

# Catchability of reef fish species in traps is strongly affected by water temperature and substrate

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**ABSTRACT:** It is commonly assumed in surveys that the likelihood of capturing or observing individuals of a given species is constant. Yet evidence is building that catchability, or the likelihood of catching an individual present at a site, can vary. We used 5465 paired trap-video samples collected along the southeast US Atlantic coast in 2015–2018 to estimate trap catchabilities of 6 reef fish species (gray triggerfish *Balistes capriscus*, red porgy *Pagrus pagrus*, vermilion snapper *Rhomboplites aurorubens*, black sea bass *Centropristis striata*, red snapper *Lutjanus campechanus*, white grunt *Haemulon plumierii*) as the ratio of trap catch to standardized site abundance from corresponding videos. Species-specific trap catchabilities were then related to 2 primary predictor variables: water temperature and percent of the visible bottom consisting of rocky substrate. Water temperature strongly influenced trap catchabilities for all species after standardizing for all other variables. The 4 warm-water species displayed strong positive relationships between catchability and temperature; of these species, the smallest absolute increase in catchability occurred for vermilion snapper (0.0 at ~14°C to 0.05 at ~28°C) and the largest occurred for white grunt (0.0 at ~14°C to 0.49 at ~28°C). The 2 cooler-water species displayed either a dome-shaped (red porgy) or negative relationship (black sea bass) between catchability and temperature. Furthermore, trap catchabilities for all species declined substantially (42–80%) as the percent hard bottom of the site increased. Only when catchability is properly accounted for can results be considered unbiased and subsequent management advice be considered accurate.

**KEY WORDS:** Detection · Detectability · Capture probability · Detection probability · Trap · Survey · GAM

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## 1. INTRODUCTION

The likelihood of capturing or observing an individual or species with a particular sampling gear is a critical variable for most ecological studies because it links the sampling process to site abundance (Williams et al. 2002). Many terms have been used to describe the likelihood of catching or observing an animal with sampling gear, but detectability or detection probability is mostly used to describe whether a species is encountered (i.e. presence–absence data), while catchability or capture probability is mostly used to describe whether an individual is encountered (i.e. catch data). In the fisheries literature, catchability has been de-

finied in slightly different but related ways: (1) the likelihood of capturing an individual known to be present at a site, (2) the proportion of available fish in the population that would be caught by a unit of effort, or (3) the constant of proportionality between catch rate and absolute abundance (Baranov 1918, Gulland 1964, Ricker 1975, Caddy 1979, Arreguín-Sánchez 1996).

Though not universal, it is often assumed that detectability and catchability from traditional sampling gears in ecological surveys are constant across space, time, habitats, and environmental conditions. For instance, animals are often surveyed across multiple habitat types, and habitat use or selection is then

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inferred from variation in catch rates among habitats (Manly et al. 2002, Bacheler et al. 2012, Livernois et al. 2020). Moreover, changes in catch rates or sightings over time are commonly assumed to reflect temporal changes in abundance (Maunder & Punt 2004, Moro et al. 2020), locations of high catch rates across a landscape are often presumed to indicate biological hotspots (Prendergast et al. 1993, Fredston-Hermann et al. 2020), and species distribution models use the relationship between temperature and catch rates to predict how climate change will influence species distributions (Monk 2014, Klippel et al. 2016, Morley et al. 2018). Many of these studies depend on the critical assumption that either all individuals or species available for capture are captured or that they are captured at a constant rate (Arreguín-Sánchez 1996, Moriarty et al. 2020).

There is increasing evidence that detectability or catchability can vary (Issaris et al. 2012, Katsanevakis et al. 2012). Catchability of fish by fishing fleets is known to vary and has almost universally increased over time with equipment and technology improvements (Robins et al. 1998, Wilberg et al. 2009). Catchability of fish has also been shown to vary in standardized surveys using trawls (Sissenwine & Bowman 1978, Nielsen 1983, Fraser et al. 2007), longlines (Ward 2008), traps (Robichaud et al. 2000), electrofishing (Speas et al. 2004, Hangsleben et al. 2013), hook-and-line (Arreguín-Sánchez & Pitcher 1999), and video (Bacheler et al. 2014). There is also recent recognition that many fishing gears selectively harvest the most active or bold individuals in a population, and given that these traits are heritable, catchability may decline over time for these evolving fish stocks (Askey et al. 2006, Biro & Post 2008, Alós et al. 2012).

Fish traps are a commonly used gear to index marine reef fish and invertebrate abundance in various places around the world (e.g. Recksiek et al. 1991, Jones et al. 2003, Wells et al. 2008, Rudershausen et al. 2010, Shertzer et al. 2016, Bacheler & Ballenger 2018), despite the fact that trap catchability has rarely been examined. Robichaud et al. (2000) showed that catchability was positively correlated with reef fish mobility and negatively correlated with percent reef cover and substrate rugosity. Geraldini et al. (2009) found that American lobsters *Homarus americanus* had higher trap catchability on soft sediments compared to rocky substrate, which ultimately obscured their strong preference for rocky substrate. Similarly, Bacheler et al. (2014) showed that 3 species of reef fish were more likely to be detected on soft sediments compared to rocky reefs, but also that

water temperature strongly affected detectability for some species. To account for variability in trap catchability, Gwinn et al. (2019) used a Bayesian state-space model with data from traps and attached video cameras to show that vermilion snapper *Rhomboplites aurorubens* abundance declines were likely stronger than previously recognized.

In this study, we used paired trap and video data collected over a broad area along the southeast US Atlantic coast to examine patterns in trap catchability of various economically important reef fish species. Previous work in the region used presence–absence data (e.g. Bacheler et al. 2014), but here we examined paired trap catches and video counts to make inferences about trap catchability on an individual (not species) level. We were specifically interested in how trap catchability of various reef fish species was influenced by bottom water temperature and substrate. Given that fish are ectothermic, many studies have observed a positive relationship between catchability in passive sampling gears and water temperature (Arreguín-Sánchez 1996), but feeding motivation and presumably catchability should eventually decline when water temperature increases beyond the thermal niche of the species (Hayward & Arnold 1996). In some instances, catchability of fish has also been shown to be influenced by habitat or substrate, although the mechanisms for this phenomenon are not well understood (Green et al. 2013, Bacheler et al. 2014). This study expands our mechanistic understanding of the strengths and drawbacks of passive sampling gears, and improves our understanding of the sampling used to index animal abundance.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Sampling for this study occurred in temperate continental shelf and shelf break waters along the southeast US Atlantic coast (hereafter, SEUS) between North Carolina and Florida (Fig. 1). The continental shelf in the SEUS is large (>100 000 km<sup>2</sup>) and varies in width from approximately 10 km in southern Florida to 130 km off Georgia. Substrate in the SEUS mostly consists of sand and mud, but sampling in this study targeted patches of hard (rocky) substrate that are intermittently distributed throughout the SEUS (Powles & Barans 1980, Schobernd & Sedberry 2009). Hardbottom habitats in the SEUS (i.e. temperate rocky reefs) range from flat limestone pavement, sometimes covered in a sand veneer, to high-relief

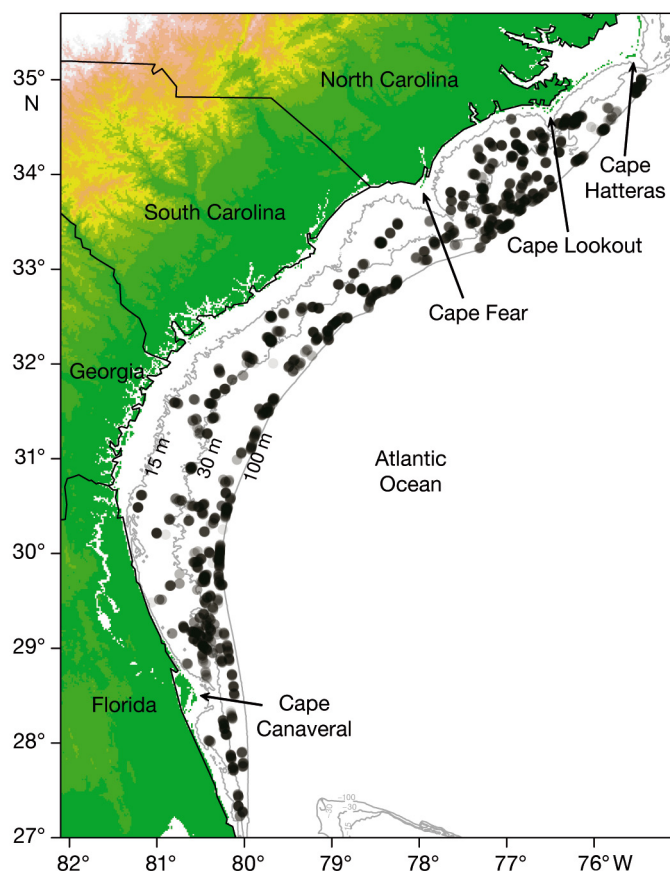


Fig. 1. Locations of chevron trap and video sampling on or near hardbottom reefs by the Southeast Reef Fish Survey along the southeast US Atlantic coast, 2015–2018. Each dot represents a trap-video deployment included in the analysis, and the darker the symbol, the greater overlap among sampling points

rocky ledges (Kendall et al. 2008). These temperate reefs often provide substrate for various species of attached biota (e.g. sponges, soft corals, algae) and critical habitat for a diverse assemblage of reef-associated fish species (Bacheler & Smart 2016, Bacheler et al. 2019).

## 2.2. Sampling

We used fishery-independent trap and video data collected by the Southeast Reef Fish Survey (SERFS) in 2015–2018 for this study. SERFS consists of 3 fishery-independent programs that work collaboratively in the SEUS using identical methodologies (as described below) to sample reef fishes: (1) the Southeast Fishery-Independent Survey, (2) the Marine Resources Monitoring, Assessment, and Prediction program of the South Carolina Department of Natu-

ral Resources, and (3) the Southeast Area Monitoring and Assessment Program – South Atlantic. All programs are funded by the National Marine Fisheries Service to sample reef fishes in the region. We used SERFS data from 2015–2018 here, a time when trap and video data were collected by SERFS in a consistent manner.

Stations were selected for sampling using a simple random sampling design. Out of approximately 4000 stations on or near hardbottom, 1500 were selected for sampling each year. Most stations sampled in this study (80%) were randomly selected stations. Some stations (17%) were sampled even though they were not randomly selected for sampling in a given year, primarily to increase efficiency while on research cruises. Some new hardbottom stations (3%) were sampled each year based on information from fishermen, charts, sonar mapping, or historical data, and included in the analyses if hardbottom was detected. Sampling occurred during daylight hours each year between April and October on the RV ‘Savannah,’ RV ‘Palmetto,’ SRVx ‘Sand Tiger,’ and NOAA Ship ‘Pisces.’

We estimated catchability of reef fishes in chevron fish traps by using a paired sampling design, specifically by attaching video cameras to fish traps. Chevron traps used in our study were 1.7 m × 1.5 m × 0.6 m in size, with a total volume of 0.91 m<sup>3</sup> (Fig. 2). They were constructed from plastic-coated galvanized 2 mm diameter wire mesh (mesh size = 3.4 × 3.4 cm), and the trap mouth was shaped like a teardrop that measured approximately 18 cm wide and 45 cm high (Bacheler et al. 2013a). Each trap was baited with 24 menhaden (*Brevoortia* spp.). In our study, chevron traps were deployed in groups of 6 or fewer, but each trap was separated from other simultaneously soaking traps by at least 200 m to provide independence among traps (Bacheler et al. 2018). Traps soaked for approximately 90 min, and any trap not fishing correctly (e.g. bouncing or dragging due to waves or current, trap mouth obstructed) was excluded from analysis. All fish caught in chevron traps were enumerated and measured for total length.

Two high-definition underwater cameras were attached to each chevron trap deployed in our study. GoPro Hero 3+/4 cameras were used, one being attached over the mouth of the trap and one attached over the nose of the trap, each looking outward away from the trap (Fig. 2). The camera over the trap mouth was always used to count fish as well as score substrate, current, and water clarity, whereas the camera over the trap nose was only used to score substrate, current, and water clarity in the opposite direction. Videos were excluded from analysis if they



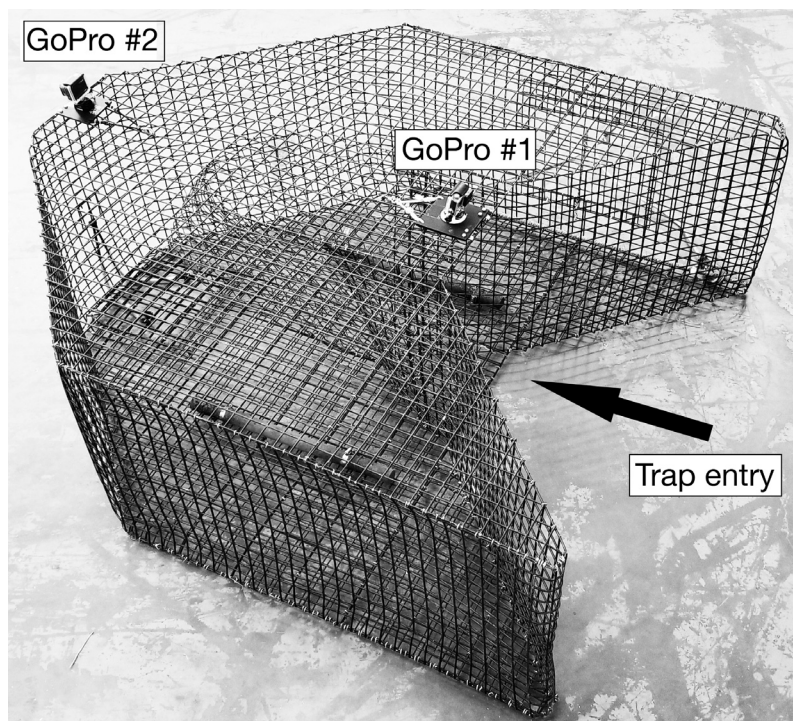


Fig. 2. Chevron trap outfitted with 2 outward-looking GoPro Hero 3+/4 cameras deployed by the Southeast Reef Fish Survey, 2015–2018. Videos from GoPro 1, attached over the trap mouth, were used to count fish and record habitat information, while GoPro 2 was only used to record habitat information in the opposite direction

were unable to be read for any reason (e.g. too dark, video out of focus, files corrupt). Samples were only included in our analyses if traps fished and video cameras recorded without any problems; if either was missing, that sample was excluded. Valid traps with corresponding valid video samples are hereafter referred to as 'trap-video samples.'

Following Bacher et al. (2014), characteristics of the water and substrate were estimated at each site using various approaches. Depth was estimated using ship-board sonar, trap soak time (min) was calculated as the trap retrieval time minus the trap deployment time, and bottom temperature was measured for each group of simultaneously deployed traps using a conductivity-temperature-depth cast deployed within 2 m of the bottom. The remaining variables were visually estimated from both video cameras attached to the trap at each site. Percent hardbottom was estimated as the percent of the bottom substrate that consisted of hard, consolidated sediment at least 10 cm in diameter (hereafter used interchangeably with 'substrate'). For each station sampled, percent hardbottom estimates were generated for each of the 2 cameras and a mean value was calculated for the site. Particle

movement was used to estimate the direction of the prevailing water current relative to the camera positioned over the trap mouth; current direction was scored categorically as 'away,' 'side-ways,' or 'towards.' Water clarity was scored as 'poor' if the substrate could not be seen, 'fair' if the substrate but not the horizon could be seen, and 'good' if the horizon could be seen in the distance. In our study, samples with a water clarity score of 'poor' (<1% of all samples) were excluded because percent hardbottom information was not available. Samples with soak times <50 min or >150 min rarely occurred so they were excluded, as were any samples that were missing data for depth, bottom temperature, soak time, percent hardbottom, current direction, or water clarity.

Six species of reef fishes were present in at least 10% of trap-video samples and examined in our study (hereafter, 'focal species'). These focal species were gray triggerfish *Balistes capriscus*, red porgy *Pagrus pagrus*, vermilion snapper *Rhomboplites aurorubens*, black sea bass *Centropristis striata*, red snapper *Lutjanus campechanus*, and white grunt *Haemulon plumieri*. Each of these focal species is economically important and the target of recreational and commercial fishing effort in the SEUS.

### 2.3. Estimating site abundance and trap catchability

Catchability of reef fish in chevron traps at each site can be calculated as the trap catch of a particular species divided by its known site abundance. Here, we estimated site abundance of the 6 focal species as the video SumCount of fish observed on video (Schorbernd et al. 2014). Video SumCount was specifically calculated as the sum of all individuals of a particular species over a series of frames in a video sample. We began enumerating fish on video 10 min after the trap landed on the bottom to allow time for the trap to settle, and read snapshots every 30 s thereafter over a 20 min time interval for a total of 41 snapshots. SumCount was used because it has been shown to track site abundance of reef fish linearly when the

number of video frames read is consistent (Schobernd et al. 2014).

Using video to estimate site abundance of reef fishes, however, can be affected by the water current direction relative to the camera view and water clarity. For instance, current direction has been shown to influence video counts because fish tend to aggregate on the down-current side of baited traps; thus, video cameras facing down-current (i.e. a current direction of 'away') may be expected to have higher video counts than cameras pointed up-current (i.e. a current direction of 'towards;' Bacheler et al. 2014). Moreover, fewer individuals may be expected to be counted when water clarity is fair compared to good. These 2 variables must be accounted for when using video counts of fish around baited traps to make inferences about true site abundance.

We accounted for the effects of current direction and water clarity on video SumCounts of our focal reef fish species using generalized additive models (GAMs), which are a nonparametric regression approach that can relate response variables to predictor variables using different error distributions (Hastie & Tibshirani 1990, Wood 2006). In this case, the 2 predictor variables (current direction and water clarity) were included in our GAMs as categorical variables:

$$y = f(\text{currdir}) + f(\text{waterclarity}) \quad (1)$$

where  $y$  is the species-specific video SumCount at a site,  $\text{currdir}$  is the current direction at the site,  $\text{waterclarity}$  is the water clarity at the site, and  $f$  is a categorical function. One GAM was developed for each of our focal species. All GAMs in this study were developed, coded, and analyzed using the 'mgcv' library 1.8-28 (Wood 2011) in R version 3.6.1 (R Core Team 2019).

To assess model fit, we compared various data transformations and error distributions using the 'gam.check' function in the 'mgcv' library. We evaluated the nominal data and 2 data transformations (fourth root, log) and 4 error distributions (Gaussian, Poisson, negative binomial, Tweedie) on model fit; note that some transformation and error distribution combinations were not possible due to data requirements. Models incorporating the Tweedie distribution with a fourth-root transformation fit best for all 6 species, so they were used here.

We used these final GAMs to estimate the effects of current direction and water clarity on video SumCounts for each of the 6 species evaluated. Means for each level of the 2 categorical variables were used to develop adjustment factors for each of the current direction and water clarity combinations for each of

the 6 species. Adjustment factors were then used to standardize video SumCount values for variable current direction and water clarity to more accurately reflect true site abundance.

Chevron trap catchability ( $q$ ) was then calculated separately for each focal species ( $i$ ) in each trap ( $j$ ) sampled using the following equation:

$$q_{ij} \sim \frac{T_{ij}}{N_{ij}} \quad (2)$$

where  $T$  is the number of individuals caught in the chevron trap, and  $N$  is the product of the video SumCount and adjustment factor estimated in Eq. (1). Typically  $0 \leq q \leq 1$ , but here the denominator is not absolute abundance but a linearly scaled version of it, so  $q$  can be  $>1$ .

#### 2.4. Effects of water temperature and substrate on catchability

To determine whether trap catchability of the focal species varied by bottom water temperature or substrate, we developed a second set of GAMs. These species-specific GAMs examined the relationships between chevron trap catchability ( $q$ ) for each species and 4 predictor variables that we hypothesized might influence trap catchability: bottom water temperature, percent hardbottom, soak time, and depth. Bottom water temperature and percent hardbottom were our 2 primary variables of interest, but soak time and depth were also included to standardize trap catchability for the effects of these 2 variables. Trap soak times varied from 50–150 min in our study, so it was important to standardize trap catchability for variable effort (Bacheler et al. 2013b). Depth was included to standardize for variability in trap catchability across depths, either due to the effects of depth alone or other variables that may be related to depth (e.g. ambient light levels). Variance inflation factors revealed no multicollinearity among predictor variables.

We related trap catchability to these 4 predictor variables as:

$$q = s(\text{temp}) + s(\text{substrate}) + s(\text{soak}) + s(\text{depth}) \quad (3)$$

where  $q$  is the species- and site-specific trap catchability estimated in Eq. (2),  $\text{temp}$  is the bottom water temperature ( $^{\circ}\text{C}$ ),  $\text{substrate}$  is the percent hardbottom of the substrate,  $\text{soak}$  is the soak time of the chevron trap,  $\text{depth}$  is the bottom depth (m), and  $s$  is a nonparametric cubic spline smoothing function. We evaluated the same 3 data transformations and

Table 1. Annual trap and video sampling by the Southeast Reef Fish Survey, 2015–2018, included in the analyses. Values for date, latitude, bottom water temperature, and depth are provided as mean (range); dates are given as mo/d

Year	N	Date	Latitude (°N)	Bottom water temperature (°C)	Depth (m)
2015	1355	7/3 (4/21–10/22)	31.9 (27.3–35.0)	22.7 (13.6–28.5)	39 (16–110)
2016	1397	8/2 (5/4–10/26)	32.2 (27.2–35.0)	23.9 (15.5–29.3)	41 (17–115)
2017	1405	7/5 (4/26–9/29)	32.0 (27.2–35.0)	22.7 (14.8–28.2)	40 (15–111)
2018	1308	6/21 (4/25–10/4)	31.9 (27.2–35.0)	22.5 (13.6–27.9)	40 (16–114)
Overall	5465	7/9 (4/21–10/26)	32.0 (27.2–35.0)	22.9 (13.6–29.3)	40 (15–115)

4 error distributions as described above. A fourth-root data transformation with a Gaussian error distribution fit best for all focal species, but note that model results were insensitive to different transformations and error distributions.

For each species-specific GAM developed, we used Akaike's information criterion (AIC) to compare full models (shown in Eq. 3) to reduced models that contained fewer predictor variables (Burnham & Anderson 2002). AIC seeks parsimony by identifying models that explain the most variation in the data with the fewest parameters. We were specifically focused on whether trap catchability varied significantly by bottom water temperature or substrate; in other words, for each species, would AIC retain or exclude these 2 variables? For each species, the model configuration with the lowest AIC value was considered the best model, which was indicated by  $\Delta$ AIC of 0. We also show all competing models within 2  $\Delta$ AIC units of the best model, given that these competing models have nearly equivalent empirical support as the best model (Burnham & Anderson 2002).

### 3. RESULTS

A total of 5465 trap-video samples were analyzed in our study, ranging from a low of 1308 in 2018 to a high of 1405 in 2017 (Table 1). Sampling was temporally consistent each year, beginning in late April or early May and continuing through the end of September or October. Moreover, latitudes, bottom water temperatures, and depths sampled among years were similar (Table 1).

Of the 6 focal species examined, gray triggerfish was observed in the most videos (44%), followed by red porgy (38%), vermilion snapper (34%), black sea bass (30%), red snapper (30%), and white grunt (18%; Table 2). That trend differed for traps, where black sea bass (38%) was present in traps more often than any other species. Black sea bass was also the only species that was more often caught in traps than

Table 2. Video and trap frequency of occurrences for 6 reef fish species sampled by the Southeast Reef Fish Survey, 2015–2018. A total of 5516 trap-video samples were included in the analyses. %FO: percent frequency of occurrence

Species	%FO on video	%FO in traps	%FO in traps when observed on video
Gray triggerfish	44	29	53
Red porgy	38	23	56
Vermilion snapper	34	22	54
Black sea bass	30	38	95
Red snapper	30	14	43
White grunt	18	16	67

observed on video (Table 2). When reef fish species were known to be present at a site based on video observations, the species most likely to be caught in the corresponding traps was black sea bass (95%), while red snapper was least likely (43%).

Current direction had a strong and consistent influence on video SumCounts across all 6 species (Table 3; Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m642p179\\_supp.pdf](http://www.int-res.com/articles/suppl/m642p179_supp.pdf)), whereas water clarity had a weak effect on all species except red porgy (Table 3; Fig. S2). Trap catchability for

Table 3. Generalized additive models relating video SumCount (sum of all individuals of a particular species over a series of frames in a video sample) of 6 reef fish species to current direction and water clarity built on data from the Southeast Reef Fish Survey, 2015–2018. Dev expl: deviance explained by the model. Degrees of freedom are shown for each term, and asterisks denote significance at the following alpha levels: \* = 0.05; \*\* = 0.01; \*\*\* = 0.001

Model	Dev expl	$s_1(\text{curdir})$	$s_2(\text{waterclarity})$
Gray triggerfish	11.6	2***	1
Red porgy	14.0	2***	1***
Vermilion snapper	4.1	2***	1
Black sea bass	6.0	2***	1
Red snapper	4.2	2***	1
White grunt	3.5	2***	1

each focal species was then calculated using video SumCount values that were standardized for the effects of current direction and water clarity.

We found large differences in trap catchability among focal species, with median trap catchability being smallest for red snapper (median = 0.0, mean = 0.3) and largest for black sea bass (median = 3.5, mean = 10.2; Fig. 3). Trap catchability for all focal species varied significantly by bottom water temperature, percent hardbottom, soak time, and depth (Table 4; Figs. S3 & S4). For all species, full models that retained all 4 predictor variables were the best models based on AIC (Table 4). Only white grunt had a candidate model ( $\Delta AIC = 1.2$ ) that excluded 1 of our 2 predictor variables of interest (substrate; Table 4), suggesting weak effects of this predictor variable on trap catchability of white grunt.

Trap catchability for all 6 focal species varied substantially across the range of bottom water temperatures encountered in trap-video sampling for this study. There was a strong positive relationship between trap catchability and bottom water temperature for 4 species (i.e. gray triggerfish, vermilion snapper, red snapper, white grunt). From the coldest to warmest water temperatures sampled in our study (i.e. ~13–29°C), mean trap catchability increased the least for vermilion snapper (0.002 to 0.051, ~2000%) and the most for white grunt (0.001 to 0.487, ~65 000%; Fig. 4). Mean black sea bass trap catchability displayed a weaker negative relationship with bottom water temperature, declining 84% from the coldest to warmest water sampled. The last species, red porgy, displayed a weak dome-shaped relationship between mean trap catchability and bottom water temperature that peaked at approximately 20°C (Fig. 4).

Unlike the inconsistent effects of water temperature, trap catchability for all 6 reef fish species declined consistently as the percent hardbottom of the site increased. The substrate variable was included in the best GAMs for all 6 species based on AIC (Table 4), and the declines appeared to take a linear or exponential decay form, depending on the species (Fig. 5). The difference in mean trap catchability from sampling on sand (0%

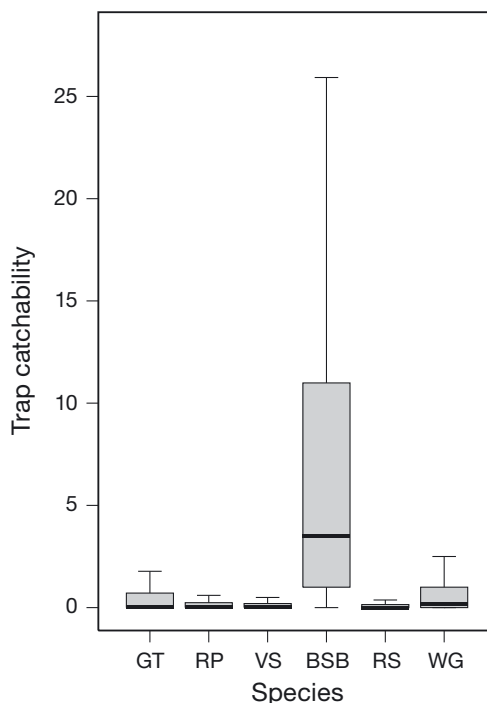


Fig. 3. Chevron fish trap catchability for 6 reef fish species collected by the Southeast Reef Fish Survey, 2015–2018. For each species, the thick horizontal line is the median catchability, the start and end of each box represent the 1st and 3rd quartiles, and the whiskers are 1.5 times the interquartile range. GT: gray triggerfish; RP: red porgy; VS: vermilion snapper; BSB: black sea bass; RS: red snapper; WG: white grunt

Table 4. Generalized additive models of trap catchability for 6 reef fish species when observed on corresponding videos from the Southeast Reef Fish Survey, 2015–2018. Only the best models or models within 2  $\Delta AIC$  values of the best models are shown for each species. Predictor variables are defined in Section 2.4. Dev expl: deviance explained by each model; ex: predictor variable was excluded from that particular model. Estimated degrees of freedom are shown for each term, and asterisks denote significance at the following alpha levels: \*0.05; \*\*0.01; \*\*\*0.001

Model	Dev expl	$\Delta AIC$	$s(temp)$	$s(substrate)$	$s(soak)$	$s(depth)$
Gray triggerfish						
Full	5.3	0.0	1.0***	1.0**	2.4***	2.4*
Red porgy						
Full	3.4	0.0	2.3	1.7**	3.1*	7.0***
Vermilion snapper						
Full	7.5	0.0	1.0***	2.7***	2.3**	7.3***
Black sea bass						
Full	9.0	0.0	3.7**	1.9***	1.0	4.8***
Full – soak	8.9	1.3	3.7**	1.9***	ex	5.0***
Red snapper						
Full	2.3	0.0	1.0**	1.0*	2.0	6.1**
Full – soak	2.0	1.5	1.0**	1.0*	ex	6.2**
White grunt						
Full	13.7	0.0	4.2***	1.0	1.6	4.3***
Full – soak	13.5	0.6	4.1***	1.0	ex	4.4***
Full – soak – substrate	13.2	1.2	4.0***	ex	ex	4.3***



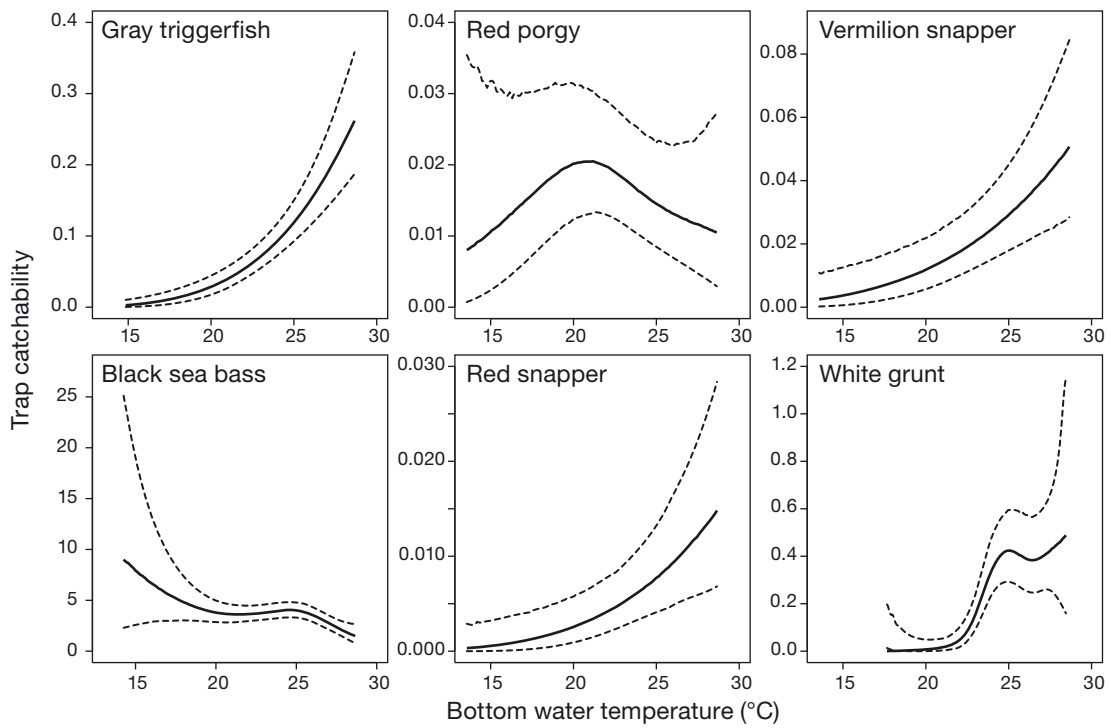


Fig. 4. Catchability of 6 reef-associated fish species in chevron traps as a function of the bottom water temperature, based on sampling from the Southeast Reef Fish Survey, 2015–2018. Solid lines are the predicted trap catchability and dashed lines are 95% confidence intervals

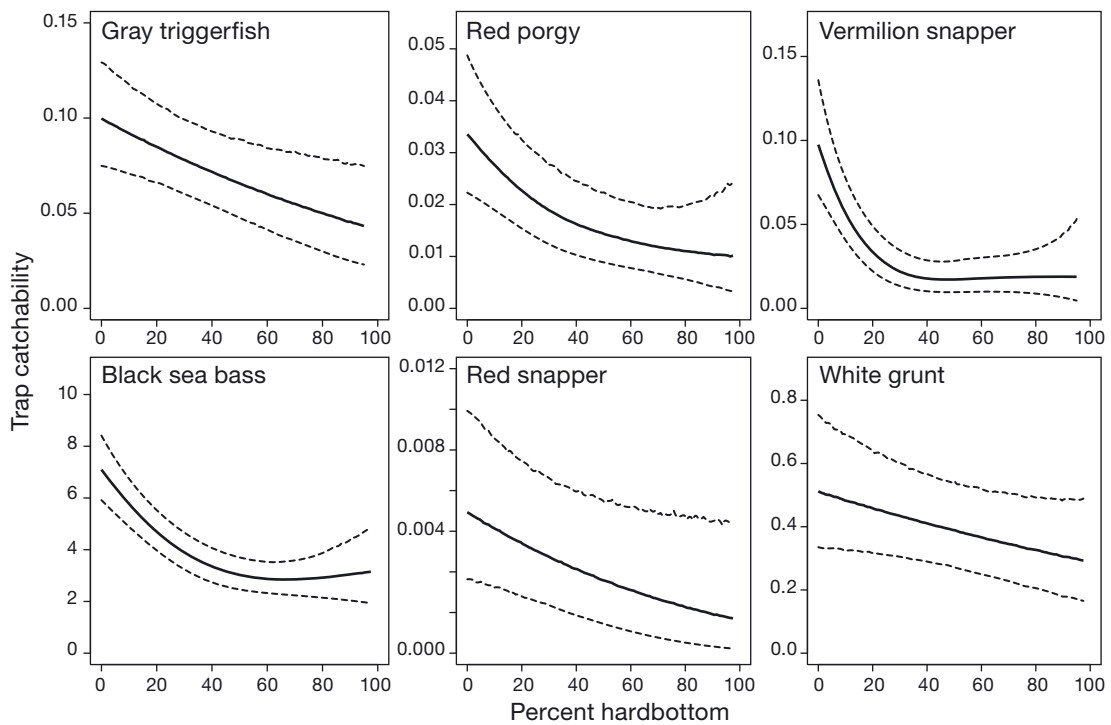


Fig. 5. Catchability of 6 reef-associated fish species in chevron traps as a function of the percent of the observed substrate that was hardbottom (e.g. 0% = sand; 100% = rock), based on sampling from the Southeast Reef Fish Survey, 2015–2018. Solid lines are the predicted trap catchability and dashed lines are 95% confidence intervals



hardbottom) to sampling on rock (100% hardbottom) was the largest for vermilion snapper (−80%), red snapper (−76%), and red porgy (−70%), and the least for white grunt (−42%; Fig. 5).

#### 4. DISCUSSION

It is commonly assumed in ecological studies that all individuals or species available for capture are captured at a constant rate (Arreguín-Sánchez 1996, Katsanevakis et al. 2012). We have shown, however, that the catchability of 6 species of reef fishes from 5 different families in baited fish traps is highly variable and strongly affected by water temperature and substrate near the trap. These results suggest that studies examining habitat use, biological hotspots, or temporal trends cannot rely upon catch information alone because catch is a product of both abundance and catchability. In other words, abundance and catchability are confounded, and only by estimating catchability can the underlying abundance signal be extracted from catch data (Langseth et al. 2016). It would be misguided, for example, to identify and protect a ‘biological hotspot’ based on large catches if those catches were solely due to high catchability and not abundance.

Water temperature strongly influenced the catchability of reef fish in baited fish traps in ways that are consistent with their life histories. Fish are ectothermic, so catches in passive gears tend to be higher in warmer water compared to colder water up to the point where water temperature increases beyond the thermal niche of the species (Hayward & Arnold 1996). In our study, the 4 reef fish species more commonly found in warmer waters of the SEUS (gray triggerfish, vermilion snapper, red snapper, and white grunt; Bacheler et al. 2019) displayed a predictable positive relationship between catchability and water temperature. Red porgy is found in deeper, cooler waters and displayed a much weaker, dome-shaped relationship, indicating that its thermal niche was lower than the 4 warmer water species. Black sea bass is a colder water species that is commonly found north of the SEUS (Fabrizio et al. 2013, Bacheler & Ballenger 2015), and was the only species in our study to display a negative relationship between catchability and water temperature.

These results have implications for research focused on the redistribution of marine organisms in response to climate change. As water temperatures increase, marine species tend to move poleward or into deeper waters to remain in the same thermal

habitat (e.g. Nye et al. 2009, Pinsky et al. 2013, Morley et al. 2018, Murphy 2020). However, a species’ thermal habitat is often quantified using catch data, which, as discussed above, may itself be strongly influenced by water temperature. Accounting for variable detection improves species distribution models by increasing their accuracy and precision (Rota et al. 2011, Lahoz-Monfort et al. 2014). As we have shown, water temperature strongly affected the catchability of marine fish in traps. We recommend that future research accounts for trends in detection in the development of species distribution models for marine fishes to minimize error in the forecasts of spatial distributions.

There are 2 mechanisms that may cause the catchability of fish to be affected by the habitat in which sampling takes place. First, the ability of sampling gears to capture fish may be influenced by the habitat itself. For instance, the presence of kelp or highly rugose substrate may obstruct the view of underwater video, resulting in lower fish counts than expected compared to unobstructed habitats. A second mechanism is that the behavior of fish may vary across habitat types. Previous research has indicated that lobsters and reef fishes are much more likely to enter traps that land on soft compared to hard substrates (Robichaud et al. 2000, Geraldi et al. 2009, Bacheler et al. 2014), a finding corroborated consistently from all 6 species examined in our study. It remains unclear why lobsters and reef fishes are more likely to be caught in traps that land on soft, unstructured habitats. We hypothesize that it may be due to the increased attractiveness of bait in areas with less prey available or the trap acting as habitat in places that normally lack habitat. Regardless, these results suggest that fish behavioral responses to sampling gears in different habitats are important for estimating catchability.

We estimated reef fish catchability using a paired gear approach, where fish counts from video cameras were standardized to provide baseline estimates of site abundance to which trap catches could be compared. An added benefit of a paired gear approach is the possible integration of data into a single index of abundance using *N*-mixture or state-space models, which explicitly account for variable catchability (MacKenzie et al. 2002, Royle & Nichols 2003, Royle 2004). For instance, Coggins et al. (2014) used paired trap-video sampling data to account for imperfect detection of red snapper. Gwinn et al. (2019) used paired trap-video data to develop a single long-term index of abundance for vermilion snapper that accounted for variable catchability; model results indi-

cated a more substantial population decline than a trap-video index of abundance that disregarded catchability. We see broad utility of adding video cameras to other passive or active sampling gears to adequately account for variable catchability.

Catchability has been defined in a variety of ways in the fisheries literature, and our definition is slightly different from those used previously. Historically, catchability was defined as the proportion of individuals in a fishing ground removed by a gear sweeping that area (Baranov 1918, Gulland 1964, Caddy 1979). However, Arreguín-Sánchez (1996) noted that this definition disregards fish behavior, so he and others instead defined catchability as the number of fish captured (or mortality rate experienced) per unit effort. Thus, variations in catchability may be due to the vulnerability of fish to the fishing gears used, the fishing strategy of fishers, or the biology and behavior of the fish themselves. Our definition of catchability, whereby the trap catch is divided by a standardized estimate of site abundance from corresponding video cameras, most closely resembles this latter definition. In our case, however, trap catch and video counts occurred on vastly different scales, so our catchabilities did not necessarily vary between 0 and 1 like other definitions. Regardless of the scale of catchability in our study, the values tracked how well the traps caught fish that were observed to be present on video.

There were some shortcomings of our work. First, we only included reef fish species in our analyses if they were captured in traps and observed on videos greater than 10% of the time. Hundreds of reef-associated fish species occur in the region, but most rarely or never enter traps (Bacheler & Smart 2016, Bacheler et al. 2019), suggesting extremely low trap catchabilities for most species in the region. Second, although traps are often used to index many species simultaneously, a downside is that the capture of predatory fish in traps may influence the subsequent capture of prey species or vice versa (Glasgow 2017). In other words, the catchability of fish caught in traps was also likely dependent upon which species were caught first, which we were unable to quantify without inward-looking videos. Third, our GAMs relating catchability to predictor variables only explained up to 14% of the species-specific model deviance, suggesting that most of the variability in trap catchability remains unexplained. Fourth, we excluded samples for which water clarity was poor (<1% of our samples) so we lack information on trap catchability in highly turbid water that may be common in other regions. Last, we assumed that catchability was

equal across all sizes and ages of fish encountered in our study, but catchability may be age- or size-dependent.

We have shown that the common assumption of ignoring variable catchability in ecological studies is unfounded. In our study, the catchability of reef fishes in traps was highly variable, being strongly affected by both the water temperature and substrate upon which the trap landed. Future studies should explicitly quantify gear-specific catchability, possibly using paired gear studies, and incorporate estimates of catchability into ecological studies, indices of abundance, and stock assessments (Maunder & Punt 2004, Wilberg et al. 2009, Langseth et al. 2016, Gwinn et al. 2019). Only after catchability and actual abundance can be disentangled can we have truly robust monitoring data that provide the foundation for unbiased ecological experiments and accurate management advice.

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