Received: 23 April 2023 | Revised: 31 January 2024 | Accepted: 27 February 2024

DOI: 10.1002/ecs2.4868

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Spatiotemporal dynamics of Atlantic reef fishes off the southeastern U.S. coast

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Funding information
National Oceanic and Atmospheric Administration (NOAA), Grant/Award Number: 80843-Z7553201

Handling Editor: Sean P. Powers

Abstract

Understanding the spatiotemporal dynamics of fish species is a central concern in fish ecology and crucial for guiding management and conservation efforts. We constructed a joint species distribution model (JSDM) to simultaneously estimate the spatiotemporal distributions and densities for 21 reef fish species in the southeastern United States (SEUS). The model separately estimates encounter probability and positive density, and accounts for unobserved spatial and spatiotemporal variation using latent factors, where the correlations among species are induced. We applied the model to video data collected from a large-scale, fishery independent survey. A clustering method was applied to the results of the JSDM to group species based on spatial and spatiotemporal synchrony in encounter probability and positive density. We found strong spatial associations among most of the reef fish species. However, species did exhibit differences in occupied habitat that varied with latitude and/or depth. Within their area of occupied habitat, almost all the species share similar spatial pattern of average density. However, for some species, annual distributions were less correlated with their expected average distributions perhaps due to differing responses to underlying spatiotemporal drivers. Some species show significant declines in abundance, for example, black sea bass, red porgy, and blueline tilefish, while a small number of species showed evidence of shifts in distribution, for example, black sea bass. The findings suggest that spatiotemporal management strategies may be of limited utility for reducing bycatch in these highly mixed reef fisheries due to high spatial correlations in occupied habitat and spatial patterns in density. Species-specific responses to environmental change may also influence the spatiotemporal structure of reef assemblages. This work suggests management attention is needed for some of the lesser known species as they are showing declining trends in abundance.

KEYWORDS
abundance, distribution shift, joint species distribution model, reef fish, southeastern United States, spatial associations, spatiotemporal synchrony

INTRODUCTION

Understanding the spatiotemporal dynamics of fish species is a central concern in fish ecology and crucial for guiding management and conservation efforts. Species distribution models (SDMs) have been widely used to map spatial distribution of a given species as a function of biotic and abiotic variables (Elith & Leathwick, 2009). However, single-species SDMs are limited because they lack any consideration of biotic interactions which are known to influence spatial distributions (Kissling et al., 2012; Pichler & Hartig, 2021) and do not leverage information across species that co-occur in the same general habitat. Stacking maps from independent, single-species SDMs can be used to provide insights on community-level patterns and processes. However, this approach can be problematic, and a better approach to estimating the combined responses of multiple species is to model their distributions jointly (Clark et al., 2014). Recently, joint species distribution models (JSDMs) have been developed as a novel analytical framework to simultaneously model the spatial distributions of multiple species while also incorporating associations among species (Pollock et al., 2014; Thorson et al., 2015, 2017; Tikhonov et al., 2017; Warton et al., 2015).

Although an ecosystem-based approach to fisheries has been widely recognized and proposed as a more effective and holistic approach for managing marine fisheries, single-species frameworks remain common in fisheries around the world (Craig & Link, 2023; Karp et al., 2023; Skern-Mauritzen et al., 2016). Ignoring species interactions can affect the ecological, biological and economic performance of a fishery management system in a complex manner (Kaplan et al., 2021; Mackinson et al., 2018; Townsend et al., 2019; Trijoulet et al., 2020). One of the most common and difficult issues facing single-species fisheries management is bycatch, which can contribute to the overfishing of nontarget species, as well as threaten protected and endangered species (Bellido et al., 2011; Pons et al., 2022). Managing bycatch is a particular challenge in mixed-stock fisheries, which are the dominant type of fishery worldwide (Calderwood et al., 2021; Cosgrove et al., 2019; Dolder et al., 2018). The mixed nature of most fisheries typically leads to high discard and mortality rates of multiple nontarget species, especially in regions where many species occupy similar habitats. The snapper-grouper fishery in the southeastern United States (SEUS) is an example of such a mixed-stock fisheries.

There are 55 species currently managed under the South Atlantic Fishery Management Council's Snapper-Grouper Fishery Management Plan. These species generally occupy naturally occurring, hard-bottom reefs on the Southeast U.S. continental shelf and upper slope (Bacheler & Smart, 2016; Parker et al., 1983). Reef-associated fishes (e.g., snappers, groupers, porgies, grunts, and tilefishes) in the SEUS provide substantial economic and social benefits to coastal communities through commercial and recreational fishing and tourism; hence, their sustainable management is of critical importance. However, despite several management efforts enacted over past decades, the abundance of many important reef fish species has declined (Bacheler & Smart, 2016), with some of these stocks currently in an overfished condition and most of them with unknown status (Table 1).

There are several challenges in managing mixed-stock reef fish fisheries in the SEUS. First, many species of reef fish require hard substrates and have other similar habitat preferences, and it is common to catch and potentially discard one species, perhaps due to single-species regulations or fisher preferences, while targeting another species (Shertzer et al., 2024). Post-release mortality of discarded fish can be high due to such factors as barotrauma, hook-inflicted injury, and depredation (Runde et al., 2019). This unintended fishing mortality can impede the rebuilding of overfished stocks and lead to overexploitation of vulnerable species. Further, because discarding is often not directly monitored and not easily observed, the magnitude of discard mortality is difficult to quantify, leading to uncertainty in stock assessment models used to inform management. For example, red snapper (*Lutjanus campechanus*), which are highly valued by recreational and commercial fishers in the SEUS, have been overexploited and depleted for the past few decades and are currently under a rebuilding plan. Although the stock has shown progress toward rebuilding, the most recent assessment (SEDAR, 2021) indicated that the stock is not yet rebuilt and is experiencing overfishing, almost entirely as a result of recreational discards (SEDAR, 2021; Shertzer et al., 2024). Unless fishers can avoid catching overfished and vulnerable species, or discard mortality can be substantially reduced, the rebuilding of overfished stocks and the sustainability of reef fish communities in general will continue to be impaired. This is particularly likely given the high recreational fishing effort in the SEUS and continued improvements in fishing technology (Craig et al., 2021). Second, the status of many reef fish species remains unknown (Table 1). Approximately 75% of the 55 species that comprise the snapper-grouper complex have not been subject to a formal stock assessment (Wade et al., 2023), in part, due to a lack of data necessary for their assessment. The life-history characteristics of many of these species (e.g., late-maturing, slow-growing, and protogynous) make them particularly vulnerable to overexploitation. Developing indices of abundance and spatial distribution for these unassessed species is an important step for their assessment and management. Also, many of these species are relatively rare and have

TABLE 1 List of reef fish species included in the multispecies vector auto-regressive spatiotemporal model (VAST), including the total number of encounters (i.e., number of individuals recorded in videos, 2011–2021) for all years combined and stock status for each species, which were determined from their last stock assessment.

Common name	Scientific name	Overfishing?	Overfished?	Encounters
Gray triggerfish	*Balistes capriscus*	Yes	No	72,494
Blueline tilefish	*Caulolatilus microps*	No	No	717
Black sea bass	*Centropristis striata*	Yes	Yes	54,772
Graysby	*Cephalopholis cruentata*	Unknown	Unknown	6575
Rock hind	*Epinephelus adscensionis*	Unknown	Unknown	1935
Goliath grouper	*Epinephelus itajara*	No	Unknown	548
Red grouper	*Epinephelus morio*	Yes	Yes	1682
Snowy grouper	*Epinephelus niveatus*	Yes	Yes	608
White grunt	*Haemulon plumierii*	Unknown	Unknown	62,048
Hogfish	*Lachnolaimus maximus*	Yes	Yes	2776
Mutton snapper	*Lutjanus analis*	No	No	1708
Red snapper	*Lutjanus campechanus*	Yes	Yes	130,035
Gray snapper	*Lutjanus griseus*	Unknown	Unknown	17,825
Sand tilefish	*Malacanthus plumieri*	Unknown	Unknown	4913
Yellowmouth grouper	*Mycteroperca interstitialis*	Unknown	Unknown	412
Gag	*Mycteroperca microlepis*	Yes	Yes	8661
Scamp	*Mycteroperca phenax*	No	Unknown	19,776
Yellowtail snapper	*Ocyurus chrysurus*	No	No	369
Red porgy	*Pagrus pagrus*	No	Yes	146,799
Vermilion snapper	*Rhomboplites aurorubens*	No	No	665,160
Greater amberjack	*Seriola dumerili*	No	No	14,124

sparse observational data (e.g., yellowmouth grouper and rock hind), therefore estimating their fine-scale spatial distributions is challenging using single-species SDMs. Third, bottom temperatures in the South Atlantic have increased in recent years accompanied by other oceanographic changes (Craig et al., 2021). It is not yet clear how these reef fishes are responding to these environmental changes, but shifts in spatial distribution are a likely response. Shifting spatial distributions have a number of management consequences, particularly when they occur across management jurisdictional boundaries, such as mismatches between quota allocations and regional abundance, that can limit the performance of fishery management systems (Baudron et al., 2020). Therefore, assessing distribution shifts and delineating stock boundaries are crucial for the effective assessment and management of mobile fish stocks.

JSDMs are a novel and effective ecological tool for modeling species co-occurrence and are becoming increasingly prevalent in fisheries (Dolder et al., 2018; Stock et al., 2020). JSDMs estimate spatial distributions of multiple species simultaneously as well as the correlations among species and also allow for the incorporation of explanatory covariates. However, a number of challenges still remain in their applications. For example, the model dimensionality and complexity scales quadratically with the number of species, which can lead to convergence issues and difficulty in interpreting model output. Further, patterns in the spatiotemporal distribution of fish communities are likely shaped by numerous abiotic and biotic processes that operate simultaneously and with interacting effects, making them difficult to measure and include in the model. Recent developments in latent variable models make simultaneous estimation for multiple species more feasible (Warton et al., 2015). Latent factors represent unmeasured variables (missing predictors) that capture the main axes of covariation across species and provide a flexible way to model via spatial and spatiotemporal covariance structures (Dolder et al., 2018). The number of factors can be significantly smaller than the number of species, hence reducing the dimensionality of the model. The use of spatial latent factors was recently introduced in the context of fish community dynamics by Thorson et al. (2016).

The goal of this research is to quantify the spatiotemporal dynamics of reef fish species in the SEUS using new application of spatial dynamic factor analysis as a JSDM that allows for the simultaneous estimation of spatiotemporal densities for multiple species. The model accounts for unobserved spatial and spatiotemporal variation using latent factors, where the correlations among species are estimated. We apply the model to estimate the distributions of 21 reef fish species as well as the correlations among species. We then apply a clustering method to group species based on spatial and spatiotemporal synchrony in encounter probability and positive density. The correlation and cluster analyses indicate the degree to which reef fish species can be separated into distinct assemblages and, hence, whether spatial targeting to harvest more selectively and reduce bycatch is practical. We also develop indices of relative abundance for each species based on the estimated spatiotemporal densities. Incorporating the spatiotemporal correlations among species into the JSDM allows for estimation of abundance trends for infrequently encountered species (i.e., density of one species is informative about the density of correlated species). Finally, we compute the center of gravity (COG) for each species as an indicator of potential shifts in spatial distributions over time. We interpret these results in terms of their implications for multiple management challenges facing the snapper-grouper fishery in SEUS.

MATERIALS AND METHODS

Study area and data sources

We used video data from a large-scale, fishery-independent survey, that is, the Southeast Reef Fish Survey (SERFS), from 2011 to 2021. Sampling was conducted in a similar manner each year except for 2020 when no survey was conducted due to the COVID-19 pandemic (Link et al., 2021). The SERFS survey samples the primary habitat of reef fish (i.e., hard-bottom substrate) on the continental shelf and upper slope of the U.S. South Atlantic between Cape Hatteras, North Carolina, and St. Lucie Inlet, Florida (Figure 1). The sampling universe consists of approximately 4300 stations on known hard-bottom reef habitat, from which about 1500 were selected to be sampled each year since 2011 following a simple random sampling design. The spatial extent of the survey has been relatively stable over time (Appendix S1: Figure S1). Sampled stations were always separated by at least 200 m in a given year to provide independence between samples. Sampling occurred during daylight hours between April and October. A high-definition video camera was attached to a baited Chevron trap deployed at each station. The trap and attached camera were allowed to soak for 90 min. Videos were read in the lab following standard protocols beginning 10 min after the trap landed on the bottom and commencing for 20 min. A total of 41 frames (every 30 s) were read for 107 key species using the approach described in Schobernd et al. (2013). Additional details regarding the survey design and sampling methodology can be found in Bacheler and Shertzer (2020). We calculated the annual percentage frequency of occurrence (i.e., the percentage of stations in which the species was observed on video) for each species from 2011 to 2021. Species with an annual percentage occurrence ≥1% for any of the 10 years were included in the analyses. This filtering resulted in 21 species for analysis (Table 1).

Spatial dynamic factor analysis

We implemented the spatial dynamic factor analysis framework described by Thorson et al. (2015) to model the spatiotemporal dynamics of the SEUS reef fish community and to estimate species co-occurrence and the strength of associations among species in space and time. The model is simultaneously fit to data for multiple species by modeling response variables, that is, presence/absence and catch rate (number of individuals observed per frame), as a multivariate process using latent factors. A latent factor is a variable that cannot be directly observed, but whose effect can be detected and summarized through other variables (Latimer et al., 2009). The model includes two types of latent factors representing spatial and spatiotemporal variation, respectively. The spatial distribution of individual species over time is described by a set of common latent trends (between 1 and the total number of species) through a factor analysis decomposition. The common latent trends consist of spatial factors representing unobserved time-invariant effects and spatiotemporal factors representing unobserved time-variant effects. The value of each factor (referred to as a factor coefficient) varies spatially and is estimated as a distance-based Gaussian random field, where the random effects describing the spatial patterning are assumed to be drawn from a multivariate normal distribution. The factor coefficients are common to all species but loadings for each factor, which represent the association of species with each factor, vary across species.

More specifically, the density of each species at a given location is estimated using two separate linear predictors, p_1 and p_2, which are transformed to predict encounter probability (r_1) and positive catch rates (r_2).

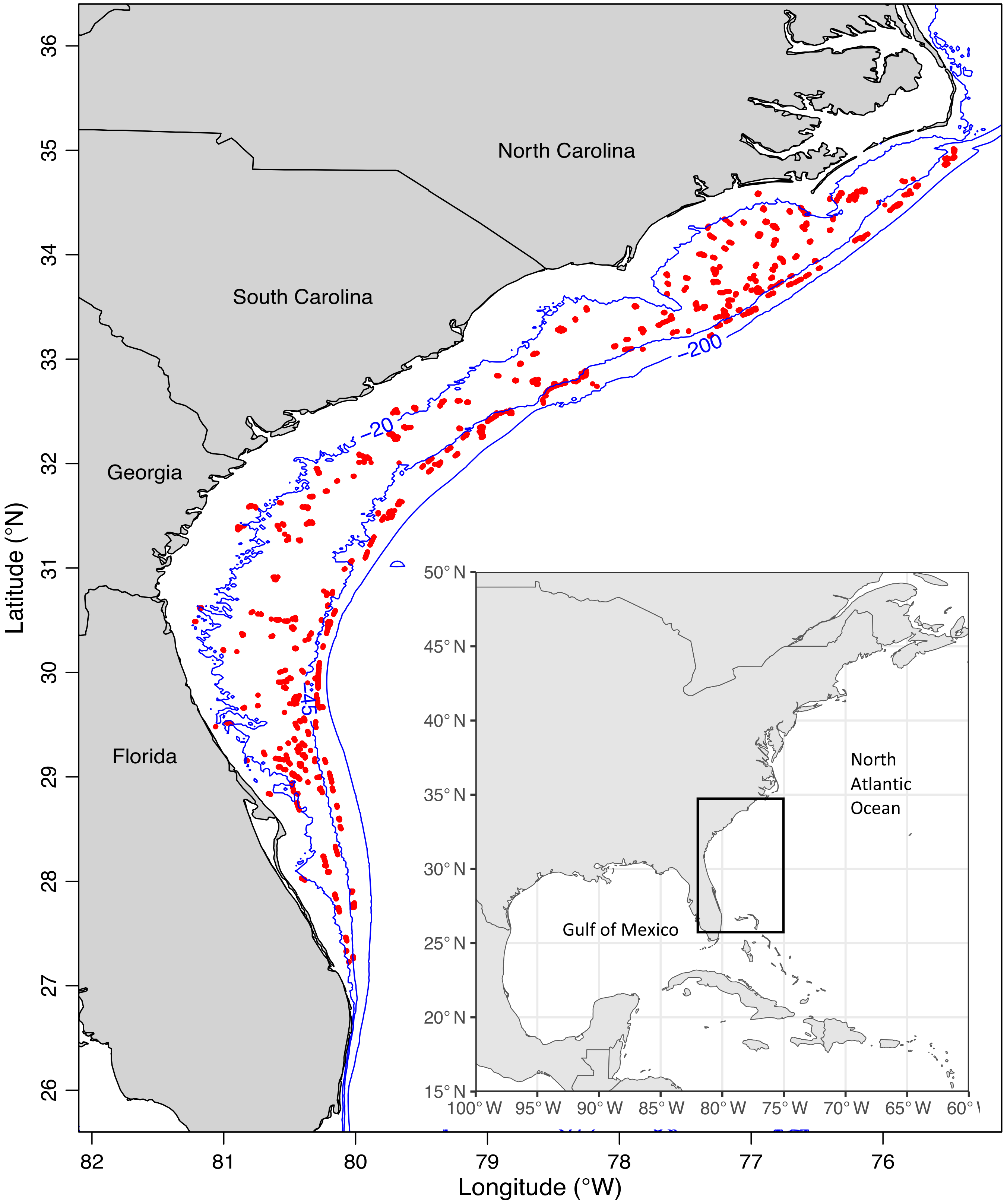


FIGURE 1 Map of study region depicting southeastern United States Atlantic Ocean. The red dots are the sampling locations from 2011 to 2021. Blue isobaths appear at 20, 45, and 200 m.

This "Poisson-link" delta model ensures that both predictors have an additive effect on log-density, $\log(r_1 \times r_2)$ (Thorson, 2019) and uses a complementary log–log link to transform p_1 to encounter probability r_1. The linear predictors at the location s for species k and time t are modeled as

$$p_*(s_i,t_i,k_i) = \beta_*(k_i) + \sum_{f=1}^{n_f} L_{\omega *}(k_i,f)\omega_*(s_i,f) + \sum_{f=1}^{n_f} L_{\varepsilon *}(k_i,f)\varepsilon_*(s_i,t_i,f), \quad (1)$$

where subscript * indicates a particular predictor (first or second). $\beta_*(k_i)$ is the intercept for species k. We specified the intercept to be constant over time so that all changes over time are attributed to spatiotemporal variation. $\omega_*(s_i,f)$ is the coefficient of spatial factor f at location s, representing predicted spatial variation occurring at the location s of sample i for factor f. $L_*(k_i,f)$ is the loading matrix that generates spatial and spatiotemporal covariation among species (i.e., loadings matrix multiplied by its transpose is equal to the covariance among species resulting from the factor), representing association of species k with factor f. $\varepsilon_*(s_i,t_i,f)$ is the coefficient of spatiotemporal factor f of sample i at location s and time t. Both $\omega_*(*,f)$ and $\varepsilon_*(*,t,f)$ were assumed to follow a multivariate normal distribution, $\mathrm{MVN}(0,R)$. R is the spatial correlation matrix computed based on a Matérn function (Thorson, 2019). The stochastic partial differential equation (SPDE) approximation to Gaussian random field was used to improve computational efficiency (Lindgren et al., 2011). The solution to a specific SPDE is a Gaussian random field with a Matérn function (Lindgren et al., 2011). A first-order autocorrelation was specified for $\varepsilon_*(*,t,f)$ among years:

$$\varepsilon_*(*,t,f) = \begin{cases} \mathrm{MVN}(0,R) & \text{if } t=1 \\ \mathrm{MVN}(\rho\varepsilon_*(*,t-1,f),R) & \text{if } t>1 \end{cases}, \quad (2)$$

where ρ was fixed at 1 and estimated for $\varepsilon_1(*,t,f)$ and $\varepsilon_2(*,t,f)$, respectively.

We started by specifying three latent trends, that is, $n_f = 3$, with 600 knots ($n_s = 600$) to approximate the distribution of the 21 species. A vector auto-regressive spatiotemporal (VAST) model creates a mesh of discrete locations (i.e., knots) to approximate the sampling area, and the knots are determined by a k-mean cluster algorithm to reflect the sampling intensity. Estimated spatial and spatiotemporal factors and loading matrices were rotated using principal components analysis (PCA) rotation to summarize and visualize community-level covariations. This PCA rotation was used to identify a factor that explained the maximum proportion of covariation among encounter probability and catch rates of the 21 species.

In summary, the density of each species is described by the product of the two linear predictors (i.e., encounter probability and positive catch rate), each consisting of three latent trends. Each latent trend includes two components, that is, spatial and spatiotemporal variation. Following Thorson (2019), we interpret the spatial component as a species' fundamental niche (expected spatial density on average) and the spatiotemporal component as a species' biological and environmental responses (e.g., aggregate environmental impacts and life-history responses influencing density). We interpret the first linear predictor (i.e., encounter probability) as a species' distribution (i.e., occupied habitat) and the second linear predictor as the spatial pattern of a species' density (e.g., hotspots within their distribution).

Parameter estimation

Parameters were estimated using the publicly available R package VAST for VAST models (Thorson, 2019). The VAST model assimilates presence/absence and count data to estimate population density over space and time for multiple species simultaneously (Thorson, 2019). Models can be specified with different levels of complexity. We treated the following effects as fixed within the model: intercept parameters for each species (β_1 and β_2), spatial decorrelation and the shape of geometric anisotropy of the Matérn function, the loading matrices (L_1 and L_2), temporal correlation for the coefficient of spatiotemporal factor, and the magnitude of residual variation in positive catch rates for each species. The coefficient of the spatial and spatiotemporal factors (ω_* and ε_*) for the number of "knots" were treated as random effects to account for unmeasured variables that cause observations to be correlated in space or in space and time. The Laplace approximation was used to approximate the marginal likelihood of fixed effects while integrating the joint likelihood with respect to random effects using Template Model Builder. The value of the random effects was predicted by maximizing the joint likelihood, which is defined as the product of the probability of the random effects (given fixed effects) and the probability of the data. We checked the gradient of the marginal log-likelihood for model convergence (i.e., <0.0001). Further details regarding VAST can be found in Thorson (2019).

Derived quantities

After all parameters were estimated, quantities of particular interest were derived, including the total abundance for each species in each year $[I(k,t)]$, the centroid of the distribution for each species in each year $[X(k,t)]$, and the covariance among species $[V]$:

$$I(k,t)=\sum_{s=1}^{n_s} a(s)\times p_1(s,t,k)\times p_2(s,t,k), \tag{3}$$

where $a(s)$ is the area associated with knot s and the other terms are as defined earlier.

$$X(k,t)=\sum_{s=1}^{n_s}\frac{x(\text{east},\text{north})\times a(s)\times p_1(s,t,k)\times p_2(s,t,k)}{I(k,t)}, \tag{4}$$

where $x(\text{east},\text{north})$ represents the easting and northing (in kilometers) for location s.

$$V=LL^T, \tag{5}$$

where L is $L_{\omega 1}$, $L_{\omega 2}$, $L_{\varepsilon 1}$, or $L_{\varepsilon 2}$ as defined above (Equations 1 and 2).

The estimates of total abundance $[I(k,t)]$ can only be directly interpreted when sampling effort is measured in units of area, for example, a bottom trawl with a known area swept. In this study, we assumed the area of attraction of the traps was constant across space and time so that the resulting absolute abundance estimates will be proportional to the underlying total abundance with an unknown constant coefficient. This assumption does not affect the interpretation of spatial and temporal patterns in relative abundance or other derived quantities (e.g., COGs), which is our primary interest.

Cluster analyses

We applied Ward's hierarchical clustering (Ward, 1963) to group species based on the covariance matrix among species, V, where the distance $d(k_1,k_2)$ between each pair of species, k_1 and k_2, is computed as

$$d(k_1,k_2)=\sqrt{V(k_1,k_1)+V(k_2,k_2)-2V(k_1,k_2)}, \tag{6}$$

where $V(k_1,k_1)$ and $V(k_2,k_2)$ are the variance of the spatial or spatiotemporal component for species k_1 and k_2, respectively, and $V(k_1,k_2)$ is the covariance between the two species (Omori & Thorson, 2022). We computed the average silhouette width to determine the optimal number of clusters using the R package "factoextra." The silhouette width measures the quality of a clustering, that is, how similar an object is to its own cluster (cohesion) compared with other clusters (separation). The average silhouette width was computed for different numbers of clusters, and the optimal number was chosen as the one that maximized the average silhouette width.

RESULTS

The model with three factors successfully converged (i.e., gradients for all the model parameters were less than 0.0001 and the Hessian matrix was positive definite), with the first two factors explaining the majority of the spatial (>96%) or spatiotemporal (>74%) variation.

Spatial variation and correlation

The average (2011–2021) density estimates indicate that some species (e.g., black sea bass, vermilion snapper, and red porgy) have higher density than others (e.g., goliath grouper, snowy grouper, and yellowmouth grouper; Figure 2). Species also show different spatial patterns, with some found mostly in deep waters on the Southeast U.S. continental shelf and upper slope (e.g., blueline tilefish, snowy grouper, red porgy), while others are common across the entire shelf (e.g., gray triggerfish and vermilion snapper; Figure 2). Latitudinal gradients were also evident for some species. For example, black sea bass tend to have higher density in the inshore and southern waters, while white grunt are more concentrated in the inshore northern waters (Figure 2).

Nearly all (i.e., >95%) of the spatial variation in encounter probability is explained by the first two latent factors (Figure 3A). The first two rotated factors (of the three considered) accounted for 84.9% and 13% of the total spatial variation, respectively. Factor 1 shows low encounter probabilities in inshore waters, particularly in the south and the north of the study region, and higher encounter probabilities in mid-shelf waters in the central region of the study area (Figure 4). All the species have positive associations with Factor 1 (i.e., positive loadings; Figure 3A), suggesting their distributions share a varying degree of similarity with the spatial pattern of Factor 1, depending on the loadings. For example, species with high Factor 1 scores tended to have stronger latitudinal gradients in encounter rate with high probability of presence in the northern and central areas (e.g., yellowtail snapper and yellowmouth grouper), while species with low Factor 1 scores tended to be broadly distributed throughout the survey area (e.g., gray triggerfish and gag) sometimes with higher occurrence in the southern areas (e.g., black sea bass).

Factor 2 appears to be associated primarily with differences between inshore and offshore waters, with high encounter probability inshore and low encounter

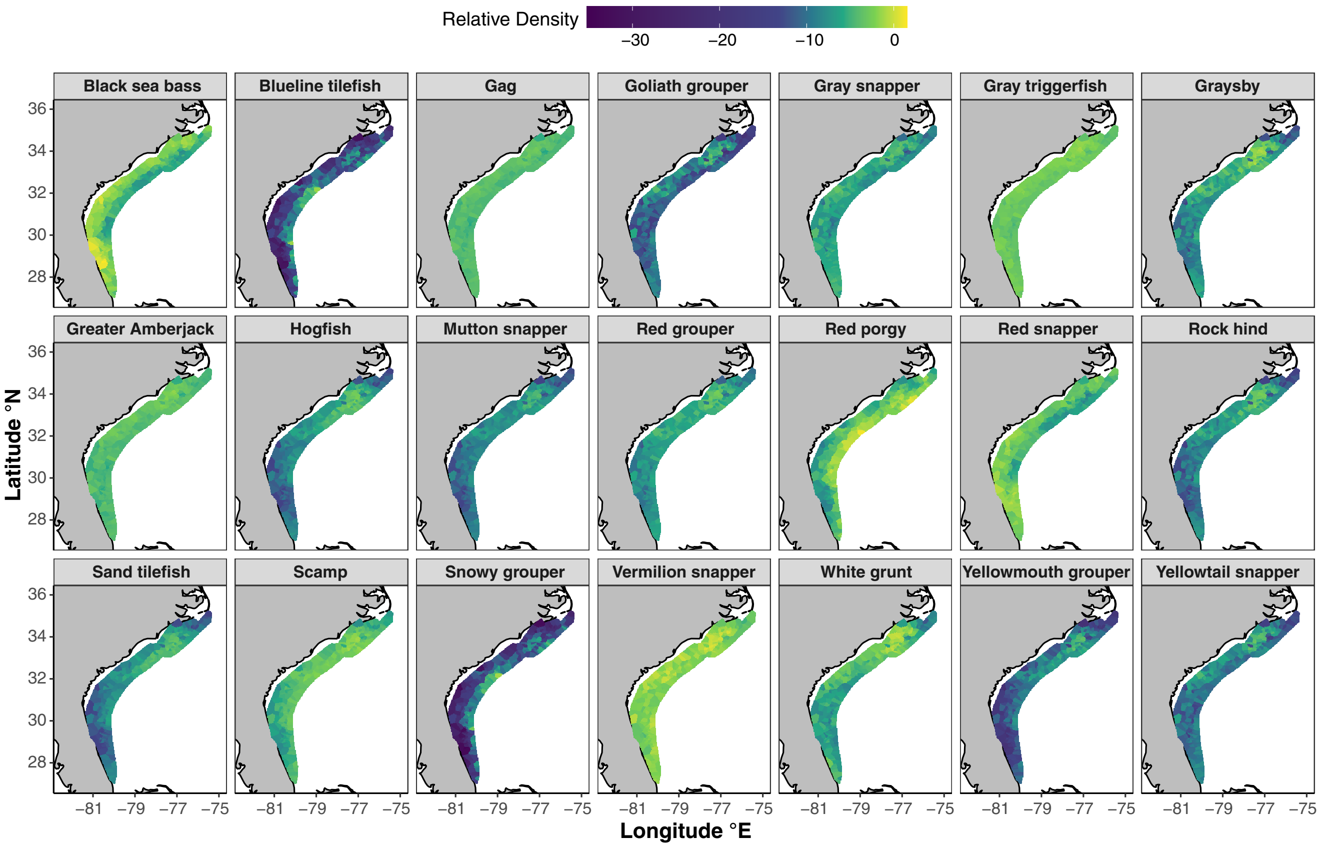


FIGURE 2 Estimated average relative density (logarithmic scale) of each reef fish species across all Southeast Reef Fish Survey years (2011–2021).

probability offshore (Figure 4). Most species showed positive associations with Factor 2 and these were primarily inshore and mid-shelf species (e.g., white grunt and black sea bass). Only red porgy, scamp, blueline tilefish, and snowy grouper, which have higher encounter probability in deeper, offshore waters, had negative associations with Factor 2 (Figure 2). In fact, blueline tilefish and snowy grouper, two species restricted to deep offshore waters along the shelf-slope break, had the most extreme factor scores on both Factor 1 and Factor 2. Therefore, Factor 2 appears to separate shallow to mid-shelf species from those that occur mostly in deeper shelf and shelf-break waters.

For positive density within the occupied area, the first two rotated factors explained 84.3% and 12.3% of the total spatial variation in positive density, respectively (Figure 5A). Factor 1 did not show clear spatial patterns. Factor 2 appeared to be associated with latitudinal variations with generally high values in the north and low values in the south (Figure 6). All the species are positively associated with Factor 1, except for vermilion snapper (Figure 5A). Factor 2 shows hot spots of high density in northern, mid-shelf waters and low-density patches in southern inshore waters and in the extreme north of the study region (Figure 6). Species are separated into two groups with positive and negative Factor 2 loadings, respectively (Figure 5). Species with a positive association with Factor 2 tend to have a hot spot in the northern shelf and/or a low-density area in the southern inshore waters (e.g., goliath grouper and white grunt) though this pattern was not always evident across all species (Figure 2).

Almost all reef fish demonstrated some degree of positive correlation with one another, with correlations ranging from −0.16 to 1 (median correlation = 0.89) for encounter probability (Figure 7A) and −0.89 to 1 (median correlation = 0.91) for density (Figure 7B). For encounter probability, the exceptions were a weak negative correlation between the encounter probability of black sea bass and that of red porgy and snowy grouper (Figure 7A). Black sea bass are more often found inshore, while red porgy and snowy grouper mainly occur further offshore (Figure 2). Further the density pattern of vermilion snapper was negatively correlated with that of 19 of the 20 other species (goliath grouper was the exception), with negative correlations ranging from −0.23 to −0.89 (median = −0.57).

Based on the Ward's hierarchical clustering analysis, the reef fish separate into three groups in terms of

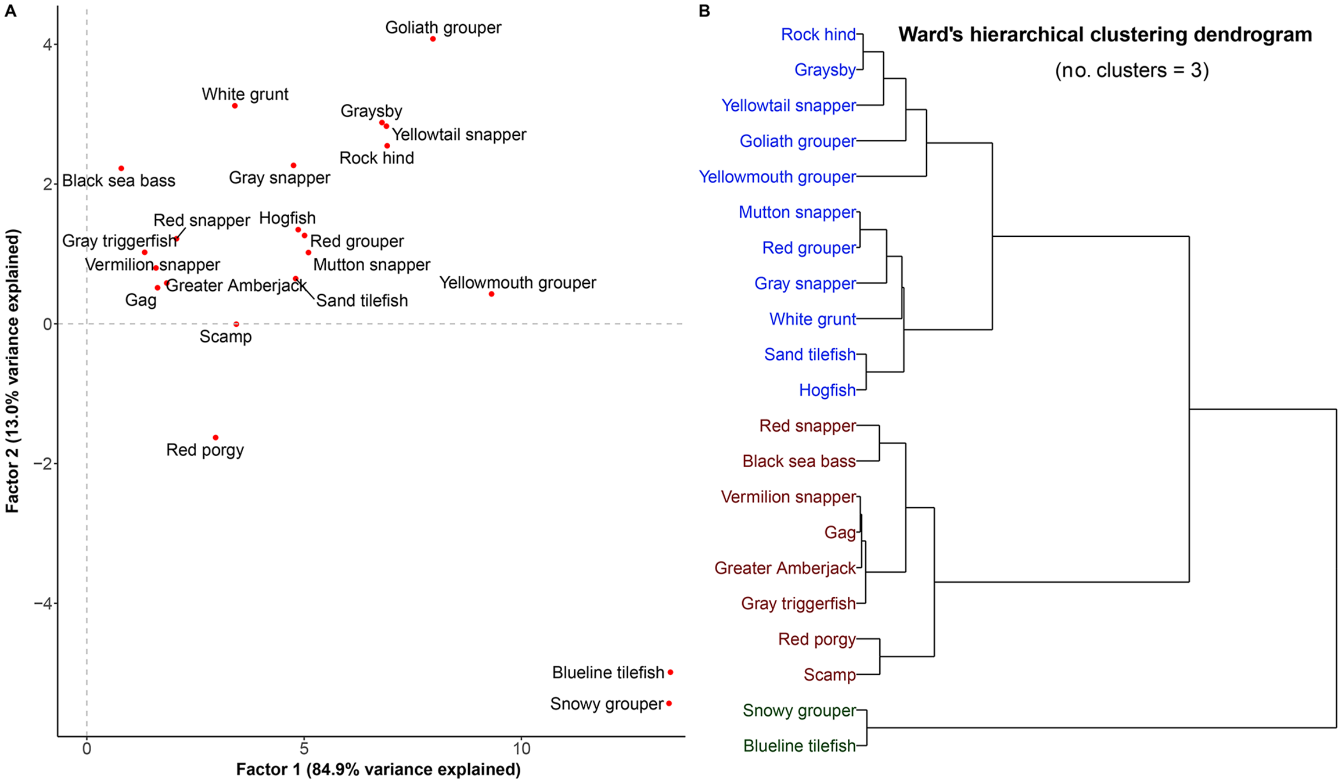


FIGURE 3 (A) Loadings of the first two factors after a principal components analysis rotation from the spatial component for the spatial encounter probability and (B) dendrogram based on Ward's hierarchical clustering analysis. Colored text in the dendrogram represents identified clusters.

occupied habitat (Figure 3B). These three groups are characterized by species that (1) mainly occupy deep offshore waters (snowy grouper and blueline tilefish); (2) have broad latitudinal and depth distributions across the entire shelf (e.g., gag, gray triggerfish, greater amberjack, and vermillion snapper); and (3) show high latitudinal heterogeneity in distribution (e.g., yellowmouth grouper, yellowtail snapper, rock hind, hogfish, sand tilefish, and goliath grouper). Ward's hierarchical clustering analysis based on density suggests two groups: (1) vermillion snapper and goliath grouper and (2) the remaining 21 species (Figure 5B), indicating that within the species' occupied habitats, nearly all of the species share similarity in average spatial patterns of density (e.g., hotspots), with the exception of vermillion snapper and to some extent goliath grouper (Figure 7B).

Spatiotemporal variation and correlation

Maps of the spatiotemporal factors are different than those for the spatial factors, suggesting that different drivers affect the average spatial distribution of species (i.e., occupied habitat and density pattern) and the interannual differences in distribution. Spatiotemporal factors for encounter probability showed a similar spatial pattern driving species distribution from year to year (Figure 8). However, factors for positive density did not show the same spatial pattern driving species' hot spots over time (Figure 9).

The first two rotated factors of the three considered explained 65.7% and 17.8% of the total spatiotemporal variation in encounter probability, respectively. Factor 1 shows hotspots in the north (e.g., off central North Carolina) and in the south (e.g., offshore waters of Florida and Georgia), particularly in mid-shelf and deep waters (Figure 8). All the species are positively associated with Factor 1 (Figure 10A), suggesting that the underlying drivers represented by Factor 1 influence the annual changes in distribution of these species in a similar way. Factor 2 appears to be the mirror image of Factor 1, with the highest values in the middle of the study region (e.g., southern North Carolina to South Carolina), particular in mid-shelf and shallow depths, and low values elsewhere (Figure 8). Black sea bass, red porgy, and vermilion snapper, and white grunt have large positive loadings for Factor 2 while mutton snapper, goliath grouper, yellowmouth grouper, and sand tilefish have large negative loadings (Figure 10A).

The first two rotated factors accounted for 59.9% and 22.3% of the total spatiotemporal variation in density,

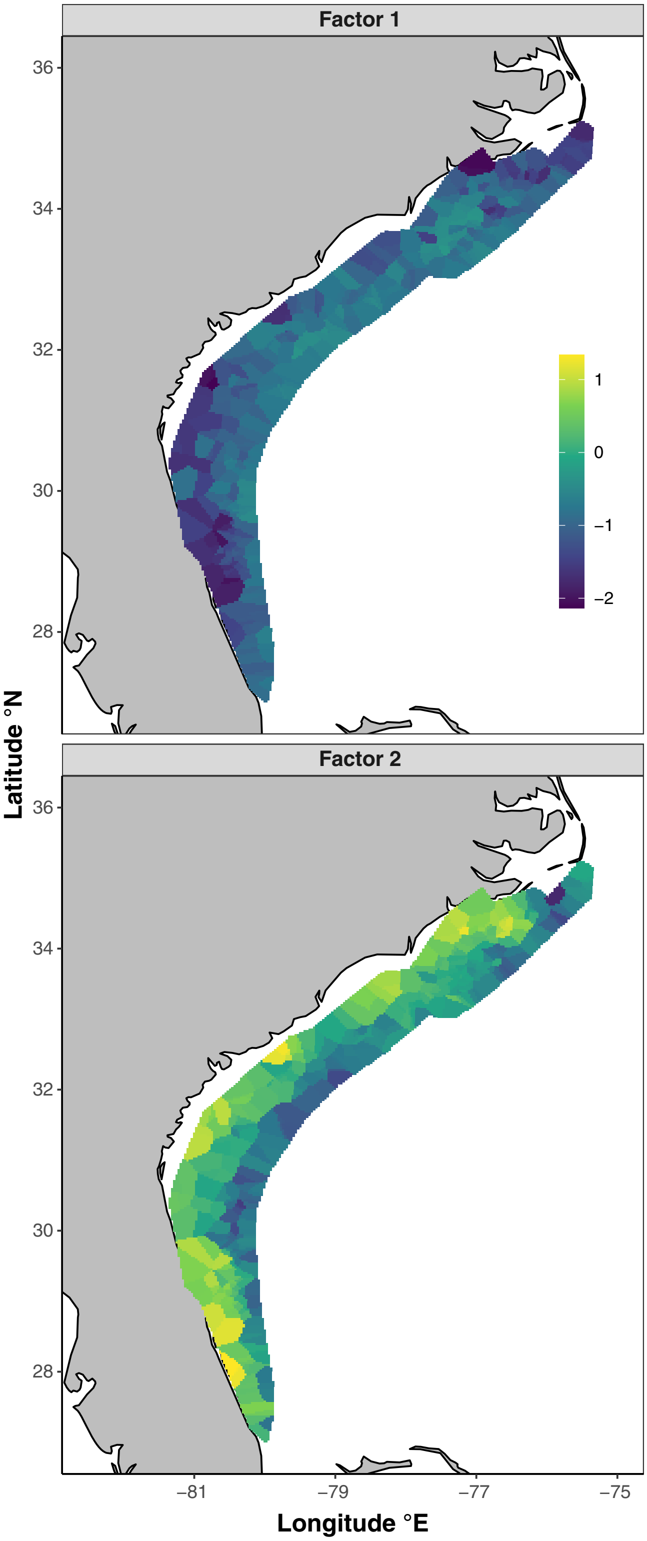


FIGURE 4 Maps of the first two factors after a principal components analysis rotation from the spatial component for the spatial encounter probability.

respectively (Figure 11A). Factor 1 appears to be associated with differences between the northern region (low values) and the southern regions of the study area (high values, Figure 9). All the species except sand tilefish have a positive Factor 1 loading, suggesting that the underlying drivers represented by Factor 1 influence their interannual pattern in a similar way. The spatiotemporal patterns in Factor 2 are less consistent over time (Figure 9), suggesting the effects of drivers represented by Factor 2 on species density vary over time and space. Some species show a positive association (e.g., greater amberjack, vermilion snapper, and sand tilefish) with Factor 2 while others show a negative association (snowy grouper, goliath grouper, white grunt, and yellowmouth grouper).

Most of the species showed strong, mostly positive correlations in spatiotemporal encounter probability (Figure 12A), with correlation coefficients ranging from −0.33 to 0.99 (median correlation = 0.67). The exceptions were blueline tilefish, snowy grouper, black sea bass, gag, red porgy, white grunt, and vermilion snapper, which showed negative correlations with one to four other species. Correlations for spatiotemporal positive density were mostly positive as well (Figure 12B). In general, the spatiotemporal correlations (median correlation = 0.56) show fewer high positive values compared to the spatial correlations (Figure 7). This suggests that though species may have high overlap in their occupied habitat and similar average spatial patterns in density, they may respond to spatiotemporal drivers in different ways so that their annual distributions may be less correlated. For example, red snapper has high positive correlations with black sea bass, greater amberjack, and hogfish for average positive density (Figure 7B); however, their spatiotemporal correlations are low (Figure 12B), suggesting these high correlations are not stable over time.

Ward's hierarchical clustering analysis separates the species into two clusters (Figure 10B) in terms of spatiotemporal variability in occupied habitat, and the separation is driven more by Factor 2 (Figure 10A), which reflects the contrast between the south and north. Species separate into three groups in terms of spatiotemporal variability in density (Figure 11B), and the separation is also driven more by Factor 2 (Figure 11A), which does not show clear spatial pattern over time.

Derived quantities

The 21 species showed highly variable patterns in abundance from 2011 to 2022 (Figure 13). The most abundant species in the survey are vermilion snapper, red porgy, red snapper, black sea bass, and gray triggerfish (Table 1, Figure 13). The least common species are yellowmouth grouper, yellowtail snapper, snowy grouper, goliath grouper, and blueline tilefish. The species show different

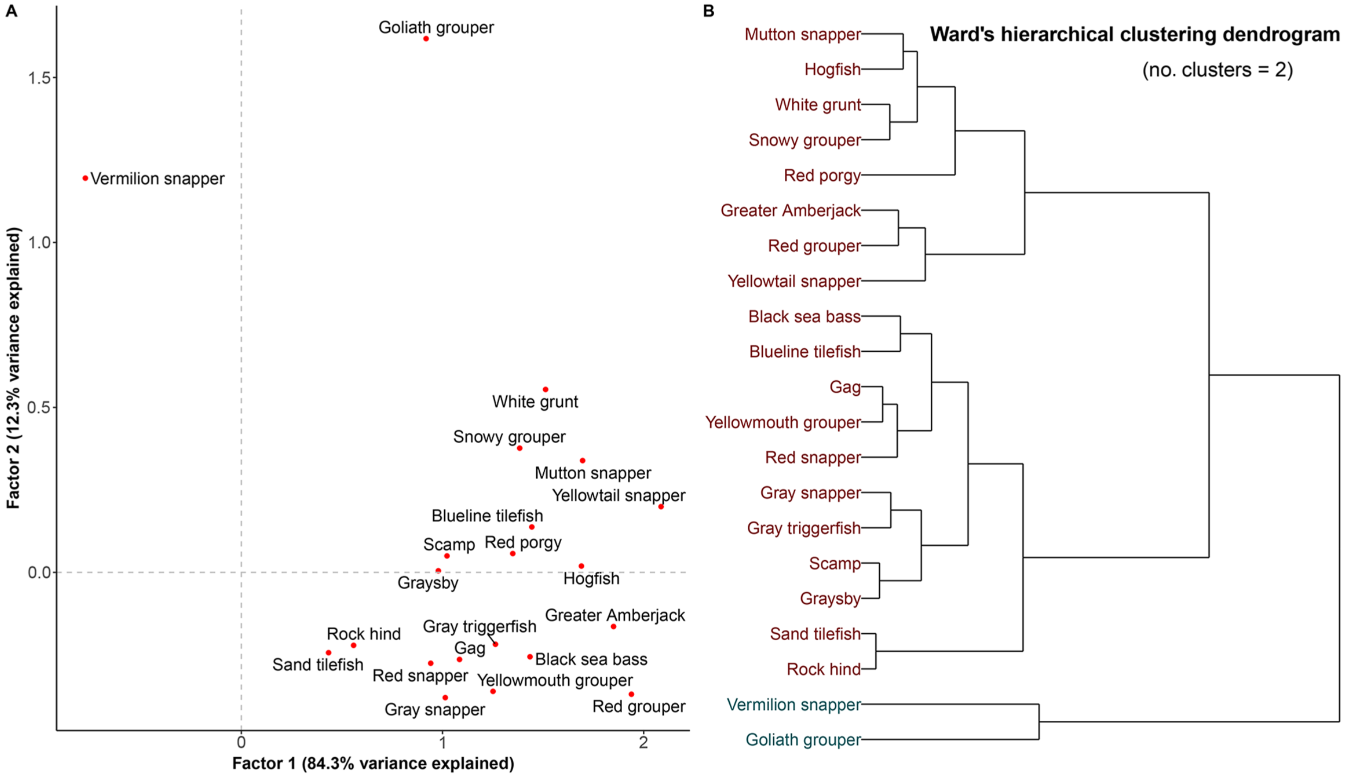


FIGURE 5 (A) Loadings of the first two factors after a principal components analysis rotation from the spatial component for the spatial positive density and (B) dendrogram based on Ward's hierarchical clustering analysis. Colored text in the dendrogram represents identified clusters.

temporal patterns, with some species showing positive trends throughout the modeled years (e.g., goliath grouper, graysby, mutton snapper, gray snapper, and vermilion snapper), while some species show decreasing trends either throughout all the modeled years (e.g., black sea bass) or over the most recent (since 2017–2021) years (e.g., blueline tilefish, gray triggerfish, hogfish, rock hind, scamp, and white grunt).

Among the 21 species, there are nine species that showed significant trends in their COG, that is, either northing/easting or both (Figure 14). Black sea bass and sand tilefish show significant positive trends in their easting and northing, suggesting that their distribution shifted northward and to deeper waters from 2011 to 2021 (Figure 14). Gag, hogfish, and red porgy show the opposite pattern, with significant negative trends in easting and northing, suggesting their distributions shifted southward and to shallower water over the same time period (Figure 14). However, the uncertainty associated with their COGs is high. The COG of mutton snapper and red grouper also show negative trends, but driven primarily by a more northward and offshore distribution in the early years (2011–2013) compared with the later years (2014–2021). Goliath grouper and snowy grouper showed slight shifts inshore and offshore, respectively, but the pattern was weak.

DISCUSSION

We simultaneously modeled 21 reef fish species in the SEUS Atlantic Ocean using a JSDM to quantify trends in their occurrence, abundance, and spatial distribution, as well as the correlations among species. We found that species can be separated into a few assemblages that share similar associations with the common spatial or spatiotemporal factors estimated from the model. However, the composition of the species assemblages varied across the four grouping variables, encounter probability (occupied habitat), positive density (hotspots), spatial variation (fundamental niche), and spatiotemporal variation (environmental responses), suggesting that a complex set of potentially interacting factors underlies patterns in spatial distribution. The high spatial correlations in encounter probability among the majority of the species indicates their occupied habitats exhibit a high degree of spatial overlap. The main difference in occupied habitat was between species with a widespread distribution throughout the study area versus those with a more limited distribution to inshore, offshore, or more northern waters. The similar spatial patterns in average density among most species indicates that regions of the shelf supporting high densities of one species likely also

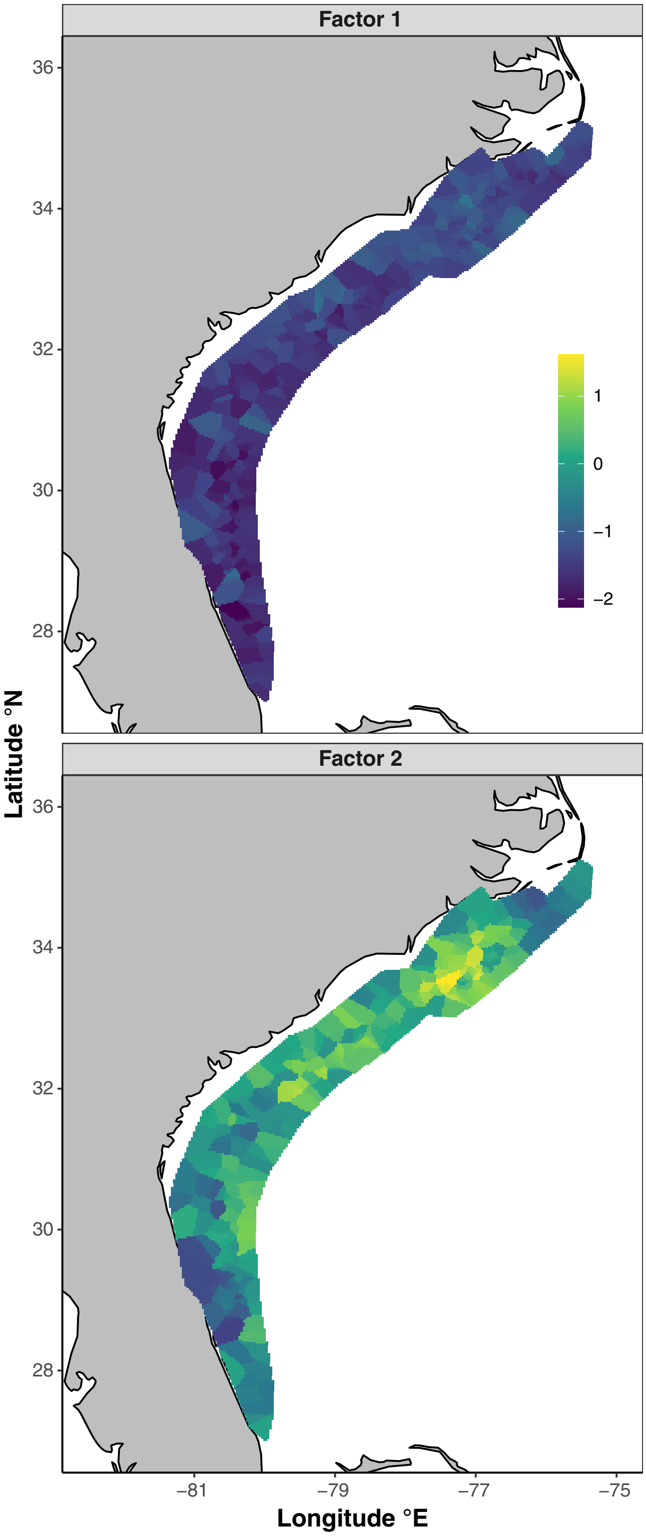
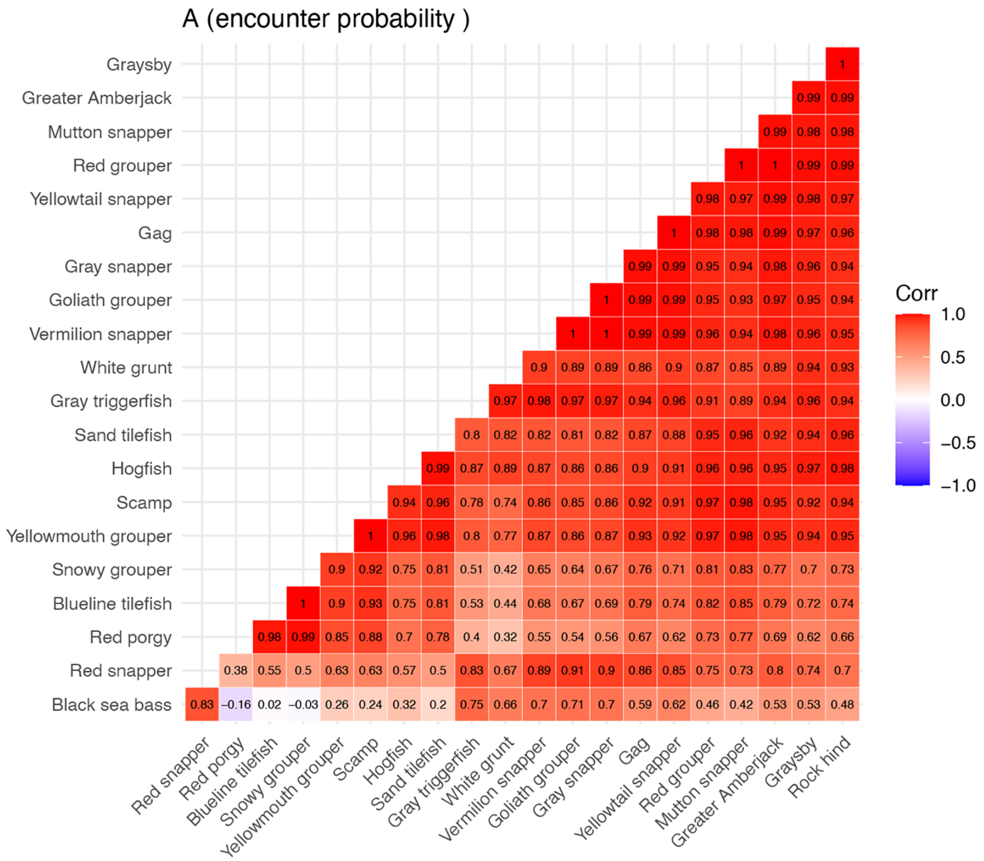


FIGURE 6 Maps of the first two factors after a principal components analysis rotation from the spatial component for the spatial positive density.

support high densities of other species. For example, multiple species had their highest average densities in the northern and central regions of the SEUS off of southern North Carolina and South Carolina, suggesting these regions may be particularly important to the productivity of this reef fish complex.

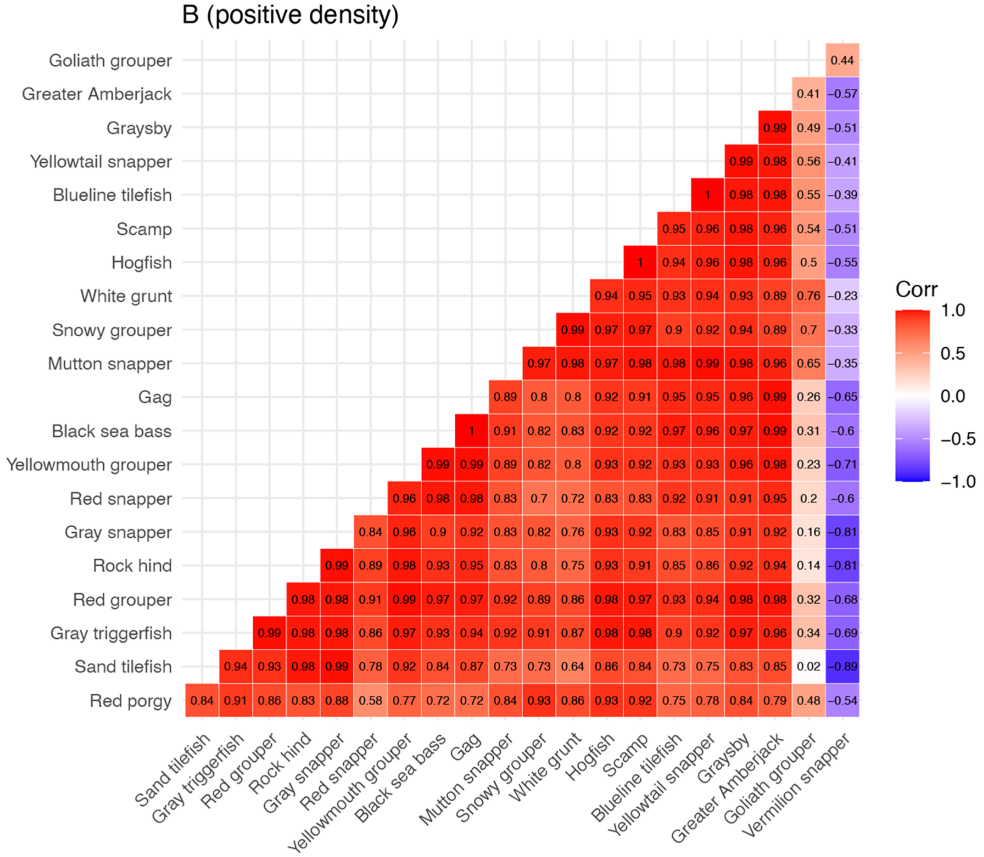
While the spatial correlations in occupied habitat and average density were high among the 21 reef fish species, the spatiotemporal correlations were generally weaker, indicating that the annual distributions of individual species were less correlated compared with their expected average distributions over the study time period (2011–2021). Some species with large positive correlations in average spatial distribution even show negative spatiotemporal correlations (e.g., sand tilefish and white grunt), suggesting the spatial associations among some species are not stable over time. This could occur due to annual differences in spatial patterns of recruitment, movement, and mortality. Several reef fishes have shown declining recruitment over the study period while a few have shown increases (Wade et al., 2023). The SERFS survey samples young (e.g., age-1) age classes of several species and sampling occurs over a protracted period (May–September). Therefore, interannual and seasonal variability in recruitment and mortality processes (including fishing mortality) may lead to annual variation in spatial distributions. Also, recent studies suggest some species (i.e., red snapper and scamp) receive annually varying numbers of recruits from the Gulf of Mexico into the South Atlantic through the Florida Straits (Brothers et al., 2023; Karnauskas et al., 2022), and this may be another source of variation influencing spatial distributions in the South Atlantic. Even so, most of the spatiotemporal correlations in our study were positive, suggesting many species may respond in a similar manner to spatiotemporal drivers and, as a result, may be consistently found in higher densities in the same locations from year to year.

The JSDM applied here is a purely latent model (i.e., no covariates), and two latent factors, a spatial factor representing the average spatial distribution and a spatiotemporal factor representing annual variation in spatial distribution, explained most (i.e., ~80% to 90%) of the variation in spatial patterns in the survey data. While our approach is correlational in nature, the latent factors represent the integrated effects of biotic and abiotic processes that influence species' spatial dynamics and are key elements that link individual species. The two latent factors often showed spatial patterns that appeared to vary in relation to depth and latitude. For example, the spatial component for encounter probability appears to be associated with the difference between inshore and offshore waters (Factor 2, Figure 4), while that for average density appears to vary more latitudinally. Therefore, potential environmental drivers affecting species' spatial distributions likely reflect some aspect of



A (encounter probability)

	Red snapper	Red porgy	Blueline tilefish	Snowy grouper	Yellowmouth grouper	Scamp	Hogfish	Sand tilefish	Gray triggerfish	White grunt	Vermilion snapper	Goliath grouper	Gray snapper	Gag	Yellowtail snapper	Red grouper	Mutton snapper	Greater Amberjack	Graysby	Rock hind
Graysby																				1
Greater Amberjack																			0.99	0.99
Mutton snapper																		0.99	0.98	0.98
Red grouper																	1	1	0.99	0.99
Yellowtail snapper																0.98	0.97	0.99	0.98	0.97
Gag															1	0.98	0.98	0.99	0.97	0.96
Gray snapper														0.99	0.99	0.95	0.94	0.98	0.96	0.94
Goliath grouper													1	0.99	0.99	0.95	0.93	0.97	0.95	0.94
Vermilion snapper												1	1	0.99	0.99	0.96	0.94	0.98	0.96	0.95
White grunt											0.9	0.89	0.89	0.86	0.9	0.87	0.85	0.89	0.94	0.93
Gray triggerfish										0.97	0.98	0.97	0.97	0.94	0.96	0.91	0.89	0.94	0.96	0.94
Sand tilefish									0.8	0.82	0.82	0.81	0.82	0.87	0.88	0.95	0.96	0.92	0.94	0.96
Hogfish								0.99	0.87	0.89	0.87	0.86	0.86	0.9	0.91	0.96	0.96	0.95	0.97	0.98
Scamp							0.94	0.96	0.78	0.74	0.86	0.85	0.86	0.92	0.91	0.97	0.98	0.95	0.92	0.94
Yellowmouth grouper						1	0.96	0.98	0.8	0.77	0.87	0.86	0.87	0.93	0.92	0.97	0.98	0.95	0.94	0.95
Snowy grouper					0.9	0.92	0.75	0.81	0.51	0.42	0.65	0.64	0.67	0.76	0.71	0.81	0.83	0.77	0.7	0.73
Blueline tilefish				1	0.9	0.93	0.75	0.81	0.53	0.44	0.68	0.67	0.69	0.79	0.74	0.82	0.85	0.79	0.72	0.74
Red porgy			0.98	0.99	0.85	0.88	0.7	0.78	0.4	0.32	0.55	0.54	0.56	0.67	0.62	0.73	0.77	0.69	0.62	0.66
Red snapper		0.38	0.55	0.5	0.63	0.63	0.57	0.5	0.83	0.67	0.89	0.91	0.9	0.86	0.85	0.75	0.73	0.8	0.74	0.7
Black sea bass	0.83	−0.16	0.02	−0.03	0.26	0.24	0.32	0.2	0.75	0.66	0.7	0.71	0.7	0.59	0.62	0.46	0.42	0.53	0.53	0.48



B (positive density)

	Sand tilefish	Gray triggerfish	Red grouper	Rock hind	Gray snapper	Red snapper	Yellowmouth grouper	Black sea bass	Gag	Mutton snapper	Snowy grouper	White grunt	Hogfish	Scamp	Blueline tilefish	Yellowtail snapper	Graysby	Greater Amberjack	Goliath grouper	Vermilion snapper
Goliath grouper																				0.44
Greater Amberjack																			0.41	−0.57
Graysby																		0.99	0.49	−0.51
Yellowtail snapper																	0.99	0.98	0.56	−0.41
Blueline tilefish																1	0.98	0.98	0.55	−0.39
Scamp															0.95	0.96	0.98	0.96	0.54	−0.51
Hogfish														1	0.94	0.96	0.98	0.96	0.5	−0.55
White grunt													0.94	0.95	0.93	0.94	0.93	0.89	0.76	−0.23
Snowy grouper												0.99	0.97	0.97	0.9	0.92	0.94	0.89	0.7	−0.33
Mutton snapper											0.97	0.98	0.97	0.98	0.98	0.99	0.98	0.96	0.65	−0.35
Gag										0.89	0.8	0.8	0.92	0.91	0.95	0.95	0.96	0.99	0.26	−0.65
Black sea bass									1	0.91	0.82	0.83	0.92	0.92	0.97	0.96	0.97	0.99	0.31	−0.6
Yellowmouth grouper								0.99	0.99	0.89	0.82	0.8	0.93	0.92	0.93	0.93	0.96	0.98	0.23	−0.71
Red snapper							0.96	0.98	0.98	0.83	0.7	0.72	0.83	0.83	0.92	0.91	0.91	0.95	0.2	−0.6
Gray snapper						0.84	0.96	0.9	0.92	0.83	0.82	0.76	0.93	0.92	0.83	0.85	0.91	0.92	0.16	−0.81
Rock hind					0.99	0.89	0.98	0.93	0.95	0.83	0.8	0.75	0.93	0.91	0.85	0.86	0.92	0.94	0.14	−0.81
Red grouper				0.98	0.98	0.91	0.99	0.97	0.97	0.92	0.89	0.86	0.98	0.97	0.93	0.94	0.98	0.98	0.32	−0.68
Gray triggerfish			0.99	0.98	0.98	0.86	0.97	0.93	0.94	0.92	0.91	0.87	0.98	0.98	0.9	0.92	0.97	0.96	0.34	−0.69
Sand tilefish		0.94	0.93	0.98	0.99	0.78	0.92	0.84	0.87	0.73	0.73	0.64	0.86	0.84	0.73	0.75	0.83	0.85	0.02	−0.89
Red porgy	0.84	0.91	0.86	0.83	0.88	0.58	0.77	0.72	0.72	0.84	0.93	0.86	0.93	0.92	0.75	0.78	0.84	0.79	0.48	−0.54

FIGURE 7 Interspecies correlations for (A) spatial encounter probability and (B) positive density.

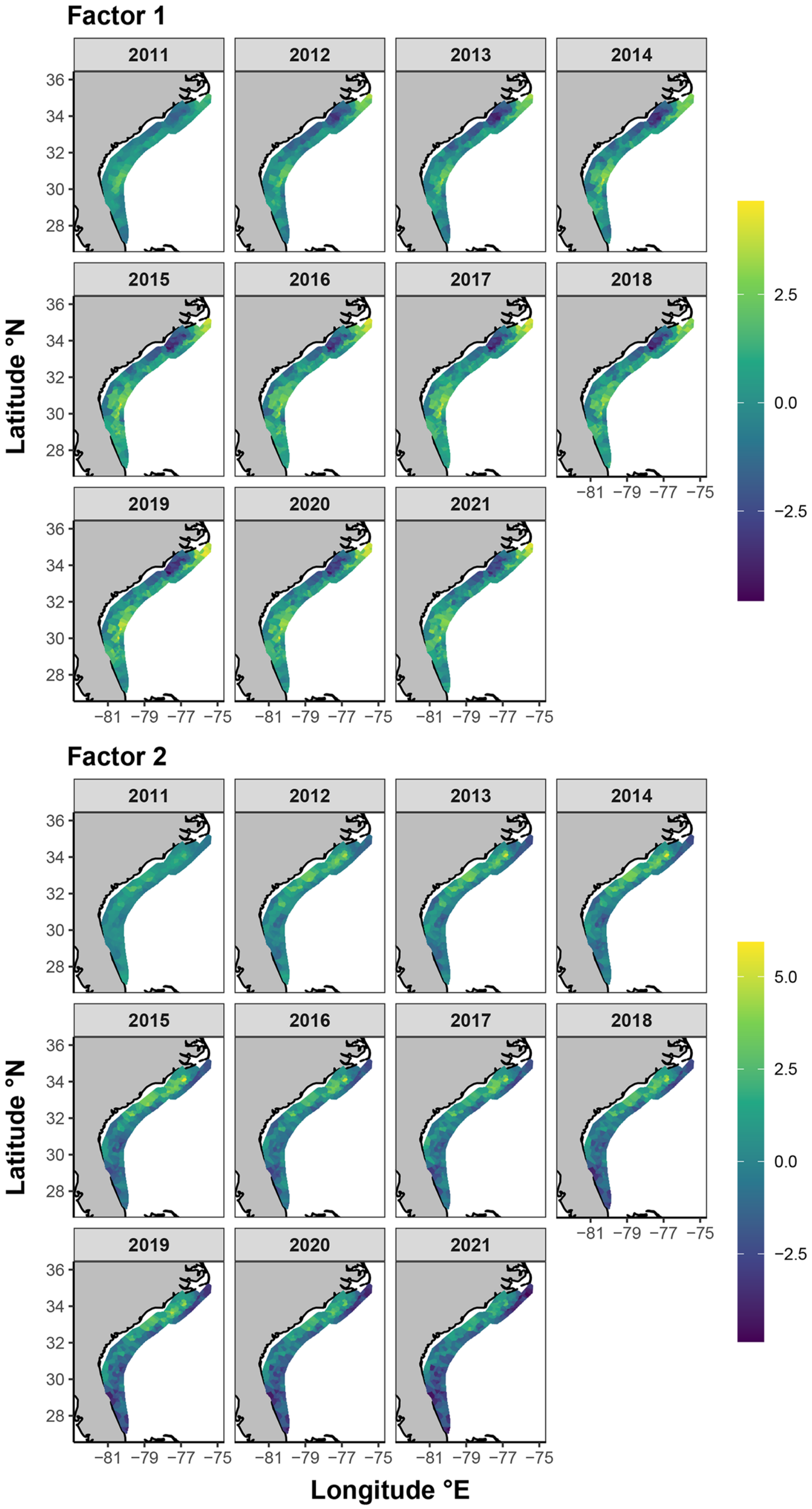


FIGURE 8 Maps of the first two factors after a principal components analysis rotation from the spatiotemporal component for the spatial encounter probability.

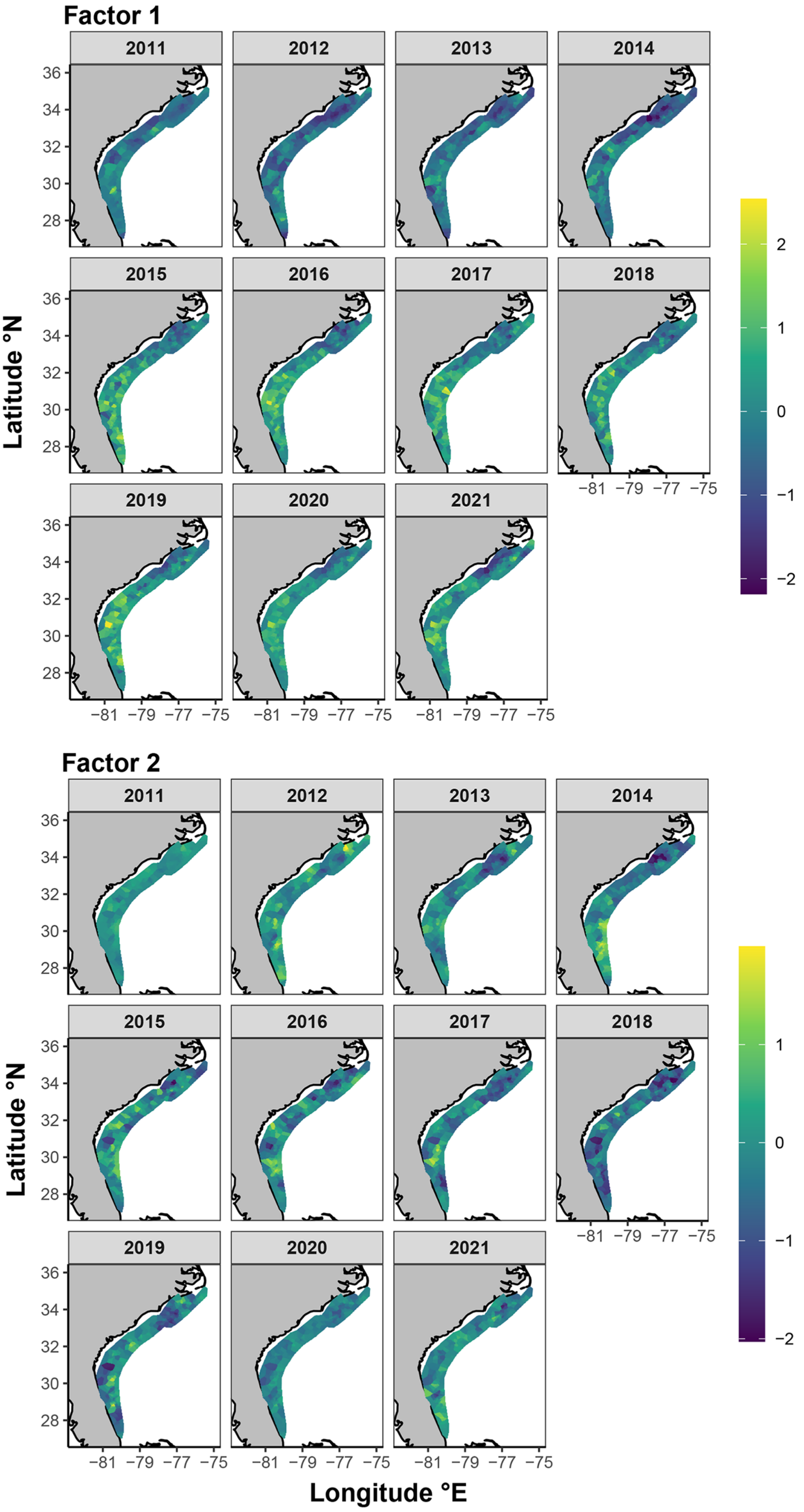


FIGURE 9 Maps of the first two factors after a principal components analysis rotation from the spatiotemporal component for the spatial positive density.

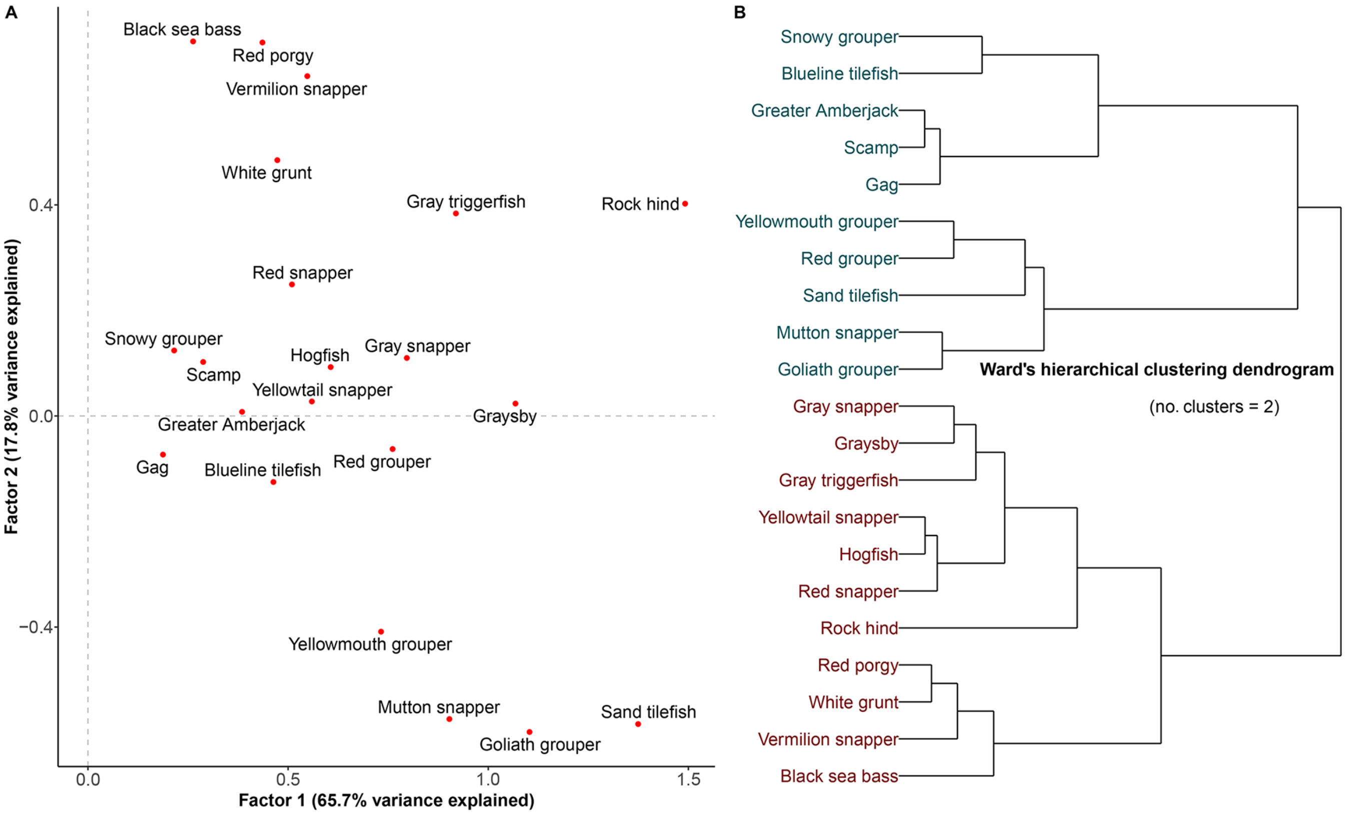


FIGURE 10 (A) Loadings of the first two factors after a principal components analysis rotation from the spatiotemporal component for the spatial encounter probability and (B) dendrogram based on Ward's hierarchical clustering analysis. Colored text in the dendrogram represents identified clusters.

the environment that vary with depth, latitude, distance to shore, or their interactions. Depth has previously been shown to be a major driver structuring reef fish assemblages in the SEUS (Bacheler et al., 2016; Sedberry & Van Dolah, 1984) as has distance to the Gulf Stream (Glasgow et al., 2021), which varies latitudinally given the geography of the continental shelf (i.e., narrow in the most northern and southern latitudes and wider in the middle latitudes). Other potential environmental covariates represented by the latent factors may be substrate and bottom temperature. The SERFS survey samples known hard-bottom habitats, and the high correlations of most species with the first spatial and spatiotemporal factors may represent the general distribution of hard-bottom habitat on the shelf, which are a requirement for most of these species. Although hard-bottom habitats (e.g., rock/coral rubble) support some of the highest levels of biodiversity in the SEUS, species may have different specific habitat preferences with respect to the type of hard bottom (Bacheler & Smart, 2016; Glasgow et al., 2021). For example, snowy grouper and blueline tilefish are typically associated with high-relief hard bottom, while other species appear to be habitat generalists that occur on multiple types of structured habitats (e.g., black sea bass). It is not surprising that the maps of the spatiotemporal factors for encounter probability and positive density were different from those for the spatial factors, because drivers that affect species' fundamental niche are likely to be different than those that determine interannual variability in occupied habitat and spatial patterns in density (e.g., recruitment).

Indices of abundance were developed for all 21 of the modeled species from the JSDM. JSDMs that incorporate species associations can have better predictive performance compared with single-species models (Stock et al., 2020). Incorporating species associations can be particularly helpful for developing abundance indices for data-limited species with sparse observation data. Our results are consistent with prior studies indicating that reef fish abundance in the SEUS has declined over the last 25–30 years (Bacheler & Smart, 2016) and suggest that some species have continued to decline since their last stock assessment (e.g., black sea bass, blueline tilefish, and red porgy; Figure 13). Updating the JSDM periodically with new survey data is an efficient means of providing abundance information for unassessed species and for the intervening years between stock assessments for assessed species, which can often span 5–7 years.

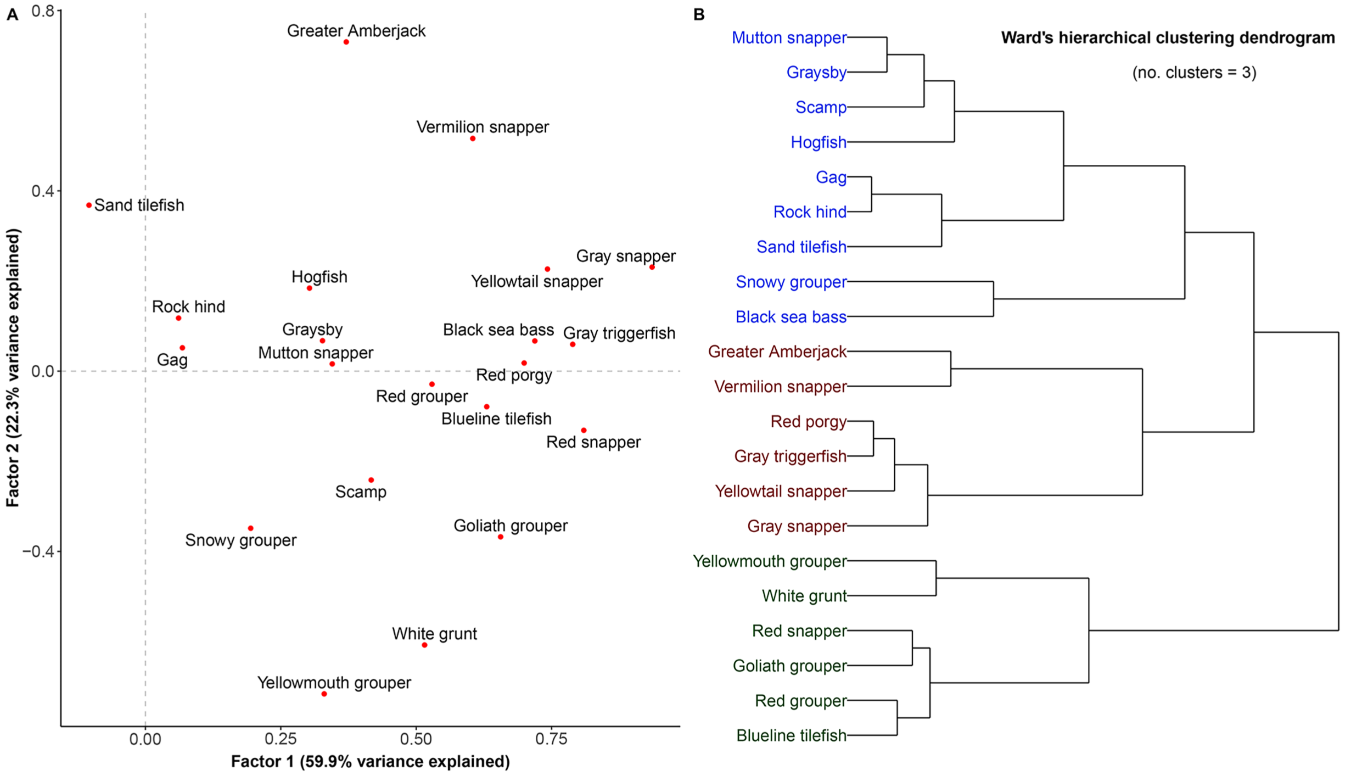
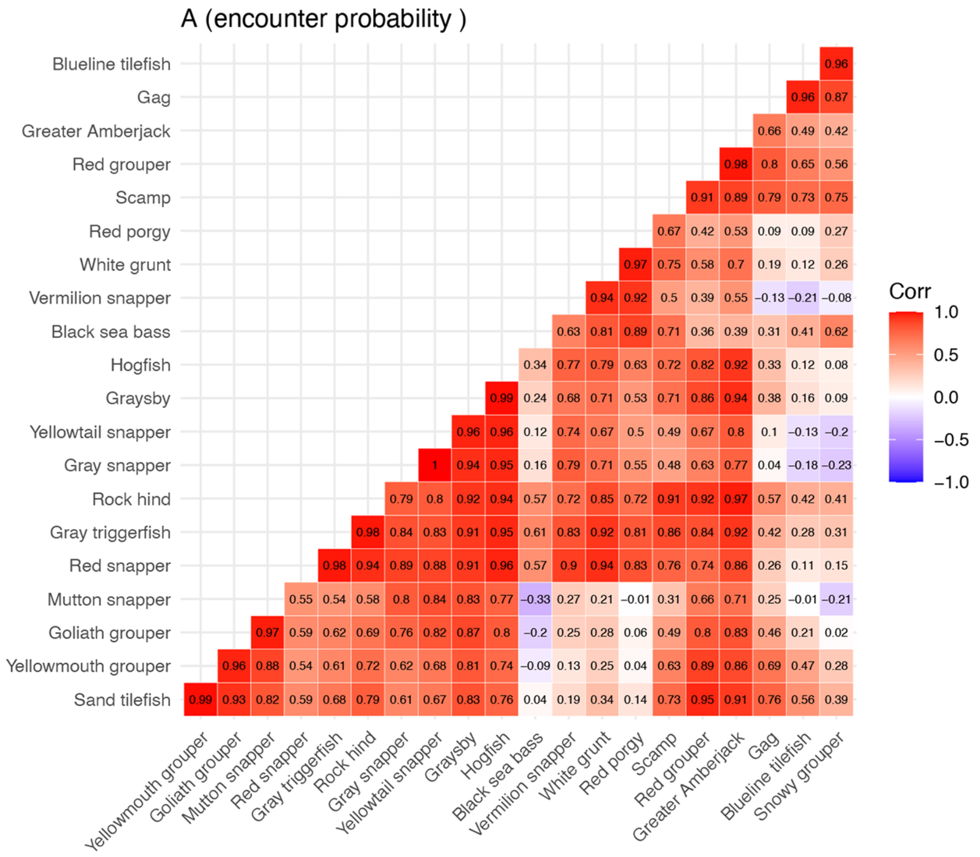


FIGURE 11 (A) Loadings of the first two factors after a principal components analysis rotation from the spatiotemporal component for the spatial positive density and (B) dendrogram based on Ward's hierarchical clustering analysis. Colored text in the dendrogram represents identified clusters.

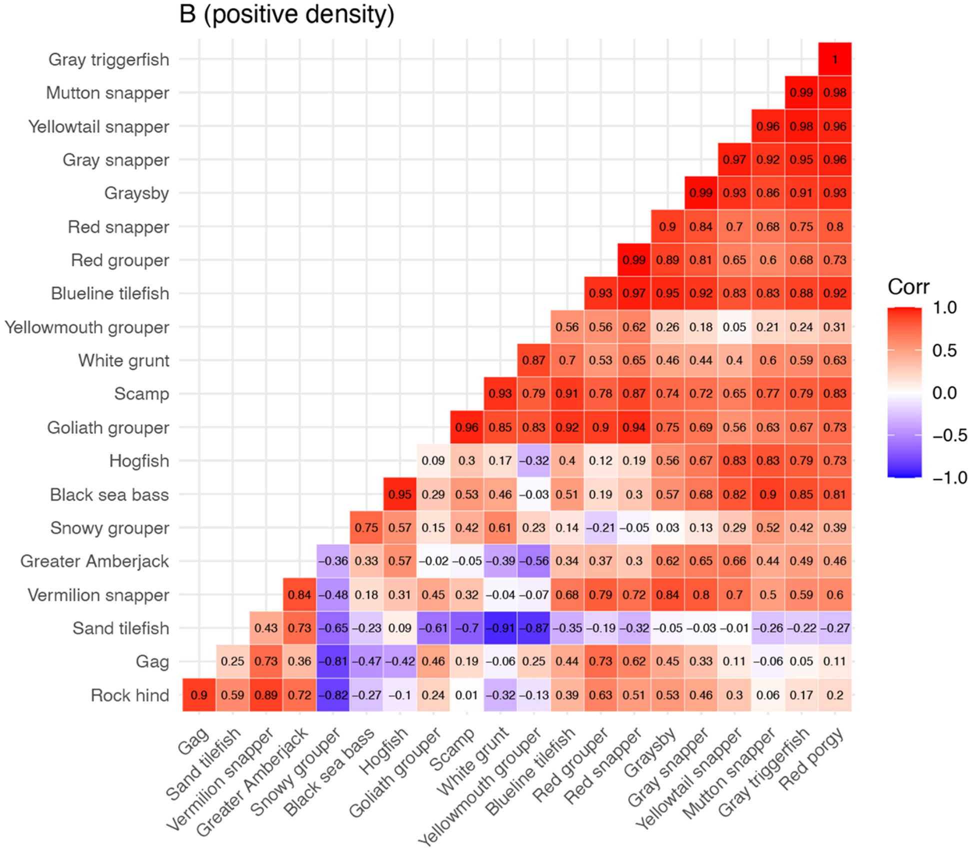
Information on shifting species' spatial distributions is becoming increasingly important as climate-induced distribution shifts have been documented (Baudron et al., 2020; Gervais et al., 2021; Hastings et al., 2020) and are projected to increase in the future (Pinsky et al., 2013). We developed estimates of COG from the JSDM, which can be used to identify distribution shifts (Thorson & Barnett, 2017). Most modeled species did not show strong evidence of significant changes in COG over the 11-year period investigated here. Based on linear trend analysis, very few species had significant trends in "northing" and "easting," and there were more negative than positive slopes for both, which is the opposite expected under temperature-induced shifts in distribution to the north or to deeper waters. Black sea bass is one exception where there has been a significant shift to both more northerly and to deeper waters within the South Atlantic region since 2011. Similar shifts in distribution have also been documented for black sea bass stocks and other stocks in the mid-Atlantic and New England shelf (Lucey & Nye, 2010; Nye et al., 2009). Whether these changes in black sea bass distribution are due to movement of propagules or adults, or due to spatial changes in productivity, is unknown. Some studies have reported that substrate-associated species may not shift spatial distributions in response to changing temperature and other hydrographic conditions compared with more pelagic species (Roberts et al., 2020). Even so, a number of oceanographic changes have been documented in the U.S. South Atlantic that may alter the spatial dynamics of the SEUS reef fish complex (Craig et al., 2021). For example, the spatial distributions of several marine species assemblages in the SEUS have shown responses to recent increases in ocean temperatures after a long historical period of stable temperatures in the region (Morley et al., 2017), suggesting future temperature variability will affect many of the species investigated here.

We made several simplifying assumptions that deserve further investigation. First, we did not include any catchability covariates in the model. Thus, catchability was assumed to be constant over time and space and across species. Bacheler and Shertzer (2020) suggested that catchability of the video survey can be affected by water current direction, water clarity, and temperature. Interestingly, we found that the average density pattern of vermilion snapper was negatively correlated with almost all of the other species (Figure 7B). Vermilion snapper typically occur higher in the water column, so their catchability and survey catch rates may be more variable compared with species more closely associated



A (encounter probability)

	Yellowmouth grouper	Goliath grouper	Mutton snapper	Red snapper	Gray triggerfish	Rock hind	Gray snapper	Yellowtail snapper	Graysby	Hogfish	Black sea bass	Vermilion snapper	White grunt	Red porgy	Scamp	Red grouper	Greater Amberjack	Gag	Blueline tilefish	Snowy grouper
Blueline tilefish																				0.96
Gag																			0.96	0.87
Greater Amberjack																		0.66	0.49	0.42
Red grouper																	0.98	0.8	0.65	0.56
Scamp																0.91	0.89	0.79	0.73	0.75
Red porgy															0.67	0.42	0.53	0.09	0.09	0.27
White grunt														0.97	0.75	0.58	0.7	0.19	0.12	0.26
Vermilion snapper													0.94	0.92	0.5	0.39	0.55	−0.13	−0.21	−0.08
Black sea bass												0.63	0.81	0.89	0.71	0.36	0.39	0.31	0.41	0.62
Hogfish											0.34	0.77	0.79	0.63	0.72	0.82	0.92	0.33	0.12	0.08
Graysby										0.99	0.24	0.68	0.71	0.53	0.71	0.86	0.94	0.38	0.16	0.09
Yellowtail snapper									0.96	0.96	0.12	0.74	0.67	0.5	0.49	0.67	0.8	0.1	−0.13	−0.2
Gray snapper								1	0.94	0.95	0.16	0.79	0.71	0.55	0.48	0.63	0.77	0.04	−0.18	−0.23
Rock hind							0.79	0.8	0.92	0.94	0.57	0.72	0.85	0.72	0.91	0.92	0.97	0.57	0.42	0.41
Gray triggerfish						0.98	0.84	0.83	0.91	0.95	0.61	0.83	0.92	0.81	0.86	0.84	0.92	0.42	0.28	0.31
Red snapper					0.98	0.94	0.89	0.88	0.91	0.96	0.57	0.9	0.94	0.83	0.76	0.74	0.86	0.26	0.11	0.15
Mutton snapper				0.55	0.54	0.58	0.8	0.84	0.83	0.77	−0.33	0.27	0.21	−0.01	0.31	0.66	0.71	0.25	−0.01	−0.21
Goliath grouper			0.97	0.59	0.62	0.69	0.76	0.82	0.87	0.8	−0.2	0.25	0.28	0.06	0.49	0.8	0.83	0.46	0.21	0.02
Yellowmouth grouper		0.96	0.88	0.54	0.61	0.72	0.62	0.68	0.81	0.74	−0.09	0.13	0.25	0.04	0.63	0.89	0.86	0.69	0.47	0.28
Sand tilefish	0.99	0.93	0.82	0.59	0.68	0.79	0.61	0.67	0.83	0.76	0.04	0.19	0.34	0.14	0.73	0.95	0.91	0.76	0.56	0.39



B (positive density)

	Gag	Sand tilefish	Vermilion snapper	Greater Amberjack	Snowy grouper	Black sea bass	Hogfish	Goliath grouper	Scamp	White grunt	Yellowmouth grouper	Blueline tilefish	Red grouper	Red snapper	Graysby	Gray snapper	Yellowtail snapper	Mutton snapper	Gray triggerfish	Red porgy
Gray triggerfish																				1
Mutton snapper																			0.99	0.98
Yellowtail snapper																		0.96	0.98	0.96
Gray snapper																	0.97	0.92	0.95	0.96
Graysby																0.99	0.93	0.86	0.91	0.93
Red snapper															0.9	0.84	0.7	0.68	0.75	0.8
Red grouper														0.99	0.89	0.81	0.65	0.6	0.68	0.73
Blueline tilefish													0.93	0.97	0.95	0.92	0.83	0.83	0.88	0.92
Yellowmouth grouper												0.56	0.56	0.62	0.26	0.18	0.05	0.21	0.24	0.31
White grunt											0.87	0.7	0.53	0.65	0.46	0.44	0.4	0.6	0.59	0.63
Scamp										0.93	0.79	0.91	0.78	0.87	0.74	0.72	0.65	0.77	0.79	0.83
Goliath grouper									0.96	0.85	0.83	0.92	0.9	0.94	0.75	0.69	0.56	0.63	0.67	0.73
Hogfish								0.09	0.3	0.17	−0.32	0.4	0.12	0.19	0.56	0.67	0.83	0.83	0.79	0.73
Black sea bass							0.95	0.29	0.53	0.46	−0.03	0.51	0.19	0.3	0.57	0.68	0.82	0.9	0.85	0.81
Snowy grouper						0.75	0.57	0.15	0.42	0.61	0.23	0.14	−0.21	−0.05	0.03	0.13	0.29	0.52	0.42	0.39
Greater Amberjack					−0.36	0.33	0.57	−0.02	−0.05	−0.39	−0.56	0.34	0.37	0.3	0.62	0.65	0.66	0.44	0.49	0.46
Vermilion snapper				0.84	−0.48	0.18	0.31	0.45	0.32	−0.04	−0.07	0.68	0.79	0.72	0.84	0.8	0.7	0.5	0.59	0.6
Sand tilefish			0.43	0.73	−0.65	−0.23	0.09	−0.61	−0.7	−0.91	−0.87	−0.35	−0.19	−0.32	−0.05	−0.03	−0.01	−0.26	−0.22	−0.27
Gag		0.25	0.73	0.36	−0.81	−0.47	−0.42	0.46	0.19	−0.06	0.25	0.44	0.73	0.62	0.45	0.33	0.11	−0.06	0.05	0.11
Rock hind	0.9	0.59	0.89	0.72	−0.82	−0.27	−0.1	0.24	0.01	−0.32	−0.13	0.39	0.63	0.51	0.53	0.46	0.3	0.06	0.17	0.2

FIGURE 12 Interspecies correlations for (A) spatiotemporal encounter probability and (B) positive density.

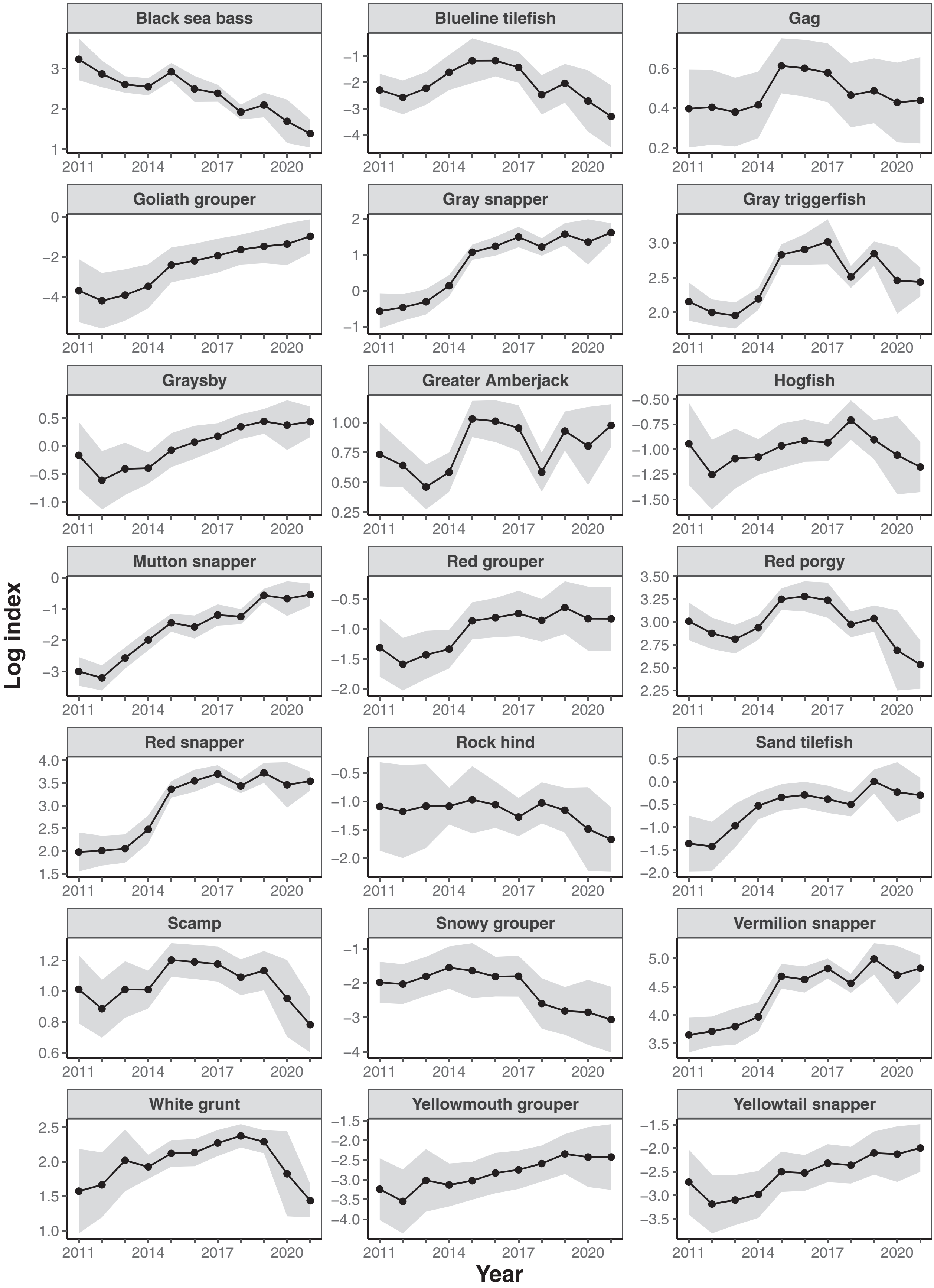


FIGURE 13 Species-specific abundance index (black line and points) with 95% CI (gray shading) for modeled reef fish species. No data were collected in 2020.

with bottom structure. Second, we did not account for the possibility that species may show ontogenetic changes in spatial distribution. Combining all age/size classes may have contributed to some of the differences in the correlations of the species with the spatial and spatiotemporal latent factors, particularly if recruitment to hard-bottom habitats or mortality (natural and fishing) among age and size classes varies spatially over the study region. Third, the JSDM estimates density hotspots by sharing information among all the species, which results in a shrinkage, whereby rare species showing similar patterns in distribution and abundance to more common species with which they are correlated. We recommend future research grouping species a priori based on traits. Finally, spatial aspects of the SERFS video survey and potential effects on inferences regarding species' spatial dynamics warrant further consideration. For example, the spatial coverage of the

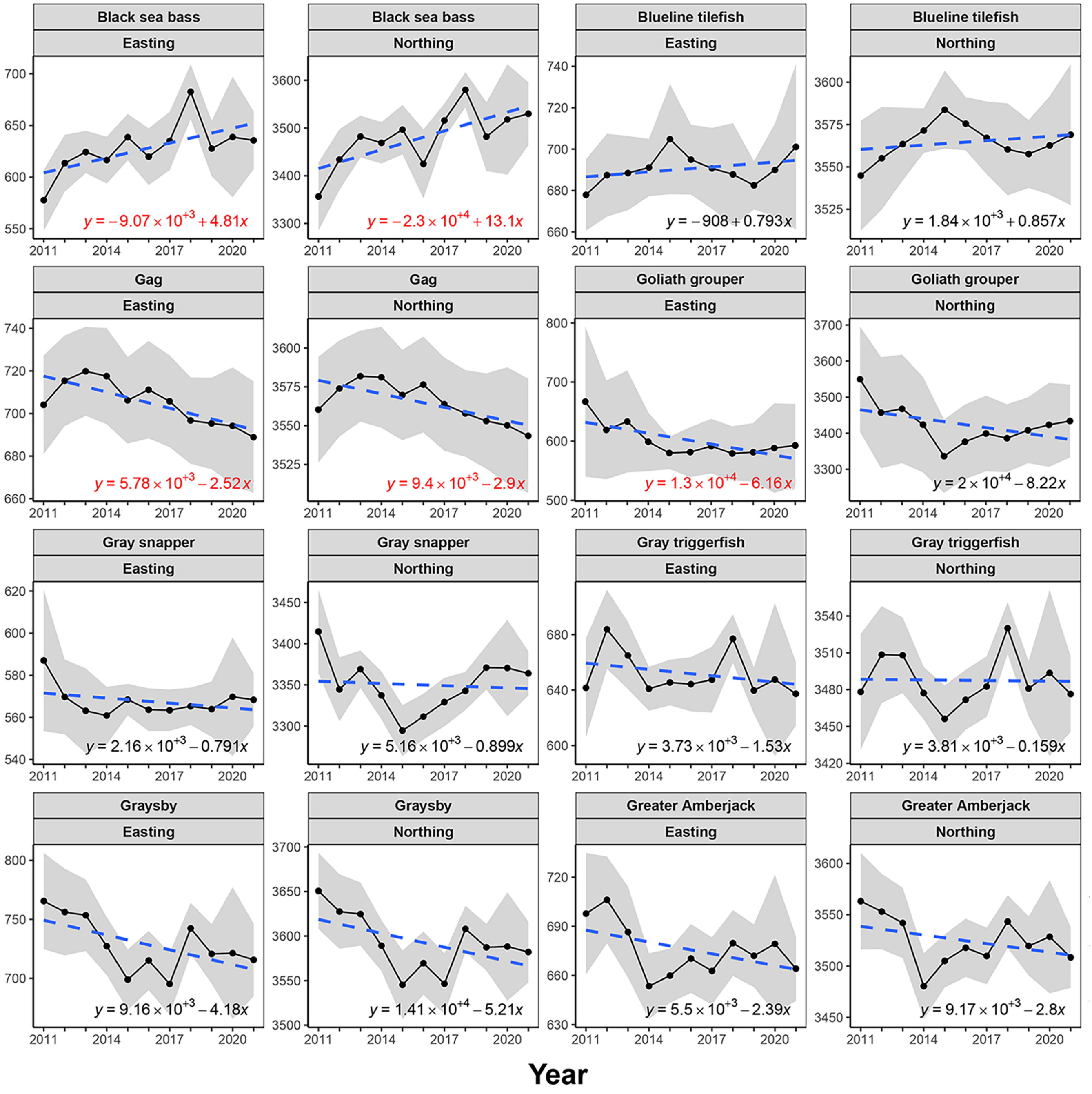


FIGURE 14 Estimated easting and northing (black line and points) of the center of gravity with 95% CI (gray shading) for modeled reef fish species. The blue dashed line is the regression line and the estimated equations are shown at the bottom-right corner of each panel with significant relationships in red.

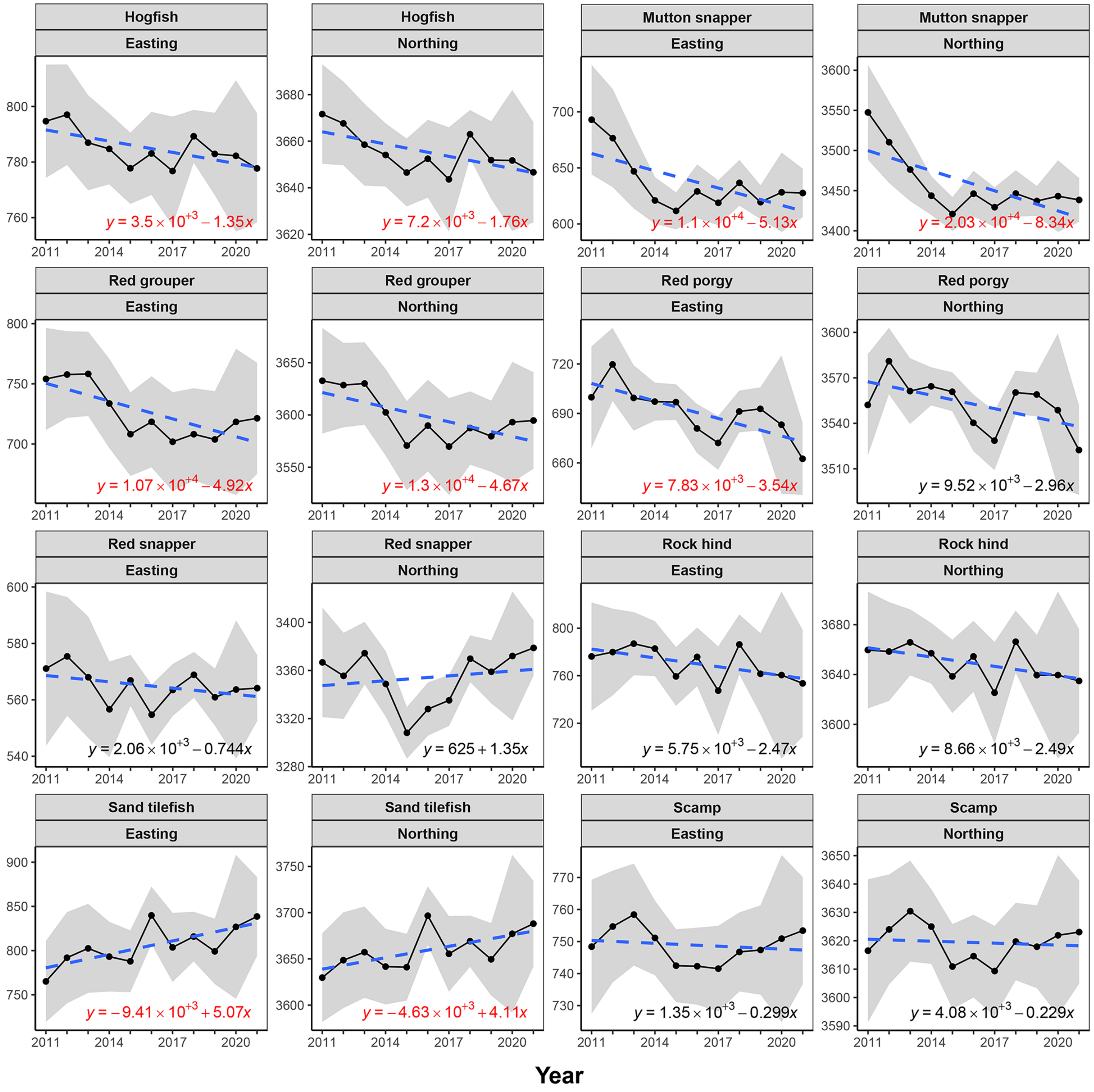


FIGURE 14 (Continued)

video survey has varied slightly over time, with some northern areas not sampled in the first year (i.e., 2011) and some variation in sampling intensity with depth occurred across some years (Appendix S1: Figure S1). Further, the sampling universe of SERFS only includes known hard-bottom habitat, and the amount of hard bottom that exists in the SEUS is uncertain (Steward et al., 2022). If the survey does not sample a significant portion of hard-bottom habitat within the survey footprint or if species also occupy habitats other than hard bottom, then inferences on species' spatial distributions may be biased. This could be particularly important for detecting range shifts or expansions. Although the predictions for unsampled areas were based on the spatiotemporal autocorrelation estimated within the model, additional work is needed to determine how survey design affects estimates of abundance and spatial distribution.

Our study is motivated by the need to address bycatch of overfished and vulnerable species in highly mixed reef fisheries of the SEUS, potentially using spatiotemporal fishery management strategies. Spatiotemporal modeling

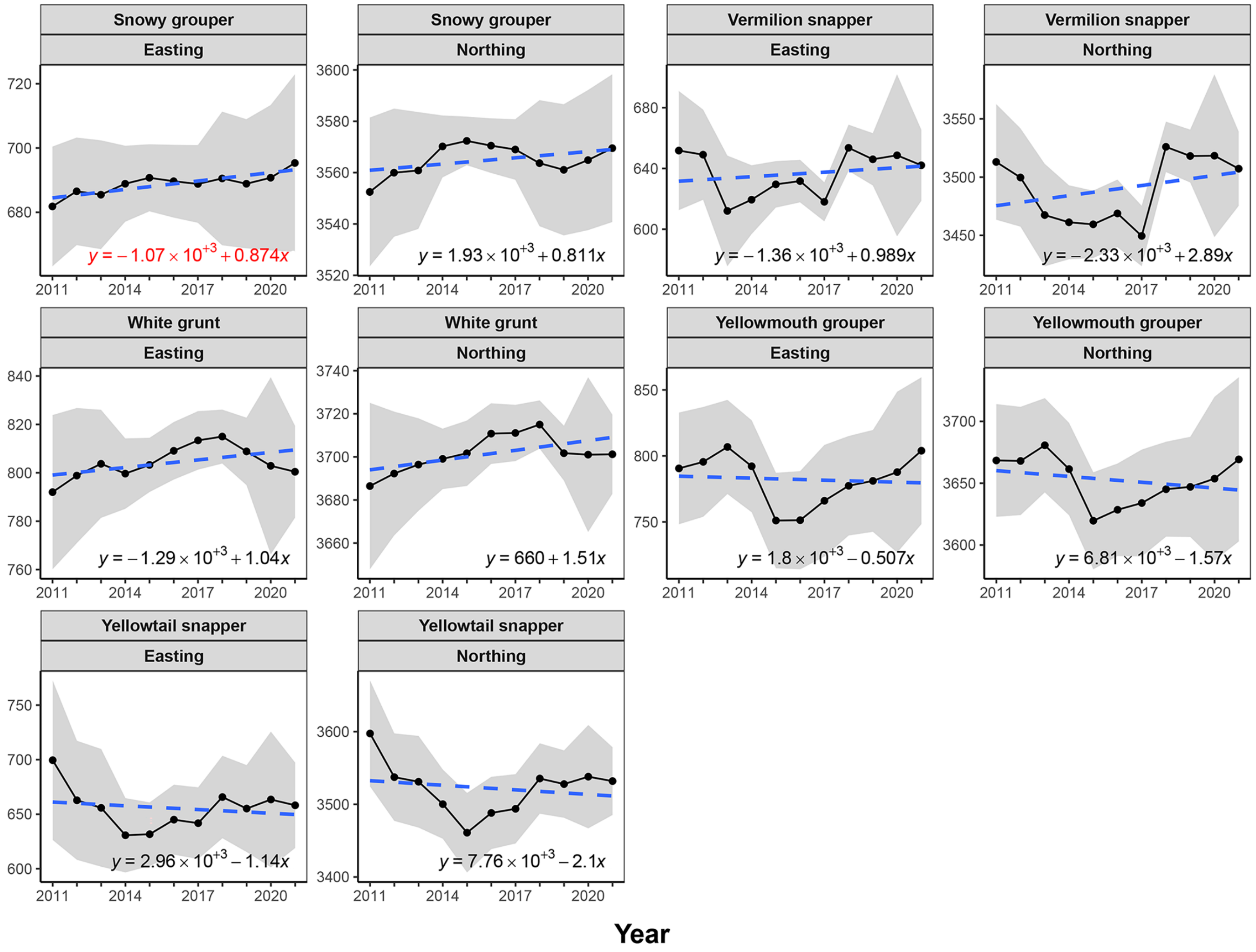


FIGURE 14 (Continued)

has been used to provide insights on the effectiveness of spatial targeting in mixed stock fisheries (Dolder et al., 2018). Although distinct species assemblages where common spatial patterns emerge may be identified, species within an assemblage show similar spatial patterns, where potential for spatial targeting can be limited (Dolder et al., 2018). Our results demonstrate that mixed reef fish fisheries in SEUS showed strong associations among most of the 21 species considered. Only a few species assemblages were identified based on spatial and spatiotemporal synchrony in encounter probability and positive density, and species within an assemblage were difficult to separate spatially. Additionally, the species composition within an assemblage changed depending upon the grouping variable. Therefore, for most of the species considered, spatial targeting may not be an effective management strategy to selectively target a particular species. Correlations were generally stronger based on occupied habitat and average density than based on interannual variability, suggesting high correlation in average density may not persist from one year to the next. This suggests that dynamic spatial closures may be more efficient than static spatial closures in minimizing discard mortality within this reef fish complex. However, this requires an understanding of the underlying mechanism that drives the interannual variability in distribution and some capacity to predict conditions for a given fishing season. An important next step to better inform spatial management (e.g., spatial closures of various sizes, locations, and durations) would be to develop an integrated risk spatial surface map by combining predicted average density map for each species weighted by individual species risk (Hazen et al., 2018), perhaps determined from the relative status (e.g., overfishing) of species or based on management or stakeholder (e.g., fishers) concerns. For example, overfished and vulnerable species could be given higher weighting values. A simulation study can be conducted to further quantify the extent to which spatiotemporal management measures can reduce bycatch of overfished and vulnerable species. Fleet dynamics with and without constraints on spatiotemporal management measures can be simulated on the estimated reef fish community spatial structure. The performance of each scenario can then be evaluated in terms of the total amount of dead discards of overfished and vulnerable species and landings of healthy species.

Besides spatial management strategies, the multispecies model applied in this study can be used to develop and evaluate multispecies management strategies. Historically, regulations for the reef-associated fishes in the SEUS have been established on a species-by-species basis, but fishing effort applies to the complex given the high correlations among species. Therefore, single-species output controls can result in a substantial amount of dead discarded bycatch which is a waste of natural resources (Shertzer et al., 2024). The modeling approach developed in this study can be paired with a fleet dynamic model to predict realized catches for each species given targeting of particular species within the reef fish complex. This will allow managers to examine the impacts of a single-species total allowable catch on other species.

Understanding the spatiotemporal distribution of fish species is a central focus of fisheries ecology, and important for guiding management and conservation efforts. This study provided a more holistic understanding of how common reef species in the SEUS coexist and covary in space and time and identified trends and similarities in their abundance and distribution. The findings suggest that spatiotemporal management strategies to avoid harvest of particular species may not be effective for reducing bycatch in these highly mixed reef fisheries due to high spatial correlations in occupied habitat and spatial pattern of density. Varying responses to environmental changes may influence the structure of emerging reef assemblages. Management attention is needed for some of the species with unknown status as they are showing a declining trend in abundance.

ACKNOWLEDGMENTS

We thank James Thorson and two anonymous reviewers for providing constructive feedback on earlier versions of this manuscript. This research was supported by funding from Grant 80843-Z7553201 from the National Oceanic and Atmospheric Administration (NOAA). The findings and conclusions expressed herein are those of the authors and do not necessarily reflect the view of NOAA or any of its subagencies.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Cao et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.10943451.

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SUPPORTING INFORMATION

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

How to cite this article: Cao, Jie, J. Kevin Craig, and Matthew D. Damiano. 2024. "Spatiotemporal Dynamics of Atlantic Reef Fishes off the Southeastern U.S. Coast." *Ecosphere* 15(6): e4868. https://doi.org/10.1002/ecs2.4868