Influence of soak time and fish accumulation on catches of reef fishes in a multispecies trap survey

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Abstract—Catch rates from fishery-independent surveys often are assumed to vary in proportion to the actual abundance of a population, but this approach assumes that the catchability coefficient (q) is constant. When fish accumulate in a gear, the rate at which the gear catches fish can decline, and, as a result, catch asymptotes and q declines with longer fishing times. We used data from long-term trap surveys (1990–2011) in the southeastern U.S. Atlantic to determine whether traps saturated for 8 reef fish species because of the amount of time traps soaked or the level of fish accumulation (the total number of individuals of all fish species caught in a trap). We used a delta-generalized-additive model to relate the catch of each species to a variety of predictor variables to determine how catch was influenced by soak time and fish accumulation after accounting for variability in catch due to the other predictor variables in the model. We found evidence of trap saturation for all 8 reef fish species examined. Traps became saturated for most species across the range of soak times examined, but trap saturation occurred for 3 fish species because of fish accumulation levels in the trap. Our results indicate that, to infer relative abundance levels from catch data, future studies should standardize catch or catch rates with nonlinear regression models that incorporate soak time, fish accumulation, and any other predictor variable that may ultimately influence catch. Determination of the exact mechanisms that cause trap saturation is a critical need for accurate stock assessment, and our results indicate that these mechanisms may vary considerably among species.

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Robust fishery-independent survey data are a critical component of modern fisheries stock assessments (Pennington and Stromme, 1998). Catch rates from fishery-independent surveys often are assumed to vary in proportion to the actual abundance of a fish population and, therefore, provide a relative measure of annual changes in abundance that can be used as a tuning index in a stock assessment (Kimura and Somerton, 2006). The basic assumption of this approach is that the catchability coefficient (q), or the efficiency of a fishery or survey gear, is constant over space, time, and over the range of environmental conditions encountered in a survey (Hilborn and Walters, 1992).

It is also typically assumed that q is not influenced by the amount of time a particular fishing gear is fished (Hamley, 1975). When the rate at which a fishing gear catches fish declines as fish accumulate in it, the fishing gear becomes saturated and q declines as fishing times increase (Miller, 1979; Olin et al., 2004). Therefore, catch rates tend to increase asymptotically rather than proportionally with fish abundance, and at high levels of abundance, catch rates are an insensitive indicator of change (Ricker, 1975). Numerous mechanisms have been shown to cause gear saturation, which can be broadly categorized as space limitation of gear, increased gear avoidance, interspecific competition, bait degradation or consumption of bait, or fishing gear that causes local depletion of fish (Kennedy, 1951; Richards et al., 1983; Olin et al., 2004). Depending on the exact mechanism that causes gear saturation, the catch at which a fishing gear becomes saturated may or may not reflect actual abundance (Beverton and Holt, 1954).

Although saturation in gill nets, longlines, and trawl nets has been well studied (Ragonese et al., 2001; Olin et al., 2004; Rodgveller et al., 2008), there has been a paucity of empirical research on the presence of trap saturation. Traps are widely used, especially in sensitive habi-

tats (e.g., seagrass meadows and coral reefs), and are sometimes the only feasible method of sampling in these habitats because of their relatively low effect on substrate and benthic communities (Miller, 1990). Clearly, the catch of fishes or invertebrates in traps cannot continue to increase linearly with soak time because the space inside a trap is finite and will eventually become filled with animals to the point at which no additional individuals can enter (Bennett, 1974; Austin, 1977; Miller, 1990). Models have been developed to describe the relationship between catch per trap and soak time, with the intention of using those models to standardize catch for different soak times (Munro, 1974; Somerton and Merritt, 1986; Zhou and Shirley, 1997). Unfortunately, these approaches to standardization do not account for landscape (e.g., depth) or environmental effects (e.g., water temperature) on catch. Nor do they help us understand how the catch of one species may be influenced by the catches of other species.

One recent method to examine these drawbacks has been to model the catch of a species as a function of soak time and fish accumulation (i.e., the total number of individuals of all species caught by a fishing gear; Olin et al., 2004) after accounting for other variables that may influence catch. In other words, catch rates can first be standardized by all of the predictor variables in the model building process (Lo et al., 1992; Maunder and Punt, 2004), and then the specific effects of soak time and fish accumulation can be extracted and examined independently of other predictor variables (Li et al., 2011). For example, Li et al. (2011) showed that gill nets became saturated with Yellow Perch (*Perca flavescens*) because of the total number of individuals caught in a gill net but not because of increased soak times. These results indicate that Yellow Perch catch rates decline when, for instance, this species sees fish already caught in the gill net, and not for reasons associated purely with increased soak time (i.e., when all the Yellow Perch in an area are caught, which takes some time).

In our study, we used a standardized catch approach to examine the influence of soak time and fish accumulation on the catches of several reef fish species from long-term fishery-independent, multispecies trap surveys occurring in the southeastern U.S. Atlantic (SEUS) from North Carolina to Florida. The inclusion of soak time and fish accumulation separated mechanisms that cause gear saturation into 2 groups: those mechanisms related to fish accumulation (e.g., agonistic behaviors or bait depletion) and those mechanisms related to the length of time a trap soaks (e.g., local depletion of the target species or loss of bait freshness). We developed a delta-generalized-additive model (delta-GAM) that was able to accommodate both nonlinearities between the response and predictor variables and zero-inflation (i.e., a high proportion of zero catches; Martin et al., 2005). This approach allowed us to determine whether trap saturation occured because of either soak time or fish accumulation, or both, and then we used the model to predict relative abundance after accounting for the influence of soak time and fish accumulation.

Materials and methods

Study area

In our study reef fish species associated with hard substrates were sampled on the continental shelf and continental shelf-break in the SEUS. The continental shelf and shelf-break in the SEUS are dominated by sand and mud substrates, within which areas of hard, rocky substrates ("hard bottom") occur and a highly diverse reef fish assemblage associates. 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; Glasgow, 2010). Hard bottom areas often host diverse epifauna that can provide food and shelter for reef fishes. The major oceanographic feature of the SEUS is the Gulf Stream, which influences outer sections of the continental shelf as it flows northward. Consistently warm Gulf Stream waters along the outer SEUS shelf allow tropical and subtropical species to inhabit areas at least as far north as North Carolina (Miller and Richards, 1980). For our study, sampling occurred on continental shelf and shelf break habitats from approximately Cape Lookout, North Carolina, to St. Lucie Inlet, Florida (Fig. 1).

Sampling approach

The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program of the South Carolina Department of Natural Resources has used chevron fish traps to index reef fish abundance since the late 1980s. Since 2009, MARMAP funding for reef fish sampling has been supplemented by the cooperative Southeast Area Monitoring and Assessment Program—South Atlantic (SEAMAP-SA) administered by the National Marine Fisheries Service. We analyzed MARMAP data from 1990 through 2011, during which time sampling with chevron fish traps was conducted in a consistent manner (as described later in this section). We also included in our analyses 2010–11 data from the Southeast Fishery-independent Survey (SEFIS), which the National Marine Fisheries Service created in 2010 to increase fishery-independent sampling in the SEUS, because sampling methods were identical. Hereafter, the 2 sampling programs are referred to as "MARMAP/SEFIS."

Hard bottom sampling stations included in the analyses were selected for sampling in 1 of 3 ways. First, most sites were selected randomly from the MARMAP/SEFIS sampling frame that consisted of approximately 2000 sampling stations on hard bottom habitat. Second, some stations in the sampling frame were sampled op-

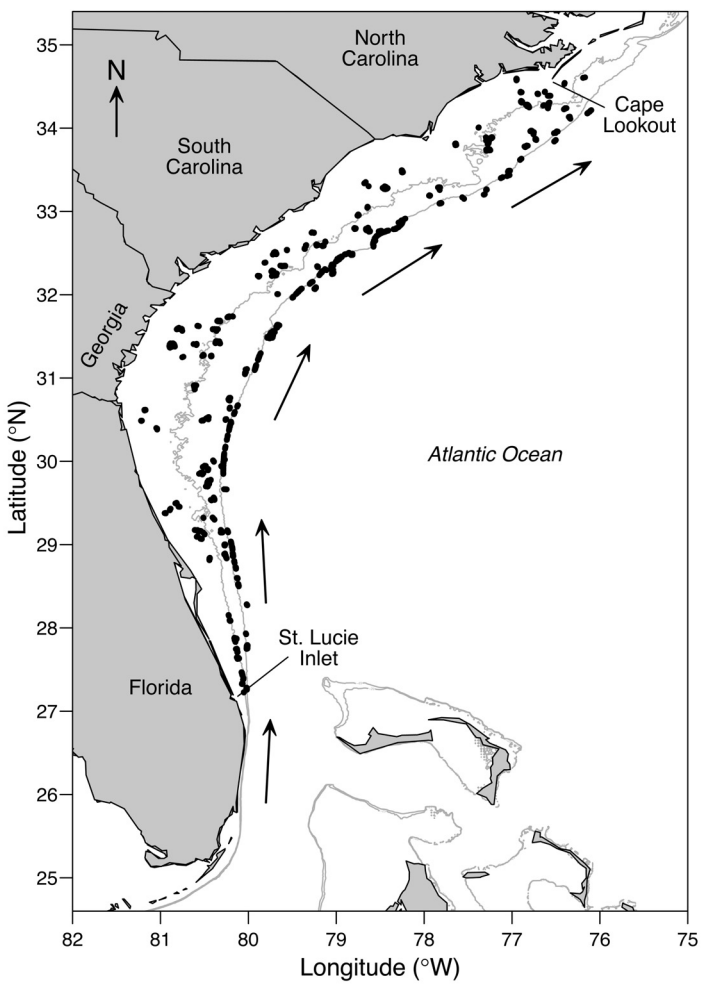

Figure 1

Spatial distribution of samples of reef fish species (black circles) collected in chevron traps during 2 long-term, fishery-independent survey programs in the southeastern U.S. Atlantic—the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11)—for examination of the relationship between soak time, fish accumulation, and catch of 8 reef fish species. Note that black circles overlap in many instances. Gray lines indicate 35- and 70-m depth contours (derived from bathymetry data), and arrows indicate the approximate path of the Gulf Stream.

portunistically even though they were not selected randomly for sampling in a given year. Third, new hard-bottom stations were added during the study period through the use of information from fishermen, charts, and historical surveys. These new locations were investigated with a vessel echosounder or drop cameras and sampled if hard bottom habitat was present. We assumed that the catch of each species was influenced similarly at all stations by the various predictor variables (described later). All sampling for this study occurred during daylight hours between March and October and was conducted on 1 of 4 vessels: MARMAP and SEAMAP-SA used the RV *Palmetto* (1990–2011), and SEFIS used the RV *Savannah* (2010–11), NOAA Ship *Nancy Foster* (2010), and NOAA Ship *Pisces* (2011).

Chevron fish traps were deployed at each station sampled in this study. Chevron traps were constructed from plastic-coated, galvanized 2-mm-diameter wire (mesh size=3.4 cm^2) and shaped like an arrowhead that measured 1.7 m × 1.5 m × 0.6 m, with a total volume of 0.91 m^3 (Fig. 2) (Collins, 1990). The mouth openings of traps were shaped like a teardrop and measured approximately 18 cm wide and 45 cm high. Each trap was baited with 24 menhaden (*Brevoortia* spp.): 16 were attached to freely accessible stringers and 8 were placed loosely inside. Traps typically were deployed in a group of 6. The minimum distance between individual traps was approximately 200 m to provide some measure of independence between traps.

Because the primary purpose of MARMAP/SEFIS sampling was to provide standardized catch information for reef fish species in the SEUS, a soak time of 90 min was targeted for each trap. We were not able to soak traps for a wide range of experimentally chosen amounts of time. However, for many different reasons, soak time was somewhat variable, ranging from 9 to 270 min (mean: 97.6 min and standard deviation of the mean [SD]=12.8) (Fig. 3). All trap deployments that did not fish properly (e.g., traps that dragged in current) were excluded from analysis. Soak times were variable enough to allow an examination of the ways in which fish catch was related to variability in soak time.

We included in our analyses the 8 most commonly caught reef fish species in the MARMAP/SEFIS trap surveys: Black Sea Bass (*Centropristis striata*), Tomtate (*Haemulon aurolineatum*), Red Porgy (*Pagrus pagrus*), Bank Sea Bass (*Centropristis ocyurus*), Gray Triggerfish (*Balistes capriscus*), Vermilion Snapper (*Rhomboplites aurorubens*), *Stenotomus* spp., and Sand Perch (*Diplectrum formosum*) (Table 1). *Stenotomus* spp. may represent more than one species, but, for the purpose of discussion, we will refer to this taxon as a single species and the group of taxa studied as 8 species of fish. Fish coloration, shape, and meristics were used to identify individuals to genus and species levels with field guides (e.g., Robins et al., 1986; Hoese and Moore, 1998; McEachran and Fechhelm, 1998; Carpenter, 2002; Humann and Deloach, 2002; McEachran and Fechhelm, 2005). Black Sea Bass, Red Porgy, Gray Triggerfish, and Vermilion Snapper are targeted by commercial and recreational fishermen in the SEUS. The 8 species included in our analyses were the most common species caught in the traps in the MARMAP/SEFIS surveys by both frequency of occurrence and mean catch per trap (Table 2). Additional species were not analyzed if their frequency of occurrence was less

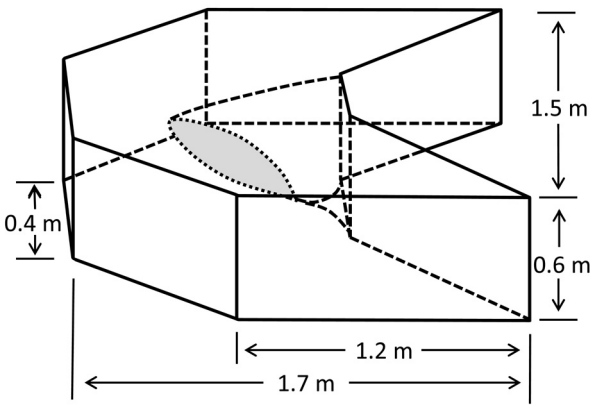

Figure 2

Schematic of the design of the chevron trap used to sample reef fish species in 1990–2011 by the Marine Resources Monitoring, Assessment, and Prediction Program and the Southeast Fishery-independent Survey. The gray oval is the mouth opening of the trap (~18 cm wide and 45 cm high), and the total trap volume is 0.91 m^3.

than 15%, but individuals of all species were included in analyses of fish accumulation.

Data analyses

We used a generalized additive modeling approach to test the hypothesis that trap catch of reef fishes was influenced by soak time and fish accumulation. GAMs use nonparametric smoothing functions to account for nonlinearities between predictor and response variables (Hastie and Tibshirani, 1990; Bacheler et al., 2009). GAMs extend traditional additive models by allowing for alternative distributions of underlying random variation, just as generalized linear models allow for alternative distributions in linear models.

We developed delta-GAMs because there was a high proportion of zero observations (>50%) for the catch of each species that could not be modeled appropriately with standard statistical distributions. We considered zero-inflated models, but they were challenging to work with because they rarely converged, and when they did, model solutions were often unreasonable. Therefore, we developed a delta-GAM for each of the 8 species. Each delta-GAM contained 2 submodels that estimated the influence of soak time and fish accumulation on catch:

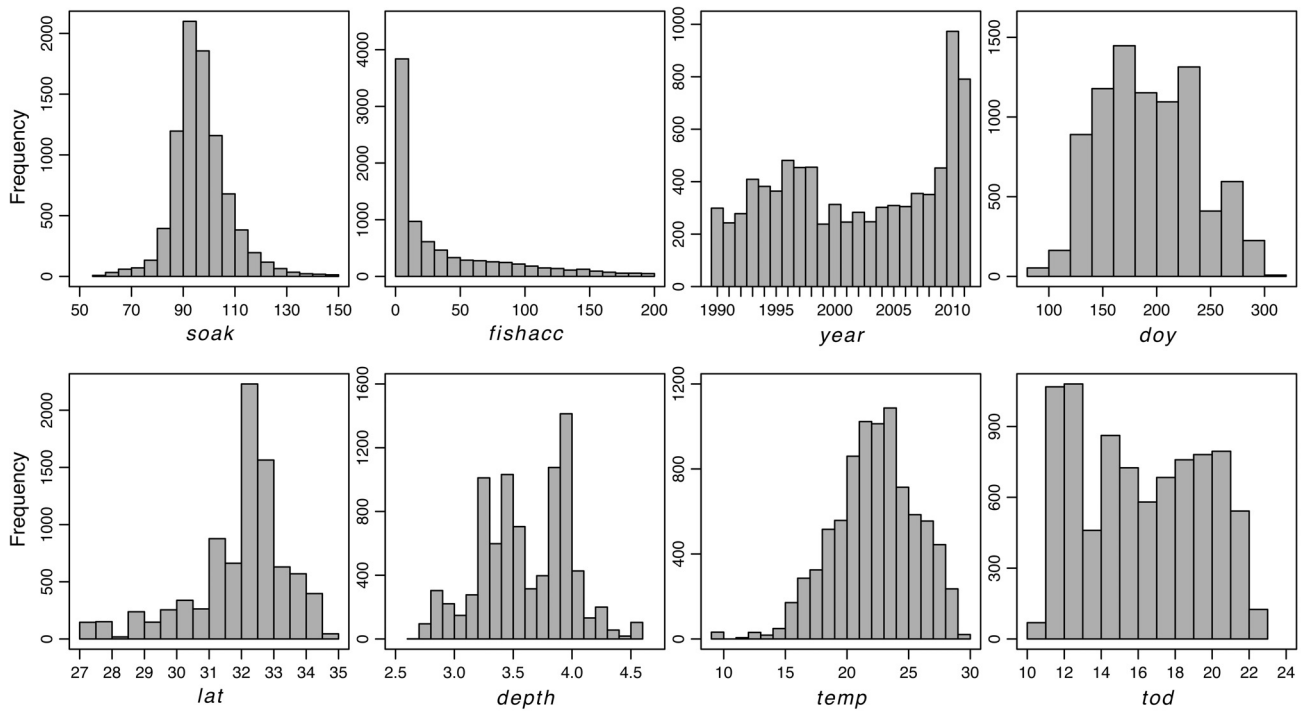

Figure 3

Histograms of predictor variables used in the delta-generalized-additive models of reef fish catch from trap surveys conducted by the Marine Resources Monitoring, Assessment, and Prediction Program and the Southeast Fishery-independent Survey in the Atlantic Ocean from North Carolina to Florida during 1990–2011. Variables were soak time (*soak*; min), fish accumulation (*fishacc*; total fish per trap), year of sampling (*year*), day of the year (*doy*), latitude (*lat*; °N), depth of sampling (*depth*; m), bottom water temperature (*temp*; °C), and time of day (*tod*; Coordinated Universal Time).

Table 1

Life history characteristics of the 8 fish species analyzed in our study of soak time and fish accumulation as mechanisms that can cause trap saturation. Characteristics come from data sets of 2 sampling programs in the southeastern U.S. Atlantic: the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11). L_∞=maximum length; $L_{maturity}$=length at maturity; A_{max}=maximum age in years; f=fish; i=invertebrates; PH=protogynous hermaprodite; SH=sequential hermaphrodite; GO=gonochoristic. All lengths are total lengths in centimeters.

Common name	Scientific name	L_∞	$L_{maturity}$	A_{max}	Diet	Reproduction
Bank Sea Bass	*Centropristis ocyurus*	33[a]	14[a]	9[a]	f,i[a]	PH[a]
Black Sea Bass	*Centropristis striata*	50[a]	16[a]	11[a]	f,i[b]	PH[a]
Gray Triggerfish	*Balistes capriscus*	48[a]	19[a]	12[a]	i[f]	GO[a]
Red Porgy	*Pagrus pagrus*	51[a]	25[a]	20[a]	f,i[e]	PH[a]
Sand Perch	*Diplectrum formosum*	24[k]	19[k]	8[k]	f,i[l]	SH[a]
Tomtate	*Haemulon aurolineatum*	35[c]	18[a]	17[a]	i[d]	GO[a]
Vermilion Snapper	*Rhomboplites aurorubens*	51[a]	15[g]	13[a]	f,i[h]	GO[a]
	Stenotomus spp.	46[l]	18[i]	15[j]	i[l]	GO[a]

Sources: [a] MARMAP (unpubl. data); [b] Sedberry (1988); [c] Manooch and Barans (1982); [d] Sedberry (1985); [e] Manooch (1977); [f] Kurz (1995); [g] Zhao et al. (1997); [h] Sedberry and Cuellar (1993); [i] O'Brien et al. (1993); [j] Finkelstein (1969); [k] Bubley and Pashuk (2010); [l] South Atlantic Fishery Management Council (http://www.safmc.net/).

one modeling the presence-absence of each species and another modeling the positive catches only (Lo et al., 1992; Pennington, 1996; Stefansson, 1996). The overall effects of a particular predictor variable on catch were then obtained by multiplying the effects from each submodel (Maunder and Punt, 2004; Murray, 2004; Li et al., 2011).

We examined the influence of 8 predictor variables on the catch of 8 reef fish species: soak time, fish accumulation, year, depth, time of day, day of the year, water temperature, and latitude (Fig. 3). In this study, we were particularly interested in how soak time and fish accumulation influenced the catch of each species after accounting for variability in the other 6 predictor variables. To accomplish this goal, we first fitted the delta-GAM, and then we predicted catch for a range of values for soak time and fish accumulation, fixing all other predictor variables to their own mean, except the variable *year*, which was fixed at year 2000 (i.e., the midpoint of the time series; results were invariant to the year chosen). Soak time (*soak*) was the number of minutes a trap soaked between deployment and retrieval, and fish accumulation (*fishacc*) was the total number of individuals of all fish species caught

Table 2

Catch information, mean length, and frequency of occurrence (FO) for each of the 8 most common species of reef fishes in the data sets of 2 sampling programs in the southeastern U.S. Atlantic: the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11). Mean proportion of catch is the mean proportion of catch in each trap that was composed of a single species. Fork length was measured for all species, except Black Sea Bass (*Centropristis striata*) and Bank Sea Bass (*C. ocyurus*), which were measured for total length. SD=standard deviation of the mean.

Species	FO	Mean (SD) catch per trap	Mean (SD) proportion of catch	Mean (SD) length (cm)
Bank Sea Bass	0.301	1.4 (3.9)	0.06 (0.17)	22.5 (3.0)
Black Sea Bass	0.408	10.2 (21.8)	0.20 (0.30)	23.6 (4.5)
Gray Triggerfish	0.263	0.9 (3.3)	0.06 (0.18)	31.3 (7.0)
Red Porgy	0.364	2.0 (4.4)	0.13 (0.26)	27.1 (4.6)
Sand Perch	0.184	0.6 (1.8)	0.03 (0.13)	22.8 (1.6)
Stenotomus spp.	0.203	6.5 (19.8)	0.09 (0.20)	15.6 (2.0)
Tomtate	0.403	9.3 (21.9)	0.18 (0.28)	18.1 (1.9)
Vermilion Snapper	0.263	3.0 (9.9)	0.07 (0.17)	23.7 (3.9)

in a trap. We limited our analysis to *soak* between 50 and 150 min and to *fishacc* less than 200 total fish per trap because of low small sample sizes outside of these ranges (i.e., <2% of all observations). *Year* was included as a categorical variable (1990–2011), but all other variables were included as continuous variables. Depth (*depth*) was measured in meters for each trap deployment; depths were recorded in a range of 13–218 m over the course of the surveys used in our study. Because of small sample sizes, samples collected at depths >100 m were excluded from our analyses and remaining depths were log-transformed to achieve normality. Time of day (*tod*) was measured in Coordinated Universal Time, and day of the year (*doy*) was the day of the year that the trap sample was collected. Water temperature (*temp*) was bottom water temperature measured in degrees Celsius for each group of 6 simultaneously deployed traps, and latitude (*lat*) was the latitude (degrees north) at which the samples were collected. Longitude was not included because of its statistically significant correlation ($P<0.001$) with depth that occurred because of the north–south orientation of our study area.

Before the development of models, multicollinearity among predictor variables was examined because its presence can cause erratic model behavior and should be avoided (Zar, 1999). We assessed the severity of multicollinearity among predictor variables through calculation of the variance inflation factor (VIF) for each variable, which measures the amount of variance that is inflated for each variable as a result of its collinearity with other predictor variables. 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)—thus indicating no significant multicollinearity among predictor variables in our data set.

We also included *fishacc* as a predictor variable in our GAMs. Because trap catch often was composed of a mixture of fish species in the multispecies survey, the contribution of a single species to the *fishacc* variable was generally small, but there were instances when the catch in traps was dominated by a single species. Inclusion of samples in which the catch was dominated by a single species may have positively biased the reported deviance of the models for those particular species, but the functional relationship between single species catch and *fishacc* was not affected. If catch of a single species was influenced entirely by *fishacc*, the relationship between the 2 variables would have been perfectly linear. By definition, then, any deviation from a linear relationship between the 2 variables could not have been the result of a potential lack of independence. Because we were primarily interested in the shape of the relationship between catch and *fishacc*, we agree with Li et al. (2011) that the inclusion of the *fishacc* variable is a useful approach to examine trap saturation due to fish accumulation.

Initially, a full model was fitted on the presence-absence data for each species. Following Li et al. (2011), we used a binomial GAM submodel to estimate the probability of presence for each species being caught in individual traps (η), which was assumed to be an independent draw from a binary variable with a probability of success p:

$$E(p) = \upsilon^{-1}(\eta); \tag{1}$$

$$\eta = \alpha + g_1(soak) + g_2(fishacc) + \sum_{j=3}^{N} g_j(x_j),$$

where $E(p)$ = the expectation of p;
υ = the logit link function;
α = the intercept;
soak = soak time;
fishacc = fish accumulation;
g_j are smoothing functions,
N = the number of predictor variables in the model; and
x_j = the jth remaining explanatory variable.

We next coded a positive-catch GAM submodel that related the Gaussian fourth-root transformed catch of each reef fish species when caught to the 8 predictor variables. We compared the error structure of log-normal, log-gamma, and Gaussian (with a fourth-root transformation) distributions using the Akaike information criterion (AIC; Burnham and Anderson, 2002) for each full model:

$$\text{AIC} = -2\log\left(\mathcal{L}(\hat{\theta} \mid y)\right) + 2K, \tag{2}$$

where $\left(\mathcal{L}(\hat{\theta} \mid y)\right)$ = the log-likelihood; and
K = the number of parameters of each model.

The model with the lowest AIC value was considered the best model in the model set. For all species, the Gaussian distributions with fourth-root transformations had the lowest AIC values and were therefore considered the most parsimonious distributions for the positive-catch submodels.

For the positive-catch GAM submodel, we used the following equation:

$$y^{0.25} = a' + h_1(soak) + h_2(fishacc) + \sum_{j=3}^{N} h_j(x_j), \tag{3}$$

where y = the trap catch of a particular reef fish species;
a' = the intercept;
h_j are smoothing functions;
N = the number of predictor variables in the model; and
x_j = the jth remaining explanatory variable.

For each reef fish species, we then compared the full GAM submodels containing 8 predictor variables to various reduced models that contained fewer predictor variables. We compared various binomial GAM submodels with the unbiased risk estimator (UBRE) score,

Table 3

Final generalized additive models (GAMs) for 8 species of reef fishes in our study. Data were obtained from 2 sampling programs in the southeastern U.S. Atlantic: the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11). Binomial GAMs were constructed with presence-absence data, and Gaussian GAMs were constructed with only positive catch. The best model for each species was the one with the lowest unbiased risk estimator (binomial GAM) or generalized cross validation (Gaussian GAM) scores (see the *Materials and methods* section for full descriptions). *N*=number of samples from chevron traps that were included in each model. Dev. exp.= the percentage of deviance explained by each model, *ex* means that the covariate was excluded from the final model, g_1… g_7 are nonparametric smoothing functions, *f*=a categorical function, *soak*=soak time, *fishacc*=fish accumulation, *year*=year, *doy*=day of the year, *lat*=latitude, *depth*=bottom depth, *temp* =bottom temperature, and *tod*=time of the day. Estimated degrees of freedom and statistical significance are shown for each term: *=*P*≤0.10, **=*P*≤0.05, ***=*P*≤0.01.

Model and species	*N*	Dev. exp.	g_1 (*soak*)	g_2 (*fishacc*)	f_1 (*year*)	g_3(*doy*)	g_4(*lat*)	g_5(*depth*)	g_6(*temp*)	g_7(*tod*)
Binomial GAM										
Bank Sea Bass	8530	28.8	ex	3.0***	21***	8.6***	8.1***	8.9***	6.3***	8.3***
Black Sea Bass	8530	63.6	ex	3.0***	21***	2.6***	8.6***	8.2***	8.1***	1.0**
Gray Triggerfish	8530	20.6	5.5***	3.0***	21***	8.9***	8.8***	5.8***	4.8***	8.1**
Red Porgy	8530	27.0	1.6*	3.0***	21***	8.0***	8.9***	7.8***	8.5***	5.1**
Sand Perch	8530	37.5	1.7***	6.8***	21***	ex	7.0***	7.8***	6.1	1.0***
Stenotomus spp.	8530	61.4	3.3***	7.4***	21***	ex	5.9***	6.0***	7.9***	8.1***
Tomtate	8530	46.9	5.6***	8.2***	21***	2.8***	8.9***	8.3***	7.1***	2.0*
Vermilion Snapper	8530	38.0	1.6	8.6***	21***	1.0***	8.2***	7.1***	7.1***	8.2***
Gaussian GAM										
Bank Sea Bass	2571	22.1	ex	2.9***	21***	8.9***	8.2***	8.5***	6.8***	3.9***
Black Sea Bass	3476	64.4	ex	8.1***	21***	7.9***	8.6***	7.2***	1.6***	4.8***
Gray Triggerfish	2244	18.9	2.3**	2.9***	21***	1.0***	7.5***	7.4***	1.0	7.7***
Red Porgy	3104	21.4	3.4*	2.0***	21***	2.1	8.8***	8.8***	2.2	1.0**
Sand Perch	1568	26.5	ex	2.8***	21***	5.3	8.9***	2.7***	3.4*	ex
Stenotomus spp.	1733	48.6	4.0*	4.0***	21***	1.0	8.8***	7.9***	5.4**	4.8**
Tomtate	3437	51.2	ex	7.0***	21***	6.2**	8.8***	8.8***	7.7***	4.4**
Vermilion Snapper	2240	36.1	ex	6.4***	21***	ex	8.0***	5.4***	1.6***	ex

which is effectively a rescaled AIC approach that is well suited for binomial models (Wahba, 1990). For the positive-catch GAM submodels, we used generalized cross validation (GCV; a measure of the out-of-sample prediction mean squared error) to select the most parsimonious combination of predictor variables. For each approach, the model for each species with the smallest UBRE or GCV score was selected as the best model in that particular model set. In addition, we evaluated the model diagnostics for each final model selected by UBRE or GCV. In all cases, residuals in final models met assumptions of normality and constant variance. All models were coded and analyzed in R,[1] vers. 2.14.1 (R Development Core Team, 2011) with the mgcv library, vers. 1.7-13 (Wood, 2008).

We used 2 methods to test for the presence or absence of spatial autocorrelation, which is the situation where samples near one another are often more similar than 2 samples farther apart. First, we developed generalized additive mixed models (GAMMs) for each species with the same covariates as the GAM models presented previously. GAMMs are spatially explicit regression models that allow for spatially correlated error distributions (Venables and Ripley, 2002). Using positive-catch data, we found that the coefficient of multiple determination (R^2) and parameter significance values from the GAMMs were nearly identical to GAM model results for all 8 species. Binomial GAMMs built on presence-absence data never converged for any species. Second, we developed semivariograms for each species for each year using the R package geoR, vers. 1.7-2 (R Development Core Team, 2011). There were no consistent patterns in the relationship between the semivariance of the model residuals and distance between sampling points, indicating negligible spatial autocorrelation in the residuals.

The overall influence of *soak* or *fishacc* on reef fish catch was calculated as the product of the binomial and positive-catch submodels, and the variance of the overall model was estimated with a bootstrapping approach. We resampled the predictions (*N*=10,000) for both submodels at average values of all other predictor variables according to the pointwise estimates of error that were assumed to be distributed normally. For the combined (overall) predictions, we multiplied the simulated point estimates of error for each submodel. The

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

95% confidence interval was estimated as the 0.025 and 0.975 quantiles of the 10,000 point estimates.

Results

The assumption of independence of predictor variables was met in our study. There were no statistically significant relationships between any of the predictor variables included in our analyses (VIF<4), and, in particular, *soak* and *fishacc* variables were unrelated (r^2<0.001). *Fishacc* was the total number of individuals of all species caught in a trap, whereas the response variable (i.e., catch) was the total number of individuals of each species caught in a trap. Moreover, no single species composed more than 20% of total trap catch (Table 2).

Overall, 8530 samples collected from chevron traps in the 22-year span of MARMAP/SEFIS surveys were included in our analyses (annual mean: 388 [SD 179]). Sampling occurred between March and October, and there were no obvious changes in the seasonality of sampling across years. The spatial coverage of the surveys, in contrast, expanded southward in the mid-1990s to include sampling sites in central Florida.

Of the 8 reef fish species included in our analyses, Black Sea Bass had the highest frequency of occurrence (0.408) and Sand Perch had the lowest (0.184; Table 2). Unstandardized catch per trap ranged from 0.6 for Sand Perch to 10.2 for Black Sea Bass. Mean lengths ranged from 15.6 cm fork length for *Stenotomus* spp. to 31.3 cm fork length for Gray Triggerfish (Table 2).

The binomial GAMs explained 20.6–63.6% of the deviance in presence-absence patterns of the 8 reef fish species (Table 3). Models that explained the least deviance were the ones for Gray Triggerfish (20.6%) and Red Porgy (28.8%), and models for Black Sea Bass (63.6%) and *Stenotomus* spp. (61.4%) explained the most deviance. All 8 predictor variables were selected in the binomial model for each species on the basis of UBRE scores, with the exceptions of *soak* for Black Sea Bass and Bank Sea Bass and *doy* for *Stenotomus* spp. and Sand Perch (Table 3). The *fishacc* variable was retained in the binomial models for all species.

The Gaussian GAMs explained 18.9–64.4% of the deviance in the positive-catch values of the 8 reef fish species (Table 3). The most deviance was explained by the models for Black Sea Bass (64.4%) and Tomtate (51.2%), and models for Gray Triggerfish (18.9%) and Red Porgy (21.4%) explained the least deviance (Table 3). On the basis of GCV scores, *soak* was excluded from the models for Black Sea Bass, Bank Sea Bass, Tomtate, Vermilion Snapper, and Sand Perch. Moreover, *doy* was excluded from the Vermilion Snapper model, and *tod* was excluded from the models for Vermilion Snapper and Sand Perch. The *fishacc* variable was included in all 8 models.

Over the range of *soak* values examined, predicted overall catch was invariant to *soak* for 3 species (Black Sea Bass, Bank Sea Bass, and Vermilion Snapper), positively related to *soak* for 2 species (Red Porgy and Gray Triggerfish), and negatively related to *soak* for the remaining 3 species (Tomtate, *Stenotomus* spp., and Sand Perch; Fig. 4). For most species, the influence of *soak* on the probability of obtaining nonzero catch was very similar to its influence on the estimated overall catch when present (Fig. 4). With a doubling of *soak* from 60 to 120 minutes, estimated catch approximately doubled for Red Porgy (106% increase) and Gray Triggerfish (95%) but increased little for Black Sea Bass (20%), Bank Sea Bass (9%), and Vermilion Snapper (8%; Table 4). The estimated overall catch of Sand Perch (–71%), Tomtate (–32%), and Sand Perch (–26%) declined when *soak* doubled (Table 4). Note that confidence intervals were larger for Gray Triggerfish and *Stenotomus* spp. than for the other 6 species.

The relationship between the overall catch of the 8 reef fish species and *fishacc* displayed one of 3 patterns (Fig. 5). The overall catch of Black Sea Bass, Tomtate, Vermilion Snapper, and Sand Perch generally was related linearly to *fishacc*, indicating that the rate of catch of these species was not strongly influenced by the catch of individuals of all species in the trap. Alternatively, the overall catch of Red Porgy, Bank Sea Bass, and Gray Triggerfish reached an asymptote at *fishacc* values between 50 and 100, indicating that individuals of these 3 species were much less likely to enter a trap once 50 to 100 total individuals of all species were caught in it. The last pattern was displayed by *Stenotomus* spp., the overall catch of which was exponentially related to *fishacc*, indicating that *Stenotomus* spp. were more likely to enter a trap once large numbers of individual of all species were caught (Fig. 5). All 8 species had relatively narrow 95% confidence intervals surrounding overall mean estimates.

Discussion

Fishery-independent survey data form a critical component of modern stock assessments because they produce indices of abundance that are assumed to vary in proportion to the actual abundance of a population (Pennington and Stromme, 1998). Whether or not indices of abundance track actual abundance is a complex topic that has been the subject of much research (Harley et al., 2001; Kimura and Somerton, 2006). The basic assumption of this approach is that q does not change over space, time, or environmental conditions (Hilborn and Walters, 1992). In our study, we tested whether q was influenced by 2 additional variables, the length of time the trap was soaked and fish accumulation. For the species in our study, there was no clear relationship between life history traits and mechanisms of trap saturation (Table 1). We found evidence of trap saturation for most of the reef fish species examined, but the responses were species-specific. Trap saturation was observed for some reef fishes across the range of soak

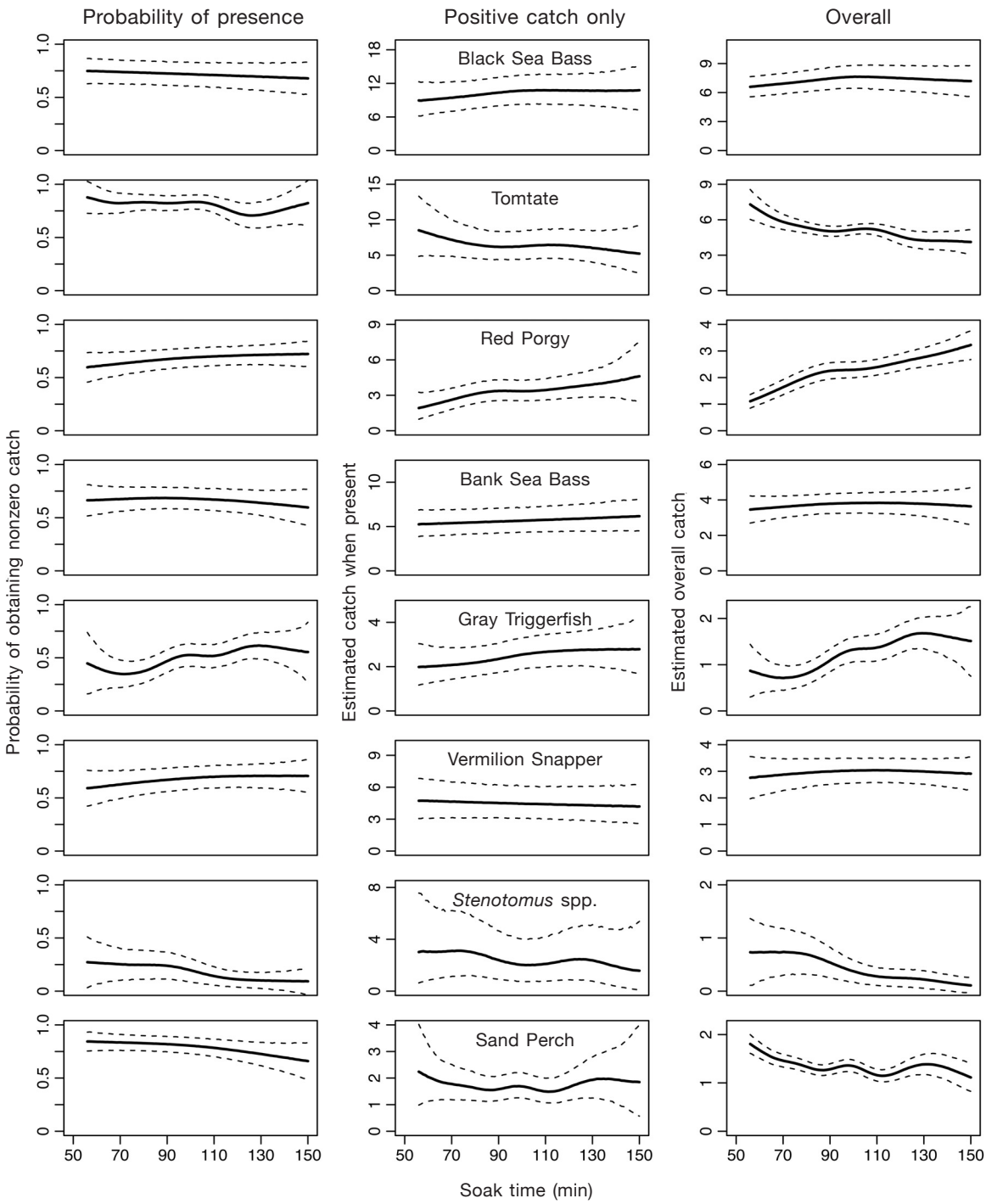

Figure 4

Relationship between soak time and the probability of obtaining a nonzero catch (probability of presence) (left column), estimated catch when present (middle column), and estimated overall catch (right column) for 8 species of reef fishes on the basis of data from trap surveys conducted in the southeastern U.S. Atlantic by the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11). Binomial generalized additive models (GAMs) were used to estimate probability of obtaining nonzero catch. Gaussian GAMs were used to estimate catch when present. Overall catch was determined through the combination of binomial and Gaussian GAM estimates. Dashed lines indicate 95% confidence intervals.

times examined, and, for others, because of fish accumulation in the trap.

A number of methods have been developed to determine if gear saturation is occurring. Addison and Bell (1997) used a simulation approach to show that the relationship between lobster catch and abundance was asymptotic, a problematic result because models would predict an even spatial distribution of lobster catches across a study area despite a true underlying aggregated distribution. Some researchers have documented gear saturation by the fact that the cumulative catch of individuals in traps that are periodically emptied is often much higher than the catch in traps that were hauled and redeployed without being emptied (Miller, 1979; Robertson, 1989). Alternatively, Li et al. (2011) developed a delta-GAM to quantify the relationship between catch of Walleye (*Sander vitreus*) and Yellow Perch and soak time or fish accumulation at average values of all other covariates in the model. We used the Li et al. (2011) modeling approach to show that chevron traps became saturated for all 8 reef fish species examined across a range of values for soak time or fish accumulation. There are 3 major benefits of this approach. First, it is possible to test for trap saturation through the use of long-term survey data, as long as there has been sufficient variation in soak time. Second, the relationship between catch and soak time or fish accumulation can be quantified after accounting for variation due to the other predictor variables in the model. Last, zero-inflation, the situation where a large number of zero observations in a data set cannot be properly accounted for with traditional statistical distributions, can be properly accounted for through the use of a delta model.

Table 4

Percent change in estimates of overall catch per trap for 8 reef fish species when soak time doubled (from 60 to 120 min) on the basis of data from 2 sampling programs in the southeastern U.S. Atlantic: the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11). Catch was estimated with a delta-generalized-additive model where mean values of all other predictor variables were used. Species are arranged from highest to lowest percent change in catch per trap.

Species	Estimated catch at 60 min	Estimated catch at 120 min	Percent change
Red Porgy	1.25	2.57	106
Gray Triggerfish	0.80	1.56	95
Black Sea Bass	6.45	7.71	20
Bank Sea Bass	3.51	3.83	9
Vermilion Snapper	2.79	3.02	8
Sand Perch	1.67	1.24	–26
Tomtate	6.78	4.58	–32
Stenotomus spp.	0.99	0.29	–71

Our study was improved by the inclusion of the *fishacc* variable in the models. If the rate at which a species entered the trap was unaffected by the number of individuals (of all species) already caught in a trap, then one would expect a positive, linear relationship between the catch of a species and the *fishacc* variable (Li et al., 2011). We showed that catches of Red Porgy, Bank Sea Bass, and Gray Triggerfish plateaued once a moderate number of total individuals were already caught in a trap, indicating that these species are more sensitive to species interactions and, therefore, much less likely to enter a trap once it began filling up. These results are consistent with previous work that has shown that behavioral interactions in and around traps can strongly influence the catch of target species (Addison and Bell, 1997; Jury et al., 2001; authors, personal observ.). In contrast and, perhaps, more surprisingly, Black Sea Bass, Tomtate, Vermilion Snapper, and Sand Perch continued to enter a trap at about the same rate no matter how many total individuals of all species were caught in it. A primary benefit of inclusion of a predictor variable for fish accumulation in our model was that it allowed us to distinguish between species that saturated the gear because of fish accumulating in a trap from the species that appeared to saturate the gear because of the amount of time a trap soaked. In addition, the inclusion of the *fishacc* variable standardized the catch of each of the 8 reef fish species to a common total catch of all species in the trap. In other words, we were able to remove variations in the catch of each reef fish species that were attributable to species-specific responses to fish accumulation. The inclusion of a variable for fish accumulation in a standardization model is one straightforward approach that can be used to account for some species interactions.

Our results indicate that catch per trap, not catch per trap minute, should be the response variable used in future standardization models for all the species we examined. If catch is invariant to soak time and catch per unit of effort (CPUE) is used as the response in a catch standardization model, then CPUE on average would be lower in traps with longer soak times than in traps with shorter soak times. Soak-time-dependent CPUE could become a serious problem if soak time for traps was longer in some years than in others because real changes in the relative abundance of a species would be confounded with the effects on CPUE due to changes in soak time. Instead, we recommend the use of a model-based approach with catch as the response variable and soak time and fish accumulation as predictor variables to properly account for any variation in catch due to these 2 factors.

Whether catch data from trap surveys can be used to index reef fish abundance ultimately depends on the underlying mechanisms responsible for the observed

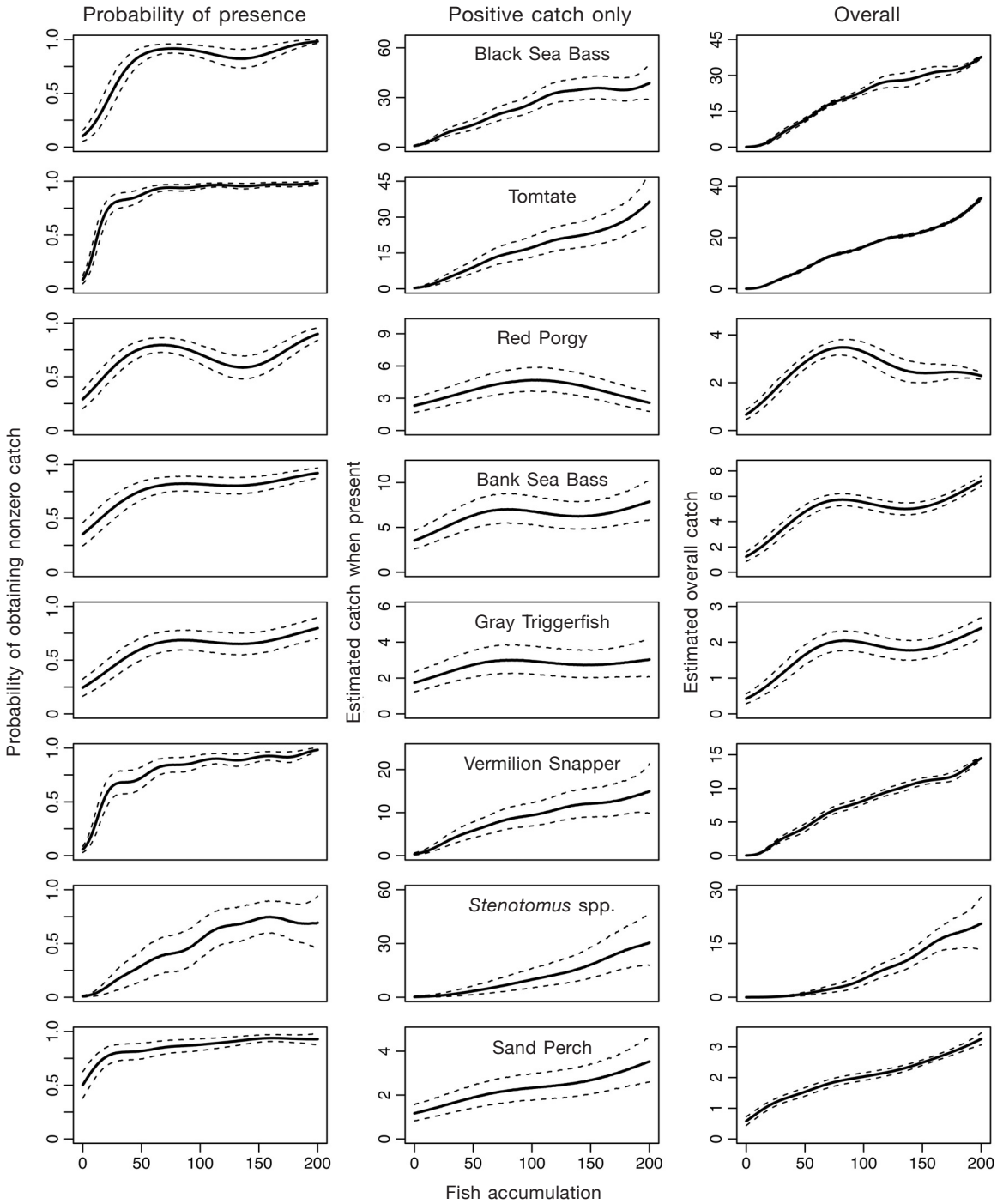

Figure 5

Relationship between fish accumulation (total fish per trap) and the probability of obtaining a nonzero catch (probability of presence) (left column), estimated catch when present (middle column), and estimated overall catch (right column) for 8 species of reef fishes on the basis of data from trap surveys conducted in the southeastern U.S. Atlantic by the Marine Resources Monitoring, Assessment, and Prediction Program (1990–2011) and the Southeast Fishery-independent Survey (2010–11). Binomial generalized additive models (GAMs) were used to estimate probability of obtaining nonzero catch. Gaussian GAMs were used to estimate catch when present. Overall catch was determined through the combination of binomial and Gaussian GAM estimates. Dashed lines indicate 95% confidence intervals.

trap saturation. For instance, if catch reaches an asymptote because most or all of the individuals in a local area have been caught, then catch is likely a good index of abundance. But catch may not reflect actual abundance if trap saturation occurs because of space limitation in the gear, negative species interactions, increasing avoidance of the gear due to individuals already being caught, handling time limitations, or bait deterioration or consumption of bait (Kennedy, 1951; Munro, 1974; Olin et al., 2004). If traps become saturated at a level of catch unrelated to actual abundance, then statistical models for censored data may be useful (Bagdonavicus et al., 2011). Another factor that may affect trap saturation is changes in feeding motivation of fishes with time of day or light levels. In our study, changes in feeding with time of day were not related to catch because all trapping was done during daylight hours. Light levels, therefore, were driven by water clarity more than by time of day. However, preliminary occupancy and *N*-mixture modeling for a few species has shown that water clarity does not appear to influence the detection probability of traps.[2] In our study, we could not identify the exact mechanisms responsible for trap saturation; therefore, this topic clearly requires more research.

Catches of Tomtate, *Stenotomus* spp., and Sand Perch declined with increasing soak times, indicating that at least some individuals of these 3 species may have escaped from the trap. These results are consistent with our own observations and a growing body of literature that indicates that some fish, crab, and lobster species frequently escape from traps and pots (Jury et al., 2001; Cole et al., 2004; Sturdivant and Clark, 2011). Tomtate, *Stenotomus* spp., and Sand Perch were among the 3 smallest fish species examined in our study, and their small size may have allowed them to escape through the narrow trap entrance more easily than could species of larger size. Size was the only life-history trait (Table 1) that influenced catch. An alternative explanation for the decreased catch of these 3 species during soak times over 100 min is that they had a longer time over which they may have been exposed to and eaten by predatory fish species caught in the same trap. We consider this explanation less likely because the diets of predatory fishes caught in traps only occasionally contain freshly consumed Tomtate and *Stenotomus* spp. (Goldman[3]), but the 2 explanations are not mutually exclusive. Experimental work should be conducted with underwater video to quantify entry and exit rates of reef fishes in fish traps—research that can provide significant insights into the catch dynamics and species interactions of marine organisms (e.g., Jury et al., 2001; Cole et al., 2004; Sturdivant and Clark, 2011).

[2] Bacheler, N., and L. Coggins. 2012. Unpubl. data. Beaufort Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[3] Goldman, S. 2012. Personal commun. Marine Resources Monitoring, Assessment, and Prediction Program, South Carolina Department of Natural Resources, Charleston, SC 29422.

Delta-GAMs provided a convenient analytical approach that helped us understand the influence of soak time and fish accumulation on the catch of reef fish species in a multispecies trap survey. The primary benefit of a delta-GAM is that the effects of soak time and fish accumulation can be understood after accounting for variation in total fish catch that might be due to all the other predictor variables in a model (Li et al., 2011). By accounting for soak time, fish accumulation, and other predictor variables, we found an improvement over previous (primarily gill net) studies that focused on only those predictor variables that were directly related to the gear saturation process itself (e.g., Minns and Hurley, 1988; Hansen et al., 1998; Akiyama et al., 2007). A secondary benefit of delta-GAMs is that they can account for zero-inflation. It is important to note that delta-GAMs, which are composed of separate submodels that must be combined, have been criticized as less elegant than the recently developed zero-inflated GAMs to account for zero-inflation (Chiogna and Gaetan, 2007; Liu and Chan, 2011). In our study, zero-inflated models were challenging to work with because they rarely converged, and, when they did, model solutions were often unreasonable.

There were some potential drawbacks of our experimental design and analyses. First, the range of soak times used in our study (50–150 min) was relatively narrow, and broader insights into the catch dynamics of species in traps would have been possible if large numbers of traps had been soaked for much shorter or longer periods of time. Second, the *fishacc* variable was made up partially of the catch of each individual species (Olin et al., 2004; Li et al., 2011), but we do not consider this aspect of our study to be a problem because we were interested primarily in the shape of the relationship between catch and fish accumulation, not necessarily in the significance of *fishacc* in the delta-GAMs. Third, the *fishacc* variable did not distinguish large, predatory species from smaller, nonpredatory species caught in the trap; future analyses could separate the catch of potential predators from smaller species.

Conclusions

We showed that the rate at which reef fish species entered traps in long-term programs of fishery-independent surveys decreased either over a range of soak times or over a range of fish accumulation levels. Trap saturation occurred for all 8 reef fish species that we examined; therefore, we recommend that future studies use catch standardization on raw catch or CPUE data (Maunder and Punt, 2004). It is also extremely important to understand the exact mechanisms that cause fish to saturate fishing gears, and our results indicate that these mechanisms may vary considerably among species. Ultimately, whether catch or CPUE can be used to index abundance will depend on a clear-

er understanding of the mechanisms that cause gear saturation.

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