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ARTICLE

Fine-scale behavior of red snapper (*Lutjanus campechanus*) around bait: approach distances, bait plume dynamics, and effective fishing area

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Abstract: The behavior of fish around bait is poorly understood despite it being important for the fish catching process and estimating relative abundance. We used a fine-scale acoustic positioning system to quantify the movements of 26 red snapper (*Lutjanus campechanus*) around 120 bait deployments in 2019 at a natural reef site (~37-m deep) in North Carolina, USA. There were 39 instances of tagged red snapper approaching bait during four baiting days, some of which approached due to apparent sensory cues (28%), while most approached incidentally (72%). Tagged red snapper approached bait from initial distances of 1 to 1147 m (median = 27 m; mean = 86 m), and took 0–77 min (mean = 22 min) to approach. Fish were more likely to approach bait if they were located close to, and down-current of, the bait at deployment. Our estimated effective fishing area of 2290 m^2 (within which >50% of red snapper responded to bait) could be used along with video counts and other information to estimate densities of red snapper.

Résumé : Le comportement des poissons autour d'appâts demeure mal compris, malgré son importance pour le processus de capture et l'estimation de l'abondance relative de poissons. Nous utilisons un système de positionnement acoustique à échelle fine pour quantifier les déplacements de 26 vivaneaux rouges (*Lutjanus campechanus*) aux alentours de 120 déploiements d'appâts effectués en 2019 dans un site récifal naturel (~37 m de profondeur) en Caroline du Nord (États-Unis). Trente-neuf cas où des vivaneaux rouges se sont approchés d'appâts ont été recensés durant quatre jours d'appâtage, certaines de ces approches étant motivées par des signaux sensoriels apparents (28 %), alors que la plupart étaient le fruit du hasard (72 %). Les vivaneaux rouges marqués ont parcouru des distances initiales de 1 à 1147 m (valeur médiane = 27 m; moyenne = 86 m) et ont pris de 0 à 77 min (moyenne = 22 min) pour s'approcher d'appâts. Les poissons étaient plus susceptibles de s'approcher d'appâts s'ils se trouvaient à proximité ou en aval courant de l'appât au moment de son déploiement. La superficie de pêche effective estimée de 2290 m^2 (dans laquelle >50 % des vivaneaux rouges ont réagi aux appâts) pourrait être utilisée de concert avec des dénombrements vidéo et d'autres renseignements pour estimer la densité de vivaneaux rouges. [Traduit par la Rédaction]

Introduction

Many long-term scientific surveys of demersal, reef-associated fish species use catch data from baited gears or video counts from underwater cameras to index fish abundance over time (Kimura and Somerton 2006; Schobernd et al. 2014). These standardized fishery-independent surveys often form the backbone of stock assessment models and are valuable because they are not generally subject to changes in catchability (e.g., gear or technological improvements) over time like most fishery-dependent data sources (Harley et al. 2001; Maunder and Punt 2004). The main assumption of scientific surveys is that yearly changes in catch rates or video counts reflect corresponding changes in actual abundance. In general, these abundance changes are only estimable in a relative sense, and estimates of absolute abundance often remain unattainable due to difficulties in understanding how fish respond to sampling gear (but see Shertzer et al. 2020). To calculate absolute abundance from scientific surveys one must either census the population, which is often unrealistic, or estimate habitat-specific densities that can be extrapolated to abundance using a habitat map of a broader region. Thus, for surveys that rely on baited gear that attract fish, understanding fish approaches to bait may begin to bridge the gap between estimating relative and absolute abundance.

Stock assessments are improved when scientific surveys can provide annual estimates of absolute instead of relative abundance (Maunder and Piner 2015). Absolute abundance is challenging to estimate because bait is often used to maximize encounter rates of economically important predatory and scavenger species (Harvey et al. 2007), and bait attracts individuals from a potentially broad and usually unknown area (DeBose and Nevitt 2008). Despite the challenges, some approaches have been developed to provide estimates of the effective fishing area of baited gears (Miller 1975; Eggers et al. 1982; Miller and Hunte 1987). An alternative approach has been to model bait plume dynamics; this technique can be used to estimate abundance when combined with a thorough understanding of the sensory and movement biology of the study species (Sainte-Marie and Hargrave 1987; Priede et al. 1994). However, there are significant drawbacks of these approaches including, for example, having to know the spatial arrangement and densities of individuals across the seafloor, the sizes of fish

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that are available within the effective fished area, or the sensitivity of olfaction and exact swimming speeds towards bait for the species of interest.

Another approach to scale up relative abundance to absolute abundance is by quantifying the fine-scale movement behavior of fish around baited gears. Most related early behavioral work employed laboratory or mesocosm experiments (Zhou and Shirley 1997; Watson et al. 2009), but technological innovations now make such studies possible in natural settings. For instance, Løkkeborg and Fernö (1999) used a stationary acoustic positioning system to track Atlantic cod (*Gadus morhua*) around a string of baits in a fjord in Norway. More recently, fine-scale acoustic telemetry positioning systems have been used to quantify the behavior of gray triggerfish (*Balistes capriscus*; Bacheler et al. 2018) and European lobsters (*Homarus gammarus*; Lees et al. 2018) around bait in the open ocean. Theoretically, fish density can be estimated by using the spatial pattern of attraction to baited gears to define the sampled area combined with the catchability or sightability of responding individuals.

Here, we quantified the fine-scale behavior of a demersal reef fish, red snapper (*Lutjanus campechanus*), around bait at a natural reef site in the open ocean off North Carolina, USA. Red snapper are an economically important and intensively managed species along the southeast United States Atlantic coast (hereinafter, SEUS) and Gulf of Mexico (Cowan et al. 2011; SEDAR 2021). Movement rates of red snapper are relatively low and tend to be higher at night than during the day (Topping and Szedlmayer 2011*a*; Piraino and Szedlmayer 2014; Bacheler et al. 2021) and some individuals may move long distances (Patterson et al. 2001; Patterson 2007). Moreover, site fidelity and residence time of red snapper around artificial reefs are high (Topping and Szedlmayer 2011*b*; Williams-Grove and Szedlmayer 2016*a*). The most recent red snapper stock assessment in the SEUS used relative abundance data from baited traps and video as key inputs (SEDAR 2021), but management advice could be improved if annual absolute abundance estimates were available from these surveys. In this study, we used an acoustic positioning system to track the fine-scale movements of red snapper for four months, during which time we deployed bait to elicit behavioral responses and calculate area sampled.

Our objectives were four-fold. Our first objective was to quantify the total number of red snapper approaching bait using telemetry and quantify the likelihood that a fish was observed on video if it was known to approach bait (i.e., the "sightability" of red snapper). Our second objective was to determine the influence of initial distance, current direction, and depth of the fish on the probability that transmitter-tagged red snapper would approach bait. Our third objective was to use model predictions to develop a heat map showing the area of attraction (i.e., effective fishing area) of red snapper to bait. Our last objective was to estimate the proportion of fish finding bait using apparent sensory cues compared to fish finding bait through incidental movements and to evaluate the bait response of red snapper on days with and without bait. Elucidating the behavior of red snapper around bait in their natural environment improves our mechanistic understanding of the sampling process using baited gears and may eventually allow us to bridge the gap between estimating relative and absolute abundance.

Materials and methods

Study area

This study took place at the "Chicken Rock" area approximately 35 km east of Cape Lookout, North Carolina, USA (Fig. 1). The area is approximately 36.5–38.5 m deep, and the seafloor is composed of a mix of sand and low-relief (<1 m) hardbottom with which red snapper generally associate. The Chicken Rock area is fished by recreational and commercial fishers. The specific area was chosen for this study because (1) a multibeam sonar seafloor map was available for the site from the National Centers for Coastal Ocean Science (Fig. 2), (2) it has a relatively flat seafloor that lacks acoustic shadows or dead zones that would impact fish tracking, and (3) it is consistently utilized by red snapper.

Vemco positioning system

Fine-scale movements of red snapper were quantified using a Vemco positioning system (VPS). VPS uses coded acoustic transmitters and an array of moored underwater receivers to provide a sequence of high-resolution ($\sim$1 m) spatial positions for transmitter-tagged fish (Espinoza et al. 2011; Bacheler et al. 2018). Specifically, acoustic signals from transmitter-tagged fish must be detected by at least three receivers, which then allows for triangulation based on the precise time offsets between the transmitter and receivers. Given the importance of time synchronization among receivers, we used Vemco VR2AR receivers that included their own sync tags. Detection range of transmitters is a critical element of VPS studies, since receivers spread too far apart may not allow for at least three acoustic detections, while receivers spaced too closely result in a study area that is unnecessarily small (Espinoza et al. 2011). Detection range in our study was assumed to be 300–800 m based on previous studies in the region (Bacheler et al. 2015, 2018).

Receiver and reference tag deployment

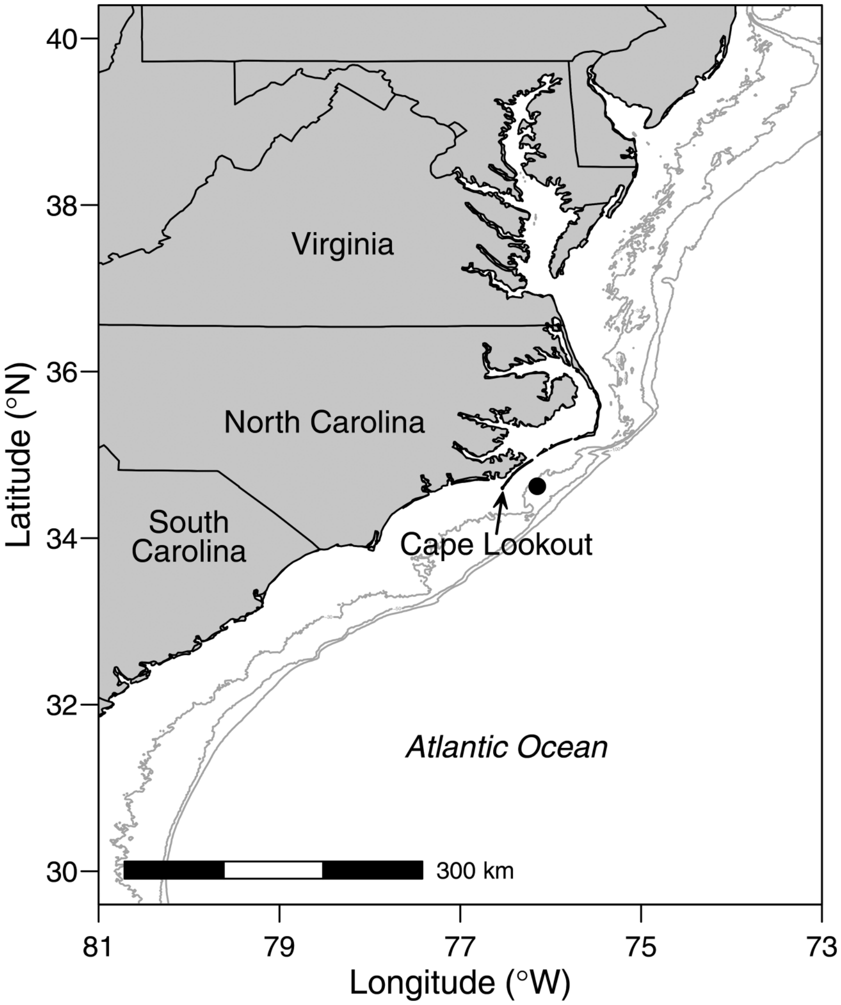
We deployed 20 Vemco VR2AR receivers at the Chicken Rock area on 17 April 2019. Receivers were deployed in a 3 × 7 grid, minus a single receiver in the northeast corner of the array. Receivers were spaced 200 m apart based on empirically estimated detection ranges (Bacheler et al. 2015, 2018). Thus, the size of the receiver array was approximately 400 m × 1200 m (0.48 km^2; Fig. 2). Each receiver was attached to 8-mm diameter Amsteel Blue dyneema line, which was connected to a 36-kg steel weight for mooring on one end and a 28-cm diameter plastic float with 8.8 kg of buoyancy on the other end. The mooring line length for each receiver was 1–3 m long based on the known depth at each receiver deployment location, so that after deployment all receivers were on a horizontal plane approximately 35 m deep. Receivers were retrieved at the end of the study using built-in acoustic releases.

A reference transmitter (Vemco V13T-1x) with a temperature sensor was deployed in the receiver array on 17 April 2019. There were two purposes for the deployment of the reference transmitter in the study area. First, it provided continuous water temperature information that was used to calculate sound speed velocity that was critical for the VPS analyses. Second, positions estimated for the reference transmitter were compared to its known location to estimate daily horizontal positional errors (m) of the VPS. The reference transmitter operated at 69 kHz, had a 550–650 s random ping interval, and was attached to a 3 m long, 8 mm diameter Amsteel Blue line with a mooring weight at one end and a float on the other.

Fish tagging

Red snapper were captured for tagging via hook-and-line sampling on 7 May 2019 on the F/V *Merry Marlin* and 13 August 2019 on the R/V *Ocellatus*. All fish were caught within the study array during daylight hours using circle or J-style hooks and reeled to the surface quickly. Once on board the vessel, fish in good condition (i.e., jaw-hooked) were dehooked and tagged externally. We attached transmitters externally to red snapper for three reasons. First, external transmitters are detected over longer distances than surgically implanted transmitters (Dance et al. 2016). Second, external transmitter attachment is generally faster than surgery (Jepsen et al. 2015). It was important for us to minimize the time in which fish were held at the surface, because post-release survival of fish caught from deep water is affected by the

Fig. 1. Location of the 2019 fine-scale telemetry study (black circle) where responses of tagged red snapper (*Lutjanus campechanus*) to bait were quantified. Gray lines indicate 30, 50, and 100 m isobaths. Map projection is WGS84 and coordinate system is latitude–longitude.



amount of time spent at the surface (Burns et al. 2002). Last, external attachment tends to be less invasive than surgical implantation of transmitters. Treatment of red snapper followed the recommendations described in National Research Council of the National Academies (2011).

The external tagging approach was developed in collaboration with Craig A. Harms (Director of the Marine Health Program and Doctor of Veterinary Medicine, North Carolina State University). We sought an approach that was quick to apply but would entirely detach from fish when it failed, allowing fish to fully recover. We attached transmitters to a 30-cm segment of 0.89-mm diameter stainless steel wire by first wrapping the wire around the non-transmitting end of the transmitter, gluing it with marine adhesive (3M 5200), and covering the attachment area with heat shrink tubing. The remaining ~15 cm of wire was straightened and the end was sharpened. We used Vemco V13P-1x transmitters that operated at 69 kHz, had a 130–230 s pulse interval, a 613-day battery life, and were 13 mm wide and 46 mm long (weight = 13 g in air). Each transmitter included a pressure sensor that measured the depth of each fish.

Fish were measured for total length (mm) and their head and eyes were covered in a wet towel to reduce their movement during handling. The sharpened transmitter wire was inserted through the dorsal musculature of the fish approximately 25 mm posterior to, and 25 mm ventral of, the insertion of the fish's first dorsal spine. As the transmitter was pushed tight against the fish's left side, the wire emerged from approximately the same location on the right side of the fish. An aluminum washer was threaded onto the emergent wire, followed by a #1 double steel crimp, which were held firmly against the right side of the fish. The steel crimp was then attached to the wire with a swager, and the remaining wire beyond the crimp was removed. The transmitter and aluminum washer had been previously labeled with numeric identification. The towel was removed and fish were attached to a weighted SeaQualizer fish release tool, which transported fish to a depth of approximately 31 m before they were released from the device. The total surface time for each fish was approximately 90 s.

Eliciting red snapper bait approaches

We evaluated tagged red snapper responses to bait during four daytime sampling periods that occurred on 15 May, 23 May, 24 August, and 30 August 2019. Baited traps were deployed throughout the study area on each sampling period. We use "bait" and "baited traps" interchangeably because these results may apply to other baited gears. Traps were 0.48 m × 0.60 m × 0.60 m in size, constructed out of plastic-coated square wire mesh (38 mm × 38 mm mesh size), and baited with 2 kg of *Brevoortia* spp. in a central bait well. During the first sampling period, traps were baited with whole *Brevoortia* spp. and trap

Fig. 2. Study area where red snapper (*Lutjanus campechanus*) behavioral responses to bait were quantified in 2019, showing locations of receivers, receivers with attached current probes (Receivers (current)), reference transmitter, tagging locations, and baited sampling periods. Background map shows bathymetry of the study area. Map projection is WGS84 and coordinate system is UTM.

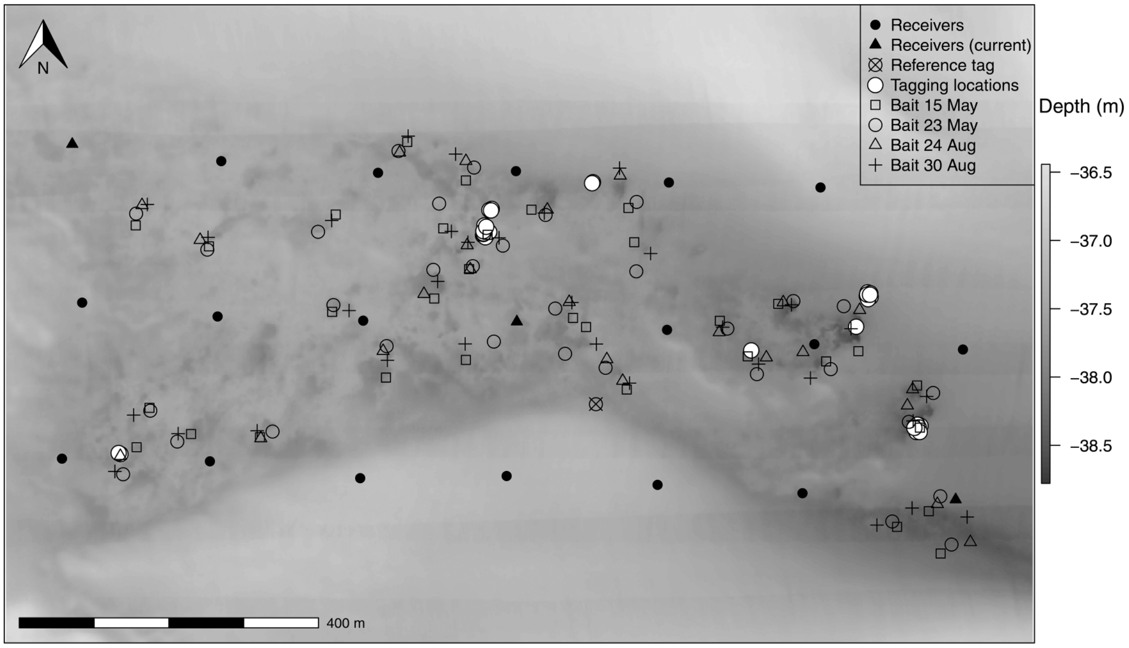


Fig. 3. Red snapper (*Lutjanus campechanus*) with an externally attached acoustic transmitter (#33) observed on video by a baited trap-mounted camera on 24 August 2019. [Colour online.]

funnels were closed to prevent the capture of fish, but few red snapper approaches were observed on these related videos. Therefore, in the final three sampling periods, bait fish were cut in half and trap funnels were left open in an attempt to maximize red snapper approaches by encouraging the formation of a bait plume. Eight traps were set in the study area simultaneously, and soak times were approximately 70–80 min per trap. Traps were weighted with steel rebar and had their own line to a surface float. We attached a GoPro Hero 4 outward-looking camera on top of each trap to visually determine if tagged red snapper approached bait (Fig. 3). Moreover, we attached one Vemco V13-1x transmitter (540–660 s pulse interval, 69 kHz frequency) to each trap to provide exact bait locations via the VPS acoustic receiver array.

Bait deployment locations were pre-selected throughout the study to target hardbottom identified from the multibeam sonar map. Traps were always deployed at least 100 m from each other in an attempt to maintain independence. Bottom water current magnitude and direction were determined for each minute of the study using TCM-1 current probes (Lowell Instruments) that were attached to three separate receiver buoys deployed for the duration of our study. Mean minute-by-minute values of current magnitude and direction were then associated with each baited trap based on its deployment and retrieval time.

Exploratory data analyses

We first explored the precision and accuracy of our VPS. We estimated horizontal positional error of the reference transmitter as the difference between its known location and its estimated VPS position each time it emitted a signal (approximately every 10 min). We used a boxplot displaying daily median, 25th, and 75th percentiles of horizontal positional error throughout the study. Boxplots were used to assess the accuracy of fish positions on days when sampling with bait occurred and whether changes were evident over the course of the study.

For illustrative purposes, we next provided six examples of red snapper movements around baited traps that showed a variety of bait response behaviors. The six examples were chosen to represent the diversity of observed behaviors of red snapper around bait.

We then determined the sightability of tagged red snapper that approached bait. We quantified the number of tagged red snapper approaching bait, defined as fish that had at least one detection within 20 m of bait, and compared it to the number of tagged red snapper observed on each trap's video. Distances less than 20 m resulted in many fewer approaches and therefore more limited sample sizes, and distances greater than 20 m increased uncertainty about whether fish actually approached bait. Thus, we chose a distance of 20 m (same as used by Bacheler et al. 2018) and note that model results here and below were found to be insensitive to the distance used. The intent of this approach was to understand how each fish's initial distance to the bait and initial position relative to current direction influenced their response to bait. We only included samples in this analysis if videos recorded for the entire length of the baited trap deployment, and any tagged red snapper observed on video were noted. In some videos, the fish number could be identified on the transmitter or aluminum washer. However, because fish numbers could not always be reliably observed on video, it was often impossible to determine if we were observing the same tagged fish repeatedly or if we were observing multiple tagged fish. Therefore, we limited our analysis to the presence or absence of tagged red snapper on video compared to the presence or absence of fish approaching bait from VPS. We also noted any situations where tagged red snapper were observed on video but lacked an official approach from VPS data.

Next, we developed a visual representation of all baited trap and tagged red snapper combinations by centering the bait in each plot and rotating the fish position along with its current direction such that the current direction vector pointed from north (0°) to south (180°). As an example, if the initial fish position was directly north of the bait by 100 m, and water current was moving eastward, the fish position was rotated clockwise 90° (now shown as "east" of the bait by 100 m) so that current was moving down (i.e., "north" to "south" on the map). Once fish were repositioned relative to current direction, we determined whether fish approached bait after its introduction.

One challenge in summarizing the approaches of red snapper to bait is that some fish may be approaching due to specific sensory cues like smell, while others may swim within 20 m of bait given their normal swimming behaviors. We attempted to distinguish fish approaching incidentally from those approaching based on sensory cues by examining the movements of tagged red snapper on days immediately preceding sampling with bait. Here, we determined whether tagged red snapper incidentally approached (at the same time of day) locations where bait was deployed the following day. "Day of" sampling and "day before" bait approach data were used to determine the relative importance of red snapper approaching locations incidentally compared to approaching due to specific sensory cues (see below). The number of responses from "day of" and "day before" were pooled to obtain overall estimates, but were also calculated for each sampling period to obtain ranges of these estimates. This analysis assumes that the number of tagged red snapper available was the same between "day before trapping" and "day of trapping", which was the case in our study.

Generalized additive mixed models

We used generalized additive mixed models (GAMMs) to understand the drivers of behavior of red snapper around bait. These models are analogous to generalized linear mixed models that can include random effects or account for various correlational structures in the data, but can also easily allow for nonlinear functions of continuous predictor variables (Wood 2006). Various model structures and error distributions can be used with GAMMs, and they are highly flexible, easy to interpret, and widely used (Hastie and Tibshirani 1990).

Our first GAMM determined the predictor variables that were related to tagged red snapper approaching bait. We used a binomial (logistic) model because response data were binary — tagged red snapper either approached bait (i.e., pinged within 20 m of a baited trap) or not. Five predictor variables were included in our binomial model based on our hypotheses and previous research. The first predictor variable was the initial distance between the bait and tagged fish at the moment when the bait was deployed (dist). We hypothesized that red snapper would display an inverse relationship between response rate and initial distance to bait because of sensory cues (Westerberg and Westerberg 2011; Bacheler et al. 2018). The second predictor variable was the initial fish position relative to the bait and current direction (cur); we hypothesized that red snapper would be more likely to approach bait if they were initially down-current from the baited trap due to increased detection of the bait plume (Løkkeborg et al. 1989; DeBose and Nevitt 2008). The third predictor variable was the initial depth of the fish (depth) at bait deployment. We hypothesized that fish initially farther off the bottom would be less likely to approach bait than fish closer to the bottom. The fourth predictor variable was sampling period (period), which was included as a random effect categorical variable to control for any differences in the responses of red snapper due to variation in environmental conditions or bait among the four sampling periods (e.g., water temperature, bottom current magnitude, water clarity, whole versus cut bait). The last predictor variable was the unique tagged fish (fish), which was also included as a random effect to control for any differences in intrinsic individual red snapper behavior.

The binomial GAMM was coded as follows:

$$\eta = \alpha + s_1(\mathrm{dist}) + s_2(\mathrm{cur}) + s_3(\mathrm{depth}) + f_1(\mathrm{period}) + f_2(\mathrm{fish}) \tag{1}$$

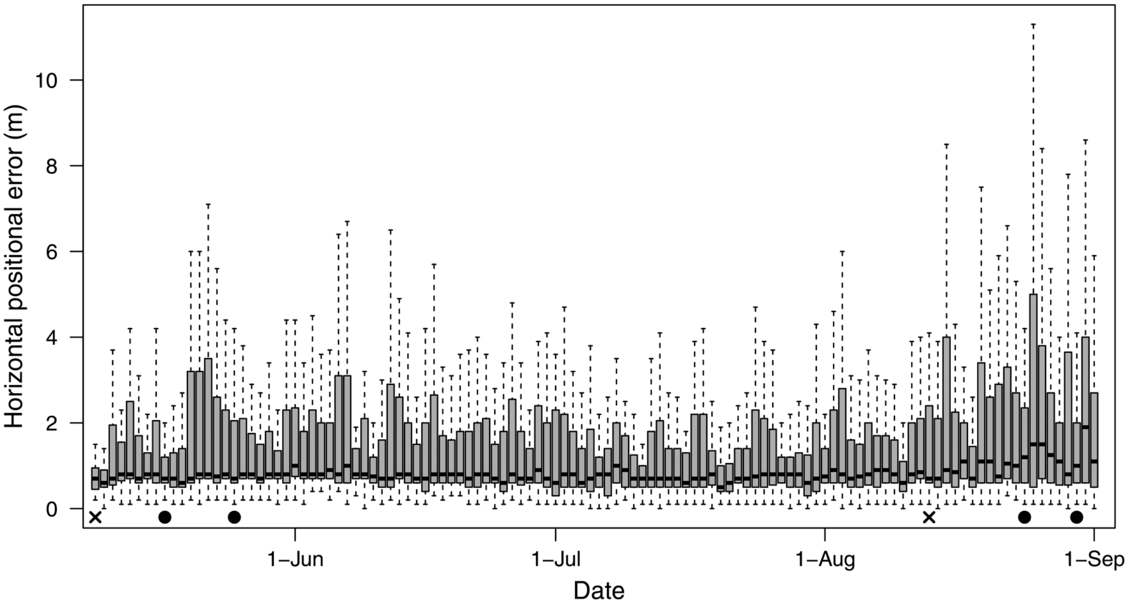
where η is the probability that a tagged red snapper approached bait, α is the model intercept, s_1–s_3 are cubic spline smoothers, and f_1–f_2 are categorical functions. GAMMs were coded and analyzed using the mgcv library (version 1.8-31; Wood 2011) in R (version 3.6.3; R Core Team 2020).

We used the Akaike information criterion (AIC; Burnham and Anderson 2002) to determine which predictor variables should be included in the final model. We compared the model including all five predictor variables (hereinafter, "Full model") to reduced models containing all combinations of fewer predictor variables. The best model was defined by having the lowest AIC score, which we provide as ΔAIC values (ΔAIC value of best model = 0.0).

We next developed a heat map to show the predicted response probability of tagged red snapper to bait that was based on GAMM predictor variable effects. We created a grid (x axis: –200 to 200 m; y axis: –200 to 200 m) around hypothetical bait located at the origin (0, 0). For each 1-m cell of the grid, we predicted the response probability of red snapper using our GAMM based the predictor variables of the model, and assuming the current was moving down (180°). We then displayed the response probability surface of tagged red snapper around bait as a heat map, which is analogous to the effective fishing area for a baited video system.

Last, we developed an additional, second GAMM that was coded exactly like eq. 1 except it evaluated a "day" effect by including red snapper response data from "day before" and "day of" sampling, as described above. If the day variable was included in the best model identified by ΔAIC, it would suggest that red snapper

Fig. 4. Horizontal positional error (m) of the reference transmitter during the telemetry study at the Chicken Rock area in Raleigh Bay, North Carolina, USA, in 2019. Horizontal positional error was estimated as the distance between the known location of the reference transmitter and its various estimated positions each day over the course of the study. The horizontal black lines are daily medians, the gray bars indicate daily 25th and 75th percentiles, whiskers are 1.5 times the interquartile range, the "×" symbol along the *x* axis refers to days when fish were tagged, and filled circles indicate sampling periods with baited traps.



were more likely to respond to bait itself than to incidentally respond to the same areas lacking bait 24 hours earlier; in other words, inclusion of the day variable evaluated potential bait responses of red snapper. We followed this GAMM with a comparison of the minimum distances between each trapping location and tagged red snapper on the "day of" trapping compared to the "day before" trapping when the same baited trap locations were used exactly 24 h preceding each recapture effort (but with no baited traps deployed). We used a Welch's two-sample *t* test to test for differences in means between these two groups; this test was used because it is reliable when the samples have unequal sample sizes and variances.

Results

VPS positional error

Daily median positional error rates of the reference transmitter ranged from 0.5 to 1.9 m over the course of the study, with most daily medians around 1.0 m (Fig. 4). On the four bait sampling days, daily median positional error rates ranged from 0.7 to 1.5 m, suggesting high spatial accuracy of tagged red snapper on all bait sampling days.

Field tagging

A total of 42 red snapper were tagged externally with transmitters in this study: 23 fish on 7 May 2019 and 19 fish on 13 August 2019 (Table 1). Fish ranged in size from 390 to 860 mm total length (mean = 698 mm), with estimated weights of 0.9 to 9.8 kg (mean = 5.6 kg). The tag weight to red snapper body weight ratio ranged from 0.1% to 1.4% (mean = 0.3%). After censoring positions from fish that lost tags or died (i.e., transmitters stopped moving), there were a total of 218 105 detections of tagged red snapper in the study area from 7 May to 1 September 2019, ranging from 0 to 26 060 detections per fish (mean = 5592 detections per fish; Table 1).

Sampling with bait

Thirty-two baited traps were deployed during each of the four sampling periods except during the third sampling period, when 24 baited traps were deployed (Table 2). Thus, a total of 120 baited traps were deployed in this study to examine behavioral responses of tagged red snapper. The minimum distance between simultaneously deployed baited traps across all sampling periods was 107 m (mean = 488 m). There were 11–16 tagged red snapper alive and in the study area during each of the four sampling periods, for a total of 26 unique individuals available across all sampling periods (Table 2).

Red snapper behavior around bait

Many (*N* = 15) tagged red snapper approached bait at least one time in our study. Most (73%) of these fish approached multiple baited traps throughout the study. Fish #33 had the most approaches to bait (*N* = 8). Of the 120 baited traps deployed in the study, 24% (*N* = 29) had at least one tagged red snapper approach. For baited traps that had approaching red snapper, most (69%; *N* = 20) attracted only one red snapper, 28% (*N* = 8) attracted two red snapper, and 3% (*N* = 1) attracted three red snapper.

Red snapper appeared to display behavioral responses to bait in some instances but not others (Fig. 5). In these examples, the baited trap was placed centrally in each plot, the bathymetry map is provided as background, arrows show the current direction and magnitude at the beginning and end of the baited trap soak, and locations of tagged red snapper during the baited trap soak were shown as filled circles, where colours were coded from white (bait deployment) to black (bait retrieval) and sizes of circles were scaled to depth of the fish. A greater proportion of tagged red snapper responded to baited traps in sampling periods 3 (11 of 16 fish; 69%) and 4 (8 of 12 fish; 67%) compared to periods 1 (5 of 11 fish; 45%) or 2 (4 of 12 fish; 33%). Generally, it appeared as though fish initially closer to, and down-current of, baited traps were more likely to approach than fish further away and up-current, but there were examples of tagged red snapper initially close to baited traps or down-current that did not approach (Fig. 5).

There were 109 videos that recorded the full trap soak and were analyzed for tagged red snapper. A total of 25 of these baited videos had at least one tagged red snapper approach based on VPS, and

Table 1. Information for transmitter-tagged red snapper (*Lutjanus campechanus*) at the Chicken Rock area in Raleigh Bay, North Carolina, in 2019.

No.	ID	Date of tagging	TL (mm)	BW (kg)	Tag:BW (%)	No. of positional observations	Fate on 1 Sept. 2019
1	4290	7 May 2019	520	2.18	0.6	0	Tag loss
2	4291	7 May 2019	700	5.30	0.2	17 208	Alive in study area
3	4292	7 May 2019	720	5.77	0.2	20 785	Harvest
4	4293	7 May 2019	685	4.97	0.3	604	Tag loss
5	4294	7 May 2019	665	4.55	0.3	15 201	Tag loss
6	4295	7 May 2019	785	7.47	0.2	799	Tag loss
7	4296	7 May 2019	635	3.96	0.3	2 755	Emigration
8	4297	7 May 2019	680	4.86	0.3	16 635	Tag loss
9	4298	7 May 2019	720	5.77	0.2	3 664	Alive in study area
10	4299	7 May 2019	750	6.52	0.2	4 698	Tag loss
11	4300	7 May 2019	740	6.26	0.2	1 290	Tag loss
12	4301	7 May 2019	860	9.81	0.1	22 384	Tag loss
13	4302	7 May 2019	500	1.94	0.7	6	Emigration
14	4303	7 May 2019	705	5.41	0.2	265	Emigration
15	4304	7 May 2019	710	5.53	0.2	3 005	Tag loss
16	4305	7 May 2019	760	6.78	0.2	26 060	Alive in study area
17	4306	7 May 2019	765	6.91	0.2	20 316	Tag loss
18	4307	7 May 2019	740	6.26	0.2	5 208	Tag loss
19	4308	7 May 2019	720	5.77	0.2	13 505	Tag loss
20	4309	7 May 2019	795	7.75	0.2	12 427	Tag loss
21	5228	7 May 2019	390	0.92	1.4	12	Emigration
22	5229	7 May 2019	690	5.08	0.3	6 755	Tag loss
23	5230	7 May 2019	730	6.01	0.2	1 316	Tag loss
24	5231	13 Aug. 2019	530	2.31	0.6	0	Emigration
25	7269	13 Aug. 2019	735	6.13	0.2	2 481	Alive in study area
26	7270	13 Aug. 2019	750	6.52	0.2	303	Alive in study area
27	7271	13 Aug. 2019	760	6.78	0.2	2 063	Alive in study area
28	7272	13 Aug. 2019	715	5.65	0.2	27	Tag loss
29	7273	13 Aug. 2019	735	6.13	0.2	12 501	Tag loss
30	7274	13 Aug. 2019	750	6.52	0.2	23	Predation
31	7275	13 Aug. 2019	685	4.97	0.3	2 294	Tag loss
32	7276	13 Aug. 2019	425	1.19	1.1	1 743	Tag loss
33	7277	13 Aug. 2019	790	7.61	0.2	3 653	Tag loss
34	7278	13 Aug. 2019	520	2.18	0.6	1	Predation
35	7279	13 Aug. 2019	695	5.19	0.3	3	Predation
36	7280	13 Aug. 2019	685	4.97	0.3	0	Predation
37	7281	13 Aug. 2019	750	6.52	0.2	3 518	Alive in study area
38	7282	13 Aug. 2019	720	5.77	0.2	386	Alive in study area
39	7283	13 Aug. 2019	775	7.19	0.2	2 397	Alive in study area
40	7284	13 Aug. 2019	845	9.31	0.1	86	Alive in study area
41	7285	13 Aug. 2019	745	6.39	0.2	1 677	Alive in study area
42	7286	13 Aug. 2019	755	6.65	0.2	51	Alive in study area

Note: Individual body weight (BW) was estimated using a total length (TL) to weight conversion, and "Tag:BW" is the ratio of transmitter weight in air to estimated fish BW in air × 100.

Table 2. Information about each of the four sampling periods used to elicit response behaviors of tagged red snapper (*Lutjanus campechanus*) to bait.

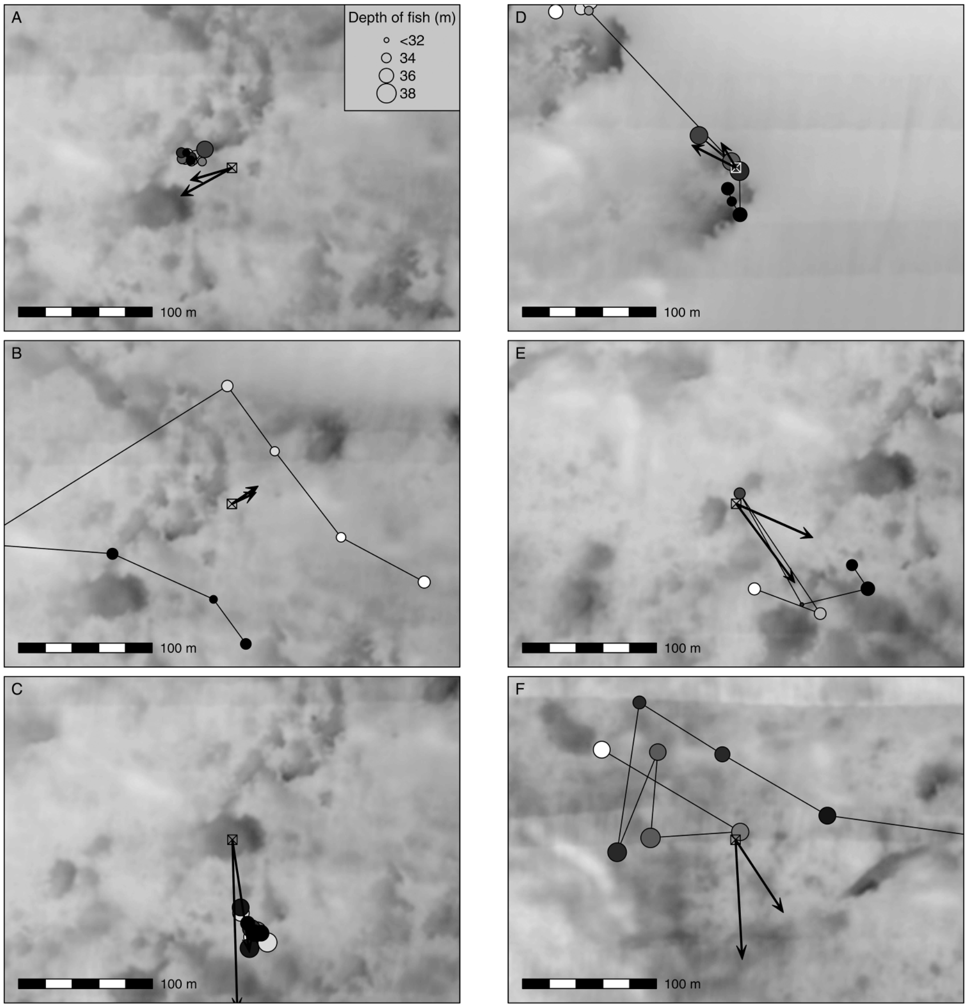
Date	Period	Baited traps	No. of RS in array	No. of RS responses
15 May 2019	1	32	11	5
23 May 2019	2	32	12	4
24 Aug. 2019	3	24	16	18
30 Aug. 2019	4	32	12	12
Overall	1, 2, 3, 4	120	26 unique	39

Note: "No. of RS in array" is the number of tagged red snapper that were alive in the array at some point during each sampling period, and "No. of RS responses" is the number of responses of tagged red snapper to baited traps, where a "response" is defined as a fish having at least one acoustic detection within 20 m of a baited trap.

tagged red snapper were observed in 18 of 25 associated videos (72%). Identifying fish numbers were visible in 13 of these 18 videos (72%). There were three instances where tagged red snapper were observed on video but were not detected within 20 m of the baited trap by the VPS array. All three instances involved tagged fish that were detected multiple times just beyond 20 m from bait.

There were 39 instances of tagged red snapper approaching baited traps (Table 2; Fig. 6). The initial distance between tagged red snapper and baited traps ranged from 1–1147 m (median = 27 m, mean = 86 m), and fish took 0–77 min to approach bait (mean = 22 min). The minimum distance between the 39 approaching red snapper and baited traps ranged from 1–19 m (mean = 8 m). A total of 28 approaches occurred by red snapper within 20 m of baited trap locations on the day preceding baited trap sampling and could be considered incidental in their approach (Fig. 6). Half of these approaching fish were within 20 m of trap locations at deployment, and the other half

Fig. 5. Movements of tagged red snapper (*Lutjanus campechanus*) around baited traps. In each plot, baited traps are located in the middle of the plot (white or black box with ×), and arrows indicate bottom current compass heading (°) and magnitude (shorter arrows = lower current magnitude; longer arrows = higher current magnitude) at the beginning and end of the baited trap soak. Positions from individual fish are displayed as filled circles, where shading of the filled circles represent the spectrum of baited trap soak time (white = trap just deployed; black = end of trap deployment) and size of the points is the depth of the fish. Left column plots show examples of tagged red snapper that did not approach bait, while right column plots show examples of fish approaching bait. Sampling period (SP) and fish tag numbers in each panel are: (A) SP 1, tag 15; (B) SP 2, tag 6; (C) SP 3, tag 16; (D) SP 2, fish 2; (E) SP 4, tag 31; (F) SP 3, tag 29. Map projection is WGS84 and coordinate system is UTM.



approached from distances up to 128 m over the course of up to 20 min. Given that 28 approaches occurred at locations one day previous to actual baited trap sampling and 39 approaches occurred to baited traps, it appears that 72% (range = 56%–100%) of red snapper approached incidentally to bait and 28% (range = 0%–44%) approached due to sensory cues from the baited trap (Fig. 6).

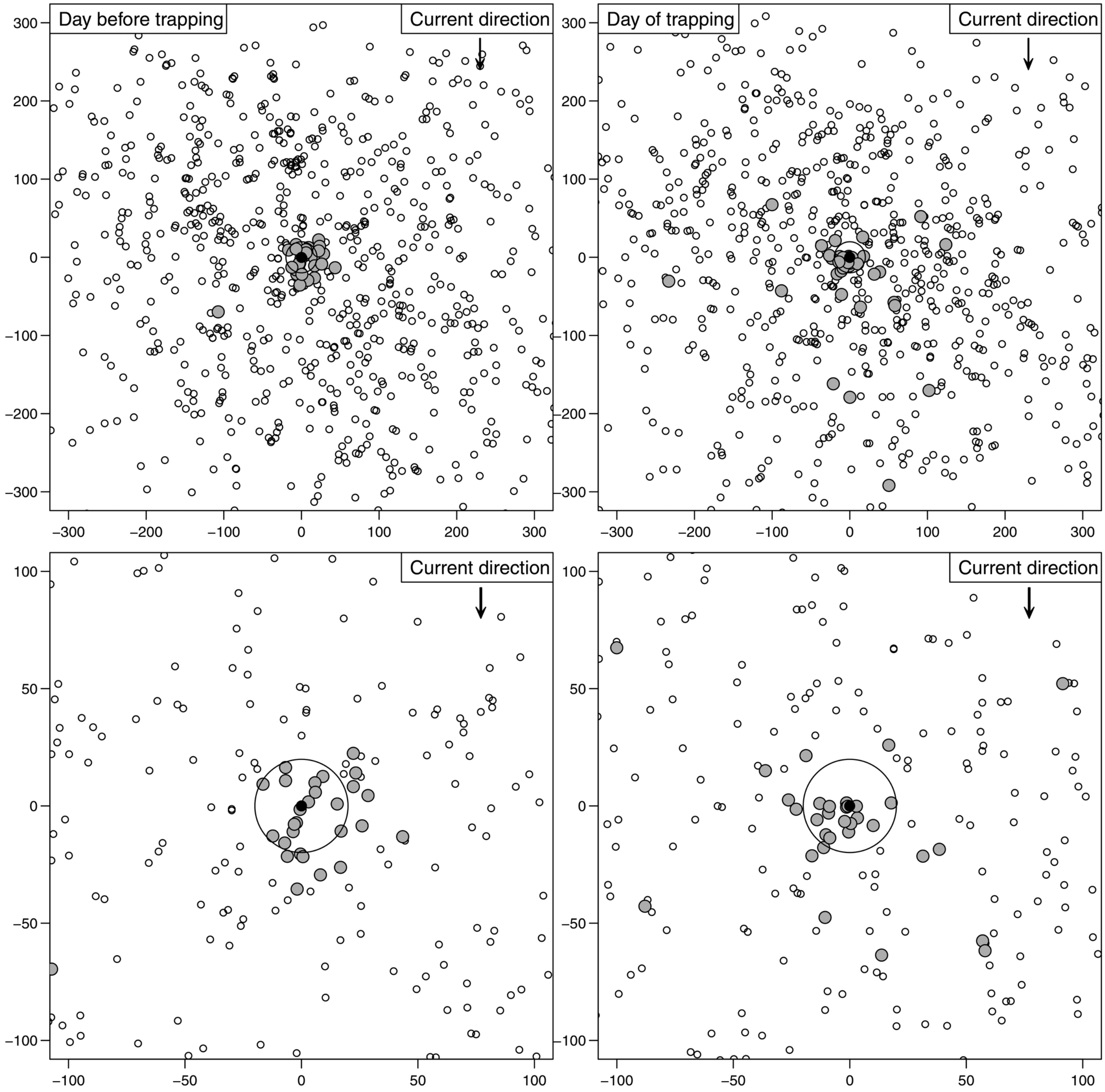
Generalized additive mixed models

Our first GAMM evaluated the influence of five predictor variables on whether or not tagged red snapper approached baited traps. The best model based on ΔAIC included dist, cur, and fish and explained 47.8% of the model deviance (Table 3). The next best model had a ΔAIC of 2.8 and included dist, cur, fish, and period, while other models had ΔAIC values > 16. As expected, there was an inverse relationship between the probability of a tagged red snapper responding to a baited trap (our response variable) and dist out to approximately 50 m, beyond which the probability of fish responding was less than 0.10 (Fig. 7). The relationship between the probability of red snapper responding to bait and cur was consistent with our hypothesis, being higher for fish down-current of bait and less likely up-current (Fig. 7).

The heat plot of predicted response probabilities of tagged red snapper displayed a pattern that reflected the GAMM effects of dist and cur (Fig. 8). Tagged red snapper were most likely to approach bait if they were initially close to it, but were also more likely to approach if they were down-current from bait compared to up-current (Fig. 8). The effective fishing area within which at least 50% of tagged red snapper responded to bait was 2290 m^2.

The day predictor variable was included in our second GAMM based on ΔAIC. The best GAMM here included dist, cur, fish, and day, explained 59.1% of the model deviance, and had a ΔAIC value of over 30 points lower than the second best model (Table 4). The probability of tagged red snapper response was higher during days when baited traps were deployed (day of) compared to preceding days when no baited traps were deployed (day before; Fig. 9). Specifically, tagged red snapper with an initial distance of 50 m down current from sampling locations had a 13% response rate on the "day of" compared to 6% on the "day before" (Fig. 9). Moreover,

Fig. 6. Bait responses of tagged red snapper (*Lutjanus campechanus*) in relation to their initial distance from baited traps and current direction combined over all four sampling periods in 2019 ("Day of trapping"; right column), and "responses" of tagged fish to the same baited trap locations (but with no traps deployed) exactly 24 h preceding each recapture effort ("Day before trapping"; left column). All plots are scaled so that the baited trap location is shown in the center of the plot (filled black circle) and the current direction (heading; °) is straight down. Open circles indicate the initial position for fish that did not at any point approach within 20 m of baited traps (or the same trap locations the previous day), and each filled gray circles indicate initial positions for fish that at some point approached within 20 m of baited traps or trap locations the previous day. Top row shows broad view, and bottom row shows zoomed-in views of the same data. Map projection is WGS84 and coordinate system is UTM.



minimum distances between baited traps and tagged red snapper were shorter on the "day of" compared to the "day before" ($t = 2.39$; $p = 0.01$; Fig. 10).

Discussion

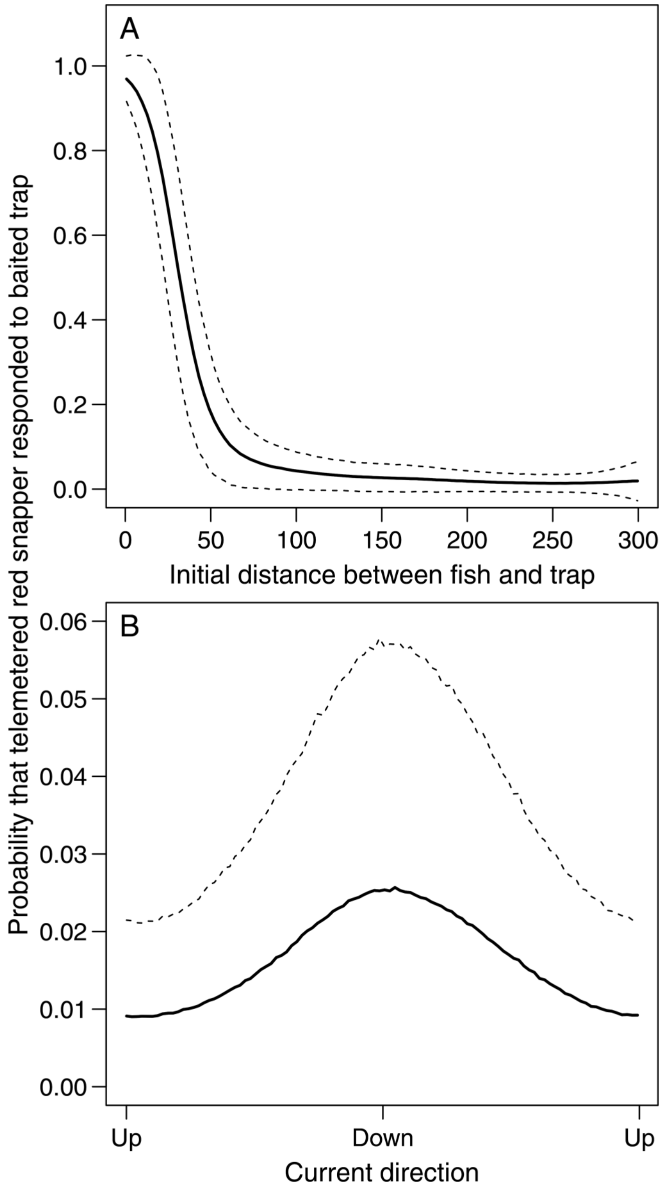
Quantifying fish behavior around baited sampling gears improves our mechanistic understanding of the sampling process and helps to bridge the gap between estimating relative and absolute site abundance. We quantified movement patterns of tagged red snapper around 120 baited traps, and individual positions from fish were highly precise in space and time. The two main drivers of red snapper bait responses were initial distance and current direction relative to the bait, which were important across all sampling periods. We improved on the work of Bacheler et al. (2018) by attaching transmitters to traps to acquire more precise

Table 3. Model selection for the binomial generalized additive mixed model relating whether or not tagged red snapper (*Lutjanus campechanus*) approached (i.e., were detected within 20 m of) baited fish traps to five predictor variables: initial distance between tagged fish and the baited fish trap (dist), the initial location of the tagged fish based on the relative bait location and current direction (cur), the initial depth of the tagged fish (depth), the sampling period (period, included as a random effect), and unique fish (fish, included as a random effect).

Model	DE	ΔAIC	*s*(dist)	*s*(cur)	*s*(depth)	*f*(period)	*f*(fish)
Full – period – depth	47.8	0.0	3.9^{***}	1.5^{*}	Ex	Ex	25^{***}
Full – depth	46.9	2.8	3.9^{***}	1.5^{*}	Ex	3	25^{***}
Full – period	48.7	16.4	4.0^{***}	1.5^{*}	1	Ex	25^{***}
Full	48.2	21.5	4.0^{***}	1.5^{*}	1	3	25^{***}

Note: Degrees of freedom are shown for the factor (*f*) terms, and estimated degrees of freedom are shown for smoothed terms (*s*). DE is the deviance explained by the model, ΔAIC 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 Full is the model that includes all three predictor variables. Only the four best candidate models are shown. Asterisks denote significance at the following alpha levels: *, $\alpha = 0.05$; ***, $\alpha = 0.001$.

Fig. 7. Probability that tagged red snapper (*Lutjanus campechanus*) approached baited traps related to two predictor variables using binomial generalized additive mixed models: (A) the initial distance between tagged fish and the bait and (B) the fish position relative to the bait and current direction. Black lines are means and dashed lines are 95% confidence intervals.



bait locations and deploying current probes that collected continuous water current information. The end result was a heat map that showed the response probabilities of red snapper around bait, which we used to infer the area over which red snapper approach bait (i.e., effective fishing area).

Our heat map of response probabilities of red snapper around bait can be used to make inferences about the cues causing red snapper to approach bait. We showed that most red snapper do not use cues but instead find bait incidentally, generally when they were located relatively close (<50 m) to baited traps initially. Red snapper were much more likely to approach bait incidentally (72%) compared to another demersal reef-associated fish species, gray triggerfish (i.e., 33%; Bacheler et al. 2018), suggesting that red snapper movement rates are naturally higher than gray triggerfish or that red snapper are less motivated to approach bait based on sensory cues. However, there was evidence of dependence on olfaction because red snapper were more likely to approach bait from down-current directions, consistent with scavenging organisms that approach bait plumes (Smith 1985; Løkkeborg et al. 1989; Zhou and Shirley 1997; Stiansen et al. 2010). It also appears as though red snapper approached baited traps from other current directions when initial distances were short (<50 m), suggesting red snapper also use vision or auditory cues to find nearby baited traps in lieu of a bait plume.

The general behavior of red snapper around bait was not unexpected given our knowledge of other marine scavenger and predator species. Many fish species rely upon olfaction, or olfaction combined with other cues, to find bait or home to their natal streams (Dittman and Quinn 1996; Mitamura et al. 2005; Plenderleith et al. 2005; DeBose and Nevitt 2008). Median response distances of red snapper to bait (26 m) were similar to the response distances of most lobster, crab, and fish species examined in other studies (Sainte-Marie and Hargrave 1987; Jernakoff and Phillips 1988; Skajaa et al. 1998; Smith and Tremblay 2003; Watson et al. 2009; Bacheler et al. 2018; Lees et al. 2018). The exception is that a few tagged red snapper approached baited traps from substantially greater distances (one fish over 1 km away) than has been noted for most other species except sharks (Gardiner et al. 2012), which could be the result of other stimuli besides olfaction (e.g., sound).

The heat map of response probabilities of red snapper and their catchability or sightability may be used to make inferences about actual site abundance of red snapper. For example, red snapper counts from video gear first need to be expanded based on the estimated sightability of individuals, because not all fish approaching bait were observed on video (or captured by baited gears). It is also important to determine the proportion of fish detected within 20 m of baited traps but that do not actually find the trap, which we were unable to determine in our study. Next, the total area over which those fish were distributed before bait deployment can be determined using the heat map approach we

Fig. 8. Heat map of the predicted response probabilities of red snapper (*Lutjanus campechanus*) around bait based on generalized additive mixed model results for the effects of initial distance and current direction. In this plot, bait is marked with a white "×" symbol, black shade is higher response probability, light gray shade is lower response probability, current direction in this example is straight down, and *x* and *y* axes are measured in metres. The three black contour lines indicate 5% (large outer contour), 25% (middle), and 50% (inner) response probabilities, and the white area outside the outer 5% contour line has a 0%–4% response probability. A bait response was defined as observing an acoustic detection from a tagged red snapper within 20 m of baited traps.

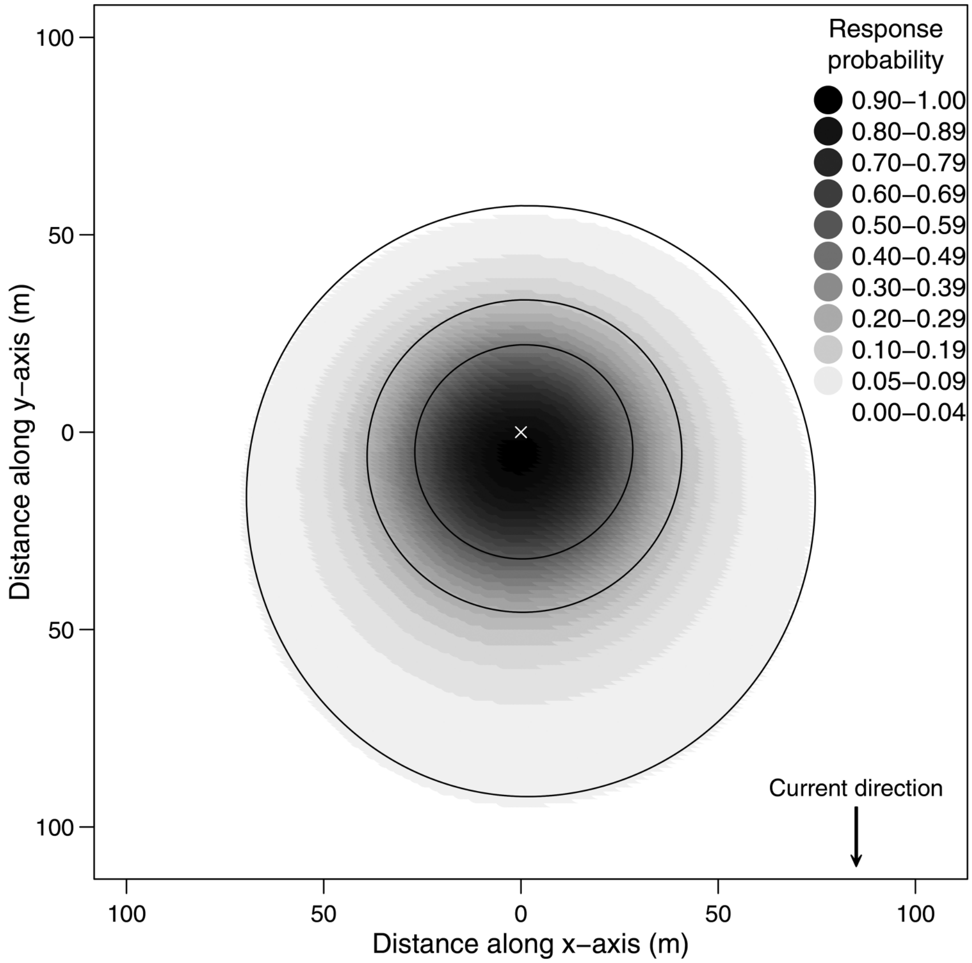


Table 4. Model selection for binomial generalized additive mixed model relating whether or not tagged red snapper (*Lutjanus campechanus*) approached (i.e., detected within 20 m of) baited fish traps to six predictor variables: initial distance between tagged fish and the baited fish trap (dist), the initial location of the tagged fish based on the relative bait location and current direction (cur), the initial depth of the tagged fish (depth), the sampling period (period, included as a random effect), the unique fish (fish, included as a random effect), and the day of sampling ("day before" versus "day of" sampling).

Model	DE	ΔAIC	*s*(dist)	*s*(cur)	*s*(depth)	*f*(period)	*f*(fish)	*f*(day)
Full – period – depth	59.1	0.0	5.3***	1.8*	Ex	Ex	25***	1*
Full – depth	58.9	30.3	5.3***	1.8*	Ex	3	25***	1*
Full – period	59.8	77.6	5.4***	1.9*	1.0	Ex	25***	1*
Full	59.4	85.0	5.3***	1.8*	1.0	3	25***	1*

Note: Degrees of freedom are shown for the factor (*f*) terms, and estimated degrees of freedom are shown for smoothed terms (*s*). DE is the deviance explained by the model, ΔAIC 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 Full is the model that includes all three predictor variables. Only the four best candidate models are shown. Asterisks denote significance at the following alpha levels: *, $\alpha = 0.05$; ***, $\alpha = 0.001$.

developed or using other approaches such as kernel density estimation (e.g., Williams-Grove and Szedlmayer 2017). Density of red snapper at that location can be calculated as the total number of red snapper estimated from video after accounting for sightability divided by the area over which red snapper approached. If habitat maps exist, density can be estimated across each habitat type and summed by the amount of each habitat type in the total area to estimate total red snapper abundance. The critical assumption of this approach is either that the response probabilities of red snapper are invariant across different environmental conditions like variable water clarity or current speeds (which is unlikely; Bacheler et al. 2014; Bacheler and Shertzer 2020), or that the variability can be accounted for by sampling across the influential factors. We did not evaluate how variation in habitat

Fig. 9. Probability of tagged red snapper (*Lutjanus campechanus*) responding to bait at an initial distance of 50 m down current of the sampling location on the "day of" or "day before" sampling using generalized additive mixed models. "Day of" sampling was the four days of sampling with baited traps, while "day before" sampling used the same baited trap locations exactly 24 h preceding each the four sampling days but did not include any baited trap deployments.

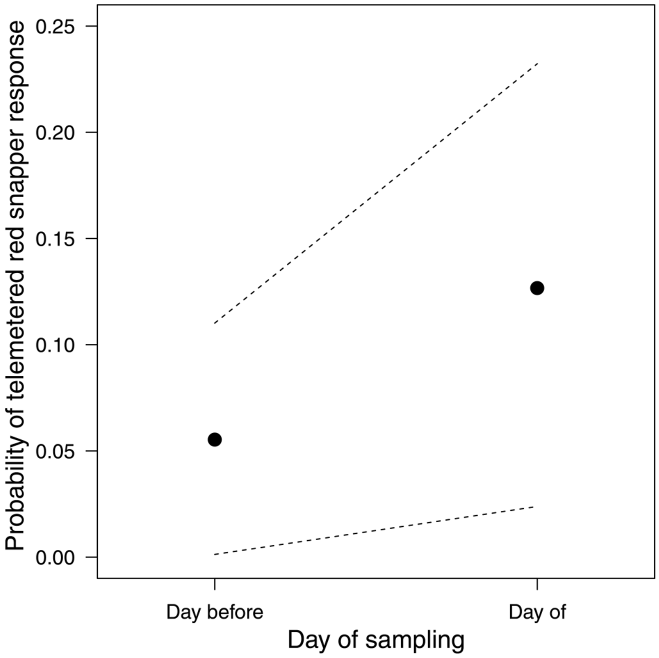
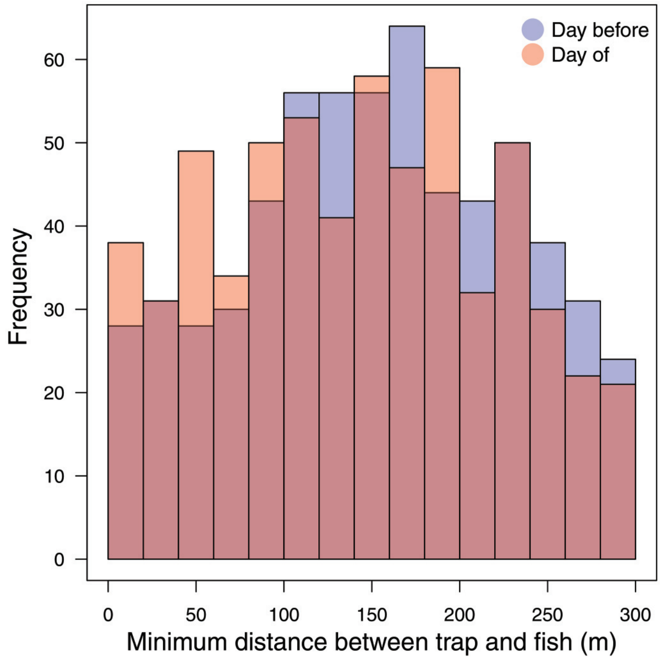


Fig. 10. Histogram of the minimum distance between each trapping location and tagged red snapper (*Lutjanus campechanus*) on the "day of" trapping (red bars) compared to the "day before" trapping (blue bars) when the same baited trap locations were used exactly 24 h preceding each recapture effort (but with no baited traps deployed). [Colour online.]



type and likely important environmental conditions (e.g., water clarity, current speed) influenced red snapper response probabilities, despite their importance for fish behavior (Stoner 2004); future research could examine this topic for red snapper.

To estimate site abundance using baited video, the proportion of fish approaching bait that are also observed on video (i.e., sightability) must also be estimated. In our study, sightability of red snapper was approximately 72%, meaning that 28% of fish ($N = 7$) that approached baited traps were not observed on the corresponding videos. Our sightability estimate is within the range of estimated video detection probabilities for four other reef-associated fish species in the SEUS (i.e., 57%–88%; Bacheler et al. 2014). In the current study, there were three ways fish may have been missed on video. First, video cameras were only looking a single direction away from baited traps, so any red snapper on the other side of the baited trap would not have been observed. Second, fish may have been far enough off the bottom to be located near the bait based on VPS data but not visible on video closer to the bottom; analysis of depth data in our study suggests this was unlikely because red snapper were nearly always near the bottom when horizontally close to traps. Third, it is possible that red snapper entered a halo of 20 m around bait but did not actually approach any closer to the baited trap, so it may not have been possible to be observed. During preliminary analyses, we used an alternative halo distance of 10 m to classify fish as having approached baited traps, which would mitigate this third issue. But the two downsides of this 10 m approach were that the number of red snapper responses declined from 39 to 27, resulting in convergence issues with GAMMs, and there were likely many fish that actually found baited traps but did not have VPS positions within 10 m. However, for GAMMs that did converge, results were very similar to results using a 20-m distance. We believe a 20 m distance was a reasonable tradeoff to deal with these various issues.

We deployed baited traps on four different days throughout the late spring and summer of 2019, but sampling period was removed from final GAMMs based on AIC. The sampling period variable used in the analyses can be thought of as a surrogate for other variables such as current magnitude, water clarity, bottom temperature, environmental conditions, or bait and trap differences that could affect red snapper responses to bait. The exclusion of sampling period from the final GAMMs suggests that either red snapper bait responses are relatively unaffected by environmental variability, environmental variability among sampling periods was minimal, or the power to test for a sampling period effect was low.

We encourage more widespread use of VPS and other techniques to understand the fine-scale behavior of fish around various types of sampling gears to better estimate the effective fishing area and capture efficiency of those gears. In addition to bait responses, fine-scale behavioral information gathered from these systems can be used to quantify movement patterns (Piraino and Szedlmayer 2014; Skerritt et al. 2015; Herbig and Szedlmayer 2016), home ranges (Piraino and Szedlmayer 2014; Alós et al. 2016), responses to storms (Bacheler et al. 2019), habitat use (Freitas et al. 2016; Stieglitz and Dujon 2017), and mortality rates (Williams-Grove and Szedlmayer 2016*b*; Bohaboy et al. 2020; Runde et al. 2021) of a variety of fishes and invertebrates. For instance, it would be useful to understand how fish behaviorally respond to divers, underwater vehicles, or hook-and-line sampling (Willis et al. 2000; Bozec et al. 2011; Lees et al. 2018). VPS studies are most useful when transmitter detection ranges are high and quantified well, fish survive the tagging process and retain their tags, and site fidelity of the species of interest is high (Espinoza et al. 2011).

There were some shortcomings of this study. First, we made inferences about red snapper bait responses from periodic location data, where positions were available every 2–4 min. Yet it is well known that movement distances can be underestimated using intermittent location data (Rowcliffe et al. 2012). In our study, there were three instances where tagged red snapper were detected on videos but did not appear to approach baited traps based on VPS, and the most likely explanation is that fish swam from outside the 20-m halo to the bait and back between VPS acoustic detections. We could reduce the probability that fish approach bait undetected by VPS by increasing the halo size (e.g., 30 m), but that would increase the chance that fish are subsequently scored as approaching based on VPS but do not actually approach the bait, as described above. Thus, we believe a 20-m halo size provided the best tradeoff between these two competing issues. Using transmitters that ping more frequently could also be useful.

Second, the sampling period variable evaluated the effects of environmental conditions on red snapper bait response rate, but ideally we would have evaluated individual environmental variables like water temperature, current magnitude, or water clarity separately. It is likely red snapper bait responses vary across their geographic range due to variability in these or other environmental conditions. Third, we examined alternative response variables for our GAMMs (e.g., minimum distance between fish and bait, initial distance divided by the minimum distance) so a subjective cutoff value like 20 m did not have to be used. Model fits for those response variables were poor (i.e., data were highly non-normal and left skewed), which prevented their use, but the covariate relationships were similar to our models using the 20 m halo distance. Fourth, a majority of tagged red snapper approached more than one baited trap in our study, suggesting some amount of nonindependence among baited trap samples. However, there was only one instance where a tagged red snapper approached two simultaneously soaking baited traps, suggesting the level of nonindependence in this study was negligible. Future studies could deploy fewer traps at any given time to increase spacing among traps, but the downside is that sample sizes would decline accordingly.

There have been several previous attempts at estimating absolute abundance from surveys using baited gears (e.g., Miller 1975; Eggers et al. 1982; Miller and Hunte 1987; Sainte-Marie and Hargrave 1987; Priede et al. 1994), but their utility has been limited due to strong assumptions or difficulties with implementation (but see Shertzer et al. 2020). We address this issue using a different approach, whereby the fine-scale movement behaviors of red snapper were quantified around baited trap deployments, building on the work of Bacheler et al. (2018) and Lees et al. (2018). Fine-scale acoustic positioning systems can provide some of the information necessary to estimate absolute density of marine fishes, including the effective fishing area of baited gears and the catchability or sightability of individual fish. As we have shown, these systems can also provide additional information that help reveal the normally hidden behaviors of demersal marine fishes.

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