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Decadal-scale decline of scamp (*Mycteroperca phenax*) abundance along the southeast United States Atlantic coast

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ABSTRACT

Scamp (*Mycteroperca phenax*) are a long-lived, economically important grouper species for which population trends are unknown along the southeast United States Atlantic coast (SEUS). We analyzed fishery-independent chevron trap (1990–2016) and underwater video (2011–2015) data using two-stage generalized additive models to elucidate changes in scamp relative abundance and mean size across the SEUS. A total of 1813 scamp were caught in 15609 trap samples across 27 years of sampling, and the proportion of traps catching scamp declined from a peak of 18.0% in 1994 to 2.5% in 2016. Likewise, mean scamp relative abundance declined 92% from its peak in 1995 to its lowest point (2016) in the time series. We observed a 29% decline of scamp relative abundance on videos between 2011 and 2015 (N = 6061 video samples), which closely matched the declining trend of trap relative abundance for the same years. Mean annual coefficients of variation were higher for traps (0.41) than video (0.20), but traps were essential given the much longer time series of trap data. Trap and video spatial predictions for scamp were consistently highest on the middle and outer continental shelf (40–100 m deep) between southern North Carolina and Georgia. Mean scamp total length increased approximately 130 mm over the course of the study due to the disproportionate declining catch of small scamp from traps since the early 2000s. Two hypotheses for potential recruitment failure of scamp in the SEUS are recruitment overfishing (increased F) and increased mortality on egg, larval, or juvenile stages (increased M).

1. Introduction

Reef-associated fish species occur in tropical, subtropical, and temperate regions of the world and are often heavily targeted by fishermen (Bellwood et al., 2004). Reef fishes face numerous threats including climate change, ocean acidification, habitat loss, introduced species, and overfishing (Parker and Dixon, 1998; Coleman et al., 1999; Ballew et al., 2016). Moreover, life-history traits of many reef fish species make them particularly vulnerable to overfishing, including long life spans, slow growth, late maturity, the formation of large spawning aggregations, and hermaphroditism (Coleman et al., 1996; Wyanski et al., 2000); all the above complicate effective reef fish conservation and management.

Fishery-independent survey data form the backbone of many reef fish stock assessments (Pennington and Stromme, 1998; Kimura and Somerton, 2006). Trawls are the most commonly used gear in fishery-independent surveys on non-reef habitats because they can be used to estimate fish densities from total trawl catch and area swept by the net (Adams et al., 1995; Kotwicki et al., 2011). Because reef habitats are highly rugose, bottom trawls are not able to sample them efficiently and, therefore, cannot provide reliable fishery independent abundance and distribution data. Instead, the most commonly used methods to sample fish in reef habitats are traps (Munro, 1974; Collins, 1990; Bacheler et al., 2013a), underwater visual census (Whitfield et al., 2014), hook-and-line (Harms et al., 2010), longlines (Ellis and DeMartini, 1995; Mitchell et al., 2014), acoustics (Jones et al., 2012), underwater video (Willis and Babcock, 2000; Bacheler and Shertzer, 2015), and manned or unmanned underwater vehicles (Adams et al., 1995; Karpov et al., 2012). With some exceptions (e.g., Jones et al., 2012; Whitfield et al., 2014), sampling gears in reef habitats provide estimates of relative abundance, not density, because the area sampled by sampling gears is often very difficult to estimate (Kimura and Somerton, 2006).

Scamp (*Mycteroperca phenax*) are a reef-associated grouper species for which fishery-independent data will be useful in determining trends in population abundance along the southeast United States Atlantic coast (hereafter, "SEUS"). Scamp are a moderately long-lived (~25–30 years), slow-growing, hermaphroditic, economically

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important grouper species that associates with hard-bottom temperate reefs from Cape Hatteras, North Carolina, through the Gulf of Mexico (Smith, 1971; Matheson et al., 1986; Harris et al., 2002; Lombardi-Carlson et al., 2012). Scamp typically inhabit rocky pavement, outcropping, and ledge habitats that are often covered in soft corals, sponges, and algae (Gilmore and Jones, 1992; Kendall et al., 2008).

In the SEUS, scamp are typically harvested by recreational and commercial hook-and-line fisheries. Outside of a wintertime spawning closure, recreational fishers can currently harvest up to 3 scamp per person per day over 508-mm total length, while commercial fishers have the same minimum size limit but no trip limit. Recreational or commercial fishing for scamp closes in the SEUS when their respective annual catch limits are reached. There is also a geographic pattern to scamp catches, whereby more scamp are typically harvested in the northern compared to southern SEUS (Manooch et al., 1998). The only stock assessment of scamp in the SEUS occurred in 1998, and it indicated scamp were not overfished and overfishing was not occurring (Manooch et al., 1998). Subsequently, Harris et al. (2002) showed that scamp sex ratios in the SEUS were becoming more skewed towards females over time and egg production was declining due to the loss of older, larger females, suggesting that scamp were becoming vulnerable to exploitation.

Here we examine long-term fishery-independent chevron trap and shorter-term underwater video data to evaluate the temporal and spatial patterns of scamp abundance in the SEUS. There were two primary objectives of our work. First, spatio-temporal variation in scamp abundance was evaluated, and then we assessed whether this variation was influenced by landscape or environmental variables. Second, given the results from the first objective, we evaluated whether recruitment failure may have been partially or completely responsible for declining scamp abundance over time. These results are timely given that a new, comprehensive, statistical catch-at-age model for scamp in the SEUS is scheduled to be developed in 2019 to assess the status of the SEUS scamp stock, and robust fishery-independent indices of abundance like those presented herein will be central to the success of that assessment.

2. Methods

2.1. Study area

Sampling in this study targeted patchily-distributed hard-bottom habitats found across the continental shelf and shelf break in the SEUS. Our sampling stretched across a broad latitudinal range (27–35° N) extending from Cape Hatteras, North Carolina, in the north to St. Lucie Inlet, Florida, in the south. Most of the SEUS continental shelf and shelf break is composed of unconsolidated sand and mud substrates, but patches of hard-bottom temperate reefs naturally occur throughout the region (Fautin et al., 2010). Scamp strongly associate with these hard-bottom habitats (Kendall et al., 2008), which range from flat limestone pavement habitats to high-relief ledges, often covered in sponges, algae, and soft corals (Schobernd and Sedberry, 2009).

2.2. Scamp sampling approach

We used data derived from the Southeast Reef Fish Survey (SERFS) to make inferences about scamp in the SEUS. The SERFS is a collaborative survey and research program comprising three groups funded by the National Marine Fisheries Service (NMFS) that sample the reef-associated fish community identically in the SEUS. The first is the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program, housed at the South Carolina Department of Natural Resources (SCDNR), which NMFS has funded since the 1970s. The MARMAP program has used chevron traps since 1990 to survey reef fishes associated with hard-bottoms in the SEUS. The Southeast Area Monitoring and Assessment Program, South Atlantic Region (SEAMAP-SA) Reef Fish Complement, also funded by NMFS and housed at SCDNR, has sampled in the SEUS since 2009 and has primarily focused on evaluating previously un-sampled hard-bottom habitats in the SEUS. The third program, created in 2010 by the NMFS-Beaufort Laboratory, is the Southeast Fishery-Independent Survey, which added to the MARMAP and SEAMAP-SA Reef Fish Complement by allowing for an additional increase in overall survey effort and the implementation of underwater video.

Based on a sampling frame of known hard-bottom stations in the SEUS, SERFS either used simple random (1990–2014) or stratified random (2015–2016) sampling to select stations. The impetus for the move to stratified random sampling in the most recent years was to make the SERFS robust to future expansions or contractions of the sampling frame of known hard-bottom stations, to prepare the survey for potential changes in resource allocation, and to ensure appropriate spatial coverage annually. The twelve current strata were delineated by four depth (< 30 m, 30–42 m, 43–63 m, > 63 m) and three latitude bins (< 29.71°N, 29.71–32.61°N, > 32.61°N) based on multivariate clustering of long-term SERFS trap data. Sample allocation to strata in the recent years was designed to approximate the spatial distribution of the randomly selected stations selected for sampling in 2013 and 2014, resulting in a very similar spatial and depth distribution of sampled points in 2015–2016 compared to 2013–2014. While most stations were randomly selected in our study, some stations in the sampling frame were sampled opportunistically in a given year despite not being randomly sampled in order to increase sampling efficiency during research cruises (~3% of all stations included in our analyses). Additionally, some new hard-bottom stations were found using the vessel echosounder and sampled, and were included in our analyses in the year they were discovered if these new stations sampled hard-bottom habitat. All sampling occurred during daylight hours on the R/V *Palmetto* (1990–2016), R/V *Savannah* (2010–2016), NOAA Ship *Nancy Foster* (2010), NOAA Ship *Pisces* (2011–2016), and NOAA Ship SRVx *Sand Tiger* (2016) between spring and fall each year.

SERFS has used chevron traps (see Collins (1990) for a complete gear description) since 1990 to sample reef-associated fish species in the SEUS. Previous studies have shown that chevron trap catches are highly related to local (true) abundance for various reef fish species (Bacheler et al., 2013b,c; Shertzer et al., 2016). Each chevron trap was baited with 24 menhaden (*Brevoortia* spp.) and soaked for approximately 90 min. Chevron traps were typically deployed in groups of up to six traps, with no traps being closer than 200 m from any other trap in a given year to provide independence between samples (Bacheler et al., 2013a). Scamp trap catch-per-unit-effort (CPUE) was calculated as the number of individuals caught in a trap sample (CPUE = Catch/Trap). Trap soak time was included as a predictor variable (see below), based on the recommendations of Bacheler et al. (2013a). Chevron trap samples were excluded from the analysis if the validity of the catch was suspect due to trap behavior (e.g., trap moved or was damaged) or if any information was missing from the sample.

Beginning in 2011, the SERFS program attached high-definition video cameras over the mouth and nose of each trap to provide additional data on the abundance and distribution of reef fish. In 2011–2014, the program attached Canon Vixia HF-S200 video cameras in Gates HF-S21 housings over the mouth of each trap deployed, facing away from the trap. In 2015, the survey replaced Canon cameras with GoPro Hero 3+ cameras. Fish were only counted on cameras attached over the mouth of each trap. However, an additional camera (GoPro Hero or Nikon Coolpix S210/S220) was placed over the nose of the trap in order to quantify habitat information in the opposite direction (see below; Bacheler et al., 2014). Videos were excluded from our analyses if they were too dark to identify fish, out of focus, corrupt, or if evidence existed (e.g., bouncing, moving) that the trap may not have behaved as anticipated.

Scamp relative abundance from video was calculated using a derivation of the MeanCount approach (Fig. 1; Schobernd et al., 2014). The most common video reading metric is *MaxN* (Ellis and DeMartini,



Fig. 1. Scamp (*Mycteroperca phenax*) observed on an underwater video collected by the Southeast Reef Fish Survey in 2015 off north Florida in 54 m of water.

1995), which is the maximum number of individuals of a given species observed in a single video frame. Schobernd et al. (2014) showed that *MaxN* was nonlinearly related to true abundance, however, and proposed using the MeanCount approach instead because it was proportionally related to true abundance. MeanCount is calculated as the mean number of individuals of a given species across a series of snapshots within a video. A potential downside of MeanCount is that the precision of MeanCount may be lower than for *MaxN* (Campbell et al., 2015, but see Schobernd et al., 2014). In our study, MeanCount was calculated as the mean number of individuals of scamp across snapshots spaced 30 s apart beginning 10 min after the trap landed on the bottom (to allow time for the trap to settle) and lasting a total of 20 min. Thus, we read 41 frames from each video in our study. We used a derivation of MeanCount called SumCount, which was simply the sum of all scamp individuals observed across all video frames in our analysis. When the number of frames read was the same, as was the case in our study, MeanCount and SumCount are exactly linearly related. SumCount was used here instead of MeanCount because some of the error distributions we considered required count (instead of continuous) data.

A side-by-side camera calibration study took place in 2014 to develop a camera calibration factor between Canon and GoPro cameras. Cameras were deployed on traps next to one another, facing away from the trap mouth, and the subsequent videos were read using the SumCount metric for a variety of species that included scamp. Scamp were observed on 10 pairs of calibration videos, and Canon cameras observed a mean of 39.4% fewer scamp than their paired GoPro cameras, which was also similar to the difference in fields of view between cameras and the calibration factors for other similar species. Therefore, scamp video counts using GoPro cameras in 2015 were reduced by 39.4% to make 2015 video data consistent with data collected by Canon cameras in 2011–2014.

Characteristics of the water were obtained for each station sampled in our study. We used the vessel's echosounder to estimate depth (m) and each ship's global positioning unit to estimate latitude and longitude. Bottom water temperature (°C) for each group of simultaneously deployed traps was measured using a "conductivity-temperature-depth" cast. For samples that included video cameras (i.e., 2011–2015), three habitat variables were visually estimated from each of the two cameras attached to traps in our study (see Bacheler et al. (2014) for more details). The percent of the visible substrate that was hard-bottom (hereafter referred to as "substrate") was estimated for each camera, and a mean value was calculated for each station sampled. Substrate relief was the maximum relief visually estimated in three categories: low (< 0.3 m), moderate (0.3–1.0 m), or high (> 1.0 m). Substrate size was the predominant size of hard-bottom estimated in three categories: N/A (no hard-bottom present), coarse (a majority of hard-bottom was ≤ 1.0 m in diameter, i.e., cobble), and continuous (a majority of hard-bottom was > 1.0 m in diameter, i.e., ledges). Current direction was estimated as "away", "sideways", or "towards" based on the movement of visible particles in the water relative to the view field of the video camera over the trap mouth. 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. Trap and video samples were excluded from our analyses if any variables pertinent to the gear were missing or unknown.

2.3. Data analyses

Our first objective was to quantify the relative abundance of scamp in the SEUS using chevron trap (1990–2016) and underwater video (2011–2015) data. Raw (unstandardized) trap catches and video counts of scamp were not used because annual changes in the spatial and temporal distribution of sampling or environmental variability would be confounded with annual changes in scamp abundance (Maunder and Punt, 2004; Bacheler et al., 2014). Instead, we used spatially explicit generalized additive models (GAMs) to relate trap catch or video counts to variables that were *a priori* hypothesized to influence scamp catch or counts. A GAM is a nonparametric regression approach that uses local smoothers to fit nonlinear relationships between response and predictor variables (Wood, 2006). Various error distributions can also be fit with GAMs (Hastie and Tibshirani, 1990).

Scamp trap catch and video counts were zero-inflated, meaning that there were more zeros than expected based on various GAM error distributions. Therefore, we used delta-GAMs to model the trap catch and video counts of scamp in our study. Delta-GAMs contain two submodels: one that modeled the presence-absence of scamp and another that modeled the trap catch or video counts when scamp were present (Lo et al., 1992; Pennington, 1996; Stefansson, 1996). The overall effects of a particular predictor variable on trap catch or video counts were obtained by multiplying the effects from each submodel (Maunder and Punt, 2004; Murray, 2004; Li et al., 2011).

We examined the influence of six predictor variables (hereafter, covariates) on the trap catch of scamp using delta-GAMs. These covariates were year (*y*; 1990–2016), depth (*d*; m), bottom water temperature (*temp*; °C), day of the year (*doy*), soak time of the trap (*soak*; min), and position (*pos*). We excluded samples deeper than 100 m or

soak times less than 50 min or greater than 150 min due to low sample sizes. Position was a bivariate smooth covariate (i.e., surface) that was developed using the latitude and longitude of the sample (Bacheler and Smart, 2016). No covariates exhibited multicollinearity given that the variance inflation factors were less than three for all covariates (Neter et al., 1989).

We first developed a binomial GAM submodel that related scamp presence or absence in a chevron trap (η) to the six covariates described above (hereafter referred to as the *base* trap model), which was assumed to be an independent draw from a binary variable with a probability of presence being π and the probability of absence being 1 − π:

$$\eta \sim \text{Bernoulli}(\pi), \tag{1}$$

$$E(\eta) = \pi \text{ and } \text{var}(\eta) = \pi \times (1 - \pi), \tag{2}$$

$$\text{logit}(\pi) = \alpha + f_1(y) + s_1(d) + s_2(temp) + s_3(doy) + s_4(soak) + s_5(pos), \tag{3}$$

where logit is the logit link function, α is the model intercept, f is a categorical function, and s is a cubic spline (smoothed) function. All GAMs were coded and analyzed in R version 3.3.3 (R Core Team, 2017) using the mgcv library 1.8–16 (Wood, 2011).

The positive catch GAM submodels related the number of scamp caught in a given trap (ϖ) to the same six covariates described above. Various error distributions were compared for the positive catch GAM including Gaussian with a fourth root or log transformation, Tweedie, Poisson, and negative binomial. Based on various model diagnostics (e.g., quantile–quantile plot, residual plots) using the "gam.check" function in the mgcv library in R, the Poisson model outperformed all other distributions so was used here:

$$\varpi \sim P(\lambda), \tag{4}$$

$$E(\varpi) = \lambda \text{ and } \text{var}(\varpi) = \lambda, \tag{5}$$

$$\log(\lambda) = \alpha + f_1(y) + s_1(d) + s_2(temp) + s_3(doy) + s_4(soak) + s_5(pos). \tag{6}$$

For each GAM submodel described above, base models were compared to various reduced models that contained fewer covariates. We used Akaike's information criterion (AIC) for all model selection (Burnham and Anderson, 2002). AIC balances the number of parameters of a model with its fit, and attempts to find the most parsimonious model that explained the most variation in the data with the fewest parameters. Models with the lowest AIC values were considered the best model in the set; here, we compared ΔAIC values, which was a measure of each model relative to the best model in the set. Thus, the best models have ΔAIC values of zero, and other models in the set have ΔAIC values greater than zero.

Calculating combined effects required that the same covariates be present in each submodel, so if one submodel retained a variable based on AIC, it was necessarily included in both submodels. All final GAMs met the assumptions of normality and constant variance. The degree of flexibility in the smoothed covariates was determined automatically using the built-in algorithm in the mgcv library.

The GAMs for video counts of scamp were coded similarly to the trap submodels (Eqs. (3) and (6), above) except soak time was removed (since all videos were read consistently over the same time frame) and five additional variables were included: substrate (*sub*; %), water clarity (*wc*), current direction (*cur*), substrate relief (*rel*), and substrate size (*size*):

$$\text{logit}(\pi) = \alpha + f_1(y) + s_1(d) + s_2(temp) + s_3(doy) + s_4(pos) + s_5(sub) + f_2(wc) + f_3(cur) + f_4(rel) + f_5(size), \tag{7}$$

$$\log(\mu) = \alpha + f_1(y) + s_1(d) + s_2(temp) + s_3(doy) + s_4(pos) + s_5(sub) + f_2(wc) + f_3(cur) + f_4(rel) + f_5(size), \tag{8}$$

where Eq. (7) was the binomial video GAM and Eq. (8) was the positive video GAM.

In both equations, substrate was a continuous variable, while the other four covariates were categorical variables. Unlike the positive trap catch model above, the best fitting positive video count submodel used a Gaussian error distribution with log-transformed video SumCounts.

The second objective of our work was to evaluate whether recruitment failure may have been partially or completely responsible for the observed decline in scamp abundance over time. To address this objective, we developed additional GAMs. The first was a GAM that modeled mean length of scamp in traps as the response variable in relation to the same six predictor variables in Eqs. (3) and (6). Declining abundance is often associated with declining size for reef fish like scamp that are harvested with minimum size limits. This length-based GAM tested whether the lengths of scamp caught in SERFS traps over time have changed significantly. Since traps that failed to catch scamp were excluded from this length model, we developed a single GAM, not a delta-GAM, because length data were not zero inflated. Here, trap samples were weighted by the total number of scamp caught in each trap, so that mean length based on many fish in a trap was weighted more heavily than a mean length comprising a single fish caught in the trap. A Gaussian error distribution without a transformation fit the data better than any other distribution, so it was used for the length-based GAM.

Lastly, we modeled the trap catch of small and large scamp separately over time in an attempt to explain why the lengths of scamp may have changed, as inferred from our length-based GAM above. We used the same delta-GAM submodels as shown in Eqs. (1)–(6) to model the trap catch of small scamp (< 500 mm total length) separately from the catch of large scamp (≥500 mm total length) from 1990 to 2016. We chose a cutoff size of 500 mm because there were enough scamp smaller and larger than this size to model separately; a smaller cutoff length resulted in too few samples to model in the small group. Both positive trap catch submodels (for small and large fish) used a Poisson error distribution.

3. Results

A total of 15,609 trap samples were included in our analyses over the 27 years of the survey, ranging from a low of 253 samples in 1999 to a high of 1478 in 2016 (Table 1; Fig. 2). Sampling generally commenced in the spring and terminated in fall (commonly April or May through September or October; Table 1). Depths sampled among years was similar, ranging from approximately 15–95 m each year. The spatial extent of sampling, however, expanded from approximately 30–34° N in the early 1990s to 27–35° N since the late 1990s. A primary benefit of including spatial position as a covariate in our GAMs was to standardize for changes in the spatial distribution of sampling among years.

A total of 1813 scamp were caught in chevron traps since 1990 in a total of 1074 traps. Scamp trap catch ranged from 1 to 8 individuals (Figs. 2 and 3). Percent frequency of occurrence of scamp was highest in 1994 at 18.0%, and lowest in 2016 at 2.5% (6.9% overall; Table 1). With the exception of a single year (2007), percent frequency of occurrence was above 10% between 1990 and 2004 and below 10% from 2005 to 2016.

We included 6061 video samples in our analyses between 2011 and 2015, ranging from 662 in 2011 to 1416 in 2014 (Table 2). Dates, depths, and latitudes sampled were very similar among the five years of video data collection. Scamp were present in 704 videos, with a percent frequency of occurrence (%FO) ranging from 8.2% in 2013 to 15.1% in 2011 (overall %FO = 11.6; Table 2). Scamp SumCount among video samples ranged from 1 to 222 (Fig. 3).

The best binomial GAM relating the presence or absence of scamp in chevron traps (1990–2016) to covariates was the base model that included all six covariates and explained 24.9% of the deviance in scamp

Table 1
Annual sampling information for the 27 years of chevron trapping by the Southeast Reef Fish Survey, 1990–2016, along the southeast United States Atlantic coast. *N* = number of chevron trap samples included in the analyses each year, FO = frequency of occurrence or number of samples in which scamp were caught, and %FO = percent frequency of occurrence or the percent of traps deployed each year in which scamp were caught.

Year	*N*	Scamp FO	Unstandardized scamp %FO	Date range	Depth range (m)	Latitude (°N)
1990	313	32	10.2	4/23–8/9	17–93	30.4–33.8
1991	278	30	10.8	6/11–9/24	17–95	30.8–34.6
1992	288	29	10.1	3/31–8/13	17–62	30.4–34.3
1993	396	41	10.4	5/10–8/13	16–94	30.4–34.3
1994	394	71	18.0	5/9–10/26	16–93	30.7–33.8
1995	363	52	14.3	5/3–10/26	16–60	29.8–33.7
1996	488	67	13.7	4/29–9/16	14–100	27.9–34.3
1997	465	83	17.8	5/5–9/29	15–97	27.9–34.6
1998	467	51	10.9	5/5–8/18	14–92	27.4–34.6
1999	253	32	12.6	6/2–9/28	15–79	27.3–34.4
2000	346	46	13.3	5/16–10/19	15–100	29.0–34.3
2001	259	36	13.9	5/23–10/24	14–91	27.9–34.3
2002	288	29	10.1	6/17–9/24	13–94	27.9–34.0
2003	255	26	10.2	6/3–9/22	16–92	27.4–34.3
2004	316	40	12.7	5/5–10/28	14–91	29.0–34.0
2005	322	32	9.9	5/3–9/29	15–69	27.3–34.3
2006	312	12	3.8	6/6–9/28	15–94	27.3–34.4
2007	358	40	11.2	5/21–9/24	15–92	27.3–34.3
2008	354	11	3.1	5/5–9/30	14–92	27.3–34.6
2009	464	13	2.8	4/23–10/8	14–91	27.3–34.6
2010	896	37	4.1	5/4–10/27	14–92	27.3–34.6
2011	769	29	3.8	5/19–10/26	14–93	27.2–34.5
2012	1198	42	3.5	4/24–10/10	15–98	27.2–35.0
2013	1363	49	3.6	4/24–10/4	15–100	27.2–35.0
2014	1482	53	3.6	4/23–10/21	15–99	27.2–35.0
2015	1444	54	3.7	4/21–10/22	16–100	27.3–35.0
2016	1478	37	2.5	5/4–10/26	17–100	27.2–35.0
Overall	15609	1074	6.9	3/31–10/28	13–100	27.2–35.0

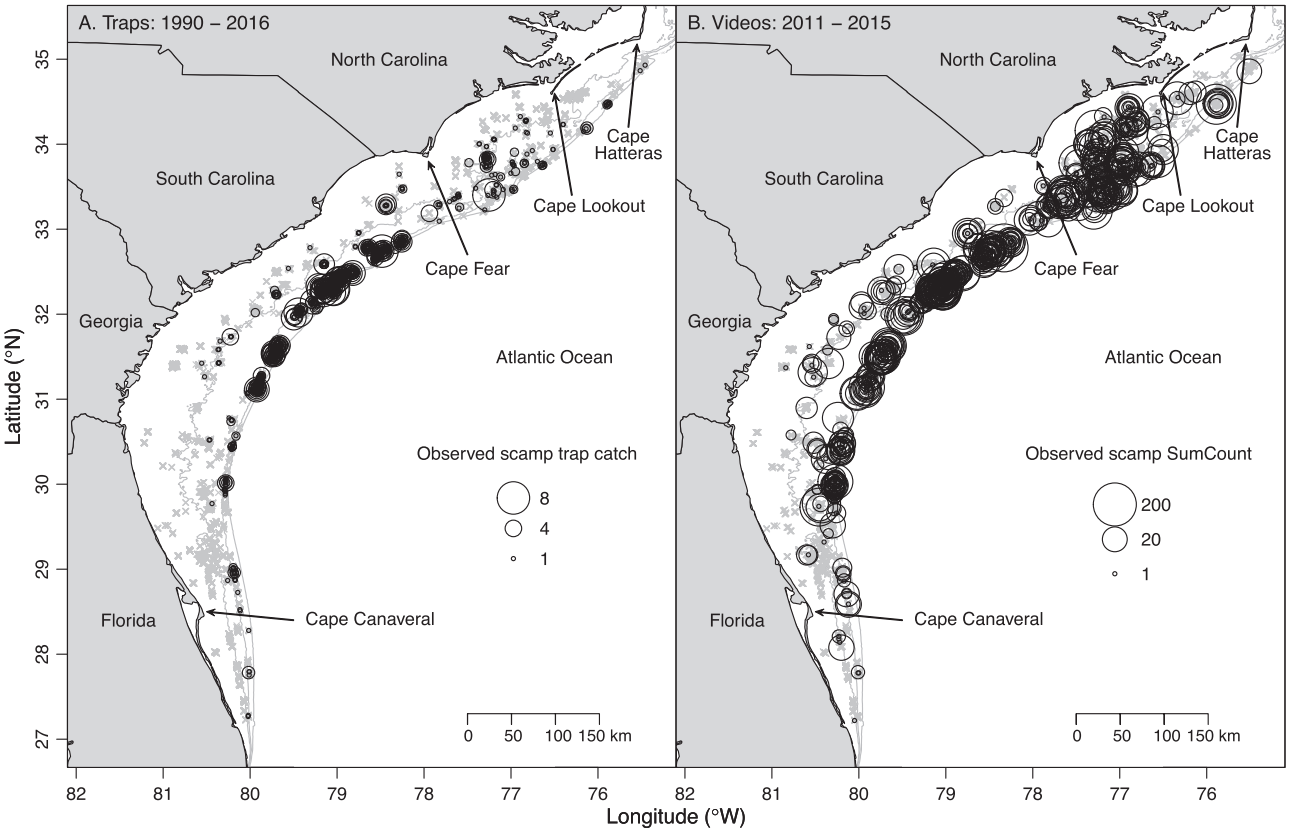


Fig. 2. Trap catch (A) and video counts (B) of scamp (*Mycteroperca phenax*) along the southeast United States Atlantic coast. Each gray "×" marks the location of a trap or video sample where no scamp were observed, while the black bubbles mark locations where scamp were observed; bubble size was scaled to the number of scamp caught in traps or observed on video, and bubbles often overlap. Note that traps were deployed in 1990–2016, while videos were attached to traps in 2011–2015.

Table 2
Annual sampling information for the 5 years of underwater video collection by the Southeast Reef Fish Survey, 2011–2015, along the southeast United States Atlantic coast. *N* = number of underwater video samples included in the analyses each year, FO = frequency of occurrence or number of video samples in which scamp were observed, and %FO = percent frequency of occurrence or the percent of underwater videos deployed each year in which scamp were observed.

Year	Camera	*N*	Scamp FO	Unstandardized scamp %FO	Date range	Depth range (m)	Latitude (°N)
2011	Canon	662	100	15.1	5/19–10/26	15–93	27.2–34.5
2012	Canon	1223	105	8.6	4/24–10/10	15–98	27.2–35.0
2013	Canon	1360	111	8.2	4/24–10/4	15–100	27.3–35.0
2014	Canon	1416	209	14.8	4/23–10/21	15–99	27.2–35.0
2015	GoPro	1400	179	12.8	4/21–10/22	16–96	27.3–35.0
Overall		6061	704	11.6	4/21–10/26	15–100	27.2–35.0

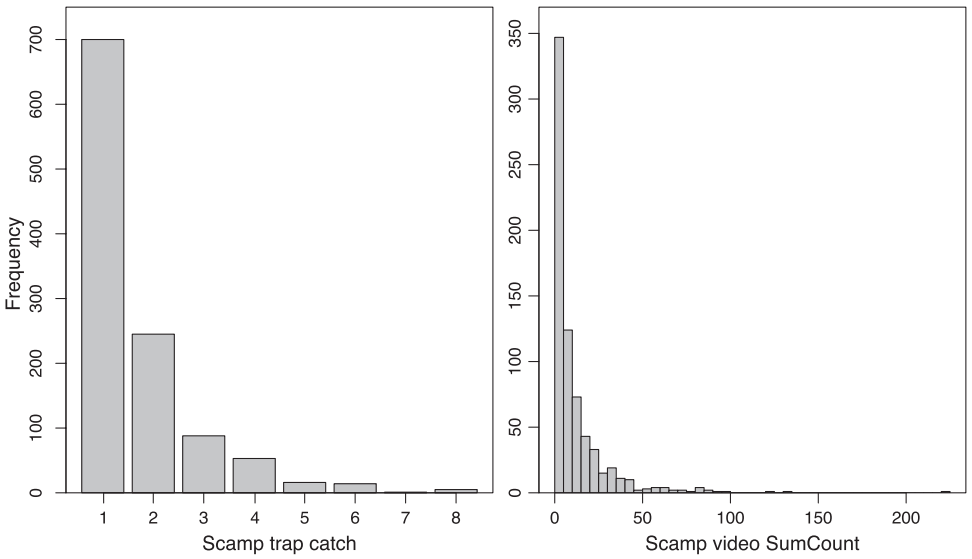


Fig. 3. Histograms of scamp (*Mycteroperca phenax*) trap catch and video counts from the Southeast Reef Fish Survey for each sample included in the analyses. Note that trap data were collected in 1990–2016, while video data was collected in 2011–2015. Note different y-axis scales between plots.

Table 3
Model selection for the spatially explicit generalized additive models for the catch of scamp *Mycteroperca phenax* in traps (A and B) or counts of scamp on video (C and D) deployed by the Southeast Reef Fish Survey. Traps were deployed in 1990–2016, while video cameras were attached to traps in 2011–2015. Degrees of freedom are shown for factor (*f*) terms, and estimated degrees of freedom are shown for smoothed terms (*s*). Asterisks denote significance at the following alpha levels: *0.05, **0.01, ***0.001; *N* = sample size; AIC = Akaike information criterion; Dev = deviance explained by the model; *y* = year of the sample; *d* = bottom depth; *temp* = bottom water temperature; *doy* = day of the year; *soak* = trap soak time; *pos* = position of the sample; *sub* = percent of bottom substrate that was hard bottom; *wc* = water clarity; *cur* = current direction relative to the video camera; *rel* = maximum substrate relief; *size* = predominant size of hard-bottom; ex = covariate was excluded from model based on AIC; NA = covariate was not applicable to that particular model.

Model	*N*	ΔAIC	Dev	*f*(*y*)	*s*(*d*)	*s*(*temp*)	*s*(*doy*)	*s*(*soak*)	*s*(*pos*)	*s*(*sub*)	*f*(*wc*)	*f*(*cur*)	*f*(*rel*)	*f*(*size*)
A. Binomial trap submodel														
Base	15609	0.0	24.9	26***	5.3**	2.7***	8.2***	1.8**	27.2***	NA	NA	NA	NA	NA
Base minus *soak*	15609	7.7	24.7	26***	5.3**	2.7***	8.2***	ex	27.3***	NA	NA	NA	NA	NA
Base minus *depth*	15609	15.0	24.5	26***	ex	2.7***	8.1***	1.6**	27.8***	NA	NA	NA	NA	NA
Base minus *doy*	15609	18.2	24.4	26***	5.3**	2.9***	ex	1.8**	27.2***	NA	NA	NA	NA	NA
B. Positive trap submodel														
Base	1074	0.0	20.8	26***	1.8*	2.0*	2.7	1.7*	4.3	NA	NA	NA	NA	NA
Base minus *doy*	1074	4.7	19.3	26***	2.1*	2.2**	ex	1.7*	4.2	NA	NA	NA	NA	NA
Base minus *temp*	1074	4.8	19.7	26***	2.0	ex	3.2*	1.7*	4.5*	NA	NA	NA	NA	NA
Base minus *pos*	1074	5.5	20.2	26***	1.9*	2.1*	8.0	1.4*	ex	NA	NA	NA	NA	NA
C. Binomial video submodel														
Base minus *doy*, *temp*, *wc*	6061	0.0	32.6	4**	4.0**	ex	ex	NA	24.6***	1.9***	ex	2**	2***	2***
Base minus *doy*, *temp*	6061	1.4	32.6	4**	4.0**	ex	ex	NA	24.6***	1.9***	2	2**	2***	2***
Base minus *doy*	6061	1.8	32.7	4**	4.0***	1.9	ex	NA	24.7***	1.8***	2	2**	2***	2***
Base	6061	3.6	32.7	4**	4.0***	1.8	1.0	NA	24.8***	1.8***	2	2**	2***	2***
D. Positive video submodel														
Base minus *temp*, *size*, *sub*, *wc*, *rel*	704	0.0	11.6	4***	1.0*	ex	1.0*	NA	3.4***	ex	ex	2***	ex	ex
Base minus *temp*, *size*, *sub*, *wc*	704	0.3	13.0	4***	4.5	ex	1.0*	NA	3.5**	ex	ex	2***	2	ex
Base minus *temp*, *size*, *sub*, *wc*, *rel*, *doy*	704	2.7	11.0	4***	1.0*	ex	ex	NA	3.5***	ex	ex	2***	ex	ex
Base minus *temp*, *size*, *sub*	704	3.0	13.2	4***	4.7	ex	1.0*	NA	3.6**	ex	2	2***	2	ex

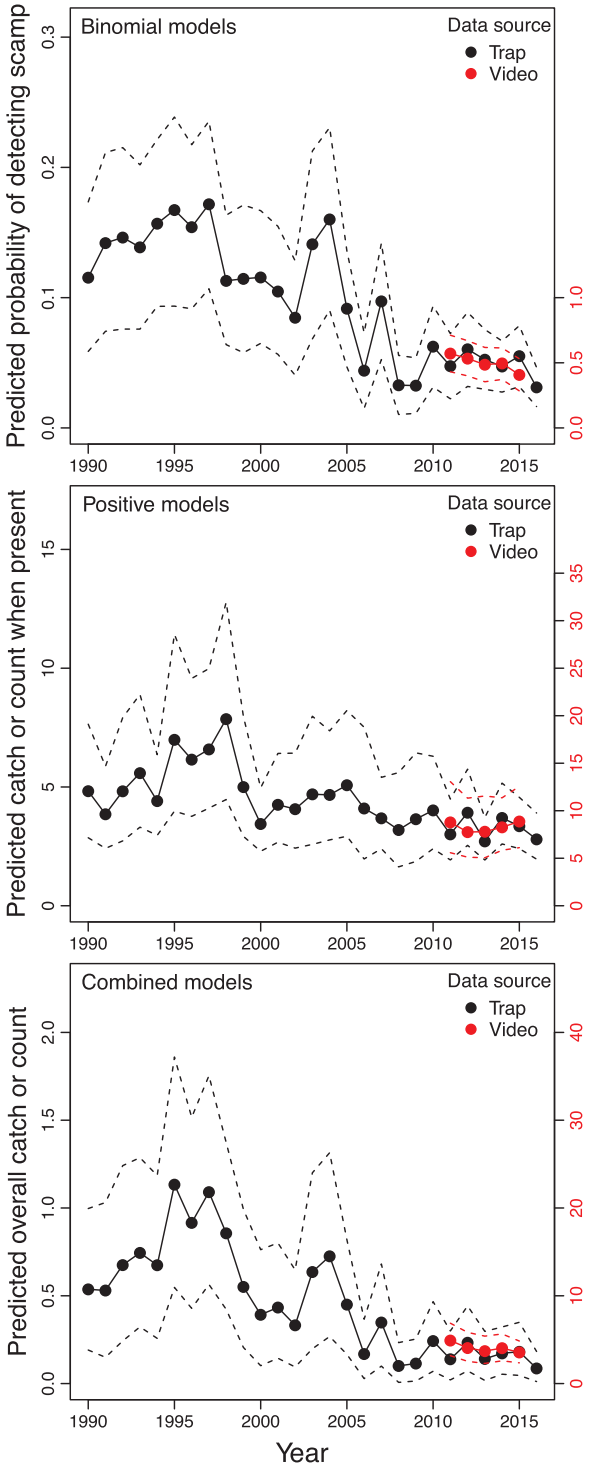


Fig. 4. Predicted annual trap catch (black) or video SumCounts (red) of scamp (*Mycteroperca phenax*) using binomial (top) and positive catch submodels (middle), as well as their combined effects (bottom), based on Southeast Reef Fish Survey trap (1990–2016) and video data (2011–2015) using generalized additive models. Filled circles indicate mean values at average values of all other model covariates and dashed lines indicate 95% confidence intervals. Note the right y-axes used for video results. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

catch (Table 3). The second best model (excluding soak time) had a ΔAIC value of 7.7, and other reduced models were considerably worse. The best positive trap catch GAM was also the base model that included all six covariates and explained 20.8% of the deviance, followed by the

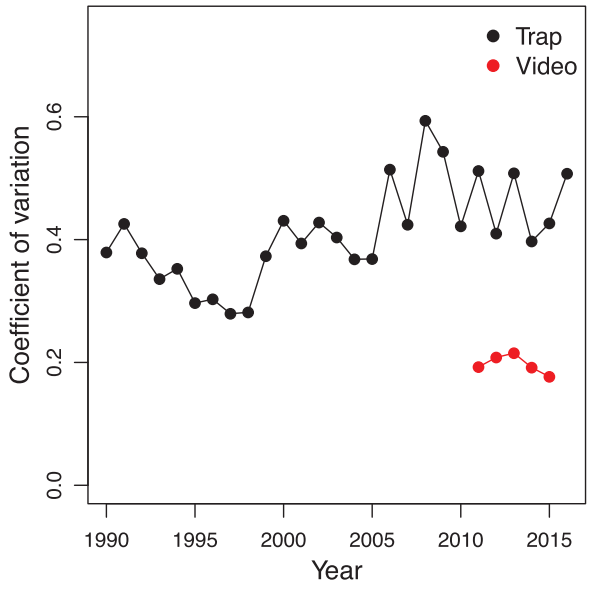


Fig. 5. Annual coefficient of variation (standard deviation divided by the mean) for scamp (*Mycteroperca phenax*) caught in traps (black) or observed on video (red) by the Southeast Reef Fish Survey along the southeast United States Atlantic coast. Trapping occurred in 1990–2016, while video data collection occurred in 2011–2015. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

model excluding day of the year (ΔAIC = 4.7; Table 3). Thus, all six covariates were included in the binomial and positive trap catch submodels to calculate overall effects.

Results were somewhat different for the delta-GAM relating video counts of scamp (2011–2015) to covariates. The best binomial GAM relating the presence or absence of scamp on video to ten covariates was the submodel that excluded day of the year, bottom temperature, and water clarity. This best model explained 32.6% of the deviance and was better than the second model that excluded day of the year and bottom temperature only (ΔAIC = 1.4; Table 3). The best positive video count submodel explained much less deviance (11.6%) than the binomial submodel and excluded five variables: bottom temperature, water clarity, substrate, substrate size, and substrate relief. The best positive video count submodel was only slightly better than the second best model (ΔAIC = 0.3) excluding the same covariates except substrate relief (Table 3). Thus, the final binomial and positive count video submodels included all covariates except bottom temperature and water clarity to estimate overall effects.

Predicted (standardized) trap catch of scamp declined significantly over the study period (Fig. 4). The trap binomial model mirrored the unstandardized %FO of scamp, consisting of high values until approximately 2005 (mean = 0.13) and much lower values after that time (mean = 0.05), a 62% decline (Fig. 4). The positive trap submodel (i.e., the number of scamp caught when present) displayed a smaller decline (33%) over the same time period (Fig. 4). Given the multiplicative nature of the combined temporal effect, declines of scamp from 1990–2005 to 2006–2017 overall were more severe (74%; Fig. 4). Point estimates suggests a 92% decline in abundance from the year of scamp maximum relative abundance in 1995 to its lowest relative abundance in 2016.

Although the video time series (5 years) was much shorter than the trap time series, declines of scamp were still apparent (Fig. 4). The likelihood of observing scamp on video decreased 29% between 2011 and 2015, although the numbers observed when present were similar over time (Fig. 4). These results translated to an overall decline of 29% of scamp on video between 2011 and 2015 (Fig. 4). Despite being different in absolute terms, trap and video time series for scamp matched very closely in relative pattern (Fig. 4).

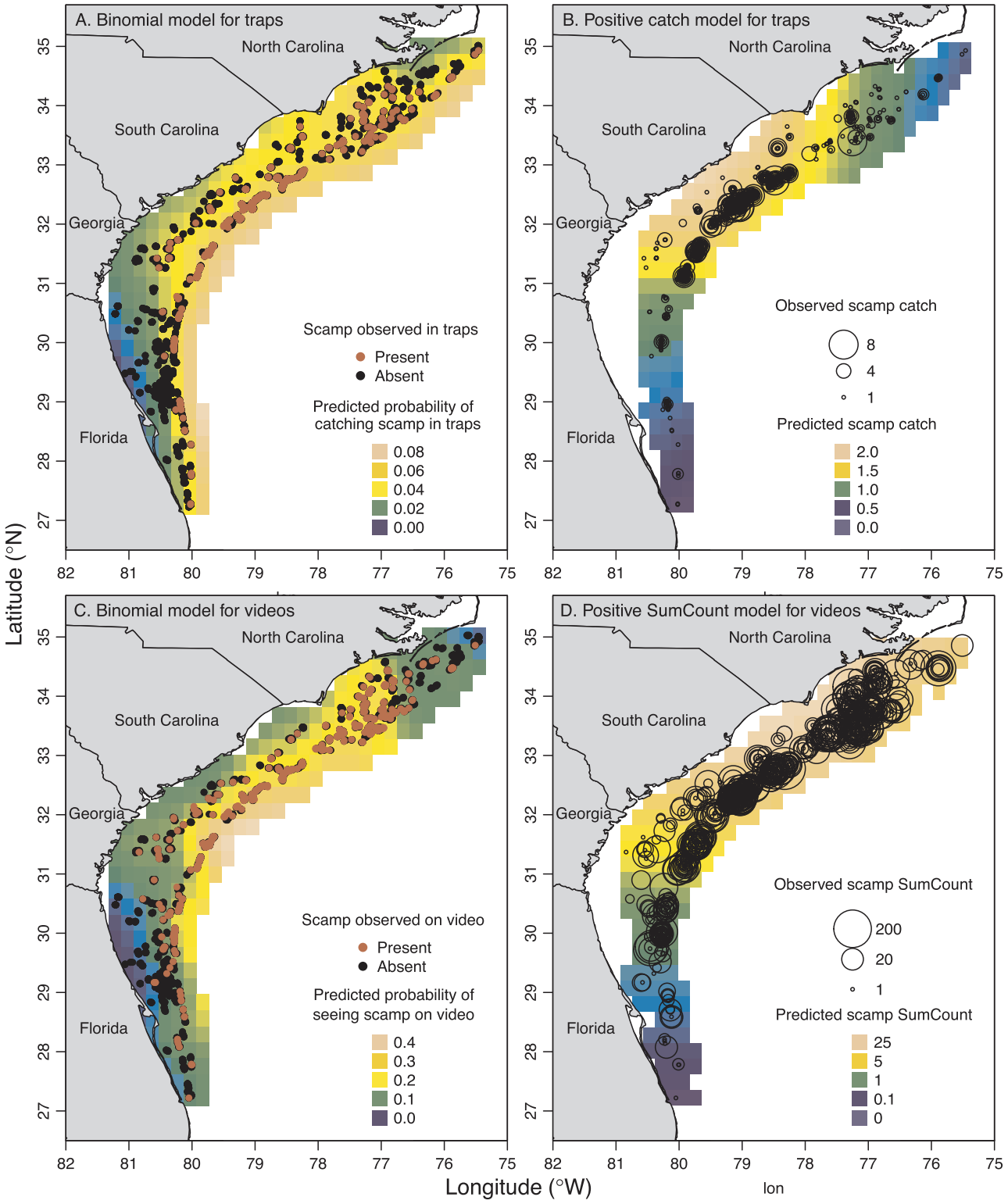


Fig. 6. Partial effects of position on the spatial distribution of scamp (*Mycteroperca phenax*) based on trap catches (A, B) and video counts (C, D). The left column shows the results of binomial generalized additive models for traps (A) and video (C), where orange indicates the highest likelihood of observing scamp and blue indicates the lowest likelihood. Overlaid on these plots are red points indicating scamp were present in traps or video, and black points indicating their absence. The right panels show the positive catch generalize additive models for traps (B) or video (D), where orange shows highest predicted trap catch or video SumCounts and blue shows the lowest predicted catch or counts. Overlaid on these plots are black bubbles scaled to the observed trap catch (1990–2016) or video SumCounts (2011–2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The annual coefficients of variation (CV) for the scamp video-based index of abundance were smaller than the CVs for the trap-based index of abundance (Fig. 5). The CVs for traps ranged from 0.28 (1997) to 0.59 (2008), with an overall mean (1990–2016) of 0.41 (Fig. 5). Alternatively, the CVs for video (2011–2015) ranged from 0.17 (2015) to 0.22 (2013), with a mean of 0.20. For direct comparison, the mean trap-based CV from the same years as the video index (2011–2015) was 0.45 (Fig. 5), which was 108% greater than the video-based CVs.

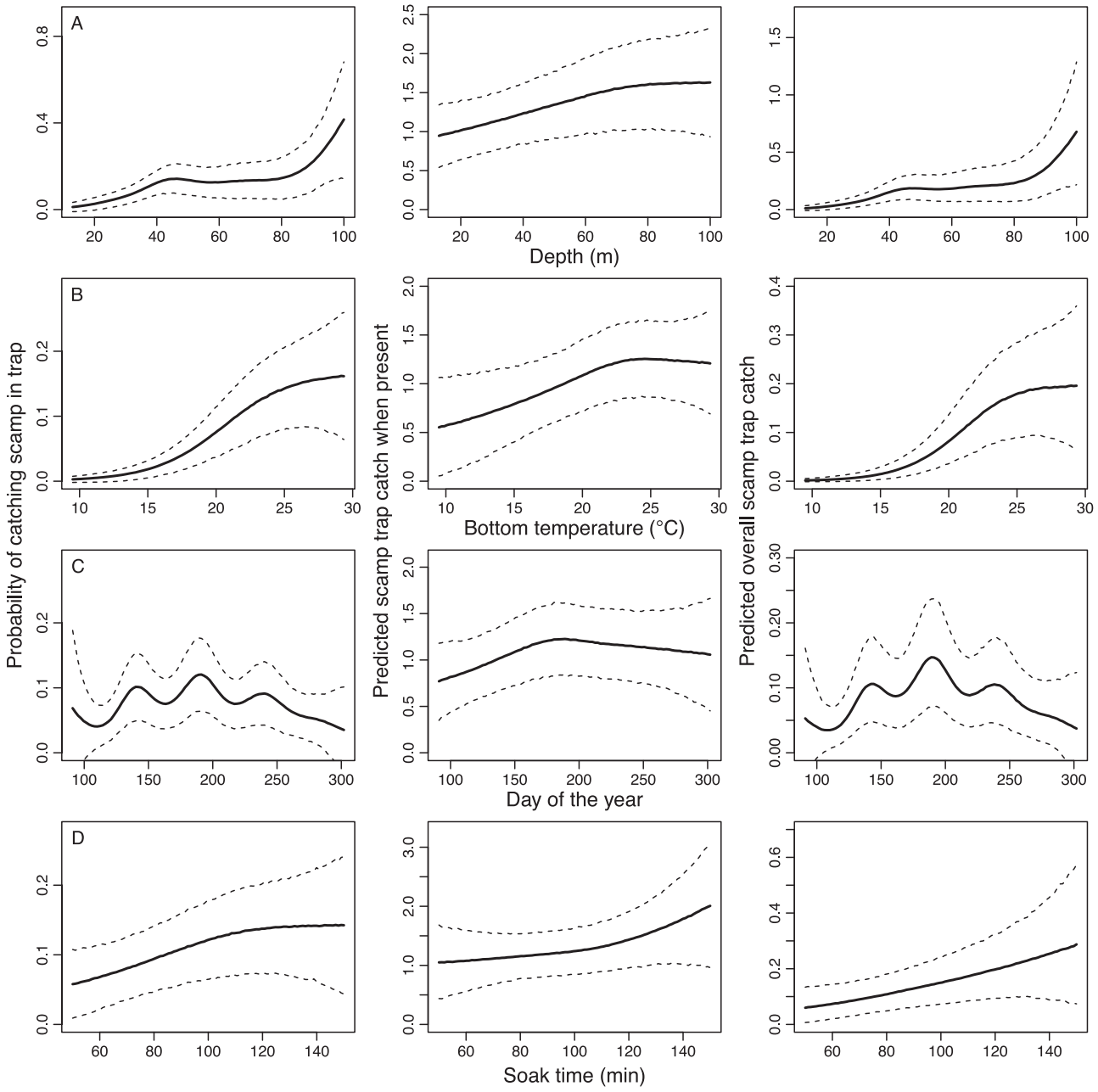


Fig. 7. Predicted trap catch of scamp (*Mycteroperca phenax*) as a function of depth (A), bottom temperature (B), day of the year (C), and soak time (D) using generalized additive models built upon Southeast Reef Fish Survey in 1990–2016. Binomial modeling results are shown in the left column, positive trap catch results are shown in the middle column, and their combination (overall effects) are shown in the right column. Solid lines are the predicted scamp catch per trap at average values of all other covariates and dashed lines represent 95% confidence intervals.

Trap- and video-based spatial predictions were generally consistent with one another and matched observations closely (Fig. 6). The binomial submodel for traps predicted the highest likelihood of catching scamp (> 8%) at the continental shelf break and lowest inshore off Florida, whereas the highest predicted scamp per trap when present occurred primarily in waters off South Carolina and southern North Carolina and lowest at the northern and southern ends of the SEUS (Fig. 6). The binomial submodel for videos predicted a similarly high likelihood of observing scamp on video in the deepest waters at the continental shelf break (> 40%), but over a more narrow latitudinal range than trap-based predictions (i.e., southern North Carolina through Georgia; Fig. 6). The highest scamp SumCount per video was predicted to occur in southern North Carolina through northern South Carolina, and lowest throughout much of Florida (Fig. 6).

Specific covariate effects for the binomial submodel, positive catch submodel, and combined overall trap catch were similar to one another. Scamp were more commonly caught in deeper water with warmer bottom temperatures during the summer months, and traps soaking for a longer amount of time had a higher likelihood of catching scamp than traps soaking for a smaller amount of time (Fig. 7). Based on the width of 95% confidence intervals (CIs), the relationships between depth or bottom temperature and scamp catch were stronger (narrower CIs) than day of the year or soak time (wider CIs; Fig. 7).

Observations of scamp on video varied significantly across the six covariates included in the best model. Like the trap-based covariate effects for depth, scamp were observed on video much more commonly in deeper water compared to shallower water (Fig. 8). Scamp on video were also observed in areas with more hard-bottom, in later sampling periods, and when the current was away from the camera. Moreover, scamp were more likely to be observed on video in higher relief,

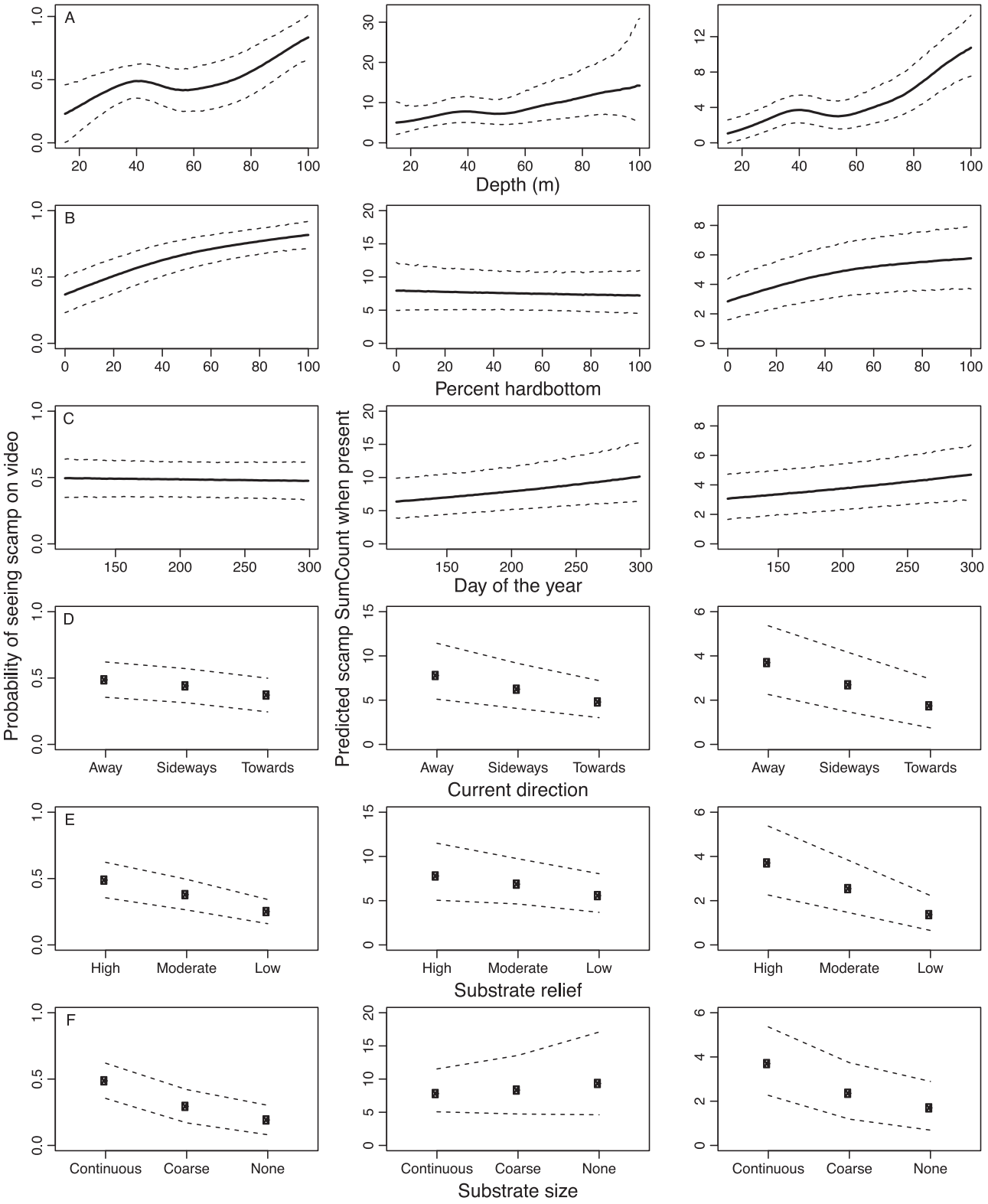


Fig. 8. Predicted video counts of scamp (*Mycteroperca phenax*) as a function of depth (A), percent hard-bottom (B), day of the year (C), current direction (D), substrate relief (E), and substrate size (F) using generalized additive models built upon Southeast Reef Fish Survey in 2011–2015. Binomial modeling results are shown in the left column, positive video count results are shown in the middle column, and their combination (overall effects) are shown in the right column. Solid lines or filled points are scamp predictions per trap at average values of all other covariates and dashed lines represent 95% confidence intervals.

continuous hard-bottom habitats (Fig. 8).

The best GAM for estimating mean length of scamp caught in chevron traps over time (1990–2016) retained four covariates (year, depth, day of the year, and position) and excluded two covariates (bottom temperature and soak time; Table 4). Based on this best model, predicted scamp length increased over time in our survey. Annual mean predicted scamp length ranged from 445 mm total length in 2003 to 574 mm total length in 2012, with an overall mean of 500 mm total

Table 4
Model selection for the spatially explicit generalized additive models for mean length (A) or abundance of small (< 500 mm total length; B and C) or large (≥500 mm total length; D and E) scamp *Mycteroperca phenax* caught in traps deployed by the Southeast Reef Fish Survey, 1990–2016. Degrees of freedom are shown for factor (*f*) terms, and estimated degrees of freedom are shown for smoothed terms (*s*). Asterisks denote significance at the following alpha levels: *0.05, **0.01, ***0.001; *N* = sample size; AIC = Akaike information criterion; Dev = deviance explained by the model; *y* = year of the sample; *d* = bottom depth; *temp* = bottom water temperature; *doy* = day of the year; *soak* = trap soak time; *pos* = position of the sample; ex = covariate was excluded from model based on AIC.

Model	*N*	ΔAIC	Dev	*f*(*y*)	*s*(*d*)	*s*(*temp*)	*s*(*doy*)	*s*(*soak*)	*s*(*pos*)
A. Length model									
Base minus *soak, temp*	1074	0.0	35.2	26***	4.0	ex	1.0*	ex	26.1***
Base minus *temp*	1074	1.9	35.2	26***	4.0	ex	1.0*	1.0	26.1***
Base minus *soak*	1074	2.1	35.5	26***	3.8	3.5	1.0*	ex	26.1***
B. Binomial submodel for small scamp									
Base	15609	0.0	25.9	26***	4.3	2.2***	8.6***	1.0*	27.9***
Base minus *depth*	15609	3.8	25.6	26***	ex	2.3***	8.6***	1.0*	28.2***
Base minus *soak*	15609	4.3	25.7	26***	4.3	2.2***	8.6***	ex	27.9***
C. Positive submodel for small scamp									
Base minus *y, d, temp, doy, pos*	442	0.0	5.2	ex	ex	ex	ex	1.0**	ex
Base minus *y, temp, doy, pos*	442	1.6	5.6	ex	1.0	ex	ex	1.0*	ex
Base minus *y, doy, pos*	442	2.7	6.3	ex	1.0	1.0	ex	1.0*	ex
D. Binomial submodel for large scamp									
Base	15609	0.0	26.6	26***	4.7***	2.7***	2.2	1.0*	27.4***
Base minus *soak*	15609	3.2	26.5	26***	4.7***	2.8***	2.2	ex	27.4***
Base minus *doy*	15609	3.3	26.5	26***	4.7***	2.9***	ex	1.0*	27.4***
E. Positive submodel for large scamp									
Base minus *doy, soak, pos*	799	0.0	15.0	26*	1.0	1.9	ex	ex	ex
Base minus *doy, soak*	799	1.5	15.7	26*	1.0*	1.9	ex	ex	2.0
Base minus *doy*	799	2.6	16.0	26	1.0*	1.8	ex	1.0	2.0

length across all years. Mean scamp length increased from 476 mm total length in 1990 to 2005 to 534 mm total length in 2006–2016, a 12% increase (Fig. 9). The largest mean predicted scamp length captured in traps occurred in the last five years of the trap survey (mean = 566 mm total length), a 19% increase over mean lengths in 1990–2005 (Fig. 9).

The best binomial submodels for the catch of small (< 500 mm) and large scamp (≥500 mm) over time (1990–2016) retained all covariates (year, depth, bottom temperature, day of the year, soak time of the trap, and position; Table 4). Fewer covariates were retained in the positive trap catch submodels for small and large scamp, including just soak time in the small scamp positive catch submodel and year, depth, and bottom temperature in the large scamp positive catch submodel (Table 4). Thus, binomial and positive catch submodels for small and large scamp retained all covariates to calculate overall effects.

Declines over time were observed for both predicted small (< 500 mm total length) and large (≥500 mm total length) scamp caught in traps (Fig. 9). Predicted small scamp trap catch ranged from 0.01 (2013) to 0.90 (1997), with much lower predicted catches in the late 2000s and 2010s compared to the 1990s and early 2000s (Fig. 9). Specifically, predicted small scamp trap catch decreased from a mean of 0.46 (1990–2005) to 0.10 (2006–2016), a decline of 79%. Declines were even more substantial (90%) when comparing predicted small scamp catch from 1990 to 2005 to the last five years of the survey (2012–2016; Fig. 9). A 99% decline was observed from the year of highest small scamp relative abundance (1997) to the lowest (2013). Predicted large scamp trap catch declined 70% from a mean of 0.22 in 1990–2005 to 0.07 in 2006–2016 (Fig. 9), and a 91% decline was observed for large scamp between the year of highest relative abundance (1995) and lowest relative abundance (2006).

4. Discussion

We found significant declines in the relative abundance of scamp over three decades of fishery-independent chevron trap sampling in the SEUS. Declines were observed for both small and large scamp over time, but the increase in mean size of scamp caught in the trap survey combined with the greater rate of decline for small scamp compared to large scamp over time suggests that recruitment failure may have occurred since at least the mid-2000s. Moreover, traps and video gears both appeared to adequately sample scamp in the SEUS based on various inferences including gear-specific CVs, model diagnostics, consistency in covariate relationships, and similar predicted temporal and spatial patterns in scamp abundance. Our results support the need for a stock assessment of scamp in the SEUS, and these data will likely play a central role in that assessment.

Over a 20 year period from the mid-1990s to the mid-2010s, our results indicated that scamp relative abundance potentially declined by 90% in the SEUS. This level of decline for scamp is similar to various high-profile (but controversial) declines of predatory fish species around the world (e.g., Myers and Worm, 2003; Baum et al., 2003). Scamp are a relatively long-lived, slow-growing, and hermaphroditic species (Matheson et al., 1986; Harris et al., 2002), and fish species with those characteristics often cannot sustain very high levels of exploitation (Coleman et al., 1999; Huntsman et al., 1999). Despite the late 1990s stock assessment conclusion of not overfished and overfishing not occurring (Manooch et al., 1998), there were some warning signs occurring as early as the early 2000s that scamp may have been overexploited in the SEUS. For instance, Harris et al. (2002) showed that exploitation of scamp was increasing throughout the 1990s, causing skewed sex ratios and the disappearance of older, larger fish that disproportionately contribute to reproduction. It is also likely that scamp abundance in 1990 had been reduced from virgin abundance given historical commercial catches of the species (see https://www.st.nmfs.noaa.gov/commercial-fisheries/); thus, declines of scamp in the SEUS relative to virgin abundance were likely higher than estimated in our study.

The near disappearance of small scamp from chevron trap catches since the early 2000s suggests recent recruitment failure of scamp may have occurred in the SEUS. Recruitment failure has been documented for other reef-associated fish species in the SEUS including red grouper (*Epinephelus morio*; SEDAR, 2017), and there are two potential hypotheses for possible recruitment failure. First, recruitment overfishing may be occurring, where spawning biomass has been depleted by direct exploitation to a level where reproductive capacity has been significantly reduced (Hilborn and Walters, 1992), or sperm limitation has occurred due to skewed sex ratios. Second, egg, larval, or juvenile

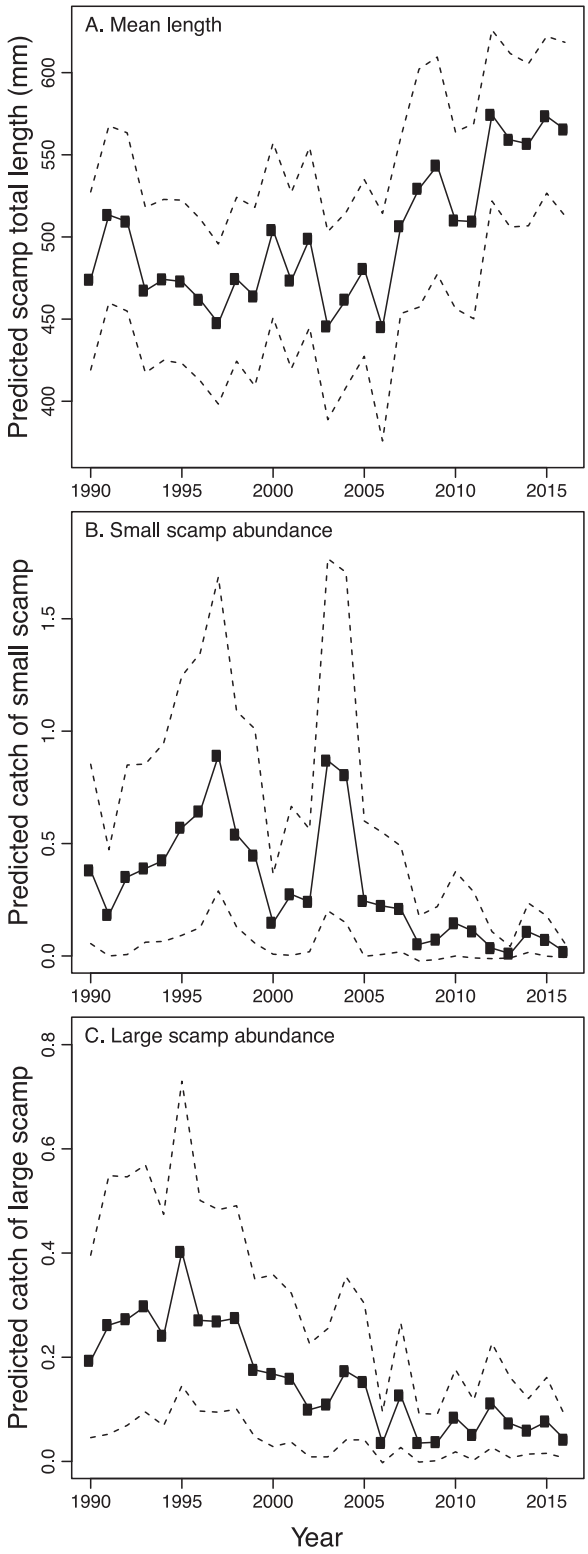


Fig. 9. Predicted annual scamp (*Mycteroperca phenax*) total length (mm; A), abundance of small scamp (< 500 mm total length; B), and abundance of large scamp (≥ 500 mm total length; C) using spatially explicit generalized additive models built on Southeast Reef Fish Survey chevron trap data along the southeast United States Atlantic coast, 1990–2016. Filled circles are mean predictions at average values of all other model covariates and dashed lines represent 95% confidence intervals.

scamp mortality may have increased. Possible explanations for increased egg, larval, or juvenile mortality include changes in environmental conditions, the introduction of the highly predatory and non-native red lionfish (*Pterois volitans*; Morris and Whitfield, 2009; Ballew et al., 2016) that may eat juvenile scamp, the increased abundance of other native piscivores, or loss of other forage fish species available to piscivores leading to increased predation on juvenile scamp.

Scamp were not encountered broadly throughout the SEUS, instead primarily occurring on the middle and outer continental shelf between southern North Carolina and Georgia. These results are similar to previous studies that have found similar spatial distributions of scamp in the SEUS (Manooch et al., 1998; Harris et al., 2002; Bacheler et al., 2016). Middle and outer continental shelf habitats that scamp inhabit in the SEUS are relatively deep, which is problematic given that a high proportion of landed scamp must be released because they are smaller than the minimum size limit (35%; Rudershausen et al., 2007). Predicted mortality of released scamp (e.g., due to barotrauma) is therefore relatively high (i.e., 23–35%; Rudershausen et al., 2007; Pulver, 2017). Unfortunately, there are no easy solutions to reduce the capture of sublegal scamp or increase their survival upon release given that increasing hook size does not reduce the catch of sublegal scamp and sublegal fish occur in the same areas as larger, legal-sized scamp (Bacheler and Buckel, 2004; Rudershausen et al., 2007). Circle hooks generally result in a reduced incidence of deep, traumatic gut or gill hooking of groupers, which could increase their post-release survival, but the results for scamp in particular have been mixed (Bacheler and Buckel, 2004; Sauls and Ayala, 2012). Survival of released scamp may also be improved with the wider adoption of venting or use of descending devices that may reduce the effects of barotrauma (Butcher et al., 2012).

The coefficients of variation for scamp relative abundance using video were approximately half as large as they were for traps, a result that has similarly been found for many reef-associated fish species in Australia (Harvey et al., 2012). Our results are also consistent with previous work that documented scamp having much higher frequency of occurrence on video (12%) compared to traps (1%) in Georgia and Florida waters (Bacheler et al., 2013b). But these results cannot be generalized to all reef fish because some species like black sea bass (*Centropristis striata*) and red grouper (*Epinephelus morio*) are more commonly caught in traps than observed on video in the SEUS (Bacheler et al., 2013b). Moreover, chevron trap sampling provides valuable information including fish length, weight, otoliths for ageing, and reproductive tissue that can be used to estimate age at maturity, the timing of sex change, and reproductive output. Last, the chevron trap time series is much longer than the video time series, making it particularly important for scamp management. Thus, we believe that using traps and video in combination provides much more useful information than either gear by itself.

The covariate relationships for trap and video models were useful to help understand the biology and ecology of scamp, but they can also be used to make inferences about gear-specific detectability and the robustness of the GAMs. For instance, both trap and video models indicated an increasing relative abundance of scamp in deeper (i.e., 60–100 m) water in our survey, which is consistent with previous work on scamp (Rudershausen et al., 2007; Pulver, 2017). Scamp were also more commonly observed in high-relief ledge habitats with large amounts of hard-bottom, similar to the findings of Kendall et al. (2008). There was a strong, positive relationship between scamp trap catch and bottom water temperature, however, that was absent for scamp video counts, likely due to temperature affecting scamp feeding rates and their subsequent capture in baited traps (e.g., Bacheler et al., 2014). Video detection of scamp was not influenced by bottom temperature or water clarity, but was affected by the direction of the current, presumably because they would tend to aggregate on the down-current side of the baited trap (e.g., Bacheler et al., 2014). The consistency of our models between gears and covariate combinations suggests that our GAMs were robust.

There were some shortcomings of our study on scamp in the SEUS. First, the spatial extent of sampling increased over time, which may

have influenced study results. We believe any related potential bias in scamp relative abundance or mean length was negligible because trends in southern North Carolina through Georgia (which has been sampled consistently since 1990) were nearly identical to the overall study area, similar to the results of Bacheler and Ballenger (2016) for black sea bass (*Centropristis striata*). Second, our study was correlational and, thus, causation could not be determined. Third, we used an arbitrary length cutoff of 500 mm total length to separate small and large scamp in our analyses because sample sizes of each group were sufficient for modeling, but the downside is that this cutoff lacked reference to scamp biology. Last, our models explained 5–35% of the deviance in scamp relative abundance or mean length. Thus, 65–95% of the deviance was left unexplained by our models, suggesting that other unmeasured variables (e.g., social interactions, prey or predator abundance) are likely important in determining scamp relative abundance and mean length in the SEUS. Moreover, binomial submodels outperformed positive submodels based on model deviance, suggesting that it is easier to model scamp distribution than scamp abundance.

Despite these shortcomings, we demonstrated that scamp have experienced a strong and significant decline in the SEUS over the last three decades, perhaps due to recruitment failure stemming from recruitment overfishing or increased mortality on the egg, larval, or juvenile stages from invasive lionfish or other predatory species. The sustainable management of scamp in the SEUS is dependent upon elucidating the exact mechanism causing recruitment failure, because without any improvement in recruitment, scamp abundance will likely not increase, regardless of any management measures. And as was the case for Atlantic cod (*Gadus morhua*) in the northwest Atlantic Ocean or red snapper (*Lutjanus campechanus*) in the SEUS, the rebuilding time for severely depleted long-lived fish species could be many years or decades.

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