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Surface Conditions Drive Changes In Groundfish Species' Populations Along California Coast

Danielle Marie Fabian
California State University, Monterey Bay, dfabian@csumb.edu

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SURFACE CONDITIONS DRIVE CHANGES IN GROUNDFISH SPECIES'

POPULATIONS ALONG CALIFORNIA COAST

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A Thesis

Presented to the

Faculty of the

School of Natural Sciences

California State University Monterey Bay

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Environmental Science

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by

Danielle Marie Fabian

Term Completed: Spring 2020

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

The Undersigned Faculty Committee Approves the

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POPULATIONS ALONG CALIFORNIA COAST
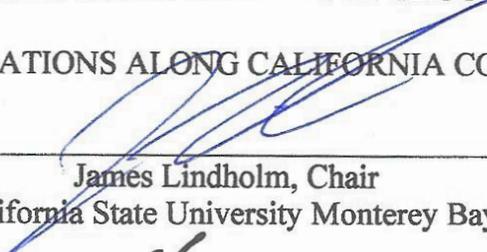
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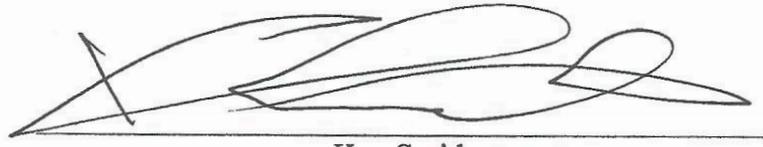
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Monterey Bay Aquarium Research Institute, Moss Landing, California
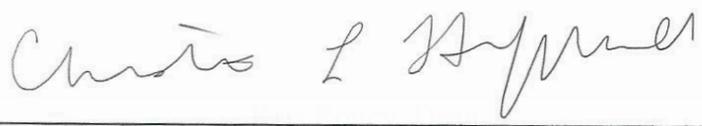
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Christine Huffard
Monterey Bay Aquarium Research Institute, Moss Landing, California

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Kris Roney, Dean
Associate VP for Academic Programs and Dean of Undergraduate and Graduate Studies

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11 May 2020
Approval Date

DEDICATION

To my family. You guys have been my biggest fans and have supported me tirelessly and selflessly throughout this chapter in my life. I could not have done it without you.

To my friends – you know who you are . Thank you for motivating me to keep going when I was tired through pep talks and words of wisdom, and for lifting my spirits in times of need.

To Jacob Stivers. Thank you for being there for me during the home stretch.   You are my rock.

I am forever grateful for all of you.

The fact that a cloud from a minor volcanic eruption in Iceland—a small disturbance in the complex mechanism of life on the Earth—can bring to a standstill the aerial traffic over an entire continent is a reminder of how, with all its power to transform nature, humankind remains just another species on the planet Earth.

Slavoj Žižek

ABSTRACT

Surface Conditions Drive Changes In Groundfish Species'
Populations Along California Coast
by
Danielle Marie Fabian
Master of Science in Environmental Science
California State University Monterey Bay, 2020

Oceans display physical variability over a range of temporal and spatial scales, influencing factors such as larval dispersal, nutrient availability, species migration, and biodiversity. Such variability is vulnerable to the effects of climate change. Larvae and juveniles are particularly susceptible to changes in ocean variability, and changes in the early life stages of species populations ultimately impacts the adult stages. Physical consequences stemming from climate driven variability, including a loss of key prey species and changes in depth distributions of vulnerable fish species, could ultimately impact ecosystem services and threaten human food security and fisheries. The deep sea benthopelagic groundfish play significant roles in biogeochemical and ecological processes on a global scale. Macrourids, the most common benthopelagic fish in the deep sea, are important benthic and midwater predators; making it critical to understand changes in their population structures over time. Macrourid larvae reside in surface waters, where they are more vulnerable to climate driven variability. Merluccius productus (M. productus) is a commercially important benthopelagic groundfish species with a life history similar to Macrourids. The combination of surface waters exhibiting more changes in physical variability compared to the deep sea and the vulnerability of larvae to oceanographic variability makes observing these benthopelagic species particularly important for understanding the full-depth interactions and climate-related changes. This project focuses on studying correlations between changes in the life stages of Macrourid species' and M. productus' populations over time in relation to changes in climate and surface ocean conditions. Four research questions are addressed; Q1 & Q2) Has groundfish (specifically Macrourid spp. (Q1) and M. productus (Q2)) population structure changed over time in relation to changing climate and surface-ocean conditions?; and Q3 & Q4) Has the depth range of groundfish species (specifically Macrourid spp. (Q3) and M. productus (Q4)) changed over time with changing climate and surface-ocean conditions? With increasing changes in climate and surface-ocean conditions over time, there is a significant change in both Macrourid species' population structure and M. productus population structure over time (Q1 and Q2). With increasing changes in climate and surface-ocean conditions over time, there is no significant change in M. productus' depth distribution over time (Q4). Regarding potential changes in Macrourid species' depth distributions, Q3 couldn't be answered due to insufficient data. This study increases our understanding of how potential impacts of changing climate and surface-ocean conditions on M. productus' population structure and depth distribution could affect Macrourid populations. Findings also provide valuable insight for: 1) predicting and managing consequences of climate change and 2) management of coastal and marine resources and fisheries in the future.

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CHAPTER 1

INTRODUCTION

CLIMATE CHANGE EFFECTS ON ENVIRONMENTAL VARIABILITY & FISHERIES

Deep sea groundfish along continental margins play vital roles within their ecosystems (Hamilton et al. 2004), including major biogeochemical cycles (Ragueneau et al. 2000; Street-Perrott et al. 2008), acting as an important process contributing to marine primary production and carbon export to the deep sea (Tréguer and De La Rocha 2013; Schneider et al. 2008). The eastern division of the North Pacific is highly biodiverse, containing a combination of subarctic, temperate, and subtropical groundfish species (Therriault et al., 2016). An east to west diversity gradient is present there, with higher diversity and the majority of fish biomass occurring within coastal nearshore areas and the continental shelf, compared to the less diverse oceanic realm (Mueter and Norcross, 2002). Due to the great depths that deep sea groundfish reside in, the data needed to understand and monitor these species is lacking (Therriault et al., 2016). Grenadiers, of the family Macrouridae (Neat and Burns 2010), are the most common benthopelagic groundfish in the deep sea (Jeffreys et al. 2010; Matsui et al. 1991). For the sake of consistency, "grenadiers" will be referred to as Macrourids for the entirety of this paper. Macrourids are important benthic and midwater predators (Morley & Belchier, 2002) and some species are targeted by fisheries. Many Macrourids, including four of the five focal species of this research project, are benthopelagic (Hiroaki et al. 2002). The adult stages reside in the deep sea, inhabiting the water just above the seafloor, while the larvae are planktonic and reside in the upper water column (Allen et al. 2006). The pelagic larvae is ultimately the link between the surface water and their adult habitat – the seafloor (e.g. Stein & Pearcy, 1982). The extent to which Macrourid, and other deep sea benthopelagic groundfish, populations are coupled to surface conditions, and the role that different marine species interactions play within this coupling are examples of important unresolved questions in the field of marine ecology that need to be addressed regarding these species.

Oceans display physical variability over a range of temporal and spatial scales (Brierley and Kingsford 2009; Fraschetti et al. 2005; Powell et al. 2006), influencing factors such as larval dispersal (Botsford et al. 1994), physiology (Hinrichsen 2009), nutrient availability (Kamykowski et al. 2002), species migration (Wegner et al. 2003), production, and biodiversity (Lindegren et al. 2016). In California waters, groundfish species' populations experience different degrees of physical variability interannually, depending on the depth range and relative spatial location of groundfish species' populations residing in the California Current Ecosystem (CCE) (Bograd et al., 2019). The combination of three different source waters and various currents within the California Current Ecosystem allows for great spatial diversity in physical and biological processes (Strub *et al.*, 1990; Mendelssohn *et al.*, 2003). Species residing in regions further north and closer to the coast experience more extreme temperature variation due to the cooling of waters, both at the surface and at depth, from the intrusion of Subarctic water and upwelling in the spring and summer (Mendelssohn *et al.*, 2003; King et al., 2011). By contrast, annual thermocline variability in the southern and offshore regions is very low, partially due to subtropical water dominating these regions and stratification reduction in the seasonal mixed layer during the summer and autumn months (King et al., 2011).

Similarly, surface waters exhibit more changes in physical variability compared to the deep sea (McLeod et al. 2009; Davies et al. 2007). Shallower living groundfish species, such as *Merluccius productus* (*M. productus*) may experience more extreme physical variability compared to groundfish living deeper in the water column, such as *Coryphaenoides armatus* (*C. armatus*); and therefore, may are more directly affected by such variability (Peterson et al., 2006; Bailey et al., 1982). However, changes in the surface waters ultimately affect deep sea ecosystems, impacting deep sea species either directly or indirectly (Kuhnz et al., 2014; Moore et al., 2013). For instance, extended periods of high-nutrient conditions caused by upwelling result in high productivity in surface waters (Pickett & Paduan, 2003; Bograd et al., 2019), which eventually leads to increased food supply reaching the deep sea in the form of particulate organic carbon (Buesseler et al., 2008; Steinberg et al., 2012). Additionally, *M. productus* carrion has been found to be the largest food source for various groundfish species, including Macrourids (Drazen et al., 2009; Dufault et al., 2009), making up 61% of

pelagic biomass in the California Current ecosystem (CCE) (Agostini et al., 2006; Drazen et al., 2012). Although physical variability in the surface waters may not directly affect deep sea Macrourids, these species are dependent on the carrion of *M. productus'* populations, which are more sensitive to such variability (Agostini, 2005). For instance, the location of spawning can shift slightly with temperature (Agostini, 2005). Direct physical variability effects on *M. productus* populations could in turn indirectly affect Macrourids and other deep sea groundfish species . The extent to which physical variability affects deep sea benthopelagic species, both directly and indirectly, are two important and unresolved questions that need to be addressed in the field of marine ecology.

Physical ocean variability among and within all marine ecosystems is vulnerable to the effects of climate change (Brierley and Kingsford 2009; Doney et al. 2012), primarily due to temperature increases (Rosenzweig et al., 2008). Since the mid-1800s, there has been a tremendous increase in carbon dioxide (CO_2) in the atmosphere due to the combustion of fossil fuels on a global scale (Karnosky 2003; Patz et al. 2014). This rise in C02 aggravates the greenhouse gas effect (Peters 1985; Recent Global Warming 2002), making the planet warmer than it otherwise would be (Recent Global Warming 2002; Mitchell 1989; Schneider 1989). Additional effects of climate change include: rising sea levels, rising global mean sea-surface temperatures (SST), increased ocean acidity, perturbed regional weather patterns, altered ocean circulation, changes in the extent of oxygen-deficient dead-zones, and changed nutrient loads (Brierley and Kingsford 2009; Doney et al. 2011). Marine biological processes are affected by such physical consequences, which could ultimately impact ecosystem services and threaten human food security (Brander 2007; Pecl et al. 2017). For example, significant changes in physical ocean variability caused by ocean warming (Rosenzweig et al., 2008) can affect the conditions of larvae and juveniles (Pansch et al. 2012), as well as the timing of reproduction and reproductive output (Velaquez 2003; Pankhurst and Munday 2011; Petrik et al. 2015).

Larvae and juveniles are particularly susceptible to changes in ocean variability (Pansch et al. 2012; Heath 1992), and changes in the early life stages of species populations ultimately impacts the adult stages (Pankhurst and Munday 2011; Heath 1992). Juveniles and

larvae may not be able to survive the changes in salinity, temperature, and pH that are tolerated by adult stages (Rijnsdorp et al. 2009; Byrne and Przeslawski 2013). Similarly, if the hatching time of larval eggs does not coincide with food availability, survival rates may be affected (Brierley and Kingsford 2009; Fiksen and Jorgensen 2011). Changes in food availability could stem from temperature-driven phenological changes that could alter the timing of plankton blooms (Berner et al. 2018); ultimately leading to a loss of food supply for prey species, and potentially causing shifts in prey species distributions (Brierley and Kingsford 2009). The loss of key prey species could negatively impact remaining predators that not only play an important role within their ecosystems, but that are also deemed important in commercial fisheries (Young et al. 2015; Ripple et al. 2014). The combination of surface waters exhibiting more changes in physical variability compared to the deep sea (McLeod et al. 2009; Davies et al. 2007) and the vulnerability of larvae to oceanographic variability change (biological and physical) (Pansch et al. 2012; Heath 1992) makes observing deep sea benthopelagic species particularly important for understanding the interactions and feedbacks between marine systems and climate-related changes. Changes in surface water conditions probably affect larval stages of these species. Although adult fishes living in the deep sea may experience fewer negative effects caused by changing climate and surface conditions than their pelagic larvae and juveniles, effects on the early life stages will ultimately affect the adult populations and the fisheries dependent upon them (Johnson et al. 2011). In addition, direct impacts of increasing changes in climate and surface-ocean conditions on the more sensitive shallower species may potentially affect deep sea benthopelagic species indirectly.

Another concern is that extremely vulnerable fish species have exhibited changes in depth distribution relating to changing water conditions (Nye et al. 2009; Cheung et al. 2010). Fishing effort is venturing to deeper depths with increasing depletion of economically important species in shallower water (Norse et al. 2012; Yoklavich et al. 2000), and changes in depth distributions can potentially impact the risk of individuals being caught as bycatch (Gilly et al. 2013; Roberts 2002). In addition, Macrourids generally have slow recovery rates from fishing mortality (Norse et al., 2012), due to high longevity and slow growth rates (Clark, 2001), and Macrourid species that are commercially exploited may be overfished

(Shotton 2005). The combination of slow recovery rates and overfishing could potentially result in a fishery collapse within a short time period (Large et al. 2003; Shotton 2005). A good example for showing the importance of monitoring Macrourid species' populations can be seen in reference to the commercially targeted species, *Coryphaenoides acrolepis* (*C. acrolepis*), and the non-target species, *Coryphaenoides armatus* (*C. armatus*). These two species overlap on the slope. *Coryphaenoides armatus*, although of little interest to fisheries, is often caught as bycatch and is difficult to differentiate from *C. acrolepis* (Iwamoto et al. 2015). Both *C. acrolepis* and *C. armatus* are known to have pelagic larvae (e.g. Stein & Pearcy, 1982). It is important to assess if there is any change in *C. acrolepis* and *C. armatus* pelagic larval density and benthopelagic adult fishes with the change in climate and surface conditions in order to provide insight necessary to manage fisheries in the future. Accidental misclassification could result in fishermen wrongly assuming that the target species', *C. acrolepis*, population is thriving. In reality, it might be declining at a rapid rate. This could result in overexploitation and collapse of fisheries, which in turn, could negatively affect local communities as a whole. Misidentification could also lead to overexploitation of the non-target species, potentially disrupting deep-sea ecosystems (Gjerde 2006). For instance, declining groundfish populations, resulting from anthropogenic climate change and overfishing, could potentially create shifts in marine phytoplankton communities (Pershing et al. 2015; Katz et al. 2009).

Given the extent to which deep sea benthopelagic groundfish are coupled to surface conditions and the vulnerability of their early life stages to changes in physical variability, the goal of this thesis is to better understand, how increasing changes in climate and surface-ocean conditions over time are affecting deep sea benthopelagic groundfish species off the coast of California. To achieve this, this study monitors changes occurring in larval and adult life stages of environmentally and economically important benthopelagic fish species with changes in climate and surface-ocean conditions. Findings from this study have the potential to provide valuable insight for the global climate change discussion in that it sheds light on both the direct effects and potential indirect effects of changing climate and surface conditions on economically and ecologically important benthopelagic groundfish species. In

turn, such insight can be incorporated into the management of coastal and marine resources to aid in the protection of both fisheries and the marine ecosystems they depend on.

FOCAL SPECIES

The five focal species in this study are: *C. armatus*, *Coryphaenoides leptolepis* (*C. leptolepis*), *Coryphaenoides yaquinae* (*C. yaquinae*), *C. acrolepis*, and *M. productus*, commonly known as North Pacific hake. For the sake of consistency, Pacific hake will be referred to as *M. productus* for the entirety of this thesis. All of the *Coryphaenoides* species are included in the family Macrouridae (Cohen et al. 1990). Although not a Macrourid, *M. productus* is a benthopelagic groundfish species and is included in the study due to its similar life history (Melnychuk et al. 2013; Cohen et al. 1990). *Merluccius productus* and Macrourids are all included in the order Gadiformes (Iwamoto et al. 2015). For this study, Macrourids were analyzed as a group and *M. productus* was analyzed independently as a single species. Due to difficulty distinguishing *C. armatus, C. leptolepis,* and *C. yaquinae* from one another at the long-term time series study site, all three species were grouped together as one complex (*Coryphaenoides armatus-leptolepis-yaquinae* complex or Macrourid species complex) for analyses at this site. The following are brief descriptions of the Macrourid focal species in this project:

Coryphaenoides acrolepis:

Coryphaenoides acrolepis is a benthopelagic mid-slope Macrourid species that is significantly more abundant than any other large fish species living on the continental slope (Cohen et al. 1990). Commercially, this species is the North Pacific's most important Macrourid species (Koslow 1996; Laptikhovsky et al., 2013). It is a non-migratory species that resides in the North Pacific at a depth range of 400-1800 meters (Matsui et al. 1991; Cohen et al. 1990). This species has pelagic larvae (Iwamoto T. 1999). Due to its economic importance, it is necessary to monitor potential changes in abundance of this species over time to avoid overfishing (as recommended for groupers: Mangubhai et al. 2011).

Coryphaenoides armatus:

   Coryphaenoides armatus is a deep-slope upper continental rise Macrourid species found in all the world's oceans, at depths between 800 and 4,000 meters (Merrett and Haedrich 1997; Cohen et al. 1990). This species is known to grow slowly, potentially living up to 75 years of age (Cohen et al. 1990). Distribution of *C. armatus* is likely driven by migration in response to variation in food availability (Drazen et al. 2012; Bailey et al. 2006). *Coryphaenoides armatus*, although of no interest to fisheries, is often caught as by-catch and is difficult to differentiate from *C. acrolepis* (Iwamoto et al. 2015). This species has pelagic larvae (Iwamoto T. 1999).

Coryphaenoides yaquinae:

   Coryphaenoides yaquinae is an abyssal Macrourid species that is confined to abyssal depths encompassed within the Pacific Ocean (Jamieson et al. 2012). Although preferring deeper depths, the species is known to inhabit a depth range of 3400 to 5800 meters (Wilson and Waples 1983). *Coryphaenoides yaquinae* is closely related to *C. armatus*, and the two species are almost indistinguishable from one another based on physical characteristics alone (Smith et al. 1979; Jamieson et al. 2012). While generally segregated by depth, the two species co-exist on the Pacific continental margin between the 3400-4300 meter depth ranges (Jamieson et al. 2012; Endo and Okamura 1992). This species has pelagic larvae (Iwamoto T. 1999).

Coryphaenoides leptolepis:

   Coryphaenoides leptolepis is commonly referred to as the "Ghostly Grenadier" and is listed as Least Concern because the species has no known predators and resides outside the range of fisheries (Iwamoto 2015). It is a bathydemersal species, inhabiting a depth range of 610-4000 meters, and can grow to 62 centimeters in length (Iwamoto 2015). *Coryphaenoides leptolepis* is native to the northeast and eastern central Pacific, as well as the western central, eastern central, northwest, and northeast Atlantic (Wilson and Attia 2003; Iwamoto 2015). Due to a lack of commercial importance and depth range, very little is known about *C. leptolepis* (Iwamoto 2015). This species has pelagic larvae (Iwamoto T. 1999).

Merluccius productus:

Merluccius productus, of the family Merlucciidae, is commonly referred to as the Pacific hake (Carrera et al. 2006). It is a benthopelagic species (Essington et al. 2011) with pelagic larvae (Leaman and Beamish 1984) and is important prey for many larger fishes and marine mammals (Hoff et al. 2015). Within U.S. waters, *M. productus* is considered one of the most important commercial fishery species (NOAA, Pacific whiting (hake)). *Merluccius productus* resides in surface waters and depths up to 1,000 meters and is native to the eastern Pacific (Cohen et al. 1990). It inhabits coastal and oceanic areas but resides mainly on the continental shelf (Alverson and Larkins 1969; Cohen et al. 1990). *Merluccius productus* is a highly migratory species and can grow to 91 centimeters in length (Beamish et al. 2005; Hoff et al. 2015). Currently, this species is the most abundant groundfish population in the California Current system, with more *M. productus* caught than all other groundfish species combined (Fisheries and Oceans Canada 2018).
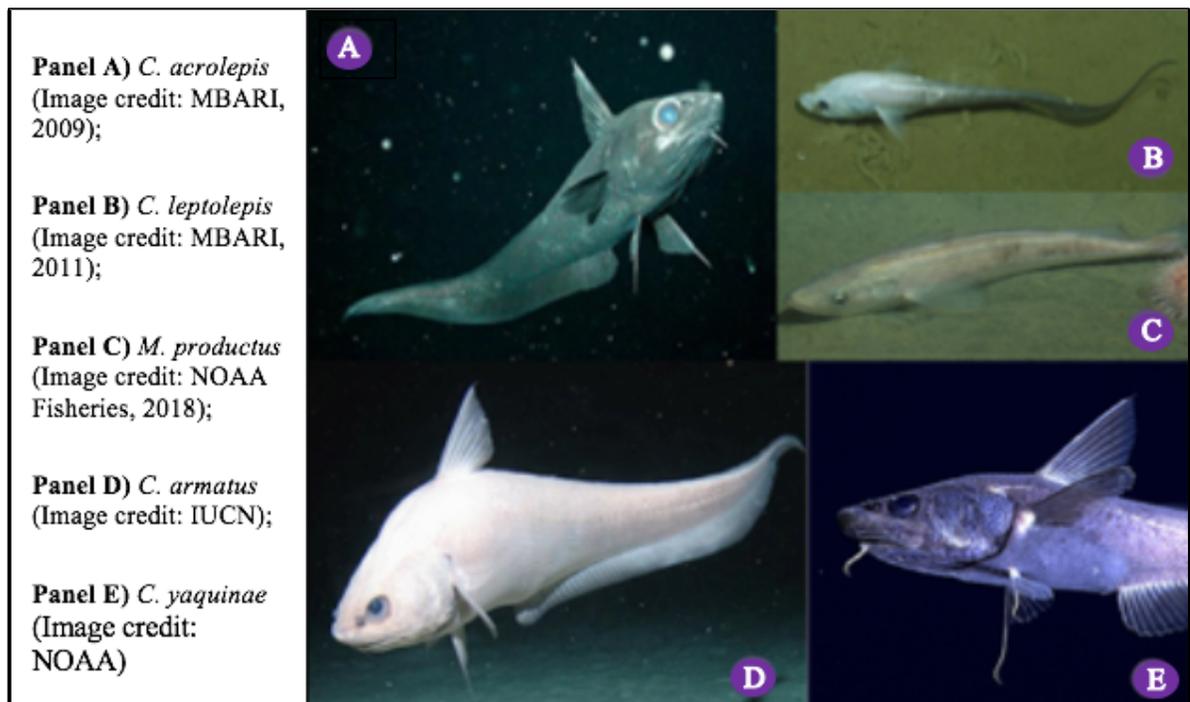
Figure 1. Panels A-E showing separate images of the benthopelagic groundfish focal species chosen for this study.

ENVIRONMENTAL VARIABLES

In order to monitor potential changes occurring in larval and adult life stages of Macrourids and *M. productus* in relation to changes in climate and surface-ocean conditions, five environmental variables were chosen and compared to Macrourid and *M. productus* data. Certain variables, despite not being classified as "climate" or "surface-ocean condition" variables, were chosen due to their strong relationships with climate and surface-ocean conditions. The five environmental variables used in the study are the following: sea surface temperature (SST), particulate organic carbon (POC) flux reaching the deep sea, carbon to nitrogen ratio (C:N) of sinking particulate matter, net primary production (NPP), and the Multivariate ENSO index (MEI). NPP, POC and C:N are indicators of food supply (Buesseler et al., 2008; Steinberg et al., 2012), however, they are useful for monitoring climate-related changes because such changes affect NPP, POC, and C:N (Moore et al., 2013), ultimately affecting factors such as export efficiency and the community structures of abyssal and deep-sea ecosystems (Kuhnz et al., 2014; Moore et al., 2013). Climate change is predicted to increase certain phytoplankton C:N ratios (Burkhardt et al., 1999). Increased C:N ratios could result in decreased export efficiency (Burkhardt et al., 1999), likely resulting in less POC reaching the seafloor in deeper waters (Moore et al., 2013)). By contrast, export efficiency is expected to increase due to climate-related declines in primary production, ultimately increasing export efficiency of POC (Arteaga et al., 2018; Chavez et al., 2011). This predicted increase in export efficiency will likely outweigh the declines caused by increased C:N ratios of phytoplankton (Chavez et al., 2011). Regardless, C:N, NPP, and POC are useful in assessing associations between fish populations and climate/surface-ocean conditions (Moore et al., 2013). Throughout the remainder of this paper, the variables relating to "climate and surface-ocean conditions" mentioned above, including indirect indicators of food supply, will be referred to as "environmental variables" for the sake of simplicity.

APPROACH

This project focuses on studying correlations between changes in deep-sea benthopelagic groundfish populations over time in relation to changes in climate and surface ocean conditions, as well as changes in indirect indicators of food supply. Four research

questions are addressed in this project; Q1) Has Macrourid population structure (abundance, body length, biomass) changed over time in relation to changing climate and surface-ocean conditions? Q2) Has *Merluccius productus'* population structure (abundance, body length, biomass) changed over time in relation to changing climate and surface-ocean conditions? Q3) Has the depth range of Macrourid species changed over time with changing climate and surface-ocean conditions? Q4) Has the depth range of *Merluccius productus* changed over time with changing climate and surface-ocean conditions? Question 1 addresses Macrourids using two separate means: 1) analyzing a time-series of benthic imagery annotations, and 2) analyzing Macrourid data collected from external sources. Questions 2-4 were addressed strictly through mined external data. Questions 2 and 4 address potential changes relating to *M. productus*. Due to separate data collection methods for Q1, there are separate component hypotheses for each method, as well as for each of the various fish variables obtained within the mined data. Further details regarding each question, their component hypotheses, and the population structure variables used are given below (See Appendix A).

This thesis involves a two-part study to address the four research questions. Part 1 of the study addresses Q1. Part 2 of the study addresses all four questions. Part 1 of the study involved conducting an hourly benthic imagery annotation to determine changes in adult Macrourid spp. abundance during a 6-year period at a station in the northeast Pacific (Sta. M). The annotation focused on data collected from 2011 to 2017. For Part 2 of the study, two existing NOAA databases (ERDDAP & FRAM; see methods section) were examined to determine potential changes in *M. productus* and Macrourid population structures/depth-distributions over time (2011-2017). The databases contained data from a continuous 64-year time-series, however, only data from the study period (2011-2017) relating to life stages of *M. productus* and Macrourid species residing along the California coast were used in analyses. Population structure and depth distribution data collected at Sta. M and obtained from NOAA databases were then compared to environmental variables relating to climate and surface-ocean conditions to determine if similar temporal trends occurred along the California coast.

CHAPTER 2

METHODS

STUDY AREA

Station M (Sta. M) is an abyssal station in the northeast Pacific, approximately 220 km west of Point Conception along the central California coast (34º 50'N, 123º 00'W). The station is approximately 4,100 m deep. This time series study is maintained by the Smith lab at the Monterey Bay Aquarium Research Institute (MBARI) and has been monitored consistently since 1989 (Smith et al., 2020).

Figure 2. Station M. (Image Credit: MBARI)
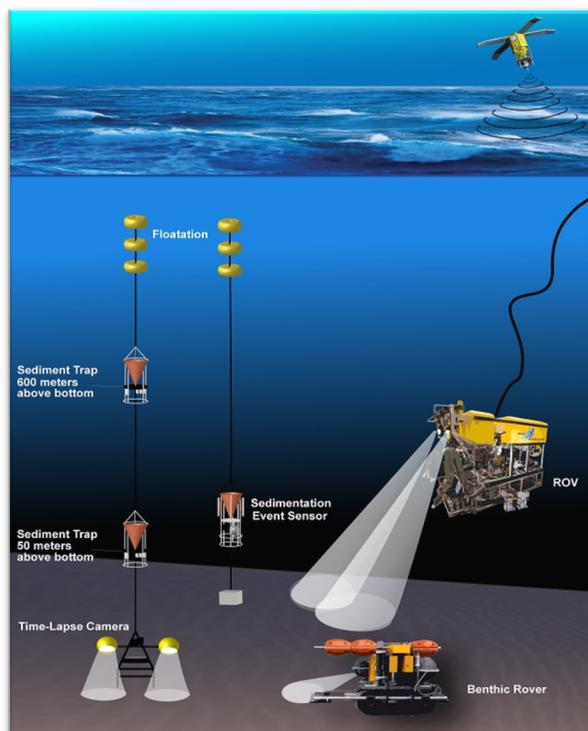
Figure 3. Instruments currently deployed at Sta. M (Image credit: MBARI)

INSTRUMENTATION

A number of autonomous long-term instruments have been deployed on the seafloor at Sta. M to collect various types of data. The instruments used in part 1 of this study are currently deployed at Sta. M and include 2 sediment traps moored 600 and 50 meters above the seafloor (mab) (Smith et al., 2013), as well as 2 benthic time-lapse cameras (Smith et al., 2017). The sediment traps collect particulate

matter that falls through the water column, eventually reaching the seafloor (Smith et al., 2013). The traps collect sinking material at 10-day intervals with a rotating carousel of 21 bottles (Smith et al., 1994). Once recovered, these bottles are taken back to the lab where the contents are analyzed for total and organic carbon, allowing for estimates of POC flux (Smith et al., 2013). The time-lapse cameras took a still image of the seafloor every hour for the duration of this study period (Smith et al., 1993), with gaps for periods when the camera systems were being serviced or did not work (Smith et al., 1994). Continuous deployment periods range from 3 to 12 month time spans. The cameras are mounted on a titanium frame at angles of 1) 35º in the vertical plane and 31º in the horizontal plane (Smith 1993), and the camera lens is situated approximately 2 m above the seafloor (Smith et al., 1994). The fields of view extend to 6.5 m from the tripod frame base and begins at 1.8 m in front of the cameras. An area of the seafloor, approximately 20 m², is illuminated by the two strobes on either side of the camera housings (Lemon, 2018). High-resolution digital imagery is used for deployments since 2007 (Sherman & Smith, 2009. Time-lapse imagery allows for observational estimates of various factors, including species' abundances and spatial patterns of individual organisms (Lemon, 2018). Satellite color imagery is also used to obtain SST and regional surface water chlorophyll, providing the data necessary for estimating NPP in surface waters above Sta. M (Smith et al., 2017). Around Sta. M, a radius of 100 km was used for the daily satellite sensing (Smith et al., 2017). Refer to Smith et al., 2017 for a description of full methods.

IMAGE ANALYSIS (PART 1)

Each hourly image from the time-lapse camera, taken from 2007 to 2017, was reviewed for presence of identifiable Macrourids using MBARI's open-source Video Annotation and Reference System (VARS) software (Schlining & Stout, 2006). VARS allows for annotation at any level of detail, including measurements of individual animals on the sea floor and comments on behavior and color. However, individuals in this study were not measured because they were typically in the water column. The VARS software stores all of the data and annotations within the system (Schlining & Stout, 2006). The lower 75% of each 20 m² image was used as an effective field of view due to the uneven

lighting and angle of the tripod images, increasing confidence in the identification of Macrourid species.

Figure 4. Time-lapse camera tripod image. The number of individual Macrourids present is counted for each hourly image (indiv./hr) and averaged weekly.

QUESTION 1(A):

Has Macrourid species complex' population structure changed over time in relation to changing climate and surface-ocean conditions?

Null Hypothesis: With changes in climate and surface-ocean conditions over time, there is no significant change (increase or decrease) in Macrourid species complex' abundance.

Alternative Hypothesis: With changes in climate and surface-ocean conditions over time, there is a significant change (increase or decrease) in Macrourid species complex' abundance.

Counts of all benthopelagic Macrourid species present at Sta. M from 2011-2017 were analyzed to determine changes in Macrourid abundance. The three dominant species present at Sta. M were *C. armatus*, *C. leptolepis*, and *C. yaquinae*. As a proxy for local abundance, counts of individuals per frame were determined. Counts were determined by visually counting the number of individuals present in each image's effective field of

view every hour. Due to difficulty distinguishing the three species from one another in the images, all three species were grouped together as one complex (*Coryphaenoides armatus-leptolepis-yaquinae complex*) when counting the number of individuals present. The number of fish present per hour (i.e. per image) was averaged over each week. Weekly averaged Macrourid count data were compared to the environmental variables to determine potential correlations between changes in fish populations at Sta. M. and climate. As previously stated, the variables used in the study included the following: sea surface temperature (SST), particulate organic carbon flux (POC flux), net primary production (NPP), carbon to nitrogen ratio (C:N) in the sinking particulate matter, and the Multivariate ENSO Index (MEI). Once these variables used in the data analyses were extracted for the entire time-series, they were averaged to obtain weekly averages to compare to weekly averaged fish count data using statistical analyses.

MINING DATA FROM OUTSIDE SOURCES (PART 2)

Existing NOAA databases containing data from a continuous 64-year time-series were examined to obtain Macrourid spp.' population structure and depth-distribution data for all life stages of the species present at Sta. M when data were available. Additionally, similar data for the shallower living *M. productus*, *C. acrolepis*, and all deep-sea Macrourid species residing along the California coast were obtained and included in the analyses when data were available. All extracted data falls within the time period of 2011 to 2017. The two NOAA databases include the data server ERDDAP and the data warehouse FRAM (refer to the Literature Cited section for links to both sources).

QUESTIONS 1(B)-4:

Q1(B) & Q2) Has groundfish (specifically Macrourid spp. (Q1) and M. productus (Q2)) population structure changed over time in relation to changing climate and surface-ocean conditions?

Q3 & Q4) Has the depth range of groundfish species (specifically Macrourid spp. (Q3) and M. productus (Q4)) changed over time with changing climate and surface-ocean conditions?

The collected NOAA groundfish data were also averaged (weekly) and compared to the same physical variables as the fish density data from Sta. M via statistical analyses to address the separate research questions. Comparing early life stage data to adult abundance data provides valuable insight into possible larval or juvenile density decline due to climate and surface conditions. A decline in adult fish populations will reflect this early life-stage density decline and can be predicted in the future. Early life stage data, adult abundance data, and other data relating to population structure obtained from NOAA databases were then compared to the adult fish density data collected at Sta. M for the study period (2011-2017) to determine if there are similar temporal trends in population structure occurring at Sta. M and along the California coast. Values derived from statistical analyses on Sta. M and NOAA mined data were assessed to determine possible and/or similar trends. The mined fish variables used in population structure analyses included the following: 1) regional (CA) Macrourid spp. biomass, 2) regional Macrourid spp. catch per unit effort (CPUE), 3) regional and local (relating to Sta. M) *M. productus* biomass, 4) regional and local *M. productus* CPUE, 5) regional Macrourid body length, 6) regional *M. productus* body length, 7) regional Macrourid spp.' larval abundance, and 8) regional *M. productus'* larval abundance.

Depth-distribution data were also extracted along with the NOAA time-series quantitative data to assess any changes in species' depth distributions over time. Statistical analyses were used to determine any potential relationships between changes in species' depth distributions over time and changes in climate and surface conditions. Depth-distribution data were compared to the same environmental variables as the fish density data from Sta. M in statistical analyses. Findings from statistical analyses were compared between Macrourid spp. and *M. productus* to determine similar trends among the different species regarding depth-distributions. The mined fish variables included in depth-distribution analyses were the following: 1) regional Macrourid spp. depth, and 2) regional and local *M. productus* depth.

STATISTICAL ANALYSES:

All data derived from Sta. M annotations and mined NOAA sources were averaged to obtain weekly averages to compare averaged fish population structure variables using three methods of statistical analyses, including; 1) Man-Kendall Trend Test, 2) Cross correlation (CC) analyses, and 3) Spearman's rho. Weekly averages for all previously stated fish variables were obtained and ranked using Excel. In order to detect any statistically significant trends in the time-series (2011-2017) data, the Mann-Kendall method was applied. Simply put, the Mann-Kendall method was used to establish whether Macrourid and *M. productus* variables were increasing or decreasing consistently over time. This is the first step in answering the study questions because we must first establish possible trends in fish variables before we can determine how climate and surface-ocean conditions are affecting or causing such trends. CC analyses were used to determine the separate relationships and the degree of correlation between changes in fish populations, at Sta. M and along the California coast, and changes in climate and surface ocean conditions over time. CC analyses were run in the statistical program R, and accounted for time lags between variables, as well as measured similarity between the variable series. To evaluate the linear relationship between variables, scatter plots were created to incorporate the shifted weekly variables and fish variables. To evaluate the monotonic relationship between variables (i.e., the strength of association between two variables), as well as for comparison purposes, Spearman's rho was used alongside CC analyses. Lag periods, correlation strengths (+, -), and Spearman's rho values, derived from CC analyses on Sta. M and mined data, were assessed to determine possible trends over time. In other words, CC analyses and Spearman's rho were used to answer the remaining portions of this study questions, by determining relationships (and relationship strengths) between Macrourid and *M. productus* population structure variables and variables relating to climate and surface-ocean conditions. CC analyses also allowed us to determine the lag times of the relationships, i.e., the amount of time it takes for fish variables to change in relation to changes in the associated environmental variables.

CHAPTER 3

RESULTS

Findings from this study provided answers to the four research questions addressed in this thesis. These questions are relisted below. Page numbers for the complete list of research questions, their associated component hypotheses, and statistical analyses results tables can be found in the Table of Contents. Three of the fourteen fish variables used in the Mann-Kendall analyses showed significant trends over the time-series (2011-2017). Macrourid length and abundance increased significantly over the 7-year period (Macr. spp. comp.' abundance: $p < 0.0001$; Macr. length: $p = 0.0023$). Similarly, local *Merluccius productus* biomass significantly increased over time (*M. productus* biomass: $p = 0.0170$).

Population Structure:

Question 1:

HAS MACROURID SPECIES' POPULATION STRUCTURE CHANGED OVER TIME IN RELATION TO CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?

QUESTION 2:

HAS MERLUCCIUS PRODUCTUS' POPULATION STRUCTURE CHANGED OVER TIME IN RELATION TO CHANGING CLIMATE AND SURFACE OCEAN CONDITIONS?

Depth:

QUESTION 3:

HAS THE DEPTH RANGE OF MACROURID SPECIES CHANGED OVER TIME WITH CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?

QUESTION 4:

HAS THE DEPTH RANGE OF MERLUCCIUS PRODUCTUS CHANGED OVER TIME WITH CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?

1.) *Macrourid Species Complex' Abundance*

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
Macrourid species complex' abundance (# ind. /hr/ week)	*Coryphaenoides armatus* *Corphaenoides leptolepis* *Coryphaenoides yaquinae*	Sta. M	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	A	*Has Macrourid species complex' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species complex' abundance.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species complex' abundance.	Spearman Rank

Cross correlation analysis showed a positive relationship between MEI and Macrourid species complex' abundance (rho = 0.40; p = 0.0000), with the strongest correlation when fish abundance was lagged 56 weeks after MEI data (Refer to Table 1 in Appendix B). There was significant evidence of a moderate monotonic association between these two variables (rho = 0.40; p = 0.0000). An inverse relationship was found between NPP and Macrourid species complex' abundance (rho = -0.35; p = 0.0000), with the strongest correlation present when fish abundance was lagged 50 weeks after NPP data. A significantly weak monotonic trend was exhibited over the time series between these two variables (rho = -0.35; p = 0.0000). An inverse relationship between Macrourid species complex' abundance and C:N was also found (rho = -0.32; p = 0.0000), with the strongest correlation present when fish abundance lagged 67 weeks after changes in C:N data. A significantly weak monotonic relationship between these two variables over time was determined (rho = -0.32; p = 0.0000).

Relating back to the research question (Q1(A)), results from the Mann-Kendall tests, carried out on Macrourid species complex' abundance, showed a significant increasing trend in the series over time (alpha < 0.05; See Table # above). Results from the Mann-Kendall analysis, in combination with the findings mentioned above from CC and Spearman rank analyses, allow us to reject the null hypothesis (Ho) and accept the alternative hypothesis (Ha), which is stated below.

(Q1(A)): HAS MACROURID SPECIES COMPLEX' POPULATION STRUCTURE CHANGED OVER TIME IN RELATION TO CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?

HA: WITH INCREASING CHANGES IN CLIMATE AND SURFACE OCEAN CONDITIONS OVER TIME, SPECIFICALLY IN REGARD TO MEI, NPP AND C:N, THERE IS A SIGNIFICANT INCREASE IN MACROURID SPECIES COMPLEX' ABUNDANCE; THEREFORE, THERE IS A SIGNIFICANT CHANGE IN MACROURID SPECIES COMPLEX' POPULATION STRUCTURE OVER TIME.

2.) *Macrourid Body Length*

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	D	*Has Macrourid sp.' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species' body lengths.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species' body lengths.	Spearman Rank

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
Macrourid length (cm) (Regional)	*Nezumia stelgidolepis* *Albatrossia pectoralis* *Coryphaenoides acrolepis* *Nezumia liolepis*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

The two strongest negative relationships associated with Macrourid body length were with NPP and C:N (NPP: rho = -0.58, p = 0.0000; C:N: rho = -0.53, p = 0.0004). Strongest correlations were found when fish lengths were lagged 56 weeks after NPP data and 39 weeks after C:N data (Refer to Fig. in Appendix). There is significant evidence of independent moderate monotonic associations between these two variables and Macrourid length (NPP: rho = -0.58, p = 0.0000; C:N: rho = -0.53, p = 0.0004). A positive relationship between Macrourid length and SST was found (rho = 0.40; p = 0.0005) with the strongest correlation when fish abundance was lagged 30 weeks after SST data. A significantly moderate monotonic relationship existed between these two variables over time (rho = 0.40; p = 0.0005). Lastly, a positive association was found between Macrourid length and MEI (rho = 0.35; p = 0.0023), when fish lengths were lagged 23 weeks behind NPP data. The two variables exhibited a significantly weak monotonic relationship over time (rho = 0.35; p = 0.0023).

Relating back to the research question (Q1(F)), results from the Mann-Kendall tests, carried out on Macrourid lengths, showed a significant increasing trend in the time-

series (alpha < 0.05; See Table # above). Results from the Mann-Kendall analysis, in combination with the findings mentioned above from CC and Spearman rank analyses, allow us to reject the null hypothesis (Ho) and accept the alternative hypothesis (Ha), which is stated below.

> **(Q1(F)):** *HAS MACROURID SP.' POPULATION STRUCTURE CHANGED OVER TIME IN RELATION TO CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?*

> **HA:** WITH INCREASING CHANGES IN CLIMATE AND SURFACE OCEAN CONDITIONS OVER TIME, SPECIFICALLY IN REGARD TO NPP, C:N, SST, AND MEI, THERE IS A SIGNIFICANT INCREASE IN MACROURID LENGTHS; THEREFORE, THERE IS A SIGNIFICANT CHANGE IN MACROURID SP.' POPULATION STRUCTURE OVER TIME.

3.) *Local Merluccius productus Biomass*

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	A	Has Merluccius productus' population structure changed over time in relation to changing climate and surface-ocean conditions?	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* biomass.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* biomass.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus biomass (kg per ha/der) (Regional & Local)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Overall, local *M. productus'* biomass data were found to have the strongest relationships between the climate/surface ocean condition variables out of the three fish variables exhibiting trends over time. More specifically, SST exhibited the strongest association with local biomass. The relationship between local *M. productus'* biomass (kg per ha/der) data and SST was positive (rho = 0.75; p = 0.0005), with the strongest correlation present when local *M. productus'* biomass was lagged 6 weeks after SST data (Refer to Fig in Appendix). There is significant evidence of a strong monotonic association between these two variables (rho = 0.75; p = 0.0005). A positive relationship between local *M. productus'* biomass and MEI was also found (rho = 0.76; p = 0.0003). The strongest correlation occurred when local *M. productus'* biomass was lagged 15

weeks after MEI data. A significantly strong monotonic relationship was determined between these two variables over time (rho = 0.76; p = 0.0003). Lastly, NPP was found to be inversely associated with local *M. productus*' biomass data (rho = -0.68; p = 0.0027), with the strongest correlation when local *M. productus*' biomass was lagged 2 weeks after NPP data. A significantly strong monotonic relationship existed between these two variables over time (rho = -0.68; p = 0.0027).

Relating back to the research question (Q1(D)), results from the Mann-Kendall tests, carried out on local *M. productus*' biomass, showed a significant increasing trend in the series over time (alpha < 0.05; See Table # above). Results from the Mann-Kendall analysis, in combination with the findings mentioned above from CC and Spearman rank analyses, allow us to reject the null hypothesis (Ho) and accept the alternative hypothesis (Ha), which is stated below.

(Q1(D)): Has Merluccius productus' population structure changed over time in relation to changing climate and surface-ocean conditions?

Ha: With increasing changes in climate and surface ocean conditions over time, specifically in regard to SST, MEI, and NPP, there is a significant increase in local *Merluccius productus*' biomass; therefore, there is a significant change in *Merluccius productus*' population structure over time.

4.) *Other Noteworthy Relationships*

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	B	Has Merluccius productus' population structure changed over time in relation to changing climate and surface ocean conditions?	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* CPUE.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* CPUE.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus CPUE (num per ha/der) (Regional & Local)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	D	*Has Merluccius productus' population structure changed over time in relation to changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* larval abundance.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* larval abundance.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus larval abundance (10 m^2) (Regional)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
4	A	*Has the depth range of Merluccius productus changed over time with changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* depth distribution.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* depth distribution.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus depth (m) (Regional & Local)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

The associations discussed below are statistically significant and noteworthy, despite lacking trends over time, as determined by the Mann-Kendall tests. The strongest statistical relationship existed between local *M. productus* depth data and C:N. The relationship between local *M. productus* depth and C:N was positive (rho = 0.90; p = 0.0046), with the strongest correlation when local *M. productus* depth data were lagged 3 weeks after C:N data. There was a very strong monotonic association between these two variables (rho = 0.90; p = 0.0046). The second strongest relationship existed between local *M. productus* catch per unit effort (CPUE) data and SST. The relationship between these two variables was positive (rho = 0.86; p < 2.2 e^(-16)), with the strongest correlation when local *M. productus* CPUE was lagged 6 weeks behind SST data. A very strong statistically significant monotonic association between these two variables over time was found (rho = 0.86; p < 2.2 e^(-16)). The third strongest relationship existed between the same local *M. productus* CPUE data and NPP. The relationship between these two variables was negative (rho = -0.80; p = 0.0001), with the strongest correlation when local *M. productus* CPUE was lagged 2 weeks behind NPP data. A very strong monotonic association between these two variables was determined (rho = -0.80; p =

0.0001). Lastly, *M. productus*' larval abundance was significantly associated with C:N, SST, and NPP. The separate relationships of C:N and SST with *M. productus*' larvae were both positive (C:N: rho = 0.58, p = 0.0000; SST: rho = 0.55, p = 0.0000). The strongest correlation was present when *M. productus*' larval abundance data were lagged 4 weeks after C:N data and when lagged 14 weeks after SST data, respectively. *M. productus*' larvae were determined to have a significantly inverse association with NPP (rho = -0.45; p = 0.0003), with the strongest correlation when *M. productus*' larvae were lagged 2 weeks behind NPP. Results determined independent and statistically significant moderate monotonic associations between *M. productus*' larvae and these three variables (C:N: rho = 0.58, p = 0.0000; SST: rho = 0.55, p = 0.0000; NPP: rho = -0.45; p = 0.0003).

Relating back to the research question (Q1(E)), results from the Mann-Kendall tests, carried out on local *M. productus* CPUE, showed a computed p-value greater than the significance level (alpha = 0.05); and can therefore be interpreted as local *M. productus* CPUE lacking a significant trend in the series over time (See Table # above). Results from the Mann-Kendall analysis, in combination with the findings mentioned above from CC and Spearman rank analyses, lead us to the conclusion that one cannot reject the null hypothesis (Ho), which is stated below.

> *(Q1(E)):* HAS MERLUCCIUS PRODUCTUS' POPULATION STRUCTURE CHANGED OVER TIME IN RELATION TO CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?
>
> *Ho:* WITH INCREASING CHANGES IN CLIMATE AND SURFACE OCEAN CONDITIONS OVER TIME, SPECIFICALLY IN REGARD TO SST AND NPP, THERE IS NO SIGNIFICANT CHANGE IN LOCAL MERLUCCIUS PRODUCTUS' CPUE; THEREFORE, THERE IS NO SIGNIFICANT CHANGE OVER TIME IN MERLUCCIUS PRODUCTUS' POPULATION STRUCTURE IN RELATION TO LOCAL MERLUCCIUS PRODUCTUS' CPUE, SST AND NPP.

The null hypothesis could not be rejected on account of there being no significant trend in local *M. productus* CPUE over time. It is worth noting that local *M. productus* CPUE, and therefore local *M. productus* population structure, did exhibit changes in relation to environmental variables (SST and NPP) despite the lack of a significant trend over time. Similarly, results from the Mann- Kendall test carried out on regional *M.*

productus' larvae (Q1(I)) showed a computed p-value greater than the significance level (alpha = 0.05); and can therefore be interpreted as regional *M. productus'* larvae lacking a significant trend in the series over time (See Table # above). Results from the statistical analyses lead us to the conclusion that one cannot reject the null hypothesis (Ho), which is stated below.

> **(Q1(I)):** HAS MERLUCCIUS PRODUCTUS' POPULATION STRUCTURE CHANGED OVER TIME IN RELATION TO CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?
>
> **Ho:** WITH INCREASING CHANGES IN CLIMATE AND SURFACE OCEAN CONDITIONS OVER TIME, SPECIFICALLY IN REGARD TO C:N, SST AND NPP, THERE IS NO SIGNIFICANT CHANGE IN REGIONAL MERLUCCIUS PRODUCTUS' LARVAE; THEREFORE, THERE IS NO SIGNIFICANT CHANGE OVER TIME IN MERLUCCIUS PRODUCTUS' POPULATION STRUCTURE IN RELATION TO REGIONAL MERLUCCIUS PRODUCTUS LARVAE, C:N, SST, AND NPP.

The null hypothesis could not be rejected on account of there was no significant trend in regional *M. productus'* larvae over time. It is worth noting that regional *M. productus'* larvae, and therefore *M. productus'* population structure, did exhibit changes in relation to environmental variables (C:N, SST, and NPP) despite the lack of a significant trend over time. Finally, results from the Mann-Kendall test carried out on local *M. productus* depth (Q2(B)) showed a computed p-value greater than the significance level (alpha = 0.05); and can therefore be interpreted as local *M. productus* depth lacking a significant trend in the series over time (See Table # above). Results from the statistical analyses lead us to the conclusion that one cannot reject the null hypothesis (Ho), which is stated below.

> **(Q2(B)):** HAS THE DEPTH RANGE OF MERLUCCIUS PRODUCTUS CHANGED OVER TIME WITH CHANGING CLIMATE AND SURFACE-OCEAN CONDITIONS?
>
> **Ho:** WITH INCREASING CHANGES IN CLIMATE AND SURFACE OCEAN CONDITIONS OVER TIME, SPECIFICALLY IN REGARD TO C:N, THERE IS NO SIGNIFICANT CHANGE IN LOCAL MERLUCCIUS PRODUCTUS' DEPTH DISTRIBUTION OVER TIME.

The null hypothesis could not be rejected on account of there being no significant trend in local *M. productus* depth over time. Like the two previous variables mentioned above, it is worth noting that local *M. productus* depth, and therefore local *M. productus'*

depth distribution, did exhibit changes in relation to environmental variables (C**:**N) despite the lack of a significant trend over time. In summary, the answers to the two research questions, determined from the results, are as follows:

Q1 & Q2: With increasing changes in climate and surface-ocean conditions over time, there is a significant change in both Macrourid species' population structure and *M. productus* population structure over time.

Q4: With increasing changes in climate and surface-ocean conditions over time, there is no significant change in *M. productus*' depth distribution over time.

Q3: Regarding potential changes in Macrourid species' depth distributions, this question couldn't be answered due to insufficient sampling sizes in the mined Macrourid species depth data.

CHAPTER 4

DISCUSSION & CONCLUSIONS

Findings from this study provide a clearer picture of how marine ecosystems are being affected by changes in climate and surface ocean conditions over time. For instance, shifts in nekton abundance within the California Current ecosystem (CCE) have been observed in various studies (Zeidberg & Robison, 2007; Brodeur et al., 2006; Drazen et al., 2012). Changes in Macrourid abundance over time are driven by carrion fluxes (Drazen et al., 2008; Jeffreys et al., 2010; Drazen et al., 2012). *Merluccius productus* nekton being the main source of carrion supply for benthopelagic Macrourids (Drazen et al., 2009; Dufault et al., 2009; Drazen et al., 2012). Prior to this study, a similar time-series analysis was conducted for an earlier period, 1989-2007, by Drazen et al. (2012) with the goal of evaluating whether changes in Macrourid abundance over time were driven by changes in *M. productus* carrion supply. The goal of this thesis study, however, was to determine: 1) whether Macrourid spp. and/or *M. productus* population structures have changed over time in relation to changing climate and surface-ocean conditions and 2) whether the depth ranges of Macrourid spp. and/or *M. productus* have changed over time with changing climate and surface-ocean conditions. While the two studies sought to answer different questions, results from this thesis study corroborate Drazen et al., 2012's findings for the CCE area, as well as for the vicinity of Sta. M. Comparing observations from the two studies, one presenting weekly averages and one presenting x-scale data, can give broader scale insights into how changes in climate and surface ocean conditions might be indirectly influencing population structures and depth distributions of fish species', expanding our understanding in ways that would not be possible using findings from this study alone. More specifically, comparing findings can increase our understanding of how potential impacts of changing climate and surface-ocean conditions on *M. productus'* population structure and depth distribution could indirectly affect Macrourid populations, due to their close relationship with *M. productus.* It is worth noting that, although *M. productus* was a focal species for both studies, fish variables (*M. productus biomass* & larval abundance vs. *M. productus* egg abundance) used in the analyses were not directly comparable to one another due to life-

stage differences. Despite this, it is still beneficial to compare the findings indirectly, giving insight into trends occurring over the life-history of *M. productus*.

4.1) Macrourid & *Merluccius productus* Observations (2011-2017)

Comparable to Drazen et al. (2012) findings for the years 1989-2007, we observed continued increases in both local Macrourid abundance at Sta. M and regional Macrourid length over the period 2011-2017. Local Macrourid abundance was moderately associated with MEI (+) and weakly associated with NPP (-) and C:N (-). Local Macrourid body length was moderately associated with NPP (-), C:N (-), and SST (+), and weakly associated with MEI (+). When *M. productus* data from the region were localized within 100 nmi of Sta. M, we observed an increase in *M. productus* biomass over time, despite lacking a regional trend. Additionally, out of the fish variables exhibiting trends over time, local *M. productus* biomass was found to have the strongest relationships with climate/surface condition variables. More specifically, strong associations were found between local *M. productus* biomass and SST (+), MEI (+), and NPP (-). Similarly, local *M. productus* CPUE was also strongly associated with SST (+) and NPP (-). Despite lacking a trend over time, regional *M. productus* larval abundance was also significantly correlated to SST (+) and NPP (-), as well as C:N (+). It is worth noting that *M. productus* larval abundance data were not localized for this study.

Similar to this study, Drazen et al. (2012) observed a significant increase in local Macrourid abundances over the time period 1989-2007 and found significant correlations (+) between *M. productus* egg abundance and local Macrourid abundance at all spatial scales. Aside from a four year gap in data between the two time-series studies, combining findings sheds light on the temporal trend occurring from 1989-2017 at Sta. M, in reguards to increased Macrourid abundances .Increases in *M. productus* egg abundance were followed by increases in Macrourid abundance following a lag of 6-7 months at the 100 nautical miles (nmi) scale (Drazen et al., 2012). Correlations between *M. productus* egg abundance and Macrourid abundance were strongest when egg abundances were localized to Sta. M at this smaller spatial scale resolution of 100 nmi, compared to the broader regional (CA) scale. When comparing Macrourid abundances at Sta. M with

annual estimates *of M. productus* female spawning stock biomass, for the entire North American west coast, no significant correlations were found. Drazen et al. (2012) also observed a significant increase in average local Macrourid size over time. Combining Macrourid size and abundance allowed for biomass estimates to be assessed, in which a ~6 fold increase in Macrourid biomass was observed over the time period. Changes in local Macrourid population structure was determined to follow metrics for *M. productus* biomass, suggesting *M. productus* carrion supply may be the driving factor contributing to changes in some Macrourid population structures (Drazen et al., 2012).

As previously mentioned, results from this study found increases in local *M. productus* biomass, local Macrourid abundance, and regional Macrourid length over time. Despite lacking Macrourid biomass data, observed increases in the abundance and length of local Macrourids over time matches findings from Drazen et al. (2012). The two studies used different analyses to assess Macrourid and *M. productus* populations, however, we can still compare the findings indirectly to gain further insight into what the separate results might signify. Observed positive correlations between local *M. productus* egg abundance and local Macrourid abundance (Drazen et al., 2012) suggest that an increase in one variable would lead to an increase in the other. *M. productus* larval abundance was not found to increase over time in this thesis study, however, an increasing trend over time may have been observed if the larval data had been localized relative to Sta. M. Regardless, Drazen et al. (2012) found that changes in local *M. productus* biomass were followed by changes in local Macrourid population structure. Findings from this thesis study compliment this finding, in that we observed increases in both local *M. productus* biomass and local Macrourid abundance and length. It is also worth noting that all local *M. productus* variables (biomass, CPUE, & larval abundance) were all significantly correlated with SST (+) and NPP (-), suggesting changes in local larval abundance, driven by SST and/or NPP, are likely to somewhat resemble changes in local adult biomass.

4.2) Spatial Scale & Location Significance

As previously stated, *M. productus* carrion has been found to be the largest and most important food source for Macrourids (Drazen et al., 2009; Dufault et al., 2009), making up 61% of pelagic biomass in the California Current ecosystem (CCE) (Agostini et al., 2006; Drazen et al., 2012). For this study, spatial scale was a determining factor in the significance of the observed findings. When localized to Sta. M, we observed significant increases in Macrourid abundance and length, as well as increased *M. productus* biomass over time. When cross correlations were run for the broader region of California waters, these trends were not significant. Similar to findings from this study, Drazen et al., 2012 found that the relationships between *M. productus* egg abundance and Macrourid abundance increased significantly when localized to Sta. M at 100 nmi. Sta. M is unique for many reasons, including spatial, temporal and biogeochemical processes (Smith et al., 2006); which may explain the significance found when localizing the datasets. In regard to Macrourid population structure dynamics, various studies suggest location of *M. productus* spawning may be more of a factor than spawning stock size (Bailey 1982; Mullin et al., 2000; Horn & Smith, 1997; Drazen et al., 2012).

Station M, underlying part of the California Current (CC) (Smith et al., 2017), lies within the inshore region known as the Southern California Bight (SCB) (Bograd et al., 2015). POC flux varies seasonally and interannually at this site (Ruhl, 2008). The CCE is an important and highly productive upwelling region due to Ekman transport (Pickett & Paduan, 2003; Bograd et al., 2019). The California Undercurrent (CU) has a strong impact on the SCB, particularly in regard to areas over the continental slope (Bograd et al., 2015; Bograd et al., 2019). The southern CCE region acts as a transitional boundary between various water masses, including the Pacific Equatorial Water (PEW), Eastern North Pacific Central Water (ENPCW), and the Pacific Subarctic Upper Water (PSUW) (Brodeur et al., 2003; Bograd et al., 2019). PEW, ENPCW, and PSUW strongly influence the CU, lateral shifts in the North Pacific subtropical gyre boundary, and the CC respectively (Bograd et al., 2019). These water masses have different physical properties and their separate relative influences can vary interannually (Bograd et al., 2019). Such variations can have multi-scale consequences on ecosystem structure and biogeochemical processes (Bograd et al., 2015).

Merluccius productus is a highly valued target species for fisheries around the world, including US and Canadian fisheries (Agostini et al., 2006). Fish yields between these two countries are strongly influenced by interannual biomass distribution of the species. Substantial variability in year-class strength upsets this distribution, potentially impacting the fisheries in a negative way (Agostini et al., 2006). Studies found that year-class strength may depend on survival of the larval stages, specifically the late stage (Hollowed, 1992; Smith, 1985b). Locations such as Sta. M and the SCB are significant for the US and Canadian fisheries for this reason. Studies have determined the SCB, where *M. productus* nursery grounds are located, and regions west of Point Conception (Sta. M) are favorable to the survival of *M. productus* larvae, and late stage larvae have been shown to congregate in these areas regularly (Hollowed, 1992; Walker et al., 1987). This is largely due to the layered physical structure of this particular region (Sta. M and SCB) (Hollowed, 1992). The survival of *M. productus* larvae may rely on reduced offshore advection (Bailey et al., 1982; Bailey, 1981). The layered structure of the region results in subsurface waters from the CU being directed onshore while surface waters stemming from the CC are directed offshore (Hollowed, 1992). Nearshore, offshore transport is minimized (Morgan & Fisher, 2010). This, combined with the diurnal vertical migration of *M. productus* larvae, reduces offshore advection, allowing larvae to remain in the study region where prey abundance is high (Hollowed, 1992).

Prey availability is another important factor contributing to the survival or mortality of *M. productus* larvae (Bailey, 1981). Prey is more than abundant in the study area (Sta. M) due to the high productivity of the region. Extended periods of high-nutrient conditions caused by upwelling in this region result in high productivity (Pickett & Paduan, 2003; Bograd et al., 2019). Increases in phytoplankton from optimal-nutrient conditions results in high zooplankton abundances (Danger et al., 2007; Vanni, 1987). *Calanus pacificus* is a primary prey item for *M. productus* adults. Increased abundances of phytoplankton cause increased production in this prey species, which are then prey for larval *M. productus* (Hollowed, 1992). This is in line with findings from this thesis study, in that NPP was found to be significantly and positively associated with *M. productus*

regional biomass and CPUE. Local *M. productus* biomass and CPUE were found exhibiting inverse trends associated with NPP. This makes sense in theory because *M. productus* adults migrate north, a long distance away from Sta. M, to feed and are less dependent on NPP associated with the Sta. M region. The influence of NPP on *M. productus* larval abundance, Macrourid length, and local Macrourid abundance in this study were less clear. Significant inverse associations between NPP and these three variables were observed. It is possible that abundance changes of dominant zooplankton species could result in a loss of prey for *M. productus* larvae, negatively affecting Macrourid population structure as well (Brodeur et al., 2006). Another possibility is that observed correlation directions associated with the relationships between NPP and Macrourid length/*M. productus* larvae could potentially switch to positive correlations if length and larval abundance data were localized to Sta. M.

Carbon to nitrogen ratios (C:N) were selected as a food supply variable focused on in this study and goes hand in hand with NPP. Higher C:N ratios in mixed layer waters signifies the use of nitrogen for primary production, resulting in increased food supply for larvae (Körtzinger et al., 2001). Higher C:N ratios also denote more refractory, lower food quality at abyssal depths and hence less nitrogen compared to carbon (Burkhardt et al., 1999). By contrast, lower C:N ratios in mixed layer waters signifies higher food quality in the sinking particulate matter food for Macrourids in the deep sea (Körtzinger et al., 2001). C:N ratios were significantly and positively associated with *M. productus* larval abundance. The influence of C:N ratios on adult fishes in this study were less clear. Significant inverse associations between C:N ratios and local Macrourid abundance and length were observed. These findings make sense in theory, in that higher C:N ratios signify lower quality food for Macrourids in the deep-sea (Ken Smith, pers. comm.), and increased food supply for larvae in the shallower mixed layer waters. Not surprisingly, C:N had the strongest correlations with *M. productus* (+) and Macrourid depth ranges (-) among the environmental variables analyzed in this study.

In addition to spawning location, the spawning migration route of *M. productus* may be another potential factor contributing to the significance of the localized small

spatial scale in relation to Station M and fish associations. Factors including temperature, depth, upwelling, and currents within the CCE contribute significantly to the migration route taken by *M. productus* adult fishes (Peterson et al., 2006; Bailey et al., 1982). Upwelling plays a significant role in the life-stages of *M. productus*, in that for at least half of the year, adults reside in upwelling regions (Cushing, 1971). *M. productus* travel south at a depth of 350-400 m via the CC to warmer offshore waters in the fall and winter, in order to spawn where larvae can take advantage of productive upwelling (Cushing, 1971; Drazen et al., 2012). Point Conception is considered the southern boundary of the major CCE upwelling zone (Cudaback et al., 2005). The location of spawning can vary slightly with temperature, with observed shifts towards the equator during cold years and shifts poleward during warm years (near Point Conception) (Agostini, 2005). Winds north of Point Conception influence inner shelf currents, specifically the inshore Davidson current (Mazzini et al., 2014). Adult fish take advantage of this countercurrent as the upwelling season advances, riding it north in the spring and summer at a depth of <100 m in order to feed (Cushing, 1971; Stauffer, 1985). Studies have suggested changes in Macrourid length and abundance may be due to migration patterns associated with *M. productus* migrations (Drazen et al., 2012; Priede et al., 2003; King & Priede, 2008), which aligns with results from this study.

As stated above, temperature plays a significant role in the patterns exhibited by *M. productus* life stages throughout the year (Agnostini, 2005). SST has an effect on spawning location (Agnostini, 2005) and NPP (Körtzinger et al., 2001), which in turn affects *M. productus* year-class strength and larval abundance (Hollowed, 1992), consequently affecting local Macrourid population structure (Drazen et al., 2012). Results from this study reflect this, in that local *M. productus* larvae and adult biomass, as well as local Macrourid length, are significantly associated with SST. SST is one of the six variables associated with the MEI index (Sukresno, 2010); an assessment of ENSO that considers atmospheric and oceanic variables of tropical Pacific (Wolter & Timlin, 2011). Studies have shown source water contributions (PEW, ENPCW, and PSUW) of the CCE are affected by the ENSO cycle, specifically in relation to PEW during La Nina events (Bograd et al., 2019). During these events, changes in depth distribution of this water

source, in combination with fluctuations of upwelling strength, result in primary producers gaining better access to the nutrient-rich waters below (Bograd et al., 2019). During such events, scientists have observed southern shifts in *M. productus* spawning activity (Drazen et al., 2012). Findings from this study compliment this, in that MEI was found to be positively associated with local *M. productus* biomass, Macrourid abundance and length.

4.3 Potential Impacts of Climate and Fishing Pressure

Climate and fishing pressure can have drastic impacts on marine ecosystems, including the deep-sea (Overland et al., 2010). Increases in anthropogenic climate change has the potential to dramatically alter biogeochemical processes within the world's oceans, and the population structures of important fish species targeted by fisheries (Doney, 2010). In light of anthropogenic climate change, ENSO events have become more frequent and have increased in intensity in recent years, and this is predicted to continue in the future (Cai et al., 2015). In addition, ENSO events have been assumed to resemble future warming events (Meehl et al., 2000), which are predicted to cause sea level rise and increases in surface water temperatures along the coast, upwelling, and stratification (Hoegh-Guldberg & Bruno, 2005; DiNezio et al., 2010). Additionally, thermocline depth is expected to get deeper (DiNezio et al., 2010). La Nina events have also been found to impact near surface expression of source waters mentioned above, and this is known to cause amplified low pH and hypoxic events (Bograd et al., 2019). Macrourid and *M. productus* populations residing in the CCE could be affected by changes in climate in various ways, including those residing in the vicinity of Point Conception and the SCB. For instance, the location of *M. productus* spawning shifts in regard to temperature, moving poleward in warm years (Agnostini, 2005). As previously stated, *M. productus* is one of the most important and largest commercial groundfish species in the U.S. (Drazen et al., 2012; Zeidberg & Robison, 2007), and shifts in the distribution of biomass can affect the annual yields for Canadian and US fisheries (Agostini et al., 2006). In addition, the most valuable fish migrate further north (Emmett et al., 2006; Agostini et al., 2006). Increased surface temperature may result in further migrational shifts northward, potentially benefitting northern US and Canadian fisheries.

By contrast, these shifts could potentially reduce abundance in waters off California (Emmett et al., 2006). Aside from shifts in distribution, surface warming may also cause declines in zooplankton-copepod abundances (Smith, 1985a) and community composition changes due to nutrient changes (Pinhassi et al., 2006; Suikkanen et al., 2013) and greater offshore transport (Bakun et al., 2015). Declines in zooplankton-copepod abundances could mean a decrease in the food source for *M. productus* larvae (Sumida & Moser, 1980) (reducing year-class success) and thus a decrease in food for Macrourids and other species relying on *M. productus* carrion (Bailey, 1981; Hollowed, 1992; Dufault et al., 2009; Brodeur et al., 2003). By contrast, surface warming may favor *M. productus* populations in California waters. During warmer years, spawning locations shift poleward near Point Conception, as previously stated. Spawning in this location reduces offshore advection for larvae, increasing their chances of survival. This study's findings are in line with this assumption because we found positive correlations between SST and *M. productus* larval abundance. Reduction in year-class success from shifts in larval distributions may negatively impact fisheries in future years as well (Agostini et al., 2006). Increased temperature also leads to low productivity (Behrenfeld et al., 2006). Many species will likely move closer to the coast and northward (Cushing, 1971), however, some species may not be able to. For instance, the habitat range of the deep-sea Macrourid *C. yaquinae* is limited to the North Pacific central gyre (Drazen et al., 2012). *C. yaquinae* may not be able to adapt or relocate as the regions with low productivity expand in the gyre, likely reducing the abundance of their food source (Drazen et al., 2012).

Finally, a big impact of climate change on marine ecosystems (i.e. a significantly higher stress level) stems from declining midwater oxygen concentrations and shoaling of oxygen minimum zones (OMZs) (Booth et al., 2012). OMZ expansion in the Eastern Pacific was found to be correlated with CU intensification (Czeschel et al., 2012). Such intensification of the CU can significantly affect the CCE (Bograd et al., 2019). CU intensification is one of the factors contributing to the poleward shift in *M. productus* feeding and spawning grounds (Bograd et al., 2019). Shoaling of the thermocline and OMZs could potentially affect vertical migrations of *M. productus* larvae and could

compress the vertical habitat of adult fish as well, making them more vulnerable to commercial fishing (Gilly et al., 2013). One study found that in summer 1955, a short-term shift in water masses (from PSUW to PEW) at certain depths caused variations in "depth and thermosteric anomaly surfaces on either side of the transition" (Blanton & Pattullo, 1970]. These two OMZ zones, were separated by an oxygen enriched zone caused by vertical mixing. The enriched zone was located within my study site area near Point Conception (Blanton & Pattullo, 1970). This may be a clue as to why the location of Sta. M was primarily significant for correlations relating to *M. productus* (i.e. local biomass, local CPUE, and local depth range). This region and regions with similar characteristics (i.e. upwelling and location relative to currents) should be considered in future fishery and climate-mitigation decisions, as they are extremely important areas for fisheries and marine ecosystems. Future climate variation could alter the water properties of source waters (Bograd et al., 2015), causing variation in OMZ zones and other factors. Locations such as Sta. M may provide safe zones in the future for *M. productus* and other species in light of future climate impacts; unless upwelling of hypoxic waters occurs (Booth et al., 2012); in which the impacts would be devastating. Lastly, climate-related factors such as OMZ shoaling has resulted in a range expansion for the Humboldt Squid, potentially contributing to top-down forcing on local *M. productus* populations (Gilly et al., 2013; Zeidberg & Robison, 2007). Range expansions and increases in Humboldt Squid abundance within these ranges have been correlated with declines in *M. productus* biomass (Mooney & Zavaleta, 2016; Zeidberg & Robison, 2007), and studies have determined this species' principal prey over the coastal California slope and shelf is *M. productus*. (Zeidberg & Robison, 2007). Increased predation, schooling structure changes, and competition between and among Humboldt squid and *M. productus* could potentially threaten fisheries, Macrourid populations, and the ecosystems they reside in (Gilly et al., 2013).

Regarding fisheries, increased bycatch from commercial fishing can positively impact Macrourid populations short term due to increased carrion fluxes (Dayton et al., 2003; Drazen et al., 2012; Wallace, 2015). However, commercial overfishing may lead to a reduction in carrion flux in the deep-sea, negatively impacting Macrourids and other

species long-term (Wallace, 2015; Drazen et al., 2012). This is especially true for species whose migration patterns reflect that of *M. productus*, and who may have grown dependent on bycatch as their primary food source (Gage et al., 2005). Macrourids and other scavengers may expand their populations in response to bycatch, potentially altering the balance of ecological function (Gage et al., 2005). Additionally, overfishing can potentially lead to shifts in population structure. Such shifts could negatively impact recruitment of *M. productus* larvae, as well as cause shifts in the location and range of adult spawning (Horn & Smith, 1997). Future studies should seek to understand trends and the state of primary producers and zooplankton populations, as well as *M. productus* and Macrourid stocks, and bycatch distribution ranges/intensities in order to better predict, mitigate, and adapt to climate change and commercial fishing related impacts.

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APPENDIX A

LIST OF HYPOTHESIS

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	A	*Has Macrourid species complex' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species complex' abundance.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species complex' abundance.	Spearman Rank

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables						Time-Series
Macrourid species complex' abundance (# ind. /hr/ week)	*Coryphaenoides armatus* *Corphaenoides leptolepis* *Coryphaenoides yaquinae*	Sta. M	POC	C_N	MEI	SST	NPP		2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	B	*Has Macrourid sp.' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species' biomass.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species' biomass.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables						Time-Series
Macrourid biomass (kg per ha/der) (Regional)	*Nezumia stelgidolepis* *Albatrossia pectoralis* *Coryphaenoides acrolepis* *Nezumia liolepis* *Coryphaenoides cinereus* *Coelorinchus scaphopsis* *Malacocephalus laevis* *Grenadier unident.*	Mined	POC	C_N	MEI	SST	NPP		2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	C	*Has Macrourid sp.' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species' CPUE.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species' CPUE.	Spearman Rank

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables						Time-Series
Macrourid CPUE (num per ha/der) (Regional)	*Nezumia stelgidolepis* *Albatrossia pectoralis* *Coryphaenoides acrolepis* *Nezumia liolepis* *Coryphaenoides cinereus* *Coelorinchus scaphopsis* *Malacocephalus laevis* *Grenadier unident.*	Mined	POC	C_N	MEI	SST	NPP		2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	D	*Has Macrourid sp.' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species' body lengths.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species' body lengths.	Spearman Rank

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
Macrourid length (cm) (Regional)	*Nezumia stelgidolepis* *Albatrossia pectoralis* *Coryphaenoides acrolepis* *Nezumia liolepis*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
1	E	*Has Macrourid sp.' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid sp.' larval abundances.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid sp.' larval abundances.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
Macrourid larval abundance (10 m^2) (Regional)	*Nezumia sp.* *Albatrossia pectoralis* *Coryphaenoides acrolepis* *Macrouridae sp.*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	A	*Has Merluccius productus' population structure changed over time in relation to changing climate and surface-ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* biomass.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* biomass.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus biomass (kg per ha/der) (Regional & Local)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	B	*Has Merluccius productus' population structure changed over time in relation to changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* CPUE.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* CPUE.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus CPUE (num per ha/der) (Regional & Local)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	C	*Has Merluccius productus' population structure changed over time in relation to changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* body lengths.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* body lengths.	Spearman Rank

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus length (cm) (Regional)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
2	D	*Has Merluccius productus' population structure changed over time in relation to changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* larval abundance.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* larval abundance.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus larval abundance (10 m^2) (Regional)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
3	A	*Has the depth range of Macrourid species changed over time with changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in Macrourid species' depth distributions.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in Macrourid species' depth distributions.	Spearman Rank

Fish Variable	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
Macrourid depth (m) (Regional)	*Nezumia stelgidolepis* *Albatrossia pectoralis* *Coryphaenoides acrolepis* *Nezumia liolepis* *Coryphaenoides cinereus* *Coelorinchus scaphopsis* *Malacocephalus laevis* *Grenadier unident.*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

Question #	Question Section	Question & Hypotheses	Statistical Tests
4	A	*Has the depth range of Merluccius productus changed over time with changing climate and surface ocean conditions?*	Mann-Kendall
		Ho: With increasing changes in climate and surface ocean conditions over time, there is no significant change in *Merluccius productus'* depth distribution.	Cross Correlation Analysis
		Ha: With increasing changes in climate and surface ocean conditions over time, there is a significant change in *Merluccius productus'* depth distribution.	Spearman Rank

Fish Variables	Species Included	Data Source	Climate/Surface Condition Variables					Time-Series
M. productus depth (m) (Regional & Local)	*Merluccius productus*	Mined	POC	C_N	MEI	SST	NPP	2011-2017

APPENDIX B

RESULTS TABLES

MACROURIDS (GROUPED)

Variables			Cross Correlation			Spearman Rank		Mann-Kendall Trend Tests (Time Series Trend)				
Fish Variable	Scale	Environmental Variable	Correlation	Lag (# weeks)	Direction (+/-)	rho	P-Value	Hypothesis	Trend	S (Test Statistic)	Trend Direction	P-Value
Macrourid spp. complex' abundance	Local (Sta. M)	POC	-0.23	6	(-)	-0.22	0.001	Ha	Yes	8590	Increasing	< 0.0001
		C_N	-0.31	67	(-)	-0.32	0.000					
		SST	0.21	22	(+)	0.20	0.001					
		NPP	-0.36	50	(-)	-0.35	0.000					
		MEI	0.39	56	(+)	0.40	0.000					
Macrourid biomass	Regional	POC	0.33	0	(+)	0.27	0.042	H0	No	NA	NA	NA
		C_N	0.24	1	(+)	0.29	0.043					
		SST	-0.15	2	(-)	-0.15	0.181					
		NPP	-0.23	3	(-)	-0.28	0.010					
		MEI	0.24	102	(+)	0.21	0.073					
Macrourid CPUE	Regional	POC	-0.29	14	(-)	-0.24	0.041	H0	No	NA	NA	NA
		C_N	0.26	3	(+)	0.25	0.084					
		SST	-0.13	3	(-)	-0.13	0.244					
		NPP	-0.16	3	(-)	-0.20	0.072					
		MEI	0.14	50	(+)	0.15	0.181					
Macrourid depth	Regional	POC	0.27	3	(+)	0.23	0.099	H0	No	NA	NA	NA
		C_N	-0.33	2	(-)	-0.35	0.020					
		SST	0.19	36	(+)	0.14	0.254					
		NPP	-0.20	25	(-)	-0.23	0.048					
		MEI	0.15	8	(+)	0.15	0.211					
Macrourid length	Regional	POC	0.27	0	(+)	0.04	0.801	Ha	Yes	640	Increasing	0.0023
		C_N	-0.48	39	(-)	-0.53	0.000					
		SST	0.33	30	(+)	0.40	0.001					
		NPP	-0.52	56	(-)	-0.58	0.000					
		MEI	0.34	23	(+)	0.35	0.002					

Table #1. Table of statistical analyses results for relationships between Macrourid spp.' variables and environmental variables. Gray and bold cells represent most significant findings.

MERLUCCIUS PRODUCTUS

Fish Variable	Scale	Environmental Variable	Correlation	Lag (# weeks)	Direction (+/-)	rho	P-Value	Hypothesis	Trend	S (Test Statistic)	Trend Direction	P-Value
			Cross Correlation			**Spearman Rank**		**Mann-Kendall Trend Tests (Time Series Trend)**				
M. productus biomass	Regional	POC	-0.25	4	(-)	-0.21	0.101					
		C_N	0.34	2	(+)	0.32	0.024					
		SST	-0.19	38	(-)	-0.17	0.114	H0	No	NA	NA	NA
		NPP	0.34	12	(+)	0.35	0.001					
		MEI	-0.20	4	(-)	-0.23	0.033					
M. productus CPUE	Regional	POC	0.31	16	(+)	0.30	0.013					
		C_N	0.35	18	(+)	0.33	0.007					
		SST	-0.27	39	(-)	-0.27	0.012	H0	No	NA	NA	NA
		NPP	0.30	7	(+)	0.34	0.002					
		MEI	-0.26	1	(-)	-0.29	0.008					
M. productus biomass	Local	POC	0.25	0	(+)	0.07	0.839					
		C_N	-0.53	3	(-)	-0.55	0.171					
		SST	0.73	6	(+)	0.75	0.000	Ha	Yes	63	Increasing	0.017
		NPP	-0.53	2	(-)	-0.68	0.003					
		MEI	0.68	15	(+)	0.76	0.000					
M. productus CPUE	Local	POC	0.53	7	(+)	0.47	0.070					
		C_N	0.45	0	(+)	0.53	0.148					
		SST	0.83	6	(+)	0.86	< 2.2e-16	H0	No	NA	NA	NA
		NPP	-0.67	2	(-)	-0.80	0.000					
		MEI	0.48	15	(+)	0.55	0.018					
M. productus depth	Regional	POC	0.35	14	(+)	0.30	0.010					
		C_N	0.34	39	(+)	0.31	0.027					
		SST	0.22	1	(+)	0.30	0.006	H0	No	NA	NA	NA
		NPP	0.24	16	(+)	0.26	0.017					
		MEI	-0.13	0	(-)	-0.15	0.180					
M. productus depth	Local	POC	-0.58	8	(-)	-0.58	0.016					
		C_N	0.57	3	(+)	0.90	0.005					
		SST	-0.32	6	(-)	-0.30	0.232	H0	No	NA	NA	NA
		NPP	0.20	12	(+)	0.26	0.294					
		MEI	0.10	6	(+)	0.07	0.794					
M. productus length	Regional	POC	-0.39	4	(-)	-0.45	0.000					
		C_N	0.24	2	(+)	0.22	0.125					
		SST	-0.25	4	(-)	-0.28	0.010	H0	No	NA	NA	NA
		NPP	-0.22	15	(-)	-0.24	0.028					
		MEI	0.23	52	(+)	0.25	0.024					
M. productus larval abundance	Regional	POC	-0.32	5	(-)	-0.20	0.168					
		C_N	0.64	4	(+)	0.58	0.000					
		SST	0.58	14	(+)	0.55	0.000	H0	No	NA	NA	NA
		NPP	-0.39	2	(-)	-0.45	0.000					
		MEI	-0.18	0	(-)	-0.17	0.198					

Table #2. Table of statistical analyses results for relationships between *M. productus'* variables and environmental variables. Gray and bold cells represent most significant findings.

APPENDIX C

RESULTS PLOTS

VARIABLES OVER TIME

Environmental Variables
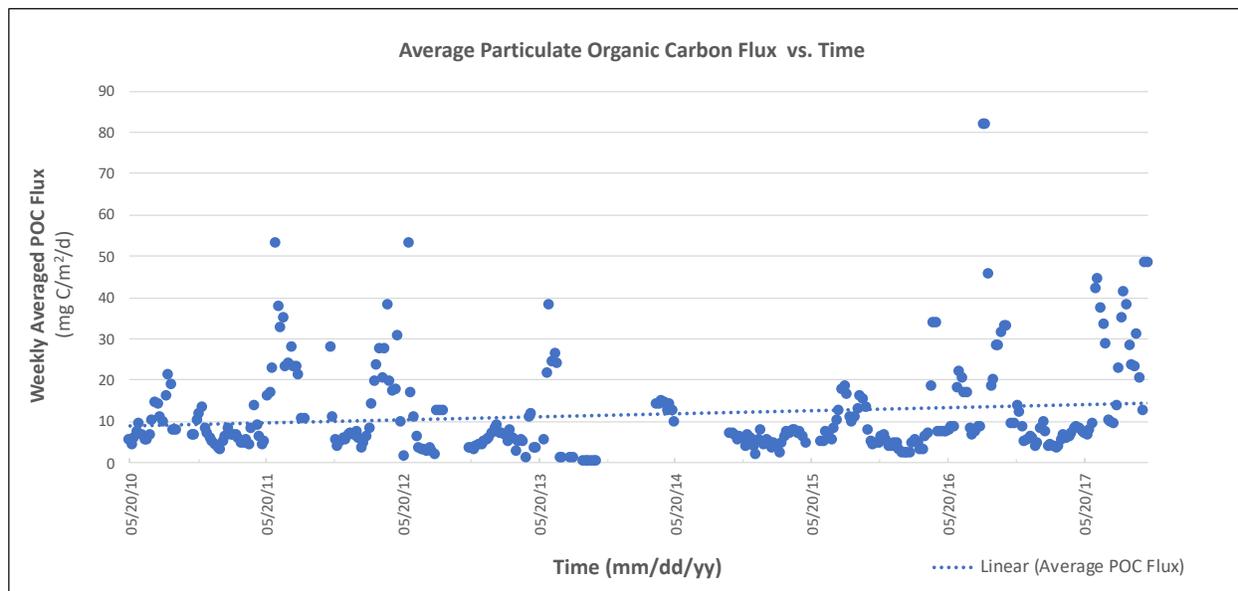
Plot 1. Weekly averaged POC flux (mg C/m^2/d), at Station M, during the 2011-2017 study period.
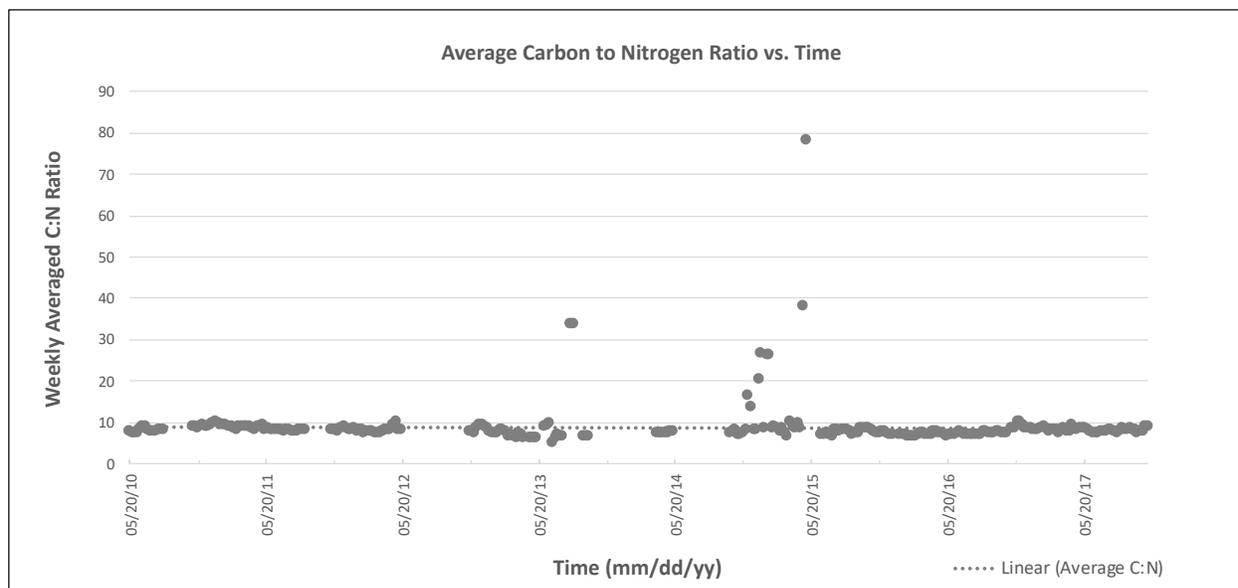
Plot 2. Weekly averaged carbon to nitrogen ratios, at Station M, during the 2011-2017 study period.
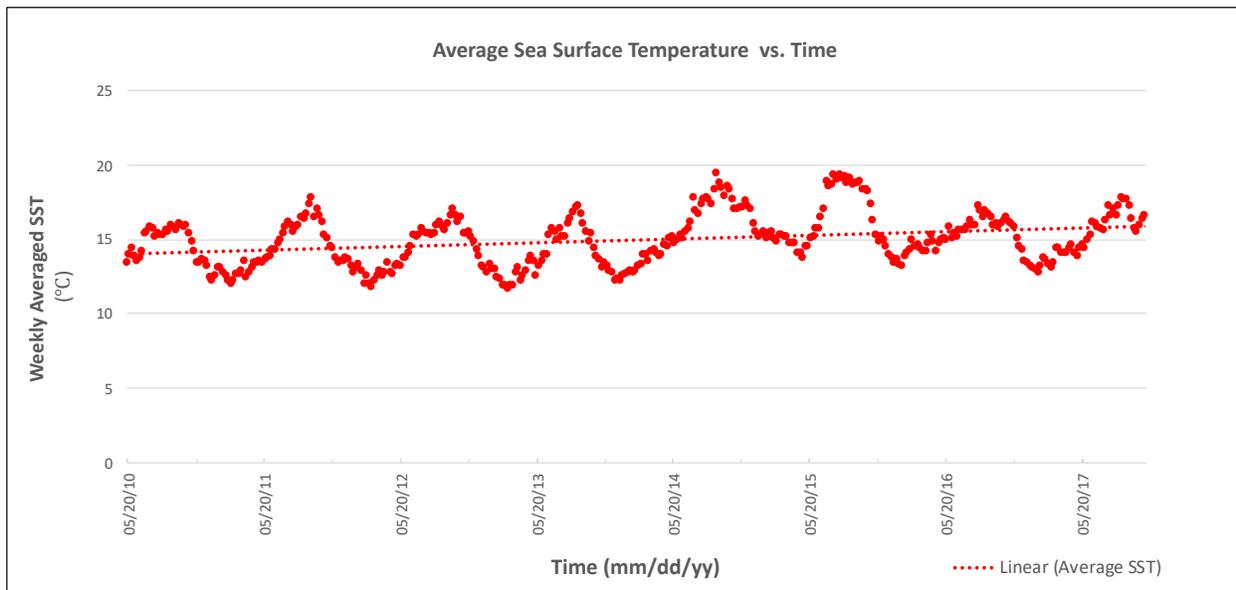
Plot 3. Weekly averaged SST (°C), for the California coast, during the 2011-2017 study period.
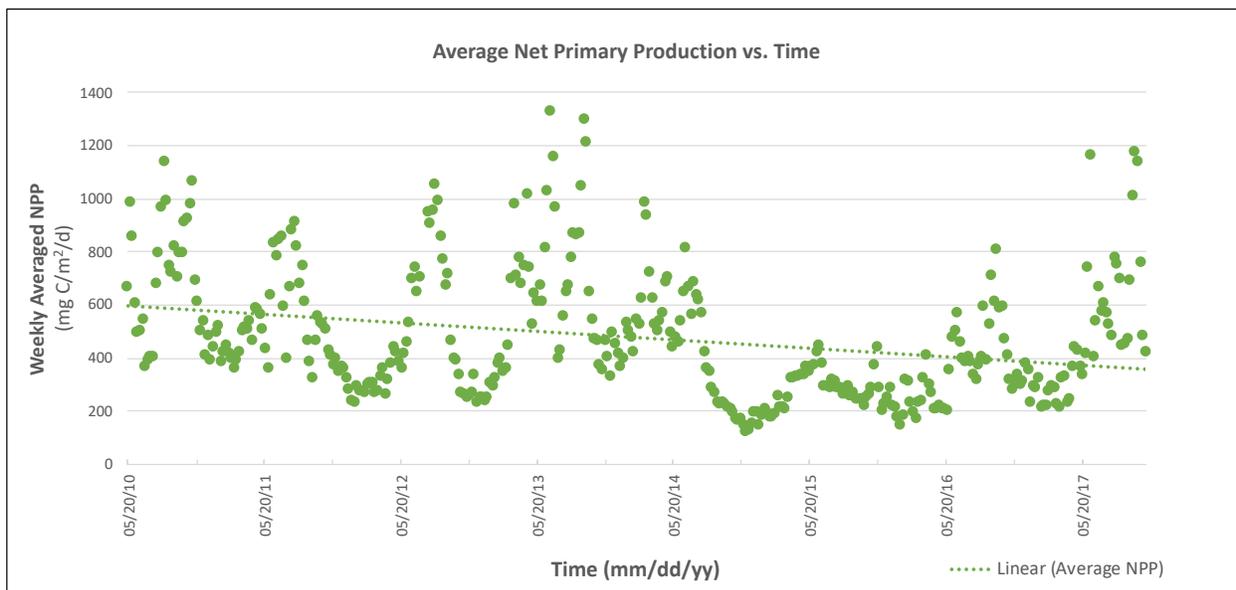
Plot 4. Weekly averaged NPP (mg C/m2/d), at Station M, during the 2011-2017 study period.
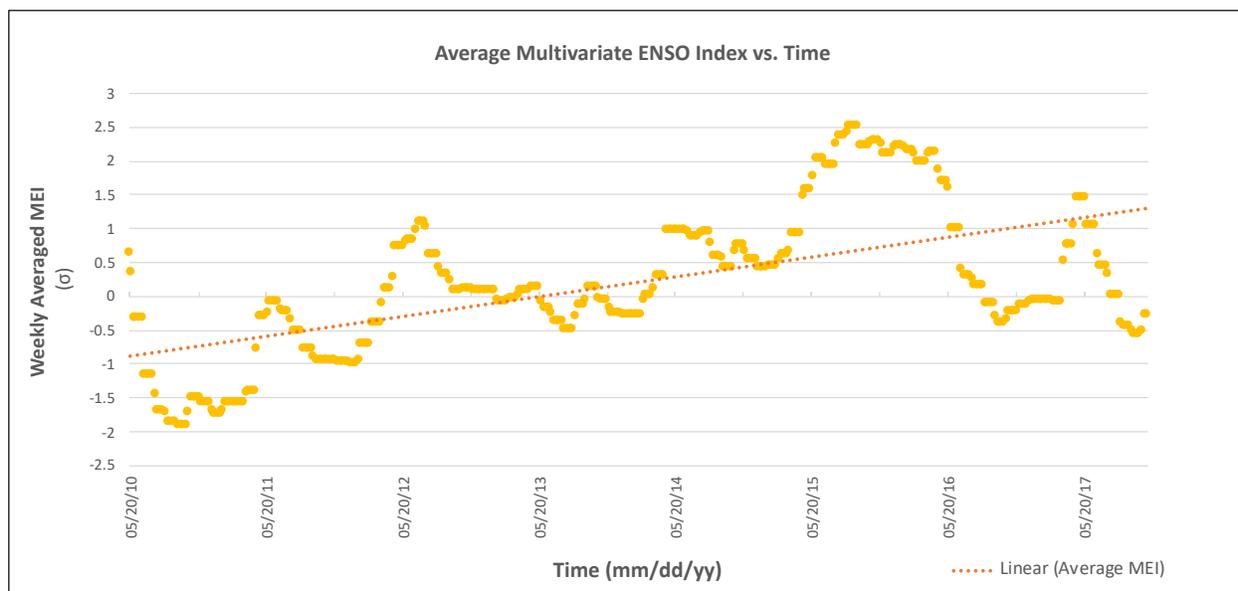
Plot 5. Weekly averaged MEI (σ), for the California coast, during the 2011-2017 study period.

Macrourid Variables
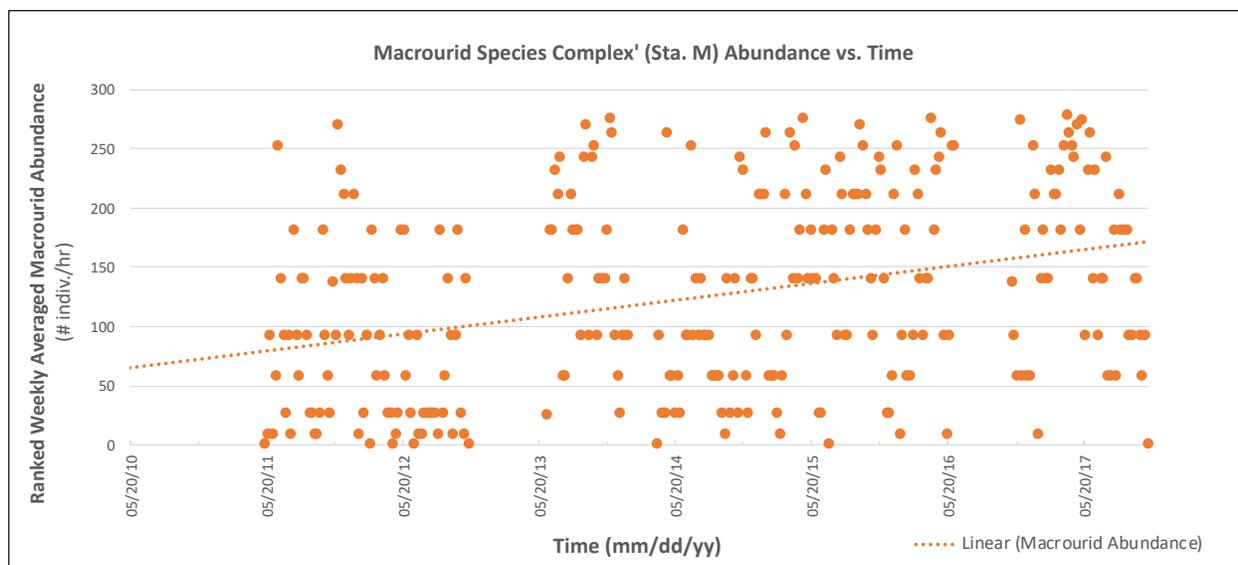
Plot 6. Ranked weekly averaged Macrourid species complex' abundance (# indiv./hr), at Station M, during the 2011-2017 study period.
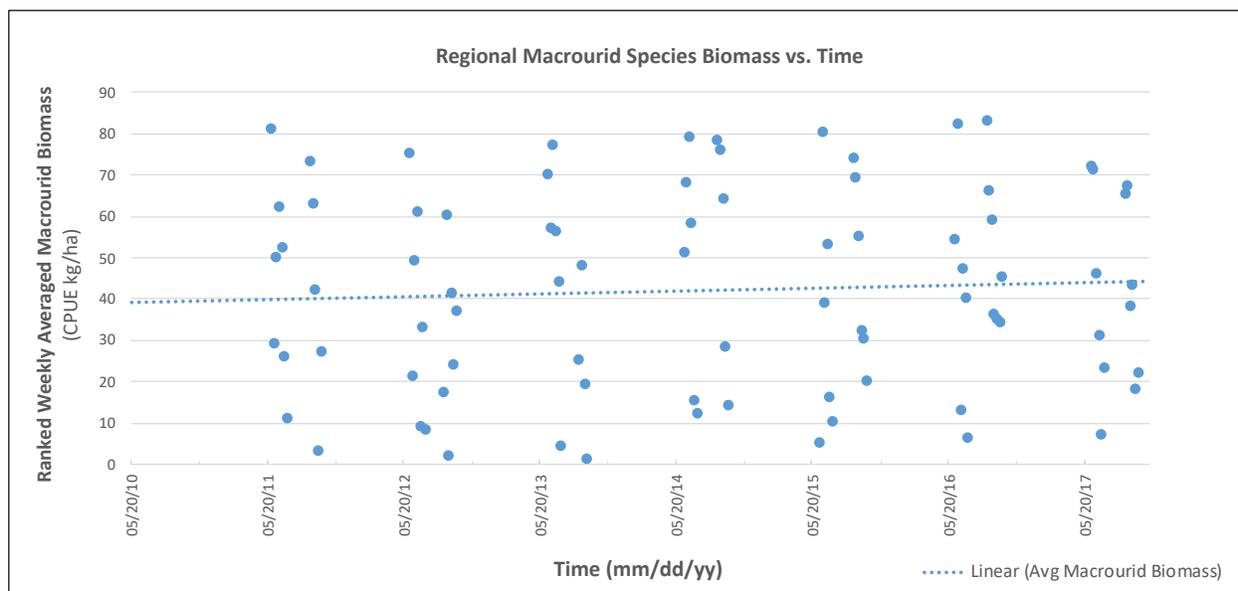
Plot 7. Ranked weekly averaged regional Macrourid spp.' biomass (CPUE kg/ha), for the California coast, during the 2011-2017 study period.
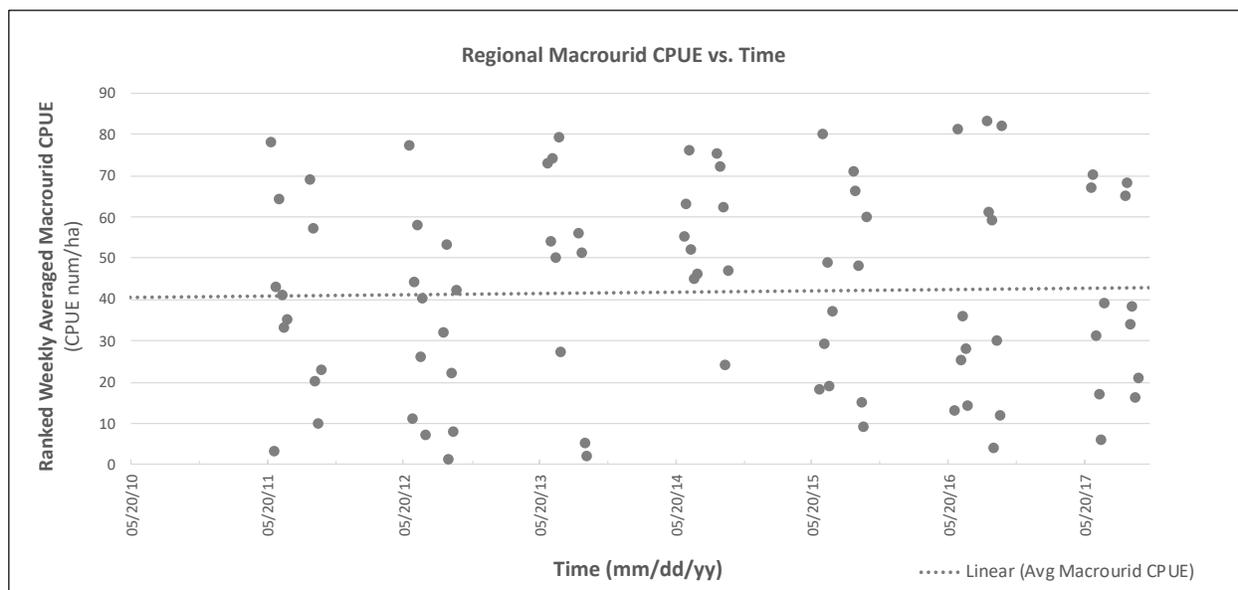
Plot 8. Ranked weekly averaged regional Macrourid spp.' CPUE (num/ha), for the California coast, during the 2011-2017 study period.
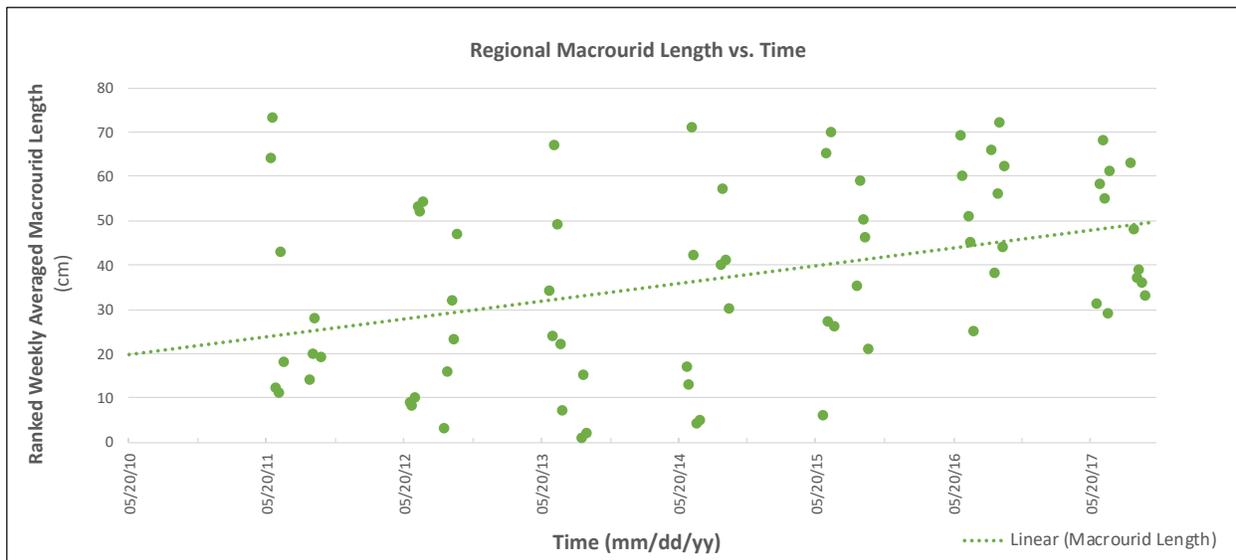
Plot 9. Ranked weekly averaged regional Macrourid spp.' length (cm), for the California coast, during the 2011-2017 study period.
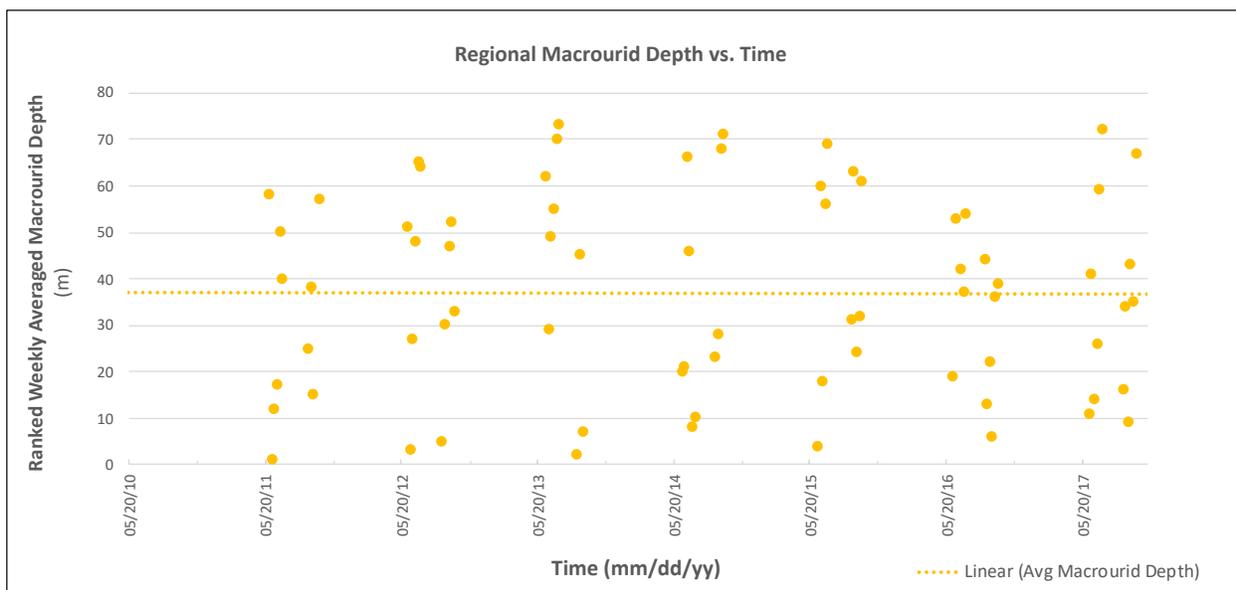
Plot 11. Ranked weekly averaged regional Macrourid spp.' depth (m), for the California coast, during the 2011-2017 study period.

Merluccius Productus **Variables**
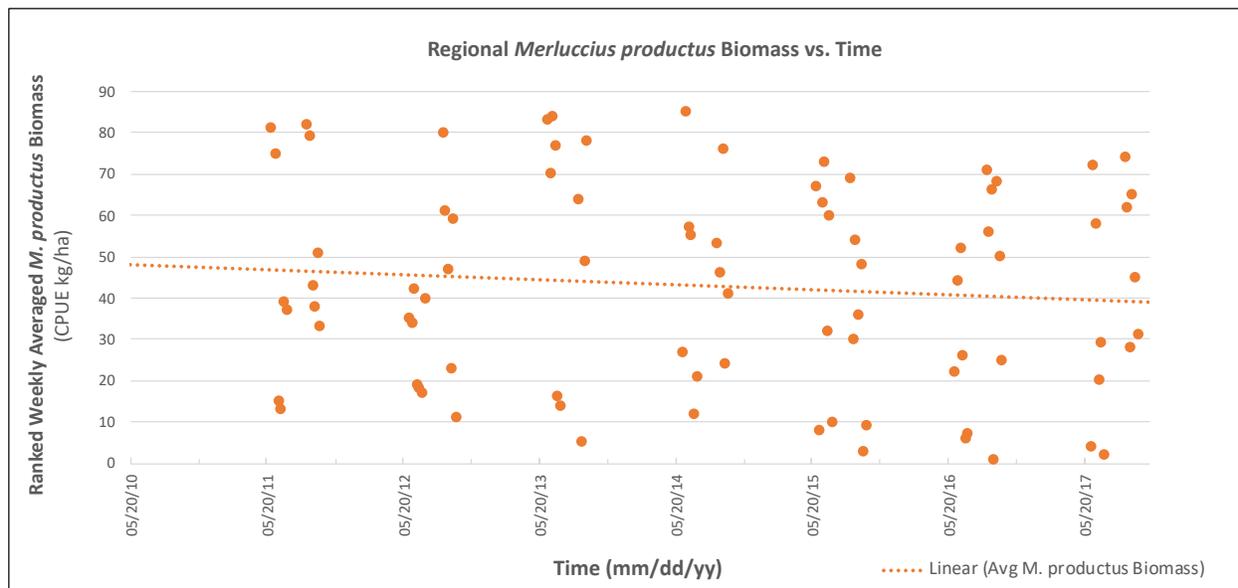
Plot 12. Ranked weekly averaged regional *M. productus* biomass (CPUE kg/ha), for the California coast, during the 2011-2017 study period.
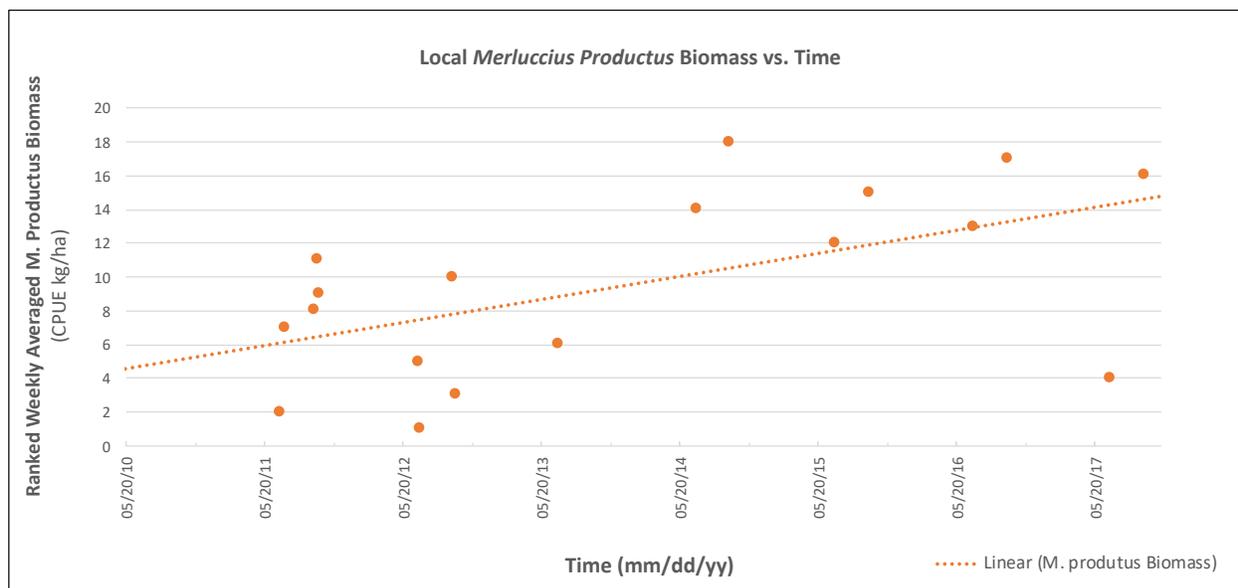
Plot 13. Ranked weekly averaged *M. productus* biomass (CPUE kg/ha), localized within 100 nmi of Station M, during the 2011-2017 study period.
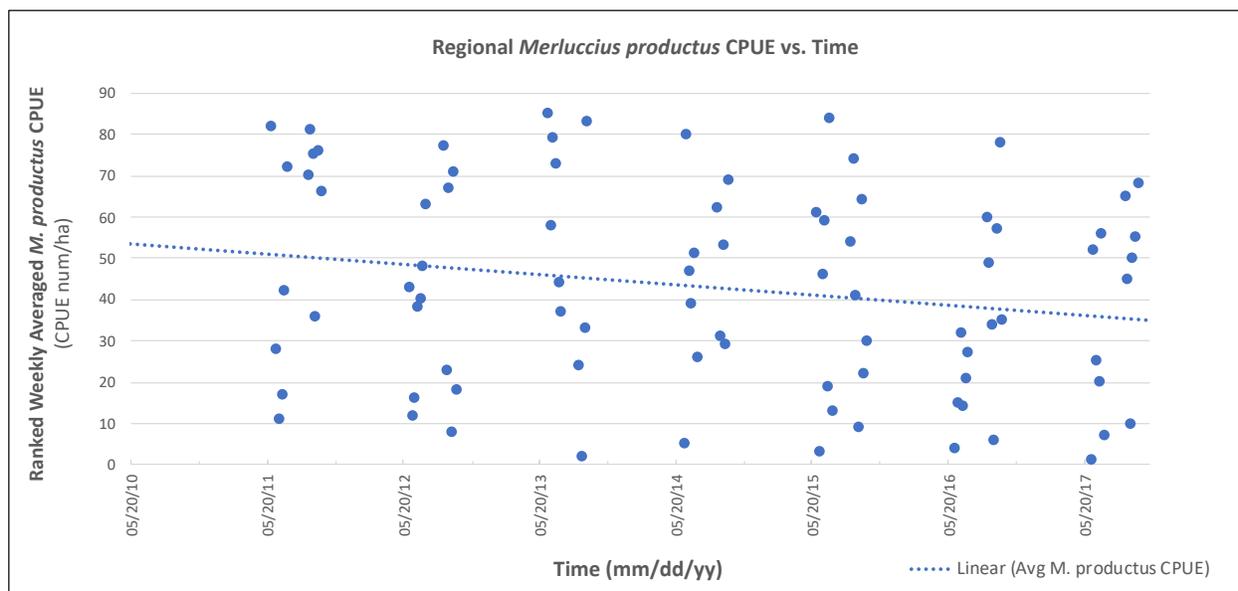
Plot 14. Ranked weekly averaged regional *M. productus* CPUE (num/ha), for the California coast, during the 2011-2017 study period.
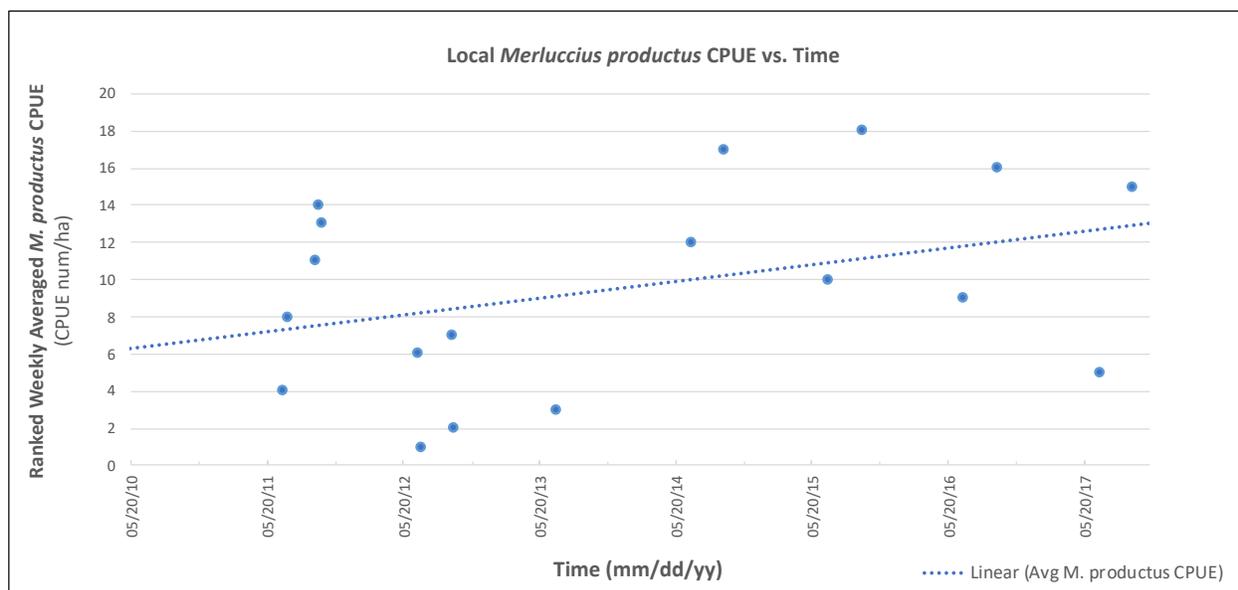
Plot 15. Ranked weekly averaged *M. productus* CPUE (num/ha), localized within 100 nmi of Station M, during the 2011-2017 study period.
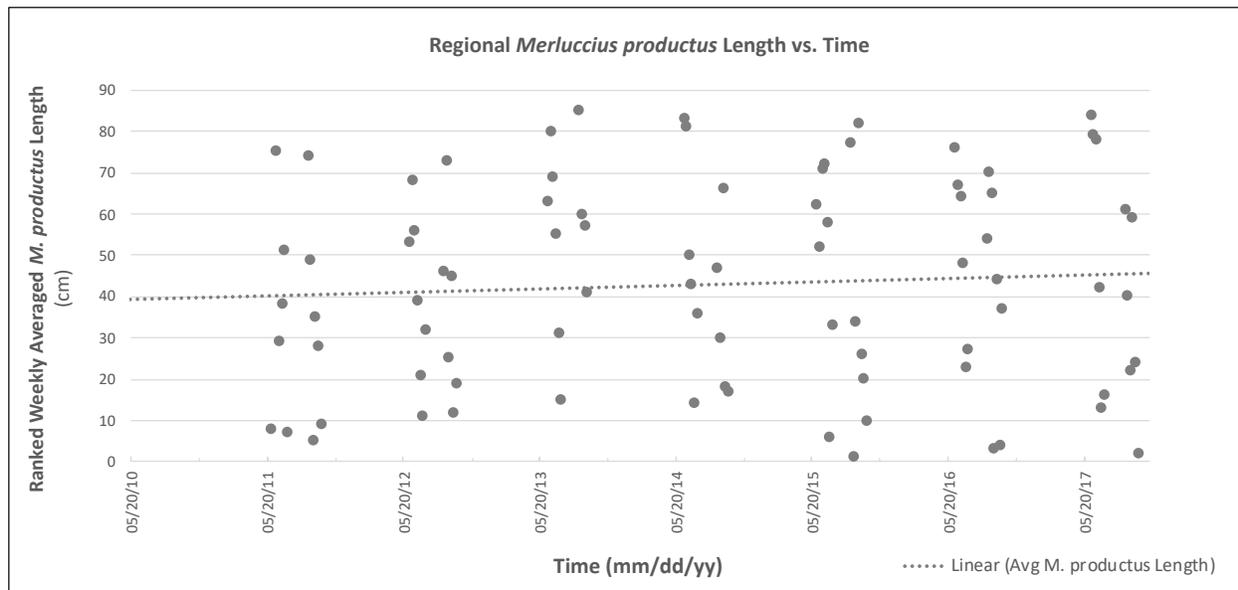
Plot 16. Ranked weekly averaged regional *M. productus* length (cm), for the California coast, during the 2011-2017 study period.
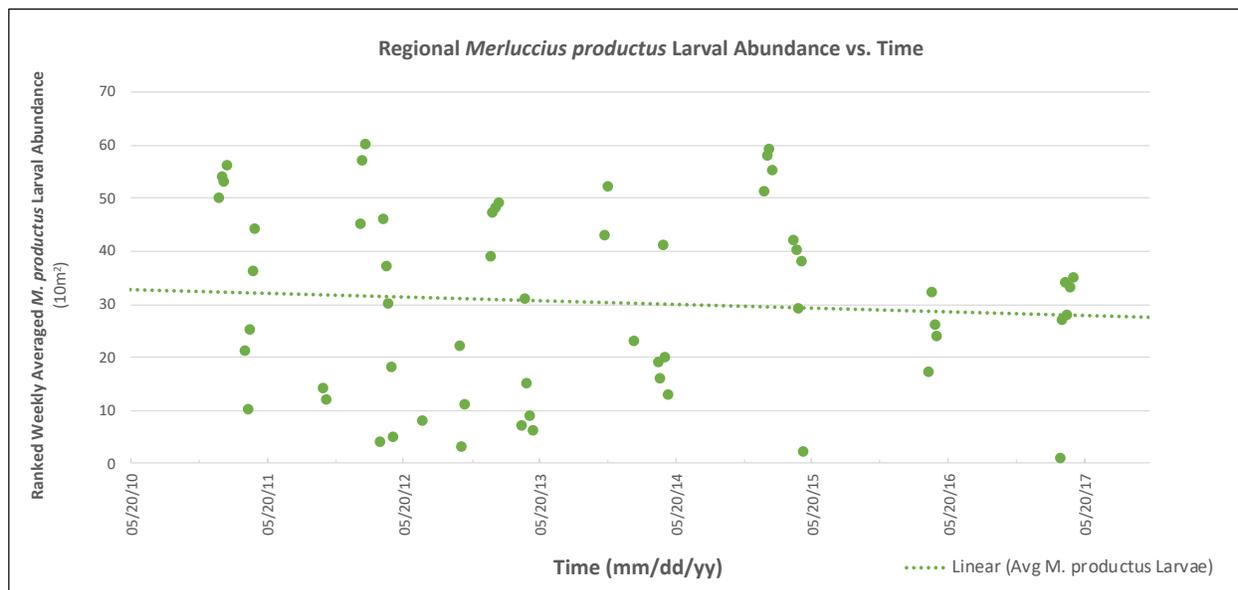
Plot 17. Ranked weekly averaged regional *M. productus* larval abundance (10m²), for the California coast, during the 2011-2017 study period.
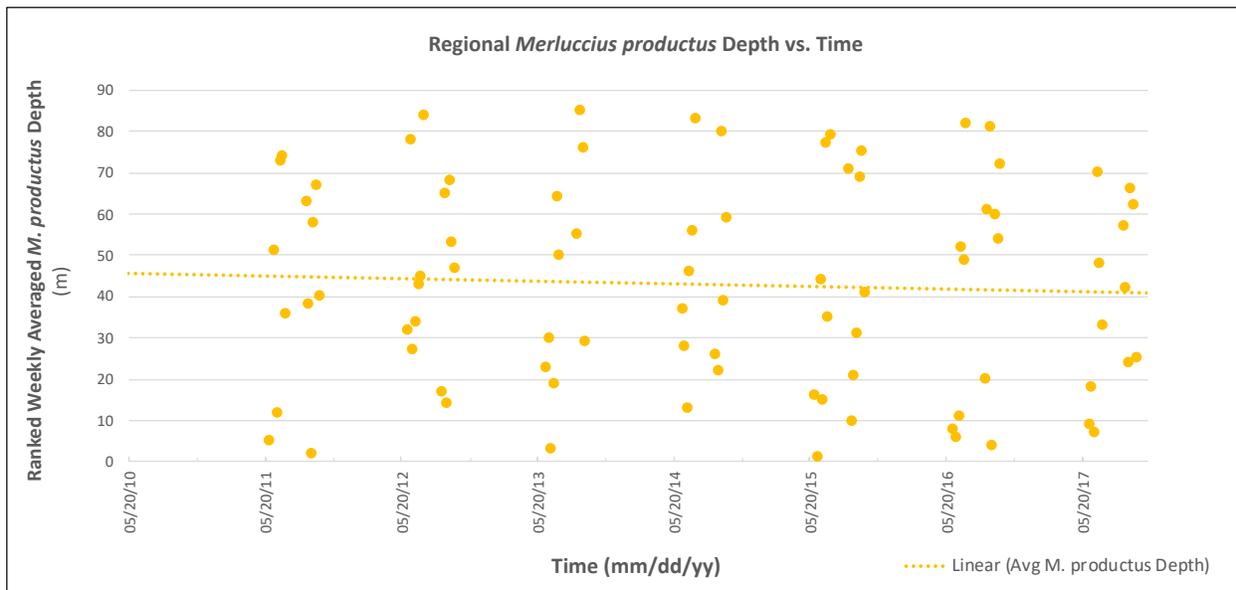
Plot 18. Ranked weekly averaged regional *M. productus* depth (m), for the California coast, during the 2011-2017 study period.
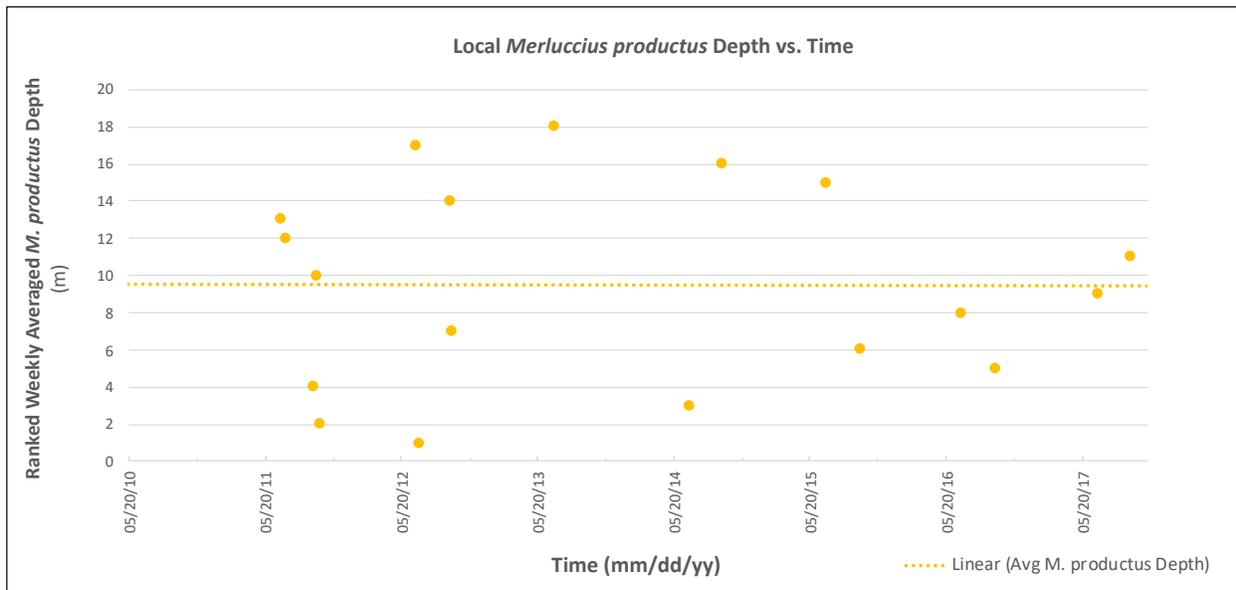
Plot 19. Ranked weekly averaged *M. productus* depth (m), localized within 100 nmi of Station M, during the 2011-2017 study period.

MACROURID PLOTS
CROSS CORRELATION   SCATTER PLOT

MEI Leads Macrourid Length

value of correlation vs. lag–number of weekly increments

0.34   0

Regional Macrourid Length Follows MEI vs. Lag (Weeks)

R^2 is 0.1041 lag = 0 weeks

NPP Leads Macrourid Length

value of correlation vs. lag–number of weekly increments

−0.52   0

Regional Macrourid Length Follows NPP vs. Lag (Weeks)

R^2 is 0.3173 lag = 0 weeks
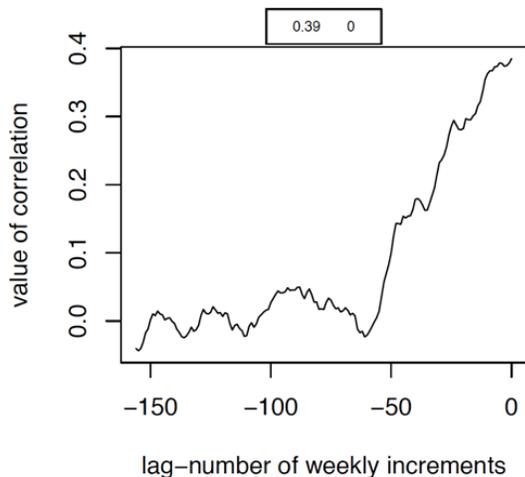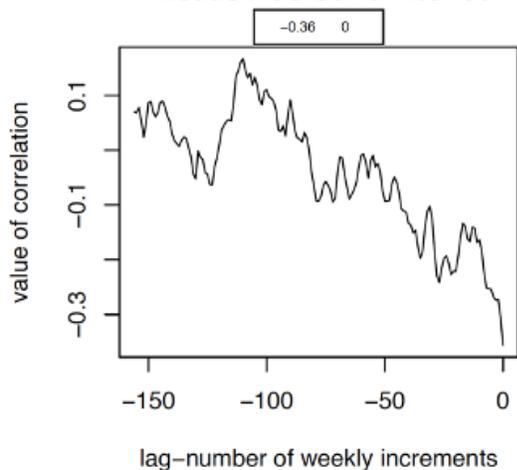
C_N Leads Macrourid Length

value of correlation vs. lag–number of weekly increments

−0.48   0

Regional Macrourid Length Follows C_N vs. Lag (Weeks)

R^2 is 0.2871 lag = 0 weeks

MERLUCCIUS PRODUCTUS PLOTS
CROSS CORRELATION   SCATTER PLOT
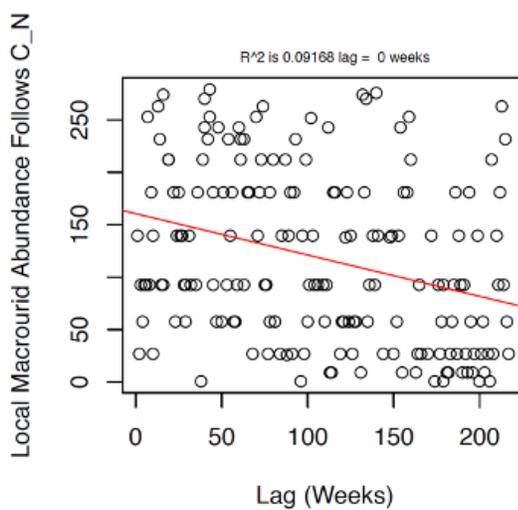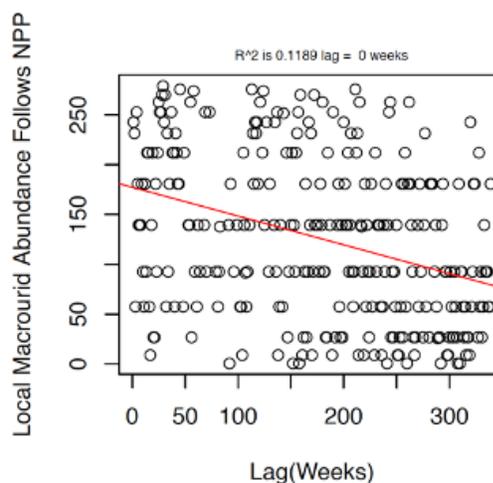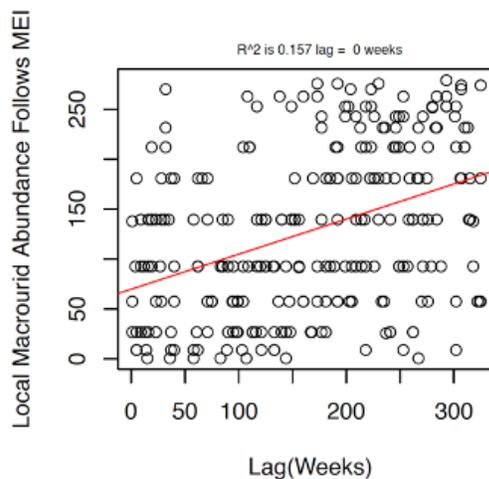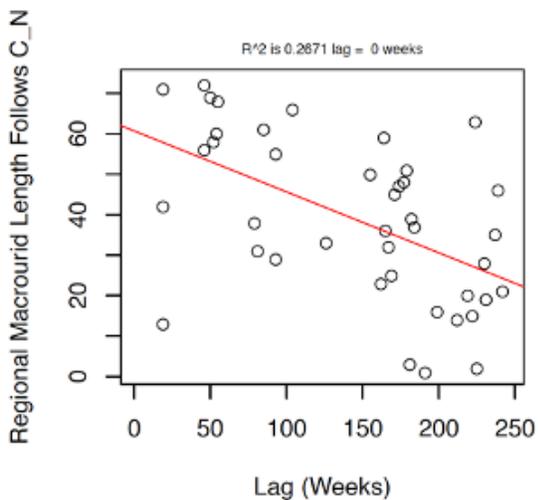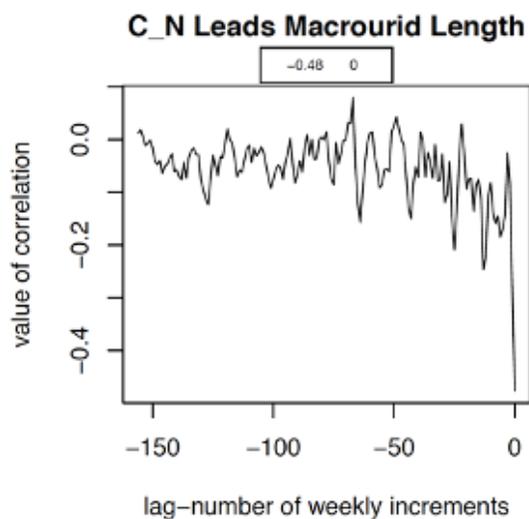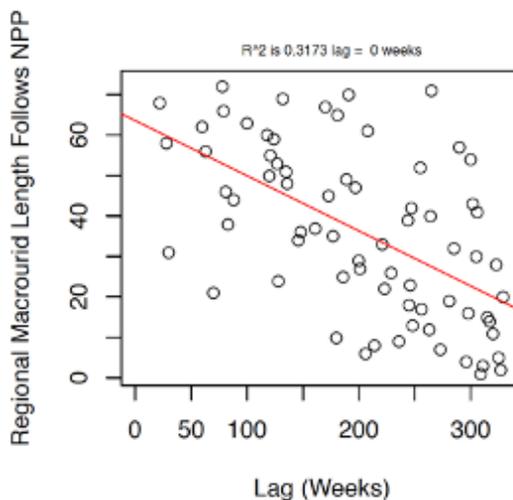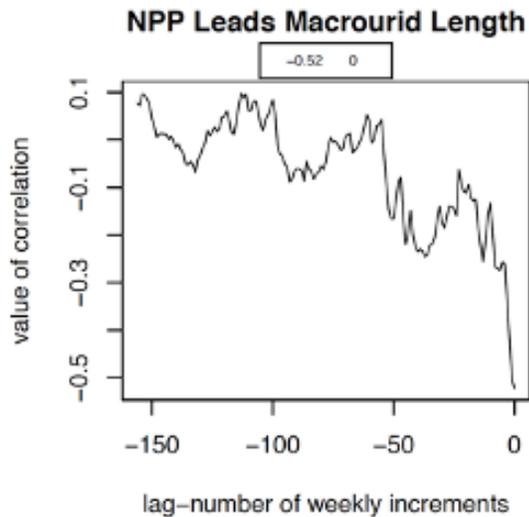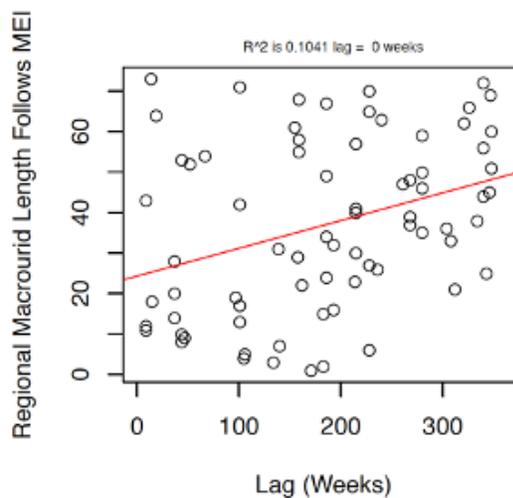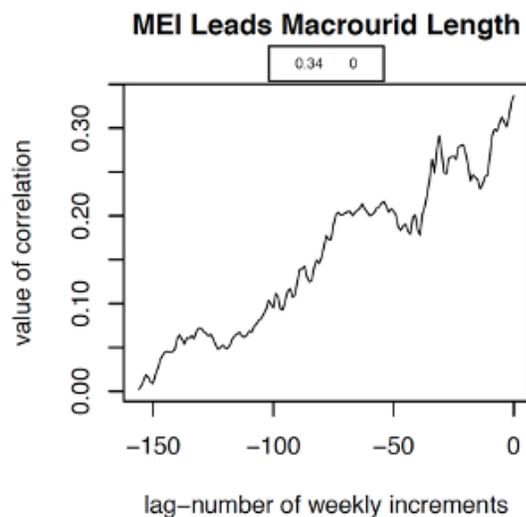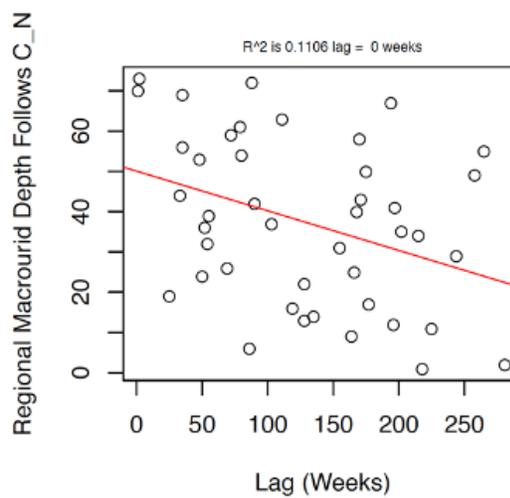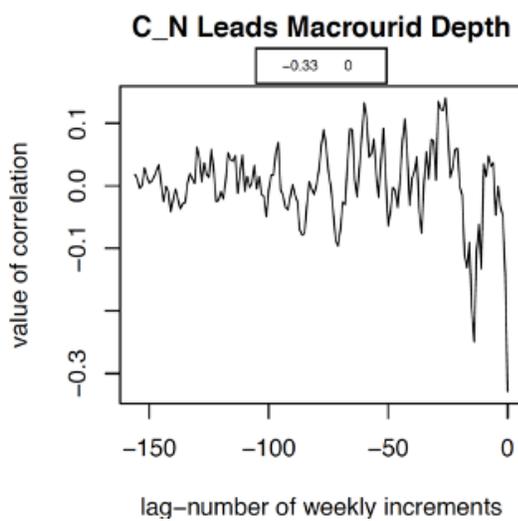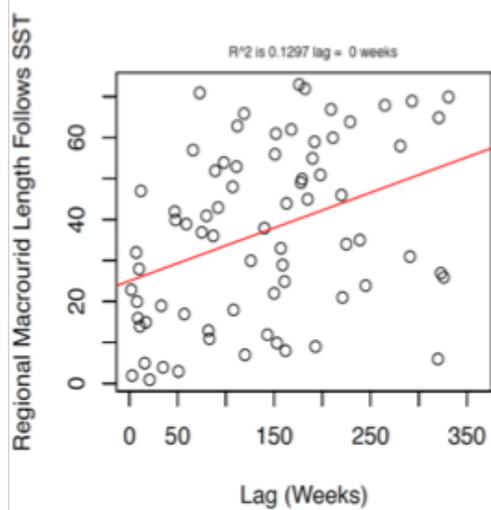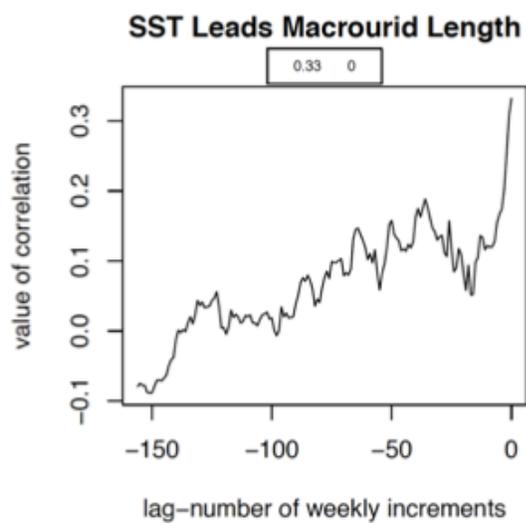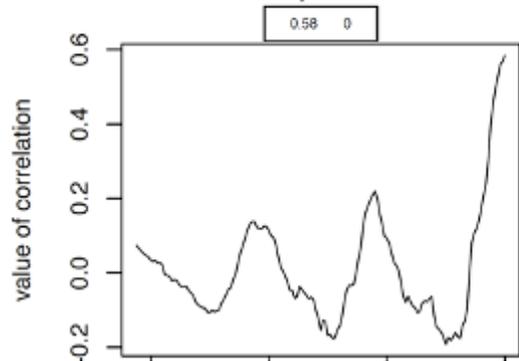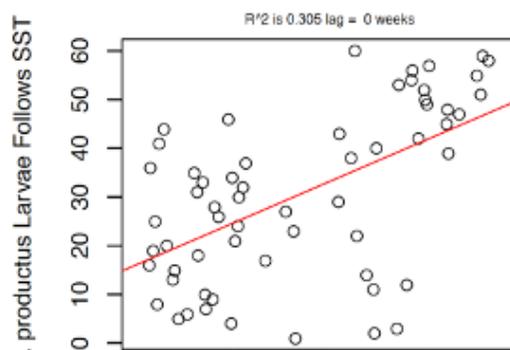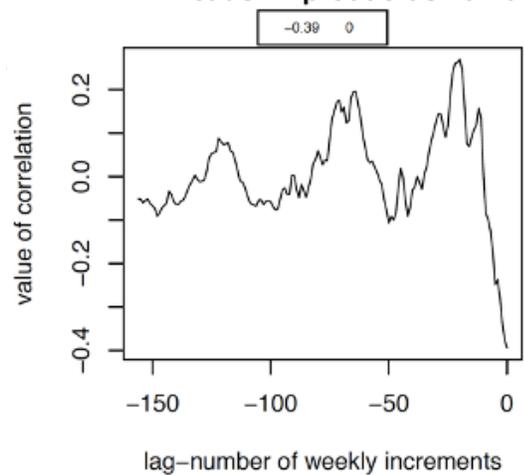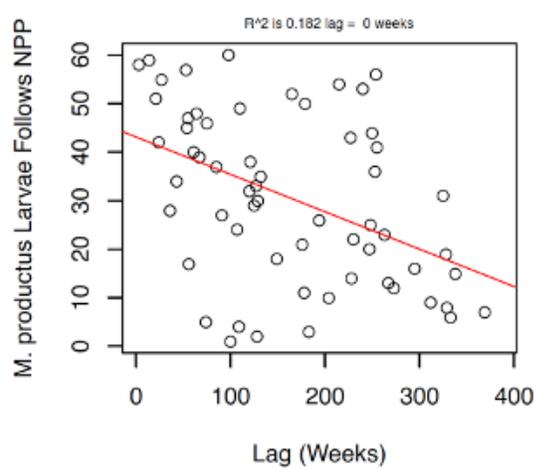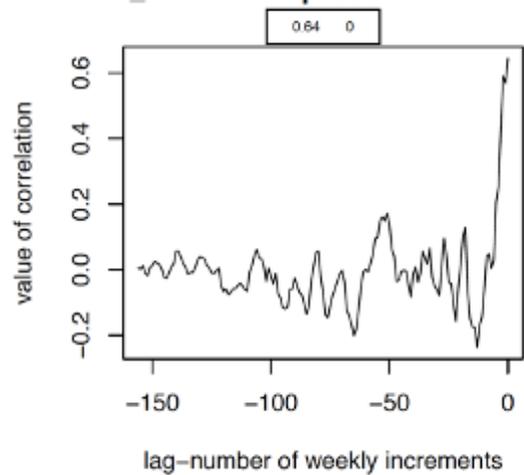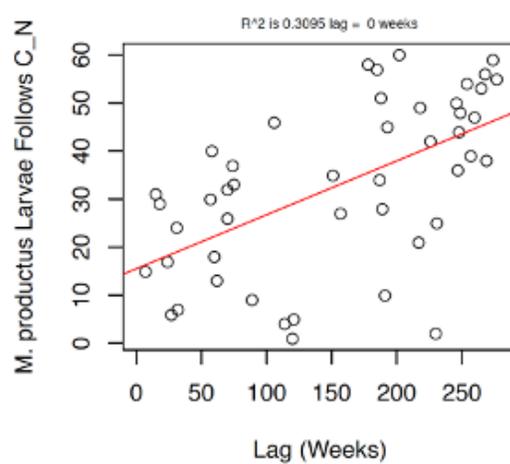
C_N Leads M. productus Depth

0.57   0

value of correlation
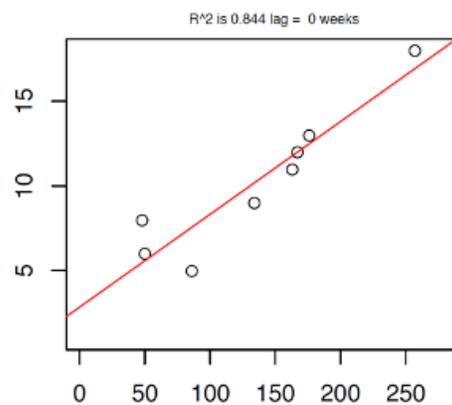
POC Leads M. productus Depth

−0.58   0

value of correlation

lag−number of weekly increments

SST Leads M. productus Depth

−0.32   0

value of correlation

lag−number of weekly increments

R^2 is 0.844 lag = 0 weeks

Local M. productus Depth Follows C_N

R^2 is 0.2804 lag = 0 weeks
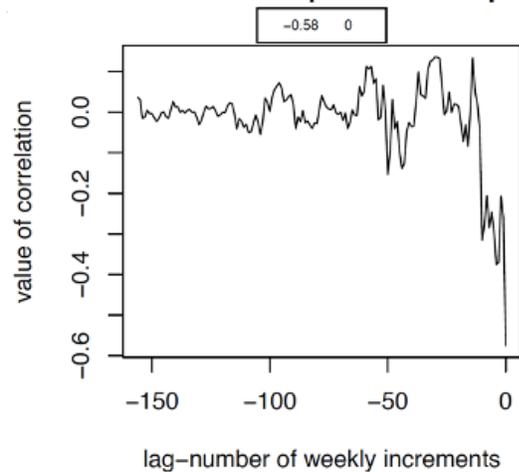
Local M. productus Depth Follows POC

Lag (Weeks)

R^2 is 0.05802 lag = 0 weeks

Local M. productus Depth Follows SST

Lag (Weeks)