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Abstract

Understanding spatial ecology and predicting animal movements in response to environmental changes, such as anthropogenic climate change and multidecadal variability, is critical for effective conservation strategies. Niche structuring is key to some coastal shark species and size classes coexisting in the US Atlantic and Gulf of Mexico to limit interspecific and intraspecific interaction. Data from four fishery-independent bottom longline surveys were used to evaluate the abiotic ecological niches of eight species of small and large coastal sharks. Gaussian mixture models separated length composition data into 14 size categories for ecological niche analysis. Generalized additive mixed effect models were fit and coupled with output from dynamic high-resolution ocean models to predict suitable abiotic habitats, evaluate potential shifts in distribution, and explore the impacts of large-scale climatological trends on abiotic habitats from 1994 to 2019. The abiotic niche for small coastal sharks generally tended toward warmer, high salinity, shallow bottom waters close to shore. No overarching niche was found for large coastal sharks, but appreciable ontogenetic differences were seen. Most taxa analyzed exhibited declining annual trends in higher quality habitats, particularly during fall months. The analysis provided evidence of shifts north along the Atlantic, to deeper offshore waters in the Atlantic and Gulf of Mexico, and the potential to redistribute in response to multidecadal climate variability for multiple species. The analytical framework described could aid in developing various spatiotemporal management measures, and results provide insight into the habitat characteristics of several species over broad spatiotemporal ranges and through ontogeny.

KEYWORDS
coastal sharks, distribution shifts, ecological niche, Gaussian mixture models, generalized additive mixed effect models, habitat predictions

1 | INTRODUCTION

Global ocean temperatures have gradually risen over the past 50 years as additional heat trapped by anthropogenic greenhouse gas emissions is absorbed by aquatic ecosystems (IPCC, 2014; Levitus et al., 2000). The Atlantic Ocean has recently been disproportionately impacted by warming and is experiencing some of the fastest temperature increases worldwide (Burrows et al., 2011; Levitus et al., 2005;

Pershing et al., 2015). Warming along the US Atlantic coast may also be due to shifts in the position of the Gulf Stream (Alexander et al., 2020; Chen et al., 2020; Gonçalves Neto et al., 2021; Todd & Ren, 2023). Although several studies have focused on characterizing climate change impacts on the US northwest Atlantic shelf (Cheng et al., 2019; Kleisner et al., 2017; Saba et al., 2016), the southeastern United States and Gulf of Mexico (GOM) shelves have received significantly less attention likely due to a slower warming rate and the emphasis placed on other climate change effects (e.g., sea level rise; Piecuch et al., 2018; Ezer, 2019; Ruela et al., 2020).

Large-scale naturally occurring climatological trends co-occur with climate change and may offset or intensify environmental changes (Stine et al., 2009; St. Laurent et al., 2021). The North Atlantic Oscillation (NAO), which measures pressure difference over the North Atlantic and impacts temperature and precipitation across the North Atlantic region; the Atlantic Multidecadal Oscillation (AMO), which encompasses basin-wide sea surface temperature, circulation patterns, and sea level pressure; and the Gulf Stream Index (GSI), which evaluates northern shifts in the Gulf Stream, directly impact climate patterns and affect fish survival and ecosystem organization through bottom-up control in the southeastern United States and GOM (Nye et al., 2009, 2014; Peterson, Belcher, et al., 2017; Stenseth et al., 2002). Documented impacts of multidecadal variability and climate change include poleward and offshore shifts toward deeper waters in distribution (Free et al., 2019; Nye et al., 2014), adjustments in spawning timing (Asch, 2015; Shoji et al., 2011), and changes in migration patterns (Kessel et al., 2014; Langan et al., 2021; Lea et al., 2018). As climate-related impacts are anticipated to continue for the foreseeable future and could alter ecosystem structure, efforts to characterize niche structure and habitat shifts of marine fauna in response to environmental change become increasingly important.

As mid- to upper-level trophic predators, sharks have a stabilizing effect on marine ecosystems, and loss of animals through either population declines or shifts in distribution ultimately affects high-value fisheries and overall ecosystem health (Britten et al., 2014; Ferretti et al., 2010). Healthy shark populations contribute to increased biodiversity, which enhances the resilience of marine ecosystems by maintaining a diverse array of species with different ecological roles (Stevens et al., 2000). The large coastal shark complex (LCS; e.g., sandbar shark; *Carcharhinus plumbeus*, see more examples below) experienced a rapid decline in abundance from the mid-1970s to 1990s due to overexploitation along the southeast US coast and within the GOM (Baum et al., 2003; Burgess et al., 2005; Baum & Blanchard, 2010). In contrast, the small coastal shark complex (SCS; e.g., Atlantic sharpnose shark; *Rhizoprionodon terraenovae*, see more examples below) underwent a less pronounced decline (Peterson, Belcher, et al., 2017). Both complexes appear to be recovering (Carlson et al., 2012; Peterson, Belcher, et al., 2017; E. Cortés, personal communication) with SCS species generally recovering more quickly than LCS species, but recovery is slow due to low intrinsic rates of population growth (Musick, 1999; Peterson et al., 2022).

LCS species display a high potential to shift distributions in response to climate change as water temperature is a key abiotic driver of latitudinal and depth distribution (Hare et al., 2016), while studies focusing on SCS species are lacking. Increasing water temperatures and salinity changes could impact the physiological processes (Harding et al., 2022; Pegado et al., 2020; Ubeda et al., 2009), swimming activity (Ferreira et al., 2015; Hyatt et al., 2017; Papastamatiou et al., 2013; Payne et al., 2018), and coastal distribution (Niella et al., 2020) of LCS and SCS species.

Further, overlapping distributions for coastal shark species are well documented (Harry et al., 2016; Heupel, 2007; Last et al., 2011), and competition for resources such as habitats can adversely affect species through decreased growth and survivorship (Bangley et al., 2018; Heupel et al., 2019). Coastal sharks generally undergo ontogenetic shifts in habitat utilization to limit inter- and intraspecific interactions with smaller individuals largely occupying warmer, shallower, and fresher inshore areas compared to larger animals (Grubbs, 2010). Research on shark habitat utilization has primarily focused on smaller individuals in nurseries, where salinity and depth are significant factors (Latour et al., 2022), with limited research on larger individuals due to challenges associated with their larger activity space and data limitations. Few studies have examined ecological niches and abiotic habitat utilization of species and size categories within the SCS and LCS in the southeastern United States and GOM, even though such information can aid efforts to understand population-level responses to climate change.

An ecological niche, or the environment with the abiotic conditions required for a species' survival and growth, is a critical component to a species distribution (Soberon & Peterson, 2005). Methods for quantifying and assessing factors influencing species' ecological niches have grown significantly thanks to continued conceptual and computational advances (Broennimann et al., 2012). Results from these analyses enable ecologists and resource managers to address ecological and biogeographic questions regarding mechanisms underlying geographic ranges including strategies for conservation, impacts of climate change, and changes in the overlap of distributions or ecological niches among species (Peterson et al., 2015; Rödder & Engler, 2011; Warren et al., 2019). Applying ecological niche models (ENMs) has become increasingly useful (Elith & Leathwick, 2009; Robinson et al., 2017); however, studies have not been evenly distributed across taxonomic groups with comparatively few studies concentrating on elasmobranchs (Melo-Merino et al., 2020).

This study addresses this knowledge gap through four objectives: (1) develop ENMs for multiple size categories of eight Atlantic coastal shark species inhabiting the southeast coast of the United States and GOM using data from multiple fishery-independent surveys that collectively sample an extensive spatiotemporal range, (2) use ENMs to predict habitat suitability and associated variability across that range over a 26-year hindcast period, (3) investigate potential shifts in predicted habitat suitability by estimating the centers of gravity (COGs) for multiple metrics, and (4) evaluate potential relationships between COGs and three large scale climatological indices (NAO, GSI, and AMO). Achieving these objectives will provide insights into the conservation implications of ocean warming on multiple marine predators.

2 | METHODS

2.1 | Data sources and size categories

Catch, effort, and environmental data from four fishery-independent bottom longline surveys spanning 1996 to 2019 were the basis of this study; namely, the Virginia Shark Monitoring and Assessment Program Longline Survey (VASMAP), the Southeast Fisheries Science Center Bottom Longline Survey (SEFSC), the South Carolina Coastal Longline Survey (SC), and the Georgia Red Drum Longline Survey (GA; Figure 1, Table S1). These surveys collectively cover a large spatial footprint relative to the target species' home ranges and synoptically measure environmental variables during sampling. These environmental variables were classified as static (depth [m] and distance from shore [km]) or dynamic (bottom temperature [C°] and salinity). Bottom environmental variables for GA were predicted from sampled surface values using a linear regression fit to data from a complementary survey (SouthEast Area Monitoring and Assessment Program-South Atlantic Coastal Trawl Survey) filtered to the same spatial and temporal range so as to include GA in the analysis as only surface measurements were collected (SEAMAP-SA Data Management Work Group, 2012).

Data from eight shark species were analyzed, including four SCS (blacknose shark, *Carcharhinus acronotus*, with Atlantic (A.) and GOM (G.) stocks examined separately; Atlantic sharpnose shark, bonnethead, *Sphyrna tiburo*; and finetooth shark, *C. isodon*) and four LCS (sandbar shark, the Atlantic stock of blacktip shark, *C. limbatus*; spinner shark, *C. brevipinna*; tiger shark, *Galeocerdo cuvier*). Species were selected based on several factors, including data availability, hypothesized distribution shifts, and a gap in prior research on certain species (Chin et al., 2010; Hare et al., 2016; Quinlan et al., 2023). Small and large coastal shark designations distinguish management units along the US Atlantic coast (NMFS 1993).

Length composition data (natural body curved total length, TL [mm]) indicated that multiple size categories were sampled across and within surveys. A species-specific modal analysis was conducted to identify the number of size categories present, as the ages or sizes at which coastal sharks undergo ontogenetic shifts in habitats are unknown for most data-limited species. Gaussian mixture models (GMMs) were fitted under the assumption that length data comprised a set of Gaussian distributions, $m(y)$, such that

$$m(y) = \sum_{k=1}^{K} \pi_k N(y|\mu_k, \boldsymbol{\Sigma}_k), \qquad (1)$$

where for the k^{th} mixture component, $k \in \{1,\ldots,K\}$, π_k is the mixing coefficient (weight) such that $0 \leq \pi_k \leq 1$ and $\sum_{k=1}^{K} \pi_k = 1$, μ_k is the mean, and $\boldsymbol{\Sigma}_k$ is the covariance matrix. The number of size categories for each species was selected based on a 10-fold cross-validation analysis and analyst judgment. GMMs were fitted using the R package *mixtools* (Young et al., 2020), and size categories were separated at the intersection of two adjacent Gaussian curves. A single size

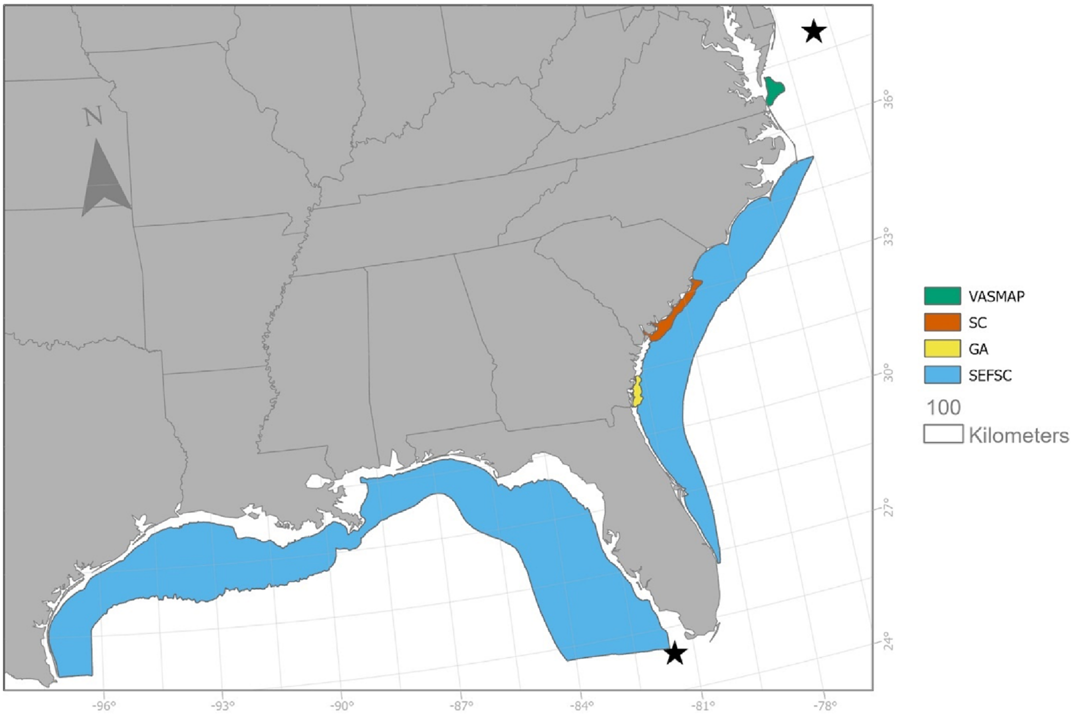

FIGURE 1 Map of the spatial extent of the four fishery-independent longline surveys used in this study: the Virginia Shark Monitoring and Assessment Program Longline Survey (VASMAP), the South Carolina Coastal Longline Survey (SC), the Georgia Red Drum Longline Survey (GA), and the Southeast Fisheries Science Center Bottom Longline Survey (SEFSC). Stars represent reference points for the two regions (Atlantic and Gulf of Mexico) that were used to calculate the center of abundance.

category was assumed for extremely data-limited species (>92% frequency of 0 or with no clear size categories).

The sufficiency of a survey for a particular size category was evaluated following a rubric based on previous Highly Migratory Species (HMS) stock assessments (ICCAT, 2012). The criteria included, among other metrics, survey geographic and temporal coverage, sampling design, and an overall proportion positive (longline sets where at least one target animal was captured) of at least 0.05. For surveys deemed sufficient, spatiotemporal filtering was applied to optimize representativeness. If a year's proportion positive was >0.03 then months and stations (if fixed) were assessed individually and removed if <0.03, while the whole year was removed if the encounter rate was <0.03.

2.2 | Ecological niche modeling

Preliminary data exploration revealed two initial findings: (i) a high frequency of zero observations (despite data filtering) and (ii) nonlinear relationships between catch and environmental variables for all size categories. A variety of discrete count distributions were considered to accommodate the former, including the negative binomial (NB), Sichel (SI), and zero-altered negative binomial (ZANB). Generalized additive mixed effect models (GAMMs, Lin & Zhang, 1999) were applied to address the latter since these models assume no a priori effect shape between the response and predictor variables. The general form of a GAMM is as follows:

$$g(E(\boldsymbol{y}|\boldsymbol{b})) = \beta_0 + \sum\nolimits_{j=1}^{p} f_j(\boldsymbol{x}_j) + \boldsymbol{Zb} + \boldsymbol{\delta}, \tag{2}$$

where $E(\boldsymbol{y}|\boldsymbol{b})$ is the expected value of the response vector $\boldsymbol{y}$, defined as animal count per longline, conditioned on the random effects $\boldsymbol{b}$, β_0 is the model intercept, f_j are the smooth functions, $\boldsymbol{x}_j$ are the vectors of survey-derived environmental variables, $\boldsymbol{Z}$ is the random-effect design matrix, $\boldsymbol{\delta}$ is the offset variable, expressed as sampling effort scaled to 100 hooks h^{-1}, and $g(.)$ is the monotonic link function.

GAMMs were fitted using the generalized additive models for location, scale, and shape (GAMLSS) regression framework (*gamlss* R package; Stasinopoulos & Rigby, 2007). Residuals of preliminary model fits were evaluated for spatial and temporal autocorrelation, and the results indicated both forms were minor (small Moran's I value and acceptable autocorrelation function and partial autocorrelation function plots; Zuur et al., 2009). Correlation and collinearity of environmental variables were assessed using scatter plot matrices and variance inflation factors (VIFs) with highly correlated covariates ($\gtrsim$0.7) or large VIFs (>10; Peterson, Belcher, et al., 2017) not mutually included in any model parameterization. Cubic smoothing splines were applied, and the number of knots was held to <5 to avoid overparameterization. Year, month or season, and survey were categorically defined and included as random effects to account for any survey or temporal effects while enabling ENMs to be predicted outside of surveyed years and areas. Month and season were never mutually included in a model. Model parameterizations ranged from fully saturated to including each environmental variable separately. Model selection was based on Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002) and 10-fold cross-validation analysis where the root mean square error, mean absolute error, and Pearson correlation coefficients between predicted and observed values were assessed.

Model validation was achieved through diagnostic plots (QQ plots and residuals), assessment of overdispersion, and simulation analysis to ensure the response distribution could accommodate the frequency of zeros. From the selected model, curves of each covariate were generated using marginal means (Searle et al., 1980), and uncertainty estimates were generated from 1000 nonparametric bootstrapped samples (Efron & Tibshirani, 1994).

2.3 | Hindcast projections

The ENMs were coupled with a hindcast climate data set to evaluate shifts in the quality and availability of abiotic habitats. Climate data for hindcast projections extended from May 1 to November 30 for 1994–2019. Static climate data consisted of bathymetry data, obtained from ETOPO 2022 (https://www.ngdc.noaa.gov/mgg/global/global.html) at a 15 arc-second resolution, and distance from shore, the shortest distance between the center point of each grid cell to the coast. Both were held constant across time. Dynamic climate data consisted of bottom temperature and salinity values from Hybrid Coordinate Ocean Model (HYCOM) + Navy Coupled Ocean Data Assimilation (NCODA) Global 1/12° Reanalysis (GLBv0.08) over the southeastern US shelf waters within the 200-m isobath from the mouth of the Chesapeake Bay (~37.5°N) to the lower range of the surveys (27°N) and within the 200-m isobath of the US GOM (Ferris, 2020). HYCOM values were recorded every 3 hours and were combined with static environmental variables to form a complete prediction data set. The prediction data were filtered to match the observed domains (temporal and environmental variables) and trimmed to coincide with species-specific distributions reported in the literature (Castro, 2010).

The ENMs projected relative abundance over the modified climate data sets, where year was fixed to allow for comparisons, with predictions assumed to represent habitat suitability values. Annual and monthly suitability values for a grid cell were calculated by averaging ENM predictions across years and months, respectively. Suitability values were then deconstructed into five suitability quantiles of Low (0–25), Medium-Low (25–50), Medium (50–75), Medium-High (75–90), and High (90–100), to enable evaluation over time across species-specific size categories. Quantile limits were chosen to facilitate the assessment of habitat suitability across the entire range, with a special focus on the higher quality habitats (Medium-High and High). These limits were kept constant across years and months for each species-specific size category. For each region (Atlantic and GOM), the proportion of grid cells classified in each suitability quantile was calculated across years ($n = 26$) and months ($n = 2$–7 depending on species-specific size category), with associated coefficients of variation (CVs) to characterize uncertainty. Mann–Kendall non-parametric tests (Mann, 1945) evaluated whether temporal trends in these proportions were monotonic, which may be linear or non-linear, while significance was assessed through a median-based regression (Komsta, 2019).

2.4 | Habitat metrics

ENM predictions were the basis for COGs as model-based estimations are more robust than metrics estimated from raw data (Thorson et al., 2016) and annual averages are more representative of the species' overall distribution and habitat suitability than monthly averages, which can be influenced by seasonal and temporal fluctuations (Nye et al., 2009). Annual COGs were calculated separately for each region to characterize patterns in the available habitat for each species-specific size category. COGs for depth of occurrence (DEPTH, m), distance from shore (DFS, km), and temperature (TEMP, °C) were based on the equation:

$$COG_{\text{year}} = \frac{\sum_{i=1}^{k}(x_i * t_i)}{\sum_{i=1}^{k} t_i}, \tag{4}$$

where x_i is the depth, distance from shore, or bottom temperature for grid cell i; t_i denotes the ENM prediction; and k is the total number of species-specific size category grid cells in the study area (Friedland et al., 2021). The center of abundance (COA) was calculated as the distance from a set reference point to the center of the ENM prediction (sensu Nye et al., 2009). The reference point in the Atlantic was north of all samples (38°N, 74°W—80 km off the coast of the Delmarva Peninsula) and east in the GOM (24.9°N, 81.5°W—entrance into the GOM off the southern tip of Florida) to enable evaluation of latitudinal and longitudinal shifts, respectively. Steps to calculate COA were as follows: (1) the latitude and longitude coordinates of each grid cell were converted to across- and along-shelf distances from the reference points due to the curvilinear nature of the coastline, (2) Equation (4) was used to calculate the predicted ENM-weighted mean for across- and along-shelf locations, (3) those predicted mean locations were back-transformed to mean latitude and mean longitude values, and (4) the distance between the reference point and the center of ENM prediction per year was based on the great circle distance formula:

$$\begin{aligned} d = Acos[(\sin(\mathrm{Ref}_{lat})) * \sin(mlat)] \\ + \cos\{\mathrm{Ref}_{lat} * \cos(mlat) * \cos[mlon - \mathrm{Ref}_{lon}]\} \end{aligned} \tag{5}$$

where *mlat* and *mlon* are the mean latitude and longitude of the center of ENM prediction and Ref_{lat} and Ref_{lon} are the latitude and longitude of the reference points, respectively. For this metric, lower COA corresponds to positions in the northeast portion of the Atlantic prediction area and positions closer to the southern tip of Florida in the GOM. The proportion of grid cells with suitable habitat (PROP), defined as the fraction of grid cells with an ENM prediction greater than the cumulative average in the species-specific domain, was computed to evaluate potential habitat expansions or contractions. Temporal trends for COGs were evaluated by median-based regression with a Mann–Kendall test to assess if trends were monotonic.

Relationships between COGs and AMO, GSI, and NAO (*ecodata* R package; Beltz, 2024) were explored because each directly impacts climate patterns and has been shown to affect fish populations and distributions in the southeast US Atlantic coast and GOM (Collins et al., 2013; Stenseth et al., 2002). Relationships between COGs and climate indices were assessed with a median-based regression with Bonferroni correction applied for multiple tests and a Mann–Kendall test evaluated if trends were monotonic.

3 | RESULTS

3.1 | Data summary and size categories

Of the species considered, the results of the GMMs revealed 18 size categories across seven species with no discernable size categories identified for spinner sharks and only a single size category for blacknose (A.) sharks (Table 1). All other species displayed two or three separate size categories. Although size categories were evident for blacknose (G.), bonnethead, and finetooth sharks, most could not be reliably modeled even when combined with adjacent data limited size categories due to the high frequency of zero observations (>92%); accordingly, only size categories with enough data were considered (Table 2). High degrees of overlap between a subset of GMM components were observed for multiple species (Atlantic sharpnose and tiger sharks) and those were merged into a single size category as the likelihoods were relatively comparable.

For SCS species in the Atlantic, data from GA and SC were used in most analyses of species-specific size categories (Table 1). SEFSC was the next most utilized survey for SCS species and the VASMAP survey provided data for only large Atlantic sharpnose sharks. Surveys used for LCS were more variable across species and size categories. VASMAP contributed to at least one size category of all LCS, while GA informed only small blacktip sharks. Surveys used for species with multiple size categories (Atlantic sharpnose, blacktip, sandbar, and tiger sharks) varied across size categories (Table 1).

The ranges of environmental variables and the number of longline sets differed across species-specific size categories depending on the contributing surveys (Table 1 and Figure 2). Overall, the minimum and maximum number of sets for the size categories were 1463 and 7726 for small blacktip and large Atlantic sharpnose sharks, respectively, while the frequency of zero observations ranged from 49.9% for large Atlantic sharpnose sharks to 91.7% for small sandbar sharks.

3.2 | Ecological niche models

The ZANB and SI distributions received the most empirical support across species and size categories, followed by the NB distribution

TABLE 1 The size category (Size cat.) designation, size range (total length; mm), years and surveys utilized, total longline sets, and frequency of a longline set not capturing the species size category of interest (Zero %) for each species size category for small coastal (top) and large coastal shark (bottom) species following Gaussian mixture model analysis. Italics denote size categories identified in the GMM analysis that were not modeled further due to data limitations.

Species	Size cat.	Size range (mm)	Years	GA	SC	SEFSC	VASMAP	Sets	Zero (%)
Small coastal sharks									
Atlantic Sharpnose	Small	168–566	1996–2019	✓	✓	✓		5226	78.5
	Large	567–1223	1996–2019	✓	✓	✓	✓	7726	49.9
Blacknose (A.)	One	410–663	2006–2019	✓	✓	✓		4411	74.6
Blacknose (G.)	*Small*	*475–692*	*2001–2017*			✓		*2687*	*98.1*
	Medium	*693–897*	*2001–2017*			✓		*1432*	*94.2*
	Large	898–1500	2001–2017			✓		1894	73.7
Bonnethead	*Small*	*450–810*	2007–2019	✓				*2516*	*92.2*
	Medium	811–980	2007–2019	✓	✓			1865	88.7
	Large	*981–1257*	2007–2019	✓	✓			*3105*	*92.3*
Finetooth	*Small*	*604–784*	*2007–2018*		✓			*3728*	*98.0*
	Large	785–1616	2007–2018		✓			2223	87.8
Large coastal sharks									
Blacktip (A.)	Small	465–809	2007–2019	✓	✓			1463	86.5
	Large	810–2000	1996–2019		✓		✓	2348	86.0
Sandbar	Small	539–835	1995–2019		✓		✓	2012	91.7
	Medium	836–1530	1996–2019		✓		✓	2758	81.8
	Large	1530–2580	1996–2019			✓	✓	3282	80.8
Spinner	All	660–2350	1996–2019		✓	✓	✓	3708	88.0
Tiger	Small	600–1017	2001–2017			✓		1528	88.5
	Large	1018–3500	1996–2019			✓	✓	2665	88.3

Note: Surveys considered were the Georgia Red Drum Longline Survey (GA), the South Carolina Coastal Longline Survey (SC), the Southeast Fisheries Science Center Bottom Longline Survey (SEFSC), and the Virginia Shark Monitoring and Assessment Program Longline Survey (VASMAP) with check marks denoting when a survey was deemed sufficient for a particular size category. Atlantic and Gulf of Mexico stocks that were examined separately are denoted after species name by A. or G., respectively.

(Table 2). For all size categories that were modeled further, the GAMMs fit the data well and acceptable diagnostic plots were evident for all species except Atlantic sharpnose shark. Although spatial autocorrelation was detected in the residuals for the small and large Atlantic sharpnose shark models, the marginal means from a spatial GAMM (*sdmTMB* R package; Anderson et al., 2022) did not differ considerably; thus, traditional GAMMs were applied to maintain a common modeling framework.

Salinity and temperature were the most frequently included covariates in the selected ENMs across species and size categories. AIC, 10-fold cross-validation, and diagnostic plots supported ENMs that included salinity as either a linear or smoothed covariate, and only the large tiger shark model did not include temperature (Tables 2 and S2). Depth and distance from shore were also retained frequently across models.

The marginal predictions from each ENM scaled by their respective means (hereafter predictions) showed that SCS species were generally associated with warm, high salinity, shallow waters close to shore, with only slight differences between species and size categories (Figure 2a). The highest predictions for dynamic environmental variables for bonnethead, blacknose (A.), and small Atlantic sharpnose sharks, arbitrarily defined as the top 15%, occurred at or near the extremes of the observed variable domains (Figure 2a). The depth prediction for large Atlantic sharpnose sharks revealed an association with deeper waters than other SCS. For blacknose (G.) sharks, predicted distance from shore coincided with areas farther offshore than other species-specific size categories, and peak salinity predictions for finetooth sharks occurred at lower values when compared to other SCS species. Uncertainty in marginal predictions for the SCS was generally high given fairly wide 95% confidence intervals (Figure S1).

Predictions for LCS showed appreciable differences across species and size categories (Figure 2b). The highest abundances for blacktip sharks were predicted to occur in warmer waters and areas closer to shore or shallower when compared to other LCS species, except for medium-sized sandbar sharks. For tiger sharks, peak salinity predictions were generally higher than other LCS predictions. The highest abundances for spinner and small sandbar sharks were predicted to be found in cooler waters, but those for spinner sharks were linked to comparatively higher salinities. Large sandbar shark predictions

TABLE 2 Information regarding the most supported ecological niche model for each species and size category (Size cat.) including the model distribution and components, when applicable (Distr: Comp), significant covariates within the model with options of bottom water temperature (Temp; °C), bottom salinity (Sal), depth (m), and distance from shore (Dist; km), and significant random effects. Potential random effects include month, season, survey, and year.

Species	Size cat.	Distr: comp	Covariates	Random effect
Small coastal sharks				
Atlantic sharpnose	Small	NB	$f(Temp_{k=5}) + Depth + Sal$	Month, survey, year
	Large	ZANB: trNB	$f(Temp_{k=4}) + f(Depth_{k=3}) + Sal$	Month, survey, year
		ZANB: B	$f(Temp_{k=4}) + f(Depth_{k=3}) + Sal$	Month, survey, year
Blacknose (A.)		NB	$f(Temp_{k=5}) + f(SA_{k=5}) + f(Depth_{k=3})$	Month, survey, year
Blacknose (G.)	Large	SI	$f(Temp_{k=5}) + f(Sal_{k=3}) + f(Dist_{k=5})$	Month, year
Bonnethead	Medium	SI	$f(Temp_{k=3}) + f(Dist_{k=3}) + Sal$	Survey
Finetooth	Large	ZANB: trNB	$Depth$	Month
		ZANB: B	$f(Temp_{k=4}) + f(Sal_{k=3}) + f(Dist_{k=3}) + f(Depth_{k=3})$	Year
Large coastal sharks				
Blacktip (A.)	Small	SI	$f(Temp_{k=5}) + f(Sal_{k=4}) + f(Depth_{k=5})$	Year
	Large	ZANB: trNB	$f(Temp_{k=3})$	Month, survey
		ZANB: B	$f(Temp_{k=3}) + f(Sal_{k=3}) + f(Dist_{k=3})$	Month, survey, year
Sandbar	Small	SI	$f(Temp_{k=3}) + f(Sal_{k=3}) + f(Depth_{k=4}) + f(Dist_{k=4})$	Season, survey
	Medium	ZANB: trNB	$f(Temp_{k=5}) + f(Dist_{k=3})$	Survey
		ZANB: B	$f(Temp_{k=5}) + f(Sal_{k=3}) + f(Dist_{k=5})$	Survey, year
	Large	ZANB: trNB	$f(Temp_{k=3}) + f(Dist_{k=3}) + f(Depth_{k=4})$	Month, survey
		ZANB: B	$f(Temp_{k=4}) + f(Sal_{k=3}) + f(Depth_{k=3}) + f(Dist_{k=3})$	Month, survey, year
Spinner	All	SI	$f(Temp_{k=4}) + f(Sal_{k=5}) + f(Depth_{k=5})$	Season, survey, year
Tiger	Small	SI	$f(Temp_{k=3}) + f(Dist_{k=3}) + Sal$	Month, year
	Large	SI	$f(Sal_{k=4}) + f(Depth_{k=3})$	Month, survey, year

Note: Acronyms for model distributions and components are as follows: B, binomial; NB, negative binomial; SI, Sichel; trNB, truncated negative binomial; ZANB, zero-altered negative binomial. Atlantic and Gulf of Mexico stocks that were examined separately are denoted after species name by A. or G., respectively.

peaked at cooler waters and locations farther offshore compared to other LCS species. Like the SCS, uncertainty in the LCS predictions was relatively high (Figure S2).

Ontogenetic differences among peak predictions were observed for both SCS and LCS. Atlantic sharpnose shark was the only SCS with multiple size categories modeled, and predictions showed visible differences across the observed temperature and depth ranges with smaller animals linked to warmer and shallower waters when compared to larger individuals. ENM predictions for salinity differed among size categories for blacktip sharks; higher predictions for small animals were associated with lower salinities with the opposite relationship for large individuals. For small- and medium-sized sandbar sharks, higher ENM predictions occurred for areas closer to shore and at the lowest observed salinities for each size category. Medium-sized sandbar sharks were associated with warmer waters than their small-sized counterparts, but marginal mean curves were relatively similar with high uncertainty (Figure S2). In contrast, higher predictions for large sandbar sharks coincided with cooler, higher salinity, and deeper, offshore waters. Salinity predictions for both size categories of tiger sharks were generally similar.

3.3 | Hindcast projections

Predictions over the HYCOM grid for both SCS and LCS illustrated regions of consistently highly suitable habitat with modest variability for each species-specific size category over the 26 years (maps of annual suitability and variability in the month of September, a month when all size categories were sampled, for small Atlantic sharpnose sharks, Figure 3, and large sandbar sharks, Figure 4, are shown as representatives of SCS and LCS, respectively; see supplementary materials for maps of all other species-specific size categories, Figures S3–14). Highly suitable habitat for Atlantic SCS occurred in coastal waters with high variability at the mouths of estuaries and along the offshore edge of those areas. In the GOM, suitable habitat was predominantly located in water associated with the Mississippi River Delta and along the west coast of Florida. Offshore waters were generally less suitable and variable for both regions (Figures S3–S7). Overlap in highly suitable habitats among species was evident (Figures 3 and S4–S6).

Among the smaller LCS, except for small tiger sharks, highly suitable habitats also appeared to overlap with those of the SCS. Highly suitable habitat was evident in near coastal waters and at the mouths

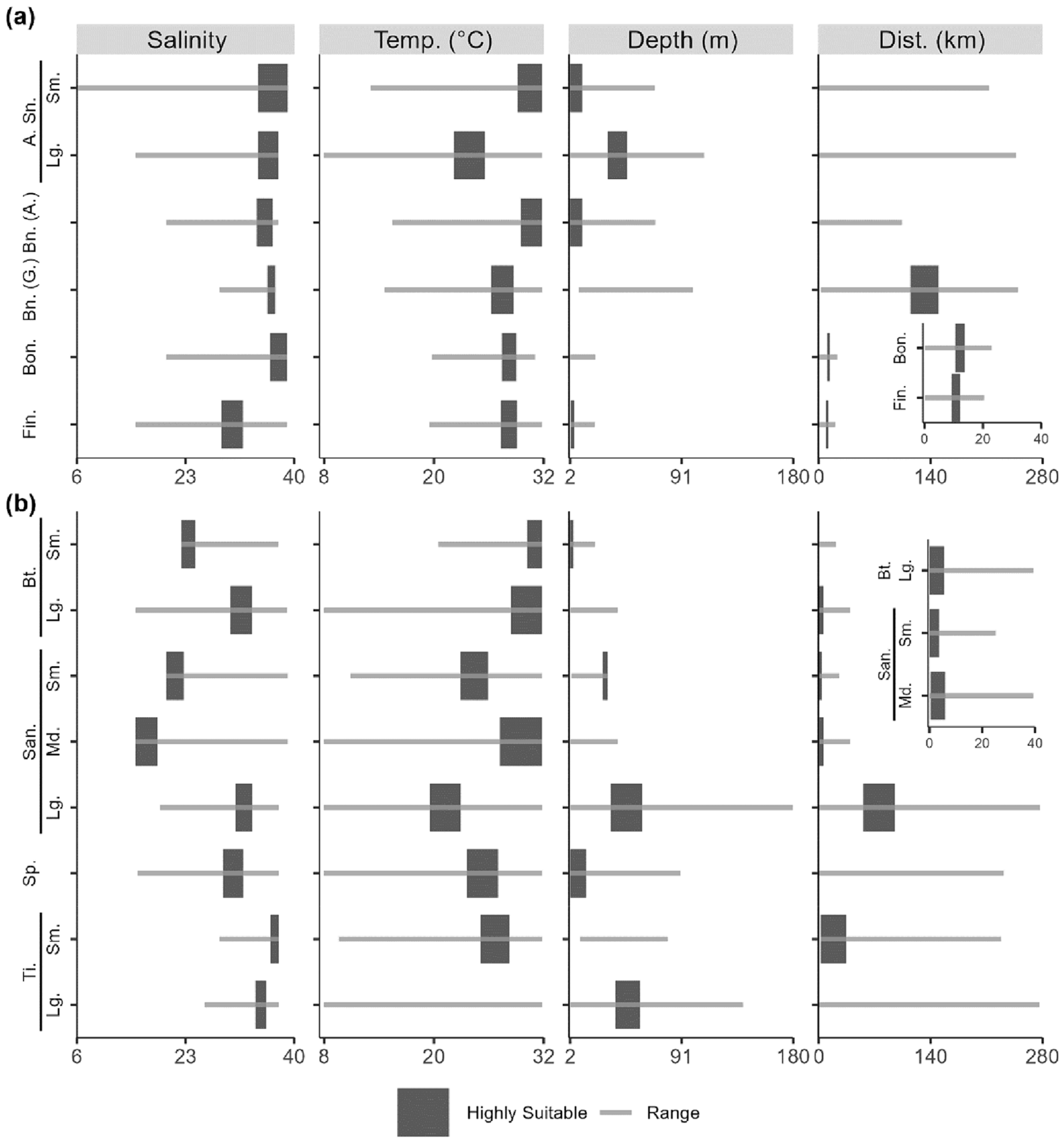

FIGURE 2 The highest predicted scaled relative abundance, arbitrarily defined as the top 15% of all ecological niche model (ENM) predictions (thick dark gray line), plotted over the range of each environmental covariate (thin light gray line) for bottom salinity, bottom water temperature (Temp; °C), depth (m), and distance from shore (Dist.; km) for species-specific size categories of (a) small coastal and (b) large coastal sharks. The absence of a thick line denotes covariates that were not included in the most supported ENM for a size category. Insets of the highest predicted scaled relative abundance close to shore are included for visual analysis. Acronyms for sizes and species are as follows: Sm., small; Md., medium; Lg., large; A. Sn., Atlantic sharpnose sharks; Bn. (A.), Atlantic stock of blacknose sharks; Bn. (G.), Gulf of Mexico stock of blacknose sharks; Bon., bonnethead; Fin., finetooth sharks; Bt., Atlantic stock of blacktip sharks; San., sandbar sharks; Sp., spinner sharks; Ti., tiger sharks.

of estuaries and rivers along the Atlantic coast, and variability was present at the boundaries to deeper waters. Areas off the east coast of Florida, South Carolina, and southern North Carolina in the Atlantic and along the west coast of Florida and Texas coastline in the GOM displayed highly suitable habitats for small tiger sharks. For spinner sharks, highly suitable habitats included coastal waters from Georgia to Virginia and the Mississippi River Delta in the Atlantic and GOM, respectively. Highly suitable habitats for large LCS varied across species, although common hot spots included offshore waters in the Atlantic and the Mississippi River Delta and the west coast of Florida in the GOM (Figures S8–S14).

SCS species largely displayed a significant decrease in higher quality habitat and an increase in lower quality habitat (Figure 5a,b). Examples include a significant increase in the Medium-Low quantile and a significant decrease in the High quantile for bonnethead sharks in the Atlantic and small Atlantic sharpnose sharks in both regions and a significant increase in the Low quantile and decrease in the Medium quantile for blacknose (A.) sharks in the Atlantic and blacknose (G.) and large Atlantic sharpnose sharks in the GOM (Figure 5a,b). The CVs for the more suitable quantiles were often larger than those of the less suitable ones. Higher suitability quantiles decreased during fall months (September, October, and

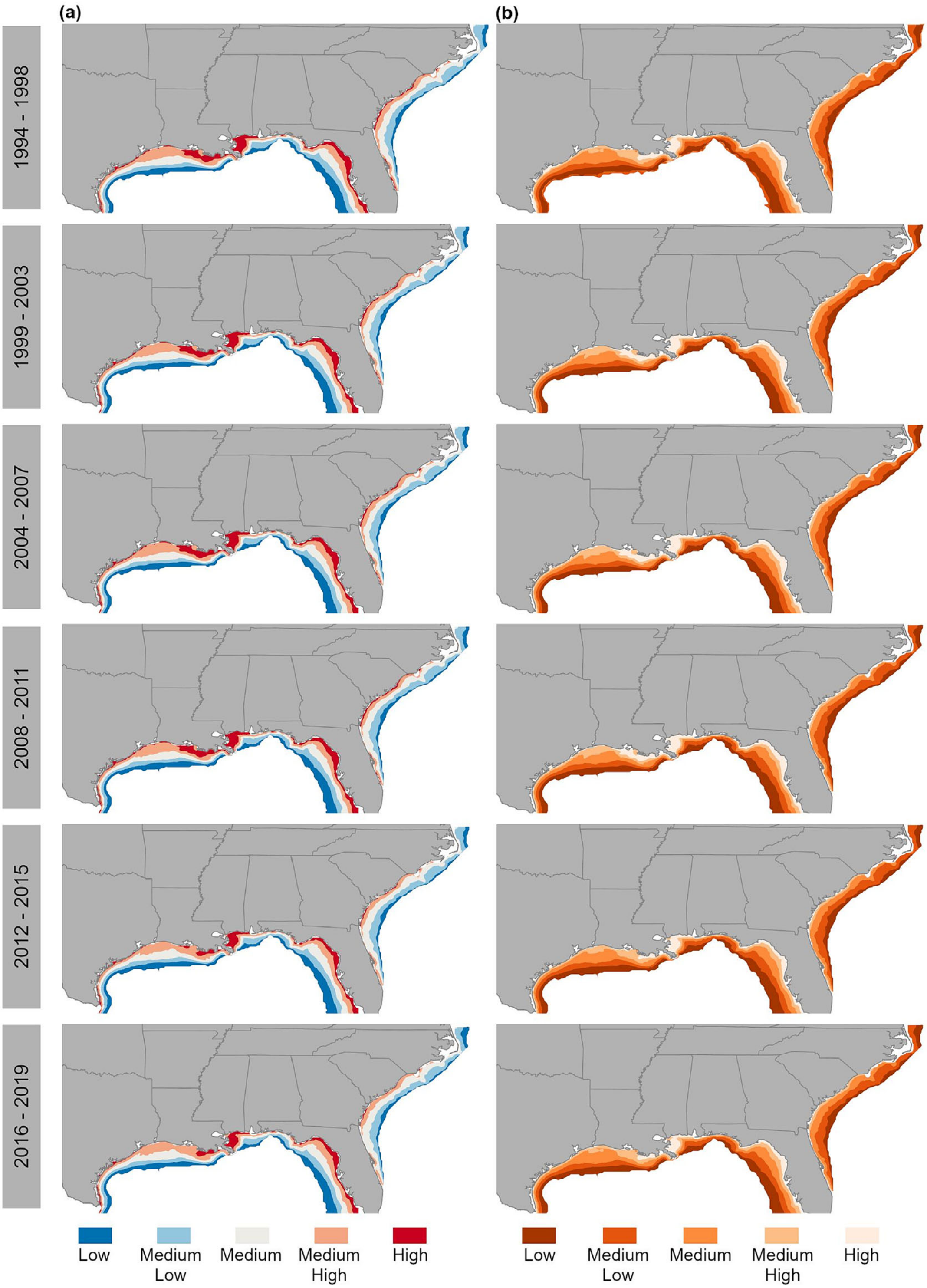

FIGURE 3 Visual representation of predicted yearly (a) habitat suitability and (b) habitat variability (coefficient of variation) for the month of September based on an ecological niche model for small Atlantic sharpnose shark broken down into six time periods of 1994–1998, 1999–2003, 2004–2007, 2008–2011, 2012–2015, and 2016–2019. Habitat suitability and variability predictions were broken down into suitability and variability quantiles of Low (0–25), Medium-Low (25–50), Medium (50–75), Medium-High (75–90), and High (90–100) where High represents higher suitability and variability, respectively. Warmer colors display areas of higher habitat suitability, and cooler tones represent lower suitability. For habitat variability, darker colors are lower variability, while light colors are high variability.

November) across size categories and regions, except for finetooth sharks in the Atlantic (Figure 6a,b). Trends in the earlier months were more variable across size categories and rarely significant. Monthly CVs were again larger for the higher suitability quantiles but were also larger across all quantiles in the later months (Figure 6a,b).

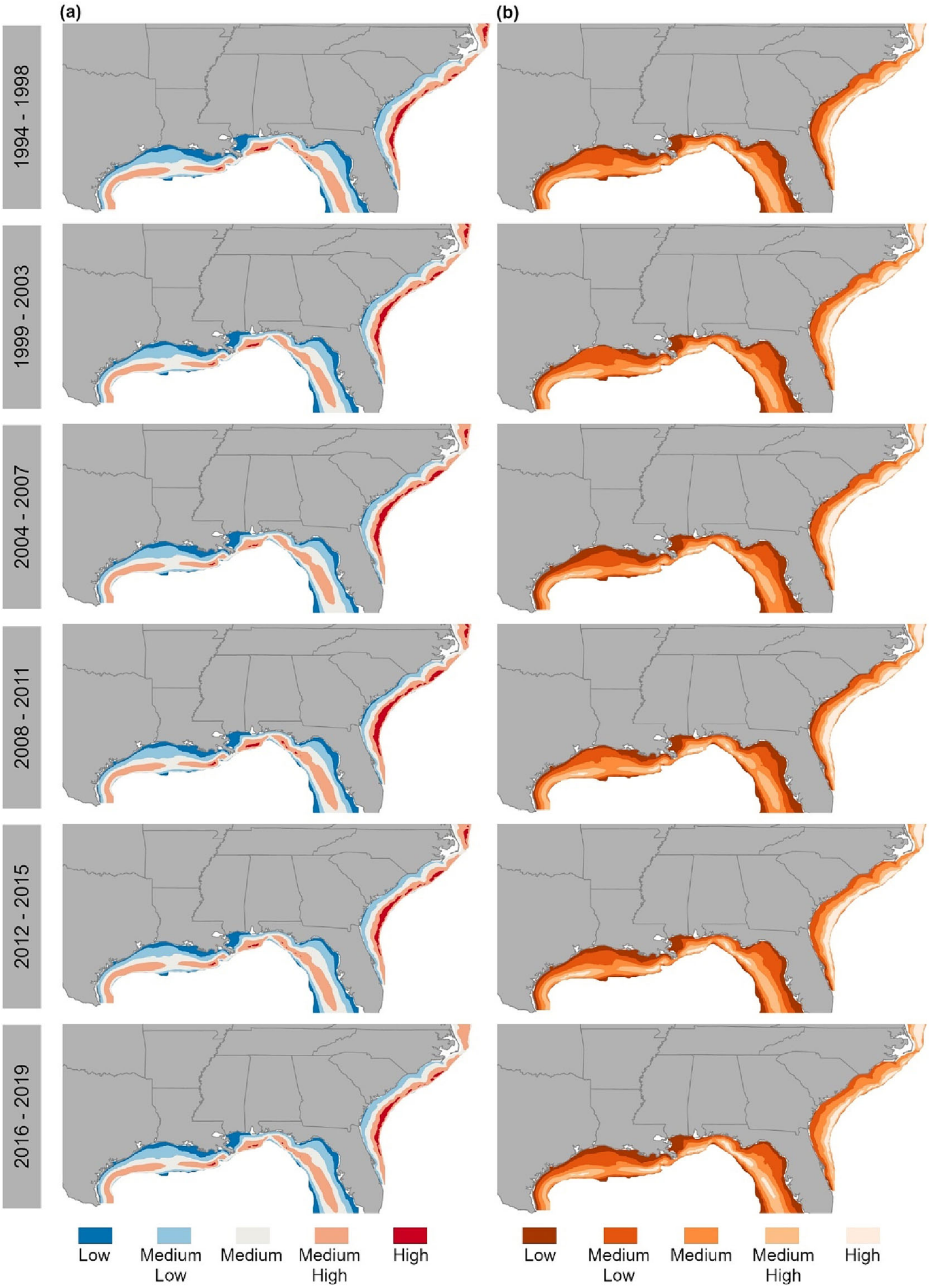

FIGURE 4 Visual representation of predicted yearly (a) habitat suitability and (b) habitat variability (coefficient of variation) for September based on an ecological niche model for large sandbar shark broken down into six time periods of 1994–1998, 1999–2003, 2004–2007, 2008–2011, 2012–2015, and 2016–2019. Habitat suitability and variability predictions were broken down into suitability and variability quantiles of Low (0–25), Medium-Low (25–50), Medium (50–75), Medium-High (75–90), and High (90–100) where High represents higher suitability and variability, respectively. Warmer colors display areas of higher habitat suitability, and cooler tones represent lower suitability. For habitat variability, darker colors are lower variability, while light colors are high variability.

Annual patterns of suitability quantiles were more varied for LCS when compared to SCS (Figure 5c,d). Species size categories displayed one of two general patterns: a significant decrease in higher quality habitat and subsequent increase in the amount of lower quality habitat or the inverse. In the Atlantic, small and large blacktip, small and medium sandbar, spinner, and small tiger sharks displayed the former

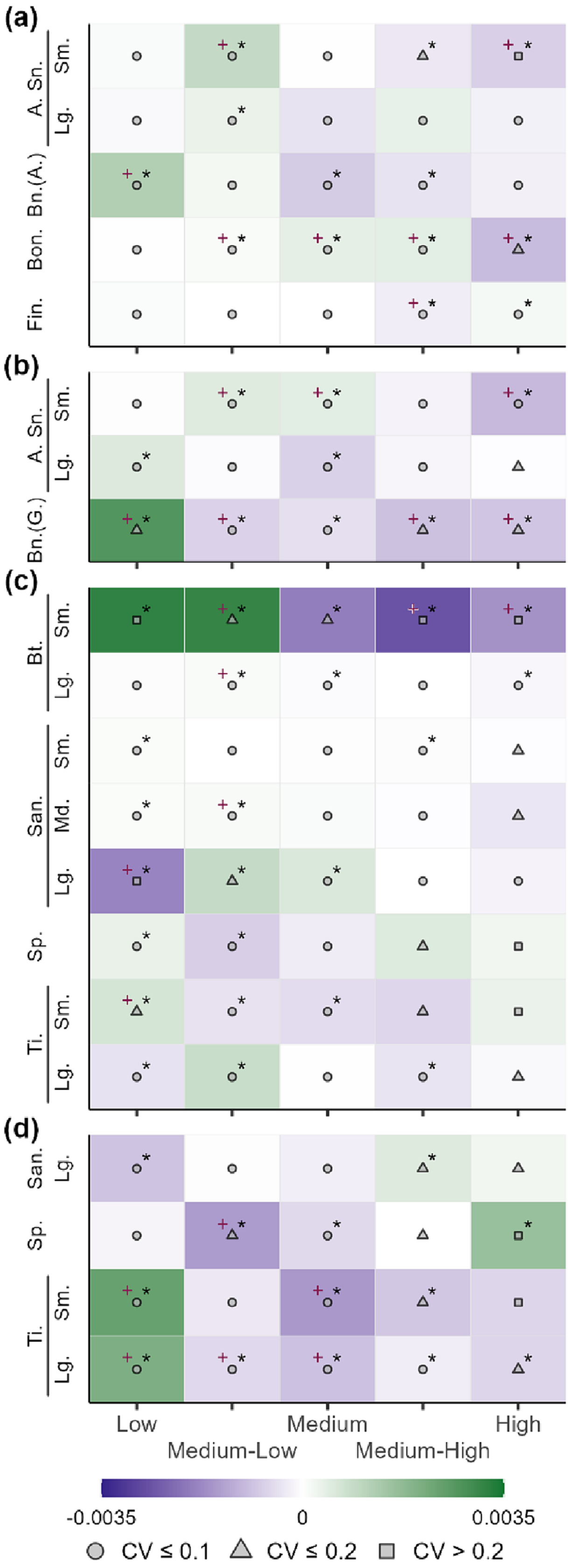

FIGURE 5 Temporal trends from 1994 to 2019 for five suitability quantiles (Low: 0–25; Medium-Low: 25–50; Medium: 50–75; Medium-High: 75–90; High: 90–100) for four species of small coastal shark (SCS) in the Atlantic (a) and Gulf of Mexico (b) and four species of large coastal shark (LCS) in the Atlantic (c) and Gulf of Mexico (d). The magnitude and direction of slopes were determined by median-based regression with positive slopes (green tones) representing an increase in the proportion of grid cells for a quantile and negative slopes (purple tones) a decrease. Asterisks within a cell indicate a significant ($p < .05$) slope according to median regression, and plus signs indicate a significant ($p < .1$) monotonic trend according to the Mann–Kendall test. Secondary symbols represent the size of the coefficient of variation for the proportion of grid cells allocated into a suitable quantile with circles for $CV \le 0.1$, triangles for $CV \le 0.2$ and squares for $CV > 0.2$. Acronyms for sizes and species are as follows: Sm., small; Md., medium; Lg., large; A. Sn., Atlantic sharpnose sharks; Bn. (A.), Atlantic stock of blacknose sharks; Bn. (G.), Gulf of Mexico stock of blacknose sharks; Bon., bonnethead; Fin., finetooth sharks; Bt., Atlantic stock of blacktip sharks; San., sandbar sharks; Sp., spinner sharks; Ti., tiger sharks.

trend while larger sandbar sharks exhibited the latter (Figure 5c). Higher quality habitat for large sandbar and spinner sharks significantly increased but decreased for small and large tiger sharks in the GOM (Figure 5d). An exception to these patterns was large tiger sharks in the Atlantic as both Low and Medium-High quantiles significantly decreased while Medium-Low increased. Very few trends were significant according to Mann–Kendall tests ($p > .1$), which is likely a reflection of the difference in power between the Mann–Kendall tests and median-based regression analyses (Wang et al., 2020). CVs were generally higher for the LCS than SCS across quantiles, and within those, more uncertainty was associated with higher quantiles. Months examined and subsequent temporal trends differed widely across species-specific size categories because of variations in the surveys selected (Figure 6c,d). The higher quality habitat decreased in November in the Atlantic but showed no change in the GOM. Over the later summer and early fall months, patterns largely followed the respective annual trends. Associated uncertainty was larger in earlier and later months and in end quantiles compared to summer months and middle quantiles, respectively (Figure 6c,d).

3.4 | Habitat metrics

Significant trends in COGs for SCS were found in both regions (Figure 7a,b), though nonlinearity was common (Figure S15a,b). COA decreased significantly for small Atlantic sharpnose and bonnethead sharks in the Atlantic (northward) and small and large Atlantic sharpnose sharks in the GOM (eastward) but increased for large Atlantic sharpnose and finetooth sharks in the Atlantic (southward). Trends for DFS and DEPTH consistently aligned with some size categories significantly increasing (offshore and deeper; small Atlantic sharpnose sharks in the Atlantic and both size categories of Atlantic sharpnose sharks in the GOM) and others decreasing (inshore and shallower; large Atlantic sharpnose and finetooth sharks in the

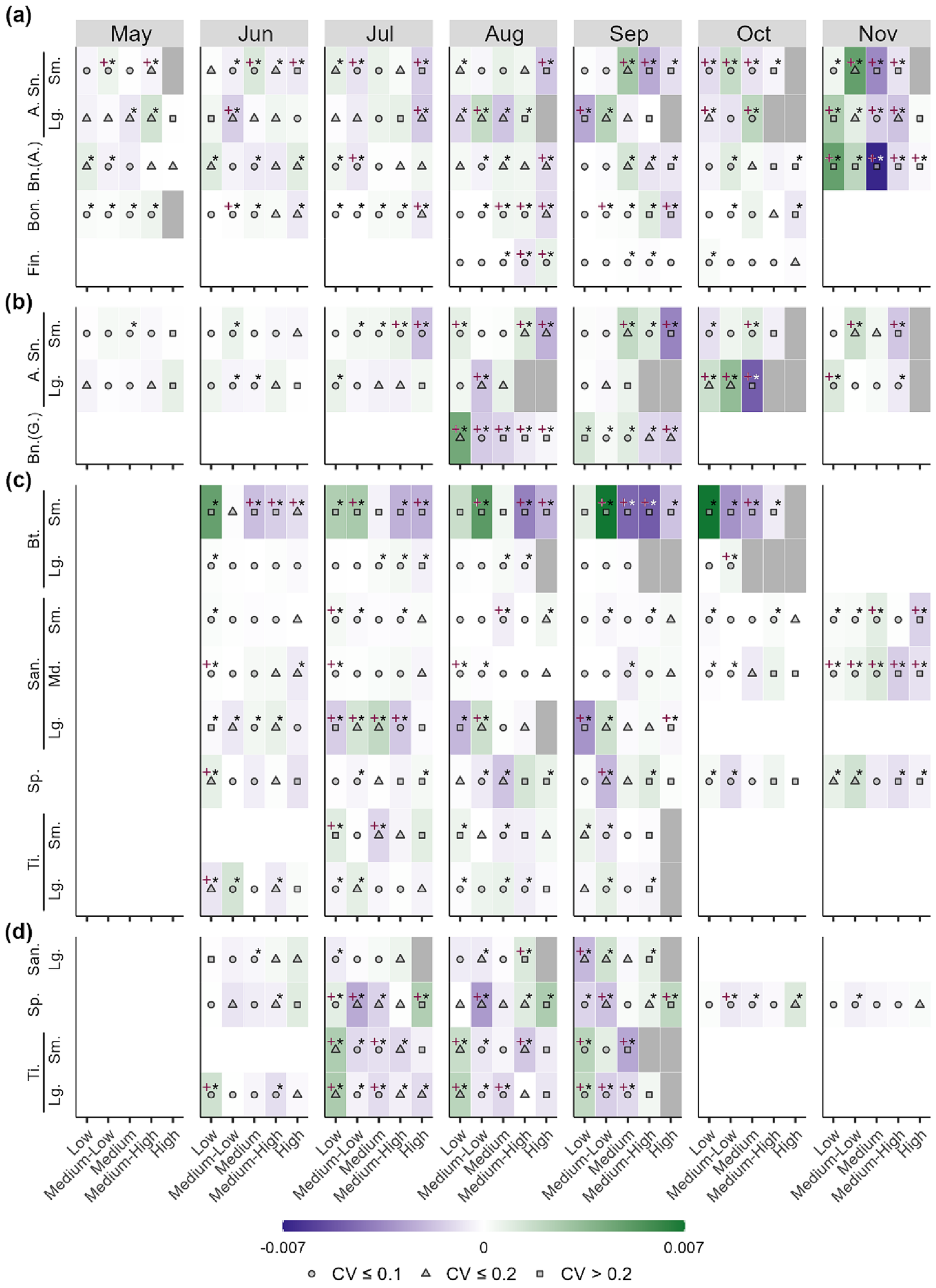

FIGURE 6 Monthly temporal trends from 1994 to 2019 as determined by a median-based regression for the proportion of grid cells assigned to five habitat suitability quantiles (Low: 0–25; Medium-Low: 25–50; Medium: 50–75; Medium-High: 75–90; High: 90–100) for four species of small coastal shark (SCS) in the Atlantic (a) and Gulf of Mexico (b) and four species of large coastal shark (LCS) in the Atlantic (c) and Gulf of Mexico (d). Months are separated and labeled at the top of each column. Positive slopes (green tones) represent an increase in the proportion of grid cells for a quantile and negative slopes (purple tones) represent a decrease. Grey boxes indicate where more than 4 years had no grid cells assigned to that quantile for a given month and were not further analyzed. Asterisks within a cell indicate a significant ($p < .05$) slope according to median regression, and plus signs indicate a significant ($p < .1$) monotonic trend according to the Mann–Kendall test. Secondary symbols represent the size of the coefficient of variation for the proportion of grid cells allocated into a suitable quantile with circles for $CV \leq 0.1$, triangles for $CV \leq 0.2$, and squares for $CV > 0.2$. Breakpoints for quantiles were calculated separately for each size category but held constant across months and years. Acronyms for sizes and species are as follows: Sm., small; Md., medium; Lg., large; A. Sn., Atlantic sharpnose sharks; Bn. (A.), Atlantic stock of blacknose sharks; Bn. (G.), Gulf of Mexico stock of blacknose sharks; Bon., bonnethead; Fin., finetooth sharks; Bt., Atlantic stock of blacktip sharks; San., sandbar sharks; Sp., spinner sharks; Ti., tiger sharks.

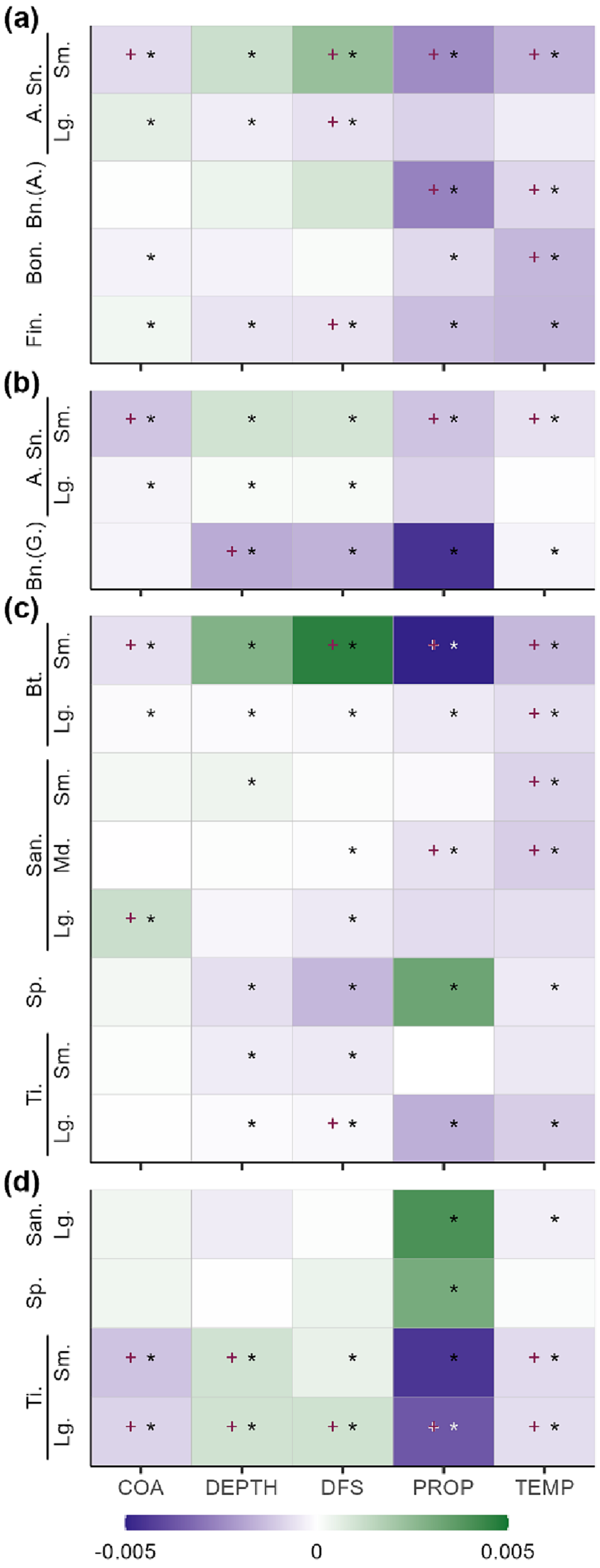

FIGURE 7 Temporal trends from 1994 to 2019 as determined by a median-based regression for five centers of gravity for four species of small coastal shark (SCS) in the Atlantic (a) and Gulf of Mexico (b) and four species of large coastal shark (LCS) in the Atlantic (c) and Gulf of Mexico (d). The five COGs assessed include the center of abundance (COA; km), mean depth of occurrence (DEPTH; m), mean distance from shore of occurrence (DFS; km), the proportion of grid cells with a prediction from associated ecological niche model greater than average prediction (PROP), and mean temperature of occurrence (TEMP, °C). Positive slopes (green tones) represent an increase and negative slopes (purple tones) represent a decrease. Asterisks within a cell indicate a significant ($p < .05$) slope according to median regression, and plus signs indicate a significant ($p < .1$) monotonic trend according to the Mann–Kendall test. Acronyms for sizes and species are as follows: Sm., small; Md., medium; Lg., large; A. Sn., Atlantic sharpnose sharks; Bn. (A.), Atlantic stock of blacknose sharks; Bn. (G.), Gulf of Mexico stock of blacknose sharks; Bon., bonnethead; Fin., finetooth sharks; Bt., Atlantic stock of blacktip sharks; San., sandbar sharks; Sp., spinner sharks; Ti., tiger sharks.

Atlantic and blacknose (G.) sharks in the GOM). Trends in PROP and TEMP were negative for all SCS in both regions, though they were not significant for large Atlantic sharpnose sharks in either region.

Fewer trends in COGs were significant for LCS compared to SCS (Figure 7c,d), and nonlinearity patterns were often present (Figure S15c,d). COA decreased significantly for small and large blacktip sharks along the Atlantic (northward) and small and large tiger sharks in the GOM (eastward). Large sandbar sharks along the Atlantic were the lone size category with a significant increase in COA (southward). Similar to SCS, trends in DEPTH and DFS were often in tandem, though a few size categories displayed significant trends for only one COG (an increase in DEPTH for small sandbar sharks and a decrease in DFS for medium and large sandbar sharks in the Atlantic). PROP and TEMP commonly declined in both regions, but PROP significantly increased for spinner sharks in the Atlantic and large sandbar and spinner sharks in the GOM.

Climate indices and COGs were significantly related for multiple SCS size categories (Figure 8a,b). AMO was rarely significantly related to a COG besides COA, with size categories exhibiting positive (large Atlantic sharpnose and finetooth sharks in the Atlantic) and negative (small Atlantic sharpnose and bonnethead sharks in the Atlantic and large Atlantic sharpnose sharks in the GOM) trends. Both DEPTH and DFS were often positively related to GSI and NAO in the Atlantic (e.g., small Atlantic sharpnose sharks) but showed negative trends in the GOM (e.g., blacknose (G.) sharks). PROP was only significantly related to GSI for bonnethead sharks in the Atlantic but was frequently negatively related to climate indices in the GOM. Large Atlantic sharpnose shark was the only SCS size category where TEMP was significantly positively related to GSI and NAO, as most other size categories showed negative relationships.

For the LCS, relationships between COGs and the GSI and NAO were similar across species and size categories but often showed the opposite pattern when related to AMO. AMO was not significantly related to COGs in the Atlantic (except for COA of small

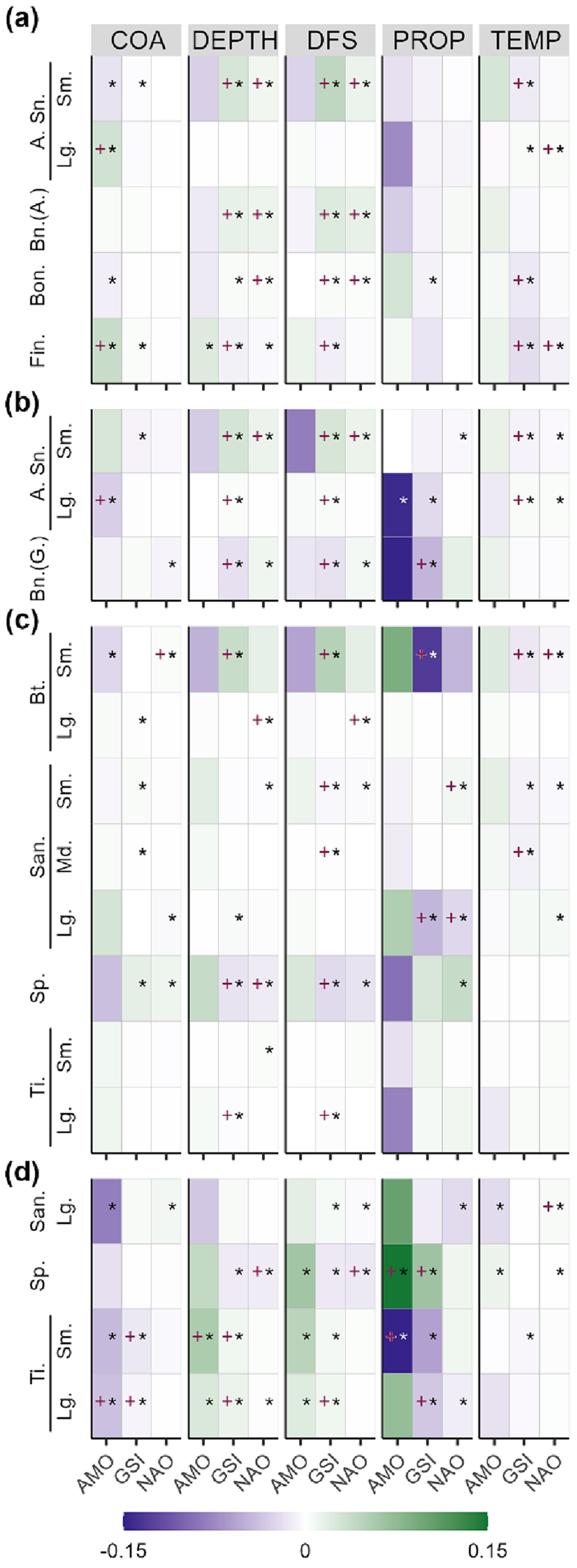

FIGURE 8 Trends between three large-scale climatological trends and five centers of gravity (COGs) as determined by a median-based regression and Mann–Kendall test for four species of small coastal sharks in the Atlantic (a) and Gulf of Mexico (b) and four stocks of large coastal sharks in the Atlantic (c) and Gulf of Mexico (d). The three large-scale climatological trends are the Atlantic Multidecadal Oscillation (AMO), the Gulf Stream Index (GSI), and the North Atlantic Oscillation (NAO), and the five COGs assessed include the center of abundance (COA; km), mean depth of occurrence (DEPTH; m), mean distance from shore of occurrence (DFS; km), the proportion of grid cells with a prediction from associated ecological niche model greater than the average prediction (PROP), and mean temperature of occurrence (TEMP, °C). Positive slopes (green tones) represent an increase, and negative slopes (purple tones) represent a decrease. Asterisks within a cell indicate a significant ($p < .05$) slope according to median regression, and plus signs indicate a significant ($p < .1$) monotonic trend according to the Mann–Kendall test after accounting for multiple tests by applying Bonferroni correction. Acronyms for sizes and species are as follows: Sm., small; Md., medium; Lg., large; A. Sn., Atlantic sharpnose sharks; Bn. (A.), Atlantic stock of blacknose sharks; Bn. (G.), Gulf of Mexico stock of blacknose sharks; Bon., bonnethead; Fin., finetooth sharks; Bt., Atlantic stock of blacktip sharks; San., sandbar sharks; Sp., spinner sharks; Ti., tiger sharks.

blacktip sharks) but showed significant relationships with multiple size categories for all COGs in the GOM. Significant trends between COGs and climate indices were detected for large blacktip, small and medium sandbar, and small and large tiger sharks along the Atlantic, but slopes were very small (Figure 8c). In contrast, small blacktip, large sandbar, and spinner sharks in the Atlantic showed significant relationships across most COGs when compared to GSI and NAO. Significant trends were more common for species and size categories in the GOM, particularly for large tiger and spinner sharks (Figure 8d).

4 | DISCUSSION

Studies of habitat utilization of marine populations have predominately focused on teleost species (Melo-Merino et al., 2020), and those involving sharks have often targeted younger ages in nursery habitats due to the close proximity to shore (Latour et al., 2022; Ward-Paige et al., 2015) or examined species groups to mitigate the challenges of limited data (Birkmanis et al., 2020). This study is the first to investigate the habitat characteristics of several shark species through ontogeny and over a broad spatiotemporal extent. Resultant ENMs fit the data well and documented appreciable interspecific and intraspecific differences in ecological niches for coastal sharks. The quantity of higher quality habitat decreased throughout the time series for most SCS and some LCS with directional trends in COG for some size categories indicating potential shifts north along the Atlantic or toward cooler or deeper offshore waters in both regions. These results improve our understanding of coastal shark ecology along the southeast US coast and suggest potential population-level responses of coastal sharks to climate change and multidecadal variability.

4.1 | Size categories

The documented ontogenetic shifts in abiotic habitat utilization for coastal shark species (Grubbs, 2010; Speed et al., 2010) suggest that species-specific ENMs could miss important intraspecific habitat associations and motivated decomposing length composition data into size categories. GMMs are a useful tool when only length composition data are available as they allow for an objective statistical approach as opposed to a subjective visual examination (Campana, 2001; Sethi et al., 2017). However, estimated thresholds may not necessarily align with age classes. For example, the estimated size categories for sandbar sharks aligned well with age groups (small; <1.11, medium; 1.11–6.93, large; >6.93 years) but not for blacktip sharks (small; <0.6, large; >0.6 years) based on von Bertalanffy growth model parameters for sexes combined (Deacy & Moncrief-Cox, 2019; Hale & Baremore, 2014). Limited research has been conducted on whether shifts in habitat utilization occur at specific ages for shark species (Grubbs, 2010). By utilizing fitted GMMs, this study was able to provide a more detailed and refined understanding of abiotic habitat utilization throughout ontogeny.

The GMMs often yielded cryptic model components (multiple curves within an observed length mode) or highly overlapping components. Cryptic components may represent sampling variability given the different surveys, sampling designs, and data limitations but could also be due to combining different sexes or maturity stages within a single size category. However, due to the high proportion of zeros in the data set, cryptic and overlapping components were combined into single size categories to ensure successful ENM fitting. The differences in gear characteristics and sampling protocols (i.e., hook type, hook size, bait, soak time, etc.) across surveys likely impacted selectivity and subsequent estimated size category thresholds (Afonso et al., 2012). All surveys except VASMAP use circle hooks, which are associated with higher catch rates (Curran & Bigelow, 2011) while not affecting species diversity (Ingram et al., 2005). Larger hook sizes select against smaller animals (Løkkeborg & Bjordal, 1992) and the relatively large hook used by VASMAP likely explains the absence of small Atlantic sharpnose shark encounters. Differences in bait between surveys could also affect the sizes of animals sampled given ontogenetic shifts in diet (Heupel et al., 2014; Weltersbach et al., 2019), and the short soak times for GA and SC (<1 hour) could potentially reduce encounter rates with larger, more mobile individuals (Peterson, Gartland, et al., 2017). Although the surveys used cover a sizable portion of the home range of most target species, data from the survey covering the largest area (SEFSC) represents a single annual snapshot (July–September) of sampled populations in depths greater than 9 m across both regions. Therefore, important size categories and maturity stages may be absent from the size composition data analyzed given the complex spatiotemporal migration patterns of coastal sharks, particularly the LCS (Kohler & Turner, 2020). Nevertheless, survey data analyzed in this study constitute a large portion of fishery-independent information routinely used in shark stock assessments in the southeastern United States (SEDAR, 2017, 2020) and represent the best available population-level information.

4.2 | Ecological niche models

Differences in estimated marginal means between management complexes and species support the notion of limited interspecific and intraspecific interactions within the respective abiotic niche structures. As previously noted, the LCS had no overarching ecological niche and these noted differences in estimated marginal means support studies highlighting that large-bodied, less productive species are risk-averse and utilize different areas with age and size (Cortés et al., 2012; Duncan & Holland, 2006). Further, individual management practices may be best for LCS species as previous studies have noted significant differences in the population dynamics and life history characteristics (Casey, 2006; Castro, 2010) and differences in habitat utilization may indicate varying interactions between species and their shared habitat that should be assessed on an individual basis (Barker & Schluessel, 2005). Differences in ecological niches between size categories of species that do not utilize nursery areas (Atlantic sharpnose and tiger sharks) could reduce predation and competition (Heithaus, 2001; Heupel et al., 2007). For species exploiting nursery areas (blacktip and sandbar sharks), salinity emerged as important given that movements of larger animals away from nursery habitats correspond with shifts toward higher salinities (Grubbs & Musick, 2007; Heupel & Simpfendorfer, 2002; Santander-Neto et al., 2020). A similarity analysis could more formally evaluate if differences in estimated marginal means are examples of niche partitioning.

This is the first study to evaluate the importance of abiotic factors for several shark species through ontogeny and over a broad spatiotemporal extent; however, previous studies have investigated the effects of temperature, salinity, and depth for juveniles (Heithaus et al., 2007; Heupel & Simpfendorfer, 2008; Ortega et al., 2009; Ubeda et al., 2009) and adults (Crear et al., 2021; Osgood et al., 2021). The results of this study are consistent with previous work, such as lower salinity and warmer water being important environmental factors for finetooth (Ward-Paige et al., 2015) and blacktip sharks (DeAngelis et al., 2008; Froeschke et al., 2010), respectively. There are also important differences between studies, which could be related to the spatiotemporal scale or because different subsets of the population were examined. For example, salinity was a significant environmental variable in this study for both size categories of blacktip sharks but was not significant in Ward-Paige et al.'s (2015) study. The sizable spatial range of this study corresponds with large ranges in environmental variables compared to studies focusing on a single (DeAngelis et al., 2008; Heupel et al., 2006) or a few bays and estuaries (Froeschke et al., 2010; Ward-Paige et al., 2015). Further, differences in the size range and sex ratio of the sharks being studied could impact the significance and range of abiotic factors, highlighting the importance of considering the specific population being studied (Drymon et al., 2020).

Abiotic factors beyond those considered here (e.g., substrate, dissolved oxygen, and turbidity) were significantly correlated with the relative abundance of shark species in previous studies (Birkmanis et al., 2020; Ward-Paige et al., 2015). Unfortunately, data on these covariates are not routinely collected in all four surveys included here and could not be evaluated in ENMs. The abiotic environment is only one component of a realized niche (Peterson et al., 2015; Soberon & Peterson, 2005) and biotic forcing, such as predator–prey interactions, also shapes habitat utilization (Selden et al., 2018). Interspecific and intraspecific prey partitioning has been documented for coastal shark species, as have ontogenetic shifts in diet composition (Cortés, 1999; Wetherbee et al., 2012). Future synoptic sampling of predators and associated prey fields could generate valuable biotic covariates for ENMs and, in turn, yield greater insight into shark habitat ecology.

4.3 | Hindcast projections

Coupling ENMs with historical climate data in the Atlantic and GOM facilitated the identification of regions associated with expected highly suitable habitats for coastal sharks and shifts in the timing and area of this habitat from 1994 to 2019. Suitable habitat predictions aligned well with documented distributions (Castro, 2010), and the distributions of suitable habitat for each species and size category were relatively consistent throughout the hindcast period, recognizing that annual and monthly averaging approaches could have obscured finer-scale variability in suitable habitat. While domains of historical abiotic data were constrained to mirror those included in the ENMs, data could extend beyond the combined spatial sampling frame to more fully capture known spatial distributions of these species.

For most SCS and LCS, the relative abundance increased with temperature, suggesting warming in the Atlantic and GOM due to climate change may have had minimal adverse effects on the quality of available habitat. However, the ecological niche of a species is molded by a suite of abiotic and biotic factors that shape its geographic distributions (including distributional shifts; McHenry et al., 2019). Mobile elasmobranchs tend to have narrow thermal sensitivity (Lear et al., 2019), but salinity also limits a species' range through physiological mechanisms related to osmoregulation stress (Bernal et al., 2012). Precipitation has increased throughout the southeastern United States (Bishop, Williams, & Seager, 2019; Bishop, Williams, Seager, Fiore, et al., 2019) and sea levels are projected to rise rapidly along parts of the eastern US coastline (Landerer et al., 2007; Piecuch et al., 2018; Yin et al., 2009), both of which could potentially affect salinity in coastal waters. Changes in coastal salinity could offset the potential benefits of increased temperature on the extent of suitable habitat available to coastal shark species. Further, coastal waters and the higher quality habitat may become more variable given the increase in frequency and intensity of heatwaves and tropical storms (Frölicher et al., 2018; Patricola & Wehner, 2018), which can significantly impact coastal environments (Gutowsky et al., 2021; Osgood et al., 2021) and the distribution and residency time of individuals (Doney et al., 2012).

Investigations of shifts in migration times for coastal sharks are limited except for a documented shift to earlier in the year and northward locations for tiger sharks in the eastern United States (Hammerschlag et al., 2022). Higher quality habitat declined over the latter fall months for the majority of both SCS and LCS and could suggest earlier migrations from summer to winter habitats. However, long-term temporal patterns in the extent of higher quality habitat coincide with the relatively large variability, which may be attributable to the fact that the hindcast projections were conducted over a known migration, likely obscuring consistent trends in migration timing.

The analytical framework used here to identify temporal trends in the landscape of suitable habitats could aid in developing various management measures (SEDAR, 2020). For example, time/area closures are considered valuable management strategies to control harvest and ensure sustainable shark populations (Bonfil, 1999; Cortés, 2002; Ellis et al., 2009; Musick et al., 2000), but the changing spatiotemporal distributions of these animals could impact the efficacy of these measures (Davies et al., 2021; Santora et al., 2021). Quantifying spatiotemporal patterns in suitable habitats presents the opportunity for more dynamic management approaches that could refine species-specific regulations at appropriate temporal and spatial scales (Dunn et al., 2016; Lewison et al., 2015). Further, identifying essential fish habitats associated with higher habitat suitability, with a particular focus on defining changes in critical habitats throughout ontogeny (Ellis et al., 2009), could prove valuable.

4.4 | Habitat metrics

Few studies have assessed how coastal shark populations will respond to environmental change, even though their spatiotemporal distributions will likely shift in response to climate change (Chin et al., 2010; Diaz-Carballido et al., 2022; Hare et al., 2016). Further, large-scale climatological patterns are known to affect shark populations (Peterson, Belcher, et al., 2017; Witt et al., 2012), and natural phenomena may temper or intensify these impacts (Schlaff et al., 2014). The evaluation of trends in COGs over time and in relation to climatological indices revealed directional changes in the suitable habitat of several coastal shark species and identified hypothesized drivers of these trends.

Although not all trends were visually linear, which is unsurprising given the natural variability in climate data, the highly suitable habitat appeared to decrease throughout the time series for all SCS and most LCS. Directional trends in DEPTH, DFS, and COA indicated potential shifts north along the Atlantic (e.g., small Atlantic sharpnose, bonnethead, and blacktip sharks) or toward deeper offshore waters in both regions (e.g., small blacktip sharks in the Atlantic, small and large tiger sharks in the GOM, and small Atlantic sharpnose sharks in both regions), which mirrors patterns observed for several teleost fishes (Bowers & Kajiura, 2023; Kleisner et al., 2017; Nye et al., 2009). Directional trends were less common for LCS compared to SCS, and besides small blacktip sharks, significant trends were relatively small. Habitat for SCS species is generally more specialized and constricted than the LCS, likely due to narrow ranges of peak relative abundance for the ENM variables considered. Habitat changes do not occur uniformly across space which may result in habitat fragmentation that could limit geographic ranges through reduced connectivity (Caldwell & Gergel, 2013).

Warm phase AMO, associated with increased rainfall in Florida and heightened hurricane activity in the Atlantic Ocean, was associated with northward or southward shifts in the Atlantic for some SCS size categories. Northward shifts mirror the general movements of teleost fishes poleward (Nye et al., 2014), but Atlantic sharpnose sharks exhibited shifts in both directions at different sizes (northward for small and southward for large individuals), highlighting the importance of investigating the specific needs and vulnerabilities of sharks through ontogeny. In contrast, except for small blacktip sharks, no significant impacts were noted for LCS in the Atlantic but were commonly present in the GOM for all COGs evaluated. Populations in the GOM may be more sensitive to changes in environmental conditions associated with the AMO than populations in the southeastern Atlantic due to differences in their physiology (Speed et al., 2010), underscoring the importance of investigating the specific needs and vulnerabilities of shark populations and developing region-specific management approaches to protect marine ecosystems.

Overall, COGs were more frequently significantly related to GSI and NAO for SCS species over LCS, likely due to SCS species being constrained to specific habitats such as shallow coastal areas and estuaries, whereas LCS species are more widely distributed (Kohler & Turner, 2020). Only COGs for two size categories (blacknose (G.) and small tiger sharks in the GOM) displayed conflicting trends between GSI and NAO, which is unsurprising given that the position of the Gulf Stream and Gulf Stream Wall may be linked to NAO intensity (Taylor et al., 1998). Positive GSI and NAO values indicate an increase in water temperature along the southeast US coast and could expand higher quality habitat offshore for warmer water size categories, such as small Atlantic sharpnose sharks. Conversely, cooler water species (e.g., finetooth, large Atlantic sharpnose, blacknose (G.), spinner, and large sandbar sharks) largely displayed no or very small directional shifts except for spinner sharks, which showed a significant shift to inshore waters. Possible explanations include increased hypoxic waters close to shore, which spinner sharks utilize (W. Driggers, personal communication), but the absence of size categories prevented a more detailed ontogenetic analysis. Movement inshore could increase interaction with fishing gears and humans (Afonso et al., 2017; Dulvy et al., 2014) but may support improved recruitment and increased nursery utilization (Peterson, Belcher, et al., 2017). Decreased higher quality habitat for large sandbar sharks was linked to positive GSI and NAO values with visible declines off the coast of Virginia in more recent years. Previous findings noted a decrease in the relative abundance of sandbar sharks off the Virginia coast in high NAO years (Peterson, Belcher, et al., 2017), and this could partially explain the southward shift in COA as the GSI and NAO were predominately positive for the last 8 years of the time series. Although several significant trends were detected between COGs in the GOM and GSI, underlying mechanisms for these relationships remain unclear as GSI is an Atlantic-focused index. Further research investigating additional large-scale climatology indices could provide insight into an overarching climatological trend impacting the Gulf Stream Wall location and environmental conditions within the GOM.

All COGs were calculated annually, but the months over which data were analyzed and predictions were computed generally differed across species-specific size categories (May–November for small Atlantic sharpnose sharks versus August–September for blacknose (G.) sharks). Maintaining consistent temporal resolution would require generating predictions for months not reflected in the underlying observed data used to construct the ENMs. Overcoming this challenge would require modifications to the temporal extent of monthly sampling for several surveys. Further, while ENMs were fit to the best available population-level data, uncertainty for models was generally high and could affect the conclusions about habitat utilization or shifts in distribution. However, large confidence errors do not necessarily indicate poor model performance, as some level of uncertainty is expected in any model, and the models performed well given the complexity and limitations of the data. Evaluating COGs over an extended period would likely provide deeper insight into potential long-term patterns of habitat quality and availability, but this is the longest period possible given the data. Additionally, COG results were based on the benthic climate model layer because of the gear and target species biology; however, target species utilize the entire water column which is an important consideration when interpreting patterns and shifts in COGs. It is also important to note that all COGs were calculated from hindcast projections that did not include measures of uncertainty. Bootstrapping ENM models and predicting each iteration across the climate data set could provide estimates of uncertainty in habitat availability and COG predictions but was not attempted here due to long processing times. As computing power increases and processing times decline, estimating uncertainty in COGs would enhance interpretation.

CONCLUSION

Studies on shark habitat ecology over relatively large spatial scales and ontogeny are limited. The availability of long-term fishery-independent datasets for coastal shark species provided an opportunity to assess the impacts of environmental factors on suitable habitats for multiple species and size categories. Models developed here revealed that abiotic niches of coastal shark species varied by taxon size. The combination of ENMs and climate data aided in the characterization of spatiotemporal patterns in suitable habitats. The higher quality habitat declined for most species-specific size categories, particularly during fall months, and directional trends in COGs revealed potential shifts north along the Atlantic and to deeper offshore waters in the Atlantic and GOM for multiple taxa examined. Further, climate oscillations may cause redistributions that could increase encounter rates between the coastal sharks and fishers, like those seen in some teleost fisheries (Báez et al., 2021). In recent years, fisheries managers have recognized the need to enhance spatial resource management measures for coastal sharks, including the designation of marine protected areas and closed areas (Crear et al., 2021; NOAA Highly Migratory Species Office, personal communication). The analytical framework used here to identify temporal trends in the landscape of suitable habitat can aid in developing these various management measures designed to rebuild and maintain sustainable coastal shark populations in the southeast United States and GOM.

AUTHOR CONTRIBUTIONS

Kaitlyn A. O'Brien, Enric Cortés, William B. Driggers III, Bryan S. Frazier, and Robert J. Latour contributed to the study design. William B. Driggers III, Bryan S. Frazier, and Robert J. Latour provided SEFSC, SC, and VASMAP survey data, respectively. Statistical analyses were conducted by Kaitlyn A. O'Brien with input from Robert J. Latour. The first draft of the manuscript was written by Kaitlyn A. O'Brien and subsequently revised by comments from Enric Cortés, William B. Driggers III, Bryan S. Frazier, and Robert J. Latour. All authors approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no competing interests.

DATA AVAILABILITY STATEMENT

Catch data from GA and SEAMAP-SA Coastal Trawl Survey data are publicly accessible online with access information provided in the main text. Catch data from SC, SEFSC, and VASMAP are available from the respective author (see Author Contributions) upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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