

Behavior of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale acoustic tracking

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ABSTRACT: Most reef fish surveys use bait to attract individuals to bite hooks, enter traps, or be counted on underwater video. The behavior of fish around baited gears, however, is poorly understood despite its importance for estimating catchability. We used a fine-scale acoustic positioning system to elucidate the movement behaviors of 11 telemetered gray triggerfish *Balistes capriscus* around 54 baited fish traps deployed at a 37 m deep site in Raleigh Bay, North Carolina, USA. Median positional error rates from a reference transmitter were 1–2 m, suggesting fish positions were accurate and precise. Overall, 104 170 spatial positions were determined for gray triggerfish over the 42 d study. There were 27 instances of telemetered gray triggerfish responding to baited fish traps. These fish responded from initial distances up to 312 m (mean = 68 m) from traps and spent 4–95% (mean = 35%) of their time within 20 m of traps. Using generalized additive models, we determined that telemetered gray triggerfish were most likely to respond to baited traps when they were initially located close to (<100 m), and down-current from, baited traps. There were substantial differences in gray triggerfish responses and water clarity across the 3 recapture periods, suggesting gray triggerfish use vision, olfaction, and perhaps sound to locate bait. Our modeling approach is general, and could be used to quantify the behavior of myriad organisms around sampling gears in various types of aquatic systems.

KEY WORDS: Animal behavior · Bait · Telemetry · Vemco positioning system · Movement · Baited remote underwater video station · BRUVS · Trap · Reef

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INTRODUCTION

Many ecological surveys and modern stock assessments require information on temporal trends in abundance of the species of interest, which is usually provided by scientific (i.e. fishery-independent) surveys (Kimura & Somerton 2006). For fish species that associate with hardbottom reef habitats, scientific surveys typically sample with traps, underwater visual census, hook-and-line, acoustics, underwater video, or underwater vehicles to provide abundance

information (Karpov et al. 2012, Whitfield et al. 2014, Bacheler et al. 2017). Estimating relative abundance without knowing the sampling area assumes that the area remains constant among samples, which is unlikely to be true given the effect of environmental variation on fish movement and feeding behavior (Stoner 2004). In some instances, scientific surveys of reef fishes provide absolute abundance and density information for stock assessments (e.g. Ault et al. 2005, Rooper et al. 2012), but most of these examples come from underwater visual census, underwater

vehicles, or acoustics gears that are unbaited and take place over relatively small spatial scales. For baited gears, the area sampled can be difficult to estimate because it at least partially depends on the spatial and temporal dynamics of the bait plume.

Because absolute abundance is much more informative than relative abundance, a variety of approaches have been developed to estimate the area sampled by baited gears. A theoretical 'effective fishing area' of baited fish traps has been estimated by dividing the trap catch by the density of fish at a sampling location, the latter being determined by divers or underwater photographs (Miller 1975, Miller & Hunte 1987). Eggers et al. (1982) developed a method to estimate the area fished by using baited traps or hooks along a ground line spaced at different distances apart from one another. Others have estimated deep-water scavenger fish abundance by modeling bait plume dynamics and scavenger fish sensory and movement biology (Sainte-Marie & Hargrave 1987, Priede et al. 1994). Each of the methods has significant limitations and assumptions that diminish its utility for most baited surveys of reef fishes (Kimura & Somerton 2006).

More recent studies have examined bait responses directly in laboratory or mesocosm experiments. Zhou & Shirley (1997) showed that red king crabs *Paralithodes camtschaticus* approached baited traps placed in a large laboratory tank from the downstream direction, likely using chemical cues to detect and approach baited traps. Watson et al. (2009) tracked acoustically tagged American lobsters *Homarus americanus* in an underwater enclosure and related their movements to baited traps. American lobsters approached traps from a mean distance of 11 m, and the authors calculated an area of bait influence of 380 m² (Watson et al. 2009). It would not be feasible to quantify the bait responses of most fish species in laboratory or mesocosm experiments because they likely respond to bait over larger spatial scales.

We used a fine-scale acoustic positioning system deployed on a natural offshore hardbottom reef and sand area to describe the behavior of a demersal reef fish, gray triggerfish *Balistes capriscus*, around baited traps (hereafter, 'traps'). Gray triggerfish are a commercially and recreationally important reef fish species along the southeast US Atlantic coast (i.e. SEUS; SEDAR 2016). They are also one of the most numerous species captured in the Southeast Reef Fish Survey (i.e. SERFS), a fishery-independent trap and video survey that has sampled in the SEUS since 1990 (Bacheler & Smart 2016). Standardized trap

catch of gray triggerfish from SERFS was one of the primary sources of relative abundance in the most recent gray triggerfish stock assessment (SEDAR 2016).

We tested 3 specific hypotheses: (1) telemetered gray triggerfish would be more likely to respond to traps when they were initially in close proximity; (2) fish would be more likely to respond to traps if they were initially down-current from the trap because of the bait plume; and (3) fish initially closest to traps would respond to traps more quickly than fish initially located farther away. Our study is novel because we directly quantify the behavior of fish around traps in their natural environment. Such information could prove useful for standardizing sampling data to estimate relative abundance, for example, by better accounting for the effects of water clarity or bait plume characteristics on catchability. More importantly, this study takes a step toward understanding the effective area sampled, which is necessary for estimating absolute abundance.

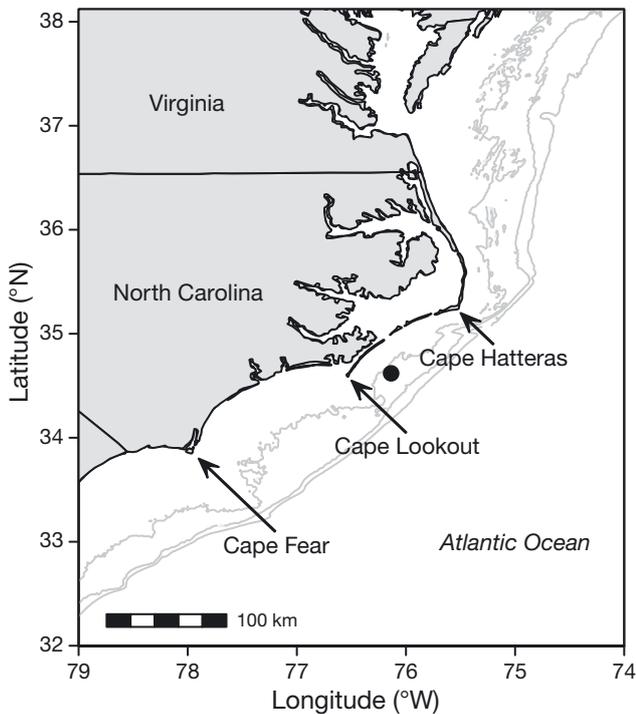
MATERIALS AND METHODS

Study area

Our study took place at a natural temperate hard-bottom reef and sand area approximately 35 km east of Cape Lookout, North Carolina, USA (Fig. 1). This general area is known locally as the 'Chicken Rock' and was chosen due the relatively flat seafloor (i.e. depth ranged 36.5–38.5 m) and high historic catches of gray triggerfish in the area by the SERFS (Bacheler & Smart 2016). Moreover, a multibeam seafloor bathymetry map was available for the Chicken Rock area (C. Taylor unpublished data; Fig. 2), which assisted us in selecting the exact location for this study.

Holding tank study

We first conducted a holding tank study to estimate gray triggerfish post-tagging survival and transmitter retention. We elected to attach transmitters externally to gray triggerfish in this study because externally attached transmitters have been found to be detected significantly more often at a given distance than surgically-implanted transmitters in marine fishes (Dance et al. 2016). Transmitters can also be attached externally much more quickly than they can be surgically implanted (Jepsen et al. 2015), which



was important in our study because we wanted to minimize the surface interval experienced by each fish to reduce barotrauma (Burns et al. 2002).

We attached transmitters to 5 gray triggerfish in tanks at the NOAA-Beaufort laboratory in Beaufort, North Carolina. These fish were held indoors in round tanks that were 1.8 m in diameter and 0.9 m deep with recirculating seawater. Fish were fed squid daily to satiation and water temperature ranged 22–25°C during our holding tank study. Fish were measured before tagging (mm fork length), and their body weight (g) was estimated using the fork length–weight relationship provided by Burton et al. (2015).

Our external transmitter attachment technique was developed under the advice and guidance of Dr. Craig Harms (Director of the Marine Health Program

Fig. 1. Location of the 2017 fine-scale telemetry study of gray triggerfish *Balistes capriscus* between Cape Lookout and Cape Hatteras, North Carolina, USA, indicated by the filled circle. Gray lines indicate 30, 50, and 100 m isobaths

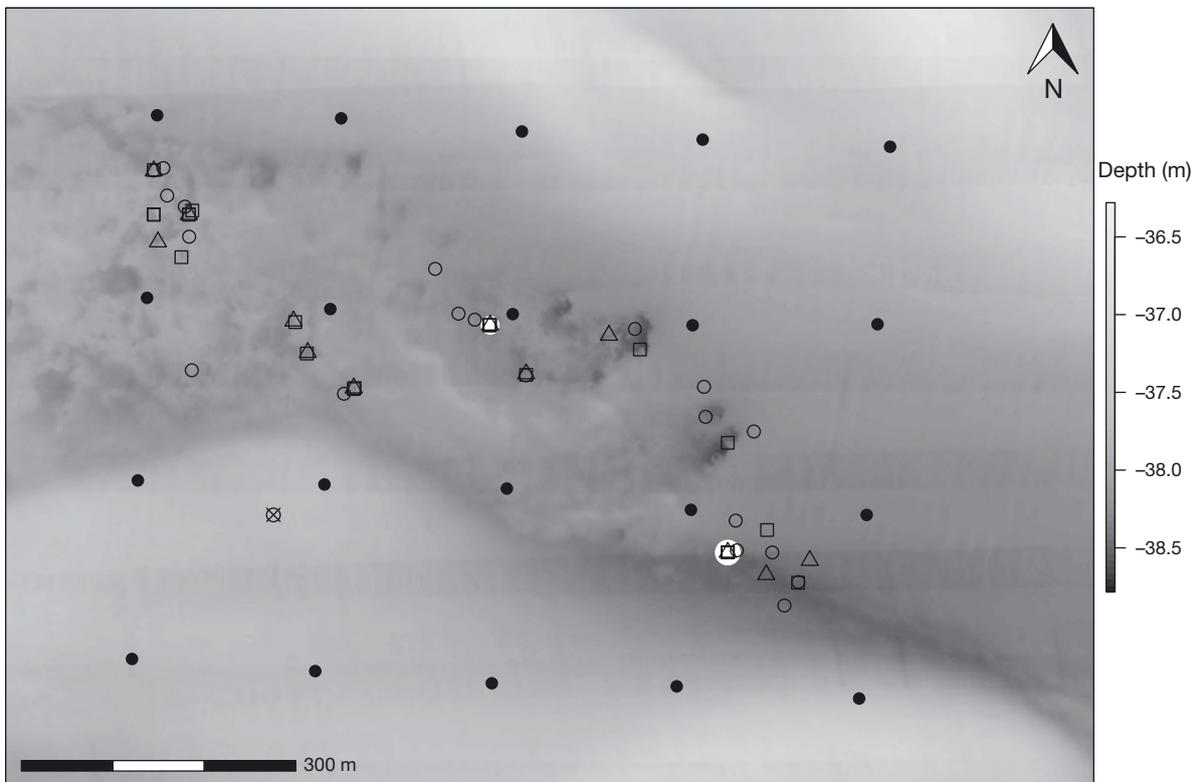


Fig. 2. Study area of the gray triggerfish *Balistes capriscus* telemetry positioning system in the Chicken Rock area of Raleigh Bay, North Carolina, 2017. Background map shows the bathymetry of the study area, with lighter (darker) colors being shallower (deeper) water. Underwater receivers are shown with a filled black circle, reference tag location is shown by an open circle with an x, tagging locations where gray triggerfish were caught are shown by white circles scaled to the number of fish tagged at each location, and recapture locations are open circles, squares, and triangles for recapture periods 1, 2, and 3, respectively (see 'Materials and methods', section 'Recapture events')

and Doctor of Veterinary Medicine, North Carolina State University). We used dummy V13-1x transmitters (Vemco) in our holding tank study. These transmitters were 36 mm long, 13 mm in diameter, and weighed 11 g in air and 6 g in water. A cap was epoxied onto the end of the transmitter opposite from the transducer, and a 20 cm length of no. 1 (0.4 mm diameter) polydioxanone absorbable suture (PDS II; Ethicon) was tied around, and epoxied to, the center of the transmitter.

Transmitters were attached to gray triggerfish on 8 May 2017 by first passing a sharpened surgical awl approximately 15 mm ventral to the anterior edge of the soft dorsal fin, which created a hole for the absorbable suture to be passed through the fish's back. A second passage was created with the same awl about 10 mm posterior to the third dorsal spine (and approximately 25 mm anterior from the first passage), and the absorbable suture was passed through the fish's back a second time and then through a small hole in the end cap of the transmitter. The transmitter was affixed to the side of the fish by attaching an aluminum crimp to the suture material beyond the hole in the end cap, and the excess suture material was cut just beyond the crimp. Absorbable suture material was used so that transmitters would eventually become detached from fish without any harm to the fish. The external attachment procedure took 90 to 120 s in air for each fish in the laboratory, and we did not irrigate gills during transmitter attachment. All 5 fish were released into 1 of the recirculating tanks after transmitter attachments. Surgical awls were soaked in Cidex® OPA (Advanced Sterilization Products) for 15 min for sterilization, and then rinsed with sterile water before using on fish. Tagged gray triggerfish were monitored for 92 d.

Vemco positioning system

We used a Vemco positioning system (VPS) to quantify the behavior of telemetered gray triggerfish around fish traps. A VPS fine-scale tracking system can provide meter-level spatial resolution of telemetered fishes (Espinoza et al. 2011), including those in relatively deep water (Piraino & Szedlmayer 2014). A VPS study has been used previously to understand the movement patterns of gray triggerfish around artificial reefs in the northern Gulf of Mexico (Herbig & Szedlmayer 2016).

The VPS system uses coded acoustic transmitters and an array of receivers to detect and record their transmissions. Vemco then uses the time offsets of

individual acoustic transmissions being detected on multiple receivers to determine the spatial positions of tagged animals. For VPS to be successful, time must be synchronized across all receivers, which is typically accomplished in a VPS study by using sync tags that are either deployed independently throughout the receiver array or built into the receivers themselves. To determine spatial positions, transmissions must be detected on a minimum of 3 receivers, and detection on more than 3 receivers increases the precision of spatial locations. Thus, an essential element of a VPS study is that the detection range of transmitters is estimated well. If receivers are spread too far apart from one another, exact fish positions cannot be determined, whereas the study area becomes unnecessarily small if receivers are moved too close to one another.

Receiver deployment

We deployed 20 Vemco VR2AR acoustic receivers at the Chicken Rock area on 31 August 2017. Each receiver not only recorded acoustic signals from all transmitters detected, but also included its own Vemco V16 sync tag that was used for time corrections among receivers. Receivers were deployed in a 4 × 5 grid that covered an area of low-relief hardbottom (reef) and softbottom (sand) habitats (Fig. 2). In our study, receivers were spaced every 200 m based on detection ranges from a previous reef fish telemetry study that used slightly smaller (i.e. V9) transmitters but occurred in similar depths in North Carolina (Bacheler et al. 2015). Thus, our study area was 600 m × 800 m in size (0.48 km²).

Recovering all receivers was critical to the study, given the requirements of the VPS. Each receiver was attached to a 36 kg steel weight for mooring and a 28 cm diameter hard plastic float with 8.8 kg of buoyancy (Mooring Systems) using 8 mm Amsteel® Blue dyneema rope (Rigging Warehouse). The line length between the mooring weight and each receiver varied between 1.5 and 3.5 m given the known depth at each specific receiver deployment location, resulting in all 20 receivers being in a horizontal plane approximately 35 m deep after deployment. Our VR2AR receivers also included an acoustic release for retrieval at the conclusion of the study. Last, a reference transmitter (Vemco V13T-1x) with a temperature sensor was deployed in the southwest corner of the receiver array (Fig. 2) to provide continuous water temperature information that was subsequently used in the VPS analyses, as well as to esti-

mate positional error of transmitters in the array because the reference tag location was known exactly. The reference tag operated at 69 kHz, had a 550–650 s ping interval, and was attached to a 4 m long Amsteel® Blue line that was weighted on one end and had a float on the other.

Field tagging

Gray triggerfish were captured for tagging in the receiver array using traps on 15 September 2017 using the RV ‘Ocellatus.’ Small traps (hereafter, ‘triggerfish traps’) were used to capture fish for tagging in this study; these traps were 60 × 60 × 48 cm in size and constructed out of plastic-coated square wire mesh (38 × 38 mm mesh size), baited with approximately 2 kg of frozen *Brevoortia* spp., and soaked for 50–80 min before retrieval. Four traps in total were used during the collection of gray triggerfish for tagging (but only 2 of them caught gray triggerfish), and each was deployed independently with a line to the surface and a surface float. Traps were set in areas that appeared to contain some hardbottom reef habitat from the multibeam bathymetry map. The surface water, bottom water, and air temperatures were all approximately 26°C during tagging.

Upon trap retrieval, gray triggerfish were emptied into a 300 l holding tank filled with ambient seawater. To minimize the chance of release mortality, only gray triggerfish actively swimming in the holding tank were chosen for transmitter attachment, and a maximum of 5 gray triggerfish were tagged from each trap to facilitate a short surface interval (Burns et al. 2002). The external transmitter attachment procedure was exactly the same as used in the holding tank experiment, with the exception that some excessively bloated fish were vented after tagging using a 16-gauge hollow needle to allow the fish to swim back to the bottom (see Table 1). All fish were tagged with Vemco V13-1x transmitters that operated on a frequency of 69 kHz, weighed 11 g in air, had a 110–250 s ping interval, and had an estimated battery life of 904 d. Each telemetered gray triggerfish swam towards the bottom after tagging and release.

Recapture events

We conducted 3 separate daytime recapture events to quantify the behavioral responses of telemetered gray triggerfish to traps. The first recapture event

occurred on the RV ‘Savannah’ on 30 September 2017, 15 d after tagging. We used chevron fish traps in the first recapture period, which were arrowhead-shaped fish traps that measured 1.7 × 1.5 × 0.6 m, with a volume of approximately 0.91 m³ (Collins 1990, Bacheler et al. 2017). Chevron fish traps are regularly used to capture gray triggerfish in the SEUS by the SERFS (Bacheler & Smart 2016). Chevron traps were baited with approximately 4 kg of *Brevoortia* spp., and a soak time of 90 min was targeted for each trap (mean = 93.7 min, range = 70–112 min). Four chevron traps were deployed independently in the study area at any given time (mean distance between traps = 279 m), and every 90 min, traps were retrieved, rebaited, and redeployed in a new location.

The second recapture period occurred on 6 October 2017 (21 d after tagging) and the third recapture period occurred on 27 October 2017 (42 d after tagging) using smaller research vessels. During the second and third recapture periods, 6 baited ‘triggerfish traps’ (the same as used during tagging) were deployed simultaneously (mean distance between traps was 190 m in the second recapture period and 182 m in the third recapture period). Triggerfish traps were used in the second and third recapture period due to vessel size limitations. Soak times averaged 80 and 85 min in the second and third recapture periods, respectively. We also attached 1 GoPro® Hero 4 camera on the top of every trap deployed during each recapture period, facing outward; tagged and untagged gray triggerfish were counted on videos, and any fish that appeared to have lost transmitters (i.e. fish with 2 holes in upper back) were noted. All receivers were retrieved after the third recapture period on 27 October 2017.

Bottom water current direction and magnitude were determined by attaching tilt current meters to some traps in all 3 recapture periods. We used TCM-1 tilt current meters (Lowell Instruments) that included 3-axis accelerometers and magnetometers to measure tilt and bearing, which were then converted to current magnitude and direction using the TCM-1 software. For each group of simultaneously deployed chevron or triggerfish traps, 1 to 3 traps included a tilt current meter. Each current meter calculated current magnitude and direction 120 times min⁻¹, and the estimated current direction and magnitude for a given trap was the mean of all of these values across the trap’s soak time. If a particular trap was missing current direction and magnitude data, information from other simultaneously deployed traps with a current meter was used. Current magnitude and direc-

tion were very similar among simultaneously soaked traps and within each day. Water clarity was scored as poor, fair, or good based on the qualitative classification scheme described by Bacheler et al. (2014).

Exploratory data analyses

Prior to quantitative data analysis, we explored the data for broad patterns in the precision of our telemetry system and the behavior of telemetered gray triggerfish around traps. First, we examined the daily positional error estimates of the reference transmitter in the receiver array. Error was calculated as the difference between the known reference tag location and its estimated VPS position each time it emitted a signal. We visualized positional error with a boxplot showing daily median, 25th, and 75th percentiles. Daily boxes were developed to determine if any changes in positional error over the course of this study were evident.

Second, we plotted locations of a subset of individual telemetered gray triggerfish that either responded or did not respond to traps. To visualize responses spatially, the location of the trap was placed centrally in a plot, an arrow indicated current direction and magnitude, and the locations of telemetered gray triggerfish during the trap soak time were colored from white (trap just deployed) to black (trap about to be retrieved) to ease interpretation. Six responses from 4 fish were chosen because they represented the wide variety of observed behaviors of gray triggerfish around traps.

Third, we graphically summarized data from all telemetered fish and traps by scaling locations so that the trap was centered and the current direction was straight down, which required rotating data from each trap in the study for alignment. The goal was to visualize which fish responded to traps and how their initial distance from the trap, as well as their initial position relative to the trap with respect to current direction, influenced their responses. For this summary, we chose a threshold distance of 20 m between telemetered fish and traps to qualify fish as having responded to fish traps to allow for some uncertainty in the trap location.

One challenge of quantifying the responses of gray triggerfish to traps is that some fish may respond due to sensory cues, while others may incidentally discover a trap given their normal swimming patterns. In an attempt to distinguish fish responding incidentally from those responding to specific sensory cues, we examined movements of gray triggerfish around

trap deployment locations on days immediately preceding recapture efforts. We determined whether telemetered gray triggerfish were located within 20 m of those trap locations during the time period when traps were deployed the following day. A side-by-side comparison of these 2 figures was used to determine the relative importance of fish responding randomly compared to responding to specific sensory cues. This analysis assumed that normal swimming behaviors were exhibited on the day before each recapture period.

Quantitative data analyses

We assembled individual-level behavioral information about each of the telemetered gray triggerfish that responded to traps in our study. For each individual that responded to a baited trap, we determined the amount of time it spent within 20 m of the trap as the number of detections within that radius divided by the total number of detections during the trap soak time. We also determined (1) the time elapsed from trap deployment until each fish entered within 20 m of the trap, (2) the mean, minimum, and maximum distance between each fish and traps during the trap soak, and (3) the number of separate visits each telemetered fish made within 20 m of traps. To count as separate visits, telemetered fish must have been detected within 20 m of the trap (visit no. 1), then move more than 20 m from the trap, and then swim within 20 m of the trap a second time (visit no. 2).

To quantify the behavior of telemetered gray triggerfish around traps, we used generalized additive models (GAMs) to test for the influence of predictor variables in 2 sets of analyses (described below). GAMs are a regression modeling technique that can relate a response variable to multiple predictor variables nonlinearly (Wood 2006). A major advantage of GAMs compared to linear or additive models is their flexibility in fitting different error distributions (Hastie & Tibshirani 1990). All models were coded and analyzed using the *mgcv* library (version 1.8-17; Wood 2011) in R version 3.4.3 (R Core Team 2017).

GAM analysis 1

Our first GAM analysis examined which predictor variables were correlated with whether or not telemetered gray triggerfish responded to traps. We used binomial GAMs because our response data

were inherently binary (i.e. a fish did or did not respond to a trap). However, spatial uncertainty occurred in some cases because of our inability to pinpoint the exact location of traps. We knew the deployment location of traps within about 3 m, but water current during the trap descent may have moved traps some distance away from their deployment location. To account for trap location uncertainty, we developed 4 binomial GAMs, each with different threshold distances used to define a response: 10, 20, 30, and 40 m from the trap deployment location. Thus, these 4 GAMs were used to determine how sensitive our results were to threshold size. Consistency among these 4 models would suggest our binomial GAM results were robust to uncertainty in the exact trap location. Only fish alive and in the study area during recapture periods were included in the analyses.

Three predictor variables were included in the binomial GAMs based on our specific hypotheses and previous research. The first predictor variable was the initial distance between the trap and fish locations when the trap was deployed (*dist*). We hypothesized that telemetered gray triggerfish would be more likely to respond to traps when they were initially in close proximity. Initial distance was included as a smoothed, continuous variable in the binomial GAMs. The second predictor variable was the initial fish position relative to the trap and current direction (*cur*). We hypothesized that fish would be more likely to respond to traps if they were initially down-current from the trap because of the bait plume (Zhou & Shirley 1997, Bacheler et al. 2014). Current direction was included in the binomial GAMs as a smoothed, continuous, circular variable. The last predictor variable included in our binomial GAMs was recapture period (*period*). Recapture period was included as a categorical variable to control for any differences in the responses of telemetered gray triggerfish due to trap type, bait amount, water clarity, or any other conditions that varied among the 3 recapture periods. We attempted to include recapture period as a random effect in this GAM and models below, but in each case models failed to converge due to low sample sizes. Thus, we included recapture period as a fixed effect.

The binomial GAMs were formulated as:

$$\eta = \alpha + s_1(\text{dist}) + s_2(\text{cur}) + f_1(\text{period}) \quad (1)$$

where η is the probability of a telemetered gray triggerfish responding to a trap, α is the model intercept, s_1 and s_2 are nonparametric smoothing functions, and f_1 is a categorical function.

GAM analysis 2

There was broad variability in the time it took telemetered gray triggerfish to approach within 20 m of traps, and thus our second GAM analysis focused on the predictor variables that may have influenced this timing. Instead of modeling binary data, the response variable here was the time it took fish to move within 20 m of the traps. Various model diagnostics (e.g. quantile–quantile plot, residual plots) suggested GAMs with a Gaussian error distribution outperformed other distributions, such as Poisson or negative binomial, for modeling these data. We related this response variable to the same 3 predictor variables and formulations as our binomial GAMs above. This GAM was formulated as:

$$y = \alpha + s_1(\text{dist}) + s_2(\text{cur}) + f_1(\text{period}) \quad (2)$$

where y is the time it took telemetered gray triggerfish to respond to traps and all other variables are defined in Eq. (1).

Model comparison

For each of the GAM analyses, we applied model selection techniques to examine the importance of the predictor variables. Specifically, we compared models containing all 3 predictor variables (hereafter, 'Base' models) to reduced models containing all combinations of fewer predictor variables. Model comparisons were made using Akaike's information criterion (AIC; Burnham & Anderson 2002). To improve clarity, we presented Δ AIC scores that were calculated as the difference between AIC scores of each model and that of the best performer (lowest AIC). We focus the presentation of results on the best performing models in the model set, although models with Δ AIC scores < 2 might have similar support (Burnham & Anderson 2002).

RESULTS

Holding tank study

Fish in the holding tank study ranged from 335–405 mm fork length at tagging (853–1502 g), and the transmitter weight to fish weight ratio ranged from 0.7 to 1.3% in air. No fish died during the 92 d study, but gray triggerfish lost their transmitters at 14, 35, 77, 81, and 91 d after tagging. The first fish lost its transmitter because the knot and epoxy failed, but

the subsequent 4 fish lost their transmitters when the absorbable suture material broke near the crimp.

Positional error of transmitters

The positional error of transmitters was determined from the reference tag deployed in the receiver array at a known location throughout the entire study. Median positional error rates ranged from approximately 1 m early in the study to just over 2 m by the end of the study (Fig. 3), suggesting high spatial precision of telemetered gray triggerfish. Spatial precision also appeared to be unaffected by 2 storms that passed by the study area, Hurricane Jose on 17–19 September 2017 and Hurricane Maria on 25–27 September 2017.

Field tagging

Thirty gray triggerfish were tagged externally with transmitters and released into the study area on 15 September 2017 (Table 1, Fig. 2). The lengths of gray

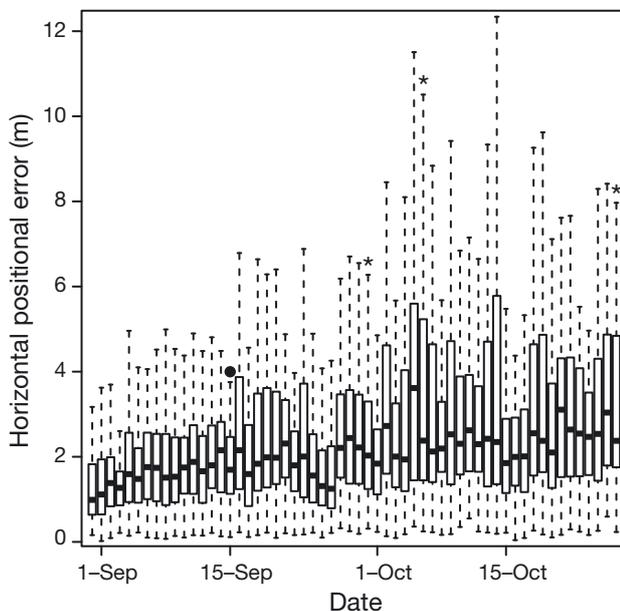


Fig. 3. Horizontal positional error (m) of a reference transmitter deployed at a known location. The estimated position of the reference tag each time it emitted an acoustic signal was compared to its actual, known position to determine the horizontal positional error on each day of the study. Daily boxes show median horizontal positional error rates by the thick horizontal black line, bottom and top of boxes provide 25th and 75th percentiles, respectively, and whiskers are 1.5 times the interquartile range. The filled circle denotes the day when gray triggerfish *Balistes capriscus* were tagged, and asterisks denote the 3 days on which recapture efforts occurred

triggerfish tagged in the field (mean = 291 mm fork length; range = 250–335 mm) were smaller than fish tagged in our holding tank study, which translated to a higher tag weight to body weight ratio (mean = 2.0%; range = 1.3–3.0%) for field-tagged fish. Most of the fish tagged in the field (73%) were vented to allow them to swim back down to the bottom immediately after tagging (Table 1).

Recapture events

Three recapture events occurred 15, 21, and 42 d after tagging, during which we monitored responses of telemetered gray triggerfish to traps (Table 2). Bottom current direction and compass heading (on a 0–359° scale) were similar among recapture periods 1 and 2, but were weaker and in the opposite direction during recapture period 3 (Table 2). Bottom temperature was very similar among the 3 recapture periods (25.7–27.2°C), whereas water clarity was quite different, being poor, fair, and good in recapture periods 1, 2, and 3, respectively (Table 2). Twenty chevron traps were deployed in recapture period 1, 24 triggerfish traps in period 2, and 12 triggerfish traps in period 3. A total of 201 gray triggerfish were recaptured in period 1, 203 in period 2, and 173 in period 3, but no telemetered gray triggerfish were recaptured during the study.

Gray triggerfish behavior around traps

Overall, 137 183 spatial positions were available for the 30 telemetered gray triggerfish in our study. The precise spatial positions allowed us to determine that 13 fish emigrated from the study area, 6 fish either lost their transmitter or died in the study area, and 11 fish were alive and remained in the study area until the end of the study (Table 1). Excluding spatial positions for fish after their transmitters stopped moving resulted in a total of 104 170 spatial positions for fish alive in the study area (mean: 3472 positions fish⁻¹; range = 63–11 789; Table 1). Eight telemetered gray triggerfish were detected and alive in the study area during recapture period 1, 10 during period 2, and 11 during period 3.

Telemetered gray triggerfish responded to traps in some instances but not others (Fig. 4). Trap response rate was variable across recapture periods, with 3 of 8 fish responding to at least 1 trap in period 1 (38%), 7 of 10 responding in period 2 (70%), and 5 of 11 responding in period 3 (45%). It appeared that fish

Table 1. Information for individual gray triggerfish *Balistes capricus* tagged at the Chicken Rock area in Raleigh Bay, North Carolina, USA, on 15 September 2017. Individual body weight (BW) was estimated using a fork length (FL) to weight conversion (Burton et al. 2015), and 'Tag:BW' is the ratio of transmitter weight in air to estimated fish BW in air $\times 100$. 'Vent' shows whether a fish did or did not have its swim bladder punctured with a hollow needle to allow the fish to swim back to the bottom. Asterisks note fish shown in Fig. 4

| Tag | FL (mm) | Estimated BW (g) | Tag:BW (%) | Vent | Estimated positions (n) | Last day detected | Fate |
|-----|---------|------------------|------------|------|-------------------------|-------------------|------------------|
| 30 | 335 | 868 | 1.3 | Yes | 1764 | 27 Sep | Emigrated |
| 31* | 270 | 458 | 2.4 | Yes | 4321 | 10 Oct | Lost tag or died |
| 32 | 290 | 566 | 1.9 | Yes | 235 | 29 Sep | Emigrated |
| 33 | 265 | 433 | 2.5 | Yes | 1668 | 2 Oct | Lost tag or died |
| 34 | 275 | 483 | 2.3 | No | 2002 | 29 Sep | Lost tag or died |
| 35 | 335 | 868 | 1.3 | No | 982 | 1 Oct | Emigrated |
| 36 | 310 | 690 | 1.6 | Yes | 7884 | 27 Oct | Alive in array |
| 37* | 280 | 510 | 2.2 | No | 6992 | 27 Oct | Alive in array |
| 38 | 250 | 364 | 3.0 | No | 8491 | 27 Oct | Alive in array |
| 39 | 273 | 473 | 2.3 | No | 1263 | 23 Sep | Lost tag or died |
| 40* | 325 | 794 | 1.4 | Yes | 1079 | 1 Oct | Lost tag or died |
| 41 | 275 | 483 | 2.3 | No | 178 | 18 Sep | Emigrated |
| 42 | 268 | 448 | 2.5 | No | 242 | 15 Oct | Emigrated |
| 43 | 320 | 758 | 1.5 | Yes | 661 | 26 Sep | Emigrated |
| 44 | 295 | 595 | 1.8 | Yes | 8223 | 27 Oct | Alive in array |
| 45 | 312 | 703 | 1.6 | Yes | 92 | 15 Sep | Emigrated |
| 46 | 285 | 537 | 2.0 | Yes | 4345 | 27 Oct | Alive in array |
| 47 | 268 | 448 | 2.5 | Yes | 8881 | 27 Oct | Alive in array |
| 48 | 315 | 723 | 1.5 | Yes | 837 | 22 Sep | Lost tag or died |
| 49 | 285 | 537 | 2.0 | Yes | 5061 | 27 Oct | Alive in array |
| 50 | 305 | 657 | 1.7 | Yes | 204 | 18 Sep | Emigrated |
| 51 | 318 | 744 | 1.5 | Yes | 1320 | 24 Sep | Emigrated |
| 52* | 275 | 483 | 2.3 | Yes | 10912 | 27 Oct | Alive in array |
| 53 | 250 | 364 | 3.0 | Yes | 167 | 27 Sep | Emigrated |
| 54 | 270 | 458 | 2.4 | Yes | 9018 | 27 Oct | Alive in array |
| 55 | 308 | 677 | 1.6 | Yes | 63 | 16 Sep | Emigrated |
| 56 | 312 | 703 | 1.6 | Yes | 5028 | 27 Oct | Alive in array |
| 57 | 305 | 657 | 1.7 | Yes | 370 | 20 Sep | Emigrated |
| 58 | 255 | 386 | 2.8 | No | 11 789 | 27 Oct | Alive in array |
| 59 | 315 | 723 | 1.5 | Yes | 98 | 17 Sep | Emigrated |

Table 2. Information about each of the 3 trap recapture periods used to elicit response behaviors of telemetered gray triggerfish *Balistes capricus* to baited traps. Bottom current velocity and direction (heading) were determined with water current probes attached to traps. Ch: chevron fish trap, Tr: homemade trap designed to specifically catch gray triggerfish. Water clarity scores were based on the qualitative classification scheme described by Bacheler et al. (2014)

| Recapture period | Date | Research vessel | Trap | Traps deployed (n) | Current velocity (m s^{-1}) | Current heading ($^{\circ}$) | Bottom temperature ($^{\circ}\text{C}$) | Water clarity |
|------------------|--------|-----------------|------|--------------------|--|--------------------------------|---|---------------|
| 1 | 30 Sep | 'Savannah' | Ch | 20 | 1.1 | 42 | 26.6 | Poor |
| 2 | 6 Oct | 'Ocellatus' | Tr | 24 | 1.2 | 46 | 27.2 | Fair |
| 3 | 27 Oct | 'Regulator' | Tr | 12 | 0.8 | 211 | 25.7 | Good |

were more likely to respond relatively quickly to traps when they were initially close to the traps. It was rare that telemetered gray triggerfish stayed near a trap for long periods of time; they often visited for short periods (<10 min) and then left, sometimes returning to the trap later in the trap soak (Fig. 4).

When rescaled by trap location and current direction, it appeared that nearly half (48%) of teleme-

tered gray triggerfish responded to traps when the initial distance between fish and traps was less than 50 m (Fig. 5). Moreover, fish down-current or perpendicular to the current appeared more likely to respond to traps than fish up-current. However, there were numerous telemetered gray triggerfish that did not appear to respond to traps even though they were initially located within 100 m of traps (Fig. 5).

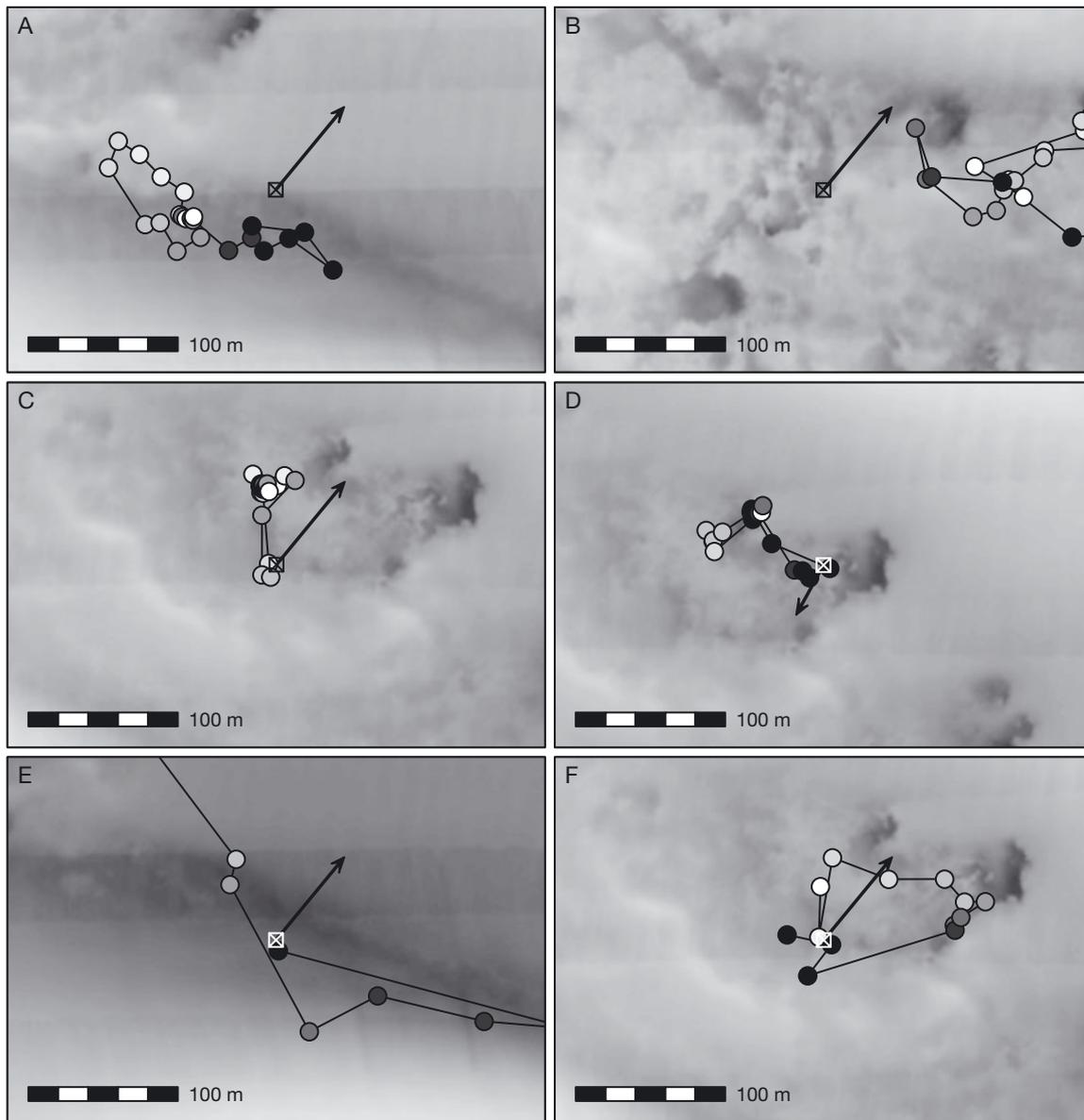


Fig. 4. Swimming behavior of telemetered gray triggerfish *Balistes capriscus* around baited fish traps. In each plot, the trap is located in the middle of the plot (white or black box with ×), and the arrow indicates bottom current compass heading (°) and magnitude. Positions from a single telemetered gray triggerfish are plotted on each plot, and colors of the filled circles represent the spectrum of trap soak time (white = trap just deployed; black = trap retrieved). Recapture periods (RP) and individual fish tag numbers in each panel are: (A) RP 1, tag 52; (B) RP 2, tag 31; (C) RP 1, tag 52; (D) RP 3, tag 37; (E) RP 1, tag 40; (F) RP 2, tag 37

Nine telemetered gray triggerfish approached within 20 m of trap locations on the day preceding recapture periods and could be considered random responders (Fig. 5). Most of these fish (67%) were initially located within 50 m of the locations where traps were deployed the following day, suggesting gray triggerfish are more likely to incidentally discover traps when traps are deployed close to their initial position. Given that there were 27 instances of tele-

metered gray triggerfish responding to traps during the 3 recapture periods (see below), 33% responded incidentally to traps and 67% responded due to sensory cues from the bait or trap (Fig. 5).

There were 27 instances when telemetered gray triggerfish were at some point located within 20 m of traps across the 3 recapture periods: 3 in period 1, 17 in period 2, and 7 in period 3 (Table 3). Some (60%) of these telemetered gray triggerfish responded to mul-

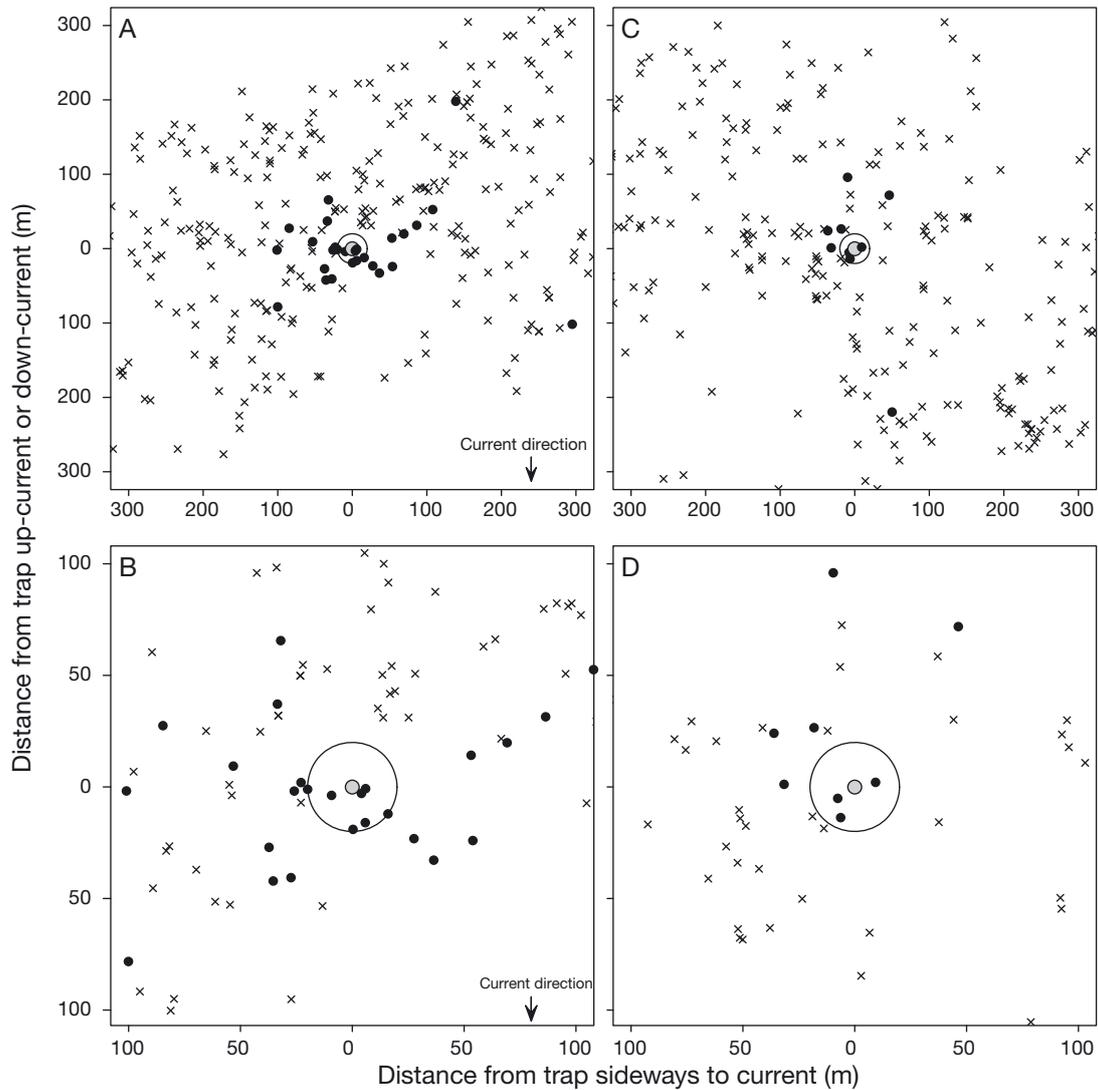


Fig. 5. Trap responses of telemetered gray triggerfish *Balistes capriscus* in relation to their initial distance from traps and current direction during 3 recapture efforts in 2017 (left column), and 'responses' of telemetered fish to the same trap locations (but with no traps deployed) exactly 24 h preceding each recapture effort (right column). In the left column, data from all telemetered fish and all traps are scaled so that the trap is shown in the center of each plot and the current direction (heading; °) is straight down; in the right column, current direction was unknown so plots are unscaled. Each × shows the initial positions of fish that did not approach within 20 m of baited traps (or trap locations the following day), and each black filled circle indicates fish that approached within 20 m of baited traps or trap locations the following day; open circles indicate a 20 m radius around each location. (A,C) Broad view; (B,D) zoomed-in views of the same data

tiple traps, with fish no. 37 responding to the most traps in our study ($N = 6$). Moreover, some traps (47%) had multiple telemetered gray triggerfish respond to them. The mean initial distance between telemetered fish and traps was 68 m (range: 5–312 m). Telemetered gray triggerfish that responded to traps spent a mean of 35% of their time within 20 m of traps, but there was substantial variability among individuals (range = 4–95%) and recapture period (mean = 12% in period 1, 30% in period 2, and 57% in period 3; Table 3). Only 7 of the 27 instances of triggerfish responding to

traps (26%) spent more than 50% of their time within 20 m of traps. Some telemetered gray triggerfish were already within 20 m of traps when traps were deployed, but other telemetered fish took up to 87 min to respond to traps (mean response time = 33 min). Of fish responding to traps, the mean distance between telemetered gray triggerfish and traps ranged from 10 to 195 m (mean = 54 m). The minimum distance between the 27 telemetered gray triggerfish and fish traps ranged from 1 to 17 m among fish (mean = 7 m), and the maximum distance among fish ranged from

Table 3. Summary information for the 27 instances of telemetered gray triggerfish *Balistes capriscus* responding to baited fish traps at the Chicken Rock area of Raleigh Bay, North Carolina, in 2017. Here, a fish response was determined if it entered a 20 m halo around a baited fish trap ('within 20 m' in table)

| Transmitter no. | Recapture period | Trap number | Total detections during trap soak time | Detections within 20 m | Proportion of detections within 20 m | Time (min) to approach within 20 m | Initial distance between fish and trap (m) | Mean distance (m) to trap (range) during trap soak | Number of separate visits inside 20 m |
|-----------------|------------------|-------------|--|------------------------|--------------------------------------|------------------------------------|--|--|---------------------------------------|
| 33 | 1 | 4 | 14 | 2 | 0.14 | 16 | 20 | 89 (12–196) | 2 |
| 40 | 1 | 9 | 11 | 1 | 0.09 | 81 | 312 | 167 (7–323) | 1 |
| 52 | 1 | 18 | 25 | 3 | 0.12 | 28 | 49 | 48 (5–63) | 1 |
| 37 | 2 | 3 | 21 | 7 | 0.33 | 29 | 127 | 51 (2–127) | 2 |
| 49 | 2 | 3 | 14 | 3 | 0.21 | 66 | 49 | 37 (11–68) | 2 |
| 52 | 2 | 3 | 23 | 1 | 0.04 | 81 | 46 | 43 (15–67) | 1 |
| 37 | 2 | 9 | 17 | 9 | 0.53 | 0 | 10 | 32 (1–57) | 2 |
| 52 | 2 | 9 | 17 | 10 | 0.59 | 0 | 17 | 21 (15–30) | 3 |
| 44 | 2 | 10 | 18 | 3 | 0.17 | 12 | 72 | 120 (7–263) | 1 |
| 37 | 2 | 15 | 22 | 4 | 0.18 | 24 | 55 | 45 (2–67) | 1 |
| 52 | 2 | 15 | 18 | 5 | 0.28 | 0 | 19 | 26 (9–42) | 4 |
| 31 | 2 | 16 | 17 | 7 | 0.41 | 76 | 55 | 46 (7–119) | 2 |
| 44 | 2 | 16 | 26 | 2 | 0.08 | 87 | 242 | 195 (6–396) | 1 |
| 36 | 2 | 20 | 19 | 8 | 0.42 | 29 | 73 | 35 (8–74) | 2 |
| 37 | 2 | 20 | 14 | 1 | 0.07 | 43 | 120 | 84 (16–145) | 1 |
| 37 | 2 | 21 | 13 | 2 | 0.15 | 11 | 36 | 60 (4–111) | 2 |
| 52 | 2 | 21 | 19 | 3 | 0.16 | 67 | 59 | 55 (5–105) | 1 |
| 31 | 2 | 22 | 13 | 2 | 0.15 | 10 | 20 | 40 (17–46) | 1 |
| 44 | 2 | 22 | 13 | 10 | 0.77 | 15 | 101 | 24 (9–101) | 2 |
| 47 | 2 | 22 | 20 | 10 | 0.50 | 34 | 50 | 33 (7–90) | 2 |
| 36 | 3 | 2 | 21 | 20 | 0.95 | 0 | 6 | 10 (3–22) | 1 |
| 58 | 3 | 2 | 22 | 19 | 0.86 | 0 | 5 | 10 (3–26) | 3 |
| 44 | 3 | 3 | 20 | 1 | 0.05 | 71 | 92 | 62 (15–104) | 1 |
| 49 | 3 | 5 | 16 | 13 | 0.81 | 5 | 23 | 12 (5–32) | 2 |
| 36 | 3 | 7 | 14 | 10 | 0.71 | 15 | 26 | 23 (3–80) | 1 |
| 37 | 3 | 8 | 16 | 4 | 0.25 | 49 | 54 | 51 (5–82) | 1 |
| 44 | 3 | 9 | 19 | 7 | 0.37 | 51 | 89 | 47 (1–89) | 1 |
| Mean | | | 17.8 | 6.1 | 0.35 | 34 | 68 | 54 (7–108) | 1.6 |

22 to 396 m (mean = 108 m). Most telemetered gray triggerfish (14 of 27 fish; 52%) visited the trap a single time, 10 (37%) visited twice, 2 (7%) visited 3 times, and 1 fish (4%) visited 4 times (Table 3).

GAMs

Our first GAM analysis tested the influence of 3 predictor variables on the binary response of gray triggerfish to traps. We developed 4 GAMs in this first analysis, each with a different distance threshold between fish and trap (i.e. 10, 20, 30, and 40 m). In our study, there were 20 instances where telemetered gray triggerfish approached within 10 m of traps, 27 instances within 20 m, 35 within 30 m, and 47 within 40 m. The base model that included all 3 predictor variables (i.e. initial distance, current direction, and recapture period) had the lowest Δ AIC values for the 20, 30, and

40 m models, whereas the best 10 m model excluded recapture period (Table 4). The deviance explained by these GAMs was relatively high, ranging from 45.3% for the 10 m model to 62.6% for the 30 m model.

The partial effects of predictor variables on the responses of telemetered gray triggerfish to traps were similar among the 4 GAMs. Telemetered gray triggerfish were much more likely to respond to traps if their initial distance from traps was less than 100 m; the probability of telemetered gray triggerfish responding to traps more than 100 m away was close to 0 for all 4 models (Fig. 6). Across all 4 models, telemetered gray triggerfish were much more likely to respond to traps when the fish were initially located down-current or perpendicular to the current than up-current of the trap (Fig. 6). In the 20, 30, and 40 m models, telemetered gray triggerfish were most likely to respond to traps in the second recapture period, but inferences were limited by the large

Table 4. Model selection for generalized additive models that related whether or not telemetered gray triggerfish *Balistes capriscus* responded to (i.e. approached within 10, 20, 30, or 40 m of baited fish traps) 3 predictor variables: (1) initial distance between telemetered fish and the baited fish trap (*dist*), (2) initial location of the telemetered fish based on the relative trap location and current direction (*cur*), and (3) the recapture period (*period*). Degrees of freedom are shown for factor (f_1) term, and estimated degrees of freedom are shown for nonparametric, smoothed terms (s_1 and s_2). Dev. ex. is the deviance explained by the model, Δ AIC is the Akaike information criterion of each model relative to the best model in the set, ex means that predictor variable was excluded from the model, and Base is the model that includes all 3 predictor variables.

Only the 3 best candidate models are shown for each radius size

| Model | Dev. ex. (%) | Δ AIC | $s_1(\text{dist})$ | $s_2(\text{cur})$ | $f_1(\text{period})$ |
|-----------------------------------|--------------|--------------|--------------------|-------------------|----------------------|
| 10 m radius | | | | | |
| Base – <i>period</i> | 45.3 | 0.0 | 1.5 | 3.1 | ex |
| Base | 47.1 | 1.2 | 1.4 | 3.2 | 2 |
| Base – <i>period</i> – <i>cur</i> | 41.1 | 1.7 | 1.8 | ex | ex |
| 20 m radius | | | | | |
| Base | 58.9 | 0.0 | 1.8 | 3.7 | 2 |
| Base – <i>period</i> | 56.3 | 0.8 | 1.9 | 3.3 | ex |
| Base – <i>period</i> – <i>cur</i> | 49.5 | 9.4 | 2.2 | ex | ex |
| 30 m radius | | | | | |
| Base | 62.6 | 0.0 | 3.7 | 5.0 | 2 |
| Base – <i>period</i> | 58.8 | 4.5 | 3.5 | 4.5 | ex |
| Base – <i>cur</i> | 52.4 | 16.1 | 3.6 | ex | 2 |
| 40 m radius | | | | | |
| Base | 56.5 | 0.0 | 3.5 | 4.6 | 2 |
| Base – <i>period</i> | 54.8 | 0.2 | 3.4 | 4.1 | ex |
| Base – <i>period</i> – <i>cur</i> | 50.2 | 6.3 | 3.3 | ex | ex |

amount of variability in each of these 3 relationships (Fig. 6). The recapture period variable was excluded from the 10 m model based on Δ AIC. Error in trap locations likely did not influence our results given the similarities in fish responses across a range of threshold distances, so we used 20 m for the remainder of our analyses and interpretations.

The second GAM analysis sought to explain the variability in the time it took telemetered gray triggerfish to respond to traps. The only statistically significant predictor was their initial distance from traps; current direction and recapture period were excluded based on Δ AIC (Table 5). The initial distance of telemetered gray triggerfish from traps explained 63.0% of the variability in response time, and there was generally a positive relationship between the 2 variables (Fig. 7).

DISCUSSION

The ability to infer absolute site abundance from relative abundance data using baited gears would be an enormous advance for reef fish stock assessments

and ecological surveys (Kimura & Somerton 2006). The first step in converting relative abundance to absolute abundance is understanding the behavior of the species of interest around baited gears (Watson et al. 2009) and how those behaviors are influenced by environmental variability (Stoner 2004). We analyzed the behavior of gray triggerfish around baited traps using an acoustic positioning system, which provided spatially precise, temporally extensive, individual-level position data for telemetered gray triggerfish around 54 traps. To our knowledge, our study is novel because it is the first to directly quantify fine-scale movements of fish around baited gears in their natural habitat, and is a significant first step towards estimating absolute abundance of gray triggerfish around baited gears.

Gray triggerfish responded to traps over broader spatial scales than most organisms in previous studies. For instance, the response distance for American lobsters has been estimated at 9–17 m by Smith & Tremblay (2003) and 11 m by Watson et al. (2009). Max-

imum response distances for other invertebrate species can be greater, however, such as 48 m for the edible crab *Cancer pagurus* (Skajaa et al. 1998), 120 m for juvenile western rock lobsters *Panulirus cygnus* (Jernakoff & Phillips 1988), and 125 m for European lobsters *Homarus gammarus* (Lees et al. 2018). Similarly, using swimming speed and time at arrival information, a deepwater scavenging fish (*Coryphaenoides* sp.) responded to bait over spatial scales of at least 15–67 m (Sainte-Marie & Hargrave 1987). Gray triggerfish responded to traps at a mean distance of 68 m, and 81% of all gray triggerfish responding to traps did so within an initial distance of 100 m, although 1 fish found a trap from an initial distance of more than 300 m. It is likely that various fish species could respond to bait over greater distances than gray triggerfish (e.g. sharks; Gardiner et al. 2012), but it appears that technological or methodological hurdles have limited inferences about bait responses to all but the slowest-moving species in previous studies.

Gray triggerfish appear to use multiple sensory systems to find traps. Olfaction was important because gray triggerfish were more likely to respond to

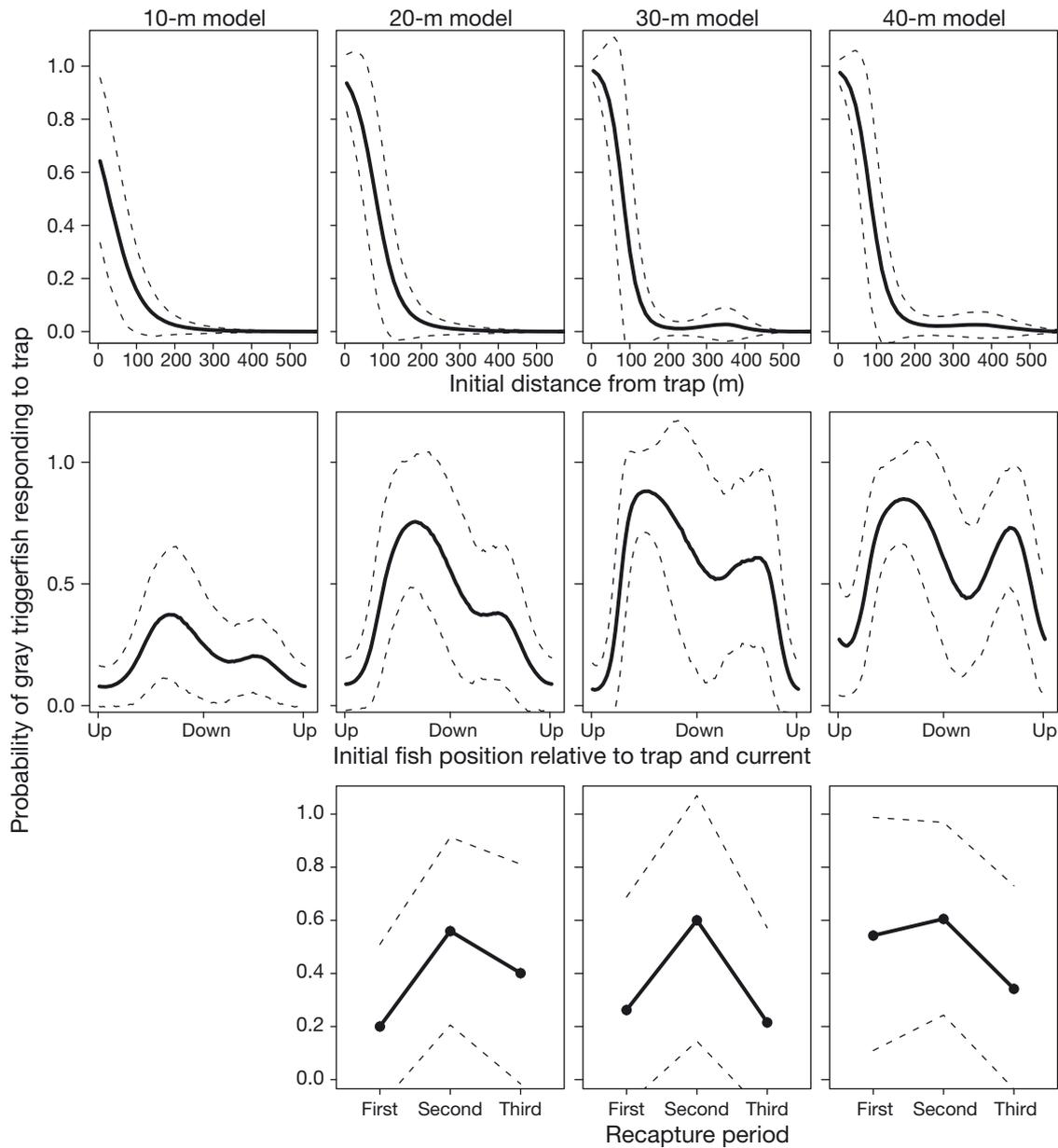


Fig. 6. Partial effects of 3 covariates on the probability that telemetered gray triggerfish *Balistes capriscus* responded to baited traps, using a binomial generalized additive model. Each plot was based on different assumptions about whether or not gray triggerfish responded to baited fish traps by determining if gray triggerfish approached within 10, 20, 30, or 40 m of baited traps as the response variable. In each plot, the solid line is the mean effect and dashed lines are 95% confidence intervals. Missing plot indicates that covariate was not included in the final model

Table 5. Model selection for generalized additive models that related the time it took telemetered gray triggerfish *Balistes capriscus* to enter a 20 m halo around baited traps to 3 predictor variables. Variables and degrees of freedom values are defined in Table 4

| Model | Dev. ex. (%) | ΔAIC | $s_1(dist)$ | $s_2(cur)$ | $f_1(period)$ |
|---------------------|--------------|------|-------------|------------|---------------|
| Base – cur – period | 63.0 | 0.0 | 4.1 | ex | ex |
| Base – period | 65.1 | 2.4 | 4.1 | 1.0 | ex |
| Base – cur | 65.0 | 2.5 | 4.1 | ex | 2 |

traps when they were initially down-current compared to up-current of the trap, consistent with scavenging organisms that respond to bait plumes (Smith 1985, Zhou & Shirley 1997, Stiansen et al. 2010). Three lines of evidence also suggest that vision is important to gray triggerfish finding traps. First, we showed that

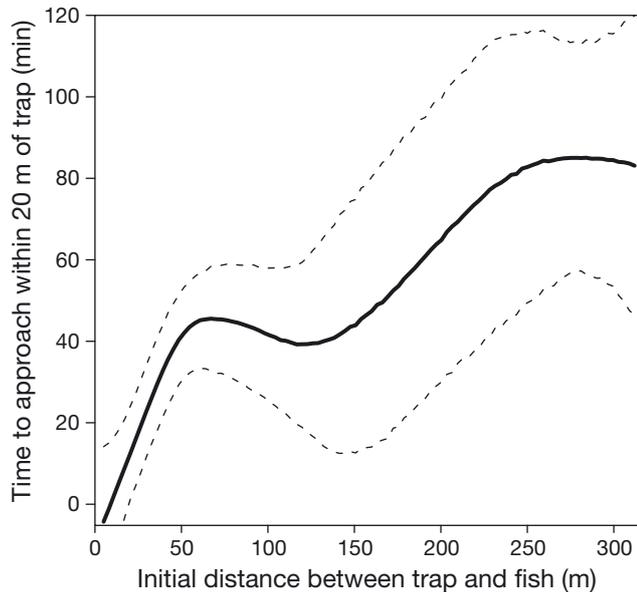


Fig. 7. Relationship between the time it took telemetered gray triggerfish *Balistes caprisicus* to enter a 20 m halo around baited traps and the initial distance between the trap and fish. The solid line is the mean effect and dashed lines are 95% confidence intervals

gray triggerfish responded to traps when they were close to traps, regardless of the current direction. Second, gray triggerfish were less likely to respond to traps in the first recapture period when water clarity was poor (0.15 fish responses trap⁻¹) compared to the second (0.71 responses trap⁻¹) and third recapture periods (0.58 responses trap⁻¹) when water was much clearer, despite twice as much bait being used in the first recapture period. Other potential explanations for differences in gray triggerfish responses could be differences in trap type, amount of bait, vessel noise, or other oceanic conditions. Third, telemetered gray triggerfish spent much less time in close proximity to traps in the first recapture period when water clarity was poor (14% of their time) compared to the other 2 recapture periods (30% in period 2 and 57% in period 3). However, there were instances of telemetered gray triggerfish responding to traps from up-current or sideways to the current from distances beyond the likely visibility horizon, suggesting that other mechanisms such as sound (e.g. Stiansen et al. 2010) may also be important for them to locate and respond to traps.

While there is a dearth of studies examining the behavior of fish around baited gears, some insights may be gleaned from studies examining the behavior of pelagic fish species around fish aggregating devices (FADs), for which many studies exist. Residence time of pelagic species at FADs is a primary

variable of interest in such studies, and has been shown to vary from less than 1 d for some tuna species (Govinden et al. 2013) to over 5 d for oceanic triggerfish *Canthidermis sufflamen* (Dagorn et al. 2007), dolphinfish *Coryphaena hippurus* (Taquet et al. 2007), bigeye tuna *Thunnus obesus* (Ohta & Kakuma (2005), and silky sharks *Carcharhinus falciformis* (Filmlalter et al. 2015). In a major advance, Capello et al. (2016) described a method to estimate tuna relative abundance that employs traditional survival models that are built on continuous residence and absence times of tunas around FADs; the authors noted that it is also theoretically possible to estimate the absolute abundance of tunas if the total number of tunas at 1 FAD is known. Likewise, gray triggerfish aggregated around traps in our study, so a similar method of obtaining absolute abundance may be possible.

The VPS acoustic system we employed here may be useful to understand the behavior of fish and invertebrates around various types of fishing gears. VPS systems have been used successfully to quantify the movement patterns (Herbig & Szedlmayer 2016, Piraino & Szedlmayer 2014, Skerritt et al. 2015), habitat use (Freitas et al. 2016, Stieglitz & Dujon 2017), and mortality rates (Williams-Grove & Szedlmayer 2016) of a variety of fishes and invertebrates. Moreover, Lees et al. (2018) used VPS to quantify responses of European lobsters to baited traps in the UK. We envision VPS being used to understand the behavior of fish around passive gears like hook-and-line, baited or unbaited traps, gill nets, and underwater video arrays, as well as around active gears like seines or trawls. It could also be used to understand the behavior of fishes around divers or manned or unmanned underwater vehicles conducting transect surveys to determine if estimated fish densities are biased, for instance, via fish flight responses from, or attraction to, divers or underwater vehicles (Willis et al. 2000, Bozec et al. 2011). Success can be maximized in VPS studies if the site fidelity of the study organism, transmitter retention, post-tagging survival, and transmitter detection range are all as high as possible (Espinoza et al. 2011).

Video cameras attached to traps confirmed the response of telemetered gray triggerfish to traps in some instances. Videos were not analyzed during recapture period 1 because water clarity was poor, but 4 telemetered gray triggerfish were observed on videos during recapture period 2, and 2 telemetered gray triggerfish were observed on videos during recapture period 3. In 1 instance, the transmitter number could be identified for a telemetered fish

during recapture period 2 (fish no. 52 was observed at trap no. 9). There were 2 instances in recapture period 2 where individuals were observed with 2 holes in their upper back (trap nos. 9 and 21), indicative of fish that had lost their transmitters.

Understanding the behavior of fish around baited gears can also guide the approach used to standardize catch or count data to estimate fish relative abundance (Maunder & Punt 2004, Stoner 2004). For instance, the behavioral responses of gray triggerfish often depended on recapture period, which in our study varied in terms of trap type, amount of bait used, and water clarity. These results suggest that SERFS (and other trap or video surveys) should continue consistently using the same trap type and amount of bait, as well as continue accounting for water clarity when standardizing indices of abundance. It was not possible to test for the influence of current magnitude on gray triggerfish behavior around traps in our study due to lack of replicates, so that topic requires further study given its importance in bait plume dynamics.

Our study had some shortcomings. First, there was some uncertainty in the exact trap locations due to water currents moving the traps laterally after deployment, which forced us to use 4 distances from the trap to score fish as having responded to traps or not. There was a high degree of consistency among models with different threshold distances, however, suggesting that our modeling results were insensitive to the distance used. Future VPS studies should attach transmitters to traps for more exact trap locations (see Lees et al. 2018). Second, a majority of individuals responded to more than 1 trap in our study, suggesting some amount of non-independence among trap samples that could not be accounted for. However, there was only 1 instance where a telemetered fish responded to 2 simultaneously soaking traps located 132 m apart in our study, so the level of non-independence was unknown but likely negligible. Third, although 27 telemetered gray triggerfish responded to traps in our study, none were actually caught in traps. It is unclear if this indicates that tagged gray triggerfish experienced trap shyness after being caught and tagged previously, or that catchability was simply very low in our study, or both. Fortunately, in our study, the VPS positional data allowed us to quantify the behavior of gray triggerfish without the need for catching fish in traps. Fourth, while the time between detections was short (2–4 min) in our study, spatial positions were not continuous, so we assumed straight-line movements of gray triggerfish between these spatial positions. Last, it would

have been useful to deploy some unbaited traps to help disentangle the effects of olfaction, sound, and vision on gray triggerfish responses to baited traps.

It is challenging to convert catch rates or relative abundance from baited gears to absolute abundance in fish surveys. It is widely assumed that catch rates from baited gears are proportional to true abundance, yet any variable that influences fish feeding motivation, swimming behavior, or ability to detect, approach, and attack a bait will influence the catchability of fish and thus decouple catch rates and actual abundance (Engås & Løkkeborg 1994, Sigler 2000). Therefore, catch rates from baited gears may reflect more about the behavior of fish than their abundance (Stoner 2004). Given that stock assessments and ecological surveys depend on survey data that assume catch is proportional to abundance, more studies are clearly needed to test this critical assumption. There is necessity not only for studies such as the one presented here, but also for examinations of how fish behaviors may change with variability in water temperature, water clarity, light level, current velocity, and ambient prey density (Stoner 2004).

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