*Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 12:205–219, 2020

ISSN: 1942-5120 online
DOI: 10.1002/mcf2.10118

ARTICLE

# Spatial Patterns in Relative Abundance and Habitat Use of Adult Gray Snapper off the Southeastern Coast of the United States

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*Abstract*

**Gray Snapper *Lutjanus griseus* is an economically and ecologically important species in the estuarine and coastal environments of the southeastern United States. Previous research has focused primarily on juvenile Gray Snapper due to their accessible inshore distribution and ecological importance, while adults, which often occur offshore and are the main focus of fishing pressure, remain poorly understood. Seven years of baited underwater video data (2011–2017; $N = 8{,}379$ videos; ~14,000 h of video) were collected along the continental shelf between North Carolina and Florida (~100,000 km$^2$) to better understand the ways in which the relative abundance of Gray Snapper varied by space, time, habitats, and environmental conditions. Adult Gray Snapper were observed on 6.9% of the videos overall, but they were much more commonly observed in Florida (16.9% of the videos) compared with the states that are north of Florida (1.4% of the videos). We used delta-generalized additive models to determine that adult Gray Snapper primarily occurred in high-relief hardbottom sites south of St. Augustine, Florida, in warm water less than 50 m deep, after accounting for imperfect detection on video. Temporal variability was relatively minor despite relatively high precision (the mean annual coefficient of variation = 24%). Fifteen large aggregations of Gray Snapper (i.e., >20 individuals counted on a single frame) were observed on video, but it is unclear whether these aggregations indicated potential spawning aggregation sites. This work provides greater insight into the ecology of Gray Snapper during their important coastal-ocean adult life stage, which will improve their management and conservation.**

Underwater video has become a common approach for monitoring the abundance, distribution, and diversity of reef-associated marine fish around the world (Murphy and Jenkins 2010; Mallet and Pelletier 2014), and the benefits of using underwater video are significant. Video is a nonextractive sampling gear, which is ideal for monitoring ocean biodiversity, especially in no-take reserves (Cappo et al. 2003; Bacheler et al. 2016b). Video data can be collected in locations where bottom structure, depth, or fish behavior limit the effectiveness of traditional sampling gears like underwater visual census or traps (Jones et al. 2012; Rooper et al. 2012). Video can also be baited, which often increases the power to detect change (Harvey et al. 2007). Moreover, video is often less size- (Cappo et al. 2004; Morrison and Carbines 2006) and species-selective (Ellis and DeMartini 1995; Bacheler et al. 2013) than extractive fishing gears like traps, trawls, or hooks. Last, video provides behavioral information on species and habitat from each sampling site (Mallet and Pelletier 2014).

Gray Snapper *Lutjanus griseus* is an economically (Burton 2001) and ecologically important fish species (Claro

Subject editor: Kenneth Rose, University of Maryland Center for Environmental Science, Cambridge

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Received October 30, 2019; accepted March 20, 2020

1991) with a poorly understood adult life stage that would benefit from video sampling (Figure 1). Gray Snapper (also known as Mangrove Snapper) are found in the estuarine and marine waters of the western Atlantic Ocean from North Carolina to Brazil, including the Caribbean, Gulf of Mexico, and Bermuda (Starck and Schroeder 1971; Rutherford et al. 1989b; Andrade and Santos 2019). Larval Gray Snapper settle out of their planktonic stage into estuarine seagrass beds, mangroves, or oyster reefs (Allman and Grimes 2002; Denit and Sponaugle 2004) where they reside until subadult or adult life stages. Adults are thought to move offshore into coral or rocky reef habitats where they aggregate to spawn in summer months during the new (Starck and Schroeder 1971; Manooch and Matheson 1984; Domeier et al. 1996) or full moon (Claro and Lindeman 2003). Gray Snapper are rarely captured in the ocean using traditional sampling gears like traps or longlines, but are observed on video frequently (Bacheler et al. 2013). Gray Snapper are thought to be overfished in the Florida Keys (Ault et al. 2005) and in the Gulf of Mexico (SEDAR 2018), but stock status has not been formally analyzed by state or federal agencies along the southeastern U.S. Atlantic Continental Shelf (hereafter, "SEUS"). Most of the Gray Snapper harvest in the southeastern United States occurs in Florida.

Despite the well-studied habitat use, abundance, and distribution patterns of juveniles (e.g., Rutherford et al. 1989a; Chester and Thayer 1990; Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002; Whaley et al. 2007; Faunce and Serafy 2007, 2008; Lara et al. 2008; Flaherty et al. 2014), there is a paucity of information about adult Gray Snapper. The few studies that have been conducted suggest that adult Gray Snapper associate with oyster reefs, seagrass, and mangroves in bays (Rooker and Dennis 1991; Nagelkerken et al. 2000; Luo et al. 2009) or around temperate or tropical reefs or artificial habitats in the coastal ocean (Farmer and Ault 2011; Friedlander et al. 2013; Bacheler et al. 2016a; Reeves et al. 2018). For instance, Luo et al. (2009) found that adult Gray Snapper moved from mangroves during the day to seagrass beds at night and emigrated from bays to the ocean for the summer spawning season. Farmer and Ault (2011) used ultrasonic telemetry to track one adult Gray Snapper in the Dry Tortugas National Park that associated with coral reef habitats during the day and made long migrations beyond the study area at night. In a preliminary analysis, Bacheler et al. (2016a) used baited underwater video data in the SEUS and found a strong negative correlation between the relative abundance of Gray Snapper and latitude. Despite these studies, the temporal and spatial dynamics of adult Gray Snapper in the ocean remain unresolved (SEDAR 2018).

FIGURE 1. Gray Snapper observed on an underwater video that was collected in 2017 by the Southeast Reef Fish Survey off St. Augustine, Florida, in 38 m of water.

Here, 7 years of extensive baited underwater video data were used to elucidate the abundance and distribution patterns of adult Gray Snapper in the SEUS, a broad area ranging from North Carolina to southern Florida (Figure 2). Our objectives were (1) to quantify the temporal dynamics of Gray Snapper from 2011–2017 across the SEUS, (2) to describe the spatial patterns of abundance and distribution for Gray Snapper in the SEUS, building on the preliminary results for Gray Snapper by Bacheler et al. (2016a), (3) to determine the use of habitats and environmental conditions by Gray Snapper in the coastal ocean, and (4) to identify the locations and timing of large aggregations of Gray Snapper to make inferences about potential spawning aggregations that have been noted elsewhere (Domeier et al. 1996; Domeier and Colin 1997). By focusing on adults in the coastal ocean, our results fill a gap in our understanding of the ecology and ontogeny of Gray Snapper.

## METHODS

*Study area.*— The continental shelf in the SEUS (area = 100,000 km$^2$) is dominated by unconsolidated sediments, with patches of consolidated hardbottom interspersed throughout the region. Sampling for this study targeted these patches of hardbottom between Cape Hatteras, North Carolina, and Port St. Lucie, Florida (Figure 2). The hardbottom in the region ranges from flat pavement rock, which is sometimes covered by a thin veneer of sand, to highly rugose limestone ledges that are covered in sponges, algae, and soft corals (Schobernd and Sedberry 2009).

*Video sampling.*— The data were collected throughout 1990–2017 by various agencies as part of the Southeast Reef Fish Survey (SERFS). The SERFS is a fishery-independent sampling program that is composed of three collaborating groups: the Marine Resources Monitoring, Assessment, and Prediction program, housed at the South Carolina Department of Natural Resources (SCDNR;

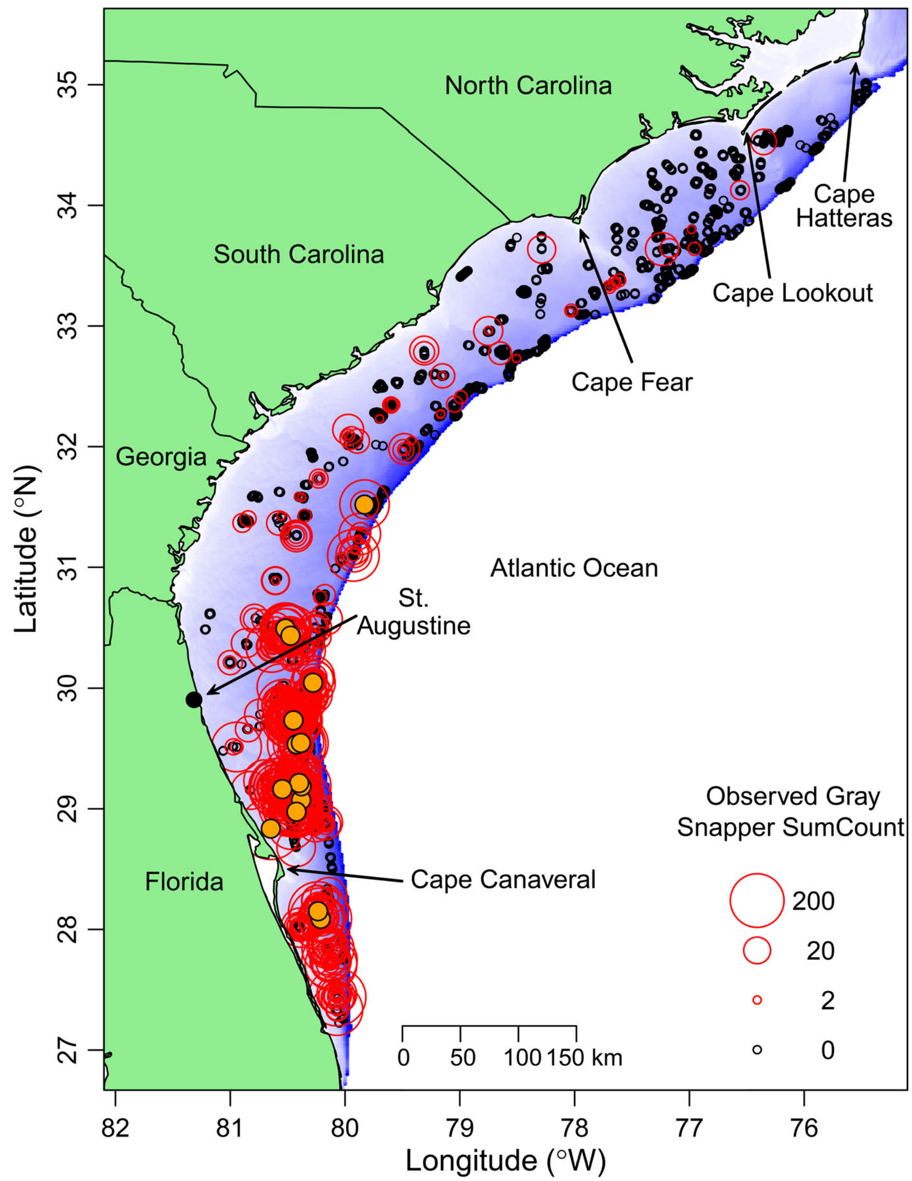


FIGURE 2. Gray Snapper video counts from the Southeast Reef Fish Survey along the Atlantic coast of the southeastern United States, 2011–2017. The black open circles mark the locations where no Gray Snapper were observed on video, and the red open circles mark the locations where Gray Snapper were observed. The size of the red bubbles was scaled to the number of Gray Snapper that were observed on the video (i.e., SumCount), and the orange filled circles denote Gray Snapper aggregations (i.e., >20 individuals observed on a single video frame). Note that the orange and red bubbles are plotted on top of the black bubbles, bubbles often overlap, and water depth is shown in blue (light blue = 5 m, dark blue = 100 m).

1990–2017), the Southeast Area Monitoring and Assessment Program–South Atlantic Region (2009–2017), also housed at SCDNR, and the Southeast Fishery-Independent Survey (2010–2017), housed within the National Marine Fisheries Service. Each program has been funded by the National Marine Fisheries Service, and each used standardized sampling methods as described below. Video cameras were implemented by SERFS region-wide in 2011.

A simple random sampling design was used to select hardbottom stations that were to be sampled by SERFS each year. A station was a discrete sampling location on hardbottom in the SEUS, but note that some of the samples landed on sand adjacent to hardbottom. Approximately 1,500 stations were randomly selected to be sampled annually out of a sampling frame of ~4,000 known hardbottom stations. Most of the stations that were included in our analyses were randomly selected (74%). In addition to the randomly selected points, some of the stations that were not selected for sampling in a given year were sampled opportunistically in order to increase the sampling efficiency during research cruises

(10%). Others were new stations that were discovered by using a fisheries echosounder or multibeam sonar mapping, or they were points that were provided by fishers. These points were included in the analyses if hardbottom habitat or reef-associated fish species were present on video (16%).

The Southeast Reef Fish Survey has used baited chevron fish traps to sample reef-associated fish species since 1990, and in 2011 cameras were attached to all of the traps to account for low capture rates of many fish species including Gray Snapper (Bacheler et al. 2013, 2017). Chevron fish traps were baited with 24 menhaden *Brevoortia* spp., soaked for approximately 90 min, and deployed greater than 200 m from one another to provide some measure of independence between trap samples (i.e., to minimize spatial autocorrelation). All of the chevron traps that have been deployed by SERFS since 2011 have had two cameras attached to them, one over the mouth and one over the nose of the trap, looking in opposite directions. During 2011–2014, SERFS attached Canon Vixia HF-S200 video cameras in Gates HF-21 housings over the mouth of each trap that was deployed, facing away from the trap. In 2015, Canon cameras were replaced by GoPro Hero 3+ or 4 cameras. Only cameras that were attached over the mouth of each trap were used to count fish, while the second camera, attached over the nose of each trap (GoPro Hero, GoPro Hero 3+/4, or Nikon Coolpix S210/S220), was used to quantify habitat, water current direction, and water clarity in addition to collecting these variables with the camera over the mouth. Videos were excluded from the analyses if the traps bounced or moved, videos were too dark or out of focus to identify fish, the camera view was obstructed, or if the video files were corrupt.

This study used a derivation of the MeanCount approach to determine the relative abundance of Gray Snapper on video. MeanCount is calculated as the mean number of individuals that is observed on a series of snapshots within a video, which in a study by Schobernd et al. (2014) was determined to be proportional to abundance using laboratory, simulation, and empirical data. In our study, Gray Snapper were quantified on 41 snapshots, each spaced 30 s apart beginning 10 min after the trap landed on the bottom and lasting 20 min in total. A SumCount approach, which is linearly related to MeanCount when the number of frames is the same, was then used to calculate the total number of Gray Snapper observed across all 41 frames. We used SumCount instead of MeanCount in our study because some of the error distributions that we considered (e.g., Poisson, negative binomial) required count data.

Because the fish were counted on two different camera types in this study, we conducted a side-by-side calibration study to develop a Gray Snapper-specific calibration factor between the Canon and GoPro cameras. During 2014, 143 traps were deployed with Canon and GoPro cameras attached side-by-side over the trap mouth and subsequent videos were read using SumCount for video footage that was recorded at exactly the same times on the two different camera types. Gray Snapper were observed on 14 pairs of the calibration videos, and the Canon cameras observed a mean of 29% fewer Gray Snapper than GoPro cameras (Figure 3), which is similar to the difference in fields-of-view between cameras. Therefore, Gray Snapper video counts on GoPro cameras during 2015–2017 were reduced by 29% to make the video data in those years consistent with the video data that were collected from the Canon cameras during 2011–2014.

At each station that was sampled, features of the water and substrate were obtained in various ways. Depth (m) was estimated by using the vessel echosounder, and latitude and longitude were acquired from the vessel global positioning unit. Bottom water temperature (°C) was measured for each group of simultaneously deployed traps by using a "conductivity-temperature-depth" cast. Two habitat variables were included in our analyses, following Bacheler et al. (2014). First, the percentage of the visible substrate that was hardbottom (hereafter, "percent hardbottom"; range = 0–100%) was estimated for each of the two cameras (i.e., one over the mouth and one over the nose) and a mean value was used for each station. Substrate relief was the maximum relief of the substrate, which was visually estimated in three categories: low (<0.3 m), moderate (0.3–1.0 m), or high (>1.0 m). Using the movement of particles in the water column, current

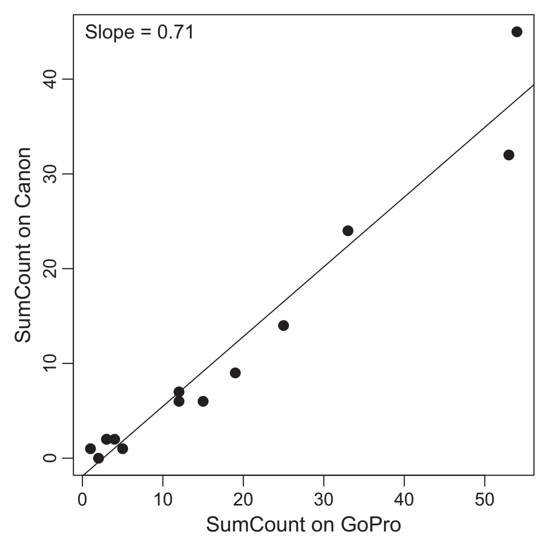


FIGURE 3. Baited video SumCounts for Gray Snapper observed on paired GoPro Hero 3+ and Canon Vixia HF-S200 cameras ($N = 14$) that were deployed by the Southeast Reef Fish Survey in 2014, which were used as a calibration factor between the cameras.

direction was estimated as "away," "sideways," or "towards" relative to the outward-facing camera over the trap mouth used to count fish. Last, water clarity was scored as "poor" if the substrate was not visible, "fair" if substrate could be seen but not the horizon, and "good" if the horizon was visible in the distance. If any of these variables was missing, that sample was excluded from analyses.

*Generalized additive models.—* We developed generalized additive models (GAMs) to relate video counts of Gray Snapper to temporal, spatial, habitat, and environmental variables. A GAM is a regression technique that can be used to examine the potentially nonlinear relationships between a response variable (in our case, Gray Snapper SumCount) and predictor variables. Local smoothers are used to model nonlinearity (Wood 2006), and GAMs can incorporate different types of error distributions (Hastie and Tibshirani 1990).

Video counts of Gray Snapper were zero-inflated beyond what could be accounted for by using traditional GAM error distributions. To account for zero-inflation, we used delta-GAMs to model video counts (Lo et al. 1992; Pennington 1996; Stefánsson 1996). The delta-GAMs contained two submodels, one modeling the presence or absence of Gray Snapper on the video (hereafter, "binomial submodel") and another that modeled video counts of Gray Snapper only when they were present (hereafter, "positive submodel"). The binomial submodel describes the distribution patterns of Gray Snapper, while the positive submodel helps to elucidate school size and abundance patterns when fish are present. For the combined model, the overall effects of a particular predictor variable on the video counts were obtained by multiplying the effects of each submodel (Maunder and Punt 2004; Murray 2004; Li et al. 2011; Bacheler and Ballenger 2018).

We examined nine predictor variables in our delta-GAMs that were hypothesized a priori to affect the video counts of Gray Snapper, the first four of which were categorical variables and five of which were smoothed, continuous variables. Year was included to test for changes in relative abundance of Gray Snapper over time, and substrate relief was included because many species of reef fish in the region tend to more closely associate with higher relief than with lower relief hardbottom habitats (Kendall et al. 2008; Schobernd and Sedberry 2009; Bacheler and Ballenger 2018). Water clarity was included to account for the effects of water clarity on sightability (Bacheler et al. 2014), and current direction was included to standardize for variability in video counts based on the direction of the bait plume (e.g., Bacheler and Ballenger 2018). The five continuous variables (i.e., latitude, depth, percent hardbottom, bottom temperature, and day of the year) were included because each has been shown to influence the abundance and distribution of reef fishes in the region (Kendall et al. 2008; Bacheler et al. 2014; Bacheler and Ballenger 2015, 2018). None of the predictor variables that were included in our delta-GAMs exhibited multicollinearity with each other based on variance inflation factors (Neter et al. 1989). In particular, bottom water temperature was not significantly collinear with depth, latitude, or day of the year in our study, likely due to summertime upwelling that may occur throughout the study area but most commonly occurs in Florida (Hyun and He 2010).

The full binomial submodel related the presence or absence of Gray Snapper on video to the nine predictor variables (hereafter, "full model"). The presence or absence of Gray Snapper on video was assumed to be an independent draw from a binary variable, where the probability of presence was $\pi$ and the probability of absence was $1-\pi$. Here we used the binomial error distribution with a logit link:

$$\begin{aligned}\mathrm{logit}(\eta) = \alpha &+ f_1(year) + f_2(rel) + f_3(wc) \\ &+ f_4(cd) + s_1(lat) + s_2(depth) \\ &+ s_3(hb) + s_4(temp) + s_5(doy)\end{aligned}, \qquad (1)$$

where $\eta$ is the presence or absence of Gray Snapper on video, $\alpha$ is the model intercept, *year* is the year, *rel* is the substrate relief, *wc* is water clarity, *cd* is current direction, *lat* is latitude, *depth* is water depth, *hb* is percent hardbottom, *temp* is the bottom water temperature, *doy* is the day of the year, $f_{1-4}$ are categorical functions, and $s_{1-5}$ are cubic spline (smoothed) functions. All of the GAMs were coded in R version 3.4.3 (R Core Team 2017) by using the mgcv library 1.8-24 (Wood 2011) in RStudio version 1.1.456.

The positive submodel related nonzero SumCounts of Gray Snapper to the same nine predictor variables (also called "full" model). We explored five potential error distributions for the positive submodels: Gaussian with a log transformation, Gaussian with a fourth-root transformation, Tweedie, Poisson, and negative binomial. Based on various model diagnostics using the "gam.check" function, the Gaussian error distribution with a log transformation outperformed all of the other distributions and was used:

$$\begin{aligned}\log(y) = \alpha &+ f_1(year) + f_2(rel) + f_3(wc) + f_4(cd) \\ &+ s_1(lat) + s_2(depth) + s_3(hb) + s_4(temp) \\ &+ s_5(doy)\end{aligned}, \qquad (2)$$

where $y$ is the nonzero SumCount of Gray Snapper and all of the other variables remain the same as in equation (1).

*Model selection.—* The full models were compared with models with all combinations of fewer predictor variables by using Akaike's information criterion (AIC; Burnham and Anderson 2002). Akaike's information criterion seeks parsimony by searching for the models that explain the greatest amount of variation with the fewest number of parameters. The best models in each model set were those with the lowest AIC values; for clarity we present ΔAIC values, which compare each model with the best model in the set. Thus, the best models have ΔAIC values = 0 and the other models in the set have ΔAIC values that are greater than 0. Models with ΔAIC values <2 are generally considered to be indistinguishable from the best models, but for simplicity we only present the covariate effects from the best models. We allowed the built-in algorithm in the mgcv library to determine the amount of flexibility in the smoothed covariates, and final models met the assumptions of constant variance and normality.

The models can be made spatially explicit with the inclusion of a position variable that combines latitude and longitude into a single variable (Ciannelli et al. 2012). A two-dimensional surface smoother can then be used to estimate relative abundance across the study area (Bacheler and Ballenger 2015). We compared a simple latitude variable with the position variable using AIC, and for both submodels the latitude variable was more parsimonious (it had a lower AIC) than the position variable, perhaps because latitude and depth sufficiently capture most of the spatial variability in video counts of Gray Snapper in the SEUS. Therefore, latitude was used in all of the GAMs in our study instead of position.

Developing delta-GAMs by using the mgcv library requires that the same predictor variables be present in both submodels if they are to be combined statistically into an overall model. Thus, predictor variables were only removed from each GAM submodel if AIC chose to remove it from both of the submodels. If AIC chose to remove a predictor variable from one submodel but not the other, it was retained in both models. The end result is that our final chosen models for each submodel were not necessarily the best models based on AIC.

*Gray Snapper aggregations.*— We sought to identify potential spawning aggregation sites for Gray Snapper, but given that our survey occurred during daylight hours and Gray Snapper spawn at night (Claro and Lindeman 2003), observing actual Gray Snapper spawning in our study was not possible. Instead, we noted the locations and timing of large aggregations of Gray Snapper that were observed on video in our study to make inferences about potential spawning locations. An "aggregation" of Gray Snapper in our study was defined as a minimum of 20 individual Gray Snapper being counted on a single video frame, which was chosen arbitrarily. Using a kernel density estimator, we then visually compared the locations and timing of the Gray Snapper aggregations on video with the locations and timing of all Gray Snapper on video. Differences in latitude, depth, seasonality, and percent hardbottom might suggest that Gray Snapper migrate to specific, unique areas for spawning at particular times of the year.

## RESULTS

A total of 8,379 underwater videos (~14,000 h of video) were included in our analyses spanning from 2011 to 2017 (Table 1). The fewest samples were from 2011 (585), and the most were from 2015 (1,393). The spatial distribution of sampling reflected the patchy distribution of hardbottom habitat in the SEUS (Figure 2). Day of year, depth, and latitude of sampling were similar among years (Table 1). Sampling typically began in late April or May and ended in late September or October, and took place over a wide range of water depths (i.e., 15–115 m), but yearly mean water depths were similar. Bottom water temperature ranged from 12.4°C to 29.3°C over the course of the study, and annual mean water temperature varied from a low of 21.3°C in 2011 to a high of 23.9°C in 2015.

Gray Snapper were observed on 6.9% of the SERFS videos over the course of the study, ranging from a low of 5.6% in 2012 to 8.5% in 2015 (Figure 4). Across all of the videos, the SumCount for Gray Snapper ranged from 0 to 230 (overall mean = 1.1), and the overall median nonzero SumCount was 4. Thus, the video data were overdispersed and zero-inflated. Median SumCounts were fairly invariant across years, ranging from 3 in 2011, 2013, 2014, and 2016 to 6 in 2015 (Figure 4). Most of the Gray Snapper that were observed on video were in Florida (the percentage of occurrence in Florida = 16.9%; Figure 2). Gray Snapper were observed as far north as Cape Lookout, North Carolina, but the percentage of occurrence (the proportion of video samples in which Gray Snapper were observed) and SumCount at the locations where Gray Snapper were present appeared to decline substantially north of Florida (Figure 2). For instance, Gray Snapper were only observed on 1 out of 827 video samples (0.1%) north of Cape Lookout, North Carolina.

The best binomial GAM relating the presence or absence of Gray Snapper on video to predictor variables was the model that excluded year and day of the year and explained 34.0% of the model deviance (Table 2). Five other competing models, including the full model, had ΔAIC values of 4.6 or less. The best positive GAM explained 11.0% of the model deviance and excluded day of the year, percent hardbottom, current direction, and water clarity (Table 2). Only one predictor variable, day of the year, was excluded from both the best binomial submodel and the best positive submodel, so the final models that were used for all of the subsequent analyses only excluded this single variable (Table 2). The final binomial and positive models excluding day of the year were only slightly worse than the best models based on ΔAIC

TABLE 1. Annual sampling information for video data that were collected by the Southeast Reef Fish Survey during 2011–2017 along the Atlantic coast of the southeastern United States. $N$ = number of video samples included in the analyses. Mean values are provided for date, depth, latitude, and bottom temperature, and ranges are shown in parentheses.

| Year | $N$ | Date | Depth (m) | Latitude (°N) | Bottom temperature (°C) |
|---|---|---|---|---|---|
| 2011 | 585 | 7/26 (5/19–10/26) | 41.9 (15–93) | 30.7 (27.2–34.5) | 21.3 (14.8–28.8) |
| 2012 | 1,076 | 7/11 (4/24–10/10) | 40.3 (15–106) | 31.9 (27.2–35.0) | 22.1 (12.9–27.8) |
| 2013 | 1,220 | 7/17 (4/24–10/4) | 38.1 (15–100) | 31.3 (27.3–35.0) | 22.1 (12.4–28.1) |
| 2014 | 1,378 | 7/11 (4/23–10/21) | 39.2 (15–110) | 31.9 (27.2–35.0) | 23.4 (16.1–29.3) |
| 2015 | 1,393 | 7/4 (4/21–10/22) | 38.4 (16–110) | 31.9 (27.3–35.0) | 22.6 (13.6–28.5) |
| 2016 | 1,390 | 8/2 (5/4–10/26) | 40.8 (17–115) | 32.2 (27.2–35.0) | 23.9 (15.5–29.3) |
| 2017 | 1,337 | 7/2 (4/26–9/29) | 38.9 (15–100) | 31.9 (27.2–35.0) | 22.6 (14.8–28.2) |
| Overall | 8,379 | 7/14 (4/21–10/26) | 39.4 (15–115) | 31.8 (27.2–35.0) | 22.7 (12.4–29.3) |

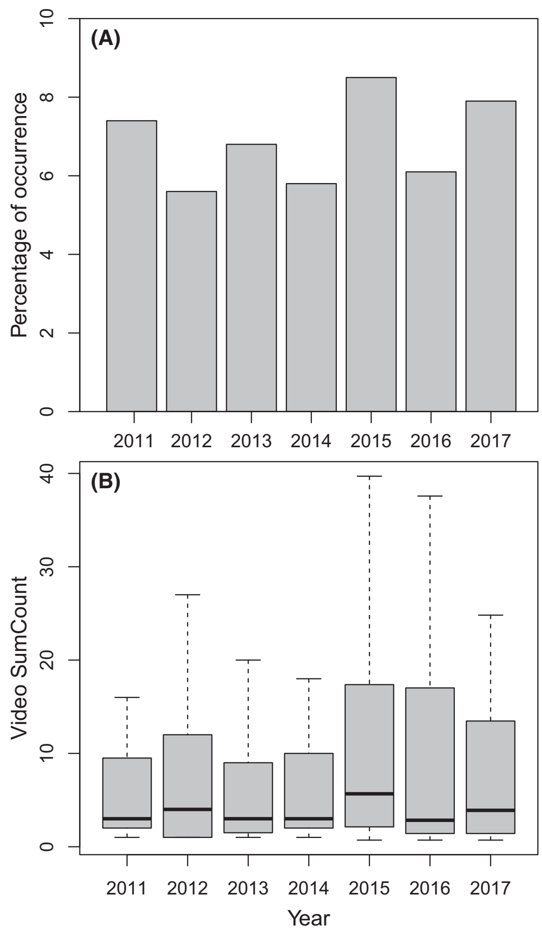


FIGURE 4. Uncalibrated video data for Gray Snapper that were collected by the Southeast Reef Fish Survey in 2011–2017. **(A)** Annual percentage of occurrence of Gray Snapper on baited videos, which was calculated as the percentage of all videos in which Gray Snapper were observed each year. **(B)** Boxplot of annual video SumCounts of Gray Snapper for baited videos in which they were observed. The annual boxes show the median SumCounts by the thick horizontal black line, the bottom and top of boxes provide the 25th and 75th percentiles, respectively, and the whiskers are 1.5 times the interquartile range.

(i.e., 3.3 and 4.2, respectively), but they explained more model deviance than the best binomial (34.2% versus 34.0%) and positive models (12.8% versus 11.0%; Table 2).

Video counts of Gray Snapper were related to the four categorical predictor variables in different ways. The year effect was similar among the binomial, positive, and combined models, decreasing slightly from 2011 to 2014, being higher in 2015, and lower again in 2016 and 2017 (Figure 5). The overall coefficient of variation around the year effect was 24%. Gray Snapper were also more likely to be observed on video, and in higher numbers, on high relief than on low relief substrates when the water clarity was good. Current direction was weakly related to the video counts; SumCount was slightly lower when the current was towards the camera (Figure 5).

Latitude and depth were the predictor variables that most strongly associated with the video counts. Gray Snapper were much more commonly observed on video south of 30°N latitude (approximately St. Augustine, Florida) compared with northward locations (Figure 6). There was a slight negative relationship between latitude and SumCount for Gray Snapper when they were present in the SEUS, and the combined model showed that overall SumCount declined substantially with increasing latitude. A similar relationship was observed for depth, where Gray Snapper were most likely to be observed on video, and had highest SumCounts when present, in water less than 50 m deep. The combined model mirrored these relationships, with the highest relative abundance of Gray Snapper in water less than 50 m deep, peaking at approximately 35 m (Figure 6).

The relationships between the video counts for Gray Snapper and percent hardbottom and bottom temperature were also similar. Gray Snapper were more likely to be observed on video in places where a large percentage of the substrate was hardbottom (>20%) and the water temperature was warm (>22°C); the likelihood of Gray Snapper presence below these values was lower (Figure 6).

TABLE 2. Model selection for the delta-generalized additive models relating Gray Snapper video counts to nine predictor variables using data from the Southeast Reef Fish Survey, 2011–2017. The top six binomial models and the top six positive models, based on ΔAIC values, are shown; the full models include all predictor variables and the reduced models exclude one or more predictor variables ("ex" means that the variable was excluded from the model). The abbreviations are as follows: DE is the deviance explained by the models, degrees of freedom are shown for the categorical variables ($f_{1–4}$), estimated degrees of freedom are shown for smoothed variables ($s_{1–5}$), *year* is year, *rel* is substrate relief, *wc* is water clarity, *cd* is current direction, *lat* is latitude, *depth* is water depth, *hb* is percent hardbottom, *temp* is bottom water temperature, and *doy* is day of the year. Asterisks denote significance at the following alpha levels: *0.05, **0.01, ***0.001, and † indicates the final models used for all of the analyses.

| Model | ΔAIC | DE | $f_1$ (*year*) | $f_2$(*rel*) | $f_3$(*wc*) | $f_4$ (*cd*) | $s_1$(*lat*) | $s_2$(*depth*) | $s_3$(*hb*) | $s_4$(*temp*) | $s_5$ (*doy*) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Binomial model | | | | | | | | | | | |
| Full – *doy* – *year* | 0.0 | 34.0 | ex | 2*** | 2*** | 2 | 4.5*** | 5.6*** | 7.9*** | 8.3*** | ex |
| Full – *year* | 1.1 | 34.1 | ex | 2*** | 2*** | 2 | 4.4*** | 5.8*** | 7.8*** | 8.3*** | 1.7 |
| Full – *doy* – *year* – *cd* | 2.2 | 33.8 | ex | 2*** | 2*** | ex | 4.5*** | 5.6*** | 7.9*** | 8.3*** | ex |
| Full – *doy*† | 3.3 | 34.2 | 6 | 2*** | 2*** | 2 | 4.6*** | 5.6*** | 7.9*** | 8.6*** | ex |
| Full | 4.0 | 34.2 | 6 | 2*** | 2*** | 2 | 4.5*** | 5.5*** | 7.8*** | 8.5*** | 1.8 |
| Full – *doy* – *cd* | 4.6 | 34.1 | 6 | 2*** | 2*** | ex | 4.6*** | 5.6*** | 7.9*** | 8.5*** | ex |
| Positive model | | | | | | | | | | | |
| Full – *doy* – *hb* – *cd* – *wc* | 0.0 | 11.0 | 6** | 2*** | ex | ex | 2.8*** | 2.2* | ex | 1.0 | ex |
| Full – *doy* – *hb* – *cd* | 0.5 | 11.5 | 6** | 2** | 2 | ex | 2.5*** | 2.2* | ex | 1.0 | ex |
| Full – *doy* – *hb* – *cd* – *wc* – *temp* | 1.2 | 10.5 | 6*** | 2*** | ex | ex | 2.8*** | 2.2* | ex | ex | ex |
| Full – *doy* – *hb* – *cd* – *temp* | 1.7 | 10.9 | 6** | 2** | 2 | ex | 2.4*** | 2.3* | ex | ex | ex |
| Full – *doy* – *hb* | 1.8 | 11.9 | 6*** | 2** | 2 | 2 | 2.6*** | 2.3* | ex | 1.0 | ex |
| Full – *doy*† | 4.2 | 12.8 | 6** | 2* | 2 | 2 | 2.6*** | 2.3* | 4.1 | 1.0 | ex |

However, the influence of these two variables on Gray Snapper abundance when present was minimal. The combined effects, therefore, mirrored the effects from each of the binomial models, with the relative abundance of Gray Snapper being positively related to percent hardbottom and bottom temperature (Figure 6).

A total of 15 aggregations of Gray Snapper were observed across the 7 years of our study. More aggregations were observed during 2015–2017 ($N = 12$) when GoPro cameras were used (with a wider field-of-view) than during 2011–2014 ($N = 3$) when Canon cameras were used (Table 3). Aggregations of Gray Snapper were observed between 28.1°N and 31.5°N and 21–54 m deep (Figure 2) across a wide variety of values of percent hardbottom, substrate reliefs, and moon phases (Table 3). Most of the aggregations were observed in late spring ($N = 11$) or late summer ($N = 4$; Table 3). The locations and timing of the aggregations were very similar to the locations and timing of all of the Gray Snapper that were observed on video (Figure 7).

## DISCUSSION

In this study, baited underwater video was used to provide baseline estimates of the abundance and distribution of adult Gray Snapper broadly across the SEUS. Typical sampling gears for reef fish (like traps) rarely capture adult Gray Snapper (Bacheler et al. 2013, 2017), so here we used underwater video to index the abundance and distribution of adult Gray Snapper broadly across the SEUS. Gray Snapper were commonly observed on video in Florida but decreased northward to North Carolina, becoming extremely rare north of Cape Lookout, North Carolina. Gray Snapper were most commonly observed in warmer compared to colder water at depths less than 50 m, and they were more likely to be observed in high-relief hardbottom habitats than in low-relief habitats with less hardbottom. Temporal variability in the abundance and distribution of Gray Snapper from 2011 to 2017 was relatively minor, while precision was relatively high. Our work expands the collective knowledge about the ecology of Gray Snapper during their important coastal-ocean adult life stage.

While the spatial distribution of Gray Snapper ichthyoplankton and juveniles in the SEUS has been described in detail, the distribution of adults has been elusive. Eggs and larvae are exported northward from Florida spawning grounds via the Gulf Stream, and they have been collected as far north as the Outer Banks, North Carolina (Hettler and Barker 1993). Juveniles commonly inhabit inshore mangrove forests and seagrass beds in the southeastern United States (Rutherford et al. 1989a; Chester and Thayer 1990; Serafy et al. 1997; Flaherty et al. 2014), but they have been collected in estuaries as far north as Massachusetts (Sumner et al. 1911). In contrast, the distribution of adult Gray Snapper in the SEUS is poorly known. While some adult Gray Snapper have been found inshore prior to making seasonal offshore spawning migrations

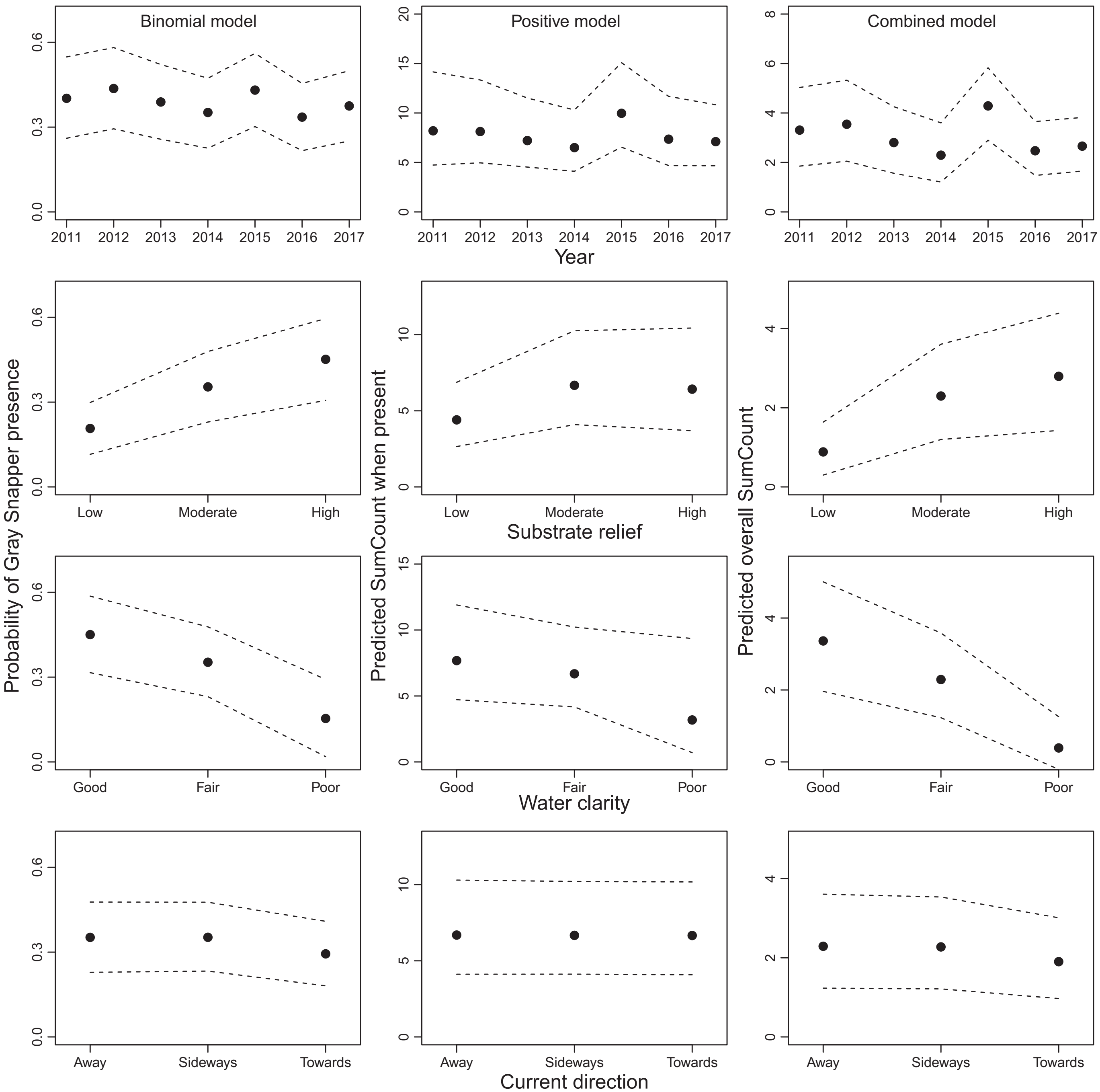


FIGURE 5. Predicted video counts of Gray Snapper related to four categorical variables (year, substrate relief, water clarity, and current direction) using a delta-generalized additive model that was built on baited video data that were collected by the Southeast Reef Fish Survey during 2011–2017. The binomial model results are shown in the left column, the positive model results are shown in the middle column, and their combinations (overall effects) are shown in the right column (note the different *y*-axis scales). The filled points are the predictions for Gray Snapper at the average values of all of the other covariates, and the dashed lines represent 95% confidence intervals.

(Nagelkerken et al. 2000; Serafy et al. 2003; Sheridan and Hays 2003), most are thought to inhabit offshore subtropical or temperate reef habitats year-round from the Florida Keys (Schmidt et al. 1999; Bohnsack et al. 1999) northward to North Carolina (Bacheler et al. 2016a). Chester et al. (1984) stated that the northernmost regular fishery catches of Gray Snapper occurred in northern Florida and increased southward. Similarly, we found high abundance of adult Gray Snapper in Florida northward to approximately St. Augustine (~30°N), beyond which abundance

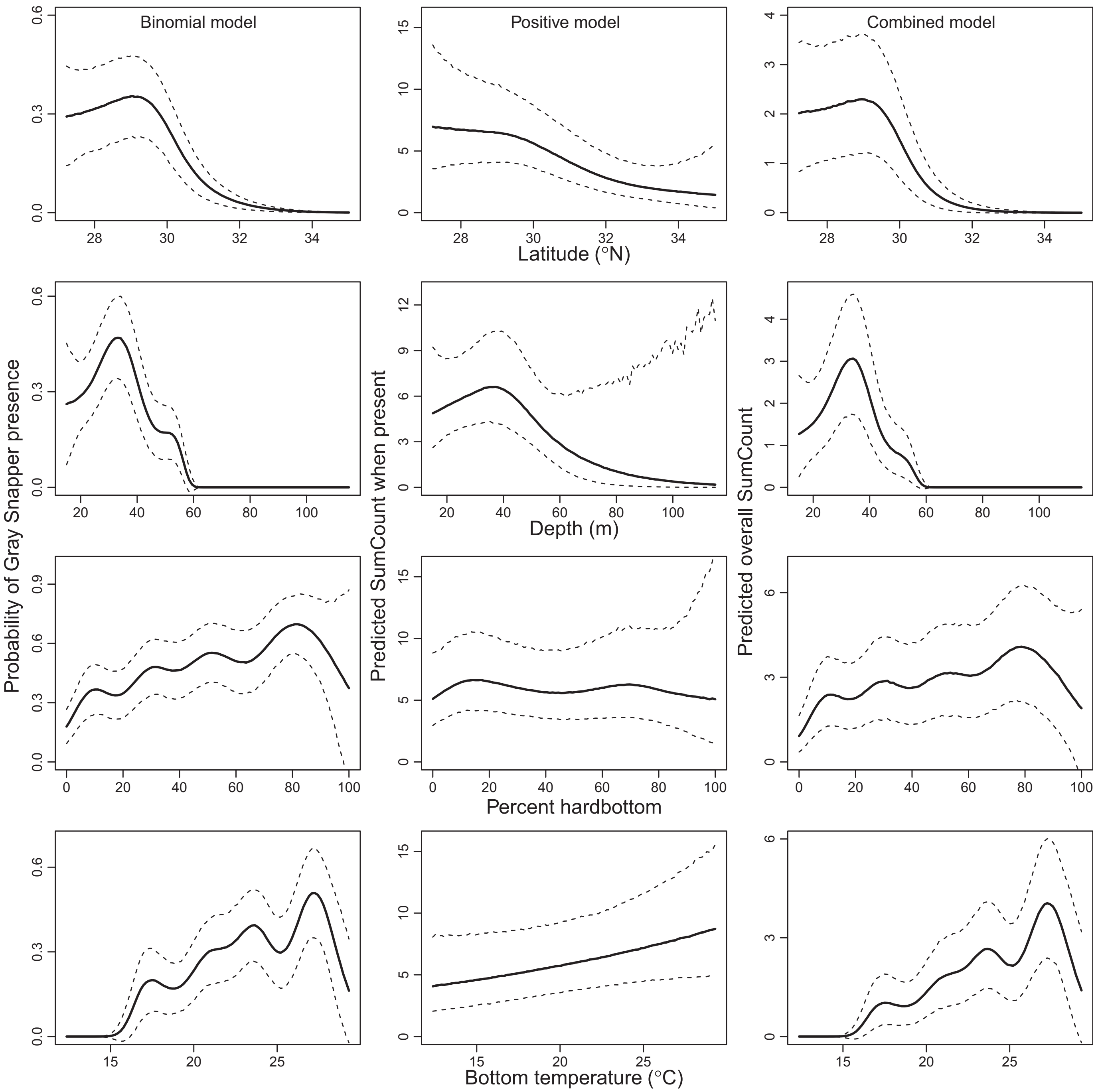


FIGURE 6. Predicted video counts of Gray Snapper related to four smoothed variables (latitude, depth, percent hardbottom, and bottom temperature) using a delta-generalized additive model that was built on baited video data collected by the Southeast Reef Fish Survey during 2011–2017. The binomial model results are shown in the left column, the positive model results are shown in the middle column, and their combination (overall effects) are shown in the right column (note the different *y*-axis scales). The solid black lines are the predictions for Gray Snapper at the average values of all of the other covariates, and the dashed lines represent 95% confidence intervals.

declined precipitously. Overall, video-based abundance of Gray Snapper in South and North Carolina was only slightly above zero. It is not known why the abundance of adult Gray Snapper north of 30°N latitude is so much lower than further south, but prey abundance, predator distributions, or proximity to optimal spawning habitats are potential mechanisms that could be explored.

Juvenile and adult Gray Snapper in nearshore or estuarine environments tend to exhibit diel movement patterns of habitat use, occupying complex habitats like mangroves

TABLE 3. Locations and timing of Gray Snapper aggregations observed on videos collected by the Southeast Reef Fish Survey along the Atlantic coast of the southeastern United States during 2011–2017. Gray Snapper aggregations were defined as locations where at least 20 individuals were observed on a single video frame. The values for *N* represent the maximum frame count of Gray Snapper on that particular video.

| Date | *N* | Latitude (°N) | Depth (m) | Substrate (%) | Substrate relief | Moon phase (%) |
|---|---|---|---|---|---|---|
| 5/28/2012 | 55 | 28.1 | 29 | 2 | Low | 47 |
| 9/23/2013 | 30 | 30.4 | 38 | 5 | Low | 83 |
| 5/05/2014 | 28 | 29.5 | 44 | 10 | Moderate | 35 |
| 4/27/2015 | 23 | 29.0 | 24 | 10 | Low | 64 |
| 5/26/2015 | 31 | 31.5 | 49 | 13 | Moderate | 57 |
| 5/28/2015 | 26 | 30.0 | 54 | 78 | Moderate | 75 |
| 5/29/2015 | 21 | 29.2 | 24 | 8 | Low | 83 |
| 6/11/2015 | 25 | 29.2 | 32 | 20 | Moderate | 30 |
| 5/08/2016 | 40 | 29.1 | 31 | 40 | Low | 4 |
| 9/11/2016 | 21 | 28.2 | 24 | 50 | Moderate | 69 |
| 9/24/2016 | 23 | 29.2 | 30 | 19 | Moderate | 38 |
| 4/26/2017 | 29 | 29.7 | 34 | 53 | Moderate | 1 |
| 5/05/2017 | 21 | 28.8 | 21 | 28 | Moderate | 74 |
| 6/23/2017 | 32 | 30.5 | 36 | 0 | Low | 1 |
| 8/04/2017 | 31 | 29.5 | 38 | 10 | Low | 90 |

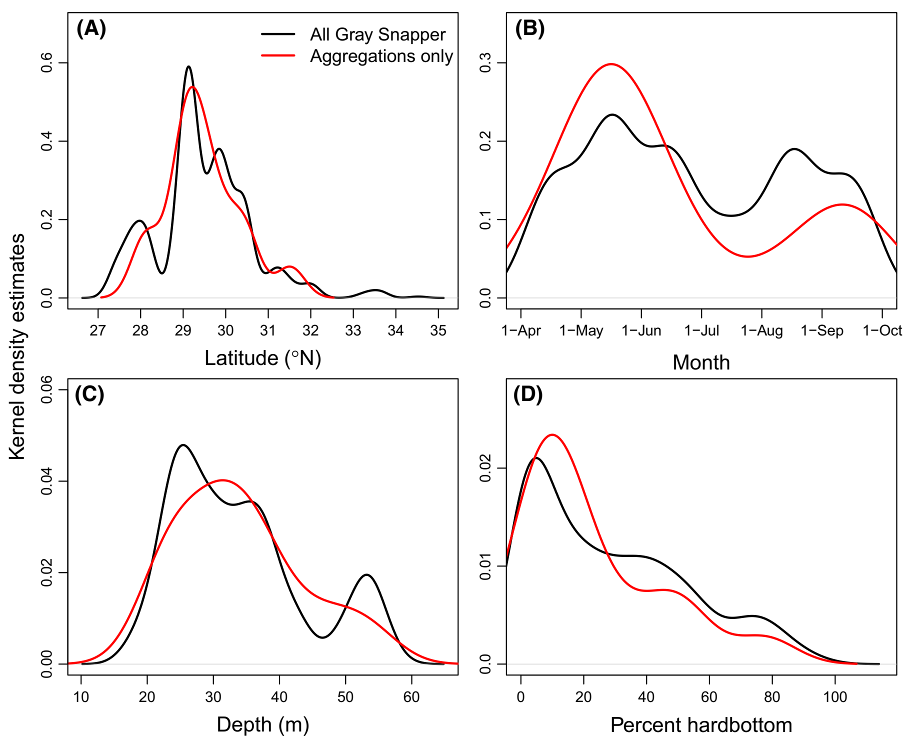


FIGURE 7. Kernel density estimates of sites where Gray Snapper were present on baited video (black lines) and sites where aggregations of Gray Snapper (>20 individuals observed on a single frame) were seen on video (red lines) from samples that were collected by the Southeast Reef Fish Survey, 2011–2017. Kernel density estimates are shown for four predictor variables: **(A)** latitude (°N), **(B)** month, **(C)** depth (m), and **(D)** percent hardbottom.

during the day and moving into seagrass habitats to feed at night (Luo et al. 2009; Flaherty et al. 2014). Various sources have stated that adult Gray Snapper generally associate with coral reef habitats (Springer and Woodburn 1960; Moe 1963; Starck and Schroeder 1971; Domeier et al. 1996), but few specifics are available. Farmer and Ault

(2011) tracked one adult Gray Snapper near the Dry Tortugas, Florida, that associated with coral reef habitats during the day but made routine nocturnal migrations out of the study area. We found that adult Gray Snapper did not use all of the reef habitats equally during the day, being more common in high-relief sites with a high proportion of hardbottom than in lower-relief, patchy habitats across the SEUS. Adult Gray Snapper in this study inhabited deeper depths (mean = 35 m) than have been reported in most previous studies. For instance, Domeier et al. (1996) documented adult Gray Snapper at inshore (5–6 m deep) and offshore (9–15 m deep) reef sites near Key West, Florida.

Spawning aggregation sites for Gray Snapper are mostly unknown outside of Cuba, so the discovery of spawning aggregation sites in the United States would be important for the management and conservation of this species. In Cuba, spawning aggregation sites were found at depths of 20–30 m and spawning activity occurred at night on the full moon in the summer months (Claro and Lindeman 2003). Denit and Sponaugle (2004) back-calculated birthdates for juvenile Gray Snapper by using otoliths in the SEUS and found that spawning was more likely on new or first-quarter moons. It is unclear whether the aggregations of Gray Snapper that were observed in the present study were indicative of spawning aggregations, but these aggregations were generally deeper than the spawning aggregations described by Claro and Lindeman (2003), and were observed across all moon phases. Furthermore, the aggregations of Gray Snapper observed on video in the present study occurred in the same general locations and at the same times as Gray Snapper observed at lower abundance, which is unexpected for a species that presumably migrates to specific spawning aggregation sites (Domeier and Colin 1997). That said, the unique coloration patterns and nipping and nudging behaviors of Gray Snapper, often observed far up in the water column, are indicative of spawning activity. More work is clearly needed to verify whether any of the aggregations that were observed were actual functional spawning aggregations.

Temporal trends of adult Gray Snapper abundance in the SEUS are mostly unknown. The only stock assessments of Gray Snapper in the SEUS indicated that the spawning stock ratio was far below sustainable levels in 1988 (NMFS 1990, 1991) but improved when data through 1991 were included (Huntsman et al. 1992, 1993). In the Florida Keys, Gray Snapper declined substantially between 1979 and 1988, based on an annual survey using an underwater visual census approach, but modest increases subsequently occurred through 1998 (Bohnsack et al. 1999). In the Gulf of Mexico, total Gray Snapper biomass declined by approximately 75% between 1950 and 1980 and has stayed relatively low and constant since that time (SEDAR 2018). Our results suggest that the abundance of Gray Snapper in the coastal ocean has been constant or perhaps slightly declined in recent years, but whether a preceding broad-scale decline occurred during the last half of the twentieth century, similar to the Gulf of Mexico, will remain elusive until a new formal stock assessment is conducted.

There were some shortcomings of our study. First, a delta-GAM approach with two submodels that were manually combined to determine the overall effects of each predictor variable on the abundance of Gray Snapper were used to account for zero inflation in the dataset. The downside was that developing these models in the mgcv library required the same predictor variables to be included in each submodel, which resulted in one or more predictor variables being included in submodels that would have been excluded based on AIC alone. Second, our regression models were naturally correlative, so ascribing causation is tenuous. Third, some Gray Snapper were likely missed in our study because no gear samples reef fish perfectly (Bacheler et al. 2017). Fourth, lasers or stereo-video systems were not used in this study, so the sizes of the Gray Snapper that were observed were unknown, but based on previous studies these individuals were presumed to be adults (Burton 2001; Flaherty-Walia et al. 2016; Andrade and Santos 2019). Last, our study was conducted exclusively during daylight hours, so the behavior and habitat use of Gray Snapper offshore during nighttime hours remains unclear.

While previous research on Gray Snapper has primarily focused on life stages that occur in accessible nearshore environments like seagrass beds and mangroves, this research provided a broad examination of adult Gray Snapper ecology in offshore oceanic environments over a large spatial area. Video was used to determine the influence of space, time, habitat, and the environment on the relative abundance of adult Gray Snapper while also providing some information on the locations and timing of Gray Snapper aggregations. The long-term population trend of adult Gray Snapper in the SEUS remains mostly unknown, but given the broad-scale declines of Gray Snapper that have been observed in the Gulf of Mexico (SEDAR 2018), this should be a research focus. The identification and protection of spawning aggregation sites of Gray Snapper in the SEUS would also be important because fish are often highly vulnerable to fishing while they are aggregating (Domeier and Colin 1997). This work provides greater insight into the ecology of Gray Snapper during their important coastal-ocean adult life stage, which will improve their management and conservation.

## ACKNOWLEDGMENTS

We thank Southeast Fishery–Independent Survey, Marine Resources Monitoring, Assessment, and Prediction program, and Southeast Area Monitoring and Assessment Program–South Atlantic Region staff members and numerous volunteers for their field assistance and video reading, and we are also grateful to the captains and crews of the RV *Palmetto*, RV *Savannah*, SRVx [small research vessel] *Sand Tiger*, and National Oceanic and Atmospheric Administration (NOAA) Ship *Pisces* for providing the platforms for sampling. We also thank A. Chester, A. Hohn, T. Kellison, and three anonymous reviewers for providing comments on earlier versions of this manuscript and the U.S. National Marine Fisheries Service for funding. The use of trade, product, industry, or firm names or products, software, or models, whether commercially available or not, is for informative purposes only and does not constitute an endorsement by the U.S. Government or NOAA. The views and opinions expressed or implied in this article are those of the authors and do not necessarily reflect the position of the U.S. National Marine Fisheries Service, NOAA. There is no conflict of interest declared in this article.

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