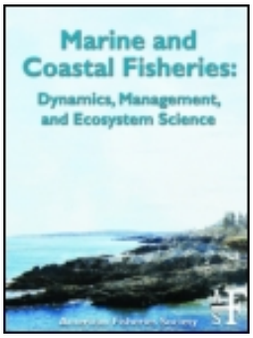

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ARTICLE

Spatial and Temporal Patterns of Black Sea Bass Sizes and Catches in the Southeastern United States Inferred from Spatially Explicit Nonlinear Models

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Abstract
Temporal and spatial variability in abundance often results from the effects of environmental and landscape variables interacting over multiple spatial scales, and understanding the complex interplay among these variables is key to elucidating the drivers of a species' population dynamics. We used a spatially explicit, variable-coefficient, generalized additive modeling approach with 24 years of fishery-independent trap data (N = 11,726 samples) to elucidate the spatiotemporal dynamics of size and size-specific CPUE of Black Sea Bass *Centropristis striata* along the southeastern Atlantic coast of the United States. Black Sea Bass catch exhibited complex spatial and temporal dynamics that were influenced by environmental, landscape, and sampling effects. Black Sea Bass were more commonly caught inshore than offshore, but were significantly smaller inshore and southward and larger offshore and northward in the study area. Moreover, the spatial distribution of Black Sea Bass changed as abundance varied within and among sampling seasons. Standardized mean length of Black Sea Bass also increased by more than 20% over the study period, from 230 mm TL in the early 1990s to 280 mm TL after 2010. These results elucidate the spatial and temporal dynamics of Black Sea Bass, inform population structure and indices of abundance, and provide an analytical framework that can be easily adapted to other species and systems.

All species exhibit spatial variability in abundance across a landscape, and elucidating the spatial patterns in size and abundance is key to understanding community dynamics, variation in life history traits, and temporal changes in abundance (Dunning et al. 1992; Jackson et al. 2001; Ciannelli et al. 2013). Spatial variability in abundance can result from larval or juvenile dispersal patterns, habitat patchiness, environmental variability, landscape features, or biotic interactions such as predation or competition (Levin 1992; Brown et al. 1995). While the focus of most historical studies has been on temporal variability in abundance or density, researchers now recognize that understanding spatial variability and dynamics is key to describing a species' ecology and explaining temporal abundance patterns

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(Cadrin and Secor 2009; Bartolino et al. 2011; Ciannelli et al. 2012).

Recent analytical advances have helped us understand the complex interplay between environmental and landscape influences on the spatial dynamics of organisms (Lehmann et al. 2002; Bacheler et al. 2009). For instance, Ciannelli et al. (2012) used a spatially explicit nonlinear regression modeling approach to show that at low levels of abundance Arrowtooth Flounder *Atheresthes stomias* distribution was influenced solely by water temperature, but their distribution expanded into new habitats in a nonadditive fashion with increasing water temperature when abundance was high. Bacheler et al. (2012) used a similar modeling approach to document density-dependent estuarine habitat use of Red Drum *Sciaenops ocellatus* after removing variability in catches due to various environmental and landscape effects.

Another fish species for which spatially explicit modeling would be useful to explicate temporal and spatial dynamics is the Black Sea Bass *Centropristis striata*, a protogynous serranid that occurs in nearshore waters of the U.S. Atlantic Ocean and Gulf of Mexico (Lavenda 1949; Wenner et al. 1986; Hood et al. 1994). Two Black Sea Bass stocks have been identified along the U.S. Atlantic coast, separated at Cape Hatteras, North Carolina (Roy et al. 2012; McCartney et al. 2013). The northern stock is thought to migrate offshore and southward in colder winter months, then back inshore and northward when water warms in spring and summer (Musick and Mercer 1977; Moser and Shepherd 2009; Fabrizio et al. 2013). South of Cape Hatteras, however, Black Sea Bass movement rates appear to be lower, perhaps lacking seasonal migrations altogether.

Recreational and commercial fishers harvest Black Sea Bass throughout their range primarily using pots and hook and line (Coleman et al. 2000; McGovern et al. 2002). Along the southeastern U.S. Atlantic Coast (SEUS), size limits have increased from 203 mm TL in the 1980s and 1990s to 279 mm TL (commercial sector) or 330 mm TL (recreational sector) by 2015. While commercial harvest of Black Sea Bass is substantially greater in North Carolina than in states to its south, recreational harvest is similar among states in the SEUS, and historically, fishing by both sectors generally occurred year-round except when quotas had been met. However, there have been management changes to the fishing year of both the commercial and recreational sectors, gear restrictions implemented on the timing and use of certain gears of the Black Sea Bass fishery, and in-season closures of one or both sectors in recent years. These actions, coupled with regional differences in dominant weather patterns in the SEUS limiting access to Black Sea Bass habitat, have led to changes in the timing of peak landings in the calendar year across years and across subregions of the SEUS within a year.

We used long-term, spatially extensive monitoring data in a spatially explicit regression-modeling framework to determine the environmental, landscape, and temporal predictors of Black Sea Bass size and CPUE along the SEUS. Black Sea Bass is an ideal species with which to use a spatially explicit modeling approach because they can be sampled efficiently (Bacheler et al. 2013c), catches generally reflect abundance (Bacheler et al. 2013b), and their spatial and temporal dynamics in the SEUS are poorly understood (Sedberry et al. 1998). There were two specific objectives of our work. Our first objective was to quantify the spatial and temporal patterns of Black Sea Bass size and size-specific CPUE throughout the SEUS after correcting for the influences of environmental variation and landscape features. Our second objective was to determine whether annual or seasonal variation in Black Sea Bass sizes or size-specific CPUE was spatially variable; in other words, whether temporal changes in Black Sea Bass sizes or catches occur more strongly in some locations than in others. Our aim was to improve our understanding of the seasonal movement patterns and temporal and spatial dynamics of Black Sea Bass in the SEUS to benefit their stock assessment by elucidating their population structure and improving annual indices of abundance. We also intended to provide an analytical framework that can be easily adapted to other species and systems.

METHODS

Study area.—We used long-term, fishery-independent, chevron-trap data to elucidate the spatial and temporal patterns of Black Sea Bass lengths and catches in the SEUS between North Carolina and Florida (Figure 1). In 1990, the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program began using chevron traps to index reef fish abundance in the SEUS. Since 2009, MARMAP funding has been supplemented by the Southeast Area Monitoring and Assessment Program–South Atlantic to allow for an expansion of coverage of the survey into historically undersampled areas. In 2010, the Southeast Fishery-Independent Survey began chevron-trap sampling cooperatively and identically in the region to increase sample sizes. Collectively these programs are now known as the Southeast Reef Fish Survey (SERFS); we used SERFS data from 1990 through 2013 in our analyses.

Sampling by SERFS targets hard substrates in continental shelf and shelf-break waters in the SEUS, the preferred habitat of Black Sea Bass (Powles and Barans 1980; Sedberry and Van Dolah 1984). The continental shelf and shelf-break in the SEUS are dominated by sand and mud substrates, but Black Sea Bass generally associate with the scattered patches of hard, rocky substrates ("hard bottom") that occur in the region (Kendall et al. 2008; Fautin et al. 2010). Hard-bottom habitats sampled in our study ranged in complexity from flat limestone pavement, sometimes covered with a sand or gravel veneer, to high-relief rocky ledges (Schobernd and Sedberry 2009; Glasgow 2010). Sampling in our study occurred between Cape Hatteras, North Carolina, and St. Lucie Inlet, Florida (Figure 1).

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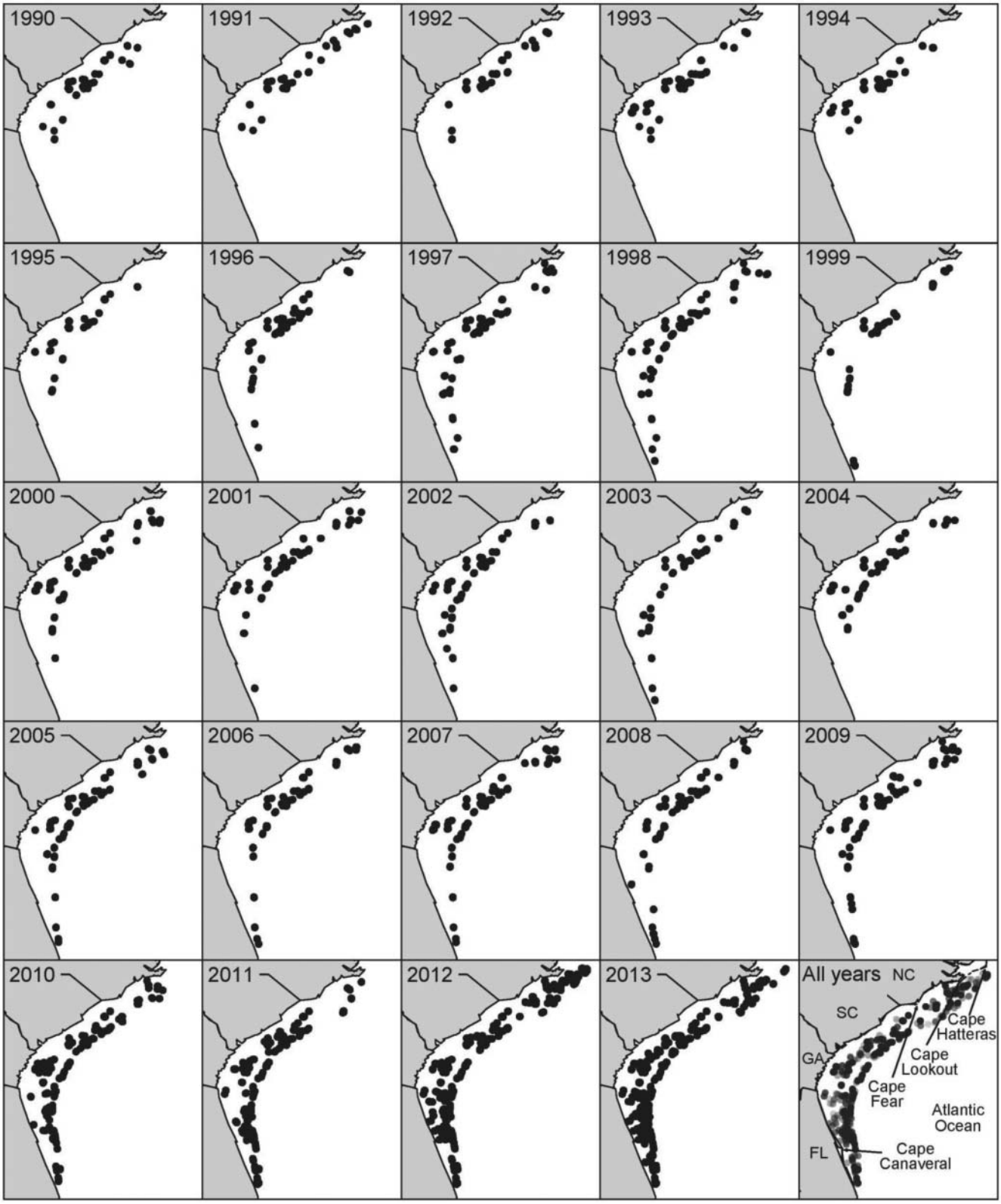

FIGURE 1. Spatial distribution of chevron-trap sampling for Black Sea Bass by the Southeast Reef Fish Survey between North Carolina and Florida, 1990–2013. Each point represents a single chevron-trap deployment included in the analysis. Note that symbols often overlap. In the bottom right panel, all sampling from 1990 to 2013 is shown and the darker the symbol, the greater the overlap among points.

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Sampling design and gear.—Hard-bottom sampling stations were selected for sampling in one of three ways. First, most sites were randomly selected from the SERFS sampling frame that consisted of approximately 1,000 sampling stations in the early 1990s to more than 3,000 sampling stations in the 2010s, all located on hard-bottom habitat. Second, some stations in the sampling frame were sampled opportunistically even though they were not randomly selected for sampling in a given year. Third, new hard-bottom stations were added during the study period through the use of information from fishers, charts, and historical surveys. These new locations were investigated using the vessel's echo sounder or drop cameras and sampled if hard bottom was detected. All sampling for this study occurred during daylight hours between late March and early November and was conducted on the RV *Palmetto* (1990–2013), RV *Savannah* (2010–2013), NOAA Ship *Nancy Foster* (2010), or NOAA Ship *Pisces* (2011–2013) using identical methods.

Chevron fish traps were deployed at each station sampled in our study. Black Sea Bass are caught very effectively in chevron traps (Bacheler et al. 2013c), and catches appear to be strongly and positively related to true abundance at a site (Bacheler et al. 2013b). Chevron traps were constructed from plastic-coated, galvanized, 2-mm-diameter wire (mesh size = 3.4 cm^2) and were shaped like an arrowhead that measured 1.7 × 1.5 × 0.6 m with a total volume of 0.91 m^3 (Collins 1990). Trap-mouth openings were shaped like a teardrop and measured approximately 18 cm wide and 45 cm high. Each trap was baited with 24 menhaden *Brevoortia* spp. Traps were typically deployed in groups of six, and each trap in a set was deployed at least 200 m from all other traps in a given year to provide some measure of independence between traps. A soak time of 90 min was targeted for each trap deployed, and any trap not fishing properly (e.g., dragged due to current, damaged upon retrieval) was excluded from analysis. All Black Sea Bass caught in chevron traps were enumerated and measured for length (mm TL).

Data analysis.—We related mean length or catches of small or large (defined below) Black Sea Bass to various predictor variables using a spatially explicit, variable-coefficient, generalized additive model (Bacheler et al. 2009, 2010; Bartolino et al. 2011). A generalized additive model (GAM) is a nonlinear, nonparametric, regression model that does not require a priori specification of the functional relationship between the response and predictor variables (Venables and Dichmont 2004; Wood 2008). The GAMs extend traditional additive models by allowing for alternative error distributions, just as generalized linear models allow for alternative error distributions of linear models. The addition of variable-coefficient terms can be used to determine specific locations where Black Sea Bass sizes or catches are expected to increase or decrease with changes in any of the predictor variables in the model (Bacheler et al. 2009).

We developed two broad classes of spatially explicit GAMs to understand more about the spatial and temporal patterns of Black Sea Bass in the SEUS. The first model used mean Black Sea Bass TL (mm) in each trap as the response variable for the GAM (hereafter, "length model"). Here, chevron-trap samples were weighted in the model by the total number of Black Sea Bass caught in each trap, so that a mean length based on many fish in a trap was weighted more heavily than a mean length comprising only a single fish in a trap. Chevron-trap samples that failed to catch Black Sea Bass were excluded from this analysis. Mean lengths from the remaining, positive trap catches were log transformed to achieve normality. The second model type used the trap catch of small or large Black Sea Bass as the response variable (hereafter, "catch models"). Small Black Sea Bass were defined as <235 mm TL, and large Black Sea Bass were ≥235 mm TL, roughly the cutoff between age-2 and age-3 Black Sea Bass caught in traps (McGovern et al. 2002); 235 mm TL was also the modal size of Black Sea Bass caught in traps in our study (see Figure 2). While arbitrary, the 235-mm cutoff between small and large Black Sea Bass was chosen because sample sizes of these two groups were sufficient in chevron traps each year. Moreover, large Black Sea Bass have not been observed excluding small Black Sea Bass from entering traps, and asymptotic catch of Black Sea Bass is highly related to local abundance (Bacheler et al. 2013b, 2013c). Catch of small or large Black Sea Bass was fourth-root transformed, which resulted in better model fit than any other types of transformations or error distributions using standard model diagnostics (e.g., Bacheler et al. 2013a). Unlike the length model described above, chevron traps that did not catch any Black Sea Bass were included in the catch models.

We examined the influence of various predictor variables on the mean length or catch of Black Sea Bass. For the length model, six primary variables were considered for inclusion based on our hypotheses and previous knowledge: year (y) was included as a factor variable, and bottom temperature (°C; *temp*), day of the year (*doy*), and spatial position (latitude and longitude; *pos*) were included in the model as smoothed variables. In addition, two variable-coefficient terms were included: an interaction between spatial position and year and an interaction between spatial position and day of the year. The former allows for interaction between the spatial position smoother and year while the latter allows for the local effect of the spatial position smoother to vary seasonally (i.e., within the sampling season). Thus, the base length model ("$\text{Base}_{\text{length}}$") was formulated as:

$$z_{doy,y,pos} = f_1(y) + g_1(doy) + g_2(temp) + g_3(pos) + g_4(pos \cdot y) + g_5(pos \cdot doy) + e_{doy,y,pos},$$

where $z_{doy,y,pos}$ is the log-transformed mean TL of Black Sea Bass on day of the year *doy* in year y at spatial position *pos*, *temp* is bottom temperature, f_1 is a categorical function, $g_{1–5}$ are nonparametric smoothing functions, and $e_{doy,y,pos}$ is the

random error assumed to be normally distributed with a mean of zero and finite variance.

Catch models were coded similarly except five additional variables were included based on the results of Bacheler et al. (2013a). Station type was included as a factor variable and described any potential variation in catch between randomly selected stations and those newly found and sampled for the first time. Depth (m), time of day (Coordinated Universal Time), trap soak time (min), and moon phase were each included as smoothed variables. The base catch models ("$\text{Base}_{\text{catch}}$") were formulated as:

$$x_{doy,y,pos} = a + f_1(y) + f_2(type) + g_1(depth) + g_2(doy) + g_3(tod) + g_4(soak) + g_5(temp) + g_6(moon) + g_7(pos) + g_8(pos \cdot y) + g_9(pos \cdot doy) + e_{doy,y,pos},$$

where $x_{doy,y,pos}$ is the fourth-root transformed catch of small or large Black Sea Bass on day of the year *doy* in year *y* at spatial position *pos, type* is the station type, *depth* is bottom depth, *tod* is time of day, *soak* is the soak time of the trap, *moon* is the moon phase, f_{1-2} are categorical functions, g_{1-9} are nonparametric smoothing functions, and $e_{doy,y,pos}$ is the random error assumed to be normally distributed with a mean of zero and finite variance.

All base models were compared to reduced models using the Akaike information criterion (AIC; Burnham and Anderson 2002). The AIC approach balances the number of parameters of a model and its log-likelihood, and the model with the lowest AIC values is considered the best model out of the candidate models investigated given the data set used (Burnham and Anderson 2002). We used the mgcv library (Wood 2004, 2011) in R (R Development Core Team 2013) to construct and compare all models. For smoothed and variable coefficient terms, estimated degrees of freedom were chosen using automatic software selection. There was no significant multicolinearity among predictor variables given that the variance inflation factor was less than three for all variables (Neter et al. 1989). Also, there were no consistent patterns in the relationship between the semivariance of the model residuals and distance between sampling points, indicating negligible spatial autocorrelation in the residuals. Furthermore, there were no obvious trends in residuals over space, suggesting no spatial bias in model fit. Last, models only using data from 2010 to 2013, during which time the survey expanded spatially (see Table 1), were very similar to models incorporating the full data set (i.e., 1990–2013), as was a model that only examined Black Sea Bass caught in South Carolina and Georgia over the entire time series.

Three additional landscape variables were considered for inclusion in the catch models: rugosity (a measure of the roughness of the seafloor), slope of slope (a measure of the curvature or shape of the seafloor), and predicted hard bottom (the likelihood of being hard bottom: Dunn and Halpin 2009). Since bottom-mapping information does not exist for most of our sampling locations, we calculated the first two metrics using data from the Coastal Relief Model (National Centers for Environmental Information, NOAA), which provided depth data for our entire study area at a resolution of approximately 90 m (~8,100-m^2 cells). Rugosity and slope of slope were calculated for each 90-m grid cell in our study area by comparing its depth to the depth of the eight surrounding grid cells using the Benthic Terrain Modeler in ArcGIS 10.2. Moreover, we obtained predicted hardbottom data from Dunn and Halpin (2009). For both small and large Black Sea Bass catch models, all three landscape variables were excluded based on AIC values, likely due to the weak habitat relationships displayed by Black Sea Bass (Kendall et al. 2008) and poor accuracy of the Coastal Relief Model (Dunn and Halpin 2009).

The overall influence of predictor variables on mean length or catch of Black Sea Bass was calculated using a bootstrapping approach described by Bacheler et al. (2013a). Briefly, we resampled the predictions ($N = 10{,}000$) for each model at mean values of all other predictor variables according to the pointwise estimates of error that were assumed to be normally distributed. Since average values did not exist for categorical variables (year and station type), the model predicted at all combinations of these categorical variables using the "expand. grid" function in R. Mean latitude and longitude values were not used because average values would be placed in the middle of the Atlantic Ocean (outside the range of our study area), so we instead used a latitude of 32°N and a longitude of 80°W (i.e., mid-continental shelf off southern South Carolina). All 95% CIs were estimated as the 0.025 and 0.975 quantiles of the 10,000 point estimates. To visualize spatial effects across the study area, a grid of 0.05° × 0.05° was created over the study area and mean Black Sea Bass length or catch was predicted for each cell given the depth (from the U.S. Coastal Relief Model, National Geophysical Data Center, NOAA), latitude, and longitude of each cell and mean values of all other model predictor variables. Black Sea Bass predictions only applied to hard bottom areas within each cell.

RESULTS

Overall, 11,726 chevron-trap deployments were included in the catch models, ranging from 250 samples in 1999 to 1,514 in 2013 (annual mean = 489, SD = 333; Table 1; Figure 1). Seasonality of sampling was relatively constant over the 24 years, and sampling commenced in late April through May and terminated in late September through October in most years (Table 1). Likewise, the range of depths sampled annually was relatively constant, ranging from approximately 15 to 95 m in most years. In contrast, the spatial extent of sampling increased from approximately 30–34°N in the early years of the survey to 27–35°N in later years; however, the long time series and large number of samples taken throughout the entire

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TABLE 1. Sampling information for the 24 years included in the analysis of the Southeast Reef Fish Survey chevron-trap data. N = number of trap samples included each year, the number of small Black Sea Bass is the total number of small Black Sea Bass < 235 mm TL caught in traps in a given year, and the number of large Black Sea Bass is the total number of large Black Sea Bass ≥ 235 mm TL caught in traps in a given year.

Year	N	Dates sampled	Depth range (m)	Latitude range (°N)	Number of small Black Sea Bass	Number of large Black Sea Bass
1990	310	Apr 23–Aug 9	17–93	30.4–33.8	4,172	1,843
1991	268	Jun 11–Sep 24	17–95	30.8–34.6	2,824	1,079
1992	291	Mar 31–Aug 13	17–62	30.4–34.3	2,708	1,551
1993	412	May 10–Aug 13	16–94	30.4–34.3	2,122	1,138
1994	409	May 9–Oct 26	16–93	30.7–33.8	2,323	1,325
1995	376	Apr 17–Oct 26	16–60	29.9–33.7	2,170	777
1996	498	Apr 29–Oct 17	14–95	27.9–34.3	2,282	1,489
1997	476	Apr 21–Sep 29	15–97	27.9–34.6	2,300	1,513
1998	466	Mar 31–Oct 5	14–92	27.4–34.6	2,450	1,335
1999	250	May 18–Oct 6	15–79	27.3–34.4	2,278	1,215
2000	352	May 16–Oct 19	15–95	29.0–34.3	2,518	1,653
2001	276	May 23–Oct 24	14–91	27.9–34.3	1,838	1,455
2002	298	Jun 17–Nov 5	13–94	27.9–34.0	1,765	1,033
2003	276	Jun 3–Sep 22	16–92	27.4–34.3	941	854
2004	319	May 5–Oct 28	14–91	30.0–34.0	2,156	2,980
2005	338	May 3–Oct 20	15–69	27.3–34.3	2,121	2,235
2006	309	Jun 6–Oct 19	15–94	27.3–34.4	1,624	1,424
2007	361	May 21–Sep 24	15–92	27.3–34.3	1,811	1,455
2008	354	May 5–Sep 30	14–92	27.3–34.6	1,634	1,526
2009	458	Apr 23–Oct 8	14–91	27.3–34.6	1,501	2,196
2010	990	May 4–Oct 27	14–92	27.3–34.6	3,907	5,838
2011	817	May 3–Oct 26	14–93	27.2–34.5	7,444	5,501
2012	1,308	Apr 24–Oct 10	15–98	27.2–35.0	9,709	7,360
2013	1,514	Apr 24–Oct 4	15–92	27.2–35.0	10,565	8,766
Total	11,726	Mar 31–Oct 28	13–98	27.2–35.0	75,163	57,541

latitudinal extent in later years likely minimized any effects of inconsistent latitudinal sampling on GAM models (Table 1). Catch of small Black Sea Bass ranged from 0 to 137 individuals per trap, and catch of large Black Sea Bass ranged from 0 to 160 individuals per trap.

A total of 5,230 (44.6%) out of 11,726 chevron traps deployed in our study caught Black Sea Bass and were included in the length model. The annual percent frequency of occurrence of Black Sea Bass in chevron traps ranged from 27% in 2003 to 64% in 1990. Overall mean Black Sea Bass TL was 259 mm (SD = 47; range = 100–520 mm; Figure 2). The largest catches of Black Sea Bass had mean lengths of between 200 and 350 mm TL and were generally caught in depths of less than 45 m (Figure 3). Moreover, mean Black Sea Bass length appeared to increase with depth (Figure 3).

The best length model for Black Sea Bass excluded bottom temperature from the $\text{Base}_{\text{length}}$ model; the $\text{Base}_{\text{length}}$ model and all other reduced models had AIC scores of at least 23 points higher than the best model (Table 2). The best length model explained 54.4% of the deviance in Black Sea Bass mean length and included year, day of the year, position, position × year, and position × day of the year (Table 2). The best catch models for small and large Black Sea Bass were the $\text{Base}_{\text{catch}}$ models, which explained 53.6% and 52.3% of the deviance in catch, respectively. Based on AIC scores, none of the reduced models compared favorably with the $\text{Base}_{\text{catch}}$ models. $\text{Base}_{\text{catch}}$ models for small and large Black Sea Bass included year, station type, depth, day of the year, time of the day, soak time, bottom temperature, moon phase, position, position × year, and position × day (Table 2).

Predicted mean TL of Black Sea Bass increased over the study period from approximately 230 mm in the early 1990s to approximately 280 mm after 2010 (Figure 4A). Increases in predicted mean length were gradual over the time series, perhaps increasing most dramatically between 2008 and 2009 (Figure 4A). The predicted catch of small Black Sea Bass was relatively constant between 1990 and 2010 at ~2–4 Black Sea Bass/trap, but increased in 2011–2013 to ~6–7 fish/trap (Figure 4B). The predicted catch of large Black Sea Bass increased throughout the study period from fewer than 1 fish/trap in the mid-1990s to ~4 fish/trap in 2011–2013 (Figure 4C).

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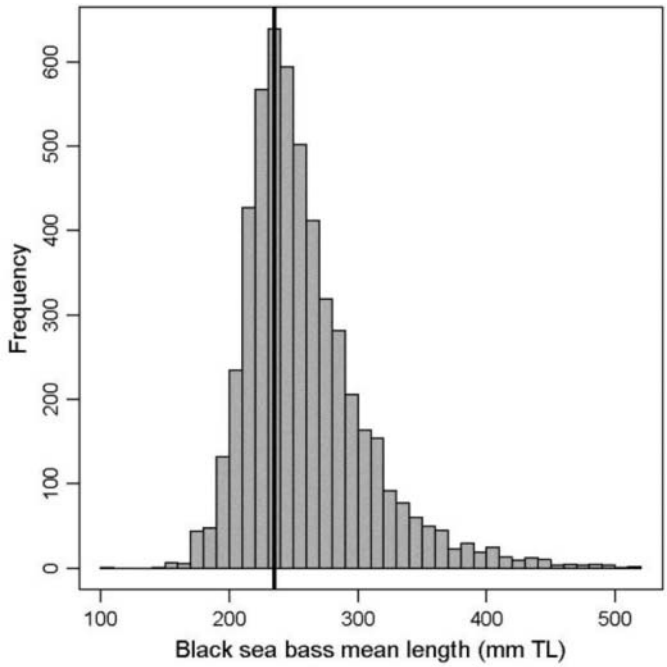

FIGURE 2. Mean length frequency distribution of Black Sea Bass (mm TL) caught in chevron traps by the Southeast Reef Fish Survey between North Carolina and Florida, 1990–2013. The black vertical line shows the cutoff used in this paper (i.e., 235 mm TL) between small and large Black Sea Bass.

Most of the effects of the smoothed predictor variables on Black Sea Bass mean length or catch were nonlinear. The predicted mean length of Black Sea Bass gradually decreased from approximately 260 mm TL on day of the year 100 (April 10) to 240 mm TL on day of the year 255 (September 12), but increased after that time to over 250 mm by day of the year 300 (October 27), although CIs were wide (Figure 5). Predicted catch of small and large Black Sea Bass was influenced very similarly by five of the six smoothed predictor variables. Mean catch of both small and large Black Sea Bass declined exponentially with increasing depth, declined throughout the sampling season, increased with time of day, displayed a dome-shaped response to bottom temperature, and appeared to be lowest during full moons (Figure 6). In contrast, the catch of large Black Sea Bass reached an asymptote beyond a soak time of 100 min, while the catch of small Black Sea Bass increased linearly with soak time over the range of soak times examined in this paper (Figure 6). The precision of estimates was highest for depth and day of the year and lowest for time of day and moon phase (Figure 6).

The predicted mean length of Black Sea Bass was spatially variable, generally smallest in shallower depths and off Cape Canaveral, Florida, and highest in deeper waters off North Carolina, South Carolina, Georgia, and northern Florida (Figure 7A). The predicted catch of small and large Black Sea Bass was also spatially variable, highest inshore in South Carolina, Georgia, and around Cape Canaveral and lowest in deep waters and off southern Georgia and northern Florida (Figure 7).

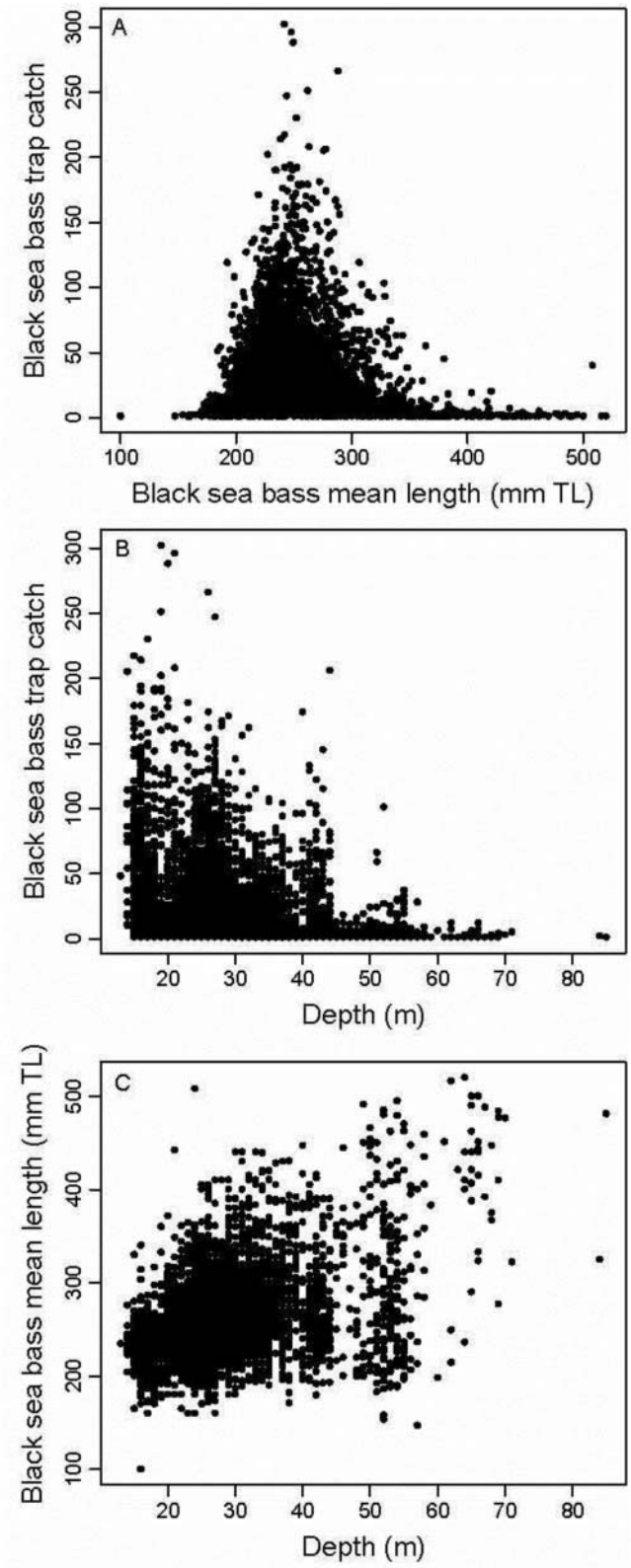

FIGURE 3. Relationship between (**A**) total Black Sea Bass catch (all sizes, number per trap) and Black Sea Bass mean length (mm TL), (**B**) total Black Sea Bass catch and depth (m), and (**C**) Black Sea Bass mean TL and depth in Southeast Reef Fish Survey chevron-trap sampling, 1990–2013.

TABLE 2. Model selection for the spatially explicit generalized additive models for mean length of Black Sea Bass, catch of small Black Sea Bass, or catch of large Black Sea Bass in chevron traps by the Southeast Reef Fish Survey, 1990–2013. Degrees of freedom are shown for factor (*f*) terms, and estimated degrees of freedom are shown for nonparametric, smoothed terms (*g*). Asterisks denote significance at the following alpha levels: *0.05, **0.01, ***0.001; Dev = deviance explained by the model; AIC = Akaike information criterion; *y* = year of the sample; *type* = station type; *depth* = bottom depth; *t* = day of the year; *tod* = Coordinated Universal Time; *soak* = trap soak time; *temp* = bottom temperature; *moon* = moon phase; *pos* = position of the trap sample; NA = covariate was not applicable to that particular model. Only the four best models are shown for each response variable.

Model	Dev	AIC	*y*	*type*	*depth*	*t*	*tod*	*soak*	*temp*	*moon*	*pos*	*pos·y*	*pos·t*
Black Sea Bass mean length													
$\text{Base}_{\text{length}}$[a] − *temp*	54.4	−7,639	23***	NA	NA	7.1***	NA	NA	NA	NA	21.0***	28.8***	26.1***
$\text{Base}_{\text{length}}$ − *doy*	54.1	−7,616	23***	NA	NA	NA	NA	NA	5.9***	NA	20.1***	29.7***	25.9***
$\text{Base}_{\text{length}}$ − *temp* − *doy*	53.9	−7,598	23***	NA	NA	NA	NA	NA	NA	NA	20.9***	28.8***	26.8***
$\text{Base}_{\text{length}}$	53.8	−7,597	23***	NA	NA	6.3***	NA	NA	6.9***	NA	3.7***	29.8***	27.7***
Small Black Sea Bass catch													
$\text{Base}_{\text{catch}}$[b]	53.6	23,030	23***	1***	2.8***	3.6***	2.2***	1.9***	4.5***	4.0***	26.7***	29.5***	24.6***
$\text{Base}_{\text{catch}}$ − *type*	53.5	23,040	23***	NA	2.8***	3.9***	2.2***	2.2***	4.5***	4.0***	26.7***	29.6***	23.9***
$\text{Base}_{\text{catch}}$ − *moon*	53.5	23,048	23***	1***	2.8***	3.5***	2.2***	1.8***	4.5***	NA	26.7***	29.6***	25.1***
$\text{Base}_{\text{catch}}$ − *temp*	53.5	23,048	23***	1***	2.8***	3.3***	2.1***	1.9***	NA	4.1***	26.7***	29.6***	24.1***
Large Black Sea Bass catch													
$\text{Base}_{\text{catch}}$	52.3	21,681	23***	1***	2.7***	5.5***	1.0***	2.8***	4.7***	4.6***	26.9***	30.0***	28.0***
$\text{Base}_{\text{catch}}$ − *tod*	52.2	21,698	23***	1***	2.7***	5.4***	NA	2.8***	4.7***	4.6***	26.9***	29.9***	28.2***
$\text{Base}_{\text{catch}}$ − *moon*	52.1	21,714	23***	1***	2.7***	5.2***	1.0***	2.8***	4.7***	NA	26.9***	30.0***	28.3***
$\text{Base}_{\text{catch}}$ − *doy*	52.1	21,715	23***	1***	2.8***	NA	1.0***	2.8***	4.6***	4.6***	26.9***	29.9***	27.4***

[a]$\text{Base}_{\text{length}}$ is: $z_{doy,y,pos} = f_1(y) + g_1(doy) + g_2(temp) + g_3(pos) + g_4(pos \cdot y) + g_5(pos \cdot doy) + e_{doy,y,pos}$.
[b]$\text{Base}_{\text{catch}}$ is: $x_{doy,y,pos} = f_1(y) + f_2(type) + g_1(depth) + g_2(doy) + g_3(tod) + g_4(soak) + g_5(temp) + g_6(moon) + g_7(pos) + g_7(pos \cdot y) + g_7(pos \cdot doy) + e_{doy,y,pos}$.

There were significant spatially variable effects of year on mean Black Sea Bass length and the catch of small and large Black Sea Bass (Figure 8). Over the course of the study, mean Black Sea Bass length increased throughout the region (Figure 4A), but mean length increased disproportionately more off Cape Canaveral and inshore areas of South Carolina and Georgia and increased the least off Cape Lookout, North Carolina, and deep waters off Georgia (Figure 8A). Catches of small and large Black Sea Bass increased considerably in North Carolina, northern Florida, and inshore areas of South Carolina and Georgia, while they decreased disproportionately off Cape Canaveral and offshore areas of South Carolina and Georgia (Figure 8B, C).

The spatially variable effects of day of the year on mean Black Sea Bass length and the catch of small and large Black Sea Bass were also significant, but were not nearly as strong as the effects of year (Figure 8D–F). Mean Black Sea Bass length was more likely to decrease during the sampling season (spring–fall) off Cape Canaveral, inshore areas in South Carolina, and around Cape Lookout (Figure 8D). The catch of small Black Sea Bass tended to increase during the sampling season off Cape Lookout (Figure 8E) and increased off both Cape Lookout and Cape Canaveral for large Black Sea Bass (Figure 8F).

DISCUSSION

The spatial and temporal distributions of marine fish species can be ecologically complex and mediated by myriad interacting variables (Dingsør et al. 2007; Ciannelli et al. 2012). We found complex spatial and temporal dynamics of Black Sea Bass that were influenced by environmental, landscape, and sampling effects over the 24 years of the survey. Moreover, the spatial distribution of Black Sea Bass was not static among or within sampling seasons, but instead changed temporally over both seasonal and annual time scales. Standardized mean length of Black Sea Bass has also increased over time as a result of a higher proportional abundance of large Black Sea Bass in the SEUS. These results elucidate the spatial and temporal dynamics of Black Sea Bass, inform spatial management approaches, and provide an analytical framework that can be easily adapted to other species and systems.

The spatial dynamics of Black Sea Bass vary along the U.S. Atlantic coast. North of Cape Hatteras, Black Sea Bass undertake yearly migrations southward and offshore in fall and inshore and northward in the spring (Musick and Mercer 1977; Moser and Shepherd 2009; Fabrizio et al. 2013). However, Black Sea Bass do not appear to migrate across Cape Hatteras; Moser and Shepherd (2009) tagged over 16,000 Black Sea Bass north of Cape Hatteras, and not a single tag

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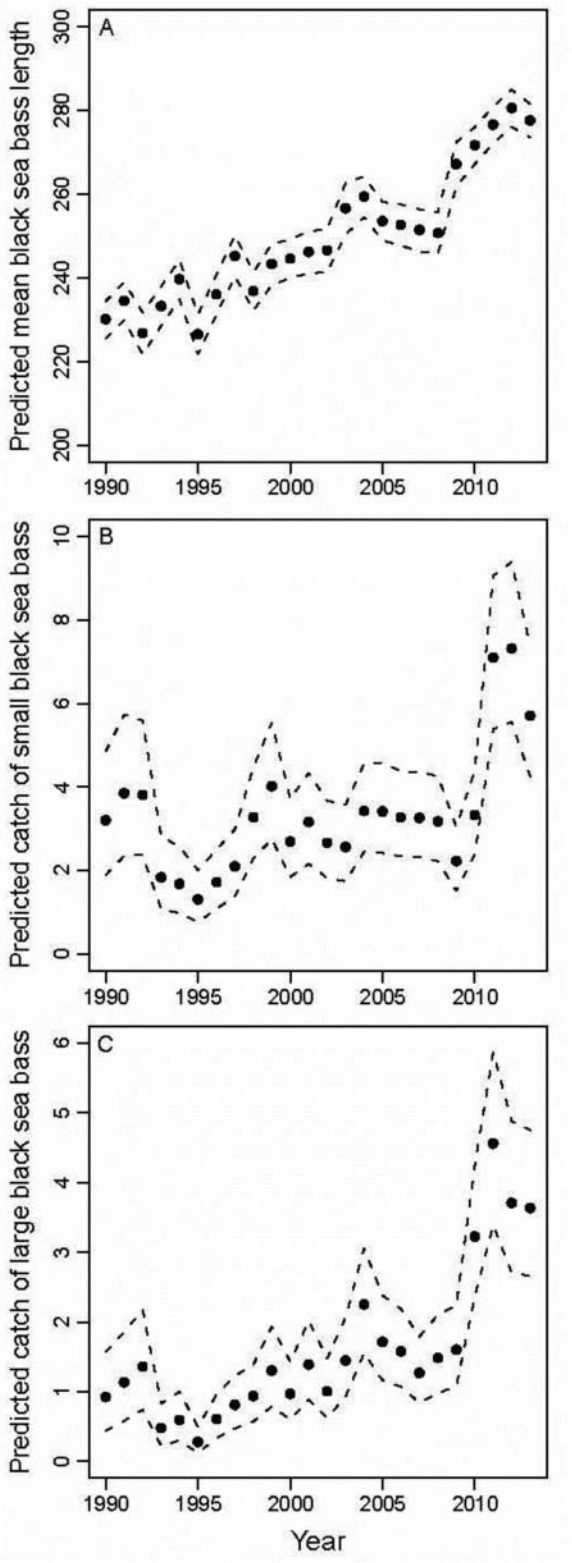

FIGURE 4. Predicted annual (**A**) mean Black Sea Bass length (mm TL), (**B**) catch of small Black Sea Bass, and (**C**) catch of large Black Sea Bass from spatially explicit generalized additive models built upon chevron-trap data, 1990–2013. Filled circles are mean predictions at average values of all other model covariates and dashed lines represent the 95% CI.

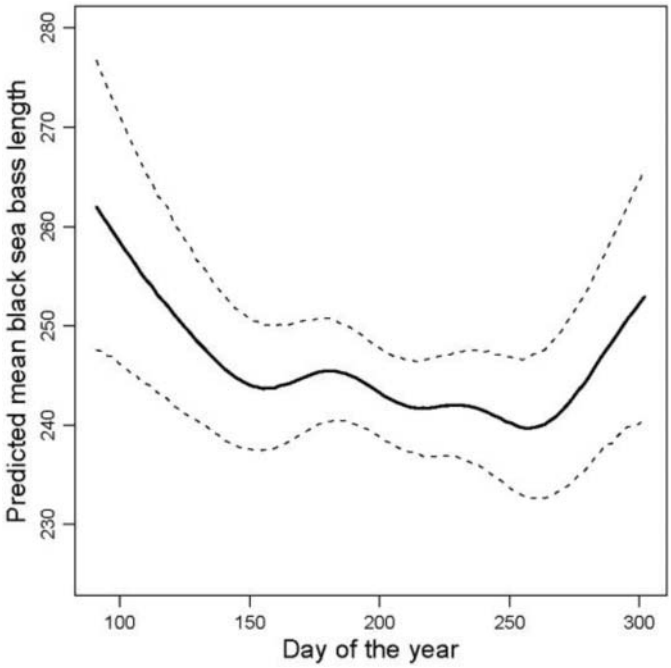

FIGURE 5. Predicted mean length of Black Sea Bass (mm TL) as a function of the day of the year using a spatially explicit generalized additive model built from Southeast Reef Fish Survey chevron-trap data, 1990–2013. The solid line is the predicted mean length of Black Sea Bass at average values of all other covariates, and dashed lines represent the 95% CI.

return (out of 2,800 returns) occurred south of Cape Hatteras. In the SEUS (i.e., south of Cape Hatteras), we found no clear evidence of inshore–offshore migration of Black Sea Bass over the seasonal time scale of this study (late March through early November). However, we did observe changes in the spatial distribution of sizes and catches of Black Sea Bass at smaller spatial scales within and among years. For instance, mean Black Sea Bass length tended to increase more in locations inshore in South Carolina, Georgia, and Florida over the course of the study than elsewhere, but seasonally showed modest declines off Cape Lookout, inshore off South Carolina, and off Cape Canaveral. Changes in the spatial structure of marine fishes may reflect migratory behaviors (Block et al. 2001), but habitat preferences (Gregory and Anderson 1997) and the spatial patterns of fishery harvest (Bartolino et al. 2012) can also influence observed spatial patterns. The potentially multiple, interacting forces causing Black Sea Bass to exhibit spatially variable sizes and catches are not known and deserve research attention.

The spatial patterns of Black Sea Bass were not consistent throughout the entire SEUS. Black Sea Bass tended to be smaller inshore and larger offshore, as has been previously noted (Sedberry et al. 1998; Steimle et al. 1999), but in our study small fish persisted into offshore waters around and south of Cape Canaveral. Black Sea Bass sizes and size at age can be positively related to latitude along the U.S. Atlantic coast, where individuals attain the largest body sizes north of

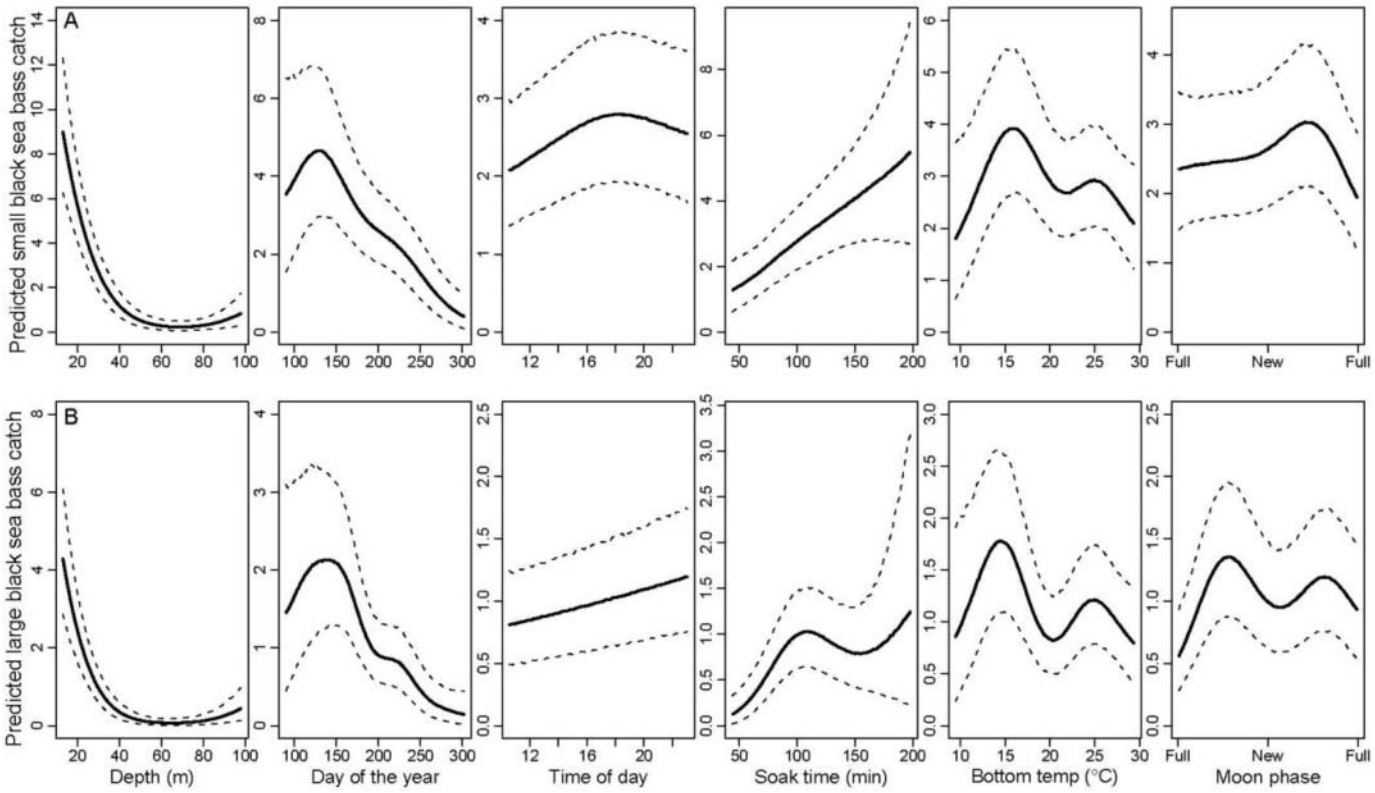

FIGURE 6. Predicted catch of (**A**) small or (**B**) large Black Sea Bass as a function of depth (m), day of the year, time of day (Coordinated Universal Time), soak time (min), bottom temperature (°C), or moon phase using spatially explicit generalized additive models built using Southeast Reef Fish Survey chevron-traps data, 1990–2013. Solid lines are the predicted Black Sea Bass catch per trap at average values of all other covariates, and dashed lines represent the 95% CIs.

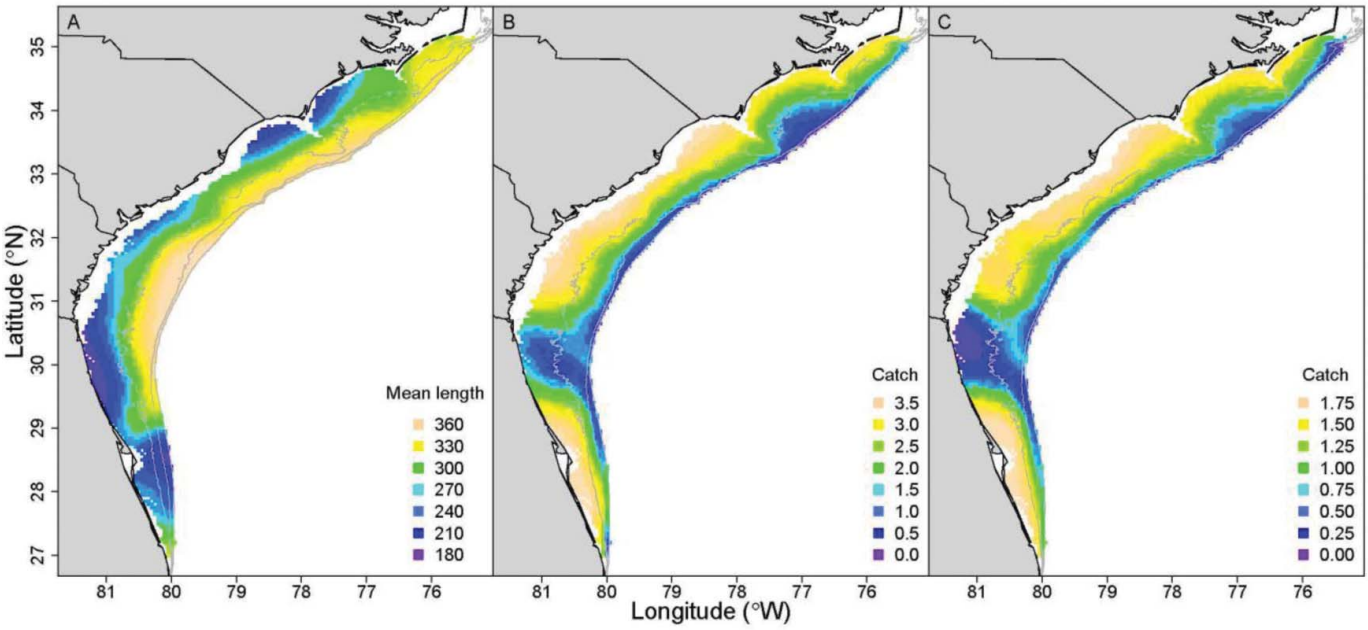

FIGURE 7. Predicted (**A**) mean Black Sea Bass length (mm TL), (**B**) catch of small Black Sea Bass, and (**C**) catch of large Black Sea Bass across the study area given spatial position and depth of each cell and average values of all other covariates using spatially explicit generalized additive models built on chevron-trap data in 1990–2013. Gray lines indicate the 30-, 50-, and 100-m isobaths.

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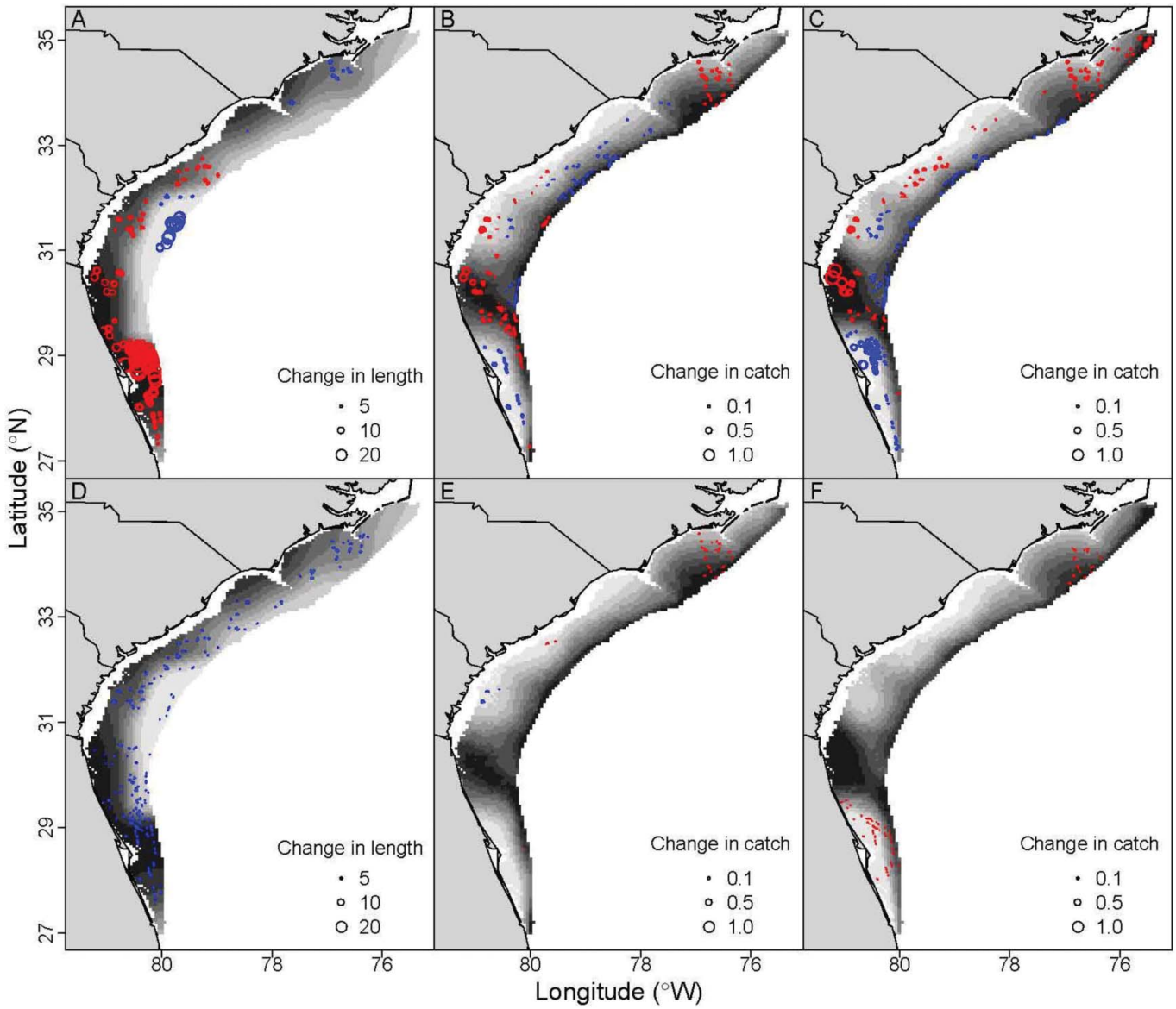

FIGURE 8. Spatially explicit variable-coefficient generalized additive model plots for the effects of (**A**, **B**, **C**) annual or (**D**, **E**, **F**) seasonal changes on the spatial distribution of (A, D) mean length of Black Sea Bass, (B, E) catch of small Black Sea Bass, and (C, F) catch of large Black Sea Bass in the Southeast Reef Fish Survey, 1990–2013. Light gray grid cells denote large mean size or catch, and black grid cells denote small mean size or catch. Overlaid on grid cells are red or blue circles, which indicate a disproportionate increase or decrease, respectively, in mean length or catch with an increase in the covariate. Size of the colored circles is scaled to the size of the positive or negative effect, and effects not significantly different from zero are excluded.

Cape Hatteras (Mercer 1978; Wenner et al. 1986). Even within the SEUS, Black Sea Bass can attain a larger size at age in North and South Carolina than those in Georgia and Florida (McGovern et al. 2002). But instead of a gradual change throughout the SEUS, we found that the depth distribution of Black Sea Bass sizes was similar over a broad range of latitudes (29.5–35°N), only changing qualitatively around Cape Canaveral.

Standardized mean length of Black Sea Bass increased significantly over the 24 years of the trap survey. During the 1970s and 1980s, harvest and fishery mortality rate of Black Sea Bass were high, which likely caused declines in mean length (Vaughan et al. 1995; McGovern et al. 2002). The stabilization of mean lengths and fishery-independent catch rates in the 1990s was attributed to the implementation of size limits, the prohibition of trawling, and reduced fishery harvests in the 1980s and 1990s (McGovern et al. 2002). When a population is heavily harvested, fish sizes tend to decline due to the selective removal of larger individuals from the population, both because of immediate effects of losing the largest individuals but also because of the potential long-term selection for early maturing and slower growing individuals (Conover and

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Munch 2002; Olsen et al. 2004). Since the 1990s, Black Sea Bass mean length has increased by approximately 20 mm in the SEUS because of the relative increase in the number of large Black Sea Bass in the population, perhaps due to increased minimum size limits in the recreational fishery over the same time frame, and suggests there are few, persistent, selective effects on length for this population. This finding also hints at lower recent mortality rates of large Black Sea Bass in the SEUS.

The spatial dynamics and covariate effects were surprisingly similar between small and large Black Sea Bass in the SEUS. Most species tend to display ontogenetic changes in relation to environmental and habitat variables due to physiological and behavioral differences across ontogeny (Werner and Gilliam 1984; Mitchell et al. 2014). For Black Sea Bass in the SEUS, maturity occurs between 135 and 235 mm TL (McGovern et al. 2002), so some small and all large Black Sea Bass in our study were mature. We found that small and large Black Sea Bass varied similarly by depth, season, time of day, bottom temperature, moon phase, and spatial position. It is likely that the most significant ontogenetic changes for Black Sea Bass occur at fish sizes smaller than those caught in our survey, so that by the time they are caught in our survey, Black Sea Bass appear to behave similarly.

Small and large Black Sea Bass did differ significantly in their relationship to soak time in our trap survey. The catch of small Black Sea Bass increased linearly as soak time increased, whereas the catch of large Black Sea Bass reached an asymptote at longer soak times. Bacheler et al. (2013b) showed that the catch of Black Sea Bass in chevron traps reached an asymptote at a soak time of around 60 min and further suggested that catch at saturation is likely related to true abundance around the trap. Our results indicate that small and large Black Sea Bass may be responding differently to the trapping process, which was not accounted for in Bacheler et al. (2013b). One explanation for this difference in response of large and small Black Sea Bass to the trapping process is due to size-based selectivity of Black Sea Bass to the chevron-trap gear, which may not fully select for small Black Sea Bass.

There were some drawbacks of our study design. First, predictions of absolute mean lengths or catches of small and large Black Sea Bass were dependent upon the values or levels of the covariates chosen. In most cases we were able to use average values of covariates, but in some instances selection needed to occur manually. For instance, using mean latitude and longitude values would have resulted in unreasonable Black Sea Bass predictions from deep, offshore waters of the Atlantic Ocean; instead, values were chosen approximately in the center of the SEUS study area. Regardless, the covariate values or levels used only influence absolute but not relative values. Second, the latitudinal extent of sampling increased over time, which could have influenced study results. We believe bias is unlikely because mean length and catch rate information from the core of the study area (i.e., South Carolina and Georgia), which has been sampled consistently since 1990, was nearly identical to that from the entire study area. However, mean length or catch information north of Cape Lookout, North Carolina, or south of Cape Canaveral, Florida, should be interpreted with caution due to low sample sizes. Third, spatial predictions were only developed for chevron traps deployed on hard-bottom sites, so inferences can only be made for hard-bottom (not sand or mud) substrates throughout the SEUS. Fourth, our regression models explained approximately 50–55% of the deviance in catch or length, suggesting that unmeasured variables, such as other characteristics of the site, interactions with other species, or fishery spatial structure, are important. Last, we assumed that the size-selectivity patterns of chevron traps were constant over space and time. Chevron-trap selectivity patterns would also need to be known in order to translate our length and catch predictions to make inferences about the population.

Despite these caveats, our study demonstrated that Black Sea Bass exhibited annual and seasonal variability in sizes and catches that had a unique spatial component unrelated to obvious inshore–offshore migrations. Black Sea Bass also appeared to have benefited from recent management actions by exhibiting increased mean length and fishery-independent trap catches; most significantly, large Black Sea Bass appeared to increase almost fourfold from the mid-1990s to the 2010s. The spatially explicit analytical approach we employed allowed us to quantify the spatial, temporal, environmental, and landscape correlates of Black Sea Bass size or catch in the SEUS, and provides important information if spatial management measures are considered in the future (Murphy and Jenkins 2010; Cardinale et al. 2011). Our results also suggest that little coastwide inshore–offshore or north–south movements by Black Sea Bass in the SEUS occurrs between spring and fall. The major benefits of a variable-coefficient modeling approach are that this approach is flexible and can be adapted to a variety of species and systems, it can test for myriad covariate effects simultaneously, and the results can be straightforward to interpret.

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