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Spatiotemporal dynamics and habitat use of red snapper (*Lutjanus campechanus*) on the southeastern United States Atlantic continental shelf

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ABSTRACT

Red snapper (*Lutjanus campechanus*) is an iconic marine fish species along the southeast United States coast. Despite its ecological and economic importance, surprisingly little is known about red snapper biology and habitat use on the southeast United States Atlantic continental shelf (SEUS). We used data from a long-term baited trap and video survey (2011–2022), as well as from remotely operated vehicle (ROV) sampling (2021–2023), to quantify temporal changes in relative abundance, patterns of spatial distribution, and habitat use of red snapper in the SEUS. Using generalized additive models, we showed that red snapper increased in relative abundance from 2011 to 2022 by ~ 1000 % in both trap and video samples. Red snapper relative abundance was highest in mid-shelf waters off the east coast of Florida, Georgia, and, to a lesser extent, off the Outer Banks of North Carolina; red snapper were less common off southern North Carolina and South Carolina. Highest relative abundance of red snapper occurred in locations with a moderate amount of natural structured habitat and high seafloor complexity and were never observed at randomly selected ROV stations (n = 197) lacking structured habitat. These results increase our understanding of the spatial and temporal distribution of red snapper, improve our knowledge of red snapper habitat use, and can be used when scaling local density estimates to the entire SEUS.

1. Introduction

Red snapper (*Lutjanus campechanus*) is a large, early maturing (~ age-2), long-lived (maximum observed age = 51 years), predatory fish species that occurs from Cape Hatteras, North Carolina, to the Yucatan Peninsula, including the Gulf of Mexico (Manooch and Potts, 1997; Hoese and Moore, 1998; SEDAR, 2021). Red snapper are found across a wide range of water depths on the continental shelf and shelf-break, from relatively shallow coastal habitats to deep mesopelagic habitats (Camber, 1955), but they are most commonly found in depths of 20–100 m (Gallaway et al., 1999; Mitchell et al., 2014; Bacheler et al., 2016). Benthic juveniles are mainly found over substrates consisting of shell hash and sand (Gallaway et al., 1999; Geary et al., 2007), while adults tend to associate with natural and artificial structure such as coral reefs, rocky outcroppings and ledges, oil rigs, and shipwrecks (Moseley, 1966; Powles and Barans, 1980; Williams-Grove and Szedlmayer, 2016; Dance and Rooker, 2019; Chatterjee et al., 2024).

Red snapper are an iconic species in the southeast United States (Cowan Jr. et al., 2011), and significant recreational and commercial fisheries for red snapper have operated in the region for many decades (White and Palmer, 2004; SEDAR, 2018, 2021). On the southeast United States Atlantic continental shelf (hereafter, SEUS), red snapper commercial landings increased throughout the 1950s and 1960s and peaked at 473,000 kg in 1968, followed by a long decline through the 1990s (Manooch III et al., 1998). Recreational landings temporally lagged behind the commercial harvest, peaking at 280,800 kg in 1985, but also

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have generally declined since that time (SEDAR, 2021). Since the late 1990s, however, the recreational sector has made up the majority of red snapper removals in the SEUS (Shertzer et al., 2019). Most of the red snapper harvest in the SEUS has occurred on the east coast of Florida, followed distantly by South Carolina, North Carolina, and Georgia.

A bleak stock assessment for SEUS red snapper in 2009 precipitated a number of red snapper-related actions (SEDAR, 2009). First, red snapper in the SEUS were determined to have been overfished since 1960 and overfishing was continuing to occur; multiple subsequent stock assessments since that time have produced similar results (SEDAR, 2010, 2017, 2021). Second, in response to the 2009 stock assessment, a fishery closure was enacted in 2010 that, aside from some short, periodic recreational and commercial fishing seasons, has continued to the present day (SEDAR, 2021). Third, the primary fishery-independent survey in the region (see Smart et al. (2020) for details) was expanded and strengthened given the loss of fishery-dependent data that was expected to occur during a fishery closure (Williams and Carmichael, 2009). Fourth, fishery-independent longline studies were funded in 2010 and 2011 that found no evidence of “cryptic biomass” (i.e., unobserved biomass) of large (> 850 mm total length) and old (> age-10) red snapper on the outer shelf that are generally unavailable to fisheries or surveys, with implications for estimating selectivity, as suggested by some stakeholders in the SEUS (Mitchell et al., 2014; SEDAR, 2021). Lastly, the U.S. Congress allocated \$1.5 M in funding in 2020 (and an additional ~ \$3.3 M in funding in subsequent years) to estimate red snapper age 2+ population size in the SEUS (SARSRP, 2020),

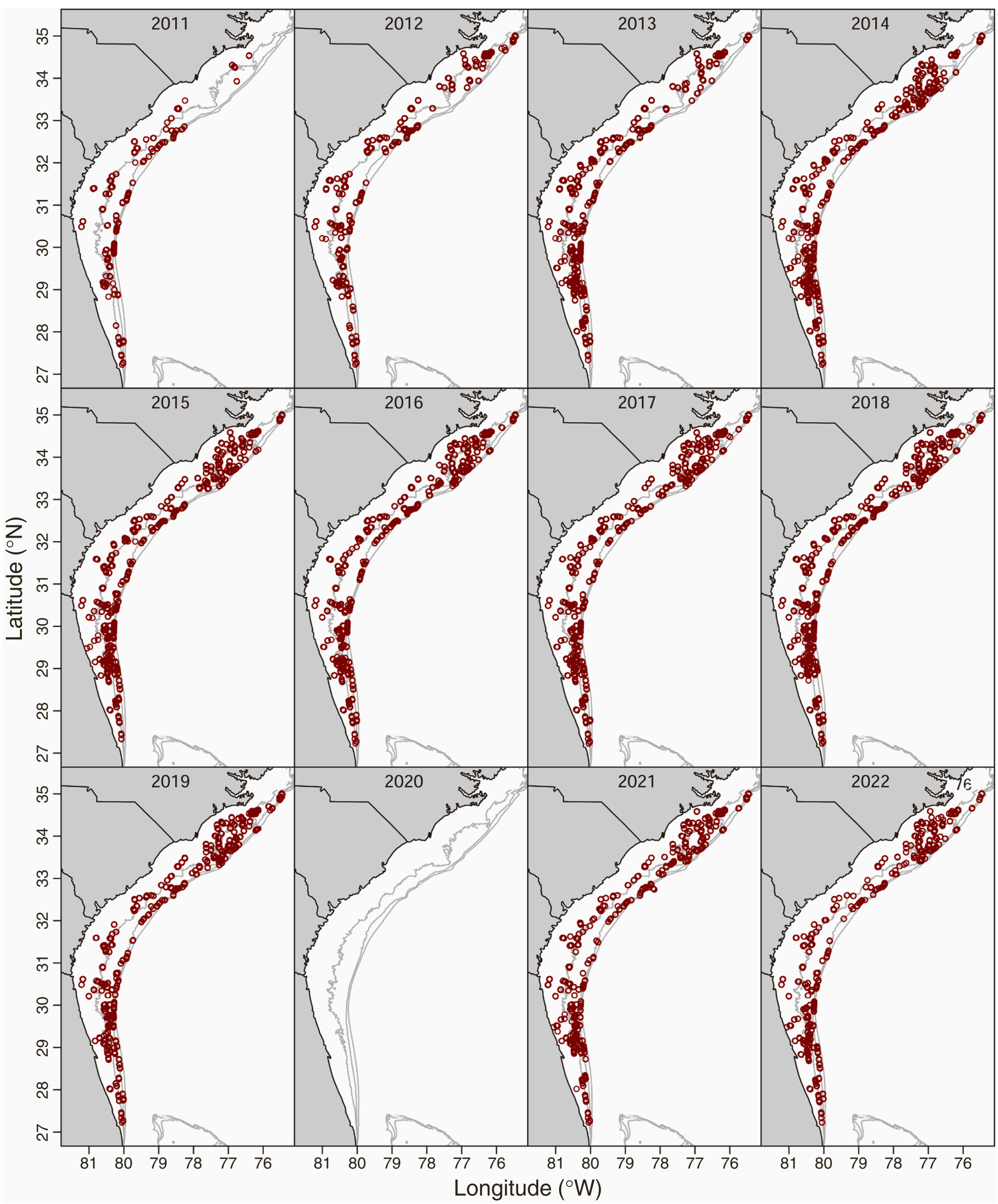

Fig. 1. Stations sampled ($n = 13{,}217$) by the Southeast Reef Fish Survey each year between 2011 and 2022 using chevron traps and attached video cameras. Isobaths indicate 30, 50, and 100-m depths. No sampling occurred in 2020 due to the COVID-19 pandemic.

highlighting the importance and high-profile nature of red snapper in the SEUS.

Despite substantial resources being allocated to red snapper assessment and management in the SEUS, some fundamental questions remain unanswered that are the focus of the present work. Our first objective was to quantify the temporal change in relative abundance for red snapper in the SEUS since the closure in 2010, and our second objective was to elucidate the spatial distribution of red snapper in the SEUS. Information about the temporal and spatial patterns of red snapper abundance in the SEUS would provide important data for potential future management actions. Our third objective was to identify the habitats that red snapper most commonly associated with, including whether adult red snapper regularly occur over unconsolidated substrates (e.g., sand, mud). Adult red snapper are thought to use unconsolidated habitats in some portion of their Gulf of Mexico range (Cowan, 2011); however, it is possible that these unconsolidated habitats are adjacent to unknown reefs or manmade structures (Stunz et al., 2021). If this were also true in the SEUS, it could mean that an unobserved biomass of red snapper exists outside of areas or habitats targeted by fisheries and surveys and thus population size could be underestimated in stock assessments. Addressing these questions will increase our understanding of the spatial and temporal distribution of red snapper in the SEUS, improve our understanding of red snapper habitat use, and can be used when scaling density estimates to the entire SEUS in the ongoing project to estimate red snapper abundance.

2. Material and methods

2.1. Study area

Sampling for this study occurred on the SEUS continental shelf and shelf-break, specifically between Cape Hatteras, North Carolina, and St. Lucie Inlet, Florida (Fig. 1). This is a large area (~ 100,000 km^2) stretching across a broad latitudinal range (27–35°N). Approximately 97 % of the seafloor on the SEUS shelf is composed of unconsolidated sand and mud substrates, but there are patches of naturally occurring temperate rocky reef habitat scattered throughout the region (Steward et al., 2022). Red snapper associate with hardbottom reef habitats (Bacheler et al., 2022; Chatterjee et al., 2024), which range from flat pavement habitats, sometimes covered in a layer of sand, to high-relief (> 1 m) rocky ledges (Schobernd and Sedberry, 2009). Red snapper are also found on artificial reefs within the SEUS (Paxton et al., 2020), but those associations were not part of this study because artificial reefs account for only ~ 0.1 % of structured habitat in the SEUS (Steward et al., 2022).

2.2. Trap and video sampling

We used trap and video data from the Southeast Reef Fish Survey (SERFS) to make inferences about red snapper abundance, distribution, and habitat use on the SEUS shelf. The SERFS is a collaborative fishery-independent survey composed of three groups funded by the U.S. National Marine Fisheries Service. The first is the Marine Resources Monitoring, Assessment, and Prediction program at the South Carolina Department of Natural Resources (SCDNR), which has been sampling in the region using various sampling gears since the 1970s. The second is the Southeast Area Monitoring and Assessment Program (South Atlantic Region) Reef Fish Complement, also housed at SCDNR, which has operated since 2009. The third is the Southeast Fishery-Independent Survey, which was created in 2010 to partner with SCDNR to increase sampling effort and implement underwater video as an additional sampling gear. These three groups have sampled reef fishes collaboratively in the SEUS since 2011 using identical trap and video gears as described below.

A simple random sampling design has been used annually to select stations for sampling. From a sampling frame of approximately 4300 stations known to have natural reef structure, ~ 1500 stations were randomly selected for sampling each year. Most stations analyzed in our study were randomly selected (86 %), but some stations (9 %) were sampled despite not being randomly selected to increase sampling efficiency during research cruises. The remaining stations (5 %) were new stations found using the vessel echosounder and were included if hardbottom was present. Sampling took place on one of four research vessels: the R/V *Savannah*, the R/V *Palmetto*, the NOAA Ship *Pisces*, or the SRVx *Sand Tiger*. Sampling occurred during daylight hours between April and October each year.

We analyzed trap and video data collected by SERFS during 2011–2022 (note no sampling occurred in 2020 due to the COVID-19 pandemic). Traps were large (1.7 × 1.5 × 0.6 m; volume = 0.91 m^3), were shaped like an arrowhead ("chevron") when viewed from above, had a mesh size of 3.4 × 3.4 cm, were soaked for approximately 90 min, and were baited with 24 menhaden (*Brevoortia* spp.) totaling approximately 4 kg (Collins, 1990; Bacheler et al., 2013a). Traps were deployed independently with their own line to buoys on the surface, with no traps being closer than 200 m to another trap in a given year to minimize spatial autocorrelation (McGovern et al., 2002; Bacheler et al., 2018, 2022). Typically, three or four groups of six simultaneously soaking traps were deployed each day, totaling 18–24 traps, and these traps were often deployed across multiple areas. Red snapper catch per unit effort was the catch of red snapper per trap, and soak time was included as a predictor variable in the trap model to standardize for variable effort (Bacheler et al., 2013b; Bacheler, 2024). Trap-based relative abundance of red snapper is defined as the standardized trap catch of red snapper. Trap samples were excluded from analyses if any information was missing for the sample or the validity of the catch was dubious for any reason (e.g., trap moved or was damaged).

Video cameras have been attached to all chevron traps deployed by SERFS since 2011 to provide additional data on the abundance and distribution of reef fish, as well as to enable the quantification of habitat, water clarity, and water current at each station sampled. Canon Vixia HF-S200 video cameras in Gates HF-S21 housings were attached over the mouth of traps (facing outward) in 2011–2014, and were used to enumerate fish. Canon cameras had a 102° linear field of view and recorded at 1080p resolution at 30 frames per second. A second camera (GoPro® Hero or Nikon Coolpix S210/S220) was attached over the nose of each trap (also facing outward) and was used to quantify habitat in the opposite direction. In 2015–2022, all cameras were replaced with GoPro® Hero3+ or Hero4 cameras that had a linear field of view of 123° and recorded at 1080p resolution at 30 frames per second. Video samples were excluded from analyses if cameras did not record or if videos were corrupt, out of focus, or dark.

Video-based relative abundance of red snapper was defined as the standardized counts of red snapper from video using a version of the MeanCount metric. MeanCount is the mean number of individuals of a particular species of interest observed across a series of snapshots within a video, and has been shown to be proportionally related to true abundance (Schobernd et al., 2014). Here, MeanCount was calculated as the mean number of red snapper observed on snapshots every 30 s beginning 10 min after the trap landed on the bottom and lasting a total of 20 min, for a total of 41 snapshots. For our analyses, we used a derivation of MeanCount called SumCount because some of the error distributions we considered required count data. SumCount was the sum of all red snapper individuals observed across all 41 frames of the video, and SumCount is proportional to MeanCount when the number of frames read is the same, as was the case in our study (i.e., only samples with 41 frames read were included; Bacheler et al., 2020).

Because two types of video cameras with different characteristics were used to count fish in our study since 2011, a side-by-side camera calibration study took place in 2014 to develop a camera calibration factor between Canon and GoPro cameras (see Bacheler et al. (2023) for full details). In short, Canon and GoPro cameras were deployed on traps next to one another throughout 2014, facing away from the trap mouths, and subsequent videos were read using SumCount for red snapper. Red snapper were observed on 31 pairs of calibration videos, and from these samples, GoPro cameras observed 65 % more red snapper than Canon cameras. Therefore, index values generated from Canon cameras in 2011–2014 were increased by 65 % to make those years consistent with estimates generated from GoPro cameras in 2015–2022 (Bacheler et al., 2023).

In addition, each ship's global positioning unit was used to estimate latitude and longitude, and the ship's echosounder was used to estimate depth (m). Bottom water temperature (°C) was measured using a "conductivity-temperature-depth" cast within 2 m of the seafloor for each group of simultaneously deployed traps. Soak time (min) was the number of minutes each trap soaked from deployment to the start of the retrieval process. The last four variables were estimated using video cameras attached to traps. The percent of the visible substrate that was hardbottom or reef (hereafter referred to as "structured habitat") was estimated for the two cameras on each trap, and a mean value was calculated for each station sampled. Maximum substrate relief (m) was the maximum relief visually estimated in three categories: low (< 0.3 m), moderate (0.3–1.0 m), or high (> 1.0 m), and visual estimation was aided by the fact that cameras were attached to traps 0.6 m off the seafloor. Water clarity was classified as "low" if substrate could not be seen, "moderate" if substrate could be seen but not the horizon, and "high" if the horizon was visible in the distance. Lastly, current direction was estimated as "away", "sideways", or "towards" based on the movement of visible particles in the water relative to the view field of the video camera over the trap mouth. Trap and video samples were only included in analyses if all predictor variables were available.

2.3. Trap and video data analyses

Our first and second objectives were to quantify the temporal and spatial patterns of red snapper relative abundance from 2011 to 2022. We first examined the proportion of trap samples catching red snapper and the proportion of video samples where red snapper were observed, as well as the nominal mean trap catch (individuals caught per trap) and nominal video counts (mean SumCount per video sample) of red snapper, by year. But annual changes in the spatial and temporal distribution of sampling or environmental variability can be confounded with annual changes in red snapper abundance. Therefore, we used generalized additive models (GAMs; Hastie and Tibshirani, 1990) to relate trap catch or video counts to predictor variables in order to standardize for the influence of those variables on red snapper catches or counts. A GAM is a nonparametric regression approach that uses local smoothers to fit nonlinear relationships between response and predictor variables, and can incorporate various error distributions (Wood, 2017).

Our trap GAM related the trap catch of red snapper to ten predictor variables (Table 1). These predictor variables were: year of the sample (*year*), water clarity (*wc*), current direction (*cur*), maximum substrate relief (*rel*), trap soak time (*soak*), depth (*depth*), bottom water temperature (*temp*), day of the year (*doy*), structured habitat (*sh*), and position (*pos*). Position was a bivariate smooth predictor surface that was created using the combination of longitude and latitude of the sample (Bacheler and Smart, 2016). We excluded samples with soak times less than 50 min and greater than 150 min, bottom temperatures less than 16° and greater than 29°C, and depths greater than 60 m deep due to low sample sizes. Variance inflation factors were less than three for all predictor variables, suggesting no multicollinearity among predictor variables (Neter et al., 1989).

Our trap GAM was:

$$y = f(year) + f(wc) + f(cur) + f(rel) + s(soak) + s(depth) + s(temp) + s(doy) + s(sh) + s(pos) \quad (1)$$

where y is the trap catch of red snapper, f is a categorical function, and s is a cubic spline (smoothed) function. All GAMs were coded in R version 4.1.1 (R Core Team, 2021) using the mgcv library 1.8–23 (Wood, 2011). We used cubic spline smoothers due to their computational efficiency for large datasets and broad usage in ecological studies; the spline's knot locations were determined using restricted maximum likelihood, as implemented by the mgcv library (Wood, 2011). We compared three error distributions given our count response variable: Poisson, negative binomial, and Tweedie error distributions. The best fitting model was the negative binomial error distribution based on model diagnostics and convergence rates from the "mgcv::gam.check" function; residuals were approximately normal and exhibited constant variance.

We compared the full trap model containing all ten predictor variables to reduced models that contained fewer predictor variables using backward selection based on Akaike's information criterion (AIC). AIC attempts to find the most parsimonious model that maximizes fit with the fewest predictor variables (Burnham and Anderson, 2002). The best (i.e., most parsimonious) model is the one with the lowest AIC value, and we report ΔAIC values here, where the best model has a value of 0 and all other models have ΔAIC values greater than 0. Models with ΔAIC values of less than 2 are thought to have similar support from the data, while those with ΔAIC values greater than 2 have less support (Burnham and Anderson, 2002).

Our second GAM related video SumCount of red snapper to nine predictor variables (Table 1). The same predictor variables from the trap model were included in the video model with the exception of soak time, since that variable is not relevant to the video model. Our video GAM was:

$$y = f(year) + f(wc) + f(cur) + f(rel) + s(depth) + s(temp) + s(doy) + s(sh) + s(pos) \quad (2)$$

where y is the video SumCount of red snapper and all other variables are the same as the trap model (Eq. (1)). The best fitting video GAM was again a negative binomial error distribution, and model residuals were approximately normal and exhibited constant variance.

We used the final (best) trap and video GAMs to specifically address our three objectives. To estimate temporal trends in relative abundance, our first objective, we used the trap and video GAMs to estimate the year effect at mean values of all continuous predictor variables and midpoint levels of factor variables. To address our second objective (elucidate red snapper spatial distribution), we used GAMs to predict red snapper trap catches and video SumCounts at 90-m grid cells (≤ 60 m deep) across the SEUS shelf given the latitude, longitude, and depth of each cell and mean or midpoint values of all other predictor variables. These GAMs predict red snapper relative abundance across the SEUS shelf, but note that standardized trap catches and video SumCounts only apply to reef habitats in cells and assume structured habitat is homogenous across the SEUS continental shelf. For our third objective (quantify habitat use), we used trap and video GAMs to quantify the relationships between trap catch or video SumCounts and predictor variables (e.g., structured habitat, maximum substrate relief, depth, bottom temperature, day of

Table 1
Predictor variables included in generalized additive models for red snapper (*Lutjanus campechanus*) catch in traps or counts in video samples from the Southeast Reef Fish Survey, 2011–2022.

Predictor variable	Abbreviation	Type	Units
Year	*year*	Categorical	-
Water clarity	*wc*	Categorical	-
Current direction	*cur*	Categorical	-
Relief	*rel*	Categorical	-
Soak time	*soak*	Continuous	Minutes
Depth	*depth*	Continuous	Meters
Bottom water temperature	*temp*	Continuous	Degrees Celsius
Day of the year	*doy*	Continuous	Day
Structured habitat	*sh*	Continuous	Percent
Position	*pos*	Continuous	Degrees

the year, year, current direction, water clarity, and position). Since we did not quantify the availability of habitats or environmental conditions, we only describe the use of these predictors by red snapper and not their preference or selection for them. The major strength of the GAM approach is that trap catch or video counts can be standardized to account for any variability in, and shape of, predictor variable relationships.

2.4. Remotely operated vehicle sampling

We used video data from a remotely operated vehicle (ROV) to further address our third objective. A drawback of trap and video sampling described above is that it is difficult to make inferences about the habitats that red snapper associate with because only reef habitats are targeted by SERFS sampling. Thus, traps landing on sand are often located close to reef habitats and are therefore not truly random samples; in other words, sand stations close to reef habitat likely contain many more red snapper than sand stations far from any reef habitat (Bacheler et al., 2022). A second drawback is that baited traps and videos attract fish from some unknown local area, so estimating absolute abundance or density is difficult (Bacheler et al., 2022).

To address these issues, we used an ROV to sample randomly selected stations in 2021–2023 in the SEUS. Transect sampling was conducted at randomly selected sites along the continental shelf from north of Cape Hatteras, North Carolina, to North Key Largo, Florida, with a VideoRay Pro4 mini ROV (dimensions: 36 cm long, 28 cm tall, 22 cm wide; mass: 4.8 kg). The sampling frame, encompassing the continental shelf from 10–160 m deep and from just south of the Virginia–North Carolina border to North Key Largo, Florida, was divided into six regions from 24.42° to 36.22° N. Sites were allocated to regions relative to shelf area from 10 to 160 m depths; however, disproportionately higher sampling was focused in the Florida Keys to test whether red snapper were present in that region. Within regions, site locations were selected with a random number generator to select integer latitude and longitude and then decimal degrees within the specific depth range. ROV transects were flown as close to selected GPS coordinates at each site as sea conditions allowed. Each randomly selected site was sampled one time during the three-year period.

The ROV was tethered to the surface where it was controlled by a pilot via an integrated control box with a video monitor to observe video captured by the ROV's forward camera. High-resolution digital video was captured with a GoPro Hero6 digital camera in 2021–2022, and a GoPro Hero11 in 2023. GoPro cameras were encased in an underwater housing that was mounted to the top of the ROV's float block and angled at 45° to the seabed. Both cameras recorded widescreen video at 1080p resolution and 60 frames per second, but the GoPro Hero6 cameras had a horizontal field of view of 123° the GoPro Hero11 cameras had a horizontal field of view of 118°. At each study site, the ROV descended to the seabed and a 100-m transect was flown between 1 and 2 m off bottom depending on visibility. A second transect was flown 100 m from the endpoint of the first transect. The ROV position on the seabed was tracked and recorded with an acoustic ultrashort baseline acoustic positioning system.

Digital sample videos were analyzed to enumerate all red snapper observed during each transect. Transect width was estimated from the ROV's height off bottom given the angle of the camera (45°) to the seabed and the camera's field-of-view following the method of Patterson et al. (2014). Red snapper density per transect was estimated as the count divided by the area sampled (transect width × length). Red snapper density per site was then estimated as the mean between the two transect samples conducted at that site. Two habitat variables were also scored at each site: structured habitat (%) and habitat complexity. Structured habitat was visually estimated as the percent of the transect covered by structured habitat (i.e., rocks or attached biota, measured in 5 % intervals), and habitat complexity was a qualitative assessment of the complexity of the seafloor. A habitat complexity score of 1 was the least complex habitat, such as sand, shell hash, or mud. A score of 2 was moderately complex and included the presence of soft or stony corals, sponges, and macroalgae. Lastly, a score of 3 was the most complex and included rocky hardbottom habitats which were often higher relief (> 1 m) reefs and ledges.

To specifically address our third objective, we related red snapper densities from ROV videos to structured habitat and habitat complexity. We examined red snapper densities at four levels of structured habitat (0 %, 5–20 %, 25–50 %, and 55–100 %) and at the three levels of habitat complexity. We tested for a significant effect of these two habitat variables separately on red snapper densities using Kruskal-Wallis tests and an alpha level of 0.05.

3. Results

3.1. Trap and video sampling

From 2011 to 2022, a total of 13,217 chevron traps were deployed and included in our analyses, slightly more than the number of videos collected and included ($n = 12{,}577$; Table 2). Excluding 2020 (when no sampling occurred), the fewest trap and video samples were available from 2011, and the most were available from 2018 (Table 2). Sampling was quite consistent each year across dates, depths, and latitudes (Table 2; Fig. 1). In total, 10,671 red snapper were caught in the 13,217 traps deployed, with the highest trap catch of red snapper being 88; these red snapper ranged in size from 159 to 991 mm total length (mean = 443 mm total length; Fig. S1). The highest red snapper SumCount was

Table 2
Annual sampling information for the 11 years of chevron trap and video sampling by the Southeast Reef Fish Survey, 2011–2022, on the southeast United States Atlantic continental shelf and included in this study. No sampling occurred in 2020 due to the COVID-19 pandemic.

Year	Number of trap samples	Number of video samples	Mean date (range)	Mean depth (m; range)	Mean latitude (°N; range)
2011	516	488	27 Jul (19 May–25 Oct)	39 (15–59)	30.8 (27.2–34.5)
2012	939	909	11 Jul (24 Apr–10 Oct)	36 (15–59)	31.9 (27.2–35.0)
2013	1185	1116	15 Jul (24 Apr–4 Oct)	36 (15–59)	31.3 (27.3–35.0)
2014	1349	1268	10 Jul (23 Apr–21 Oct)	36 (16–59)	31.8 (27.2–35.0)
2015	1313	1280	1 Jul (21 Apr–22 Oct)	36 (15–59)	31.8 (27.3–35.0)
2016	1302	1252	3 Aug (4 May–26 Oct)	36 (16–59)	32.1 (27.2–35.0)
2017	1326	1254	3 Jul (26 Apr–29 Sep)	36 (15–59)	31.9 (27.2–35.0)
2018	1512	1453	24 Jun (25 Apr–4 Oct)	36 (16–59)	31.9 (27.2–35.0)
2019	1431	1367	1 Jul (30 Apr–25 Sep)	37 (15–59)	32.0 (27.2–35.0)
2020	0	0	-	-	-
2021	1308	1246	29 Jun (28 Apr–29 Sep)	34 (16–59)	31.8 (27.2–35.0)
2022	1036	944	10 Jul (26 Apr–27 Sep)	35 (16–59)	31.6 (27.2–35.0)
Total	13,217	12,577	9 Jul (21 Apr–26 Oct)	36 (15–59)	31.8 (27.2–35.0)

1408, or a mean of 34.3 red snapper observed per frame.

The nominal proportion of traps catching red snapper and video samples in which red snapper were observed increased during our study. The nominal proportion positive of red snapper in traps was 0.073 in 2011, but it increased nearly linearly to 0.226 in 2022 and the proportion positive for all traps was 0.152 (Fig. 2A). Although red snapper were observed nearly twice as often on video than they were caught in traps, the increase in proportion positive on video similarly increased from 0.207 in 2011 to 0.355 in 2022 and the proportion positive for all videos was 0.291 (Fig. 2A). Even more substantial increases were observed in the nominal mean red snapper trap catches and mean SumCounts over time. Nominal mean red snapper catch (including zeros) increased from 0.09 to 1.41 fish/trap (~ 1500 % increase) between 2011 and 2022, while nominal video SumCounts of red snapper increased from 1.50 to 20.90 fish over the same time frame (~ 1300 % increase; Fig. 2B). Red snapper were most commonly caught in traps or observed in video samples off northern Florida and Georgia and less commonly in South Carolina and southern North Carolina, but catches and counts increased again north of Cape Lookout, North Carolina (Fig. 3).

3.2. Trap and video generalized additive models

The best trap GAM based on AIC included all predictor variables except maximum substrate relief and trap soak time, explaining 46.1 % of the model deviance (Table 3). There was also some evidence for a trap model excluding maximum substrate relief but including soak time, which had a ΔAIC value of 0.7 and also explained 46.1 % of the deviance; no other models were supported by the data as evidenced by ΔAIC values > 2 (Table 3). The best video model was the full model containing all nine predictor variables, which explained 44.3 % of the model deviance; none of the reduced models were supported by the data (Table 3).

Standardized red snapper relative abundance increased rapidly over the 12-year study. Standardized trap catches and video SumCounts of red snapper showed a similar increase as nominal values and were very similar to one another, generally increasing over the study (Fig. 4). Standardized trap catches increased from 0.37 to 3.90 fish per trap (~ 1000 % increase), while standardized video SumCounts increased from 4.2 to 52.4 fish (~ 1100 % increase).

There were strong patterns in the spatial distribution of red snapper relative abundance across the SEUS, and standardized trap catches and video SumCounts were nearly identical (Fig. 5). Standardized red snapper relative abundance was highest around Cape Canaveral, Florida, declining northward to Cape Lookout, North Carolina. In both models, however, relative abundance increased again between Cape Lookout and Cape Hatteras, North Carolina, which is consistent with nominal trap and video data (Fig. 3). Relative abundance was also highest mid-continental shelf, declining inshore and offshore, except off central Florida where relative abundance was high across the shelf depths surveyed (15–59 m). Lowest red snapper relative abundance occurred in northern South Carolina and southern North Carolina (Fig. 5).

Standardized red snapper relative abundance was influenced by habitat variables in specific ways, and there was a high degree of similarity between trap and video models. Red snapper relative abundance from video was highest at approximately 40 m deep, being lower in shallower and deeper water (Fig. 6A). Trap-based relative abundance of red snapper was highest in slightly deeper water, but confidence intervals at those deeper depths were large. Standardized relative abundance from traps and videos generally declined throughout the year, increased with bottom water temperature, and displayed a dome-shaped relationship with structured habitat (Fig. 6B–D). Standardized red snapper trap catches and video counts were also higher when water current was moving away from the trap mouth and video cameras (Fig. 6E). Standardized red snapper video counts were positively related to water clarity and maximum substrate relief, while standardized red snapper trap catches were somewhat negatively related to water clarity; maximum substrate relief was excluded from the trap GAM, suggesting no effect of that variable on trap catches of red snapper (Fig. 6F–G).

3.3. Remotely operated vehicle sampling

In total, 282 remotely operated vehicle samples were collected in 2021–2023 (Table 4). The ROV sampling primarily occurred during summer months, but in 2021 occurred into October. Sampling occurred across the continental shelf in depths ranging from 5 to 138 m and

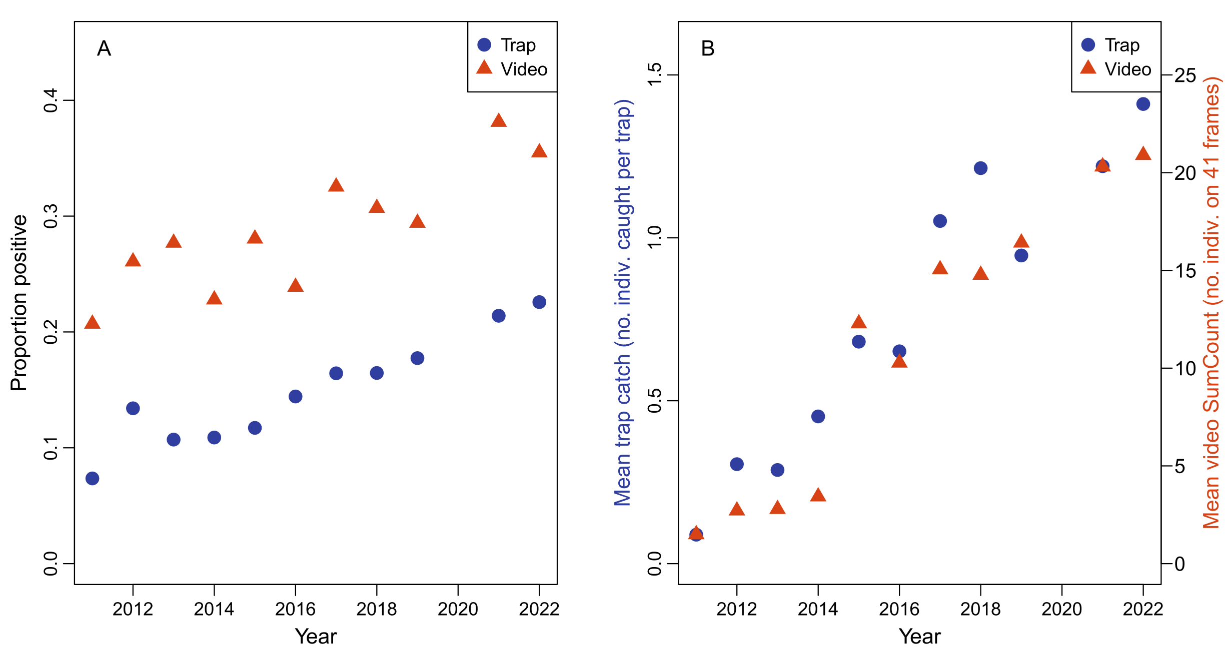

Fig. 2. (A) Nominal proportion of trap or video samples capturing or observing red snapper (*Lutjanus campechanus*) from the Southeast Reef Fish Survey on the southeast United States Atlantic continental shelf, 2011–2022. (B) Nominal mean trap catch (individuals per trap) and mean video SumCount (sum of red snapper individuals across 41 video frame) of red snapper, 2011–2022. Note that no sampling occurred in 2020 due to the COVID-19 pandemic.

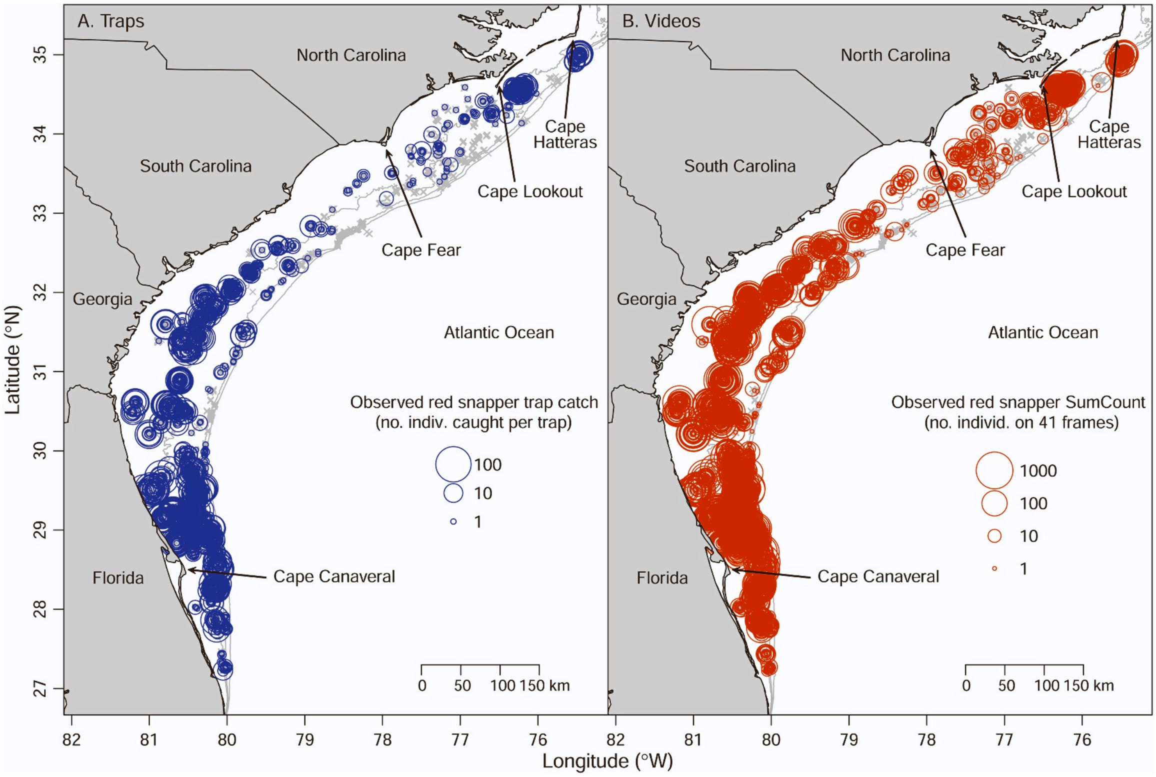

Fig. 3. Bubble plot showing the geographic distribution of nominal trap catches (left plot) and video counts (right plot) of red snapper (*Lutjanus campechanus*) on the southeast United States Atlantic continental shelf, 2011–2022. Bubble size is scaled to the number of red snapper caught in traps or observed on video, and each gray 'x' indicates a sample where no red snapper were caught or observed. Note that symbols overlap.

Table 3
Model selection for generalized additive models for red snapper (*Lutjanus campechanus*) catch in traps or counts in video samples from the Southeast Reef Fish Survey, 2011–2022, on the southeast United States Atlantic continental shelf. Degrees of freedom are shown for factor (*f*) terms, and estimated degrees of freedom are shown for smoothed terms (*s*). Asterisks denote significance at the following alpha levels: *0.05, **0.01, ***0.001; AIC = Akaike information criterion; DE = deviance explained by the model; *year* = year of the sample; *cur* = current direction; *wc* = water clarity; *rel* = maximum substrate relief; *depth* = bottom depth; *doy* = day of the year; *temp* = bottom water temperature; *soak* = trap soak time; *sh* = structured habitat; *pos* = position (i.e., latitude and longitude) of the sample; ex = predictor variable was excluded from the model; NA = predictor variable was not applicable to that particular model. Full models included all predictor variables, and the minus sign after "Full" indicates that one or more predictor variables were excluded from that particular model.

Model	ΔAIC	DE	*f*(*year*)	*f*(*cur*)	*f*(*wc*)	*f*(*rel*)	*s*(*depth*)	*s*(*doy*)	*s*(*temp*)	*s*(*soak*)	*s*(*sh*)	*s*(*pos*)
Trap model												
Full – *rel* – *soak*	0.0	46.1	10^{***}	2^{***}	2	ex	8.0^{***}	4.5^{**}	4.2^{***}	ex	5.2^{***}	27.9^{***}
Full – *rel*	0.7	46.1	10^{***}	2^{***}	2	ex	8.0^{***}	4.5^{**}	4.2^{***}	1.0	5.1^{***}	27.9^{***}
Full – *rel* – *wc* – *soak*	2.6	46.0	10^{***}	2^{***}	ex	ex	8.0^{***}	4.3^{***}	4.1^{***}	ex	5.1^{***}	27.9^{***}
Full – *rel* – *wc*	3.2	46.0	10^{***}	2^{***}	ex	ex	8.0^{***}	4.4^{***}	4.1^{***}	ex	5.1^{***}	27.9^{***}
Full – *soak*	3.4	46.1	10^{***}	2^{***}	2	2	8.0^{***}	4.5^{**}	4.2^{***}	ex	5.1^{***}	27.9^{***}
Video model												
Full	0.0	44.3	10^{***}	2^{***}	2^{**}	2^{***}	2.0^{***}	4.5^{***}	1.6^{***}	NA	5.7^{***}	28.5^{***}
Full – *wc*	8.0	44.2	10^{***}	2^{***}	ex	2^{***}	2.0^{***}	4.6^{***}	1.7^{***}	NA	5.7^{***}	28.5^{***}
Full – *doy*	15.2	44.0	10^{***}	2^{***}	2^{***}	2^{***}	2.0^{***}	ex	1.0^{***}	NA	5.5^{***}	28.5^{***}
Full – *wc* – *doy*	25.0	43.9	10^{***}	2^{***}	ex	2^{***}	2.0^{***}	ex	1.0^{***}	NA	5.5^{***}	28.5^{***}
Full – *temp*	25.8	44.0	10^{***}	2^{***}	2^{***}	2^{***}	2.0^{***}	3.6	ex	NA	5.6^{***}	28.5^{***}

latitudes ranging from 24.4 to 36.2° N (Table 4). Red snapper were observed on 7 of the 282 ROV video samples (2.5 %), and the ROV samples positive for red snapper were found from Cape Hatteras, North Carolina, to the Florida Keys (Fig. 7). Red snapper were observed in water depths ranging from 21.3 to 95.1 m (mean = 42.7 m). The highest density of red snapper observed in ROV video samples was 0.77 fish per 100 m^2.

There was a strong relationship between observing red snapper via ROV and seafloor habitat. Zero red snapper were observed at sites lacking, or having a small amount (≤ 20 %) of, structured habitat and a habitat complexity score of 1 (Fig. 8). Red snapper were observed in the highest proportion of samples, and had highest mean densities, at sites with a moderate amount of structured habitat (25–50 %; Fig. 8A,C) and a habitat complexity score of 3 (Fig. 8B,D). Moreover, there was a strong effect of the amount of structured habitat ($p < 0.0001$), as well as habitat complexity ($p < 0.0001$), on mean densities of red snapper (Fig. 8).

4. Discussion

We used long-term sampling with three sampling gears at a broad regional scale to elucidate the temporal, spatial, and habitat patterns of red snapper on the SEUS shelf. Standardized relative abundance of red snapper increased by approximately three orders of magnitude from 2011 to 2022, generally consistent with recent stock assessment results

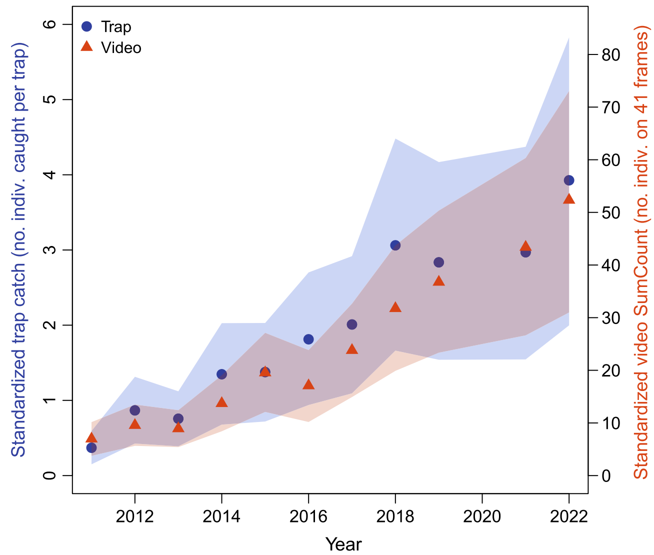

Fig. 4. Standardized trap catches (number of individuals per trap) and video SumCounts of red snapper (*Lutjanus campechanus*) using generalized additive models from the Southeast Reef Fish Survey on the southeast United States Atlantic continental shelf, 2011–2022. Points indicate mean values (traps = blue; video = orange) and shaded areas indicate 95 % confidence intervals. Standardization used mean values of continuous variables and midpoint levels of all categorical variables.

in the region (SEDAR, 2021). The data also indicated red snapper are not homogenously distributed throughout the SEUS, instead being most common in mid-shelf waters from Cape Canaveral, Florida, northward to Georgia and again off Cape Hatteras, North Carolina, and less common off southern North Carolina and northern South Carolina. Relative abundance and densities of red snapper were highest at moderate levels of structured habitat and lower at both low and high levels of structured habitat. Furthermore, not a single red snapper was observed on the 197 ROV transects that lacked structured habitat. Clearly, red snapper appear to have spatial and habitat preferences on the SEUS shelf, which is similar to findings reported for the Gulf of Mexico shelf off western Florida (Stunz et al., 2021).

There is high certainty that red snapper have increased in abundance in the SEUS since the fishing closure in 2010. The most recent red snapper stock assessment in the SEUS estimated that age-1 + red snapper abundance increased from around 651,630 individuals in 2011 to 2,700,500 individuals in 2020, a 314 % increase (SEDAR, 2021). Red snapper catch rates have also increased dramatically (2025 %) between 2012 and 2018 from a fishery-independent survey using repetitive timed drops of baited hook-and-line gear off the east coast of Florida (Christiansen et al., 2020). We similarly documented large increases in red snapper relative abundance (i.e., 960–1482 %) in the SEUS, and there was strong agreement in our study between sampling gears (i.e., traps, video) and whether or not the indices were standardized. Moreover, our trap and video GAMs explained a substantial amount of deviance (44.3–46.1 %) and models fit well, suggesting the pattern of increased red snapper relative abundance is real and not spurious.

Nominal trap catches, nominal video counts, and standardized trap catches and video SumCounts indicated that red snapper were most abundant off central and northern Florida, less abundant off Georgia,

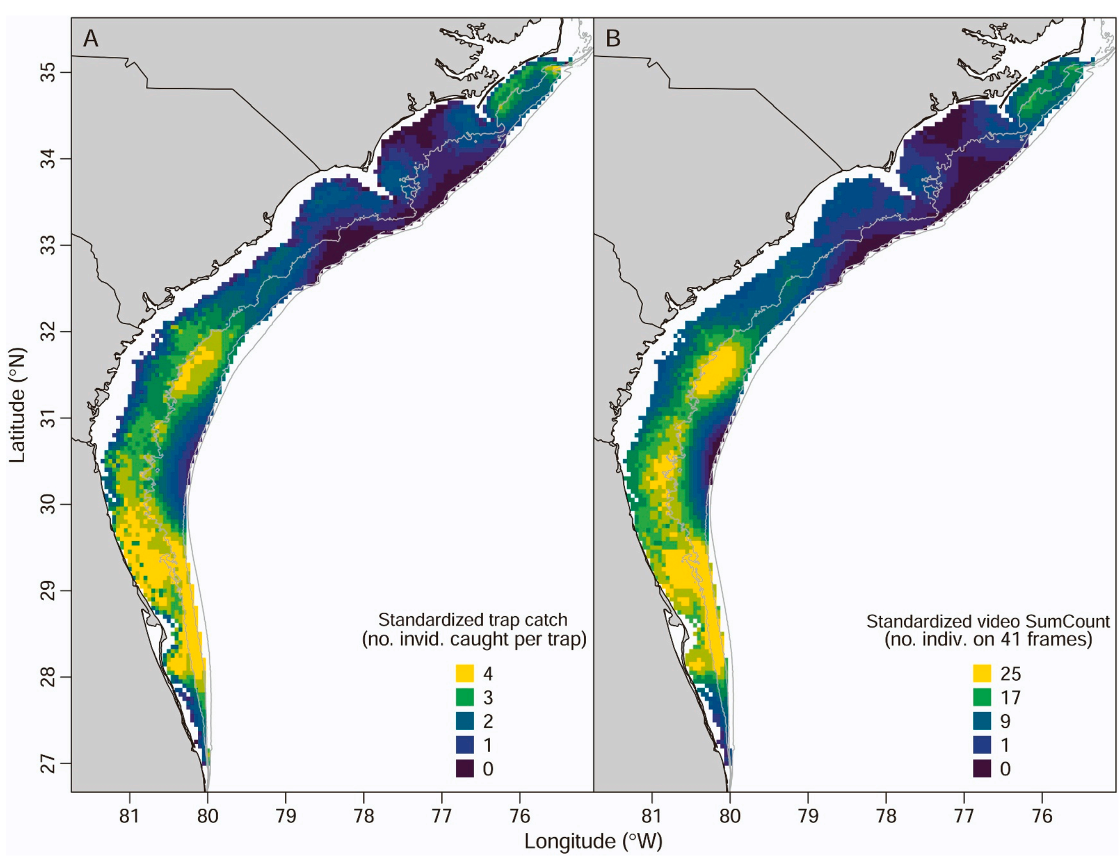

Fig. 5. Standardized trap catches (A) and video SumCounts (B) of red snapper (*Lutjanus campechanus*) from the Southeast Reef Fish Survey on the southeast United States Atlantic continental shelf, 2011–2022. Standardized trap catches or video SumCounts were based on the spatial position and depth of each cell at mean or midpoint values of all other model predictor variables using generalized additive models. Gray isobaths indicate 30, 50, and 100 m deep. Note that the spatial distribution of structured habitats is not being considered and many grid cells likely do not contain structure.

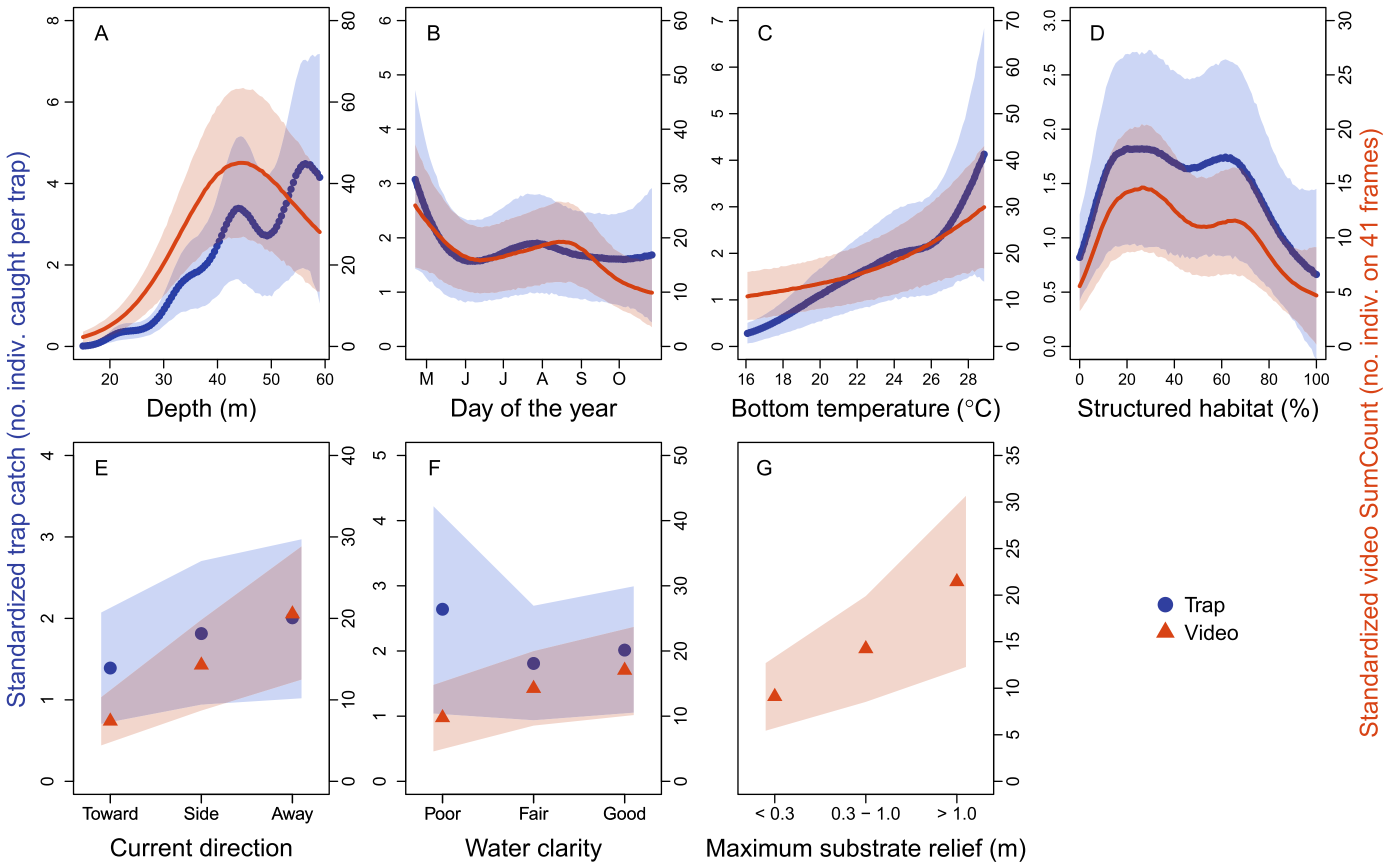

Fig. 6. Standardized trap catches and video SumCounts of red snapper (*Lutjanus campechanus*) as a function of (A) depth (m), (B) day of the year, (C) bottom temperature (°C), (D) structured habitat, (E) current direction, (F) water clarity, and (G) maximum substrate relief using generalized additive models from data collected by the Southeast Reef Fish Survey on the southeast United States Atlantic continental shelf, 2011–2022. Lines or points are mean estimates at mean or midpoint values of all predictor variables and shaded areas are 95 % confidence intervals. Mean trap values are indicated by blue filled circles or thick blue lines and mean video values are indicated by orange triangles or thin orange lines. Note that maximum substrate relief was excluded from the trap model based on Akaike information criterion (AIC), so those results are not shown.

Table 4
Annual sampling information for the 3 years (2021–2023) of remotely operated vehicle surveys on the southeast United States Atlantic continental shelf.

Year	Number of ROV stations	Mean date (range)	Mean depth (m; range)	Mean latitude (°N; range)
2021	148	19 Aug (28 Jun–25 Oct)	35 (5–138)	30.4 (24.4–36.2)
2022	85	15 Jul (27 Jun–10 Aug)	42 (6–132)	29.2 (24.6–32.9)
2023	49	15 Jul (2 Jun–28 Jul)	39 (15–113)	34.4 (32.9–35.6)
Total	282	3 Aug (2 Jun–25 Oct)	36 (5–138)	30.7 (24.4–36.2)

southern South Carolina, and North Carolina's Outer Banks, and rare off southern North Carolina and northern South Carolina. It is unclear why red snapper display this spatial pattern of abundance that is unlike any other reef fish in the region (Bacheler et al., 2016), but it may be related to red snapper's ability to survive and even thrive in periodic summertime upwelling events by being able to move vertically above cold, upwelled water (Bacheler et al., 2021). These upwellings are driven by the position of the Gulf Stream and prevailing winds and are much more common in Florida and the Outer Banks of North Carolina than elsewhere along the SEUS shelf (Hyun and He, 2010). Regardless of the reason, these results align well with previous studies in the region that have also used trap and video data from SERFS but employed different analytical approaches (Coggins et al., 2014; Bacheler et al., 2016; Cao et al., 2024). These data might be useful, for instance, to create targeted and efficient marine protected areas to reduce discard mortality of red snapper (e.g., Farmer and Karnauskas, 2013), to implement other spatial management measures (Farmer et al., 2017; Shertzer et al., 2024), or for estimating total population size of red snapper in the entire SEUS region. This latter application could be accomplished by scaling the relative spatial abundance estimated across the region (Fig. 5) to absolute abundance using point estimates of density obtained at specific locations (e.g., Zulian et al., in press).

Adult red snapper (> age-2) have been shown to associate with various types of natural and artificial structured habitats, such as coral reefs, rocky outcroppings and ledges, oil rigs, and shipwrecks (Moseley, 1966; Powles and Barans, 1980; Williams-Grove and Szedlmayer, 2016; Dance and Rooker, 2019; Chatterjee et al., 2024). Our results from trap, stationary video, and ROV video samples are consistent with these previous studies but go further to show that adult red snapper appear to disproportionately use moderate levels of structured habitat, showing less affinity for continuous reef habitats and more affinity for patchy reef habitats composed of a mix of rock, coral and sponge, and sand habitats. The use of patchy reef and sand habitats by adult red snapper may be related to their feeding and predator avoidance behaviors; red snapper feed over various types of sand, mud, and structured habitats (Camber, 1955; Bradley and Bryan, 1975; Szedlmayer and Lee, 2004; McCawley et al., 2006; Tarnecki and Patterson, 2015; Schwartzkopf et al., 2017), but are thought to find refuge in structured habitats (Wells et al., 2008). Patchy mosaics of sand and reef habitats may provide red snapper with the ability to maximize the ratio of foraging rate to predation risk

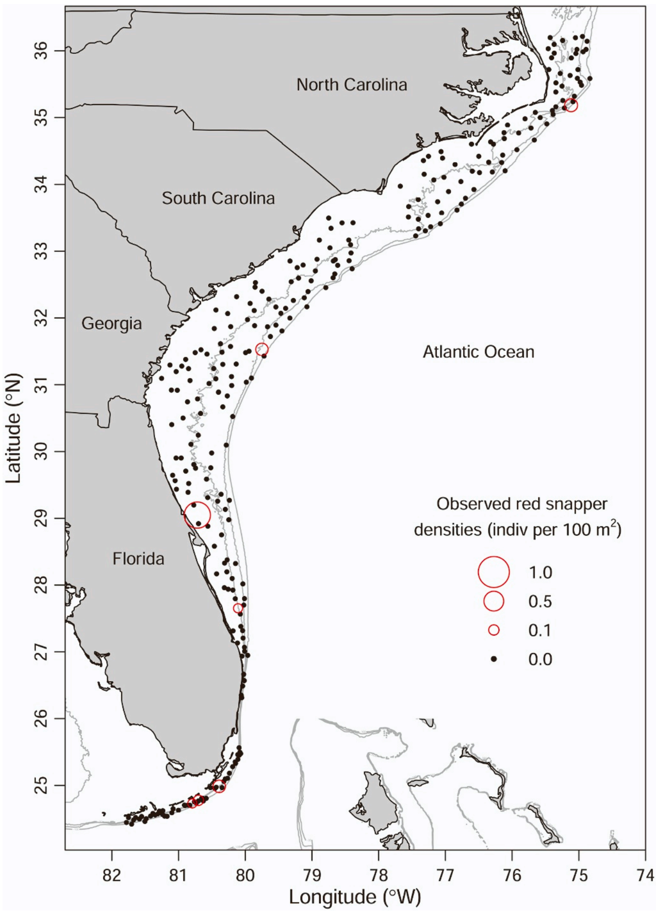

Fig. 7. Bubble plot showing red snapper (*Lutjanus campechanus*) density estimates (fish per 100 m^2) at randomly selected locations on the southeast United States Atlantic continental shelf, 15–150 m deep, using a remotely operated vehicle, 2021–2023. Bubble size is scaled to the density of red snapper estimated by remotely operated vehicle video samples, and each black point indicates a sample where no red snapper were observed.

(Gilliam and Fraser, 1987).

There has been uncertainty about habitat use by large (> 850 mm total length), old red snapper (> age-10) in the Gulf of Mexico, specifically whether they prefer structured habitat or move off reefs to spend most of their time over sand and mud habitats (Patterson, 2007; Szedlmayer, 2007; Gallaway et al., 2009). The prevailing hypothesis in the Gulf of Mexico is that old red snapper have declining vulnerability to the fishery and surveys because of their tendency to move off structured habitats as they age (Cowan, 2011; Cowan Jr. et al., 2011). These conclusions are mostly based on Gulf of Mexico longline surveys that have caught old red snapper over presumably unconsolidated sand and mud habitats (Henwood et al., 2004; Mitchell et al., 2004). Telemetry studies have consistently shown that adult red snapper associate closely with natural or artificial structured habitats and only appear to use unstructured habitats when periodically transiting from reef to reef (Piraino and Szedlmayer, 2014; Williams-Grove and Szedlmayer, 2016, 2017; Everett et al., 2020; Bacheler et al., 2021; Froehlich et al., 2021; Chatterjee et al., 2024). But telemetry may not fairly assess the degree of off-reef habitat use of red snapper, however, because (1) old (> 10-year-old) red snapper are rarely tagged in telemetry studies, (2) telemetry studies tend to be short-term while red snapper tend to slowly diffuse away from tagging sites (Patterson III et al., 2001; Patterson, 2007; Addis et al., 2013), and (3) once telemetered red snapper leave a telemetry array, they are typically not tracked unless they are detected at another array. Old red snapper appear to use unstructured habitats near the shelf break in the western Gulf of Mexico but red snapper of any size were not found over unstructured habitat in the eastern Gulf of Mexico (Stunz et al., 2021), and our ROV results are consistent with the findings in the eastern Gulf of Mexico. The lack of red snapper found over unstructured habitat in the SEUS may also be due to the overall rarity of age-10 + red snapper in the region (i.e., < 2.5 % of all red snapper; SEDAR, 2021). If it is rare for red snapper to disassociate with structured habitats as they grow larger and older, it suggests that a significant cryptic biomass of red snapper does not exist in the SEUS.

Red snapper were associated with environmental variables and other characteristics of the stations sampled in ways that were consistent with previous studies. Standardized red snapper trap catches and video counts were positively related to bottom water temperature, peaked at about 40-m deep (i.e., mid-shelf waters), and declined somewhat throughout the year, consistent with previous work in the SEUS (Mitchell et al., 2014; Bacheler et al., 2016; Bacheler and Shertzer, 2020). Standardized red snapper relative abundance was positively related to maximum substrate relief on video, but maximum substrate relief was excluded from the trap model; this result is also consistent with previous studies that have shown trap catchability of red snapper is lower when high-relief hardbottom habitat is present (Bacheler et al., 2014; Bacheler and Shertzer, 2020). In addition, red snapper were more likely to be caught in traps or observed on video when the current was moving away from the trap mouth and video camera used to count fish (Coggins et al., 2014; Bacheler et al., 2014, 2016). Red snapper were also somewhat more likely to be observed on video when water clarity was good compared to poor, but the same relationship did not occur for trap catches, where red snapper were slightly more likely to be caught when water clarity was poor. Gregory and Northcote (1993) introduced the motivation hypothesis, suggesting that heightened turbidity could amplify feeding motivation by reducing the risks of predation. But with regards to red snapper, the reason for this increased trap catchability in turbid water is unknown. One potential yet untested explanation is that red snapper may be less wary of the trap or line in turbid water.

There were some limitations of our red snapper study in the SEUS. First, trap and video gears were paired in our study, so they were not truly independent. Second, our study was correlational and therefore causation could not be determined (Altman and Krzywinski, 2015). Third, our GAMs explained ~ 45 % of the deviance in red snapper trap catches or video counts, which is relatively high for studies of this type (e.g., Bacheler and Ballenger, 2018). However, this implies ~ 55 % of the deviance was unexplained by our models, suggesting other unmeasured variables (e.g., predator or prey abundance, social interactions) are important for estimating red snapper relative abundance in the SEUS. Fourth, 197 ROV stations were sampled over sand in our study and not a single red snapper was observed; more ROV sampling over sand in conjunction with bathymetric mapping would increase our confidence that red snapper do not generally disassociate with structured habitats in the SEUS. Fifth, our inferences about red snapper habitat use only pertain to the spring through fall time period because no sampling occurred in this study during winter, but note previous studies have not observed seasonal differences in red snapper habitat use (Bacheler et al., 2021). Lastly, we estimated red snapper relative abundance using traps and videos, but being able to estimate absolute abundance would greatly benefit their assessment and management.

Red snapper are an iconic reef-associated fish species with a long history of exploitation in the SEUS. Trap and camera data clearly demonstrate red snapper abundance has increased markedly on the SEUS shelf over the last 15 years. Furthermore, red snapper are heterogeneously distributed across the region, and their presence and abundance are strongly correlated to hardbottom habitat on the SEUS shelf. Confidence in our results is high given the strong agreement among sampling gears and broad spatial and temporal scale of sampling in our study. These results increase our understanding of the spatial and temporal distribution of red snapper, improve our understanding of red snapper habitat use, and can be used when scaling density estimates to

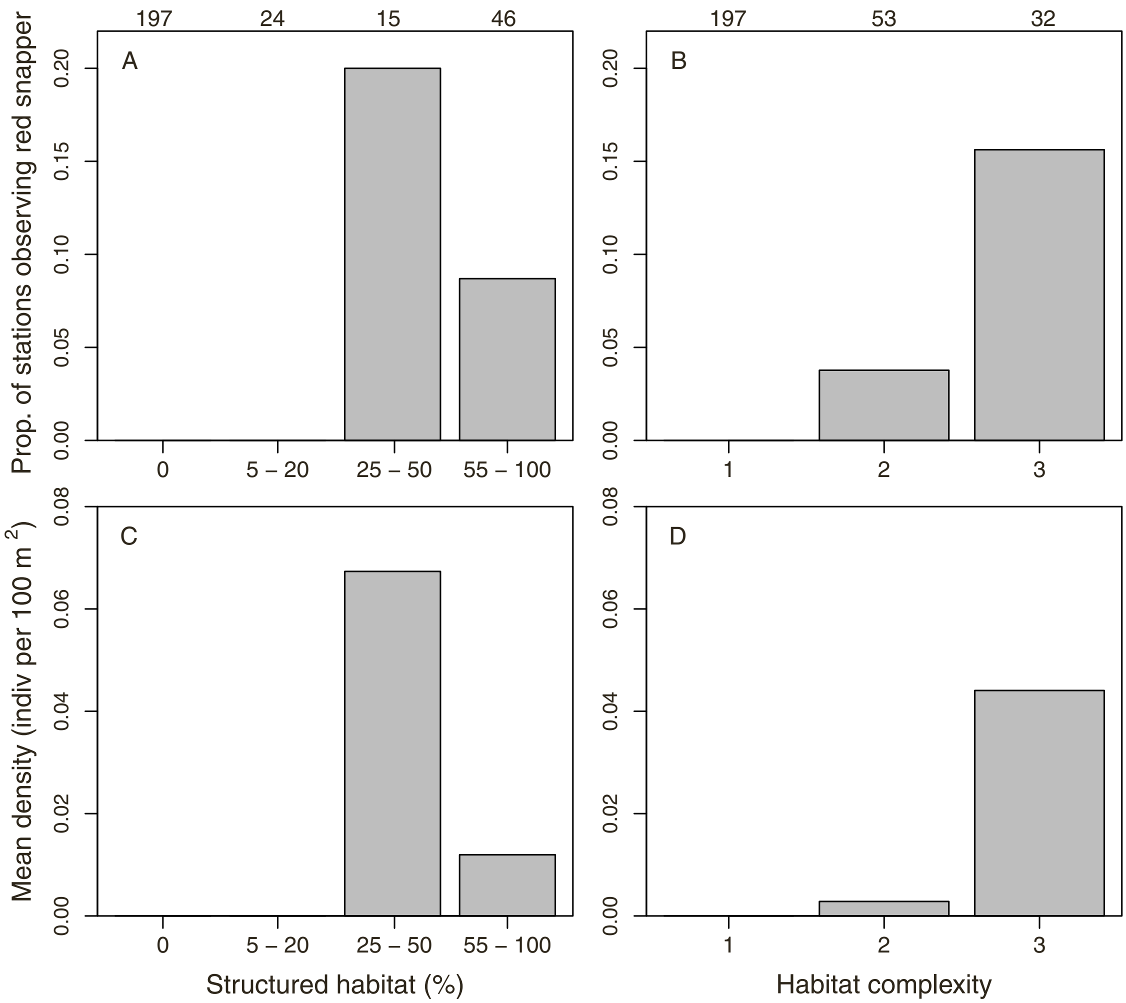

Fig. 8. The proportion of stations where red snapper (*Lutjanus campechanus*) were observed (A, B) and their associated mean densities (fish per 100 m^2; C, D) as a function of the percent of the seafloor containing structured habitat (A, C) and habitat complexity (B, D) from remotely operated vehicle video samples on the southeast United States Atlantic continental shelf, 2021–2023. Numbers at the top of each column indicate the number of remotely operated vehicle samples that were available in each habitat category.

the entire SEUS shelf. Future studies that explore ways to scale relative abundance estimates to density and further evaluate our hypothesis that red snapper rarely use unstructured habitats on the SEUS shelf will provide critical information for stock assessments and management actions.

CRediT authorship contribution statement

Krishna Pacifici: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Viviane Zulian:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Jeffrey Buckel:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Nathan Hostetter:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Joseph Tarnecki:** Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Kyle Shertzer:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **William Patterson:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Nathan Bacheler:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Walter Bubley:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Research Program, and South Carolina Sea Grant. Our work was carried out under a Scientific Research Permit issued to NMB on 24 Nov 2020 and was carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for animal experiments (http://europa.eu.int/scadplus/leg/en/s23000.htm) and the Uniform Requirements for manuscripts submitted to Biomedical journals (http://www.nejm.org/general/text/requirements/1.htm).

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The scientific results and conclusions, as well as any views and opinions expressed herein, are those of the authors and the U.S. Geological Survey, but do not necessarily reflect those of the National Marine Fisheries Service. Data availability questions can be emailed to the corresponding author at nate.bacheler@noaa.gov.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107200.

References

Addis, D.T., Patterson III, W.F., Dance, M.A., Ingram Jr., G.W., 2013. Implications of reef fish movement from unreported artificial reef sites in the northern Gulf of Mexico. Fish. Res. 147, 349–358. https://doi.org/10.1016/j.fishres.2013.07.011.

Altman, N., Krzywinski, M., 2015. Association, correlation and causation. Nat. Methods 12, 899–900. https://doi.org/10.1038/nmeth.3587.

Bacheler, N.M., 2024. A review and synthesis of the benefits, drawbacks, and considerations of using traps to survey fish and decapods. ICES J. Mar. Sci. 81, 1–21. https://doi.org/10.1093/icesjms/fsad206.

Bacheler, N.M., Ballenger, J.C., 2018. Decadal-scale decline of scamp (*Mycteroperca phenax*) abundance along the southeast United States Atlantic coast. Fish. Res. 204, 74–87. https://doi.org/10.1016/j.fishres.2018.02.006.

Bacheler, N.M., Bartolino, V., Reichert, M.J.M., 2013b. Influence of soak time and fish accumulation on catches of reef fishes in a multispecies trap survey. Fish. Bull. 111, 218–232. https://doi.org/10.7755/FB.111.3.2.

Bacheler, N.M., Berrane, D.J., Mitchell, W.A., Schobernd, C.M., Schobernd, Z.H., Teer, B. Z., Ballenger, J.C., 2014. Environmental conditions and habitat characteristics influence trap and video detection probabilities for reef fish species. Mar. Ecol. Prog. Ser. 517, 1–14. https://doi.org/10.3354/meps11094.

Bacheler, N.M., Gillum, Z.D., Gregalis, K.C., Schobernd, C.M., Schobernd, Z.H., Teer, B. Z., 2020. Spatial patterns in relative abundance and habitat use of adult gray snapper off the southeastern coast of the United States. Mar. Coast. Fish. 12, 205–219. https://doi.org/10.1002/mcf2.10118.

Bacheler, N.M., Runde, B.J., Shertzer, K.W., Buckel, J.A., Rudershausen, P.J., 2022. Fine-scale behavior of red snapper (*Lutjanus campechanus*) around bait: approach distances, bait plume dynamics, and effective fishing area. Can. J. Fish. Aquat. Sci. 79, 458–471. https://doi.org/10.1139/cjfas-2021-0044.

Bacheler, N.M., Schobernd, Z.H., Berrane, D.J., Schobernd, C.M., Mitchell, W.A., Geraldi, N.R., 2013a. When a trap is not a trap: converging entry and exit rates and their effect on trap saturation of black sea bass (*Centropristis striata*). ICES J. Mar. Sci. 70, 873–882. https://doi.org/10.1093/icesjms/fst062.

Bacheler, N.M., Schobernd, Z.H., Berrane, D.J., Schobernd, C.M., Mitchell, W.A., Teer, B. Z., Gregalis, K.C., Glasgow, D.M., 2016. Spatial distribution of reef fish species along the southeast US Atlantic coast inferred from underwater video survey data. PLoS One 11, e0162653. https://doi.org/10.1371/journal.pone.0162653.

Bacheler, N.M., Shertzer, K.W., Buckel, J.A., Rudershausen, P.J., Runde, B.J., 2018. Behavior of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale acoustic tracking. Mar. Ecol. Prog. Ser. 606, 133–150. https://doi.org/10.3354/meps12780.

Bacheler, N.M., Shertzer, K.W., Runde, B.J., Rudershausen, P.J., Buckel, J.A., 2021. Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. Sci. Rep. 11, 9580. https://doi.org/10.1038/s41598-021-88806-3.

Bacheler, N.M., Shertzer, K.W., Schobernd, Z.H., Coggins Jr, L.G., 2023. Calibration of fish counts in video surveys: a case study from the Southeast Reef Fish Survey. Front. Mar. Sci. 10, 1183955. https://doi.org/10.3389/fmars.2023.1183955.

Bacheler, N.M., Shertzer, K.W., 2020. Catchability of reef fish species in traps is strongly affected by water temperature and substrate. Mar. Ecol. Prog. Ser. 642, 179–190. https://doi.org/10.3354/meps13337.

Bacheler, N.M., Smart, T.I., 2016. Multi-decadal decline in reef fish abundance and species richness in the southeast USA assessed by standardized trap catches. Mar. Biol. 163, 26. https://doi.org/10.1007/s00227-015-2774-x.

Bradley, E., Bryan, C.E., 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970–1974. Proc. Gulf Carib. Fish. Inst. 27, 77–106.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York.

Camber, C.I., 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Fl. St. Board Conserv. Tech. Ser. 12, 1–64.

Cao, J., Craig, J.K., Damiano, M., 2024. Spatio-temporal dynamics of reef fishes in the Southeastern United States Atlantic Ocean. Ecosphere 15, e4868. https://doi.org/10.1002/ecs2.4868.

Chatterjee, N., Wolfson, D., Kim, D., Velez, J., Freeman, S., Bacheler, N.M., Shertzer, K., Taylor, J.C., Fieberg, J., 2024. Modeling individual variability in habitat selection and movement using integrated step-selection analyses. Methods Ecol. Evol. 15, 1034–1047. https://doi.org/10.1111/2041-210X.14321.

Christiansen, H.M., Switzer, T.S., Brodie, R.B., Solomon, J.J., Paperno, R., 2020. Indices of Abundance for Red Snapper (*Lutjanus campechanus*) from the FWC Fish and Wildlife Research Institute (FWRI) Repetitive Timed Drop Survey in the U.S. South Atlantic (SEDAR73-WP06). SEDAR, North Charleston, SC.

Coggins Jr, L.G., Bacheler, N.M., Gwinn, D.C., 2014. Occupancy models for monitoring marine fish: a Bayesian hierarchical approach to model imperfect detection with a novel gear combination. PLoS One 9, e108302. https://doi.org/10.1371/journal.pone.0108302.

Collins, M.R., 1990. A comparison of three fish trap designs. Fish. Res. 9, 325–332. https://doi.org/10.1016/0165-7836(90)90051-V.

Cowan Jr., J.H., 2011. Red snapper in the Gulf of Mexico and U.S. South Atlantic: data, doubt, and debate. Fisheries. vol. 36, pp. 319–31. 〈https://doi.org/10.1080/03632415.2011.589318〉.

Cowan Jr., J.H., Grimes, C.B., Patterson III, W.F., Walters, C.J., Jones, A.C., Lindberg, W. J., Sheehy, D.J., Pine III, W.E., Powers, J.E., Campbell, M.D., Lindeman, K.C., Diamond, S.L., Hilborn, R., Gibson, H.T., Rose, K.A., 2011. Red snapper management in the Gulf of Mexico: science- or faith-based? Rev. Fish Biol. Fish. vol. 21, pp. 187–204. 〈https://doi.org/10.1007/s11160-010-9165-7〉.

Dance, M.A., Rooker, J.R., 2019. Cross-shelf habitat shifts by red snapper (*Lutjanus campechanus*) in the Gulf of Mexico. PLoS One 14, e0213506. https://doi.org/10.1371/journal.pone.0213506.

Everett, A.G., Szedlmayer, S.T., Gallaway, B.J., 2020. Movement patterns of red snapper *Lutjanus campechanus* based on acoustic telemetry around oil and gas platforms in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 649, 155–173. https://doi.org/10.3354/meps13448.

Farmer, N.A., Heyman, W.D., Karnauskas, M., Kobara, S., Smart, T.I., Ballenger, J.C., Reichert, M.J.M., Wyanski, D.M., Tishler, M.S., Lindeman, K.C., Lowerre-Barbieri, S. K., Switzer, T.S., Solomon, J.J., McCain, K., Marhefka, M., Sedberry, G.R., 2017. Timing and locations of reef fish spawning off the southeastern United States. PLoS One 12, e0172968. https://doi.org/10.1371/journal.pone.0172968.

Farmer, N.A., Karnauskas, M., 2013. Spatial distribution and conservation of speckled hind and Warsaw grouper in the Atlantic Ocean off the southeastern U.S. PLoS One 8, e78682. https://doi.org/10.1371/journal.pone.0078682.

Froehlich, C.Y.M., Garcia, A., Cintra-Buenrostro, C.E., Hicks, D.W., Kline, R.J., 2021. Structural differences alter residence and depth activity of red snapper (*Lutjanus campechanus*) at two artificial reefs. Fish. Res. 242, 106043. https://doi.org/10.1016/j.fishres.2021.106043.

Gallaway, B.J., Cole, J.G., Meyer, R., Roscigno, P., 1999. Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. Trans. Am. Fish. Soc. 128, 713–726. https://doi.org/10.1577/1548-8659(1999)128<0713:DOEHFJ>2.0.CO;2.

Gallaway, B.J., Szedlmayer, S.T., Gazey, W.J., 2009. A life history review of red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Rev. Fish. Sci. 17, 48–67. https://doi.org/10.1080/10641260802160717.

Geary, B.W., Mikulas, J.J., Rooker, J.R., Landry, A.M., Dellapenna, T.M., 2007. Patterns of habitat use by newly settled red snapper in the northwestern Gulf of Mexico. Am. Fish. Soc. Symp 60, 25–38. https://doi.org/10.47886/9781888569971.

Gilliam, J.F., Fraser, D.F., 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecol 68, 1856–1862. https://doi.org/10.2307/1939877.

Gregory, R.S., Northcote, G.T., 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can. J. Fish. Aquat. Sci 50, 233–240. https://doi.org/10.1139/f93-026.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman & Hall, London.

Henwood, T., Ingram, W., Grace, M., 2004. Shark/snapper/grouper longline surveys. National Marine Fisheries Service (SEDAR 07-DW-08). 〈https://sedarweb.org/documents/s7dw08-shark-snapper-grouper-longline-surveys/〉.

Hoese, H.D., Moore, R.H., 1998. Fishes of the Gulf of Mexico, 2nd ed. Texas A&M Press, College Station.

Hyun, K.H., He, R., 2010. Coastal upwelling in the South Atlantic Bight: a revisit of the 2003 cold event using long term observations and model hindcast solutions. J. Mar. Syst. 83, 1–13. https://doi.org/10.1016/j.jmarsys.2010.05.014.

Manooch III, C.S., Potts, J.C., 1997. Age and growth of red snapper, *Lutjanus campechanus*, Lutjanidae, collected along the southeastern United States from North Carolina through the East Coast of Florida. J. Elisha Mitchell Sci. Soc. 113, 111–122.

Manooch III, C.S., Potts, J.C., Vaughan, D.S., Burton, M.L., 1998. Population assessment of red snapper from the southeastern United States. Fish. Res. 38, 19–32. https://doi.org/10.1016/S0165-7836(98)00112-X.

McCawley, J.R., Cowan Jr, J.H., Shipp, R.L., 2006. Feeding periodicity and prey habitat preference of red snapper, *Lutjanus campechanus* (Poey, 1860), on Alabama artificial reefs. Gulf Mex. Sci. 24, 14–27. https://doi.org/10.18785/goms.2401.04.

McGovern, J.C., Collins, M.R., Pashuk, O., Meister, H.S., 2002. Temporal and spatial differences in life history parameters of black sea bass in the southeastern United States. N. Am. J. Fish. Manag. 22, 1151–1163. https://doi.org/10.1577/1548-8675(2002)022<1151:TASDIL>2.0.CO;2.

Mitchell, K.M., Henwood, T., Fitzhugh, G.R., Allman, R.J., 2004. Distribution, abundance, and age structure of red snapper (Lutjanus campechanus) caught on research longlines in the U.S. Gulf of Mexico. National Marine Fisheries Service SEDAR 07-DW-09. ⟨https://sedarweb.org/documents/s7dw09-distribution-abundance-and-age-structure-of-red-snapper-lutjanus-campechanus-caught-on-research-longlines-in-u-s-gulf-of-mexico/⟩.
Mitchell, W.A., Kellison, G.T., Bacheler, N.M., Potts, J.C., Schobernd, C.M., Hale, L.F., 2014. Depth-related distribution of post-juvenile red snapper in southeastern U.S. Atlantic Ocean waters: ontogenic patterns and implications for management. Mar. Coast. Fish. 6, 142–155. https://doi.org/10.1080/19425120.2014.920743.
Moseley, F.M., 1966. Biology of the red snapper, *Lutjanus aya* Bloch, of the northwestern Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Texas 11, 90–101.
Neter, J., Wasserman, W., Kutner, M.H., 1989. Applied Linear Regression Models, second ed. Irwin, Homewood.
Patterson III, W.F., 2007. A review of movement in Gulf of Mexico red snapper: implications for population structure. Am. Fish. Soc. Symp 60, 221–235. https://doi.org/10.47886/9781888569971.
Patterson III, W.F., Tarnecki, J.H., Addis, D.T., Barbieri, L.R., 2014. Reef fish community structure at natural versus artificial reefs in the northern Gulf of Mexico. Proc. Gulf Carib. Fish. Inst. 66, 4–8.
Patterson III, W.F., Watterson, J.C., Shipp, J.L., Cowan Jr, J.H., 2001. Movement of tagged red snapper in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 130, 533–545. https://doi.org/10.1577/1548-8659(2001)130<0533:MOTRSI>2.0.CO;2.
Paxton, A.B., Newton, E.A., Adler, A.M., Van Hoeck, R.V., Iversen Jr., E.S., Taylor, J.C., Peterson, C.H., Silliman, B.R., 2020. Artificial habitats host elevated densities of large reef-associated predators. PLoS One 15 (9), e0237374. https://doi.org/10.1371/journal.pone.0237374.
Piraino, M.N., Szedlmayer, S.T., 2014. Fine-scale movements and home ranges of red snapper around artificial reefs in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 143, 988–998. https://doi.org/10.1080/00028487.2014.901249.
Powles, H., Barans, C.A., 1980. Groundfish monitoring sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42, 21–35.
R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. ⟨https://www.r-project.org/⟩.
SARSRP, 2020. The South Atlantic Red Snapper Research Program. Sea Grant and National Marine Fisheries Service. ⟨https://www.scseagrant.org/south-atlantic-red-snapper-research-program/⟩.
Schobernd, Z.H., Bacheler, N.M., Conn, P.B., 2014. Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. Can. J. Fish. Aquat. Sci. 71, 464–471. https://doi.org/10.1139/cjfas-2013-0086.
Schobernd, C.M., Sedberry, G.R., 2009. Shelf-edge and upper-slope reef fish assemblages in the South Atlantic Bight: habitat characteristics, spatial variation, and reproductive behavior. Bull. Mar. Sci. 84, 67–92.
Schwartzkopf, B.D., Langland, T.A., Cowan, J.H., 2017. Habitat selection important for red snapper feeding ecology in the northwestern Gulf of Mexico. Mar. Coast. Fish. 9, 373–387. https://doi.org/10.1080/19425120.2017.1347117.
SEDAR, 2009. SEDAR 15: Stock Assessment Report 1 (SAR 1) for South Atlantic Red Snapper. SEDAR, North Charleston, SC. ⟨https://sedarweb.org/documents/sedar-15-stock-assessment-report-south-atlantic-red-snapper/⟩.
SEDAR, 2010. SEDAR 24: Stock Assessment Report for South Atlantic Red Snapper. SEDAR, North Charleston, SC. ⟨https://sedarweb.org/documents/sedar-24-stock-assessment-report-south-atlantic-red-snapper/⟩.
SEDAR, 2017. SEDAR 41: Stock Assessment Report for South Atlantic Red Snapper. SEDAR, North Charleston, SC. ⟨https://sedarweb.org/documents/sedar-41-corrected-assessment-workshop-report-south-atlantic-red-snapper-april-2017/⟩.
SEDAR, 2018. SEDAR 52: Stock Assessment Report for Gulf of Mexico rEd Snapper. SEDAR, North Charleston, SC. ⟨https://sedarweb.org/documents/sedar-52-gulf-of-mexico-red-snapper-final-stock-assessment-report/⟩.
SEDAR, 2021. SEDAR 73: South Atlantic Red Snapper Stock Assessment Report. SEDAR, North Charleston, SC. ⟨https://sedarweb.org/documents/sedar-73-stock-assessment-report-south-atlantic-red-snapper/⟩.
Shertzer, K., Crosson, S., Williams, E., Cao, J., DeVictor, R., Dumas, C., Nesslage, G., 2024. Fishery management strategies for red snapper in the southeastern U.S. Atlantic: a spatial population model to compare approaches. N. Am. J. Fish. Manag. https://doi.org/10.1002/nafm.10966 (XX, XXX–XXX.
Shertzer, K.W., Williams, E.H., Craig, J.K., Fitzpatrick, E.E., Klibansky, N., Siegfried, K.I., 2019. Recreational sector is the dominant source of fishing mortality for oceanic fishes in the southeast United States Atlantic Ocean. Fish Manag. Ecol. 26, 621–629. https://doi.org/10.1111/fme.12371.
Smart, T.I., Bubley, W.J., Glasgow, D.M., Reichert, M.J.M., 2020. Spatial distribution changes and habitat use in red porgy in waters off the Southeast U.S. Atlantic coast. Mar. Coast. Fish. 12, 381–394. https://doi.org/10.1002/mcf2.10135.
Steward, D.N., Paxton, A.B., Bacheler, N.M., Schobernd, C.M., Mille, K., Renchen, J., Harrison, Z., Byrum, J., Martore, R., Brinton, C., Riley, K.L., Taylor, J.C., Kellison, G.T., 2022. Quantifying spatial extents of artificial versus natural reefs in the seascape. Front. Mar. Sci. 9, 980384. https://doi.org/10.3389/fmars.2022.980384.
Stunz, G.W., Patterson III, W.F., Powers, S.P., Cowan Jr, J.H., Rooker, J.R., Ahrens, R.A., \Boswell, K., Carleton, L., Catalano, M., Drymon, J.M., Hoenig, J., Leaf, R., Lecours, V., Murawski, S., Portnoy, D., Saillant, E., Stokes, L.S., Wells, R.J.D., 2021. Estimating the Absolute Abundance of Age-2+ Red Snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico. Mississippi-Alabama Sea Grant Consortium, NOAA Sea Grant. ⟨https://www.harteresearch.org/sites/default/files/inline-files/Great%20Red%20Snapper%20Count_Final%20Report.pdf⟩.
Szedlmayer, S.T., 2007. An evaluation of the benefits of artificial habitats for red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. Proc. Gulf Carib. Fish. Inst. 59, 223–230.
Szedlmayer, S.T., Lee, J.D., 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. Fish. Bull. 102, 366–375.
Tarnecki, J.H., Patterson III, W.F., 2015. Changes in red snapper diet and trophic ecology following the Deepwater Horizon oil spill. Mar. Coast. Fish. 7, 135–147. https://doi.org/10.1080/19425120.2015.1020402.
Wells, R.J.D., Cowan Jr, J.H., Fry, B., 2008. Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 361, 213–225. https://doi.org/10.3354/meps07425.
White, D.B., Palmer, S.M., 2004. Age, growth, and reproduction of the red snapper, *Lutjanus campechanus*, from the Atlantic waters of the southeastern U.S. Bull. Mar. Sci. 75, 335–360.
Williams, E.H., Carmichael, J., 2009. Final Report of the South Atlantic Fishery Independent Monitoring Program Workshop. Beaufort, North Carolina.
Williams-Grove, L.J., Szedlmayer, S.T., 2016. Acoustic positioning and movement patterns of red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 553, 233–251. https://doi.org/10.3354/meps11778.
Williams-Grove, L.J., Szedlmayer, S.T., 2017. Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Fish. Res. 190, 61–70. https://doi.org/10.1016/j.fishres.2017.01.003.
Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. Roy. Stat. Soc. B Stat. Meth. 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.
Wood, S.N., 2017. Generalized Additive Models: An Introduction With R. Chapman & Hall/CRC, Boca Raton. https://doi.org/10.1201/9781315370279.
Zulian, V., Pacifici, K., Bacheler, N.M., Buckel, J.A., Patterson III, W.F., Reich, B.J., Shertzer, K.W., Hostetter, N.J., 2024. Integrating mark-resight and count data to estimate effective sampling area and fish density. Can. J. Fish. Aquat. Sci. ⟨https://doi.org/10.1139/cjfas-2023-0373⟩. (In press).