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UNIVERSITY OF SAN DIEGO

San Diego

What drives larval condition for Northern Anchovy (*Engraulis mordax*)? Implications for coastal pelagic species recruitment fluctuations and fishery management practices

A thesis submitted in partial satisfaction of the
requirements for the degree of

Master of Science in Environmental and Ocean Sciences

by

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DEDICATION

To my mom and dad, who relentlessly supported my pursuit of higher education and raised me to be an empowered, curious, and ambitious woman. I love you.

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ABSTRACT

Discerning the causes of population boom and bust cycles for coastal pelagic species (CPS) has been a major focus of fisheries management research since the early 20th century. One factor that has been linked to year-class strength is larval survival, which can be heavily influenced by larval condition, growth rate, maternal investment, and environmental variables such as water temperature, salinity, oxygen, and chlorophyll *a*. Condition was determined by the following morphological measurements: standard body length (SL), muscular height at the anal fin (MHA), and muscular height at the pectoral fin (MHP). Maternal investment (size-at-hatch) was quantified by sagittae otolith core diameter and larval growth rate was quantified by the width of the otolith increments. The SL, MHA, MHP, recent growth rate (average otolith increment widths of last 3 days of life), survival (age), and maternal investment were measured for 127 two to eight week-old larvae collected from San Diego to San Francisco from 2009-2019. Linear Regressions and Generalized Linear Mixed Models (GLMMs) were then used to analyze what relationships the environment and maternal investment had with larval condition, survival, and recent growth rate. GLMMs demonstrated that larval condition and survival increased when fish had larger otolith core diameters. Larval condition also increased when fish were collected from more southern latitude waters with slightly above average temperatures (residual of 0.25), low chlorophyll, and low salinity. Larval survival also increased when fish were collected in water with colder temperatures and low chlorophyll concentrations. Larval growth rate had no significant relationships to environmental variables or

otolith core diameter. Finally, when mapping the lifelong growth rate trajectories for various years and stations with at least 5 fish replicates, it was found there is a significant difference in larval growth trajectories between years with differing levels of recruitment success, faster otolith growth occurred during high recruitment years. This preliminary finding supports that larval growth rates could have huge implications for year-class strength but further analyses are needed. Overall, it was concluded that maternal investment and environmental conditions have a very important role in controlling larval condition and survival. Future fisheries studies should analyze the relationship between larval condition and recruitment success as well as determine what drives maternal investment and how it is best measured.

CHAPTER 1: INTRODUCTION

1.1. Introduction

20th Century Fishery Oceanography

Since the early 20th century, a main focus of fisheries research, in order to manage population sizes, has been to understand recruitment fluctuation (Hjort 1926; Houde 2008). For many species, recruitment (also referred to as year-class strength) is defined as the biomass of larvae that survive early life stages to become juvenile fish, which have a high probability to reach sexual maturity and contribute to population growth (James et al. 2003). For small pelagic fish species (also known as small ray-finned fish or coastal pelagic species (CPS)), that experience drastic population fluctuations due to high recruitment variability, it is crucial to understand which trophodynamic and hydrodynamic conditions lead to population booms and busts in order to effectively manage their populations (Peck et al. 2014). This field of science, fishery oceanography, investigates oceanic processes that impact marine ecosystems and the ecosystem's relationship to the abundance, distribution, and availability of fishery species (Hare 2014). As an applied science, the goal of fishery oceanography is to provide best practices for scientists, managers, and fishers to ensure long-lasting and sustainable fishery populations, and understanding the mechanisms that actually drive recruitment variability is thus fundamental to the field (Hare 2014).

For coastal pelagic species worldwide, their short life span, generation time, high fecundity, and strong relationship to lower trophic levels and bottom-up processes leads naturally-occurring population boom and bust cycles that are

closely linked to environmental changes (Chavez et al. 2003; McClatchie et al. 2017); yet, it is still unclear what causes these fluctuations in both population size and recruitment success for most CPS (Checkley et al. 2017; Bode et al. 2018; Peck et al. 2021; Swalethorp et al. 2022). In 1914, a Norwegian fishery biologist, Johan Hjort, published seminal hypotheses explaining what causes small pelagic's recruitment variability: migration patterns, larval survival, parental investment, prey availability, and larval dispersal (Hjort 1914). Hjort's hypotheses set the stage and opened the floodgates for fisheries investigation. Over the past century, fishery biologists have published evidence for many hypotheses that different abiotic and biotic factors impact fish species' recruitment variability and hence population size (Hare 2014). For example, variability in predation, the physiology of the environment (temperature, salinity, oxygen, etc...), growth rate, fishing pressure, adult prey, and adult predation can impact fish recruitment variability (Odum et al. 1955; Beverton 1957; Fry 1971; Anderson 1988; Bailey & Houde 1989; Neill et al. 1994). In short, to answer the question of what influences small pelagic fish recruitment and population size, it can be concluded that 'almost everything' does, from the quality of a mother's eggs to the day her offspring die (Lasker 1985). The challenge, then, is to determine 'what limits clupeoides mostly?'(and)... When, in the life cycle does this occur?" (Lasker 1985)

Although multiple abiotic and biotic factors can influence CPS recruitment variability, some factors hold a greater influence on adult mortality versus larval mortality (Hare 2014). For example, fishing pressure is more relevant to adult survival while prey abundance and distribution is more relevant

to prerecruit survival (Hare 2014). Here, we focus on what impacts survival in early life. Hjort originally hypothesized, which others later built upon, the concepts that year-class strength is influenced by: quality and quantity of eggs (maternal investment), feeding success of larvae (Hjort's Critical Period, Lasker's Stable Ocean, Cushing's Match-Mismatch, and Cury and Roy's Optimal Environmental Window hypotheses), and whether currents move larvae to locations with ideal environmental conditions for survival (Hjort's Aberrant Drift hypothesis) (Hjort 1914; Lasker 1981; Cury & Roy 1989; Cushing 1990; Houde 2008). On average, although sea temperature can modify the larval development timeline drastically, most small pelagic fish hatch roughly three days after fertilization and have a larval duration of 70-90 days (Butler et al. 1993; Peck et al. 2013; Davison et al. 2017). By day four of the larval stage, larvae have absorbed their yolk sack and need to start feeding on prey in order to survive (Hunter 1977). Although many larval fish start feeding prior to complete yolk sac absorption, the yolk sac provides a critical energy supply that allows larvae to develop their hunting and swimming skills (Rønnestad et al. 2013). Complete yolk-sac absorption marks the start of Hjort's "Critical Period." With minimal swimming capabilities and a depleted yolk-sac, larvae are very vulnerable during the Critical Period; if they are unsuccessful at capturing prey, they will die from starvation, weakening the species' year-class strength and recruitment success (Lasker 1985).

There are several subsequent hypotheses that state conditions at which fish are more likely to survive and avoid starvation during the Critical Period and the

entire larval stage. First, Cushing's Match-Mismatch hypothesis, which has been supported by many fish stocks (*Clupea harengus*, *Gadus morhua*, *Hippoglossoides platessoides*, and *Oncorhynchus nerka*) spiny lobsters (*Jasus edwardsii*), and Dungeness crab (*Metacarcinus magister*), states that a match in timing with spawning and larval development with phytoplankton blooms will lead to an optimal prey environment for larval fish, decreasing larval mortality (Cushing 1990; Moloney et al. 1994). This is mainly because phytoplankton blooms support an abundance of appropriately-sized zooplankton for larval fish to eat (Cushing 1990). For the Northern Anchovy (*Engraulis mordax*), larval growth rates have also been closely linked to the size and abundance of prey, finding that anchovy prefer to feed on larger zooplankton and phytoplankton species (Rykaczewski 2019). Cushing hypothesized that temperate fish, which includes the Northern Anchovy in the California Current Ecosystem (CCE), have a fixed spawning time with peaks during the spring and fall when there are phytoplankton blooms (Cushing 1990). Major spawning events for anchovy occur in February and March, which could align with plankton production (Hunter, 1977). Lasker's Stable Ocean hypothesis, which has been supported specifically for the Northern Anchovy, states that high larval feeding and survival happens when there is an increase in frequency of relaxed coastal upwelling (Lasker 1981, 1985). Calm periods induce vertical stratification, which increases feeding opportunities with optimal prey aggregations (Houde 2008). Despite high larval survival under Stable Ocean conditions for the Northern Anchovy, there was no significant link with recruitment strength (Lasker 1981). A possible explanation for this could be

Cury and Roy's Optimal Environmental Window Hypothesis, which states that recruitment strength in Ekman-type upwelling ecosystems is dome-shaped, meaning that the highest recruitment occurs under moderate winds, which create high food encounters and vertical stratification without high offshore advection (Cury & Roy 1989; Houde 2008). The Match-Mismatch, Stable Ocean, and Optimal Environmental Window hypotheses all attempt to explain when there is sufficient prey availability for larvae during the larval stage, increasing their chance of survival and recruitment success.

Closely related to prey availability is larval growth rate and morphology, two more hypothesized indicators of larval survival. The well-supported Stage Duration Hypothesis states that faster-growing larvae are more likely to survive to the recruitment stage than slower-growing larvae (Fontes et al. 2011). Due to small body size and limited swimming mobility, it is assumed the larval life stage has the highest mortality as larvae are much more likely to die from predation or starvation than their post-settlement counterparts (Fontes et al. 2011). For many species, the less time in the larval-stage the better, making growth rate an excellent indicator of a survival and recruitment strength (Fontes et al. 2011). The Stage Duration Hypothesis has been supported specifically for the Northern Anchovy, when delayed upwelling in 2005 slowed larval growth and significantly weakened anchovy year-class strength compared to the 2006 year-class (Takahashi et al. 2012). Another widely accepted hypothesis in fishery science is the Bigger-Is-Better Hypothesis, which states larger-at-age larvae are more likely to survive and contribute to recruitment (Suthers 1992; Fontes et al. 2011).

Morphometrics, such as body length and body height at the pectoral and anal fins, have been used as indicators of recruitment strength not only because of their link to larval survival but to growth rate and starvation as well (Suthers 1992). In particular, anal and pectoral depth have been shown to quickly decline when larvae are malnourished while body length is thought to be independent from starvation (Ferron & Leggett 1994). The Bigger-Is-Better Hypothesis is also supported by maternal investment, or the amount of energy a female spends on the nutritional quality of her eggs for a particular spawning event (Kindsvater et al. 2012; Garrido et al. 2015). Greater maternal investment has been closely linked to larger size-at-hatch, faster growth rates, resilience to starvation, and greater larval survival (Beldade et al. 2012; Hixon et al. 2014; Garrido et al. 2015; Lubzens et al. 2017). In summary, previous studies have shown larval growth rate, body morphometrics, and maternal investment should be strongly correlated to larval survival and recruitment success, supporting the Stage Duration and Bigger-Is-Better hypotheses (Suthers 1992; Fontes et al. 2011; Garrido et al. 2015).

There is a well-established way to quantify larval growth rate: analyzing a fish's largest ear bone, the sagittae otolith. In 1971, it was discovered by Pannella that otoliths of many temperate fish species have daily growth increments during the larval stage that can accurately age larvae to the day (Pannella 1971). For Northern Anchovy specifically, it has been found that daily growth increments form in the sagittae otolith after yolk sac absorption, usually day 5 of the fish's life (Brothers et al. 1976). Since increments are formed daily, the width between

these growth increments can be used to quantify a fish's growth rate (Figure 2.4; Geffen 1982). Using the preserved otoliths of the anchovy larvae at the SWFSC, the average larval growth rates for anchovy larvae from 2009-2019 can be quantified to determine whether anchovy growth rates are affected by the environment and whether recruitment is higher in years when larvae are growing faster. In addition to larval growth, the core diameter of the larva's otolith can give insight to its size-at-hatch (Garrido et al. 2015). The core, which is assumed to be influenced by maternal investment, is the dark center of the otolith surrounded by daily growth increments that is the only portion of the fish's ear bone that develops prior to feeding (Ruttenberg et al. 2005; Sun et al. 2020). The core diameter has been linked to larval size-at-hatch and survival-at-age for European Sardine (*Sardina pilchardus*) and eight species of rockfish (Genus *Sebastes*) (Garrido et al. 2015; Fennie et al. 2022). In short, the otolith core can be used as a proxy for size-at-hatch, which can be the result of maternal effects as well as intrinsic factors like temperature and additive genetic variation and these factors' interactions (Johnson et al. 2010; Politis et al. 2014). A fish's otolith can provide information about larval age, growth rate, and size-at-hatch (maternal investment), all of which give important implications for larval condition, survival, and recruitment (Kindsvater et al. 2012; Fontes et al. 2011).

Natural Anchovy Population Fluctuations off the California Coast

Sediment cores from the Santa Barbara Basin (SBB) have preserved historical abundance data for two of the most common coastal pelagic species in the California Current Ecosystem (CCE): the Northern Anchovy (*Engraulis*

mordax) and the Pacific Sardine (*Sardinops sagax*) (Baumgartner et. al. 1992; Litz et al. 2008). Since the SBB is adjacent to major spawning grounds for the anchovy and sardine, it contains both species' scales in annual-layered sediments due to its lack of bioturbation and oxygen (Pike & Kemp 1997). By taking sediment core samples from the SBB, scientists can calculate scale deposition rates, which are then used as a proxy to estimate the abundance of anchovies and sardines (Baumgartner et. al. 1992). Using this method, natural population fluctuations were found for anchovies and sardines throughout the last 2,000 years (Baumgartner et. al. 1992). This finding supported the idea that coastal pelagic species have naturally-occurring boom and bust cycles, even in the absence of anthropogenic fishing pressure (Baumgartner et. al. 1992; McClatchie et al. 2017). Since A.D. 270, anchovy and sardine abundances remained at relatively low or high levels in 50-70 year-long cycles (Baumgartner et. al. 1992). During these cycles, scale-deposition rates for both species could be high, low, or one species could be dominating while the other is recovering (Baumgartner et. al. 1992). In recent history, the population cycles of the Pacific Sardine and Northern Anchovy, have been linked to Pacific-wide changes in atmospheric and ocean circulation, such as the Pacific Decadal Oscillation (PDO) and in the broader sense, seasonality and solar irradiance (Pike & Kemp 1997). Throughout the 20th century, scientists believed sea temperature and the PDO were the best predictors for anchovy and sardine abundance: anchovies thrived under colder water temperatures when the PDO was in its negative phase and sardines thrived under warmer water temperatures when the PDO was in its positive phase (Chavez et al.

2003). Due to potential shifts, expansions, and contractions in the habitat range of sardines and anchovies over the past 2,000 years, it is hard to know for sure if their population fluctuations were historically linked to the PDO.

Despite their ecological importance and role in understanding our marine world through climate change, it is still unclear which environmental variables drive the abundance and geographical range of the Northern Anchovy (Litz et al. 2008). In order to have the best management practices for coastal pelagic species conservation, scientists must be extremely familiar with the oceanic processes that occur in their habitats (Litz et al. 2008). Home to the Northern Anchovy is the California Current Ecosystem (CCE), which constitutes the eastern portion of the Central Pacific Gyre and is a subarctic water mass (King et al. 2011). Throughout the year, the California Current (CC) provides a stream of cold, low-salinity, high oxygen, and moderate chlorophyll water in the upper 50 meters of the water column that ranges from 50 to 100 km offshore the coast of California (King et al. 2011). On an annual basis, the CCE is largely influenced by two atmospheric pressure systems: the Aleutian Low (AL) in the wintertime and the North Pacific High (NPH) during the summertime (King et al. 2011). When the AL weakens, the CC typically strengthens and moves closer to shore. In addition, wind-fueled upwelling increases, leading to high biological productivity from February to September during summertime in the California Current Ecosystem (Pike & Kemp 1997; King et al. 2011). For the Northern Anchovy, a species that resides in the upper 50 meters of the water column, the largest spawning events typically

occur in February and March, which are aligned with the beginning of the upwelling season (Hunter 1977).

The habitat of the Northern Anchovy also undergoes interannual and decadal environmental fluctuations, affected by two widespread ocean-climate variability patterns: the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) (King et al. 2011). In general, a negative PDO index indicates low SST and La Niña climate patterns in the CCE while a positive index indicates high SST and El Niño climate patterns; the PDO index oscillates between cold and warm regimes roughly every 20 to 30 years (Chavez et al. 2003). Ranging from Alaska to California, the PDO reveals information about the region's upwelling strength; when the California Current Ecosystem is in a cold regime, the PDO is in its negative phase, which is associated with increased upwelling, bringing colder waters to the surface (Chhak & Di Lorenzo 2007). From 1950 until 2000 Northern Anchovy dominated the CCE during the cold regime, when the PDO was in a negative phase and SSTs were cooler, while the Pacific Sardine dominated in the warm regime (Chavez et al. 2003).

In the last decade, recent studies have shown significant changes in climate patterns in the CCE. The NPGO no longer explains salinity in the CCE and studies have shown an increase in its coupling with the PDO, which has the possibility to create longer-lasting marine heatwaves in the Northeast Pacific (Joh & Di Lorenzo 2017; Thompson et al. 2018). In 2014, a marine heat wave off of the Gulf of Alaska persisted southward, elevating the sea surface temperatures off the coast of California to record-high levels (Bond et al. 2015). For the following

two years, one of the strongest El Niño events in recent history caused 2014-2016 to be the warmest 3-year sea-surface temperature (SST) period recorded in the CC (Jacox et al. 2018). Contrary to previous assumptions, this warming led to an anchovy-dominated regime and record-high recruitment success for the 2015-year class (Thompson et al. 2019). Until 2014, it was believed that water temperature, which co-varies with zooplankton size and species, was a major determinant for anchovy abundance: Northern Anchovy dominated in the cold regime while Pacific Sardine dominated in the warm regime (Chavez et al. 2003; Thompson et al. 2018). With recent marine heatwaves in the midst of climate change and recurring climate patterns no longer being reliable indicators of ocean climate or ichthyoplankton abundance, it is becoming increasingly important to determine what impacts recruitment for anchovy (Thompson et al. 2018).

In the CCE, Northern Anchovy are a staple food source for marine mammals, seabirds, squid, and economically important predatory fish, giving their absence the potential to drive ecosystem functioning through trophic cascades (McClatchie et al. 2018). It has been hypothesized when anchovies are low in abundance, the mesopelagic Pacific Mackerel (*Scomber japonicus*) would dominate, impacting California coast predators that gravitate towards sea-surface food sources, such as the Brown Pelican (*Pelecanus occidentalis*; Schwartzlose & Alheit 1999). Other studies have shown a correlation between low anchovy abundance with California sea lion reproduction failure and increased mortality (Melin et al. 2008; MacCall et al. 2016). In the Northeast Pacific, more than half of the Chinook salmon's diet by weight was the Northern Anchovy (Dale et al.

2017). Many studies have shown synchronous declines in small pelagic species correlate with negative ecosystem impacts from brown pelican breeding failure to the disappearance of important predators such as large piscivorous flatfish and dolphins (Kaplan et al. 2017). Without Northern Anchovy in the CCE, many other species could suffer increased mortality, potentially resulting in diminished ecosystem functioning (Kaplan et al. 2017).

The Data Archive of Northern Anchovy

To better understand how the environment impacts anchovy larval survival (growth rate, maternal investment, and body condition) and recruitment success, both ichthyoplankton and oceanographic climate data has been collected in the CCE since 1949 by The California Cooperative Oceanic Fisheries Investigation (CalCOFI) (Davison et al. 2017). The winter and spring cruises carry out 11 transects with a total of 113 sampling stations between San Francisco and San Diego; CalCOFI is one of few oceanic datasets with a timescale long enough to capture population fluctuations to address what variables impact larval survival and recruitment success (Ohman & Smith 1995). Northern Anchovy larvae reside in the upper 122 meters of the water column (Davison et al. 2017). Since 1978, CalCOFI ichthyoplankton sampling cruises have run quarterly using 0.71 meter diameter bongo nets down to a depth of 210 meters (Davison et al. 2017). Since 1997, plankton from the port side of the bongo net have been preserved in ethanol while the starboard side is stored in formalin, as ethanol preservation allows for isotope analysis. In addition, hydrographic profiles are conducted using a CTD

and fluorometer to measure temperature, salinity, chlorophyll-a, nutrients, and oxygen, at each station, generally ranging from 20-500 meters, with some cruises collecting as shallow as 5 meters (Ohman & Smith 1995; McClatchie et al. 2018). From the CalCOFI cruises, the Southwest Fisheries Science Center (SWFSC) in La Jolla, California has archived ichthyoplankton samples. Specifically, cruises conducted in the late winter and early spring have captured 2-8 week-old Northern Anchovy larvae as this species' major spawning events occur in February and March (Hunter 1977). Northern Anchovy have a 10-13 week-long larval period, meaning the preserved 2-8 week-old larvae survived the Critical Period, or the period in which first-feeding larvae's yolk sacs are absorbed and they must eat prey to avoid starvation (Hunter 1977; Houde 1987).

Recruitment indices for the Northern Anchovy have been quantified by ongoing midwater rockfish trawl surveys off the coast of California by NOAA's Southwest Fisheries Science Center since 1983 (Ralston et al. 2015). In 1990, abundance estimates for pelagic species were standardized among 40 different stations; sampling occurred at night in May and June and were standardized for 15 minutes at target depth of 30 meters (Ralston et al. 2015). Stations ranged within three different regions of the southern California coast: south, south central, and core. The core region ranges from 36.5°N-37.5°N and captures the Monterey Bay area, the south central region ranges from 35°-36.5°N and captures areas south of Monterey and north of Point Conception, and the south region ranges from 32.5°-35°N and captures areas south of Point Conception to San Diego. All recruitment sampling regions are shown in Figure 2.2 in bright green.

By establishing an abundance baseline for Northern Anchovy young-of-the-year, these trawl surveys were able to produce recruitment indices for 2009, 2010, 2013, 2015-2017, and 2019 (Ralston et al. 2015). With the recruitment data and the CalCOFI data, the relationship between larval condition and environmental conditions can be compared to recruitment strength.

The Pursuit of Multiple Hypotheses to Explain the 2016 Population Boom

In the 20th century, fishery oceanographers believed they grasped what controls Northern Anchovy and Pacific Sardine recruitment variability with their population sizes being strongly correlated with the PDO and SST. However, the anchovy boom during the 2014-2016 marine heatwave underlined the importance of understanding coastal pelagic species recruitment variability “lies in the pursuit of multiple hypotheses” (Hare 2014). While Johan Hjort’s hypotheses catapulted our understanding of what impacts small pelagic fish recruitment variability, much is left to be explored. The following research analyzes how larval growth, condition, maternal investment, and environmental conditions can help explain Northern Anchovy recruitment fluctuations from 2009-2019. This research has four main objectives, to determine whether there is: a significant relationship between larval growth rates and condition with recruitment strength (i), a significant relationship between maternal investment and recruitment strength (ii), a significant relationship between oceanographic variables (temperature, salinity, oxygen, chlorophyll, prey availability, and dynamic height) with larval growth rate, condition, and recruitment strength.

1.2. Statement of Hypotheses

In conjunction with the Critical Period, Stage Duration, and Bigger-is-Better Hypotheses, the following research hypothesized that the growth rate of larval anchovy will be faster and maternal investment will be higher for years with high recruitment (Takahashi et al. 2012; Lubzens et al. 2017). Supporting the Stable Ocean and Match-Mismatch Hypotheses, the following research hypothesized that phytoplankton and zooplankton communities will have above average abundance during good recruitment years (Houde 2008; Thompson et al. 2018; Pizzaro et al. 2019). Finally, it is hypothesized that recruitment strength will be higher during periods with upwelled water characteristics such as: above average SST, high salinity, low oxygen, and high chlorophyll *a* concentrations (King et al. 2011; Thompson et al. 2018; Bograd et al. 2019).

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CHAPTER 2: How maternal investment and environmental variables impact larval condition, growth, and survival of Northern Anchovy: implications for recruitment success and fishery management

2.1 Abstract

Discerning the causes of population boom and bust cycles for coastal pelagic species (CPS) has been a major focus of fisheries management research for over a century. Year-class strength is contingent on larval survival and condition, which can be influenced by larval size at age and growth rate. These two factors, in turn, can be affected by maternal investment and environmental variables such as water temperature, salinity, oxygen, and chlorophyll *a*. We evaluated each of these factors from 127 two to eight week-old Northern Anchovy (*Engraulis mordax*) larvae off the coast of San Diego to San Francisco collected from 2009-2019. Sagittae otoliths were analyzed to determine larval age (otolith ring-count), size-at-hatch as an index of maternal investment (otolith core diameter) and growth rate (otolith increment width). Size at age was determined by computing the residuals between age and the following larval condition measurements: standard body length (SL), muscular height at the anal fin (MHA), and muscular height at the pectoral fin (MHP). Linear regressions revealed that SL, MHA, MHP and average recent otolith growth (average of last 3 increment widths) were significantly correlated, indicating that fish that were larger at age were also growing faster. Generalized Linear Mixed Models (GLMM) demonstrated that fish age (survival) was positively correlated to core diameter,

and negatively correlated with water temperature and chlorophyll; SL was positively correlated with core diameter, negatively correlated with salinity and latitude; MHA was positively correlated with core diameter, negatively correlated with latitude, and largest at slightly above average temperatures (residual= 0.25); and MHP was positively correlated with core diameter and negatively correlated with chlorophyll. Average recent growth rate was not significantly correlated with core diameter or any environmental factor.

However, lifelong growth rate trajectories showed that fish were growing faster in years with high recruitment. This preliminary finding supports that larval growth rates could have important implications for year-class strength; however further analyses are needed. Overall, maternal investment, intermediate water temperature, low chlorophyll and low salinity optimized larval survival to older ages and morphological condition. Future fisheries studies should analyze the relationship between larval condition and recruitment success as well as understanding what drives maternal investment and how it is best measured.

2.1.1 Key Words

Coastal pelagic species, Northern Anchovy, larval condition, maternal investment, recruitment

2.2 Introduction

The Northern Anchovy (*Engraulis mordax*; henceforth anchovy) is one of the most common Coastal Pelagic Species (CPS) in the California Current Ecosystem (CCE) (Pike & Kemp 1997; Litz et al. 2008; Sydeman et al. 2020). CPS are critical components of many marine ecosystems, transferring nutrients and energy to higher trophic levels, and often supporting large commercial fisheries (Alder et al. 2008). Although no large commercial fishery exists for the Northern Anchovy in the United States, learning about Northern Anchovy population dynamics can translate to better fishery management practices for other species of anchovies around the world, which in combination with sardines (*Sardinops sp.*, another CPS), total around 13% of global fishery landings (Checkley et al. 2017). CPS species worldwide have naturally-occurring boom and bust population cycles due to short life spans, high fecundity, and strong relationships to lower trophic levels and bottom-up processes (De Moor et al. 2011; McClatchie et al. 2017; Bode et al. 2018; Swalethorp et al. 2022; Salvattecchi et al. 2022). CPS species also feed economically and ecologically important predators (Peck et al. 2014). For example, when anchovy abundances were low in the CCE, brown pelicans exhibited breeding failure (Kaplan et al. 2017; McClatchie et al. 2018), the abundance of large piscivorous fishes and dolphins decreased (Kaplan et al. 2017; McClatchie et al. 2018), and sea lion pup mortality greatly increased (Melin et al. 2008; McClatchie et al. 2018). CPS species are also ecosystem indicators, as assemblage structure and abundance has been linked to large-scale oceanographic dynamics, such as El Niño and La Niña (Chavez et al.

2003; Thompson et al. 2019). Despite this global pattern and the economic and ecological importance of CPS, fishery scientists still do not fully understand what drives CPS recruitment variability and population fluctuations (Houde 2008).

To better understand long term CPS population dynamics, several studies have been able to estimate anchovy and sardine population fluctuations since AD 270 by using sediment core analysis of scale-deposition rates as a proxy for population abundance (Baumgartner et al. 1992; Pike & Kemp 1997; McClatchie et al. 2017). For example, anchovy scales have been collected from the annual-layered anoxic sediments of the Santa Barbara Basin, which lacks bioturbation and is within major anchovy and sardine spawning grounds (Baumgartner et al. 1992; Pike & Kemp 1997). Scale-deposition rates showed that population cycles of anchovy and Pacific Sardine (*Sardinops sagax*; henceforth sardine) in the CCE last roughly 50-70 years (Baumgartner et al. 1992). During these cycles, scale-deposition rates for both species could be high, low, or one species could be dominating while the other is recovering (Baumgartner et al. 1992). The population cycles of the Pacific Sardine and Northern Anchovy have been closely linked to Pacific-wide changes in atmospheric and oceanic circulation, particularly the Pacific Decadal Oscillation (PDO) (Pike & Kemp 1997; Chavez et al. 2003). The PDO is calculated through multivariate analysis on monthly sea surface temperature (SST) and sea surface height anomalies in the North Pacific (Newman et al. 2016). Typically, a negative PDO index indicates low SST and La Niña climate patterns for California while a positive index indicates high SST and El Niño climate patterns (Chavez et al. 2003). El Niño and La Niña are defined by

the SST at the equator (NOAA's Oceanic Niño Index; <https://www.ncei.noaa.gov/access/monitoring/enso/sst>), this means the PDO positive or negative indices cannot fully explain the El Niño/ La Niña conditions as it is a measure of the SST in the North Pacific (McClatchie 2016). In general, the PDO index oscillates between cold and warm regimes roughly every 20 to 30 years (Chavez et al. 2003; Chhak & Di Lorenzo 2007), whereas El Niño/La Niña has a 2-7 year periodicity (NOAA's Oceanic Niño Index; <https://www.ncei.noaa.gov/access/monitoring/enso/sst>). Throughout the 20th century, fishery oceanographers believed that the cold/warm PDO conditions, which influence zooplankton size and community composition, was an important predictor of anchovy abundance (Chavez et al. 2003; Thompson et al. 2018). From 1950-2000, anchovy dominated the CCE during the cold regime, when the PDO was negative, while sardine dominated in the warm regime when the PDO was in a positive phase (Chavez et al. 2003; Thompson et al. 2018). However, a 2013-2016 Pacific Marine Heatwave contradicted the 20th century assumption that the PDO was a robust predictor of anchovy population fluctuation (Chavez et al. 2003). The Pacific Marine Heatwave was a giant warm water mass, which caused the California coast to have record-high ocean temperatures throughout 2014-2016 (Bond et al. 2015; Jacox et al. 2018). The Pacific Marine Heatwave was the consequence of a 2013 Gulf of Alaska surface warming event ("The Blob") that traveled southward to California and a strong 2015 El Niño event (Bond et al. 2015; Jacox et al. 2018). Contrary to previous assumptions, this water warming led to an anchovy-dominated regime with high recruitment success for

the 2015-year class, causing a historical and unpredicted population boom in 2016 (Thompson et al. 2019). “The Blob” highlighted that understanding CPS recruitment variability requires pursuing many hypotheses (Hare 2014).

In 1914, a Norwegian fishery biologist, Johan Hjort, published the first hypotheses explaining what causes CPS recruitment variability: migration patterns, larval survival, parental investment, prey availability, and larval dispersal (Hjort 1914; Hare 2014). Arguably, his most influential hypothesis, the Critical Period, states recruitment success is heavily influenced by larval survival as each year-class is likely to have high mortality among first-feeding larvae, which influences the number of individuals that can survive into adulthood (Hjort 1914 and 1926). Once the yolk-sac is absorbed, larvae with minimal swimming capabilities become vulnerable to starvation (Lasker 1985). Hjort’s conclusion that early larval survival was the best predictor for recruitment strength was well-received and set the stage for more than a century of fisheries investigation. Over the past century, a priority for fishery scientists has been to analyze how abiotic and biotic factors impact larval survival and recruitment variability (Hare 2014). Specifically, it has been shown that some factors hold a greater influence on adult mortality versus larval mortality (Hare 2014). For example, fishing pressure is more relevant to adult survival (if a fishery is present) while the environment (water temperature, salinity, etc...), prey abundance, maternal investment, and larval dispersal is more relevant to prerecruit survival (Hare 2014; Garrido et al. 2015). In short, to answer the question of what influences CPS recruitment and population size, it can be concluded that ‘almost everything’ does, from the

moment an egg is fertilized to the day it starts spawning (Lasker 1985). My research seeks to understand the factors that affect larval anchovy viability by investigating the relationships maternal investment (otolith size-at-hatch) and the environment (water temperature, salinity, oxygen, and chlorophyll *a*) have on larval survival (age), larval condition (morphology), and larval otolith growth rates.

Following Hjort's Critical Period hypothesis, there have been several subsequent hypotheses that try to determine the environmental conditions that facilitate larval survival. Cushing's Match-Mismatch hypothesis states that a match in timing of larval production with phytoplankton blooms increases larval survival (Cushing 1990). The match-mismatch hypothesis has been supported by many fish stocks (*Clupea harengus*, *Gadus morhua*, *Hippoglossoides platessoides*, and *Oncorhynchus nerka*), spiny lobster (*Jasus edwardsii*), and Dungeness crab (*Metacarcinus magister*; Cushing 1990). When larval production and phytoplankton blooms occur at the same time, phytoplankton will support small zooplankton creating an abundance of appropriately-sized zooplankton for the fish larvae to eat (Cushing 1990). Cushing hypothesized that temperate fish, which includes anchovy, have a fixed spawning time that has evolved to match peaks in phytoplankton blooms (Cushing 1990). Major spawning events for anchovy occur in February and March, which could align with spring plankton production (Hunter 1977). Cushing's hypothesis was an important extension of Hjort's Critical Period hypothesis as it postulated that starvation could cull a year class even subsequent to the few days after yolk sac absorption.

Lasker's Stable Ocean hypothesis, which has been supported specifically for the anchovy states that high larval feeding and survival happens during calm periods when there is an increase in frequency of relaxed coastal upwelling (Lasker 1981, 1985). Calm periods induce vertical stratification, which promotes feeding success through optimal aggregations of larvae and prey (Houde 2008). Going a step further beyond larval survival, Cury and Roy's Optimal Environmental Window hypothesis links upwelling to recruitment strength (Cury & Roy 1989). The hypothesis states that recruitment strength in Ekman-type (wind-driven) upwelling ecosystems is dome-shaped, meaning high recruitment occurs under moderate winds and upwelling intensity, which promotes high food encounters through vertical stratification in the absence of strong offshore advection (Cury & Roy 1989; Houde 2008). The Match-Mismatch, Stable Ocean, and Optimal Environmental Window hypotheses all attempt to explain which biological (e.g., phytoplankton blooms) and physical (e.g., upwelling) processes increase prey availability for larvae during their larval stage, increasing their chance of survival and contribution to recruitment success.

A second group of hypotheses attempt to explain what about the larvae itself (growth rate, morphology, and size-at-hatch) can build its resilience against mortality. For example, the Stage Duration Hypothesis suggests that the less time in the larval-stage the better the fish's chances for survival and recruitment to adult populations (Houde 1987; Fontes et al. 2011). Studies testing Stage Duration show that larval growth rates have an inverse relationship to larval stage duration, meaning that faster-growing larvae are more likely to survive and

contribute to recruitment than slower-growing larvae (Houde 1987; Fontes et al. 2011). This has been supported specifically for the Northern Anchovy, when delayed upwelling in 2005 was related to slowed larval growth and significantly weakened anchovy year-class strength compared to the 2006 year-class (Takahashi et al. 2012). Another widely-accepted hypothesis is the Bigger-Is-Better hypothesis, which states larger larvae-at-age are more likely to survive and contribute to recruitment (Suthers 1992; Fontes et al. 2011). It should be noted that there have been a few studies demonstrating predator selection against faster growth rates since they may target larger individuals, especially when there is a high predation (Biro et al. 2004; Sundström et al. 2005). Body morphometrics, such as body length and muscular height at the pectoral (MHP) and anal fins (MHA), have been shown to be strongly correlated to larval growth rate and have been used as a key indicator of recruitment strength (Suthers 1992). Maternal investment, or the amount of energy a mother spends on the quality and quantity of her eggs, has been known to influence larval size-at-hatch, which can be estimated by the portion of a larva's sagittae and lapilli otoliths that is developed prior to larval feeding (Grønkjær & Schytte 1999; Vigliola & Meekan 2002; Raventós & Macpherson 2005; Ruttenberg et al. 2005; Garrido et al. 2015). Known as the core, this portion of the otolith is identified as the dark shaded region in the middle of the otolith before daily growth increment formation at the onset of feeding, about 4 to 6 days into the larval stage (Ruttenberg et al. 2005; Sun et al. 2020). For European Sardine larvae (*Sardina pilchardus*) and eight different species of California rockfish larvae (Genus *Sebastes*: *S. goodei*, *S.*

hopkinsi, *S. jordani*, *S. mystinus*, *S. paucispinis*, *S. rufus*, *S. serranoides*, and *S. wilsoni*), the core diameter had a significant positive correlation to larval size-at-hatch and larval survival-at-age (Ruttenberg et al. 2005; Garrido et al. 2015; Fennie et al. submitted). With compelling evidence that maternal investment could be measured by otolith core diameter, which corresponds to larval size-at-age and survival, this study investigates the relationship between larval size-at-hatch with larval survival, condition, and growth rates in wild-caught Northern Anchovy.

To improve the understanding of CPS recruitment fluctuations and their management, my study looks at how larval condition (body length and muscular height and the anal and pectoral fins), larval survival (age), and larval recent growth rates (average growth rate from last 3 days of life) for 2-8 week-old Northern Anchovy captured from 2009-2019 are influenced by larval size-at-hatch (larger otolith core diameter) and environmental conditions (temperature, salinity, chlorophyll *a*, and oxygen). By addressing these relationships, this research addresses the century-old objective of fisheries oceanography to understand what impacts CPS larval survival in order to forecast their recruitment variability and improve their management. For the Northern Anchovy in particular, this study provides novel insight to the importance of larval size-at-age for larval condition, survival, and growth rates. It is hypothesized that larvae who experienced larger size-at-hatch (larger otolith core diameter) and upwelled water (cold temperature, high salinity, high chlorophyll, low oxygen) would have better condition (longer and more muscular), better survival (older), and faster average

recent growth rates (average otolith growth during the last 3 days of life) as anchovy thrived under these conditions in the past (Chavez et al. 2003, Rykaczewski & Checkley 2008).

2.3 Sample Collection and Lab Methods

Anchovy Samples

Anchovy larvae were sorted from ethanol-preserved ichthyoplankton samples from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises that conduct plankton and CTD sampling from 75-113 sampling stations from the U.S./Mexico border north to San Francisco (32°N-38°N; 117°W-124°W). CalCOFI cruises collect plankton by towing a dual bongo frame through the water column from 210 meters depth to the surface, while the ship is underway at 1-2 knots (CalCOFI Net

Sampling: https://calcofi.com/index.php?option=com_content&view=article&id=265:bongo-calbobl-net&catid=152&Itemid=846). Bongo nets are held at depth for 30 seconds then retrieved at 20m per minute. The bongo nets are 71cm in diameter and 3m in length with a 505µm mesh size (Kramer 1972; Smith & Richardson 1977). After each cruise, the plankton samples collected from the bongo nets are preserved in ethanol (port side) and formalin (starboard side). Prior to my study, the formalin-preserved ichthyoplankton samples were already identified, and the standard length (SL) of each larval anchovy was recorded. Here, I targeted relatively large larvae (> 13 mm; future research will conduct compound-specific stable isotope analysis on the larvae, and only larger larvae are suitable for this work) and focused on stations where several had been recorded in

the formalin preserved sample. I then sorted the larvae from the ethanol preserved samples since ethanol preserves the otoliths well and allowed analysis of growth rate, age, and core size. A total of 127 ethanol-preserved anchovy larvae were sorted from 8 years (from 2009-2019) and a total of 14 cruises and 19 sampling stations (Figure 2.1 and Table 2.10). Each larva was then placed in an individual sample tube filled with a 95% ethanol solution for further morphometric and otolith analysis.

Larval Morphometrics

Larval condition was quantified by three morphometrics: standard body length (SL), muscular height at the anal fin (MHA), and muscular height at the pectoral fin (MHP). To ensure the most accurate morphometric measurements, each fish was soaked in water for 20 seconds to reduce dysmorphia and brittleness caused by ethanol preservation (King & Porter 2004). Using tweezers, larvae were carefully straightened and measured. SL was measured as the distance from the tip of the larvae's snout to the beginning of the caudal fin (Figure 2.3) and was analyzed using 0.7x coarse focus (10 units of the calibrated scale equaled 2.5mm) to the nearest hundredth mm. MHP was the muscular height at the pectoral fin's attachment point to the body (Figure 2.3). MHA was the muscular height immediately posterior to the anal fin (Figure 2.3). MHP and MHA were measured using 2.5x coarse focus (10 units of the calibrated scale equaled 0.75mm) to the thousandth by using an Olympus SZX2-ILLD microscope with a SDF Plapo 0.5xPF objective lens.

Otolith Analysis

Otolith extraction from sorted and measured larvae followed established protocols (Swalethorp et al. 2016). Each larva was decapitated using a scalpel for easier removal of the sagittae otoliths. The sagittae otoliths were removed from the larvae using fine needles underneath a Olympus SDF Plapo microscope using 0.5xPF objective lens magnification. Once isolated under the microscope, the extracted sagittae otoliths (sometimes the left, right, or both otoliths) were placed flat-side down on a mounting slide and coated with clear nail polish.

Digital images of each otolith were taken using a LEICA Stereozoom S9i microscope camera with a 40x objective lens. An image of a calibrated slide was captured with the same camera and magnification in order to quantify the number of image pixels per μm . The calibrated slide was measured 10 times, to get an average measurement of $1\mu\text{m}$ per 4.66 pixels. For all of the otolith's increment counts, increment widths, and core diameter, the clearest digital image was analyzed, either from the right or left otolith. Otolith core diameters and increment widths were measured using ImageJ.

Daily growth increments on the otoliths were counted to age each anchovy and width between each increment was measured to analyze the anchovies' full growth rate histories and recent growth rate (average of last 3 days of life). Henceforth, larval growth rates refer to the measured otolith growth (daily increment width) as a proxy for somatic growth. Otolith core diameter was used

as a proxy for size-at-hatch, which is believed to be larger with greater maternal investment (Garrido et al. 2015).

To reduce the error of aging each anchovy, each otolith was read at least two times by the same reader (Sun et al. 2020; Swieca 2022). Measurements for the number of increments and their widths were taken along the longest radius from the otolith's core to the outermost edge when possible and increment widths were quantified as the distance between two adjacent increments (Swalethorp et al. 2016) (Figure 2.4). For otoliths with unclear increments, the initial dark band at least 8 μ m or more from the core's center was used for the first growth increment (Swalethorp et al. 2016). This method is based upon previous studies demonstrating that the first growth increment of the otolith is usually 8-13 μ m away from the core center (Bolz, 1983). The outermost band for each otolith was counted as an increment. For the first read, a live image was juxtaposed with a still image to avoid counting sub-daily increments. For the second read, only a still image was used. If the first two reads were within 5% of one another, the larger increment count out of the two was used to age the anchovy. If the two reads were not within 5% of each other, a third read was conducted using the same still image as the 1st and 2nd reads. If the 3rd read was within 5% of either the 1st or 2nd read, the largest increment count was used to age the anchovy. If the 3rd read differed more than 5% from the 1st and 2nd reads, the otolith and fish were not used in further analysis. Choosing a 5% threshold for all counts was based on a previous study (Swieca 2022).

Oceanographic Data

The precise time, latitude, and longitude of each larva's capture was recorded by CalCOFI through their 73-year long monitoring of a fixed sampling grid (Figure 2.1). Using CalCOFI's CTD bottle data, temperature, salinity, oxygen, and chlorophyll *a* for each larva's sampling location, I analyzed the level of impact environmental variables have on larval condition, survival, and growth rate. The "Final 1m-Binned" downcast CTD data was selected for the environmental variables (See: <https://calcofi.org/data/oceanographic-data/ctd-cast-files/>). Since the sampling location 83.3-39.4 (line-station) only had CTD data up to 10 meters in depth, the temperature, salinity, chlorophyll *a*, and oxygen for each location was averaged over the first 10m.

Recruitment

Anchovy recruitment indices were generated using midwater trawls from NOAA's Rockfish Recruitment and Ecosystem Analysis Survey (RREAS; Sakuma et al. 2006, 2016). RREAS collects samples by towing a Cobb midwater trawl at 30 m for 15 minutes at night in late spring/early summer. Transects are located within five regions off California: North (N) from Cape Mendocino to the Oregon Border, North Central (NC) from San Francisco to Cape Mendocino, Core (C) from San Francisco to Monterey Bay, South Central (SC) from Monterey Bay to Point Conception, and South (S) from Point Conception to the U.S./Mexican border. The survey has been conducted annually in late spring/early summer in the Core region since 1990 and the other regions since 2004. The

highest recruitment numbers are typically found in the southernmost region where there are four transects with four stations within each transect (Sakuma et al. 2006). Fish are counted and processed on the ship, and anchovies that are less than 100 mm are classified as young of the year.

2.3.1 Statistical Analysis

Growth and Condition

It was first evaluated whether fish that were larger were also growing faster. To account for the positive correlation between larval morphometrics and average recent growth rate with larval age, Generalized Additive Models (GAM) were used and implemented through the package mgcv (Wood 2006) to model age against each condition variable. To prevent overfitting, the number of knots in the GAM was limited to 3. Residuals of GAMs were then calculated to determine age-adjusted condition values. All further analysis used age-adjusted residuals for SL, MHA, MHP, and average recent growth rate. Age-adjusted morphology (SL, MHA, MHP) equaled the larval condition, or the overall health of the fish. To analyze the relationships between age-adjusted morphometrics (SL, MHA, MHP) and age-adjusted average recent growth rate (last 3 days), four linear regressions using each pair of condition indices were used.

Maternal Investment, Environment and Condition

To discern whether maternal effects alone affected larval condition at capture, linear models were used to correlate core width against age, and age-adjusted SL, MHA, MHP and recent growth. Preliminary inspection of the core

width~age relationship revealed that most younger larvae had small cores, average sized larvae had a mixture of core sizes, while older larvae had mostly large cores. Natural breaks in core distribution were identified, and the percentage of small and large larvae that had above-average core widths was determined.

The combined effects of maternal investment (core diameter) and oceanographic variables on age (an index of survival) and the four age-adjusted condition variables (morphology and recent growth) was then evaluated. Because multiple fish were often collected from the same station, individual fish were not statistically independent from one another. Thus, five Generalized Linear Mixed-effects Models (GLMM) were used to determine the relationships between larval age, average recent otolith growth rate, SL, MHA, and MHP (each as a response variable in an individual GLMM) and environmental explanatory variables as fixed effects: temperature, salinity, chlorophyll *a*, and oxygen, location (latitude), and size-at-hatch (core diameter). Early visualizations of the data indicated response variables had parabolic relationships with temperature and salinity, so these explanatory variables were modeled as both 1st order (linear) and 2nd order (parabolic) variables in the GLMM. All response variables and fixed effects were centered by their mean and scaled by two standard deviations to improve computational speed and stability and to make coefficients directly comparable (Gelman 2008). Multiple fish from the 127 sorted anchovies were captured from the same sampling location and year, violating the statistical assumption of independence for each larva. A GLMM is useful because it includes random effects that allow non-independent data to be explicitly grouped (Gomes 2022).

Thus, the interaction of sample location and year was used as a random effect (intercept) in each GLMM. Following Cole et al., 2022, we fit GLMMs with the R package ``glmmTMB`` (Magnusson et al. 2017), checked model residuals with the ``DHARMA`` package (Hartig et al. 2017), and checked collinearity between predictor variables with Variance Inflation Factors, using the ``performance`` package (Lüdtke et al. 2021). There were no residual or collinearity issues detected in any of the models. The conditional pseudo- R^2 values, which can be interpreted as the variance explained by the entire GLMM model (both fixed and random effects), were calculated using the methods from Nakagawa & Schielzeth 2013.

Growth and Recruitment

To discern temporal recruitment dynamics, young of the year anchovy from each year and region was averaged and plotted. A horizontal line depicting average recruitment across all years and locations was included to evaluate whether recruitment was below or above average in a given location/year.

To determine if larvae were growing faster in above-average recruitment years, the entire otolith growth increment trajectories of larvae was examined using a Linear Mixed-Effects Model (`lme` function in the `nlme` package, Pinheiro et al., 2014). To control for sample size errors, only CalCOFI cruises with at least 5 anchovy larvae and only growth increments with a minimum of 5 replicates were chosen for analysis. Because young of the year data was collected in early summer, larvae collected in summer or fall could not possibly have contributed to

the sampled recruits, so growth trajectories were only analyzed from winter (2013, 2015, 2016) and spring (2015, 2017). An approach similar to that outlined in previous studies (Swalethorp et al. 2016; Malanski et al. 2020; Malca et al. 2022) was used, where the model was fit to growth increment width as the dependent variable and year as a fixed effect. Growth increment number was nested by individual larvae and included as a random effect applied to both intercepts and slopes. Consecutive growth increments widths are autocorrelated by nature (Campana et al. 1995; Campana 1996; Chambers 1995), and to correct for this the model was refitted with an autocorrelation structure using the `corCAR1` function using growth increment number as the continuous time covariate. The maximum likelihood was used to estimate slopes and level of significance to adjust for the unbalanced design as individual larvae differed in number of growth increments. The model was run separately for winter and spring and included an interaction term for growth increment number and year. If the interaction was insignificant, the term was dropped and the model re-run.

Outliers

When outliers were identified and removed from analyses, no significant changes were made to the relationships found in the GAM, linear regressions, or GLMM, so outliers were not discarded.

2.4 Results

Growth and Condition

All morphometric variables (including average recent growth rate) had significant positive correlations with one another (Figures 2.6a-c). Age alone affected all morphometric variables as there were significant, positive relationships between average recent growth rate, SL, MHA, and MHP with age (Figure 2.5 and Table 2.1). Thus, age-adjusted residuals were used for all further analysis.

Maternal Investment, Environment and Condition

Larvae that were larger at age were also growing faster at age as there were significant, positive relationships between the age-adjusted residuals of SL, MHA, and MHP with the age-adjusted residuals of average recent growth rate (Figure 2.8 and Table 2.2). All morphometrics (SL, MHA, and MHP) had significant positive linear relationships with one another (p-value $<2.2e-16$).

There were significant, positive relationships between larval age and the age-adjusted residuals of SL, MHA, and MHP with size-at-hatch (core diameter; Figures 2.7 & 2.9 and Table 2.3). Older larvae had larger otolith core diameters than younger larvae (Figure 2.9). In detail, 71% (12 out of 17) fish older than 33 days had core diameters larger than the average core diameter of all 127 larvae analyzed; additionally, 75% (9 out of 12) fish younger than 20 days had core diameters smaller than the average core diameter of all 127 larvae analyzed

(Figure 2.9). There was no relationship between size-at-hatch and age-adjusted residuals of average recent growth rate (Figure 2.7 and Table 2.3).

From the five GLMM models, age-adjusted residuals of SL had a negative linear relationship with salinity and latitude and a positive linear relationship with size-at-hatch (core diameter; Figure 2.10 and Table 2.4). The GLMM for SL had a conditional R^2 value of 0.33 and an intercept value of -0.23. Age-adjusted residuals of MHA had a positive linear relationship with size-at-hatch (core diameter), a positive linear trend within a negative parabolic relationship with temperature, and a negative linear relationship with latitude (Figure 2.10 and Table 2.5). The GLMM for MHA had a conditional R^2 value of 0.40 and an intercept value of -0.23. Age-adjusted residuals of MHP had a positive linear relationship with size-at-hatch (core diameter) and a negative linear relationship with chlorophyll *a* (Figure 2.10 and Table 2.6). The GLMM for MHP had a conditional R^2 value of 0.43 and an intercept value of -0.34. Age-adjusted residuals of average recent growth rate did not have any significant relationships with explanatory variables (Figure 2.10 and Table 2.7). Larval age had a positive linear relationship with size-at-hatch (core diameter) and negative linear relationships with temperature and chlorophyll *a* (Figure 2.10 and Table 2.8). The GLMM for larval age had a conditional R^2 value of 0.46 and an intercept value of -0.25.

Growth and Recruitment

Recruitment was highly dynamic over the course of the study (2009-2019; Figure 2.11). Among regions, mean young of the year abundance was highest in S in the study period in all years except 2009, 2013 and 2014 when it was highest in SC and second highest in S. Recruitment changed dramatically in S during this study. From 2008-2014, recruitment in S was extremely low with the nadir being 2013 when only two individuals were captured. Recruitment in S dramatically rose from very low to above average in 2015 in S and was higher in 2017-2019 than in any other year on record (Figure 2.11).

There were also significant differences in winter/spring larval growth trajectories among the years when data was available (2013, 2015, 2016, and 2017; Figure 2.12 and Table 2.9). In winter larvae from 2013 differed significantly in their growth trajectories from 2015 and 2016 ($df = 1735$, $t = 2.134$, $p = 0.033$). Figure 2.12 shows the slope of the 2015 and 2016 growth trajectories appearing steeper and with wider growth increments compared to 2013. Larvae from 2015 had significantly wider growth increments than the other years ($df = 58$, $t = 5.177$, $p < 0.001$), while 2016 larvae had wider increments than 2013 but narrower than 2015 ($df = 58$, $t = 2.773$, $p = 0.008$). In spring larvae from 2015 had significantly wider increments than 2017 ($df = 30$, $t = 3.760$, $p < 0.001$). These results demonstrate that larval growth histories in 2015-2016 were much faster than 2017, and particularly 2013 which was a low recruitment year.

2.5 Discussion

This research describes how the environment and size-at-hatch impact the morphology, growth rate, and survival of 2-8 week old Northern Anchovy (*Engraulis mordax*) larvae from winter, spring, summer, and fall between 2009-2019. Across all collection seasons, larger-at-age larvae had faster recent growth rates than smaller-at-age larvae. In addition, larvae collected in the winter and spring had faster larval growth during years with higher recruitment, suggesting faster larval growth may contribute to a stronger year class by potentially shortening the duration of the larval period as stated in the Stage Duration hypothesis. For the most part, larvae that were in better condition had larger cores (high maternal investment) and were located in the southern region of the study area in water with intermediate temperature, low salinity, and low chlorophyll concentrations.

My finding that anchovy with larger standard body lengths (SL) and greater muscular heights at the anal (MHA) and pectoral (MHP) fins had faster average growth rates during their last three days of life supports that otolith growth relates to overall body condition. It also verifies otolith increments as a reliable indicator for recent or past larval condition and growth for anchovy. Larval condition and growth are important predictors for year-class strength as the Bigger-is-Better and Stage Duration hypotheses state that larger-at-age larvae and larvae with shorter larval stages are more likely to survive and contribute to recruitment (Houde et al. 1987; Suthers 1992; Fontes et al. 2011). Faster larval growth rates have been associated with higher year-class strength in anchovy off

Oregon and Washington in the California Current Ecosystem (Takahashi et al. 2012). Specifically, the June 2005 cohort of anchovy larvae experienced delayed upwelling and had significantly slower growth rates than the August 2005 and July 2006 cohorts (Takahashi et al. 2012). It was suggested that delayed upwelling in the spring of 2005 caused low food availability for larval anchovy as different water temperatures co-vary with zooplankton size and species (Chavez et al. 2003; Takahashi et al. 2012; Thompson et al. 2018). Notably, my study also found that recruitment was very low in 2013 when larvae were growing significantly slower than in sample years with above average recruitment. To better understand the causes of anchovy recruitment dynamics, future research could focus on quantifying actual larval diet and larval prey fields. Additionally, to make direct comparisons with Takahashi et al. (2012), further analysis should note any significant differences in upwelling timing and strength between years with varying recruitment strength and larval growth rates.

Since it is well-supported that larval morphology and growth rates can be reliable predictors for larval survival and recruitment success, it is crucial to understand what impacts larval condition and growth rate in order to improve the management of coastal pelagic species (Suthers 1992; Fontes et al. 2011). A main finding of this study was that larval size at hatch, as indexed through otolith core diameters, is positively correlated with longer SL, greater MHA and MHP, and older age (better survival). Other studies have shown otolith core size has a positive linear relationship to larval survival for eight different species of California Rockfish (Genus *Sebastes*) (Fennie et al. submitted) and European

Sardine (*Sardina pilchardus*; Garrido et al. 2015). Since the otolith core is developed prior to larval hatching, it is likely a function of maternal investment (Ruttenberg et al. 2005; Johnson et al. 2010). If greater maternal investment is expressed by a larger core diameter and yields a larger size-at-hatch, maternal investment has strong implications for improved larval survival from the Bigger-is-Better hypothesis (Fontes et al. 2011). Contrary to the rockfish study (Fennie et al. submitted), the current study does not support the finding that larger otolith core diameters are correlated to faster larval growth rates. Since only 5 out of 7 rockfish species had a significant relationship between larger core diameters to faster larval growth, it is possible this correlation is species specific. A lack of correlation between core diameter and average recent growth rate could indicate that maternal investment only influences larval growth rate during early portions of the larval stage for anchovy. Beyond using otolith cores to proxy size-at-hatch, maternal investment has also been expressed in egg size, yolk-sac size, and embryonic metabolic rates (Chambers & Leggett 1996; Heath et al. 1999; Bang et al. 2006; Sogard et al. 2008; Garrido et al. 2015; Fennie et al. submitted). As otolith core diameter becomes an increasingly supported indicator for size-at-age and survival-at-age, it is important for future studies to determine how maternal investment is most reliably expressed and what influences its strength. In summary, otolith core diameter appears to be a reliable predictor for larval size-at-age and survival-at-age for the Northern Anchovy.

In addition to size at hatch, larval survival and condition were also correlated to certain environmental variables. For the most part, fish were in better

condition and lived to an older age in water that had intermediate water temperature, low salinity and low chlorophyll. This is contrary to many studies for coastal pelagic species off of the California coast that have shown links between upwelling (cold, saline, high chlorophyll water) with improved reproduction, recruitment strength, larval survival, and faster larval growth rates (Lasker 1975; Rykaczewski & Checkley 2008; Checkley & Barth 2009; Takahashi et al. 2012). A potential explanation to this discrepancy is that there may be a dome-shaped relationship between recruitment and upwelling strength (Optimal Environmental Window Hypothesis; Roy et al. 1992). A proposed reason for the dome-shaped relationship is that if upwelling is too low, there will be insufficient production to provide larval prey and if upwelling is too high, then wind-induced offshore transport has the potential to decrease larval survival by transporting larvae to offshore, unfavorable prey environments for feeding success (Lasker 1981; Peterman & Bradford 1987; Rothschild & Osborn 1988; MacKenzie & Leggett 1991). Since this study was unable to directly correlate recruitment strength to larval survival or condition-at-age, it is unclear whether this study supports anchovy's recruitment strength has a dome-shaped relationship to upwelling strength. This study simply supports that larval condition and survival does not have a linear relationship to upwelling, which is not surprising given the remarkably strong linear relationship otolith core diameter has to larval survival and condition. To thoroughly assess the Optimal Environmental Window Hypothesis, future studies could determine if anchovy larval condition also has a dome-shaped relationship to upwelling strength.

It is widely accepted by fishery scientists that larval growth rate in pelagic species is impacted by water temperature and/or prey availability (Meekan et al. 2003; Takahashi et al. 2012; Robert et al. 2014). Since all anchovy in this study were greater than 13mm in SL, it is likely their diet consisted exclusively of copepodites and adult copepods, rather than species of phytoplankton (Swieca 2022). For larval Japanese Anchovy (*Engraulis japonicus*), average larval growth rates during the last 10 days of life were most strongly impacted by the larval prey field once copepod density reached sufficient abundance (<100mg dry weight per m²; Takahashi & Watanabe 2005). Unfortunately, this study only had estimates of phytoplankton abundance through chlorophyll *a* and not zooplankton abundance. For my study, it is possible zooplankton abundance, rather than water temperature, had the biggest influence on recent growth rates. Better information on potential larval prey would help resolve the relationship between anchovy prey availability and recruitment.

In summary, this study found evidence that larger sagittae otolith core diameters are strongly correlated with higher larval condition and survival. From previous studies, this implies that larger-at-hatch larvae are more robust and outlive smaller-at-hatch larvae (Garrido et al. 2015; Fennie et al. 2022). With an increasing number of studies showing larger otolith core diameters are significantly correlated to larger size-at-hatch and improved larval survival, it is crucial future studies further analyze the extent to which greater maternal investment yields larger otolith core diameters. Additionally, future work should compare varying expressions of maternal investment (egg size, yolk-sac size,

otolith core diameter, and embryonic metabolic rates) and discuss which proxy is the most reliable predictor for larval growth rate, condition, and survival (Chambers et al. 1996; Heath et al. 1999; Bang et al. 2006; Sogard et al. 2008; Garrido et al. 2015; Fennie et al. 2022). Beyond maternal investment, this study also found that larvae are generally in better condition under water conditions that are not associated with upwelling: intermediate water temperature with low chlorophyll and salinity. The recruitment boom and exceptionally fast larval growth history during the marine heat (Figures 2.11 and 2.12) wave is counter to 20th century predictions that anchovy recruitment is high under colder water temperatures (Chavez et al. 2003; Fontes, 2011; Bond et al. 2015). This study also found a trend for years with higher recruitment strength during the winter and spring to be associated with faster larval growth rates, which is consistent with the Bigger-is-Better and Stage Duration hypotheses. A potential explanation for this relationship between recruitment and growth rate could be the Optimal Environmental Window Hypothesis (Cury & Roy 1989). Since upwelling has strong implications for water temperature and the larval prey field, it is important future work investigates ichthyoplankton prey field data in relation to both upwelling strength/timing and CPS recruitment strength. Since the collection stations for the study were both inshore and offshore, it is possible the larvae were exposed to a variable amount of coastal upwelling (Figure 2.1). Both maternal investment and upwelling may be important predictors of *Engraulis mordax* recruitment success, but without knowing the best proxy for maternal investment

or having reliable prey field data, future work is needed to conclude these potential links with CPS recruitment strength.

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Figure 2.1: A map of all 113 CalCOFI stations consisting of 11 transect lines ranging from San Diego to San Francisco. Offshore stations are defined as stations west of station 60 in each transect (McClatchie et al. 2018). Red circles indicate the locations of the 127 larvae analyzed for this study.

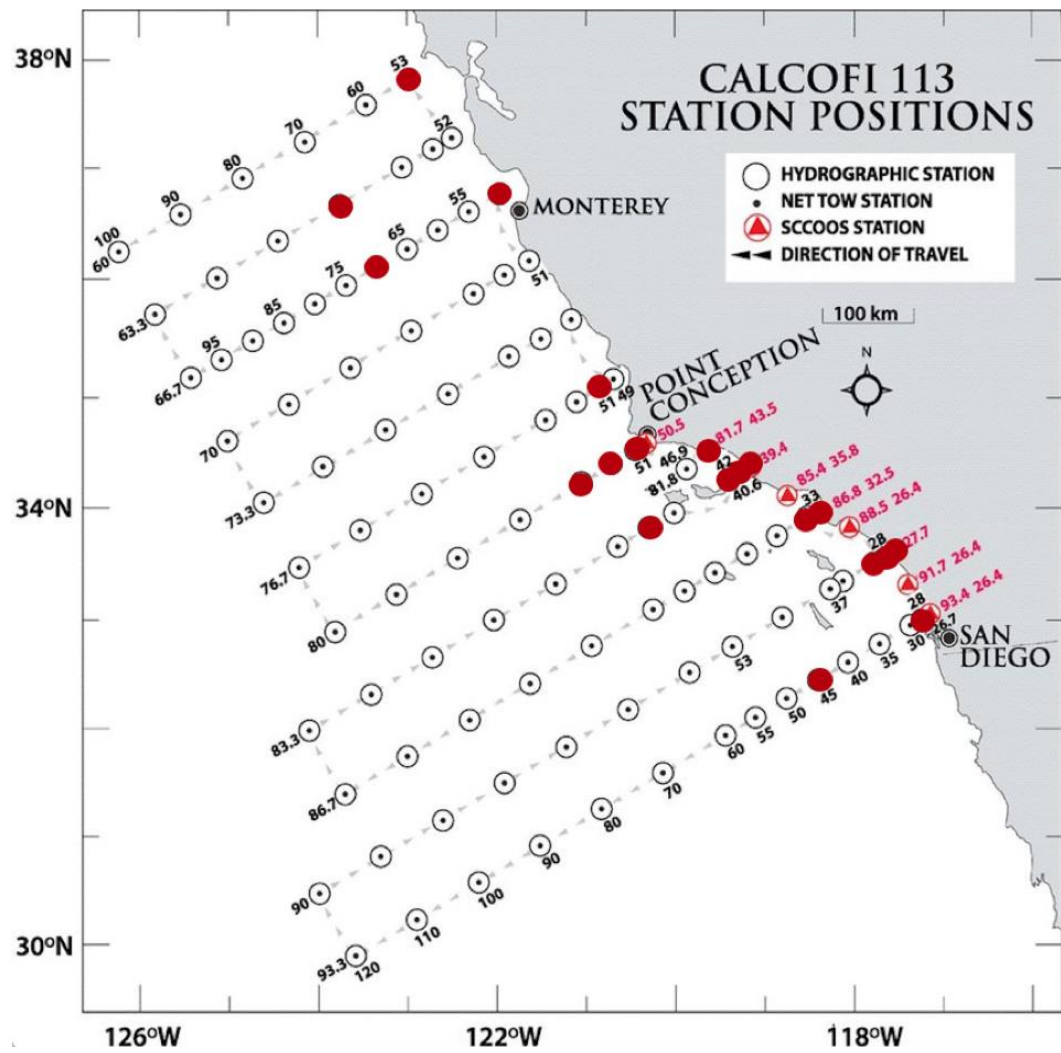


Figure 2.2: Map of the sampling sites (bright green) of NOAA's Rockfish Recruitment and Ecosystem Analysis Survey (RREAS) that was used to estimate anchovy recruitment strength. RREAS has been collecting data off the coast of southern California since 2004. Sampling sites are categorized into five stratas off the coast of California: North (N), North Central (NC), Central (C), South Central (SC), and South (S). The CalCOFI sampling sites are shown in orange.

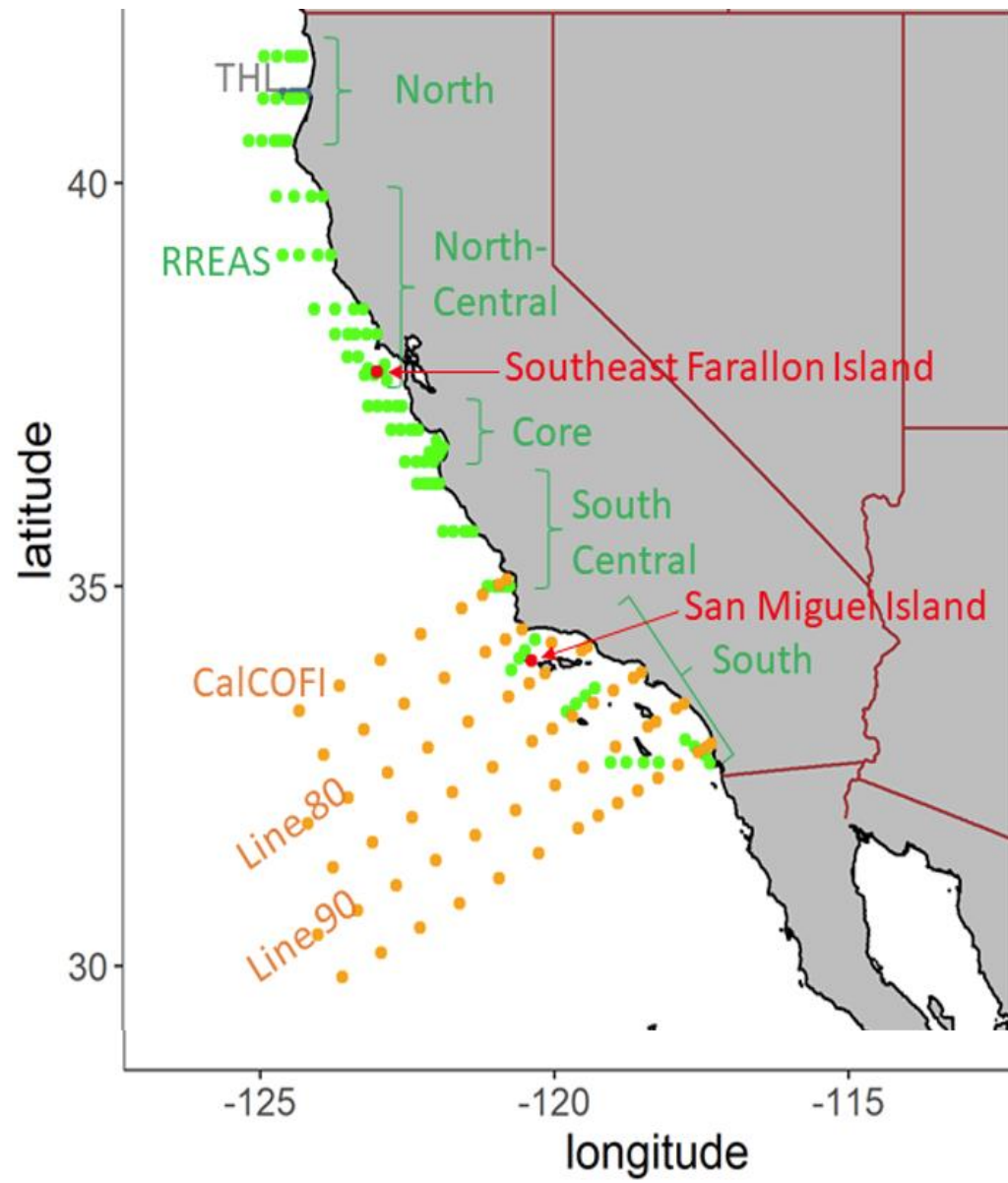


Figure 2.3: Body morphometrics of a 3-week old *anchovy*. A) muscular height at the anal fin (MHA) (solid line). B) muscular height at the pectoral fin (MHP) (solid line). C) standard body length (SL; dashed line). (Henry, 2015).

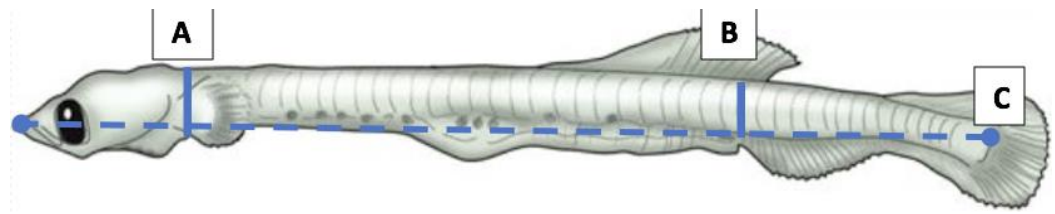


Figure 2.4: A) Northern Anchovy sagittae otolith with its core circled, which was used as a proxy for larval size-at-hatch, assumed to be influenced by maternal investment. The longest axis from the core is labeled “Radius.” B) Individual otolith increments, which were used to age each larva. Blue lines show the increment widths, which quantify larval growth rate.

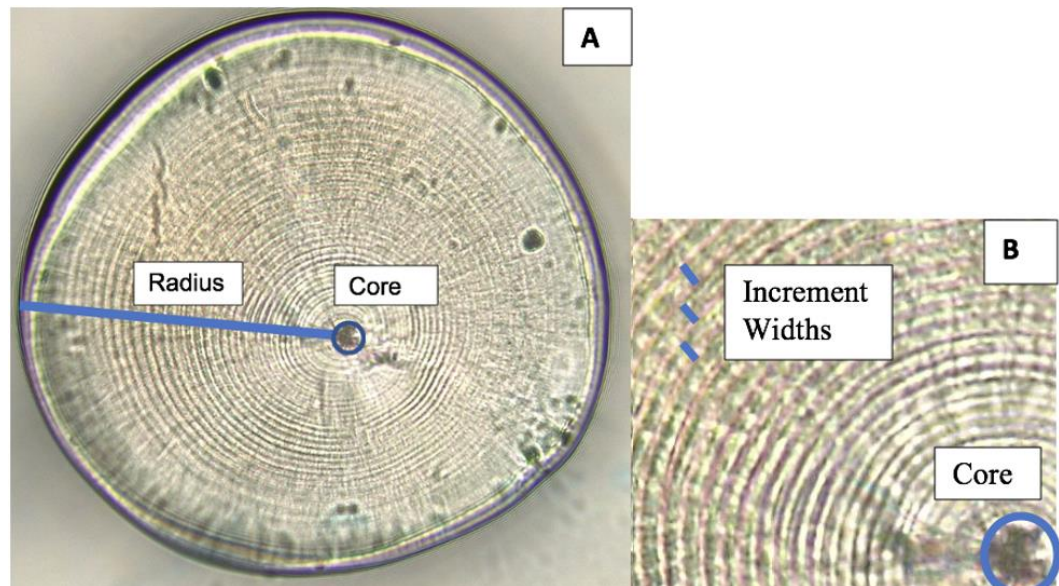


Figure 2.5: A Generalized Additive Model (GAM) showing the relationships between age with raw (not age-adjusted) standard length (A), muscular height at the pectoral fin (B), muscular height at the anal fin (C), and average recent growth rate (D).

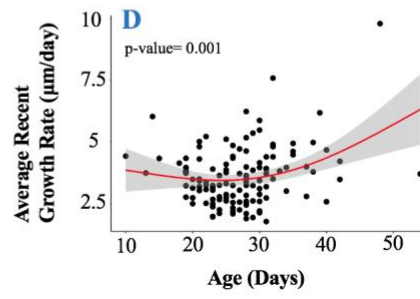
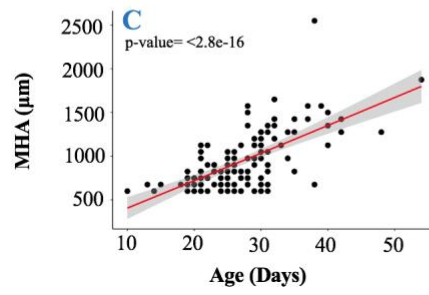
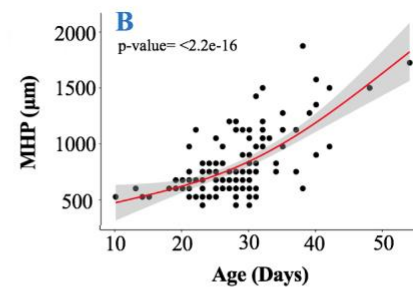
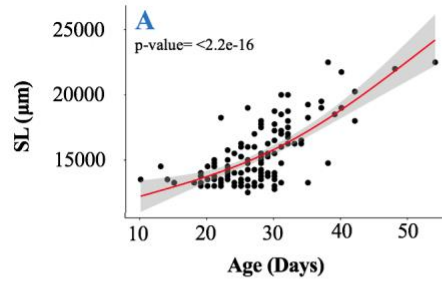


Figure 2.6a: Linear regression of the significant positive relationships between age-adjusted standard length (A), muscular height at the anal fin (B), and muscular height at the pectoral fin (C) with age-adjusted average recent growth rate.

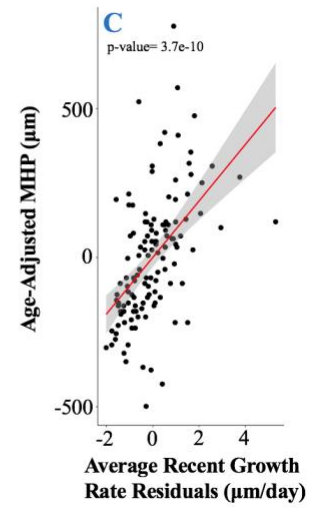
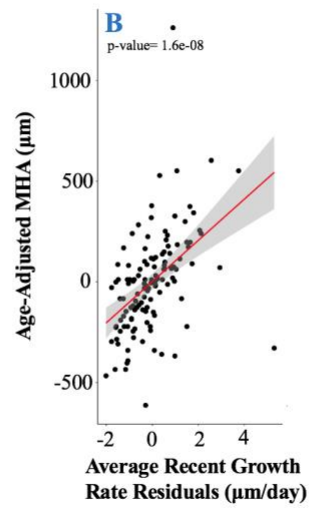
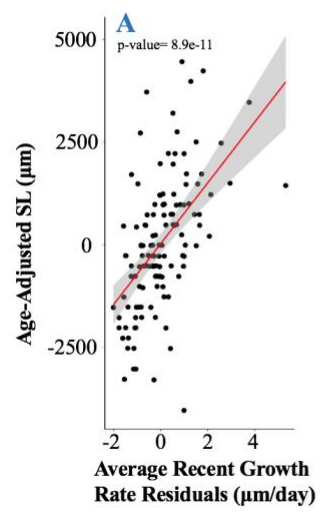


Figure 2.6b: Positive linear relationships between age-adjusted muscular height at the anal fin with standard length (A) and muscular height at the pectoral fin (B).

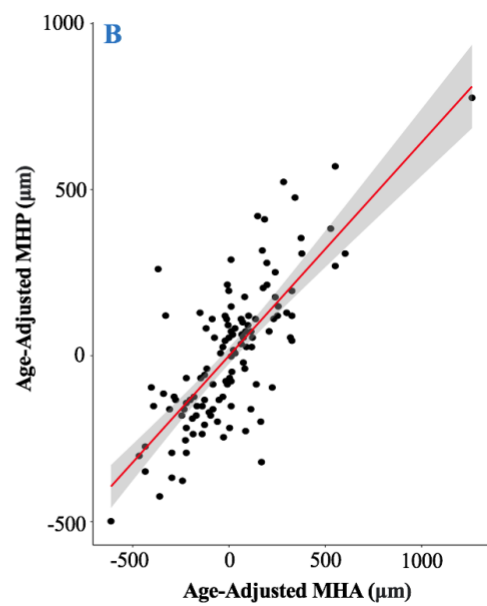
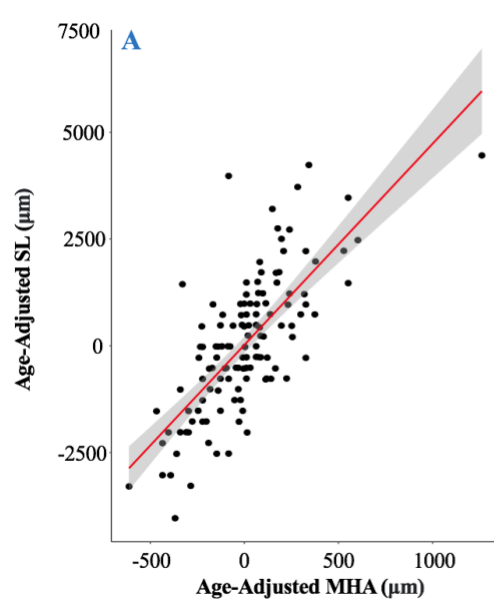


Figure 2.6c: Positive linear relationship between age-adjusted muscular height at the pectoral fin with standard length.

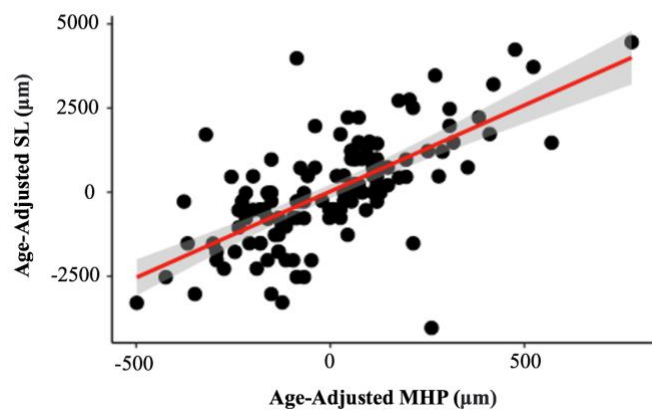


Figure 2.7: Summary of all the linear relationships between core diameter and age-adjusted standard length (A), muscular height at the anal fin (B), muscular height at the pectoral fin (C), and average recent growth rate (D). Core diameter had a significant positive linear relationship with all variables except average recent growth (D).

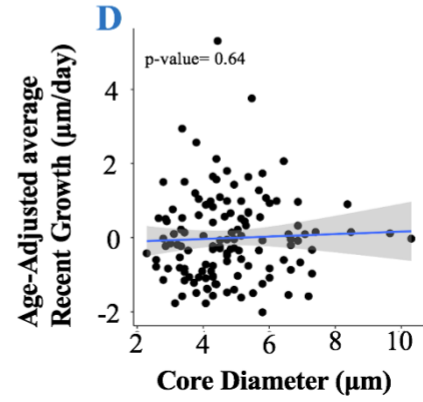
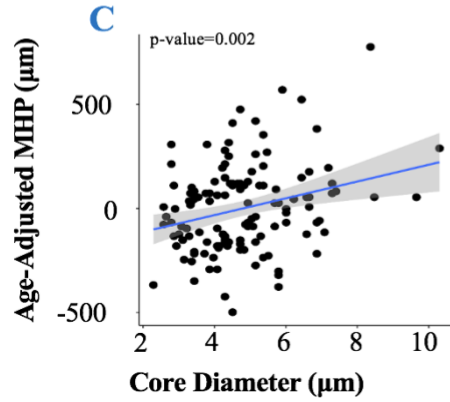
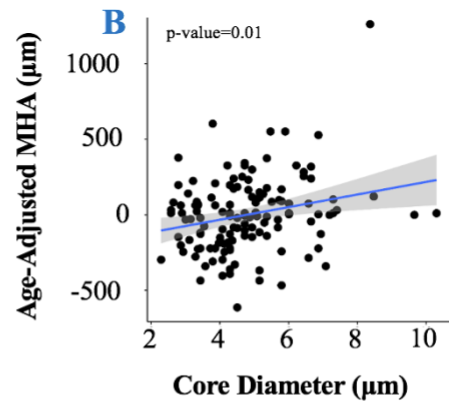
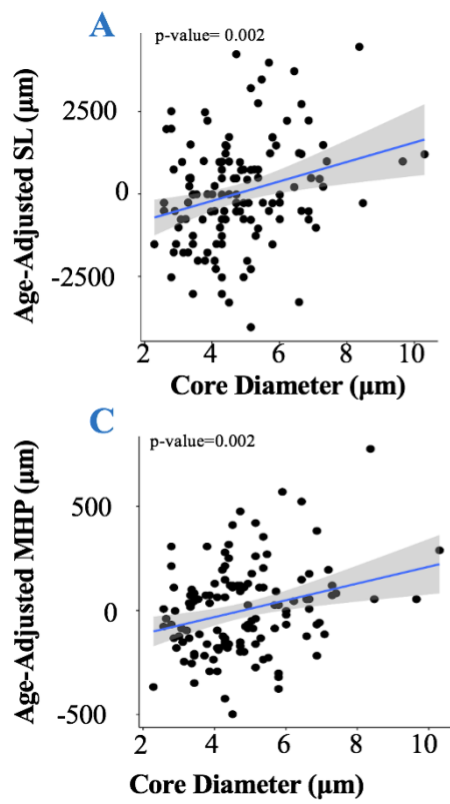


Figure 2.8: Significant positive relationship between age and core diameter. 12 of 17 (71%) fish older than 33 days had cores larger than average and 9 of 12 (75%) fish younger than 20 days had cores smaller than average.

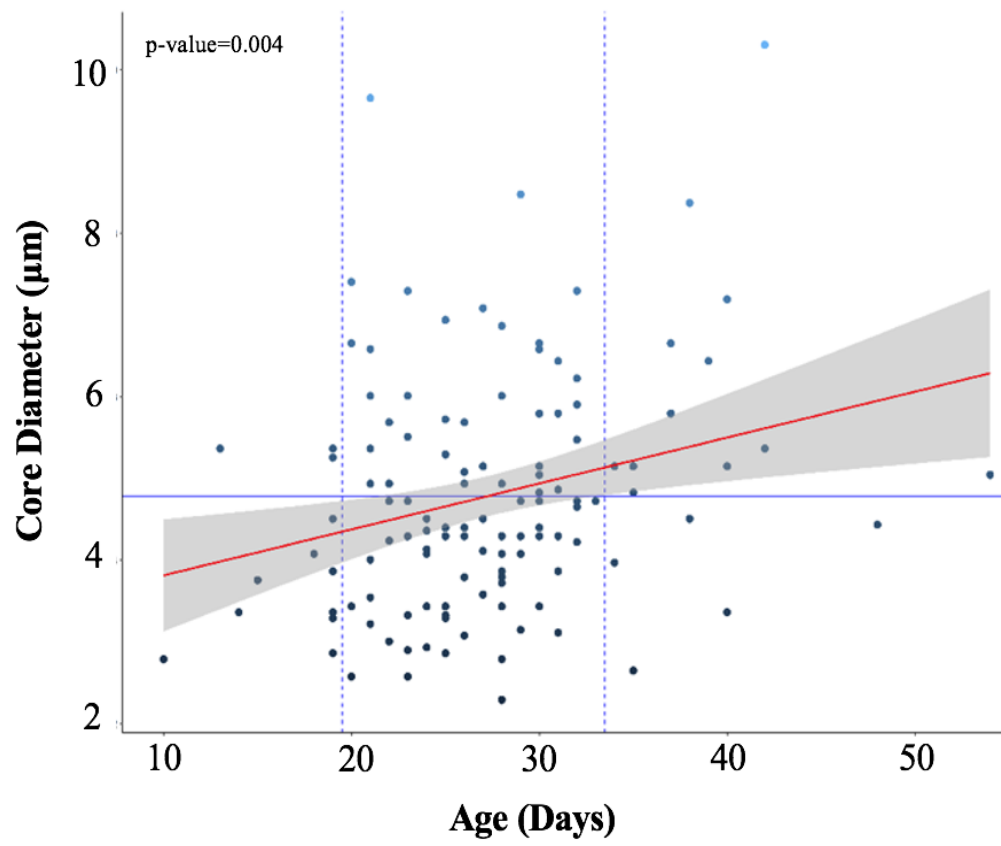


Figure 2.9: Summary of the 5 GLMM models showing the slope and 95% confidence intervals between response variables: age, MHA (age-adjusted muscular height at the anal fin), MHP (age-adjusted muscular height at the pectoral fin), SL (standard length), and average recent growth rate (last three otolith increment widths) with the explanatory variables (fixed effects): temperature, salinity, chlorophyll *a*, oxygen, location (latitude), and size-at-hatch (core diameter). Temperature and salinity were modeled as both 1st order (linear) and 2nd order (parabolic) variables. All response variables and fixed effects were centered by their mean and scaled by two standard deviations to improve computational speed and stability and to make coefficients directly comparable (Gelman 2008). If the confidence interval does not cross the 0 y-intercept line, the relationship is significant at a p-value = 0.05 threshold.

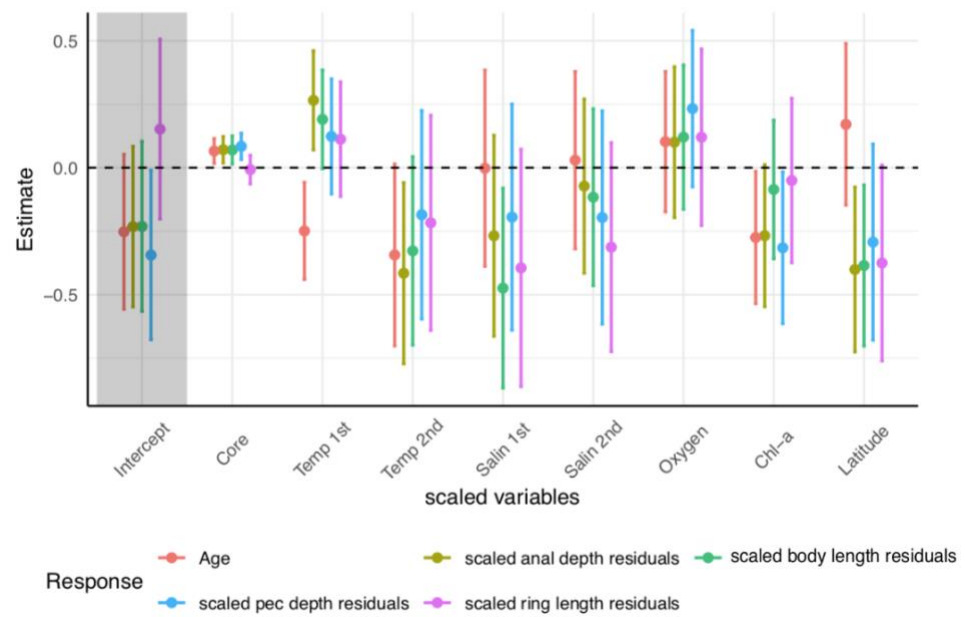


Figure 2.10: Mean ln young-of-the-year anchovy abundance from the Rockfish Recruitment and Ecosystem Analysis Survey (RREAS) in North (N), North Central (NC), Core (C), South Central (SC), and South (S) region. The horizontal line that intercepts with the y-axis shows the average number of young-of-the-year for anchovy across all points. The vertical line delineates the start of the Marine Heatwave in 2015 when recruitment abruptly increased in all regions relative to 2014. Note that data has been collected from 1990 to 2022 in the C, and from 2004 to 2022 in the other regions except 2020 when the survey was restricted to just C due to the covid 19 pandemic.

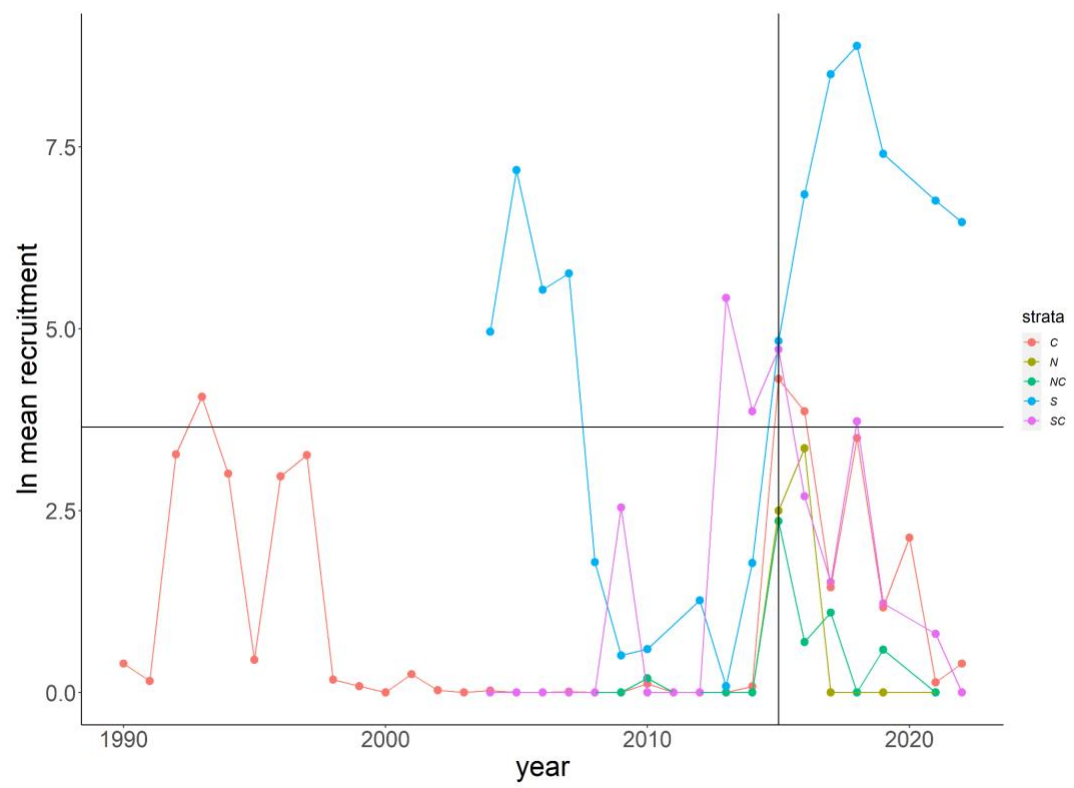


Figure 2.11: Average growth trajectories for larvae from winter and spring cruises in 2013, 2015, 2016, and 2017. Error bars represent the standard errors of the years' average increment width per larval age.

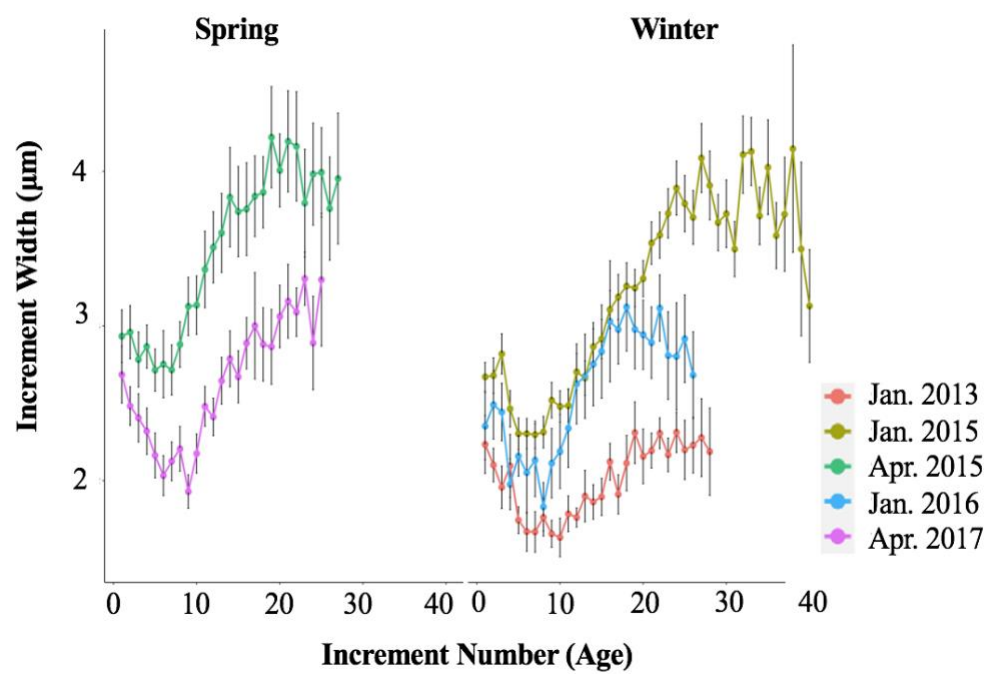


Table 2.1: Summary of GAM relationships of average recent growth rate, SL, MHA, and MHP with age.

	Average Recent Growth Rate ($\mu\text{m}/\text{day}$)	Standard Body Length (μm)	Muscular Height at the Pectoral Fin (μm)	Muscular Height at the Anal Fin (μm)
p-value	0.001	<2.2e-16	<2.2e-16	<2.8e-16
Adjusted R²	0.10	0.54	0.46	0.41
Slope (edf)	1.88	1.87	1.87	1.005
Intercept	3.64	15,351.60	795.70	947.46

Table 2.2: Summary of linear regression relationships between age-adjusted SL, MHA, and MHP with age-adjusted average recent growth rate.

	Age-Adjusted SL	Age-Adjusted MHA	Age-Adjusted MHP
p-value	8.9 e-11	1.6 e-08	3.7 e-10
Adjusted R²	0.28	0.22	0.26
Slope	3.837e-04	0.002	0.003
Intercept	-1.75 e-02	-0.009	-0.009

Table 2.3: Summary of the linear regression p-values between core diameter with:
age and age-adjusted residuals of SL, MHA, MHP, and average recent growth
rate.

	Age	Age-Adjusted SL	Age-Adjusted MHP	Age-Adjusted MHA	Age-Adjusted Average Recent Growth Rate
p-value	0.004	0.002	0.002	0.01	0.64
Adjusted R²	0.06	0.06	0.07	0.05	-0.01
Slope	1.16	294.84	40.32	41.74	0.03
Intercept	21.67	-1388.80	-193.11	-199.68	-0.17

Table 2.4: GLMM showing the relationships between age-adjusted standard length (SL; the response variable) with the explanatory variables and fixed effects of: temperature, salinity, chlorophyll *a*, oxygen, location (latitude), and size-at-hatch (core diameter).

	Core	Temp 1 st	Temp 2 nd	Salinity 1 st	Salinity 2 nd	Oxygen	Chlorophyll <i>a</i>	Latitude
p-value	0.01	0.05	0.08	0.02	0.51	0.41	0.54	0.02
Slope	0.07	0.19	-0.33	-0.47	-0.12	0.12	-0.09	-0.39

Table 2.5: GLMM showing the relationships between age-adjusted muscular height at the anal fin (MHA; the response variable) with the explanatory variables and fixed effects of: temperature, salinity, chlorophyll *a*, oxygen, location (latitude), and size-at-hatch (core diameter).

	Core	Temp 1 st	Temp 2 nd	Salinity 1 st	Salinity 2 nd	Oxygen	Chlorophyll <i>a</i>	Latitude
p-value	0.01	0.01	0.02	0.18	0.68	0.51	0.06	0.02
Slope	0.07	0.27	-0.42	-0.27	-0.07	0.10	-0.27	-0.40

Table 2.6: GLMM showing the relationships between age-adjusted muscular height at the pectoral fin (MHP; the response variable) with the explanatory variables and fixed effects of: temperature, salinity, chlorophyll *a*, oxygen, location (latitude), and size-at-hatch (core diameter).

	Core	Temp 1 st	Temp 2 nd	Salinity 1 st	Salinity 2 nd	Oxygen	Chlorophyll <i>a</i>	Latitude
p-value	0.001	0.29	0.38	0.39	0.36	0.14	0.04	0.14
Slope	0.08	0.12	-0.19	-0.19	-0.20	0.23	-0.32	-0.29

Table 2.7: GLMM showing the relationships between age-adjusted average recent growth rate (the response variable) with the explanatory variables and fixed effects of: temperature, salinity, chlorophyll a , oxygen, location (latitude), and size-at-hatch (core diameter).

	Core	Temp 1 st	Temp 2 nd	Salinity 1 st	Salinity 2 nd	Oxygen	Chlorophyll <i>a</i>	Latitude
p-value	0.79	0.33	0.32	0.10	0.14	0.50	0.76	0.06
Slope	-0.01	0.11	-0.22	-0.39	-0.31	0.12	-0.05	-0.38

Table 2.8: GLMM showing the relationships between survival (age; the response variable) with the explanatory variables and fixed effects of: temperature, salinity, chlorophyll a , oxygen, location (latitude), and size-at-hatch (core diameter).

	Core	Temp 1 st	Temp 2 nd	Salinity 1 st	Salinity 2 nd	Oxygen	Chlorophyll <i>a</i>	Latitude
p-value	0.01	0.01	0.06	0.99	0.87	0.47	0.04	0.29
Slope	0.07	-0.25	-0.34	-0.002	0.03	0.10	-0.27	0.17

Table 2.9: LME showing the significant differences between years' average larval growth trajectories.

	2013	2015	2016	2017
p-value	0.03	<0.001	0.008	< 0.001
t-test	2.1	5.2	2.8	3.8
df	1735	58	58	30

Table 2.10: Throughout 2009-2019 the 127 anchovies that were analyzed were collected from 19 sampling locations (line-station), 8 years, and 6 months.

Cruise	Year	Month	Ship	Line	Station	Number of Anchovies
1501NH	2015	January	New Horizon	60	53	10
1601RL	2016	January	Reuben Lasker	60	53	1
1501NH	2015	January	New Horizon	63.3	70	3
1501NH	2015	January	New Horizon	66.7	50	10
1501NH	2015	January	New Horizon	76.7	51	10
1511OC	2015	November	RV Oceanus	76.7	51	4
1501NH	2015	January	New Horizon	80	51	2
1601RL	2016	January	Reuben Lasker	80	51	1
1501NH	2015	January	New Horizon	80	55	5
1704SH	2017	April	Bell M. Shimada	80	60	4
1301SH	2013	January	Bell M. Shimada	81.7	43.5	7
1301SH	2013	January	Bell M. Shimada	83.3	39.4	2
1511OC	2015	November	RV Oceanus	83.3	39.4	2
1301SH	2013	January	Bell M. Shimada	83.3	40.6	1
1607OS	2016	July	Ocean Starr	83.3	40.6	6
1704SH	2017	April	Bell M. Shimada	83.3	42	3

1704SH	2017	April	Bell M. Shimada	83.3	55	3
1601RL	2016	January	Reuben Lasker	86.7	35	4
1504NH	2015	April	New Horizon	86.8	32.5	9
1601RL	2016	January	Reuben Lasker	86.8	32.5	3
1008NH	2010	August	New Horizon	90	27.7	7
1108NH	2011	August	New Horizon	90	27.7	6
1307NH	2013	July	New Horizon	90	27.7	1
0907M2	2009	July	McArthur II	90	28	10
1110NH	2011	October	New Horizon	90	28	1
1904RL	2019	April	Reuben Lasker	90	28	1
1604SH	2016	April	Bell M. Shimada	90	30	3
1504NH	2015	April	New Horizon	93.3	28	6
1704SH	2017	April	Bell M. Shimada	93.3	45	2