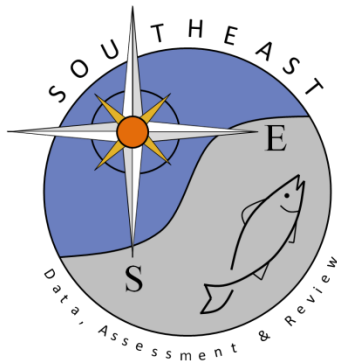


Discard mortality rates of red snapper *Lutjanus campechanus* after barotrauma and hook trauma: 6 insights from using acoustic telemetry in the US South Atlantic

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Discard mortality rates of red snapper *Lutjanus campechanus* after barotrauma and hook trauma: insights from using acoustic telemetry in the US South Atlantic

P.J. Rudershausen¹, B.J. Runde², R.M. Tharp¹, J.H. Merrell¹, N.M. Bacheler³, W.F. Patterson III⁴, and J.A. Buckel¹

¹*North Carolina State University, Department of Applied Ecology, Center for Marine Sciences and Technology, 303 College Circle, Morehead City, NC 28557*

²*The Nature Conservancy, 652 Peter Jefferson Pkwy STE 190, Charlottesville, VA 229113*

³*Southeast Fisheries Science Center, National Marine Fisheries Service, Beaufort, NC 28516*

⁴*University of Florida, Fisheries and Aquatic Sciences, 7922 NW 71st St., Gainesville, FL 32653*

Abstract

Objective: We studied discard mortality of red snapper *Lutjanus campechanus*, a reef species that experiences barotrauma and hook trauma in its US hook and line fisheries. Annual numbers of discarded red snapper far exceed those harvested in federal fisheries management regions, a phenomenon that emphasizes the importance of quantifying discard fates.

Methods: To estimate discard mortality, three-dimensional movement data were collected using acoustic telemetry tags and a 3 km² array of receivers deployed in 2019 and in 2023 at a natural reef area 38 m deep off North Carolina. Release treatments were jaw-hooked or deep-hooked fish; all fish were returned to depth with a recompression device. We assigned a fate for each released red snapper based on movement profiles revealed by the acoustic detection data; fates included: discard mortality, lost tag, emigrated/harvested, or alive within an array when receivers were retrieved. A Kaplan-Meier survivorship analysis was used to estimate rates of discard survival for each release treatment.

Results: Mean proportional rates of discard mortality (1-survival) (2.5, 97.5 confidence intervals) were 0.063 (0.001, 0.122) for jaw-hooked recompressed fish and 0.875 (0.543, 0.966) for deep-hooked recompressed fish.

Conclusion: Our study provides estimates of discard mortality for red snapper at a depth where the species is often captured in US South Atlantic commercial and recreational fisheries. Our estimate of discard mortality for deep-hooked red snapper is among the highest published rates for fish in this release condition and demonstrates that deeply hooked red snapper will likely die.

Impact statement: The results from using acoustic telemetry to study discard mortality rates of recompressed red snapper highlight the need for aggressive outreach regarding the benefits and

requirements of fishing with conservation gears, such as circle hooks recompression tools, to reduce deep hooking and thus facilitate recovery of the US Atlantic red snapper stock.

Keywords: red snapper, discard mortality, acoustic telemetry

Introduction The red snapper *Lutjanus campechanus* is a prized reef species that aggregates on low- and medium-relief reef habitats in tropical and sub-tropical waters on the western Atlantic and Gulf of Mexico continental shelf (Mitchell et al. 2014; Bacheler et al. 2016; Karnauskas et al. 2017; Dance and Rooker 2019). Management approaches to address overfishing and the overfished status of red snapper have been debated in the US Gulf of Mexico and Atlantic federal waters for decades (Hood et al. 2007; Cowan 2011). The most recent stock assessment for Atlantic red snapper concluded that the stock remains overfished with overfishing occurring (SEDAR 2021). This stock is in a decades-long rebuilding period (SEDAR 2021), an extended timeline that is partly due to unrestricted recreational effort and estimated high numbers of dead discards (Shertzer et al. 2024). The impact of recreational discards is partly a consequence of red snapper belonging to a mixed-species fishery such that bycatch and live release of non-targeted fish are common (Campbell et al. 2014; Shertzer et al. 2019; Shertzer et al. 2024). Many of these live releases die from pressure trauma (barotrauma) or hook trauma (Campbell et al. 2014). These frequent discard mortality events have implications for the effectiveness of closed seasons and possession-based regulations, both of which are used to federally manage red snapper. For these types of regulations to be effective in this mixed species fishery with some species open to harvest while others are closed, a relatively high percentage of discarded fish must survive the catch and release experience (Arlinghaus et al. 2007).

Barotrauma can be lethal to reef fish captured at depth if it is severe enough and left untreated by the angler. Barotrauma results from rapid expansion yet slow diffusion of internal

body gases because physoclistous fish such as red snapper lack a pneumatic duct which would otherwise allow for more rapid gas exchange between the air bladder and the digestive tract (Cook et al. 2019; Kerr et al. 2023). Barotrauma in physoclistous fish caught from continental shelf habitats (to 200 m) can result in both obvious and latent injuries such as a ruptured air bladder, stomach eversion, exophthalmia, and intestinal prolapse (Rudershausen et al. 2007; Hannah et al. 2008; Overton et al. 2008). Barotrauma mitigation gears include descending (recompression) devices, which forcefully return fish to a depth (pressure) where they can resume self-regulating their buoyancy (Drumhiller et al. 2014). While their use is not mandatory, recompression devices are required aboard any vessel fishing for or in possession of snapper-grouper species in the US Atlantic region (SAFMC 2019; NARA 2020) given they can increase post-release survival of reef species in this and other regions (Hochhalter and Reed 2011; Hannah et al. 2012; Curtis et al. 2015; Runde and Buckel 2018). Hook trauma is an additional source of mortality in hook-and-line reef fisheries (Overton et al. 2008; Campbell et al. 2014; Rudershausen et al. 2014). Species-, condition-, and depth-specific estimates of discard mortality among reef fish experiencing barotrauma or hook trauma are important for assessment because they increase the accuracy of estimated numbers of total annual removals (harvests plus dead discards) from a stock (SAFMC 2010).

Acoustic telemetry has been recently used to better understand fates of released fish by collecting data that can be used to calculate three-dimensional movement profiles of electronically tagged individuals (Curtis et al. 2015; Bohaboy et al. 2020; Runde et al. 2021; Wegner et al. 2021; Bohaboy et al. 2022). The use of an Acoustic Positioning System (APS) aids in assigning fates of tagged fish by synchronizing detection times among data-collecting receivers within the array (Espinoza et al. 2011). Acoustic arrays allow for studies of discard

94 fates with more ecological realism relative to studies which used equipment such as cages, tanks,
95 or hyperbaric chambers (e.g., Gitschlag and Renaud 1994; Diamond and Campbell 2009;
96 Drumhiller et al. 2014) that eliminate sources of discard mortality, such as predation, that would
97 otherwise occur in the wild. Acoustic telemetry additionally represents an improvement over
98 previous studies that assumed immediate discard condition or a fish's ability to submerge
99 predicted its long-term fate (e.g., Campbell et al. 2014; Pulver 2017). This is because acoustic
100 telemetry studies account for both immediate and delayed sources of discard mortality. The
101 likelihood of obtaining data from electronically tagged fish monitored with passive acoustic
102 arrays is also greater than from conventional tagging methods that typically rely on physical
103 recaptures to obtain post-release data. Long-term fates determined from telemetry data include
104 mortality, emigration or human removal from the array (harvest), tag loss, or survival past a
105 certain timepoint post-release or over the duration that an acoustic array collects data (Bohaboy
106 et al. 2020; Villegas-Ríos et al. 2020; Runde et al. 2021; Wegner et al. 2021). The process of
107 assigning discard fates using acoustic tagging is aided by collecting movement data from known
108 negative and positive controls. Negative controls are tagged individuals intentionally sacrificed
109 and then released dead to help understand and distinguish movements of predated tagged fish,
110 and therefore movement profiles of the non-focal species after predation has occurred, from
111 tagged survivors (Yergey et al. 2012; Muhametsafina et al. 2014; Runde et al. 2020; Runde et al.
112 2021; Wegner et al. 2021). Positive controls are tagged survivors later recaptured or resighted;
113 they are useful to help identify movement patterns of tagged conspecifics not resighted but based
114 on movement data are presumed to have survived catch and release (Capizzano et al. 2019;
115 Bohaboy et al. 2020). Lastly, published decision trees can be utilized to objectively assign fates

(e.g. discard mortality, lost tag, survival) from depth and speed profiles of acoustic tags (Bohaboy et al. 2020; Runde et al. 2021).

In this study, we use acoustic telemetry data to estimate discard mortality for red snapper caught from a 38-m-deep natural reef area off North Carolina. This research was part of a larger study to estimate absolute abundance of red snapper in the US Atlantic region using data and analyses independent of a formal stock assessment (SCSG 2020). This larger abundance estimation study required the construction and maintenance of an acoustic array that we opportunistically used to estimate mortality of electronically tagged red snapper released in different conditions. This study builds on previous acoustic telemetry research into red snapper discard fates in the US Atlantic (Runde et al. 2021) by estimating discard mortality rates of fish with hook trauma. A limitation using acoustic telemetry to study discard mortality is that small sample sizes of tagged individuals (oftentimes due to the price of acoustic tags) can result in relatively imprecise estimates of mortality (Campbell et al. 2014; Curtis et al. 2015). Here, we address the sample size and imprecision issue in the earlier study on red snapper in the southeast US Atlantic (Runde et al. 2021) by adding new red snapper fate data collected within an array in 2023.

Methods We estimated fates of red snapper caught from an area roughly 3.2 km² in size with much of this area comprised of low-relief (~ 1 m) natural reef habitats in waters roughly 38 m deep in Raleigh Bay, North Carolina (Figure 1). We deployed an array of acoustic release receivers encompassing the study area in 2019 and again in 2023. In 2019, we deployed an array of 20 acoustic release receivers (model ‘VR2AR’, Innovasea, Bedford, Nova Scotia, Canada) on the seafloor in a gridded pattern with spacing among them configured to eliminate gaps in detection coverage over the study area based on prior telemetry studies at the same site (Bacheler

et al. 2018). In 2023, we deployed 21 VR2AR receivers in essentially the same area and depth as 2019; this array and receiver spacing of roughly 300 m between receivers was designed in consultation with the manufacturer of the acoustic tags and receivers to eliminate potential gaps in detection based on the approximate transmission distance of the acoustic tags (Figure 1). The area in 2023 was slightly larger than the array in 2019 to encompass more natural reef habitat, which may have been destinations for red snapper emigrating from the 2019 array area. Such an array like we used permits calculations of positional information of tagged fish using time-offsets of tag detections at different receivers within the array and synchronization of times among receivers using transmitters inside each VR2AR. Locating reference tags at known locations within the array (identical tags as those used for fish; see below) was an additional means of calculating horizontal positional error (Figure 1). For red snapper studied in 2019, fate was assigned based on data collected by the acoustic array from 7 May (first day of tagging) to 16 December (receiver retrieval date). For red snapper studied in 2023, fate was assigned from data collected between 11 August and 16 November.

Fish were captured and tagged over multiple dates each study year. Red snapper were captured with hook and line at various locations within the study area using natural baits affixed to J-hooks or circle hooks ranging from 4/0 to 8/0 in size and fished on or near the sea floor (within 1 m). Thus, we assumed that captured red snapper were ascended through the full depth of the study site (38 m), even though red snapper vertical movements away from the sea floor are not uncommon (Bacheler et al. 2021; Bohaboy et al. 2022). While circle hooks are required by regulation for the reef fishery in a sub-region of the US South Atlantic (SAFMC 2020), we fished with both circle and J-hooks to produce a range of hooking locations and conditions, as J-hooks result in higher rates of deep hooking (Sauls and Ayala 2012). Upon capture, each red

snapper was measured for total length (mm) with the hooking location and any signs of hook trauma (location of the hook, obvious bleeding) recorded. We considered deeply hooked fish to be individuals with hook trauma (hooked in either the gills, esophagus, or stomach); in most instances of deep hooking, the leader material was cut and hook left in the fish. After unhooking or cutting the leader, a wet towel was placed over the fish's head prior to tagging.

We used Vemco V13P-1x acoustic transmitters to electronically tag red snapper. This tag type contains an internal sensor to provide pressure (depth) data with each transmission. Tags were attached to fish using an external wire tagging method in 2019 and external spaghetti tagging method in 2023; both of these tagging techniques are described elsewhere and tested for retention and effects on fish health in lab trials on another reef species (black sea bass *Centropristis striata*) (Runde et al. 2022). Both of these external attachment methods anchor the acoustic tags through the dorsal musculature and thus do not interfere with experimental treatments intended to study the effects of barotrauma mitigation. Despite differences in tag retention between the two tagging methods, our decision tree for inferring fates (Runde et al. 2021) and 'right-censoring' method for estimating survival (see below) allowed us to account for tag loss regardless of its cause or when it occurred after tagging. Each of these tagging methods takes approximately 60 seconds to apply; we assumed that this did not affect discard fate and this belief was corroborated by low estimated discard mortality among recompressed red snapper in the earlier study on this topic (Bacheler et al. 2021; Runde et al. 2021). These handling times are likely representative of the recreational fishery based on observations of dehooking and handling times on North Carolina headboat trips targeting reef fishes (P.J. Rudershausen, pers. obs.).

All tagged red snapper were released by descending to 30 m deep with a 'SeaQualizer' device. When the SeaQualizer failed to release fish at depth, an inverted barbless hook was

utilized to descend fish to the seafloor. Fish that fell off either recompression device were netted at the surface and re-descended if they did not submerge on their own. Additionally, five tagged red snapper were sacrificed and purposely recompressed dead in 2019 to serve as negative controls (Yergey et al. 2012; Capizanno et al. 2019; Runde et al. 2020). Movement profiles of these tags (i.e., their scavengers) were used to infer discard mortality of unknown-fate fish that exhibited similar profiles.

Data analysis Acoustic detection data were processed by the tag and receiver manufacturer (Innovasea, Inc., New Bedford, Nova Scotia, Canada), to produce a time series of three-dimensional estimates of each tagged fish's position (Espinoza et al. 2011). Discard fates of red snapper were determined by analyzing three-dimensional movement profiles provided by fine-scale acoustic position data obtained from downloading receiver data (Bohaboy et al. 2020; Runde et al. 2021). We used fine-scale position data to estimate minimum swimming speed by calculating Euclidean (straight-line) distance between a tag's successive three-dimensional positions. Calculations of swimming speeds (distance/time) were conducted when subsequent detections of an individual tag occurred less than 30 minutes apart.

Red snapper fate was determined using a previously published dichotomous decision tree (Runde et al. 2021). This decision tree used information on movement profiles of negative controls tagged in 2019 and positive controls (fish known to be alive after tagging) that were recaptured via hook and line by researchers or fishers, or resighted in videos used to identify tag numbers hand-written on the outward-facing surface of the electronic tags. The video resighting data of live fish were obtained by affixing underwater cameras to baited fish traps to obtain fine-scale position information of red snapper as part of a study on movements of tagged individuals within the array deployed in 2019 (Bacheler et al. 2021). Using daily movement profiles

208 generated from data collected from each tagged fish release, one of four fates was assigned to
209 each fish: alive within the array (Figure 2), permanently emigrated from the array or removed
210 from the array via harvest, lost tag (Figure 3), or discard mortality (Figure 4). Red snapper alive
211 and residing within the array were distinguished from predated conspecifics by having small
212 daily movement patterns over known reef habitat, speeds typically less than 0.5 m/sec (in 2019),
213 or less than 1 m/sec with brief speeds above 2 m/sec (in 2023). Further, movement of red
214 snapper often occurs in the lower half of the water column based on previously published fine-
215 scale red snapper movement behaviors (Bohaboy et al. 2020; Bacheler et al. 2021; Runde et al.
216 2021) and movement data obtained from positive controls before the date on which each was
217 respectively resighted or recaptured in those studies and in this study. In contrast to movements
218 of live fish, data on negative controls and fish that experienced discard mortality were
219 characterized by frequent movements to near-surface waters, speed bursts exceeding 2 m/sec,
220 and emigration from the array's reef habitat within hours of tagging; each of these movement
221 behaviors indicate shark predation or movement of dolphins *Tursiops truncatus* to the surface to
222 breathe within the array (Runde et al. 2021; Bohaboy et al. 2022). Tag loss was considered in
223 cases where there was stationarity of detections or movement speeds less than the horizontal
224 position error data supplied by reference tags within the array. There is a potential that some fish
225 assigned a tag loss fate were predated red snapper where the tag was not consumed but the
226 majority of the tag loss fates (22/25) occurred at ≥ 7 days after capture and, if they did result from
227 predation, it would likely not be considered a result of the catch and release process. Non-
228 ceasing detections that met the depth and speed criteria for a living red snapper were considered
229 tagged fish still alive when receivers were retrieved while detections that ceased before this time
230 but had movement speeds of a live fish were considered tagged red snapper emigrants.

Emigration is further identified by regular movement detections and patterns reflective of live red snapper followed by no detections after a certain timepoint (Curtis et al. 2015; Runde et al. 2021). Discard mortality was assumed to be the sole source of mortality in this study for tags not recovered through harvest reports. Natural mortality is another possibility but the numbers would likely be very low given the short-term duration of the data collection within each study year.

We conducted preliminary model fitting to the binary survival/mortality data to determine whether sea surface water temperature, fish total length, and/or year were meaningful covariates or factors of survival/mortality. This was done by fitting a Cox proportional hazards model (Cox 1972) to data on survival/mortality and time-to-event (e.g., survival to end of study, mortality, tag loss, emigration). Cox models evaluate the instantaneous ‘risk’ of an event at time t conditioned on survival to that time (Cox 1972). The Cox modeling approach is suited to estimate relative rates of post-release survival of fish from tag-recapture or tag-detection studies because it permits staggered entry of newly tagged individuals and does not require that the researcher know the fate of every tagged individual upon conclusion of the study. This type of survival analysis in studies of catch and release mortality assumes that tagging artifacts and natural mortality act on treatment groups in the same way, tag reporting rates are equal among groups, the probability of mortality is not influenced by time of entry into the study population, and studied individuals are randomly encountered. Three pairs of Cox models were fitted was fitted via maximum likelihood by using the *R* software (R 2021) package *survival* (Therneau 2024) and the *coxph* function run through this package. All models contained hooking location as a factor. The first pair included models with- and without water temperature, the second models with- and without fish total length, and the third models with- and without year. For each

pair, a likelihood ratio test (LRT) was conducted in base *R* to compare to the fuller vs. lesser (simpler) model; a non-significant probability value ($p > 0.05$) for the LRT indicates that the simpler model provides an adequate fit to the data.

We conducted a nonparametric Kaplan-Meier survival analysis that is designed to estimate absolute survival rates for known (or inferred) fates biological data (Efron 1988; Pollock et al. 1989; Dudley et al. 2016). The Kaplan-Meier approach can account for staggered entry of individuals into the study population (i.e., multiple tagging dates) as well as right censoring of individuals no longer members of the studied population. Right censoring in an acoustic telemetry study occurs due to reported harvest of tagged fish, emigration from the array, lost tag, or discard mortality. The Kaplan-Meier approach estimates survival S at time t ($S(t)$). $S(t)$ represents the conditional probability of surviving beyond that time given a study individual has survived just prior to that time. Via the Kaplan-Meier procedure, an absolute survival rate was estimated for each treatment of red snapper releases. The Kaplan-Meier survival analysis and associated survival plots were conducted in *R* (R Core Team 2021) using the package *survival* with the *Surv* and *survfit2* functions (Therneau 2024). When fitted in *R*, the Kaplan-Meier analysis uses each individual's time-to-fate data (in our case, days) and binary data for its fate assignment; dead = 1, alive = 0. Products from these software applications include an estimated mean and precision about the survival rate for each release treatment. From this output of the Kaplan-Meier survival analysis we calculated the mean and confidence interval (CI) for discard mortality as (1-survival probability) for each release treatment. Fitting of the *survfit2* function permits the estimation of survival at any timepoint after the entry of each individual into the study (date of tagging).

Results We assigned fates to 79 tagged red snapper caught and released alive within the acoustic arrays deployed in 2019 and 2023. Total length ranged from 390 to 845 mm and averaged 649 mm. The live releases included 63 fish jaw-hooked and 16 deep-hooked fish (Table 1). Seven fish swam down on their own after they fell off the recompression device boatside; these fish were not included in our analyses. In addition to the five negative controls recompressed in 2019, movement data from nine fish either resighted or recaptured in 2019 and three resighted in 2023 served as positive controls to assist in fate assignments. Daily horizontal position error in the 2019 array averaged 1.0 m and ranged from 0.5 to 1.9 m. Daily horizontal position error in the 2023 array averaged 2.9 m and ranged from 1.3 to 6.2 m.

In general, fate classifications differed between treatments. The majority of discard fates for jaw-hooked red snapper included individuals that were alive within the array at the end of its deployment or lost their tags. In contrast, the majority of tags for deep-hooked red snapper were individuals that experienced discard mortality (Table 2). All fish believed to have suffered discard mortality experienced this fate on their day of capture and release (Day 0), with the exception of a single deep-hooked fish that experienced discard mortality on Day 1 (one day after tag and release) (Figure 5; Table 1). Survival was higher for jaw-hooked fish relative to deep-hooked fish (Figures 5 & 6). The mean (2.5/97.5 CI) rate of discard survival for the jaw-hooked treatment was 0.937 (0.878, 0.999) while the mean rate of discard survival for the deep-hooked treatment was 0.125 (0.034, 0.457) equating to discard mortality of 0.063 (0.001, 0.122) for the jaw-hooked group and 0.875 (0.543, 0.966) for the deep-hooked group (Figure 6).

A likelihood ratio test (LRT) comparing Cox proportional hazards models with- vs. without sea surface water temperature was non-significant ($p=0.828$). Similar results were found

for LRTs comparing models with- vs. without fish total length ($p=0.472$) and with- vs. without year ($p=0.360$).

Discussion Our study reveals that discard outcomes for recompressed red snapper are likely to be very different for fish with or without hook trauma. Fish that experience hook trauma (deep hooking) have poor survival even when the effects of barotrauma are mitigated by utilizing a descender device. In contrast, jaw-hooked fish had high survival when descended, which translated into a much lower discard mortality rate than rates used in the Atlantic red snapper assessment (SEDAR 2021). The conservation benefit of this level of discard mortality reduction by using recompression for improving US Atlantic red snapper stock health has also been demonstrated in the recent scientific literature through simulation of different management approaches (Shertzer et al. 2024). We anticipate that results of this study will be useful for stock assessment scientists to consider as input for the forthcoming 2025-26 benchmark assessment modeling of the US South Atlantic red snapper stock ('SEDAR 90').

Using acoustic telemetry and inferring fates based on daily movements allowed us to account for immediate and delayed sources of mortality, which can both influence long-term fates of discarded red snapper (Campbell et al. 2014). We contend that telemetry studies provide greater ecological realism than many previous studies investigating red snapper discard mortality. Our estimates of condition-specific discard mortality assume that fates obtained from the telemetry data are accurately assigned.

Our project is timely because it updates estimates of discard mortality that can be used to improve the accuracy of assessments of US Atlantic red snapper, a stock that is experiencing overfishing due in part to excessive numbers of recreational dead discards (SAFMC 2023; Shertzer et al. 2024). Combining red snapper fate information from two studies allowed us to

increase the 95% confidence interval precision for estimated discard mortality for the jaw-hooked recompressed group from 0.00, 0.17 (Runde et al. 2021) to 0.00, 0.12 (this study). This a release condition that could predominate in the red snapper fishery if recompression usage recommendations and hook type recommendations were more widely followed than may currently be the case (Scyphers et al. 2013). Usage rates of recompression devices to mitigate barotrauma in red snapper may be very low in the US South Atlantic region (Vecchio et al. 2020). Recent (2020) projections using Marine Recreational Information Program (MRIP) data estimated that 21% fewer red snapper would experience discard mortality if recompression was hypothetically used 100% of the time to mitigate barotrauma in US South Atlantic red snapper instead of 0% of the time (Vecchio et al. 2020).

Capture-related mortality among fish can result from pressure- and or hook-related trauma (Bartholomew and Bohnsack 2005) but can also be impacted by environmental conditions (e.g. water temperature) and deck time (Benoît et al. 2010; Capizzano et al. 2019). It is possible that our condition-specific discard mortality estimates are biased high relative to conducting year-round releases of red snapper, given that our study was conducted in summer and thermal stress increases red snapper discard mortality (Campbell et al. 2014; Curtis et al. 2015; Bohaboy et al. 2020). However, preliminary model fits showed that the inclusion of sea surface water temperature into a Cox proportional hazards models did not improve the fit relative to a model without this covariate. A similar result was found when including fish total length in preliminary Cox proportional hazards modeling. Any tagging-related influences on discard mortality would bias our estimates high relative to their true rates in the absence of tagging. Recompression may confer an incidental benefit of reducing water-column predation as fish are descended towards the bottom (Drymon et al 2020; Runde et al. 2022).

Our estimate of discard mortality for hook-traumatized red snapper is higher than in previous studies (see Campbell et al. 2014). We are unsure what may have contributed to these differences among studies. For example, Burns and Restrepo (2002) estimated that red snapper with hook trauma had a discard mortality rate of 43 percent, less than half our mean rate. We attribute the high rate of discard mortality of this group to hook trauma because intermittent releases of recompressed red snapper lacking hook trauma had a much lower mortality rate. Bohaboy et al. (2020), like us, also used acoustic telemetry to estimate discard mortality and found that red snapper with hook trauma had a discard mortality rate roughly five-fold greater than conspecifics without it. The effect of hook trauma was estimated to be even greater in the current study; fish suffering it had a 14-fold higher discard mortality than fish without it. However, multiplying the 97.5 confidence interval for the relative rate of discard mortality of hook-traumatized fish from Bohaboy et al. (2020) study by our mean mortality rate of non-hook traumatized fish results in mortality estimates overlapping between studies for hook-traumatized fish. Given that acoustic telemetry is considered a state-of-the-art technique for understanding long-term fates of released fish, we recommend that these results from hook-traumatized fish be considered when updating hook-type regulations and assessments. The mortality effect from deep hooking underscores the need to use circle hooks as a conservation tool to reduce rates of hook trauma in reef species (Bacheler and Buckel 2004; Sauls and Ayala 2012). Furthermore, release mortality rates associated with deep hooking could be even higher in the recreational fishery if attempts are made to remove deeply set hooks (as opposed to leaving them embedded) and if descender devices are not used (Fobert et al. 2009; Cooke and Danylchuk 2020; Bohaboy et al. 2020).

In assigning fates, we used results provided by a growing body of literature that has studied fine-scale red snapper movements via acoustic telemetry (Bohaboy et al. 2020; Bacheler et al. 2021; Runde et al. 2021; Bohaboy et al. 2022). In 2019, daily median horizontal positional error rates ranged from 0.5 to 1.9 m while in 2023 these values ranged from 1.3 to 6.2 m. We attribute the difference in maximal horizontal error to differences in array designs between years. In 2023, to cover a larger detection area, the distance between adjacent receivers was 300 m, a 50% increase over the distance in 2019 of 200 m. However, including a year effect did not improve the fit of a Cox proportional hazards model in preliminary testing so we find it unlikely that differences in positional error contributed to differences in survival outcomes based on the year that the data were collected. We used known-fate information provided by positive and negative controls to better understand movement profiles for each of the various fates assigned to tagged fish that were not known-fate controls (Capizzano et al. 2019). In our 2023 positive control data, there were often intermittent speeds greater than 2 m/sec; this was greater than in 2019 and we suspect it is because of the greater spacing between receivers, higher error in location, higher resolution (0.3 m) and reduced accuracy (± 3.4 m) of tags in 2023 than the resolution (0.15 m) and accuracy (± 1.4 m) of tags in 2019. It is likely that these increases in error contributed to occasional spurious positions of live red snapper, which in turn could have led to spikes in estimated velocity of live red snapper above 2.0 m/s (values which were not seen in 2019). In 2023, we observed these velocity spikes in several fish, including some positive controls; therefore, we are confident that such velocity estimates are not representative of discard mortalities.

Red snapper discard mortality has been extensively studied. This is a testament to the popularity and historic importance of its fisheries in the US Atlantic and Gulf of Mexico. Direct

comparisons between our results and those of other studies must be made with caution for a variety of reasons, such as differing regions and depths, handling and tagging practices, and overall methodology. A meta-analysis of Gulf of Mexico red snapper discard mortality research predicted proportional mortality rates of 0.341 and 0.364 in waters 35 and 40 m deep, respectively (Campbell et al. 2014), but those authors estimated depth-specific rates regardless of whether barotrauma mitigation occurred or not. Recent research into red snapper fish discard mortality using acoustic technologies (Curtis et al. 2015; Runde et al. 2021 Bohaboy et al. 2022; this study) firmly refutes the suggestion by Wilde (2009) that the effects of barotrauma cannot be reversed through human intervention or wound healing. Given the pressure gradient between the surface and depths fished in this study, it is likely that all red snapper had barotrauma despite only a fraction of studied individuals displaying some of its obvious forms (Rummer 2007). Roughly 10 percent of red snapper caught from shallower depths (30 m) were unable to submerge following release in another study of red snapper discard mortality (Campbell et al. 2010). Recompressed Gulf of Mexico red snapper caught from waters 30, 50, and 55 m deep had greater rates of survival than surface releases in previous acoustic telemetry studies (Curtis et al. 2015; Bohaboy et al. 2020). Discard mortality rates of jaw-hooked recompressed fish from those two studies were slightly higher than ours but direct comparisons are difficult owing to differing depths where studies were conducted. Bohaboy et al (2020) reported red snapper discard mortality was halved in recompressed fish compared to surface releases at depths of 30 and 55 m. Studies suggest that 31-40 m depths where red snapper are commonly found in the US Atlantic (Bacheler et al. 2016; Vecchio et al. 2020; Bacheler et al. 2024) and where this study occurred are depths over which barotrauma mitigation appears important for improving discard survival of reef fish (Runde et al. 2021; Rudershausen et al. 2022). Work on red snapper discard

mortality also suggests that for effective barotrauma mitigation, it may not be necessary to return fish all the way to the bottom (Sauls et al. 2016; Runde et al. 2021; this study).

Self-submersing fish were not included in our analysis because a primary goal was to understand discard mortality rates of fish treated with barotrauma mitigation. As such, we did not have a true insight into mortality rates of untreated fish because, when possible, we re-collected fish if they fell off the recompression device and began the recompression process again. Seven fish that escaped our re-collection efforts self-submersed on their own. Studying discard mortality rates of surface-released red snapper over a range of depths would be a useful research topic given our observations that some red snapper self-submerge at the depth of the study area. This would help refine depth-specific guidance for using barotrauma mitigation on red snapper. Some depths where recreational anglers catch red snapper in the US Atlantic (Vecchio et al. 2020) may sufficiently shallow (<30 m) that the benefits of rapid release of untreated fish may outweigh taking the time to mitigate barotrauma (South Atlantic Fishery Management Council Advisory Panel Meeting, October 2024, personal communication).

Mortality-by-condition, such as estimated in this study, does not provide all the information required to estimate numbers of dead discards in either the recreational or commercial fishery. An accurate estimate of the proportion of live releases that die (i.e., discard mortality rate) is only possible when comprehensive data are available on both mortality-by-condition and also proportion-by-condition, the latter of which could be obtained through onboard observers, creel surveys, or citizen science initiatives to collect fishery-dependent samples on angler practices (Campbell et al. 2014). Some of these data on usage of hook types and barotrauma mitigation have been collected for a sub-section of the region and for specific fishing modes (Vecchio et al. 2020; Runde et al. 2021). Researchers could obtain contemporary

fishery-dependent information on the frequency of various angling practices and apply these gears and techniques in field experiments where discard mortality is estimated. Such an approach was recently taken to estimate discard mortality for the hook and line dolphinfish *Coryphaena hippurus* fishery in the western North Atlantic (Rudershausen et al. 2019).

The circle hook requirement for the US South Atlantic reef fishery is latitude-specific (required north of 28° N) (SAFMC 2020) so proportion-by-condition information is needed over finer spatial scales than the entire range of the stock. Runde et al. (2021) used data on circle hook usage for one recreational mode in the US Atlantic (headboats) to estimate deep hooking rates and overall discard mortality rates for the red snapper recreational fishery. For the US Atlantic recreational reef fishery, such estimates of proportional releases by condition are needed in both sub-regions (south and north of 28° N) and for all recreational fishing modes: private, for-hire, and headboat. Red snapper discard mortality increases with depth of capture (Campbell et al. 2014; Curtis et al. 2015; Pulver 2017; Bohaboy et al. 2022), which further complicates efforts to estimate total numbers of dead discards in federal fisheries management regions since the federal marine recreational fishery-dependent sampling program (MRIP) does not collect depth-specific information on reported harvests or releases.

The fate of released fish is an increasingly important issue in conserving stocks of reef fishes in the US South Atlantic federal fisheries management region due to high numbers of regulatory discards (Rudershausen et al. 2007; Overton et al. 2008) and increasing recreational fishing activity over recent years (Shertzer et al. 2019; MRIP 2024). For example, the number of released red snapper exceeded the number harvest by roughly 25-fold in the US Atlantic in 2023 (MRIP 2024). Predictions indicate that high discard mortality for some snapper/grouper species coupled with increasing recreational fishing activity in the US Atlantic will, within the next

decade, lead to annual numbers of total annual allowable removals being comprised exclusively of discards with no allowable landings (SAFMC 2023). Thus, spatial data on commercial and recreational usage rates of conservation tools are urgently needed to better estimate the numbers of dead discards of red snapper and other reef species.

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Figure 1. Grayscale bathymetric map depicting the study area and acoustic receiver locations in Raleigh Bay, North Carolina used to collect movement data on electronically tagged red snapper *Lutjanus campechanus* in 2023. The same general location was utilized in the 2019 study, with a map of receiver locations provided in Runde et al. (2021). Locations of red snapper released alive are shown in yellow for 2019 and blue for 2023. Locations of red snapper sacrificed and released dead (negative controls) in 2019 are shown in red (there were no negative controls in 2023). Multiple releases occurred at some locations shown on the map. Down-facing triangles are locations of reference tags within the 2023 array while up-facing triangles are locations of acoustic receivers.

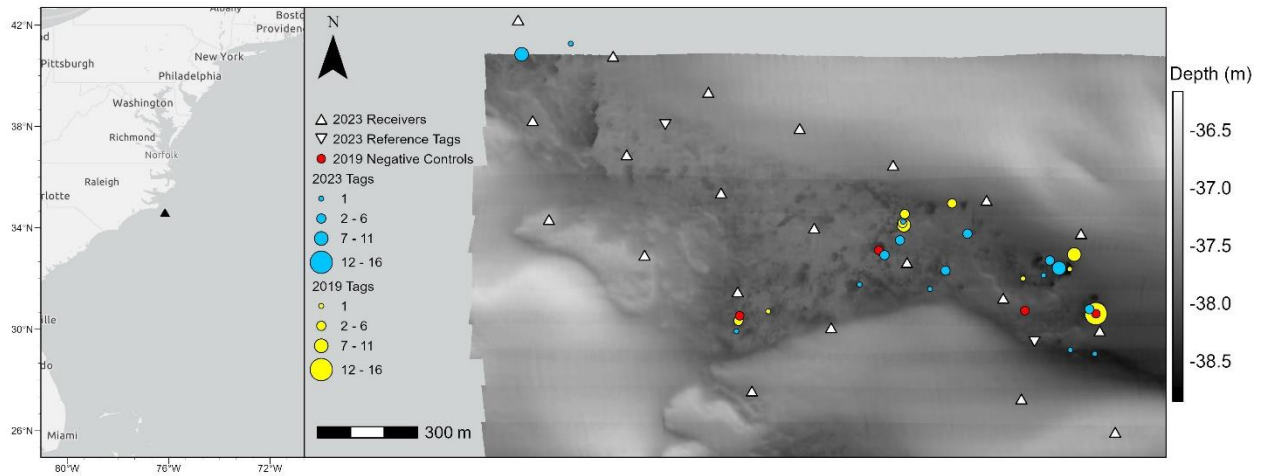


Figure 2. Representative daily movement profile of a red snapper *Lutjanus campechanus* released in 2023 within an array of acoustic receivers deployed in Raleigh Bay, North Carolina to determine discard fates. This fish was considered a positive control in that it was later observed alive with an underwater camera. The left panel depicts a bathymetric map displaying one day (24 h) of movement data (red track line) within the array of receivers (black circles) before the resighting date. The right panel depicts the depth occupied by the fish (left y-axis: black line) and its speed (m/s) (right y-axis: red line) throughout the 24-hour cycle (x-axis) of areal movement displayed in the left panel. Gaps in the red line on the right panel denote periods where fish speed was not calculated because consecutive detections occurred more than 30 minutes apart.

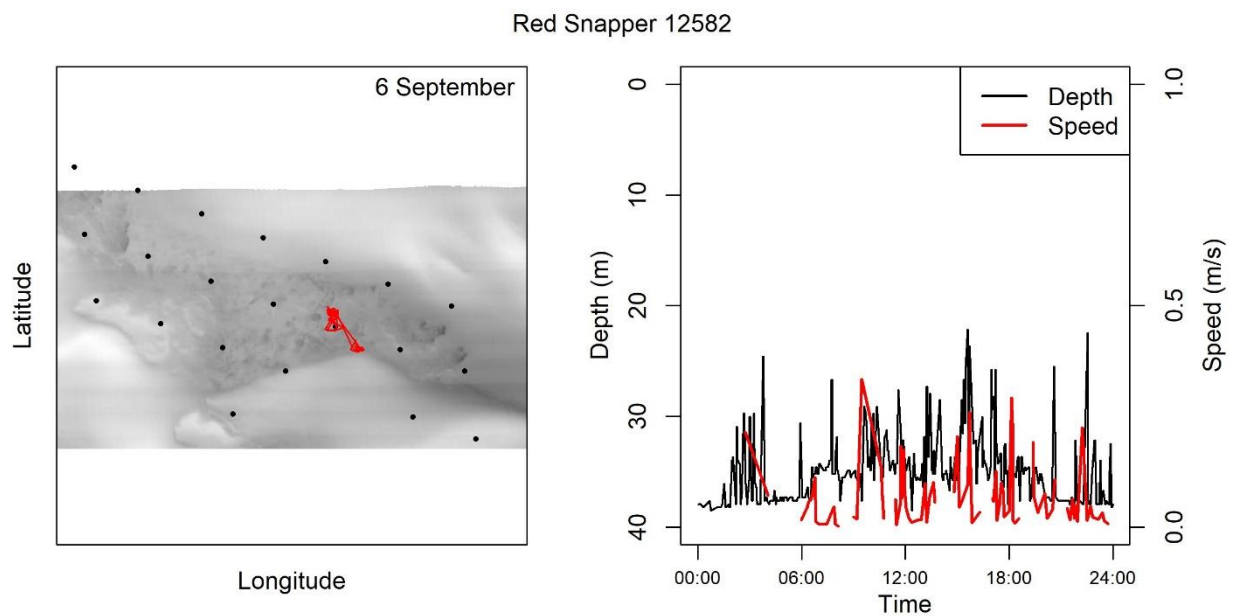


Figure 3. Representative daily movement profile of a red snapper *Lutjanus campechanus* released alive in 2023 within an array of acoustic receivers deployed in Raleigh Bay, North Carolina to determine red snapper discard fates. This fish was evaluated to have lost its tag. The left panel depicts a bathymetric map of fish movement (red track line) within the array of receivers (black circles) on the day that the tag was lost. The right panel depicts the depth occupied by the tag (left y-axis: black line) and its speed (m/s) (right y-axis: red line) throughout the 24-hour cycle (x-axis) on the day of tag loss (shedding). Gaps in the red line on the right panel denote periods where tag speed was not calculated because consecutive detections occurred more than 30 minutes apart.

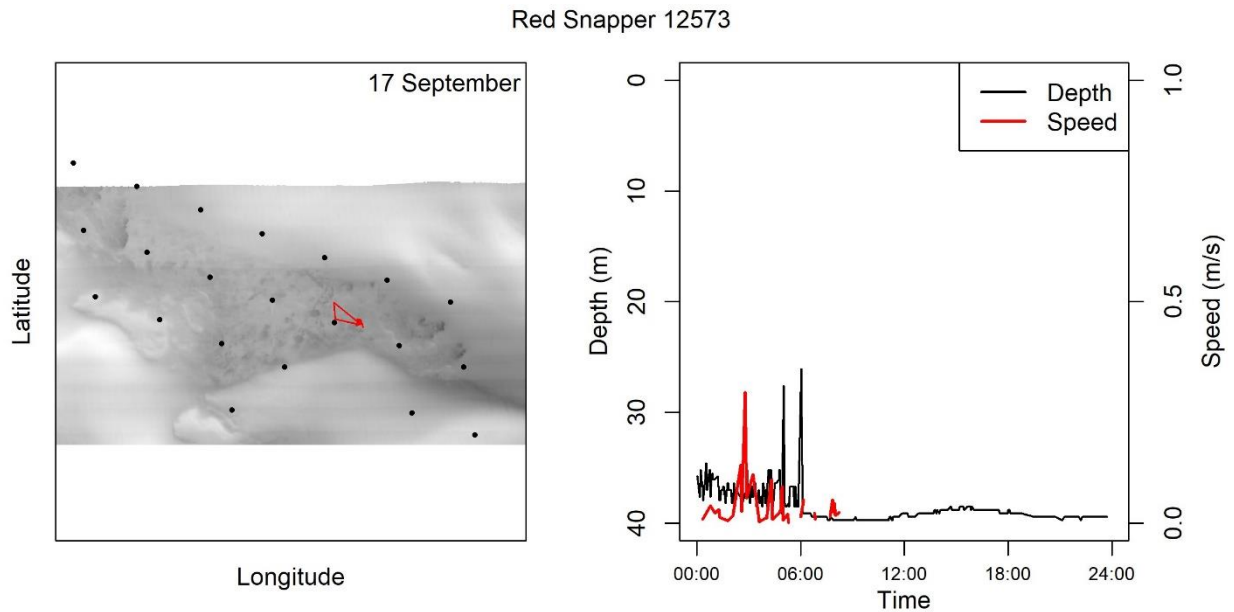


Figure 4. Representative daily movement profile of an acoustic tag used to mark a red snapper *Lutjanus campechanus* released in 2023 within an array of acoustic receivers deployed in Raleigh Bay, North Carolina to determine red snapper discard fates. This fish was estimated to suffer discard mortality. The left panel depicts a map of tag movement (red track line) within the array of receivers (black circles) on the day that the fish was released and subsequently died. The right panel depicts the depth occupied by the tag (left y-axis: black line) and its speed (m/s) (right y-axis: red line) throughout the 24-hour cycle (x-axis) on the day of release and post-release death. The range of the scale of the right y-axis on the right panel differs from Figures 2 and 3. The gaps in the red line on the right panel denote periods where tag speed was not calculated because consecutive detections occurred more than 30 minutes apart.

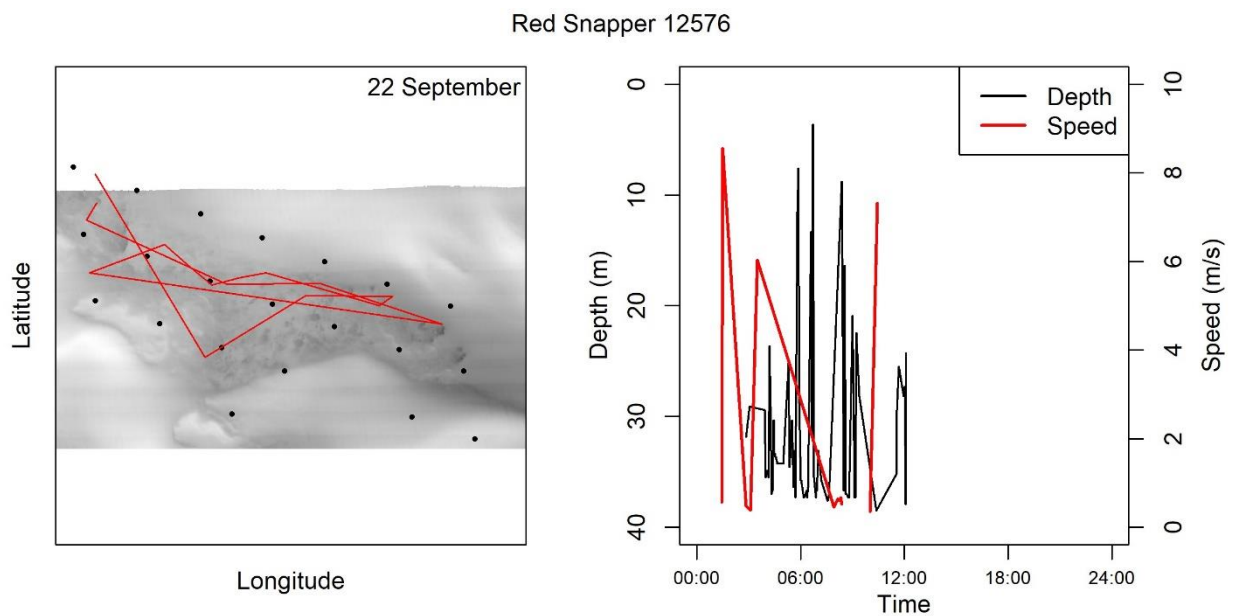


Figure 5. Mean (line) and 95% confidence interval (CI) (shaded area) for survival probability (y-axis) vs. time (days) post-release (x-axis) for red snapper *Lutjanus campechanus* studied for fates using an acoustic array deployed in waters 38 m deep in Raleigh Bay, North Carolina. Survival was estimated with a Kaplan-Meier analysis for each of two different release treatments: jaw-hooked and recompressed (blue line and shading) and deep-hooked and recompressed (orange line and shading). No jaw-hooked recompressed fish died after the day of release (after Day 0), hence the horizontal line and shaded area (blue). Plus symbols ('+') at top of the graph panel denote instances of censoring individuals of each treatment type.

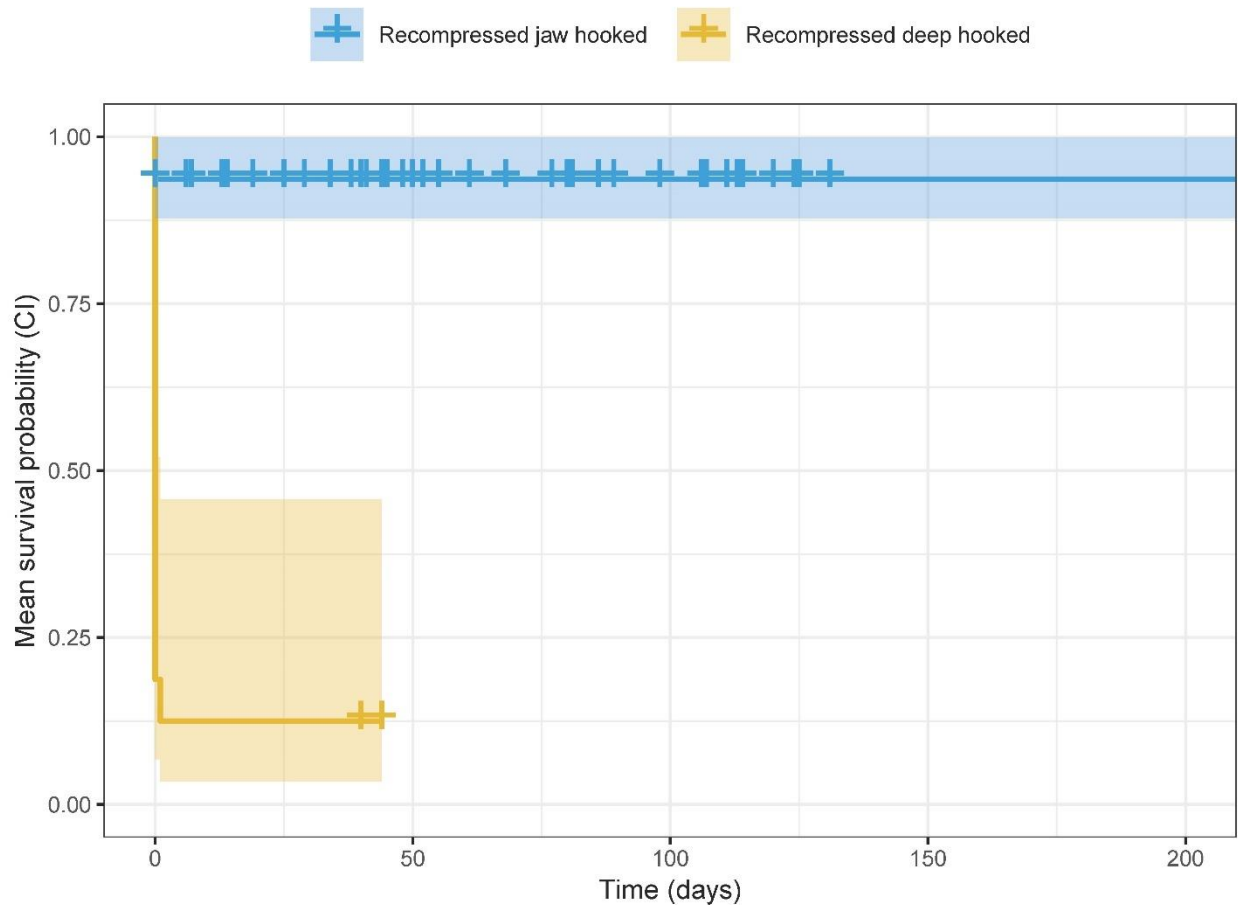
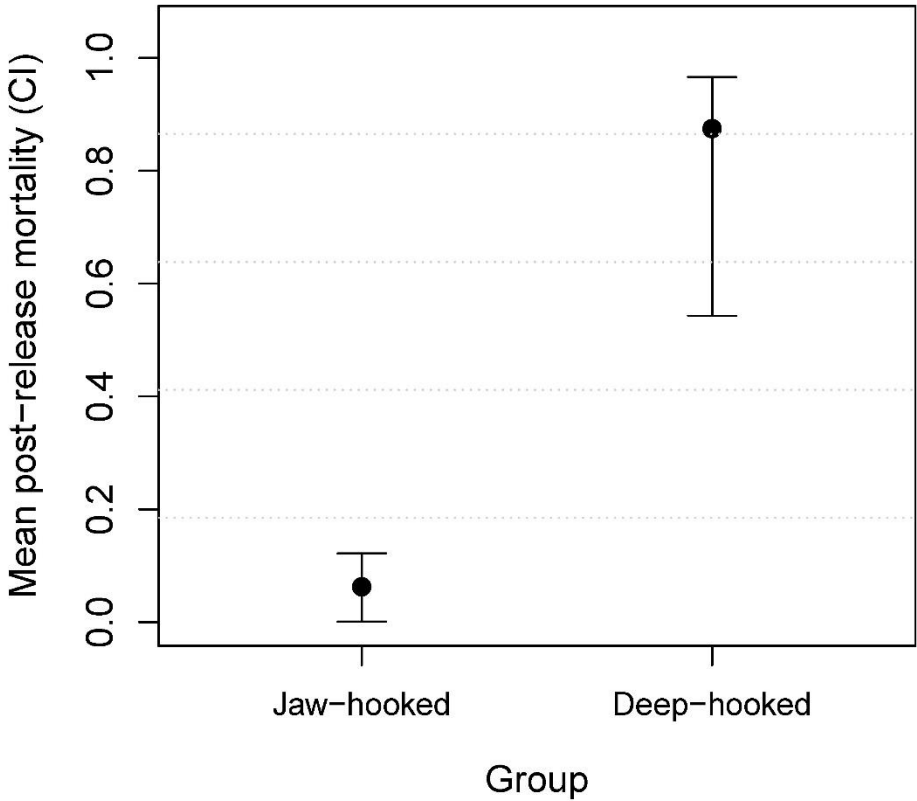


Figure 6. Means \pm 95% confidence intervals (CI) (horizontal lines) for two estimates of proportional discard mortality probability (y-axis) of recompressed red snapper *Lutjanus campechanus* caught from waters 38 m deep in Raleigh Bay, North Carolina. Discard mortality (1-survival) was estimated using results from a Kaplan-Meier analysis for two different treatments (x-axis): A) jaw-hooked and B) deep-hooked fish. All fish were release at depth with a descender device.



838 Table 1. Information on 79 red snapper *Lutjanus campechanus* acoustically tagged and released
839 in a variety of conditions in 2019 and 2023 in waters 38 m deep in Raleigh Bay, North Carolina.
840 Tagged fish were released at depth a descender device, monitored with an array of acoustic
841 receivers, and their fate estimated based on movement profiles. Fish assigned a fate of alive at
842 the end of the study were considered still alive when the acoustic receivers were removed from
843 the seabed. TL = total length (mm). Deep-hooked = hooked in the gill, esophagus, or stomach.
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Fish #	Date tagged	TL (mm)	Deep-hooked?	Assigned fate	Days: tagging to fate
1	7 May 2019	520	No	Lost tag	0
2	7 May 2019	700	No	Emigrated	131
3	7 May 2019	720	No	Harvested	113
4	7 May 2019	685	No	Lost tag	6
5	7 May 2019	665	No	Lost tag	98
6	7 May 2019	785	No	Lost tag	29
7	7 May 2019	635	No	Emigrated	50
8	7 May 2019	680	No	Lost tag	113
9	7 May 2019	750	No	Lost tag	19
10	7 May 2019	790	No	Lost tag	79
11	7 May 2019	500	No	Discard mortality	0
12	7 May 2019	705	No	Emigrated	81
13	7 May 2019	710	No	Lost tag	13
14	7 May 2019	760	No	Alive at study's end	223
15	7 May 2019	740	No	Lost tag	55
16	7 May 2019	720	No	Lost tag	68
17	7 May 2019	795	No	Lost tag	114
18	7 May 2019	390	Yes	Discard mortality	0
19	7 May 2019	690	No	Lost tag	44
20	7 May 2019	730	No	Lost tag	7
21	13 Aug 2019	735	No	Emigrated	107
22	13 Aug 2019	750	No	Emigrated	44
23	13 Aug 2019	760	No	Alive at study's end	125
24	13 Aug 2019	715	No	Lost tag	0
25	13 Aug 2019	735	No	Lost tag	34
26	13 Aug 2019	750	No	Discard mortality	0
27	13 Aug 2019	425	No	Lost tag	61
28	13 Aug 2019	790	No	Lost tag	48
29	13 Aug 2019	695	No	Discard mortality	0
30	13 Aug 2019	685	Yes	Discard mortality	0
31	13 Aug 2019	750	No	Lost tag	111
32	13 Aug 2019	720	No	Emigrated	124
33	13 Aug 2019	775	No	Emigrated	124
34	13 Aug 2019	845	No	Emigrated	120
35	13 Aug 2019	745	No	Emigrated	124
36	13 Aug 2019	755	No	Emigrated	106
37	30 Aug 2019	410	No	Emigrated	77
38	22 Sep 2019	475	No	Lost tag	45

39	11 Aug 2023	550	Yes	Discard mortality	0
40	11 Aug 2023	560	No	Lost tag	68
41	19 Aug 2023	735	No	Lost tag	14
42	19 Aug 2023	730	Yes	Discard mortality	0
43	19 Aug 2023	510	No	Discard mortality	0
44	19 Aug 2023	655	Yes	Emigrated	40
45	19 Aug 2023	585	No	Lost tag	38
46	19 Aug 2023	645	No	Alive at study's end	89
47	19 Aug 2023	725	No	Lost tag	29
48	19 Aug 2023	625	Yes	Discard mortality	0
49	19 Aug 2023	550	Yes	Discard mortality	0
50	19 Aug 2023	525	No	Alive at study's end	89
51	19 Aug 2023	530	No	Alive at study's end	89
52	19 Aug 2023	660	No	Alive at study's end	89
53	28 Aug 2023	630	Yes	Discard mortality	0
54	28 Aug 2023	670	No	Alive at study's end	80
55	28 Aug 2023	670	No	Alive at study's end	80
56	28 Aug 2023	620	Yes	Discard mortality	0
57	28 Aug 2023	585	Yes	Discard mortality	0
58	28 Aug 2023	675	No	Alive at study's end	80
59	28 Aug 2023	715	No	Alive at study's end	80
60	28 Aug 2023	470	No	Alive at study's end	80
61	28 Aug 2023	540	Yes	Discard mortality	0
62	28 Aug 2023	615	No	Alive at study's end	80
63	28 Aug 2023	680	Yes	Discard mortality	1
64	28 Aug 2023	430	No	Lost tag	29
65	28 Aug 2023	520	Yes	Lost tag	44
66	28 Aug 2023	665	Yes	Discard mortality	0
67	28 Aug 2023	680	No	Alive at study's end	80
68	25 Sep 2023	585	No	Alive at study's end	52
69	25 Sep 2023	585	No	Alive at study's end	52
70	25 Sep 2023	595	No	Alive at study's end	52
71	25 Sep 2023	605	No	Lost tag	40
72	25 Sep 2023	565	Yes	Discard mortality	0
73	25 Sep 2023	560	No	Alive at study's end	52
74	25 Sep 2023	525	Yes	Discard mortality	0
75	25 Sep 2023	605	No	Alive at study's end	52
76	25 Sep 2023	590	No	Alive at study's end	52
77	25 Sep 2023	545	No	Alive at study's end	52
78	25 Sep 2023	760	No	Emigrated	41
79	25 Sep 2023	780	No	Alive at study's end	52

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848 Table 2. Sample size (n) and proportion, by release condition, for each of five assigned fates of
849 79 red snapper *Lutjanus campechanus* acoustically tagged and released as recompressed fish in
850 two different hooking conditions in 2019 and 2023 within an acoustic array deployed in waters
851 38 m deep in Raleigh Bay, North Carolina. Fish were assigned discard fates based on individual
852 movement profiles within the array. Deep-hooked = hooked in the gill, esophagus, or stomach.
853

Release condition	Fate									
	Alive		Emigrated		Harvested		Lost tag		Discard mortality	
Jaw-hooked	21	0.33	12	0.19	1	0.02	25	0.40	4	0.06
Deep-hooked	0	0	1	0.06	0	0	1	0.06	14	0.88

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