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Article

Discard mortality rates of Red Snapper after barotrauma and hook trauma: Insights from using acoustic telemetry in the U.S. South Atlantic

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ABSTRACT

Objective: We studied discard mortality of Red Snapper *Lutjanus campechanus*, a reef species that experiences barotrauma and hook trauma in its U.S. 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-km^2 array of receivers deployed in 2019 and 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 the array when the receivers were retrieved. A Kaplan–Meier survivorship analysis was used to estimate the rates of discard survival for each release treatment.

Results: Mean proportional rates of discard mortality (1 − survival) were 0.063 (95% CI = 0.001–0.122) for jaw-hooked recompressed fish and 0.875 (0.543–0.966) for deep-hooked recompressed fish.

Conclusions: Our study provides estimates of discard mortality for Red Snapper at a depth where the species is often captured in U.S. 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.

KEYWORDS: acoustic telemetry, discard mortality, Red Snapper

LAY SUMMARY

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 and recompression tools, to reduce deep hooking and effects of barotrauma and thus facilitate recovery of the U.S. Atlantic Red Snapper stock.

INTRODUCTION

The Red Snapper *Lutjanus campechanus* is a prized reef species that aggregates on low- and medium-relief reef habitats in tropical and subtropical waters on the western Atlantic and Gulf of Mexico continental shelf (Bacheler et al., 2016; Dance & Rooker, 2019; Karnauskas et al., 2017; Mitchell et al., 2014). Management approaches to address overfishing and the overfished status of Red Snapper in the U.S. Gulf of Mexico and

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Atlantic federal waters have been debated for decades (Cowan, 2011; Hood et al., 2007). The most recent stock assessment for Atlantic Red Snapper concluded that the stock remains overfished, with overfishing occurring (Southeast Data, Assessment, and Review, 2021). This stock is in a decades-long rebuilding period (Southeast Data, Assessment, and Review, 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 nontargeted fish are common (Campbell et al., 2014; Shertzer et al., 2019, 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 for this mixed-species fishery, in which some species are 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 fishes 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 fishes 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 fishes 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 (Hannah et al., 2008; Overton et al., 2008; Rudershausen et al., 2007). 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). Although their use is not mandatory, recompression devices are required aboard any vessel fishing for or in possession of snapper–grouper species in the U.S. Atlantic region (National Archives and Records Administration, 2020; South Atlantic Fishery Management Council [SAFMC], 2020) given that they can increase the postrelease survival of reef species in this and other regions (Curtis et al., 2015; Hannah et al., 2012; Hochhalter & Reed, 2011; Runde & Buckel, 2018). Hook trauma is an additional source of mortality in hook-and-line reef fisheries (Campbell et al., 2014; Overton et al., 2008; Rudershausen et al., 2014). Species-, condition-, and depth-specific estimates of discard mortality among reef fishes 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 the fates of released fish by collecting data that can be used to calculate three-dimensional movement profiles of electronically tagged individuals (Bohaboy et al., 2020, 2022; Curtis et al., 2015; Runde et al., 2021; Wegner et al., 2021). The use of an acoustic positioning system 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 fates with more ecological realism relative to studies that use equipment such as cages, tanks, or hyperbaric chambers (e.g., Diamond & Campbell, 2009; Drumhiller et al., 2014; Gitschlag & Renaud, 1994), as the latter studies eliminate sources of discard mortality (e.g., predation) that would otherwise occur in the wild. Acoustic telemetry additionally represents an improvement over previous studies, which assumed that immediate discard condition or a fish's ability to submerge could be used to predict its long-term fate (e.g., Campbell et al., 2014; Pulver, 2017). This is because acoustic telemetry studies account for both immediate and delayed sources of discard mortality. The likelihood of obtaining data from electronically tagged fish that are monitored with passive acoustic arrays is also greater than from conventional tagging methods, which typically rely on physical recaptures to obtain postrelease data. Long-term fates determined from telemetry data include mortality, emigration or human removal from the array (harvest), tag loss, or survival past a certain time point after release or over the duration for which an acoustic array collects data (Bohaboy et al., 2020; Runde et al., 2021; Villegas-Ríos et al., 2020; Wegner et al., 2021). The process of assigning discard fates using acoustic tagging is aided by collecting movement data from known negative and positive controls. Negative controls are tagged individuals that are intentionally sacrificed and then released dead to help understand and distinguish the movements of predated tagged fish—and therefore the movement profiles of the nonfocal species after predation has occurred—from the movements of tagged survivors (Muhametsafina et al., 2014; Runde et al., 2020, 2021; Wegner et al., 2021; Yergey et al., 2012). Positive controls are tagged survivors that are later recaptured or resighted; they are useful to help identify movement patterns of tagged conspecifics that are not resighted but, based on movement data, are presumed to have survived catch and release (Bohaboy et al., 2020; Capizzano et al., 2019). Lastly, published decision trees can be utilized to objectively assign fates (e.g., discard mortality, lost tag, or survival) from the depth and speed profiles of acoustic tags (Bohaboy et al., 2020; Runde et al., 2021).

In this study, we used 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 U.S. Atlantic region using data and analyses independent of a formal stock assessment (South Carolina Sea Grant, 2020). This larger abundance estimation study required the construction and maintenance of an acoustic array that we opportunistically used to estimate the mortality of electronically tagged Red Snapper that were released in different conditions. This study builds on previous acoustic telemetry research into Red Snapper discard fates in the U.S. Atlantic (Runde et al., 2021) by estimating discard mortality rates of fish with hook trauma. A limitation of using acoustic telemetry to study discard mortality is that small sample sizes of tagged individuals (often 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 from the earlier study on Red Snapper in the southeast U.S. Atlantic (Runde et al., 2021) by adding new Red Snapper fate data collected within an array in 2023.

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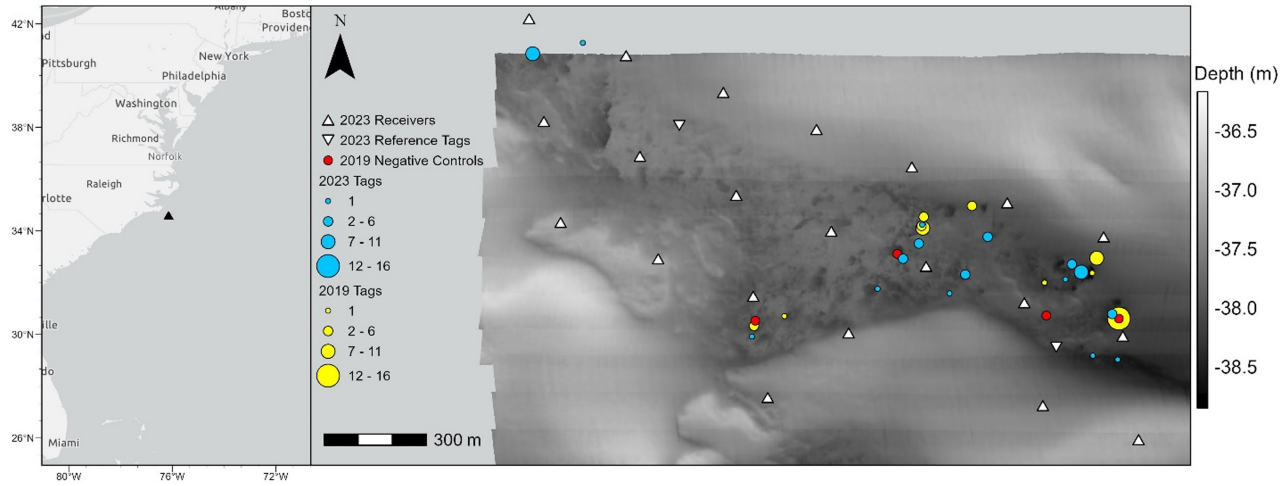

Figure 1. Grayscale bathymetric map depicting the study area and acoustic receiver locations in Raleigh Bay, North Carolina, used to collect movement data on electronically tagged Red Snapper in 2023. The same general location was utilized in the 2019 study (a map of receiver locations for 2019 is provided 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 that were 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. Downward-facing triangles represent the locations of reference tags within the 2023 array, while upward-facing triangles represent the locations of acoustic receivers.

METHODS

We estimated the fates of Red Snapper caught from an area roughly 3.2 km^2 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, New 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 Innovasea Model VR2AR receivers in essentially the same area and depth as 2019; this array and receiver spacing of roughly 300 m between receivers were 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 array area in 2023 was slightly larger than that in 2019 to encompass more natural reef habitat, which may have been a destination for Red Snapper emigrating from the 2019 array area. An array like the one we used permits calculations of positional information for 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 (tags identical to 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 May 7 (first day of tagging) to December 16 (receiver retrieval date). For Red Snapper studied in 2023, fate was assigned from data collected between August 11 and November 16.

Red Snapper were captured and tagged over multiple dates during each study year. Fish were captured with hook and line at various locations within the study area using natural baits that were affixed to J-hooks or circle hooks ranging from 4/0 to 8/0 in size and that were fished on or near the seafloor (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 seafloor are not uncommon (Bacheler et al., 2021; Bohaboy et al., 2022). Although circle hooks are required by regulation for the reef fishery in a subregion of the U.S. South Atlantic (SAFMC, 2020), we fished with both circle hooks and J-hooks to produce a range of hooking locations and conditions, as J-hooks result in higher rates of deep hooking (Sauls & Ayala, 2012). Upon capture, each Red Snapper was measured for total length (mm), and the hooking location and any signs of hook trauma (e.g., obvious bleeding) were recorded. We considered deeply hooked fish to be individuals with hook trauma (hooked in the gills, esophagus, or stomach); in most instances of deep hooking, the leader material was cut and the hook was left in the fish. After the leader was unhooked or cut, 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 the fish using an external wire-tagging method in 2019 and an external spaghetti-tagging method in 2023; both tagging techniques are described elsewhere and were tested for retention and effects on fish health in laboratory trials on another reef species (Black Sea Bass *Centropristis striata*; Runde, et al., 2022a). Both external attachment methods anchor the acoustic tags through the dorsal musculature and thus do not interfere with experimental treatments that are 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 the "right-censoring" method for estimating survival (see below)

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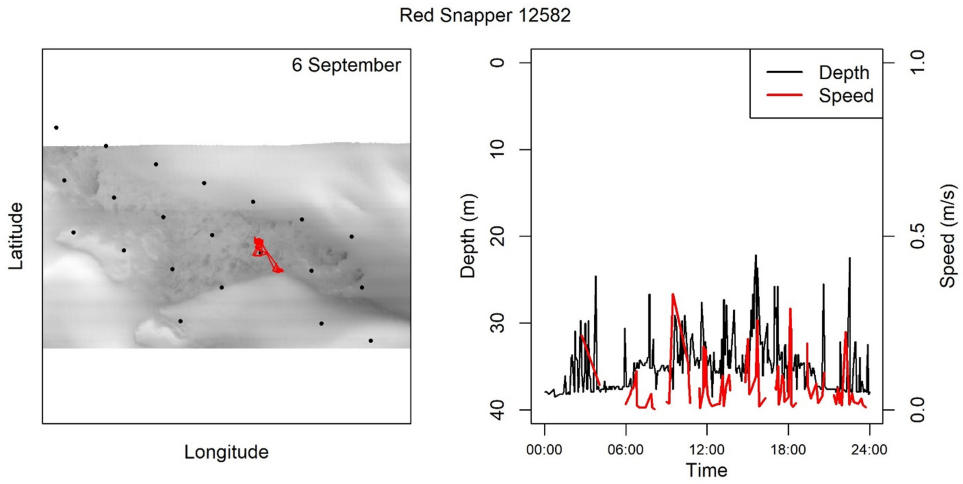

Figure 2. Representative daily movement profile of a Red Snapper released in 2023 within an array of acoustic receivers deployed in Raleigh Bay, North Carolina, to determine discard fates. This fish was considered a positive control in that it was later observed alive with an underwater camera. The left panel depicts a bathymetric map displaying 1 d (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 (m) occupied by the fish (left *y*-axis; black line) and its speed (m/s; right *y*-axis; red line) throughout the 24-h cycle (*x*-axis) of areal movement displayed in the left panel. Gaps in the red line on the right panel denote periods for which fish speed was not calculated because consecutive detections occurred more than 30 min apart.

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 s 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, personal observation).

All tagged Red Snapper were released by descending to 30-m depth with a SeaQualizer device. If 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 redescended if they did not submerge on their own. Additionally, five Red Snapper that were tagged in 2019 were sacrificed, and the dead individuals were recompressed to serve as negative controls (Capizzano et al, 2019; Runde et al., 2020; Yergey et al., 2012). 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) 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 the 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 the 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 min 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 (1) recaptured via hook and line by researchers or fishers or (2) resighted in videos used to identify tag numbers that were handwritten on the outward-facing surface of the electronic tags. The video resighting data for live fish were obtained by affixing underwater cameras to baited fish traps to obtain information on the fine-scale position 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 generated from data collected from each tagged fish release, one of four fates was assigned to each fish: alive within the array (Figure 2), permanently emigrated from the array or removed from the array via harvest, lost tag (Figure 3), or discard mortality (Figure 4). Red Snapper that were alive and residing within the array were distinguished from predated conspecifics by having small daily movement patterns over known reef habitat, speeds typically less than 0.5 m/s (in 2019), or speeds less than 1 m/s, with brief speeds above 2 m/s (in 2023). Further, movement of Red Snapper often occurs in the lower half of the water column based on previously published fine-scale Red Snapper movement behaviors (Bacheler et al., 2021; Bohaboy et al., 2020; Runde et al., 2021) and based on movement data obtained from positive controls before the date on which each was respectively resighted or recaptured in those studies and the present study. In contrast to the movements of live fish, data on negative controls and fish that experienced discard mortality were characterized by frequent movements to near-surface waters, speed bursts exceeding 2 m/s, and emigration from the array's reef habitat within hours of tagging; each of these movement

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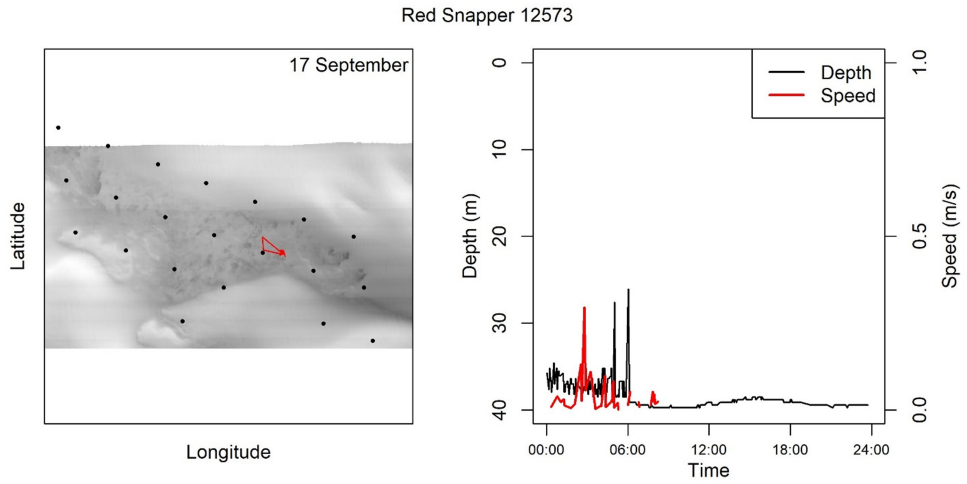

Figure 3. Representative daily movement profile of a Red Snapper released alive in 2023 within an array of acoustic receivers deployed in Raleigh Bay, North Carolina, to determine discard fates. This fish was evaluated as having lost its tag. The left panel depicts a bathymetric map of fish movement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

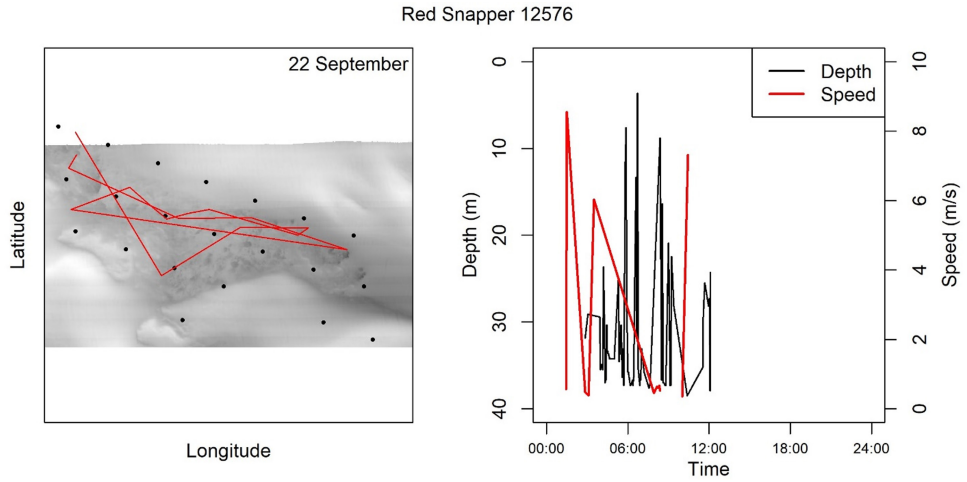

Figure 4. Representative daily movement profile of an acoustic tag used to mark a Red Snapper released in 2023 within an array of acoustic receivers deployed in Raleigh Bay, North Carolina, to determine discard fates. This fish was estimated to have suffered discard mortality. The left panel depicts 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 (m) occupied by the tag (left *y*-axis; black line) and its speed (m/s; right *y*-axis; red line) throughout the 24-h cycle (*x*-axis) on the day of release and postrelease death. The range of the right *y*-axis scale on the right panel differs from that in Figures 2 and 3. The gaps in the red line on the right panel denote periods for which tag speed was not calculated because consecutive detections occurred more than 30 min apart.

behaviors indicate shark predation or movement of common bottlenose dolphins *Tursiops truncatus* to the surface to breathe within the array (Bohaboy et al., 2022; Runde et al., 2021). Tag loss was considered in cases where there was stationarity of detections or movement speeds less than the horizontal position error data supplied by reference tags within the array. Some fish that were assigned a tag loss fate may have been predated Red Snapper from which the tag was not consumed, but the majority of the tag loss fates (22/25) occurred at or beyond 7 d postcapture; therefore, if those tag losses were due to predation, it was unlikely to have resulted from the catch-and-release process. Nonceasing detections that met the depth and speed criteria for a living Red Snapper were considered to represent tagged fish that were still alive when receivers were retrieved, while detections that ceased before this time but had the movement speeds of a live fish were considered to represent 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 time point (Curtis et al., 2015; Runde et al., 2021). Discard mortality was assumed to be the sole source of mortality in this study for tags that were not recovered through harvest reports. Natural

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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 survival/mortality and time-to-event data (e.g., survival to end of study, mortality, tag loss, or 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 the relative rates of postrelease survival of fish from tag-recapture or tag-detection studies because it permits staggered entry of newly tagged individuals and does not require the researcher to know the fate of every tagged individual upon the 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 via maximum likelihood by using the coxph function in the R package survival (R Core Team, 2021; Therneau, 2024). All models contained hooking location as a factor. The first pair included models with and without water temperature, the second pair included models with and without fish total length, and the third pair included models with and without year. For each pair, a likelihood ratio test (LRT) was conducted in base R (R Core Team, 2021) to compare the fuller and lesser (simpler) models; a nonsignificant probability value ($P > 0.05$) for the LRT would indicate that the simpler model provided an adequate fit to the data.

We conducted a nonparametric Kaplan–Meier survival analysis that is designed to estimate absolute survival rates for known-fate (or inferred-fate) biological data (Dudley et al., 2016; Efron, 1988; Pollock et al., 1989). 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 that are 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, tag loss, or discard mortality. The Kaplan–Meier approach estimates survival S at time t ($S[t]$), with $S(t)$ representing the conditional probability of surviving beyond time t given that 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 95% CI for discard mortality as 1 − survival probability for each release treatment. Fitting of the survfit2 function permitted the estimation of survival at any time point after the entry of each individual into the study (date of tagging).

RESULTS

We assigned fates to 79 tagged Red Snapper that were 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 jaw-hooked fish 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 that were recompressed in 2019, movement data from nine fish either resighted or recaptured in 2019 and three fish 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.

We found that hooking location was an important predictor of survival/mortality in Cox proportional hazards models but not sea surface temperature, fish total length, or year. The LRT comparing Cox proportional hazards models with versus without sea surface water temperature was nonsignificant ($P = 0.828$). Similar results were found for the LRTs comparing models with versus without fish total length ($P = 0.472$) and with versus without year ($P = 0.360$). Thus, we estimated survival rate by hook treatment alone.

In general, fate classifications differed between hook 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 individuals that lost their tags. In contrast, the majority of fates for deep-hooked Red Snapper were individuals that experienced discard mortality (Table 2). All fish that were believed to have suffered discard mortality experienced this fate on their day of capture and release (day 0) except for a single deep-hooked fish that experienced discard mortality on day 1 (1 d after tagging and release; Figure 5; Table 1). Survival was higher for jaw-hooked fish than for deep-hooked fish (Figures 5 and 6). The mean rate of discard survival for the jaw-hooked treatment was 0.937 (95% CI = 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 (95% CI = 0.001–0.122) for the jaw-hooked group and 0.875 (0.543–0.966) for the deep-hooked group (Figure 6).

DISCUSSION

Our study reveals that discard outcomes for recompressed Red Snapper are likely to be very different for fish with versus 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 the rates used in the Atlantic Red Snapper assessment (Southeast Data, Assessment,

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Table 1. Information on 79 Red Snapper that were acoustically tagged and released in a variety of conditions during 2019 and 2023 in waters 38 m deep in Raleigh Bay, North Carolina. Tagged fish were released at depth with a descender device and monitored with an array of acoustic receivers, and their fates were estimated based on movement profiles. Fish that were assigned a fate of alive at the end of the study were considered still alive when the acoustic receivers were removed from the seabed (TL = total length, mm; deep-hooked = hooked in the gill, esophagus, or stomach).

Fish number	Date tagged	TL (mm)	Deep-hooked?	Assigned fate	Days from tagging to fate
1	May 7, 2019	520	No	Lost tag	0
2	May 7, 2019	700	No	Emigrated	131
3	May 7, 2019	720	No	Harvested	113
4	May 7, 2019	685	No	Lost tag	6
5	May 7, 2019	665	No	Lost tag	98
6	May 7, 2019	785	No	Lost tag	29
7	May 7, 2019	635	No	Emigrated	50
8	May 7, 2019	680	No	Lost tag	113
9	May 7, 2019	750	No	Lost tag	19
10	May 7, 2019	790	No	Lost tag	79
11	May 7, 2019	500	No	Discard mortality	0
12	May 7, 2019	705	No	Emigrated	81
13	May 7, 2019	710	No	Lost tag	13
14	May 7, 2019	760	No	Alive at study's end	223
15	May 7, 2019	740	No	Lost tag	55
16	May 7, 2019	720	No	Lost tag	68
17	May 7, 2019	795	No	Lost tag	114
18	May 7, 2019	390	Yes	Discard mortality	0
19	May 7, 2019	690	No	Lost tag	44
20	May 7, 2019	730	No	Lost tag	7
21	Aug 13, 2019	735	No	Emigrated	107
22	Aug 13, 2019	750	No	Emigrated	44
23	Aug 13, 2019	760	No	Alive at study's end	125
24	Aug 13, 2019	715	No	Lost tag	0
25	Aug 13, 2019	735	No	Lost tag	34
26	Aug 13, 2019	750	No	Discard mortality	0
27	Aug 13, 2019	425	No	Lost tag	61
28	Aug 13, 2019	790	No	Lost tag	48
29	Aug 13, 2019	695	No	Discard mortality	0
30	Aug 13, 2019	685	Yes	Discard mortality	0
31	Aug 13, 2019	750	No	Lost tag	111
32	Aug 13, 2019	720	No	Emigrated	124
33	Aug 13, 2019	775	No	Emigrated	124
34	Aug 13, 2019	845	No	Emigrated	120
35	Aug 13, 2019	745	No	Emigrated	124
36	Aug 13, 2019	755	No	Emigrated	106
37	Aug 30, 2019	410	No	Emigrated	77
38	Sep 22, 2019	475	No	Lost tag	45
39	Aug 11, 2023	550	Yes	Discard mortality	0
40	Aug 11, 2023	560	No	Lost tag	68
41	Aug 19, 2023	735	No	Lost tag	14
42	Aug 19, 2023	730	Yes	Discard mortality	0
43	Aug 19, 2023	510	No	Discard mortality	0
44	Aug 19, 2023	655	Yes	Emigrated	40
45	Aug 19, 2023	585	No	Lost tag	38
46	Aug 19, 2023	645	No	Alive at study's end	89
47	Aug 19, 2023	725	No	Lost tag	29
48	Aug 19, 2023	625	Yes	Discard mortality	0
49	Aug 19, 2023	550	Yes	Discard mortality	0
50	Aug 19, 2023	525	No	Alive at study's end	89
51	Aug 19, 2023	530	No	Alive at study's end	89
52	Aug 19, 2023	660	No	Alive at study's end	89
53	Aug 28, 2023	630	Yes	Discard mortality	0
54	Aug 28, 2023	670	No	Alive at study's end	80
55	Aug 28, 2023	670	No	Alive at study's end	80
56	Aug 28, 2023	620	Yes	Discard mortality	0

(*Continued*)

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Table 1. (*Continued*)

Fish number	Date tagged	TL (mm)	Deep-hooked?	Assigned fate	Days from tagging to fate
57	Aug 28, 2023	585	Yes	Discard mortality	0
58	Aug 28, 2023	675	No	Alive at study's end	80
59	Aug 28, 2023	715	No	Alive at study's end	80
60	Aug 28, 2023	470	No	Alive at study's end	80
61	Aug 28, 2023	540	Yes	Discard mortality	0
62	Aug 28, 2023	615	No	Alive at study's end	80
63	Aug 28, 2023	680	Yes	Discard mortality	1
64	Aug 28, 2023	430	No	Lost tag	29
65	Aug 28, 2023	520	Yes	Lost tag	44
66	Aug 28, 2023	665	Yes	Discard mortality	0
67	Aug 28, 2023	680	No	Alive at study's end	80
68	Sep 25, 2023	585	No	Alive at study's end	52
69	Sep 25, 2023	585	No	Alive at study's end	52
70	Sep 25, 2023	595	No	Alive at study's end	52
71	Sep 25, 2023	605	No	Lost tag	40
72	Sep 25, 2023	565	Yes	Discard mortality	0
73	Sep 25, 2023	560	No	Alive at study's end	52
74	Sep 25, 2023	525	Yes	Discard mortality	0
75	Sep 25, 2023	605	No	Alive at study's end	52
76	Sep 25, 2023	590	No	Alive at study's end	52
77	Sep 25, 2023	545	No	Alive at study's end	52
78	Sep 25, 2023	760	No	Emigrated	41
79	Sep 25, 2023	780	No	Alive at study's end	52

Table 2. Sample size (*n*) and proportion (Prop), by release condition, for each of five assigned fates of 79 Red Snapper that were acoustically tagged and released as recompressed fish during 2019 and 2023 within an acoustic array deployed in waters 38 m deep in Raleigh Bay, North Carolina. Fish were assigned discard fates based on individual movement profiles within the array (deep-hooked = hooked in the gill, esophagus, or stomach).

	Fate									
	Alive		Emigrated		Harvested		Lost tag		Discard mortality	
Release condition	***n***	**Prop**	***n***	**Prop**	***n***	**Prop**	***n***	**Prop**	***n***	**Prop**
Jaw-hooked	21	0.33	12	0.19	1	0.02	25	0.40	4	0.06
Deep-hooked	0	0.00	1	0.06	0	0.00	1	0.06	14	0.88

and Review, 2021). The conservation benefit of this level of discard mortality reduction by using recompression for improving U.S. 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 the results of this study will be useful for stock assessment scientists to consider as input for the forthcoming 2025–2026 benchmark assessment modeling of the U.S. South Atlantic Red Snapper stock (i.e., 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 the fates obtained from the telemetry data were accurately assigned.

Our project is timely because it updates estimates of discard mortality that can be used to improve the accuracy of assessments of U.S. 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% CI 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 is 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 U.S. South Atlantic region (Vecchio et al., 2020). Recent (2020) projections using Marine Recreational Information Program data estimated that 21% fewer Red Snapper would experience discard mortality if recompression was hypothetically used 100% of the time to mitigate barotrauma in U.S. 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 & 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

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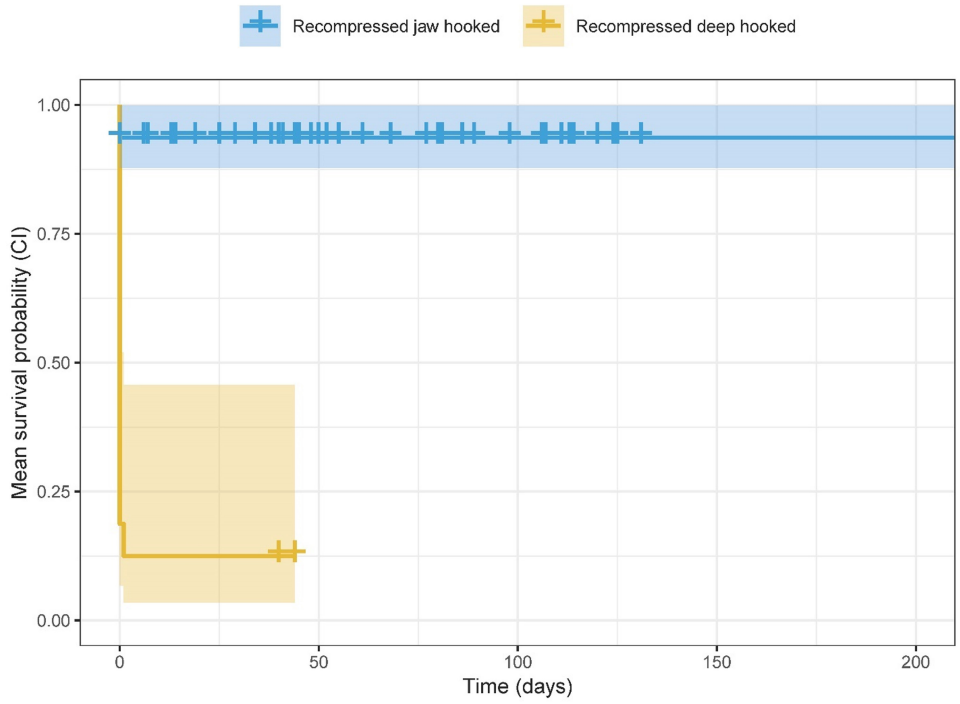

Figure 5. Mean survival probability (line; *y*-axis; with 95% CI shown as shaded area) versus time (d) postrelease (*x*-axis) for Red Snapper that were studied for fates using an acoustic array deployed in waters 38 m deep in Raleigh Bay, North Carolina. Survival was estimated with a Kaplan–Meier analysis for each of two different release treatments: jaw-hooked and recompressed fish (blue line and shading), and deep-hooked and recompressed fish (orange line and shading). No jaw-hooked recompressed fish died after the day of release (after day 0); hence, the line and shaded area are horizontal. The plus symbols (+) denote instances of censoring individuals of each treatment type.

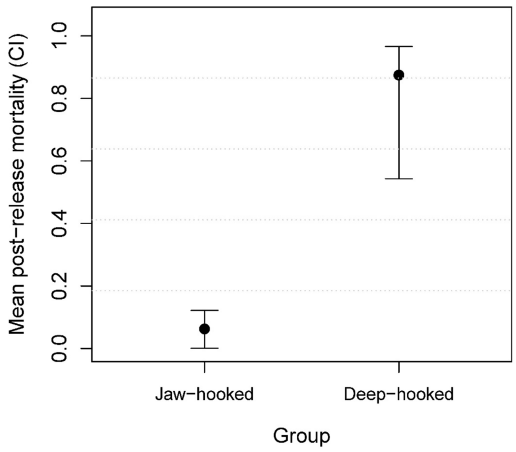

Figure 6. Mean (±95% CI) estimates of proportional discard mortality probability (*y*-axis) for recompressed Red Snapper caught from waters 38 m deep in Raleigh Bay, North Carolina. Discard mortality (1 − survival) was estimated using results from a Kaplan–Meier analysis for two different treatments (*x*-axis): jaw-hooked fish and deep-hooked fish. All fish were released at depth with a descender device.

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 (Bohaboy et al., 2020; Campbell et al., 2014; Curtis et al., 2015). However, model fits showed that the inclusion of sea surface water temperature into a Cox proportional hazards model did not improve the fit relative to a model without this covariate. A similar result was found when including fish total length in 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., 2022b).

Our estimate of discard mortality for hook-traumatized Red Snapper is higher than those reported in previous studies (see Campbell et al., 2014). We are unsure what may have contributed to the differences among studies. For example, Burns and Restrepo (2002) estimated that Red Snapper with hook trauma had a discard mortality rate of 43%, or 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 fivefold greater than that of conspecifics without hook trauma. The effect of hook trauma was estimated to be even greater in the current study; fish suffering trauma had a 14-fold higher discard mortality than fish without trauma. However, multiplying the upper limit of the 95% CI for the discard mortality multiplier of hook-traumatized fish from the 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

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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 & Buckel, 2004; Sauls & 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 (Bohaboy et al., 2020; Cooke & Danylchuk, 2020; Fobert et al., 2009).

In assigning fates, we used results provided by a growing body of literature that has studied fine-scale Red Snapper movements via acoustic telemetry (Bacheler et al., 2021; Bohaboy et al., 2020, 2022; Runde et al., 2021). 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 of 200 m in 2019. 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 in which 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/s; this was greater than in 2019, and we suspect that it was due to the greater spacing between receivers, higher error in location, and higher resolution (0.3 m) and reduced accuracy (±3.4 m) of tags in 2023 relative to 2019 (resolution: 0.15 m; accuracy: ±1.4 m). These increases in error likely contributed to occasional spurious positions of live Red Snapper, which in turn could have led to spikes in the estimated speed of live Red Snapper above 2.0 m/s (values that were not seen in 2019). In 2023, we observed these speed spikes in several fish, including some positive controls; therefore, we are confident that such speed 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 Red Snapper fisheries in the U.S. 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. Recent research into Red Snapper discard mortality using acoustic technologies (Bohaboy et al., 2022; Curtis et al., 2015; Runde et al., 2021; 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 the 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. Roughly 10% of Red Snapper caught from shallower depths (30 m) were unable to submerge after 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 (Bohaboy et al., 2020; Curtis et al., 2015). Discard mortality rates of jaw-hooked recompressed fish from those two studies were slightly higher than the rate observed here, but direct comparisons are difficult owing to the differing depths at which studies were conducted. Bohaboy et al. (2020) reported that 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 U.S. Atlantic (Bacheler et al., 2016, 2024; Vecchio et al., 2020) and where this study occurred, are the depths over which barotrauma mitigation appears important for improving the discard survival of reef fish (Rudershausen et al., 2023; Runde et al., 2021). 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 (Runde et al., 2021; Sauls et al., 2016; this study).

Self-submersing fish were not included in our analysis because a primary goal was to understand discard mortality rates of fish that were treated with barotrauma mitigation. As such, we did not have a true insight into mortality rates of untreated fish because, when possible, we recollected fish if they fell off the recompression device and then began the recompression process again. Seven fish that escaped our recollection 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-submersed at the depth of the study area. This would help to refine depth-specific guidance for using barotrauma mitigation on Red Snapper. Some depths at which recreational anglers catch Red Snapper in the U.S. Atlantic (Vecchio et al., 2020) may be sufficiently shallow (<30 m) that the benefits of rapidly releasing untreated fish may outweigh the benefits of taking the time to mitigate barotrauma (SAFMC, personal communication).

Mortality-by-condition, such as estimated in this study, does not provide all the information required to estimate the numbers of dead discards in either the recreational fishery or the 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 subsection of the region and for specific fishing modes (Runde et al., 2021; Vecchio et al., 2020). Researchers could obtain contemporary fishery-dependent information on the frequency of various angling practices and could apply

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these gears and techniques during field experiments in which discard mortality is estimated. Such an approach was recently taken to estimate discard mortality in the hook-and-line fishery for Dolphinfish *Coryphaena hippurus* in the western North Atlantic (Rudershausen et al., 2019).

The circle hook requirement for the U.S. 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 U.S. Atlantic (headboats) to estimate deep-hooking rates and overall discard mortality rates for the Red Snapper recreational fishery. For the U.S. Atlantic recreational reef fishery, such estimates of proportional releases by condition are needed in both subregions (south and north of 28°N) and for all recreational fishing modes: private, for-hire, and headboat. Red Snapper discard mortality increases with the depth of capture (Bohaboy et al., 2022; Campbell et al., 2014; Curtis et al., 2015; Pulver, 2017), 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 (Marine Recreational Information Program) 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 U.S. South Atlantic federal fisheries management region due to high numbers of regulatory discards (Overton et al., 2008; Rudershausen et al., 2007) and increases in recreational fishing activity over recent years (National Marine Fisheries Service, 2024; Shertzer et al., 2019). For example, the number of released Red Snapper exceeded the number harvested by roughly 25-fold in the U.S. Atlantic during 2023 (National Marine Fisheries Service, 2024). Predictions indicate that high discard mortality for some snapper/grouper species coupled with increasing recreational fishing activity in the U.S. Atlantic will, within the next decade, lead to 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.

DATA AVAILABILITY

Data are available upon request to the corresponding author.

ETHICS STATEMENT

Fish were tagged under North Carolina State University animal welfare protocols, Institutional Animal Care and Use Committee permit 28-284-O.

FUNDING

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CONFLICTS OF INTEREST

Brendan Runde holds the position of associate editor for the *North American Journal of Fisheries Management* and has not peer reviewed or made any editorial decisions for this paper.

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