Summer 2021

Characterizing the Temporal and Spatial Distribution of the Cannonball Jellyfish (*Stomolophus meleagris*) in the South Atlantic Bight

Lauren G. Faulk

Characterizing the Temporal and Spatial Distribution of the Cannonball Jellyfish (*Stomolophus meleagris)* in the South Atlantic Bight

by

Lauren G Faulk

Bachelor of Science
University of South Carolina, 2019

Submitted in Partial Fulfillment of the Requirements

For the Degree of Master of Science in

Biological Sciences

College of Arts and Sciences

University of South Carolina

2021

Accepted by:

Joshua Stone, Director of Thesis

Tammi Richardson, Reader

Daniel Speiser, Reader

Tracey L. Weldon, Interim Vice Provost and Dean of the Graduate School

ABSTRACT

The cannonball jellyfish, *Stomolophus meleagris*, is commercially harvested throughout its range in the tropical and sub-tropical Americas, including in the South Atlantic Bight, where an estimated 4,000 tons (less than 2.4% of the estimated stock in South Carolina during the spring) are harvested annually. Like many Scyphozoan jellyfish, cannonball jellies have high interannual variability and little is known about the environmental drivers of their distribution and phenology. To better understand the ecology of this targeted species, we used fisheries-independent abundance data of cannonball jellyfish from 2001 to 2019 collected by the Southeast Area Monitoring and Assessment Program (SEAMAP) throughout the coastal zone of the South Atlantic Bight. Average biomass is highest in the spring off the coast of Georgia and lower South Carolina (south of Charleston), and the largest jellyfish occur during the spring months. The lowest biomass occurs in the summer months when smaller jellyfish occur. This could indicate that adult cannonball jellyfish occur offshore in the spring, move inshore toward estuarine habitats to release larvae, then juvenile cannonballs move out of the estuaries as they mature throughout the summer and fall, and finally the surviving adults are detected offshore again the next spring. The seasonal and spatial variability described does not appear to be connected to temperature, salinity, chlorophyll-a concentration, or river discharge, but is perhaps influenced by distance from estuarine habitats and wind direction. Interannual variability in biomass is evident in the cannonball jellyfish of the

South Atlantic Bight, but no long-term trends or strong correlations with the aforementioned environmental parameters were detected. Further analyses remain necessary in order to pin-point the drivers behind the variability seen in the cannonball jellyfish of the South Atlantic Bight.

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

INTRODUCTION

Cnidarian jellyfish have flourished in Earth's oceans since the Cambrian Period, and have been understudied for many years mostly due to difficulties in sampling and lack of proper methodology and collection gear (Young and Hagadorn 2010). Despite the widespread abundance of jellyfish, and the increasing acceptance of their influential role in marine ecosystems there are still substantial gaps in the knowledge of the phenology and general ecology of most known species (Purcell 2005). Jellyfish continue to draw human attention not only for their economic impacts by stinging swimmers, closing beaches, clogging powerplant intake pipes and overwhelming fishing nets, but also ecologically by predating on plankton and fish, protecting juvenile marine life, and playing a significant role in biogeochemical processes and cycles (Shimomura 1959, Brodeur 1998, Graham et al 2003, Burnett 2001, Matsueda 1969, Rajagopal et al 1989, Crum et al 2014; Lebrato et al 2012).

JELLYFISH DESCRIPTION & LIFE CYCLE

Jellyfish (Phylum: Cnidaria, Class: Scyphozoa) are radially symmetrical and have one opening that acts as both the mouth for food intake and the anus for waste excretion (Wright et al 2021). Jellyfish are characterized by an umbrella-like, or bell, body shape with flowing tentacles armed with nematocysts, or stinging-cells, that swim by contracting their muscular bell (Wright et al 2021). Jellyfish generally follow a metagenetic life cycle (Agassiz 1860) that consists of two stages – a smaller benthic polyp stage and a larger mobile, free-swimming medusa stage. The medusa stage reproduces sexually to create planula larvae, which in turn can settle into polyps and then asexually strobilate, by means of transverse fission from one individual into one or many ephyra, or immature medusae. The polyp stage, also known as scyphistomae, can also asexually reproduce through budding off a frustule, a non-eating mobile polyp which will move and establish a new colony or by branching to create a polyp colony.

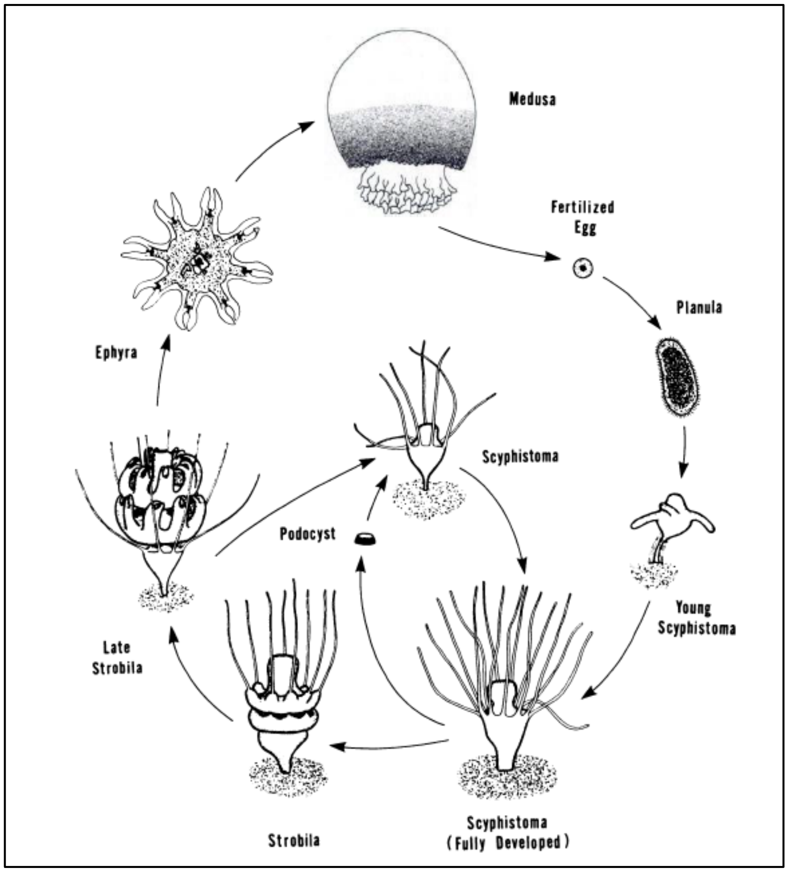

Figure 1.1 Jellyfish Life Cycle: Diagram of the scyphozoan jellyfish life cycle using *Stomolophus meleagris* as the example (Roundtree 1982).

Success in polyp reproduction and recruitment likely hinges on habitat quality among other things (Valiela et al 2001; Duarte et al 2013). Polyps can also encyst in an effort to survive poor conditions (Adler & Jarms 2009; Arai 2009; Lucas et al 2012; Schiariti et al 2014). Most medusae die off within a year (Purcell 2005). It is important to note that there is immense variety and plasticity seen in jellyfish life cycles (Boero et al 2008; Lucas and Dawson 2014; Wright et al 2021). For example, many scyphozoan jellyfish spend most of their life in the medusa stage, while some spend the more of their lifetime as a polyp and some only exhibit one stage (holobenthic or holoplanktonic) (Wright et al 2021). For most species, the factors that trigger progression from one life stage to the other are uncertain but may include chemical cues, food availability or seasonal changes in environmental parameters like temperature and salinity (Purcell 2005).

CLIMATE CHANGE

Previously, it was believed that increasing temperature associated with climate change could potentially lead to spatial and temporal spreading and increased population sizes of jellyfish (Purcells 2005). More recent literature suggests that the relationships between jellyfish biomass and climate are much more complex than previously assumed, and that jellyfish populations are not significantly increasing long-term (Brodeur et al 2008; Condon et al 2013). Brodeur et al (2008) concluded that it is likely that several confounding biotic and abiotic factors are to blame for the apparent increase in jellyfish populations.

Literature suggests that basin-wide climate oscillations are potentially linked to changes in jellyfish abundance (Anderson & Piatt 1999; Ottersen et al 2001, Raskoff 2001, Austin 2002, Beaugrand 2003, Lynam et al 2004, Purcell & Decker 2005; Brodeur et al 2008). Studies performed in vitro under controlled laboratory conditions employ drastic variation in treatment conditions, like temperature or salinity, compared to the more gradual, subtle circumstances found *in situ*. Seeing jellyfish not only survive but also reproduce under the extreme changes invoked in the laboratory setting suggests extraordinary potential to endure and thrive under climate change conditions (Purcell 2005). But it is important to note that different species, and even different populations of the same species, may react completely differently given the same environmental conditions and changes (Pederson & Smidt 2000; Lucas 2001; Purcell 2005).

ROLE OF JELLYFISH IN MARINE ECOSYSTEMS

Jellyfish are well-known predators of plankton, specifically zooplankton and ichthyoplankton, which has the potential to significantly impact higher tropic levels through cascading effects (Deason & Smayda 1982; Suchman et al 2008; Condon et al 2012; Ruzicka et al 2020; Pitt et al 2007, 2009; West et al 2009; Wright et al 2021). As predators, jellyfish are known to have detrimental effects on the biomass, abundance, and size distribution of zooplankton (Moller 1980; Mills 1995; Purcell & Arai 2001). Mass aggregations of jellyfish, termed “blooms”, can easily dominate local ecosystems and exhaust local zooplankton populations. During blooms and under normal circumstances, jellyfish have the potential to hinder fish species through both competition for prey and directly preying on them (Brodeur et al 2008; Shoji et al 2009; Brodeur et all 2011; Ruzicka et al 2012; Schnedler-Meyer et al 2016; D’Ambra et al 2018; Tilves et al 2018).

Historically, jellyfish were viewed as trophic dead-ends, meaning the nutrients ingested by jellyfish are not transmitted to higher trophic levels (Verity & Smetacek 1996; Sommer et al 2001). It is now known that sea turtles and over one hundred species of fish prey on jellyfish (Arai 1988; Ates 1988; Mianzan et al 2001; Purcell & Arai 2001; Arai 2005; Pauly et al 2009; Cardona et al 2012; Heaslip et al 2012). In addition to predation in the water column, jellyfish may also become a meal for benthic organisms when they die and sink down to the seafloor (Henschke et al 2013; Sweetman et al 2014).

JELLYFISH FISHERY

Jellyfish were viewed as a nuisance to fishers because at high abundances they can overwhelm and burst nets while trawling for other commercially important marine organisms (Broadhurst & Kennelly 1996). This dilemma inspired the development of the prototype gear modification that eventually became the turtle excluder device (TED) (Jones & Rudloe 1995). Fishers implemented a series of bars in their nets that pushed organisms larger than the gap, like jellyfish or turtles, to an exit hatch while still allowing smaller organisms, like shrimp, to pass through into the cod end of the net (Jenkins 2012). This adjustment proved to be successful in reducing the jellyfish bycatch by more than 80% (Huang et al 1987). However, jellyfish are not viewed as a nuisance everywhere, as jellyfish have been harvested in Asian counties like China, Thailand, Malaysia, Korea, Japan, Taiwan, and Singapore for human consumption for over 1700 years (Lopez-Martinez & Alvarez-Tello 2013; Brotz et al 2017). Now these edible jellyfish outside of eastern Asia are the focus of an up-and-coming fishery in many countries. As demand for this ocean commodity grew and local jellyfish fishery establishments collapsed, the jellyfish fishery scene began to spread into the Western

Hemisphere with varied levels of success (Brotz er al 2017). The fishery produces a significant amount of catch globally, surpassing one million tons, but currently the Americas contribute only about 3% of that global catch (Brotz 2016; Brotz & Pauly 2016).

Jellyfish are commercially harvested using a myriad of collection gear such as hand or dip nets, various types of seines, hooks, trawl nets and sometimes combinations of these (Brotz et al 2017). Just like any fishery, it is vital to set size limits and utilize specific mesh sizes to efficiently catch mature medusae and limit the catch of juveniles and bycatch. There are many factors that influence the distribution of jellyfish in the water column, including currents, rain, wind, and light intensity, which in turn influences the choice of fishing gear (Graham et al 2001; Brotz et al 2017). Scyphozoan jellyfish in the order Rhizostomeae are typically targeted as the "edible jellyfish" because the texture and consistency of their tissues results in the desired chewy yet crunchy quality (Brotz et al 2017).

Jellyfish focused fisheries have been attempted in Argentina, Canada, Ecuador, Honduras, Mexico, Peru, Nicaragua and the United States with various levels of success (Brotz et al 2017). Argentina is focused on *Lychonorhiza lucerne*, a species that does not have a history of being fished for human consumption (Brotz et al 2017). *L. lucerne* is under research along the northern coast of Buenos Aires province to see if it can generate a quality product for consumption since it is a nuisance to already established fisheries and local tourism and has the potential to provide a needed economic boost to the local fishers (Nagata et al 2009; Brotz et al 2017). The jellyfish fishery in Argentina has been limited by the lack of credible economic and ecological information, and as a result remains at a developmental impasse (Brotz et al 2017). Canada attempted to target Aurelia spp. in both the Pacific and Atlantic, but ultimately ceased due to inadequate demand for the product. These jellyfish did not produce the crunchy texture consumers desire (Sloan & Gunn 1985). In the first year of attempting to fish for jellies, Ecuadorian shellfish fishers landed 78,000 tons of jellyfish thought to be *Stomolophus meleagris*, in only a few months in 2014 (Brotz et al 2017). The Ecuadorian jellyfish fishery is still landing tons of catch. Honduras is exploring the exploitation potential of *Stomolophus* species in the Gulf of Fonseca in the Pacific Ocean (Brotz et al 2017). Mexico initially focused its jellyfish fishing efforts on the Gulf of Mexico near Tabasco but shifted its fishery to the state of Sonora in the Gulf of California one year later in 2001 (Lopez-Martinez & Alvarez-Tello 2013; Brotz et al 2017). This fishery brings in 10,000 to 15,000 tons on average each year and has attempted to implement management measures to maintain the stability and longevity of the industry (Brotz et al 2017). The initial attempt at establishing a jellyfish fishery in Nicaragua deteriorated, but in 2013 and 2014 the interest in starting the fishery revived (Brotz et al 2017). Peru attempted to exploit *Chrysaora plocamia* with the hope to eventually extend the fishery into Chile, but semaeostome jellyfish are less desirable than Rhizostomes so this fishery remains undeveloped (Brotz et al 2017).

The United States is the home a historical, cancelled fishery in Washington State and an active, growing fishery in the southeastern states. The jellyfish *Aequorea victoria* was harvested in the Puget Sound until the 1990s for bioluminescence research that specifically focused on isolating aequorin and green fluorescent protein (GFP) (Shimomura 1995). These jellyfish were harvested until synthetic versions of these proteins became available because GFP is a significant genetic marker (Zimmer 2005; Brotz et al 2017). On the opposite side of the country, several attempts were made to establish fisheries for the edible *Stomolophus meleagris*. The first attempt occurred in the 1970s in Florida but lacked the necessary involvement and willingness of fishers (Rudloe 1992; Brotz et al 2017). The next attempt began gaining traction in the 1980s in Florida and Georgia, and officially launched in 1991 with monetary support from the US Department of Commerce (Brotz et al 2017). Florida attempted to establish a fishery in the panhandle but faced many obstacles including pollution from processing, lack of knowledge and small jellyfish. Consumers preferred the jellyfish without the dark coloration around the bell, so focus shifted into the Gulf of Mexico where jellyfish are still harvested for consumption (Brotz et al 2017). Georgia began licensing six to twelve shrimp fishers to harvest jellyfish in 1998 for the processing facility in Darien, GA and became an official fishery in 2013.

CONCLUSION

Most jellyfish species exhibit clear seasonality, and high interannual variability. These enigmatic life history traits coupled with lack of research in the field and unsustainable traditional fishing practices can lead to uncertainty and instability that can prevent progress in the industry (Brotz et al 2017). The polyp stage of the jellyfish life cycle may allow populations to combat fishing pressures and prevent stock collapse but there remains more to be learned about the population dynamics of jellyfish in order to implement appropriate management and foster a healthy fishery (Brotz et al 2017). In this paper, we will explore variability and drivers of biomass of *Stomolophus meleagris* in the South Atlantic bight on seasonal, spatial and interannual scales.

CHAPTER 2: CANNONBALL JELLYFISH (STOMOLOPHUS MELEAGRIS)

INTRODUCTION

Stomolophus meleagris (Phylum: Cnidaria, Class: Scyphozoa, Order: Rhizostomeae, Family: Stomolophidae), or cannonball jellyfish, are found in the western Atlantic from New England to Brazil, the eastern Pacific from southern California to Ecuador, and the western Pacific from the Sea of Japan to the South China Sea (Kramp 1961; Larson 1976; Omori 1978; Griffin & Murphy 2005). This jellyfish is one of the most prevalent scyphozoans in the western Atlantic along the coast of the southeastern and Gulf States of the United States (Mayer 1910; Kraeuter & Setzler 1975; Burke 1976; Calder & Hester 1978; Griffin & Murphy 2005). Cannonball jellyfish are commonly referred to as “jellyballs” by locals because they lack long, trailing tentacles. They do, however, have several short oral arms accompanied by scapulets, or oral folds located at the base of the bell (Griffin & Murphy 2005). These jellyfish are regularly found in both estuarine and coastal waters with temperatures from 23.84 to 31.72 degree Celsius (23.7 degrees Celsius on average) and salinities ranging from 15.011 to 36.637 parts per thousand (34.2 ppt on average) (Griffin & Murphy 2005; SEAMAP data). Cannonball jellyfish are known to feed on zooplankton, including commercially important species such as larval red drum (Duffy et al. 1997; Griffin & Murphy 2005) and the veliger stage of the mollusk life cycle (Larson 1991; Griffin & Murphy 2005). Although *S. meleagris* is not listed or considered to be in danger of extinction, it is an ecologically important species for conservation because it is a primary prey species for Atlantic spadefish, butterfish, and the endangered leatherback sea turtle (Hayse 1989; Phillips et. al 1969; Griffin & Murphy 2005, Page 2015). In addition to its ecological importance, the cannonball jellyfish is also economically significant.

For 1700 years, jellyfish in the order Rhizostomeae, including the cannonball jellyfish, have been harvested in eastern Asia for consumption (Lopez-Martinez & Alvarez-Tello 2013). Although *S. meleagris* jellyfish were originally seen as a pest for shrimpers in the US and Mexico, they are now commercially targeted throughout their range, including the waters adjacent to the southeastern United States where an estimated 4,000 tons are harvested annually. Since the US commercial fishery began in 1998, *S. meleagris* has become an economically valuable United States export, emerging as the third largest fishery by weight in the state of Georgia (Page 2015).

Like many Scyphozoan jellyfish, cannonball jellies have high interannual variability, but little is known about the environmental drivers of their distribution and phenology. And despite their economic importance, no stock-assessment or analysis of their population dynamics in the South Atlantic Bight has been conducted. To better understand the ecology of this species, we will analyze data from a long-term time series of cannonball jellyfish collected from the South Atlantic Bight.

The area of coastal water along the southeastern United States that spans from Cape Canaveral, Florida up to Cape Hatteras, North Carolina is known as the South

Atlantic Bight. The continental shelf of the South Atlantic Bight is slimmer at both extremities, approximately 50 kilometers off the coast of Cape Canaveral and 30 kilometers off the coast of Cape Hatteras, and wider in the center, maxing out at 120 kilometers near Savannah, Georgia (Atkinson et al 1983; Blanton et al 2003). The coastal region of the South Atlantic Bight, especially from central South Carolina down to northern Florida, is dominated with inlets and rivers but also strongly influenced by the Gulf Stream (Blanton et al 2003). According to Atkinson et al (1983), the hydrographic properties of the South Atlantic Bight are split into three distinct regions (inner, middle and outer shelf). The inner continental shelf is influenced by riverine input, tidal fluxes and atmospheric dynamics the most (Atkinson et al 1983; Blanton et al 2003). The middle continental shelf is controlled mostly by the tides, and winds and oftentimes Gulf Stream (Atkinson et al 1983; Blanton et al 2003). Lastly, the outer portion of the continental shelf is unsurprisingly dictated by Gulf Stream (Atkinson et al 1983; Blanton et al 2003).

Weber and Blanton (1980; 1985) established five seasonal wind periods for the South Atlantic Bight – winter, spring, summer, fall and mariner’s fall. Studies by Bumpus (1973) illustrated that surface flows generally align with the three main wind regimes (Winter, Summer and Mariners’ Fall) detailed above (Blanton et al 2003). The Winter period is coupled with offshore surface flows. The Summer period is coupled with poleward flows. Lastly, the Mariners’ Fall period is coupled with surface flows toward the equator (Bumpus 1973; Weber & Blanton 1980; Blanton et al 2003).

AIMS OF THIS THESIS:

- QUESTION: Is there clear seasonality in cannonball jellyfish biomass in the sampling region?
    - HYPOTHESIS: Cannonball jellyfish biomass in the sampling region will be highest in the spring months.
    - RATIONALE: In 1910, cannonball jellyfish were documented as abundant off the coasts of Florida, Georgia and South Carolina during the winter and spring (Mayer 1910).
- How does latitude impact cannonball jellyfish seasonality?
    - HYPOTHESIS: Jellyfish biomass will be highest off the coast of Georgia & South Carolina, and lowest off the three regions in North Carolina.
    - RATIONALE: Cannonball jellyfish are considered to be the most common scyphozoan jellyfish off the coast of South Carolina and Georgia (Krauter & Setzler 1975; Calder & Hester 1978).
- If not latitude, what drivers impact the spatial variability in cannonball jellyfish?
    - HYPOTHESIS: Temperature and chlorophyll-a concentration will have the strongest influences on spatial variability in cannonball jellyfish.
    - RATIONALE: Jellyfish are often controlled by bottom-up effects (Purcell 2012; Condon et al 2013). Warmer temperatures can positively influence phytoplankton populations. Higher abundances of phytoplankton, and higher chlorophyll-a concentrations leads to blooms in the zooplankton that jellyfish feed on.

- Do cannonball jellyfish exhibit interannual variability in the South Atlantic Bight?
    - HYPTOHESIS: Like most scyphozoan jellyfish species, cannonball jellyfish will exhibit interannual variability in the sampling region.
    - RATIONALE: The relationship between jellyfish biomass and environmental parameters seems to be more complex than originally thought. This means several biotic and abiotic factors have the ability in influence jellyfish population dynamics each year.
- If so, what drives that interannual variability?
    - HYPOTHESIS: Climatic oscillations and temperature will have the strongest influences on interannual variability in cannonball jellyfish.
    - RATIONALE: Jellyfish biomass appears to fluctuate on a decadal scale around the globe, suggesting a global-level driver, like climatic oscillations (Condon et al 2013).
- Are the cannonball jellyfish populations stable or changing long-term?
    - HYPOTHESIS: Interannual variability will be noticeable, but long-term trends will not be discernable yet given only nineteen years of data.
    - RATIONALE: Long-term trends in jellyfish can occur on decadal scales (Condon et al 2013). We need at least 20-30 years of data to describe long-term trends with confidence.

METHODS

SEAMAP

Fishery-independent data of the cannonball jellyfish has been collected by trawl and recorded since 1989 by South Carolina Department of Natural Resources Marine

Resource Division (SCDNR-MRD) through the Southeast Area Monitoring and Assessment Program – South Atlantic (SEAMAP-SA). From 1989 to 2001, SEAMAP-SA only recorded the presence or absence of *S. meleagris*, and the jellyfish were present in 43 percent of the tows (Griffin and Murphy 2005). From 2001 to present, biomass data of the cannonball jellyfish was recorded for each tow (Griffin and Murphy 2005). Trawls

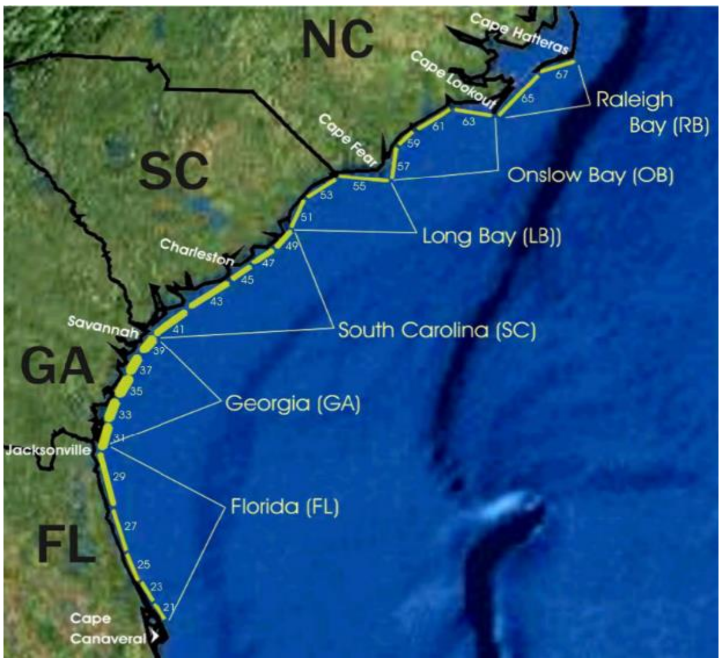

Figure 2.1 Sampling Region: Schematic of the SEAMAP-SA sampling region. Strata not drawn to scale. (SEAMAP-SA Data Management Work Group)

take place during the daylight hours in the coastal zone of the South Atlantic Bight between Cape Hatteras, North Carolina and Cape Canaveral, Florida during the spring, summer and fall from mid-April to mid-May, mid-July to early August and early October to mid-November, respectively. The sampling region is divided into 24 strata across six distinct regions – Florida (Strata 21-29), Georgia (31-39), South Carolina (41-49), Long

Bay (51-55), Onslow Bay (57-63) and Raleigh Bay (65 & 67). The strata are defined approximately by the four-meter and ten-meter depth contour. The number of stations sampled within each stratum is determined through optimal allocation annually. They aim to sample between 102 and 112 stations per season (306-336 per year) with, generally, three to five stations per strata, contingent on funding and field conditions. The jellyfish are collected using two 75-foot mongoose-type Falcon trawl nets without a Turtle Exclusion Device (TED) hauled by a 75-foot double-rigged shrimp trawler named the Lady Lisa. The trawl net was made of 1.875 inch mesh for the body, and 1.625 inch mesh for the cod end. Each trawl is pulled for 20 minutes not including wire-out (approximately 1-2 minutes) and haul-back (approximately 2-3 minutes) time at approximately 2.5 knots. The two nets are processed individually for the data collection but analyzed as one sampling event. The biomass and abundance of the total catch is measured or estimated from subsample of approximately 30-60 specimens. Additionally, surface, and bottom temperature and salinity were measured with each tow. Abundance (number of individuals/tow), biomass (kg/tow), salinity and temperature data from 2001 to 2019 was downloaded on May 24th, 2020 from https://www2.dnr.sc.gov/seamap/.

Environmental Data

In addition to the data provided by the SEAMAP-SA timeseries, environmental data was downloaded from the following programs: NASA, USGS, and NOAA. Monthly chlorophyll-a measurements (mg per cubic meter) were downloaded from NASA's Ocean Color Data center on April 5th, 2021 (https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/chlor_a/). These data were collected through MODIS-Aqua satellite mission and reported at a 4-kilometer resolution. Monthly river discharge rates (cubic feet per second) were downloaded from USGS's National Water Dashboard on May 25th, 2021 (https://dashboard.waterdata.usgs.gov/app/nwd/?region=lower48&aoi=default). Monthly mean values for the North Atlantic Oscillation index were downloaded from NOAA's Climate Prediction Center on March 10th, 2021 (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml).

Statistical Analyses

Data Cleaning

All statistical analyses were completed using RStudio Version 1.4.1106 programming language and software. The jellyfish trawl raw data displayed an individual value representing the total number and total weight recorded for each net for each tow. Because there was a set of two nets used simultaneously during every tow, making them non-independent samples, the data for both nets was combined for the statistical analysis. This resulted in an average total number of specimens and an average total weight caught for each event. In order to standardize the data to account for any variability in sampling frequency between strata, the data were grouped by year, strata, and season to produce one average value for each variable measured per sampling event. The total weight variable was also adjusted using the natural log() function to normalize the data for the analysis.

Size Proxy

A proxy for average jellyfish size was estimated by dividing the total weight measurement by the number of individuals caught for each tow event. The results were then averaged across each strata for all of the three seasons.

Standing Stock Estimate

To calculate an estimate for the standing stock of jellyfish in the sampling region, the area of each strata was estimated. The exact dimensions of the trawl net used are variable depending on water currents and tow conditions, so we calculated an estimated area for the mouth of the net using diagrams of a similar net given in a paper from Stender & Barans (1994). Next, the distance the vessel traveled in meters was calculated based on the known speed of 2.5 knots (1.28 meters/second) and the tow time of 20 minutes (1200 seconds). Finally, the area of the net opening (m^2) was multiplied by the distance the vessel traveled (meters) to produce an estimate of the total volume of water sampled through a single net.

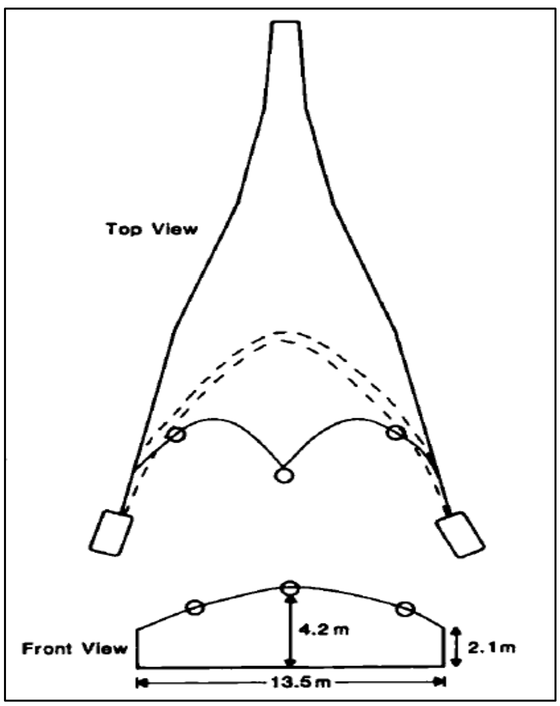

Figure 2.2 Trawl Dimensions: Diagram of the tongue trawl during tow from Stenner & Barans (1994) used to estimate the area of the net opening for the SEAMAP tows.

Next, the average total weight for each event was divided by the total volume of water sampled per tow then multiplied by 7 meters (the average depth of the sampling region) to produce a density value. The resulting density value for each event was then multiplied by the area of the corresponding strata where the tow occurred, producing a rough measure of total biomass (kg) in that stratum at that time. Finally, the total biomass values were averaged across each stratum, year, and season. This estimate of biomass is based on the assumption that we are sampling the entire water column, or the jellyfish are evenly distributed throughout the water column. As a result, the estimate for standing stock is likely conservative, given that cannonball jellyfish are known to aggregate at the surface during the day when all tows are collected.

K-means Cluster Analysis

Preliminary analyses of environmental parameters showed distinct environmental regimes within the sampling region. To explore spatial variability in jellyfish abundance, we wanted to identify similar hydrographic regions. To identify those hydrographic regions, a k-means cluster analysis was used to determine an appropriate number of clusters needed to explain trends in the data. A user-defined function was then used to determine which of the 24 strata clustered together based on surface temperature, surface salinity and chlorophyll-a concentration. An ANOVA and pair-wise analysis was conducted on the resulting clusters to ensure that the clusters were indeed statistically significantly different from one another.

Anomaly analysis

Anomaly is determined by comparing each biomass value to overall mean total biomass and logging to make the data more normal for analysis.

$$A = \log\left(\frac{total\ weight}{mean\ total\ weight}\right)$$

This produces positive values when the datapoint is above the overall mean, and negative values when the datapoint is below the overall mean. The anomaly analysis was conducted for the whole dataset, each individual season (spring, summer, and fall), and each of the major regions (Far South, South, North and Far North).

Correlations

Finally, Pearson's correlations between the jellyfish anomaly and environmental parameters like chlorophyll-a concentration, surface temperature, surface salinity, river discharge rates, and the North Atlantic Oscillation index were calculated within each year sampled, and on a one-season lag to investigate if the environmental conditions of the previous season influence the biomass measurements.

RESULTS

Estimated Standing Stock

The highest estimated biomass is 12,500 ± 18,000 kg / km^2 during the Spring in strata number 43 (Figure 4a). The lowest estimated biomass is 3 ± 8 kg / km^2 during the Summer in strata number 67 (Figure 4b). Average biomass in the Florida region ranges from 171 ± 640 kg / km^2 to 1,700 ± 11,600 kg / km^2 (Figure 3). Average biomass in the Georgia region ranges from 1,900 ± 6,300 kg / km^2 to 3,200 ± 7,000 kg / km^2 (Figure 3). Average biomass in the South Carolina region ranges 1,200 ± 3,900 kg / km^2 to 5,600 ± 13,000 kg / km^2 (Figure 3). Average biomass in the Long Bay region ranges from 923 ± 4,300 kg / km^2 to 1,400 ± 4,200 kg / km^2 (Figure 3). Average biomass in the Onslow Bay region ranges from 527 ± 2,200 kg / km^2 to 1,600 ± 7,500 kg / km^2 (Figure 3). Average biomass in the Raleigh Bay region ranges from 216 ± 1,100 kg / km^2 to 449 ± 3,000 kg / km^2 (Figure 3).

The highest total biomass (kg) measurements in the survey area occurred in South Carolina, with the majority of that biomass occurring in the Spring (157,486,000 kg) (Table 1). The second highest total biomass in the survey area occurred in Georgia waters, with the majority of that biomass occurring during the Fall (57,826,000 kg) (Table 1). The lowest total biomass (kg) occurred in Raleigh Bay, North Carolina during in Summer (16,000 kg) (Table 1).

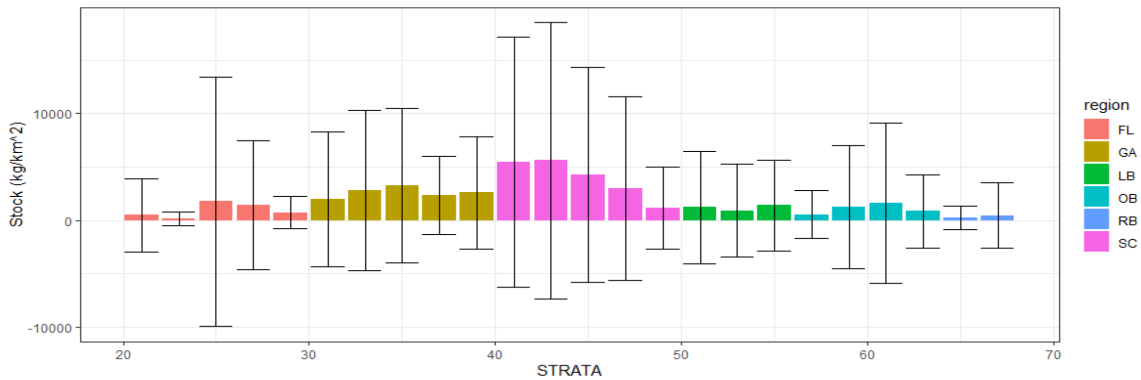

Figure 2.3 Average Standing Stock: Bar-graph displaying average estimated standing stock (kg/km^2) across the sampling region from South (strata 21) to North (strata 67) colored by region. Error bars represent calculated standard deviations.

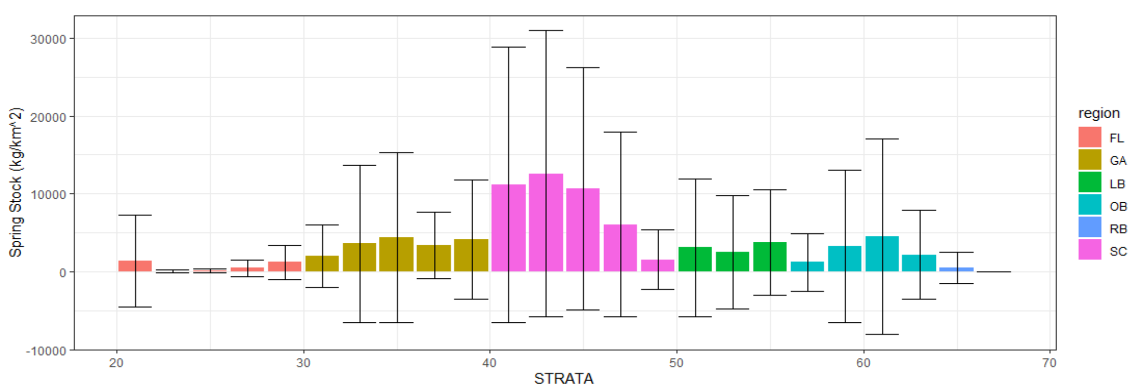

Figure 2.4a Spring Standing Stock: Bar-graph displaying average estimated standing stock (kg/km^2) across the sampling region from South (strata 21) to North (strata 67) colored by region for the Spring season. Error bars represent calculated standard deviations.

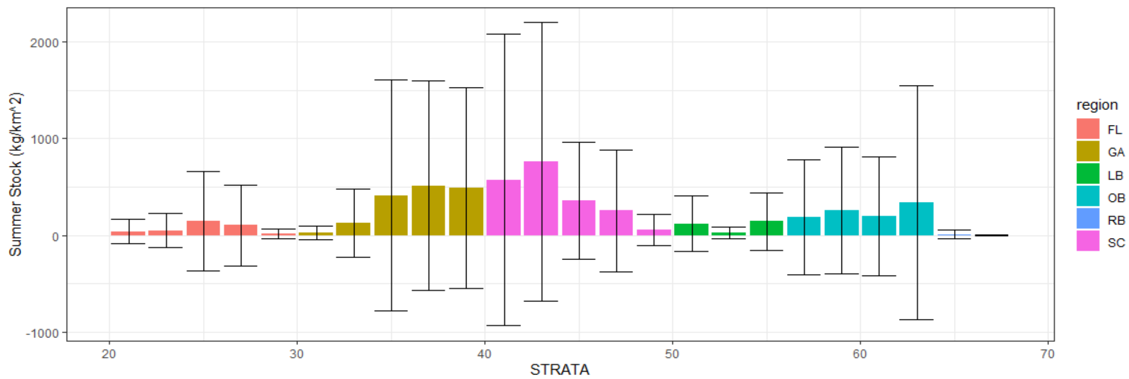

Figure 2.4b Summer Standing Stock: Bar-graph displaying average estimated standing stock (kg/km^2) across the sampling region from South (strata 21) to North (strata 67) colored by region for the Summer season. Error bars represent calculated standard deviations.

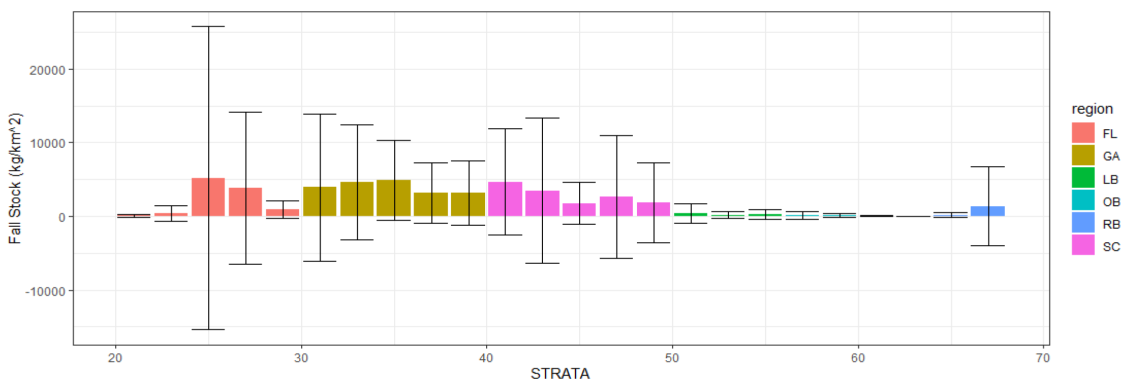

Figure 2.4c Fall Standing Stock: Bar-graph displaying average estimated standing stock (kg/km^2) across the sampling region from South (strata 21) to North (strata 67) colored by region for the Fall season. Error bars represent calculated standard deviations.

Table 2.1: Total standing stock biomass estimates (kg) for each of the regions for each of the three sampling seasons.

REGION	Total Biomass (kg) in the Spring	Total Biomass (kg) in the Summer	Total Biomass (kg) in the Fall
Florida	1,043,000	115,000	3,642,000
Georgia	49,649,000	4,636,000	57,826,000
South Carolina	157,486,000	7,835,000	63,912,000
Long Bay, NC	27,952,000	910,000	2,763,000
Onslow Bay, NC	9,209,000	929,000	404,000
Raleigh Bay, NC	548,000	16,000	1,612,000

K-means cluster analysis

The k-means cluster analysis determined four clusters to be the optimal number needed to explain the variability in the data. The Far South region includes all of the Florida region (strata 21 to 29) from a latitude of 28.74416 to 30.38673 (Table 2). The South region includes all of Georgia and the lower portion of South Carolina (strata 31 to 45) from a latitude of 30.38673 to 32.7294 (Table 2). The North region includes the upper portion of South Carolina, Long Bay and Onslow Bay (strata 47 to 63) from a latitude of 32.7294 to 34.5321 (Table 2). Finally, the Far North region includes Raleigh Bay (strata 65 and 67) from a latitude of 34.5321 to 35.2298 (Table 2). The highest average temperature occurs in the Far South region (24.79 ± 0.16 degrees Celsius), and the lowest average temperature occurs in the Far North region (23.12 ± 0.40 degrees Celsius) (Table 2). Average salinity is highest in the Far South (35.25 ± 0.38 ppm) and lowest in the Far North (33.20 ± 0.60 ppm) (Table 2). Chlorophyll-a concentration is highest on average in the Far North (8.727 ± 1.79 mg per cubic meter) and Lowest in the Far South (3.611 ± 1.36 mg per cubic meter) (Table 2).

Table 2.2: Identifying hydrographic parameters for each of the major regions that resulted from the k-means cluster analysis with standard deviation.

Cluster Name	Min. Latitude	Max. Latitude	Min. Strata	Max. Strata	Average temp	Average Salinity	Avg Chl-a conc.
Far South	28.74416	30.38673	21	29	24.79 ± 0.16	35.25 ± 0.38	3.611 ± 1.36
South	30.38673	32.7294	31	45	24.22 ± 0.27	33.52 ± 0.55	5.116 ± 1.10
North	32.7294	34.5321	47	63	23.12 ± 0.40	34.54 ± 0.49	3.830 ± 1.62
Far North	34.5321	35.2298	65	67	22.15 ± 0.41	33.20 ± 0.60	8.727 ± 1.79

Spatial Variability

A one-way ANOVA investigating average biomass as a function of strata resulted in a p-value of 0.375, while a one-way ANOVA investigating average biomass as a function of cluster resulted in a p-value of 6.3e-6. A pairwise, Tukey's Honest Significant Difference, analysis of average biomass as a function of cluster resulted in the following p-values: 0.34 for Far South and Far North, 0.03 for North and Far North, 0.00005 for South and Far North, 0.35 for North and Far South, 0.00008 for South and Far South, and lastly, 0.0007 for South and North.

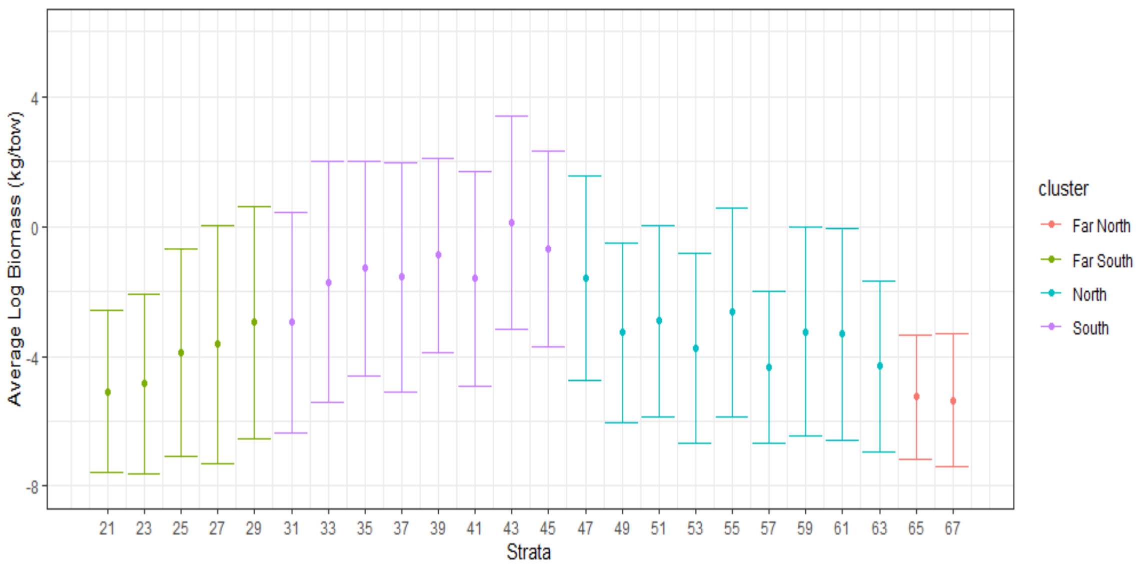

Figure 2.5 Average Log Biomass: Average natural log biomass (kg / tow) across the sampling region from south (strata 21) to north (strata 67), colored by major region. Error bars represent standard deviations.

Seasonal Variability

The highest average logged biomass is 0.929 ± 3.96 kg / tow in strata 43 during the Spring season (Figure 5a). The lowest average logged biomass is -5.94 ± 0.89 kg / tow in strata 67 during the Summer season (Figure 5b). Average logged biomass ranges from -5.37 ± 0.94 to 0.92 ± 3.96 kg / tow in the Spring season (Figure 5a). Average logged biomass ranges from -5.94 ± 0.89 to -1.40 ± 3.08 kg / tow in the Summer season (Figure 5b). Average logged biomass ranges from -4.76 ± 2.12 to 0.858 ± 3.16 kg / tow during the Fall (Figure 5c).

The average size of jellyfish is highest in the Spring (0.955 kg / individual), and lowest in the Summer (0.15 kg / individual) (Figure 6a-b). A one-way ANOVA between average size and season produced a p-value of less than 2e-16. A pairwise Tukey's Honest Significant Difference analysis of the relationship between average size and season determined a significant p-value for the relationship between Spring and Fall (0.00), and Summer and Spring (0.00), but not between Summer and Fall (0.21). A one-way ANOVA between average size and cluster produced significant p-values for Spring, Summer and Fall – 8.17e-6, 3.59e-8, and 3.3e-6, respectively.

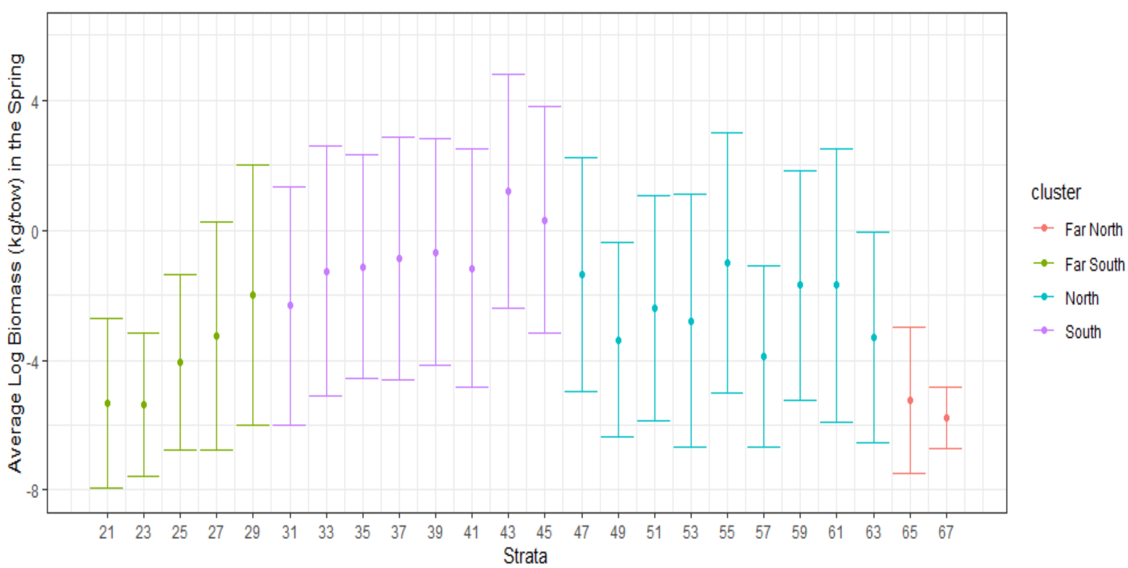

Figure 2.6a Average Spring Log Biomass: Average natural log biomass (kg / tow) across the sampling region from south (strata 21) to north (strata 67), colored by major region during the Spring sampling. Error bars represent standard deviations.

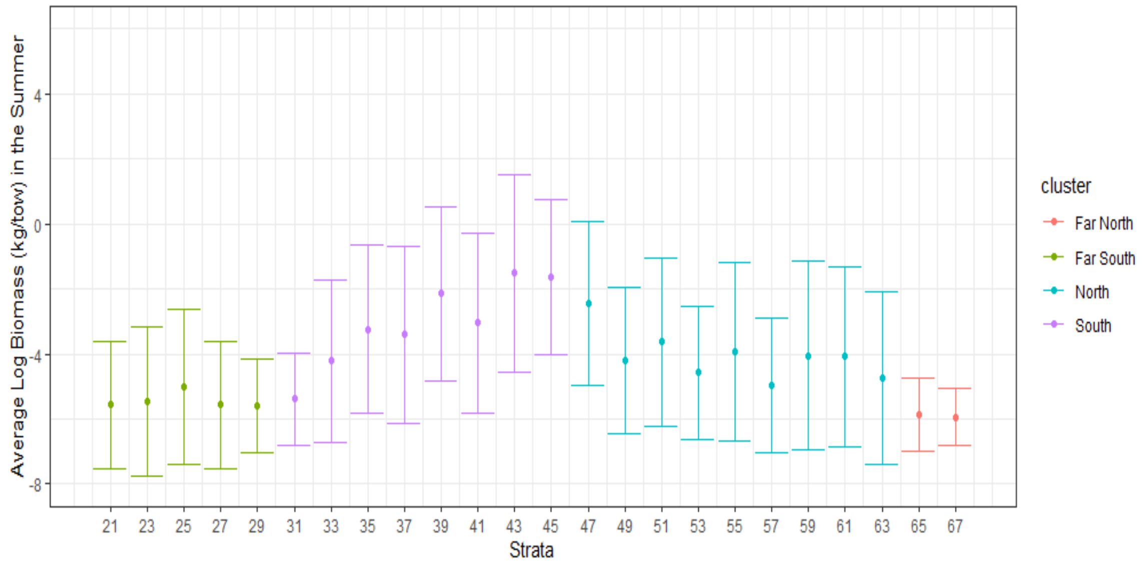

Figure 2.6b Average Summer Log Biomass: Average natural log biomass (kg / tow) across the sampling region from south (strata 21) to north (strata 67), colored by major region during the Summer sampling. Error bars represent standard deviations.

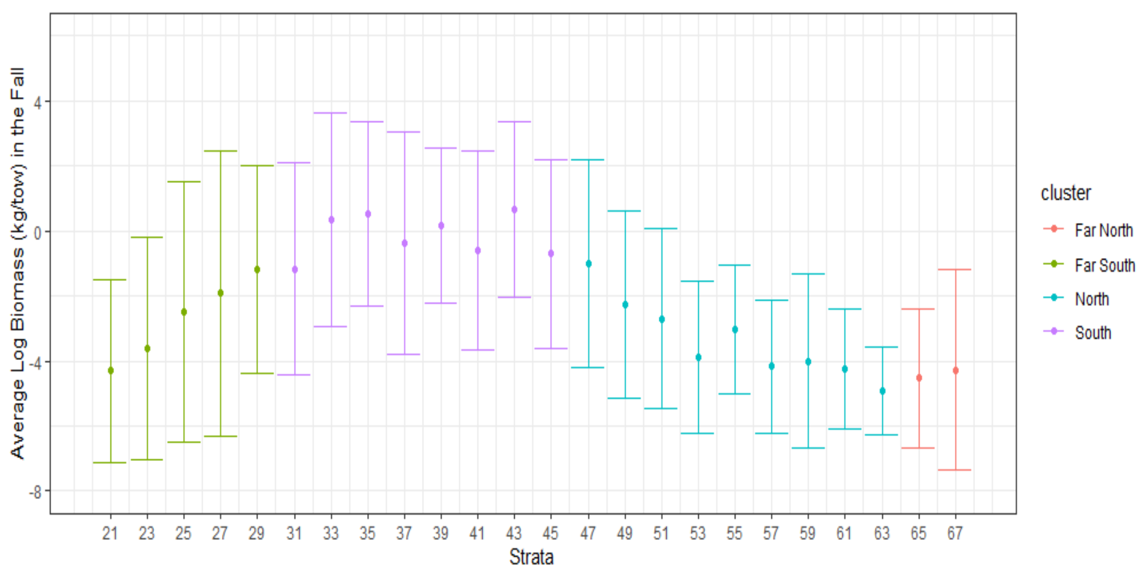

Figure 2.6c Average Fall Log Biomass: Average natural log biomass (kg / tow) across the sampling region from south (strata 21) to north (strata 67), colored by major region during the Fall sampling. Error bars represent standard deviations.

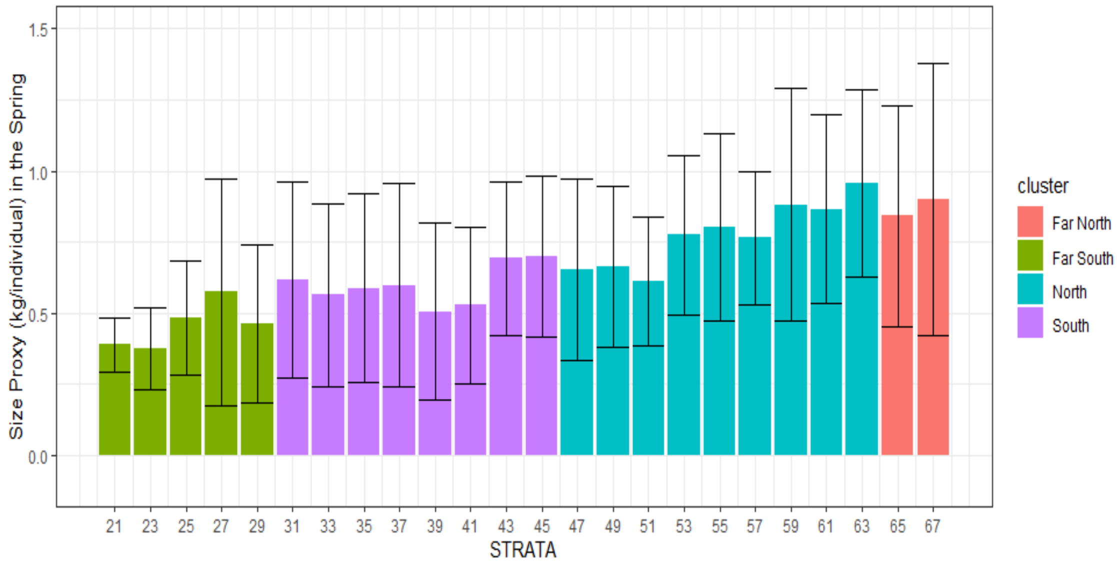

Figure 2.7a Average Spring Size Proxy: Average size proxy (kg / individual) during the Spring from south (strata 21) to north (strata 67), colored by major region. Error bars represent standard deviations.

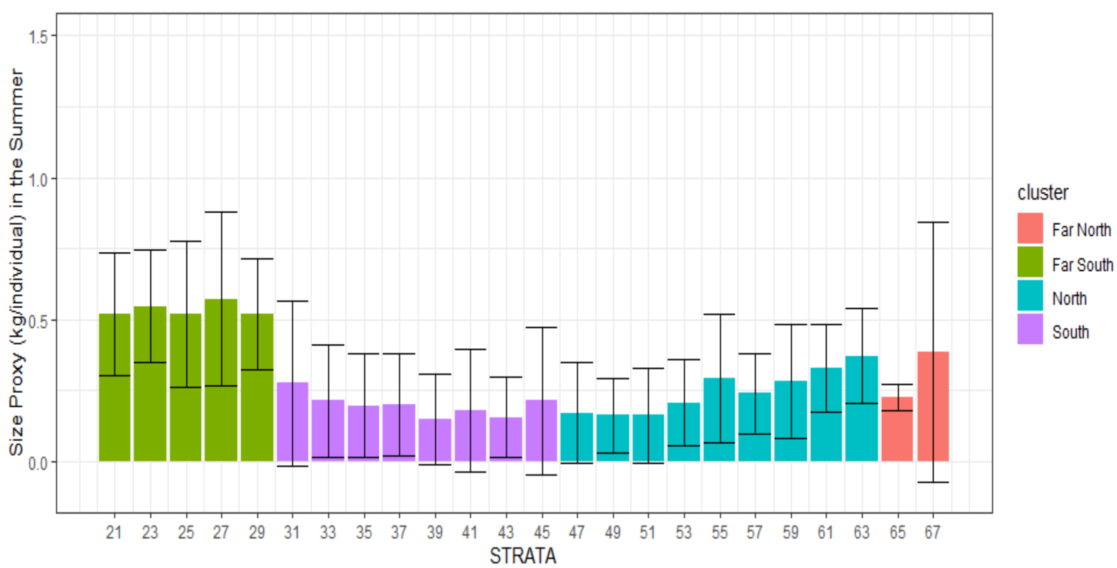

Figure 2.7b Average Summer Size Proxy: Average size proxy (kg / individual) during the Summer from south (strata 21) to north (strata 67), colored by major region. Error bars represent standard deviations.

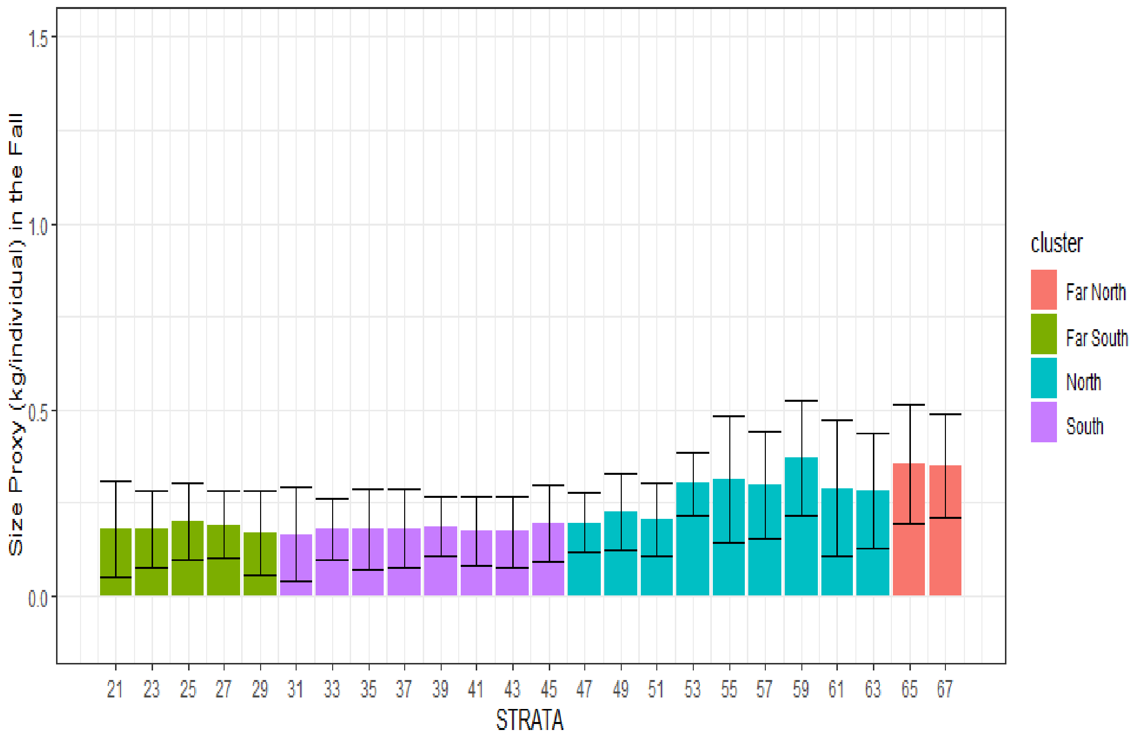

Figure 2.7c Average Fall Size Proxy: Average size proxy (kg / individual) during the Fall from south (strata 21) to north (strata 67), colored by major region. Error bars represent standard deviations.

Interannual Variability

There is interannual variability in jellyfish anomaly for the year as a whole, and for each season individually (Figure 4a-d). These graphs visually display if the biomass for each year was above or below the overall average. Positive numbers are above average, zero is average and negative numbers are below average. For the year, 2004 and 2009 fall very below average (Figure 4a). During the spring, 2004 falls very below average again (Figure 4b). During the summer, the anomaly fluctuates more drastically than the other seasons, with 2004, 2012 and 2017 being extremely below average (Figure 4c). In the fall, 2009 falls extremely below average (Figure 4d).

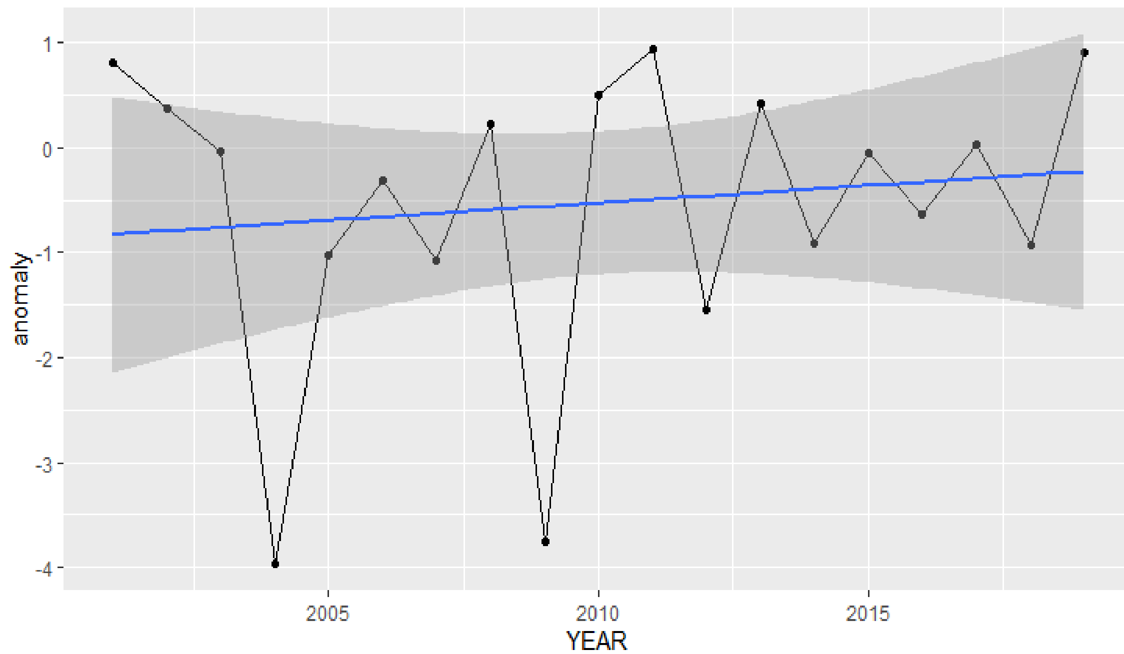

Figure 2.8 Biomass Anomaly: Interannual variability in jellyfish biomass (kg/tow) anomaly from 2001 to 2019. Linear regression has an R-squared of -0.03948.

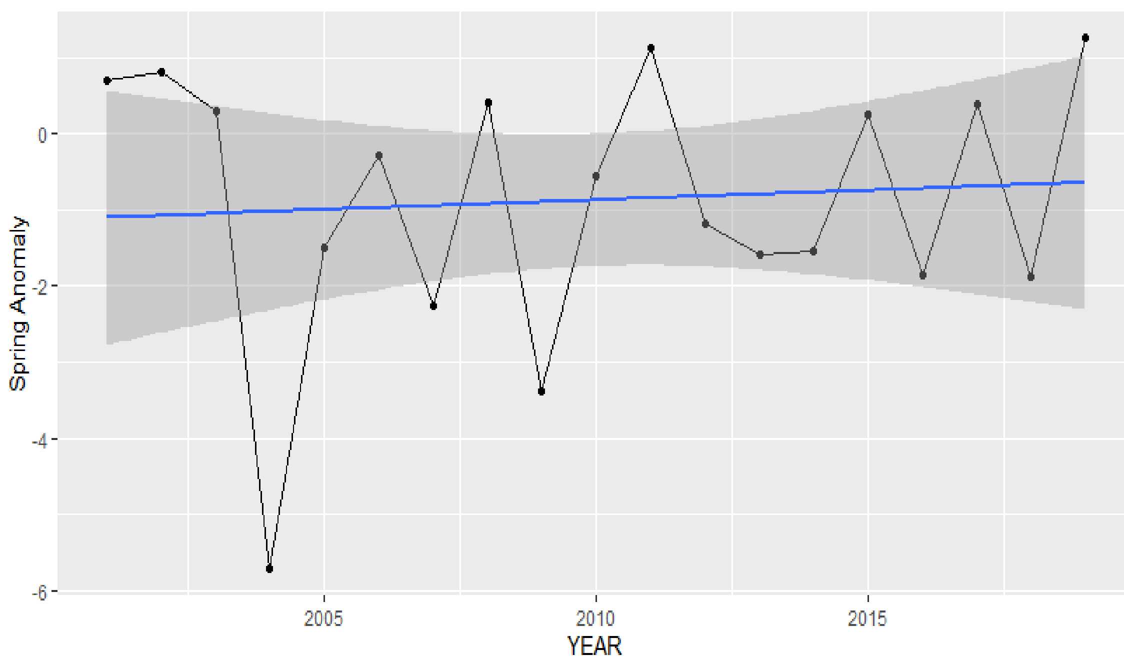

Figure 2.9a Spring Biomass Anomaly: Interannual variability in jellyfish biomass (kg/tow) anomaly during the Spring from 2001 to 2019. Linear regression has an R-squared of -0.05172.

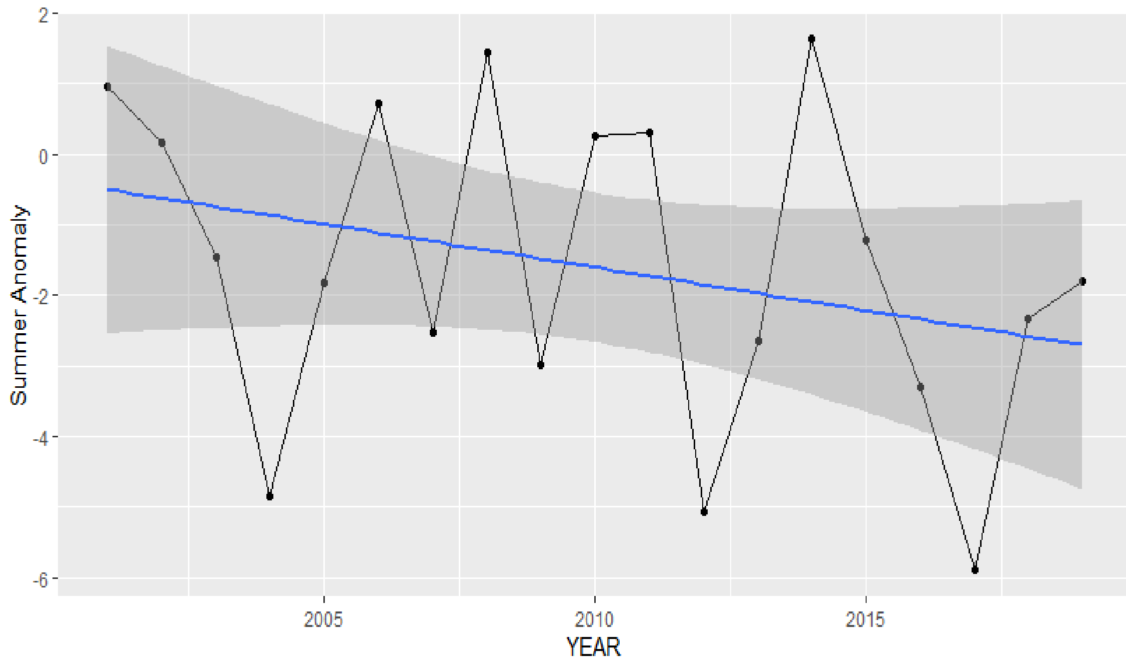

Figure 2.9b Summer Biomass Anomaly: Interannual variability in jellyfish biomass (kg / tow) anomaly during the Summer from 2001 to 2019. Linear regression has an R-squared of 0.0415.

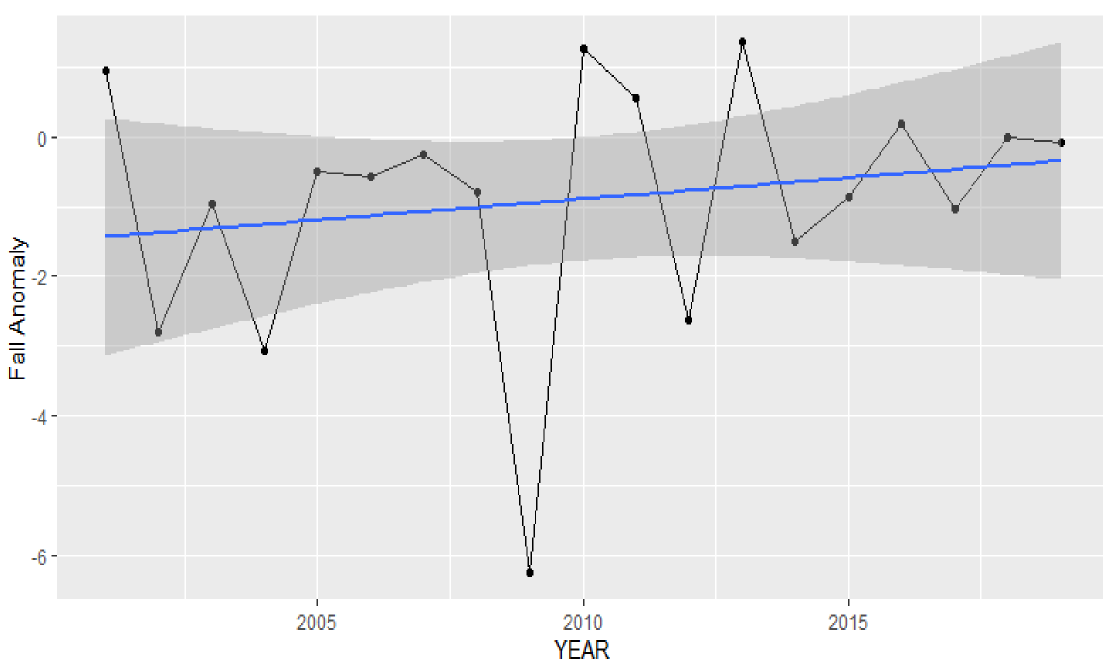

Figure 2.9c Fall Biomass Anomaly: Interannual variability in jellyfish biomass (kg / tow) anomaly during the Fall from 2001 to 2019. Linear regression has an R-squared of -0.02135.

Environmental Drivers of Seasonal and Spatial Variability

Pearson's correlations were calculated between jellyfish regional anomaly and each environmental parameter as well as seasonal jellyfish anomaly and each environmental parameter. Very few significant correlations were detected. The regional jellyfish anomaly for the Far South region was negatively correlated with temperature (Table 3). The regional jellyfish anomaly for the Far South during the Fall was negatively correlated with temperature (Table 3). The regional jellyfish anomaly for the South during the summer was negatively correlated with chlorophyll-a concentration, but this correlation was not significant (Table 3). The regional jellyfish anomaly for the Far North was negatively correlated with the North Atlantic Oscillation index (Table 3). The regional jellyfish anomaly for the Far South during the spring was positively correlated with salinity during the previous Fall (Table 3). Lastly, the regional jellyfish anomaly for the Far South during the spring was negatively correlated with the North Atlantic Oscillation index during the previous fall (Table 3).

Table 2.3: Significant correlation coefficients between jellyfish anomaly and environmental parameters. * denotes significance at alpha = 0.05, ** denotes signicance at alpha = 0.01

Comparison	Correlation Coefficient
Far South Anomaly & Temperature	-0.49 *
Far South Fall Anomaly & Temperature	-0.50 *
South Summer Anomaly & Chl a concentration	-0.42
Far North Anomaly & NAO	-0.62 **
Far South Spring Anomaly & Fall Salinity	0.49 *
Far South Spring Anomaly & Fall NAO	-0.45 *

Environmental Drivers of Interannual Variability

Pearson's correlations were calculated between jellyfish biomass anomaly and interannual averages of temperature, salinity, chlorophyll-a concentration, North Atlantic Oscillation index and river discharge but no significant correlations were detected.

DISCUSSION

Seasonal and Spatial variability

Based on statistical analyses of the SEAMAP timeseries dataset from 2001 to 2019, *Stomolophus meleagris* jellyfish exhibit both seasonal and spatial variability across the sampling region of the South Atlantic Bight from Cape Hatteras, North Carolina to Cape Canaveral, Florida. As suspected, cannonball jellyfish biomass (kg/tow) in the south region was significantly different from each of the other three major regions. This is because highest biomass (kg/tow) is observed in the south region, which includes the coastal waters of Georgia and the lower portion of South Carolina (south of Charleston). Cannonball jellyfish in the South Atlantic Bight have been historically documented as the most abundant scyphozoan off the coasts of South Carolina and Georgia, which is reflected in this timeseries (Krauter & Setzler 1975; Calder & Hester 1978).

The highest average biomass (kg/tow) was recorded during the spring sampling events. This was expected since *S. meleagris* was documented by Mayer (1910) as copious during the winter and spring in the coastal waters of Florida, Georgia, and South Carolina. The lowest average biomass (kg/tow) occurred during the summer sampling events. Low biomass in the summer within the sampling region could be a result of inshore transport toward protective habitats like estuaries and inlets where the SEAMAP coastal trawl survey does not sample. *S. meleagris* was observed occupying offshore waters during the spring and then subsequently migrating into inshore waters in the early summer by Kraueter and Setzler (1975).

The largest average size proxy (kg/individual) occurs during the spring sampling season. The average size of jellyfish (kg/individual) decreases during the summer sampling season for all of the clusters except the far south (Florida). Then in the fall, average size of jellyfish (kg/individual) decreases in the far south but remains approximately the same for the other three clusters. The lag observed in the far south region could be a result of two things 1) mis-directed, irregular migration from the south region and 2) lack of suitable habitat to reproduce once there. Roundtree (1983) also observed large cannonball jellyfish offshore during the spring, and a drop in average weight of cannonball jellyfish during the summer months in North Carolina.

Assuming the jellyfish sampled within each year are just different generations of the same population and using the average size as a proxy for age, we can assume the smaller jellyfish are the immature juveniles while the larger jellyfish are the mature adults. In this dataset, juveniles (smallest in size) are seen in the summer and fall and then adults (largest in size) are seen in the spring. A suggested seasonal pattern for the cannonball jellyfish population of the South Atlantic Bight is as follows: Mature medusae occur offshore in the spring season. At the beginning of summer, these adult medusae travel inshore towards estuarine habitats to reproduce and release their planula larvae. These larvae settle into polyps, and strobilate throughout the summer producing ephyra. As the ephyra mature and grow, they move out of the estuaries into nearshore waters throughout the summer and fall. This could explain why low biomass is detected during the summer months but increases in the fall months even though size does not generally increase, because the SEAMAP trawl survey does not sample the estuaries but as more juveniles are recruited into the sampling region in the fall, more biomass is detected. As they continue to mature, the winter surface flow pushes them offshore back into the sampling region where large adults in high abundances are then detected during the SEAMAP surveys. A pairwise Tukey HSD analysis, detected a significant difference in size between the spring and summer, and spring and fall but not during summer and fall. This supports the idea of juveniles (smaller individuals) occurring during the summer and fall, while adults (significantly larger individuals) occur during the spring.

Although this analysis provides useful insight on the spatial and temporal variability of cannonball jellyfish in the South Atlantic Bight, we were unable to detect what drives these patterns. The relationship between biomass anomaly and several environmental parameters (temperature, salinity, river discharge, and chlorophyll-a concentration) was explored, but no significant correlations emerged. These relationships were explored on a regional scale, for each season individually and on a one-season lag. A few moderate negative correlations were detected in the far south and far north regions, but upon further inspection we believe the jellyfish occurring in these extremities are drifters and not truly representative of the phenology of the species. It is very likely that the seasonal and spatial variability in cannonball jellyfish biomass observed is actually influenced by the distance from an estuary and wind direction instead.

Interannual Variability

In addition to the spatial and temporal variability described the cannonball jellyfish in the sampling region also demonstrate interannual variability in biomass anomaly throughout the SEAMAP timeseries. No long-term trends were detected in cannonball jellyfish biomass anomaly. The relationship between interannual variability in biomass anomaly and the following environmental parameters was explored: temperature, salinity, river discharge, chlorophyll-a concentration, and North Atlantic Oscillation Index. To analyze these environmental drivers, a Pearson's correlation coefficient was calculated for each relationship, but no significant or strong correlations were detected. Literature suggests that long-term trends in interannual jellyfish dynamics are likely connected to global climate oscillations that fluctuate on decadal scales, but given under 20 years of data, we cannot discern any long-term trends with certainty (Condon et al 2013).

Implications for the Jellyfish Fishery

Based on this data, large jellyfish can be commercially targeted most efficiently during the spring months off the coasts of Georgia and South Carolina. Currently, only 4,000 US tons of cannonball jellyfish are harvested annually in the South Atlantic Bight. This is approximately 3,629,000 kilograms of jellyfish, which equates to less than 2.4% of the estimated standing stock off the coast of South Carolina during the spring alone. Further research on the drivers of biomass variability and specifics of the asexual reproduction in cannonball jellyfish is still necessary in order to regulate and sustain the industry.

CONCLUSIONS

The cannonball jellyfish, *Stomolophus meleagris*, is commercially harvested throughout its range in the tropical and sub-tropical Americas, including in the South Atlantic Bight, where an estimated 4,000 tons (less than 2.4% of the estimated stock in South Carolina during the spring) are harvested annually. Like many Scyphozoan jellyfish, cannonball jellies have high interannual variability and little is known about the environmental drivers of their distribution and phenology. To better understand the ecology of this targeted species, we used fisheries-independent abundance data of cannonball jellyfish from 2001 to 2019 collected by the Southeast Area Monitoring and Assessment Program (SEAMAP) throughout the coastal zone of the South Atlantic Bight. In conclusion, average biomass is highest in the spring off the coast of Georgia and lower South Carolina (south of Charleston), and the largest jellyfish occur during the spring months. The lowest biomass occurs in the summer months when smaller jellyfish occur. This could indicate that adult cannonball jellyfish occur offshore in the spring, move inshore toward estuarine habitats to release larvae, then juvenile cannonballs move out of the estuaries as they mature throughout the summer and fall, and finally the surviving adults are detected offshore again the next spring. The seasonal and spatial variability described does not appear to be connected to temperature, salinity, chlorophyll-a concentration or river discharge, but is perhaps influenced by distance from estuarine habitats and wind direction. Interannual variability in biomass is evident in the cannonball jellyfish of the South Atlantic Bight, but no long-term trends or strong correlations with the aforementioned environmental parameters were detected. Further analyses remain necessary in order to pin-point the drivers behind the variability seen in the cannonball jellyfish of the South Atlantic Bight.

REFERENCES

Anderson, P.J. & Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series, 189, 117–123.

Arai MN. Interactions of fish and pelagic coelenterates. 1988. Can J Zool 66:1913–1927.

Arai MN. Predation on pelagic coelenterates: a review. 2005. J Mar Biol Assoc UK 85:523–536.

Ates RML. Medusivorous fishes - a review. Zool Meded. 1988. (Leiden) 62:29–42

Atkinson, L. P., T. N. Lee, J. O. Blanton, and W. S. Chandler, Climatology of the southeastern United States continental shelf waters, J. Geophys. Res., 88, 4705–4718, 1983. Brodeur, R. D. 1998. In situ observations of the association between juvenile fishes and scyphomedusae in the Bering Sea. Marine Ecology Progress Series, 163: 11–20.

Austin, H.M., 2002. Decadal oscillations and regime shifts, a characterization of the Chesapeake Bay marine climate. American Fisheries Society Symposium, 32, 155–170.

Beaugrand, G., 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuation in the hydroclimatic environment. Fisheries Oceanography, 12, 270–283.

Boero, F., Bouillon, J., Gravili, C., Miglietta, M. P., Parsons, T., and Piraino, S.: Gelatinous plankton: irregularities rule the world (sometimes), Mar. Ecol. Prog. Ser., 356, 299–310, https://doi.org/10.3354/meps07368, 2008.

Broadhurst MK, Kennelly SJ. Rigid and flexible separator panels in trawls that reduce the by-catch of small fish in the Clarence River prawn-trawl fishery, Australia. 1996. Mar Freshw Res 47:991–998

Brodeur, R. D., Decker, M. B., Ciannelli, L., Purcell, J. E., Bond, N. A., Stabeno, P. J., Acuna, E., . 2008a. The rise and fall of jellyfish in the Bering Sea in relation to climate regime shifts. Progress in Oceanography, 77: 103–111.

Brodeur, R. D., Ruzicka, J. J., and Steele, J. H. 2011. Investigating alternate trophic pathways through gelatinous zooplankton and planktivorous fishes in an upwelling ecosystem using end-to-end models. In Interdisciplinary Studies on Environmental Chemistry—Marine Environmental Modeling & Analysis, pp. 57–63. Ed. by K. Omori, X. Guo, N. Yoshie, N. Fujii, I. C. Handoh, A. Isobe and S. Tanabe. TERRAPUB, Tokyo.

Brotz L. Jellyfish fisheries—a global assessment. 2016. In: Pauly D, Zeller D (eds) Global atlas of marine fisheries: a critical appraisal of catches and ecosystem impacts. Island Press, Washington, D.C., USA, pp 110–124

Brotz L, and Pauly D. Studying jellyfish fisheries: toward accurate national catch reports and appropriate methods for stock assessments. 2016. In: Mariottini GL (ed) Jellyfish: ecology, distribution patterns and human interactions. Nova Publishers, Hauppauge.

Brotz, Lucas, et al. “Jellyfish Fisheries in the Americas: Origin, State of the Art, and Perspectives on New Fishing Grounds.” Reviews in Fish Biology and Fisheries, vol. 27, no. 1, Mar. 2017, pp. 1–29. DOI.org (Crossref), doi:10.1007/s11160-016-9445-y.

Burke, W.D. 1976. Biology and distribution of the macrocoelenterates of Mississippi Sound and adjacent waters. Gulf Resource Report 5:17-28.

Calder, D.R. and B.S. Hester. 1978. Phylum Cnidaria. In: An annotated checklist of the biota of the coastal zone of South Carolina. R.G. Zingmark (ed). University of South Carolina Press: 87-93.

Cardona L, de Quevedo IA, and Borrell A, Aguilar. A Massive consumption of gelatinous plankton by Mediterranean apex predators. 2012. PLoS One 7:e31329.

Carvalho, F.J. , Santana, D.G., and M.V. Sampaio. 2019. Modeling Overdispersion, Autocorrelation, and Zero-Inflation Count Data Via Generalized Additive Models and Bayesian Statistics in an Aphis Population Study. Ecology, Behavior, and Bionomics.

Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H. D., Sutherland, K. R., . 2012. Questioning the rise of gelatinous zooplankton in the World’s oceans. BioScience, 62: 160–169.

Crum, K. P., Fuchs, H. L., Bologna, P. A. X., and Gaynor, J. J.: Model-to- data comparisons reveal influence of jellyfish interactions on plankton community dynamics, Mar. Ecol. Prog. Ser., 517, 105–119, https://doi.org/10.3354/meps11022, 2014.

Dale R. Calder, 1982. Life history of the cannonball jellyfish, Stomolophus Meleagris L. agassize, 1860 (Scyphozoa, Rhizostomida). Biol. Bull. 149-162

D’Ambra, I., Graham, W. M., Carmichael, R. H., and Hernandez, F. J. Jr. 2018. Dietary overlap between jellyfish and forage fish in the northern Gulf of Mexico. Marine Ecology Progress Series, 587: 31–40.

Deason, E. E., and Smayda, T. J. 1982. Ctenophore-zooplankton phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972-1977. Journal of Plankton Research, 4: 203–217.

DuBose Griffin & Thomas M. Murphy. 2005. Cannonball jellyfish. SCDNR.

Duffy, J.T., C.E. Epifanio and L.A. Fuiman. 1997. Mortality rates imposed by three scyphozoans

on red drum (Sciaenops ocellatus Linnaeus) larvae in field enclosures. Journal of Experimental Marine Biology and Ecology 212:123-131.

Graham, W.M., Martin, D.L., Felder, D.L., Asper, V.L. & Perry, H.M., 2003. Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. Biological Invasions, 5, 53–69.

Hayse, J. W. 1989. Feeding habits, age, growth, and reproduction of Atlantic Spadefish Chaetodipterus faber (Pisces: Ephippidae) in South Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 88:67–83.

Heaslip SG, Iverson SJ, Bowen WD, and James MC. Jellyfish support high energy intake of leatherback sea turtles (Dermochelys coriacea): video evidence from animalborne cameras.2012. PLoS One 7:e33259

Henschke N, Bowden DA, Everett JD, Holmes SP, Kloser RJ, Lee RW, and Suthers IM. Salp-falls in the Tasman Sea: a major food input to deep-sea benthos. 2013. Mar Ecol Prog Ser 491:165–175.

Hsieh, Y-H.P., F.M. Leong, and J. Rudloe. 2001. Jellyfish as food. Hydrobiologia 451:11-17.

Huang Y, Christian P, and Colson D. Harvest and preservation of a shrimp by-catch: cannonball jellyfish (Stomolophus meleagris).1987. In: Proceedings of the 12th annual tropical and subtropical fisheries technological conference of the Americas, November 9–11, 1987. Orlando, FL, USA

James W. Page. 2015. Characterization of Bycatch in the Cannonball Jellyfish Fishery in the Coastal Waters of Georgia. Marine and Coastal Fisheries. 7(1): 190-199.

Jenkins L. Reducing sea turtle bycatch in trawl nets: a history of NMFS turtle excluder device (TED) research. 2012. Mar Fish Rev 74:26–44

Jones RP, and Rudloe J. Harvesting & processing of Florida cannonball jellyfish. Report to the Florida International Affairs Commission, Florida Department of Commerce. 1995. Southeastern Fisheries Association, Tallahassee, Florida, USA, 28 pp.

Kraeuter, J.N. and E.M. Setzler. 1975. The seasonal cycle of scyphozoa and cubozoa in Georgia estuaries. Bulletin of Marine Science 25(1):66-74.

Kramp, P.L. 1961. Synopsis of the medusae of the world. Journal of the Marine Biological Association U.K. 40:7-469.

Larson, R.J. 1976. Marine flora and fauna of the northeastern United States. Cnidaria: Scyphozoa. NOAA Tech Report NMFS Cir. 397:18p.

Larson, R.J. 1991. Diet, prey selection and daily ration of Stomolophus meleagris, a filterfeeding Scyphomedusae from the NE Gulf of Mexico Lopez-Martinez, J. & J. Alvarez-Tello. 2013. The jellyfish fishery in Mexico. Agricultural Sciences. 4(6): 57-61.

Lebrato, M., Pitt, K. A., Sweetman, A. K., Jones, D. O. B., Cartes, J. E., Oschlies, A., Condon, R. H., Molinero, J. C., Adler, L., Gaillard, C., Lloris, D., and Billett, D. S. M.: Jelly-falls historic and recent observations: a review to drive future research directions, Hydrobiologia, 690, 227–245, Https://doi.org/10.1007/s10750-012-1046-8, 2012.

Lopez-Martinez, J. & J. Alvarez-Tello. 2013. The jellyfish fishery in Mexico. Agricultural Sciences. 4(6): 57-61.

Lucas, C.H., 2001. Reproduction and life history strategies of the common jellyfish, Aurelia aurita, in relation to its ambient environment. Hydrobiologia, 451, 229–246.

Lucas, C. H. and Dawson, M. N.: What Are Jellyfishes and Thaliaceans and Why Do They Bloom?, in: Jellyfish blooms, edited by: Pitt K. and Lucas C., Springer, Dordrecht, Springer, 9–44, 2014.

Lynam, C.P., Hay, S.J. & Brierley, A.S., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnology and Oceanography, 49, 637–643.

Lynam, C.P., Brierley, A.S. & Hay, S.J., 2005. Jellyfish abundance and climate variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. Journal of the Marine Biological Association of the United Kingdom, 85, 435–450.

Matsumura, K., Kamiya, K., Yamashita, K., Hayashi, F., Watanabe, I., Murao, Y., Miyasaka, H., Kamimura, N. & Nogami, M., 2005. Genetic polymorphism of the adult medusae invading an electric power station and wild polyps of Aurelia aurita in Wakasa Bay, Japan. Journal of the Marine Biological Association of the United Kingdom, 85, 563–568.

Mayer, A.G. 1910. Medusae of the world, Hydromedusae and Scyphomedusae. Carnegie Institute Washington, Publication 109(3):735p.

Mianzan H, Pa´jaro M, Colombo GA, and Madirolas A. Feeding on survival-food: gelatinous plankton as a source of food for anchovies. 2001. Hydrobiologia 451:45–53.

Mills CE. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. 1995. ICES J Mar Sci 52:575–581.

Mo¨ller H. Scyphomedusae as predators and food competitors of larval fish. 1980. Meeresforschung 28:90–100.

Nagata RM, Haddad MA, and Nogueira M Jr. The nuisance of medusae (Cnidaria, Medusozoa) to shrimp trawls in central part of southern Brazilian Bight, from the perspective of artisanal fishermen. 2009. Pan Am J Aquat Sci 4:312–325.

NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group; (2014): MODIS-Aqua Ocean Color Data; NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. http://dx.doi.org/10.5067/AQUA/MODIS_OC.2014.0

Omori, M. 1978. Zooplankton fisheries of the world: a review. Marine Biology 48(3):199-205.

Ottersen, G., Planque, B. & Belgrano, A., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128: 1–14.

Pauly D, Graham W, Libralato S, Morissette L, and Palomares MLD. Jellyfish in ecosystems, online databases, and ecosystem models. 2009. Hydrobiologia 616:67–85.

Pedersen, S.A. & Smidt, E.L.B., 2000. Zooplankton distribution and abundance in west Greenland waters, 1950–1984. Journal of Northwest Atlantic Fisheries Science, 26, 45–102.

Phillips, P., W. D. Burke, and E. J. Keener. 1969. Observations on the trophic significance of jellyfishes in Mississippi sound with quantitative data on the associative behavior of small fishes with medusa. Transactions of the American Fisheries Society 98:703–712

Purcell JE, and Arai MN. Interactions of pelagic cnidarians and ctenophores with fish: a review. 2001. Hydrobiologia. 451:27–44.

Purcell, Jennifer E. 2005. Climate Effects on Formation of Jellyfish and Ctenophore Blooms: A Review. Journal of the Marine Biological Association of the United Kingdom, 85: 461–76.

Purcell, J.E. & Decker, M.B., 2005. Effects of climate on relative predation by ctenophores and scyphomedusae on copepods in Chesapeake Bay during 1987–2000. Limnology and Oceanography, 50, 376–387.

Rajagopal, S., Nair, K.V.K. & Azariah, J., 1989. Some observations on the problem of jelly fish ingress in a power station cooling system at Kalpakkam, east coast of India. Mahasagar Quarterly Journal of Oceanography, National Institute of Oceanography, Goa, India, 22, 151–158.

Raskoff, K.A., 2001. The impact of El Niño events on blooms of mesopelagic hydromedusae. Hydrobiologia, 451, 121–129.

Ruzicka, J. J., Brodeur, R. D., Emmett, R. L., Steele, J. H., Zamon, J. H., Morgan, C. A., Thomas, A. C., . 2012. Interannual variability in the Northern California Current food web structure: changes in energy flow pathways and an End-to-End model to investigate system response to alternate forcing scenarios. Progress in Oceanography, 102: 19–41.

Ruzicka, James, et al. "Examining the Ecological Role of Jellyfish in the Eastern Bering Sea." ICES Journal of Marine Science, edited by Rubao Ji, vol. 77, no. 2, Mar. 2020, pp. 791–802.

Schiariti A, Morandini AC, Jarms G, Paes RG, Franke S, and Mianzan H. Asexual reproduction strategies and blooming potential in Scyphozoa.2014. Mar Ecol Prog Ser 510:241–253.

Schnedler-Meyer, N. A., Mariani, P., and Kiørboe, T. 2016. The global susceptibility of coastal forage fish to competition by large jellyfish. Proceedings of the Royal Society B: Biological Sciences, 283: 20161931.

SEAMAP-SA Data Management Work Group . 2020, May. SEAMAP-SA online database. Retrieved from: http://www.dnr.sc.gov/SEAMAP/data.html by: Lauren Faulk.

Shimomura, T., 1959. On the unprecedented flourishing of ‘Eshizen-Kurage’, Stomolophus nomurai (Kishinouye), in the Tsushima Warm Current regions in autumn, 1958. Bulletin of the Japan Sea Regional Fisheries Research Laboratory, 7, 85–107.

Shimomura O. A short story of aequorin. 1995. Biol Bull 189:1–5

Shoji, J., Mizuno, K. I., Yamamoto, M., Miller, T. W., Hamaoka, H., and Omori, K. 2009. Spatial distribution and dietary overlap between Japanese anchovy Engraulis japonicus and moon jellyfish Aurelia aurita in the Seto Inland Sea, Japan. Scientia Marina, 73: 91–198.

Sloan NA, and Gunn CR. Fishing, processing, and marketing of the jellyfish, Aurelia aurita [labiata], from southern British Columbia. 1985. Can Ind Rep Fish Aquat Sci 157:29.

Sommer U, Stibor H, Katechakis A, Sommer F, and Hansen T. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. 2001. Hydrobiologia 484:11–20

Stender, B. W., and C. A. Barans. Comparison of the Catch from Tongue and Two-Seam Shrimp Nets off South Carolina. p. 19.

Suchman, C. L., Daly, E. A., Keister, J. E., Peterson, W. T., and Brodeur, R. D. 2008. Feeding patterns and predation potential of scyphomedusae in a highly productive upwelling region. Marine Ecology Progress Series, 358: 161–172.

Sweetman AK, Smith CR, Dale T, and Jones DOB. Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. 2014. Proc R Soc B 281:20142210

Tilves, U., Fuentes, V. L., Milisenda, G., Parrish, C. C., Vizzini, S., and Sabate´s, A. 2018. Trophic interactions of the jellyfish Pelagia noctiluca in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition. Marine Ecology Progress Series, 591: 101–116.

Verity PG, and Smetacek V. Organism life cycles, predation, and the structure of marine pelagic ecosystems. 1996. Mar Ecol Prog Ser 130:277–293

Young GA, Hagadorn JW. 2010. The fossil record of cnidarian medusae. Paleoworld 19:212–21

Wright, Rebecca M., et al. “Role of Jellyfish in the Plankton Ecosystem Revealed Using a Global Ocean Biogeochemical Model.” Biogeosciences, vol. 18, no. 4, Feb. 2021, pp. 1291–320. DOI.org (Crossref), doi:10.5194/bg-18-1291-2021.