithophores (F). Colour bars show the magnitude of change in biomass (mmol Pm^{-3}). A t-test was performed between the first and last 20 years of the model. If the change was not significant ($p>0.05$) an 'x' was overlaid on the map.

6.4.3 Changes to the structure of the phytoplankton community over the study period at the functional group level

Significant changes in the distribution and abundance of functional groups is predicted to occur across the North Atlantic region (Figure 6.3). The diatom group declines by ~-100% in biomass across the North Atlantic from 1990 with the exception of the sub-polar gyre, where an increase of ~+50% occurred (Figure 6.3). Diazotrophs and Other Small functional groups declines by ~-50% in the lower latitudes since 1990, but increased in the higher latitudes by ~+80% (Figure 6.3). The Other Large group had the opposite changes, with a decline of ~-250% in the high latitudes and a slight increase in the very low latitudes (Figure 6.3). The final group, Coccolithophores, demonstrate declines of ~-100% across the North Atlantic basin, with very few increases up to ~+25% in the high latitudes since 1990 (Figure 6.3).

To further examine changes to the phytoplankton community composition, the North Atlantic was divided into 5 ecological provinces as defined by Longhurst (2007) and shown in Figure 6.4. Polar plots were used to demonstrate the changes in the percentage contribution of each functional group to the total community in each of the provinces.

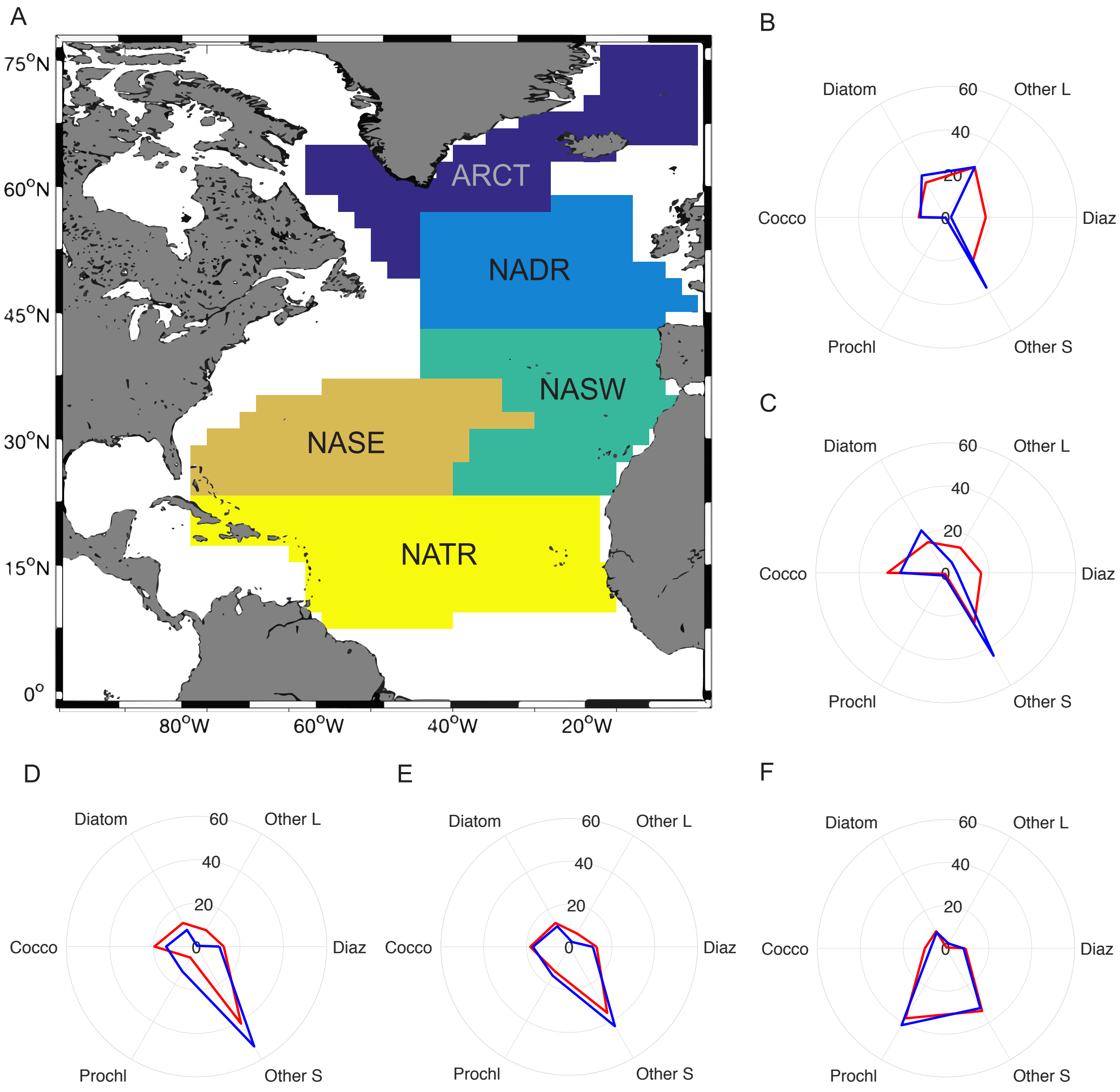

Figure 6.4: Polar plots of the modelled phytoplankton community structure in five Longhurst biogeochemical provinces of the North Atlantic basin. The regions are defined in the map (A) and are abbreviated as follows: B) ARCT – Atlantic Arctic, C) NADR – North Atlantic Drift, D) NASE -North-East Atlantic subtropical gyre, E) NASW – North-West subtropical gyre, F) NATR – North Atlantic tropical gyre. Each functional group of the phytoplankton community is shown as a percentage contribution to the total community structure (as labelled on the radial axis), averaged for each Longhurst region. The red line on the polar plots represent the community structure during the first 20 years of the model, and the blue line represents the community during the last 20 years.

The largest changes to the community structure occurred in the ARCT and NADR in the higher latitudes (Figure 6.4). Both of these areas showed an increase in contribution by Other Small up to +17% and Diatom types by +6%, while there was a decline in diazotrophs of -15% and coccolithophores by -8%, and a decline of Other Large types by -7% in the NADR (Figure 6.4a-b). The NASE and NASW had much less severe changes to the percentage contribution of each functional group, with the greatest predicted change an increase in the contribution to the total biomass of the Other Small group in the NASE of +12% (Figure 6.4c-d). Both the NASE and NASW had a decline in diatoms of up to -3% and other large types by -8%, but an increase in Prochlorococcus and other small by up to +12%, with the NASW showing the least amount of change. The NATR also experienced relatively few changes in the structure of the community with a slight decrease in the contribution of coccolithophores by -2% and an increase in Prochlorococcus types by +3%.

The polar plots presented in Figure 6.4 demonstrate that in the tropical and sub-tropical regions changes to the community structure are restricted, with no extreme switches in the functional composition of the community. In the ARCT and NADR regions, there are more substantial shifts in the structuring of the community, for example in the ARCT region there is a collapse in the presence of diazotrophs, but an increase in the presence of other small types (Figure 6.4b).

6.4.4 Changes to the smaller sized fraction of the phytoplankton community compared to the larger sized fraction

The smaller functional types represented in the model (Other Small, Diazotrophs, Prochlorococcus and Coccolithophores) dominate the phytoplankton community composition from the equator to 60°N, at which there is a switch to the larger functional types in the model (Supplementary Figure 0.12). The sub-tropical gyre is almost completely dominated by the smaller functional types.

The larger sized functional groups (Diatoms and Other Large) are predicted to have large declines in their biomass in the sub-tropical gyre region, up to -250% decline from the first 20 years of the model study, and slight declines of -50% in the rest of the North Atlantic. The larger sized functional groups are predicted to have significant increases of +35% in the sub-polar gyre and the tropical Atlantic (Supplementary Figure 0.12). The small size fraction declines across the lower latitudes and declines in the subpolar regions of the North West Atlantic, by -40%. In the high latitudes the small sized fraction increased in biomass by up to 40% by the end of 2100 (Supplementary Figure 0.12).

6.4.5 Changes to the physical environment and zooplankton population

Over the course of the modelled period the physical environment and the zooplankton abundance experienced significant changes shown by the results of the t-test for each pixel of the North Atlantic (Figure 6.5). Across the North Atlantic there were significant increases of up to 6°C in SST, apart from a small region of the sub-polar which had a significant decline of SST up to -3°C (Figure 6.5a). Changes to the MLD were largely insignificant south of 45°N and in the North West Atlantic shelf region. In the North-East there was largely shallowing of the MLD by ~100m (Figure 6.5b). Changes to nitrate were largely significant in the higher latitudes above 45°N with a decline of up to 5 mmol N m^{-3} across the study period (Figure 6.5c). Zooplankton had largely significant declines in biomass, up to 0.008 mmol P m^{-3}, particularly in the North West Atlantic shelf region, however in the sub-polar region zooplankton biomass increased by up to 0.002 mmol P m^{-3} (Figure 6.5d).

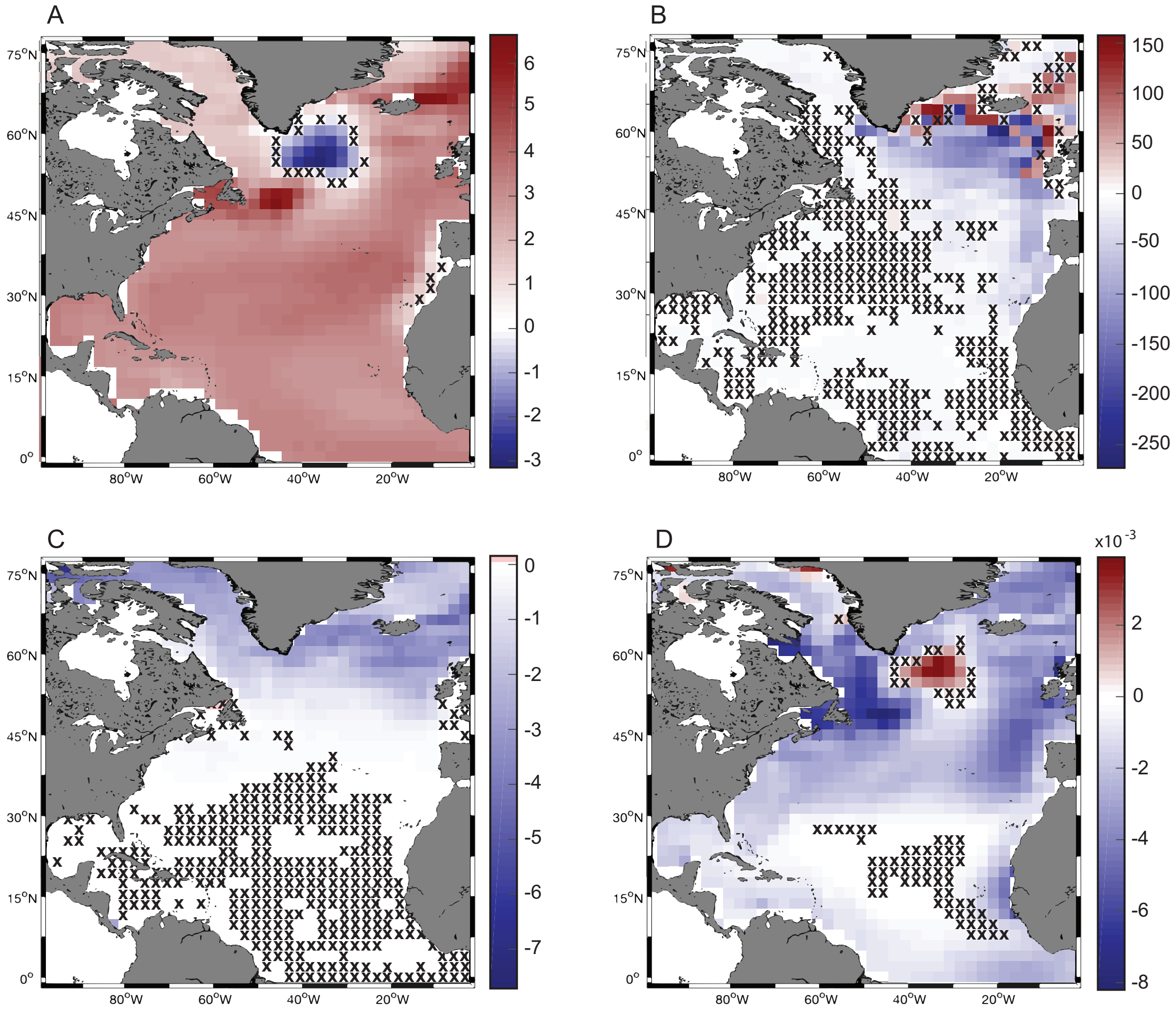

Figure 6.5: Changes to the drivers in the model between the first and last 20 years of the model run: A) sea surface temperature (℃), B) Mixed Layer Depth (m), C) Nitrate (mmol N m^{-3}), D) zooplankton biomass (mmol P m^{-3}). A t-test was performed between the first and last 20 years of the model. If the change was not significant ($p>0.05$) an 'x' was overlaid on the map.

6.4.6 The relationship between sea surface temperature, mixed layer depth, nitrate or zooplankton to phytoplankton biomass and richness.

A negative relationship between phytoplankton biomass and SST exists across broad swathes of the North Atlantic (Figure 6.6a) and between phytoplankton biomass and zooplankton (Figure 6.6d). The only area where these relationships were not significant was the boundary of the sub-polar gyre in the North West Atlantic. MLD also had a positive linear relationship with phytoplankton biomass, significantly in the sub-tropical gyre and North-Eastern drift region of the Atlantic (Figure 6.6b). Nitrate had a positive linear relationship with phytoplankton biomass from 30°N to the high latitudes, however south of 30°N this relationship was significant and negative for many areas of the sub-tropical gyre (Figure 6.6c).

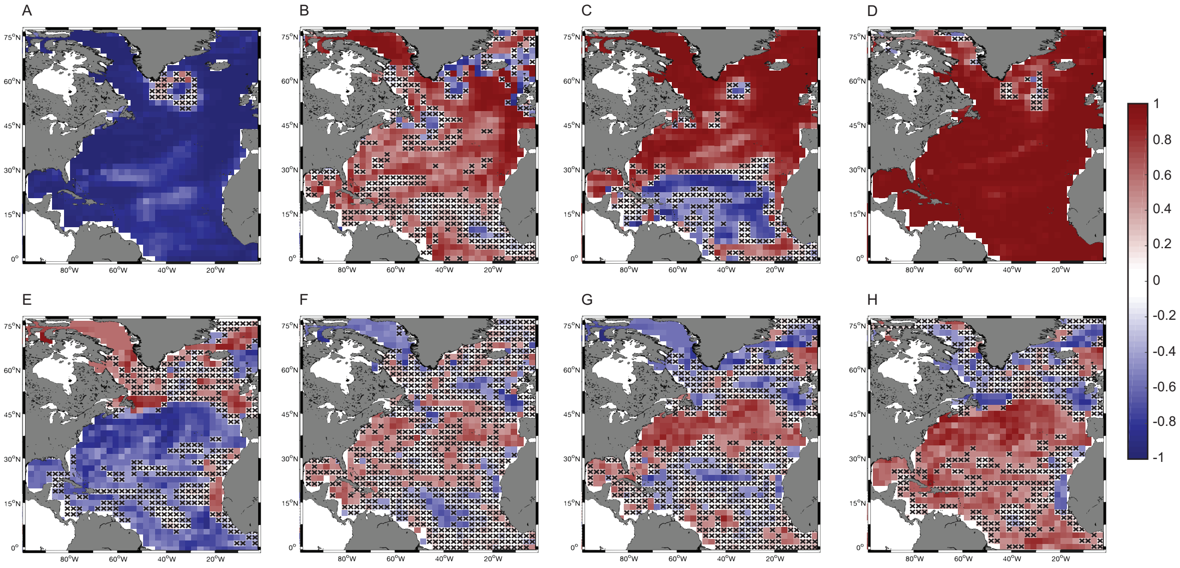

Figure 6.6: Result of Spearman's correlation analysis between phytoplankton biomass, mmol P m^{-3}, (row 1) and richness (row 2) and each of the predictor variables. A) biomass and sea surface temperature (SST), B) biomass and mixed layer depth (MLD), C) biomass and nitrate (NO3), D) biomass and zooplankton (Zoo), E) richness and SST, F) richness and MLD, G) richness and NO3, H) richness and Zoo. Spearman's coefficient is ranked between 1, a positive correlation, and -1 an inverse correlation. If the correlation was not significant (p>0.05) an 'x' was overlaid on the map.

The relationships between phytoplankton richness and the driving forces examined here were largely insignificant (Figure 6.6e-h). However phytoplankton richness in the sub-tropical region had a negative relationship with SST and a positive relationship with nitrate and zooplankton (Figure 6.6e,g,h). MLD mostly insignificant relationships with phytoplankton richness across the North Atlantic (Figure 6.6f).

6.5 Discussion

In this study, I explore projected changes in North Atlantic phytoplankton communities by using the MIT ISGM, which contains 96 phytoplankton types, defined by individual temperature ranges and optima clustered in 6 functional groups.

6.5.1 Biomass and richness overview

Changes to phytoplankton biomass and richness fit well with that observed in previous model simulations, with phytoplankton types demonstrating biogeographical patterns and tracking changes in the physical environment (Bopp et al., 2005, Barton et al., 2010, Dutkiewicz et al., 2015, Dutkiewicz et al., 2013). These include biomass increasing at higher latitudes and a geographical divide of phytoplankton types representing the smaller functional groups dominating in the lower latitudes, compared with larger types dominating north of 60°N (Figure 6.1,Supplementary Figure 0.12). In the North Atlantic sub-polar gyre region there was a small increase in phytoplankton biomass, where the physical environment had a decrease in SST over the 21st century with some deepening of the mixed layer, compared to other regions (Figure 6.5). This change reflects the controls of phytoplankton by variability in temperature, nutrients and irradiance in the model, a relationship that was not apparent with the CPR data in Chapter 4 and Chapter 5 (Dutkiewicz et al., 2015).

Although this model is a simplification of reality, the richness of phytoplankton across the North Atlantic demonstrated patterns that are consistent with in-situ observations and previous model expectations (Barton et al., 2010, Thomas et al., 2012, Barton et al., 2016). Over the modelled time period, our analysis found large regions where changes to richness were not significant, however, there were general patterns of decreased richness in the sub-tropical regions and increased richness in the higher latitudes (Figure 6.1).

6.5.2 Change point analysis

Change point analysis was used to assess abrupt changes in the biomass and richness of the community in the modelled timeseries (1990 to 2100). The best fit models were defined by the lowest AIC (Figure 6.2b).

In the subtropical regions the biomass of the phytoplankton community followed either model 2, a constant mean and variance with a change-point, or model 5, a linear trend without a change-point (Figure 6.2b). In the higher latitudes, model 5 (linear trend) and model 6 (linear trend with a change-point), were the best fit EnvCPT models (Figure 6.2b). In all cases the overall resulting trend was a decline in phytoplankton biomass over the 21st century. This decline follows the finding of previous studies including modelling (Litchman et al., 2006, Bopp et al., 2013) and in-situ studies (Boyce et al., 2010), however this in-situ trend still remains largely debated for the North Atlantic region with some studies demonstrating an increase in phytoplankton biomass (McQuatters-Gollop et al., 2011).

Results of the change-point analysis suggest that an initial shift in the phytoplankton to a lower biomass occurred in the 2030s for the lower latitude sub-tropical regions, compared to 2050s in the higher latitudes (Figure 6.2a). I hypothesise that this lagged response of phytoplankton biomass in the higher latitudes may be due to the northwards movement of smaller species as the climatic conditions continue to change, or due to a later significant change in the physical environment compared to the tropical regions. In the lower latitudes, the phytoplankton types in the model will track their thermal optima and with increasing temperatures will be driven northwards, and is demonstrated in this model output by the distribution of functional types between the beginning and end of the timeseries (Supplementary Figure 0.12). The biomass of the higher latitudes may be less affected by the initial changes to the SST and other physical parameters as this region experiences large shifts due to the seasonality of this region, as such the influence of increased SST may accumulate an effect over multidecadal timescales, than somewhere with lower seasonality.

The change-point analysis showed that the timing of abrupt shifts which declined biomass varied spatially (Figure 6.2c and d). The sub-tropical regions were best fit by model 2 (specify what model 2 is here), like the biomass, however north of 30°N the patterns of best fit model to timeseries showed little spatial coherency (Figure 6.2d). Across the North Atlantic the mean initial change-point for community richness occurred earlier than the initial change-point in community biomass (Supplementary Figure 0.10). I hypothesise that this lag between change-points in richness and biomass is a feature of the phytoplankton community responding to pressures in the external environment. As conditions change into the modelled 21st century, unfit phytoplankton types are likely to be outcompeted by types with more suitable thermal ranges and nutrient requirements. This may result in the first abrupt shift in community richness, as only competitively fit phytoplankton types remain in the modelled environment. However the change in richness may not be immediately reflected in the biomass, as the reduction in competition induced by the reduction in richness may allow the remaining phytoplankton types to increase their biomass. With another 100 years of forced model output, change-points in biomass may begin to occur as even the competitively fit phytoplankton types begin to struggle with their changing environmental conditions.

6.5.3 Change in functional groups

In this study, I also used polar plots to visualise changes to the modelled phytoplankton community structure across five Longhurst provinces of the North Atlantic region (Figure 6.4a). In the NASW and NATR regions of the lower latitudes there was clear stability in the structure of the community, which suggests that the majority of change in this region wasn't a shuffle in the functional group structure but due to the significant impact on biomass with changing climatic conditions (Figure 6.4e and f). This may be reflecting that lower latitudes are occupied by phytoplankton types that are able to adapt well in these high irradiance, low nutrient conditions, as has been described in other studies (Barton et al., 2010).

The polar plots of the higher latitude Longhurst regions, ARCT and NADR, demonstrate an increase in the smaller functional groups, particularly the Other Small group (Figure 6.4b and c). This shift in the community structure fits with previous model results showing that smaller phytoplankton types shift northwards in a warming climate (Beaugrand, 2005, Bopp et al., 2005, Thomas et al., 2012, Barton et al., 2016). Previous use of the IGSM has demonstrated phytoplankton types track their thermal optima in changing environmental conditions, even though they may still have variability in their biomass (Dutkiewicz et al., 2015). This tracking of thermal optima into the northern regions of the North Atlantic may result in the increase of smaller functional types, seen in the polar plot analysis (Figure 6.4). Theory from a recent study also suggests a mismatch between the range movements of plankton taxa and the velocity of climate change, with dinoflagellates and copepods tracking changes in climate, such as increasing SST, more closely than larger diatom species (Chivers et al., 2017). This may be another factor explaining the decline of diatoms in the higher latitudes and the replacement with other functional types.

In the higher latitudes, the model demonstrates that an increase in species richness is accompanied by a variable community structure through time (Figure 6.2 and Figure 6.3), whereas in the low latitudes a decreasing richness had little impact on the functional structure of the community, only on the species within those functional groups. Another model study by Thomas et al. (2012) found phytoplankton from polar regions had larger thermal ranges than those in tropical regions, reflecting the larger seasonality in high latitudes. Due to this natural variation in thermal niches between phytoplankton types, changes to the marine environment in the higher latitudes may result in less stress to the community than in the tropical regions (Thomas et al., 2012). This theory fits with our model results, where in the high latitudes I have the addition of smaller functional types, but not the loss of larger types that dominate north of 60°N (Figure 6.4).

6.5.4 Relationship to environmental drivers

The factors regulating phytoplankton biomass, and especially diversity, are not well understood, although the requirement of light and nutrients for successful growth has been widely demonstrated (Adjou et al., 2012). Here, I assessed four potential drivers: SST, MLD, NO3 and zooplankton abundance (Figure 6.5). Changes in the physical environment reflected patterns observed previously in other models with the North Atlantic experiencing increased SST, apart from in the central subpolar gyre where a cooling effect is predicted, shallowing of the mixed layer in the high latitudes and a decrease in nutrient supply (Bopp et al., 2013, IPCC, 2013, Dutkiewicz et al., 2015, Barton et al., 2016). These patterns reflect the theory that a rise in ocean temperature may lead to increased ocean stratification and changes to mixing which may ultimately decrease nutrient supply, and thus increasing nutrient stress for phytoplankton (Litchman et al., 2006, Bopp et al., 2013, Adjou et al., 2012). While many studies have focused on distributional patterns of phytoplankton abundance, in this study I focused on how these mechanisms may regulate the community biomass and richness through time (Barton et al., 2010, Adjou et al., 2012, Barton et al., 2016).

Temperature has a fundamental and direct effect on biological processes (Eppley, 1972, Bopp et al., 2013) and this was reflected in the strong positive Spearman correlation between phytoplankton biomass and SST (Figure 6.6a). In the higher latitudes, north of 60°N, over the course of the modelled 21st century the mixed layer was found to shoal (Figure 6.6b). A positive Spearman correlation with phytoplankton biomass suggests that as the mixed layer shoals there is an increase in phytoplankton biomass, potentially due to a reduction in light limitation as phytoplankton are maintained nearer the surface promoting conditions for growth (Figure 6.6) (Bannister, 1974, Matsumoto et al., 2014).

Many in-situ and model studies focus on the control of the physical environment, while the control of ‘top-down’ forcing from predation remains largely under studied over long timescales (Barton et al., 2014). Here I have assessed the influence of zooplankton biomass on the phytoplankton community as a ‘top-down’ factor (Figure 6.6). There is a strong positive correlation between zooplankton and phytoplankton biomass, with both variables declining through the 21st century across the North Atlantic with the exception of the sub-polar gyre region (Figure 6.6). While correlations can detail whether a relationship is positive or negative in affect, it cannot determine the exact direction of the driving forcing between the predictor and response without a-priori knowledge. I hypothesise that the negative influence of increasing SST, which reduces phytoplankton biomass in the model, also has a negative influence on the zooplankton biomass through strong predator-prey coupling (Edwards and

Richardson, 2004, Barton et al., 2016). Following a similar distributional pattern to SST with largely significant correlations in the sub-tropical gyre, zooplankton had a positive relationship with phytoplankton richness (Figure 6.6).

Spearman correlations for richness against each of the four predictor variables were mostly insignificant above 45°N and below 25°N , however, in the sub-tropical region a significant pattern was defined between phytoplankton richness, SST, nitrate and zooplankton biomass (Figure 6.6). In the high latitudes I must consider that the insignificance may be a result of the timescales of the model output used here, which is in 5 year averages, which eliminates seasonal timescales. I must also highlight that richness is a very simple metric of community structure. While richness is important for assessing the overall health and stability of a community, it is only a count measure and richness can remain constant through time even though there may be a change in community structure (Magurran, 2004). The low seasonality of the sub-tropics is hypothesised to give rise to increased richness through coexistence, while favouring smaller phytoplankton types suited to the lower nutrient conditions (Barton et al., 2010, Dutkiewicz et al., 2015, Dutkiewicz et al., 2013). Finally, I must also reflect that Spearman correlation assumes a monotonic relationship and that, due to the complexity of phytoplankton ecology, this may not always be the case.

Models are effective tools for assessing potential changes in marine phytoplankton. This study demonstrates that both the physical environment and zooplankton community have important relationships with phytoplankton across the North Atlantic basin (Figure 6.6). The results of change-point analysis suggest that I might expect abrupt shifts in richness before a shift in total community biomass, and that biomass may have significant changes in the sub-tropical regions earlier than the high latitudes (Figure 6.2). Averaged throughout the North Atlantic, abrupt changes in phytoplankton biomass occur around the model year 2035. By this point our modelled environment had experienced an average increase in SST by 1.25°C, a shoaling of the mixed layer by ~5m, a decrease in nitrate of 0.5 mmol N m^{-3} and decline in total zooplankton biomass of ~0.3 mmol P m^{-3} (Supplementary Figure 0.11).

6.5.5 Future work

As part of this study I examined the richness of the modelled community through time, however this index is an over simplification of the structure of a community. While the richness of a community can remain constant through time, the phytoplankton types that contribute to the structure of the community can still change. A change in the richness will only account for a net gain or loss of total species simplifying our understanding of community change. For an initial analysis of the modelled community, such a metric is useful to help us describe the spatio-temporal variability of the community and the use of polar plots here helped us to account for changes in the community structure. However, in future work I suggest the use of a more complex metric such as community turnover, which can assess the shuffling of phytoplankton types through time. Alternatively a more complex metric such as dissimilarity analysis could be used which is able to account for both the abundance and presence/absence of each phytoplankton type at each time point. Furthermore, the use of change-point analysis here could be future extended to explore the frequency of occurrence of change-points for each pixel of the North Atlantic and could also be applied to the change in the physical environment and zooplankton community.

6.6 Conclusions

Models are a useful tool to help us understand how phytoplankton community ecology may respond to changes to the North Atlantic environment. Changes predicted by the model fit well with previous model studies, demonstrating increased SST for all regions except the central sub-polar gyre, shoaling of the mixed layer in the higher latitudes, declines in nutrients and a decline in total zooplankton biomass.

Analysis demonstrated that 94% of the North Atlantic was significantly affected by changes in the model, of which most regions resulted in a decline in plankton biomass and richness. By utilising change-point analysis I demonstrate that as the environment changes, abrupt shifts are likely to occur in phytoplankton biomass and richness. These shifts were not geographically homogenous, with declines occurring first in the lower latitudes (2030s) and later in the higher latitudes (2050s). Our results also demonstrate that these changes are accompanied by a shift in community structure. These shifts in the higher latitudes include an increase of smaller functional types as they track thermal optima towards the poles with increasing SST, while in the sub-tropical regions the community structure remained relatively similar despite the decline in biomass.

The correlation analysis of phytoplankton and predictor variables reflect that as the environment continues to change, phytoplankton will respond negatively to a rise in ocean temperatures and shoaling of the mixed layer that may ultimately decrease nutrient supply and increase stress (Bopp et al., 2013, Litchman et al., 2006, Adjou et al., 2012).

Chapter 7 Synthesis

7.1 Summary of results chapters

This thesis aimed to examine long-term trends and variability in North Atlantic phytoplankton by using in-situ data from the CPR survey and modelled phytoplankton from the MIT IGSM. By utilising these datasets and applying a range of statistical analyses, this thesis provides a comprehensive picture of changes to phytoplankton biomass and community structure from the 1970s to the present day, and explores the potential variability within the phytoplankton community with a changing climate.

7.1.1 Long-term stability of phytoplankton community composition in the North-East Atlantic

In Chapter 4 I used data from the CPR survey to examine changes in the phytoplankton community between 1969 and 2013 in the North-East Atlantic. While previous studies had assessed changes to the community in terms of abundance, biomass or productivity, I evaluated changes in the abundance and community composition simultaneously by applying Bray-Curtis and community stability analysis. I found that on inter-annual timescales the phytoplankton community has remained largely stable in the North-East Atlantic, returning to its original state after a change in dominance between 1985 and 1995. Analysis suggested that in more recent years the community structure had become increasingly static, which may make it more prone to an eventual regime shift. Analysis of the community composition and environmental parameters found that on inter-annual timescales, phytoplankton did not have a significant relationship with the physical environment, and that other drivers such as the zooplankton community may be more important over long timescales. I suggest in this chapter that this may be due to the timescale of annual averages being used and that the interannual variability of zooplankton may be more comparable and therefore have a strong influence.

7.1.2 Inferring the inter-annual control of plankton communities across the North Atlantic

In Chapter 5 I continued to explore the potential drivers of phytoplankton at inter-annual timescales, assessing the importance of bottom up control by the physical environment and top-down control by the zooplankton community. In development from the linear relationships described in Chapter 4, this chapter used GAMs in a novel approach to explore non-linear relationships in plankton abundance and richness, using data from the CPR survey for the North-East and North West Atlantic. I found for the North-East Atlantic the phytoplankton community over inter-annual timescales had a negative linear relationship with the zooplankton community, reflecting the findings of my first results Chapter 4. However, in the North-West Atlantic there was a combination of the physical environment and the zooplankton community in shaping the response of the phytoplankton. Zooplankton responded positively in negative NAO conditions, consisting of increased SST and a decreased MLD and the relationship been phytoplankton and zooplankton suggested this also had a positive response from the phytoplankton community. This chapter demonstrated that textbook ecological assumptions of top-down and bottom-up control may not be so straight forward in the in-situ environment but I must also consider that these analyses are limited in there description of the marine environment and ecological factors may be missing.

Fundamentally, ecological communities are a set of interacting components that form a larger whole, and as such chaos can occur as a natural part of the system variability (Boeing, 2016). This is one such component that may be lacking in studies. Chaos can occur as a result of competition for limited resources, predator-prey interactions and food-chain dynamics, resulting in the apparent random nature of communities being formed of underlying patterns and feedback loops (Benincà et al., 2008, Boeing, 2016, Dakos et al., 2009). Chaos can generate variability in a community even when there this no external forcing from the physical environment, as demonstrated by a mesocosm experiment by Benincà et al. (2008).

7.1.3 Future shifts of North Atlantic phytoplankton community structures

In my final results Chapter 6, I used data from the MIT IGSM to assess changes in the biomass and community structure of the phytoplankton community in relation to changes in the physical environment and zooplankton biomass over the 21st century. This model had 96 phytoplankton types, split between 6 functional groups. I used change-point analysis as a novel approach to assess the model for abrupt changes in phytoplankton biomass and richness in the North Atlantic and assessed changes in the functional structure of the community. Results demonstrated that 94% of the North Atlantic experienced a change under the influence of a changing climate, this mainly resulted in a decreased of phytoplankton biomass across the North Atlantic, with the exception of the sup-polar gyre where a slight increase occurred. The novel use of change-point analysis demonstrated that abrupt shifts in the phytoplankton community are likely to occur earlier in the sub-tropical regions (2030s), than in the higher latitudes (2050s) which may be due to the natural seasonal variability of the higher latitudes enabling the community to be more resilient to change. Changes resulted in the sub-tropics remaining structurally similar even with an overall decline in biomass, however in the higher latitudes communities shifted to be dominated primarily by diatoms and smaller functional types.

I also assessed the relationship of the modelled phytoplankton biomass and richness to the physical environment and zooplankton, to follow the work of the previous two results chapters. Biomass had a significant relationship with many of the drivers across the North Atlantic, whereas phytoplankton richness only had significant relationships in select areas. SST had a negative relationship with phytoplankton, whereas shallower MLD and zooplankton had positive relationships. These results suggest that while the physical environment may not have a significant relationship with phytoplankton in the North-East Atlantic on the interannual timescales of the in-situ data in chapters 4 and 5, given enough time and change in the environment, these variables do have a significant influence in the structuring of marine plankton communities and may lead to an overall decline in the population. This chapter highlights the importance of models in enabling us to examine potential future change with the flexibility of a dataset with no spatial or temporal restrictions as with in-situ data.

7.2 Reflection on results and comments on the datasets used

This thesis demonstrates the importance of long timeseries to provide numerical assessments of changes in phytoplankton ecology. Reflecting on the findings of this thesis, it is apparent that when assessing the phytoplankton community, the North Atlantic should not be treated as a whole especially when exploring the relationship to driving forces. The North Atlantic can be divided in a variety of ways, but the consideration of biogeochemical provinces and hydrographic features should be applied to account for the spatial variability demonstrated here.

The primary focus of this thesis was the analysis of long-term changes in the phytoplankton community. There are very few in-situ biological datasets with a large spatial-temporal extent, especially that has not had an alteration in methodology. The CPR survey is able to provide a temporally, spatially and taxonomically extensive plankton dataset, enabling it to offer a unique perspective on changes to the plankton community since 1958 for the North Atlantic basin (Richardson et al., 2006). The CPR survey has been used to assess many aspects of phytoplankton including seasonality (McQuatters-Gollop et al., 2007a, Friedland et al., 2016), distributions (Beaugrand, 2004, McQuatters-Gollop et al., 2007a), response to external forcing

(Barton et al., 2014, Beaugrand and Reid, 2003, Chivers et al., 2017) and to assess the health of marine ecosystems (Beaugrand, 2005, McQuatters-Gollop et al., 2015).

Results from the CPR survey in Chapter 4 show that in the North Atlantic region, the phytoplankton community structure remains largely stable, even though there are inter-annual fluctuations in the abundance of individual species. I theorise that even with changes to the physical environment, the highly seasonal nature of this region means that phytoplankton have not yet been forced out of their response limits and therefore do not have a significant relationship with the physical drivers at these timescales. As previous studies have demonstrated, if I were to examine the phytoplankton community within a seasonal timescale, I would observe large variability in the composition and abundance of phytoplankton species, but between years the average structure of the community is stable (McQuatters-Gollop et al., 2007a, Lindemann and St. John, 2014, Matsumoto et al., 2014). This raises an important question of the timescales used. In this thesis I have been specific to focus my research to examine inter-annual variability, using data that has been averaged annually. This was largely defined by the temporal patchiness of the CPR survey, in which a monthly comparison would have resulted in a large mismatch of dates over the study period. The use of hourly or seasonal data over a long-term study can also create issues with the amount of “excess” data (Schreiber and Kantz, 1996, Orzack, 2012). This noise can distort available patterns and studies have demonstrated that this excess of data, even in the form of a few percent of noise, can distort algorithmic analysis (Schreiber and Kantz, 1996, Orzack, 2012). In this thesis, these problems have been managed through the use of annual averages and, in Chapter 5, the application of non-linear analysis.

The results of the model analysis demonstrate that as the climate continues to change, the phytoplankton community composition in the North Atlantic is likely to shift and shuffle, with smaller functional types increasing in abundance and larger functional types maintaining or declining in their contribution to the community biomass. This highlights an important limitation of the CPR survey, in which the large mesh size of 270μm, used to filter plankton from the water column, limits the fraction of the plankton community sampled (Richardson et al., 2006). This mesh size was originally chosen to allow sampling of large zooplankton types and phytoplankton, while reducing the clogging by smaller phytoplankton (Hardy, 1936). While some small phytoplankton types are regularly recorded as CPR practice, for example Coccolithophores have had their presence recorded since 1969 and counted since 1993, much of the smaller size fraction of the in-situ phytoplankton community remains unsampled or under sampled by the CPR (Richardson et al., 2006).

While the CPR survey only reflects the larger sized portion of the community, other studies with alternative data sources have demonstrated that a strong relationship between the small-sized fraction of plankton, such as picophytoplankton (<2µm in diameter), and sea surface temperature exists (Morán et al., 2010). This is likely due to smaller cells having a larger surface area to volume ratio increasing their physical contact with the marine environment, enhancing the ability to uptake nutrients in warmer environments in which they can be scarce. Such studies have demonstrated that as oceans continue to warm, a gradual shift to these smaller species is likely to occur as taxa track their thermal optima and the availability of nutrients, fitting with my findings in Chapter 6 (as shown in Figure 7.1), and that this may consequently impact carbon export as smaller plankton may have lower sinking velocities (Morán et al., 2010). While limitations within the CPR survey do exist, it undoubtedly provides a unique and critical perspective for the state of the ocean ecosystems and as such should have continued support in its maintenance and collection.

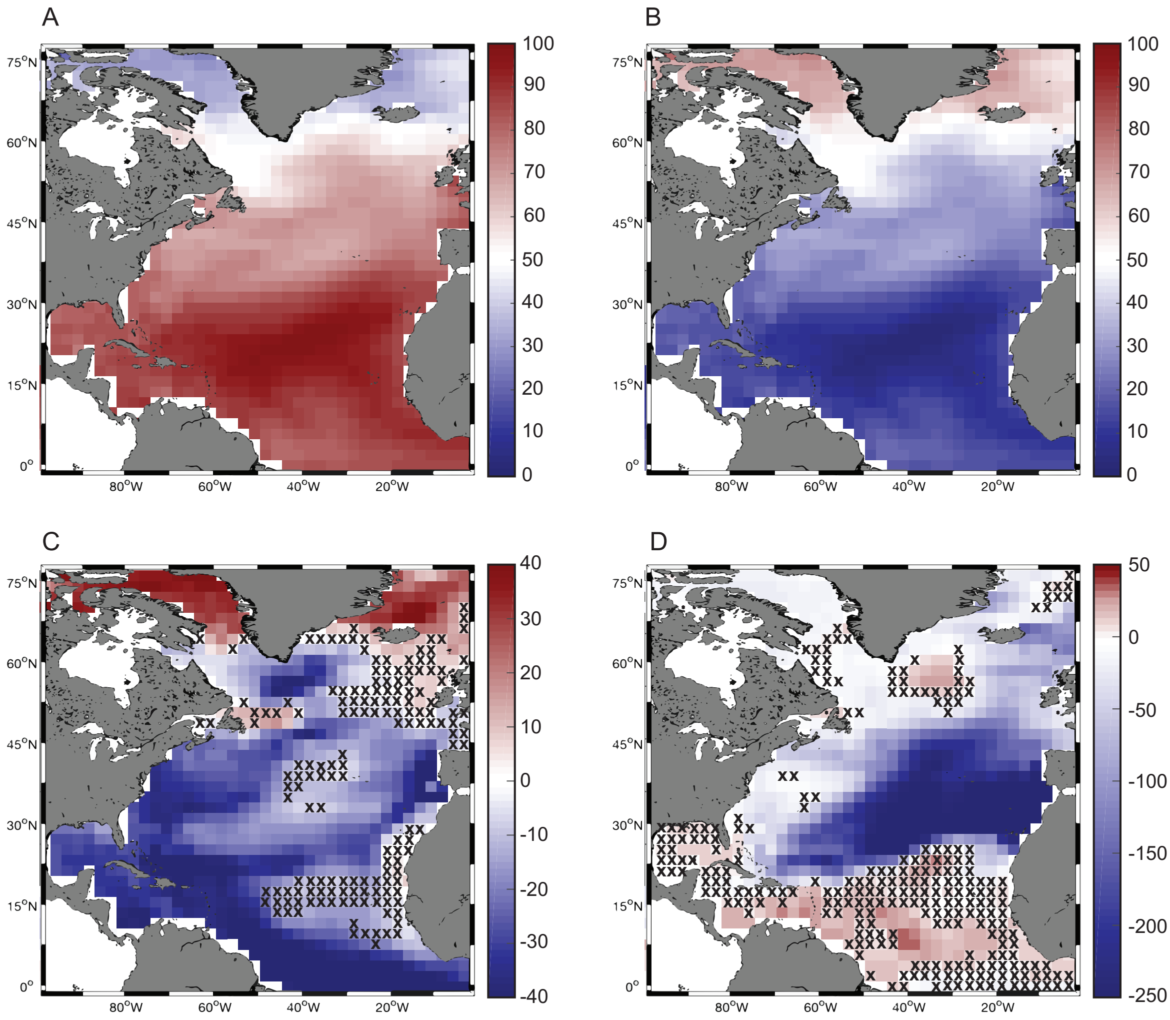

Figure 7.1: Percentage contribution of the small functional types (Other Small, Diazotrophs, Procholococcus and Coccolithophores) (A) and Large functional types (Diatoms and Other Large) (B) to the whole modelled phytoplankton community structure

and the percentage change of the small functional types (C) and Large functional types (D) between the first and last 20 years of the model. A t-test was performed between the first and last 20 years of the model. If the change was not significant (p>0.05) an 'x' was overlaid on the map

7.3 Implication of changes in phytoplankton communities to marine ecosystems

While a few sustained biological timeseries like the CPR survey exist, there has been wide discussions as to whether current in-situ timeseries are actually long enough to detect a global warming trend from natural variability and that in the North Atlantic region, a timeseries of >40 years length may be needed to distinguish climate driven trends (Henson et al., 2010). With in-situ surveys suffering from changes in methodology and a lack of funding for continuation, the use of models to represent changes in the marine environment have become increasingly popular. Models also benefit from their ability to forecast the future state of the marine environment as well as recreate current in-situ conditions, enabling their important roles in wider uses such as environmental policy and mitigation (Dutkiewicz et al., 2005, IPCC, 2013).

The results of the model analysis in Chapter 6, clearly demonstrate that as the climate continues to change the phytoplankton community will be affected and likely changes include a decline in phytoplankton biomass across the North Atlantic and a shift in composition to the smaller size fraction, which will undoubtedly have consequences for the wider marine ecosystem. With phytoplankton underpinning the marine food web, changes in community composition and biomass have the potential to drastically alter food web dynamics. While the direct impacts of such change are still widely debated, it is likely that these changes will propagate up the food chain impacting commercially important fish stocks, seabirds and mammals (Richardson and Schoeman, 2004, Worm et al., 2006).

Marine phytoplankton also have a profound role in regulating atmospheric CO_2, and the structure and biomass of the in-situ community ultimately affect the flux of carbon to the seafloor (Falkowski et al., 1998). Diatoms are well documented to aggregate when required nutrients become limited and, upon death, can sink out of the upper ocean, exporting organic matter (Bopp et al., 2005). Collectively they may account for 40% of the global carbon export and as the marine environment continues to change, their decline may ultimately impact the amount of carbon stored in the deep ocean (Tréguer and Pondaven, 2000, Bopp et al., 2005, Tréguer et al., 2017).

The smaller sized fraction of the phytoplankton community have wide distributions across the North Atlantic region, as demonstrated from the IGSM model output in Figure 7.1, and in-situ datasets contribute to a large proportion of the phytoplankton biomass and productivity (Bell and Kalff, 2001, Morán et al., 2010). While the large functional types of phytoplankton dominate the role of carbon transport to the deep ocean, a study has also demonstrated the importance of smaller types in carbon export and with their competitive advantage in a warming ocean, should not be overlooked when assessing changes to the community structure (Richardson and Jackson, 2007).

7.4 Future work

The work achieved in this thesis can be developed in several ways. This effort was confined to the limits of the North Atlantic basin, primarily due to the sampling efforts of the CPR survey. However, the analysis applied throughout this thesis could be applied to any region with an appropriate timeseries and taxonomic resolution.

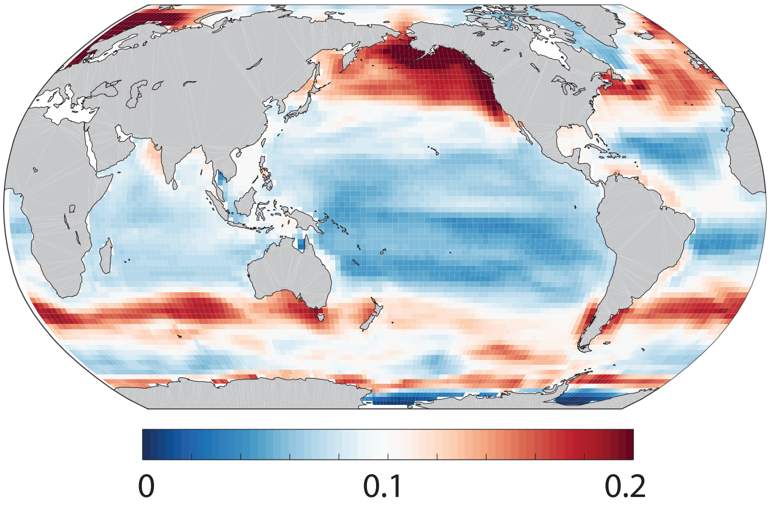

Figure 7.2: Results of Bray-Curtis analysis applied globally to IGSM dataset between 1990-2100. Values for Bray-Curtis Analysis range between 0, indicating no change in community composition, to 1, indicating no overlapping similarity in community composition. The methodology of Bray-Curtis analysis can be found in section 4.3.3.2.

The IGSM for example is a global model and additional work has demonstrated that patterns of change to community biomass and richness are expected worldwide and will continue to be greatest in the high latitude regions (Figure 7.2).

7.4.1 Structural equation modelling

An important finding of Chapter 5 was the non-linear relationships between the phytoplankton community and its drivers, reflecting that marine ecosystems are complex (Beaugrand, 2003). A limitation of this work however was that GAMs do not include the relative direction of driving forces. A development of this analysis would be to use structural equation modelling (SEMs), which through the application of hypotheses determined from a-priori understand of interactions, allow for directionality to be added and can provide more information on driver importance over various spatio-temporal scales (Arhonditsis et al., 2006). Like GAMs, SEMs are flexible and allow the exploration of many ecological datasets while providing a robust way to study independencies even among correlated variables (Arhonditsis et al., 2006). SEMs would be a natural progression of the work in Chapter 5, and could also be extended to include higher trophic levels enabling an examination of changes to wider food web dynamics, if the data of sufficient resolution was available.

7.4.2 Extending work with the IGSM

Output provided for the model analysis in Chapter 6 included information from the Control experiment, which provides a “no climate change” baseline, and the Climate experiment in which the marine environment is forced with changes to SST, mixing, circulation and sea-ice (Dutkiewicz et al., 2015). However, the analysis applied here could also be applied to other model experiments from the IGSM, including the ALL experiment which includes changes in pCO_2. Several in-situ studies have highlighted the future impact of increasing ocean acidification as pCO_2 levels rise with anthropogenic activity (Doney et al., 2009, Beare et al., 2013, Dutkiewicz et al., 2015). A previous study by Dutkiewicz et al. (2015) introduced the impact of changing pCO_2 to marine phytoplankton groups in the IGSM, concluding it had a significant impact on the ecological fitness of the modelled functional types. While this study examined changes in the community based upon richness metrics, a more complex approach could be applied as in Chapter 4, with the difference between model experiments explored (Dutkiewicz et al., 2015).

While the IGSM captures a range of phytoplankton through the simulation of 6 functional groups, each containing 16 phytoplankton types, the model does not take into account the size of each phytoplankton type and the zooplankton community is limited to two types, a small and large grazer (Dutkiewicz et al., 2013, Dutkiewicz et al., 2015). Changes to body size have important implications for planktonic organisms as it can influence the acquisition of nutrients, vital for growth, and Gardner et al. (2011) described the effects to be as universally important as changes in phenology and distribution.

Improving our understanding of size changes in the plankton community and modelling the relationships between size structure, nutrient acquisition, phenology and distributions will greatly increase our overall understanding of the impact of climate change on marine ecology and functioning (Gardner et al., 2011). While this feature is missing from the IGSM used in this thesis, the continued development of the model by MIT has led to a modified version that will include a complex marine ecosystem incorporating both functional and size diversity (Dutkiewicz et al., 2015). This expansion aims to include 8 functional types which includes 51 plankton types (2 pico-prokaryotes, 2 pico-eukaryotes, 5 coccolithophore, 5 diazotrophs, 11 diatoms, 10 mixotrophic dinoflagellates, and 16 zooplankton) ranging from 0.6µm to 2500µm in equivalent spherical diameter. A graphical representation of this model design is shown in Figure 7.3.

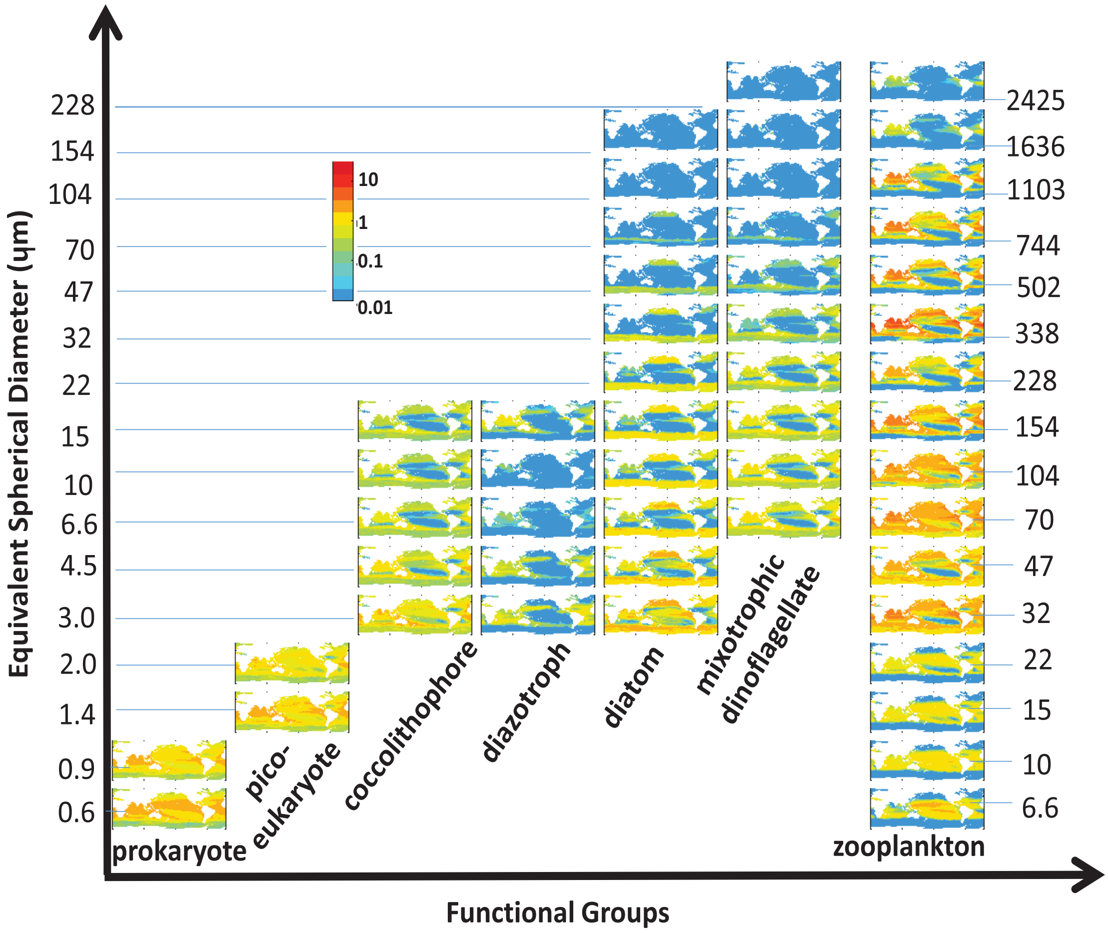

Figure 7.3: Graphical representation of the modified IGSM from Dutkiewicz et al. (2015). X-axis represents the 8 planktonic functional groups (prokaryote, pico-eukaryote, coccolithophore, diazotroph, diatom, mixotrophic dinoflagellate and zooplankton).

Y-axis represents the size for the phytoplankton and zooplankton groups. For each plankton type and size class, a map of biomass mean between 0-50m (mgC / m^3*) is shown.*

The addition of size categories to the model could lead to the analysis of changes in size distribution as the climate continues to change, as well as the ability to include size as a factor when calculating changes in community structure. This version of the IGSM also contains many more size categories of zooplankton taxa, unlike the small and large groups used in Chapter 6. This expansion would therefore allow for the more detailed examination of predator-prey dynamics and could be extended to a global study, outside the remit of this thesis.

7.5 Final remarks

It is highly likely that the diversity and biomass of the plankton community will be impacted by changes to the future climate. Biodiversity losses in the tropics and gains in the high latitudes will result in large structural changes to the community as warm water species follow their thermal optima northwards (Thomas et al., 2012, Beaugrand et al., 2015). With this shift and shuffle in phytoplankton community structure, it is likely that this will consequently be reflected in changes to the function and structure of the marine food web and biogeochemical processes. The continuation of long-term biological surveys, such as the Continuous Plankton Recorder survey will be vital to track changes in the marine environment, while models continue to drive our understanding of future changes.

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Appendix A Taxonomic data from the Continuous Plankton Recorder survey

Supplementary Table 3: Summary of every plankton type used from the CPR survey in thesis analysis. CPR number is the unique code assigned by the CPR survey program and the given name that number represents is shown. The type of plankton is defined: Phytoplankton (P), Zooplankton (Z) and the CPR sampling method is defined: Phytoplankton traverse (P/T), Zooplankton traverse (Z/T) and Zooplankton Eyecount (Z/E).

CPR number	Name	Type	Sample method
101	Paralia sulcata	P	P/T
102	Skeletonema costatum	P	P/T
103	Thalassiosira spp.	P	P/T
104	Dactyliosolen antarcticus	P	P/T
107	Rhizosolenia styliformis	P	P/T
108	Rhizosolenia hebetata semispina	P	P/T
112	Chaetoceros(Hyalochaete) spp.	P	P/T
113	Chaetoceros(Phaeoceros) spp.	P	P/T
114	Odontella sinensis	P	P/T
116	Thalassiothrix longissima	P	P/T
117	Thalassionema nitzschioides	P	P/T
121	Ceratium fusus	P	P/T
122	Ceratium furca	P	P/T
123	Ceratium lineatum	P	P/T
124	Ceratium tripos	P	P/T
125	Ceratium macroceros	P	P/T
126	Ceratium horridum	P	P/T
127	Ceratium longipes	P	P/T
128	Ceratium arcticum	P	P/T
133	Polykrikos schwartzii cysts	P	P/T
152	Asteromphalus spp.	P	P/T
154	Bacteriastrum spp.	P	P/T
157	Odontella aurita	P	P/T
165	Coscinodiscus concinnus	P	P/T
166	Coscinodiscus spp. (Unidentified)	P	P/T
167	Detonula confervacea	P	P/T
169	Eucampia zodiacus	P	P/T
170	Fragilaria spp.	P	P/T

171	Guinardia flaccida	P	P/T
172	Gyrosigma spp.	P	P/T
173	Hemiaulus spp.	P	P/T
175	Leptocylindrus danicus	P	P/T
176	Navicula spp.	P	P/T
177	Cylindrotheca closterium	P	P/T
178	Rhaphoneis amphiceros	P	P/T
179	Planktoniella sol	P	P/T
180	Rhizosolenia acuminata	P	P/T
182	Rhizosolenia bergonii	P	P/T
187	Rhizosolenia setigera	P	P/T
190	Stephanopyxis spp.	P	P/T
192	Surirella spp.	P	P/T
196	Pterosperma spp. (Total)	P	P/T
198	Silicoflagellates	P	P/T
199	Nitzschia spp. (Unidentified)	P	P/T
203	Pachysphaera spp.	P	P/T
221	Ceratium arietinum	P	P/T
224	Ceratium bucephalum	P	P/T
226	Ceratium candelabrum	P	P/T
230	Ceratium extensum	P	P/T
232	Ceratium hexacanthum	P	P/T
237	Ceratium massiliense	P	P/T
238	Ceratium minutum	P	P/T
240	Ceratium pentagonum	P	P/T
247	Ceratium trichoceros	P	P/T
250	Cladopyxis spp.	P	P/T
251	Dinophysis spp. Total	P	P/T
253	Gonyaulax spp.	P	P/T
254	Oxytoxum spp.	P	P/T
255	Protoperidinium spp.	P	P/T
257	Podolampas spp.	P	P/T
259	Prorocentrum spp. Total	P	P/T
271	Glenodinium spp.	P	P/T
818	Phalacroma spp.	P	P/T
950	Scrippsiella spp.	P	P/T
980	Actiniscus pentasterias	P	P/T
981	Nitzschia longissima	P	P/T
984	Gyrodinium spp.	P	P/T
1000	Proboscia alata	P	P/T
1001	Leptocylindrus mediterraneus	P	P/T
1002	Proboscia inermis	P	P/T
1596	Rhizosolenia pungens	P	P/T
1627	Nitzschia bicapitata	P	P/T
1634	Eucampia spp.	P	P/T

10375	Phalacroma rotundatum	P	P/T
10615	Asterionellopsis glacialis	P	P/T
10620	Prorocentrum spp. ('Exuviaella' type)	P	P/T
10622	Ephemera planamembranacea	P	P/T
10623	Pseudo-nitzschia delicatissima complex	P	P/T
10624	Pseudo-nitzschia seriata complex	P	P/T
10625	Trichodesmium spp.	P	P/T
10627	Gonyaulax grindleyi	P	P/T
10629	Pseudosolenia calcar-avis	P	P/T
10631	Guinardia delicatula	P	P/T
10632	Dactyliosolen fragilissimus	P	P/T
10634	Guinardia striata	P	P/T
10636	Detonula pumila	P	P/T
10641	Lauderia annulata	P	P/T
10680	Bacillaria paxillifera	P	P/T
10681	Corethron hystrix	P	P/T
10682	Proboscia curvirostris	P	P/T
10683	Proboscia indica	P	P/T
10684	Rhizosolenia imbricata	P	P/T
1	Calanus I-IV	Z	Z/T
3	Para-Pseudocalanus spp.	Z	Z/T
4	Temora longicornis	Z	Z/T
5	Acartia spp. (unidentified)	Z	Z/T
6	Centropages typicus	Z	Z/T
7	Centropages hamatus	Z	Z/T
9	Clausocalanus spp.	Z	Z/T
10	Oithona spp.	Z	Z/T
11	Corycaeus spp.	Z	Z/T
40	Calanus finmarchicus	Z	Z/E
41	Calanus helgolandicus	Z	Z/E
42	Calanus glacialis	Z	Z/E
44	Calanus hyperboreus	Z	Z/E
45	Neocalanus gracilis	Z	Z/E
47	Nannocalanus minor	Z	Z/E
48	Calanoides carinatus	Z	Z/E
50	Rhincalanus nasutus	Z	Z/E
51	Euchirella rostrata	Z	Z/E
53	Euchaeta acuta	Z	Z/E
55	Metridia lucens	Z	Z/E
56	Metridia longa	Z	Z/E
57	Pleuromamma robusta	Z	Z/E
58	Pleuromamma abdominalis	Z	Z/E
59	Pleuromamma borealis	Z	Z/E
60	Pleuromamma gracilis	Z	Z/E
61	Candacia armata	Z	Z/E

301	Acrocalanus spp.	Z	Z/T
302	Ischnocalanus	Z	Z/T
303	Candacia I-IV	Z	Z/T
304	Ctenocalanus vanus	Z	Z/T
306	Harpacticoida Total Traverse	Z	Z/T
312	Lucicutia spp.	Z	Z/T
313	Mecynocera clausi	Z	Z/T
314	Metridia I-IV	Z	Z/T
316	Microcalanus spp.	Z	Z/T
317	Oncaea spp.	Z	Z/T
321	Scolecithricella spp.	Z	Z/T
369	Heterorhabdus spp. (Unidentified)	Z	Z/E
370	Aetideus armatus	Z	Z/E
372	Anomalocera patersoni	Z	Z/E
373	Candacia bipinnata	Z	Z/E
380	Centropages bradyi	Z	Z/E
386	Eucalanus hyalinus	Z	Z/E
394	Euchaeta media	Z	Z/E
406	Heterorhabdus abyssalis	Z	Z/E
407	Heterorhabdus norvegicus	Z	Z/E
408	Heterorhabdus papilliger	Z	Z/E
411	Pleuromamma piseki	Z	Z/E
412	Pleuromamma xiphias	Z	Z/E
413	Rhincalanus cornutus	Z	Z/E
414	Sapphirina spp.	Z	Z/E
415	Scolecithrix bradyi	Z	Z/E
416	Scolecithrix danae	Z	Z/E
417	Scottocalanus persecans	Z	Z/E
418	Undeuchaeta major	Z	Z/E
419	Undeuchaeta plumosa	Z	Z/E
425	Scaphocalanus spp. (Unidentified)	Z	Z/E
428	Euchirella spp. (Unidentified)	Z	Z/E
429	Candacia spp. (Unidentified)	Z	Z/E
431	Centropages spp. (Unidentified)	Z	Z/T
434	Pleuromamma spp. (Unidentified)	Z	Z/E
435	Undeuchaeta spp. (Unidentified)	Z	Z/E
955	Pseudochirella spp.	Z	Z/E
1570	Neocalanus spp. (unidentified)	Z	Z/E
1574	Paraeuchaeta spp.	Z	Z/E
1628	Paracalanus spp.	Z	Z/T
10066	Siphonostomatoida	Z	Z/E
10588	Mesocalanus tenuicornis	Z	Z/E
10596	Subeucalanus crassus	Z	Z/E
10601	Eucalanidae (unidentified)	Z	Z/E
10604	Paraeuchaeta hebes	Z	Z/E

10605	Paraeuchaeta norvegica	Z	Z/E
10606	Euchaetidae (unidentified)	Z	Z/E

Appendix B Supplementary figures for Chapter 5

This section contains additional information regarding the GAM analysis in chapter 5. Section B.1 contains a comparison table of the initial GAM run containing all model variables and the final GAM run used in chapter 5. Section B.2 presented each of the 'gam.check' figures generated as part of the mgcv package used in the assessment of each model run.

B.1 Comparison table of GAMs

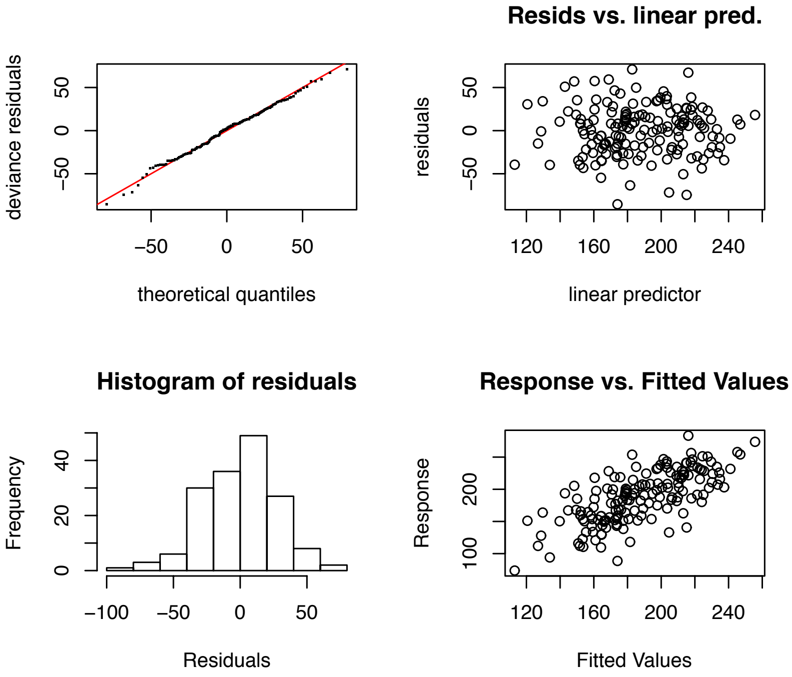
Supplementary Table 4: Summary of initial and final Generalised Additive Models for the East and West Atlantic. In both cases the model equations are given as well as the t- and f- values for the Gaussian Abundance tests and the z- and chi squared values for the Negative Binomial richness tests. Bold values for year indicate significance values (p = <0.05). For final tests of the f- and chi squared values only significant values are presented, '-' indicates the predictor was removed from the final model and 'x' indicates it was not included at all. The final column indicates the adjusted R^2 *value of the final model fit*

	Model Response	Initial (I) Final (F)	Model	*t-value*		*f-value*		Adjusted R2
				Year	**Zoo**	**PC1**	**PC2**	
East	Phytoplankton Abundance	I	*Phyto ~ s(Zoo) + s(PC1) + s(PC2) + (Year) + factor(Station)*	**-2.061**	**12.46**	0.46	2.11	49.80%
	Phytoplankton Abundance	F	*Phyto ~ s(Zoo) + (Year) + factor(Station)*	-1.76	**16.24**	-	-	50.80%
	Zooplankton Abundance	I	*Zoo ~ s(PC1) + s(PC2) + (Year) + factor(Station)*	**-3.61**	x	3.72	1.53	61.00%
	Zooplankton Abundance	F	*Zoo ~ s(PC1) + (Year) + factor(Station)*	**-3.90**	x	4.24	-	62.70%
West	Phytoplankton Abundance	I	*Phyto ~ s(Zoo) + s(PC1) + s(PC2) + (Year) + factor(Station)*	**25.45**	**30.79**	2.42	2.18	47.50%
	Phytoplankton Abundance	F	*Phyto ~ s(Zoo) + (Year) + factor(Station)*	1.63	**42.35**	-	-	40.30%
	Zooplankton Abundance	I	*Zoo ~ s(PC1) + s(PC2) + (Year) + factor(Station)*	**21.99**	x	6.227	0.02	76.90%
	Zooplankton Abundance	F	*Zoo ~ s(PC1) + (Year) + factor(Station)*	0.67	x	4.56	-	78.40%

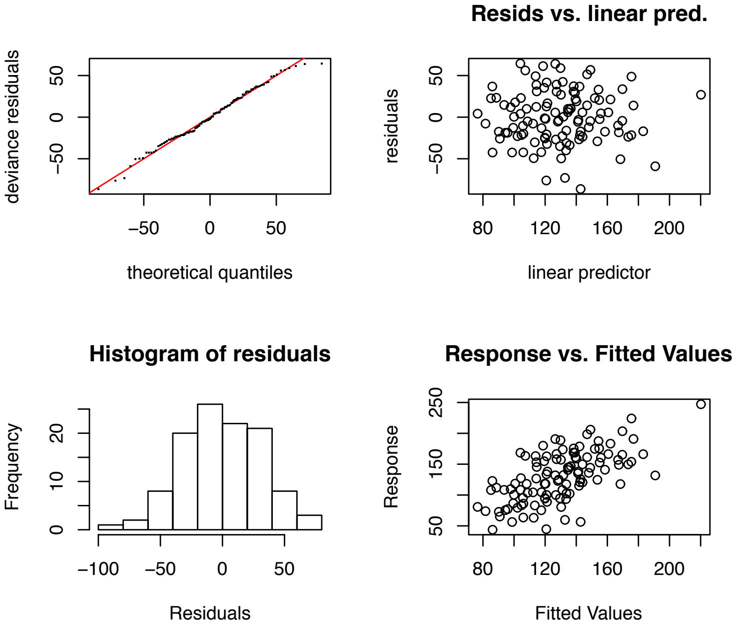
	Model Response	Initial (I) Final (F)	Model	*t-value*		*f-value*		Adjusted R2
				Year	**Zoo**	**PC1**	**PC2**	
East	Phytoplankton Richness	I	*Phyto ~ s(Zoo) + s(PC1) + s(PC2) + (Year) + factor(Station)*	0.46	**12.04**	0.01	0.06	27%
	Phytoplankton Richness	F	*Phyto ~ s(Zoo) + (Year) + factor(Station)*	0.43	**12.44**	-	-	29%
	Zooplankton Richness	I	*Zoo ~ s(PC1) + s(PC2) + (Year) + factor(Station)*	-0.93	x	5.88	0.02	67.80%
	Zooplankton Richness	F	*Zoo ~ (Year) + factor(Station)*	-0.95	x	-	-	67.80%
West	Phytoplankton Richness	I	*Phyto ~ s(Zoo) + s(PC1) + s(PC2) + (Year) + factor(Station)*	**3.7**	**35.62**	0.01	**12.34**	38.20%
	Phytoplankton Richness	F	*Phyto ~ s(Zoo) + s(PC2) + (Year) + factor(Station)*	**3.76**	**37.81**	-	12.56	44.60%
	Zooplankton Richness	I	*Zoo ~ s(PC1) + s(PC2) + (Year) + factor(Station)*	0.15	x	7.03	5.23	47.80%
	Zooplankton Richness	F	*Zoo ~ s(PC1) + s(PC2) + (Year) + factor(Station)*	0.15	x	7.03	5.23	47.80%

B.2 Final model validation figures

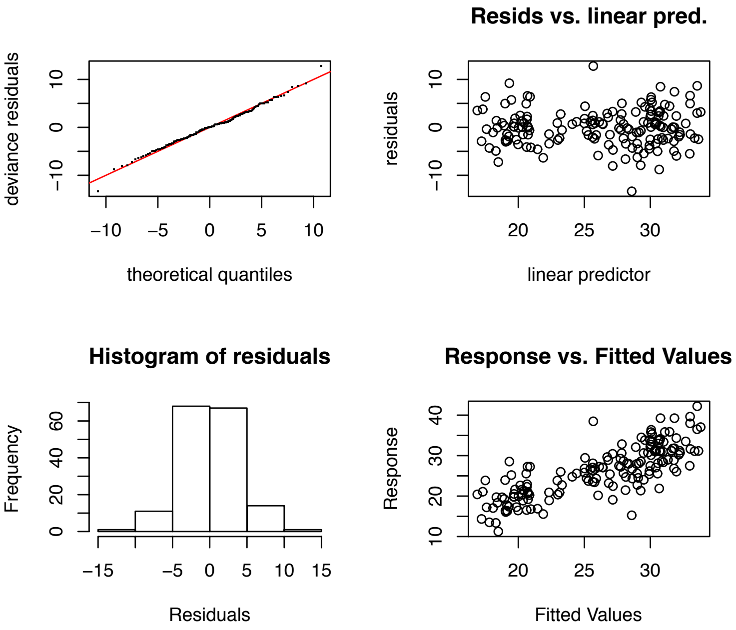
The results of the 'gam.check' in the mgcv package (Wood, 2017) in R (Team, 2016) are shown here for each of the final models.



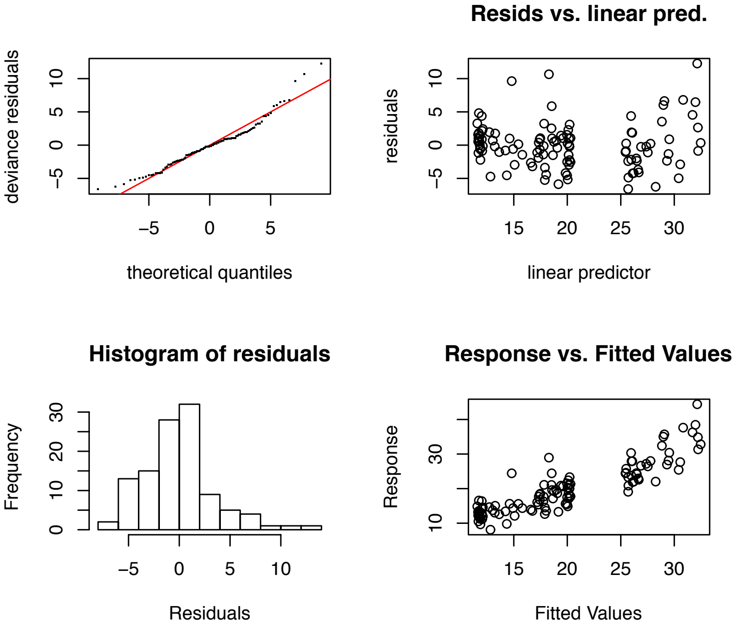
Supplementary Figure 4: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of phytoplankton abundance in the East Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.



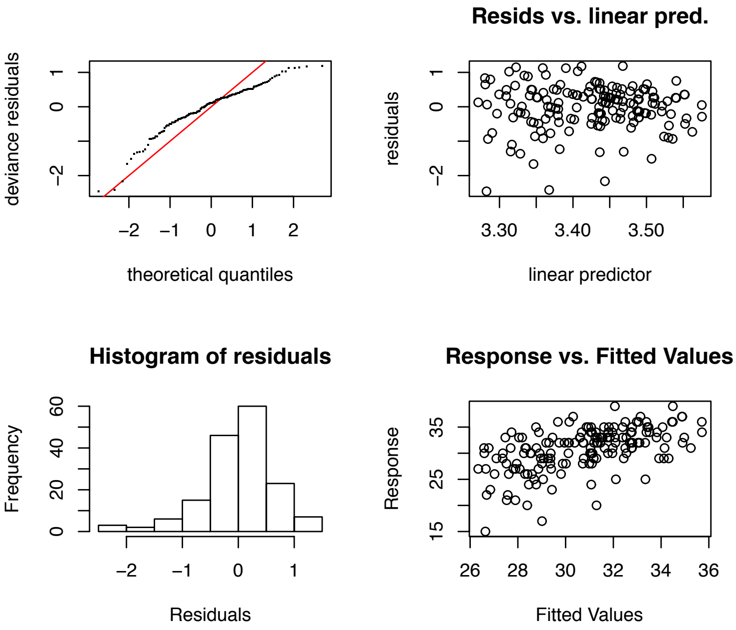
Supplementary Figure 5: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of phytoplankton abundance in the West Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.



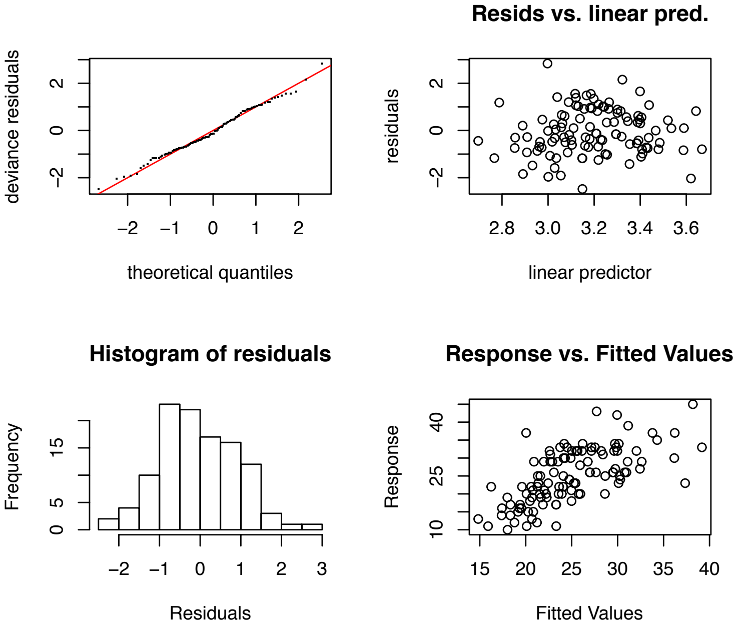
Supplementary Figure 6: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of zooplankton abundance in the East Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.



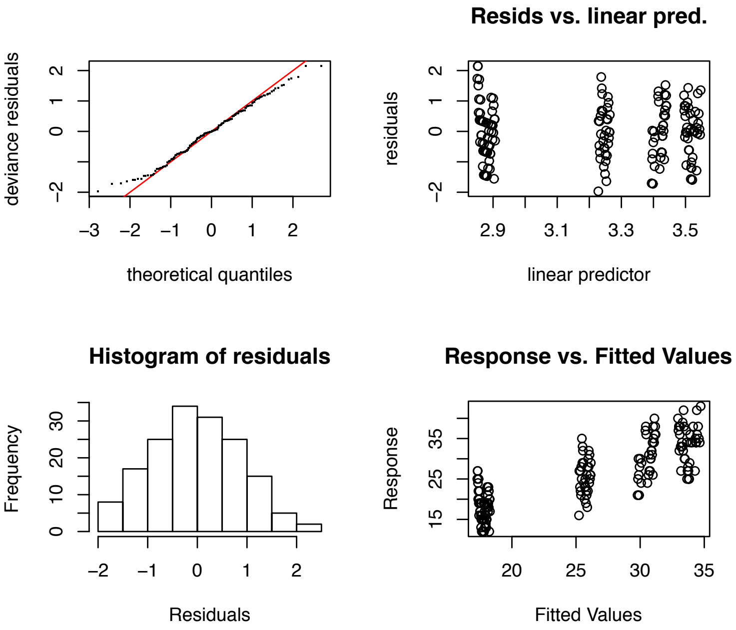
Supplementary Figure 7: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of zooplankton abundance in the West Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.



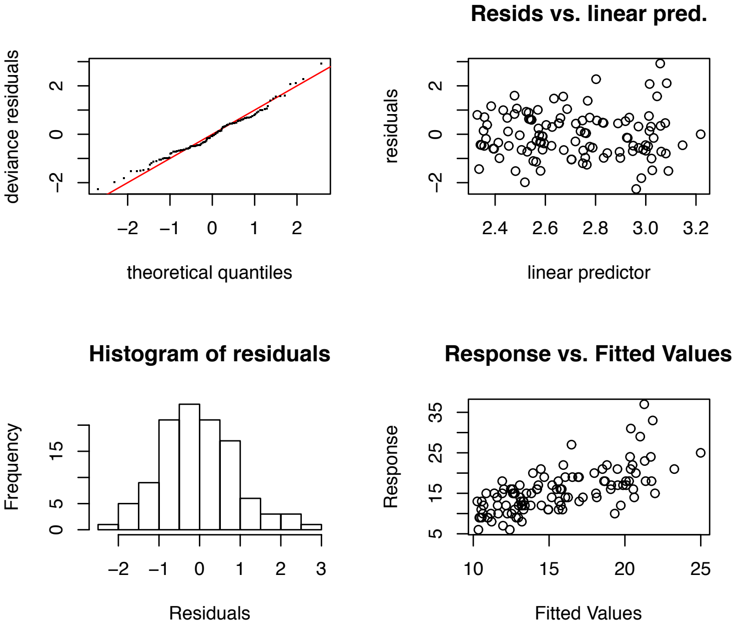
Supplementary Figure 8: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of phytoplankton richness in the East Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.



Supplementary Figure 9: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of phytoplankton richness in the West Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.

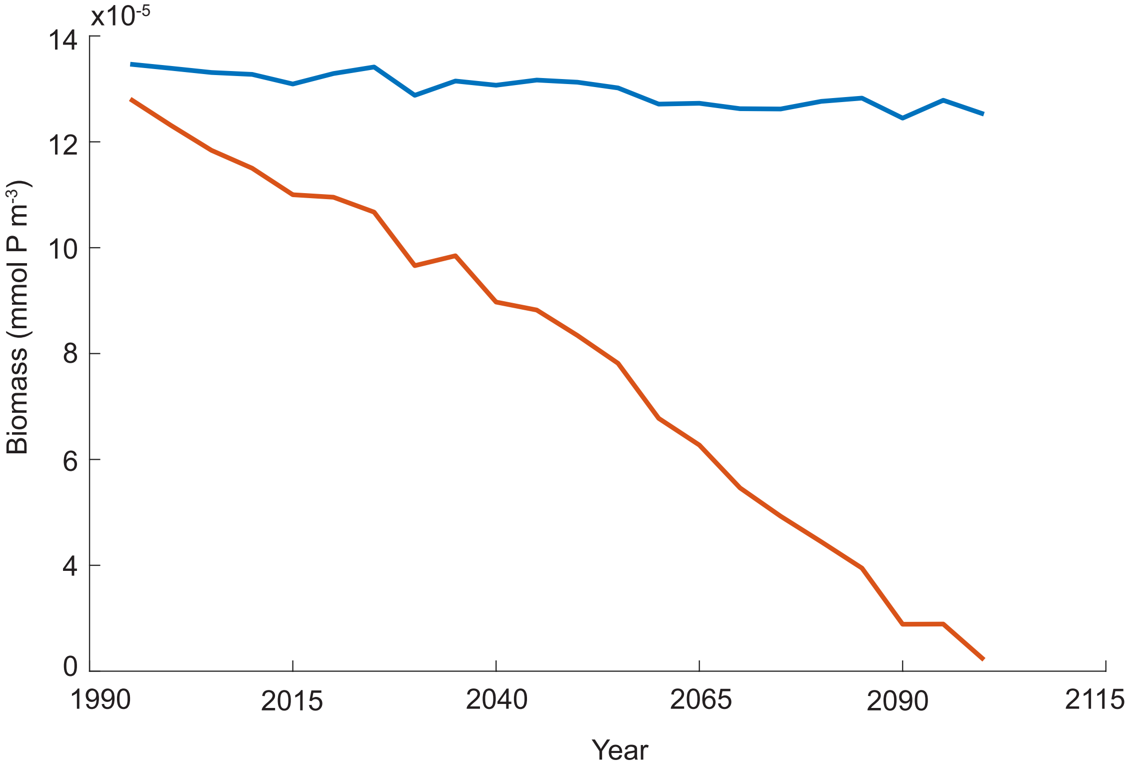


Supplementary Figure 10: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of zooplankton richness in the East Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.

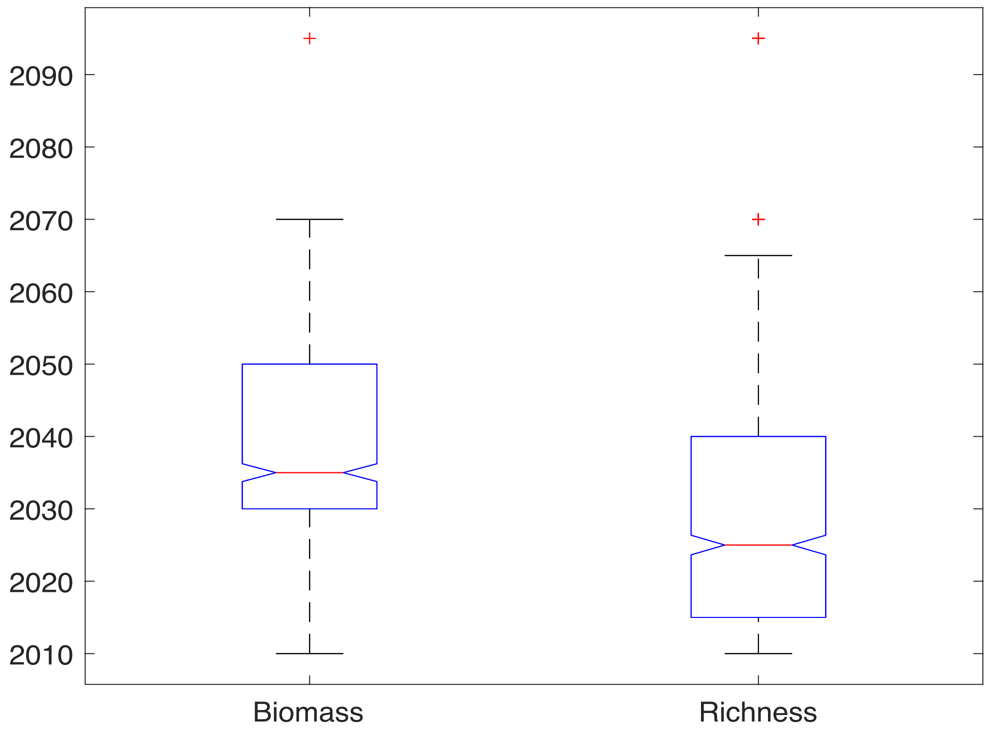


Supplementary Figure 11: Output from 'gam.check' function in the mgcv package (Wood, 2017) for the final GAM model of zooplankton richness in the West Atlantic. The 'gam.check' produces four plots. Shown here is a Q-Q plot, residuals vs linear predictor plot, a histogram of residuals and response vs. fitted values plot.

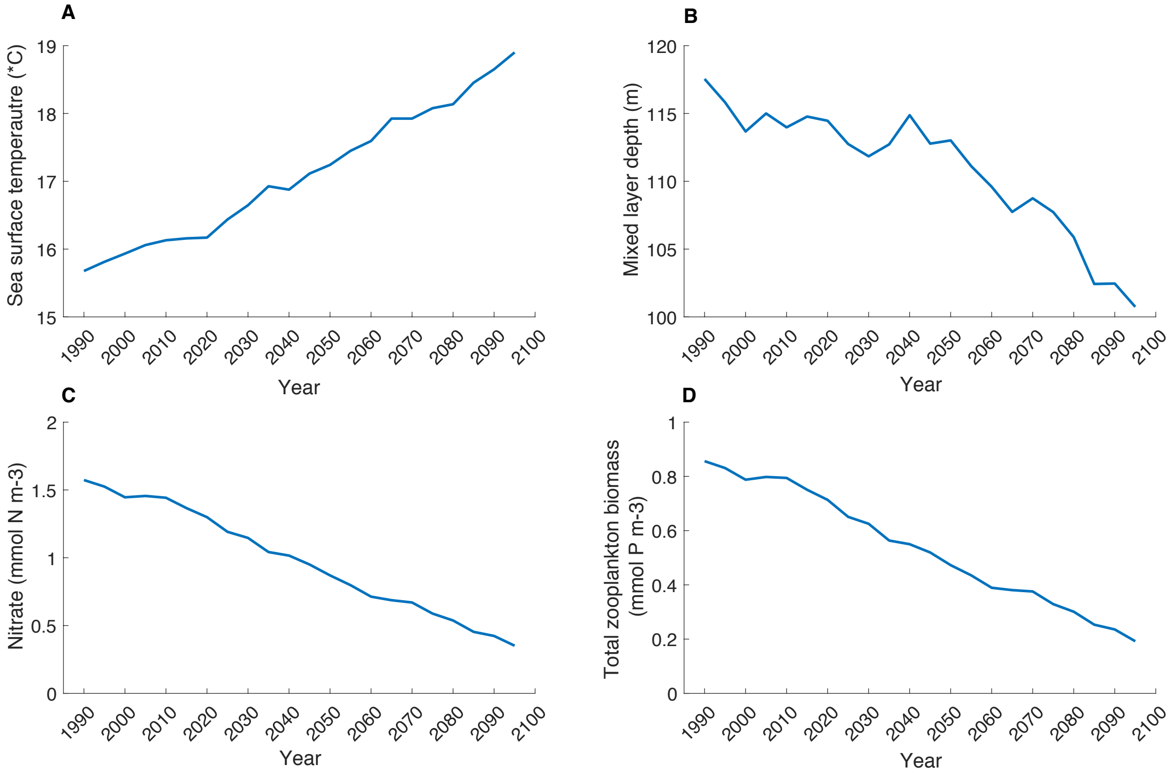
Appendix C Supplementary figures for Chapter 6



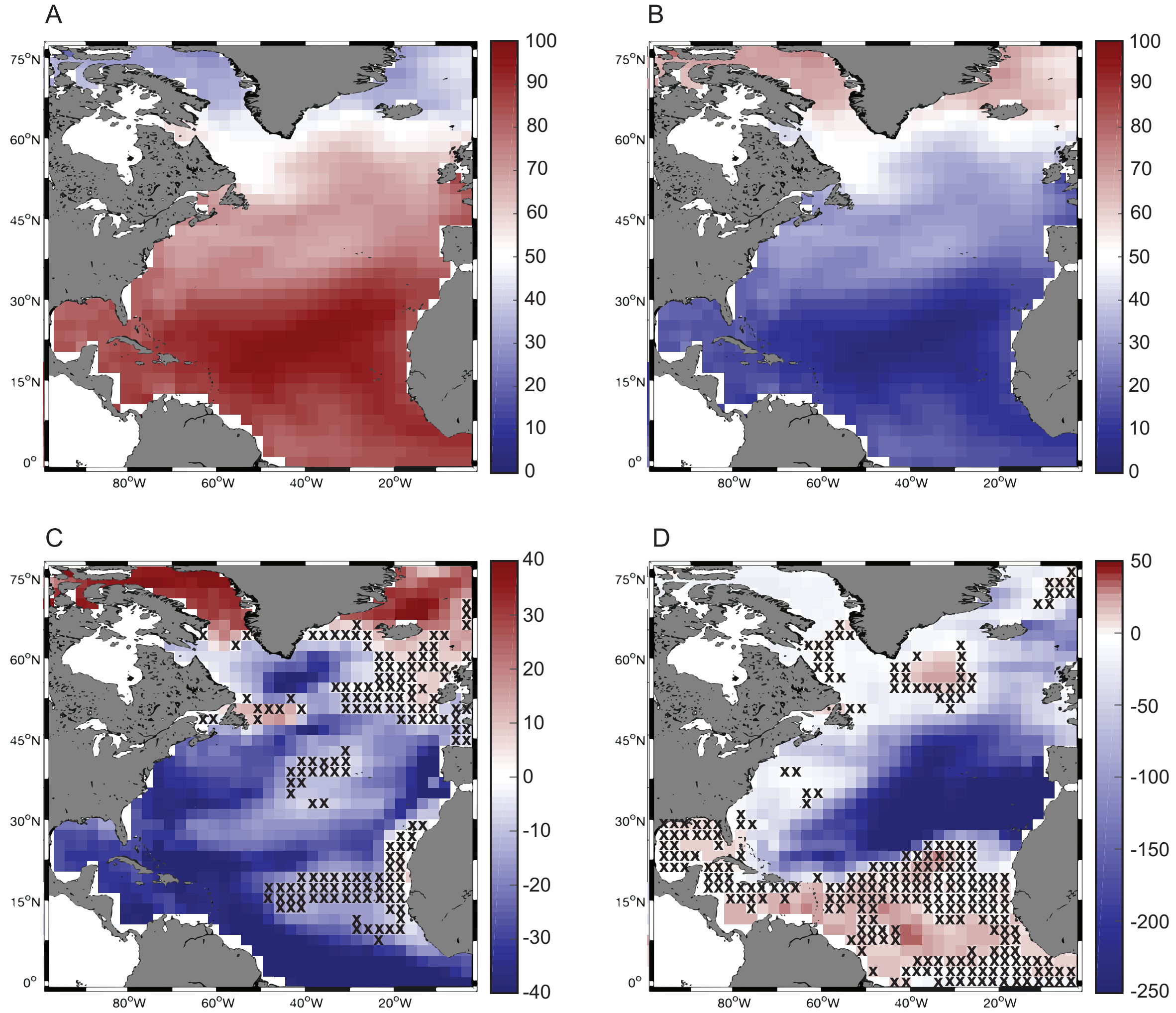
Supplementary Figure 0.9: Average North Atlantic phytoplankton biomass from two experiments in the MIT Integrated Global System Model between 1990 and 2100: A) Control experiment, blue line B) Climate (All-Other) experiment, red line.



Supplementary Figure 0.10: Boxplot for the lowest AIC models in the EnvCPT analysis of community biomass and richness across the North Atlantic region. For each box, the red central line indicates the median and the bottom and top edges of the box indicate the 25th and 75th percentiles respectively. The whiskers extend to the extremes of the data that are not considered outliers, while the outliers beyond this are plotted by the '+' symbol. As the notches of the boxplots do not overlap I can conclude, with 95% confidence, that the true medians do differ.



Supplementary Figure 0.11: Average changes to A) sea surface temperature, B) mixed layer depth, C) nitrate and D) total zooplankton biomass across the North Atlantic region between 1990 and 2100.



Supplementary Figure 0.12: Percentage contribution of the small functional types (Other Small, Diazotrophs, Procholococcus and Coccolithophores) (A) and Large functional types (Diatoms and Other Large) (B) to the whole modelled phytoplankton community structure and the percentage of change of the small functional types (C) and Large functional types (D) between the first and last 20 years of the model. For C and D, a t-test was performed between the first and last 20 years of the model. If the change was not significant (p>0.05) an 'x' was overlaid on the map