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The Response of the Zooplankton Community in the Western Gulf of Maine to a Shift in Oceanographic Conditions: 2005-2017

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THE RESPONSE OF THE ZOOPLANKTON COMMUNITY IN THE WESTERN GULF OF MAINE TO A SHIFT IN OCEANOGRAPHIC CONDITIONS: 2005-2017

By

Emma Cecile Dullaert

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Thesis Advisors: Dr. Jeffrey Runge & Dr. Lee Karp-Boss

An Abstract of the Thesis Presented
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The Gulf of Maine (GoM) harbors a productive ecosystem that supports a wide variety of marine life, providing services upon which local communities rely. The GoM ecosystem supports many important commercially harvested species, including the American lobster (*Homerus americanus*) which is the most valuable fishery in the US, Atlantic herring (*Clupea harengus*) and a variety of groundfish. The GoM is also home to the critically endangered North Atlantic right whale (*Eubalaena glacialis*), which has historically been known to feed in the eastern GoM and Bay of Fundy during the summer and fall months. In recent decades, the Gulf of Maine has experienced a rate of warming that is among the highest across the globe. Changes in circulation possibly originating from atmospheric CO_2 increase have altered the external sources of supply and physical properties of the water in the GoM. The changes in the GoM ecosystem are being described in the literature as a “regime shift” occurring around the year 2010. The 2010 oceanographic shift has been linked to changes in the biological components of the ecosystem including fisheries closings and declines in the populations of endangered species. Zooplankton represents an important link in energy transfer from lower to

higher trophic levels in the marine environment as they control the abundance and composition of phytoplankton and are a food source for consumer from pelagic forage fish to baleen whales. The objective of this study is to examine whether there were changes in the characteristics of the mesozooplankton community in the western GoM following the 2010 shift. Data from two long-term time series stations were assessed; one in Wilkinson Basin, a primary overwintering habitat for *C. finmarchicus* and an historically important feeding ground for the NARW, and one at the western margin of the MCC, an important source of advective supply and transport of zooplankton to Wilkinson Basin. This study investigates the effects on the overall mesozooplankton biomass, seasonal and longer-term change in biodiversity and community structure. The data were assessed in a time period of 5 years before and 6 years after the shift, corresponding to the availability of data in the time series. The changes observed in the mesozooplankton biomass and community structure in the western GoM support the idea that a regime shift has occurred in the GoM around the year 2010. These changes seem to be climate related and are strongly seasonal.

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TABLE OF CONTENTS

Chapter

LIST OF FIGURES

LIST OF ABBREVIATIONS

AMOC	Atlantic Meridional Overturning Current
BOEM	Bureau of Ocean Energy Management
CAST	Coastal Amplification of Supply and Transport
CMTS	Coastal Maine Time Series (previously known as DMC-2)
GoM	Gulf of Maine
ISMN	Integrated Sentinel Monitoring Network
LSW	Labrador Slope Water
MCC	Maine Coastal Current
NAO	Nort Atlantic Oscillation
NARW	North Atlantic Right Whale
NERACOOS	Northeast Regional Association for Coastal Ocean Observing Systems
NOAA	National Oceanographic and Atmospheric Administration
SSW	Scotian Shelf Water
WBTS	Wilkinson Basin Time Series (previously known as WB-7)
WSW	Warm Slope Water

CHAPTER 1

GENERAL INTRODUCTION

1.1. Origin of the Project

With the expected acceleration of global ocean warming over the coming decades, it is important to monitor regions such as the Gulf of Maine (GoM) which can serve as a model for climate-driven changes in ecosystems. This calls for a continued, integrated approach that considers physical, biological (microbial to pelagic scale), and social/political components. In response, The Northeast Regional Association of Coastal Ocean Observing Systems (NERACOOS) in collaboration with Northeast Regional Ocean Council (NROC), established the Integrated Sentinel Monitoring Network (ISMN) for assessing change in Northeast U.S. ocean and coastal ecosystems. The ultimate goal of this project is to create a base of knowledge from new and existing monitoring efforts to inform local management decisions as well as create a more broadly applicable framework for management of ecosystems facing rapid, climate driven changes (NERACOOS). The two long term time series stations included in this study, the Wilkinson Basin Time Series (WBTS) and the Coastal Maine Time Series (CMTS), are essential to monitoring potential climate driven change in the GoM ecosystem. In 2019, the two timeseries stations were integrated into the GoM Marine Biodiversity Observation Network (MBON), receiving funding from the Bureau of Ocean Energy Management (BOEM) and other government funding sources.

The objectives of my thesis research were to assist in the continuous collection of data at the two timeseries stations as well as to document potential changes in the mesozooplankton community in the GoM in terms of biomass and community structure, as well as the hydrographic properties of the surrounding environment.

1.2. Products

The outcomes of my thesis research are presented here in the format of a research article with the ultimate intention of submission for journal publication. Additionally, the historic and new data presented here were compiled and made publicly available in collaboration with a DMAC working group.

The datasets are available on the ISMN ERDDAP server:

http://ismn.erddap.neracoos.org/erddap/info/index.html?page=1&itemsPerPage=1000

CHAPTER 2

THE RESPONSE OF THE ZOOPLANKTON COMMUNITY IN THE WESTERN GULF OF MAINE TO A SHIFT IN OCEANOGRAPHIC CONDITIONS: 2005-2017

2.1. Introduction

The Gulf of Maine (GoM) is a semi-enclosed shelf sea, bordered by New England and the Canadian provinces of New Brunswick and Nova Scotia. It is separated from the Atlantic Ocean by a series of shallow banks and consists of three main basins; Jordan Basin in the eastern Gulf, Georges Basin and Wilkinson Basin in the western Gulf (Townsend et al., 2004). The circulation of water through the GoM generally flows in a counter-clockwise direction from the northeast to the southwest. The exchange of water with the Atlantic Ocean occurs primarily through the Northeast Channel, which is a deep, narrow channel bounded by Georges Bank and Browns Bank, as well as an influx of shelf waters via the Nova Scotia Current between Browns Bank and Cape Sable (Townsend et al., 2015). There are two main sources of deep water masses into the GoM: relatively colder and fresher Labrador Slope Water (LSW) from the north, entering the GoM through the Northeast Channel or by slope water intrusions onto the Scotian Shelf (Head et al. 1999; Davies et al. 2014), warmer and saltier Warm Slope Water (WSW) adjacent to the Gulf Stream, entering the Northeast Channel from the southeast (Townsend et al., 2015). An important component of the flow regime in the GoM is the Maine Coastal Current (MCC), a 30 km wide band of relatively colder water that is rich in nutrients due to the mixing of deep slope waters with the relatively nutrient poor, fresh and cold Scotian Shelf water (Pettigrew et al., 1998; 2005).

The GoM harbors a productive, but not very diverse, ecosystem that supports a wide variety of marine life, providing services upon which local communities rely (Johnson et al, 2011). The GoM ecosystem supports many important commercially harvested species. This includes the American lobster (*Homerus americanus*) which is the most valuable fishery in the US (Carloni et al., 2018, National Marine Fisheries Service, 2022). Other commercially harvested species include Atlantic herring (*Clupea harengus*) and a variety of groundfish (NOAA IEA). Another prominent species in the GoM is a small forage fish called Northern sand lance (*Ammodytes dubius*). Sand lance and herring are the primary prey for a wide variety of predatory fish, including groundfish such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), as well as marine mammals, birds, and squid, thus serving a foundational role in the GoM ecosystem (Overholtz and Link 2007; Suca et al., 2022, Staudinger et al., 2020). Due to its high levels of productivity, a variety of marine mammals frequent the GoM. The critically endangered North Atlantic right whale (*Eubalaena glacialis*) has historically been known to feed in the eastern GoM and Bay of Fundy during the summer and fall months (Baumgartner et al, 2003).

Zooplankton represents an important link in energy transfer from lower to higher trophic levels in the marine environment as they control the abundance and composition of phytoplankton and are a food source for a variety of consumers from pelagic forage fish to baleen whales. Therefore, understanding changes in zooplankton populations is critical for assessing change in the ecosystem as a whole and informs conservation of the region's marine resources. The zooplankton community in the GoM is largely dominated by copepods (Bigelow, 1924). *Calanus finmarchicus*, a lipid-rich copepod, has historically made up the majority of the mesozooplankton community in the GoM (Bigelow, 1924, Melle et al., 2014, Runge et al., 2015). Because of its high energy stores, this is the preferred prey species for the NARW and many planktivorous pelagic fish such as sand lance and Atlantic herring (Suca et al., 2022, Becker et al., 2020, Runge et al., 2015). Its abundances have also been shown to correlate strongly with lobster recruitment (Carloni et al., 2018). Therefore, *C. finmarchicus* is considered a sentinel component of the ecosystem (Baumgartner et al, 2003, Runge et al., 2012, Record et al., 2019). Other zooplankton commonly found offshore in the GoM are relatively smaller, coastal and open ocean copepods, namely species of *Centropages*, *Pseudocalanus*, *Metridia*, and *Oithona* (Johnson et al., 2017). In general, the seasonality in food availability in the GoM favors generalist feeders and species with overwintering strategies (Johnson et al., 2011).

Zooplankton populations in the GoM are maintained by local production and mortality processes and internal and external advective supply. The Gulf of St. Lawrence (GSL), through the Nova Scotia current, is the main external source of copepods, particularly *C. finmarchicus*, to the eastern GoM. The structure of the mesozooplankton community is dependent on the sources of external supply. Input of water from the GSL and incursions of LSW and WSW onto the Scotian Shelf vary depending on climatic conditions (Davies et al. 2014, Pershing et al., 2005). The Bay of Fundy and Scotian Shelf, via the MCC, are the primary source of zooplankton to the western GoM (Johnson et al., 2011, Redfield, 1941). Community structure varies spatially within the GoM depending on local conditions and advection. For example, shallow coastal regions favor copepod species that are adapted to lower salinities resulting from freshwater input or have egg carrying or resting egg strategies to alleviate risk of predation due to increased benthic pelagic interactions (Johnson et al. 2011). Influence from the offshore environment results in spatial differences in the mesozooplankton community across the Scotian shelf, whereas in the western GoM the community is relatively uniform across space (Johnson et al., 2011). The zooplankton community in the western GoM is strongly influenced by advection and mixing, both introducing copepods from the Scotian Shelf and slope waters as well as neritic species mixed in from coastal communities (Johnson et al. 2011). The life cycles of zooplankton in the GoM are strongly linked to physical ocean processes and properties such as temperature, as well as food availability. Thus, variation in their community structure is subject to seasonality and interannual and interdecadal variability (Bigelow, 1924, Johnson et al., 2011, Pershing et al., 2005).

The mechanisms controlling population dynamics of *C. finmarchicus* include production in the spring and early summer in the eastern GoM and southwest transport in the MCC, where they develop and reproduce in favorable temperature and phytoplankton conditions (known as the Coastal Amplification of Supply and Transport (CAST) hypothesis: Ji et al., 2017, Runge et al., 2015). Although the CAST hypothesis specifically applies to *C. finmarchicus*, it may hold for other zooplankton, subject to variation related to diverse life histories. Upon reaching Wilkinson Basin in late summer, *C. finmarchicus* copepodids have mostly developed to their lipid-rich, final pre adult stage (CV) and are ready to enter diapause. During the following winter/early spring, they emerge from diapause and a reproductive cycle follows supplying the spring stock for the western GoM (Runge et al., 2015, Redfield, 1941). Progression through the different stages of the life cycle depend both on the late winter spring diatom and other phytoplankton production as well as temperatures at depths below 100m, where the lipid rich stage CV copepodids spend their dormancy period from late summer to winter (Johnson et al., 2011, Ji et al., 2021). It is therefore important to consider the seasonality in the suite drivers that affect the *C. finmarchicus* life cycle in the western GoM. In the spring/early summer (Apr-Jul), the population is largely driven by local production dependent on the timing of food availability (spring phytoplankton bloom) with emergence from diapause. In the late summer/fall (Aug-Oct) and late fall/winter period (Nov-Mar), advective supply drives variations in abundance as local production decreases and part of the spring population is advected out (Ji et al., 2021). Predation also controls *C. finmarchicus* abundance, mainly in the late fall/winter period (Nov-Mar) (Ji et al., 2021, Wiebe et al., 2022).

In recent decades, the Gulf of Maine has experienced a rate of warming that is among the highest across the globe (Salisbury & Jönsson, 2018). Changes in circulation originating from atmospheric CO_2 increase have altered the external sources of supply and physical properties of the water in the GoM (Townsend et al., 2010; Record et al., 2019,; Saba et al. 2016; Seidov et al. 2021). Surface temperatures have risen at a rate of 0.12 ^{0}C/yr since 2005 (Seidov et al., 2021). Recent studies point to a likely climate-driven shift in the oceanographic regime in the GoM around 2010, characterized by a change in the sources of deep water to the GoM (Meyer-

Gutbrod et al., 2021, Record et al., 2019). Importantly, an increased influence of warm slope water (WSW) driven by a northward shift in the Gulf Stream is considered to have suppressed the flow of Labrador slope water (LSW) into the GoM (Thibodeau et al., 2018, Seidov et al., 2021). In the past, decadal scale shifts in the relative contributions of the sources of LSW and WSW have been associated with the North Atlantic Oscillation (NAO) winter index and the position of the north wall of the Gulf Stream (Pershing et al., 2005, Townsend et al., 2015, Seidov et al., 2021). Periods of higher NAO winter indices were associated with a northward migration of the Gulf Stream and greater influx of WSW, whereas low winter indices are associated with southward migration and more LSW (Townsend et al., 2015, Seidov et al., 2021). However, the recent shift does not seem to correlate with the NAO and has been shown to differ in magnitude of warm water incursion from the Gulf Stream (Townsend et al., 2015, Seidov et al., 2021). This increase in influence from WSW in the GoM is consistent with observations of weakening of the Atlantic Meridional Overturning Circulation (AMOC; Saba et al., 2016, Caesar et al., 2021, Seidov et al., 2021).

The 2010 oceanographic shift has been linked to changes in the biological components of the ecosystem including fisheries closings and declines in the populations of endangered species (Record et al., 2019, Richards and Hunter, 2021, Meyer-Gutbrod et al., 2021). Most notably, observations show that the critically endangered NARW population has shifted from their traditional summer feeding grounds in the eastern GoM and Bay of Fundy to the Gulf of St. Lawrence (Meyer-Gutbrod et al., 2021). Changes seen in the NARW population are thought to be largely driven by changes in the population of *C. finmarchicus* in the eastern GoM (Record et al., 2019, Meyer-Gutbrod et al., 2021). Declining trends in lobster recruitment in the western GoM were also shown to correlate with *C. finmarchicus* abundance (Carloni et al., 2018). The change in source waters was also linked to an overall decrease in primary productivity in the eastern GoM (Balch et al., 2022)

Changes in temperature as well as the shift in source waters to the GoM have the potential to affect ecosystem function by altering the structure of the mesozooplankton community in the GoM. In the past, decadal scale shifts in the relative abundances of *C. finmarchicus* and smaller copepods (particularly *Pseudocalanus, Oithona,* and *Centropages*) occurred concurrently with decadal shifts in sources of slope water. Periods of greater influence of WSW coincided with increased magnitude and duration of fall primary productivity related to increased stratification, higher abundances of forage fish, greater abundance of smaller copepods, and less *C. finmarchicus* (Pershing et al., 2005). Because of its predominance and foundational role in the GoM food web, the population dynamics of *C. finmarchicus* have been studied extensively in the context of the recent changes in the oceanographic regime (Record et al. 2019; Ji et al 2021; Runge et al. 2023). While order of magnitude decrease has been observed in the *C. finmarchicus* abundance in the eastern GoM, the population in the western GoM has been able to persist, presumably as a consequence of the CAST mechanism, although at lower levels (Record et al. 2019; Ji et al. 2021; Runge et al. 2023).

Apart from changes in the abundance of *C. finmarchicus* in the GoM, not much is known about the effect of the 2010 oceanographic shift on the mesozooplankton community as a whole. While egg production and growth rate generally increase with temperature (up to about 16- 19 °C in *C. finmarchicus*), development time decreases, leading to relatively smaller body size at higher temperatures (Campbell et al. 2001; Preziosi & Runge, 2014, Fields et al., 2022). Therefore, the observed increase in temperature might lead to a shift in abundance favoring smaller bodied copepods, consistent with regime shift in the GoM in the past (Pershing et al., 2005). The change in source waters may also lead to the introduction of new species which could further affect biodiversity. Because of its dominance in terms of abundance and relatively large size, *C. finmarchicus* also dominates the zooplankton biomass, which broadly represents the amount of food that is available to the next trophic level. Thus, changes in their abundance would likely be reflected in the total zooplankton biomass and consequently affect the structure of the entire ecosystem. The question remains whether potential increases in the abundances of other, likely smaller, species would be enough to offset the loss in biomass from *C. finmarchicus.* In previous regime shifts, there has been an increase in chlorophyll- a concentration in the winter, supporting increases in the abundances of *Oithona, Centropages,* and *Pseudocalanus* (Pershing et al., 2005). However, Balch et al., 2022, describe an overall decrease in primary productivity in the eastern GoM (GNATS transect from Portland, ME to Nova Scotia). The abundance of *Centropages typicus*, a subdominant copepod in the GoM, has been shown to correlate strongly with food availability, as has that of *Oithona* (Eiane & Ohman, 2004, Durbin and Kane, 2007). If a decrease in the primary productivity occurred in the western GoM, the strong winter increases in smaller bodied copepods seen in previous regime shifts might not be as pronounced in the current climate.

The oceanographic shift and its effects have been primarily described in the context of the eastern GoM. The objective of this study is to examine whether there were changes in the characteristics of the mesozooplankton community in the western GoM following the 2010 shift. The impacts on the abundance of *C.finmarchicus* in the wGoM are primarily addressed elsewhere (Runge et al., 2023; in preparation). This study investigates the effects on the overall mesozooplankton biomass, seasonal and longer term change in biodiversity and community structure. Data from two long-term time series stations were assessed; one in Wilkinson Basin, a primary overwintering habitat for *C. finmarchicus* and an historically important feeding ground for the NARW, and one at the western margin of the MCC, an important source of advective supply and transport of zooplankton to Wilkinson Basin. The data were assessed in a time period of 5 years before and 6 years after the shift, corresponding to the availability of data in the time series. Given the importance of seasonality in the life cycles of many of the dominant mesozooplankton species, and evidence for strong seasonal patterns from previous shifts, it is important to assess whether changes occur on an annual or sub-annual scale (Pershing et al., 2005). In this study, trends were divided into seasons considering the seasonality in the drivers controlling *C. finmarchicus* abundance (Ji et al. 2021). Environmental parameters of significance to the structure of the mesozooplankton community were assessed to give context to the results (ie. temperature, salinity and chlorophyll concentration).

The specific questions that guided the analysis were:

- How are the observed changes in the *Calanus finmarchicus* abundance reflected in the overall mesozooplankton biomass?

- How has the mesozooplankton community structure changed in response to changing environmental conditions?
- Are there seasonal variations in community structure?
- Is there a change in the biodiversity of the zooplankton community?

2.2. Methods

Zooplankton samples were collected at two long term time series stations in the Gulf of Maine. The Wilkinson Basin Time Series station (WBTS) is located in the western Gulf of Maine about 38 nautical miles offshore in the northwest corner of Wilkinson Basin at a depth of 250-260 m. Monthly samples were collected from the R/V *Gulf Challenger*, operating out of the University of New Hampshire's Judd-Gregg Marine Research Complex in Newcastle, New Hampshire. The timeseries covers the period from December 2004 to December 2022. The Coastal Maine Time Series station (CMTS) is located near the western margin of the Maine Coastal Current, about 5 nautical miles outside the mouth of the Damariscotta estuary at a depth of 105-110 m. Samples were collected from the R/V *Ira C*, operating out of the University of Maine's Darling Marine Center in Walpole, Maine. The timeseries covers the period April 2007 to December 2022 and primarily consists of monthly sampling during spring and summer. However, there is a gap in sampling due to a lack of funding between 2017-2019.

Water samples and environmental parameter data were acquired on each cruise using the dedicated water sampling system aboard the R/V Gulf Challenger. This system consists of a

Sea-Bird Electronics (SBE) 25Plus CTD, an SBE-55 Sampling Rosette with six four-liter Niskin bottles, a dedicated Hawboldt Industries SPR 1424/S Science winch, and a SBE-33 real-time monitoring and sampling deck unit.Each cast provides a vertical profile of physical and chemical properties of the water, which were processed using SEABIRD SBE DATA Processing version 7.22.5. The parameters analyzed in this study include salinity, temperature, and chlorophyll-a fluorescence. Prior to 2014, fluorescence was measured using IOP profilers that were calibrated annually. After 2014, in-situ fluorescence was measured using a Wetlabs Wetstar Chlorophyll Fluorometer S/N WSS-164. Water samples were collected from Niskin bottles for the determination of chlorophyll concentrations using the extraction method and calculations in Strickland and Parsons (1972) and were used for the calibration of in situ fluorometers. Samples were filtered onboard the vessel using glass fiber filters (GF/F). Samples were collected at a depth of 2, 10, 20 and 40 meters before 2020, and 0, depth of chlorophyll max, and 50 meters in 2021 and 2022.

Mixed layer depth at WBTS during the winter was estimated using density estimates derived from temperature and salinity profiles using the equation of state. To estimate the mixed layer depth for each sample, the potential density at 3 m (representing the surface) was subtracted from each density estimate. The first occurrence where this difference exceeded a threshold condition of 0.04 kg/m^3, met over at least 5 consecutive depths (1m interval), was used to represent the mixed layer depth of each profile (Cai et al., 2021). The threshold value was chosen based on visual inspection using density profiles and mixed layer estimates. To further investigate whether there was any change in the mixed layer depth, an average was taken over the whole time period for each month. These averages were subtracted from each mixed layer depth value in the corresponding month to calculate anomalies. Finally, the number of negative anomalies was divided by the total number of mixed layer values for three time periods to compare the proportion of occurrences where the mixed layer depth was deeper than the average (2004-2010, 2011-2017, 2018-2022).

The average temperature at WBTS in the estimated mixed layer, between 100-125 m (to reflect *C. finmarchicus* diapausing depth), and 200-225 m (near bottom) was calculated for each sampling date. These values were then averaged over the years before and after 2010 on an annual scale and for each season separately. To determine whether or not the changes in average temperature in each depth bin were significant, they were compared a Wilcoxon rank sum test was performed at a 95% confidence level. Temperature data were also plotted against salinity for each season separately to investigate the sources of the water mass. The data in the period before (2004-2010) and after (2011-2017) the proposed regime shift were averaged and plotted atop the Temperature-Salinity (TS) diagrams in different colors.

Samples for estimating zooplankton abundance, biomass and community composition were collected with a 200 μm mesh net. Vertical tows, from 5 m above the bottom to the surface, were conducted at a rate of 40 m/min, using a 0.75 m diameter single ring net at CMTS and a SEA-GEAR Model 9600 twin-ring net at WBTS. Two vertical casts were performed at each site. Samples from the cod ends were concentrated and poured into a 500 ml sample jar containing 50 ml of 40% buffered formaldehyde and topped off with seawater as needed, resulting in a final formaldehyde concentration of 4%. Biomass and *C.finmarchicus* abundance data are available for the entire time period, whereas the other zooplankton abundance data are only available through the end of 2017. For the purpose of the analysis of concurrent trends biomass and *C.finmarchicus* abundance only the period up to 2017 was considered for consistency. To assess whether trends in biomass continued, a separate analysis was performed on the data from 2011-2022.

In the lab, samples were split in half using a Folsom splitter under a fume hood. The half-split samples were stored in 250 ml jars; one marked for biomass and one for species composition analysis. For biomass analysis, samples were filtered on two pre-weighed filters cut from the same 200 μm mesh that is used for the nets and cod ends. The filtered samples were rinsed with 100 ml of freshwater and placed in a drying oven at 65 ^{0}C or 24-48 hours. Dried samples were removed from the oven and weighed immediately on a Mettler Toledo PG403-S DeltaRange microbalance. Sample dry weight (DW) was obtained by subtracting the initial mass of the filters from the final mass. Biomass [g/m^2] was calculated as follows:

$$Volume\ filtered\ by\ the\ net\ =\ net\ depth\ *\ net\ area$$

$$Biomass\ (g/m^2)\ =\ (sample\ DW/volume\ filtered\ by\ the\ net)\ *\ net\ depth$$

For zooplankton abundance and community composition analysis, samples were drained of formaldehyde and rinsed with filtered seawater on a 200 μm mesh sieve. The rinsed samples were then diluted with 2500 ml seawater. A 30-100 ml aliquot was taken to count

Calanus finmarchicus and other large zooplankton. A 5 ml aliquot was taken to count the smaller zooplankton in the sample. Species counts were conducted under a Leica MZ6 Modular Stereomicroscope. The counts were conducted by Rebecca Jones until 2011 and taken over by Cameron Thompson, after receiving training from Rebecca, from 2011-2017. Species abundance [individuals/m^2] was calculated as follows:

$$Dilution\ factor\ = \frac{dilution}{aliquot}$$

$$Species\ Abundance\ \left(\frac{individuals}{m^2}\right) = \frac{\#\ of\ individuals * dillution\ factor * split}{volume\ filtered\ by\ the\ net} * net\ depth$$

Data were divided into three periods considering the seasonality of the drivers in the *C. finmarchicus* population. Trends were assessed separately for the fall/winter (Nov-Mar), spring (Apr-Jul), and summer (Aug-Oct). Biomass and Chlorophyll a concentrations were monthly averaged and plotted according to season. Trends in the data were determined by linear regression and significance of the trends was determined based on p-value < 0.05. The biomass of *C. finmarchicus* present in each sample was estimated using dry weight estimates for each life stage (copepodite stages CI-CV, male, female) (. To assess the contribution of *C. finmarchicus* to the total biomass, the proportion of estimated *C. finmarchicus* dry weight to the total sample dry weight was plotted. The same regression statistics were used to determine trends and significance.

Abundance data for individual species were averaged over a 6-year period before and after the proposed regime shift in 2010 annually and for each season separately at WBTS. Note that zooplankton sampling at CMTS started in 2008, so there are only 2 years of data available before the proposed regime shift in 2010. Mean abundances for each time period were ranked, and the most abundant 17 copepod species were used for the visualization of the data. Mean abundances were plotted in order of increasing size and compared between the two time periods. The abundance value for each species represents the cumulative abundance of copepodite and adult life stages. Significance (95% confidence level) was determined based on a Wilcoxon rank sum test using individual data from all sampling dates within each of the two periods before and after 2010. The Shannon-Weiner index and and Pielou J evenness index were calculated as follows for each sample and averaged over each season for the periods before and after 2010 to identify potential changes in biodiversity. The distributions of the Pielou J indices were tested for normality, and significance was determined using a two tailed t-test.

Shannon-Wiener Diversity Index

$$H' = -\sum_{i=1}^{S} p_i \, ln \, p_i$$

Pielou J Evenness Index

$$J' = \frac{H'}{ln(S)}$$

Where p is the proportion of each species to the entire community, S is the number of species in the community. All abundance data were organized into 11 major taxonomic groups (copepoda, crustacea, urochordata, ctenophora, annelida, mollusca, bryozoa, protists, chaetognatha, cnidaria, and miscellaneous). The cumulative abundances of the species within these taxa were compared as mean abundances before and after 2010 in the same way as described for the abundances of the most common copepod species.

2.3. Results

2.3.1. Mesozooplankton Biomass and *C. finmarchicus*

On average, mesozooplankton biomass at the WBTS station before 2010 was highest in the summer and lowest in the spring. Dry weight biomass ranged from 3.8 g/m^2 to 29.6 g/m^2 in the winter, 1.3 g/m^2 to 17.2 g/m^2 in the spring, and 16.6 g/m^2 to 26.5 g/m^2 in the summer. Mesozooplankton biomass significantly decreased between 2005 and 2017 in the winter ($p = 0.016$) and the summer ($p = 0.002$) and showed no significant trend in the spring ($p = 0.199$, Fig 1.1). After 2010, mesozooplankton biomass at WBTS was highest in the spring and lowest in the winter. Dry weight ranged from 1 g/m^2 to 13.6 g/m^2 in the winter, 1.2 g/m^2 to 25.2 g/m^2 in the spring, and 8.3 g/m^2 to 14.9 g/m^2 in the summer. These trends continued during the period 2018-2022 (Fig 1.2). The spring biomass was lower during the period 2018-2022 compared to the biomass observed pre-2017. At CMTS, there was no change in biomass between 2008 and 2017 (Fig 1.1). Between 2011 and 2022, biomass significantly decreased in the summer ($p = 0.001$) and did not show any significant trend in the winter ($p = 0.536$) or spring ($p = 0.226$). Overall, the biomass after 2010 was similar in magnitude at both stations in the winter and summer, and 2-5 times higher at WBTS in the spring than at CMTS, which ranged from 0.8 to 7.7 mg/m^2 in the spring (Fig 1.1).

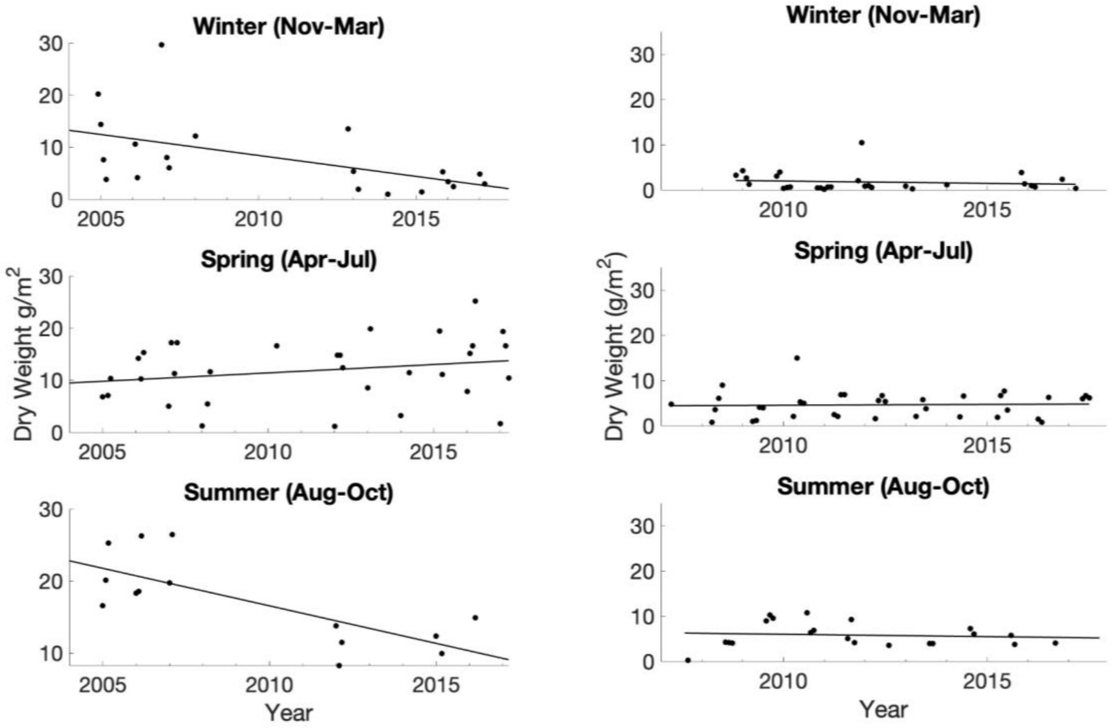

Figure 1.1. Mesozooplankton dry weight (g/m^2) at the Wilkinson Basin Time Series station (left panel) and Coastal Maine Time Series station (right panel) between 2005 and 2017. At WBTS, biomass significantly decreased in the winter ($y = -0.002x + 13.228$, *p = 0.016*, $r^2 = 0.284$) and the summer ($y = -0.003x + 22.797$, *p = 0.002*, $r^2 = 0.553$, and no significant trend in the spring ($y = 0.001x + 11.390$, *p = 0.199*, $r^2 = 0.054$). At CMTS there were no significant trends in the winter ($y = -0.000x + 2.264$, *p = 0.536*, $r^2 = 0.015$), spring ($y = -0.000x + 4.420$, *p = 0.830*, $r^2 = 0.001$), or summer ($y = -0.000x + 6.251$, *p = 0.658*, $r^2 = 0.011$). In the regression analysis x = yearday since Jan 1st, 2004 at WBTS and Jan 1st, 2007 at CMTS.

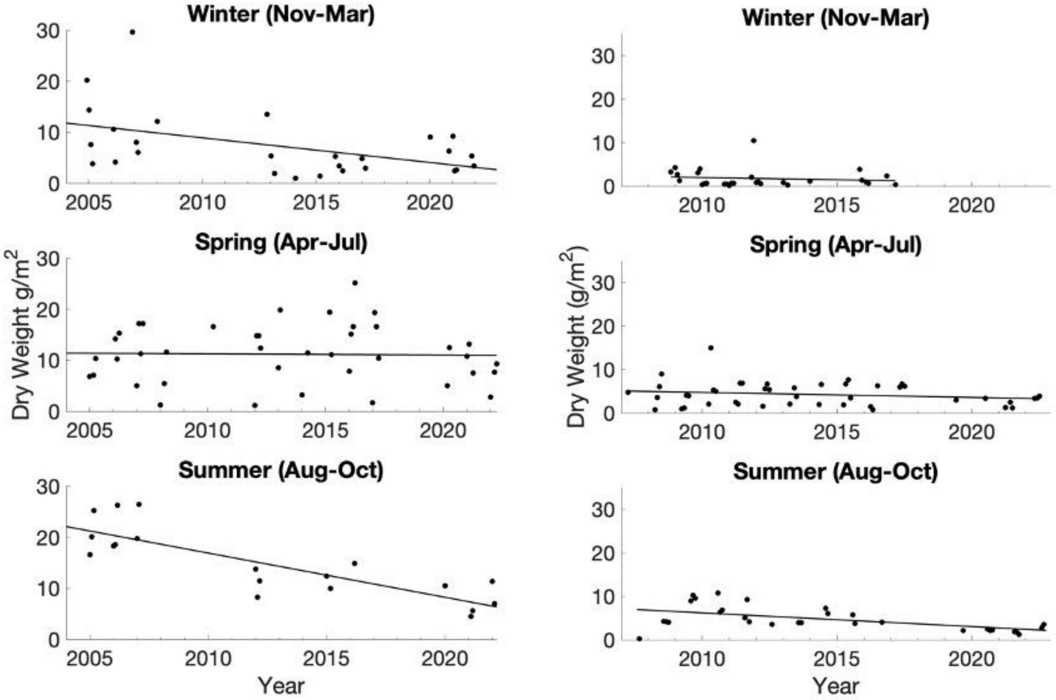

Figure 1.2. Mesozooplankton dry weight (g/m^2) at the Wilkinson Basin Time Series station (left panel) and Coastal Maine Time Series station (right panel) between 2005 and 2022. At WBTS, biomass significantly decreased in the winter ($y = -0.001x + 11.790$, $p = 0.013$, $r^2 = 0.221$) and the summer ($y = -0.002x + 22.098$, $p = 0.000$, $r^2 = 0.695$, and no significant trend in the spring ($y = 0.000x + 11.390$, $p = 0.894$, $r^2 = 0.000$). At CMTS, biomass significantly decreased in the summer ($y = -0.001x + 6.960$, $p = 0.001$, $r^2 = 0.314$), and did not show any significant trend in the winter ($y = -0.000x + 2.264$, $p = 0.536$, $r^2 = 0.015$) or spring ($y = -0.000x + 5.038$, $p = 0.226$, $r^2 = 0.035$). In the regression analysis x = yearday since Jan 1st, 2004 at WBTS and Jan 1st, 2007 at CMTS.

Prior to 2017, there was no significant change in the relative contribution of *C.finmarchicus* to the total biomass (Fig 2.1). Overall, between 2005 and 2022, *C. finmarchicus* contribution to biomass decreased significantly in the winter at WBTS but did not show any significant trend in the spring or summer (Fig 2.2).

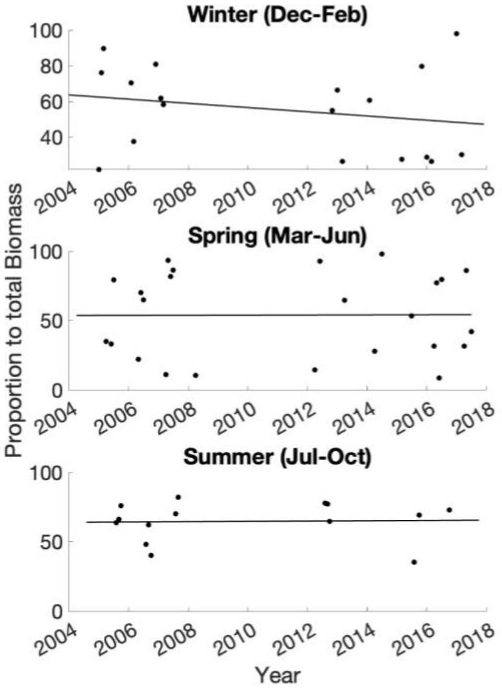

Figure 2.1. Estimated contribution (%) of *Calanus finmarchicus* (stages CI-CV) biomass, as determined by published dry weight values, to the total zooplankton biomass at the Wilkinson Basin Time Series station (WBTS) between 2005 and 2017. *Calanus* contribution to biomass decreased significantly in the winter ($y = -0.005x + 66.944$, $p = 0.032$, $r^2 = 0.2$) and did not show any significant trend in the spring ($y = 0.002x + 50.471$, $p = 0.499$, $r^2 = 0.018$) or summer ($y = -0.001x + 65.746$, $p = 0.602$, $r^2 = 0.019$). In the regression analysis x = yearday since Jan 1st, 2004.

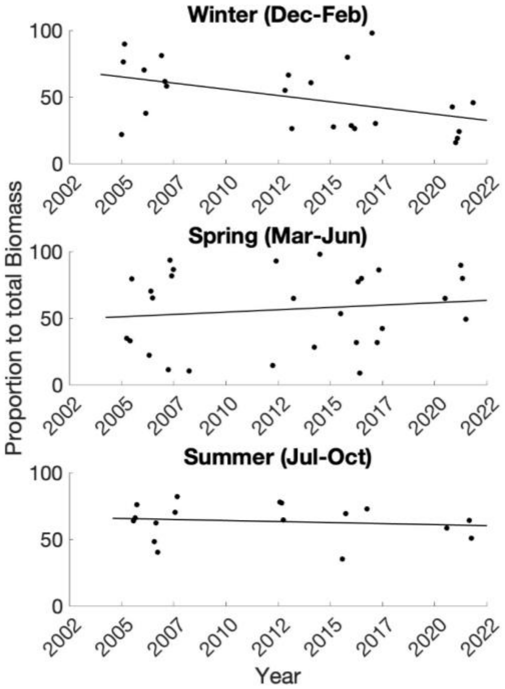

Figure 2.2. Estimated contribution (%) of *Calanus finmarchicus* (stages CI-CV) biomass, as determined by published dry weight values, to the total zooplankton biomass at the Wilkinson Basin Time Series station (WBTS) between 2005 and 2022. *Calanus* contribution to biomass decreased significantly in the winter ($y = -0.005x + 66.944$, $p = 0.032$, $r^2 = 0.2$) and did not show any significant trend in the spring ($y = 0.002x + 50.471$, $p = 0.499$, $r^2 = 0.018$) or summer ($y = -0.001x + 65.746$, $p = 0.602$, $r^2 = 0.019$). In the regression analysis x = yearday since Jan 1st, 2004.

2.3.2. Mesozooplankton Community Composition (2005-2017)

Across all years, the majority of the mesozooplankton community at both WBTS and CMTS was dominated by copepods. Altogether, 17 species of copepods made up the majority of the mesozooplankton community. The most dominant copepods at both stations include *Calanus finmarchicus, Pseudocalanus spp, Oithona spp, Metridia spp, Microcalanus spp,* and *Centropages spp* (Fig 3.1 & 4.1). Other major taxonomic groups are Crustacea, Urochordata, Mollusca, Bryozoa, Echinodermata, Annelida, Chaetognatha, Cnidaria, Ctenophora and Protists and collectively make up less than a quarter of the mesozooplankton community at both stations (Figure 5.1 & 6.1).

Annually, the proportion of copepods at WBTS decreased significantly from 93% before 2010 to 85% after 2010. There were significant increases in the contribution of most other major taxa including ctenophores, mollusks, bryozoans, chaetognaths and cnidaria (Figure 5.1). There was also an increase in the 'miscellaneous taxa' which mainly consists of trochophores. At CMTS, copepods made up 72% of the total zooplankton abundance before and 81% after 2010. The abundance of annelids decreased significantly, but no significant changes were observed in any of the other taxonomic groups (Figure 6.1). At the CMTS station, abundances of copepod species remained fairly constant during the period of study and seasonal variability was weak between 2010-2017 (Figures 4.2-4.4). It is important to note that data at CMTS start in 2008 and might not be representative of the community before the proposed regime shift.

The copepod assemblage at WBTS before 2010 was dominated by *C. finmarchicus*. The next most abundant species belonged to the genera *Oithona* and *Microcalanus pusillus* and were about 3 times less abundant than *C. finmarchicus* (Fig 3.1). After 2010, *Oithona similis* was the dominant species in terms of abundance. Abundances of smaller copepod species increased significantly, most notably in species of the genera *Centropages, Pseudocalanus* and *Metridia* (Fig 3.1). No new species were detected after the proposed regime shift in 2010, but overall, biodiversity increased during the period of study, resulting from an increase in species evenness from 0.79 to 0.98 ($p = 0.000$). Averaged over an annual scale, there was no significant observed change in the abundance of *Calanus finmarchicus* at WBTS in the pre- and post 2010 time series (Fig 3.1). The copepod community composition after 2010 differs between the two stations. In general, the total abundance is on the same order of magnitude on an annual scale and most species are present at both stations. However, their relative proportions of the total abundance are different. The relative abundances of *C.finmarchicus* and *Metridia lucens* are about twice as high at WBTS as compared to CMTS, whereas the relative abundances of *Pseudocalanus* and *Temora* are notably higher at CMTS (Fig 3.1 & 4.1).

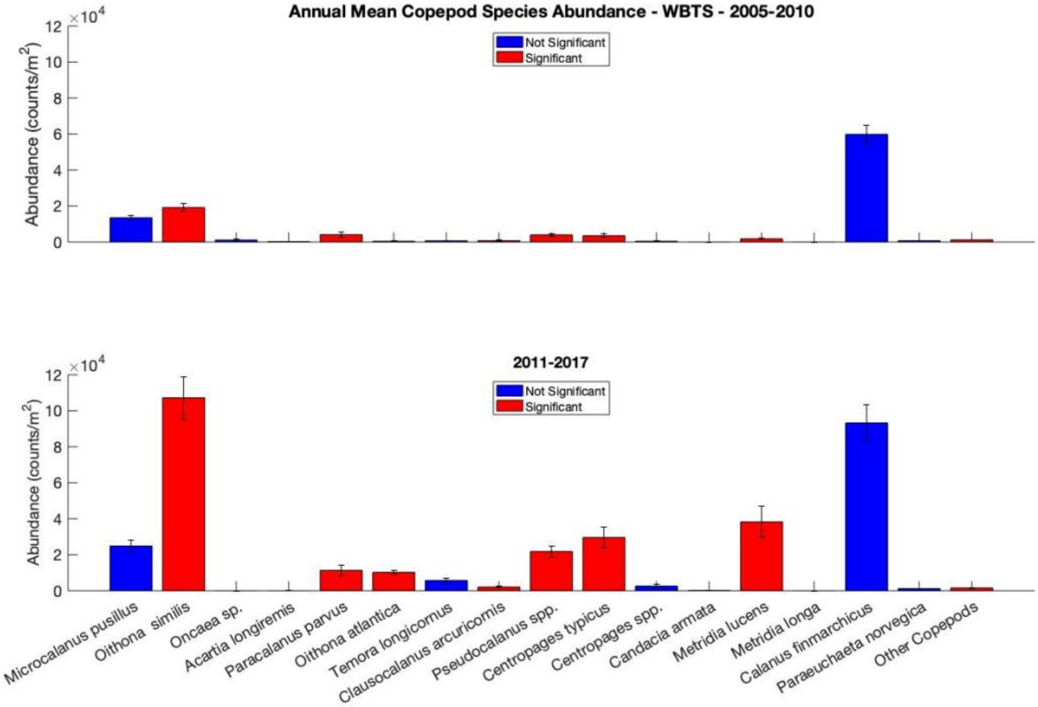

Figure 3.1. Annual mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

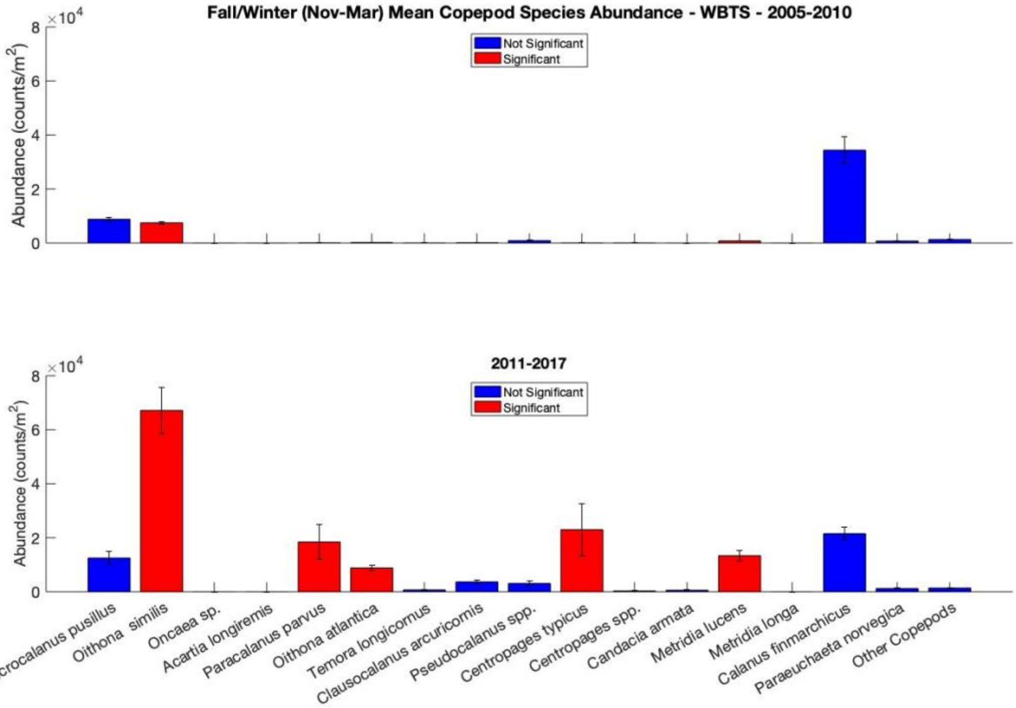

Figure 3.2. Fall/winter (November-March) mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

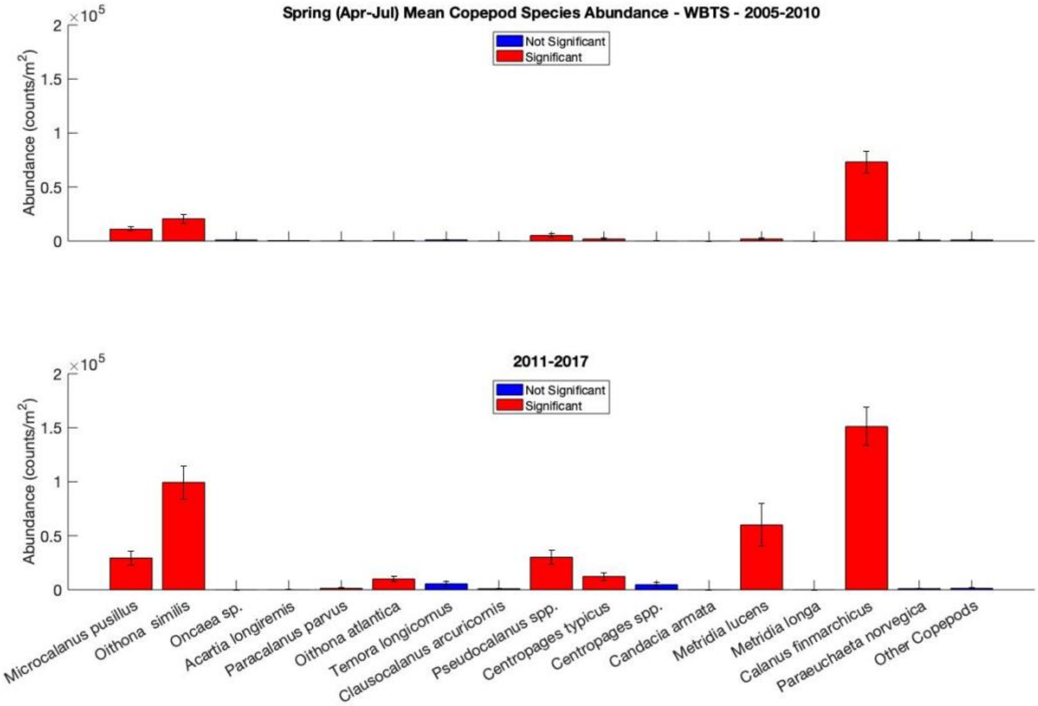

Figure 3.3. Spring (April-July) mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*$p<0.05$*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

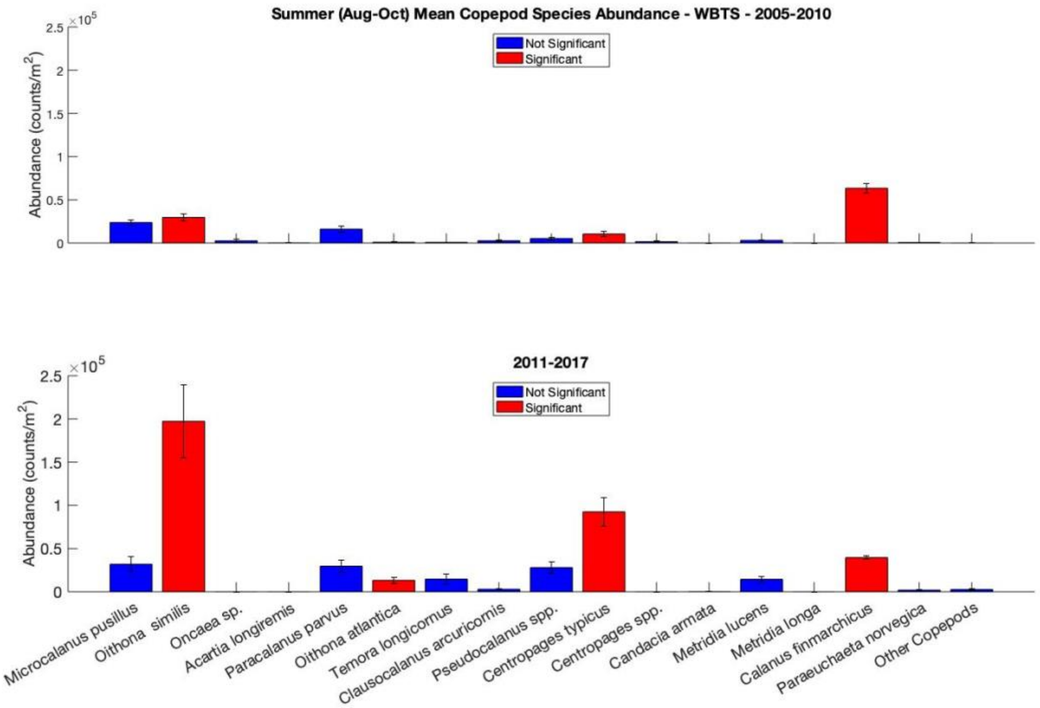

Figure 3.4. Summer (August-October) mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

The primary drivers of zooplankton abundance in the GoM are seasonally variable, and previous studies have shown notable changes in the *C. finmarchicus* population in the GoM (eg. Ji et al. 2009; 2021). Averaging over an annual scale may therefore obscure seasonal changes in the zooplankton community (Ji et al., 2010). In order to generate a better understanding of the response of the zooplankton community to the oceanographic regime shift, the results are presented for 3 periods that correspond to seasonal drivers of the *C. finmarchicus* population: fall/winter (November - March), spring (April - July), and summer (August - October).

Summer abundances of *C. finmarchicus* declined significantly in the summer after 2010 (Fig 3.4). Although a negative trend was also observed in the winter at WBTS, the change was not statistically significant (Fig 3.2). In the spring, there was a significant increase in the *C. finmarchicus* abundance (Fig 3.3). Compared to the pre-2010 period, a significant increase in the abundances of smaller copepod species was observed post 2010 across all seasons (Fig 3.2-3.4). These changes were most pronounced in the fall/winter as evidenced by a significant increase in biodiversity reflected in an increase in species evenness from 0.61 to 0.98 (*p = 0.000*). Species evenness also increased significantly in the spring from 0.66 to 0.89 (*p = 0.001*) but did not exhibit any change in the summer (0.92 to 0.93, *p = 0.3069*). Notably, there were no significant changes in the abundances of *Pseudocalanus* and *Metridia* species in the summer (Fig 3.4)

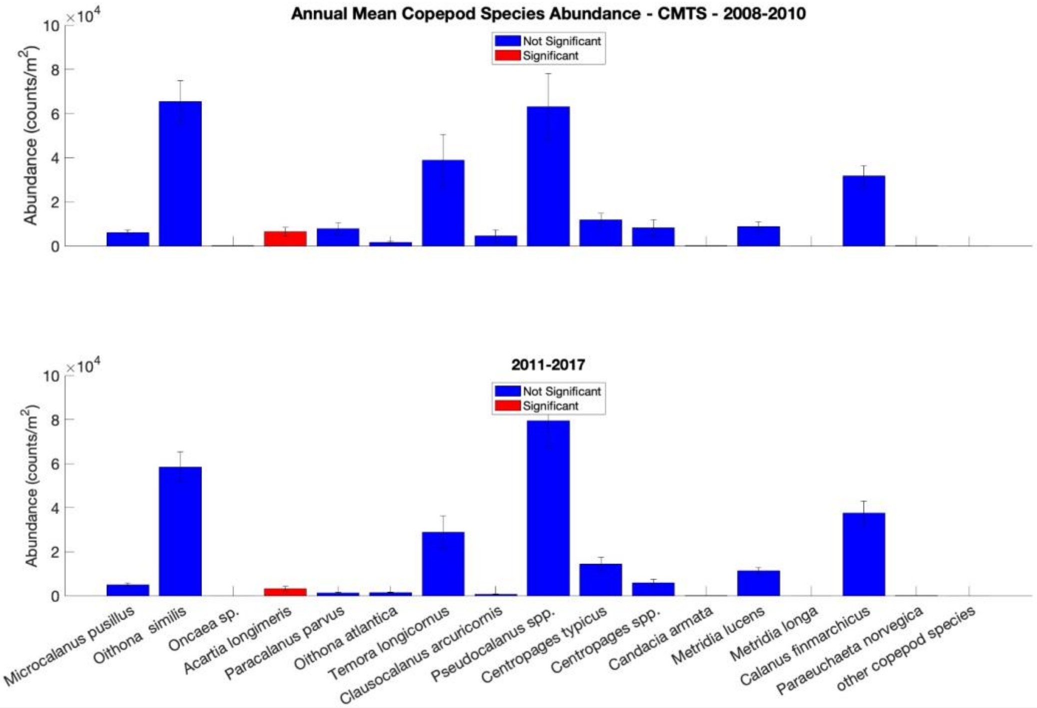

Figure 4.1. Annual mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf

of Maine at the Coastal Maine Time Series station (CMTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

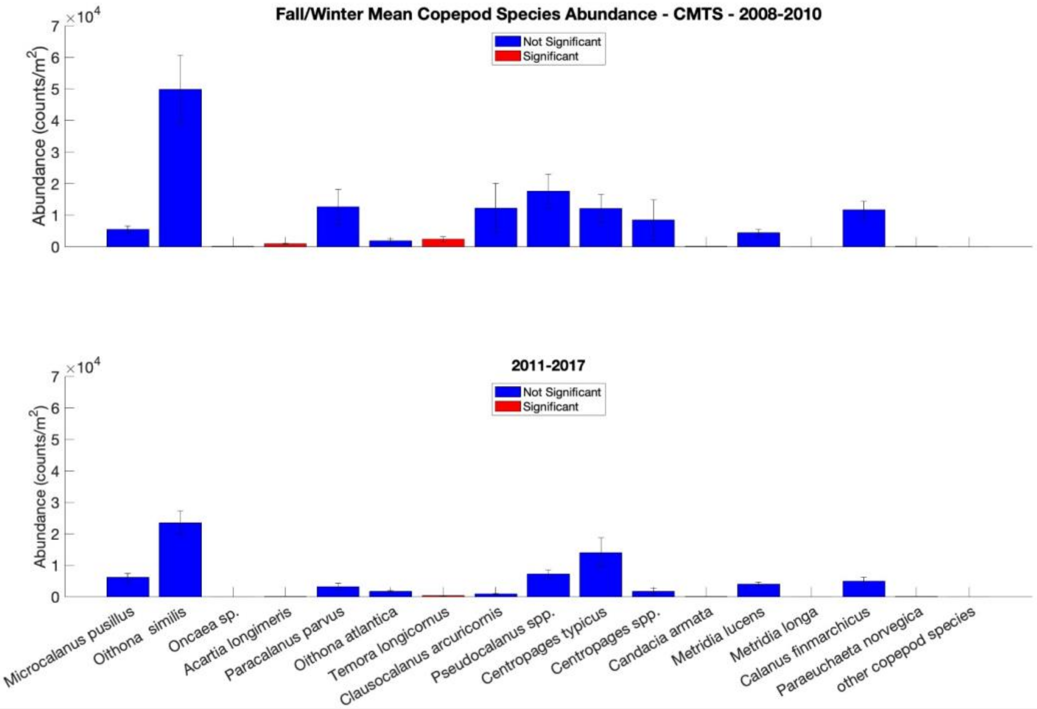

Figure 4.2. Fall/Winter (November-March) mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Coastal Maine Time Series station (CMTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

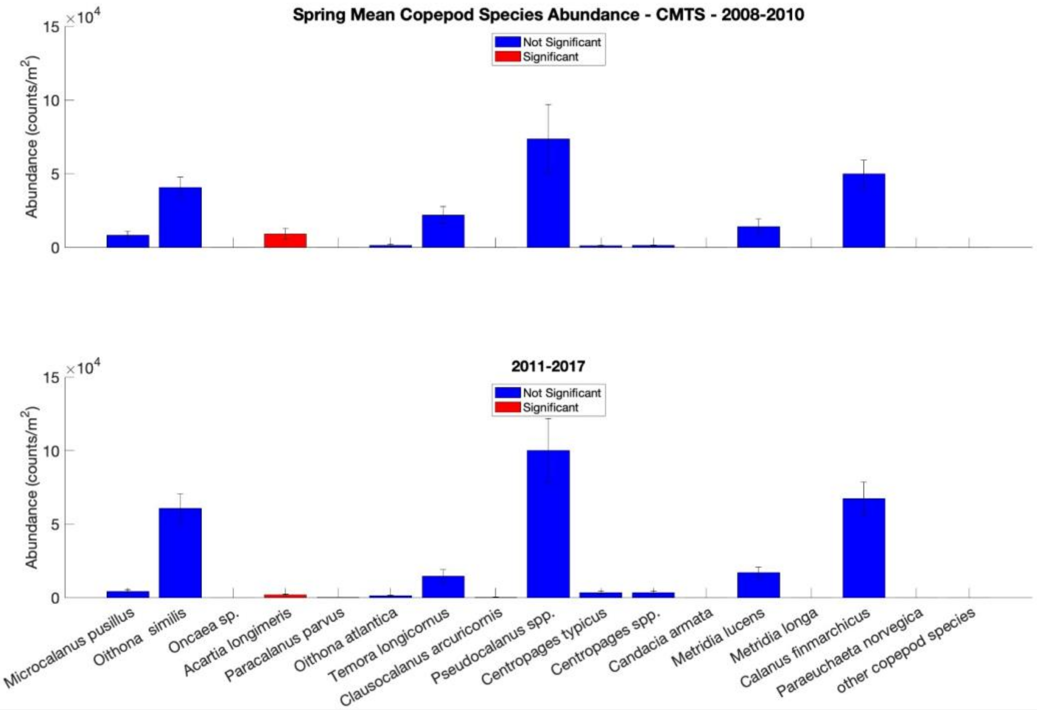

Figure 4.3. Spring (April-July) mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Coastal Maine Time Series station (CMTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

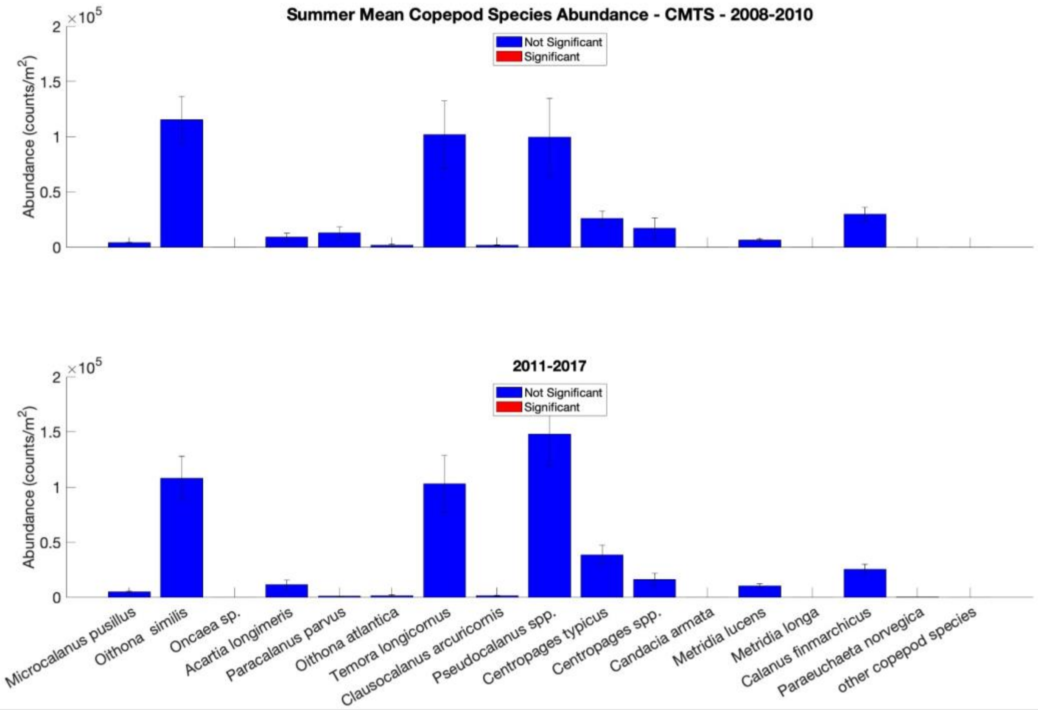

Figure 4.4. Summer (August-October) mean abundance (individuals/m2) of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Coastal Maine Time Series station (CMTS). Species are ordered by size from smallest to largest as determined by their prosome length. A Wilcoxon rank-sum test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

The most significant changes occurred in the abundances of the smaller copepods at WBTS. The abundance of *Oithona similis* increased by a factor 4 in the spring and a factor of 8 in the summer and winter. *Oithona atlantica* and *Centropages typicus* also saw significant increases across all seasons. The abundance of *Metridia lucens* increased in the fall and spring, whereas *Paracalanus parvus* saw significant increases in the fall, and *Pseudocalanus spp* increased significantly in the spring (Fig 3.2-3.4)

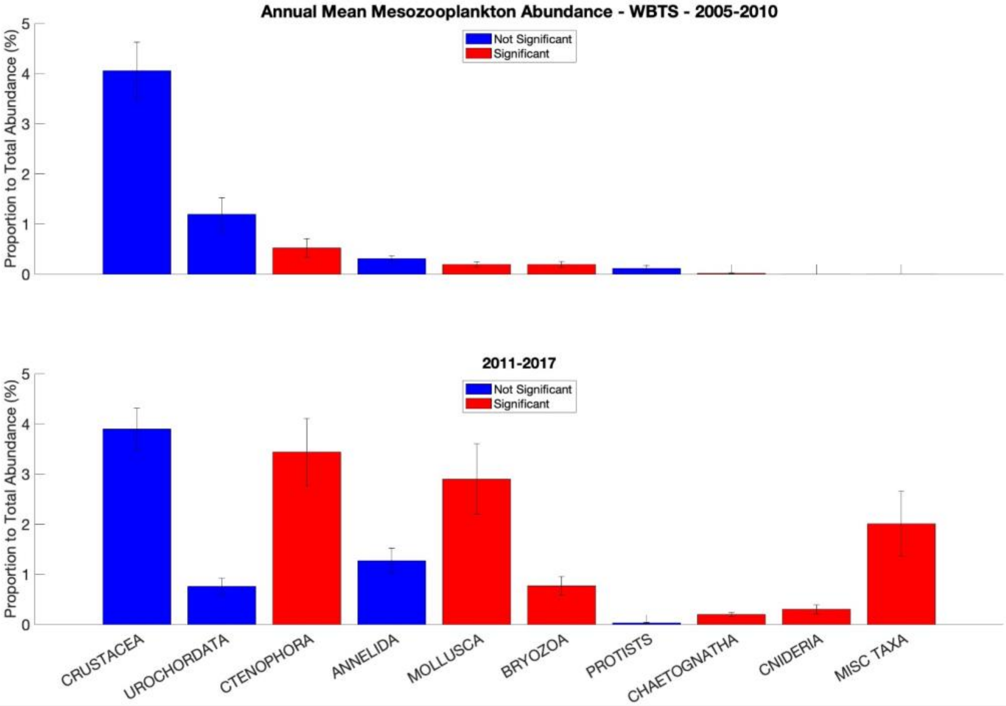

Figure 5.1. Annual mean proportion to total abundance of mesozooplankton taxa other than copepods of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A Wilcoxon rank-sum test at a significance level of 95% (*$p<0.05$*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

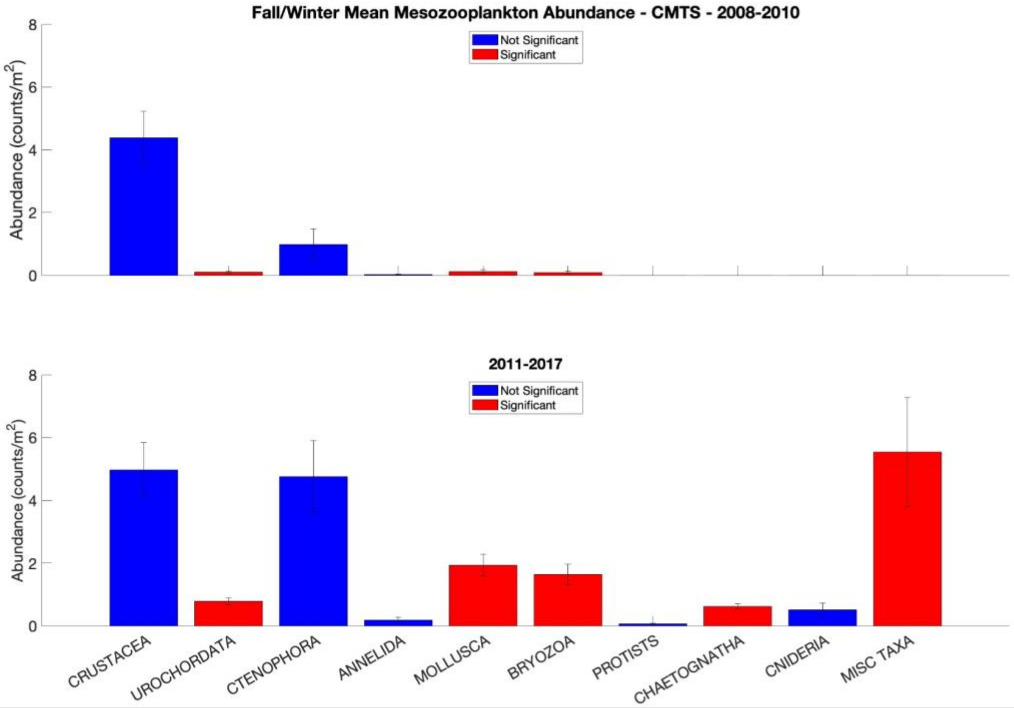

Figure 5.2. Fall/winter (November-March) mean proportion to total abundance of mesozooplankton taxa other than copepods of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A Wilcoxon rank-sum test at a significance level of 95% (*$p<0.05$*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

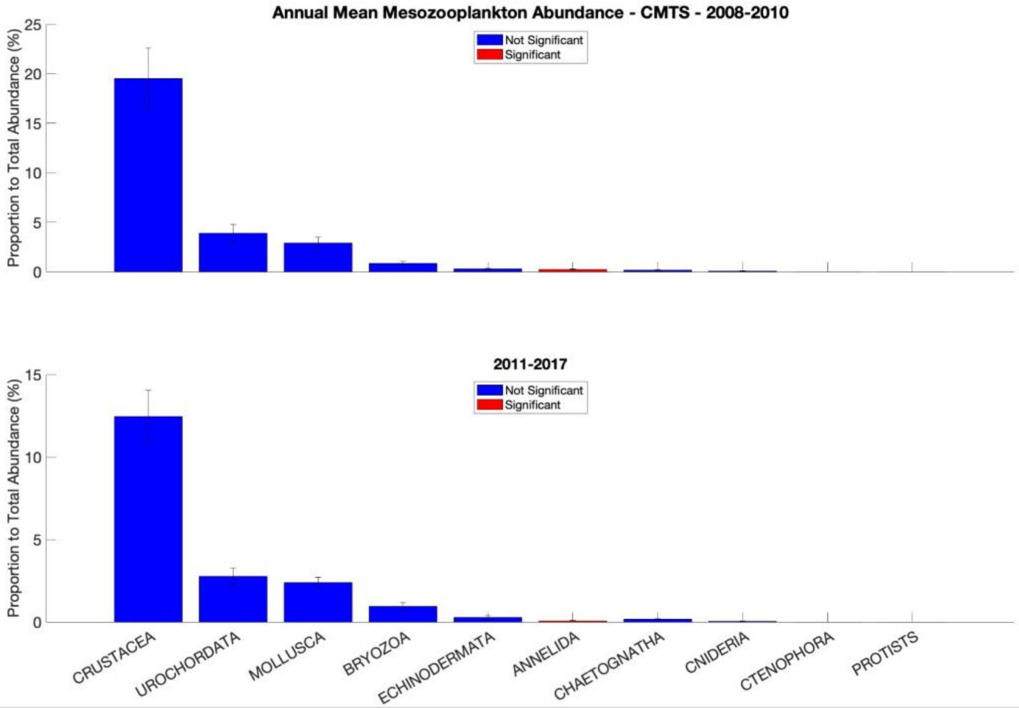

Figure 6.1. Annual mean proportion to total abundance of mesozooplankton taxa other than copepods of copepod species before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Coastal Maine Time Series station (CMTS). A Wilcoxon rank-sum test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

2.3.3. Environmental Factors

On an annual scale, the mean temperature in the estimated mixed layer, 100-125m bin, and 200-225m bin increased significantly post-2010 ($p = 0.042, 0.000, 0.000$, respectively, Fig 7.1) and the mean salinity increased significantly in the 100-125m bin only ($p = 0.000$, Fig 8.1). However, separating the data into the 3 seasonal periods reveals that the changes in temperature and salinity are not consistent throughout the year. In the fall/winter period, the mean temperature increased significantly in the mixed layer from 5.8C to 10.1 ^{0}C ($p = 0.005$) and in the 200-225m depth layer from 6.7 ^{0}C to 7.5 ^{0}C ($p = 0.017$, Fig 7.2). Salinity decreased significantly in the mixed layer in the winter from 32.8 to 32.3 (*p = 0.009*) and increased in the 200-225m depth layer from 33.9 to 34.2 (*p = 0.039*, Fig 8.2). In the spring, the temperature increased significantly in the 100-125m depth layer from 4.7 ^{0}C to 5.7 ^{0}C (*p = 0.007*, Fig 7.3). Salinity increased significantly in the mixed layer from 32.9 to 33 (*p = 0.044*, Fig 8.3). There were no significant changes in temperature or salinity at any depth in the summer (Fig 7.4 & 8.4). Overall, TS signatures are similar before and after 2010 and the water column appears to be warmer across all seasons, most notably in the winter (Fig 9.1). Especially after 2010, there is a sharp inflection in salinity and temperature around 235m.

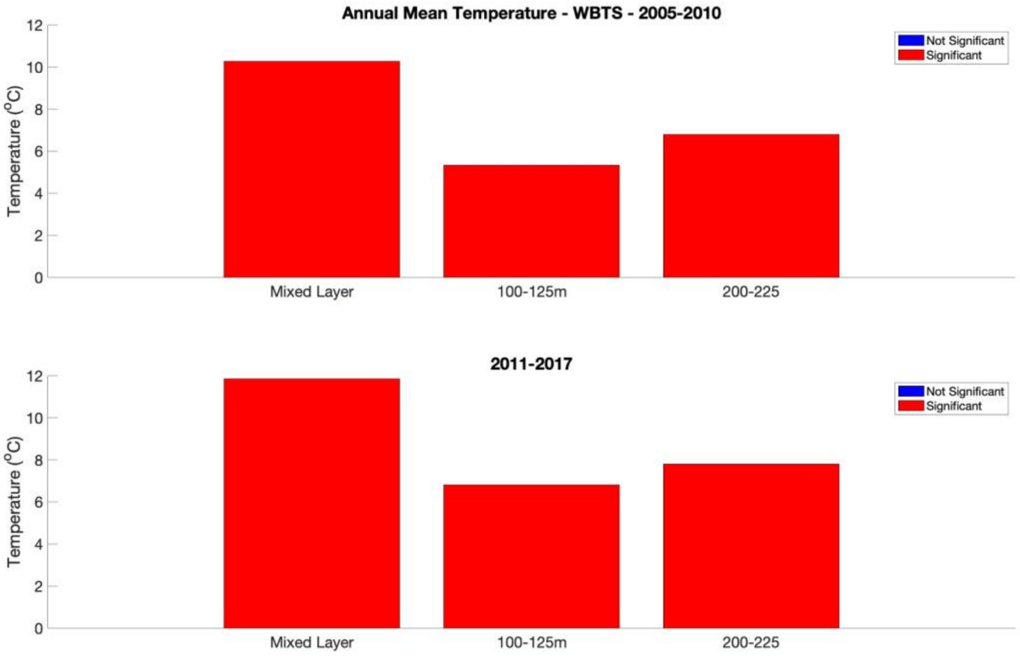

Figure 7.1. Annual mean temperature before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

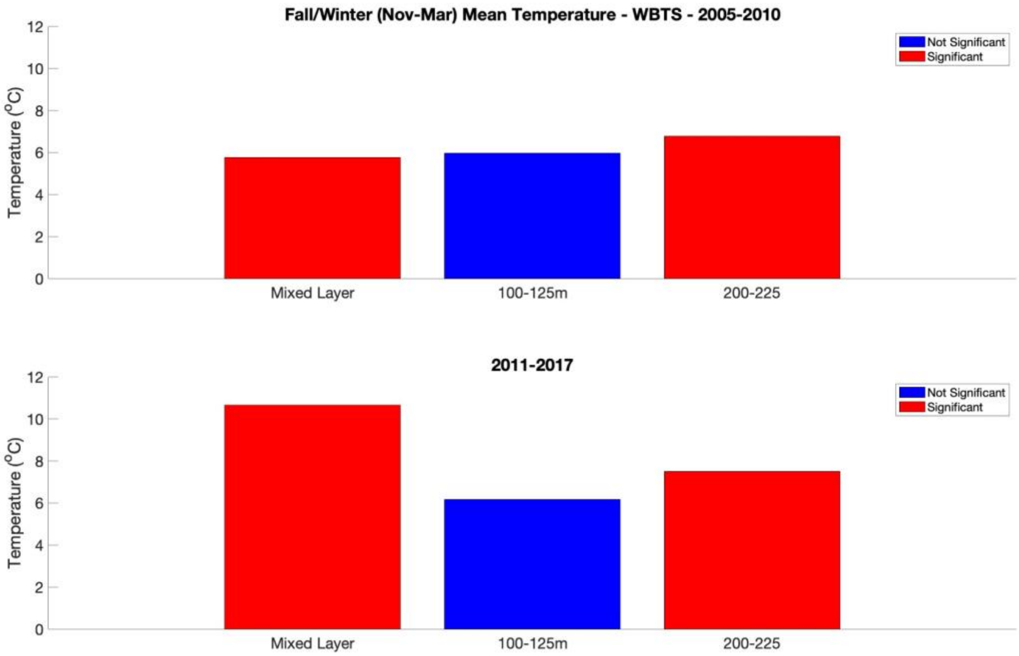

Figure 7.2. Fall/Winter (November-March) mean temperature before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% (*p<0.05*) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

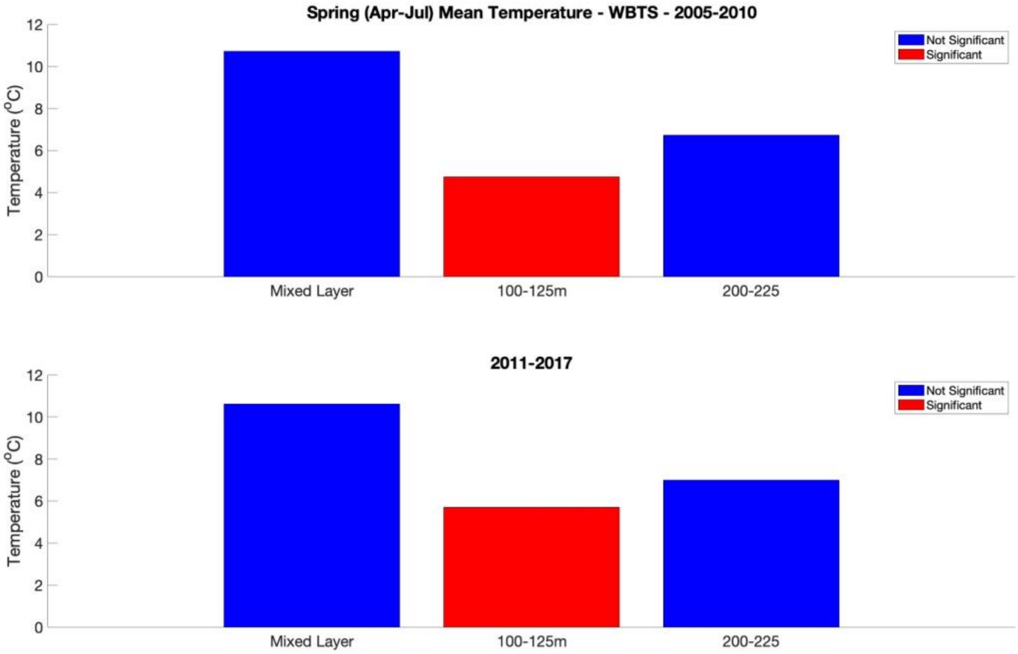

Figure 7.3. Spring (Apr-Jul) mean temperature before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

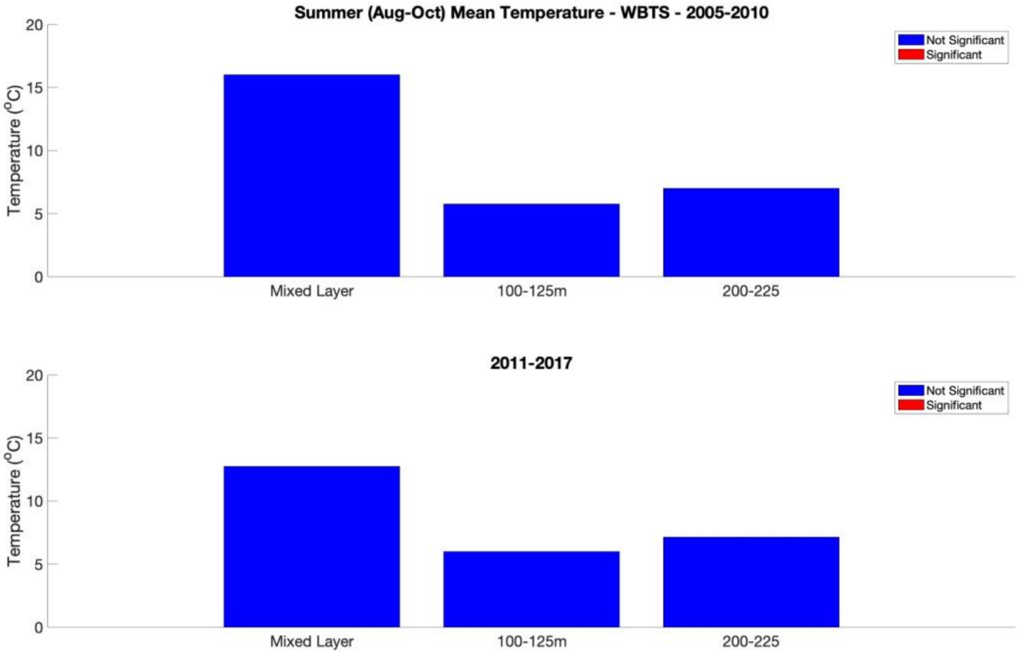

Figure 7.4. Summer (Aug-Oct) mean temperature before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the in abundance between the two time periods was statistically significant (red) or not (blue).

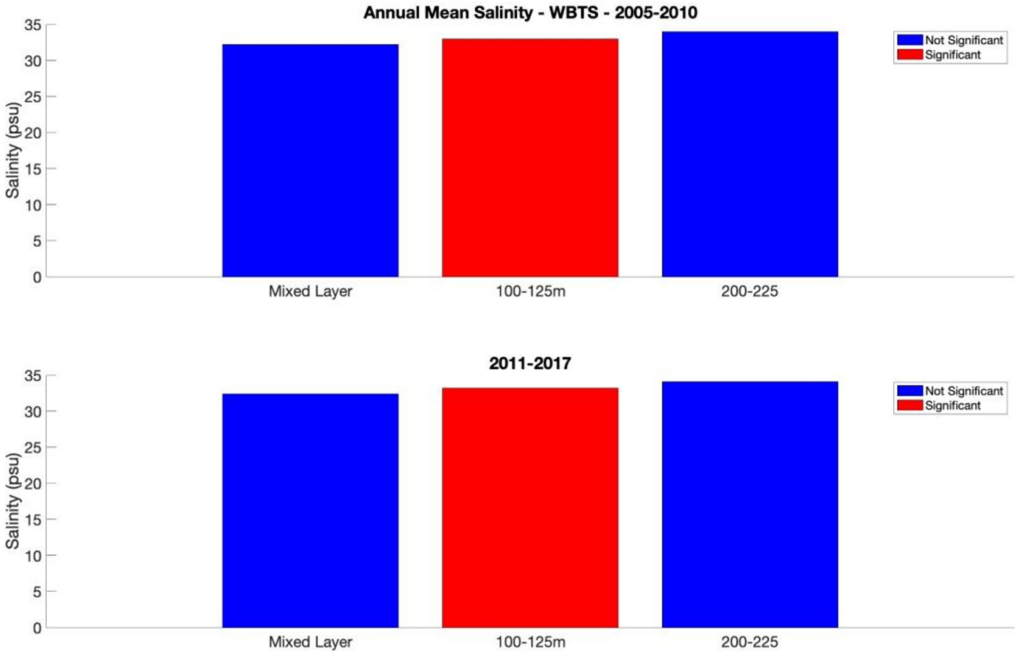

Figure 8.1. Annual mean salinity before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

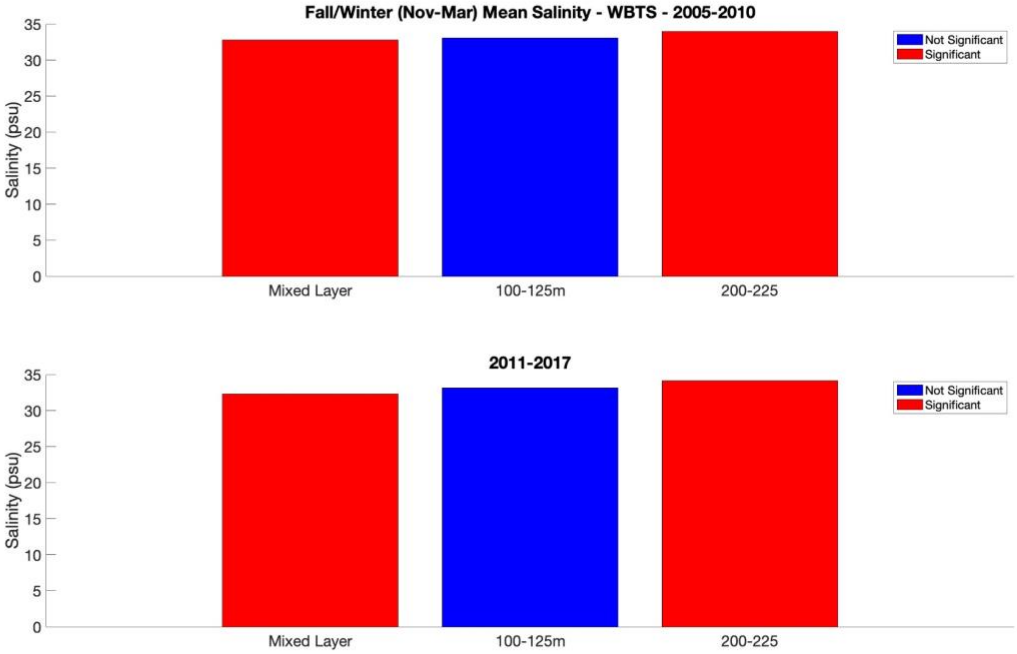

Figure 8.2. Fall/Winter (November-March) mean salinity before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

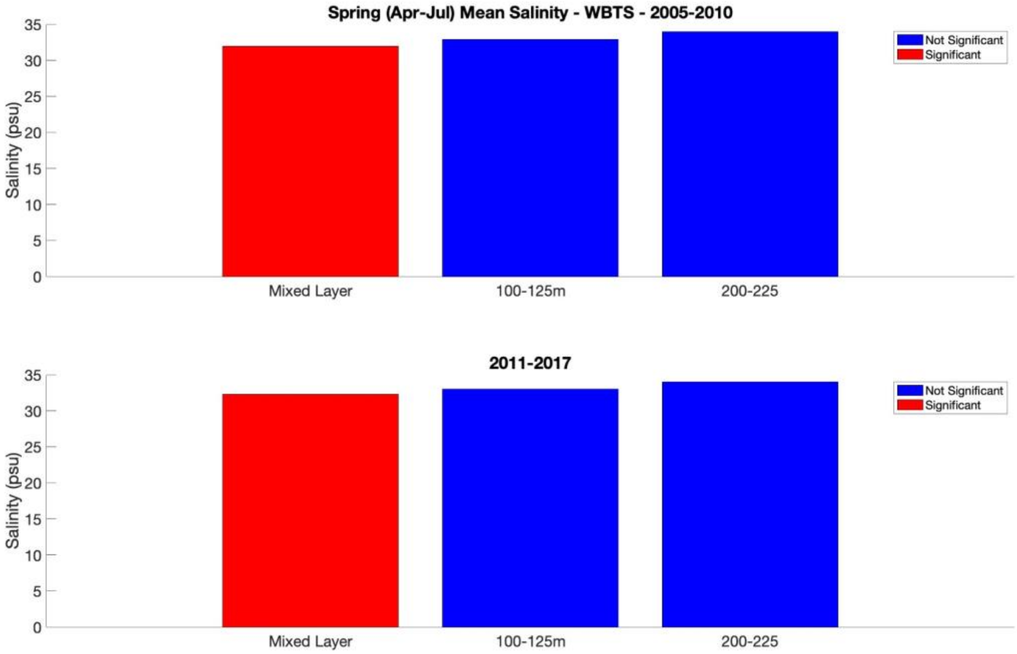

Figure 8.3. Spring (Apr-Jul) mean salinity before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

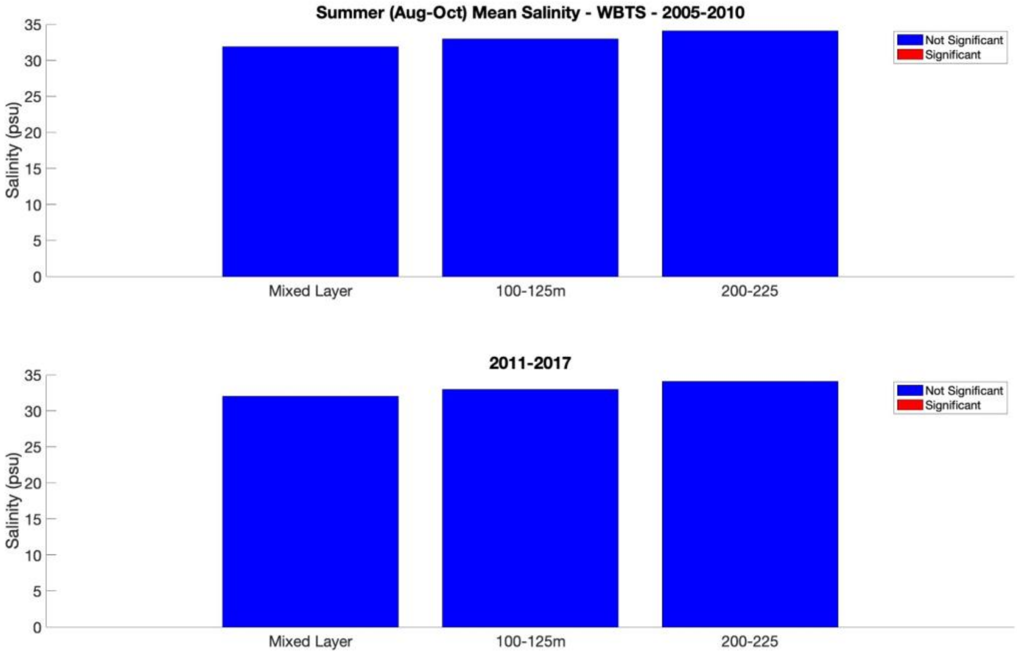

Figure 8.4. Summer (Aug-Oct) mean salinity before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

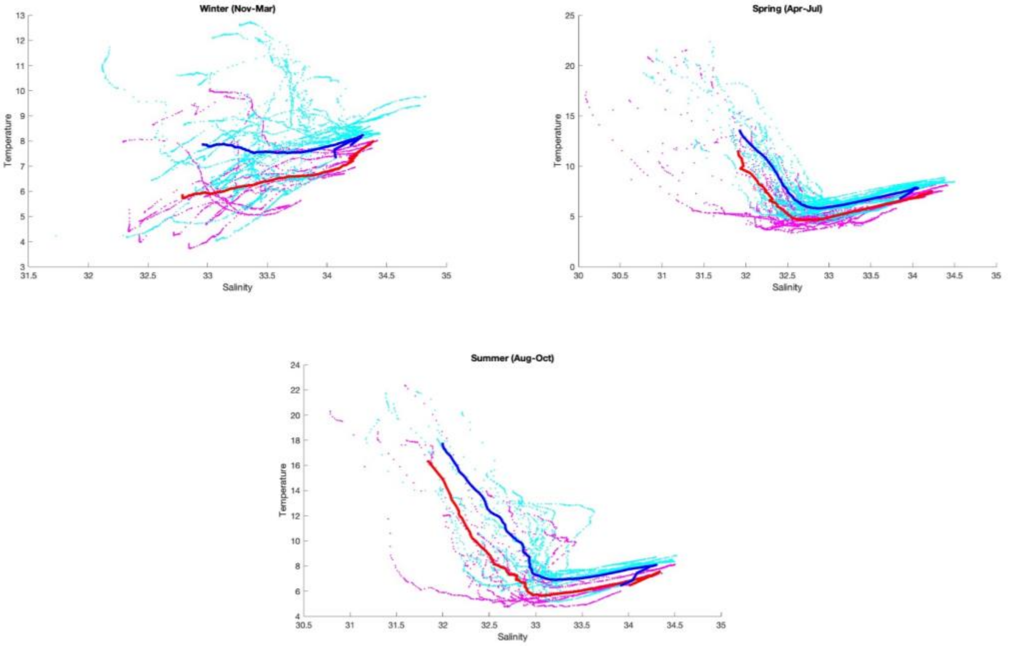

Figure 9.1. Temperature vs. Salinity at the Wilkinson Basin Time Series station (WBTS). The magenta data points are from the period before (2005-2010) the oceanographic regime shift in the Gulf of Maine (2010). The red line represents the mean for this period. The cyan data points are from the period after (2011-2017) and the blue line represents their mean.

On average the mixed layer is deepest in the fall/winter in the period before the proposed regime shift. Estimated mixed layer depth values in the fall/winter do not show a clear pattern (Fig 10.1). However, the proportion of instances where the mixed layer depth is shallower than the average for the month increases from 46.7% in 2004-2010 to 58.8% in 2011-2017 and 63.6% in 2018-2021 (Fig 10.2). Note that there are no data available for November before 2012. The seasonally averaged mixed layer depth decreased significantly between the periods pre- and post 2010 in the fall/winter from 92.1m to 31.9m ($p = 0.000$), and increased significantly in the spring from 13m to 39.2m ($p = 0.018$) and, not significantly, from 12m to 43.2m in the summer ($p = 0.068$, Fig 10.3).

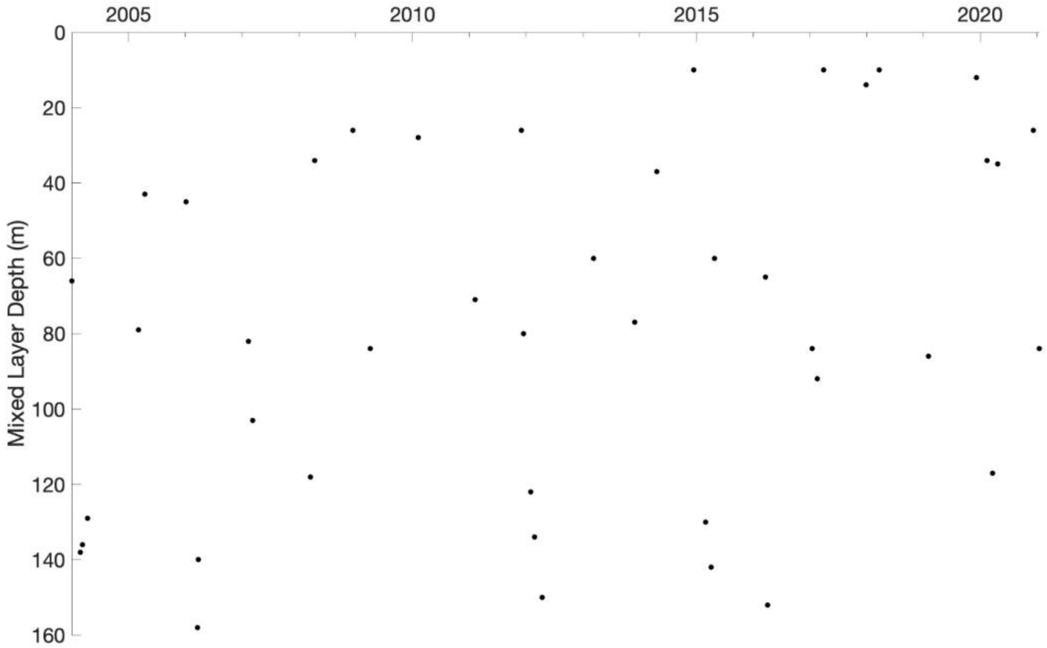

Figure 10.1. Estimated Mixed Layer depth at the Wilkinson Basin Time Series station in the fall/winter period (November-March). Mixed layer depth values represent estimates obtained using the threshold method at a density difference of 0.04kg/m^3 as compared to the density at 3m (representing the surface). This condition must be met over 5 consecutive depth measurements (1m) to account for any noise in the data.

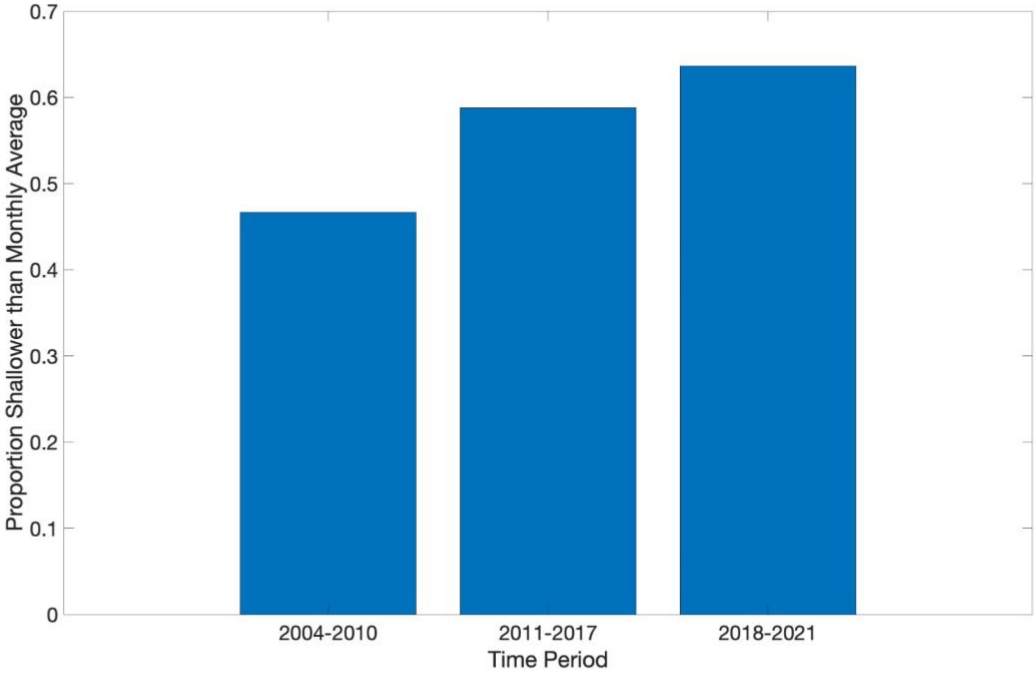

Figure 10.2. Proportion of instances where the mixed layer depth was shallower than the average in the winter months (Nov-Mar) at WBTS. Three time periods; 2004-2010 (n = 15), 2011-2017 (*n = 17*), 2018-2021 (*n = 11*).

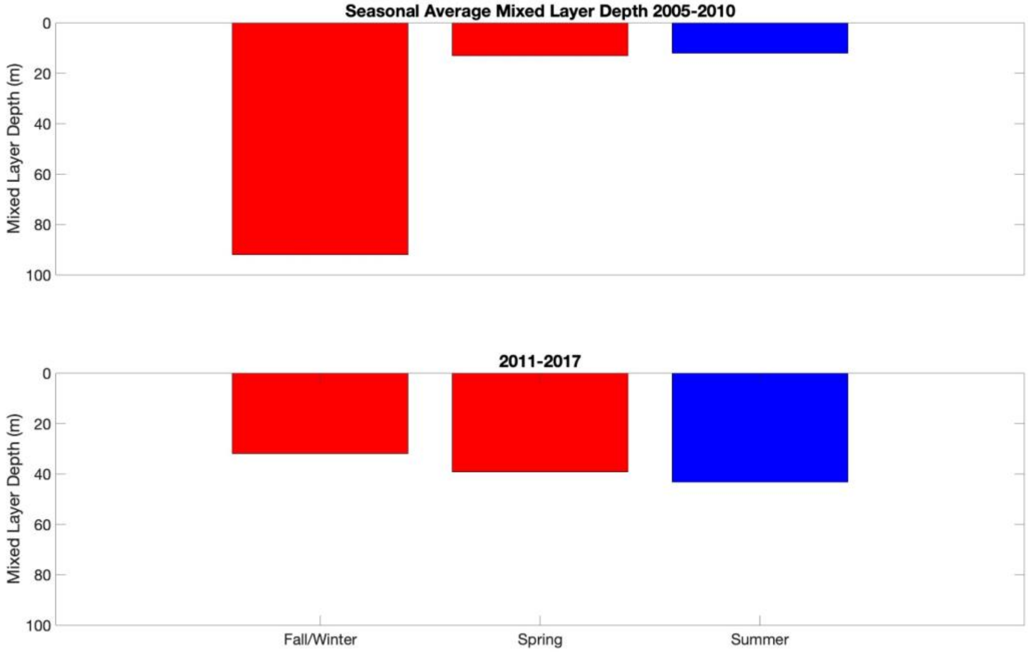

Figure 10.3. Seasonal Average Estimated Mixed Layer depth at the Wilkinson Basin Time Series station in the fall/winter period (November-March) before (2005-2010; top panel) and after (2011-2017; bottom panel) the 2010 oceanographic regime shift in the Gulf of Maine at the Wilkinson Basin Time Series station (WBTS). A two tailed t-test at a significance level of 95% ($p<0.05$) was used to determine if the change in abundance between the two time periods was statistically significant (red) or not (blue).

In general, chlorophyll-a concentration at WBTS is highest in the spring and lowest in the late fall/winter period. Before the proposed regime shift in 2010, integrated 0-50m chlorophyll-a concentration ranged from 7.8 to 40.9 mg/m^2 in the fall/winter, 18.8 to 161.6 mg/ m^2 in the spring, and 21.2 to 62.9 mg/ m^2 in the summer (Fig 11.1). In the period after 2010 concentrations were significantly higher in the winter (9.8 to 114.5 mg/ m^2; *p = 0.000*) and in the summer (33.8 to 86.3 mg/ m^2; *p = 0.000*), but not in the spring (25.4 to 214.5 mg/ m^2; *p = 0.123*) (Fig 11.1). The increasing trend in chlorophyll concentration suggests an increase in phytoplankton biomass at WBTS.

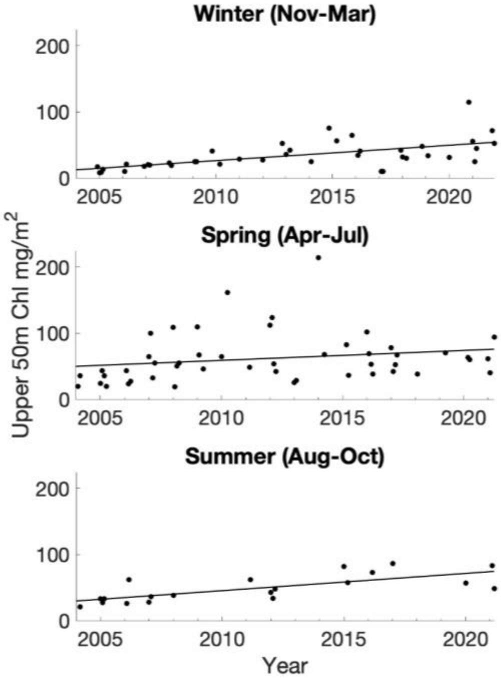

Figure 11.1. Time series of integrated chlorophyll a concentration (mg Chl a/m^2) in the upper 50m of the water column at the Wilkinson Basin Time Series station during the winter, spring and summer. Chlorophyll a standing stock significantly increased in the winter ($y = 0.007x + 11.767$, $p = 0.000$, $r^2 = 0.373$) and summer ($y = 0.007x + 28.981$, $p = 0.000$, $r^2 = 0.551$) and no significant trend in the spring ($y = 0.004x + 48.774$, $p = 0.123$, $r^2 = 0.051$). In the regression analysis x = yearday since Jan 1st, 2004.

2.4. Discussion

The objective of this study was to determine whether there were changes in the mesozooplankton community in the western GoM related to the oceanographic shift in 2010. Biomass and community structure as well as potential environmental drivers (ie. temperature and chlorophyll concentration) were investigated. Data collected at WBTS confirm a shift in the mesozooplankton total biomass and community composition after 2010. These changes vary by season and species and are consistent with seasonal drivers and life cycles of the species of zooplankton that play a role in this environment. Because sampling at CMTS started only in 2008, with few data before 2010, conclusions about changes in the mesozooplankton community in the MCC cannot be made with any confidence.

2.4.1. Hydrography

The strongest changes in the hydrographic properties of Wilkinson Basin were seen in the fall/winter period. The mixed layer became significantly warmer and fresher, whereas the deep layer (200-225m) became significantly warmer and saltier. The change in the deep layer is consistent with previous observations showing an increased influx of WSW. The explanation for a change in the mixed layer is less straightforward. The freshening could be related to an increased influx of SSW coupled with warming related to air-sea interactions. The decrease in density of the surface water is reflected in significant shallowing of the average mixed layer depth in the fall/winter post-2010. These results are consistent with those of Friedland et al.(2020) and Balch et al.(2022) who saw the most significant warming occur at the surface in the winter as well as an influx of warmer and saltier water at depth. In contrast to Balch et al.(2022), who saw significant spring cooling over a similar period, Friedland et al., 2020 observed surface warming in the spring in the GoM. In this study, there was no significant change in the temperature of the mixed layer in Wilkinson Basin, however there was a significant increase in temperature in the 100-125m layer. Balch et al, 2020, proposed the idea (originally described by Bigelow, 1927) that vernal warming can be mediated by the influx of SSW. This could potentially explain the spring pattern observed in Wilkinson Basin. In contrast to results from both studies, the average temperature and salinity at all depths in the summer did not change significantly, although the TS diagram does appear to show a warming trend. The increase we observed in phytoplankton biomass in Wilkinson Basin was not detected in the transect sampling carried out by Balch et al. (2022), who found both phytoplankton standing stock and primary productivity were declining generally in the GoM during this time period. The differences in the results between studies likely originate from the differences in sampling area. The study by Friedland at al., 2020, extends across the entire Northeast Shelf Ecosystem, and refers to the GoM in its entirety, whereas Balch et al., 2022, extends from Portland, ME to Nova Scotia, essentially excluding the wGoM. This could be an indication that the changes in the oceanographic regime differ spatially across the GoM.

2.4.2. *Calanus finmarchicus* Abundance

The *C. finmarchicus* population at WBTS is dependent on supply from the MCC in the winter and summer, local production fueled by phytoplankton in the spring, and influenced by predation mostly in the winter (Ji et al., 2021). To understand the observed changes in *C. finmarchicus*, the effect of the proposed regime shift on the seasonal drivers of its population must also be understood. A significant increase in chlorophyll concentration, indicating an increase in phytoplankton biomass at WBTS, was seen in the winter and summer, but there was no significant change in the spring. The winter increase in primary production was possibly driven by shallowing of the mixed layer during this season allowing for a longer growing period (Greene & Pershing, 2007). Increased availability of food in the fall/winter, in combination with shorter duration of diapause driven by warmer temperatures, likely contributed to stronger winter/spring reproduction of *C. finmarchicus* (e.g. Durbin et al. 2003). Greater food availability likely also drives the increase in the abundances of smaller copepods, further supported by the positive effect of increased temperature on egg production and growth rate observed in laboratory experiments (Mauchline, 1998) and natural populations (Hirst and Bunker, 2003, Bunker and Hirst, 2004). The decrease in the abundance of *C. finmarchicus* in the summer is likely due to a decrease in advective supply through the MCC (Runge et al. 2015; Record et al. 2019; Runge et al. 2023). The decline in summer abundance of *C. finmarchicus*, which between 2011-2017 was only 30% of its abundance in 2008 (Runge et al. 2023), is generally consistent with this conceptual model. Predation also affects the diapausing stock of *C. finmarchicus* in the winter (Wiebe et al., 2022). Notably, chaetognaths and cnidaria, which are important predators of *C. finmarchicus*, increased in abundance at WBTS post 2010. Due to the small aliquot taken to count other zooplankton relative to that taken for *C. finmarchicus* counts, it is likely that the more rarely occurring predators are underrepresented in the results of this study. An increase in predation pressure, primarily in the winter, may be an explanation for declining *C. finmarchicus* abundance in the winter.

2.4.3. Changes in the Mesozooplankton Community

Because *C. finmarchicus* is a keystone species in the GoM, many studies focus primarily on the effect of the 2010 regime shift on their population. However, not much was previously known about potential effects on the mesozooplankton community as a whole. In addition to assessing changes in *C. finmarchicus* abundance and how these were reflected in biomass, the abundances of other common species were assessed. Overall, there are significant increases in the abundances of smaller copepods in each season, and *Oithona similis* appears to have become dominant throughout the majority of the year (except for the spring) in terms of abundance in the period after 2010. However, *C. finmarchicus* is 5-10 times larger than other most common copepods in the Gulf of Maine (Mauchline, 1998) and it remains dominant in terms of biomass. Mesozooplankton biomass decreased significantly in the fall/winter and summer during the time period considered in this study despite increases in the abundances of small copepods, while *C.finmarchicus* abundance decreased in the summer and, although not significantly, in the fall/winter periods. There were also no significant changes in the estimated proportion of *C. finmarchicus* to the total biomass before 2017. Therefore, it can be reasonably concluded that the observed trends in zooplankton biomass were largely driven by the changes in the *C. finmarchicus* population combined with increases in abundance of the smaller copepods. In the spring, the abundance of *C. finmarchicus* increased significantly, but there was no concurrent increase in total zooplankton biomass. However, when data post-2017 is included, the spring increase in *C. finmarchicus* is not significant, which supports the idea of natural population oscillations. This increase in local production of *C. finmarchicus* is mainly in the earlier copepodite stages, which are considerably smaller than the lipid rich stage CV, and therefore do not contribute much to the biomass. While increased temperature favors higher egg production and growth rates, it also drives faster development time which results in smaller body size (Miller et al.1977; Vidal 1980).

The patterns of change observed at WBTS mostly follow those characteristic of a community shift as set forth by Pershing et al. (2005). They found that a shift in the zooplankton community in the GoM between the 1980s and 1990s, associated with a similar shift in oceanographic conditions, was best described by two ‘modes’, a small increase in *C. finmarchicus* abundance in the spring driven by increased winter production followed by a decline throughout the rest of the year and increases in the abundances of *Oithona, Centropages, Pseudocalanus,* and *Metridia* peaking at the beginning of the year and in the late spring. They also suggested that early copepodid stages of *Calanus* more closely follow the pattern of the small copepods than that of stage CV and adult *C.finmarchicus*. They characterized the patterns as a shift in abundance towards smaller copepods and suggested that it was primarily a result of changing winter conditions in primary productivity likely caused by freshening of the surface layer driving a more stratified water column.

Similar to the results of Pershing et al. (2005), the changes in the mesozooplankton community at WBTS around the proposed oceanographic regime shift in 2010 were strongest in the winter. Significant freshening and shallowing of the mixed layer in the winter was observed, and there was a concurrent increase in chlorophyll biomass. The observed increase in abundance of *C. finmarchicus* in the spring at WBTS was much greater in magnitude than observed by Pershing et al. (2005) in the central GoM. However, this study included all copepodid and adult stages, whereas Pershing et al. (2005) only considered copepodid stage CV and adults, and kept earlier copepodid stages separate. In both Pershing et al. (2005) and this study, the abundances of *Oithona, Centropages* and *Metridia* species all increased in the winter and spring. However, the abundance of *Pseudocalanus* did not change significantly in the winter and summer, and more closely followed the *C. finmarchicus* pattern with a spring increase. The increase in *Oithona similis* in this study is notably of greater magnitude relative to the other copepods compared to the shift between the 1980's and 1990's.

It is important to understand the population dynamics of GoM mesozooplankton in the context of their respective life cycles. *Oithona similis* are ubiquitous in the surface waters of the North Atlantic (Bigelow, 1924). They are generalist feeders and have low mortality rates due to their small size and low activity levels (Eiane & Ohman, 2004). They are a sac spawning species, and female fecundity and egg production rates are positively related to temperature and chlorophyll-a concentration (Ward and Hirst, 2007). Their abundance in Wilkinson basin after 2010 is highest in the spring and summer and drops off in the winter. They make up the largest proportion of total copepod abundance in the summer and winter. This is consistent with the findings in Pershing et al., 2005 and observations on the Scotian Shelf (e.g. Casault et al, 2022). *Centropages typicus* is a late fall/early winter spawner most commonly found in shelf waters (Calbet et al., 2007). Like *Oithona*, *Centropages typicus* is omnivorous and prefers motile prey such as cilliates (Calbet et al. 2007), although *Centropages* is a broadcast spawner with potentially high reproductive rates. Pseudocalanus, a sac spawner, undergoes a quiescent period, spawns in late spring/early summer, and is an herbivorous feeder (McLaren et al., 1989, Frost & Bollens, 1992). There are likely several species of *Pseudocalanus* present in the GoM which were not differentiated for the purpose of this study. The relative proportions of *Pseudocalanus* and *Centropages* are inversely related with one another in Wilkinson Basin after 2010, where *Pseudocalanus* is more abundant than *Centropages* in the spring, and *Centropages* is more abundant in the summer through the winter. This pattern is similar to that on the Scotian Shelf, however, *Centropages* is much more prominent in Wilkinson Basin (Casault et al., 2022). *Metridia lucens* is a relatively larger, broadcast-spawning copepod that undergoes diel vertical migration from the spring through fall (Batchelder & Williams, 1995). It generally has a more temperate distribution and is not usually found in waters shallower than 100m (Bigelow, 1924). Its abundance in Wilkinson Basin after 2010 peaks in the spring and is lower from the summer through the winter. In the MCC and on the Scotian Shelf the abundance of *Metridia lucens* does not peak in the spring and stays consistent throughout the year (Casault et al., 2022).

The copepod assemblage after 2010 in Wilkinson basin and in the MCC are comparable to that found on the Scotian Shelf with a few notable differences (Casault et al, 2022). As in

Wilkinson Basin, there was a decline in biomass on the Scotian Shelf driven by a decrease in the abundance of *C. finmarchicus*, and an increase in the abundance of smaller copepods, coinciding with higher temperatures (Casault et al., 2022). While *C. finmarchicus* is dominant in terms of abundance in the spring in Wilkinson Basin, it is less prominent in the MCC and on the Scotian Shelf. The higher proportion of *Pseudocalanus* relative to *Centropages typicus* in the MCC more closely resembles that on the Scotian Shelf, whereas *Centropages typicus* predominates over *Pseudocalanus* in Wilkinson Basin. In the MCC and on the Scotian Shelf, the proportional abundance of *Temora longicornus*, a coastal copepod, is much higher than in Wilkinson Basin (Casault et al., 2022). Whereas *Paracalanus parvus,* another coastal copepod, was abundant in Wilkinson Basin and on the Scotian Shelf, but not in the MCC. Peak biomass, measured as dry weight, on the Scotian Shelf reached about 6-7 g/ m^2, similar to the MCC and much lower (2-5x) than in Wilkinson Basin which, on average, ranges between 10-30 g/ m^2. Biomass in Wilkinson Basin, even after recent declining trends, is high compared to other areas in the North Atlantic and Arctic. In the Gulf of Saint Lawrence, biomass values typically range from 5-10 g/ m^2, and reach up to 20 g/ m^2 in the northwestern Gulf in the early summer (de Lafontaine, 1991). Biomass values from the Norwegian Sea are more on par with those in Wilkinson Basin, ranging from 10-20 g/ m^2 (Melle et al. 2004). Data from the Barents Sea shows a range of biomass between 5-10 g/ m^2, and has also generally experienced a decrease under warming temperatures and increases in the abundances of smaller zooplankton (Skjodal, 2023, Skjodal et al., 2022).

2.5. Conclusions

Bakun (2004) defines a regime shift as *“a persistent radical shift in the levels of abundance or productivity of multiple important components of the marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent”.* Furthermore these regime shifts are generally climate related (Bakun, 2004, Stirnimann et al., 2019). Regime shifts have not only been described in the GoM, but across marine ecosystems in general and even in lake and terrestrial ecosystems (Bakun, 2004, Stirnimann et al., 2019). In fact, Bakun (2004) describes a larger-scale regime shift in the Pacific Ocean ecosystem in the 1970’s related to the “El Niño” phenomenon that is not dissimilar in its patterns to the one currently seen in the GoM in terms of the decrease in abundance of larger zooplankton and increase in chlorophyll concentrations. A regime shift driven by extreme warming in the 1920-1930’s through the 1950-1960’s across the North Atlantic drove a northward migration of key fish species and increases in fish stocks driven by bottom-up forcing from increased phytoplankton and zooplankton abundance (Drinkwater, 2006). Most regime shifts described in the literature are related to bottom-up forcing. However, this is not always (fully) the case. Pershing et al. 2015 describe how top-down factors (trophic cascades) can drive regime shifts either partially or fully in the case of a regime shift in the Black Sea driven by the introduction of gelatinous zooplankton.

Evidence for a regime shift in the GoM, and on the Northeast (US) Continental Shelf in general, that occurred around 2010 is mounting in the literature. There has been a shift in oceanographic conditions related to the relative contributions of slope water sources driven by a much stronger than previously seen northward migration of warm water and increased atmospheric CO_2 (Seidov et al., 2021, Saba et al., 2016, Townsend et al., 2015). There have been observed shifts across multiple trophic levels. In general, many of these shifts are linked to the decreased abundance of the keystone species *C. finmarchicus* in the summer and fall/winter (Runge et al., 2023, Casault et al., 2022, Ji et al., 2021, Runge et al., 2015, Record et al. 2019). Consequently, a northward shift was observed in the distribution of the critically endangered NARW (Meyer-Gutbrod et al., 2021, Record et al., 2019). A declining abundance of *C. finmarchicus* in the GoM has also been linked to a decrease in the recruitment of the American lobster (Carloni et al., 2018) and Northern sand lance on Stellwagen Bank. Declines in lobster and sand lance and the shift in the population of the NARW have major socioeconomic and cultural impacts.

The changes that occurred in the mesozooplankton community between the periods pre- and post the proposed oceanographic regime shift in 2010 are indicative of a community shift. Decreases in the abundance of the previously dominant copepod, *Calanus finmarchicus*, drove decreases in total zooplankton biomass from the summer through winter months. This was likely driven by a decrease of *C. finmarchicus* in the source of advective supply in combination with increased predation, but neither can be confirmed within the scope of this study. Significant freshening and warming in the winter drove shallowing of the mixed layer and there was an increase in chlorophyll biomass. The observed increase in chlorophyll biomass in Wilkinson Basin in the period after the shift in 2010 was not found in the GNATS time series (Balch et al., 2021). Increased availability of chlorophyll in the fall/winter likely contributed to stronger winter/spring reproduction of *C. finmarchicus* and increases in smaller copepod abundances, further driven by the positive effect of increased temperature on egg production and growth rates. Overall, the increases in the abundances of copepod species other than *C. finmarchicus* drove an increase in species evenness in the winter and summer. However, species richness stayed relatively the same and there were no introductions of new species. The changes that occurred in Wilkinson Basin were comparable, but of higher magnitude, to those reported from a decadal shift between the 1980’s and 1990’s, and more recent changes on the Scotian Shelf with a few notable local differences. Overall, biomass and mesozooplankton abundance in Wilkinson Basin remained high compared to other places in the North Atlantic.

The changes observed in the mesozooplankton biomass and community structure support the idea that a regime shift has occurred in the GoM around the year 2010. The changes in the mesozooplankton community seem to be climate related and primarily driven by bottom-up forcing similar to many of the regime shifts described in the literature. However, there is some evidence for potential top-down forcing if, in fact, predation has increased in the winter months. Studies from the Scotian Shelf suggest that the shift has occurred more broadly over the Northeast (US) Atlantic continental shelf (Casault et al., 2022). The magnitude of the warming, and the disconnect of the current regime to the NAO raises the question of whether the results of these changes might persist into the future.

BIBLIOGRAPHY

Balch, W. M., Drapeau, D. T., Bowler, B. C., Record, N. R., Bates, N. R., Pinkham, S., ... & Mitchell, C. (2022). Changing hydrographic, biogeochemical, and acidification properties in the Gulf of Maine as measured by the Gulf of Maine North Atlantic Time Series, GNATS, between 1998 and 2018. *Journal of Geophysical Research: Biogeosciences*, *127*(6), e2022JG006790.

Batchelder, H. P., & Williams, R. (1995). Individual-based modelling of the population dynamics of Metridia lucens in the North Atlantic. *ICES Journal of Marine Science*, *52*(3-4), 469-482.

Bakun, A. (2004). Regime shifts. In: Robinson, A.R., Brink, K. (Eds.), The Sea, Vol. 13. Harvard University Press, Cambridge,Massachusetts, pp. 971–1018 (Chapter 25).

Becker, J. R., Cieri, M. D., Libby, D. A., St. Gelais, A., Sherwood, G., & Chen, Y. (2020). Temporal variability in size and growth of Atlantic herring in the Gulf of Maine. *Journal of Fish Biology*, *97*(4), 953-963.

Bigelow, H. B. (1924). *Plankton of the offshore waters of the Gulf of Maine* (No. 968). US Government Printing Office.

Bunker, A. J., & Hirst, A. G. (2004). Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. *Marine Ecology Progress Series*, *279*, 161-181.

Cai, Cassia, et al. "Mixed layer depth climatology over the northeast US continental shelf (1993–2018)." *Continental Shelf Research* 231 (2021): 104611.

Campbell, R.G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A. and Durbin, E.G., 2001. Growth and development rates of the copepod Calanus finmarchicus reared in the laboratory. Marine Ecology Progress Series, 221, pp.161-183.

Calbet, A., Carlotti, F., & Gaudy, R. (2007). The feeding ecology of the copepod Centropages typicus (Kröyer). *Progress in Oceanography*, *72*(2-3), 137-150.

Davies, K. T., Taggart, C. T., & Smedbol, R. K. (2014). Water mass structure defines the diapausing copepod distribution in a right whale habitat on the Scotian Shelf. *Marine Ecology Progress Series*, *497*, 69-85.

Durbin, E., & Kane, J. (2007). Seasonal and spatial dynamics of Centropages typicus and C. hamatus in the western North Atlantic. *Progress in Oceanography*, *72*(2-3), 249-258.

Drinkwater, K. F. (2006). The regime shift of the 1920s and 1930s in the North Atlantic. *Progress in Oceanography*, *68*(2-4), 134-151.

Eiane, K., & Ohman, M. D. (2004). Stage-specific mortality of Calanus finmarchicus, Pseudocalanus elongatus and Oithona similis on Fladen Ground, North Sea, during a spring bloom. *Marine Ecology Progress Series*, *268*, 183-193.

Fields, D. M., Runge, J. A., Thompson, C. R., Durif, C. M., Shema, S. D., Bjelland, R. M., ... & Browman, H. I. (2022). A positive temperature-dependent effect of elevated CO2 on growth and lipid accumulation in the planktonic copepod, Calanus finmarchicus. *Limnology and Oceanography*.

Frost, B. W., & Bollens, S. M. (1992). Variability of diel vertical migration in the marine planktonic copepod Pseudocalanus newmani in relation to its predators. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(6), 1137-1141.

Greene, C. H., & Pershing, A. J. (2007). Climate drives sea change. *Science*, *315*(5815), 1084-1085.

Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnology and Oceanography*, *48*(5), 1988-2010.

Ji, R., Edwards, M., Mackas, D. L., Runge, J. A., & Thomas, A. C. (2010). Marine plankton phenology and life history in a changing climate: current research and future directions. *Journal of plankton research*, *32*(10), 1355-1368.

Ji, R., Feng, Z., Jones, B. T., Thompson, C., Chen, C., Record, N. R., & Runge, J. A. (2017). Coastal amplification of supply and transport (CAST): a new hypothesis about the persistence of Calanus finmarchicus in the Gulf of Maine. *ICES Journal of Marine Science*, *74*(7), 1865-1874.

Ji, R., Runge, J. A., Davis, C. S., & Wiebe, P. H. (2021). Drivers of variability of Calanus finmarchicus in the Gulf of Maine: roles of internal production and external exchange. *ICES Journal of Marine Science*, *79*(3), 775-784.

de Lafontaine, Y. (1991). Pelagic food web interactions and productivity in the Gulf of St Lawrence: a perspective. *The Gulf of St Lawrence: small ocean or big estuary?*.

Mauchline, J. (1998). *Adv. Mar. Biol. 33: The biology of calanoid copepods*.

McLaren, I. A., Laberge, E., Corkett, C. J., & Sevigny, J. M. (1989). Life cycles of four species of Pseudocalanus in Nova Scotia. *Canadian Journal of Zoology*, *67*(3), 552-558.

Melle,W., Ellertsen, B., and Skjoldal,H. R. 2004. Zooplankton: the link to higher trophic levels. *In* The Norwegian Sea Ecosystem, pp. 137–202. Ed. by H. R. Skjoldal, R. Sætre, A. Færnø, O. A. Misund, and I. Røttingen. Tapir Academic Press, Trondheim.

Melle, W., Runge, J., Head, E., Plourde, S., Castellani, C., Licandro, P., ... & Chust, G. (2014). The North Atlantic Ocean as habitat for Calanus finmarchicus: Environmental factors and life history traits. *Progress in Oceanography*, *129*, 244-284.

Meyer-Gutbrod, E. L., Greene, C. H., Davies, K. T., & Johns, D. G. (2021). Ocean regime shift is driving collapse of the North Atlantic right whale population. *Oceanography*, *34*(3), 22-31.

National Marine Fisheries Service (2022). Fisheries of the United States, 2020. U.S. Department of Commerce, NOAA Current Fishery Statistics No. 2020. Available at: https://www.fisheries.noaa.gov/ national/sustainable-fisheries/fisheries-united-states

Overholtz, W. J. and Link, J. S. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (Clupea harengus) complex during the years 1977–2002. ICES Journal of Marine Science, 64: 83–96.

Pershing, A. J., Greene, C. H., Jossi, J. W., O'Brien, L., Brodziak, J. K., & Bailey, B. A. (2005). Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. *ICES Journal of Marine Science*, *62*(7), 1511-1523.

Pershing, A. J., Mills, K. E., Record, N. R., Stamieszkin, K., Wurtzell, K. V., Byron, C. J., ... & Koob, E. (2015). Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130265.

Pettigrew, N. R., Townsend, D. W., Xue, H., Wallinga, J. P., Brickley, P. J., & Hetland, R. D. (1998). Observations of the Eastern Maine Coastal Current and its offshore extensions in 1994. *Journal of Geophysical Research: Oceans*, *103*(C13), 30623-30639.

Preziosi, B. M., & Runge, J. A. (2014). The effect of warm temperatures on hatching success of the marine planktonic copepod, Calanus finmarchicus. *Journal of plankton research*, *36*(5), 1381-1384.

Record, N. R., Runge, J. A., Pendleton, D. E., Balch, W. M., Davies, K. T., Pershing, A. J., ... & Thompson, C. R. (2019). Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. *Oceanography*, *32*(2), 162-169.

Richards, R. A., & Hunter, M. (2021). Northern shrimp Pandalus borealis population collapse linked to climate-driven shifts in predator distribution. *Plos one*, *16*(7), e0253914.

Runge, J., Coté Jr, M., Thompson, B., Morrison, J. R., Anderson, D., Cetinić, I., ... & Morse13, R. Y. (2012) Integrated Sentinel Monitoring for the Northeast Region: Gap Assessment.

Runge, J. A., Ji, R., Thompson, C. R. S., Record, N. R., Chen, C., Vandemark, D. C., … Maps, F.(2015). Persistence of *Calanus finmarchicus* in the western Gulf of Maine during recent extreme warming. *Journal of Plankton Research*, **37**(1), 221–232.

Runge J, Karp Boss L, Dullaert E, Ji, R, Motyka J, Young-Morse R, Pugh, D, Shellito S, Vandemark D. 2023. Sustained monitoring of zooplankton populations at the Coastal Maine Time Series (CMTS) and Wilkinson Basin Time Series (WBTS) stations in the western Gulf of Maine: Results from 2005-2022. Sterling (VA): U.S. Department of the Interior, Bureau of Ocean Energy Management. 40 p. Report No.: OCS Study BOEM 2023-015. Contract No.: CA M19AC00022.

Saba, V. S., Griffies, S. M., Anderson, W. G., Winton, M., Alexander, M. A., Delworth, T. L., ... & Zhang, R. (2016). Enhanced warming of the N orthwest A tlantic O cean under climate change. *Journal of Geophysical Research: Oceans*, *121*(1), 118-132.

Salisbury, J. E., & Jönsson, B. F. (2018). Rapid warming and salinity changes in the Gulf of Maine alter surface ocean carbonate parameters and hide ocean acidification. *Biogeochemistry*, *141*, 401-418.

Seidov, D., Mishonov, A., & Parsons, R. (2021). Recent warming and decadal variability of Gulf of Maine and Slope Water. *Limnology and Oceanography*, *66*(9), 3472-3488.

Skjoldal, H. R., Eriksen, E., & Gjøsæter, H. (2022). Size-fractioned zooplankton biomass in the Barents Sea: Spatial patterns and temporal variations during three decades of warming and strong fluctuations of the capelin stock (1989–2020). *Progress in Oceanography*, *206*, 102852.

Skjoldal, H. R. (2023). Size-fractioned zooplankton biomass in the Barents Sea ecosystem: changes during four decades of warming and four capelin collapses (1980–2020). *ICES Journal of Marine Science*, fsad057.
Staudinger, M. D., Goyert, H., Suca, J. J., Coleman, K., Welch, L., Llopiz, J. K., ... & Steinmetz, H. (2020). The role of sand lances (Ammodytes sp.) in the Northwest Atlantic Ecosystem: A synthesis of current knowledge with implications for conservation and management. *Fish and Fisheries*, *21*(3), 522-556.

Stirnimann, L., Conversi, A., & Marini, S. (2019). Detection of regime shifts in the environment: Testing “STARS” using synthetic and observed time series. *ICES Journal of Marine Science*, *76*(7), 2286-2296.

Suca, J. J., Ji, R., Baumann, H., Pham, K., Silva, T. L., Wiley, D. N., ... & Llopiz, J. K. (2022). Larval transport pathways from three prominent sand lance habitats in the Gulf of Maine. *Fisheries Oceanography*, *31*(3), 333-352.

Thibodeau, B., Not, C., Zhu, J., Schmittner, A., Noone, D., Tabor, C., ... & Liu, Z. (2018). Last century warming over the Canadian Atlantic shelves linked to weak Atlantic meridional overturning circulation. *Geophysical Research Letters*, *45*(22), 12-376.

Townsend, D. W., Thomas, A. C., Mayer, L. M., Thomas, M. A., & Quinlan, J. A. (2004). Oceanography of the northwest Atlantic continental shelf (1, W). *The sea: the global coastal ocean: interdisciplinary regional studies and syntheses*, *14*, 119-168.

Townsend, D. W., Rebuck, N. D., Thomas, M. A., Karp-Boss, L., & Gettings, R. M. (2010). A changing nutrient regime in the Gulf of Maine. *Continental Shelf Research*, *30*(7), 820-832.

Townsend, D. W., Pettigrew, N. R., Thomas, M. A., Neary, M. G., McGillicuddy, D. J., & O'Donnell, J. (2015). Water masses and nutrient sources to the Gulf of Maine. *Journal of marine research*, *73*(3-4), 93-122.

Ward, P., & Hirst, A. G. (2007). Oithona similis in a high latitude ecosystem: abundance, distribution and temperature limitation of fecundity rates in a sac spawning copepod. *Marine Biology*, *151*, 1099-1110.

Wiebe, P. H., Baumgartner, M. F., Copley, N. J., Lawson, G. L., Davis, C., Ji, R., & Greene, C. H. (2022). Does predation control the diapausing stock of Calanus finmarchicus in the Gulf of Maine?. *Progress in Oceanography*, *206*, 102861.

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Emma Cecile Dullaert was born in Zwolle, Netherlands on July 14, 1999. She moved to South Burlington, Vermont in 2015 and graduated from South Burlington High School in 2017. She attended the University of Maine and graduated with Bachelor of Science degree in Marine Science in 2021. Upon graduating, she immediately transitioned into a graduate program within the School of Marine Sciences, continuing work on the project that she started as an undergraduate capstone experience. During her time as a graduate student, Emma served as the residential life director for the semester by the sea program at the Darling Marine Center in the fall of 2021 and a teaching assistant for a Field Methods in Oceanography in the fall of 2022. After receiving her degree, Emma will be joining the Boothbay Sea and Science Center as a science instructor to pursue her passions in marine science education. Emma is a candidate for the Master of Science degree in Oceanography from the University of Maine in August, 2023.