



Temporal and spatial distribution of the cannonball jellyfish *Stomolophus meleagris* in the South Atlantic Bight, USA

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ABSTRACT: The cannonball jellyfish *Stomolophus meleagris* is one of the most abundant scyphozoan jellyfish in the South Atlantic Bight (SAB) of the southeastern USA. 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 commercially targeted species, we used fisheries-independent abundance and biomass data of *S. meleagris* from 2001 to 2019 collected by the Southeast Area Monitoring and Assessment Program (SEAMAP) throughout the coastal zone of the SAB. Average biomass of *S. meleagris* is highest in the spring off Georgia and southern South Carolina, and on average, the largest jellyfish were collected during the spring months. The lowest biomass was observed in the summer months when smaller jellyfish were caught at lower abundances in the coastal zone. These patterns suggest that mature *S. meleagris* medusae occur in the offshore area in the spring and move inshore toward estuarine habitats to sexually reproduce in the summer. Juvenile *S. meleagris* medusae move out of the estuaries as they mature throughout the summer and fall, and finally the surviving adults occur offshore again the next spring. The seasonal and spatial variability across the region is not correlated with local differences in temperature, salinity, chlorophyll *a* concentration, or river discharge, but is perhaps influenced by distance from the presumed source estuarine habitats and prevailing currents. While interannual variability in jellyfish biomass is high, no long-term trends or strong correlations with the tested environmental parameters were detected.

KEY WORDS: Jellyfish blooms · Time series · Fishery · Life history

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1. INTRODUCTION

Scyphozoan jellyfish are critical components of most coastal and estuarine ecosystems (Robinson et al. 2015) but have been understudied for many years due to difficulties in sampling and lack of proper methodology and collection gear (Young & 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 the economic impacts of stinging swimmers, closing beaches, clogging powerplant intake pipes, and commercial fishing, but also for their ecological impacts of predating on plankton and fish, providing habitat for commensal species, and playing a significant role in biogeochemical processes and cycles (Purcell et al. 2007, Condon et al. 2014, Crum et al. 2014, Brotz & Pauly 2017, Steinberg & Landry 2017, Fuentes et al. 2018, Riascos et al. 2018, Bosch-Belmar et al. 2021).

Many scyphozoans (Phylum: Cnidaria, Class: Scyphozoa) follow a metagenetic life cycle that consists

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of 2 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 to form polyps. The polyps asexually strobilate, by means of transverse fission, producing 1 or many immature medusae (ephyrae). The polyp or scyphistoma stage 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 (Calder 1982, Lucas et al. 2012, López-Martínez et al. 2023).

Stomolophus meleagris (Phylum: Cnidaria; Class: Scyphozoa; Order: Rhizostomeae; Family: Stomolophidae), commonly called cannonball jellyfish, is one of the most prevalent scyphozoans along the coast of the southeastern USA (Mayer 1910, Kraeuter & Setzler 1975, Burke 1976, Calder 1982, Griffin & Murphy 2005). Globally, they 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, although the Pacific populations are likely different, multiple species within the same genus (Kramp 1961, Larson 1976, Omori 1978, Griffin & Murphy 2005, Gómez Daglio & Dawson 2017, Getino Mamet et al. 2019, López-Martínez et al. 2023). Cannonball jellyfish are large and round, and have several thick, 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 24 to 32°C and salinities ranging from 15 to 37 (Griffin & Murphy 2005). Historically, jellyfish were viewed as trophic dead-ends (Verity & Smetacek 1996, Sommer et al. 2002, Pauly et al. 2009), but recent research has observed a large diversity of vertebrates (sea turtles and over 100 species of finfish) that feed on jellyfish (Ates 1988, Mianzan et al. 2001, Arai 2005, Cardona et al. 2012, Heaslip et al. 2012, Brodeur et al. 2021, Urban et al. 2022). *S. meleagris* are known to feed on zooplankton, including planktonic larvae of commercially important species such as red drum and the veliger stage of the mollusk life cycle (Larson 1991, Duffy et al. 1997, Griffin & Murphy 2005, Alvarez-Tello et al. 2016, Gonzalez-Valdovinos et al. 2019). Although *S. meleagris* is not itself of conservation concern in the Atlantic, it is an ecologically important species because it is a primary prey species for Atlantic spadefish, butterfish, and the endangered leatherback sea turtle (Phillips et al. 1969, Hayse 1990, Griffin & Murphy 2005, Page 2015). In addition to its ecological importance, *S. meleagris* is also eco-

nomically significant, with commercial fisheries for the species in the Gulf of California and the Gulf of Mexico, and an estimated 3000 t are harvested annually in the southeastern USA (Atlantic Coastal Cooperative Statistics Program [ACCSP] 2022). Since the US commercial fishery began in 1998, *S. meleagris* has become an economically valuable US export, emerging as the third largest fishery by weight in the state of Georgia (Page 2015).

Many jellyfish are highly sensitive to environmental change due to their relatively short life-spans, metagenetic life cycle, and limited swimming ability, and populations of medusae can vary by orders of magnitude from one year to the next (Purcell 2005, Stone et al. 2019). Interannual variability in salinity, temperature, hurricanes, sea ice, and hypoxia can all have varying effects on jellyfish medusae abundances, depending on the species, location, seasonal timing, and trophic interactions of the changes (Purcell & Decker 2005, Purcell et al. 2007, 2018, Bologna et al. 2018, Stone et al. 2019, Goldstein & Steiner 2020). Long-term changes in jellyfish populations are also attributed to decadal climate oscillations and human-induced climate change (Brodeur et al. 2008, Brotz et al. 2012, Condon et al. 2013), and humans have been shown to have varying impacts on jellyfish populations, both positively and negatively (Uye 2011, Brotz et al. 2012, Henschke et al. 2018, Treible & Condon 2019, Loveridge et al. 2021). The complicated interplay between the varying effects environmental conditions have on different stages of the scyphozoan life cycle make it difficult to predict how populations may respond in the future, and evaluation of their population dynamics needs to be species- and region-specific.

Like many scyphozoan jellyfish, *S. meleagris* populations in the South Atlantic Bight have high interannual variability. However, the spatial and seasonal patterns of *S. meleagris* variability have not been quantified on a regional scale, and the environmental drivers of their population dynamics are unknown. And despite their economic importance, no stock assessment or analysis of their population dynamics has been conducted in the region. To better understand the ecology of this species, we analyze data from a long-term time series of *S. meleagris* collected from the SAB. Specifically, we aim to quantify the seasonal, interannual, and spatial variability of *S. meleagris* populations in the SAB and determine any environmental drivers of that variability. We also aim to estimate the population of *S. meleagris* with the goal of comparing the standing stock to ongoing and potential commercial harvesting of the species.

2. MATERIALS AND METHODS

2.1. Study region

The area of coastal waters along the southeastern USA that spans from Cape Canaveral, Florida (28.39°N, 80.61°W) up to Cape Hatteras, North Carolina (35.25°N, 75.54°W) is known as the South Atlantic Bight (SAB; Fig. 1). The continental shelf of the SAB is slimmer at the northern and southern extremities of the region, approximately 50 km off the coast of Cape Canaveral and 30 km off the coast of Cape Hatteras, and wider in the central portion, with a maximum of 120 km near Savannah, Georgia (~32°N) (Atkinson et al. 1983, Blanton et al. 2003). The coastal region of the SAB, especially from central South Carolina down to northern Florida, has numerous estuaries and rivers but can also be seasonally influenced by the Gulf Stream Current (Blanton et al. 2003). The hydrographic properties of the SAB are

split into 3 distinct regions: inner, middle, and outer shelf, with the inner continental shelf most influenced by riverine input, tidal fluxes, and atmospheric dynamics, the middle shelf by tides, winds, and occasionally Gulf Stream intrusion, and the conditions in the outer portion of the shelf dictated by Gulf Stream dynamics (Atkinson et al. 1983, Blanton et al. 2003).

2.2. SEAMAP sampling

Fishery-independent abundance and biomass data of *Stomolophus meleagris* was collected by bottom trawls starting in 2001 by the South Carolina Department of Natural Resources, Marine Resource Division (SCDNR-MRD) through the Southeast Area Monitoring and Assessment Program — South Atlantic (SEAMAP-SA; www.seamap.org/) (Murray 2021). Trawls take place during the daylight hours in the coastal zone of the SAB between Cape Hatteras,

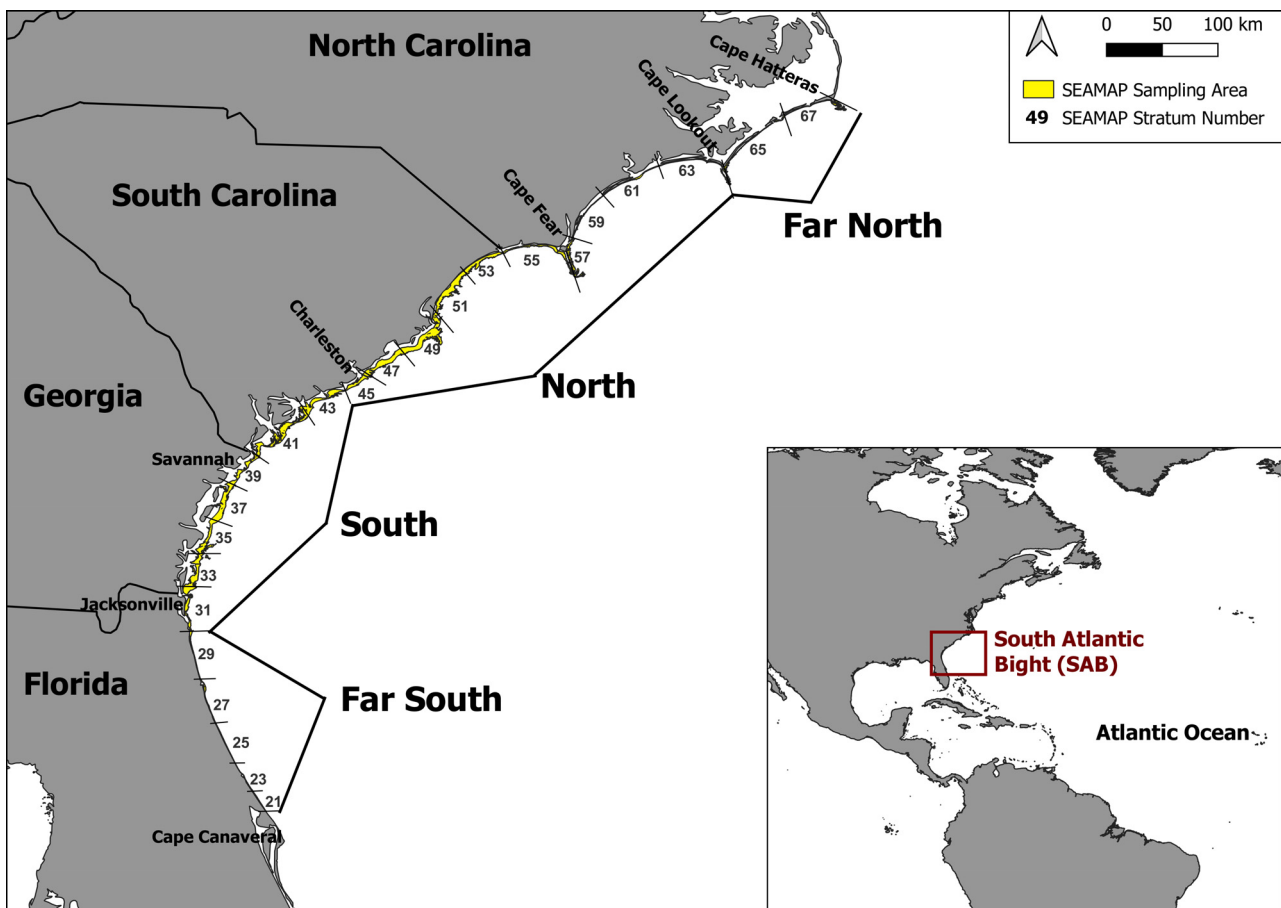


Fig. 1. SEAMAP-SA sampling region and strata. The yellow area is the sampling region between the 4 and 10 m isobaths. Numbered sampling strata are grouped by environmental region (Far South, South, North, Far North) determined in this study. Made with Natural Earth

North Carolina and Cape Canaveral, Florida during the spring (mid-April to mid-May), summer (mid-July to early August), and fall (October to mid-November). The sampling region is divided into 24 strata, and sampling occurs between the 4 and 10 m depth contour within each stratum (Fig. 1). Each season, between 102 and 112 stations are sampled in total (306 to 336 per year) with, generally, 3 to 5 stations per stratum, contingent on funding and field conditions. These sampling locations are selected randomly from a pool of stations from within each stratum. The jellyfish are collected using two 22.9 m mongoose-type Falcon bottom trawl nets without any bycatch reduction devices on the R/V 'Lady Lisa', a 22.9 m double-rigged shrimp trawler. The trawl net is made of 4.76 cm mesh for the body, and 4.13 cm mesh for the cod end. Each trawl is pulled for 20 min not including wire-out (approximately 1 to 2 min) and haul-back time (approximately 2 to 3 min) at approximately 2.5 knots (4.63 km h⁻¹). Data from both replicate nets were pooled together for this study. The biomass and abundance of the total catch was measured, unless catches were high, when a volumetric subsample of approximately 30 to 50 individuals were counted and weighed (~45% of tows where *S. meleagris* was present). Additionally, surface and bottom temperature and salinity were measured with each tow using an SBE-19 CTD (Sea-Bird Scientific). Abundance (number of individuals [ind.] tow⁻¹), biomass (kg tow⁻¹), salinity, and temperature data from 2001 to 2019 were downloaded from the SEAMAP-SA website (SC-DNR 2020).

2.3. Environmental data

In addition to the shipboard data collected by the SEAMAP-SA program, environmental data were accessed from NASA, the United States Geological Survey (USGS), and NOAA. Monthly chl *a* measurements were downloaded from NASA's Ocean Color Data from the MODIS-Aqua satellite mission, reported at a 4 km resolution, and raster cell values within each stratum were averaged within each season (spring, March to May; summer, June to August; fall, September to November; winter, December to February) (NASA 2021). Monthly river discharge rates were downloaded from the National Water Dashboard (USGS 2021), and monthly mean values for the North Atlantic Oscillation (NAO) index were downloaded from NOAA's Climate Prediction Center (NOAA 2021).

2.4. Data preparation

All statistical analyses were completed using R 4.2.3 (R Core Team 2022). Data from replicate trawls at each sampling event were combined to give 1 total catch and biomass for each sampling event. In order to standardize the data to account for the differences in sampling events between strata, a mean value was calculated for each year, strata, and season for each variable measured (jellyfish abundance, jellyfish biomass, surface and bottom temperature, surface and bottom salinity). The total biomass was natural log transformed to normalize the data for the analysis. A proxy for average jellyfish size was estimated by dividing the total biomass by the number of individuals caught from each sampling event.

2.5. Abundance and biomass estimates

To calculate an estimate for the abundance and biomass of jellyfish, the total catch (individuals or biomass) for each tow was divided by the estimated total volume of water sampled by the net during each tow. While the exact dimensions of the opening of the trawl net are variable depending on water currents and tow conditions, we calculated an estimated area of 42.5 m² for the mouth of the net opening using dimensions of a similar net from Stender & Barans (1994). The distance the vessel traveled while towing was calculated based on a vessel speed of 2.5 knots (1.28 m s⁻¹) and a tow time of 20 min plus an average of 1.5 min to deploy and 2 min to recover the net, during which time it is still collecting animals. This resulted in our estimated volume of 76 704 m³ sampled by each tow.

This estimate of jellyfish density assumes that we are sampling the entire water column, or the jellyfish are evenly distributed throughout the water column. This is likely not the case, and as a result, our estimate for abundance is likely conservative, given that for the majority of the tow, the net is only sampling the bottom 2 to 4 m of the water column and cannonball jellyfish are known to aggregate at the surface during the day when all tows are collected. The area of each stratum was calculated by totaling the area between the 4 and 10 m depth contours within the stratum boundaries as defined by SEAMAP using QGIS 3.16.0 and 3-arcsecond bathymetry data downloaded from the National Centers for Environmental Information Bathymetric Data Viewer (NOAA 2020). Total stratum area (Table S1 in the Supplement at

www.int-res.com/articles/suppl/m717p051_supp.pdf) was multiplied by an average depth of 7 m to calculate total volume of each stratum.

Medusae biomass was converted to dry weight as 4% of wet weight (Hsieh et al. 1996), and carbon content was calculated as 12.6% of dry weight (Larson 1986) for a carbon-to-wet-weight conversion of 0.5%. Carbon weight of all other species in the trawl catches was calculated using a 10% finfish carbon-to-wet-weight conversion (Czamanski et al. 2011).

2.6. *k*-means cluster analysis

To explore spatial variability in jellyfish abundance, we identified distinct hydrographic regions over which to pool data. 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 and which cluster each of the 24 strata belonged to based on surface temperature, surface salinity, and chl *a* concentration.

2.7. Anomaly analysis

Biomass anomaly for each season, year, or region is determined by dividing each biomass value by the overall median biomass and taking the \log_{10} of the resulting ratio:

$$A = \log \frac{\text{biomass}}{\text{median total biomass}} \quad (1)$$

This produces positive values when the datapoint is above the overall median, and negative values when the datapoint is below the overall median. The anomaly analysis was conducted for the whole dataset, each individual season (spring, summer, and fall), and each of the major regions identified by the *k*-means cluster analysis. When median biomass for a region and/or season was 0, the 0 value was set to a constant value (0.001 kg tow⁻¹) lower than any ob-

served biomass within any tow. This was done to still allow for an estimate of biomass anomaly without dividing by 0.

2.8. Correlations and generalized additive models

Pearson's correlations between the jellyfish biomass anomaly and environmental parameters like chl *a* concentration, surface and bottom temperature, surface and bottom salinity, river discharge rates, and the NAO index were calculated within each region, season, and year sampled, and on a 1-season lag to investigate if the environmental conditions of the previous season influence the biomass measurements. Additionally, relationships of interest between jellyfish biomass, size-proxy, and environmental parameters (surface and bottom salinity, surface and bottom temperature, and NAO index) were analyzed with generalized additive models (GAMs) using the mgcv package (version 1.8-41) and the restricted maximum likelihood (REML) estimation method in R 4.2.3 (R Core Team 2022).

3. RESULTS

3.1. Environmental regions

The *k*-means cluster analysis identified 4 clusters to optimally group strata together based on the environmental data. The strata within each cluster were all geographically contiguous, and were named as the Far South region (Florida), South (Georgia and southern South Carolina), North (northern South Carolina, Long Bay, and Onslow Bay), and Far North (Raleigh Bay) (Table 1). The highest average sampling temperature occurred in the Far South region ($24.8 \pm 0.2^\circ\text{C}$), and the lowest average temperature occurred in the Far North region ($22.2 \pm 0.4^\circ\text{C}$) (Table 1). Average salinity was highest in the Far South (35.3 ± 0.4) and lowest in the Far North (33.2 ± 0.6) (Table 1). Chl *a* concentration was highest on

Table 1. Average \pm SD yearly environmental parameters for each of the major regions identified by the *k*-means cluster analysis

Region	Latitude ($^\circ\text{N}$)		Stratum ID		Temperature ($^\circ\text{C}$)	Salinity	Chl <i>a</i> conc. (mg m^{-3})
	Min.	Max.	Min.	Max.			
Far South	28.7442	30.3867	21	29	24.8 ± 0.2	35.3 ± 0.4	3.6 ± 1.4
South	30.3867	32.7294	31	45	24.2 ± 0.3	33.5 ± 0.6	5.1 ± 1.1
North	32.7294	34.5321	47	63	23.1 ± 0.4	34.5 ± 0.5	3.8 ± 1.6
Far North	34.5321	35.2298	65	67	22.2 ± 0.4	33.2 ± 0.6	8.7 ± 1.8

average in the Far North ($8.7 \pm 1.8 \text{ mg m}^{-3}$) and lowest in the Far South ($3.6 \pm 1.4 \text{ mg m}^{-3}$) (Table 1).

3.2. Regional and seasonal patterns in *Stomolophus meleagris* abundance and biomass

Across all sampling events in the dataset, *S. meleagris* were present in 39% of tows, had an average abundance of 54 ind. tow^{-1} , and an average biomass of 18 kg tow^{-1} . Within the tows where *S. meleagris* was present, average abundance was $135 \text{ ind. tow}^{-1}$ and average biomass was 43 kg tow^{-1} . However, there was significant variability between the regions and seasons, with both abundance (ind. tow^{-1}) and biomass (kg tow^{-1}) following the same trends. One-way ANOVA tests indicated significant differences in *S. meleagris* biomass between regions ($F_{3,209} = 40.1, p < 0.001$) and seasons ($F_{2,210} = 15.6, p < 0.001$), all pair-wise comparisons between regions were significantly different (Table S2), and both spring and fall biomass were higher than that in the summer (Table S2). The South region had the highest biomass across all 3 seasons, with the highest biomass concentrated around strata 41 to 45 (Fig. 2). Average biomass was second highest in the North region, followed by the Far South, and was lowest in the Far North (Fig. 2). Seasonally within regions, spring biomass was highest in the North and South regions, and biomass was highest in the fall in the Far North and Far South regions (Fig. 3, Table S2). These seasonal and regional trends were the same for the total standing stock of each region, with the highest average biomass for any stratum during the spring in stra-

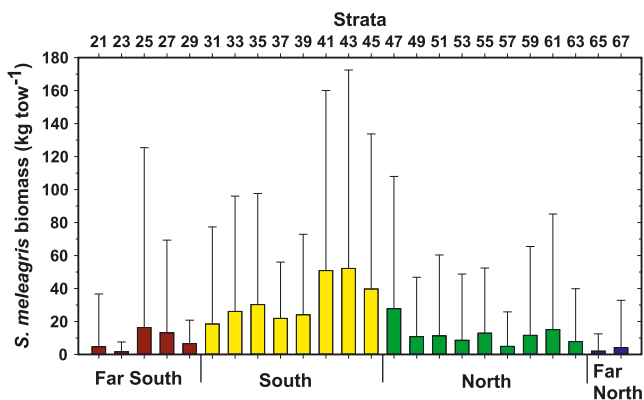


Fig. 2. Average biomass of *Stomolophus meleagris* (kg tow^{-1}) across all seasons (spring, summer, fall) and years (2001 to 2019) in each stratum of the SEAMAP trawl survey. Colors correspond to distinct geographic regions determined by *k*-means cluster analysis of environmental variables. Error bars indicate SD

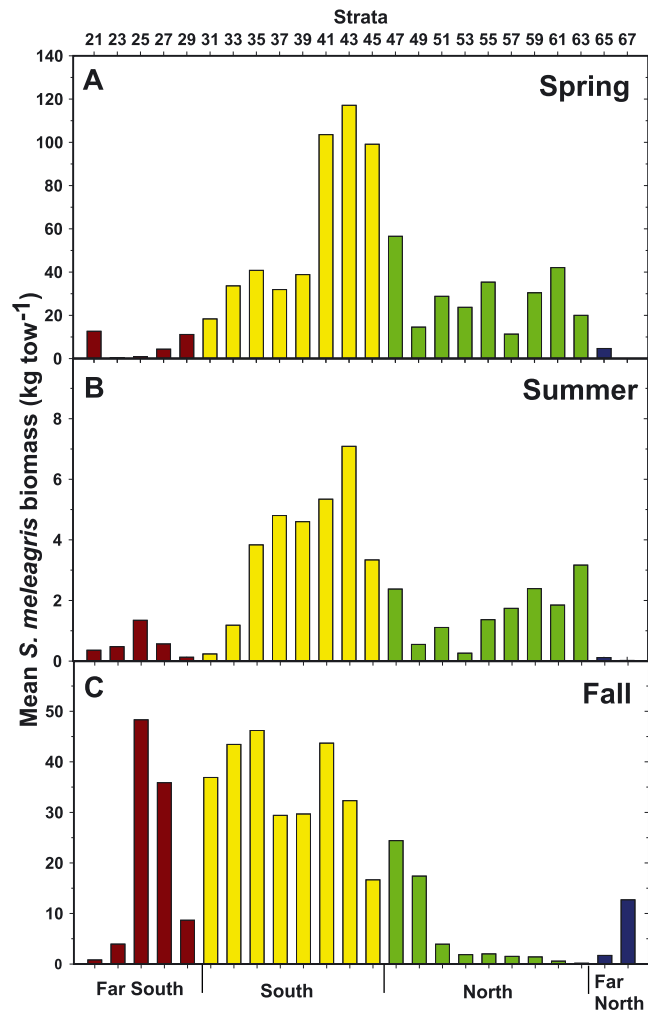


Fig. 3. Average biomass of *Stomolophus meleagris* (kg tow^{-1}) across all years (2001 to 2019) in (A) spring, (B) summer, and (C) fall in each stratum of the SEAMAP trawl survey. Colors correspond to distinct geographic regions determined by *k*-means cluster analysis of environmental variables. Note the different y-axis scales between panels

tum 41, at 3.0 million kg of *S. meleagris* within the stratum. Average annual biomass for the entire sampling region was highest in the spring at 11 million kg of *S. meleagris* (Table 2). In the South region, where *S. meleagris* biomass was highest, *S. meleagris* medusae accounted for, on average, 20.6% ($\pm 21.0 \text{ SD}$) of the wet weight and 4.8% ($\pm 7.7 \text{ SD}$) of the total carbon biomass in each trawl during the spring (Fig. 4). The proportion of medusae in the total catch was similar in the fall: 19.8% ($\pm 24.2 \text{ SD}$) of the wet weight and 3.9% ($\pm 8.2 \text{ SD}$) of the total carbon biomass. In the summer, *S. meleagris* only accounted for a small portion of the total wet weight ($4.3\% \pm 7.1 \text{ SD}$) and carbon biomass ($0.4\% \pm 0.8 \text{ SD}$).

Table 2. Total standing stock biomass estimates ($\text{kg} \times 10^3$) for each of the sampled regions (between the 4 and 10 m isobaths) for each of the 3 sampling seasons

Region	Spring total biomass	Summer total biomass	Fall total biomass
Far South	46.8	4.1	172
South	7940	502	4510
North	3070	139	1090
Far North	29.2	0.8	81.2
Total	11086	646	5853

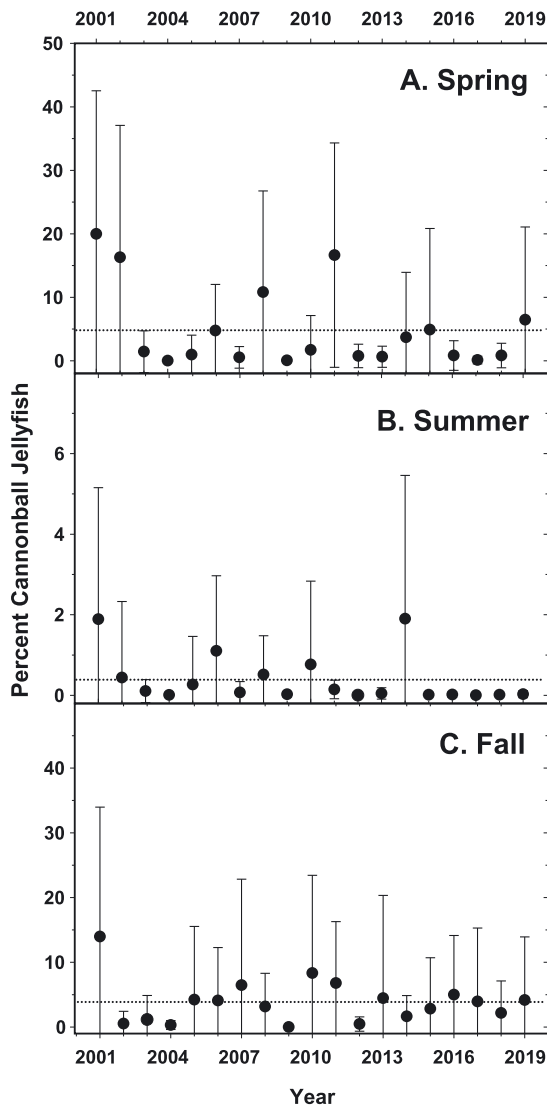


Fig. 4. Average percent *Stomolophus meleagris* of the total catch carbon biomass (converted from wet weight using Hsieh et al. 1996, Larson 1986, and Czamanski et al. 2011) across all years (2001 to 2019) in (A) spring, (B) summer, and (C) fall in the South region (strata 31 to 45) of the SEAMAP trawl survey. Error bars are SD across strata; dotted horizontal line: overall mean for each season

3.3. Changes in size-proxy

The average calculated individual biomass of *S. meleagris* across the whole dataset was $0.38 \text{ kg ind.}^{-1}$ ($\pm 0.32 \text{ SD}$). Average size-proxy across all strata was largest in the spring ($0.69 \pm 0.32 \text{ kg ind.}^{-1}$), medium in the summer ($0.24 \pm 0.22 \text{ kg ind.}^{-1}$), and smallest in the fall ($0.22 \pm 0.12 \text{ kg ind.}^{-1}$), with the differences between the seasons significantly different in a 1-way ANOVA ($F_{2,885} = 394$, $p < 0.001$) and pairwise comparisons between spring and both fall and summer significantly different (Table S3). Changes in average size-proxy between season and region were analyzed using a 2-way ANOVA, and the interaction between season and region was significant (Fig. 5; $F_{6,876} = 18.7$, $p < 0.001$). Within the spring, size-proxy

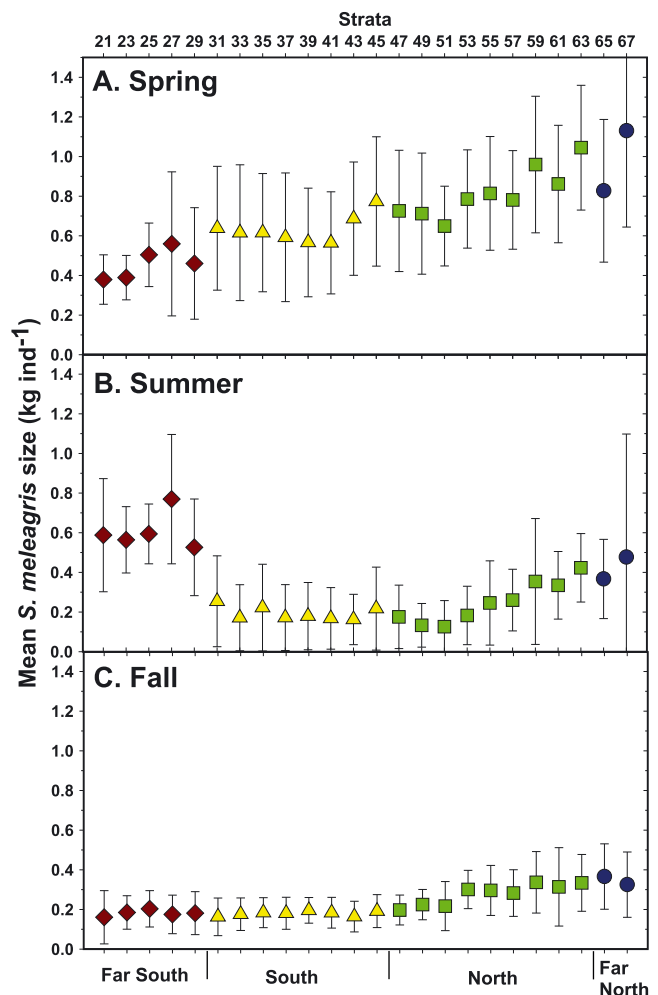


Fig. 5. Average size-proxy of *Stomolophus meleagris* (kg ind.^{-1}) across all years (2001 to 2019) in (A) spring, (B) summer, and (C) fall in each stratum of the SEAMAP trawl survey. Colors correspond to distinct geographic regions determined by k -means cluster analysis of environmental variables. Error bars indicate SD between tows

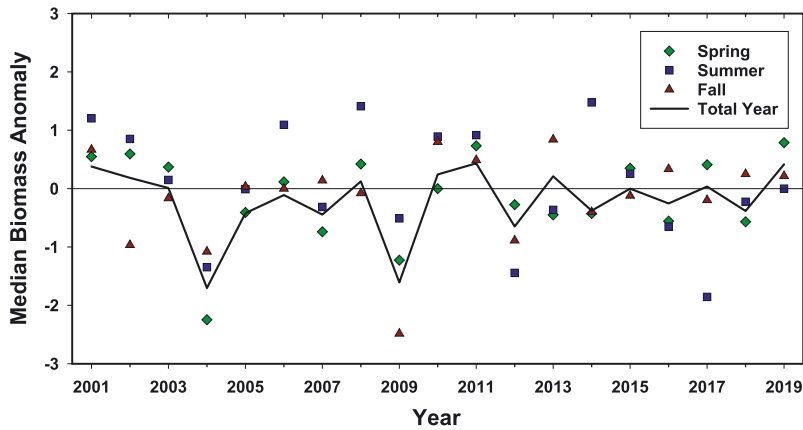
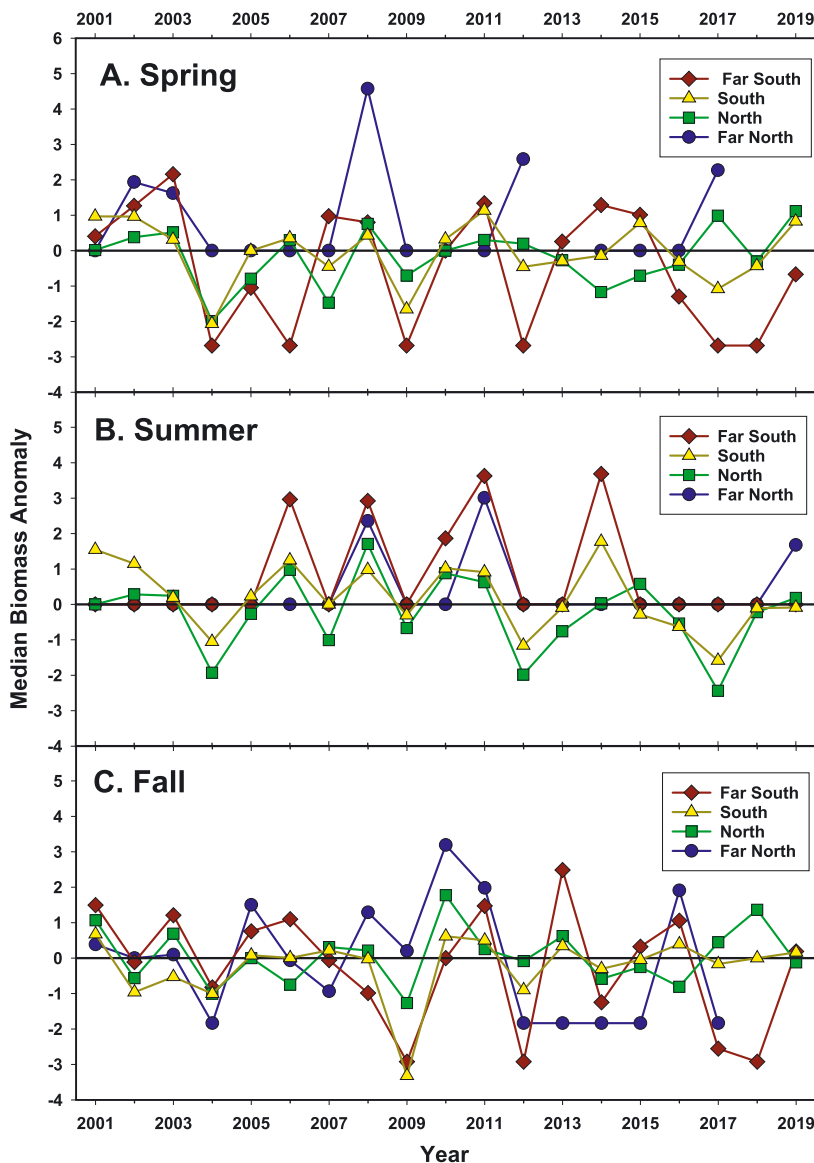


Fig. 6. Median biomass anomaly of *Stomolophus meleagris* for all combined SEAMAP strata for each season (spring, summer, and fall) and year of the survey (2001 to 2019)



increased from south to north, with all pairwise comparisons between regions significant except for between North and Far North (Table S3). During the summer, size-proxy in the Far South was significantly larger than in the South or North, and size-proxy in the Far North was significantly larger than in the South (Table S3). In the fall, there was no difference in size-proxy between the Far South and South and between the North and Far North, but it was significantly smaller in the 2 southern regions than in the 2 northern regions (Table S3).

3.4. Interannual variability

Across the entire sampling area, there was high interannual variability in *S. meleagris* biomass, but no long-term increase or decrease in biomass (Fig. 6). Biomass was particularly high in 2001, 2011, and 2019, and was lowest in 2004 and 2009. Summer biomass was positively correlated with spring biomass (Pearson's correlation = 0.478, $p = 0.038$), and fall biomass was marginally correlated with spring biomass as well (Pearson's correlation = 0.445, $p = 0.056$). Spring biomass was not correlated with the biomass anomaly from the previous year's fall (Pearson's correlation = 0.132, $p = 0.601$). Total yearly biomass anomaly was most closely correlated with spring biomass (Pearson's correlation = 0.898, $p < 0.001$), when jellyfish abundance was highest.

Between regions, interannual variability was highest in the Far South and Far North, where often no jellyfish were collected. Within each region, there was no long-term increase or decrease in biomass anomaly for the full year or any season (Fig. 7). Yearly biomass anomaly was positively corre-

Fig. 7. Median biomass anomaly of *Stomolophus meleagris* in (A) spring, (B) summer, and (C) fall for each of the 4 regions and year of the survey (2001 to 2019)

lated between adjacent regions, with significant correlations existing between Far South and South (Pearson's correlation = 0.677, $p = 0.001$), South and North (Pearson's correlation = 0.497, $p = 0.030$), and North and Far North (Pearson's correlation = 0.497, $p = 0.030$); however, no significant correlations were found between non-adjacent regions.

3.5. Environmental correlations

Annual and seasonal averages of biomass anomaly were correlated and modeled with GAMs against annual and seasonal averages of environmental parameters (temperature, salinity, chl *a* concentration, NAO index, and river discharge), but no significant correlations were detected. Additionally, Pearson's correlations (Table 3) and GAMs were calculated between the seasonal median biomass anomaly for each region and each environmental variable (bottom temperature, bottom salinity, NAO, regional chl *a*). Three primary trends were detected: (1) North spring biomass anomaly was positively correlated with North spring bottom temperature (25.2% deviance explained, $p = 0.0286$), (2) Far South and South fall anomaly negatively correlated with Far South (27.9% deviance explained, $p = 0.0201$) and South (80% deviance explained, $p = 0.0011$) fall temperature, respectively, and (3) spring size-proxy was negatively related to spring temperature and NAO in the whole survey area (36% deviance explained, $p < 0.0001$) (Fig. 8). Additionally, jellyfish biomass anomalies were compared to the environmental variables of the previous year, and the North and South spring

Table 3. Significant Pearson's correlation coefficients between jellyfish median biomass anomaly and environmental parameters. * $p \leq 0.05$; ** $p \leq 0.01$

Comparison	Correlation coefficient
Far North Summer Anomaly & North Spring Bottom Temperature	0.504*
North Spring Anomaly & North Spring Bottom Temperature	0.502*
Far South Fall Anomaly & Far South Fall Bottom Temperature	-0.528*
South Fall Anomaly & South Fall Bottom Temperature	-0.636**
North Spring Anomaly & Lagged North Summer Bottom Temperature	0.708**

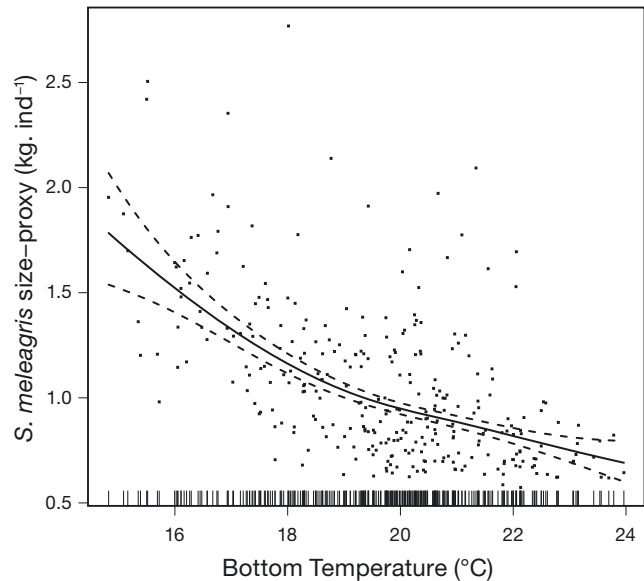


Fig. 8. Relationship between spring bottom temperature and average size-proxy of *Stomolophus meleagris* medusae in all strata across all years (2001 to 2019). Solid line: generalized additive model results; dashed lines: partial residuals (deviance explained = 36.4%)

anomaly was positively correlated with the previous summer temperature in the North (41.8% deviance explained, $p < 0.0001$), but this trend was principally driven by an outlier in 2003. No other significant correlations were observed in the dataset.

4. DISCUSSION

4.1. Seasonal and spatial variability

Based on statistical analyses of the SEAMAP time-series dataset from 2001 to 2019, *Stomolophus meleagris* jellyfish exhibit marked seasonal and spatial variability across the sampling region of the SAB from Cape Hatteras, North Carolina to Cape Canaveral, Florida. Highest biomass (kg tow^{-1}) was observed in the South region, which includes the coastal waters of Georgia and the southern portion of South Carolina (south of Charleston). *S. meleagris* in the SAB have been previously documented as the most abundant large scyphozoan off the coasts of South Carolina and Georgia (Kraeuter & Setzler 1975, Zingmark 1978). However, direct comparisons of absolute abundances in this study with previous studies are impossible, as the sampling gear used is significantly different (i.e. 1 m^2 ring net in Kraeuter & Setzler 1975), and the size classes of medusae caught are very different.

The highest average biomass (kg tow⁻¹) was recorded during the spring sampling events, although winter was not sampled in this survey. This was expected since *S. meleagris* was documented by Mayer (1910) as most abundant during the winter and spring in the coastal waters of Florida, Georgia, and South Carolina. The lowest average biomass in the survey region occurred during the summer, which could be a result of decreases in regional biomass or inshore transport toward protective habitats like estuaries and inlets where the SEAMAP coastal trawl survey does not sample. This seasonal movement in *S. meleagris* was observed by both Kraeuter & Setzler (1975) and Rountree (1983), with *S. meleagris* occupying offshore waters during the spring and then subsequently moving into inshore waters in the early summer.

The largest average size-proxy (kg ind.⁻¹) occurred during the spring sampling season. The average size-proxy of jellyfish decreased during the summer sampling season for all of the regions except the Far South (Florida). Rountree (1983) also observed large cannonball jellyfish offshore during the spring and a drop in average weight during the summer months in North Carolina. Then in the fall, average size-proxy of jellyfish decreased in the Far South but remained approximately the same for the other 3 regions. The lag observed in the Far South region could be explained by a lack of polyps and asexual reproduction in the region. The medusae that are present in the Far South could have been advected from the South region in the fall and remain there, growing in size, until a further influx of small medusae the following fall. This potential pattern is consistent with the seasonal changes in both biomass and size-proxy for the Far South. While growth of medusae could explain the seasonal patterns in size-proxy, medusae of other species are also known to decrease in size as a result of starvation (Pitt et al. 2014), which could complicate the interpretation of the size-proxy data.

Stomolophus sp. medusae in the Gulf of California first reach sexual maturity when they are at least 374 g (Carvalho-Saucedo et al. 2010), and during peak reproduction in April, average weights were 580 ± 40 g for females and 562 ± 36 g for males (Carvalho Saucedo et al. 2011). Average size-proxy of *S. meleagris* in our study was above the 374 g threshold in all regions in the spring, and in the Far South and Far North in the summer. Given the changes in average size-proxy of individuals as an estimate of maturity, the younger medusae are seen in the fall and then reproductive adults are seen in the spring. A suggested seasonal pattern for the *S. meleagris* pop-

ulation of the SAB is as follows: (1) Large, mature medusae occur offshore in the spring season. (2) During spring and early summer, these adult medusae move inshore to broadcast spawn, senesce, and die, resulting in the low abundances we see during summer sampling. (3) These planula larvae settle into polyps during the summer and begin to asexually reproduce. Polyps as young as 9 d old have been observed to begin strobilation (Calder 1982). (4) Polyps from both the current year and the previous year strobilate throughout the spring and summer to produce ephyrae. (5) As the ephyrae mature and grow into medusae, they reach a large enough size for our gear to begin capturing them during fall as they also move offshore. (6) Medusae continue to grow during winter months offshore, until they reach maturity in the spring. This timing of reproduction is consistent with *Stomolophus* sp. seasonality in the Gulf of California (López-Martínez et al. 2020).

While this suggested timing of reproduction and growth is supported by our dataset, we are unable to determine the location of polyps in relation to distance from shore, and whether the medusae are moving into and out of the sampling area (between the 4 and 10 m isobaths). Both Kraeuter & Setzler (1975) and Rountree (1983) found that young medusae first appear in coastal estuaries and nearshore waters during the late spring and summer and then move offshore during the fall and winter, where they grow and then return into nearshore environments in the spring. This proposed seasonal migration into and out of estuaries is certainly consistent with our results, and as our sampling region is often >5 km offshore, inshore migration of large medusae in late spring could explain the drop in our observed abundances during the summer.

Along-shore transport of *S. meleagris* is also probable and could follow average surface water currents. Average surface flows in the SAB generally follow 3 seasonal regimes: the winter period (November to February) is associated with offshore surface water flows, summer (June to July) with poleward flows, and the mariners' fall (October to November) period with surface flows toward the equator (Weber & Blanton 1980, Atkinson et al. 1983, Blanton et al. 2003). This seasonal pattern supports the hypothesis of offshore wintering of adults. Additionally, there could be a southward migration in the fall, consistent with seasonal shifts in the Far South size-proxy and abundance, followed by a northward migration in the spring, a possibility noted by Rountree (1983).

The location of polyps remains a major unknown, although it is likely that they are present nearshore or

in estuaries, as that is where small medusae first appear in late spring/summer (Kraeuter & Setzler 1975, Rountree 1983). Calder (1982) successfully cultured *S. meleagris* polyps at a salinity of 35.7 based on the salinity where mature medusae were collected; other salinities were not tested. Reliance of polyps on estuarine habitats for settlement and reproduction could explain the high abundances of *S. meleagris* medusae in the South and North regions, but lower abundances in the Far South and Far North. The coasts of the South and North regions are dominated by large salt-marsh-lined estuaries that have numerous oyster reefs as potential substrate for polyps as well as high exchange with oceanic waters. In contrast, the Far South and Far North regions generally have smaller estuarine area and more restricted exchange with ocean waters, which would limit medusae migrations into and out of those estuarine habitats.

4.2. Interannual variability

Although this analysis provides useful insight on the spatial and seasonal variability of cannonball jellyfish in the SAB, we were unable to detect what drives the interannual variability in total biomass. The relationships between biomass anomaly and several environmental parameters (temperature, salinity, river discharge, and chl *a* concentration) were explored, but no significant linear correlations were found. These relationships were explored on a regional scale, for each season individually, and including a 1-season lag. In some species of Scyphozoa, interannual changes in medusae populations are regulated by polyp strobilation (Purcell 2007, Prieto et al. 2010, Holst 2012, Stone et al. 2019, Loveridge et al. 2021). Without a clear understanding of where *S. meleagris* polyps occur or the environmental conditions they favor, it is difficult to predict the effects of environmental changes on their populations.

Interannual variability in medusae size-proxy was evident, and spring size-proxy was negatively related to spring bottom temperatures throughout the entire study area. This change in average size-proxy could be due to several factors: (1) smaller individuals do not survive colder winters, leaving only the largest individuals in the spring, (2) medusae grow more quickly in colder temperatures, or (3) medusae are stressed or starve in warmer winter and spring conditions and shrink in response. Additionally, food availability may vary depending on winter and spring water temperatures, influencing medusae growth and size.

S. meleagris in the sampling region did demonstrate high interannual variability in biomass anomaly throughout the SEAMAP timeseries, but no consistent, long-term trends were detected. Literature suggests that long-term trends in interannual jellyfish dynamics are likely connected to global climate oscillations that fluctuate on decadal scales (Brodeur et al. 2008, Condon et al. 2013, Robinson & Graham 2013, Quiñones et al. 2015, Decker et al. 2023), but we found no long-term changes or oscillations in *S. meleagris* abundances. Warming in the region due to global climate change is likely to have complicated effects on their life cycles. Warmer winters and springs could lead to phenological shifts in abundance and earlier initiation of sexual and asexual reproduction, but a shorter winter growing season could mean smaller medusae on average in the spring, potentially reducing reproductive output. Longer summers may lengthen the asexual reproductive period of polyps and hasten ephyrae growth but could also lead to temperature stress and mismatches in prey abundances. Without a clearer understanding of the life cycle of *S. meleagris* and the temperature optima and tolerances of both the polyps and medusae, it is difficult to make predictions about the potential effects of climate change on their populations.

4.3. Ecological impact

S. meleagris make up a large portion of the total pelagic biomass collected in the SEAMAP survey. Based on wet weight, they are the most abundant species in the core of their range (South region) during both the spring and fall. Even accounting for the lower carbon:wet weight ratio of jellyfish compared to finfish and crustaceans, *S. meleagris* are the species with the 5th (spring) and 8th (fall) highest total carbon biomass in the South region. In contrast with other high biomass species in the region, *S. meleagris* are zooplanktivorous, feeding on molluscan veligers, copepods, tintinnids, larvaceans, and other mesozooplankton (Larson 1991). Due to their high abundances, these jellyfish potentially have top-down effects on zooplankton populations. From the SEAMAP surveys, average *S. meleagris* abundances in the South region are 236 ind. tow⁻¹ in the spring (0.0031 ind. m⁻³, size-proxy of 0.64 kg ind.⁻¹) and 336 ind. tow⁻¹ in the fall (0.0044 ind. m⁻³, size-proxy of 0.18 kg ind.⁻¹). Maximum observations of *S. meleagris* in the South are approximately 8000 ind. tow⁻¹ in the spring (0.104 ind. m⁻³, size-proxy of 0.36 kg ind.⁻¹)

and approximately 10 000 ind. tow⁻¹ in the fall (0.130 ind. m⁻³, size-proxy of 0.17 kg ind.⁻¹). Using the wet weight-to-consumption formulae of Larson (1991), *S. meleagris* consume zooplankton, on average, at a rate of 1110 d⁻¹ m⁻³ in the spring and 91 d⁻¹ m⁻³ in the fall. Consumption of zooplankton at the maximum observed *S. meleagris* abundances are 6600 d⁻¹ m⁻³ in the spring and 2500 d⁻¹ m⁻³ in the fall. Typically in the South region, total mesozooplankton abundances in the spring are on the order of 10 000 ind. m⁻³ (López-Figueroa et al. 2023). Thus, *S. meleagris* has the capacity to consume approximately 10% of the mesozooplankton standing stock per day at their average spring abundance, and up to 66% at their maximum abundance. It is also worth noting that our sampling gear does not efficiently collect smaller size classes of medusae, and actual grazing rates might be higher than our estimates.

4.4. Implications for the jellyfish fishery

The US State of Georgia has an active commercial fishery of *S. meleagris* that started as an experimental fishery in 1998 and became a recognized fishery in 2013. On average, 2.9 million kg of *S. meleagris* medusae are harvested annually in the SAB (ACCSP 2022), primarily in federal waters close to Georgia (Page 2015). While expansion of the fishery is planned (Brotz et al. 2017), current harvesting has been stopped due to temporary closure of the processing plant. Based on our results, *S. meleagris* could most efficiently be commercially targeted during the spring months in the South region, where medusae are largest and most abundant. And indeed, the commercial fishery harvests in these waters during November to May, with most fishing occurring in March to May in stratum 35 (Page 2015). However, until further research is conducted into the seasonal inshore-offshore movements of these jellyfish, we caution against expansion of targeted harvest of offshore populations. If medusae move seasonally into estuaries to spawn, then offshore harvest in the spring would remove adult medusae from the population before they have a chance to reproduce. Rapid overfishing of *Stomolophus* spp. in the Gulf of California due to lack of regulation and enforcement has occurred recently (Brotz et al. 2021) and could also occur in the SAB. Our estimated spring average of *S. meleagris* standing stock in the South region (7.9 million kg) is small compared to what is commercially harvested each year on average (~2.9 million kg yr⁻¹; ACCSP 2022), which may indicate harvest is

already high. However, our sampling methodology may significantly underestimate the absolute number of medusae present in the system, as our study area was limited to a portion of the species' range (between the 4 and 10 m isobaths) and tows disproportionately sampled bottom waters, which *S. meleagris* medusae may avoid (Page 2015).

Regardless, before expansion of the *S. meleagris* fishery in the SAB, we need a much better understanding of their life cycle, seasonal migration, and environmental effects on their populations in order to avoid overfishing of this species. Most critically, a mechanistic understanding of the relative control of asexual vs. sexual reproduction on the population is needed. If asexual reproduction by the polyps is the primary control on medusae populations, then an expansion of medusae harvest is likely to be sustainable. However, if polyps are short-lived or sexual reproduction is more important in their interannual population growth, then limitations on their harvest are likely to be needed. These limitations could focus on prevention of harvesting individuals before reproduction through minimum mesh size-limits in nets, an embargo on early winter and early spring harvesting, or restricting offshore fishing before inshore migration to spawning areas occurs. Additionally, limits on total allowable catch could be implemented and adjusted based on seasonal surveys of medusae populations.

5. CONCLUSIONS

Stomolophus meleagris are the most abundant Scyphozoan jellyfish in the SAB and have high inter-annual variability. While winter months were not sampled in this study, we found average biomass of this species is highest in the spring off the coast of Georgia and southern South Carolina (South region), and the largest jellyfish occur during the spring months. The lowest biomass in the sampling region occurs in the summer months when smaller jellyfish occur. This could indicate that adult cannonball jellyfish occur offshore in the spring and move inshore toward estuarine habitats with hard substrate for polyp attachment to release larvae. Subsequently, juvenile cannonballs move out of the estuaries as they mature throughout the summer and fall, and the larger, surviving adults are detected offshore again the next spring. The seasonal and spatial variability described does not appear to be linearly related to temperature, salinity, chl *a* concentration, or river discharge, but is perhaps influenced by distance from estuarine habi-

tats and wind direction, which were not examined in this study. Interannual variability in biomass is evident in the cannonball jellyfish of the SAB, but no long-term trends or strong correlations with the aforementioned environmental parameters were detected. Further research is needed in order to pinpoint the drivers behind the variability seen in the cannonball jellyfish of the SAB, and investigations to clarify their life history are critical to sustain the commercial fishery of this species.

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LITERATURE CITED

- ACCSP (Atlantic Coastal Cooperative Statistics Program) (2022) www.accsp.org/ (accessed 28 September 2022)
- Alvarez-Tello FJ, Lopez-Martinez J, Lluch-Cota DB (2016) Trophic spectrum and feeding pattern of cannonball jellyfish *Stomolophus meleagris* (Agassiz, 1862) from central Gulf of California. *J Mar Biol Assoc UK* 96:1217–1227
- Arai MN (2005) Predation on pelagic coelenterates: a review. *J Mar Biol Assoc UK* 85:523–536
- Ates R (1988) Medusivorous fishes, a review. *Zool Meded* 62:29–42
- Atkinson LP, Lee TN, Blanton JO, Chandler WS (1983) Climatology of the southeastern United States continental shelf waters. *J Geophys Res Oceans* 88:4705–4718
- Blanton BO, Aretxabaleta A, Werner FE, Seim HE (2003) Monthly climatology of the continental shelf waters of the South Atlantic Bight. *J Geophys Res Oceans* 108:3264
- Bologna P, Gaynor JJ, Meredith R, Restaino D, Barry C (2018) Stochastic event alters gelatinous zooplankton community structure: impacts of Hurricane Sandy in a Mid-Atlantic estuary. *Mar Ecol Prog Ser* 591:217–227
- Bosch-Belmar M, Milisenda G, Basso L, Doyle TK, Leone A, Piraino S (2021) Jellyfish impacts on marine aquaculture and fisheries. *Rev Fish Sci Aquacult* 29:242–259
- Brodeur RD, Decker MB, Ciannelli L, Purcell JE and others (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Prog Oceanogr* 77: 103–111
- Brodeur RD, Buckley TW, Lang GM, Draper DL, Buchanan JC, Hibpshman RE (2021) Demersal fish predators of gelatinous zooplankton in the Northeast Pacific Ocean. *Mar Ecol Prog Ser* 658:89–104
- Brotz L, Pauly D (2017) Studying jellyfish fisheries: toward accurate national catch reports and appropriate methods for stock assessments. In: Mariottini GL (ed) *Jellyfish: ecology, distribution patterns and human interactions* Nova Publishers, New York, NY, p 313–329
- Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia* 690:3–20
- Brotz L, Schiariti A, López-Martínez J, Álvarez-Tello J and others (2017) Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Rev Fish Biol Fish* 27:1–29
- Brotz L, Cisneros-Montemayor AM, Cisneros-Mata MÁ (2021) The race for jellyfish: winners and losers in Mexico's Gulf of California. *Mar Policy* 134:104775
- Burke WD (1976) Biology and distribution of the macrocoelenterates of Mississippi Sound and adjacent waters. *Gulf Caribb Res* 5:17–28
- Calder DR (1982) Life history of the cannonball jellyfish, *Stomolophus meleagris* L. Agassiz, 1860 (Scyphozoa, Rhizostomida). *Biol Bull* 162:149–162
- Cardona L, Álvarez de Quevedo I, Borrell A, Aguilar A (2012) Massive consumption of gelatinous plankton by Mediterranean apex predators. *PLOS ONE* 7:e31329
- Carvalho-Saucedo L, García-Domínguez F, Rodríguez-Jaramillo C, López-Martínez J (2010) Variación lipídica en los ovocitos de la medusa *Stomolophus meleagris* (Scyphozoa: Rhizostomeae), durante el desarrollo gonádico, en la laguna Las Guásimas, Sonora, México. *Rev Biol Trop* 58:119–130
- Carvalho Saucedo L, Martinez J, Garcia Dominguez F, Rodríguez-Jaramillo M, Padilla Serrato J (2011) Reproductive biology of the cannonball jellyfish *Stomolophus meleagris* in Las Guasimas Lagoon, Sonora, Mexico. *Hydrobiologica* 21:77–88 (in Spanish with English Abstract)
- Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proc Natl Acad Sci USA* 110:1000–1005
- Condon RH, Lucas CH, Pitt KA, Uye S (2014) Jellyfish blooms and ecological interactions. *Mar Ecol Prog Ser* 510:109–110
- Crum KP, Fuchs HL, Bologna PAX, Gaynor JJ (2014) Model-to-data comparisons reveal influence of jellyfish interactions on plankton community dynamics. *Mar Ecol Prog Ser* 517:105–119
- Czamanski M, Nugraha A, Pondaven P, Lasbleiz M and others (2011) Carbon, nitrogen and phosphorus elemental stoichiometry in aquacultured and wild-caught fish and consequences for pelagic nutrient dynamics. *Mar Biol* 158:2847–2862
- Decker MB, Brodeur RD, Ciannelli L, Britt LL, Bond NA, DiFiore BP, Hunt GL (2023) Cyclic variability of eastern Bering Sea jellyfish relates to regional physical conditions. *Prog Oceanogr* 210:102923
- Duffy JT, Epifanio CE, Fuiman LA (1997) Mortality rates imposed by three scyphozoans on red drum (*Sciaenops ocellatus* Linnaeus) larvae in field enclosures. *J Exp Mar Biol Ecol* 212:123–131
- Fuentes VL, Purcell JE, Condon RH, Lombard F, Lucas CH (2018) Jellyfish blooms: advances and challenges. *Mar Ecol Prog Ser* 591:3–5
- Getino Mamet LN, Gómez Daglio L, García-De León FJ (2019) High genetic differentiation in the edible cannonball jellyfish (cnidaria: Scyphozoa: *Stomolophus* spp.) from the Gulf of California, Mexico. *Fish Res* 219:105328
- Goldstein J, Steiner UK (2020) Ecological drivers of jellyfish blooms—the complex life history of a 'well-known' medusa (*Aurelia aurita*). *J Anim Ecol* 89:910–920
- Gómez Daglio L, Dawson MN (2017) Species richness of jellyfishes (Scyphozoa: Discomedusae) in the Tropical Eastern Pacific: missed taxa, molecules, and morphology match in a biodiversity hotspot. *Invertebr Syst* 31:635–663
- Gonzalez-Valdovinos M, Ocampo L, Tovar-Ramirez D (2019)

- Evaluation of digestive capacity in the polyp, ephyrae, and medusae stages of the cannonball jellyfish *Stomolophus meleagris*. *Hydrobiologia* 828:259–269
- Griffin DB, Murphy TM (2005) Cannonball jellyfish. South Carolina Department of Natural Resources, Charleston
- Hayse JW (1990) Feeding habits, age, growth and reproduction of Atlantic spadefish, *Chaetodipterus Faber* (Pisces: Ephippidae), in South Carolina. *Fish Bull* 88:67–83
- Heaslip SG, Iverson SJ, Bowen WD, James MC (2012) Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PLOS ONE* 7:e33259
- Henschke N, Stock CA, Sarmiento JL (2018) Modeling population dynamics of scyphozoan jellyfish (*Aurelia* spp.) in the Gulf of Mexico. *Mar Ecol Prog Ser* 591:167–183
- Holst S (2012) Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. *Hydrobiologia* 690:127–140
- Hsieh YHP, Leong Fm, Barnes KW (1996) Inorganic constituents in fresh and processed cannonball jellyfish (*Stomolophus meleagris*). *J Agric Food Chem* 44:3117–3119
- Kraeuter JN, Setzler EM (1975) The seasonal cycle of Scyphozoa and Cubozoa in Georgia estuaries. *Bull Mar Sci* 25:66–74
- Kramp PL (1961) Synopsis of the medusae of the world. *J Mar Biol Assoc UK* 40:7–382
- Larson RJ (1976) Marine flora and fauna of the northeastern United States. Cnidaria: Scyphozoa. NOAA Tech Rep NMFS CIRC 397
- Larson RJ (1986) Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *J Exp Mar Biol Ecol* 99:107–120
- Larson RJ (1991) Diet, prey selection and daily ration of *Stomolophus meleagris*, a filter-feeding scyphomedusa from the NE Gulf of Mexico. *Estuar Coast Shelf Sci* 32:511–525
- López-Figueroa NB, Walters TL, Laureano-Rosario AE, DiGeronimo SP and others (2023) Zooplankton community variability in the South Atlantic Bight (2015–2017). *J Plankton Res* 45:312–324
- López-Martínez J, Arzola-Sotelo EA, Nevárez-Martínez MO, Álvarez-Tello FJ, Morales-Bojórquez E (2020) Modeling growth on the cannonball jellyfish *Stomolophus meleagris* based on a multi-model inference approach. *Hydrobiologia* 847:1399–1422
- López-Martínez J, Álvarez-Tello FJ, Porchas-Cornejo MA, Nevárez-López CA, Muhlia-Almazán A, Urías-Padilla KV (2023) Multiple reproduction forms in the polyps of the cannonball jellyfish *Stomolophus* sp. 2: Probable life-cycle reversal. *J Exp Zool A Ecol Integr Physiol* 339:239–252
- Loveridge A, Lucas CH, Pitt KA (2021) Shorter, warmer winters may inhibit production of ephyrae in a population of the moon jellyfish *Aurelia aurita*. *Hydrobiologia* 848:739–749
- Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. *Adv Mar Biol* 63:133–196
- Mayer A (1910) Medusae of the world, Hydromedusae and Scyphomedusae. Carnegie Institute of Washington, Publication no. 109, Washington, DC
- Mianzan H, Pájaro M, Alvarez Colombo G, Madirolas A (2001) Feeding on survival-food: gelatinous plankton as a source of food for anchovies. *Hydrobiologia* 451:45–53
- Murray S (2021) 2021–2025 SEAMAP management plan. Collection, management, and dissemination of fishery-independent data from the waters of the southeastern United States. Atlantic States Marine Fisheries Commission, Arlington, VA
- NASA (2021) Ocean Color Data Center. <https://oceancolor.gsfc.nasa.gov/> (accessed 5 April 2021)
- NOAA (2020) Bathymetric data viewer. National Centers for Environmental Information. www.ncei.noaa.gov/maps/bathymetry/ (accessed 11 November 2020)
- NOAA (2021) Climate Prediction Center. www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml (accessed 10 March 2021)
- Omori M (1978) Zooplankton fisheries of the world: a review. *Mar Biol* 48:199–205
- Page JW (2015) Characterization of bycatch in the cannonball jellyfish fishery in the coastal waters off Georgia. *Mar Coast Fish* 7:190–199
- Pauly D, Graham W, Libralato S, Morissette L, Deng Palomares ML (2009) Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* 616:67–85
- Phillips PJ, Burke WD, Keener EJ (1969) Observations on the trophic significance of jellyfishes in Mississippi Sound with quantitative data on the associative behavior of small fishes with medusae. *Trans Am Fish Soc* 98:703–712
- Pitt KA, Budarf AC, Browne JG, Condon RH (2014) Bloom and bust: why do blooms of jellyfish collapse? In: Pitt KA, Lucas CH (eds) *Jellyfish blooms*. Springer, Dordrecht, p 79–103
- Prieto L, Astorga D, Navarro G, Ruiz J (2010) Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish. *PLOS ONE* 5:e13793
- Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *J Mar Biol Assoc UK* 85:461–476
- Purcell JE (2007) Environmental effects on asexual reproduction rates of the scyphozoan, *Aurelia labiata*. *Mar Ecol Prog Ser* 348:183–196
- Purcell JE, Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. *Limnol Oceanogr* 50:376–387
- Purcell JE, Uye S, Lo WT (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar Ecol Prog Ser* 350:153–174
- Purcell JE, Juhl AR, Maňko MK, Aumack CF (2018) Overwintering of gelatinous zooplankton in the coastal Arctic Ocean. *Mar Ecol Prog Ser* 591:281–286
- Quiñones J, Mianzan H, Purca S, Robinson KL, Adams GD, Marcelo Acha E (2015) Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru. *Mar Biol* 162:2339–2350
- Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.r-project.org>
- Riascos JM, Aguirre W, Hopfe C, Morales D, Navarrete Á, Tavera J (2018) Floating nurseries? Scyphozoan jellyfish, their food and their rich symbiotic fauna in a tropical estuary. *PeerJ* 6:e5057
- Robinson KL, Graham WM (2013) Long-term change in the abundances of northern Gulf of Mexico scyphomedusae *Chrysaora* sp. and *Aurelia* spp. with links to climate variability. *Limnol Oceanogr* 58:235–253
- Robinson KL, Ruzicka JJ, Hernandez FJ, Graham WM, Decker MB, Brodeur RD, Sutor M (2015) Evaluating energy flows through jellyfish and gulf menhaden (*Brevoortia patronus*) and the effects of fishing on the north-

- ern Gulf of Mexico ecosystem. *ICES J Mar Sci* 72: 2301–2312
- Rountree RA (1983) The ecology of *Stomolophus meleagris*, the cannon ball jellyfish, and its symbionts, with special emphasis on behavior. BS thesis, University of North Carolina, Wilmington, NC
- SC-DNR (South Carolina Department of Natural Resources) (2020) Southeast Area Monitoring and Assessment Program. <https://www2.dnr.sc.gov/seamap> (accessed 24 May 2020)
- ✦ Sommer U, Stibor H, Katechakis A, Sommer F, Hansen T (2002) Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production:primary production. *Hydrobiologia* 484:11–20
- ✦ Steinberg DK, Landry MR (2017) Zooplankton and the ocean carbon cycle. *Annu Rev Mar Sci* 9:413–444
- ✦ Stender B, Barans C (1994) Comparison of the catch from tongue and two-seam shrimp nets off South Carolina. *N Am J Fish Manage* 14:178–195
- ✦ Stone JP, Steinberg DK, Fabrizio MC (2019) Long-term changes in gelatinous zooplankton in Chesapeake Bay, USA: environmental controls and interspecific interactions. *Estuaries Coasts* 42:513–527
- ✦ Treible LM, Condon RH (2019) Temperature-driven asexual reproduction and strobilation in three scyphozoan jellyfish polyps. *J Exp Mar Biol Ecol* 520:151204
- ✦ Urban P, Praebel K, Bhat S, Dierking J, Wangensteen OS (2022) DNA metabarcoding reveals the importance of gelatinous zooplankton in the diet of *Pandalus borealis*, a keystone species in the Arctic. *Mol Ecol* 31:1562–1576
- USGS (United States Geological Survey) (2021) National Water Dashboard. <https://dashboard.waterdata.usgs.gov> (accessed 25 May 2021)
- ✦ Uye Si (2011) Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia* 666:71–83
- ✦ Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar Ecol Prog Ser* 130:277–293
- ✦ Weber AH, Blanton JO (1980) Monthly mean wind fields for the South Atlantic Bight. *J Phys Oceanogr* 10:1256–1263
- ✦ Young GA, Hagadorn JW (2010) The fossil record of cnidarian medusae. *Palaeoworld* 19:212–221
- Zingmark RG (1978) An annotated checklist of the biota of the coastal zone of South Carolina. Belle W. Baruch Institute for Marine Biology and Coastal Research, Georgetown, SC

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