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Spatial Distribution Changes and Habitat Use in Red Porgy in Waters off the Southeast U.S. Atlantic Coast

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Abstract

Despite 30 years of relatively strict management measures, the Red Porgy *Pagrus pagrus* population off the southeast U.S. Atlantic coast has not met rebuilding goals and was still categorized as overfished over a decade after a moratorium (SEDAR 2020). The lack of recovery indicates that limiting fishing pressure is not enough to effectively manage population levels. Population size may be driven by spatial or habitat associations independent of fishing pressure. We defined spatial distribution and habitat associations of Red Porgy adults and recruits by using a 23-year, fishery-independent trap catch time series (1996–2019). Abundance of recruits was below the long-term average, and adults were declining for the last 8 years of the time series. In addition, the spatial distribution of recruits tended to contract to deeper waters in the center of the region when abundance was low, whereas adults remained relatively consistent in their spatial and depth distribution regardless of abundance. The independence between effective area occupied and adult abundance supports that adults persisted throughout the region, whereas recruit area occupied was proportional to abundance. Recruits and adults overlapped spatially, but there was some partitioning of habitats: recruits were more abundant in less-complex habitats (low benthic biota coverage and low availability of hard substrate) relative to more complex habitats, and adults were more abundant in more complex or warm habitats than in less-complex or cooler habitats. When overall abundance was reduced, adult abundance in more complex habitats became more similar to abundance in less-complex habitats, while there was little to no change in recruit habitat use. The center of the region had a high overlap of adults and recruits, particularly in times of reduced recruitment. If fishers cannot target adults only, there is high potential for bycatch mortality or reduced fitness for recruits, which would further reduce the likelihood of recovery.

Most economically valuable demersal fish off the southeastern U.S. (SEUS) Atlantic coast are reef associated and managed under the regional Snapper–Grouper Fisheries Management Plan by the South Atlantic Fishery Management Council (SAFMC 1991). One such species, the Red Porgy *Pagrus pagrus*, was heavily targeted well prior to the enactment of the first management measures in the 1980s. In the late 1990s, there was growing concern among fishers and managers that the population in the SEUS had declined severely; a series of strict management

measures was implemented in 1999 and 2000, beginning with an 11-month moratorium followed by greatly restricting recreational bag limits, establishing a spawning season closure, and limiting commercial landings to a small bycatch limit (SAFMC 1998a, 1998b, 2000). Subsequent stock assessments indicated that even with strict management, Red Porgy biomass had only recovered moderately and then declined again over a decade later (SEDAR 2020). Two of the greatest challenges to the management of Red Porgy (and many species in the snapper–grouper

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complex and throughout the world) are bycatch and discard mortality due to the high overlap of species distributions in the region and a lack of studies focused on spatial ecology (Hall 1996; Dunn et al. 2010).

Spatial study of fish distribution and abundance provides essential information on critical habitats, the potential for interspecific interactions, vulnerability to human activities, and appropriate assessment model structures, which may need to include subareas within a management region (Cooke et al. 2016). Examination of spatiotemporal trends also provides a potential early warning sign of impending stock collapse, as serial local depletions or range contractions can preface issues for the full stock as was seen in Atlantic Cod *Gadus morhua* and sardines *Sardinops* spp. (Lluch-Belda et al. 1989; Atkinson et al. 1997; Warren 1997; McFarlane et al. 2002). In addition, assessments and projections can be biased if spatiotemporal dynamics are not accounted for, ultimately reducing the effectiveness of management actions (Cooke et al. 2016). There are numerous examples of studies demonstrating that spatial dynamics of species, as described by a variety of metrics, vary with changes in population abundances (MacCall 1990; Hilborn and Walters 1992). Population decreases in North Sea gadoids, Bay of Biscay European Hake *Merluccius merluccius*, and spawning Common Sole *Solea solea* followed the proportional density model (Myers and Stokes 1989; Petitgas 1997, 1998), while larval Atlantic Herring *Clupea harengus* followed the constant density model (Iles and Sinclair 1982) and adult Atlantic Herring, anchovies *Engraulis* spp., and Atlantic Cod followed the basin model (Ulltang 1980; MacCall 1990; Swain and Wade 1993).

Overfished populations recover at variable rates and with varying success, generally dependent on the degree to which they were overfished and their life history, such as time to maturity and growth rates. For severely depleted populations, even strict management is unsuccessful due to Allee effects (Liermann and Hilborn 1997). In the absence of regular stock status determinations, several other metrics can serve as proxies for stock recovery, such as increases in landings or the frequency of sectors reaching their annual catch limits, increases in abundance from scientific surveys, and expansion of the length or age distributions (SEDAR 2017; Harasti et al. 2018), especially if spawning individuals become more abundant. Additionally, increases in the representation of small or newly recruited fish may preface increased abundance, as these potentially strong year-classes may persist into subsequent years (Jaworski et al. 2010). Depending on the life history of a species (e.g., age at maturity and longevity), some recovery indicators can be apparent well before others. To complement the examination of abundance trends, identification of the spatial patterns of recruitment may provide

insight into areas or habitats that are important for supporting new recruits.

The current study is aimed at defining habitat associations for and the spatial distribution of Red Porgy in the SEUS region from a fishery-independent survey. We analyzed a fishery-independent trap time series encompassing 23 years to quantify the relationships between sampling and environmental parameters (location, depth, temperature, bottom biota, and topography) and the abundance of Red Porgy adults and recruits. In addition, we tested for changes in abundance, distribution, and habitat use over time. Defining the habitat characteristics that persistently support high abundance of recruits may indicate preferred or essential habitat and better help managers to take necessary actions to improve stock rebuilding. In addition, defining areas of differential recovery or loss may help managers to develop strategies that are more likely to lead to overall recovery.

METHODS

Sampling design and study area.—Red Porgy were collected by chevron traps deployed on hard-bottom habitats at depths ranging from 15 to 115 m along the eastern U.S. continental shelf and shelf edge between Cape Hatteras, North Carolina, and St. Lucie Inlet, Florida (Figure 1). Sampling was conducted as part of a regional fishery-independent, standardized survey initiated in 1990 by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program at the South Carolina Department of Natural Resources (SCDNR). Two additional programs currently collaborate with MARMAP in this survey, collectively referred to as the Southeast Reef Fish Survey (SERFS). These programs are the Southeast Area Monitoring and Assessment Program—South Atlantic (SEAMAP-SA; also at SCDNR), which began in 2009, and the Southeast Fishery-Independent Survey (SEFIS; Southeast Fisheries Science Center, Beaufort Laboratory, Beaufort, North Carolina), which began in 2010. All partner programs' monitoring efforts are funded currently through the National Marine Fisheries Service.

Throughout the survey range, stations have been established on confirmed hard-bottom substrate and are sampled by SERFS from mid-April through mid-October of each year. Hard-bottom habitats in the region can range from flat pavement to rock ledges and pinnacles with attached invertebrates or algae. Each year, between one-third and one-half of the total number of stations available in the sampling universe are selected randomly such that no stations to be sampled are closer than 200 m in order to (1) minimize the likelihood of nearby traps attracting fish from the same location and (2) maintain statistical independence among traps. The number of stations available has increased over time and with the

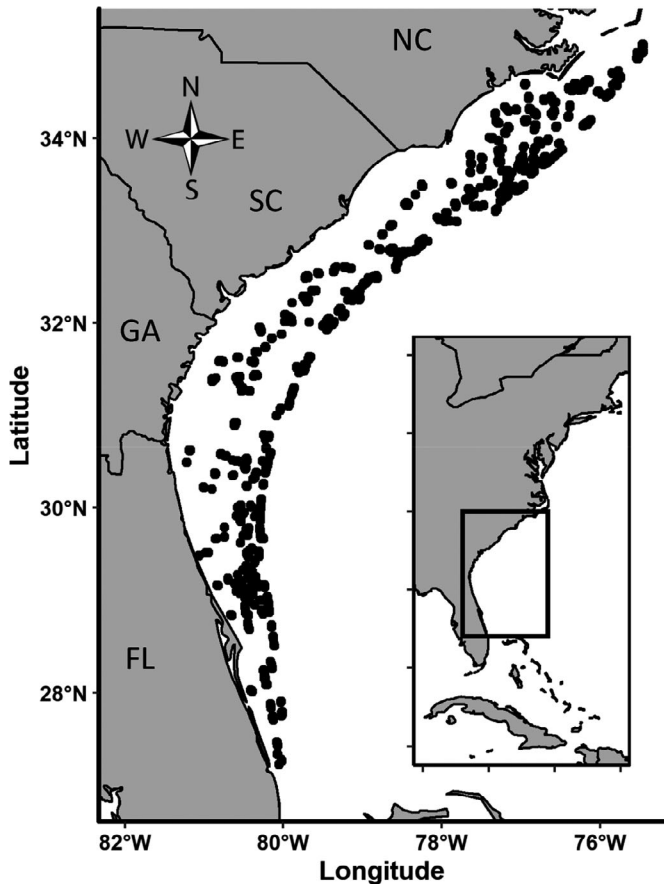


FIGURE 1. Study region and hard-bottom stations for the chevron trap survey conducted in waters off the southeastern U.S. Atlantic coast (inset).

additional SERFS partnerships. In an effort to minimize the effects of the change in the survey's spatial footprint and sampling effort over time, only samples from 1996 and later were utilized for this analysis. Standardized chevron traps were used in the region beginning in 1990, but most sampling was conducted off South Carolina, Georgia, and southern North Carolina. Starting in 1996, Florida and central North Carolina were sampled consistently, although at a much lower sampling intensity than in recent years.

Data collection.—The MARMAP program began using chevron traps in 1988 after a commercial fisherman introduced the use of this trap design in the SEUS region (Collins 1990). Currently, all three fishery-independent monitoring programs composing SERFS continue to utilize the chevron trap as their primary monitoring gear. Chevron traps are arrowhead shaped, with a total interior volume of 0.91 m^3 (Collins 1990; MARMAP 2009). Each trap is constructed of 35×35 -mm square-mesh, plastic-coated wire. Each trap possesses a single entrance funnel (“horse neck”) and a release panel to remove the catch.

Prior to deployment, each chevron trap is baited with a combination of whole or cut clupeids, with menhaden *Brevoortia* spp. most often used. Four whole clupeids on each of four stringers are suspended within the trap, and approximately eight clupeids, with their abdomens sliced open, are placed loose in the trap. An individual trap is attached to an appropriate length of 8-mm (0.3125-in) polypropylene line buoyed to the surface using a polyball buoy, a 10-m trailer line, and a Hi-Flyer buoy or another polyball. Generally, traps are deployed in sets of six when a sufficient number of stations is available in a given area. After an approximately 90-min soak time, traps are retrieved in chronological order of deployment by using a hydraulic pot hauler. All chevron trap deployments occur during daylight hours (no earlier than 30 min after sunrise and retrieved no later than 30 min before sunset).

Oceanographic data are collected via conductivity–temperature–depth instruments (CTDs) to complement most gear deployments. Sea-Bird SBE 19-, 25-, and 25Plus CTDs were used at various time points within the time series. All CTDs were calibrated annually and measured depth, temperature, and salinity. A single CTD cast in a location similar to that of traps but a minimum of 200 m away from any trap was conducted while each set of chevron traps soaked. Salinity was generally near 35 psu; therefore, we focus only on bottom temperature in the present paper. We included temperature in analyses as the average temperature ($^{\circ}\text{C}$) within 5 m of the bottom.

Bottom habitat type was determined for stations in the chevron trap universe from underwater videos. Outward-looking video cameras were added to the chevron trap survey in 2010. All cameras collected high-definition imagery of bottom features that were coded by SEFIS personnel following standard protocols, which include calibration among readers and extensive training prior to reading videos (Bacheler et al. 2014). Several habitat types were determined by these protocols, including relative vertical relief (high [$>1.0 \text{ m}$], medium [$0.3\text{--}1.0 \text{ m}$], or low [$<0.3 \text{ m}$]), percent hard-bottom substrate (0–100%), and percent biota density (amount of visible bottom covered by attached invertebrates or algae). Invertebrates and algae were combined for the current analyses, as it can be difficult to differentiate between biota types from videos due to visibility conditions, the density of fish in the frame of view, or the attached biota's distance from the trap. Since bottom type was not available for the entire time series, we conducted several preliminary analyses to test for changes in habitat characteristics over time for each station sampled with video more than four times. We found no evidence of either consistent or drastic changes in vertical relief, percent hard substrate, or biota density over time. Based on this and anecdotal evidence from historical sampling logs, any station in the trap universe with more than three video samples was assigned an average

value for these three bottom characteristics. Each station's bottom type values were then applied to collections throughout the time series that occurred on a given station. Approximately 10–13% of collections in a given year were excluded from analysis due to missing bottom type data.

Immediately after each trap was retrieved, collected fish were placed on ice in bins labeled for that deployment. Once a set of gear deployments was completed, all fish caught in each collection underwent a length frequency work-up, which consisted of identifying all fish in each collection to species level or the lowest possible taxon and then counting and measuring all fish per species per collection. An aggregate weight for each species per collection was recorded in grams wet weight. Lengths (measured to the nearest cm TL prior to 2010 or nearest mm TL since 2010) of all individual fish per species per collection were determined using an electronic fish measuring board or a measuring cradle and were recorded by hand on a paper datasheet. Following the length frequency work-up, individual fish were saved for otolith dissection to determine age. Prior to 2008, Red Porgy for aging were subsampled based on length-bins. Since 2008, either all Red Porgy were dissected for aging or fish were subsampled randomly. Fish collected by the survey were sampled for otoliths and aged in accordance with standard protocols (Smart et al. 2015).

Trap catches of Red Porgy were split into two life stages—recruits or adults—based on age compositions or sizes. Recruits were defined as fish assigned a calendar age of 0 or 1 year (Buble et al. 2018), as these individuals are below the average age at 50% maturity (Wyanski et al. 2019), while adults were defined as any age-2 or older fish. The total number of fish per trap was multiplied by the frequency of recruits or adults in the catch, determined from the age compositions of each trap. In some cases, ages were not available for a given trap, either due to loss or unreadability of otoliths or because no fish in a collection were selected for aging; in those cases, the length composition of a trap was substituted for age composition. Based on the length at 50% maturity (Wyanski et al. 2019), any fish less than 29 cm TL was categorized as a recruit, while all other fish were considered adults.

Data analysis.—The Vector-Autoregressive Spatio-Temporal (VAST) model was used to standardize Red Porgy adult and recruit abundance over time and to determine annual spatial distributions of each life stage (Thorson and Barnett 2017; Thorson 2019). In addition, the VAST model was used to estimate the center of gravity and effective area occupied by each life stage over the time series. The VAST model correlates abundance in a given sample to covariates for that sample and other factors included in the model by decomposing the time series into two components—probability of encounter and

expected catch rate—effectively creating a delta model (Maunder and Punt 2004). For Red Porgy, we included soak time as an offset; life stage, year, and vertical relief as fixed factors; latitude (°N), longitude (°W), depth (m), bottom temperature (°C), percent biota density, and percent hard substrate as continuous variables; and a Poisson error distribution. Depth, temperature, biota density, hard substrate, and vertical relief were included as covariates, which may impact catch rates. Based on preliminary analyses, the Poisson error distribution had the lowest Akaike's information criterion (AIC) relative to other error distributions (Akaike 1978). We ran the VAST model with 1,000 knots, spatial and spatiotemporal autocorrelation as random effects, and anisotropy turned off due to issues with convergence when anisotropy was included. In addition, we included a bias correction in the model to account for the change in the spatial footprint of the survey over time, since early in the time series central North Carolina and Florida were not sampled with the same effort currently employed as mentioned above.

Once the VAST model calculated the annual centers of distribution (defined as northings and eastings) and the effective area occupied, we calculated Pearson's product-moment correlation coefficients and conducted Student's *t*-tests to examine the relationship between these distribution metrics and the abundance of the two life stages.

To compare the abundance of Red Porgy adults and recruits to habitat characteristics more in-depth, we followed up the VAST analysis with two generalized linear models; abundance of either recruits or adults per hour of soak time was the response variable, and year, bottom temperature, percent hard substrate, biota density, and vertical relief were factors with a lognormal error distribution. All environmental variables also were included as interactions with year to examine changes over the time series. Continuous variables (bottom temperature, percent hard substrate, and biota density) were converted into high, medium, and low categories based on terciles (see Table 1 for details).

Traps were used only in abundance analyses if they occurred as part of the standard monitoring survey from April through October (e.g., exploratory trapping or damaged traps were not included) and with soak times

TABLE 1. Tercile values used to convert continuous habitat variables (bottom temperature, hard substrate, and biota density) into categorical factors for generalized linear models.

Factor	Low	Medium	High
Temperature (°C)	<21.21	21.21–23.63	>23.63
Hard substrate (%)	<7	7–21	>21
Biota density (%)	<11	11–22	>22

between 45 and 155 min. Bachelier et al. (2013) found that Red Porgy abundances increased in proportion to soak time through this range without signs of trap saturation. Traps that did not include values for all covariates also were dropped from analyses (e.g., no habitat data or missing temperature data). All analyses were conducted in R version 3.6.3.

RESULTS

Since 1996, an average of 662 hard-bottom monitoring stations were sampled each year using standard protocols and included in the current analyses, ranging from 146 stations in 1999 to 1,624 stations in 2018. An average of 943 adult Red Porgy was collected each year, ranging from 293 fish in 2008 to 2,491 fish in 2014. In addition, an average of 60 fish was identified as recruits each year, ranging from 13 fish in 2000 to 177 fish in 2014. Bottom type was characterized by video for 3,241 of the 4,264 chevron trap stations available in the sampling universe.

Red Porgy overall abundance for both adults and recruits has been low relative to the long-term abundance in the most recent years of the time series (Figure 2). In particular for recruits, the late 1990s and early 2000s were variable for recruit abundance in the region but generally were a high period for recruitment relative to 2008–2019. Adult abundance in the trap survey increased after the 2000 fishing moratorium, declined in 2008–2009, and recovered for a few years but has declined since 2012 (Figure 2).

Spatial distribution of Red Porgy in the SEUS varied with life stage and time, although there was a great deal of overlap between the life stages in the center of the region (Figures 3, 4). Spatial distributions created by the VAST package were converted from latitude and longitude into northings (distance from the equator) and eastings (distance from the prime meridian) in the Universal Transverse Mercator coordinate system. Recruits were encountered throughout the range of the trap survey, with hot spots over the outer shelf between Georgia and Onslow Bay, North Carolina (Figure 3). Recruit spatial distribution contracted into the center of the region and outer shelf waters during years of low abundance. This was particularly evident in the most recent years of the time series, when recruit abundance was below the long-term mean in 4 of 5 years. Adults generally were distributed over the middle and outer shelf (depths of ~40 to ~110 m) from Cape Lookout, North Carolina, to north of Cape Canaveral, Florida, with hot spots of greatest abundances over the outer shelf (60–110 m) and in Onslow Bay, North Carolina, and off South Carolina and northern Georgia (Figure 4). Adult spatial distribution was relatively consistent over time despite changes in abundance throughout the time series.

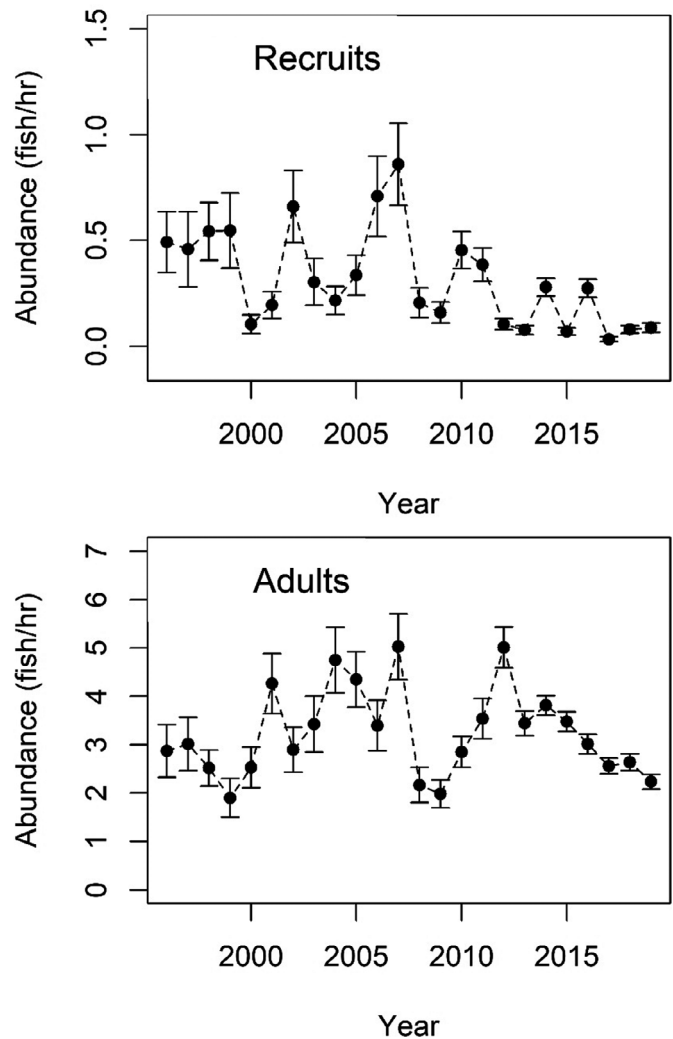


FIGURE 2. Standardized relative abundance indices (fish/h of soak time) of Red Porgy recruits and adults in a fishery-independent chevron trap survey conducted along the southeastern U.S. Atlantic coast. Points are annual means with SDs.

Ranges of Red Porgy recruits and adults showed potential but weak life stage-specific impacts of abundance changes. The center of gravity of recruits did not change much over the time series (Figure 5), primarily due to their restriction into the center of the region with decreased abundance and expansion to the edges of the region with increased abundance (Figure 3). The adult center of gravity changed only in the most recent years of low abundance, shifting southward and eastward (deeper; Figure 5). Recruit area occupied decreased in the most recent 10 years of the time series, potentially tracking reduced abundance and contracted spatial distribution (Figure 6). By comparison, adult area occupied was variable throughout the time series, with no suggestion that it tracked abundance changes (Figure 6). There was no significant

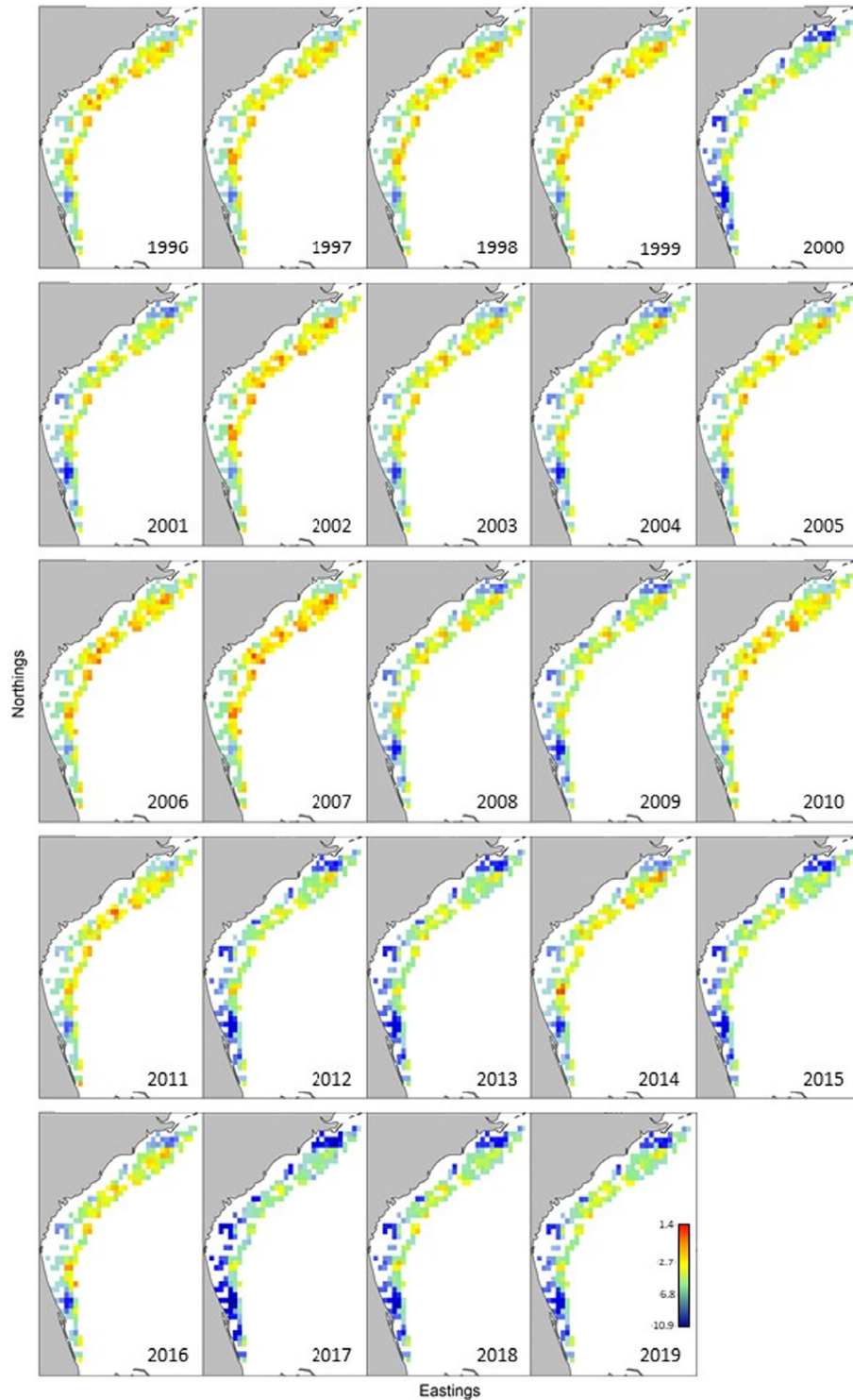


FIGURE 3. Estimated distribution of Red Porgy recruits in every year of the time series from the southeastern U.S. Atlantic chevron trap survey. Areas with colors represent the spatial domain of the survey and log-transformed relative abundance (fish/h of soak time). q

correlation between the abundance of either life stage and center-of-gravity metrics or area occupied (Table 2).

Similar to spatial distribution, Red Porgy adults and recruits inhabited similar types of habitats, although there

were some differences between the life stages. Recruit abundance was significantly related to biota density, percent hard substrate, and the interactions of biota density \times year, percent hard substrate \times year, and

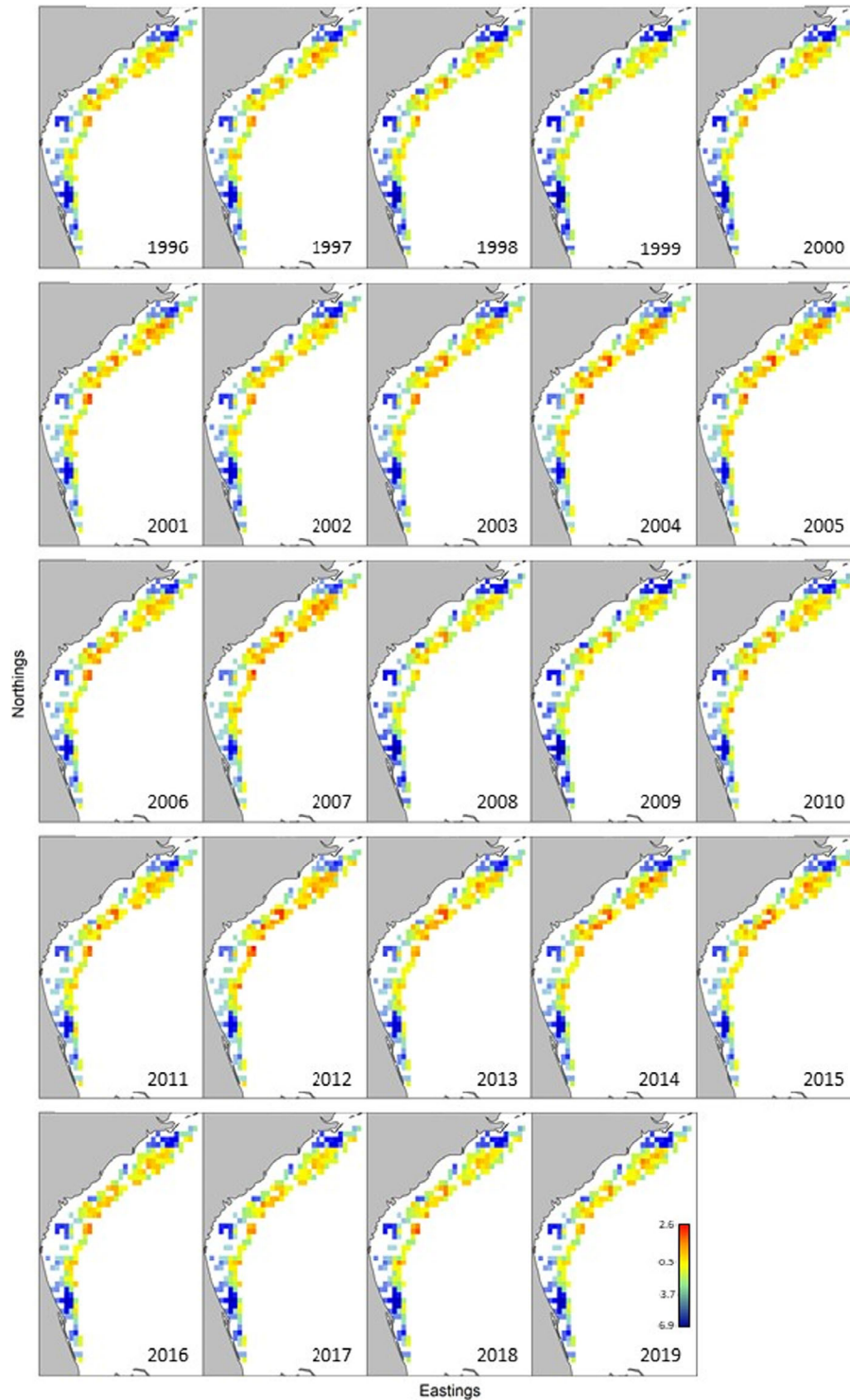


FIGURE 4. Estimated distribution of Red Porgy adults in every year of the time series from the southeastern U.S. Atlantic chevron trap survey. Areas with colors represent the spatial domain of the survey and log-transformed relative abundance (fish/h of soak time).qqqqqqqqqqqqqqqqqqqqqq

temperature \times year (Table 3). Recruit abundance was higher overall at stations with lower biota density and hard substrate relative to those with higher biota density

and hard substrate (Figure 7). Recruit abundance also declined at the end of the time series at stations with lower biota density and hard substrate to levels comparable to

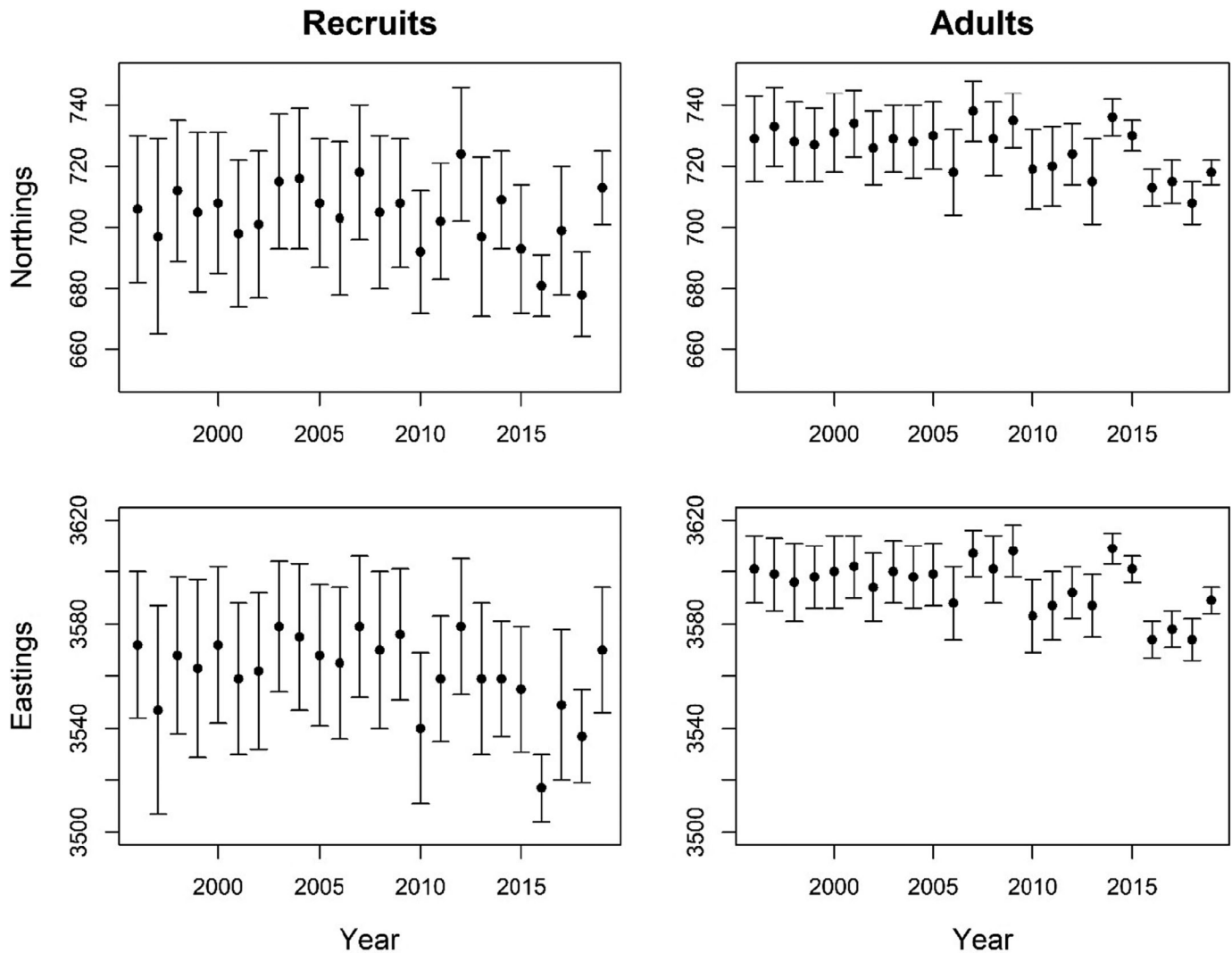


FIGURE 5. Center of gravity for Red Porgy recruits (left) and adults (right), shown in Universal Transverse Mercator projection using northings (top) and eastings (bottom). Points are the maximum likelihood estimates and the error bars represent ± 1 SE based on the Vector-Autoregressive Spatio-Temporal model.

those found at stations with higher biota density and hard substrate (Figure 7). In addition, recruit abundance declined at the end of the time series in all temperature levels (Figure 7). Adult abundance was significantly related to biota density, percent hard substrate, bottom temperature, vertical relief, and the interactions of hard substrate \times year and temperature \times year (Table 3). Adult abundance was higher overall at stations with medium and high biota densities and hard substrate compared to low biota densities and low hard-substrate coverage, in collections with medium and high temperatures relative to low temperatures, and at stations with low relief compared to medium or high relief (Figure 8). Adult abundance declined by the end of the time series at all levels of substrate, vertical relief, and temperature (Figure 8). This decline was particularly noticeable in low-relief stations

that had historically hosted the highest abundances of adults but by the end of the time series hosted adult abundances similar to those in medium and high vertical relief. In addition, there was a noticeable decline in habitat-specific adult abundance in medium and high hard-substrate stations relative to low hard substrate and in collections with medium and high temperatures relative to low temperature as overall abundance declined over time (Figure 8).

DISCUSSION

Spatiotemporal overlap between life stages may indicate shared habitat preferences, intraspecific competition, or a lack of resource partitioning. We used 23 years of a fishery-independent monitoring time series off the SEUS

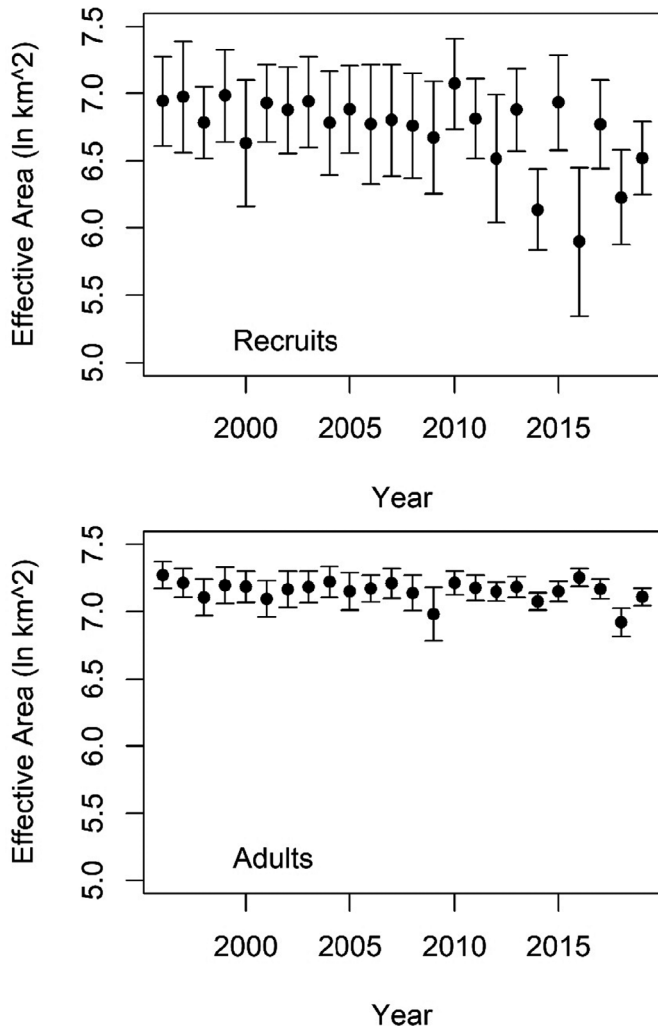


FIGURE 6. Effective area that was occupied by Red Pogy recruits and adults over the time series of the southeastern U.S. Atlantic chevron trap survey. Points are means with SDs from the Vector-Autoregressive Spatio-Temporal model.

TABLE 2. Pearson’s product-moment correlation coefficients (*r*), Student’s *t*-test values (*t*), and *P*-values for the abundance of Red Pogy recruits and adults and the following range metrics: centers of distribution (northings and eastings) and effective area occupied (Area).

Life stage	Metric	<i>r</i>	<i>t</i>	<i>P</i>
Recruits	Northings	0.186	0.886	0.385
	Eastings	0.131	0.620	0.541
	Area	0.352	1.762	0.091
Adults	Northings	0.290	1.159	0.168
	Eastings	0.240	1.159	0.258
	Area	0.224	1.080	0.291

Atlantic coast to examine spatiotemporal patterns and habitat associations of recent recruits (ages 0 and 1) and adults of Red Pogy from 1996 to 2019, a time period

during which this stock underwent a severe decline and remained low through at least 2017 (SEDAR 2020). Standardized abundances of recruit and adult Red Pogy in the trap survey have been reduced in recent years relative to the long-term trend, despite restrictive management measures. Spatial distribution of recruits tracked abundance changes over time, with contraction of spatial distribution, depth, and area occupied into the center of the region at low abundance levels. In contrast, adult spatial distribution did not track abundance over time, remaining relatively constant, although shifting southward and deeper in recent low-abundance years. Red Pogy recruits and adults overlapped in their spatial and depth distributions in the center of the region, suggesting that this is an area of potential intraspecific interactions between stages. However, recruits and adults tended to be more abundant in different bottom types and temperatures, with adults occupying more complex (high coverage of hard substrate and biota) and warm habitats and recruits occupying less-complex habitats. This finding indicates that resource partitioning among life stages is occurring even within the area of overlap.

Typical metrics used to indicate population recovery from an overfished state, short of a stock assessment, include increases in abundance from fishery-independent surveys, frequency of fishery sectors reaching their allocations before the end of the fishing year or season, size distributions (especially related to fishable fish), or evidence of strong year-classes entering the population. Red Pogy abundances from this fishery-independent trap survey increased after the enactment of a temporary moratorium in 1999. However, following the passage of Amendment 13C in 2006 by the South Atlantic Fishery Management Council, which increased the commercial quota and trip and bag limits, Red Pogy adult abundances in the trap survey returned to below or near the long-term average (SAFMC 2006). The low abundances of Red Pogy recruits in traps in the most recent years indicates that Red Pogy in the SEUS were recruitment limited in the most recent decade, with few new fish entering the fishery to replace those that were removed with relaxed catch restrictions. One method to combat low recruitment may be to take steps to reduce bycatch of small Red Pogy in the center of the region where they overlap with other exploited species, such as Black Sea Bass *Centropristis striata* and adult Red Pogy (Bublely et al. 2019; present study). Such place-based management (Lorenzen et al. 2010) may enhance year-class strength and minimize the impact of recruitment limitation. However, it currently is unknown whether the recruitment limitation is the result of decreased reproduction (mate encounter, fecundity, maturity, or fertilization success) or larval or juvenile survival.

In conjunction with the regional reductions in Red Pogy abundance in the trap survey, we saw no evidence

TABLE 3. Analysis of deviance results from generalized linear models that were used to examine Red Porgy recruit and adult habitat associations. For bottom temperature, biota density, and hard substrate, categories were based on the terciles defined in Table 1.

Factor	df	Deviance	Residual deviance	<i>F</i>	<i>P</i>
Recruits					
Year	23	56.5	2,475	16.1	<0.001
Temperature	2	0.7	2,474	2.3	0.104
Hard substrate	2	16.5	2,458	54.0	<0.001
Biota density	2	1.7	2,456	5.7	0.003
Vertical relief	2	0.2	2,456	0.5	0.602
Temperature × Year	46	26.1	2,430	3.7	<0.001
Hard substrate × Year	46	19.6	2,410	2.8	<0.001
Biota density × Year	46	16.2	2,394	2.3	<0.001
Vertical relief × Year	46	5.3	2,389	0.8	0.882
Adults					
Year	23	1,977.3	92,564	15.3	<0.001
Temperature	2	757.6	91,806	67.4	<0.001
Hard substrate	2	789.1	91,017	70.2	<0.001
Biota density	2	225.1	90,792	20.0	<0.001
Vertical relief	2	79.8	90,712	7.1	<0.001
Temperature × Year	46	1,412.2	89,300	5.5	<0.001
Hard substrate × Year	46	801.8	88,498	3.1	<0.001
Biota density × Year	46	332.1	88,166	1.3	0.093
Vertical relief × Year	46	136.2	88,030	0.5	0.997

of a reduction in the extent of adult Red Porgy occurrence, but results did suggest distribution contraction in recruits. Recruits demonstrated distributional changes consistent with the basin model in that both distribution and local abundance decreased concurrently (MacCall 1990). The constancy of extent paired with the general trend of overall abundance decreasing regionwide supported that spatial patterns of adult Red Porgy in the SEUS are most consistent with the proportional density model (Hilborn and Walters 1992). The pelagic community off Senegal also followed the proportional density model up to the point at which the population abundance had reached its lowest level and range contraction occurred, consistent with MacCall's (1990) basin model (Petitgas 1998). Based on the stock assessment history of Red Porgy in the SEUS and the continuing downward trend in abundance, it is possible and perhaps likely that adult Red Porgy in the SEUS will switch to one of these models as abundance continues to decrease. The constancy of the Red Porgy adult distribution despite declines to date also is a cause for concern that hyperstability is occurring, wherein the spatial distribution masks issues with fish abundance or availability (Walters and Martell 2004; Sarah et al. 2015).

Overall, the habitat associations defined here suggest that Red Porgy could require different habitats over their ontogeny, which complicates their management. Although not specifically tested for here, the low abundance of Red Porgy recruits in more complex habitats (high coverage of

biota and hard substrate) compared to the low abundance of adults in less-complex habitats suggests that these opposite habitats are marginal or less-preferred habitats for the two life stages of Red Porgy in the SEUS (Gaston et al. 2000). In addition, the differential abundance patterns may indicate habitat partitioning among life stages, consistent with ontogenetic differences in habitat use by other reef-associated species in the region (Glasgow 2017; Powers et al. 2018). Recruits in less-complex habitats may be relatively unprotected from predation but may take advantage of access to small invertebrates to prey upon (Goldman et al. 2016). Similar to Red Porgy, juvenile Red Snapper *Lutjanus campechanus* in the Gulf of Mexico also occur primarily on unstructured, low-relief habitats before transitioning to higher reliefs (Powers et al. 2018). The tendency of Red Porgy adult abundances to be highest in deeper waters and more complex habitats could have served as a refuge from fishing early in the exploitation history; however, with improvements in vessel instrumentation, speed, and fuel efficiency, this likely is no longer true. The differential reduction of adults in low-relief habitats also supports the idea of increased vulnerability in particular areas. Paxton et al. (2017) found that habitat characteristics played a minimal role in shaping temperate reef assemblages. Based on a 3-year video time series, Geraldi et al. (2019) found that Red Porgy abundance was not significantly related to habitat characteristics other than biota height. Our use of average habitat

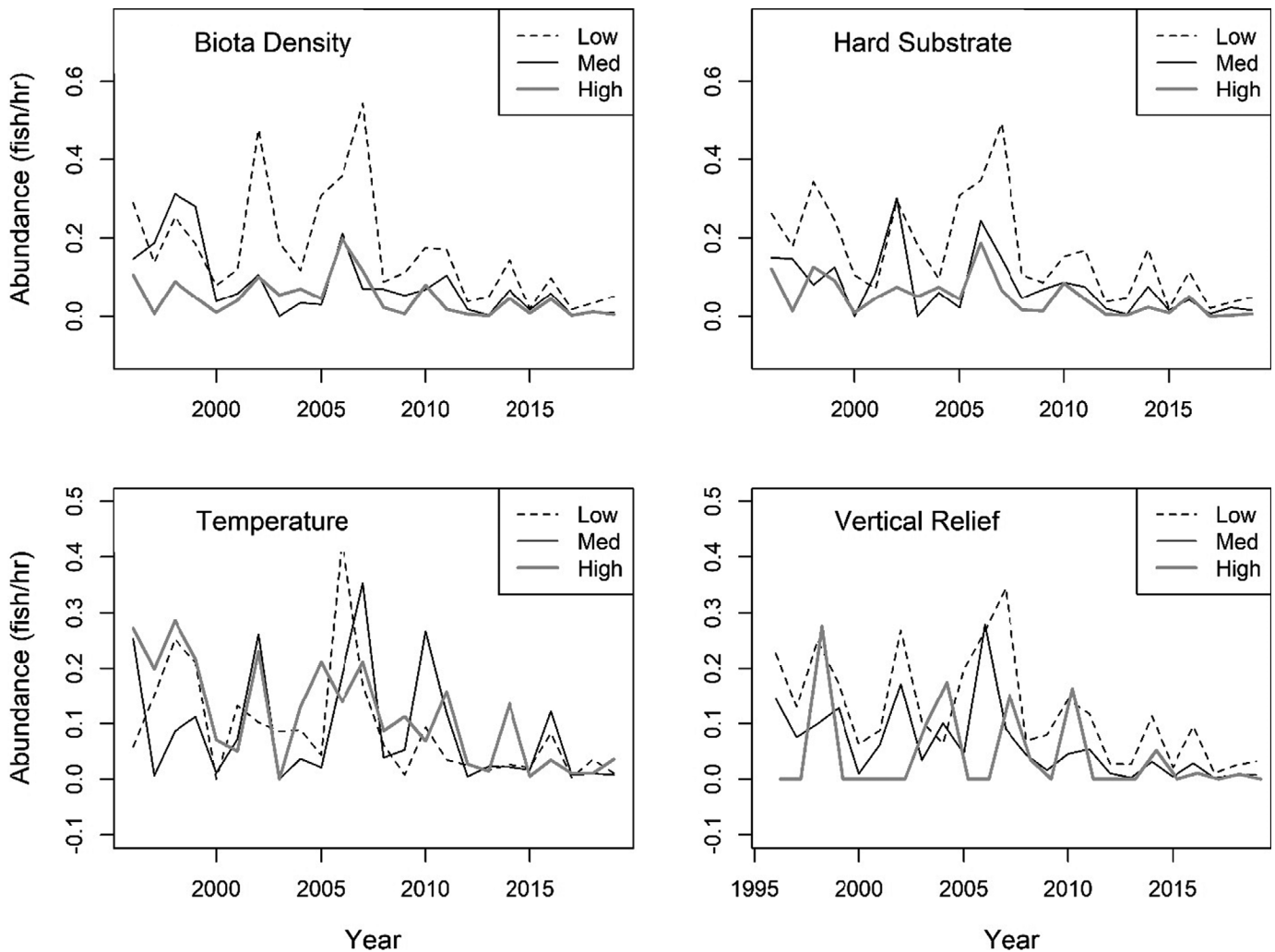


FIGURE 7. Red Pogy recruit habitat associations in the southeastern U.S. Atlantic chevron trap survey time series. Biota density, hard substrate, and bottom temperature categories (Low, Medium [Med], and High) were based on terciles given in Table 1.

characteristics from the longer video time series applied to stations sampled by the survey for the full time series and our examination of separate life stages allowed us to more thoroughly investigate habitat associations for Red Pogy, with the finding that habitat may play an important differential role for the two life stages.

A variety of options is available for examining the interplay of fish abundance, location, time, and habitat. The VAST approach was developed to allow researchers to examine spatial distribution while accounting for autocorrelation and biases that may be inherent to time series. In addition, examining multiple species (or, in this case, life stages) from the same survey independently may risk losing inferences about community- or life cycle-level properties (Clark et al. 2014; Thorson and Barnett 2017). Species distribution modeling techniques may allow differences in habitat to be inferred from spatial variation

(Latimer et al. 2009; Ovaskainen et al. 2016) but may not provide a direct test of those differences. For the current study, we employed the VAST approach in order to include spatial and spatiotemporal elements that were not well captured by other analytical approaches and also to account for the impacts of habitat covariates on the abundance of two Red Pogy life stages in the same survey. The VAST approach did have drawbacks, however, including limitations in how time was treated in the model. We considered time to be a fixed effect, partially due to each year of the survey having its own unique characteristics of station selection, cruise scheduling, and funding levels. However, other options, such as treating year as a random effect, resulted in a lack of convergence or required removing spatiotemporal autocorrelation to achieve convergence. This is possibly due to the survey design using random selection instead of fixed stations

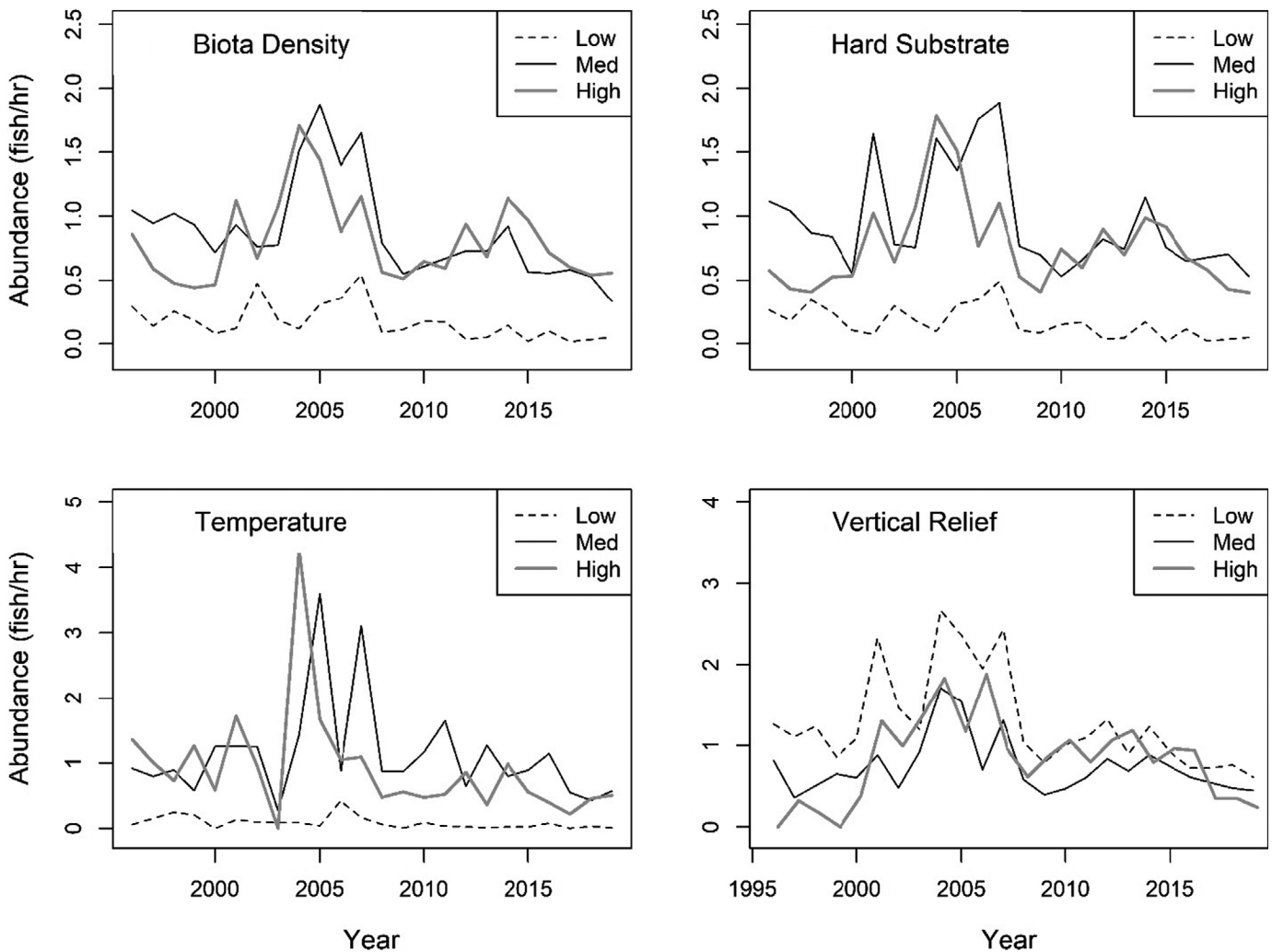


FIGURE 8. Red Pogy adult habitat associations in the southeastern U.S. Atlantic chevron trap survey time series. Biota density, hard substrate, and bottom temperature categories (Low, Medium [Med], and High) were based on terciles given in Table 1.

throughout time or even stratified random sampling, where the strata are sampled uniformly over time. Furthermore, the VAST approach did not give us a direct test of habitat associations, so we conducted supplementary analyses in the form of the generalized linear models to examine habitat use trends by the two life stages. Based on these results, it is critical to include habitat covariates in future examination of this survey's data.

Changes in the spatial distributions, habitat use, or abundance of Red Pogy have consequences for the species' exploitation and management. As areas of high local abundance become scarce, fishing for Red Pogy will become less efficient, as fishers must search for the remaining high-abundance sites (Petitgas 1998; Walters and Martell 2004). In turn, fishing behavior changes can increase effective fishing mortality once remaining hot spots are identified, thus putting potential refuges at risk (Petitgas

1998; Walters and Martell 2004). Under this scenario, not accounting for shifts in areas of occupancy and fishing effort can mask further stock declines consistent with hyperstability (Walters and Martell 2004; Sarah et al. 2015). In addition, there were recruitment pulses in 1998 and 2007, but recruitment has been consistently low since; when paired with their overfished status, this suggests that SEUS Red Pogy are at a greater risk of dramatic stock crash or local extinctions in the near future (Sale et al. 2005). The failure to incorporate spatiotemporal trends in assessments and recovery forecasts can lead to management actions that are either ineffective or counterproductive (Cooke et al. 2016). In addition, as we move toward the widespread use of marine protected areas, special management zones, and ocean zoning for multiple users, knowledge of the spatial ecology of overfished stocks is paramount to the success of these efforts and the

management of risks to recovery (Kenchington 2010; Norse 2010; Sanchirico et al. 2010; Cooke et al. 2016).

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