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ORIGINAL PAPER

Patterns in fish biodiversity associated with temperate reefs on the southeastern US continental shelf

Nathan M. Bacheler[1] · Zebulon H. Schobernd[1] · Kevan C. Gregalis[1] · Christina M. Schobernd[1] · Bradford Z. Teer[1] · Zachary Gillum[1] · Dawn M. Glasgow[2] · Neil McNeill[1] · Michael Burton[1] · Roldan Muñoz[1]

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Abstract

Temperate reef fishes provide many benefits to humans including food, sport, and ecotourism, yet remain severely understudied compared to coral reef fishes in tropical environments. We used 3 years of underwater video data ($n = 4130$ samples) from hardbottom reefs along the continental shelf of the southeastern US Atlantic coast (i.e., North Carolina to Florida; ~ 100,000 km^2) to quantify the spatial and temporal patterns of temperate reef fish biodiversity in the region. Overall, 210 taxa were identified on video from 53 families, 138 of which could be identified to the species level. Species with the highest percent occurrence were gray triggerfish (*Balistes capriscus*; observed on 45.6% of all videos), tomtate (*Haemulon aurolineatum*; 42.7%), and red porgy (*Pagrus pagrus*; 39.4%), and 23 species were observed on more than 10% of videos. Latitudinal variability swamped temporal changes (2015–2017) for most taxa. After accounting for the influence of water clarity and current direction on video detectability, generalized additive models suggested that species and family richness were highest at sites characterized by moderate depths, a high proportion of hardbottom, high substrate relief, and warm water. Our results can be used to predict areas of highest reef fish biodiversity at large (regional) and small (microhabitat) scales to improve marine protected area design, delineate essential fish habitats, and parameterize ecosystem models.

Keywords Diversity · Richness · Fisheries · Video · BRUVS · Conservation · Management · Generalized additive model · Snapper-grouper

Introduction

Reef-associated fish species provide many benefits to humans throughout tropical, subtropical, and temperate waters of the world including food, sport, and ecotourism (Coleman et al. 1999; Moberg and Folke 1999). Reef fish communities are diverse and often comprise marine biodiversity hotspots (Hughes et al. 2002; Bellwood et al. 2004), but they face a variety of threats including overharvest (Epperly and Dodrill 1995; Parker and Dixon 1998), ocean acidification (Hoegh-Guldberg et al. 2007), habitat loss (Paddack et al. 2009), nutrient loading (Carpenter et al. 1998), introduced species (Whitfield et al. 2014; Ballew et al. 2016), and climate change (Hughes et al. 2003). Moreover, life-history traits exhibited by many reef fishes make them particularly vulnerable to harvest or environmental variability including slow growth, long life spans, delayed maturity, large body size, and patchy distributions (Musick 1999; Coleman et al. 2000; Wyanski et al. 2000). In addition, many economically important reef fishes are hermaphroditic and change sex, so size-selective harvest can skew sex ratios (Coleman et al. 1996, 1999).

Temperate reef fishes along the southeastern US Atlantic coast (hereafter, "SEUS") are diverse and economically important, yet relatively little is known about their broad patterns of distribution and species richness (i.e., total number of species) in the region. The few broad-scale studies examining reef fish abundance and species richness in the SEUS have tended to focus on temporal changes. For instance, Shertzer et al. (2009)

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✉ Nathan M. Bacheler
nate.bacheler@noaa.gov

[1] Southeast Fisheries Science Center, National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, NC 28516, USA

[2] South Carolina Department of Natural Resources, Marine Resources Research Institute, 217 Fort Johnson Road, Charleston, SC 29412, USA

used recreational and commercial landings data to document gradual changes in reef fish communities over time, with more abrupt changes occurring in the 1990s. Stratton (2011) examined trap data collected over a broad spatial scale in the SEUS and noted declines in reef fish abundance since the early 1990s. Bacheler and Smart (2016) also used fishery-independent trap survey data to show that, while the temporal trends of species targeted by fishermen in the SEUS have been mixed, declines of non-targeted fish species were much more dramatic than targeted species. Using 4 years of underwater video data, Bacheler et al. (2016a) was one of the few studies that examined broad spatial trends in reef fish richness in the SEUS, finding that the highest richness occurred in outer continental shelf habitats between southern North Carolina and northern Georgia. The primary shortcoming of Bacheler et al. (2016a) was that videos were only read for some select economically important fish species, so inferences could not be made about the entire reef fish community (Klibansky et al. 2017).

Video has become one of the most commonly used methods to quantify fish biodiversity (Mallet and Pelletier 2014). It is especially useful when water depth exceeds safe limits for diving because it tends to be less selective than other sampling gears, it can be used in shallow or deep water, it provides a permanent record that can be viewed many times, and it can provide behavioral and habitat information (Willis et al. 2000; Cappo et al. 2007; Langlois et al. 2010; Mallet and Pelletier 2014; Bacheler et al. 2016a; Wellington et al. 2018). However, video sampling can be influenced by water current direction (because fish tend to aggregate down-current of bait; Bacheler et al. 2014), water clarity, and the use of bait, so accounting for those variables is critical.

Here, we use a spatially extensive video dataset that includes a broad array of species to make inferences about patterns in reef fish richness in the SEUS. We had three specific objectives. Our first objective was to

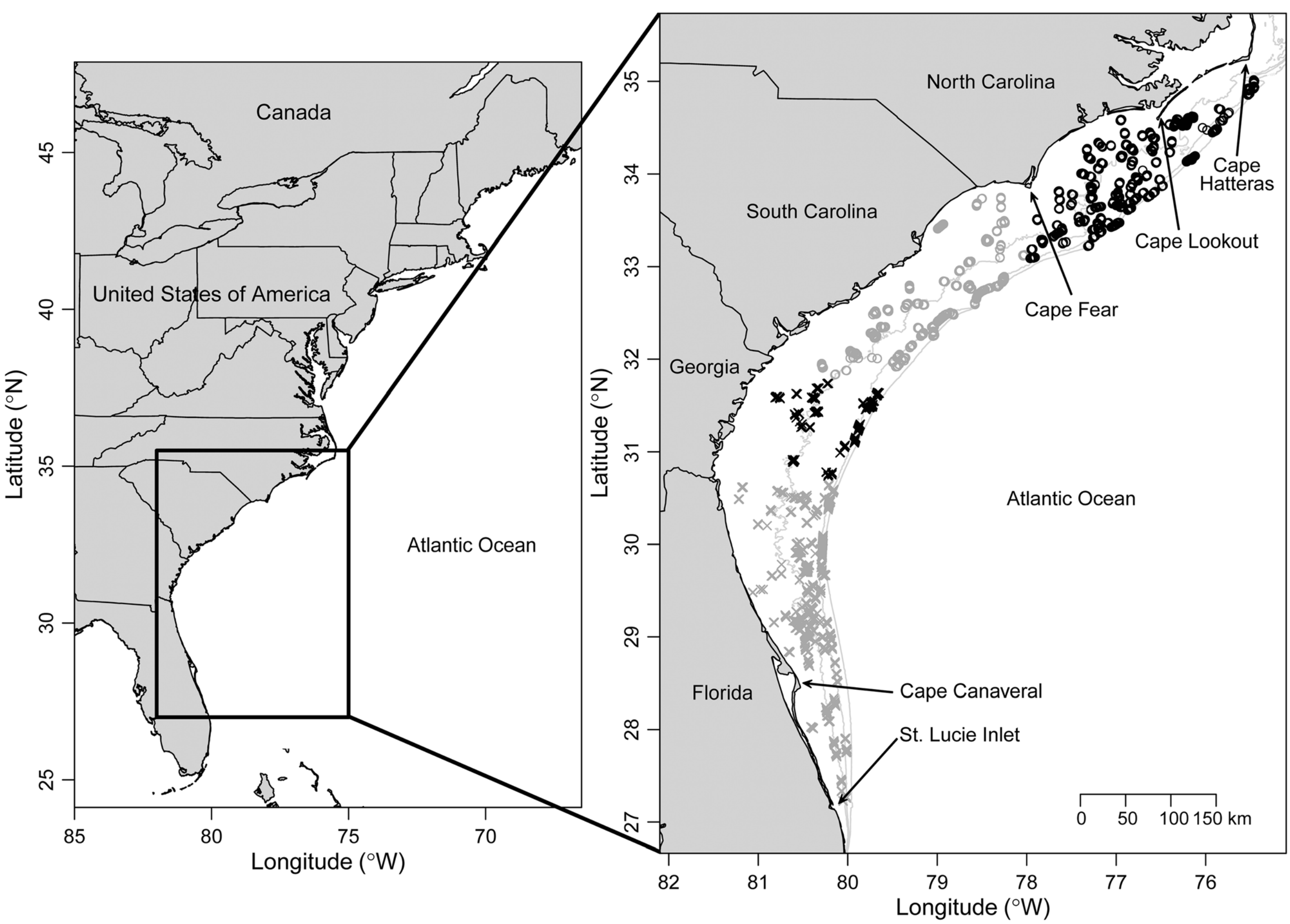

Fig. 1 Study area where underwater videos were collected on the continental shelf of the southeastern US Atlantic coast by the Southeast Reef Fish Survey in 2015–2017 (left panel). In the right panel, samples are differentiated by the state in which they were collected and analyzed: North Carolina (black open circles), South Carolina (gray open circles), Georgia (black ×), and Florida (gray ×). Light gray isobaths in the right panel indicate 30, 50, and 100 m deep, and symbols often overlap

Fig. 2 Still image from an underwater video collected by the Southeast Reef Fish Survey in North Carolina in 2015

determine which fish species and families were most and least often observed on video in the SEUS. Our second objective was to develop a species accumulation curve relating the number of species observed on video to sampling effort. Our last objective was to elucidate the broad patterns in fish biodiversity in the SEUS and how richness varied across space, time, environmental conditions, and habitat types. These results can be used to (1) predict fish biodiversity hotspots in the SEUS, (2) improve ecosystem management by quantifying the spatial distribution of reef fish species in the SEUS, and (3) unravel the environmental and habitat drivers of reef fish richness in the SEUS.

Material and methods

Study area

Sampling for this study took place on the continental shelf and shelf break (15–115 m deep) along the SEUS, a broad area (> 100,000 km^2) extending from Cape Hatteras, NC, to St. Lucie Inlet, FL (Fig. 1). Most of the SEUS consists of unconsolidated sand or mud substrate, but our sampling targeted naturally occurring hardbottom reefs that are scattered throughout the region (Parker et al. 1983; Fautin et al. 2010). These hardbottom habitats range from flat pavement habitats to high-relief rocky ledges and are often covered in attached

Table 1 Yearly sampling by state from the Southeast Reef Fish Survey (2015–2017) using chevron traps outfitted with video cameras along the southeastern United States Atlantic coast. Only stations included in the analyses are shown

State	Number	Mean date sampled (range)	Mean depth (range; m)	Mean bottom temperature (range; °C)
2015	1394	7/4 (4/21–10/22)	38.4 (16–110)	22.6 (13.6–28.5)
North Carolina	515	7/24 (5/14–9/17)	39.4 (18–100)	23.4 (20.0–27.0)
South Carolina	284	6/25 (4/21–10/22)	37.0 (16–77)	22.4 (19.0–28.0)
Georgia	126	7/13 (4/21–9/4)	42.9 (18–74)	22.7 (16.0–28.5)
Florida	469	6/14 (4/22–9/4)	36.9 (17–66)	21.9 (13.6–25.9)
2016	1395	8/2 (5/4–10/26)	40.7 (17–115)	23.9 (15.5–29.3)
North Carolina	547	7/28 (7/4–9/28)	43.0 (17–115)	23.8 (17.0–27.0)
South Carolina	336	8/8 (5/25–10/24)	38.1 (17–93)	24.2 (18.4–27.9)
Georgia	119	7/21 (6/5–10/26)	45.5 (18–75)	24.9 (21.4–29.3)
Florida	393	8/8 (5/4–9/28)	38.2 (18–85)	23.3 (15.5–28.6)
2017	1341	7/2 (4/26–9/29)	38.9 (15–100)	22.6 (14.8–28.2)
North Carolina	513	7/7 (6/1–7/31)	38.3 (15–100)	23.1 (17.2–28.1)
South Carolina	238	7/12 (5/30–9/29)	39.6 (16–93)	23.5 (17.3–27.5)
Georgia	122	7/6 (6/20–8/30)	45.9 (20–75)	22.3 (17.7–27.4)
Florida	468	6/21 (4/26–8/30)	37.3 (17–83)	21.8 (14.8–28.2)
Overall	4130	7/8 (4/21–10/26)	39.3 (15–115)	23.1 (13.6–29.3)

Table 2 Highest percent occurrence of species observed on videos collected by the Southeast Reef Fish Survey (2015–2017) along the southeastern US Atlantic coast

Rank	Species	Scientific name	2015	2016	2017	Overall
1	Gray triggerfish	*Balistes capriscus*	42.2	47.5	47.4	45.6
2	Tomtate	*Haemulon aurolineatum*	42.8	41.8	43.5	42.7
3	Red porgy	*Pagrus pagrus*	41.0	39.9	37.3	39.4
4	Almaco jack	*Seriola rivoliana*	35.4	38.7	35.7	36.6
5	Sand perch	*Diplectrum formosum*	34.7	36.1	36.7	35.8
6	Vermilion snapper	*Rhomboplites aurorubens*	33.6	36.0	35.2	34.9
7	Black sea bass	*Centropristis striata*	38.3	29.0	29.2	32.2
8	Red snapper	*Lutjanus campechanus*	28.7	24.7	34.3	29.2
9	Greater amberjack	*Seriola dumerili*	29.9	31.8	24.8	28.9
10	Blue angelfish	*Holacanthus bermudensis*	27.5	26.5	25.4	26.5
11	Bandtail puffer	*Sphoeroides spengleri*	22.3	27.4	26.8	25.5
12	Tattler	*Serranus phoebe*	20.2	21.5	16.9	19.6
13	Reef butterflyfish	*Chaetodon sedentarius*	18.6	21.1	17.2	19.0
14	Red lionfish/devil firefish	*Pterois volitans/miles*	20.0	18.3	18.0	18.8
15	White grunt	*Haemulon plumierii*	17.8	16.8	17.2	17.3
16	Scup/Longspine porgy	*Stenotomus* spp.	16.4	14.6	13.1	14.7
17	Bank sea bass	*Centropristis ocyurus*	16.3	12.3	15.1	14.6
18	Spotfin hogfish	*Bodianus pulchellus*	14.7	14.1	12.4	13.7
19	Scamp	*Mycteroperca phenax*	13.8	15.3	11.9	13.7
20	Spotfin butterflyfish	*Chaetodon ocellatus*	11.0	11.7	12.9	11.8
21	Sharpnose puffer	*Canthigaster rostrata*	14.3	9.1	11.0	11.5
22	Blue runner	*Caranx crysos*	6.8	13.9	11.9	10.8
23	Spottail pinfish	*Diplodus holbrookii*	12.6	8.8	9.3	10.3
24	Gray snapper	*Lutjanus griseus*	9.5	7.1	9.2	8.6
25	Gag	*Mycteroperca microlepis*	8.8	6.8	8.2	7.9

biota such as sponges, algae, and soft corals (Kendall et al. 2008; Schobernd and Sedberry 2009). A diverse and economically important reef fish assemblage associates with these hardbottom reefs in the SEUS (Fig. 2; Bacheler et al. 2016a; Bacheler and Smart 2016).

Sampling design

We analyzed fishery-independent video data collected by the Southeast Reef Fish Survey (SERFS). The SERFS program consists of three groups funded by the National Marine Fisheries Service that work collaboratively to sample reef fish in the SEUS using identical methodologies. The first two groups are the Marine Resources Monitoring, Assessment, and Prediction program and the Southeast Area Monitoring and Assessment program (South Atlantic Region Reef Fish Complement), both housed at the South Carolina Department of Natural Resources. The last group is the Southeast Fishery-Independent Survey that was created by, and is housed within, the National Marine Fisheries Service. The SERFS program used a simple random sampling design to sample hardbottom stations in the SEUS in 2015–2017. From a sampling frame of approximately 4000 known hardbottom points, approximately 1500 were randomly chosen for sampling each year.

While most (86%) stations sampled in our study were randomly selected, some stations in the sampling frame were sampled despite not being randomly selected in a given year in order to increase sampling efficiency during research cruises. These non-randomly selected stations made up 9% of all stations sampled and were spread out spatially. Moreover, some (5%) new hardbottom locations were found using the vessel echosounder during the study and were included in our analyses if hardbottom was present. All sampling occurred on the R/V *Savannah*, R/V *Palmetto*, SRVx *Sand Tiger*, and NOAA Ship *Pisces* during daylight hours using identical sampling methodologies as described below. Traps were typically deployed independently, with no traps being closer than 200 m from another trap to minimize spatial autocorrelation (Bacheler et al. 2018). Sampling occurred from spring through fall each year.

Table 3 Highest percent occurrence for fish families observed on videos collected by the Southeast Reef Fish Survey (2015–2017) along the southeastern US Atlantic coast

Rank	Family	Common name	2015	2016	2017	Overall
1	Serranidae	Sea basses and groupers	78.4	78.3	76.9	77.9
2	Sparidae	Porgies	77.7	79.4	74.0	77.1
3	Carangidae	Jacks	63.3	71.3	66.8	67.1
4	Labridae	Wrasses	58.9	57.8	54.3	57.0
5	Lutjanidae	Snappers	53.6	51.0	55.8	53.4
6	Balistidae	Triggerfishes	44.5	51.0	50.2	48.5
7	Haemulidae	Grunts	48.3	47.8	49.1	48.4
8	Tetraodontidae	Puffers	35.6	36.4	36.0	36.0
9	Pomacanthidae	Angelfishes	35.9	31.1	31.7	32.9
10	Chaetodontidae	Butterflyfishes	26.0	27.3	26.8	26.7

Video sampling

SERFS attaches video cameras to chevron fish traps to provide two sources of fishery-independent information for reef fishes in the region. We only examined video data in this study, since trap data have been described previously (Bacheler and Smart 2016). Chevron traps were shaped like an arrowhead, had an approximate volume of 0.91 m^3 (Collins 1990), were baited with 24 menhaden (*Brevoortia* spp.), and soaked for approximately 90 min at each station sampled in this study. High-definition GoPro® Hero 3+ or 4 cameras were attached over the mouth and nose of the chevron traps, looking outward, but to be consistent only cameras attached over the trap mouth were read for fish. Both cameras were used to score habitat, water current, and water clarity. In this study, we analyzed video data from 2015 to 2017 due to consistency during that period of camera type and video reading protocols used by the three component surveys. Video samples were excluded from our analyses if they were out of focus or too dark, the video files were corrupted, or the traps moved or bounced significantly after deployment. We recorded taxa-specific presence or absence on each video within a 20-min interval of time from 10 to 30 min after the trap landed on the bottom.

All videos were read by video readers that were able to identify taxa to the species level accurately and consistently. Individuals that could not be identified to the species level were identified to the lowest classification possible. In cases where some species within a family or genus were identifiable while others in that same family or genus were not, we often maintained taxonomic integrity by identifying all taxa in that grouping in a consistent way (i.e., all to the family or genus level). All taxa were identified to at least the family level except for those taxa in the order Pleuronectiformes (flatfishes), which could not be reliably identified to the family level using video alone and were therefore excluded from our analyses. In addition, *Stenotomus* spp. was treated as a single species here because they are difficult to visually distinguish (Powles and Barans 1980; Sedberry and Van Dolah 1984); the devil firefish (*Pterois miles*) and red lionfish (*Pterois volitans*) were also combined into a single species (lionfish, *Pterois volitans*/*miles*) for the same reason (Hamner et al. 2007). Since Serranidae is an ecologically diverse and speciose family in the SEUS, we examined them as a family but also split them into subfamily Epinephelinae (groupers) and non-Epinephelinae (sea basses) groupings when it was informative to do so. In our study, we use the term "species" for fish identified to the species level (but also including *Stenotomus* spp. and lionfish), and we use the term "taxa" for the combination of fish identified to their lowest possible taxonomic classification (i.e., species, genus, or family).

Depth was determined from the vessel echosounder, and latitude and longitude were determined via a global positioning system. Bottom water temperature (°C) for each group of traps was measured using a "conductivity-temperature-depth" cast. Following Bacheler et al. (2014), two habitat characteristics were visually estimated from each of the two video cameras attached to traps and included in our analyses. The percent of the visible substrate that was hardbottom (hereafter referred to as "substrate") was estimated for each video camera (situated ~0.5 m above the substrate), and a mean value was calculated for each station because it was a continuous variable. Substrate relief was the maximum relief visually estimated from either camera, categorized as low (< 0.3 m), moderate (0.3–1.0 m), or high (> 1.0 m). Current

Table 4 Examples of five spatial distribution trajectories for taxa observed on videos collected by the Southeast Reef Fish Survey in 2015–2017 along the southeastern US Atlantic coast. The five trajectories were (1) decreasing percent occurrence from NC to FL (NC ↘ FL), (2) increasing percent occurrence from NC to FL (NC ↗ FL), (3) lower percent occurrence in NC and FL and higher percent occurrence in SC and GA (NC ∩ FL), (4) higher percent occurrence in NC and FL and lower percent occurrence in SC and GA (NC ∪ FL), and (5) similar percent occurrence across all states (NC – FL)

Taxa	Common name	NC	SC	GA	FL	Overall
NC ↘ FL						
Centropristis striata	Black sea bass	40.0	36.6	24.5	22.3	32.2
Sphoeroides spengleri	Bandtail puffer	36.0	36.2	21.8	7.1	25.5
Haemulon plumierii	White grunt	31.9	18.8	6.8	1.9	17.3
Mycteroperca phenax	Scamp	17.4	19.3	14.7	5.4	13.7
Mycteroperca microlepis	Gag	10.0	8.3	5.7	5.8	7.9
Lachnolaimus maximus	Hogfish	12.3	10.5	3.5	1.7	7.7
Malacanthus plumieri	Sand tilefish	8.4	6.3	2.7	2.1	5.4
NC ↗ FL						
Rhomboplites aurorubens	Vermilion snapper	21.8	36.8	42.2	47.2	34.9
Lutjanus campechanus	Red snapper	14.7	16.0	34.9	53.2	29.2
Lutjanus griseus	Gray snapper	0.7	2.6	4.6	23.0	8.6
Archosargus probatocephalus	Sheepshead	2.0	2.6	1.9	18.1	7.3
Lutjanus analis	Mutton snapper	0.4	1.0	9.0	13.0	5.4
Lutjanus synagris	Lane snapper	0.0	0.0	0.0	12.0	3.8
NC ∩ FL						
Pagrus pagrus	Red porgy	35.4	55.9	46.6	31.6	39.4
Holacanthus bermudensis	Blue angelfish	21.9	33.0	30.8	26.6	26.5
Pterois volitans/miles	Lionfish	15.7	22.6	27.5	17.5	18.8
Sphyraena barracuda	Great barracuda	2.8	7.3	7.6	5.6	5.1
Pristigenys alta	Short bigeye	2.8	3.7	7.6	1.1	2.9
NC ∪ FL						
Epinephelus morio	Red grouper	2.5	0.1	0.0	1.2	1.4
NC − FL						
Haemulon aurolineatum	Tomtate	37.5	49.4	35.7	46.3	42.7
Serranus phoebe	Tattler	18.4	23.4	15.3	19.6	19.6

direction was estimated as "away," "sideways," or "towards" relative to the camera over the trap mouth, based on visible particles in the water and the direction of swaying in attached biota. Last, water clarity was classified as "low" if substrate could not been seen, "moderate" if substrate could be seen but not the horizon, and "high" if the horizon was visible in the distance. Video samples were excluded from our analyses if any of these variables were missing.

Analytical approach

Our first broad objective was to determine which fish species and families were most and least commonly observed on video in the SEUS. To accomplish this goal, we calculated the percent occurrence (i.e., the percent of video samples in which a taxon was present) for each species and family in the following ways: (1) overall percent occurrence across the entire study area and all years, (2) state-specific percent occurrences across all years, and (3) annual percent occurrences across all states. The top 25 species and top 10 families in terms of percent occurrence were then highlighted.

Our second objective was to construct a species accumulation curve to understand the relationship between the number of fish taxa observed and video sampling effort (Ugland et al. 2003). We used 200 permutations with the 3 years of video data to build the species accumulation curve, which included an overall mean and a 95% confidence interval. Our species accumulation model was developed and run using the vegan package (version 2.4-3) in R version 3.4.3 (R Core Team 2017) within R Studio version 1.1.383. Another benefit of the species accumulation curve was it could be used to assess whether all possible taxa have been observed in our study (if the curve had plateaued) or not (if the right limb of the curve continued to increase).

Our third objective was to quantify patterns in fish species and family richness over space, time, environmental conditions, and habitat. To do this, we modeled the total number of species (for only those taxa identified to the species level) or the total number of families observed on video as response variables in a GAM. A major strength of GAMs was that we could examine how patterns in fish species or family richness varied across space, environmental conditions, and habitat types after standardizing for variables that might influence fish detection on video (e.g., current direction, water clarity; Bacheler et al. 2014). Here, we developed GAMs that related the number of species or families as the response variable to a variety of predictor variables. These full (hereafter, "base") GAMs were modeled as:

$$y = s_1(d) + s_2(temp) + s_3(doy) + s_4(sub) + s_5(pos) + f_1(year) + f_2(cur) + f_3(rel) + f_4(wc)$$

where y is the number of species or families observed on video, d is depth, *temp* is bottom water temperature (°C), *doy* is day of the year, *sub* is substrate, *pos* is the position (i.e., two-dimensional combination of latitude and longitude), *year* is year, *cur* is current direction, *rel* is substrate relief, *wc* is water clarity, s_{1-5} are nonparametric smoothing functions, and f_{1-4} are categorical functions. The position variable (*pos*) was included as a random effect to account for any residual spatial autocorrelation in our dataset. All models were developed and run using the mgcv library (Wood 2011) in R version 3.4.3 (R Core Team 2017) within R Studio version 1.1.383. Predictor variables did not exhibit multicollinearity based on variance inflation factors that were less than three for all variables (Neter et al. 1989).

We compared three error distributions within each GAM, and used the "gam.check" function to visually compare model diagnostics for each. The three error distributions we considered were Poisson, negative binomial, and Tweedie distributions. The most appropriate error distributions based on the model diagnostics using the "gam.check" function were the negative binomial for the species model and Poisson for the family model, and these were used in the subsequent model selection process. All final models met the assumptions of normality and constant variance.

We compared each base model to a number of reduced models that contained fewer predictor variables using Akaike's information criterion (AIC; Burnham and Anderson 2002). AIC attempts to achieve parsimony by explaining the most variability in the data (via the model's log-likelihood) with the fewest possible parameters. AIC values for the base and all potential combinations of reduced models were compared, and the model with the lowest AIC value was considered the best model in the set. Because the differences in AIC values among models (and not absolute values) were of particular interest, we subsequently examined ΔAIC values, which were calculated as the difference in AIC values between the best model and the particular model of interest.

Last, we plotted the predicted number of species or families as a function of each of the predictor variables in our best GAMs, at average values of all other predictor variables. This includes the partial effect of position, which was predicted at average values of all other predictor variables in the model. Note that the plots showing partial effects of position are not synonymous with spatial predictions from our models. To create true spatial predictions across the study area, all other predictor variables in the model would need to be known across space, which was not possible for some predictor variables in our model (e.g., water clarity, current direction, bottom water temperature).

Results

Video sampling

A total of 4130 stations were sampled with video in 2015–2017 between Cape Hatteras, NC, and St. Lucie Inlet, FL, and included in our analyses (Table 1, Fig. 1). Sampling was relatively consistent across years in terms of total sampling effort (i.e., 1341–1395 stations sampled per year) and the number of stations sampled in each state (Table 1). Total sampling among states was variable owing to differences in the amount of coastline among states, but the density of sampling coastwide was fairly consistent (Table 1, Fig. 1). Sampling was initiated each year in late April to early May and ended in late

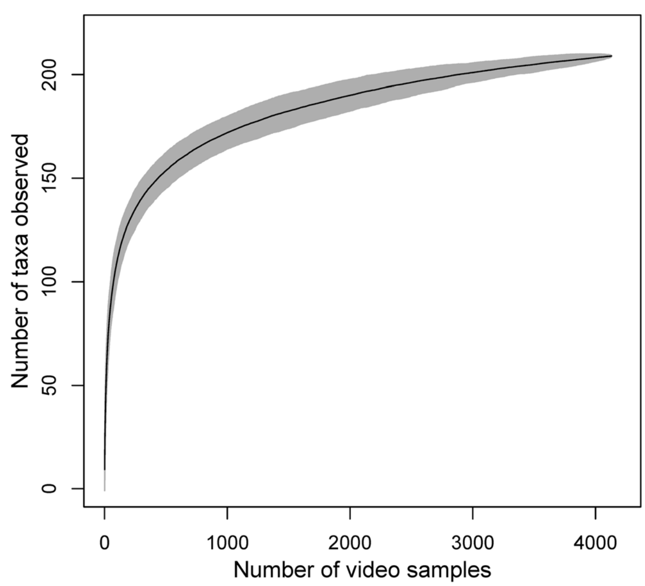

Fig. 3 Mean species accumulation curve (solid line) and 95% confidence interval (gray shading) for fish taxa observed on videos collected by the Southeast Reef Fish Survey in 2015–2017

Table 5 Model selection for generalized additive models describing the influence of predictor variables on the number of fish species or families observed on Southeast Reef Fish Survey videos in 2015–2017. Estimated degrees of freedom are shown for nonparametric, smoothed terms (*s*), and degrees of freedom are shown for factor (*f*) terms. ΔAIC is the AIC value of a particular model relative to the best model in the set, Dev is the deviance explained by each model, and Base is the full model. *d* = depth, *temp* = bottom water temperature, *doy* = day of the year, *sub* = substrate, *pos* = position, *year* = year of the sample, *cur* = current direction, *rel* = substrate relief, and *wc* = water clarity

Model	ΔAIC	Dev	$s_1(d)$	$s_2(temp)$	$s_3(doy)$	$s_4(sub)$	$s_5(pos)$	$f_1(year)$	$f_2(cur)$	$f_3(rel)$	$f_4(wc)$
Number of species											
Base	0.0	48.0	6.8	6.5	6.7	8.5	0.7	2	2	2	2
Base–*pos*	0.6	48.0	6.8	6.6	6.5	8.5	ex	2	2	2	2
Base–*year*	12.1	47.8	6.8	6.6	6.6	8.4	0.7	ex	2	2	2
Base–*year*–*pos*	12.2	47.8	6.8	6.7	6.4	8.4	ex	ex	2	2	2
Number of families											
Base	0.0	46.0	5.9	6.8	7.9	8.4	1.0	2	2	2	2
Base–*year*	10.2	45.8	5.9	6.8	7.7	8.4	1.0	ex	2	2	2
Base–*pos*	23.7	45.6	5.7	7.2	6.3	8.4	ex	2	2	2	2
Base–*year*–*pos*	32.9	45.4	5.7	7.2	6.3	8.4	ex	ex	2	2	2

September or October, and was broadly similar among states. Across the entire study, water depths ranged from 15 to 115 m and bottom temperatures ranged from 13.6 to 29.3 °C and were similar among years and states. The two exceptions were that sampling tended to occur slightly deeper in Georgia than other states (likely due to habitat availability), and bottom temperature was slightly cooler in Florida compared to states further northward due to summertime upwelling events (Table 1).

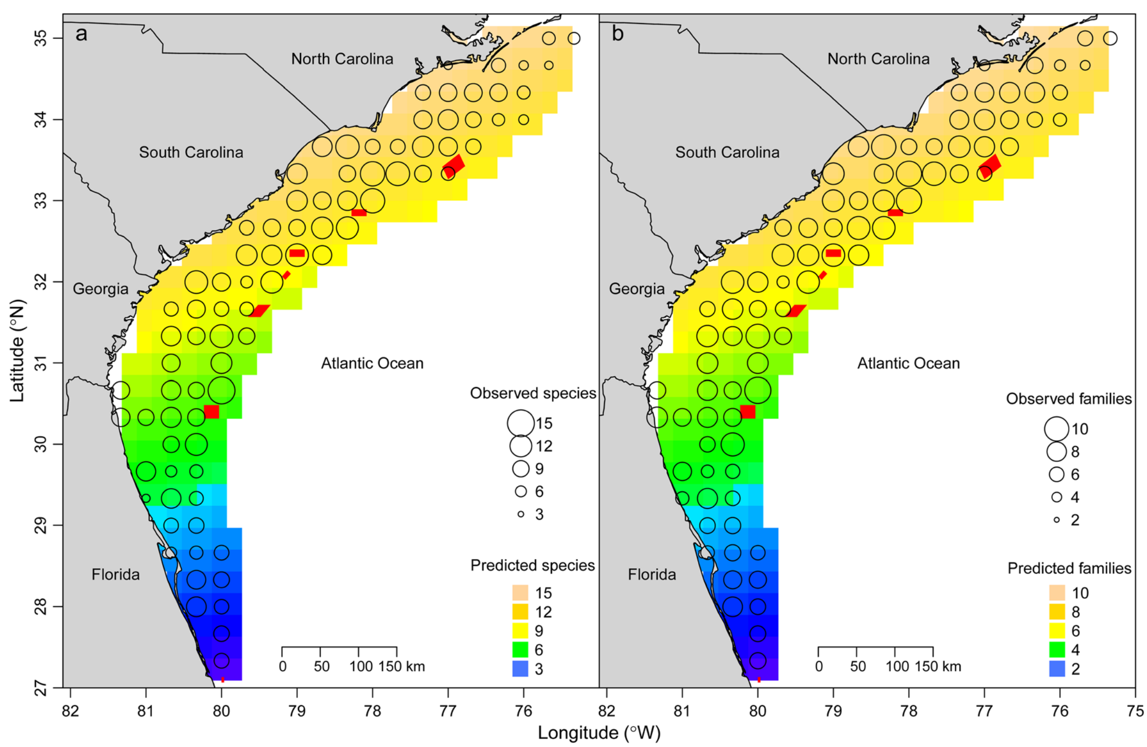

Fig. 4 Partial effect of position (latitude × longitude) on the predicted number of species (left panel) or families (right panel) using generalized additive models built on underwater video data from the Southeast Reef Fish Survey in 2015–2017. The orange background color indicates the highest predicted number of species or families, while blue indicates the fewest, and these estimates were based on average values of all other predictor variables in the models. Overlaid on position estimates are black bubbles that indicate the mean number of observed species (left) or families (right) seen on video, aggregated to one third degree bins, as well as locations of seven current marine reserves (red filled boxes)

Overall, fish observed on videos in the SEUS comprised 53 families, 138 species, and 210 taxa (Appendix Table 6). Species with the highest percent occurrence on video were gray triggerfish (*Balistes capriscus*; 45.6%), tomtate (*Haemulon aurolineatum*; 42.7%), red porgy (*Pagrus pagrus*; 39.4%), almaco jack (*Seriola rivoliana*; 36.6%), sand perch (*Diplectrum formosum*; 35.8%), vermilion snapper (*Rhomboplites aurorubens*; 34.9%), and black sea bass (*Centropristis striata*; 32.2%; Table 2). Seven species were seen on more than 30% of videos, 23 were seen on more than 10% of videos, and 62 were seen on more than 1% of videos (Table 2). Just over half of all species observed in our study ($n = 76$) were seen on less than 1% of videos, and 23 species (17% of all species observed) were observed on a single video (Appendix Table 6).

There was substantial variability in the percent occurrence among the 53 families observed on video in this study. Serranids were observed on 77.9% of videos, followed by sparids (77.1%), carangids (67.1%), labrids (57.0%), lutjanids (53.4%), balistids (48.5%), and haemulids (48.4%; Table 3). Sea basses (non-Epinephelinae serranids) were much more commonly observed (57.5%) on videos compared to groupers (Epinephelinae serranids; 24.2%). A total of 13 families were observed on more than 10% of videos, 17 families were observed on less than 1% of videos, and 3 families were observed on a single video (Appendix Table 6, Table 3).

Most fish species and families were observed in some states more than others. Some species were observed much more frequently in North and South Carolina compared to Georgia and Florida, including black sea bass, bandtail puffer (*Sphoeroides spengleri*), white grunt (*Haemulon plumierii*), scamp (*Mycteroperca phenax*), and gag (*Mycteroperca microlepis*; Table 4). Other species were more commonly observed in Florida and Georgia compared to North and South Carolina, such as vermilion snapper, red snapper (*Lutjanus campechanus*), gray

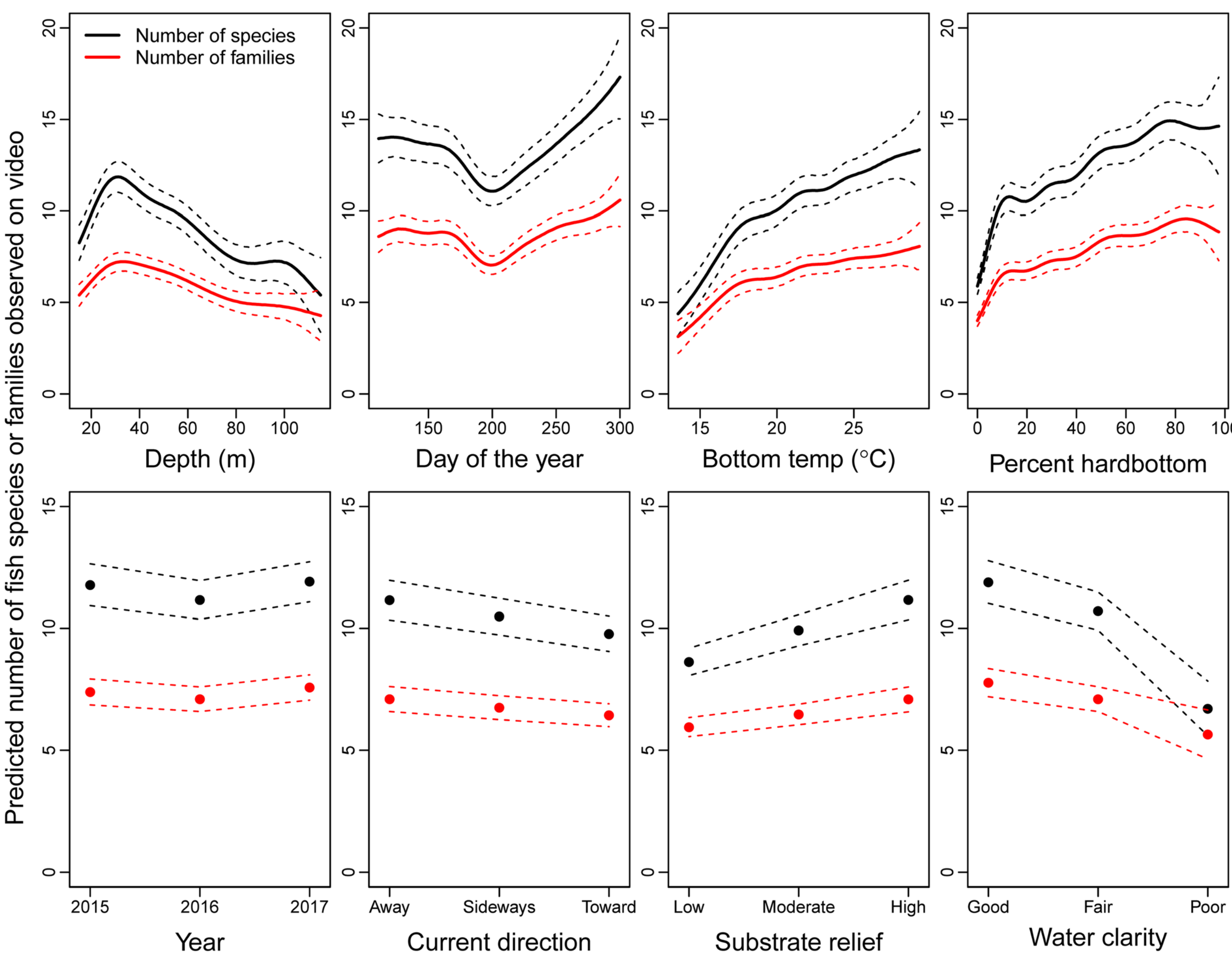

Fig. 5 Predicted number of species (black) and families (red) observed on video as a function of predictor variables using generalized additive model built on Southeast Reef Fish Survey video data from 2015 to 2017. Solid lines or points indicate predicted values at average values of all other covariates, and dashed lines are 95% confidence intervals

snapper (*Lutjanus griseus*), and sheepshead (*Archosargus probatocephalus*; Table 4). Red grouper (*Epinephelus morio*) were more commonly observed in North Carolina and Florida compared to South Carolina and Georgia, while red porgy, blue angelfish (*Holacanthus bermudensis*), lionfish (*Pterois volitans/miles*), great barracuda (*Sphyraena barracuda*), and short bigeye (*Pristigenys alta*) were more commonly observed in South Carolina and Georgia compared to North Carolina and Florida (Table 4). Tomtate and tattler (*Serranus phoebe*) appeared to have similar percent occurrences across all states.

Percent occurrence for nearly all taxa was highly consistent among the 3 years of our study, with most taxa varying less than 5% in terms of absolute percent occurrence (Appendix Table 6). The biggest decline occurred with black sea bass, which declined in percent occurrence from 38.3% in 2015 to 29.0% in 2016. The largest increase occurred with red snapper, which increased in percent occurrence from 24.7% in 2016 to 34.3% in 2017.

The species accumulation curve showed an initial rapid increase in the number of taxa observed as the number of video samples increased, after which the curve began plateauing (Fig. 3). After the first 200 video samples (i.e., 5% of total video sampling effort), 130 taxa were observed, which was approximately 62% of the total taxa observed across all 4130 videos (Fig. 3). Even at 4130 video samples, new taxa were still being observed on video, albeit at a lower rate than at a lower number of video samples, suggesting additional video effort would continue to discover new taxa in the survey.

Generalized additive models

The base GAMs relating either the number of species or families to nine predictor variables were the best models based on AIC (Table 5). Both models explained more than 45% of the model deviance and were 0.6 (species) or 10.2 (family) AIC points lower (better) than the next best models that excluded *pos* or *year* (Table 5). There was also a high degree of consistency among the GAMs, suggesting that they were robust. Subsequent results focus entirely on these best models.

The partial effect of position from the species and family GAMs were predicted to be highest in North and South Carolina and lowest in Florida (Fig. 4). Most of the spatial variation in the partial effect of position was in the latitudinal axis. The partial effects of position plots were nearly identical between species and family models, but both were only weakly related to video observations likely due to variation in other predictor variables across space (Fig. 4).

There was a high degree of consistency in the relationships between the number of species and families to the other predictor variables of the GAMs. The largest number of species and families were predicted to occur around 30 m deep, decreasing in shallower and deeper water (Fig. 5). More species and families were predicted in warmer water in spring or fall on substrates containing a large percent hardbottom. Year was included in both species and family richness models based on AIC, although there did not appear to be substantial annual variability in these two response variables over the 3-year study (Fig. 5). More species and families were observed when the current direction was away from the video camera, substrate relief was high, and water clarity was good.

Discussion

Recent advances in underwater video technology are allowing researchers to greatly improve the monitoring of reef fish communities around the world (Mallet and Pelletier 2014). Improved video monitoring is timely because myriad threats are currently facing reef fish communities including overfishing and climate change (Hoegh-Guldberg et al. 2007), and these threats can be understood and ameliorated with better data on reef fish temporal and spatial trends. We used underwater video deployed broadly across the SEUS on hardbottom reefs to make inferences about the distribution and richness of reef-associated fishes. We observed a large number of reef-associated fish species in our study, with highest fish species and family richness occurring in North and South Carolina. Although the spatial and temporal trends of exploited reef-associated fish species have been elucidated previously in the SEUS (Shertzer et al. 2009; Stratton 2011; Bacheler et al. 2016a; Bacheler and Smart 2016), ours is the first regional-scale analysis of (nearly) the entire reef fish community.

Our GAMs provided an understanding of species- and family-level richness that were standardized by various predictor factors that may have influenced detectability or distribution of reef fishes and also accounted for spatial autocorrelation. The partial effects of position suggested higher diversity in the northern half of our study area, which generally corresponds with previous analyses using long-term trap data (Bacheler and Smart 2016) and video data where only a subset of economically important species were counted and analyzed (Bacheler et al. 2016a). To create spatial predictions from our model, however, all covariates would need to be known across space, which were not available in our study. Instead, we used average values of all other predictor variables in our model, which likely explains the weak relationship between observations and the partial effects of position across the study area.

But what explains the substantial variability in reef fish species and family richness across latitudes in our study? Previous studies have found that wind forcing can cause the Gulf Stream to meander inshore during summer months, which via Ekman transport causes intrusions of cold, deep, nutrient-rich water onto the continental shelf (Atkinson 1977; Hyun and He 2010). These summertime intrusions of cold water most often occur in places where the Gulf Stream is closest to shore, namely in southern and central Florida (Blanton 1971; Smith 1983; Pitts and Smith 1997). For each of the 3 years of our study, bottom water temperatures in Florida were the coldest of any state, suggesting that some amount of upwelling occurred. Some species may simply swim away from cold water intrusions, returning after the upwelling has receded, while others may avoid areas prone to upwelling altogether. For instance, lionfish are strongly influenced by water temperature (Whitfield et al. 2014) and were encountered in our study much less frequently in Florida where upwelling occurs than South Carolina or Georgia, but it is not known what mechanism lionfish use to avoid these areas. Given that water temperature strongly influences the distribution of fishes (Tittensor et al. 2010; Langlois et al. 2011; Whitfield et al. 2014), it is not surprising that reef fish richness was highest in southern North Carolina through Georgia where cold upwelling did not occur in 2015–2017. The strong positive correlation between reef fish richness and bottom temperature found in our study provides additional evidence that reef fishes may prefer areas with warm water where upwelling rarely occurs in the SEUS.

Reef fish richness was also influenced by habitat variables. We found that reef fishes were strongly associated with the proportion of the visible substrate that was hardbottom habitat, as well as substrate relief. Previous studies have shown that reef fishes in the SEUS associate with live-bottom habitats (Miller and Richards 1980; Powles and Barans 1980; Grimes et al. 1982; Wenner 1983; Quattrini and Ross 2006; Schobernd and Sedberry 2009), but quantifying more sophisticated fish-habitat associations has been relatively rare. An exception is Kendall et al. (2008), who showed that gag (*Mycteroperca microlepis*) and scamp (*Mycteroperca phenax*) were most strongly associated with the height of undercut ledges, whereas black sea bass (*Centropristis striata*) were more often observed in areas with the highest amount of sessile biota. Our results are consistent with these previous studies and suggest that reef fish associate strongly with hardbottom habitats in the SEUS, in particular high-relief habitats in areas with substantial hardbottom, which is similar to habitat use patterns of reef fishes in other locations around the world (e.g., Roberts and Ormond 1987; Friedlander and Parrish 1998; Brokovich et al. 2006). Since we targeted hardbottom locations for sampling in our study, sand or mud habitats included in our analyses often occurred close to hardbottom sites; had sand and mud sites far from patches of hardbottom been randomly selected for sampling, we likely would have found much stronger associations of reef fish with hardbottom habitats.

There was a lack of temporal variability for most taxa in our 3-year study. High temporal consistency for most taxa suggests that temperate reef fish communities do not appear to change drastically in terms of presence/absence over time scales of up to 3 years. Our results contrast with studies of coral reef fishes that have been shown to exhibit substantial year-to-year variability (Sale and Douglas 1984) that appears mostly due to variability in recruitment (Victor 1986; Caley et al. 1996). This difference might be due to contrasting recruitment dynamics of temperate reef fishes, which are understudied compared to tropical coral reef fishes, or perhaps due to other aspects of their community dynamics or the spatial scale of study. Moreover, temporal variability may have been much larger in our study had we analyzed abundance instead of presence or absence data. Regardless, the lack of temporal variability in reef fishes in the SEUS suggests that SERFS video sampling was robust and relatively precise. If SERFS video sampling had low precision, temporal variability of reef fishes would have appeared larger.

The number of fish species encountered in a survey is not only dependent upon the number of available species, habitat, or depth of a sample but also the type of gear being used and the amount of sampling conducted. We observed 138 fish species from 4130 video samples, and the species accumulation curve suggests that more video sampling would have likely resulted in more species being encountered (Bunge and Fitzpatrick 1993; Ugland et al. 2003). The large number of species recorded in our study was fewer than is typically found in most coral reef ecosystems (Sale and Douglas 1984; Allen 2008; Smith et al. 2011), but comparable to, or higher than, most other temperate reef systems (Tittensor et al. 2010). In the SEUS, similar numbers of species were observed in a 25-year trap study (Bacheler and Smart 2016) and smaller-scale dive surveys (Whitfield et al. 2014; Bacheler et al. 2017).

There were some shortcomings of our study. First, some fish species were difficult or impossible to identify to the species level using video alone (e.g., *Calamus* spp.), so the number of species we recorded in our study was likely underestimated. Second, although video is a less selective gear than most capture gears (Cappo et al. 2003; Harvey et al. 2012), it often records fewer species than divers and may miss the most secretive, cryptic species (Bacheler et al. 2017). Third, predatory and scavenger fish species may have been overrepresented in our video samples because our video cameras were attached to baited traps. Previous work has shown that there does not tend to be concomitant decreases in herbivorous or omnivorous fishes when bait is used (Harvey et al. 2007; Dorman et al. 2012). Fourth, abundance data tend to be more informative than presence-absence data for understanding species' spatiotemporal patterns (Schobernd et al. 2014), but our video reading protocol precluded using abundance data consistently for all species in this study due to time constraints. Last, fish species with unique coloration, shading, or behaviors likely would have been identified more easily than species without those unique characteristics.

Our results are timely because some limited spatial closures have been implemented in the SEUS as a conservation and management measure (see Fig. 4), although the efficacy of these closures from a fisheries management perspective is currently unclear (Bacheler et al. 2016b).

Most of the reserves in the SEUS occur in areas with relatively high species- and family-level richness, yet these reserves ultimately only protect a small percentage of the area with highest reef fish biodiversity in the SEUS. Our results also provide information on how rare or ubiquitous each of the reef-associated fish species are in the SEUS, which is useful for ecosystem modeling (e.g., Ecopath with Ecosim; Christensen and Walters 2004) and ecosystem-based management. After standardizing for environmental conditions that may influence detectability (e.g., water clarity, current direction), using underwater video is an extremely powerful approach to understand the distribution and abundance patterns of various reef fish species, as well as the reef fish community in general.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All research activities were carried out under Scientific Research Permits issued to Todd Kellison on 29 June 2010 and Nathan Bacheler on 16 June 2015 by the US National Marine Fisheries Service, in accordance with the relevant guidelines and regulations on the ethical use of animals as experimental subjects.

Sampling and field studies All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and all necessary approvals have been obtained.

Data availability The dataset analyzed during the current study is available from the corresponding author on reasonable request.

Appendix

Table 6 State-specific and overall percent occurrence for fish taxa observed on Southeast Reef Fish Survey videos in 2015–2017. Families are shown in alphabetical order, and taxa within families are listed from highest to lowest percent occurrence

Taxon	Common name	NC	SC	GA	FL	2015	2016	2017	Overall
Acanthuridae	Surgeonfishes	10.7	6.6	4.6	4.5	7.0	7.5	7.6	7.3
Antennariidae	Frogfishes	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0
Apogonidae	Cardinalfishes	0.1	0.0	0.3	0.1	0.1	0.0	0.1	0.1
Aulostomidae	Trumpetfishes	0.3	0.3	0.3	0.0	0.1	0.1	0.5	0.2
Aulostomus maculatus	Trumpetfish	0.3	0.3	0.3	0.0	0.1	0.1	0.5	0.2
Balistidae	Triggerfishes	41.6	46.7	57.8	55.4	44.5	51.0	50.2	48.5
Balistes capriscus	Gray triggerfish	38.9	40.7	55.3	54.1	42.2	47.5	47.4	45.6
Balistes vetula	Queen triggerfish	2.9	10.5	9.8	3.8	5.1	6.2	4.9	5.4
Xanthichthys ringens	Sargassum triggerfish	0.3	0.1	0.0	0.0	0.2	0.1	0.1	0.1
Canthidermis sufflamen	Ocean triggerfish	0.1	0.0	0.0	0.1	0.1	0.1	0.0	0.1
Canthidermis maculata	Rough triggerfish	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.1
Batrachoididae	Toadfishes	0.6	0.6	2.2	0.2	1.0	0.4	0.4	0.6
Carangidae	Jacks	62.0	69.2	72.2	70.4	63.3	71.3	66.8	67.1
Seriola rivoliana	Almaco jack	37.4	40.6	43.9	31.1	35.4	38.7	35.7	36.6
Seriola dumerili	Greater amberjack	29.0	29.7	37.3	25.9	29.9	31.8	24.8	28.9
Caranx crysos	Blue runner	4.2	6.5	7.6	22.4	6.8	13.9	11.9	10.8
Seriola zonata	Banded rudderfish	2.8	7.9	11.4	8.3	7.7	5.8	5.7	6.4
Caranx ruber	Bar jack	2.0	0.9	1.1	1.2	0.8	2.3	1.3	1.5
Seriola fasciata	Lesser amberjack	0.8	1.7	0.0	0.2	0.9	0.6	0.8	0.8
Caranx bartholomaei	Yellow jack	1.0	0.3	0.0	0.5	0.6	0.4	0.7	0.6

Table 6 (continued)

Taxon	Common name	NC	SC	GA	FL	2015	2016	2017	Overall
Alectis ciliaris	African pompano	0.5	0.3	0.8	0.2	0.1	0.7	0.4	0.4
Chloroscombrus chrysurus	Atlantic bumper	0.0	0.0	0.8	0.9	0.1	0.1	0.9	0.4
Elagatis bipinnulata	Rainbow runner	0.2	0.5	0.0	0.4	0.4	0.3	0.2	0.3
Caranx hippos	Crevalle jack	0.0	0.0	0.3	0.2	0.1	0.1	0.1	0.1
Caranx lugubris	Black jack	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.0
Naucrates ductor	Pilot fish	0.0	0.1	0.3	0.0	0.1	0.0	0.0	0.0
Uraspis secunda	Cottonmouth jack	0.0	0.2	0.0	0.0	0.1	0.0	0.0	0.0
Caranx latus	Horse-eye jack	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Pseudocaranx dentex	White trevally	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Selene vomer	Lookdown	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Trachinotus carolinus	Florida pompano	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
Trachinotus falcatus	Permit	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0
Carcharhinidae	Requiem sharks	9.2	13.4	10.1	5.4	9.3	9.2	8.2	8.9
Rhizoprionodon terraenovae	Atlantic sharpnose shark	6.4	9.2	6.0	1.4	5.1	6.3	4.6	5.4
Carcharhinus plumbeus	Sandbar shark	0.8	2.4	1.6	2.9	2.7	1.3	1.7	1.9
Galeocerdo cuvier	Tiger shark	1.2	0.3	1.4	0.5	0.5	0.6	1.3	0.8
Carcharhinus brevipinna	Spinner shark	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.0
Carcharhinus acronotus	Blacknose shark	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Negaprion brevirostris	Lemon shark	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0
Centropomidae	Snooks	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0
Chaetodontidae	Butterflyfishes	20.0	35.2	29.2	28.5	26.0	27.3	26.8	26.7
Chaetodon sedentarius	Reef butterflyfish	14.2	26.9	18.8	19.5	18.6	21.1	17.2	19.0
Chaetodon ocellatus	Spotfin butterflyfish	7.7	16.4	15.5	12.7	11.0	11.7	12.9	11.8
Prognathodes aya	Bank butterflyfish	0.6	3.8	2.7	1.9	2.4	1.5	1.7	1.9
Chaetodon striatus	Banded butterflyfish	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Prognathodes aculeatus	Longsnout butterflyfish	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0
Dactylopteridae	Flying gurnards	0.0	0.2	0.0	0.0	0.1	0.1	0.0	0.0
Dasyatidae	Whiptail stingrays	1.8	4.3	2.5	2.5	3.4	2.4	1.9	2.6
Diodontidae	Porcupinefishes	0.1	0.2	0.3	0.2	0.1	0.1	0.4	0.2
Echeneidae	Remoras	2.7	6.4	9.0	8.8	5.7	6.5	5.8	6.0
Ephippidae	Spadefishes	1.4	1.9	2.2	3.5	3.1	1.7	1.9	2.3
Chaetodipterus faber	Atlantic spadefish	1.4	1.9	2.2	3.5	3.1	1.7	1.9	2.3
Fistulariidae	Cornetfishes	1.5	3.5	1.1	0.7	2.2	1.5	1.1	1.6
Ginglymostomatidae	Carpet sharks	1.0	0.9	2.7	3.0	1.7	2.3	1.3	1.8
Ginglymostoma cirratum	Nurse shark	1.0	0.9	2.7	3.0	1.7	2.3	1.3	1.8
Gymnuridae	Butterfly rays	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Haemulidae	Grunts	47.6	56.4	37.3	47.3	48.3	47.8	49.1	48.4
Haemulon aurolineatum	Tomtate	37.5	49.4	35.7	46.3	42.8	41.8	43.5	42.7
Haemulon plumierii	White grunt	31.9	18.8	6.8	1.9	17.8	16.8	17.2	17.3
Haemulon striatum	Striped grunt	0.5	9.4	0.0	1.5	2.6	3.5	1.8	2.6
Anisotremus virginicus	Porkfish	0.0	0.1	0.0	7.8	3.0	1.9	2.7	2.5
Orthopristis chrysoptera	Pigfish	0.5	0.5	1.1	0.8	0.7	0.4	0.8	0.6
Anisotremus surinamensis	Black margate	0.1	0.1	0.0	1.7	0.4	0.6	0.8	0.6
Haemulon album	White margate	0.0	0.1	0.3	0.3	0.1	0.1	0.2	0.1
Haemulon melanurum	Cottonwick	0.1	0.0	0.0	0.1	0.1	0.0	0.1	0.0
Haemulon sciurus	Blue striped grunt	0.1	0.0	0.0	0.1	0.1	0.0	0.1	0.0
Holocentridae	Squirrelfishes	4.6	6.2	6.0	9.7	7.7	5.9	6.5	6.7
Holocentrus adscensionis	Squirrelfish	3.7	5.2	5.2	8.1	5.8	5.1	5.8	5.6
Myripristis jacobus	Blackbar soldierfish	0.3	0.3	0.5	1.2	0.9	0.7	0.3	0.6

Table 6 (continued)

Taxon	Common name	NC	SC	GA	FL	2015	2016	2017	Overall
Kyphosidae	Sea chubs	0.3	0.1	0.0	0.0	0.1	0.1	0.2	0.1
Labridae	Wrasses	67.2	62.8	49.3	43.4	58.9	57.8	54.3	57.0
Bodianus pulchellus	Spotfin hogfish	10.7	20.6	9.8	14.0	14.7	14.1	12.4	13.7
Lachnolaimus maximus	Hogfish	12.3	10.5	3.5	1.7	7.2	8.7	7.2	7.7
Bodianus rufus	Spanish hogfish	5.8	1.7	1.1	3.2	4.1	3.4	3.7	3.7
Tautoga onitis	Tautog	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Lutjanidae	Snappers	35.5	43.6	64.0	78.0	53.6	51.0	55.8	53.4
Rhomboplites aurorubens	Vermilion snapper	21.8	36.8	42.2	47.2	33.6	36.0	35.2	34.9
Lutjanus campechanus	Red snapper	14.7	16.0	34.9	53.2	28.7	24.7	34.3	29.2
Lutjanus griseus	Gray snapper	0.7	2.6	4.6	23.0	9.5	7.1	9.2	8.6
Lutjanus analis	Mutton snapper	0.4	1.0	9.0	13.0	7.0	3.6	5.5	5.4
Lutjanus synagris	Lane snapper	0.0	0.0	0.0	12.0	3.2	2.7	5.7	3.8
Ocyurus chrysurus	Yellowtail snapper	0.8	0.6	1.6	1.6	1.4	0.8	1.0	1.1
Lutjanus cyanopterus	Cubera snapper	0.1	0.1	0.5	0.5	0.1	0.4	0.4	0.3
Lutjanus vivanus	Silk snapper	0.6	0.0	0.3	0.0	0.2	0.4	0.1	0.2
Lutjanus buccanella	Blackfin snapper	0.4	0.1	0.0	0.2	0.3	0.2	0.1	0.2
Lutjanus apodus	Schoolmaster	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
Lutjanus mahogoni	Mahogany snapper	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Malacanthidae	Tilefishes	9.6	8.0	4.4	2.3	5.9	7.5	6.0	6.5
Malacanthus plumieri	Sand tilefish	8.4	6.3	2.7	2.1	5.5	6.2	4.6	5.4
Caulolatilus microps	Blueline tilefish	0.9	1.7	1.6	0.2	0.4	1.1	1.3	0.9
Caulolatilus cyanops	Blackline tilefish	0.3	0.0	0.0	0.0	0.0	0.1	0.2	0.1
Caulolatilus chrysops	Goldface tilefish	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Mobulidae	Manta rays	0.1	0.0	0.0	0.2	0.1	0.1	0.1	0.1
Monacanthidae	Filefishes	12.9	18.2	15.0	5.7	13.2	12.5	9.8	11.9
Stephanolepis hispida	Planehead filefish	8.0	13.8	4.9	0.5	7.2	6.5	5.8	6.5
Aluterus monoceros	Unicorn leatherjacket	2.8	2.9	9.3	4.0	3.9	4.3	3.1	3.8
Aluterus scriptus	Scrawled filefish	0.6	0.3	0.5	0.2	0.3	0.6	0.3	0.4
Aluterus schoepfii	Orange filefish	0.1	0.6	0.3	0.1	0.4	0.1	0.1	0.2
Cantherhines pullus	Orangespotted filefish	0.2	0.2	0.0	0.0	0.2	0.1	0.1	0.1
Monacanthus tuckeri	Slender filefish	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1
Aluterus heudelotii	Dotterel filefish	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Mullidae	Goatfishes	10.5	11.9	1.9	3.6	8.0	9.0	6.3	7.8
Pseudupeneus maculatus	Spotted goatfish	9.8	11.5	1.9	2.9	7.7	8.5	5.4	7.2
Upeneus parvus	Dwarf goatfish	0.4	0.0	0.0	0.4	0.1	0.3	0.5	0.3
Mullus auratus	Red goatfish	0.2	0.1	0.0	0.5	0.2	0.1	0.4	0.2
Mulloidichthys martinicus	Yellow goatfish	0.1	0.5	0.0	0.0	0.1	0.1	0.1	0.1
Muraenidae	Morays	10.6	12.0	8.2	6.6	7.9	9.0	11.3	9.4
Myliobatidae	Eagle rays	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.0
Odontaspididae	Sand sharks	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Carcharias taurus	Sand tiger	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Ogcocephalidae	Batfishes	0.0	0.0	0.3	0.2	0.1	0.1	0.1	0.1
Ophichthidae	Snake eels	1.0	1.0	4.1	1.6	1.6	1.1	1.6	1.5
Ostraciidae	Boxfishes	1.2	5.4	3.8	1.9	3.6	2.1	1.9	2.5
Pomacanthidae	Angelfishes	26.6	42.2	36.0	33.5	35.9	31.1	31.7	32.9
Holacanthus bermudensis	Blue angelfish	21.9	33.0	30.8	26.6	27.5	26.5	25.4	26.5
Holacanthus ciliaris	Queen angelfish	2.9	6.1	5.7	7.3	6.2	4.8	4.6	5.2
Holacanthus hybrid	Hybrid angelfish	1.9	4.7	3.8	4.2	2.9	3.1	4.2	3.4
Pomacanthus paru	French angelfish	1.0	2.6	0.5	1.2	1.0	1.1	2.0	1.4

Table 6 (continued)

Taxon	Common name	NC	SC	GA	FL	2015	2016	2017	Overall
Holacanthus tricolor	Rock beauty	1.3	2.2	0.5	0.2	1.4	1.4	0.4	1.1
Pomacanthus arcuatus	Gray angelfish	0.2	1.4	0.5	1.5	0.4	1.3	1.0	0.9
Centropyge argi	Cherubfish	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Pomacentridae	Damselfishes	17.8	25.3	21.5	18.8	22.1	18.3	19.6	20.0
Pomatomidae	Bluefishes	0.0	0.1	0.3	0.0	0.1	0.0	0.1	0.0
Pomatomus saltatrix	Bluefish	0.0	0.1	0.3	0.0	0.1	0.0	0.1	0.0
Priacanthidae	Bigeyes	4.4	5.9	11.2	2.9	5.0	4.7	4.8	4.8
Pristigenys alta	Short bigeye	2.8	3.7	7.6	1.1	3.3	2.7	2.7	2.9
Priacanthus arenatus	Atlantic bigeye	1.3	0.9	2.5	1.2	1.4	1.3	1.3	1.3
Rachycentridae	Cobias	1.5	4.5	4.1	3.9	3.8	3.0	2.6	3.1
Rachycentron canadum	Cobia	1.5	4.5	4.1	3.9	3.8	3.0	2.6	3.1
Rajidae	Skates	0.3	0.0	0.5	1.1	1.1	0.2	0.2	0.5
Rhinobatidae	Guitarfishes	0.0	0.7	0.0	0.5	0.8	0.1	0.1	0.3
Rhinobatos lentiginosus	Atlantic guitarfish	0.0	0.7	0.0	0.5	0.8	0.1	0.1	0.3
Scaridae	Parrotfishes	5.1	2.2	0.5	1.2	2.4	2.9	3.1	2.8
Sciaenidae	Drums	3.2	5.1	4.9	8.1	5.4	3.7	7.1	5.4
Equetus lanceolatus	Jack-knife fish	1.1	3.6	3.5	5.9	2.7	2.4	5.2	3.4
Pareques umbrosus	Cubbyu	2.0	1.5	1.1	2.4	2.4	1.2	2.2	1.9
Pareques acuminatus	High-hat	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0
Pareques iwamotoi	Blackbar drum	0.0	0.0	0.3	0.0	0.1	0.0	0.0	0.0
Scombridae	Mackerels and tunas	2.4	3.8	3.8	2.0	2.2	2.9	3.1	2.7
Scomberomorus cavalla	King mackerel	0.1	0.1	0.5	0.2	0.3	0.3	0.0	0.2
Euthynnus alletteratus	Little tunny	0.0	0.1	0.3	0.2	0.1	0.1	0.1	0.1
Scomberomorus maculatus	Atlantic spanish mackerel	0.0	0.3	0.3	0.0	0.2	0.1	0.0	0.1
Scomberomorus regalis	Cero	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0
Scorpaenidae	Scorpionfishes	15.7	22.7	27.8	17.8	20.2	18.4	18.2	18.9
Pterois volitans/miles	Lionfish	15.7	22.6	27.5	17.5	20.0	18.3	18.0	18.8
Serranidae (overall)	Sea basses and groupers	82.6	87.5	74.1	67.1	78.4	78.3	76.9	77.9
Serranidae (Epinephelinae only)	Groupers	27.9	24.2	20.2	20.8	25.1	24.7	22.7	24.2
Mycteroperca phenax	Scamp	17.4	19.3	14.7	5.4	13.8	15.3	11.9	13.7
Mycteroperca microlepis	Gag	10.0	8.3	5.7	5.8	8.8	6.8	8.2	7.9
Cephalopholis cruentata	Graysby	2.9	3.8	3.0	1.8	2.7	2.4	3.3	2.8
Epinephelus morio	Red grouper	2.5	0.1	0.0	1.2	1.8	1.1	1.2	1.4
Epinephelus adscensionis	Rock hind	1.8	2.3	0.0	0.1	1.2	1.4	1.0	1.2
Mycteroperca interstitialis	Yellowmouth grouper	1.1	1.4	0.3	0.4	1.4	0.7	0.4	0.8
Epinephelus niveatus	Snowy grouper	0.1	1.7	1.6	0.2	0.3	0.7	0.7	0.6
Epinephelus drummondhayi	Speckled hind	0.5	0.1	0.3	0.3	0.4	0.4	0.2	0.3
Epinephelus itajara	Goliath grouper	0.1	0.0	0.0	0.8	0.3	0.4	0.1	0.3
Cephalopholis fulva	Coney	0.0	0.1	0.0	0.2	0.2	0.1	0.0	0.1
Epinephelus guttatus	Red hind	0.2	0.0	0.0	0.0	0.1	0.0	0.1	0.1
Epinephelus nigritus	Warsaw grouper	0.1	0.0	0.0	0.1	0.1	0.1	0.0	0.0
Epinephelus flavolimbatus	Yellowedge grouper	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0
Mycteroperca bonaci	Black grouper	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Mycteroperca venenosa	Yellowfin grouper	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Serranidae (except Epinephelinae)	Sea basses	62.7	63.3	53.1	48.7	59.0	56.5	56.8	57.5
Diplectrum formosum	Sand perch	34.0	44.2	38.4	31.8	34.7	36.1	36.7	35.8
Centropristis striata	Black sea bass	40.0	36.6	24.5	22.3	38.3	29.0	29.2	32.2
Serranus phoebe	Tattler	18.4	23.4	15.3	19.6	20.2	21.5	16.9	19.6
Centropristis ocyurus	Bank sea bass	18.5	14.8	17.7	8.8	16.3	12.3	15.1	14.6

Table 6 (continued)

Taxon	Common name	NC	SC	GA	FL	2015	2016	2017	Overall
Liopropoma eukrines	Wrasse bass	1.0	1.6	0.3	3.2	1.6	1.9	1.7	1.7
Paranthias furcifer	Creole-fish	0.6	0.9	0.5	0.2	0.6	0.7	0.3	0.5
Pronotogrammus martinicensis	Roughtongue bass	0.9	0.0	0.0	0.0	0.0	0.6	0.4	0.3
Centropristis philadelphica	Rock sea bass	0.3	0.1	0.5	0.2	0.2	0.4	0.0	0.2
Centropristis fuscula	Two-spot sea bass	0.1	0.0	0.3	0.1	0.2	0.0	0.0	0.1
Sparidae	Porgies	76.1	88.3	73.6	72.0	77.7	79.4	74.0	77.1
Pagrus pagrus	Red porgy	35.4	55.9	46.6	31.6	41.0	39.9	37.3	39.4
Stenotomus spp.	Scup/Longspine porgy	14.9	28.7	12.8	6.0	16.4	14.6	13.1	14.7
Diplodus holbrookii	Spottail pinfish	18.5	9.6	6.0	2.1	12.6	8.8	9.3	10.3
Archosargus probatocephalus	Sheepshead	2.0	2.6	1.9	18.1	8.3	6.1	7.5	7.3
Lagodon rhomboides	Pinfish	0.6	7.7	6.5	4.2	3.7	3.4	4.3	3.8
Sphyraenidae	Barracudas	2.8	7.3	7.6	5.6	4.0	5.7	5.4	5.1
Sphyraena barracuda	Great barracuda	2.8	7.3	7.6	5.6	4.0	5.7	5.4	5.1
Sphyrnidae	Hammerhead sharks	0.1	0.1	1.1	0.7	0.4	0.4	0.3	0.4
Sphyrna lewini	Scalloped hammerhead	0.0	0.0	0.0	0.3	0.1	0.2	0.0	0.1
Sphyrna mokarran	Great hammerhead	0.1	0.0	0.5	0.1	0.1	0.0	0.2	0.1
Synodontidae	Lizardfishes	2.0	3.7	2.2	1.2	2.1	1.4	2.9	2.1
Tetraodontidae	Puffers	46.1	51.3	31.1	15.6	35.6	36.4	36.0	36.0
Sphoeroides spengleri	Bandtail puffer	36.0	36.2	21.8	7.1	22.3	27.4	26.8	25.5
Canthigaster rostrata	Sharpnose puffer	13.1	17.1	7.4	7.1	14.3	9.1	11.0	11.5
Canthigaster jamestyleri	Goldface toby	1.3	4.8	0.8	2.3	2.3	2.4	2.2	2.3
Triglidae	Sea robins	0.6	3.0	0.3	0.2	1.0	0.6	1.3	1.0

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