EVALUATING EFFECTS OF CLIMATE CHANGE ON NEKTON DISTRIBUTION IN THE NORTH ATLANTIC USING ECOSYSTEM MODELS: CLIMATE MODEL- AND PALEOCLIMATE-DERIVED TEMPERATURE SIMULATIONS COMPARED.

by

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DEDICATION

This is dedicated to my lovely wife Emily, my son Rowley, and the rest of my family. I am forever grateful and indebted to them for their support and guidance on how to be better person.
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I would like to thank the many friends, relatives, and supporters who have made this happen. My wife Emily encouraged me to push through whatever obstacles came my way and did the work of two parents when I was frequently stuck behind a computer monitor. Drs. Christensen, Dowsett, and Verardo provided me with helpful advice and leads for future research. I would like to thank the very professional and helpful administrative personnel in the ESP Department, especially Sharon Bloomquist for their assistance with many requests.

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LIST OF ABBREVIATIONS AND SYMBOLS

Biomass.................................................................B
Carbon Dioxide..........................................................CO₂
Celsius, Degrees............................................................°C
Climate Data Operators Command Line Toolkit..........................CDO
Consumption..................................................................................Q
Coordinated Ocean-ice Reference Experiments .........................CORE
Coupled Model Intercomparison Project 5 ................................CMIP5
Ecopath with Ecosim and Ecospace Modeling Software ..............EwE
Ecotrophic Efficiency ..............................................................EE
General Circulation Model (i.e. “climate model”)..........................GCM
Geophysical Fluid Dynamics Laboratory ........................................GFDL
GFDL Earth System Model, version 2.1 .................................GFDL ESM2.1
Greenhouse Gas .......................................................................GHG
Institut Pierre Simon Laplace des Sciences de l'Environnement Global ..IPSL
IPSL Earth System Model, version 5A-LR .................................IPSL-CM5A-LR
Inter-Sectoral Impact Model Intercomparison Project ..................ISI-MIP
Large Marine Ecosystem ........................................................LME
Latitude or Longitude, Degrees ..................................................°N or °E
Mediterranean-like Region .........................................................MED
Mid-Atlantic Region ...............................................................MAT
Mid-Pliocene Warm Period .......................................................mPWP
Network Common Data Form ..................................................NetCDF
Pliocene Research, Interpretation and Synoptic Mapping Project ......PRISM
Primary Productivity ...............................................................PP
Polar-Subpolar Region ..............................................................PSP
Sea Around Us Project, The .....................................................SAUP
Sea Surface Temperature .........................................................SST or tos
Sum of Squares Error .............................................................SS
Tropical-Subtropical Region ..........................................................TST
ABSTRACT

EVALUATING EFFECTS OF CLIMATE CHANGE ON NEKTON DISTRIBUTION IN THE NORTH ATLANTIC USING ECOSYSTEM MODELS: CLIMATE MODEL- AND PALEOCLIMATE-DERIVED TEMPERATURE SIMULATIONS COMPARED.

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George Mason University, 2015
Thesis Director: Dr. Kim de Mutsert

Climate change due to increasing atmospheric greenhouse gas levels presents a potential threat to ecosystems and a challenge to effective management of natural resources. Marine ecosystems, already under significant stress due to overexploitation, are expected to experience changes by the end of century due to anthropogenic climatic change. Effective management of future marine ecosystems will require policymakers to consider the full range of potential climatic impacts, which may not be fully captured by climate model projections. Evidence from the Mid-Pliocene, a period of similarly elevated greenhouse gas levels in Earth’s recent geological past, suggests that the spatial pattern of environmental change could differ substantially from model projections.

A marine ecosystem model was created for the North Atlantic Ocean, an area of both economic significance for fisheries and disagreement between modeled and observed/reconstructed patterns of climatic change. This marine ecosystem model was
calibrated using historical landings and historical environmental data. Different spatio-temporal patterns of environmental change were then assessed using climate model output and paleoclimate reconstructions. While differences between the climate model- and paleoclimate-based warming scenarios were found, determining the full extent of such differences will require reconstructions of key environmental variables such as primary productivity, in addition to sea surface temperature. These findings demonstrate the potential for paleoclimate to inform policymaking, and suggest targets for future paleoclimate reconstructions.
CHAPTER ONE: BACKGROUND AND PURPOSE OF STUDY

Introduction

Climate Change

Humans are currently driving climatic change through an increase in radiative forcing, principally through an increase in atmospheric CO$_2$ levels due to the burning of fossil fuels (Solomon et al., 2007). Despite public confusion, a clear scientific consensus exists on the reality of anthropogenic warming (Oreskes, 2004; Doran and Zimmerman, 2009; Anderegg et al., 2010; Cook et al. 2013; Verheggen et al., 2014). Humans are responsible for essentially all of the observed warming from the middle of the 20th century to the present (Jones et al., 2013; Wigley and Santer, 2013; Huber and Knutti, 2012). Anthropogenic greenhouse gas (GHG) emissions have elevated atmospheric concentrations of CO$_2$, CH$_4$, and other known radiative forcings well above the level of natural variability for the past 800,000 years, and likely the past several million (Brook, 2008; Lüthi et al., 2008; Loulergue et al., 2008; Seki et al., 2010; Dowsett and Caballero Gill, 2010). This increase in radiative forcing necessitates warming to a higher equilibrium temperature, with significant implications for many aspects of the climate system and life on Earth. Unchecked burning of fossil fuel reserves will alter the climate for thousands of years (Archer, 2009; Eby et al., 2009).

Past instances of rapid greenhouse gas emissions in the geologic record are associated with significant climate warming and mass extinction events (Joachimski et
al., 2012; Brand et al., 2012; Sun et al., 2012; Ruhl et al., 2011; Schneebeli-Hermann et al., 2013). Many components of the climate system are already showing demonstrable changes in response to anthropogenic forcing, including: global and regional surface temperature trends, eustatic sea level, ocean heat content, combined ocean temperature and salinity patterns, surface humidity, air pressure, precipitation, the vertical structure of the atmosphere, as well as changes in the intensity and frequency of some extreme weather events, and more (Stott et al., 2010; Christidis et al., 2011; Jevrejeva et al., 2009; Sedláček and Knutti, 2012; Pierce et al., 2012; Willett et al., 2007; Gillett et al., 2005; Zhang et al., 2007; Lott et al., 2013; Stott et al., 2013; Rahmstorf and Coumou, 2011).

These climatic changes are driving concomitant changes in the biosphere (Rosenzweig et al., 2008; Walther, 2010; Chen et al., 2011; Burrows et al., 2011). Human alteration of the climate system, especially in combination with other anthropogenic stressors, poses a significant threat to biodiversity (Travis, 2003; Thomas et al., 2004; Maclean and Wilson, 2011; Barnosky et al., 2011, Harley, 2011; Bellard et al., 2012; Urban et al., 2012).

**Fisheries Management**

One such “other” anthropogenic stressor on the biosphere is the dramatic overharvesting of marine life, commonly referred to as overfishing, which can result in collapse of fish stocks, such as Atlantic cod (Hutchings and Myers, 1994; Myers et al., 1997). Although considerable debate remains over the best ways of assessing the extent of collapse within fisheries, there is near unanimous agreement that the threshold for sustainable harvesting has been reached or exceeded for numerous marine species, and that significant effort is required to prevent further collapse and to rebuild/sustain existing
fish populations (Worm et al., 2009, Worm and Branch, 2009, Costello et al., 2012). As human population continues to increase towards the middle of the 21st century, fish will play an increasingly important role as a protein source (Tidwell and Allan, 2001; Pauly et al., 2005; Godfrey et al., 2010; Rice and Garcia, 2011). The conflicting needs presented by current overharvesting and future growth in the fisheries industry demand crafting and executing effective policy to prevent further collapse. Beyond the problems presented by overharvesting, fish stocks can also be dramatically impacted by climatic driven changes (Jacobson et al., 2001; Greene et al., 2003; Glantz, 2005; Glantz and Feingold, 2005; Lehodey et al., 2006). As human influence on the global ocean increases, overharvesting and climatic change have the potential to interact synergistically and pose a greater threat to stocks than either in isolation (Harris and Tyrrell, 2001, Brander, 2005; Otterson et al., 2006; Brander, 2007; Brook et al., 2008; Hsieh et al., 2008; Perry et al., 2010; Boyd and Hutchins, 2012). Therefore, understanding the impact of climate change on marine life in the context of fisheries management needs to be a key goal in effective policymaking (Worm and Myers, 2004; Cook and Heath, 2005; Kell et al., 2005; Cheung et al., 2009; Cheung et al., 2010; Hoegh-Guldberg and Bruno, 2010; Salinger et al., 2012). Changes in fish community composition and distribution, amongst other potential responses to climatic changes, might require changes in management decisions regarding quota, or even which fisheries to maintain, close or open. The fishing industry may need to reevaluate what gear type(s) to invest in and whether ports are optimally located and/or equipped for the living marine resources that will be landed in the future.
North Atlantic as Target Region for Paleoclimate Added Value

In order to adequately meet the challenges of sustainable fishing in an anthropogenically changing climate, policymakers, industry, and other stakeholders need to be aware of the magnitude climatic change can have on fish communities (Caddy and Seijo, 2005; Hughes et al., 2005). As climatic changes do not affect species or populations in isolation, ecosystem modeling of fish communities may offer a vital source of information to stakeholders, especially when used in combination with climate model output (e.g. Hollowed et al., 2013). However, climate models are an imperfect source of information, and may underestimate the true scope of change facing a given region or ecosystem. Incorporating information from the paleoclimatic record (which represents known rather than predicted changes in climate) has the potential to complement information from climate models, and offer stakeholders a more realistic picture of what the future may hold for fish and fisheries. The North Atlantic is a region particularly suited to such an investigation, as it encompasses economically valuable fisheries, has seen overharvesting of its top marine predators (Christensen et al., 2003; Essington et al., 2006) and is not coherently simulated by climate models (Zhang et al., 2013; Kuntson et al., 2013; Wang et al., 2014). Moreover, possible paleoclimatic analogs for present and future warming of the North Atlantic differ significantly from climate model projections (Dowsett et al., 2009a; Dowsett et al., 2012; Dowsett et al., 2013), suggesting that incorporating information from the paleoclimatic record may provide additional insights in climate effects on fisheries ecosystems.
Fish Ecology and Climate Change Impact on Fisheries

Fish communities and their ecosystems can be quite sensitive to climatic changes, both in terms of “unforced” climatic variability as well as long term trends such as those occurring with anthropogenic warming. Natural sources of climatic variability can influence fisheries on timescales ranging from the seasonal to centennial (Salinger, 2013). Climatic impacts on fish come in a variety of forms. Habitat changes in response to temperature change can be both “horizontal” (i.e. equator-to-pole shifts) as well as “vertical” (shallow-to-deep water shifts); phenological behaviors (e.g. migration and spawning) can shift; physical characteristics (e.g. metabolic rates, growth) of fish can be affected; predator-prey dynamics and disease incidence can be altered; and human/fisher behavior can change with climate change as well (Brander, 1995; King et al., 1999; Edwards and Richardson, 2004; Perry et al., 2005; Pörtner and Knust, 2007; Brown et al., 2010; Pörtner and Peck, 2010; Sorte et al., 2010; Doney et al., 2012; Hobday and Evans, 2013; Cheung et al., 2013; Dell et al., 2013; Fernandes et al., 2013).

In addition to natural climatic variation on a variety of timescales, the North Atlantic is being strongly impacted by recent unprecedented global warming. In 2012, the Northeast Shelf Large Marine Ecosystem (LME) recorded its highest temperatures since observations have been made (Dawicki, 2013). Proxy-based evidence from the region also shows exceptional warming, with North Atlantic deepwater near the Gulf of St. Lawrence reaching its warmest levels in the past 1,000 years and Atlantic waters entering the Arctic at the warmest levels in the past two 2,000 years (Thibodeau et al., 2010; Spielhagen et al., 2011). Fish communities in the North Atlantic are expected to show, and in some cases are already undergoing, dramatic changes in response to anthropogenic
warming (Frank et al., 1990; Clark et al., 2003; Guisande et al., 2004; Beaugrand et al., 2008; Dulvy et al., 2008; Fogarty et al., 2008; Greene et al., 2008; Nye et al., 2009).

Efforts to identify climatic impacts on fish are growing increasingly sophisticated (e.g. Sugihara et al., 2012; Hobday and Evans, 2013). Nevertheless, stochastic processes associated with climatic variability absent a long term driver (i.e. anthropogenic climate warming) can give rise to an impression of a forced change or state shift in observational data (Doney and Sailey, 2013; Lorenzo and Ohman, 2013). Dynamic modeling of fish communities’ response to climate variability and long-term change can help both avoid incorrectly attributing responses to anthropogenic climate change as well as enable policymakers to anticipate actual anthropogenically-driven responses.

**Ecosystem-Based Management**

Perceived failures of traditional, single species, fisheries management and increased understanding of marine ecology have led to a widespread recognition of the need for Ecosystem-Based Fisheries Management (EBFM; Pauly et al., 2000; Hall and Mainprize, 2004; Pikitch et al., 2004). The value of EBFM is readily apparent when feedback mechanisms or novel interactions, rooted in ecosystem dynamics, are demonstrated to have significant impacts on fisheries that single species population modeling might otherwise fail to capture (Kordas et al., 2011; Audzijonyte et al., 2013). Even staunch advocates of traditional single species management have come to recognize the value of EBFM (Hilborn, 2011).
Ecopath with Ecosim

One of the most widely used ecosystem-based models is Ecopath with Ecosim (EwE). The Ecopath module of the EwE software package is designed to offer “snapshots” of fish ecosystems, using a mass-balance approach. It allows users to identify the relationships and biomasses of all functional groups within a modeled system. The Ecosim module allows for exploration of changes in fish ecosystems over time, through successive integrations of numerical models. Together the EwE package is used to model ecosystem interactions and environmental and policy-driven impacts on fish communities (Pauly et al., 2000; Christensen et al., 2000; Christensen and Walters, 2004; Christensen et al., 2005; Coll et al., 2009). The EwE package incorporates foraging arena theory (Walter and Martell, 2004) in species interactions to more realistically simulate predator-prey dynamics than other fish community and ecosystem modeling software (Walters and Christensen, 2007).

Ecospace

The Ecospace module of the EwE package was originally designed to evaluate spatial impacts on ecosystems, primarily to evaluate policy implications for fishing and fisheries due to the emplacement of Marine Protected Areas (Walters et al., 1999; Pauly et al., 2000; Christensen and Walters, 2004). More recently, Ecospace has incorporated spatial representation of age structure, allowing for the consideration of growth and mortality effects on biomass during spatial simulations (Walters et al., 2010). Ecospace is increasingly being utilized to examine the impacts of spatially-focused geochemical and environmental change (Steenbeek et al., 2013), not just the emplacement of MPAs.
Climate Models
The term “climate model” can refer to anything from a conceptual model used in a thought experiment, to a zero-dimensional energy balance model, to a state of the art, physics-driven simulator run on the world’s fastest supercomputers. However, in popular usage and throughout this project, the term refers to General Circulation Models (GCMs) such as those used in the IPCC Assessment Reports. GCMs are now typically coupled to dynamic ocean models, which some refer to explicitly as AOGCMs (Atmosphere-Ocean General Circulation Models), however such coupling has become so routine that the presence of a dynamic ocean model should be assumed unless otherwise indicated.

Purpose, Value, and Skill
Modeling complex systems typically serves several purposes: to enable researchers to better understand the behavior of a system, to simulate the system, and to enable predictions about the future behavior of the system. Climate models currently fulfill all of these purposes, including simulating climates of the ancient past. The skill of even (by today’s standard’s) “primitive” climate models to predict the general changes to the climate as a result of our increase in greenhouse gases has been demonstrated repeatedly (e.g. Frame and Stone, 2013; van Oldenborgh and Haarsma, 2012; Hansen et al., 2006; Hargreaves, 2010).

Use in Policy-Making
Climate models can inform policymakers by acting as “scenario generators, sources of insight into complex system behavior, and aids to critical thinking within robust decision frameworks” (Weaver et al., 2013). While rapidly advancing computational capabilities have led to significant advancements in climate model
complexity, many policy questions require input that cannot wait for subsequent
generations of models to be designed, coded, and validated. And perhaps
counterintuitively, increasing model sophistication may also lead to less rather than more
agreement about potential impacts (Trenberth, 2010; Maslin and Austin, 2012). Indeed,
some argue that climate models, imperfect as they are, are already more than sufficient to
design effective policy (Dessai et al., 2011).

**Known Issues**

**Non-Independence**

Climate models are produced by many institutions across the world. These models
are often treated as though they are independent from one another for the purposes of
statistical analyses of their output, as well as for interpreting the import of their
agreement (Masson and Knutti, 2011; Pirtle et al., 2010). In reality, however, climate
models from ostensibly different institutions are typically closely related (Masson and
Knutti, 2011; Knutti, 2013). Climate models share many assumptions and attributes - from
fundamentals like adherence to thermodynamics, to shared lines of actual code such as
parameterization routines, and even to entire components or modules, like dynamic ocean
or vegetation coupled models (Alexander and Easterbrook, 2011).

Climate models are also sometimes criticized by “skeptics” for being “tuned” to
match the observational record, and it is then claimed that their apparent success in
reproducing observed changes during this period reflects little more than calibration
rather than modeling skill. In fact, while model tuning is undertaken, this manipulation of
parameters is intended not to maximize the skill in some target simulation like the
evolution of surface temperature, but rather to most accurately match observed values for
key parameterized processes that as of yet cannot be dynamically modeled (Mauritsen et al., 2012). Nevertheless, there is a possibility that comparisons between observations and output might be unintentionally “narrowing” the field in terms of model diversity, further reducing independence and increasing the possibility of error and bias propagation (Swanson, 2013).

**Lack of Granular Skill**
While climate models have been demonstrated to be “skillful” (i.e. have smaller errors relative to another forecasting or simulation reference technique, such as persistence; Hargreaves, 2010) on large spatial and temporal scales, they are less successful with smaller scale simulations. Model skill for temperature as well as precipitation diminishes significantly on interannual to decadal temporal scales and regional and local spatial scales (Cai et al., 2009; Kim et al., 2012; Haren et al., 2013; Knutson et al., 2013). These problems are exacerbated when considered in the context of informing industry-specific policy (e.g. Ramirez-Villegas et al., 2013).

**Problems Simulating Climates Outside of the Instrumental Record**
In addition to difficulty in simulating climate on decadal and regional scales, climate models also have difficulty in correctly reproducing features of climates reconstructed from the geologic past. Comparisons between model simulations and climate proxies show significant disagreement during the Permian, late Cretaceous, and Miocene (Gibbs et al., 2002; Craggs et al., 2012; Micheels et al., 2007). Discrepancies between paleoclimate indicators from proxy records and simulations from climate models raise the possibility that important feedback processes and ocean-atmosphere dynamics are being insufficiently captured by the models.
Paleoclimate Implications for Future Climate

The Mid-Pliocene Warm Period

The Mid-Pliocene Warm Period (mPWP, sometimes also referred to as the Mid-Piacenzian) is defined as the interval from 3.264-3.025 million years ago. The mPWP occurred recently enough in geologic time that it might be useful as an analog for our present and future climate (Dowsett et al, 2007; Haywood et al., 2011; Dolan et al., 2011). State of the art climate models can reproduce some but not all features found in paleoclimatic reconstructions. These discrepancies may indicate problems in the paleoclimatic reconstructions. However, the may also indicate that we are failing to capture the behavior of key processes (perhaps relating to sea ice, the Atlantic Meridional Overturning Circulation, etc.) that can profoundly affect regional and even global climate. If so, then policy based on modeling alone can dramatically underestimate the magnitude of change we may see in response to a given increase in GHGs.

Suitability as a Paleo-Analog for Future Warming

While there have been a number of instances in the geological record of elevated greenhouse gases and/or periods of increased surface temperatures, few of these can be understood as good analogs for the current and future anthropogenic warming (Haywood et al., 2011). The climate is determined by a number of boundary conditions and dynamic relationships of which greenhouse gases are only a part. As but one example, the configuration of continents dramatically affects the Earth’s climate through many different pathways. Continents are generally lighter in coloration than open ocean, and thus have a higher albedo. Concentrating continents around the lower latitudes, where incoming solar radiation is most intense, can therefore result in a cooler climate than a
world identical except for more poleward positioning of continents. Continental configuration also has significant implications for ocean circulation, which in turn affects the ability of the climate system to absorb, transport, and release heat. Although its importance relative to other factors is still under debate, there is evidence that accumulating landmasses near the poles facilitates glaciation in those regions.

In addition to greenhouse gas levels and continental configuration, a number of other factors are at work in shaping the climate of a given time during geological history. The Mid-Pliocene Warm Period occurred recently enough (in geologic time), that most of these factors were not much different relative to the present. Continents were in more or less their present locations. While solar luminosity varies over the course of star’s life cycle, average solar output has not changed much during the last several million years. Unlike the greenhouse warming of the End Permian, the composition of ocean life and resulting ocean carbonate buffer between the mPWP and now is relatively similar (Payne and Clapham, 2012; Hönisch et al., 2012). Such similarities in most boundary conditions, in combination with elevated greenhouse gas levels and overall warmer climate, have led climate scientists to view the mPWP as an imperfect but perhaps best-available geologic analog for our enhanced greenhouse future (Dowsett et al., 2009a; Haywood et al., 2010; Robinson, 2011; Naish and Zwart, 2012; Dowsett et al., 2012). The main shortcoming of the mPWP as an analog to present and future warming is that it represents an equilibrium climatic state rather than a dynamic response to an increase in radiative forcing. As such, the remarkable rate of the change of present and future warming is not captured by mPWP conditions. On the other hand, the overall magnitude of the warming of the
mPWP is greater than would be expected in the first several hundred years of a change to comparable GHG levels. In other words, the mPWP more properly reflects the Earth System Sensitivity (ESS) rather than Equilibrium Climate Sensitivity (ECS) or the Transient Climate Response (TCR). Care must be taken to account for these differences when interpreting results based on mPWP data in an analog context.

**Climate Models and the mPWP**

Despite the similarities to the present boundary conditions, which should make simulating the climate of the mPWP relatively straightforward, climate models generally fail to accurately reproduce key features of the mPWP. In particular, climate models cannot reproduce the extreme warming in the North Atlantic (Dowsett et al., 2009a; Dowsett et al., 2009b; Dowsett et al., 2012). While there is always the possibility that the proxy data rather than the models are incorrect, the confidence in the North Atlantic proxy data is actually the highest of any area in the PRISM reconstruction (Dowsett et al., 2012). Even more concerning, this discrepancy between the proxy data and model simulations of the mPWP remains even after accounting for the known model bias in simulating present SSTs in the region. Several potential sources for the proxy-model disagreement have been identified. This inability of climate models to realistically simulate the North Atlantic during the mPWP may be an indication that one or more key processes of the region’s climate are missing or incompletely captured by the models, which could result in their underestimate of the region’s response to the current anthropogenic change.
**Topography/Bathymetry**

Although the continents themselves were in positions very similar to those at present, the surface of the Earth has changed somewhat between the two periods (Dowsett et al., 2009b). Changes in the geomorphology of the Eastern seaboard for the past ~3ma are an area of active investigation, with provisional evidence indicating possible substantial warping of the continental shelf due to convection-driven alteration of the mantle (Rowley et al., 2013). More relevantly, alterations in regional bathymetry may provide a partial explanation of the proxy-model disagreement in the North Atlantic. Variation in the subsidence of North Atlantic ridges can produce pronounced changes simulation of the North Atlantic and Artic Ocean conditions (Dowsett et al., 2009b; Robinson et al., 2011). However this explanation depends on the assumption that climate models are otherwise accurately capturing the behavior of the region, which observation-model discrepancies would appear to call into question.

**Active Atlantic Multidecadal Overturning Circulation**

The more traditional explanation for enhanced North Atlantic and Arctic Ocean warming during the mPWP is an active or enhanced Atlantic Meridional Overturning Circulation (AMOC; Raymo et al., 1996; Dowsett et al., 2009b). An increase in AMOC strength with warming stands in contrast to expectations for our future, however. Climate models typically show a decrease rather than an increase in AMOC strength with warming in the future, due to an increase in freshwater from reductions in sea and land ice in the region (Schmittner et al., 2005). Such a slowdown typically cools the region relative to an unchanging AMOC (Chang et al., 2007). However, a few climate models can produce an increase in AMOC strength and regional warming with freshwater
increases, as a consequence of strengthening of the sub-polar gyre (Kleinen et al., 2009). Extensive mPWP modeling has failed to reproduce this behavior, however, finding AMOC behavior similar to that of the preindustrial period (Zhang et al., 2013a). An alternative to the enhanced AMOC hypothesis that may be consistent with both proxy and modeling evidence regarding ocean circulation, is a change in the Antarctic wind field, which reduces Southern Ocean stratification and increases δ¹³C ventilation (Zhang et al., 2013b). However, this dynamic fails to reconcile the proxy and model data with respect to North Atlantic warming to explain the observed behavior of upwelling Antarctic Intermediate Waters and its links between windfield, productivity, and nutrient levels and more importantly also fails to reconcile the proxy and model data with respect to North Atlantic warming.

Uncaptured Feedbacks

Perhaps the most likely explanation for the inability of models to accurately simulate the North Atlantic during the mPWP is incorrect or incomplete capturing of feedback processes that affect the region, indicating it is more sensitive than current climate models suggest (Dowsett et al., 2009a). For instance, a greatly increased “Arctic amplification” effect (i.e. an increase in temperature with latitude), which could be generated by the total removal of seasonal sea ice, can bring model simulations and proxy data into much closer alignment (Ballantyne et al., 2013). Disagreements across climate models over the magnitudes and even signs of various feedbacks also suggest current modeling efforts are not realistically capturing the relevant processes driving mPWP warming (Hill et al., 2013).
**Implications for Anthropogenic Warming**

If the source of the discrepancy between models and proxy data for the mPWP North Atlantic is attributable to uncaptured feedbacks or other dynamics that continue to operate in the present, this may have significant implications for our ability to realistically model the evolution of the region under anthropogenic warming as well (Dowsett et al., 2009a). Policy that relies on model output alone could therefore potentially underestimate the true scope of potential change as the region responds to increasing greenhouse warming.

**Purpose of Study**

This project will attempt to address some of the uncertainty facing North Atlantic fisheries by exploring what differences, if any, might be expected for the environmental and ecological makeup of the region if the past (i.e. the mPWP) is a more realistic future than that projected by climate models.

The primary scientific goal of this project is intended to have relevance to management and policymaking. Despite a widespread recognition in the paleoclimate community that past instances of climatic change or different climate regimes can inform our understanding of the change humans are currently enacting on the climate system, this realization does not appear to be making its way into policy and management circles. It is hoped that incorporating mPWP data in fisheries simulations will give a broader and more realistic range of potential outcomes upon which policymakers and managers can build responses. If significant differences between paleoclimate-informed and climate model-only scenarios exist, this may have implications for the locations fishing fleets are currently deployed, the location of ports most optimal to bring in landed fish, and even
what mix of gear type is used in a certain area. Even if no significant differences arise, this will itself be a significant result, increasing confidence in management based on climate model simulations.

Finally, this project is also intended to demonstrate the practical applicability of using paleoclimate data to inform policymaking. While this project is not the first to do so, the direct application of paleoclimate data to a specific policy question remains relatively rare. It is hoped that the successful execution of this project will encourage future collaboration between paleo and policy communities, even (or especially) on questions beyond those immediately concerned with the climate system itself.

**Experimental Design**

**Study One: Calibrating an Ecopath with Ecosim model to Historical Environmental and Catch Data**

In study one (Chapter 2), I will produce an Ecopath with Ecosim model that is calibrated to changes in environmental (sea surface temperature, primary productivity) and landings data for use in future EwE and Ecospace modeling exercises.

**Study Two: Ecospace Modeling of Climate Model and mPWP-Generated Patterns of Environmental Change**

In the second study (Chapter 3), I will examine the impact of different spatial patterns of environmental change arises from climate model output of the future North Atlantic, as well as the spatial patterns reconstructed from the mid-Pliocene Warm Period. This study will consist of two sets of experiments, one using the calibrated model from the previous study, and another using the un-calibrated model default values,
allowing the impact of EwE model calibration on Ecospace simulations to be assessed as well.

**Data Sources**

*Landings Data*

I use historical landings data to calibrate biomass of the EwE model (and subregional models) in Chapter 2. Despite the significant economic and ecological importance of the marine ecosystems of the North Atlantic, long-term scientific surveys and stock assessments are lacking for all but a small number of key species or functional groups. Landings, or catch data, instead provide the basis for most estimates of large-scale abundance, community composition, and economic value for different species and functional groups. The use of catch data to represent the true state of a given fishery is not without controversy (Pauly, et al., 2013). Methodological and statistical concerns about the ability of traditional catch-based estimates of specific or aggregate fisheries or ecosystem health have been raised (de Mutsert et al., 2008; Daan et al., 2011; Branch et al., 2011; Anderson et al., 2012). Nevertheless, the importance of catch data is widely recognized, as even the harshest critics of catch-based assessments of fisheries status are quick to point out. “Catch data are a crucial part of any fisheries assessment - it is impossible to calculate the maximum weight of fish that could be harvested sustainably without knowing what is being caught each year” (Pauly et al., 2013).

This acknowledgment of value by critics of some uses of catch data reflects the fundamental fact that catch provides an effective lower bound on abundance- by definition enough fish must exist to have been harvested. To this end, using catch data only to ensure a minimum abundance level in a region avoids many of the potential
problems that arise when using the same data to infer collapse or changes in the mean
trophic level (MTL) of a fishery over time. In this study, time series of catch were used in
EwE to ensure that enough biomass of a given functional group is present in a region at
levels sufficient to not only sustain the reconstructed landings for that group itself, but its
predators and prey within the ecosystem as well.

The catch data used in Chapter 2 are historical landings from LMEs and High
Seas areas, produced by SAUP (Pauly, 2007). These data are reconstructed using official
FAO reported landings, as well as a number of additional lines of evidence. Information
taken from enforcement activities, bycatch ratios, per-capita estimates of subsistence
fishing, expert judgment, scientific surveys or stock assessments, and other methods of
estimating underreporting are combined and used to create time-point estimates, or
“anchor points” for missing or underreported data in time. Summary data are then created
by interpolating across anchor points, allowing time series of catch to be generated (Pew,
2015).

Environmental Drivers for Calibration

In addition to historical landings data, I employ historical environmental changes
as forcing functions in Chapter 2. These data are adapted from the FISH-MIP/ISI-MIP
cross-sectoral impact analysis Historical protocol (Warszawski et al., 2014; ISI-MIP,
2015). The data consist of sea surface temperature as well as small and large
phytoplankton changes derived from GFDL-ESM2.1 model ocean and ocean
biogeochemistry output, forced by the atmospheric components of the CORE reanalysis.
GFDL ESM2.1
Princeton University and the NOAA Geophysical Fluid Dynamics Laboratory’s Earth System Model version 2.1 (GFDL-ESM2.1) is an earth system model based on the CM2.1 fully coupled climate model. The CM2.1 model is comprised of atmosphere (AM2.1), land (LM2.1), and ocean (OM3.1, based on the MOM4.1 ocean model) components, connected via the Flexible Modeling System (FMS) coupler (Delworth et al., 2006). The Earth System Model (ESM) differs from the standard climate model by capturing climate-carbon interactions through the addition of dynamic land (replacing LM2.1 with LMV3) and ocean biogeochemical (TOPAZ) components, as well as incorporating dynamic, coupled atmospheric chemistry. Uniquely, the GFDL model architecture mediates the exchange between its FMS coupler (and thus the other system components) and its ocean module through its Sea Ice Simulator (SIS) interface. This setup provides advantages for interpolation as well as the treatment of a surface type that is neither properly land nor ocean, with correspondingly unique physical and dynamical characteristics, and a non-uniform spatial domain that varies over time (Alexander and Easterbrook, 2015). The data ultimately generated by the GFDL model used in Study One benefit from these advantages, as both interpolation and dynamic, physical process based ocean-sea ice-air interactions are present. An observationally-constrained, numerical weather prediction model-generated historical input (CORE, described below) are used instead of the model’s native atmospheric component. These historical reanalysis data are used to drive the combined oceanographic components of the ESM2.1 model (i.e. SIS, MOM4p1, and TOPAZ).
MOM4p1

The Modular Ocean Model (MOM) hydrostatic global ocean model from GFDL is based on the pioneering work of Bryan and Cox (Bryan and Cox, 1972a; Bryan and Cox, 1972b; Cox 1984). MOM4p1 offers a 1 degree x 1 degree resolution (with higher resolution near the equator), using non-Boussinesq (i.e. mass-conserving, but with an option for Boussinesq, or volume-conserving) equations, and provides improvements in its open boundary condition module and some physical parameterizations relative to previous versions. Additionally, version 4p1 offers a suite of different vertical coordinate schemes, which allow for greater flexibility relative to previous versions (Griffies, 2009).

While MOM4p1 has improved temperature accuracy at greater depths (reductions in both RMS temperature error and horizontal mean temperature bias relative to MOM4) compared to observations, it has a marginally higher RMS error for globally-averaged sea surface temperatures. Additionally, MOM4p1 inherits several issues from previous versions that may impact the present study, including upwelling regions that lack associated cooling and a North Atlantic current that exhibits excessive zonality (Halberg et al., 2009).

TOPAZ

In order to model carbon-ocean dynamics, GFDL ESM2.1 employs the TOPAZ (Tracers of Ocean Phytoplankton with Allometric Zooplankton) prognostic ocean biogeochemical/ecology model (Dunne et al., 2010; Gnanadesikan et al., 2011). TOPAZ is able to resolve biogeochemical-ecological interactions utilizing a wide variety (25) of tracers, including three phytoplankton groups, of which two (“small” and “large”) were used in this experiment to force primary productivity. The small and large phytoplankton
categories loosely represent cyanobacteria and diatoms respectively. Phytoplankton in TOPAZ are co-limited by light, nutrients (N, P), and iron (Fe).

TOPAZ is generally able to skillfully reproduce the distribution of phytoplankton in the North Atlantic, as well as capture broad features of its interannual variability (Henson et al., 2009). However, Continuous Plankton Recorder survey data (Richardson et al., 2006) from the region show significant community regime shifts that TOPAZ does not reproduce. This may be due to insufficiently high spatial resolution and/or low sensitivity of nutrient cycling to external forcing (Henson et al., 2009).

CORE

The ocean components of the GFDL ESM2.1 model were driven with an observationally-adjusted reanalysis of historical atmospheric forcing fields from the Coordinated Ocean-ice Reference Experiments (Large and Yeager, 2004; Griffes et al., 2009). Wind stress, freshwater, and short- and longwave radiation fluxes are prescribed as boundary conditions, and the SIS-MOM4.1-TOPAZ system were spatio-temporally forced with interannual variability relevant to the calculation of air-sea turbulent fluxes (i.e. near surface humidity, temperature, and wind speed). Much of the input data is based on the NCEP-NCAR v1 numerical weather prediction model-based reanalysis (Kalnay et al., 1996), which is corrected for biases using observational data.

Despite the overall skill of the reanalysis at large scales, potentially significant regional biases exist. Errors in the amount of insolation reaching the equatorial Atlantic and Pacific, for example, largely cancel out from a global average perspective. Eastern and Northern Atlantic low latitudes have a positive insolation bias, which is offset in global mean statistics by a negative bias in the Pacific of similar magnitude (Large and
Yeager, 2009). Thus results obtained using the CORE reanalysis for regional experiments should be viewed with more caution than the global skill of the overall product might suggest.

Environmental Drivers for Spatio-Temporal Simulations

In Chapter 3, I employ future environmental changes as spatio-temporal maps, using climate model output as well as mPWP data. The climate model data are adapted from the FISH-MIP/ISI-MIP cross-sectional impact analysis protocol. The climate model data consist of sea surface temperature as well as small and large phytoplankton derived from IPSL-CM5A-LR climate model, under a high GHG emissions scenario. The mPWP data will be adapted from the PRISM mPWP reconstruction.

IPSL-CM5A-LR Climate Model

The IPSL-CM5A-LR model has been used in a wide range of historical, present, and modeling efforts, including the CMIP5 experiments (Taylor et al., 2012). The atmosphere and land and dynamic ocean models comprising the basic GCM core are the LMDZ5A and NEMO models respectively. IPSL-CM5A-LR features a dynamic sea ice model, LIM2. In its “Earth System” form, the model also features coupled, dynamic ecological/geochemical models for both land use/vegetation and ocean: the ORCHIDEE land-surface and PISCES marine geochemistry models.

The IPSL-CM5A-LR model has an effective climate sensitivity (i.e. the globally-averaged surface temperature increase from an increase in radiative forcing equivalent to a doubling of atmospheric CO2 levels) in the upper half of the CMIP5 model range (Andrews et al., 2012; Vial et al., 2013), although this version is no longer the most sensitive, as was the case for the previous CM4 version (Webb et al., 2013).
LMDZ5A Atmosphere and Land

The atmosphere and land general circulation model core LMDZ5 comes in two versions, the “standard physics” of LMDZ5A and the “new physics” of LMDZ5B (Hourdin et al., 2013a). Although the “new physics” LMDZ5B version of the model offers some advancement in atmospheric parameterizations (e.g. turbulence, convection, and clouds) over the LMDZ5A version (Hourdin et al., 2013a, Hourdin et al., 2013b), the latter, “standard physics” version used in this experiment still exhibits more realistic behavior for some of these processes, including those relevant to climate sensitivity (Sherwood et al., 2014). The average top of atmosphere radiative flux is skillfully modeled in LMDZ5A, however this skill in the averaged representation conceals offsetting biases in vertical cloud distribution; the model produces clouds that are too optically thick, but produces too few of them (Konsta et al., 2012).

NEMO v3.2 Ocean Model System

The NEMO v3.2 ocean model system (Madec, 2008) comprises the Océan PARallélisé (NEMO-OPA) “blue ocean” ocean dynamics model, the Louvain-la-Neuve v2 (NEMO-LIM) “white ocean” sea ice model, and the Tracers in Ocean Paradigm (NEMO-TOP) “green ocean” geochemistry component, in this version using the Pelagic Interactions Scheme for Carbon and Ecosystem Studies (PISCES) biogeochemical model. The NEMO ocean modeling system is used in a number of coupled ocean-atmosphere GCMs in addition to the IPSL-CM5 models. Overall, the oceanic, and ocean-atmospheric coupled responses of the model shows improvement over previous versions. The ENSO response in IPSL-CM5A-LR is comparable or more realistic than other CMIP5 models and other versions of the IPSL model (Bellenger et al., 2014). As with most of the
CMIP5 models, IPSL-CM5A-LR is more skillfully able to capture the SST pattern of the Atlantic Multidecadal Oscillation (also known as the Atlantic Multidecadal Variability), but less realistically represents associated precipitation changes relative to CMIP3 generation models (Ruiz-Barradas et al., 2013).

The PISCES model (Aumont and Bopp, 2006, Supplementary Material) is a mixed Monod/quota model (i.e. using constant Redfield ratios for most nutrient variables but a quota approach for iron) of carbon and nutrient (phosphorous, nitrogen, iron, and silicium cycling and biogeochemistry. Plankton groups are nutrient limited, and phytoplankton are divided into two groups based on size (nanophytoplankton and diatoms), much as the TOPAZ geochemical model used in Chapter 2. The PISCES model has several notable biases, including too little surface productivity and too much productivity in deeper waters in the relatively oligotrophic mid to high latitudes of the North Atlantic, and too little productivity in the Atlantic eastern coastal upwelling region (Aumont and Bopp, 2006; Kane et al., 2011). Additionally, coupling the PISCES geochemical model to the IPSL-CM5A-LR atmosphere-ocean climate model induces a widespread cooling of the ocean surface down to 300m depth over interannual timescales due to the interplay of nutrient cycling, shortwave radiation, and ocean circulation (Mignot et al., 2013).

PRISM3 Paleoclimate Data
Reconstructed mid-Pliocene conditions for Study Two will be taken from the Pliocene Research, Interpretation and Synoptic Mapping (PRISM) project. The PRISM project is a multi-institutional effort led by the U.S. Geological Survey, in collaboration with Columbia University, the British Geological Survey, the National Science
Foundation, Northumbria University, the University of Leeds, the University of Bristol, and the University of Leicester. The PRISM products are multiproxy reconstructions of the mPWP, incorporating proxy records for SSTs, sea ice, vegetation/terrestrial biomes, and topography (including land ice). The current products from PRISM are the PRISM3 and PRSIM3D reconstructions (Dowsett et al., 2009b; Dowsett et al., 2010). PRISM3D represents a marked advancement over previous reconstructions in that it incorporates deepwater proxy data, and thus creates a three dimensional-ocean field. Future versions of PRISM will focus on a narrower “time slice” of the mid-Pliocene (Haywood et al., 2013a) and mark a shift in focus towards regions (e.g. the high latitude North Atlantic) and processes (e.g. upwelling) of particular interest. The PRISM3 global sea surface temperature reconstruction is based on the combination of several independent proxy records, including Mg/Ca foraminiferal thermometry, Uk’37 alkenones, TEX86H tetraether lipids, and assessment of floral/faunal fossil assemblages.
CHAPTER TWO: A NORTH ATLANTIC MARINE ECOSYSTEM MODEL USING ECOPATH WITH ECOSIM: DESIGN AND CALIBRATION

Introduction

As discussed in greater depth in Chapter 1, the North Atlantic is an area of particular scientific and economic interest. Anticipating the plausible evolution of the North Atlantic and its impact on fisheries is of profound economic importance as well. Suboptimal management of the region’s fisheries has already resulted in enormous economic losses, perhaps exceeding $15 billion USD in the year 2010 (Merino et al., 2013). Policy formulated on assumptions restricted to an overly-narrow range of potential outcomes risks exacerbating such inefficient management and its resultant economic consequences.

In order to explore the impact of different spatial patterns of warming on marine ecosystems in the North Atlantic, it is necessary to model the system with enough resolution and realism to satisfactorily explore (at minimum) qualitative questions, while at the same avoiding a level of complexity that becomes computationally prohibitive or creates demands that extant data (e.g. from stock assessments and commercial landings data) cannot hope to provide (Walters and Martell, 2004). Attempting to model the entire North Atlantic region at a species-level resolution is unfeasible, both from a desktop modeling software standpoint, as well as due to a dearth of population estimates for all but a relative handful of highly-commercially valued species. To that end, a North
Atlantic marine ecosystem model of intermediate complexity was created. Using the EcoOcean global model (Christensen et al., 2015) as a starting point, the model was expanded upon in several significant ways. This expanded model was then calibrated to historical landings and environmental data for the region, over a period of roughly 50 years, using Ecopath with Ecosim (EwE; Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2008).

A growing number of large area EwE models have been developed over the past decade (Colléter et al., 2013), spanning entire LMEs or Food and Agriculture Organization (FAO) Major Fishing Areas (Christensen et al., 2009), and even the global ocean (Christensen et al., 2015). However, these models typically represent their ecosystems with area-wide functional groups. This is defensible or even preferable from a modeling perspective, allowing aggregation of species into fewer, ecologically-similar roles. Area-wide functional group categorization also poses little problem when looking at the impacts of fishing over these areas, as catch data are often aggregated by functional group, as in the Sea Around Us Project (SAUP) database (Pauly, 2007). This categorization scheme becomes a bit more problematic when attempting to model the impact of temperature, however. While Ecosim provides the capability of setting temperature preferences for each group member in a model, it is only possible to use a single temperature forcing time series per simulation with this capability.

In an area as large as the entire North Atlantic, the issues a single temperature forcing poses become immediately clear. Sea surface temperatures can range from below 0°C in the polar region to above 30°C in the tropics. These different environments have
different amplitudes of seasonal temperature cycling, are influenced by natural variability over interannual to multidecadal timescales differently, and are expected to change at different rates under anthropogenic warming (Figure 1).
Figure 1: Differing Seasonal and Longer-Term Variation in Subregions.
Sea surface temperature (°C) changes for subregions (Polar-Subpolar, red; Mid-Atlantic, yellow; Mediterranean, green; Tropical-Subtropical, blue) of the North Atlantic ocean, displaying sizable differences in seasonal cycles as well as the slope of their longterm trends (dashed lines).
Using a North Atlantic-wide temperature forcing function and temperature preferences across one set of functional groups representing the entire North Atlantic would inevitably obscure much of the potential change amongst different areas and their marine ecosystems within the overall region. A number of smaller area “subregional” divisions would allow for sets of functional groups and temperature forcing functions specific to smaller areas, thus capturing spatio-temporal granularity that a North Atlantic-wide model could not.

For this study, four subregions are defined, and four Ecopath models are created and calibrated to historical landings and environmental changes in Ecosim. Once calibrated, these four subregional models can be aggregated back into a single model for North Atlantic-wide modeling.

**Materials and Methods**

**Region of Study**

The North Atlantic is defined throughout as encompassing Latitudes 0-70°N and Longitudes -90-30°E. Latitudes above 70°N were excluded due to the unreliability of data in these latitudes due to sparse observations and the presence of sea ice. This spatial extent is much larger than most regional EwE modeled areas, yet is small enough to allow for far more group members (and thus regional granularity) than would be possible in a global-scale EwE model.

**Definition of Subregions**

For the purposes of this experiment, four subregions were chosen, in order to provide enough regional distinction while not necessitating a number of model members that would preclude EwE simulations. The final subregional functional groups were
defined as four contiguous zones, comprising “Polar/Subpolar” (PSP), Mid-Atlantic (“MAT”), Mediterranean (“MED”), and “Tropical/Subtropical” (TST), based on characteristics adapted from the WOA13 decadal sea surface temperature average, the global open ocean biome divisions, and Large Marine Ecosystems/High Seas areas, described in detail below. The final subregions and their corresponding characteristics from other regional definitions are presented in Table 1.

In dividing the overall North Atlantic into smaller subregions, in order to grapple with the spatio-temporal heterogeneity found within the larger area, a number of options were considered. Large Marine Ecosystems offer a tempting classification system. LMEs are already divided into ecologically and oceanographically coherent groupings (Sherman and Alexander, 1986; Sherman, 1991, Alexander 1993). Catch data are provided by SAUP at the LME level. Additionally, EwE models have already been created for them (Christensen et al., 2009). However, individual LMEs as a scale of interest come with significant drawbacks. LMEs are small enough that environmental differences between adjoining members will be small. LMEs are so numerous that in attempting to capture the entire North Atlantic would require the inclusion of nearly 30 LME and High Seas areas. Even if the ecological relevance of including a full set of functional groups for each LME is stipulated (as used in Christensen et al. 2009, for example) multidecadal simulations with this many group members in a single model is simply beyond the computational ability of EwE in its present form.

A more suitable starting point for such larger divisions and for this purpose would be areas of sea surface temperature similarity. In an aquaplanet without boundary currents,
such divisions would neatly correspond to insolation differences and thus latitudinal bands. In the actual North Atlantic, however, the divisions are somewhat more complex. Utilizing the World Ocean Atlas 2013 (WOA13; Locarnini et al., 2013), decadal average sea surface temperatures were analyzed. The objectively analyzed mean sea surface temperature data were examined for the first decade available (1955-1964), which corresponds to the start of both the catch and environmental data as well. These data are presented as Figures 2-4, which reflect larger and smaller numbers of potential subregional divisions.

Figure 2: WOA Temperature, 32 Divisions.
Decadal (1955-64) averaged sea surface temperatures from the World Ocean Atlas 2013, with 32 divisions.
Figure 3: WOA Temperature, 16 Divisions.
Decadal (1955-64) averaged sea surface temperatures from the World Ocean Atlas 2013, with 16 divisions.
The more finely resolved divisions of sea surface temperature result in a patchwork of discontinuous areas. A smaller number of divisions reveals a relatively coherent set of subregions spanning the entire North Atlantic. These fewer, larger, coherent regions allow for a modeled population that retained some degree of geographical distinction while being computationally-friendly.

Sea surface temperature alone is perhaps not the only variable worth considering in attempting to create subdivisions, however. An interesting alternative is presented by the “global open ocean biomes” approach (Fay and McKinley, 2014). In addition to sea surface temperature, the open ocean biomes approach also considers spring and summer chlorophyll a concentrations, maximum mixed layer depth, and sea ice fraction. The

Figure 4: WOA Temperature, 8 Divisions
Decadal (1955-64) averaged sea surface temperatures from the World Ocean Atlas 2013, with 8 divisions.
time-averaged open ocean biomes are similar to the fewer, larger WOA13 sea surface temperature divisions (Figure 5). These biome divisions correspond somewhat less neatly, but still similarly, to LME and High Seas divisions. The two types of divisions are overlain in Figure 6.

**Figure 5: Open Ocean Biomes.**
Ocean biomes as defined by Fay and McKinley, 2014.
Figure 6: Open Ocean Biomes and LMEs.
Ocean biomes as defined by Fay and McKinley, 2014, with Large Marine Ecosystems superimposed.
Table 1: Subregions and Their Attributes.
The final subregions (Region) are listed (PSP: Polar/SubPolar; MAT: Mid-Atlantic; MED: Mediterranean; TST: Tropical/SubTropical), along with their corresponding characteristics from the open ocean biome (Biome) classifications (ICE: ice biome; SPSS: subpolar seasonally stratified biome; STSS: subtropical seasonally stratified biome; STPS: subtropical permanently stratified biome; EQU: equatorial biome), including maximum mix layer depth (maxMLD), chlorophyll $\alpha$ concentration (Chl $\alpha$), and fraction of sea ice coverage (Ice), and corresponding World Ocean Atlas (WOA13) decadal mean sea surface temperature and Large Marine Ecosystem/High Seas Areas.

<table>
<thead>
<tr>
<th>Region</th>
<th>Biome</th>
<th>maxMLD (m)</th>
<th>Chl $\alpha$ (mg/m$^3$)</th>
<th>WOA13 1955-64 SSTs</th>
<th>Ice (%)</th>
<th>LME/HS Areas</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSP</td>
<td>ICE</td>
<td>-2—6°C</td>
<td>≥ 0.5</td>
<td></td>
<td></td>
<td>West Greenland Shelf; Iceland Sea (60%); Barents Sea (50%); Hudson Bay;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Arctic Ocean; Arctic Archipelago; Baffin Bay-Davis Strait; HS Arctic Sea</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(10%); HS Atlantic Northeast (50%)</td>
</tr>
<tr>
<td>MAT</td>
<td>SPSS</td>
<td>≥ 0.4</td>
<td>6—14°C</td>
<td></td>
<td></td>
<td>NE US Continental Shelf; Scotian Shelf; Iceland Sea (40%); Barents Sea</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(50%); Norwegian Sea; North Sea; Baltic Sea; Celtic-Biscay Shelf; Faroe</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Plateau; HS Atlantic Northwest (34%); HS Atlantic Northeast (30%)</td>
</tr>
<tr>
<td>MED</td>
<td>STSS</td>
<td>&gt;125</td>
<td>0.16 — 0.4</td>
<td>14—20°C</td>
<td></td>
<td>Iberian Coastal; Mediterranean Sea; Black Sea; HS Atlantic Northwest (66%);</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>HS Atlantic Northeast (20%)</td>
</tr>
<tr>
<td>TST</td>
<td>STPS; EQU</td>
<td>≤ 125</td>
<td>&lt; 0.16</td>
<td>22—30°C</td>
<td></td>
<td>Gulf of Mexico; SE US Continental Shelf; Caribbean Sea; North Brazil Shelf;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Canary Current; Guinea Current; HS Atlantic Western Central (100%); HS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Atlantic Eastern Central (100%)</td>
</tr>
</tbody>
</table>
At this time, extraction of climate data from NetCDF files in irregular shapes is outside the scope of the NCL and CDO tools, so each region is also given rectangular grid coordinates for the Ecosim experiment only. These subregional coordinates are adapted from similar regional divisions used in RECCAP (the Regional Carbon Cycle Assessment Project, e.g. Gruber et al. 2009) and are provided in Table 2.

<table>
<thead>
<tr>
<th>Subregion</th>
<th>Latitudes</th>
<th>Longitudes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polar-Subpolar (PSP)</td>
<td>49°N to 70°N</td>
<td>-90°E to 30°E</td>
</tr>
<tr>
<td>Mid-Atlantic (MAT)</td>
<td>36°N to 49°N</td>
<td>-90°E to 30°E</td>
</tr>
<tr>
<td>Mediterranean (MED)</td>
<td>18°N to 36°N</td>
<td>-90°E to 30°E</td>
</tr>
<tr>
<td>Tropical-Subtropical (TST)</td>
<td>0°N to 18°N</td>
<td>-90°E to 30°E</td>
</tr>
</tbody>
</table>

In the spatially-explicit experiments described in Chapter 3 however, the subregions are not restricted to these boundaries, but arise as an emergent property of the environmental data in the model.

**EwE Model Description**

The underlying model structure, including functional group definitions and initial parameter values, used throughout this thesis was derived from the global EcoOcean model (Christensen et al., 2009; Christensen et al., 2015). The EcoOcean model was developed and used for spatio-temporal, global experiments with Ecospace, primarily to evaluate the impact of fisheries scenarios on existing stocks. A North Atlantic regional model was generated by extracting the defined geographic area out of the global
Ecospace model, resulting in a mass-balanced Ecopath model. While fishing effort is spatially explicit in the EcoOcean model, other parameters are not. Rather, in any grid cell, they contain parameter values representing a global average. As the systems being modeled are not specific to individual species, but rather comprise multiple sets of functional groups across a large and heterogeneous environment, the “default”, globally-averaged parameter values from EcoOcean can serve well for model functional group members for which catch data and its knock-on impacts have little influence.

The ecosystem structure provided in the original model slice was recreated for each subregion, resulting in a total of 204 functional groups, distributed among the four subregions. In addition to the functional group definitions and default parameter values, the original EcoOcean food web structure was retained (Appendix 3 Table 1). That is, the subregional functional groups comprise their own effectively “closed” ecosystems. This retained food web structure does allow for trophic interactions within subregions, which can significantly affect the impact of environmental change on marine ecosystem redistributions. For example, incorporating trophic interactions may result in a significant reduction of the predicted poleward expansion expected under future warming (Fernandes et al., 2013).

Retaining the original food web structure prevents functional group interactions across subregions, however. This retention is both a practical consideration due to the absence of area-wide interaction data available (such as diet matrices), as well as a conservative framework from which to explore the impact of environmental change over time. By effectively isolating the subregional ecosystems, interactions such as invasive
intra-functional group predation, competition, and dispersion are not considered. Such indirect, ecological interactions can profoundly amplify or dampen the ecological impacts of climate change beyond the direct, physiological climate effects on organisms. Therefore changes in the subregional groups in isolation might best be interpreted as a first order, rather than ‘best’ or ‘worst case’ scenario. This also allows each subregion to be modeled as its own EwE model prior to exploring spatio-temporal changes in Ecospace.

While Ecospace is capable of lengthy simulations with the more than 200 group members in the full model region, and Ecosim can do so over interannual timescales, calibrating each subregion as its own model in Ecosim offers several advantages. Ecosim runs can be performed for the full reanalysis and catch data period, rather than over 10 year periods without suffering a memory error (which occurs in longer runs of the 204 member model due to legacy reliance on some 32 bit operating system components rather than a true 64 bit software version). Running the full Ecosim model for ~10 years, saving the output, creating a new Ecosim model from results over that period and going forward another ~10 years, and repeating this process is a viable methodology, particularly if significant alterations to the modeled system may be expected (Christensen et al., 2008). However, running Ecosim over the full environmental and catch data periods ensures that the starting biomasses will be sufficient to sustain the maximum fishing pressure as well as the full range of environmental change, making Ecospace runs beginning in 1950 (rather than the end of the Ecosim simulations) a more defensible option. Calibrating each subregion as its own model in Ecosim also allows for faster simulations, which
become important during the Monte Carlo simulations discussed later in this section, which can span many thousands of Ecosim runs.

All subregional models started with the default parameter values of the EcoOcean slice. Biomass-related values were derived using catch data from SAUP, described below. Environmental data (sea surface temperature and phytoplankton productivity, described below) were derived from the CORE reanalysis forcing the ocean components of the GFDL ESM2.1 Global Coupled Climate–Carbon Earth System Model (Dunne et al., 2012), as part of the FISH-MIP ocean and fisheries sectoral experimental protocol of the ISI-MIP cross-sectoral impacts modeling effort (Warszawski et al., 2014; ISI-MIP, 2015).

Adjustments were further made if temperature changes within the first decade of the forcing data caused group populations to crash. Temperature driven crashes beyond the first decade were accepted (provided crashes did not occur when temperature forcing was turned off), as migration and dispersion were not considered in this Ecosim modeling; i.e. within the subregional models, functional groups adapted to the changing ocean temperatures could not migrate in, as would be expected in the real world and addressed in the Ecospace simulations of Chapter 3. After the catch and temperature-based iterative adjustments were made, catch and temperature drivers were turned off to ensure that the subregional models would successfully balance in the absence of external perturbations.

After the iterative biomass adjustments and environmental data forcing steps were complete, the Monte Carlo simulation tool in Ecosim was used to further reduce the Sum
of Squares error relative to the historical catch data. Each subregional model was given a large 0.49 coefficient of variation (CV) for estimating biomass, and standard CVs of 0.3 for P/B, Q/B, and EE, and a CV of 0.05 for biomass accumulation. Each subregional model was assigned 1000 trials over which Ecosim would vary the model parameters (within the range provided by the CVs) to generate a balanced Ecopath model, allowing up to 2000 simulations per trial. Parameter values generating a better fit to the historical landings data (i.e. a reduction in the SS errors) were retained for subsequent trials, allowing the thousands of Monte Carlo runs to “search” the parameter space in a random walk, progressively better-tuned to the historical data. Historical landings were used in Stock Reduction Analysis (Christensen et al., 2008, and section below), rather than a general time series function.

After the Monte Carlo simulations, each subregional model was further calibrated using the Fit to Time Series tool in Ecosim. In the vulnerabilities search, catch data were loaded as a forcing function, rather than a Stock Reduction.

**Stock Reduction Using Landings Data**

In order to bound the subregional biomasses to a first approximation of realistic values, the catch data (described below) was used in the Stock Reduction setting. Rather than treat the catch time series as a function to be fit against, the Stock Reduction removes biomass according to the reported landings. This results in a population crash of members that either do not possess enough initial biomass to support the catch-based biomass removal, or else depend on other member functional groups that are underestimated. The functional group biomass values were iteratively increased from
their EcoOcean default values by an order of magnitude until one or more groups for which there landings data were provided did not crash within the first decade of the simulation.

After this initial bracketing, functional groups that continued to crash were adjusted to support realistic trophic level distributions (i.e. proportionately greater biomass for Small Pelagics relative to Medium Pelagics relative to Large Pelagics), as well as ensuring that their total initial biomass exceeded the maximum annual landings in the group’s highest year of catch. This follows the basic principle that there cannot be fewer fish in a given functional group than the maximum amount of that group landed. Biomasses were iteratively changed upwards and downwards to approach the amount necessary to satisfy the landings data and/or the ecological consequences of prey or predator landings. These adjustments were performed until all functional groups for which catch data existed could support the historical landings in the absence of any temperature forcing.

**Landings Data**

In this study, time series of catch were used in EwE to ensure that enough biomass of a given functional group is present in a region at levels sufficient to not only sustain the reconstructed landings for that group itself, but its predators and prey within the ecosystem as well. The catch data used in this study are historical landings from LMEs and High Seas areas aggregated into the PSP, MAT, MED, and TST subregions described above (as listed in Table 1), reconstructed by SAUP (Pauly, 2007). These data
are based on official FAO reported landings and complemented by a number of additional sources (described in greater detail in Chapter 1).

**Historical Temperature and Productivity Data**

Historical sea surface temperature and phytoplankton productivity were obtained from the FISH-MIP ocean and fisheries sectoral experimental protocol of the ISI-MIP cross-sectoral impacts modeling effort (Warszawski et al., 2014; ISI-MIP, 2015). The sea surface temperature and productivity data are generated using an observationally-adjusted atmospheric reanalysis (Large and Yeager, 2004; Griffes et al., 2009) to drive the ocean and ocean geochemical components of the GFDL ESM2.1 Global Coupled Climate–Carbon Earth System Model (Dunne et al., 2012).

**Temperature Forcing**

Temperature preferences were assigned to the group members of each subregion based on the WOA13 sea surface temperature averages for the 1955-1964 decade (Table 1). The decadal average temperature of a given region was assumed to approximate the preference of marine life in the region. The resulting temperature preferences consist of normal distributions over an 8°C range (e.g. PSP members have a preferences centered at 2°C, extending from -2°C to 6°C), with the four subregions together spanning the entire (-2-30°C) North Atlantic-wide temperature range. Time series of sea surface temperature data for each subregion were generated (described in further detail below), and loaded into Ecosim as a parameter forcing function.

**Productivity Forcing**

Time series for Small and Large Phytoplankton productivity for each subregion were generated (described in further detail below), and loaded into Ecosim as a forcing
function. These time series were then enabled in Ecosim under the Apply FF (Producer) menu, for both Small and Large Phytoplankton members.

**Data Processing**

Each environmental dataset was reprojected to a 1 degree x 1 degree resolution global gridspace to match the resolution of the Ecospace model used in Chapter 3, using the Climate Data Operators toolset (CDO, 2015). The North Atlantic region was then extracted from the global dataset. Sample spatio-temporal distribution maps are presented as Figures 7-12, illustrating the impact of seasonal changes on values and distributions of the environmental variables. The impact of resolution on the data are also apparent, particularly at the land-sea boundary. The effect is negligible over large open ocean areas, but effectively reduces the amount of ocean relative to land at the coastal edge, which could impact phytoplankton, especially on smaller subregional spatial scales.
Figure 7: Spatial Distribution of Large Phytoplankton, August 1965.
Regridded, August North Atlantic distribution of Large Phytoplankton from the GFDL/CORE data (in mol/L).
Figure 8: Spatial Distribution of Large Phytoplankton, December 1965.
Regridded, December North Atlantic distribution of Large Phytoplankton from the GFDL/CORE data (in mol/L).
Figure 9: Spatial Distribution of Small Phytoplankton, August 1965.
Regridded, August North Atlantic distribution of Small Phytoplankton from the GFDL/CORE data (in mol/L).
Figure 10: Spatial Distribution of Small Phytoplankton, December 1965.
Regridded, December North Atlantic distribution of Small Phytoplankton from the GFDL/CORE data (in mol/L).
Figure 11: Spatial Distribution of Sea Surface Temperatures, August 1965. Regridded, August North Atlantic distribution of sea surface temperatures from the GFDL/CORE data (in °C).
Figure 12: Spatial Distribution of Sea Surface Temperatures, December 1965. 
Regridded, December North Atlantic distribution of sea surface temperatures from the GFDL/CORE data (in °C).

Each subregion was then further extracted from the overall North Atlantic region. These spatio-temporal datasets were then converted into time series using the R Statistical Programming Language (R Core Team, 2014) and the “ncdf4” package (Pierce, 2014). The resultant time series consist of four spatially-averaged temperature and phytoplankton datasets, which were applied as forcing functions to each subregion. The small and large phytoplankton timeseries were further processed before inclusion in Ecosim by conversion from biomass concentration (in mol/L) to a relative forcing function for each corresponding Functional Group, using the year 1959 as the “normal”, following the FISH-MIP experimental protocol. Each monthly value was divided against
the corresponding monthly value from the year 1959, resulting in values of 1 for all months in 1959 and ratios relative the 1959 value for all other years. Ecosim begins simulation runs with the first year in which “Time Series” data are available. As the landing data are available in 1950, whereas the environmental data do not begin until 1959, the 1959 values for environmental data are repeated for the years 1950-1958 as well. Ecosim models can take a decade or more to reach an equilibrium even when the underlying Ecopath model is mass-balanced (Christensen et al., 2008), so the repetition of environmental data through 1950-1959 data during this “spin up” had little impact on the experimental design or results. A subset (first and last years) of the revised environmental data are presented in Tables 3-6 (the full datasets are available as Appendix 2 Tables 1-4).
Table 3: PSP Environmental Forcings.
Time series for the first and last year of the PSP environmental forcings, including relative primary productivity changes for large phytoplankton (Lphy) and small phytoplankton (Sphy), and absolute changes in sea surface temperature in degrees Celsius (Tos).

<table>
<thead>
<tr>
<th>Year</th>
<th>Lphy</th>
<th>Sphy</th>
<th>Tos</th>
</tr>
</thead>
<tbody>
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<td>1</td>
<td>4.784817</td>
</tr>
<tr>
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</table>
Table 4: MAT Environmental Forcings
Time series for the first and last year of the MAT environmental forcings, including relative primary productivity changes for large phytoplankton (Lphy) and small phytoplankton (Sphy), and absolute changes in sea surface temperature in Celsius (Tos).

<table>
<thead>
<tr>
<th>Year</th>
<th>Lphy</th>
<th>Sphy</th>
<th>Tos</th>
</tr>
</thead>
<tbody>
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Table 5: MED Environmental Forcings.
Time series for the first and last year of the MED environmental forcings, including relative primary productivity changes for large phytoplankton (Lphy) and small phytoplankton (Sphy), and absolute changes in sea surface temperature in Celsius (Tos).

<table>
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<th>Sphy</th>
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Table 6: TST Environmental Forcings.
Time series for the first and last year of the TST environmental forcings, including relative primary productivity changes for large phytoplankton (Lphy) and small phytoplankton (Sphy), and absolute changes in sea surface temperature in Celsius (Tos).

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Results and Discussion

PSP Landings

Landings in the PSP subregion totaled around 1,000,000 tonnes/year in the early 1950s and increased for several decades. They reached their maximum in the late 1970s, at around 3,000,000 tonnes/year, declining below 1,500,000 tonnes/year by the late 1980s and early 1990s. Landings appear to have somewhat increased from that time to the mid-
2000s, totaling around 2,000,000 tonnes/year. Large Benthopelagics made up the bulk of historical landings until the early 1970s, increasing from 600,000 tonnes/year to a peak of around 1,200,000 tonnes/year in the mid-1950s. Landings of Large Benthopelagics declined significantly from their maximum, to less than 300,000 tonnes/year by the end of the record. Small Pelagics were a small part of the overall landings from the early 1950s to the mid-1960s, after which they grew rapidly as a share of the overall catch. By 1970, Small Pelagics rivaled Large Benthopelagics as the most caught functional group. As Large Benthopelagics continued their decline, Small Pelagics skyrocketed to the most heavily caught functional group, peaking in the late 1970s around 1,800,000 tonnes/year. Their landings declined from that maximum until 1990, after which they experienced a brief, albeit volatile resurgence. From the early 2000s to the end of the record, Small Pelagics appear to have rapidly declined. Medium Benthopelagics made up a relatively small share of the total catch throughout most of the record, but have surged in importance in recent years. By the late 1990s they had become the second most caught functional group, increasing from around 130,000 tonnes/year to around 500,000 tonnes/year. By the end of the historical landings record, they had become the most caught functional group, with landings nearing 700,000 tonnes/year. These data are presented as Figure 13 and in Appendix 1 Table 1.
Figure 13: PSP Landings by Functional Group.
**MAT Landings**

Landings in the MAT subregion totaled around 6,000,000 tonnes/year in the early 1950s and increased for several decades. They reached their maximum in the mid-1970s, at around 12,000,000 tonnes/year, declining to ~8,000,000 tonnes/year by the mid-2000s. Medium Pelagics made up the plurality of catches over the historical record, and were the most heavily caught functional group in all but a handful of years, being surpassed briefly by Small Pelagics in the mid-1970s to early 1980s. Medium Pelagics rebounded in the early 1980s and showed an increase in catches through the end of the landings record. From the 1950s to the 1970s, the overall trend of Medium Pelagics was mirrored by Large Benthopelagics, which comprised the second most heavily caught functional group, until the increase in Small Pelagics. Unlike Medium Pelagics, Large Benthopelagics failed to recover, and continued their decline into the early 2000s. Small Pelagics were a relatively small share of landings in the 1950 to early 1960s, but increased rapidly towards the end of the 1960s. They became the most caught functional group in the mid-1970s before declining until the 1990s. Their share of landings appears to have stabilized from the early 1990s to the end of the record. These data are presented as Figure 14 and in Appendix 1 Table 2.
Figure 14: MAT Landings by Functional Group.
Historical landings for the Mid-Atlantic (MAT) subregion, by functional group (in tonnes).
MED Landings

Total landings increased from around 1,000,000 tonnes/year in the early 1950s to around 2,000,000 tonnes/year in the early 1960s. Thereafter, landings stagnated until the late 1970s. From the late 1970s to the late 1980s, catch increased, exceeding 2,750,000 tonnes/year. Landings decline until around 2000, falling back to around 2,100,000 tonnes/year. A brief uptick is apparent towards the end of the record, with catch exceeding 2,500,000 tonnes/year. Small Pelagics were the dominant functional group caught until the early 1980s. Landings grew from under 400,000 tonnes/year in 1950 to more than 600,000 tonnes/year by the late 1970s. From this peak, catch steadily declined through the early 2000s, descending to around 425,000 tonnes/year by 2003. Landings appear to be rebounding towards the end of the record, but still fall short of peak levels (at fewer than 640,000 tonnes/year). Large Benthopelagic landings increased from less than 100,000 tonnes/year in the early 1950s to around twice that amount by the mid-1960s. Its share of the total catch increased even more rapidly until the early 1970s, reaching around 500,000 tonnes/year. After a brief decline from the mid to late 1970s, Large Benthopelagic catch again increased in importance. By 1981, it was the most landed functional group, at around 700,000. Landings increased through the late 1980s, peaking around 900,000 tonnes/year. From the late 1980s to the early 2000s, catch declined, falling below 400,000 tonnes/year by 2000, and allowing Small Pelagics to regain position as the most landed functional group. A modest rebound towards the end of the record briefly put Large Benthopelagics once again in the most caught position, but they fell again into second in the final years of the record, at around 570,000 tonnes/year. Medium Pelagics were consistently the third most landed functional group, with catch
levels remaining around 300,000 tonnes/year throughout much of the record. Landings declined from the early 1970s to the 2000s, to around 200,000 tonnes/year and occasionally below. By the mid-1990s, landings were rebounding slowly, and Medium Pelagic catch was back above 300,000 tonnes/year by the end of the record. These data are presented as Figure 15 and in Appendix 1 Table 3.
Figure 15: MED Landings by Functional Group.
Historical landings for the Mediterranean (MED) subregion, by functional group (in tonnes).
**TST Landings**

Landings in the early 1950s totaled below 1,000,000, and increased steadily in subsequent decades. By the mid-1970s, landings exceeded 5,000,000 tonnes/year. Total landings have remained relatively stable thereafter. Despite a brief uptick in the late 1980s, landings have remained around 5,000,000 tonnes/year from the mid-1970s until the end of the record. Small Pelagics comprise the largest share of landings throughout the historical record. Growing from around 500,000 tonnes/year in 1950, landings exceeded 3,500,000 tonnes/year by 1990. Landings declined somewhat into the early 1990s. Despite this decline, Small Pelagics remained the most caught functional group through the end of the record, stabilizing around 2,200,000 tonnes/year from the mid-1990s to the end of the record. Medium Pelagics made up the second most landed functional group for the majority of the record. Landings remained relatively low from the 1950s to 1960s, below 350,000 tonnes/year, before increasing rapidly in the late 1960s. From the 1970s to the 1990s, landings remained relatively stable, hovering around 1,000,000 tonnes/year. After a brief downturn in the mid-1990s, landings appear to have stabilized at a slightly higher level, around 1,100,000 tonnes/year from the late 1990s to the end of the record. Large Pelagics make up the third most caught functional group. Landings of Large Pelagics have been relatively stable from the mid-1970s to the end of the record, totaling around 400,000,000 tonnes/year. These data are presented as Figure 16 and Appendix 1 Table 4.
Figure 16: TST Landings by Functional Group.
Historical landings for the Tropical-Subtropical (TST) subregion, by functional group (in tonnes).
Parameters and Fits to Time Series
The initial values for the Biomass, Production to Biomass, Consumption to Biomass, and Ecotrophic Efficiency parameters, as well as the final results of the calibration process, are presented in Appendix 4 Tables 1-4. The most notable feature of the initial vs. final biomass estimates is their large differences in magnitude. The amount of biomass in the original Ecopath model derived from the EcoOcean Ecospace model was intentional reduced by 10E6 tonnes, presumably for ease of computation. In order to facilitate a comparison of initial to final functional group proportions (e.g. the proportion of Small to Medium to Large Pelagics), the default EcoOcean biomass values are shown as raw and “normalized” to the order of magnitude used of the final estimates. The final, calibrated fits to functional groups for which landings data are available are presented in Figures 17-20.
Figure 17: PSP Calibrated Fit to Landings.
Post-Stock Reduction Analysis fit of PSP functional group biomass to landings time series.
Figure 18: MAT Calibrated Fit to Landings.
Post-Stock Reduction Analysis fit of MAT functional group biomass to landings time series.
Figure 19: MED Calibrated Fit to Landings.
Post-Stock Reduction Analysis fit of MED functional group biomass to landings time series.
Figure 20: TST Calibrated Fit to Landings.
Post-Stock Reduction Analysis fit of TST functional group biomass to landings time series

Each panel displays the fit of the landings of the functional group to the landings data (using the Stock Reduction Method) over time, along with the Sum of Squares Error. Initial vulnerabilities for all group members were left at the model-default value of 2. The final vulnerabilities after fitting to time series are presented as Appendix 5 Tables 1-4.

In general, the fit per functional group is quite good, with most groups showing a Sum of Squares Error (SSE) of less than 10, and many with SSEs of less than 1. This is comparable to the goodness of fit obtained in smaller regional models fit explicitly to landings from their immediate area (e.g. Chistensen et al., 2009) which do not take environmental changes into account. Some crashes are observed (e.g. MAT Medium Pelagics and Molluscs, or TST Sharks). These crashes do not occur when the
environmental forcings are turned off, which suggests that temperature and/or phytoplankton changes, or a combination of these environmental factors in addition to fishing mortality, are responsible. The subregional Ecosim models in this study were not designed to accommodate regional or longer term migration/dispersion (although this capability exists, Christensen et al., 2008), which might ameliorate these crashes.

The final biomass estimates generally reflect the distribution implied by the descriptions of the SAUP historical landings data among the highest catch regions (Table 8).
Table 7: Final Biomass Estimates by Subregion (tonnes).

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>PSPFinalBiomass</th>
<th>MATFinalBiomass</th>
<th>MEDFinalBiomass</th>
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<tr>
<td>48 Phytoplankton small (nsmp)</td>
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<td>27,021</td>
<td>27,021</td>
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<tr>
<td>50 Bacteria (nbact)</td>
<td>20,717</td>
<td>20,717</td>
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<tr>
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<td>250,000,000</td>
<td>250,000,000</td>
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</tbody>
</table>

73
Of the commercially-landed group members (i.e. 1-29), the MAT subregion had the highest biomass, followed by the PSP region, in accordance with the landings data from SAUP. However, in the final biomass estimates, the MED subregion had more biomass than the TST subregion, whereas in the landings data this order was reversed. This likely reflects an overabundance of biomass in groups that lack landings time series in the MED subregional model. This overabundance could likely be mitigated by taking a more conservative approach in the iterative bracketing methodology used to find the general amount of biomass necessary to support the historical catch data, by using smaller changes in the initial adjustments and/or smaller CVs in the Stock Reduction analysis.

All subregional models were able to achieve good fits with the historical landings data in the Stock Reduction procedure in the presence of productivity forcing. However, fits were degraded for some group members when temperature forcing was included. This suggests that the temperature preferences for those groups may be too narrow, or that their food webs are too fragile due to insufficient or incorrectly allocated biomass among these members’ predators/prey.

The methodological choices made in this experiment involve tradeoffs. While functional group-level ecosystems allow for a larger area of study, data underlying their relevant parameters becomes increasingly removed from observed behavior of marine life and necessarily relies on model estimates. Functional group divisions also obscure intra- and interspecies interactions within a functional group, such as predation, competition, or turnover. To some extent, this is “limitation” is desirable - under significant environmental change, individual species may be winners and losers (due to higher
physiological tolerances for geochemical change, adaptability to ecosystem range shifts, etc.), but ecosystem roles are likely to be much more stable than particular species over time. The environmental data used in this experiment have benefits and drawbacks; the sensitivity of these findings to different observational or reanalysis datasets is an area of potential uncertainty. Different definitions of the subregions would create significant differences in the forcings used in this experiment (in sea surface temperature ranges or landings over time), as the landings and environmental forcing functions are taken from the average of these areas. The initial bracketing procedure used to estimate initial biomass was relatively quick and simple to implement, but probably errs on the side of creating group member populations that are too abundant/stable. Smaller increments of adjustment could improve this. The very act of calibrating a model against observations is itself a compromise of profound significance. While parameters are tuned to become more realistic, for the purposes of dynamic modeling, particularly for exploring alternative future scenarios, there is a danger in overfitting; a model that can reproduce historical observations with high accuracy may become less rather than more realistic in its behavior in scenarios other than the single realization provided by observations (Schmidt and Sherwood, 2014; Xiao and Friedrichs, 2014a; Xiao and Friedrichs, 2014b).

A number of avenues for future development in EwE remain. Biomass values, and the ratio between functional groups, as well as diet matrix values could be compared to smaller, extant regional EwE models, along with other parameters such as vulnerabilities. Environmental forcings like temperature and productivity could be taken from climate model scenarios of future change, although the limitations posed by the “fixed”
subregional definitions within Ecosim would remain. This could be somewhat mitigated by attempting to constrain migration and dispersion within the subregional models, however. Additional environmental variables, such as sea surface salinity, dissolved oxygen, pH, and nutrient loadings could also be explored. While such stressors are expected to be highly correlated with changes in temperature (and productivity) on large spatio-temporal scales (Bopp et al., 2013), their net impacts may interact, or even synergize and thus result in much larger change (Fabry et al., 2008; Rosa and Seibel, 2008; Hofmann and Schellnhuber, 2009; Rodolfo-Metalpa et al., 2011; Kroeker et al., 2013; Melzner et al., 2013), especially in future simulations. Responses to forcings, e.g. temperature preferences, could be allowed to vary within a subregional population rather than conform to a uniform distribution.

Conclusion
A North Atlantic marine ecosystem model of intermediate complexity was created by repurposing a regional subsample of a global Ecospace model and calibrating it to historical catch and environmental data from the region of interest. The model is the product of a series of subregional model calibrations. The calibration process involved iteratively adjusting biomass levels to withstand observed fishing pressure and forcing primary productivity and sea surface temperature with a reanalysis and ocean geochemical model-derived output. Temperature preferences for the subregional populations were derived from observed sea surface temperatures from the start of the catch data and reanalysis time series. Monte Carlo simulations were used to achieve best fits to historical landings data via Stock Reduction Analysis by varying EwE parameters
(including B, Q/B, and EE). Vulnerabilities were calibrated using historical landings as a forcing function. The resulting calibrated subregional models were aggregated into a 204 group member North Atlantic-wide model, suitable for short term Ecosim or longer term Ecospace modeling from the year 1950 onwards, involving fishing scenarios and/or environmental change. This model provides the basis for one set of the spatio-temporal modeling experiments discussed in Chapter 3.
CHAPTER THREE: THE IMPACT OF DIFFERENT SPATIAL LOADINGS OF FUTURE ENVIRONMENTAL CHANGE ON NEKTON IN THE NORTH ATLANTIC USING ECOSPACE

Introduction
Ecopath with Ecosim models are increasingly used to analyze the impacts of fisheries and environmental change, across large spatial scales (e.g. ISI-MIP, 2015).

However, traditional EwE simulations in the presence of environmental change lack the ability to examine spatial and spatio-temporal differences that might arise across different modeling scenarios or among different group members within a single model.

Fortunately, Ecospace has grown beyond its initial scope of investigating the impact of emplacing Marine Protected Areas and allows for increasingly sophisticated spatio-temporal environmental change within the EwE framework (Steenbeek et al., 2013).

Temperature and productivity data from climate model projections, as well as proxy data from the Mid-Pliocene Warm Period (mPWP), were used to assess impact of different spatial structures of future environmental change using Ecospace. Changes in biomass for the most commercially-landed functional groups were modeled to assess the impact of temperature changes with and without accompanying changes in productivity. These changes were repeated under a range of temporal resolution to see what if any influence the length of simulation timestep had on the results. Changes in spatial distributions across scenarios were also examined, and compared to previous predictions of spatial change with future warming. Further, the study was divided into two sets of experiments,
the first using the calibrated model from Chapter 2, and the second using the default values from the regional slice of the global EcoOcean model from Christensen et al. (2015). This allowed the benefits and drawbacks of EwE calibration to historical environmental and landings change to be assessed, in addition to the differences between spatio-temporal scenarios of environmental change.

Materials and Methods

Ecospace Model Description

The impact of differences between the future North Atlantic as projected by climate models and a North Atlantic that more closely resembles the mPWP was investigated using the Ecospace module of the Ecopath with Ecosim modeling software. In the experiments, a North Atlantic marine ecosystem model of intermediate complexity was used, based on a regional slice of the global EcoOcean model (Christensen et al., 2015). In the first series of experiments, the model parameters used had been calibrated to historical changes in sea surface temperatures, productivity, and commercial landings in Ecosim, described in Chapter 2. In the second series of experiments, the default model values from Christensen at al., (2015) were used.

The model boundaries were matched to the region of interest (0-70N; -90-30E), and the model resolution is 1 degree by 1 degree. The original basemap, which includes bathymetry and land mask, is taken from the Sea Around Us Project (SAUP). This basemap was reprojected with small adjustments to align with the sea surface temperature data discussed later in this section (Figure 21).
Figure 21: Ecospace Model Basemap of the North Atlantic.
Adapted from basemap and bathymetry from SAUP. Sea surface temperature gradient (red to blue representing warm to cool) provided for land-sea contrast. Note the hatching in the Pacific west of Panama denotes the area’s exclusion.
The model consists of 204 group members, which comprise four subregional ecosystems (Polar-Subpolar/PSP; Mid-Atlantic/MAT; Mediterranean-like/MED; Tropical-Subtropical/TST) of 51 functional group members each, following the classifications of the original EcoOcean global model. The subregional populations feature trophic interactions across functional groups, but do not interact across subregions. The subregion areas are not prescribed in this experiment; rather they arise as an emergent property of the functional group response to the spatial distribution of sea surface temperatures.

**IPSL-CM5A-LR Climate Model**

Modern and future projections of sea surface temperature and primary productivity data in this study were obtained from the FISH-MIP ocean and fisheries sectoral experimental protocol of the ISI-MIP cross-sectoral impacts modeling effort (Warszawski et al., 2014; ISI-MIP, 2015). These sea surface temperature and productivity data were derived from the IPSL-CM5A-LR Earth System Model (Dufresne et al., 2013), under a high emissions (RCP 8.5) scenario of future climatic change. The IPSL-CM5A-LR model components are described in detail in Chapter 1.

**Temperature Forcing**

Sea surface temperature data from the IPSL-CM5A-LR model were transformed (see Data Processing below) into a series of maps, each of which represents a monthly timestep of the model output. The total temporal coverage spans January 1950-December 2100. The sea surface temperature data were loaded into Ecospace and enabled as External Data, forcing the model SSTs’ Environmental Driver Input Map,
which allowed the data to be used in their absolute (°C) form. For each set of experiments, the model was initially run for 151 years (1950-2100) at 6, 2, and 1 timesteps per year using the depth and sea surface temperature environmental preferences only. Attempts to run the model at 12 timesteps per year resulted in the Ecopath software crashing due to insufficient memory.

**Productivity Forcing**

The phytoplankton spatiotemporal data from the IPSL-CM5A-LR model were transformed (see Data Processing below) into a series of maps, each of which represents a monthly timestep of the model output. The total temporal coverage spans January 1950-December 2100. The productivity data were loaded into Ecospace using the External Data tool. The phytoplankton data were configured as a forcing of the model’s Relative Primary Productivity Input Map. This involved adjusting the absolute mol C m⁻² data by a scalar, which relativized the data to the first year’s average. The resulting productivity forcing in a given gridcell affects all of the producer functional groups in that cell. The model was run for 151 years (1950-2100) at 6, 2, and 1 timesteps per year using the combined depth and sea surface temperature environmental preferences along with the relative primary productivity forcing.

**PRISM3 Paleoclimate Data**

Data from the mid-Pliocene Warm Period were provided by the PRISM project. The PRISM3 global sea surface temperature reconstruction is a multiproxy record utilizing a number of independent records (described in Chapter 1). The mid-Pliocene was characterized by elevated CO₂ levels and warmer than present conditions. The global
mean sea surface temperature warming is similar to that projected by climate models towards the end of the century, but with notable regional differences. Although polar amplification is present in both model projections and the PRISM reconstruction, the North Atlantic shows pronounced high latitude warming in the PRISM reconstruction that is not present in future climate projections or Pliocene modeling experiments (Dowsett et al., 2013).

**Paleotemperature Forcing**

Sea surface temperature data from PRISM3 were utilized in a similar manner as the SST data from the IPSL-CM5A-LR climate model. As the PRISM3 data are only available for a single 12-month period, the monthly data were repeated to span a period of 60 years. This was intended to provide a long enough simulation to allow the model to adjust to the imposition of the paleo-SSTs and potentially reach a new equilibrium state. The PRISM3 data were enabled as External Data, forcing the model SSTs’ Environmental Driver Input Map, which allowed the data to be used in their absolute (°C) form. For each set of experiments, the model was initially run for 60 years at 12, 6, 2, and 1 timesteps per year using the depth and sea surface temperature environmental preferences only.

**Paleoproductivity Forcing**

“Paleoproductivity” data were created based on the PRISM3 SST data (see Data Processing below) and were utilized in a similar manner as the climate model productivity data. The “paleoproductivity” data were configured as a forcing of the model’s Relative Primary Productivity Input Map. This involved adjusting the absolute
mol C m$^{-2}$ data by a scalar, which relativized the data to the first year’s average. For each set of experiments, the model was initially run for 60 years at 12, 6, 2, and 1 timesteps per year using the combined depth and sea surface temperature environmental preferences along with the relative primary productivity forcing.

Data Processing

IPSL-CM5A-LR Data

The environmental data were provided as NetCDF4 files, courtesy of FISH-MIP. The provided global sea surface temperature data were corrected for model drift (Gupta et al., 2013). This process involves removing any spurious trend in the piControl (pre-industrial control, or unforced) realizations that may occur due to flux biases imposed during model component coupling (i.e. “coupling shock”), or due to an imbalance created during initialization by to observations and/or a bias in the model physics. These global data were reprojected from the model-defined gridspace onto a 1 degree by 1 degree equal area grid.

A North Atlantic (0-70°N; -90-30°E) slice was extracted from the FISH-MIP global data. For sea surface temperature, the data were converted from kelvins to degrees Celsius. The small and large phytoplankton data were combined by merging the two variables to a common one (i.e. from large vs. small to total plankton) and combining their concentrations. In order to process the data using QGIS, all files in the NetCDF4 format were converted to the older NetCDF format. The ISI-MIP data were provided as two time periods, 1950-2005 or “Historical” and 2006-2100, or “RCP8.5” (using the 8.5 Watts/m$^2$ top of atmosphere radiative forcing scenario from the Representative Concentration Pathways). RCP8.5 represents a high emissions future. These time periods
were combined to form a continuous 1950-2100 period. In order to process the NetCDF files in QGIS, as discussed later in this section, each timestep required its own file. Thus yearly and then monthly divisions of the combined Historical + RCP8.5 datasets were performed. The drift correction and regridding were performed by ISI-MIP prior to download. The regional extraction, kelvins to degrees Celsius conversion, phytoplankton consolidation, Historical and RCP8.5 dataset combinations, and the timestep divisions were performed using the Climate Data Operators command line tools (CDO 2015). The NetCDF4 to netCDF conversion was performed using the NetCDF Operator toolkit and NCL (NCO, 2015; NCL, 2014).

**PRISM3 Data**

The PRISM3 data were also reprojected to a 1 degree by 1 degree grid, converted from kelvins to degrees Celsius, and a North Atlantic regional slice was extracted, all using CDO. In order to create a “paleo-productivity” dataset, the relationship between sea surface temperature and primary productivity was determined. While temperature and productivity are positively correlated in colder climates, under future warming, productivity is expected to decline more or less linearly with increased warming, at least on global scales (Bopp et al., 2013). Therefore, the relationship between temperature and productivity only during the RCP8.5 future scenario was used. “Baselines” for temperature and productivity were created, using the monthly average value over the period 2071-2100 (30 years being a typical length of time needed to define a climatic “normal”; Arguez and Vos, 2011). These baselines were converted from NetCDF4 formats to NetCDF. A Temperature*Productivity product was then created by multiplying these baselines. This product was then divided by the PRISM3 sea surface
temperature monthly values, resulting in a “paleo-productivity” dataset. The paleo-productivity data processing was performed using CDO, with the exception of the NetCDF4 to NetCDF conversion, which was done using NCO.

**QGIS and Bash**

In order to use the spatio-temporal data with Ecospace, the netCDF files had to be converted into the ArcInfo ASCII grid file format. This was performed using the QGIS open source geospatial information software (QGIS Development Team, 2015), using the Raster>Conversion>Translate tool, and batch processing the monthly NetCDF files. The result was several series of ArcInfo ASCII files, each representing a month of spatio-temporal data, compatible with Ecospace. As much of the data processing often involved repeatedly performing near-identical operations using the command line, Bash (Free Software Foundation, 2008) was used to perform some minor scripting.

**Temperature Preferences**

Temperature preferences for the four subregions were assigned based on the WOA13 decadal average sea surface temperature from 1955-64, as described in Chapter 2. Preferences were set using a normal distribution spanning the subregional decadal averages of the WOA13 data (e.g. PSP sea surface temperatures from -2-6°C, with a mean value of 2°C). These temperature preferences were used to create temperature response curves in Ecospace (Figures 22-25). These response curves determined the size of the habitat capacity of each gridcell for each group in the model as detailed in Christensen et al. (2014).
Figure 22: PSP Temperature Preferences.
Sea surface temperature preferences (orange curve, °C on the X-axis) for the PSP functional groups and the cumulative area corresponding to those temperatures (gray bars) in the first model year.

Figure 23: MAT Temperature Preferences.
Sea surface temperature preferences (orange curve, °C on the X-axis) for the MAT functional groups and the cumulative area corresponding to those temperatures (gray bars) in the first model year.
Figure 24: MED Temperature Preferences.
Sea surface temperature preferences (orange curve, °C on the X-axis) for the MED functional groups and the cumulative area corresponding to those temperatures (gray bars) in the first model year.

Figure 25: TST Temperature Preferences.
Sea surface temperature preferences (orange curve, °C on the X-axis) for the TST functional groups and the cumulative area corresponding to those temperatures (gray bars) in the first model year.
Depth Profiles

Depth preferences were also assigned, based not on subregion but on functional group. The values for these preferences were based on depth profiles of ~3600 Atlantic-dwelling species from FishBase (http://www.fishbase.us/). Ecopath parameter profiles for the “Atlantic Ocean” Ecosystem were downloaded. All species without depth preferences were removed. The remaining species were aggregated by functional group. Median values for minimum and maximum depths were calculated for each functional group. These response curves determined the size of the habitat capacity of each gridcell for each group in the model as detailed in Christensen et al. (2014). Depth preferences are provided in Table 8.
Table 8: Depth Preferences.
Depth preferences for each Functional Group (in meters).

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<th>Class</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
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<td>0</td>
<td>550</td>
</tr>
<tr>
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<td>Pelagics medium</td>
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<td>550</td>
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</table>
Results and Discussion

For the first series of experiments, all of the subregional populations crashed, irrespective of the combination of environmental drivers applied. These results indicate that models created, balanced, and calibrated to environmental and fisheries data in EwE will not necessarily translate into functional Ecospace models. The cause of the crashes appears to be overfitting of the EwE model to the combined historical forcings, the subregional populations were not stable even in the absence of Environmental Drivers in Ecospace, suggesting that the stability achieved in EwE was the result of compensating forces rather than genuine ecosystem stability. Future work is necessary to obtain a model that can balance calibration to the observed landings and environmental changes in the subregions that can transition successfully into a stable Ecospace model.

According to historical landings (described in Chapter 2) the most important functional groups per subregions are Large Benthopelagics, Small Pelagics, and Medium Benthopelagics for subregion PSP; Small Pelagics, Medium Pelagics, and Large Benthopelagics for subregion MAT; Small Pelagics, Large Benthopelagics, and Medium Pelagics for subregion MED; and Small Pelagics, Medium Pelagics, and Large Pelagics for subregion TST. Changes in relative biomass for these functional groups for different time resolution simulations for the second set of experiments using primary productivity and temperature forcings derived from IPSL-CM5A-LR climate model are presented in Figures 26-28. Changes in relative biomass for these functional groups with mid-Pliocene temperature and “paeloproductivity” forcing are presented in Figure 29. Changes in relative biomass for these functional groups under temperature-only forcing for IPSL-CM5A-LR and Mid-Pliocene temperature are presented in Figures 30-31.
Figure 26: Relative Biomass, Climate Model Temperature and Productivity, Bimonthly Timesteps.
Figure 27: Relative Biomass, Climate Model Temperature and Productivity, Biannual Timesteps.
Figure 28: Relative Biomass, Climate Model Temperature and Productivity, Annual Timesteps.
Figure 29: Relative Biomass, Mid-Pliocene Temperature and Productivity, Bimonthly Timesteps.
Figure 30: Relative Biomass, Climate Model Temperature Only, Bimonthly Timesteps.
Figure 31: Relative Biomass, Mid-Pliocene Temperature Only, Bimonthly Timesteps
In the bimonthly resolution (6 timesteps/year) IPSL-CM5A-LR temperature and productivity scenario (Figure 26), all functional groups saw a reduction in relative biomass until around the 1970s, after which they appeared to remain stable for several decades. In keeping with the FISH-MIP protocol, results before 1970 are considered part of the model spin up and not deemed to be a true reflection of the model population to external changes in the environment. Most functional groups show little overall trend until around 2060, after which most experience a decline. Notable exceptions include MAT and MED Large Benthopelagics, which suffer a much larger initial negative shock during model spin up and continue to decline until around 2000. This is interpreted as representing the decreasingly-available habitat that meets both the temperature and depth requirements of Large Benthopelagics in these subregions. PSP Benthopelagics, by contrast, appear to fare better, and this is interpreted as reflecting an increase in the available environment due to a reduction in sea ice cover resulting in more available open ocean with the proper depth and SST profiles. The biannual scenario (Figure 27) resulted in similar overall features. However, the decline around 2060 was noticeably weaker than in the higher resolution scenario, and MAT Small Pelagics show an early decline absent from the previous scenario as well. In the annual resolution scenario (Figure 28), the differences are even more pronounced. Not only is the 2060 downturn absent, but the MED and MAT Benthopelagics show a recovery from their initial rapid decline. The overall changes are also less than the other scenarios by a factor of 2-3. Under the annual timestep resolution, the model members are never exposed to the most extreme temperature or productivity changes, which allows them to stay within their preferred
ranges long after the higher end of those ranges have been encroached upon by summertime values in higher resolution scenarios.

Previous research has suggested warming may result (or may already be resulting) in a general poleward shift of some groups (Beaugrand et al., 2002; Rjinsborp et al., 2009; Gamito et al., 2015). The movement of warm-loving species into traditionally temperate areas has also been called “tropicalization” and has already been observed in some areas (Vergés et al., 2014). However, an expectation of mere expansion of all groups to higher latitudes with warming is likely an oversimplification. Changing climatic conditions will more likely result in a reduction of preferred environmental niche areas, as the opening of novel environments fail to compensate for the loss of preferred conditions (Ohlemüller, 2011).

In this study, the northern extents of producers and groups with the greatest mobility (e.g. Pelagics) indeed shift poleward with increasing climate model generated sea surface temperatures alone (Figures 32-34), as well as with the PRISM sea surface temperatures alone (Figures 35-36).
Figure 32: Relative Abundance, Climate Model Temperature Only, 1979.
Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
Figure 33: Relative Abundance, Climate Model Temperature Only, 2039.
Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
Figure 34: Relative Abundance, Climate Model Temperature Only, 2099.
Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
Figure 35: Relative Abundance, Mid-Pliocene Temperature Only, Initial.
Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
Some notable differences between the spatial patterns of warming between the climate model-forced and mid-Pliocene-forced groups are apparent. The mid-Pliocene-forced scenario has a much larger proportion of TST members, for example, inhabiting a larger area. Intriguingly, the lower latitudes feature less, not more, warming in the mid-Pliocene relative to climate models. The mid-Pliocene temperature forcing is also able to sustain a greater abundance of highest latitude Benthopelagics relative to the climate model temperature forcing scenario. Overall, however, both scenarios demonstrate a general expansion in groups’ higher latitude ranges.
This spatial changes over time are not simply an expansion into newly-warmed waters. Most groups also show a significant reduction at their lower latitudinal edges. These results are consistent with other modeling approaches, which find warmer species moving poleward but also experiencing high rates of local decline at their lower latitudes (Cheung et al., 2009; Jones and Cheung, 2014). This dynamic is exacerbated when changes in productivity are also taken into account (Figures 37-39).

Figure 37: Relative Abundance, Climate Model Temperature and Productivity, 1979.
Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
Figure 38: Relative Abundance, Climate Model Temperature and Productivity, 2039.
Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
The MAT and MED subregional groups experience the largest declines, especially among groups with more specialized environmental needs (e.g., Benthopelagics). These results are consistent with previous studies predicting high losses in these areas (e.g., Cheung et al., 2009).

The importance of non-temperature factors evident in the spatial maps is consistent with the relative biomass time series results. There is a larger difference between the combined temperature and productivity (Figure 39) forced system vs. temperature alone (Figure 34) using the climate model data than there is between the

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**Figure 39: Relative Abundance, Climate Model Temperature and Productivity, 2099.**
Relative abundance of Small Pelagics, Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
PRISM temperature and “paleoproductivity” information (Figure 43) vs. temperature alone (Figures 36).

Figure 40: Relative Abundance, Mid-Pliocene Temperature and Productivity Initial. Relative abundance of Small Pelagics Large Benthopelagics, Large Phytoplankton, and Small Phytoplankton (columns left to right) for PSP, MAT, MED, and TST subregions (rows top to bottom).
In fact, the differences between Figure 29 vs. Figure 31, and Figure 36 vs. Figure 43 are negligible, suggesting that little additional value was added creating the “paleoproductivity” data, and indicating a more realistic treatment of productivity is necessary. The differences between Figure 26 vs. Figure 30 as well as Figures 33-34 vs. 38-39 suggest that the later 21st century declines in the climate model scenarios are strongly influenced by changes in productivity and/or a reduction in overall environmental preferences, or the combination of these changes and temperature, rather than temperature alone. Therefore, although some significant differences exist in the
relative biomass trajectories and spatial distributions of climate model-forced vs mid-
Pliocene forced-scenarios, it is unclear how policy-relevant these differences may be in
the absence of a more comprehensive suite of environmental drivers.

The second series of experiments elucidates the importance of considering a
number of environmental variables beyond average sea surface temperature changes, and
point particularly to the significant role played by primary productivity in shaping marine
ecosystem responses to environmental change, even when productivity and other
variables, such as temperature, are quite closely correlated.

Future research areas include further refinement of the Chapter 2 EwE calibrated
model, in order to assess the difference more realistic starting biomasses and other
parameters would have on the outcome of these simulations, as well as the incorporation
of model output from a wider range of climate models to test the sensitivity of these
results to the use of the IPSL-CM5A-LR model.

Conclusion

Despite the significant differences in the spatial pattern of warming seen in the
mPWP North Atlantic ocean relative to climate model projections, temperature impacts
on marine ecosystems alone may not reflect the full scope of change marine ecosystems
face under climatic change. Changes in primary productivity in addition to temperature
changes appear to have a greater impact on the abundance and distribution of fish
communities than sea surface temperature change alone, and although cores containing
Pliocene productivity data exist (Lawrence et al., 2013) an analogously extensive mPWP
productivity reconstruction to accompany PRISM is, so far, lacking. A full suite of
mPWP variables to force marine ecosystems alongside PRISM might allow one to more thoroughly interrogate the question of whether policy designed solely on climate model projections of future oceanic change may significantly underestimate changes in the abundance and distribution of existing fisheries.

These results previously demonstrate the potential value of incorporating paleoclimatic data from periods analogous (albeit imperfectly) to our anthropogenically-warmed future. At the same time, they also emphasize the need for a wider variety of environmental variables to be reconstructed, at the regional if not global scale. The paleoclimatic community has been admirably responsive to the climate modeling community’s needs in attempting to provide target data for model comparisons. A similar interaction with the impacts and/or ecosystem modeling communities would offer many of the same mutual benefits. Such collaboration would also increase the policy-relevance of paleoenvironmental reconstructions.
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