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Black Sea Bass *Centropristis striata* Year Class Strength and Spatial Extent from Two Long-Term Surveys off the Southeast U.S. Atlantic Coast

Julie L. Vecchio *, Margaret W. Finch, Kevin R. Spanik, Amy Zimney and Tracey I. Smart

South Carolina Department of Natural Resources, Charleston, SC 29412, USA; walkermf@dnr.sc.gov (M.W.F.); spanikk@dnr.sc.gov (K.R.S.); zimneya@dnr.sc.gov (A.Z.); smartt@dnr.sc.gov (T.I.S.)
* Correspondence: vecchioj@dnr.sc.gov

Abstract: The Southeastern U.S. Atlantic coast (North Carolina to Florida, U.S.A.) has undergone considerable environmental change in recent decades, including increasing coastal water temperature and human development. The region is also home to a diverse suite of exploited reef fish species, including the southern stock of black sea bass (*Centropristis striata*). The objective of the current study was to compare trends in black sea bass year class strength and central location captured by trawls (age 0) and traps (age 2) as well as compare those trends to regional bottom temperature. We found no correlation between age 0 and age 2 abundance when comparing the same year class, suggesting that the numbers of trawl-caught juveniles cannot predict the number of adults available to the fishery. Larger year classes observed in traps were correlated with centers of abundance farther south in the region, while smaller year classes corresponded with more northerly centers of abundance. In both trawls and traps, strong year classes occurred following years with below-average regional water temperatures, and a series of recent, weak year classes correspond with recent higher-than-average water temperatures. It is unclear whether correlations between shifting centers of abundance, year class strength, and regional bottom temperature indicate a range contraction for the southern stock of black sea bass or movement into areas previously inhabited by the northern stock of the species.

Keywords: population trends; marine fish distribution; range shift; population prediction

Key Contribution: Trawl catches cannot predict black sea bass population trends, but large year classes are correlated with cooler bottom temperatures and centers of distribution farthest south.

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1. Introduction

Studies of fish spatial distribution and abundance patterns provide information on critical habitats, the potential for intra- and interspecific interactions, vulnerability to human activities, and appropriate assessment model structures, which may need to include sub-areas within a management region [1–3]. When assessments and projections lack information about spatiotemporal dynamics, biases in the results can occur. Biases, such as lacking data on portions of a population's distribution or knowledge of changes in distributions, can reduce the effectiveness of resultant management actions [1]. For example, if a species shifts its range to stay within some environmental envelope, the stock may look depleted if monitoring or fishing efforts remain in the historical range and do not account for the spatial shift. Alternately, spatiotemporal trends can provide information on potential impending stock collapse as serial local depletions or range contractions can preface declines in the full stock, as seen in Atlantic Cod (*Gadus morhua*) or sardines (*Sardinops* spp.; [4–7]).

The Southeast United States Atlantic (SEUSA), the area extending from Cape Hatteras, North Carolina, to the Florida Keys, is home to numerous exploited reef fish species. The region has undergone dramatic changes in factors that are likely to affect fish populations, including increased human population (with concomitant fishing pressure and land use changes) and declines in coastal upwelling. A concurrent decline in species richness and abundance of offshore hard-bottom-associated fish has been observed [8]. Additional factors, such as increased freshwater input, increased regional water temperature, and frequency or intensity of tropical systems, may add to the stress on the ecosystem in the future [9,10]. Most climate change scenarios predict that species follow preferred or habitable temperature regimes poleward, with many species along the east coast of the United States expected to expand or shift northward (e.g., [11–13]). However, individual species may respond to changing environments in several ways, including range shifts, population reductions due to loss of appropriate habitat (including thermal habitat), or population expansion due to increased habitat availability [12]. Suites of changing factors, such as those at play in the SEUSA, may complicate predictions. For example, red porgy (*Pagrus pagrus*) has experienced a severe population decline but no change in center of abundance or range extent [14]. In contrast, the red snapper (*Lutjanus campechanus*) population and geographic extent have both expanded in the SEUSA, coinciding with severely restricted harvest and increased juvenile recruitment [15,16].

The effect of the physiochemical environment on spatiotemporal dynamics is not static across ontogeny, as habitat use can differ markedly across the lifetime, influenced by physiological tolerances, diet shifts, or other ecological factors [14,17,18]. Because the same species may utilize multiple habitats throughout the lifespan, multiple sampling gears may be required to access all life phases of the population. Juvenile abundance surveys may foreshadow changes to the adult population, providing guidance for stock assessment forecasts or management actions that allow for sustainable fishing practices [14,19–21]. However, care must be taken because not only can environmental change impact life stages differently but erroneous conclusions may be drawn if gears are not properly aligned [22,23].

Black sea bass (*Centropristis striata*) occurs along much of the Atlantic coast of the United States in association with hard-structured habitats [24,25]. The species has historically been managed as two stocks in the northwest Atlantic Ocean, with a genetically defined barrier at Cape Hatteras, North Carolina [26–28]. The northern stock has increased in abundance and landings over the past two decades, with the northern terminus of the range shifting from southern Massachusetts to the Gulf of Maine [11,29,30]. Fish from the northern stock have historically been known to move seasonally with water temperature, spending winters in deep continental shelf water and summers in shallow coastal waters [31,32]. In recent years, black sea bass along the mid-Atlantic coast have been found to overwinter in nearshore waters, presumably due to increased winter water temperatures [33–35]. Southern stock black sea bass have never exhibited seasonal migrations [24,25,36]. While other reef fish species in the region, such as gag (*Mycteroperca microlepis*) are well known for movement from estuary to near coastal waters to offshore reefs as they grow [17,37,38], no evidence exists to suggest that black sea bass follow a similar pattern in the region [39]. Peak spawning for the southern stock is estimated to be near the end of March, with spawning occurring from February through May [40]. Population numbers and geographic extent have varied over the past forty years, with the highest estimated population in the 1980s and the lowest at present [40]. A recent climate change vulnerability model indicates that the species has a high probability of future distribution change [9]. As such, several questions remained open for black sea bass populations in the region, including whether an estimate of juvenile abundance could be generated to augment the existing adult annual estimates, whether geographic distribution is linked to population abundance, and whether water temperature or other environmental parameter changes might be associated with population reduction.

Two fishery-independent surveys, a trawl survey and a trap survey, have occurred along the continental shelf of the SEUSA for over three decades and regularly encounter black sea bass. The Southeast Area Monitoring and Assessment Program–South Atlantic Coastal Trawl Survey (CTS) uses a large falcon trawl net to sample fish and mobile invertebrates in coastal soft-bottom and flat pavement habitats from Cape Hatteras, North Carolina, to Cape Canaveral, Florida. This survey's depths range from 4.6 to 9.1 m, and sampling generally occurs within five miles of the coast. The trawl mesh size of 41.3 mm ensures the retention of most benthic-associated mobile fauna larger than approximately four centimeters [41]. The Southeast Reef Fish Survey (SERFS) uses chevron traps to sample reef habitats throughout the SEUSA at depths of 15 to 115 m [42,43]. Hard-bottom habitats in the region range from flat pavement to rock ledges with attached invertebrates or algae [44]. The catch typically consists of a subset of reef-associated fish species, including black sea bass [45,46]. Chevron trap mesh size effectively excludes fish smaller than approximately 15 cm. Since 2005, the geographic range of this survey has spanned from Cape Hatteras, North Carolina, to Cape Canaveral, Florida. In 2010, two additional funding partners were included, using identical gear to the historical survey, with the result being an intensification of sampling effort throughout the geographic range. Estimates of abundance for several species, including black sea bass, have been investigated for sampling intensity artifacts, with none being found [47,48]. Data produced by each survey (CTS and SERFS) have been used to calculate fishery-independent indices of abundance for both state and federal fisheries stock assessments (e.g., [16,40,49]).

The current study uses the long-term monitoring data produced by the two fishery-independent surveys (CTS and SERFS) to estimate abundance and spatial distribution for individual black sea bass year classes in the SEUSA over a period of twenty years, examining fish spawned in 2003 through 2022. We address several distinct objectives related to the estimation of the black sea bass population and distribution in the region. First, we estimate the size and geographic characteristics (extent and location) of individual black sea bass year classes using both trawls (age 0 fish) and traps (age 2 fish). Second, we examine the trawl estimate as a possible predictor of fishable biomass in subsequent years. Third, we assess the possibility that environmental change (through increases in regional bottom temperature) is correlated with changes in year class size, distribution, or range extent. By defining year class spatial dynamics, we contribute to the broader ecological questions surrounding black sea bass response to climate change and contribute to the ongoing transition to ecosystem-based fisheries management in the SEUSA region.

2. Materials and Methods

Here we describe both the trawl and trap surveys, including environmental covariate data collection, year class assignment from both surveys, and data analysis methods.

2.1. Trawl Field Collection

The CTS (hereafter trawl) used 22.9 m mongoose-style falcon trawl nets without turtle excluder devices and a cod end mesh size of 41.3 mm on soft-bottom or flat pavement in nearshore coastal waters (4.6–9.1 m depths; Figure 1). Trawls were towed for no more than 20 min to minimize sea turtle interactions. The full spatial range of the survey (Cape Hatteras, North Carolina, to Cape Canaveral, Florida) was targeted in each of three seasons:

spring (April and May), summer (July and August), and fall (late September to November) each year using a stratified random sampling design [41]. Briefly, the trawl survey is stratified by latitude, with station selection occurring annually from a pool of trawlable stations. The number of stations selected per stratum is determined by the variability in overall catch abundance within each stratum (higher variability = more stations selected). Through the end of 2019, the contents of two concurrently towed nets were processed. No sampling occurred from the beginning of 2020 until June 2021 due to the COVID-19 pandemic. Beginning in July 2021, only the port side net was processed, while the starboard was towed open with no catch retention. The total area swept by concurrently sampled nets (i.e., two nets from 2003 to 2019 and one net from 2021 to 2022) was calculated to represent the sampling effort. Preliminary analysis showed no ill-effects of this change in procedure on catch metrics. Upon retrieval, all black sea bass were enumerated, and the maximum total length (TL) was recorded in cm. Over 95% of black sea bass caught in trawls were between 4 and 15 cm TL.

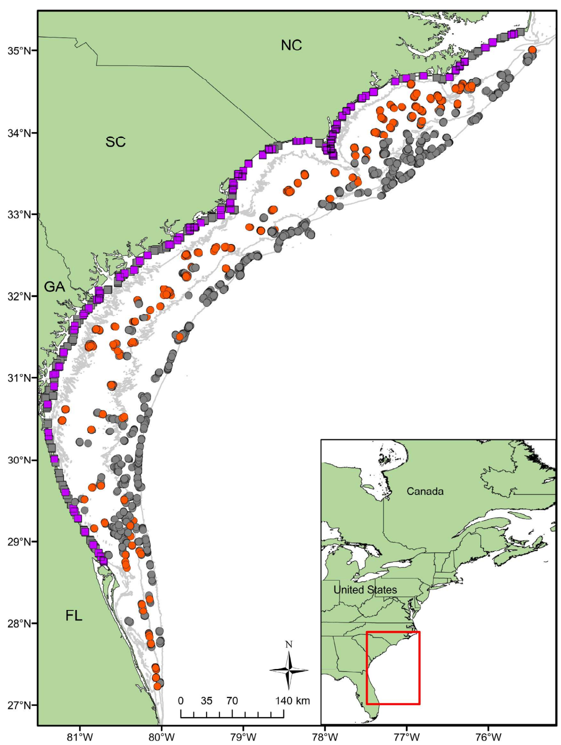

Figure 1. Sampling locations for all trap and trawl deployments included in the analyses. The red rectangle in the inset panel represents the sampling region. Purple squares represent trawls that caught black sea bass. Orange circles represent traps that caught black sea bass. Gray symbols represent deployments with no black sea bass in each respective survey. Depth contours are 20 m, 50 m, and 100 m.

2.2. Trap Field Collection

The SERFS program uses chevron traps (hereafter trap) with 35 × 35 mm square mesh on hard-bottom habitats at depths ranging from 15 to 115 m (Figure 1) throughout the SEUSA (Cape Hatteras, North Carolina, to St. Lucie Inlet, Florida, USA). All trap sampling stations were randomly selected before the beginning of the sampling season, which occurred from April to October each year. Station selection was not pre-stratified, but sampled stations were no closer than 200 m from their nearest sampled neighbor to promote independence. Sample collection was conducted in several independent, short (5–10 day) trips, the locations of which were dictated by weather conditions in various sub-regions of the sampling zone. Sampling was not systematic by geography, but chief scientists ensured regional coverage each year. Samples were relatively evenly distributed across the latitudinal gradient over the duration of each sampling season. No sampling occurred in 2020 due to the COVID-19 pandemic. Each trap was soaked for approximately 90 min, with total soak time used to calculate effort [42,47]. Upon retrieval, all black sea bass were enumerated and (TL) was recorded in cm. Over 95% of black sea bass caught in traps were larger than 15 cm TL, and black sea bass are fully recruited to the gear by age 2.

2.3. Environmental Covariate Data Collection

Location (latitude, longitude), depth (m), and time were recorded at the beginning of each trap and trawl deployment. The trap end time was recorded to determine soak time, and the trawl end location was recorded to calculate the total area swept (i.e., effort). Oceanographic data were collected via a Conductivity, Temperature, and Depth instrument (CTD) associated with each sampling event. SeaBird SBE 19, 19Plus, and 25Plus CTDs were used at various points within each time series, and each unit was calibrated bi-annually. All CTDs measured depth (m) and temperature (°C). Temperature (both trap and trawl) and salinity (psu; trawl) near the bottom during each deployment were isolated from each CTD cast.

2.4. Data Analysis

Total length, to the nearest cm, was available for all trap-caught black sea bass, while age data were available for approximately 50% of these fish. We used a multi-step process to assign likely ages to the unaged portion of the trap catch. First, we created size-at-age distributions using over 33,000 fish that had both nearest mm TL measurements and associated ages. Regional black sea bass aging procedures, including month of increment formation and criteria for advancing age beyond increment count, can be found in Bubley et al. [50]. A likely age was assigned to each fish within each 1 cm size class based on the proportion of aged fish in each length bin at that age. In this way, fish were not unilaterally assigned to a single age within each length bin. This was determined to be the best method of age estimation because black sea bass size at age is highly variable beyond age 1 [40]. Once age was assigned, each fish was assigned a birth year based on the year of capture and likely age at capture. We then selected only data on age 2 fish from each trap for analysis. We analyzed trap data collected from 2005 to 2024, beginning the trap time series with the 2003 year class.

Length was used to assign year class for trawl-caught black sea bass because these fish were rarely aged. Using the von Bertalanffy growth equation for southern stock black sea bass, we treated all fish <15 cm TL as age 0 and excluded all fish above that size from trawl analysis (<5% of total catch) [40]. The trawl dataset consisted of age 0 individuals, and we used trawl catch data from 2003 to 2022, where the year of capture was also the birth year.

Separate vector-autoregressive spatiotemporal (hereafter VAST; R Package: VAST) models were used to standardize black sea bass trap or trawl year class abundance over time and to determine annual spatial distributions of each year class in each survey [51,52]. More specifically, the VAST models were used to estimate annual geographic centers of abundance and the effective area occupied (total square km necessary to contain the estimated abundance) for each life stage over the time series. The VAST model correlates the abundance in a sample to covariates for that sample, as well as other factors included in the model. By decomposing the time series into two components, the probability of encounter and the expected catch rate, VAST effectively creates a delta model that generally performs well with zero-inflated datasets, such as multi-species fisheries surveys [53]. We included soak time (for traps) or area swept (for trawls) as offsets, year class as a fixed factor, and day of year (DOY), latitude (°N), longitude (°W), and depth (m) as continuous variables in both VAST models. The binomial error distribution was used for the presence/absence portion of the model, and the Poisson error distribution was used for the abundance model based on Akaike's Information Criterion (AIC) during preliminary model fitting [54]. We conducted the VAST model with up to 200 knots for both trawls and traps, spatial and spatiotemporal autocorrelation as random effects, and anisotropy turned on. In addition, we included a bias correction in the model to account for any change in the spatial footprint of each survey over time. Each VAST model produced four annual output parameters to describe the population and its spatial characteristics. The index of year class abundance estimates the total number of fish expected within each year class when covariates (including sampling density) are taken into consideration. The effective area occupied estimates the area needed to contain each year class given its average density. Northings and eastings represent the cardinal directions for the centroid of the population's distribution [52].

We were interested in determining how warming in the region might be related to black sea bass annual abundance and distribution [55]. We updated a time series of standardized, annual bottom temperatures used by Craig et al. [8] to demonstrate regional warming through 2022. Standardization was completed through the generalized additive model (GAM) as follows:

$$\text{Bottom Temperature} \sim \text{Year} + s\,(\text{depth}) + s\,(\text{DOY}) + s\,(\text{Longitude, Latitude}) \qquad (1)$$

The year was treated as a factor while depth, DOY, and spatial position were continuous covariates, and a lognormal error distribution was used based on AIC [54].

To quantify relationships among year classes and regional conditions, we conducted a series of correlation tests. We calculated Spearman rank correlations among the VAST annual parameters within each survey. We also tested the correlation between equivalent VAST metrics for each survey, examining whether juvenile abundance may serve as a realistic preview of the abundance of that same year class captured in subsequent years. We correlated the regional annual bottom temperature with year class strength from each survey to test if the overall water temperature was related to observed year class strength as captured by each survey. We used the following scale for interpreting correlation coefficients: 0.80–1, very high correlation; 0.60–0.79, high correlation; 0.40–0.59, moderate correlation; 0.20–0.39, low correlation; and 0.0–0.19, negligible correlation, in alignment with commonly accepted statistical practice [55]. All p-values less than 0.05 were considered to be significant correlations. All analyses were conducted in R version 4.3.0 [56].

3. Results

A total of 1019 age 0 black sea bass were captured in 5597 trawl deployments representing the year classes 2003 through 2022. Proportion positive (i.e., the number of gear deployments containing black sea bass out of all deployments) for trawls ranged from less than 0.01 to 0.13 per year, and the mean numbers of fish per trawl ranged from 0.01 to 0.43 (Table 1). A total of 40,616 age 2 black sea bass were collected in 22,094 trap deployments, representing the year classes 2003 through 2022. Proportion positive ranged from 0.09 to 0.42 per year, and mean abundance ranged from 0.35 to 4.83 per trap hour (Table 1).

Trawl and trap deployments were relatively evenly distributed throughout the region. Black sea bass were collected along the entire latitudinal extent of both surveys, and the trap survey included many stations too deep for black sea bass to be captured (Figure 1).

Table 1. Black sea bass catch summaries by year class. Trawl-caught fish are age-0. Trap-caught fish are age 2. Proportion positive is the proportion of total deployments that captured at least one black sea bass. Mean per deployment is calculated out of total deployments each year.

	Traps		**Trawls**	
Year Class	Proportion Positive	Mean per Trap	Proportion Positive	Mean per Trawl
2003	0.33	4.83	0.04	0.15
2004	0.35	4.11	0.08	0.31
2005	0.31	3.05	0.07	0.24
2006	0.32	3.03	0.05	0.32
2007	0.29	2.71	0.01	0.02
2008	0.34	3.20	0.00	0.01
2009	0.42	4.86	0.03	0.07
2010	0.40	3.64	0.04	0.05
2011	0.39	3.84	0.13	0.20
2012	0.35	2.76	0.11	0.43
2013	0.30	2.33	0.06	0.11
2014	0.24	1.47	0.05	0.09
2015	0.21	1.24	0.10	0.41
2016	0.18	1.16	0.06	0.21
2017	0.15	0.89	0.07	0.29
2018	-	-	0.04	0.15
2019	0.11	0.50	0.07	0.16
2020	0.11	0.51	-	-
2021	0.07	0.38	0.05	0.13
2022	0.09	0.35	0.02	0.03

The GAM represents the standardized regional bottom temperature with all included factors and covariates, resulting in an adjusted R^2 = 0.564 (Table 2). The year was a significant factor. The depth, day of year, and location were all significant in predicting the bottom temperature for the region. The standardized bottom temperature for the region at the end of the time series was close to 1 °C higher than the beginning of the time series. This end temperature was over 2 °C above the lowest values, recorded in 2004 and 2005 (Figure 2A). The trawl index of abundance was variable across the time series and displayed little trend over time (Figure 2B). The index of year class abundance from traps showed a 150% increase between 2003 and 2009 with a subsequent decline to record low levels of age-2 fish since at least 2016. For trawls, effective area occupied was lowest in 2015 and highest in 2013 (Figure 2C), while effective area occupied for traps showed little variability over the timeseries. Geographic center of abundance was closest to the equator for traps in 2008 and farthest north in 2013, while very little trend was observed in trawls (Figure 2D).

Annual maps of predicted abundance illustrated relatively constant year class abundances in the northern half of the survey range for both surveys, with highly variable abundances to the south (Figures 3 and 4).

Table 2. Parameter estimates for generalized regional bottom temperature model. Year is treated as a factor, and smoothed parameters use no more than 4 degrees of freedom.

Parametric Coefficients				
Factor	**Estimate**	**SE**	**t**	***p*-Value**
Intercept	−157.84	9.58	−16.47	<0.001
Year	0.09	0.005	18.88	<0.001
Smoothed Terms				
Term	**edf**	**Ref.df**	**F**	***p*-Value**
s (Depth)	2.99	3.00	789.2	<0.001
s (DOY)	2.99	3.00	3260.9	<0.001
S (Lon/Lat)	2.97	2.99	264.1	<0.001

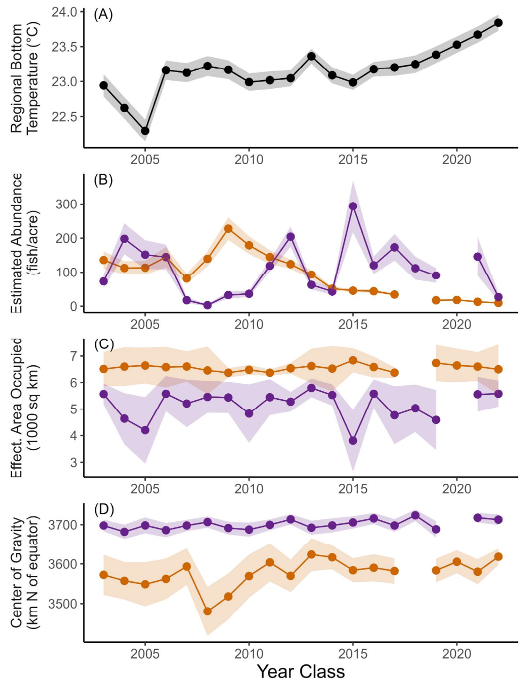

Figure 2. Average values (dots) and standard error (shading) of annual estimates across the study period. (**A**) Region-wide modeled bottom temperature. (**B**) VAST-produced index of year class abundance for trawls (purple) and traps (orange). (**C**) VAST-produced effective area occupied for each year class from trawls (purple) and traps (orange). (**D**) Northward geographic center of abundance for each year class from traps trawls (purple) and traps (orange).

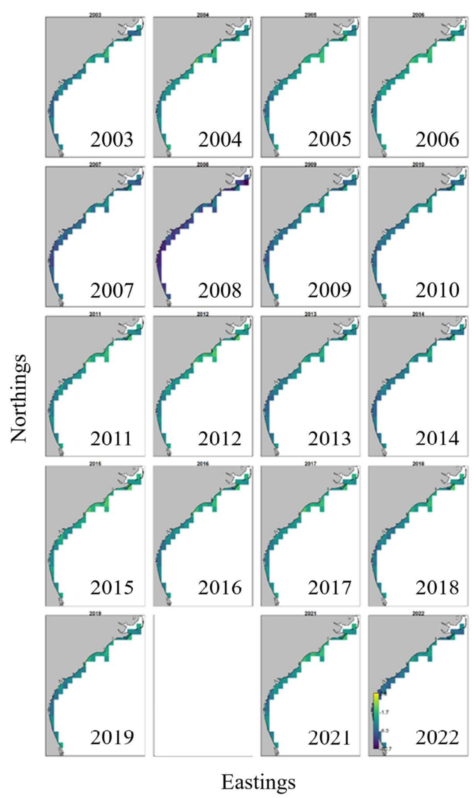

Figure 3. Predicted density of age 0 black sea bass as modeled from trawl collections for year classes 2003 through 2022. Areas with colors represent the spatial domain of the survey and relative abundance (fish/acre).

From trawls, annual northing and easting values were very highly correlated to one another (ϱ = 0.87, p < 0.001); easting was moderately correlated with effective area (ϱ = 0.46, p = 0.05), but no other VAST parameters were more than weakly correlated with one another (Table 3). From traps, year class abundance was negatively correlated with northing (ϱ = −0.56, p = 0.01), while northing and easting were positively correlated with one another (ϱ = 0.71, p < 0.001; Table 3). Correlations between the corresponding parameters from trawls and traps were never above low (ϱ between −0.03 and 0.40; Table 4). The bottom temperature showed a moderate positive correlation with effective area occupied and eastings for trawls and a moderate negative correlation with year class and effective area occupied in traps (Table 5). Larger year classes were associated with geographic centers of abundance farther south for traps, but for trawls, geographic centers did not appear to be associated with abundance (Figure 5).

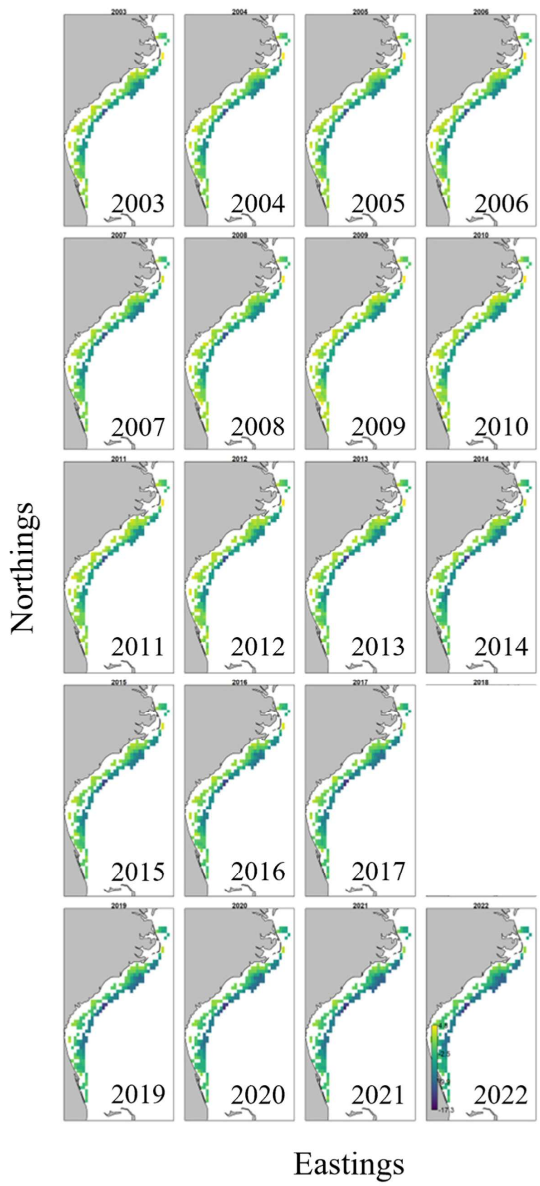

Figure 4. Predicted density of age 2 black sea bass as modeled from trap collections for year classes 2003 through 2022. Areas with colors represent the spatial domain of the survey and relative abundance (fish/acre).

Table 3. Correlation metrics for fish from the 2003 to 2022 year classes. Rho values are based on Spearman's rank correlation. The upper quadrant is the trawl-collected young of year individuals and the lower quadrant is the trap-collected two-year-old fish. Bold values represent $p < 0.05$.

	Year class Abundance	Effective Area	Easting	Northing
Year class Abundance		−0.39 $p = 0.10$	−0.09 $p = 0.72$	0.12 $p = 0.62$
Effective Area	0.23 $p = 0.22$		**0.46** **$p = 0.05$**	0.15 $p = 0.55$
Easting	−0.15 $p = 0.53$	−0.11 $p = 0.64$		**0.87** **$p < 0.001$**
Northing	**−0.56** **$p = 0.01$**	−0.14 $p = 0.55$	**0.71** **$p < 0.001$**	

Table 4. Correlations between annual indices and spatial distribution metrics of trawl-caught age 0 and trap-caught age 2 black sea bass from the 2003 to 2022 year classes. Rho values are based on Spearman's rank correlation.

	Trap	
Trawl	Year class Abundance −0.17, $p = 0.48$	Effective Area −0.03, $p = 0.88$
	Northing 0.24, $p = 0.32$	Easting 0.40, $p = 0.11$

Table 5. Correlations between annual bottom temperature and the annual spatial distribution metrics of trap-caught age 2 and trawl-caught age 0 from the 2003 through 2022 year classes.

	Bottom Temperature: Trap	Bottom Temperature: Trawl
Year class Abundance	**−0.55** **$p = 0.01$**	−0.36 $p = 0.13$
Effective Area	**−0.53** **$p = 0.02$**	0.43 $p = 0.06$
Northings	0.33 $p = 0.19$	0.33 $p = 0.17$
Eastings	0.10 $p = 0.69$	0.41 $p = 0.08$

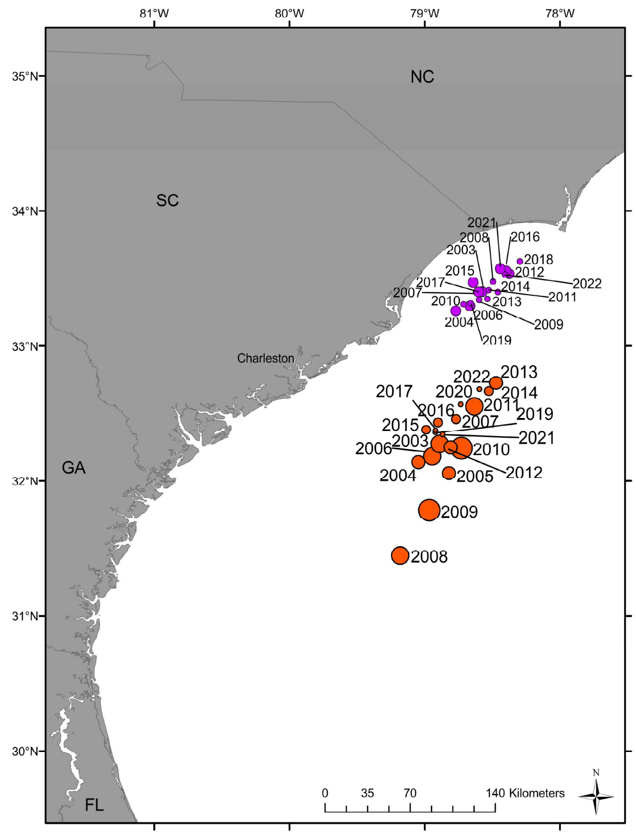

Figure 5. Geographic center of abundance and relative abundance by year class for trawls (purple) and traps (orange). The sizes of the dots are proportional to the estimated relative abundance.

4. Discussion

In the early 2010s, commercial and recreational fishery catches of southern stock black sea bass rebounded from then historically low levels following strict fishery management measures. At the time, this strong population rebound was interpreted as the direct result of newly imposed, stricter regulations. However, the subsequent population decline (beginning in 2013), while identical regulations remained in place, suggested that harvest was not the only driver of black sea bass abundance in the region [40]. Because the indices of abundance used as stock assessment inputs for black sea bass include fish only after they have been recruited to the fishery, predicting trends in the regional population has been difficult. Additionally, concerns have been raised about the expansion of the northern stock into new areas and if similar northern expansion was occurring within the southern stock. The goal of the current study was to investigate black sea bass year class variability and geographical extent in the SEUSA using data assembled from both trap and trawl gears. By comparing trends, we aimed to elucidate predictors for the southern stock black sea bass population.

A chevron trap index of black sea bass relative abundance, produced by SERFS, has served as a major input to stock assessments in the SEUSA for many years and tracks well with other fishery-independent and fishery-dependent data in the region [40]. It is clear that the trap survey encompasses the deepest depth of the species, captures the full complement of adult sizes, and reflects true abundance [43]. Black sea bass are known to be found primarily in structured, hard-bottom environments, such as shell accumulations, artificial reefs, and rocky reefs [26,57], which were targets of the trap survey [39]. The current study increases the scientific utility of the chevron trap index by including a geographic component and assigning all fish to a year class, steps that are not generally taken for individual stock assessment inputs in the region. The negligible correlation between relative abundance and effective area suggests that population density increases with increasing population size, while the high negative correlation between relative abundance and both northings and eastings indicates that the center of abundance of the species shifts toward Cape Canaveral, Florida, in high abundance years and toward Cape Hatteras, North Carolina, in low abundance years. Very high correlations between northings and eastings reflect the shape of the coast and hard-bottom availability for the region.

The mesh size of the trap selects against juvenile black sea bass by allowing the escapement of virtually all age 0 fish 39,42]. In contrast, the trawl survey captures black sea bass during their first year of life. If a species is captured during both juvenile and adult life stages, correlations can test whether juvenile indices are realistic predictors of adult abundance. While trawls sampled black sea bass sufficiently to produce an estimate of abundance with reasonable error, the VAST model of trawl-caught juveniles is neither strongly nor positively correlated to trap metrics. If trawl-caught year classes had exhibited a high correlation with trap-caught year classes, the abundance estimates produced by the trawl survey could be used to predict future fish availability within the fishery. However, the trawl survey currently appears inappropriate for estimating black sea bass recruitment to the fishery, particularly for the purposes of making management decisions.

Differences between the two abundance trends suggest that the traps and trawls are sampling geographically separate areas of the black sea bass population or that an environmental bottleneck is preventing trawl-caught juveniles from achieving the adult stage. Black sea bass in the SEUSA have not been shown to undergo seasonal migrations at any life stage [24,58]. A tagging study in the northern stock showed no movement of age 0 fish, and an isotope study of the Gulf of Mexico showed no offshore movement over the first year [59,60]. While it is true that younger life stages may be more sensitive to changes in environmental conditions [61–64], the trawl survey focused primarily on soft-bottom habitats that are less likely to support black sea bass compared to the rugose habitats sampled by traps [57,58], making migration or mortality in the second year of life an unlikely driver of the disconnect between the surveys. The geographic region in which trawls routinely encountered juvenile black sea bass in the waters of northern South Carolina consists of rock pavement with attached biota, such as sea grass and sponges, differing from most soft-bottom trawl stations (P. Webster, pers. comm.). While data from less-ideal habitat types can be valuable for combatting hyperstability in population estimates, a survey must also include core areas as a means of comparison [65,66]. The relatively consistent number of juveniles collected in this specific northern sub-area could represent a spill-over of black sea bass into a marginal rock pavement habitat from more preferred habitats [26,57,67]. Because a bottom trawl survey must have sufficient area to tow without the gear being damaged by snags, trawls may not be the most appropriate sampling gear for the species. We conclude that the trap survey is adequate for tracking the population but reflects only the sizes of fish available to recreational and commercial fisheries, while trawl abundance trends may not represent the true ecological recruitment for the species, likely due to habitat and depth limitations. A novel sampling strategy using a smaller mesh trap may fill this missing niche. Additional focused research, such as a juvenile tagging study within the stock, may elucidate ontogenetic movement for the species.

Avid anglers in the region have noted that the decline of black sea bass catch has coincided with increasing red snapper (*Lutjanus campechanus*) catches [16,40]. While no evidence has been observed for direct predation, competition between the species, for both food and space, cannot be ruled out [68]. Researchers have noted that spawning periods for the two species occur at different times of the year, with black sea bass reproducing from February to May and red snapper reproducing primarily during July and August in the region [50,69]. These differences in reproductive timing and seeming success may suggest disparate environmental needs on the part of spawning adults or larvae.

Consistent with the findings of Craig et al. [8], we observed an increasing trend in regional bottom temperature throughout the study period. Two years of low bottom temperatures, coinciding with a documented upwelling event [70], occurred in the years preceding the largest trap year classes. A weak positive correlation may represent improved physiological performance, increased food availability with upwelled nutrients, or random chance. To date, no studies have examined southern stock black sea bass temperature tolerance or preferences. However, northern stock black sea bass have displayed improved physiological performance when tested at water temperatures near the lower end of those observed in our study and increased lipid storage with higher food availability [33,71,72]. Individuals from the northern stock have demonstrated reduced metabolic performance under temperatures routinely encountered in coastal waters of the SEUSA [71,73]. Because no sampling occurred in the region during winter months, the current study did not include bottom temperatures for times that would coincide with peak spawning or the primary larval period in the region [74]. The inclusion of winter temperatures or other oceanographic parameters may improve associations between the regional environment and the success of individual year classes.

A recent climate vulnerability assessment has found that while southern stock black sea bass are moderately vulnerable to environmental change in the region, climate change exposure is very high, with particular concern regarding water temperature and changes to salinity regimes, resulting in a high risk of distribution change [9]. Our study suggests a pattern of a spatial shift with population size in the southern stock, with a southward expansion coinciding with high abundance year classes. Data from both trap and trawl analyses suggest that the center of abundance moves northward and the total population decreases as the bottom temperature increases. Genetic analysis has shown that while the northern and southern stocks are distinct north and south of Cape Hatteras, mixing does occur across this boundary, with fish captured in North Carolina being more genetically similar to the northern stock than those encountered farther south [28,75]. Over the past several years, a range shift in the northern stock black sea bass population has been observed, with documentation of a northward expansion into the Gulf of Maine and an overall increase in the stock [11,34]. The northward expansion of the northern stock is likely driven by increases in water temperature that have expanded potential thermal habitats [67]. In addition, black sea bass in the mid-Atlantic region have ceased their seasonal migration, remaining in shallower habitats throughout the year as winter temperatures have warmed [34,72,76]. Research is needed regarding whether the southern stock of black sea bass is moving northward toward the mid-Atlantic region or whether there is a geographic barrier at Cape Hatteras, which may serve to limit the total population within the southern stock. If the southern stock is sensitive to temperature and warming continues in the region, we expect a continuing trend of low abundance year classes, concentrated in the northern portion of the region. If the southern stock is near its physiological limit and oceanographic condition trends continue, an extirpation of the southern stock from the southern part of the range is increasingly possible.

Range shifts and changes in spatial distributions of exploited stocks complicate both management and industries that rely on the stock for their fishing portfolios. The current study indicates that there is cause for concern regarding changes in the distribution of black sea bass in the SEUSA. Trap survey data can produce an index of year class strength but reflect only fish that have already been recruited to the fishery. Although the trawl survey may be used to create an index of ecological recruitment, the survey does not appear to adequately represent stock recruitment due to the paucity of sampling in hard-bottom habitats. Both trap and trawl surveys indicate a core region of black sea bass persistence near the northern extent of the survey range, with changes to the population extent occurring in the southern half of the range. It remains largely unknown if the observed geographic change is driven by temperature, differential recruitment, or habitat suitability. Typical stock assessments in the SEUSA do not have a mechanism to incorporate changes in the location of a stock or a shift in the potential productivity of the stock. Within the SEUSA region, allocations to fishery sectors are rarely separated by spatial sub-area. Such considerations are becoming more commonly acknowledged, and novel approaches to stock assessment are being considered [15,77]. If the average bottom temperature in the region continues to increase, it is possible that the entire SEUSA will become less hospitable to the production of black sea bass in specific sub-regions (i.e., the southern portion). Future work should focus on the most appropriate sampling methods for juvenile black sea bass, including novel gears such as small-mesh traps or stereo video cameras, environmental impacts on the southern stock, and potential connections between the southern and northern stocks.

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Abbreviations

The following abbreviations are used in this manuscript:

SEUSA	Southeast United States Atlantic
SEAMAP-SA	Southeast Area Monitoring and Assessment Program–South Atlantic
SERFS	Southeast Reef Fish Survey
CTD	Conductivity, Temperature, and Depth instrument

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