Multi-decadal decline in reef fish abundance and species richness in the southeast USA assessed by standardized trap catches

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SEDAR68-RD20

Mar Biol (2016) 163:26
DOI 10.1007/s00227-015-2774-x

ORIGINAL PAPER

Multi-decadal decline in reef fish abundance and species richness in the southeast USA assessed by standardized trap catches

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Received: 2 July 2015 / Accepted: 23 October 2015 / Published online: 18 January 2016

Abstract Reef fish species naturally fluctuate in abundance over various temporal and spatial scales, but recent broad-scale declines in abundance have been observed worldwide and attributed to various anthropogenic influences. We used 25 years of fishery-independent trap data ($N = 11{,}237$ trap hauls) to examine the spatial and temporal variability in temperate reef fish abundance along the southeast coast of the USA, a relatively understudied region with many economically important reef fish species. Overall, 441,298 individuals from 118 species were caught in the trap survey. Number of species and total number of individuals caught in the trap survey declined over the 25 years, but when separated, nontargeted fish species declined more than fishery-targeted species. For instance, traps caught a median of 18 nontargeted individuals and a median of 2–3 nontargeted reef fish species in the early 1990s, but by the 2010s, traps caught a median of fewer than three nontargeted individuals and a median of one nontarget species. Using generalized additive models, we found that the catch of fishery-targeted and nontargeted species was positively related to bottom water temperature, while depth influenced nontargeted and fishery-targeted species in opposite ways. The substantial and consistent decline in nontargeted fish species suggests that more research and management attention should be given to these often ignored species. These results suggest that the temperate reef fish community in the southeast USA is influenced by more than just fishing, perhaps including invasive species (e.g., lionfish *Pterois volitans*), decadal-scale environmental variability, or climate change.

Introduction

Fish populations are renowned for their spatial and temporal variability, and quantifying these fluctuations has been a central focus of fisheries scientists for many decades (Iles and Sinclair 1982; Cushing 1990). Fluctuations in space and time can be driven by many factors including environmental (i.e., density-independent) and demographic (density-dependent) variables, as well as their interaction (Bartolino et al. 2012; Ciannelli et al. 2012). For reef fish species, natural fluctuations in abundance have been compounded by anthropogenic-induced changes from myriad factors such as fishing, nutrient loading, introduced species, disease, ocean acidification, and climate change (Hughes et al. 2003; Bellwood et al. 2004). Many economically important reef fish species are particularly vulnerable to anthropogenic influences because they exhibit slow growth, delayed maturity, large size, and long life spans (Parrish 1987; Coleman et al. 2000; Wyanski et al. 2000).

Historically, most of the research on, and modeling of, fish stocks has focused on temporal instead of spatial variability of fish stocks, and these efforts have provided insights into the ways that density-dependent and density-independent factors influence species dynamics (e.g., MacKenzie and Köster 2004). Elucidating the spatial structure

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Responsible Editor: K. Clements.

Reviewed by undisclosed experts.

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of a population is a common precursor to describing its ecology and managing it over appropriate spatial scales (Dunning et al. 1992). Rarely in fisheries science, however, have these spatial patterns been connected back to temporal changes in abundance (Cadrin and Secor 2009). There is increased recognition that changes in spatial structure precedes, or is accompanied by, dramatic declines in abundance over time (Ciannelli et al. 2013). Further, broad-scale community dynamics can be the result of a mosaic of top–down and bottom–up trophic forcing across the spatial landscape, which can be related to both community structure and environmental conditions (Frank et al. 2007).

Along the southeast Atlantic coast of the USA (hereafter, SEUS), many reef fish species are economically important; yet, the temporal and spatial dynamics of all except the few most common species are poorly understood. Reef fish declines have been documented in the Florida Keys (Semmens et al. 2000; Kellison et al. 2012), but elsewhere in the SEUS, temporal trends have been mixed (McGovern et al. 1998). For instance, Parker and Dixon (1998) found that some tropical fish species became more common between the 1970s and 1990s on the continental shelf of North Carolina, but some exploited species such as gag *Mycteroperca microlepis* and red snapper *Lutjanus campechanus* declined in abundance. In the same general area of North Carolina, Rudershausen et al. (2008) showed that red porgy *Pagrus pagrus*, vermilion snapper *Rhomboplites aurorubens*, gray triggerfish *Balistes capriscus*, and black sea bass *Centropristis striata* declined between the 1970s and 2000s, while red grouper *Epinephelus morio*, white grunt *Haemulon plumieri*, and bank sea bass *Centropristis ocyurus* increased in abundance.

Rarely has the fish community in the SEUS been examined holistically to understand broad changes in abundance or number of species. Shertzer et al. (2009) used recreational and commercial catches to show that community-level changes in reef fishes in the SEUS generally were gradual, with the biggest shifts occurring in the early and late 1990s. Using fishery-independent trap catches, Stratton (2011) showed that mean reef fish size has increased, but reef fish abundance has decreased consistently since 1990 despite increases in the proportion of exploited species caught by the trap survey over time. A potential drawback of these studies is that variables influencing catch rates were not incorporated into the analyses, with the exception of depth in Stratton (2011). Bacheler et al. (2014) showed that gray triggerfish and vermilion snapper, for example, were more likely to be caught in traps in the SEUS when water temperature was high.

Here, we examine trap catches to quantify the ways in which reef fish abundance and number of species have changed over 25 years in the SEUS. We summarized raw trap catches of reef fish over time in the SEUS, but we also standardized catches for many variables that are known to influence catch rates of reef fish to minimize the likelihood that variability in environmental conditions or the spatial or temporal footprint of the survey would influence results (Boulinier et al. 1998; Gotelli et al. 2010; Bacheler et al. 2013a). We hypothesized that species targeted by fishers would display declining catches over time, while nontargeted species would either show no change or increase. These results improve our understanding of the broad-scale temporal and spatial changes experienced by reef fish species in the SEUS.

Materials and methods

Study area

Sampling for this study occurred between North Carolina and the southeast coast of Florida in the SEUS. The width of the continental shelf varies in the SEUS, from as narrow as 10 km in southern Florida to over 130 km wide off Georgia (Fig. 1). The continental shelf and shelf-break (i.e., 10–100 m deep) along the SEUS are dominated by soft substrates consisting of sand and mud, but patches of hard, rocky substrate are scattered throughout the region (Powles and Barans 1980; Sedberry and Van Dolah 1984). These hard-bottom habitats range in complexity from flat limestone pavement, sometimes covered with a sand or gravel veneer, to high-relief rocky ledges (Schobernd and Sedberry 2009). Reef-associated fish species described herein associate with these patches of hard-bottom habitats and tend to avoid sand and mud habitats (Kendall et al. 2008).

Sampling

We used long-term, fishery-independent chevron trap data to quantify trends in relative abundance and number of species for reef fish in the SEUS. Chevron trap data were collected by a combination of three fishery-independent sampling programs that work collaboratively using identical methodologies to sample reef fish in the region. The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program of the South Carolina Department of Natural Resources has used chevron traps to index reef fish abundance since the late 1980s. Since 2009, MARMAP funding has been supplemented by the cooperative Southeast Area Monitoring and Assessment Program, South Atlantic. Both programs receive their funding from the US National Marine Fisheries Service. We also included in our analyses 2010–2014 data from the Southeast Fishery-Independent Survey (SEFIS), which the US National Marine Fisheries Service created in 2010 to increase

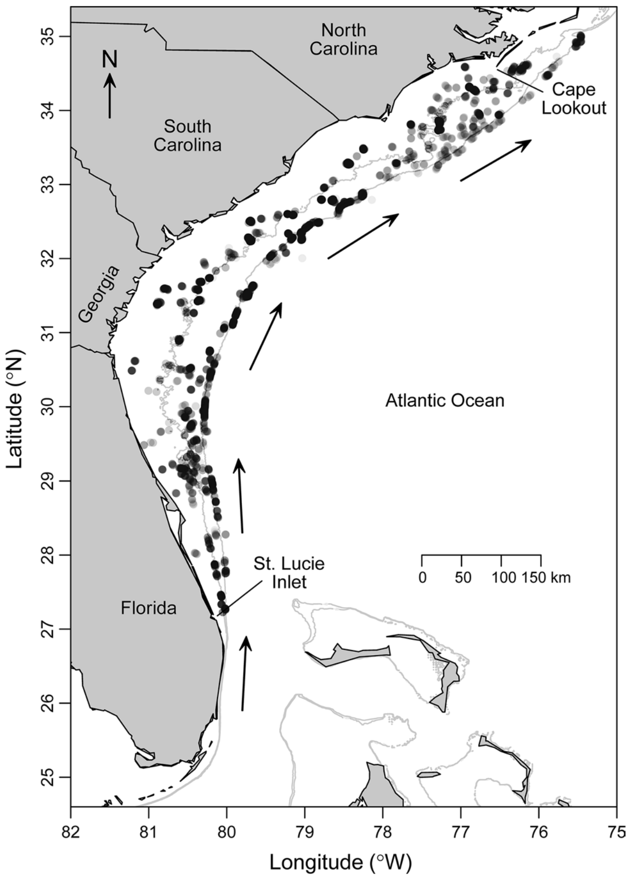

Fig. 1 Study area showing chevron trap deployments by the Southeast Reef Fish Survey used in the analyses, 1990–2014. Note that points often overlap, and *black* indicates more overlap among points (i.e., more samples), and *gray points* indicate fewer overlapping points. *Arrows* indicate the flow of the Gulf Stream, and *gray bathymetry lines* indicate 30 and 50 m depths

fishery-independent sampling in the SEUS. Hereafter, the three sampling programs are referred to as the Southeast Reef Fish Survey (SERFS). We used SERFS data from 1990 through 2014 in our analyses, a time when chevron traps were deployed throughout the region in a consistent manner (as described below).

The SERFS program randomly selected a number of stations to sample each year from a sampling frame of hard-bottom locations and deployed chevron traps on selected stations each year. In addition, some stations included in the analyses were sampled from the sampling frame even though they were not randomly selected for sampling in a given year, while others were new stations added during the study period using information from fishermen, charts, or historical surveys. These new locations were investigated using a vessel echosounder or drop cameras and sampled if hard bottom was detected, and only included in the analyses if hard bottom could be confirmed. Sampling occurred during daylight hours between late March and October aboard the RV *Palmetto*, RV *Savannah*, NOAA Ship *Nancy Foster*, or NOAA Ship *Pisces*.

Chevron traps were used in this study to estimate the local relative abundance of reef fish species. Traps are particularly well suited to sampling reef fish that live in structurally complex habitats, which are challenging to sample with other common survey techniques (Murphy and Jenkins 2010). Bacheler et al. (2013b) showed that the SERFS chevron trap catches of at least one important reef fish, black sea bass, tracked their site-specific abundance in the SEUS. Chevron traps used in this study were shaped like an arrowhead and constructed from plastic-coated galvanized 2-mm-diameter wire (mesh size = 3.4 cm^2) and measured 1.7 m long, 1.5 m wide, and 0.6 m tall, for a total volume of approximately 0.9 m^3 (Collins 1990; Bacheler et al. 2013c). Trap mouth openings were shaped like an upside down teardrop, measuring 18 cm wide and 45 cm long. Each trap was baited with 24 *Brevoortia* spp., four each on four stringers in the trap and eight loose inside the trap. Traps typically were deployed in groups of six, and each trap always was deployed at least 200 m from all other traps in a given year to provide some measure of independence among traps. The target soak time was 90 min for each trap, and any trap determined not to have fished properly (e.g., trap that dragged due to current) was excluded from analysis. All fish caught in chevron traps were identified and enumerated. In some very rare instances, individual fish caught in the trap could not be identified to species, so were identified to the lowest taxon possible.

We also collected information about each station sampled. Latitude, longitude, water depth, and time of day (Coordinated Universal Time) were collected from shipboard sensors, and soak time was determined as the elapsed time between the start of the trap deployment and the start of the trap retrieval process. Bottom water temperature (°C) was measured for each group of simultaneously deployed traps using a "conductivity–temperature–depth" cast.

Data analysis

We conducted two primary types of analyses to understand trends in relative abundance of reef fish species over the course of our study. First, we summarized raw (i.e., nominal) catches of reef fish, with the primary benefit of these analyses being that many individual species could be analyzed separately and in combination. The primary downside of using raw catches was that they were not standardized for changes in the spatial or temporal patterns of sampling or for fluctuations in environmental conditions (Kimura and Somerton 2006). Therefore, the second analytical approach we used was regression models that related trap catch to various temporal, spatial, landscape, and environmental variables. These regression models are powerful because they can quantify the temporal and spatial trends in abundance after accounting for many of the variables that influence the trap catch (Maunder and Punt 2004; Bacheler et al. 2013a). The downside of these models is that it is a big undertaking to standardize the catches of numerous reef fish species, many of which have very low catches that would require specialized zero-inflated models (Zuur et al. 2012). Instead, we used two univariate community metrics—the total number of individuals and the total number of species caught in the trap (Kenchington and Kenchington 2013)—as response variables in our regression models. Multivariate approaches were not used here given the difficulty of controlling for the spatial expansion of the survey over time. We believe these two analytical approaches (i.e., raw and standardized) used in combination are more powerful and informative than either approach alone, especially if there is strong agreement between the two.

For our analyses, we examined species of fish that were targeted by fishers separately from nontargeted fish species. Fishery-targeted species were those species targeted or highly valued by commercial or recreational hook-and-line fishers, while nontargeted species were all other species caught in the chevron trap survey. The purpose of these groupings (hereafter referred to as "species groupings") was to determine whether targeted species exhibited different spatial and temporal trends in abundance compared to nontargeted species. Even though harvest is currently prohibited for red snapper, speckled hind *Epinephelus drummondhayi*, and Warsaw grouper *Epinephelus nigritus*, these species were grouped with fishery-targeted species because of their long history of exploitation in the SEUS.

When taxa could not be identified to the species level, they were not included in the calculation of the total number of species present in the trap unless no other taxa in that same genus or family was also present in the trap. Taxonomic ambiguity exists for *Stenotomus* spp. in the SEUS, which could be a combination of *S. chrysops* and *S. caprinus* (Powles and Barans 1980; Sedberry and Van Dolah 1984); therefore, we treated *Stenotomus* spp. as a single species. All taxa identified to the generic or family level were included in calculations of the total number of individuals caught in the trap. All analyses used the catch of individuals or species in the trap (unstandardized for soak time) as response variables, based on the recommendation of Bacheler et al. (2013a).

Nominal analyses

Our first analysis using raw data was to construct a species accumulation curve for SERFS chevron trap data, in order to understand how the number of reef fish species in the SEUS increased as a function of the cumulative survey effort (i.e., number of chevron traps deployed). We used the vegan package (version 2.2-0) in R 3.1.2 (R Core Team 2014) to estimate the mean and variability of the species accumulation curve, using 200 random permutations of the 25 years of chevron trap data. We then overlaid the annual number of species caught and the corresponding effort expended each year to understand how our annual sampling of reef fish species related to the mean species accumulation curve. Years falling within the confidence interval would indicate the number of species observed in that year was not significantly different than the number of species observed from the same number of random stations across the entire dataset. The opposite would highlight years when fewer than expected species were observed.

Our second analysis using raw data was to determine whether there were obvious temporal trends for the 10 most common fishery-targeted and 10 most common nontargeted species. For this analysis, we quantified the contribution of each species to the total individuals caught for each of the two groups of species within 5-year bins between 1990 and 2014. Five-year bins were used instead of individual years in order to decrease some of the variability associated with sampling error and thereby increase our confidence in overall temporal trends.

The third analysis on raw data was developed with the explicit purpose to visualize temporal trends in occurrence and abundance for targeted and nontargeted species. For this analysis, the 10 most commonly caught fishery-targeted and 10 most commonly caught nontargeted species were examined. For each species grouping, we used stacked barplots to visualize temporal trends in each of three metrics: (1) proportion positive, which was the proportion of chevron trap samples each year in which the species was caught; (2) mean catch rate, which was the mean number of individuals of each species caught in each trap in a given year; and (3) normalized mean catch rate, which was the mean number of individuals of each species caught in each trap in a given year divided by the maximum yearly catch rate. The downside of the first two metrics is that the overall temporal trend was driven by the most common species; rare species had very little influence in the overall trend. In contrast, since the third metric was normalized to its own mean, all 10 species in each group had equal weights in the overall temporal trend.

Generalized additive models

Our next analytical approach was to use nonlinear regression models to standardize the trap catch for many variables that were hypothesized to influence trap catch. Specifically, we used generalized additive models (GAMs) to relate the trap catch to spatial, temporal, landscape, and environmental variables. A GAM is a nonparametric regression approach that uses a local smoother to fit potentially nonlinear relationships between the response and predictor variables (Wood 2006; Bacheler et al. 2009). As generalized linear models allow for alternative error distributions in linear models, GAMs extend traditional additive models by allowing for alternative error distributions (Hastie and Tibshirani 1990).

We developed GAMs using two different response variables to address our specific objectives. The first was the total number of individuals of all fish species caught in the trap, and the second was the total number of species caught in the trap. We calculated each of these two responses for three species groupings: all species combined, fishery-targeted species only, or nontargeted species only. Thus, six GAMs were developed in total. The main goal of these GAM analyses was to standardize the yearly catch of individuals or species by extracting the year effect of models at average values of all predictor variables (Maunder and Punt 2004).

We tested for the influence of year, day of the year, depth, soak time, bottom water temperature, time of day, moon phase, latitude, and longitude on the response variables. Year was the year of the sample, and day of the year was the day of the year in which the trap sample took place. Depth was measured in meters for each trap deployment; depths were recorded in a range of 13–218 m over the course of the survey, but samples 100 m and deeper were excluded from our analyses due to low sample size. Soak time was the number of minutes a trap soaked between trap deployment and the start of the trap retrieval process; we limited our analyses to soak times between 50 and 150 min because of low sample sizes outside this time. Bottom water temperature was the bottom temperature measured in degrees Celsius for each group of simultaneously deployed traps. Time of day was the time of trap deployment, measured in Coordinated Universal Time, and moon phase was the phase of the moon on the day of the trap sample. Latitude (°N) and longitude (°W) were the coordinates of the trap deployment location.

Highly collinear predictor variables can cause erratic model behavior, leading some to use GAMs based on a principle component analysis instead of traditional GAMs (Zhao et al. 2014). We tested for the presence of multicollinearity by calculating the variance inflation factor (VIF) for each predictor variable. The VIF measures the amount of variance that is inflated for each variable as a result of its collinearity with other predictor variables. We calculated the VIF for each predictor variable using the “vif” function in the HH package of R 3.1.2 (R Core Team 2014). The VIF for all predictor variables was less than 4.0, below the level generally acknowledged to be problematic (5–10; Neter et al. 1989), suggesting no significant multicollinearity among predictor variables in our dataset.

The full (“base”) GAM relating the trap catch to predictor variables was formulated as:

$$\begin{aligned} y = {} & f(year) + g_1(doy) + g_2(depth) + g_3(soak) + g_4(temp) \\ & + g_5(tod) + g_6(moon) + g_7(lon, lat), \end{aligned} \tag{1}$$

where y is one of the trap catch response variables described above, *year* is year of the sample, *doy* is day of the year of the sample, *depth* is depth of the sample, *soak* is the soak time of the sample, *temp* is the bottom temperature, *tod* is the Coordinated Universal Time, *moon* is the moon phase, *lon* is longitude, *lat* is latitude, f is a categorical function, and $g_{1–7}$ are nonparametric smoothing functions. Latitude and longitude were included together as a two-dimensional smoothed positional variable, the presence of which makes our GAMs spatially explicit. For moon phase, we used a cyclic smoother to wrap the smallest and largest values because moon phase is a naturally cyclic variable. All models were developed, coded, and analyzed in R version 3.1.2 (R Core Team 2014) using the mgcv library version 1.8-4 (Wood 2011). Estimated degrees of freedom for each smoothed predictor variable were chosen automatically by a built-in algorithm in the mgcv library and determined by the amount of flexibility in the fitted relationships between response and predictor variables.

For each GAM, we compared base models to a suite of reduced models that contained fewer predictor variables. Models were compared using the Akaike’s information criterion (AIC) and generalized cross validation (GCV); AIC balances the number of parameters of a model and its log-likelihood (Burnham and Anderson 2002), while GCV measures the out-of-sample prediction mean squared error. Since AIC and GCV agreed in all cases in our study, only AIC results are presented. For final models of the number of individuals caught, we compared gamma (with a log transformation), negative binomial, Tweedie, and Gaussian (with a log or fourth-root transformation) error distributions using model diagnostics output from the “gam.check” function in the “mgcv” library. The Gaussian distribution with a fourth-root transformation displayed the best pattern of residuals compared to any other distribution, and was selected for all three GAMs modeling the number of individuals caught. For GAMs modeling the number of species caught, we compared Poisson, negative binomial, and Tweedie distributions, and the Poisson models outperformed all other distributions based on the pattern of residuals so they were used here. All final GAM models met assumptions of normality and constant variance.

The main benefit of GAMs was that they were able to standardize the yearly catch of individuals or species by extracting the year effect of models at average values of all predictor variables. The exact values or levels chosen for prediction may have influenced the absolute estimates of individuals and species, but not the relative pattern or trends over time, which is our primary focus. An important

Table 1 Sampling information for the 25 years of chevron trap data from the Southeast Reef Fish Survey included in the analysis

Year	*N*	Dates sampled	Depth range (m)	Latitude range (°N)	Unique species caught
1990	305	4/23–8/9	17–93	30.42–33.82	41
1991	268	6/11–9/24	17–95	30.75–34.61	43
1992	288	3/31–8/13	17–62	30.42–34.32	37
1993	374	5/10–8/13	16–94	30.43–34.32	41
1994	358	5/9–10/26	16–93	30.74–33.82	48
1995	342	5/3–10/26	16–60	29.78–33.75	39
1996	371	4/29–9/16	14–95	27.92–34.32	39
1997	382	4/21–9/29	16–96	27.87–34.42	43
1998	413	3/31–8/18	14–92	27.44–34.59	49
1999	206	6/2–9/28	15–75	27.27–34.41	38
2000	252	5/16–10/19	15–95	28.95–34.28	41
2001	193	5/23–10/24	14–91	27.87–34.28	31
2002	206	6/17–9/24	13–94	27.86–33.94	40
2003	214	6/3–9/22	16–92	27.43–34.33	33
2004	270	5/5–10/28	14–91	29.00–33.97	40
2005	303	5/3–9/29	15–69	27.33–34.32	43
2006	278	6/6–9/28	15–94	27.27–34.39	31
2007	322	5/21–9/24	15–92	27.33–34.33	41
2008	303	5/5–9/30	15–92	27.27–34.59	42
2009	396	5/6–10/8	14–91	27.27–34.60	40
2010	706	5/4–10/27	14–92	27.34–34.59	52
2011	643	5/19–10/25	15–93	27.23–34.32	47
2012	1109	4/24–10/10	15–98	27.23–35.01	61
2013	1282	4/24–10/4	16–92	27.23–35.01	60
2014	1453	4/28–10/21	15–99	27.23–35.01	61
Total	11,237	3/31–10/28	13–99	27.23–35.01	118

N is the number of trap samples

secondary benefit was that we were able to quantify the form of the relationships between the catch of individuals or species and the various predictor variables included in the GAMs. For visualization, we plotted the relationship between response and predictor variables for GAMs in response space. We also fit linear models to raw mean, raw median, and standardized yearly values for each of the three species groupings × two response variables, to quantify whether the trends in relative abundance increased, decreased, or did not change over the 25-year survey. For visualization, we also extracted the partial effect of position using the vis.gam function in the mgcv library.

Last, we tested for the presence of spatial autocorrelation, where samples nearer one another tend to be more similar than samples further apart. We developed semivariograms for each of the response variables each year using the R package geoR, version 1.7-4.1. There were no consistent annual patterns in the relationship between semivariance of the model residuals and distance between sampling points, indicating no significant spatial autocorrelation in the residuals.

Results

Overall, 11,237 chevron trap samples were included in the analyses over the 25-year time period (annual mean = 449; range 193–1453; Table 1). Annual sample sizes were higher in the last 5 years of the study (mean = 1039) than the first 20 years (mean = 302). While the range of dates and depths sampled was similar across the 25 years of the study, the range of latitudes sampled was not, expanding further southward and northward over time (Table 1).

A total of 118 unique species were captured in chevron traps during our study (annual mean = 43; range 31–61), with more species generally caught in years with more sampling (Table 1). Individual chevron trap deployments caught a mean of 3.1 species (range 0–12) and 39.2 individuals (range 0–439), with only 15 % of all trap samples having zero catch. There was a positive relationship between the number of species and number of individuals caught (linear model: slope = 14.5; $F = 88.6$; $P < 0.0001$; $R^2 = 41.1$; Fig. 2).

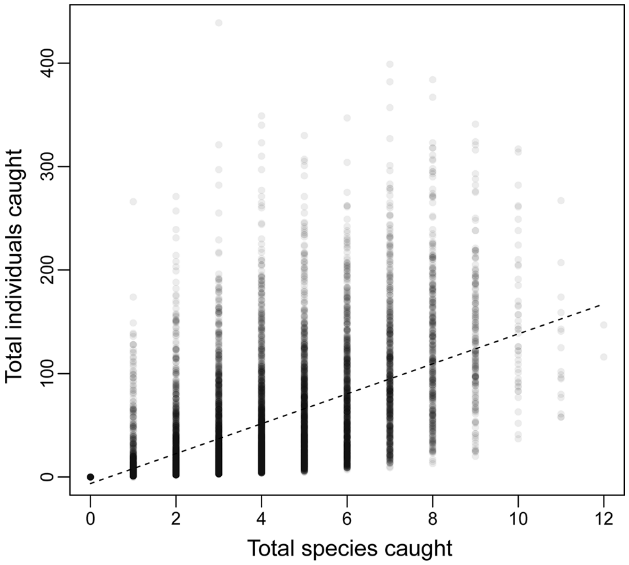

Fig. 2 Relationship between the total number of individuals caught and the total number of species in chevron traps from the Southeast Reef Fish Survey, 1990–2014. *Darker points* indicate more overlap among points, and the *dashed line* shows the linear model fit

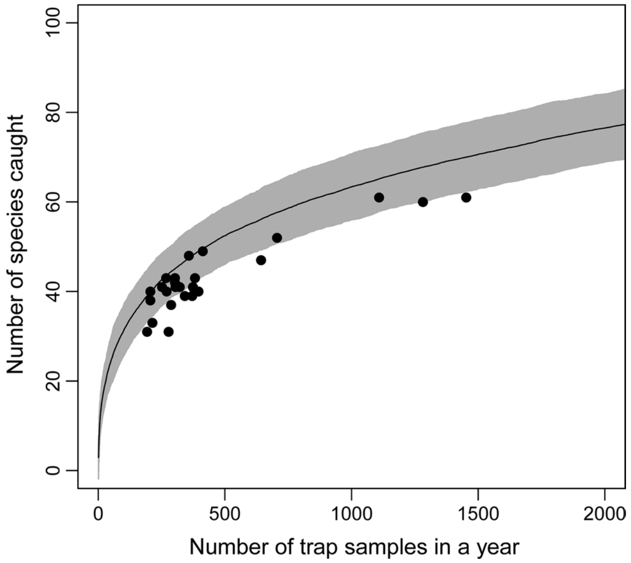

Fig. 3 Mean species accumulation curve (*solid line*) and 95 % confidence interval (*gray shading*) for reef fish species caught in chevron traps, 1990–2014, by the Southeast Reef Fish Survey. *Solid points* show the observed number of species caught and number of trap samples taken for each of the 25 years of the survey

The species accumulation curve for SERFS chevron trap data showed an initial rapid increase in the number of species observed as the number of chevron trap samples increased, but the rate of new species collected slowed as more chevron trap samples were examined (Fig. 3). In addition, eleven out of 25 years (44 %) of SERFS chevron trap sampling fell below and outside of the species accumulation curve confidence interval (Fig. 3).

Of the 441,298 total individuals caught during the study, the most commonly caught fishery-targeted species were black sea bass *Centropristis striata* (*N* = 144,781, 33 % of total), vermilion snapper *Rhomboplites aurorubens* (*N* = 29,653, 7 %), red porgy *Pagrus pagrus* (*N* = 21,784, 5 %), and gray triggerfish *Balistes capriscus* (*N* = 10,537, 2 %; Table 2). The contribution of black sea bass and red snapper to the catch of fishery-targeted species appeared to increase in later years, while the contribution of vermilion snapper, white grunt, knobbed porgy *Calamus nodosus*, scamp *Mycteroperca phenax*, red grouper *Epinephelus morio*, and snowy grouper *Epinephelus niveatus* appeared to decline (Table 2). The most commonly caught nontargeted species were tomtate *Haemulon aurolineatum* (*N* = 109,662, 25 %), *Stenotomus* spp. (*N* = 81,415, 18 %), bank sea bass *Centropristis ocyurus* (*N* = 12,877, 3 %), and sand perch *Diplectrum formosum* (*N* = 6531, 1 %). The contribution of tomtate to the nontargeted catch appeared to increase during the last 5 years, while the contribution of *Stenotomus* spp. appeared to decrease in the last 5 years (Table 2).

Declines in the proportion of positive traps, mean catch rate, and normalized catch rate were observed for the combined 10 most common nontargeted fish species over time, but obvious declines were not observed for fishery-targeted species (Fig. 4). While nontargeted declines were strong and clear, fishery-targeted species were much more variable across the 25 years of the study. As expected, the few most common species in each group tended to drive overall patterns in the proportion positive and especially mean catch rate. Nonetheless, overall downward trends were still apparent for the normalized mean catch rate plots of nontargeted species, where each of the 10 species in each group was given equal weight (Fig. 4). Increases in red snapper and black sea bass after 2009 appeared to compensate for the overall decline in the other eight fishery-targeted species (Fig. 4).

Overall, the GAMs explained 20.7–41.2 % of the deviance for models standardizing the total number of individuals or species caught in chevron traps (Table 3). Generally, models for nontargeted individuals or species explained more deviance than models for fishery-targeted individuals or species, with models built on data from all species falling in between. Moreover, GAMs modeling the number of fishery-targeted individuals caught in traps explained more deviance than models for the number of fishery-targeted species caught, but the opposite was true for models of nontargeted individuals (Table 3).

For five of six GAMs, the base model outperformed reduced models that excluded one or more predictor

Table 2 Ten most numerous fishery-targeted species and the 10 most numerous nontargeted species during Southeast Reef Fish Survey chevron trap sampling, 1990–2014, as well as the contribution of each of those species to the total number of individuals caught for each species grouping (fishery-targeted or nontargeted species) in 5-year bins

Common name	Scientific name	Total caught	Contribution of each species to the total individuals caught				
			1990–1994	1995–1999	2000–2004	2005–2009	2010–2014
Fishery-targeted species							
Black sea bass	*Centropristis striata*	144,781	54.1	55.1	66.8	57.0	74.7
Vermilion snapper	*Rhomboplites aurorubens*	29,653	23.0	19.6	13.4	18.0	6.7
Red porgy	*Pagrus pagrus*	21,784	10.8	10.0	8.9	14.8	8.4
Gray triggerfish	*Balistes capriscus*	10,537	3.3	7.9	3.1	5.1	4.7
White grunt	*Haemulon plumieri*	7169	5.2	2.8	4.2	2.3	2.6
Red snapper	*Lutjanus campechanus*	1919	0.3	0.2	0.2	0.3	1.6
Knobbed porgy	*Calamus nodosus*	1893	1.6	1.8	1.1	0.8	0.2
Scamp	*Mycteroperca phenax*	1346	0.8	1.5	0.7	0.6	0.3
Red grouper	*Epinephelus morio*	601	0.2	0.3	0.6	0.6	0.2
Snowy grouper	*Epinephelus niveatus*	355	0.1	0.3	0.2	0.1	0.1
Nontargeted species							
Tomtate	*Haemulon aurolineatum*	109,662	52.7	39.2	44.9	39.9	63.5
Stenotomus spp.	*Stenotomus* spp.	81,415	33.2	48.0	45.8	46.3	21.9
Bank sea bass	*Centropristis ocyurus*	12,877	5.9	6.0	3.6	6.0	7.0
Sand perch	*Diplectrum formosum*	6531	3.2	2.7	2.6	4.3	2.6
Spottail pinfish	*Diplodus holbrookii*	3323	1.8	1.0	1.1	1.2	2.1
Pinfish	*Lagodon rhomboides*	2762	0.8	2.2	1.2	1.0	1.0
Planehead filefish	*Stephanolepis hispidus*	1104	1.3	0.2	0.1	0.2	0.4
Spotted moray	*Gymnothorax moringa*	326	0.1	0.1	0.2	0.4	0.1
Ocellated moray	*Gymnothorax saxicola*	227	0.4	0.1	0.0	0.0	0.0
Reticulate moray	*Muraena retifera*	205	0.1	0.1	0.0	0.1	0.1

variables based on AIC values (Table 3). The only reduced model judged by AIC to be better than the base model was for the catch of nontargeted individuals, where time of day was excluded. In all other cases, models excluding time of day and moon phase were the best reduced models, but not better than base models (Table 3). Therefore, we subsequently focused our attention on the best performing models.

Mean (i.e., nonstandardized) annual catch per trap, median annual catch per trap, and standardized year effects from the GAMs displayed variable trends over time (Fig. 5). While the temporal patterns were similar among the three metrics, the standardized trends appeared to decline the least and median catches often declined the most, and nontargeted species appeared to decline more so than fishery-targeted species. The most substantial declines were observed for the median number of nontargeted individuals and species caught in traps. In the early 1990s, traps caught a median of 18 nontargeted individuals and a median of 2–3 nontargeted species, but by the 2010s, traps caught a median of fewer than three nontargeted individuals and a median of one nontarget species. In contrast, the standardized catch of fishery-targeted individuals ranged from 5 to 25 per trap, with no obvious temporal trend. When all species were examined together, declines were apparent but not as strong as the declines in nontargeted species (Fig. 5).

Sixteen out of 18 time series (two response variables × three metrics × three species groupings) were significantly negative based on linear models fitted to yearly values (20–100 % declines over the 25-year time series; Table 4). The two exceptions were the standardized catch of fishery-targeted individuals (12 % increase; $P = 0.63$) and the standardized catch of individuals of all species (27 % decline; $P = 0.11$; Table 4). Most standardized time series had a slope that was less than the corresponding slopes of mean and median catches, where a negative slope is defined as the annual loss of the number of individuals or species. For instance, there were declines of 1.36 (mean) and 1.07 (median) total individuals in chevron traps each year (resulting in 54 and 81 % declines over the entire time series, respectively), but the standardized catch of all individuals declined by 0.45 individuals per year (27 % decline). The mean and median catch of nontargeted species declined annually by 0.05 species (60–63 % decline),

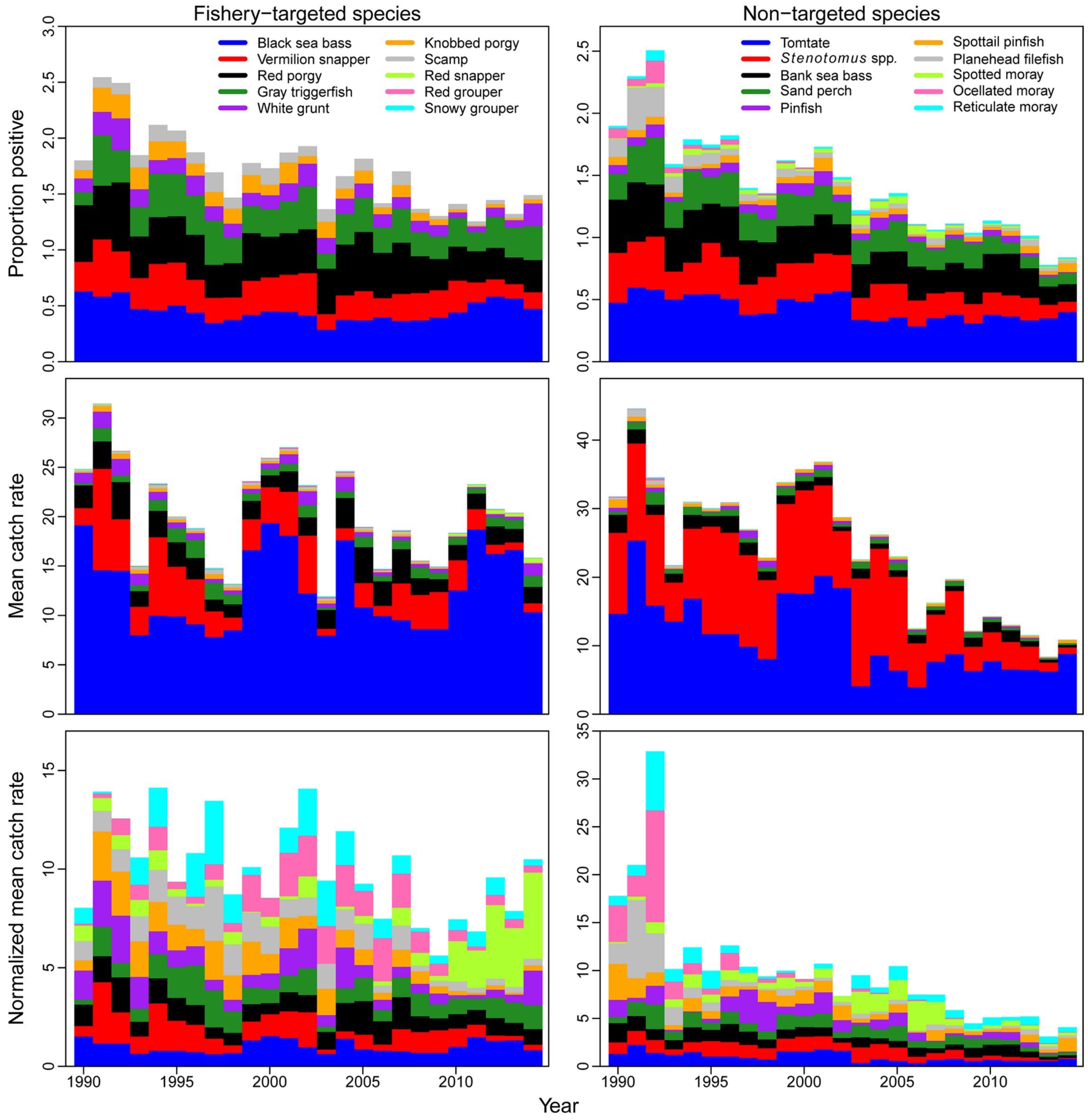

Fig. 4 *Stacked barplots* showing the proportion of traps in which the species was present (*top row*), mean catch rate (*middle row*), and normalized mean catch rate (*bottom row*) for fishery-targeted (*left column*) and nontargeted species (*right column*) from Southeast Reef Fish Survey chevron trap data, 1990–2014. Only the 10 most commonly caught fishery-targeted and 10 most commonly caught nontargeted species are shown

while the standardized catch declined by 0.04 species per year (35 % decline, Table 4).

Two-dimensional spatial effects from GAMs (at average values of all other predictor variables) indicated that fishery-targeted and nontargeted individuals and species were not distributed homogenously across the study area. All six GAMs (two response variables × three species groupings) predicted higher effects nearshore off North and South Carolina and south of Cape Canaveral, and lower effects offshore in North Carolina. Fishery-targeted species tended to have higher effects offshore in South Carolina, Georgia, and Florida than nontargeted species, which generally had higher effects inshore throughout the study area, especially in northern Florida.

The remaining predictor variables influenced the chevron trap catch in a variety of ways. With a few exceptions, the catch of individuals and species of all species groupings displayed a dome-shaped relationship with day of the year and soak time, a positive relationship with bottom temperature, and a negative relationship with depth (Figs. 6, 7). Although the effects of time of day and moon phase on the trap catch were statistically important in most cases, the effects appeared to be weak and likely not biologically important given large confidence intervals. Predictor

Table 3 Model selection of spatially explicit generalized additive models built on data from Southeast Reef Fish Survey chevron trap sampling, 1990–2014

Model	Dev. ex. (%)	AIC	$f_i(year)$	$g_1(doy)$	$g_2(depth)$	$g_3(soak)$	$g_4(temp)$	$g_5(tod)$	$g_6(moon)$	$g_7(lon, lat)$
Total individuals										
Base	36.6	28,865.6	24***	8.4***	7.4***	4.2***	8.2***	4.8*	4.1***	28.6***
Base—*tod*	36.4	28,873.0	24***	8.1***	7.5***	4.3***	8.2***	ex	3.1***	28.6***
Base—*moon*	36.4	28,883.3	24***	8.0***	7.4***	4.1***	8.2***	4.7*	ex	28.5***
Fishery-targeted individuals										
Base	30.6	27,071.9	24***	8.1***	7.6***	4.2***	7.7***	6.6*	4.8***	28.3***
Base—*tod*	30.5	27,077.7	24***	8.1***	7.6***	4.2***	7.7***	ex	4.6***	28.3***
Base—*moon*	30.3	27,102.2	24***	8.0***	7.7***	4.2***	7.7***	5.5**	ex	28.3***
Nontargeted individuals										
Base—*tod*	40.3	29,105.3	24***	8.2***	5.1***	8.4***	8.0***	ex	1.2*	28.7***
Base	40.3	29,109.6	24***	8.2***	4.9***	4.4***	7.9***	3.6	1.3*	28.7***
Base—*moon*	40.3	29,110.1	24***	8.1***	5.4***	4.4***	8.0***	1.0	ex	28.7***
Total species										
Base	35.9	44,168.2	24***	8.4***	7.0***	3.4***	7.9***	1.0*	7.2***	28.6***
Base—*tod*	35.8	44,172.1	24***	8.4***	7.0***	3.4***	7.9***	ex	7.2***	28.6***
Base—*moon*	35.8	44,184.9	24***	8.2***	7.1***	3.3***	7.9***	7.6*	ex	28.6***
Fishery-targeted species										
Base	20.9	34,985.0	24***	8.2***	6.7***	3.0***	7.9***	7.4	5.5**	28.1***
Base—*tod*	20.8	34,985.9	24***	8.2***	6.7***	2.9***	7.9***	ex	5.5**	28.1***
Base—*moon*	20.7	34,996.6	24***	8.0***	6.8***	3.0***	7.9***	7.0	ex	28.1***
Nontargeted species										
Base	41.2	29,278.2	24***	7.8***	6.8***	3.2***	7.3***	1.0**	1.0	28.6***
Base—*moon*	41.2	29,278.8	24***	7.7***	6.8***	2.9***	7.4***	1.0**	ex	28.6***
Base—*tod*	41.2	29,285.1	24***	7.8***	6.7***	3.7***	7.3***	ex	1.0	28.5***

Two response variables were used: (1) total individuals caught in the trap and (2) total species caught in the trap. Models were fit on data that included (1) all species, (2) fishery-targeted species only, and (3) nontargeted species only. Degrees of freedom are shown for factor (f) terms, and estimated degrees of freedom are shown for nonparametric, smoothed terms (g)

Dev. ex. is the deviance explained by the model, AIC is the Akaike information criterion, and "Base" and predictor variables are defined in Eq. 1

Year year of the sample, *doy* day of the year, *depth* bottom depth, *soak* soak time, *temp* bottom temperature, *tod* time of day, *moon* moon phase, *lon* longitude, *lat* latitude

Asterisks denote significance at the following alpha levels: * 0.10; ** 0.01, *** 0.001

variable effects between models for individuals and species generally were similar, but there were some differences in predictor variable effects between species groupings. For instance, the highest catch of nontarget individuals was predicted to occur at the shortest soak times, whereas the catch of fishery-targeted individuals was highest at moderate soak times (Fig. 6). Also, the highest predicted catch of fishery-targeted species occurred at the deepest depths, while the opposite was true of the catch of nontargeted species (Fig. 7).

Discussion

Quantifying changes in the diversity and structure of fish communities is a central focus of fisheries science, ecology, and conservation (Walters and Martell 2004). There are dozens of examples that highlight fish population declines or major community changes (e.g., Lekve et al. 2002; Hutchings and Baum 2005; Christensen et al. 2014), and elucidating the scale and scope of these changes is the first step in determining causation. We used trap data collected during three decades to show that reef fish generally declined in the SEUS, but declines in nontargeted reef fish species were much more dramatic and consistent than declines in fishery-targeted reef fish species. Moreover, the strong agreement between nominal analyses of raw data and standardized data using GAMs increased confidence in overall trends. These results suggest that (1) nontargeted fish species should not be ignored by research or management, because their decline may negatively affect fishery-targeted species that consume some of them, (2) declines in

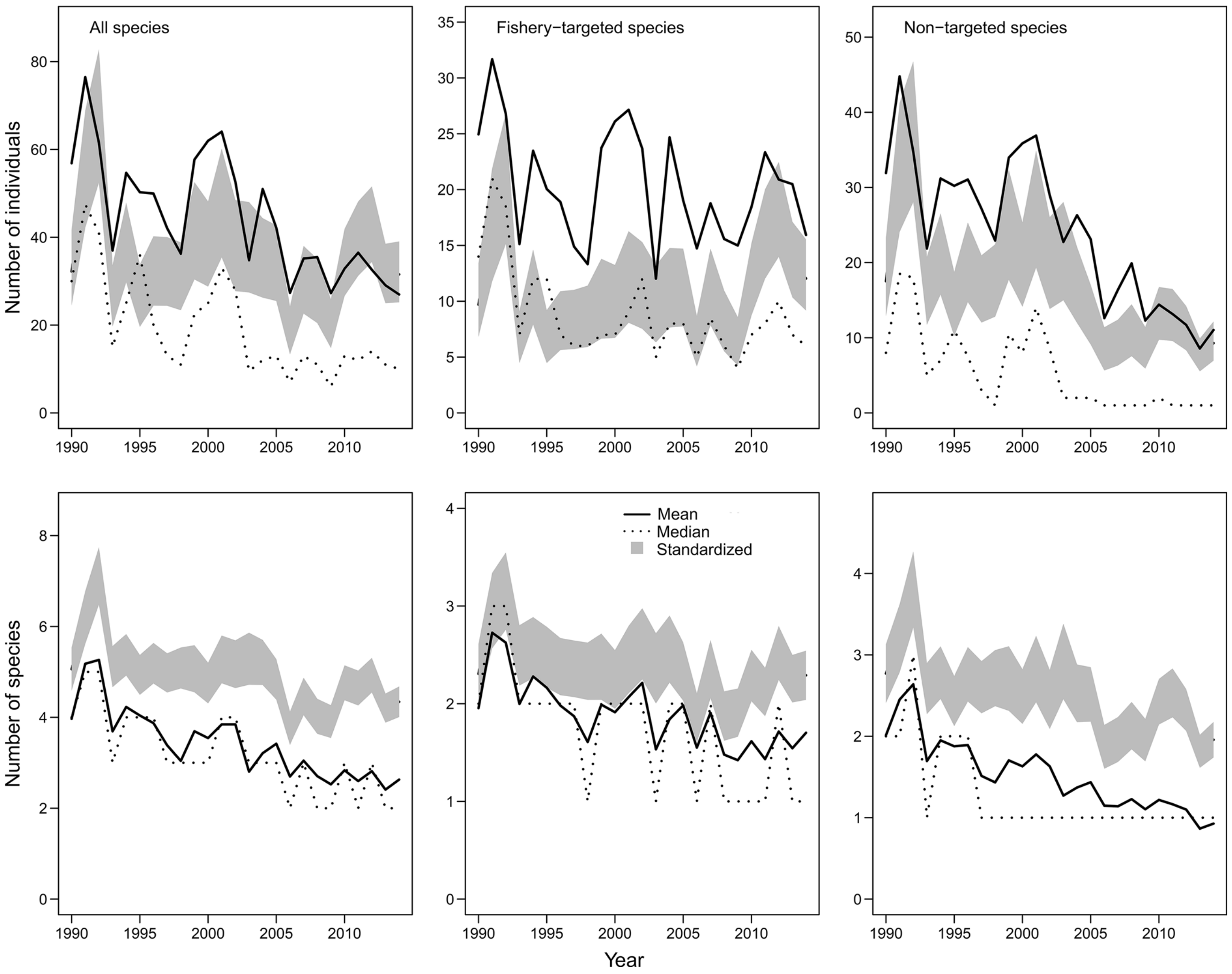

Fig. 5 Mean, median, and standardized annual chevron trap catch (*top row* number of individuals, *bottom row* number of species) from generalized additive models using Southeast Reef Fish Survey chevron trap data, 1990–2014. Shown are total individuals or species caught for all species (*left column*), fishery-targeted species only (*middle column*), or nontargeted species only (*right column*). *Shaded bands* are 95 % confidence intervals

fishery-targeted species were less drastic than nontargeted species, perhaps due to successful fisheries management in the SEUS or that abundance is being sustained at low levels after a period of decline that preceded our study, and (3) using GAMs is a powerful but straightforward approach to evaluate community changes in a univariate context, in order to standardize catches for changes in sampling or environmental conditions.

We expected nontargeted species to experience little change or perhaps even increase over time, under the assumption that fishery harvest would remove potential predators of many nontargeted species. Contrary to our main hypothesis, we observed substantial declines in catches of nontargeted reef fish species in the SEUS, which were clear using both raw and standardized catches and highly consistent among species as diverse as tomtate, planehead filefish *Stephanolepis hispidus*, and moray eels. Little attention has been paid to nontargeted reef fish species in the SEUS; those that have tended to focus on tomtate and found mixed results, likely due to the inability of separating population changes from the behavior of fishers. For instance, Shertzer et al. (2009) used nonmetric multidimensional scaling to show that tomtate decreased in prevalence more so than any other species they examined in the SEUS between 1980 and 2007. Alternatively, Parker and Dixon (1998) found that tomtate increased in headboat catches in North Carolina between the mid-1970s and early 1990s. It is unknown what could cause declines in the diverse assemblage of SEUS nontargeted species. The recent lionfish (*Pterois* spp.) invasion has resulted in broad ecological changes in the nearby Bahamas and Caribbean Sea (Lesser and Slattery 2011); however, herbivorous fish

Table 4 Results of linear models testing for temporal trends in mean, median, or standardized number of individuals or species caught in chevron traps from Southeast Reef Fish Survey sampling, 1990–2014

Model	Slope	SE	*P* value	R^2	% change
Total individuals					
Mean	−1.36	0.264	<0.001	0.53	−54
Median	−1.07	0.227	<0.001	0.49	−81
Standardized	−0.45	0.171	0.11	0.11	−27
Fishery-targeted individuals					
Mean	−0.25	0.134	0.08	0.12	−25
Median	−0.32	0.095	0.003	0.33	−61
Standardized	0.05	0.072	0.63	0.01	12
Nontargeted individuals					
Mean	−1.11	0.154	<0.001	0.69	−71
Median	−0.53	0.108	<0.001	0.51	−100
Standardized	−0.71	0.088	<0.001	0.51	−68
Total species					
Mean	−0.09	0.011	<0.001	0.72	−48
Median	−0.10	0.016	<0.001	0.62	−53
Standardized	−0.06	0.009	<0.001	0.46	−27
Fishery-targeted species					
Mean	−0.03	0.007	<0.001	0.54	−36
Median	−0.06	0.012	<0.001	0.48	−57
Standardized	−0.02	0.006	0.004	0.31	−20
Nontargeted species					
Mean	−0.05	0.006	<0.001	0.80	−60
Median	−0.05	0.011	<0.001	0.45	−63
Standardized	−0.04	0.005	<0.001	0.54	−35

"Standardized" refers to a linear model fitted to yearly catch estimates from a generalized additive model (see Eq. 1), "Slope" is the slope of a line fit to yearly values, "SE" is the standard error of the slope estimate, and " % change" is the percent change of linear model estimates between 1990 and 2014

have been most affected by the lionfish invasion in these areas (Lesser and Slattery 2011), and to date no relationship has been documented between lionfish and small generalist fish abundance (e.g., tomtate, filefish, other predators such as moray eels). Other possible explanations include climate change (Parker and Dixon 1998; Munday et al. 2008; Bell et al. 2015), decadal-scale environmental changes (Wood and Austin 2009), bycatch, complex fishing-induced community changes (Jennings et al. 2002), or synergism between fishing and environmental conditions (Kirby et al. 2009).

Given the long history of reef fish exploitation in the SEUS, we also expected to observe consistent declines in fishery-targeted species over the course of our study. While some species did appear to decline, such as vermilion snapper, knobbed porgy, and white grunt, recent increases in black sea bass and red snapper appeared to offset these declines. Black sea bass and red snapper may have increased since 2009 due to more sampling in Florida, actual increases in abundance, or a combination of the two. The net result is that our standardized analyses using the number of individuals as the response variable did not detect overall declines, even though some of the species in that group may have declined. Similarly, Rudershausen et al. (2008) compared catch rates of economically important reef fish in North Carolina between the 1970s and 2000s, finding increases for some species and decreases for others. McGovern et al. (1998) documented increased catch rates for some reef fish and declines for others in the SEUS, but also that temporal trends in catch rates were often depth-specific. Although some species have declined over the last three decades, fishing does not appear to have caused widespread declines across the suite of fishery-targeted species in the SEUS that have been observed elsewhere (Rogers and Ellis 2000; Coll et al. 2009; Paddack et al. 2009), indicating potential management success. However, the species that have shown the greatest increases also are ones that are under heavy management and have life history characteristics such as early maturity that make them more likely to respond to management measures.

A major benefit of standardizing reef fish catches using GAMs was the ability to elucidate exactly how spatial, temporal, landscape, or environmental variables were related to the number of individuals or species caught in traps. The most striking observation was the strong, positive relationship between reef fish catches and bottom water temperature. The SEUS can experience substantial variability in water temperature among years (Hyun and He 2010), so failing to standardize reef fish catches by bottom temperature would decouple the relationship between catch and true abundance (Maunder and Punt 2004). Bacheler et al. (2014) showed that water temperature influenced the ability of chevron traps to detect gray triggerfish and red porgy present at a site; the warmer the water, the more likely these two species were to be caught in traps. Bottom water temperature, however, also may influence the spatial distribution of reef fish species across a landscape, with some species leaving an area if water temperature gets too cold. Our approach did not allow for a separation of a species' detectability from its distribution or movement, so our observed relationship between reef fish catch and bottom temperature could very well be due to both phenomena.

Chevron trap efficiency varies by species and sizes of individuals; thus, some species or individuals not prone to capture could be underestimated (Coggins et al. 2014). Examples of species likely underrepresented in our study include non-scavenger species like lionfish, timid species like gag *Mycteroperca microlepis*, small species like wrasses, or large-bodied species like sharks (Bacheler et al. 2013c). It is rare in ecological studies, however, that any sampling gear is able to perfectly detect all species and

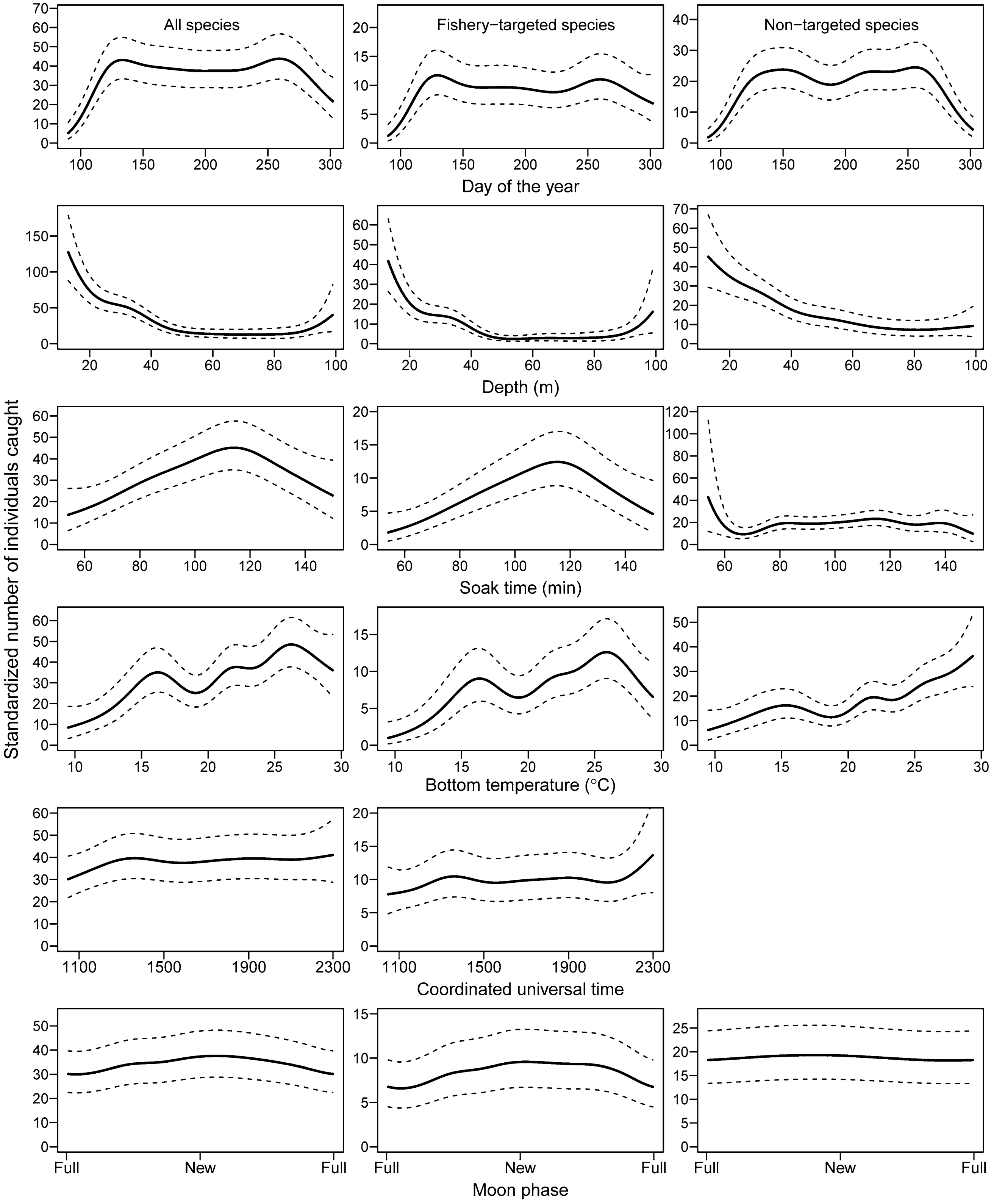

Fig. 6 Standardized number of individuals caught as a function of day of the year, depth (m), soak time (min), bottom temperature (°C), time of day (Coordinated Universal Time), and moon phase using spatially explicit generalized additive models built using Southeast Reef Fish Survey chevron traps data, 1990–2014. *Solid line* is the standardized number of individuals caught at average values of all other covariates, and *dashed lines* are 95 % confidence intervals

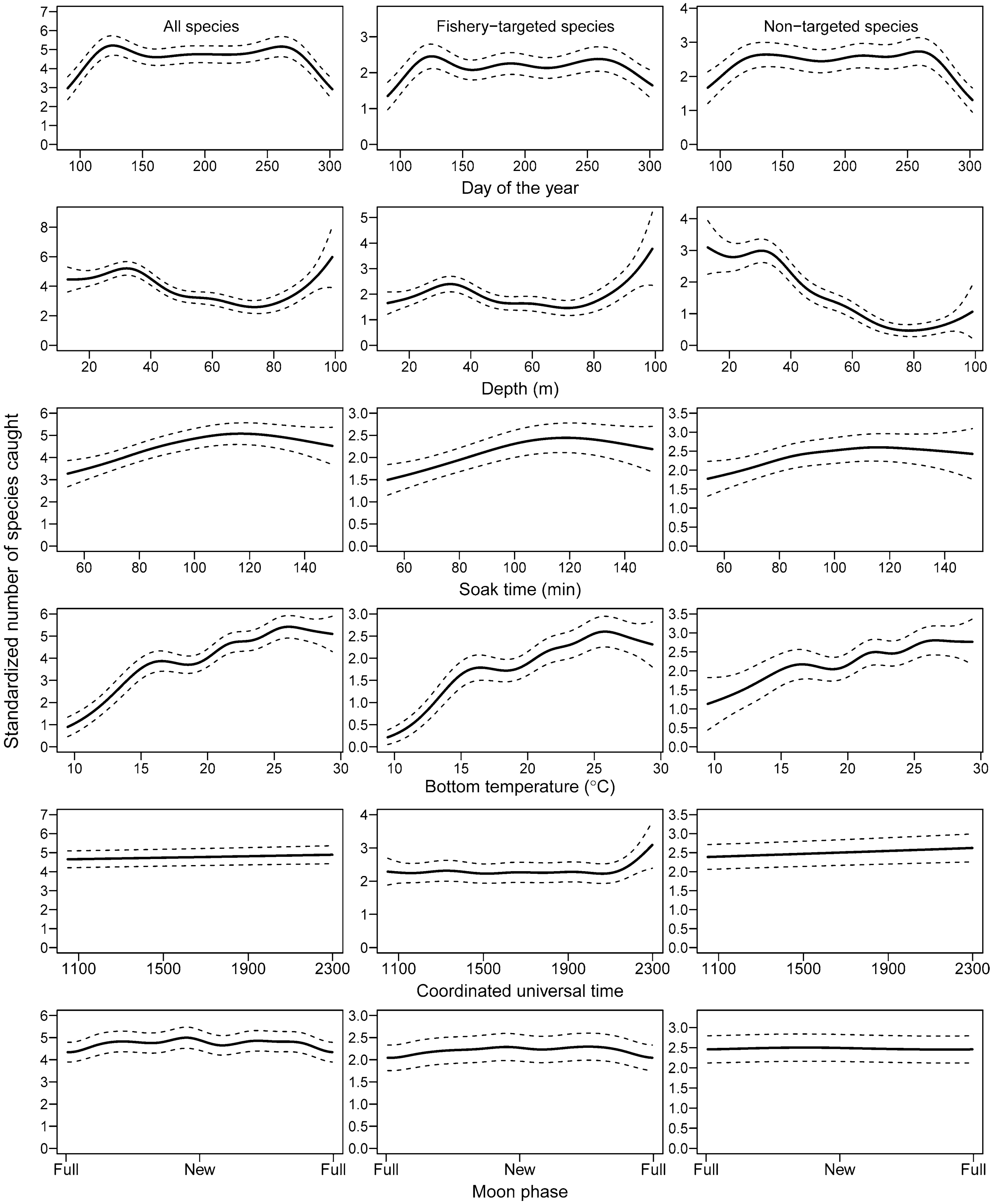

Fig. 7 Standardized number of species caught as a function of day of the year, depth (m), soak time (min), bottom temperature (°C), time of day (Coordinated Universal Time), and moon phase using spatially explicit generalized additive models built using Southeast Reef Fish Survey chevron traps data, 1990–2014. *Solid line* is the standardized number of species caught at average values of all other covariates, and *dashed lines* are 95 % confidence intervals

individuals present across a landscape (MacKenzie et al. 2002). We did not have to assume that all species or individuals were caught by the traps, but the downside of not doing so is that our results only pertain to those species that are effectively sampled by traps and not necessarily the entire reef fish community. We did assume that the catchability of reef fish species was constant over space and time, which is assumed very commonly but unlikely to always be true (Boulinier et al. 1998; MacKenzie et al. 2002; Gotelli et al. 2010). Significant violations of this assumption could influence the interpretation of our results, especially the GAM covariate plots that might actually be a product of a species' patterns of abundance and detectability (Coggins et al. 2014). We view temporal trends as being much more robust to potential violations of constant catchability because the rate of change was large and consistent over multiple decades.

The number of species or individuals across a landscape is by definition a combination of species ranging from the very common to the very rare. In our study, some species such as black sea bass and tomtate were caught in over 40 % of traps deployed, whereas 25 species were caught a single time over the 25-year trap survey (e.g., porkfish *Anisotremus virginicus*, trumpetfish *Aulostomus maculatus*). Some have emphasized the importance of rare species due to their large overall numbers and often positive relationship between the number of rare species and biodiversity in an area (Gaston 1994; Berg and Tjernberg 1996). Others have shown that common species are most important because they drive patterns in biodiversity and the delivery of ecosystem services (Lennon et al. 2004; Winfree et al. 2015). In fact, Lennon et al. (2004) argue that a minority of common species can be used as a broad surrogate for patterns in biodiversity across a landscape. Our raw analyses were weighted mostly toward common species, whereas our standardized GAM analyses (with number of species as the response variable) were influenced by common and rare species. The high level of agreement between the two approaches is encouraging and suggests that temporal trends were real and occurred for both common and rare species.

An alternative approach used to estimate diversity is species accumulation curves. The primary benefit of species accumulation curves is that they allow for estimation of the number of species in an area even when sampling is limited (Bunge and Fitzpatrick 1993). In our study, the species accumulation curve did not asymptote over 2000 (or even 10,000) samples, suggesting that rare species new to SERFS will continue to be encountered for many years to come (Gotelli and Colwell 2001). A secondary benefit of species accumulation curves is that they can be used to compare the number of species caught in a given year (with a known amount of effort) to the mean and variability of the overall species accumulation curve. We found that 11 out of 25 years of sampling fell below the confidence interval, suggesting that (1) sampling may have been somewhat clustered during some years and thus caught fewer species than expected, (2) variability in reef fish catches among years and across space was substantial in our study, and the sampling in some years did not capture that full variability that was evident when all samples were randomized, or (3) a combination of the two.

There were some drawbacks of our study design and analyses. First, we separately analyzed fishery-targeted and nontargeted species based on how we defined whether there were targeted fisheries for the species of interest. In reality, fishers may have harvested some of the non-harvested species (Bacheler and Buckel 2004), while the harvest of some fishery-targeted species like red snapper has been mostly prohibited since 2010 (Mitchell et al. 2014). Second, the latitudinal extent of sampling expanded modestly over time, which may have influenced study results. We believe this bias is unlikely because (1) survey expansion occurred during two major time periods (1995–1996 and 2012), neither of which was associated with an obvious change in raw or standardized catch of reef fish species or individuals, (2) the number of species or individuals caught in traps in the middle of the SEUS followed similar trajectories as the overall trend, and (3) we included a predictor variable, spatial position, in our GAM models to explicitly account for survey expansion over time. Third, our GAMs explained 20–41 % of the deviance in catch, suggesting that other unmeasured variables such as habitat characteristics may be important in explaining patterns in biodiversity. Fourth, microhabitat information was not available for samples in our study, so any changes in habitat over time may have influenced our results. While habitat degradation and concomitant fish declines have been observed in coral reef ecosystems (Hughes et al. 2003; Pandolfi et al. 2003), similar declines in rocky, temperate hard-bottom habitats in the SEUS have not been observed, so we consider this explanation unlikely. Last, since all SERFS samplings occurred on or near hard bottom, GAM spatial predictions only apply to hard-bottom areas throughout the SEUS.

Our results add to the growing literature documenting long-term temporal changes in fish species around the world (Lekve et al. 2002; Hutchings and Baum 2005; Christensen et al. 2014), but our finding that declines in nontargeted species were much stronger than declines in fishery-targeted species in the SEUS was unexpected. While fishery-targeted species in the SEUS are highly regulated with size and bag or trip limits and most with annual quotas, nontargeted fish species generally lack any form of management protection in the SEUS, are more vulnerable to invasive lionfish predation due to their smaller size (Muñoz et al. 2011), and may be more vulnerable to environmental changes than larger-bodied, longer-lived species. Research is now needed to understand why nontargeted species have declined.

Acknowledgments We thank the captains and crews of the RV *Palmetto*, RV *Savannah*, NOAA Ship *Pisces*, and NOAA Ship *Nancy Foster*, SERFS staff, and numerous volunteers for making field work possible. We thank N. Ballew, A. Hohn, T. Kellison, P. Marraro, K. Shertzer, and two reviewers for providing comments on earlier versions of this manuscript. This work was funded by the National Marine Fisheries Service. Data collection for this study was allowed through various Scientific Research Permits, and research followed the guidelines of the US Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training (http://grants.nih.gov/grants/olaw/references/phspol.htm#USGovPrinciples). This article does not contain any studies with human participants performed by any of the authors. The views and opinions expressed or implied in this article are those of the authors and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

Compliance with ethical standards

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

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