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ARTICLE

Discard Mortality of Red Snapper Released with Descender Devices in the U.S. South Atlantic

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Abstract
Fishery regulations mandate the release of many caught fish, elevating the importance of having accurate estimates of discard mortality. Red Snapper *Lutjanus campechanus* are overfished and undergoing overfishing in the southeast U.S. Atlantic, in part due to the high number of releases that die from discard mortality. We used acoustic telemetry to track the fine-scale movements of hook-and-line-caught Red Snapper released with descender devices at a hard-bottom site off North Carolina, USA. Movement characteristics of known-fate (live and dead) Red Snapper were used to infer fates of other individuals, from which we generated a proportional mortality estimate of 0.08 (95% CI = 0.00–0.17) for successfully descended Red Snapper with no hook trauma. This best-case mortality estimate was then used in a simulation to estimate overall Red Snapper discard mortality for the recreational fishery in the southeast U.S. Atlantic based on hooking location and a depth of approximately 37 m. For this fishery, we estimated the median proportional rate of discard mortality to be 0.13 (2.5% and 97.5% percentiles = 0.10, 0.17) if all released individuals were descended. This estimate is lower than the discard mortality values (~0.2–0.3 for the recreational fishery) used in the current Red Snapper stock assessment, but it is likely not reflective of the current reality given that descender use is not 100% in this region; this estimate is also depth specific. Increased use of descender devices will reduce discard mortality for Red Snapper, enhancing efforts to rebuild this stock.

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In recent years, estimating the quantity and disposition of released fish has been a topic of considerable interest (Cooke and Cowx 2004; Benaka et al. 2016) due to increasing numbers of discards in many fisheries, either as a response to stricter regulations or cultural changes (Quinn 1996; Catchpole et al. 2005; Suuronen and Erickson 2010; Feekings et al. 2013). In Europe, a landing obligation has banned releasing fish in certain scenarios (Guillen et al. 2018), though discarding still occurs sometimes due to noncompliance or exemptions (Villasante et al. 2019). In other regions, including the United States, discards continue to be a substantial portion of total catch for many fisheries (Zeller et al. 2018). Worldwide, estimation of discard mortality is important for determining overall fishing mortality and assessing stocks for fisheries in which discarding occurs (Viana et al. 2013; Runde et al. 2020a).

One method of estimating discard mortality in fish is with electronic tagging. Use of electronic tags and tracking gear for survival studies has become more widespread in recent years as technology has improved (Kays et al. 2015; Crossin et al. 2017). For many such studies, recapture of tagged animals is unlikely, so researchers use behavioral information provided by the tag to assign fates, such as survival or mortality (Yergey et al. 2012; Capizzano et al. 2016; Kerns et al. 2016; Hightower and Harris 2017). Movement data, including migrations, depth utilization, speed, and acceleration, have all been used to assign fates (Curtis et al. 2015; Villegas-Ríos et al. 2020), as abnormalities in these factors can often indicate mortality (Klinard and Matley 2020). Recent innovations in passive acoustic telemetry have improved such analyses by allowing for the calculation of fine-scale position information of tagged animals. Increased spatial resolution can result in reduced uncertainty when fates are assigned in discard mortality studies (Bohaboy et al. 2020).

The Red Snapper *Lutjanus campechanus* is a recreationally and commercially important reef fish in the southeast U.S. Atlantic Ocean (SEUSA) and Gulf of Mexico. In the SEUSA, Red Snapper are currently listed as overfished and undergoing overfishing (NOAA Fisheries 2020). This has led to strict harvest regulations in an effort to rebuild the stock; in recent years, recreational landings have been permitted on fewer than 10 d annually. Commercial harvest over this period has been limited to small quotas and trip limits. Despite strict regulations controlling harvest, the Red Snapper stock continues to experience high fishing mortality as a result of discard mortality (SEDAR 2021). As part of a multispecies fishery, Red Snapper are often caught when other species are targeted. Two of the dominant sources of discard mortality in Red Snapper are barotrauma and hook trauma (Burns and Restrepo 2002; Campbell et al. 2014; Bohaboy et al. 2020).

Alleviating barotrauma in released fish is possible through the use of a variety of tools, including descender devices (Theberge and Parker 2005; Pribyl et al. 2012; Drumhiller et al. 2014). Briefly, a descender (or descending) device is a removable, weighted apparatus that is capable of returning released fish to a depth where expanded gases recompress and the fish can maintain neutral buoyancy on its own (Theberge and Parker 2005). Descender devices are often preferable to puncturing an inflated fish (venting) given that they are not invasive. The effectiveness of descender devices has been demonstrated for a variety of species worldwide (Eberts and Somers 2017) and specifically for Red Snapper in the Gulf of Mexico (Drumhiller et al. 2014; Curtis et al. 2015; Ayala 2020; Bohaboy et al. 2020). In an effort to curtail high discard mortality of Red Snapper and other reef species in the SEUSA, the South Atlantic Fishery Management Council implemented Regulatory Amendment 29 to the Snapper–Grouper Fishery Management Plan (which guides management for reef fishes) in June 2020 (SAFMC 2020). This amendment requires the presence of a descender device on any vessel fishing for or possessing reef species in the SEUSA; however, use is not required and is left to the discretion of individual anglers.

Deep hooking (hooking in the gills, esophagus, or gut), which varies by hook type and offset, increases discard mortality across demersal species (Kaimmer and Trumble 1998; Overton et al. 2008; Rudershausen et al. 2014) and in Red Snapper (Burns and Restrepo 2002). Attempts to reduce mortality resulting from hook trauma include regulations requiring the use of circle hooks in most of the SEUSA (SAFMC 2010), as circle hooks have been demonstrated to have lower rates of deep hooking in reef species as compared to J-hooks (Sauls and Ayala 2012). This requirement was modified in July 2020 to specify that circle hooks must be non-offset. However, compliance with hook type regulations is known to be below 100%, and until recently anglers were permitted to use offset and non-offset circle hooks; thus, hook type usage in the fishery continues to vary (Sauls and Ayala 2012; Sauls et al. 2017). Therefore, estimates of fishery-wide discard mortality for Red Snapper should attempt to take into account the prevalence of different hook types used in the fishery and the associated differences in mortality.

The use of descender devices to mitigate barotrauma is a relatively new concept in the SEUSA, and current release practices in this region favor venting over descending (Crandall et al. 2018; Vecchio et al. 2020). As managers and scientists work to promote the use of descender devices, their ability to lobby fishery participants is limited by uncertainty in the magnitude of the benefits that could be reaped if all released Red Snapper were descended. A fishery-wide estimate of a discard mortality rate with universal descender use that incorporates both major sources of discard mortality (barotrauma and hooking injury) is needed to quantify potential reductions in dead discards and account for those conservation benefits in future stock assessments. Furthermore, an estimate of fishery-wide discard mortality for Red Snapper specific to the SEUSA would be valuable, as resource managers and stakeholders typically prefer the use of region-specific estimates of discard mortality for regulatory decision making.

Here, we took a two-stage approach to estimating fishery-wide discard mortality for Red Snapper caught in the SEUSA. First, we employed fine-scale acoustic positioning at an ocean site off North Carolina to estimate discard mortality of telemetered Red Snapper with no hook trauma after release with a descender device. Second, using our empirical estimate from the first stage as well as previously collected data on hook type, mortality from hooking, and hooking location for released Red Snapper and assuming a scenario of 100% compliance in descender use, we generated a fishery-wide discard mortality estimate for Red Snapper in the SEUSA region.

METHODS

Study site.— We performed this study at a low-relief area in Raleigh Bay, North Carolina, USA, known as the "Chicken Rock" (Figure 1). This site is a mixture of hard natural reef structure and sand and lies in approximately 37-m depth. We chose this area because (1) we had prior information suggesting high Red Snapper density at the site, (2) Red Snapper commonly occur at this depth (Bacheler et al. 2016), and (3) the majority of recreational discarding in the SEUSA takes place in depths less than 40 m (Sauls et al. 2017).

Submersible receiver deployment and retrieval.— We deployed 20 Vemco VR2AR (Innovasea, Bedford, Nova Scotia, Canada) receivers arranged in a grid at the Chicken Rock on April 17, 2019 (Figure 1). This receiver configuration allowed for a Vemco Positioning System (VPS) analysis; VPS uses time offsets of detections arriving at different receivers to calculate fine-scale positions of each tag (Espinoza et al. 2011). Each receiver was connected to a 36-kg steel ballast (below) and a 28-cm-diameter plastic trawl float (above). Each VR2AR contained an internal transmitter for time synchronization between receivers as well as an acoustic release to allow for retrieval at the termination of the study. A Vemco V13T-1x transmitter was deployed in the array on the same day for the purposes of calculating positional error and collecting water temperature information to calculate sound speed velocity throughout the duration of the study. The reference transmitter was connected to a weight below and a float above and transmitted 69-kHz pings on a 550–650-s random interval. We retrieved the receivers on December 16, 2019.

Fish capture, tagging, and data collection.— We fished for Red Snapper in the summer and fall of 2019 with hook and line using non-offset 8/0 circle hooks or J-hooks baited with Atlantic Menhaden *Brevoortia tyrannus*. Upon capture, we recorded the hooking location for each individual. Fish were measured for TL (mm) and externally tagged with Vemco V13P-1x transmitters (130–230-s random interval; 613-d battery life; 69 kHz) that contained a pressure sensor to determine the depth of each transmission (accuracy = ±1.7 m). We attached transmitters externally to reduce the harmful effects of the surface interval (Burns et al. 2002), improve detectability (Dance et al. 2016), and separate the effects of descending from incidental release of expanded abdominal gas that may occur during internal tagging (Curtis et al. 2015; Johnson et al. 2015).

Transmitters were prepared for external attachment by tightly wrapping a length of stainless-steel wire around the nontransmitting end and adhering the two with marine adhesive and heat shrink (Figure 2A). One end of the wire extended perpendicularly away from the transmitter by approximately 15 cm; this end was sharpened. When a Red Snapper was captured, a wet towel was placed over its head and the sharpened transmitter wire was inserted laterally through the dorsal musculature. The wire was pulled so that the transmitter was tight against the fish's left side (Figure 2B, C). An aluminum washer was threaded onto the protruding wire on the fish's right side, followed by a #1 steel crimp. The crimp and washer were held firmly against the fish's right side, the crimp was compressed, and the excess wire was cut. More detailed description of this approach is provided by Bacheler et al. (2021) and (in press). Each transmitter and washer were marked with a large, brightly visible individual fish number. Most Red Snapper were descended with a weighted SeaQualizer device (Figure 2B) that was set to open at a depth of 31 m, although for a few individuals the device opened at the surface prior to descent (due to user error) and the fish swam down on their own. Furthermore, several individuals returned to the surface (floated) after attempted descent; these individuals were re-descended and this repetition was noted. We recorded descended releases with a GoPro Hero 4 upward-looking camera (Figure 2B) to gather information on the disposition of each tagged fish. Total surface time for each tagged Red Snapper (other than those requiring a second descent) was approximately 90 s.

In addition to releasing live Red Snapper, we sacrificed, tagged, and descended a subset of Red Snapper to observe the behavior of scavengers or predators in the area and thereby establish a negative control for assigning fates. Other than movements that were attributable to typical tides and currents, any movements detected from these "negative control" individuals were considered to be from another animal. This methodology has been utilized in previous telemetry-based survival studies to compare movement data from known-dead individuals with the unobserved fates of live releases (Yergey et al. 2012; Muhametsafina et al. 2014; Runde et al. 2020b).

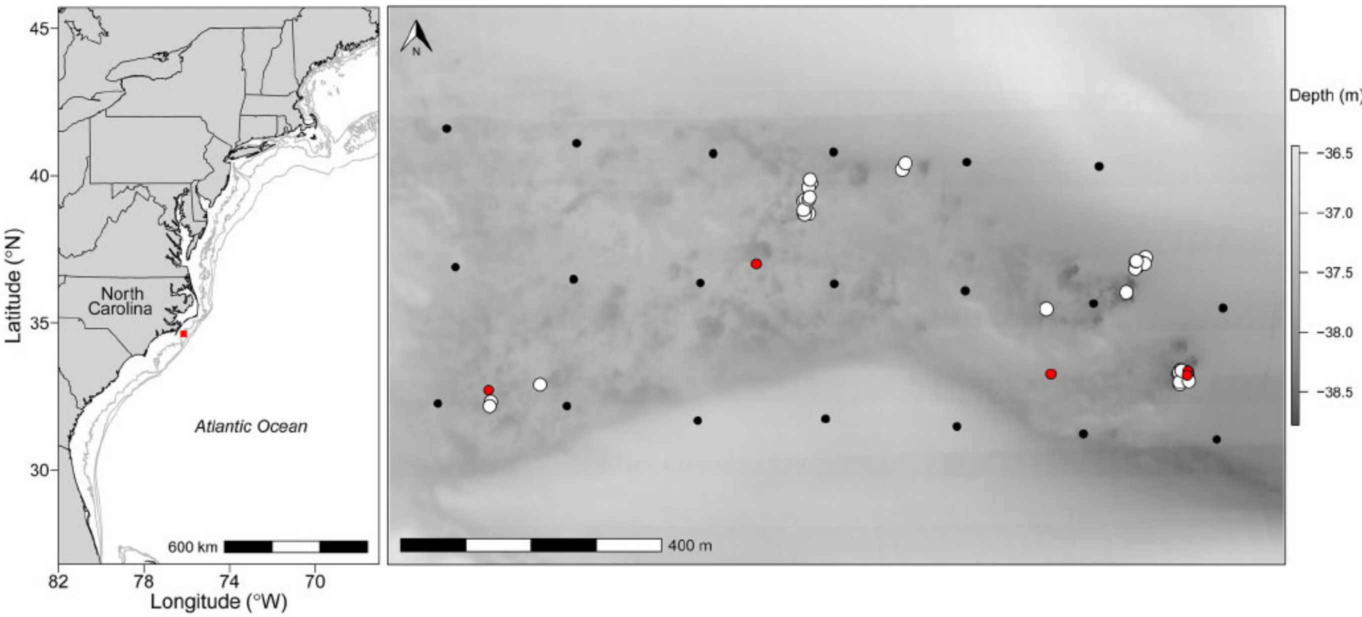

FIGURE 1. Map of the U.S. East Coast (left), showing the location of our study site (red square) off North Carolina. Gray lines represent bathymetry lines at 30-, 50-, and 100-m depth. Map of the study area (right) at the Chicken Rock in Raleigh Bay off North Carolina. Background shading shows bathymetry, where darker is deeper. Black dots represent locations of acoustic receivers, white dots represent locations of Red Snapper that were released alive, and red dots represent locations of Red Snapper that were sacrificed and descended dead.

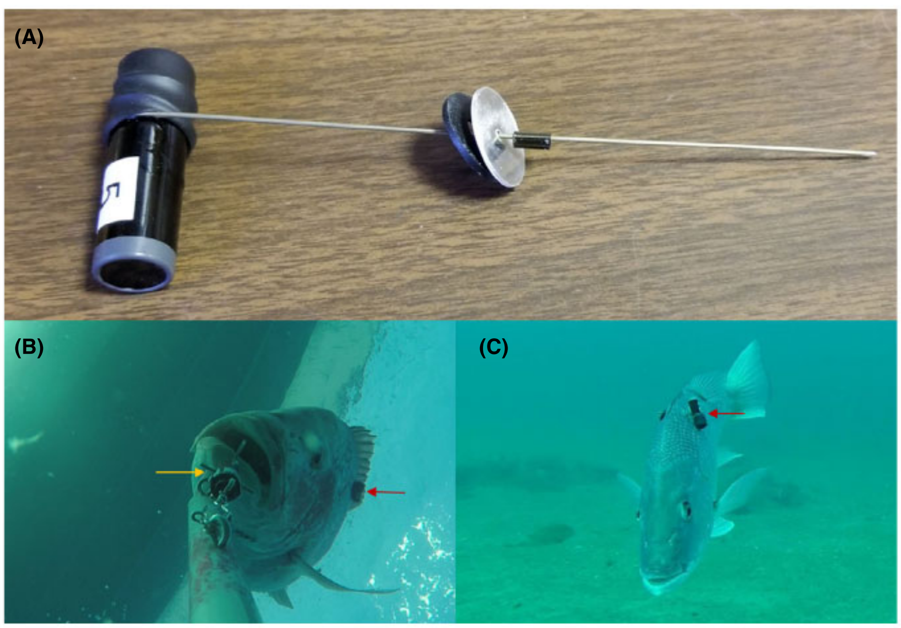

FIGURE 2. **(A)** A Vemco V13P transmitter prepared for attachment to a Red Snapper; **(B)** a freeze frame from an upward-facing video of a Red Snapper with an attached transmitter (red arrow) being descended with a SeaQualizer device (yellow arrow); and **(C)** a freeze frame from a video camera attached to bait, showing a Red Snapper with an attached transmitter (red arrow) several weeks after release.

In pursuit of research goals that were not the focus of this paper, we deployed baited fish traps within the receiver array on several occasions (Bacheler et al. 2021, and in press). Each trap was equipped with a GoPro Hero 4 outward-looking camera to record fish in the area. Videos were examined for the presence of tagged Red Snapper.

When tagged Red Snapper were observed and the transmitter number was readable, this information was recorded and was used to verify survival of specific tagged Red Snapper (i.e., positive control).

Data processing and analysis.— From VPS information, we generated time series data of Red Snapper speeds as the difference in position divided by the duration between successive detections. This resulted in minimal estimates of speed, as it arithmetically assumes that fish moved in a straight line between consecutive detections (Rowcliffe et al. 2012). Red Snapper speeds were only calculated if the temporal gap between subsequent detections was less than 20 min.

We examined time series of position, depth, and speed for each Red Snapper on a daily basis. We compared the movements of individuals that were released alive with the movements of known-fate individuals. These known-fate individuals were those that were sacrificed, tagged, and descended dead (negative controls) as well as those whose unique transmitter numbers were observed on video or those that were recaptured (positive controls). For the positive control group, we treated movement data as a positive control only from the day of tagging until the day of re-sighting or recapture (and not after). We attempted to apply hidden Markov models to these data to assign fates (sensu Runde et al. 2020b), but these attempts were unsuccessful given similarities in movements among some negative and positive control fish. Instead, from the movements of the two control groups and information provided by the reference tag, we generated a fate assignment decision tree that was used to determine whether each Red Snapper survived, lost its tag, or died (Figure 3). Deaths were inferred when movements did not match any behaviors observed in positive control individuals, and we assumed that all deaths were a result of discard mortality; given the short nature of our study, observing natural mortality was deemed unlikely. Tag loss was inferred if depth was constant at or near the seafloor and horizontal movements were no greater than what could be explained by horizontal position error (determined from the reference transmitter). When fates were uncertain, we used ancillary information to assist in fate assignment. For example, Red Snapper sometimes make vertical migrations as a result of upwelling (Bacheler et al. 2021), so if vertical movements of an uncertain-fate Red Snapper occurred during a known upwelling event, the fish was considered to be alive. For instances in which Red Snapper were determined to be alive but ceased to be detected prior to the termination of the study, we assumed that they had emigrated from the study area.

Longitudinal data can be used to describe survival over time, which can be extremely beneficial when analyzing data such as ours (Benoît et al. 2015). We used a Kaplan–Meier (KM) nonparametric survivorship procedure to estimate discard mortality for Red Snapper tagged in this study (Cox and Oakes 1984; Pollock et al. 1989). We excluded Red Snapper from this analysis if they were not descended (i.e., swam down on their own). In addition, we excluded fish if they were descended multiple times due to floating after the first attempt. We cannot assume that the rate at which the descender devices in this study failed is equivalent to the failure rate in the fishery. Furthermore, the SeaQualizer is not the only available descender, so attempting to infer fishery-wide failure rates from our study (which used only the SeaQualizer) could be misleading. Therefore, the exclusion of these few individuals from our KM estimate represents a best-case scenario that could be modified in the future if per-device and per-fishery failure rates are accurately quantified. Similarly, we excluded Red Snapper from our KM estimate if they were deeply hooked. Rates of deep hooking vary substantially depending on hook type (Table 1), and given that hook type usage differs by year and fishery sector (Table 2) we elected to focus only on jaw-hooked individuals. We incorporated deep hooking into the fishery-wide estimate of discard mortality by using proportion of deep hooking and previously published estimates of discard mortality for deep-hooked Red Snapper. Fish that were classified as having lost their tag or having emigrated from the study area were censored on the date of their last detection. Thus, the KM estimate of discard mortality applies only to successfully descended Red Snapper with no hook trauma and can be used as a baseline best-case estimate.

We used estimates of discard mortality for descended fish from our study along with information on deep hooking from prior studies to generate an estimate of discard mortality for descended Red Snapper in the SEUSA recreational fishery at approximately 37 m. In the present study, neither of the two deep-hooked individuals survived (see Results); however, from other studies it is clear that some deep-hooked Red Snapper do survive, though at a much lower rate than those that are not deep hooked (Bohaboy et al. 2020). Burns and Restrepo (2002) documented a combined immediate plus delayed hooking mortality of 0.43 for deep-hooked Red Snapper. Furthermore, Bohaboy et al. (2020) estimated that traumatic hooking increased discard mortality of Red Snapper by a factor of five. Since our mortality estimate for non-deep-hooked Red Snapper was 0.08 (see Results), a fivefold increase (0.40) is consistent with the Burns and Restrepo (2002) estimate for deeply hooked individuals. We estimated the proportion of angled Red Snapper that are deep hooked, which is known to vary by hook type. Over the past decade, four main hook types have been used in the SEUSA Red Snapper fishery: non-offset circle hooks, offset circle hooks, non-offset J-hooks, and offset J-hooks (Sauls et al. 2015). To estimate the fishery-wide rate of deep hooking, we obtained data from the Florida Fish and Wildlife

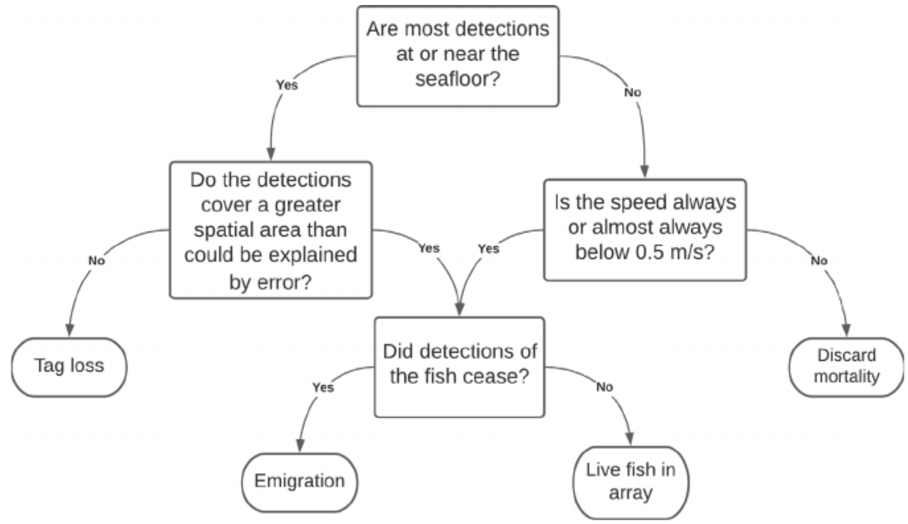

FIGURE 3. Decision tree for determining the fate of released Red Snapper.

Conservation Commission (FWC) on trends in hook type use as well as the rate of deep hooking by hook type (Sauls and Ayala 2016). The FWC has gathered information on hook type and hooking location of released Red Snapper observed from headboats since 2011 and from charter boats during the period from 2013 to 2015. To our knowledge, this is the only data set of onboard fishery-dependent observations for recreationally caught Red Snapper (and other species) in the SEUSA.

To estimate the discard mortality rate of descended Red Snapper, we used Monte Carlo simulations to estimate (1) the probability of deep hooking by the four hook types common in the fishery and (2) the survival probability of descended fish with and without hooking injuries. We generated beta distributions for the probability of each hook type (non-offset or offset circle hook or J-hook) based on annual proportions of each type used in the FWC data set (Table 2; Figure 4). Inputs for the estimation of these distributions were weighted by sample size. The four hook type probabilities were drawn from these beta distributions and normalized to sum to 1.0 within the R function rmultinom. Using these probabilities, a hook type was assigned to each individual in a virtual population of 2,000 fish. We then randomly assigned each individual a hooking location (deep or not) using the probability of deep hooking by hook type in the FWC data set. We again estimated beta distributions using annual proportions of deep hooking for each hook type weighted by sample size (Table 1; Figure 5).

After we had assigned a hooking location to each individual, we estimated mortality. For each individual that was not deep hooked, we generated a survival percentage from a normal distribution with a mean and SD taken from the KM survival estimate in the present study. For deeply hooked individuals, the survival rate was less obvious. Based on the results of Burns and Restrepo (2002) and Bohaboy et al. (2020), we elected to use a mean of 0.43 and an SD of 0.15 (which we thought captured a reasonable uncertainty in this value) for the mortality of deep-hooked fish in the Monte Carlo simulation. We drew a random value from a standard uniform distribution ($X \sim U[0, 1]$) for each fish to determine which individuals survived. If the random number was lower than the survival probability determined based on hooking location, then the individual was considered to have survived; otherwise, the individual was considered dead. We calculated the proportional mortality for the population. To estimate uncertainty, this simulation was conducted 10,000 times, with new draws from the beta distributions for probabilities of hook type and hooking location estimated in each loop. This number of iterations was sufficient to achieve stability in estimates. We generated median and 2.5% and 97.5% percentile values from the distribution of estimates; we present the median because the distribution was slightly asymmetrical. All analyses were conducted in R (R Core Team 2021).

RESULTS

Red Snapper tagging occurred on four dates in 2019: May 7, August 13, August 30, and September 22. Overall, we tagged 44 live Red Snapper. In addition, we sacrificed, tagged, and descended five Red Snapper. Red Snapper were released at several locations throughout the receiver array (Figure 1). All Red Snapper bore some sign of barotrauma, with the most common being a turgid abdomen and/or stomach eversion. Total lengths of all tagged individuals ranged from 380 to 860 mm (mean = 667 mm;

TABLE 1. Annual proportions of recreationally angled Red Snapper that were jaw hooked, categorized according to hook type, from the recreational fishery off the east coast of Florida. Sample sizes are in numbers of fish. Data are from the Florida Fish and Wildlife Conservation Commission and from Sauls and Ayala (2016).

Year	Hook type	Proportion jaw hooked	Sample size
	Charter fleet		
2013	Non-offset circle	0.969	286
	Offset circle	0.908	87
	Non-offset J	0.879	33
	Offset J	0.875	32
2014	Non-offset circle	0.946	297
	Offset circle	0.854	48
	Non-offset J	0.892	37
	Offset J	1.000	6
2015	Non-offset circle	0.900	10
	Offset circle	0.988	80
	Non-offset J	0.909	33
	Offset J	0.961	51
	Headboat fleet		
2011	Non-offset circle	0.909	22
	Offset circle	0.840	156
	Non-offset J	0.920	50
	Offset J	0.833	72
2012	Non-offset circle	0.970	33
	Offset circle	0.949	351
	Non-offset J	1.000	4
	Offset J	0.790	219
2013	Non-offset circle	0.833	12
	Offset circle	0.927	179
	Non-offset J	1.000	9
	Offset J	0.829	245
2014	Non-offset circle	0.966	29
	Offset circle	0.947	320
	Non-offset J	0.750	8
	Offset J	0.783	235
2015	Non-offset circle	1.000	8
	Offset circle	0.949	374
	Non-offset J	0.944	18
	Offset J	0.820	339
2016	Non-offset circle	1.000	24
	Offset circle	0.938	405
	Non-offset J	1.000	4
	Offset J	0.812	234
2017	Non-offset circle	0.979	47
	Offset circle	0.913	298
	Non-offset J	0.853	34
	Offset J	0.803	238
2018	Non-offset circle	1.000	1
	Offset circle	0.915	422
	Non-offset J	0.818	22
	Offset J	0.844	231
2019	Non-offset circle	0.724	29
	Offset circle	0.840	639
	Non-offset J	0.909	11
	Offset J	0.852	216
2020	Non-offset circle	NA	0
	Offset circle	0.851	121
	Non-offset J	1.000	6
	Offset J	0.864	103

Table 3). Three Red Snapper were able to escape the descender device at the surface and swim down under their own power. An additional three individuals resurfaced after initial descent and were descended a second time; the descender device failure rate in this study was therefore 7.3% (3/41, where the denominator does not include the three fish that swam down on their own). For the three fish that were descended improperly, video evidence showed that during their first decent, all three became detached from the device prematurely, and all three remained submerged after their second descent. Two Red Snapper that were descended alive were deep hooked. In total, 36 live Red Snapper were not deep hooked, were descended once only, and were therefore included in the KM survivorship procedure. Horizontal positional error varied daily from 0.5 to 1.9 m throughout the study, and most daily medians were around 1.0 m.

Eight tagged Red Snapper were observed on video and identified based on transmitter number, and one of those eight fish was subsequently recaptured. We recaptured one additional Red Snapper (tagged on May 7) during the tagging effort on August 13. Examination of movement data for these nine individuals generated a range of behavioral profiles that served as positive controls for fate assignment (Figure 6). These profiles were characterized by speeds almost always less than 0.5 m/s, with few momentary exceptions (e.g., Figure 6A), and the majority of detection locations typically matched areas of known hard-bottom structure (e.g., Figure 6B). Furthermore, positive controls usually used depths at or near the seafloor, though some fish occasionally utilized more of the water column (Figure 6C). This behavior is likely to be vertical thermotaxis that is associated with upwelling events (Bacheler et al. 2021). From the five Red Snapper that were descended dead, we obtained few detections. Four of the five disappeared from the array within 2 d of tagging, and one left the array but returned briefly and was last detected 6 d after tagging. The movement profiles from these individuals were characterized by forays to near-surface depths

TABLE 2. Annual proportions of Red Snapper caught by each of four hook types from the recreational fishery off the east coast of Florida. Sample sizes are number of fish. Data are from the Florida Fish and Wildlife Conservation Commission and from Sauls and Ayala (2016).

Year	Non-offset circle	Offset circle	Non-offset J	Offset J	Sample size
		Charter fleet			
2013	0.653	0.199	0.075	0.073	438
2014	0.765	0.124	0.095	0.015	388
2015	0.057	0.460	0.190	0.293	174
		Headboat fleet			
2011	0.073	0.520	0.167	0.240	300
2012	0.054	0.578	0.007	0.361	607
2013	0.027	0.402	0.020	0.551	445
2014	0.049	0.541	0.014	0.397	592
2015	0.011	0.506	0.024	0.459	739
2016	0.036	0.607	0.006	0.351	667
2017	0.076	0.483	0.055	0.386	617
2018	0.001	0.624	0.033	0.342	676
2019	0.032	0.714	0.012	0.241	895
2020	0.000	0.526	0.026	0.448	230

(Figure 7A), blips of relatively high speed (>0.5 m/s; e.g., Figure 7B), and wide-ranging positions that did not necessarily match locations of known hard-bottom structure (Figure 7A, B). These characteristics, along with those from the positive controls, were incorporated into our fate assignment decision tree (Figure 3). Furthermore, the number of detections per time obtained from negative control tags was very low, even for those that were detected across multiple days, likely as a result of the transmitter being inside a Red Snapper predator.

Using our decision tree (and ancillary information when necessary), we determined that the majority of Red Snapper in our study survived catch and release (Table 3). Both of the deep-hooked individuals experienced discard mortality on the day of tagging. All three Red Snapper that swam down under their own power survived. Finally, of three Red Snapper that required a second descent, one survived and two experienced discard mortality on the day of tagging. Of the 36 individuals that were included in the KM estimate, 33 survived and 3 experienced discard mortality. All three mortality events occurred on the day of tagging. Of the 33 remaining individuals, the majority

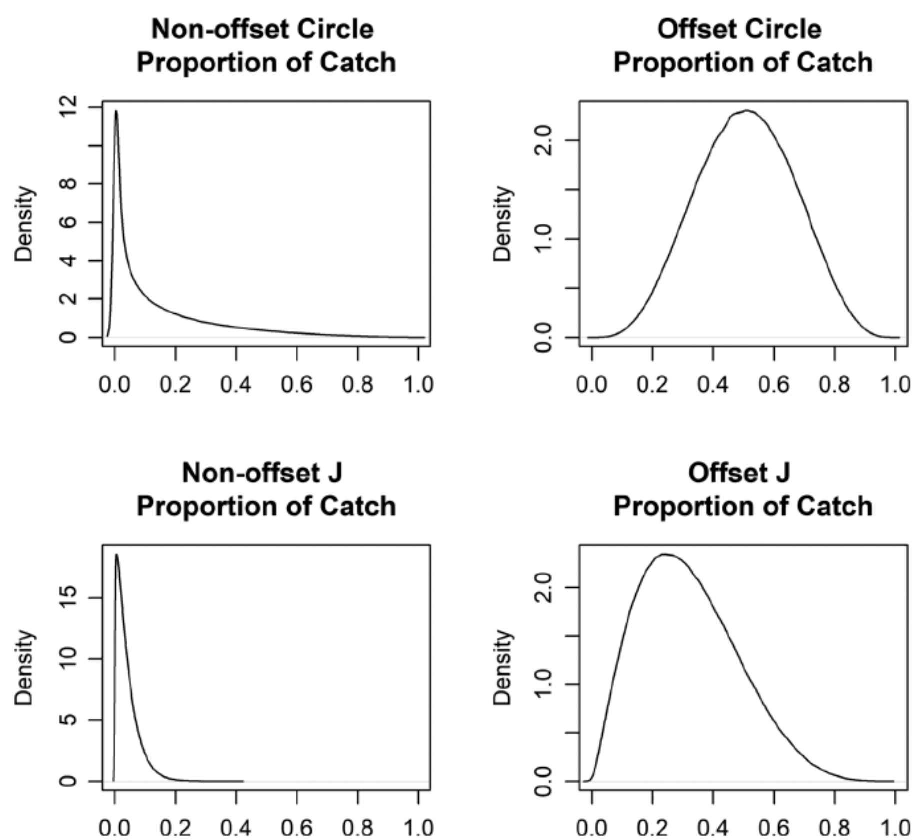

FIGURE 4. Estimated beta distributions describing the proportion of recreational Red Snapper catch with each of four hook types.

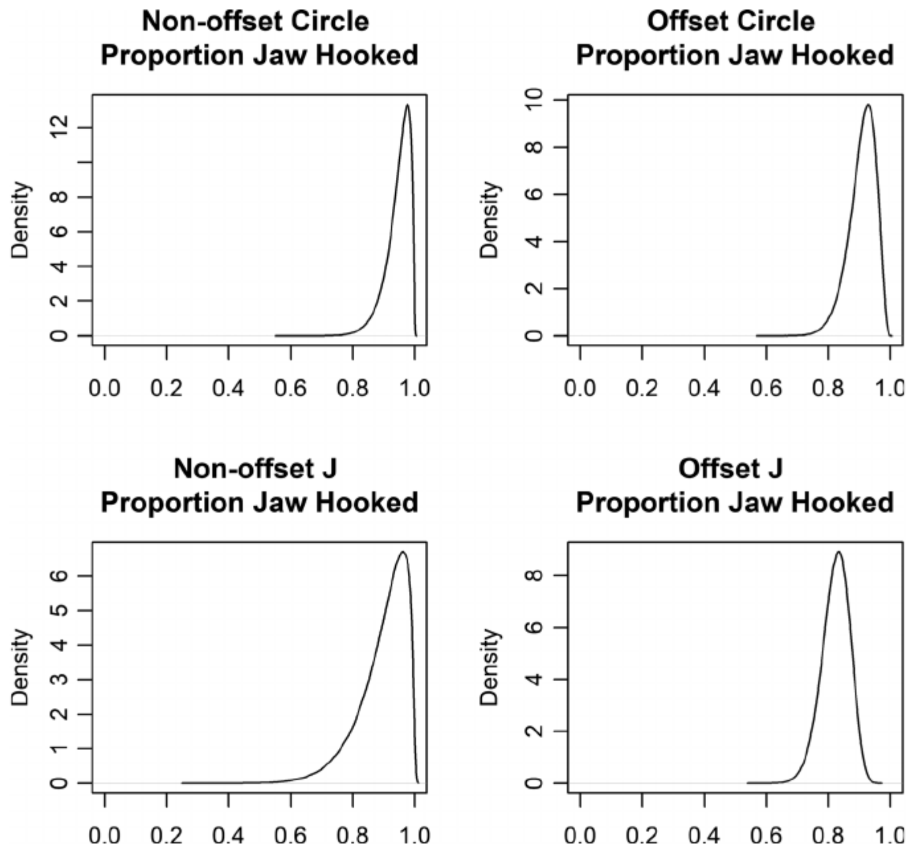

FIGURE 5. Estimated beta distributions describing the proportion of Red Snapper that became jaw hooked when caught with each of four hook types.

either lost their tags (e.g., Figure 8) or emigrated from the array prior to the termination of the study on December 16, 2019. All fish that were considered emigrations were last detected near the edge of the array.

Our overall mortality estimate for non-deep-hooked, descended fish in this study was 0.08 (95% CI = 0.00–0.17; Figure 9). At approximately 37-m depth and assuming 100% descended fish and recreational fishery-dependent hooking conditions, our Monte Carlo simulation resulted in a median estimated recreational discard mortality of 0.13 (2.5% and 97.5% percentiles = 0.10, 0.17).

DISCUSSION

We estimated a median recreational discard mortality rate of 13% for Red Snapper released at depth with descender devices. Our study did not include surface-released Red Snapper for comparison, since we descended every fish to maximize survival in pursuit of other research objectives. However, released Red Snapper sometimes float, even in depths shallower than where we worked (Campbell et al. 2010), so we are confident that our use of descenders decreased mortality. Our estimate also represents a decrease in mortality compared to previous estimates for this species—but only under the assumption that descender devices would be uniformly used and with a 0% failure rate in the fishery. These assumptions are currently aspirational, as descender use has been shown to be very low (Vecchio et al. 2020) and failures to properly descend occur with some regularity for a variety of reasons (Bellquist et al. 2019). The previous (2016) assessment for Red Snapper in the SEUSA applied discard mortality of 0.380 for the commercial fishery and 0.285 for the recreational fishery (Sauls et al. 2015; SEDAR 2017), but this assessment did not directly consider the potential for descender devices to mitigate barotrauma and improve survival. The most recent (2021) Red Snapper stock assessment in this region attempted to take into account some descender device use and modified discard mortality estimates downward for both the recreational and commercial sectors (SEDAR 2021). For the most recent time period in the assessment (post-2020), discard mortality values used in this assessment were 0.23 (sensitivity range =

TABLE 3. Information on Red Snapper tagged off the North Carolina coast in 2019. The "Times descended" column refers to whether the individual escaped prior to descending and swam down on its own (0), was descended appropriately and remained submerged (1), or floated after the initial descent attempt and had to be descended again (2). Fate assignments are our determination of what befell each fish (alive = the fish was still tagged and in the array at the end of the study; DM = the individual experienced discard mortality; descended dead = the fish was sacrificed and descended dead as a negative control). The "Days before event" column indicates the number of days that passed before the fate "event" was experienced. "Included in KM" refers to whether the individual was used for the overall survival estimate that was generated with a Kaplan–Meier survivorship procedure (N = no; Y = yes).

Fish number	Date tagged	TL (mm)	Gut hooked?	Times descended	Fate assignment	Days before event	Included in KM?
1	May 7	520	N	1	Tag loss	0	Y
2	May 7	700	N	1	Emigration	131	Y
3	May 7	720	N	1	Harvest	113	Y
4	May 7	685	N	1	Tag loss	6	Y
5	May 7	665	N	1	Tag loss	98	Y
6	May 7	785	N	1	Tag loss	29	Y
7	May 7	635	N	1	Emigration	50	Y
8	May 7	680	N	1	Tag loss	113	Y
9	May 7	720	N	0	Alive	223	N
10	May 7	750	N	1	Tag loss	19	Y
11	May 7	740	N	0	Tag loss	31	N
12	May 7	860	N	1	Tag loss	86	Y
13	May 7	500	N	1	DM	0	Y
14	May 7	705	N	1	Emigration	81	Y
15	May 7	710	N	1	Tag loss	13	Y
16	May 7	760	N	1	Alive	223	Y
17	May 7	765	N	0	Tag loss	83	N
18	May 7	740	N	1	Tag loss	55	Y
19	May 7	720	N	1	Tag loss	68	Y
20	May 7	795	N	1	Tag loss	114	Y
21	May 7	390	Y	1	DM	0	N
22	May 7	690	N	1	Tag loss	44	Y
23	May 7	730	N	1	Tag loss	7	Y
24	Aug 13	530	N	2	DM	0	N
25	Aug 13	735	N	1	Emigration	107	Y
26	Aug 13	750	N	1	Emigration	44	Y
27	Aug 13	760	N	1	Alive	125	Y
28	Aug 13	715	N	1	Tag loss	0	Y
29	Aug 13	735	N	1	Tag loss	34	Y
30	Aug 13	750	N	1	DM	0	Y
31	Aug 13	685	N	2	Tag loss	88	N
32	Aug 13	425	N	1	Tag loss	61	Y
33	Aug 13	790	N	1	Tag loss	48	Y
34	Aug 13	520	N	2	DM	0	N
35	Aug 13	695	N	1	DM	0	Y
36	Aug 13	685	Y	1	DM	0	N
37	Aug 13	750	N	1	Tag loss	111	Y
38	Aug 13	720	N	1	Emigration	124	Y
39	Aug 13	775	N	1	Emigration	124	Y
40	Aug 13	845	N	1	Emigration	120	Y
41	Aug 13	745	N	1	Emigration	124	Y
42	Aug 13	755	N	1	Emigration	106	Y
43	Aug 13	510	N	1	Descended dead	NA	N
44	Aug 30	380	N	1	Descended dead	NA	N

TABLE 3. Continued.

Fish number	Date tagged	TL (mm)	Gut hooked?	Times descended	Fate assignment	Days before event	Included in KM?
45	Aug 30	424	N	1	Descended dead	NA	N
46	Aug 30	410	N	1	Emigration	77	Y
47	Aug 30	650	N	2	Descended dead	NA	N
48	Sep 22	525	N	1	Descended dead	NA	N
49	Sep 22	475	N	1	Tag loss	45	Y

0.15–0.31) for the recreational sector and 0.32 (0.22–0.42) for the commercial sector (SEDAR 2021).

We used observer data from headboats and recreational charters as inputs to our simulation. Overall, the availability of fine-scale fishery-dependent data in the SEUSA is poor. In particular, data on hook type, hook size, hooking location, and depth of capture are extremely valuable to analyses such as ours. We applied hooking data from Florida to the entire region, though spatial differences may exist. Furthermore, although data from the commercial sector were available, they were inadequate in terms of volume and resolution for our purposes. Hook size can influence discard mortality (Muoneke and Childress 1994; Garner et al. 2014); however, we made no attempt to include hook size in our simulation given the low sample sizes that would have resulted from separating the data in this way. Finally, hook type use from the private recreational fishery remains unknown, though some self-reported data (via a mobile application) do exist (Errigo and Collier 2020). The recreational sector is responsible for a large proportion of the fishing mortality for marine fishes in the SEUSA (Coleman et al. 2004; Shertzer et al. 2019). Here, we make the assumption that hooks used by headboats and charters are representative of those used by the entire recreational fleet, but this may not be the case. If this assumption was violated and the proportion of J-hooks used by private recreational fishers differs from that used by headboats and charter vessels, then our survival estimates may be inaccurate. Improving fishery-dependent data collection across sectors—particularly for the private recreational fishery—would benefit future analyses and management.

We make an attempt to frame our findings in the context of prior work; however, comparisons are difficult given differences in methodology and measurements of interest. Campbell et al. (2014) reviewed the available literature on Red Snapper discard mortality in the Gulf of Mexico up to that point; their meta-analysis examined the association between depth and discard mortality. In our study's depth range (~37 m), they estimated recreational discard mortality of 0.14, but they did not explicitly model the influence of descender devices, as few studies at that time had tested them. In addition, many of the papers included in the Campbell et al. (2014) review quantified immediate (boat-side) mortality only, which tends to bias estimates low; our estimate includes both immediate and delayed mortality. After the Campbell et al. (2014) review, Curtis et al. (2015) and Bohaboy et al. (2020) used descender devices to release Red Snapper in the Gulf of Mexico. Curtis et al. (2015) excluded deep-hooked fish, making their estimate of 0.21 (95% CI = 0.12–0.28) analogous to our KM result of 0.08 (95% CI = 0.00–0.17); although the point estimates differ, they released the majority of their fish at 50-m depth, so a higher estimate is expected. Bohaboy et al. (2020) estimated mortality to be 0.23 (95% CI = 0.14–0.32) and noted that the vast majority of Red Snapper mortalities in their study were a result of hook injury and/or predation. Differences in predator densities between their study site and ours could have led to differences in mortality estimates. Our study is the first to use fishery-dependent data on hook type and hooking injury to modify mortality estimates when trying to extrapolate results to the fishery, though Bohaboy et al. (2020) included hooking injury in their model. In addition, some prior studies have similarly used discard mortality rate estimates to generate fishery-wide estimates by extrapolating via fishery-dependent data (e.g., Benoît et al. 2012; Sauls 2014; Sulikowski et al. 2018; Runde et al. 2019).

It is clear that compliance with the requirement to carry a descender device does not necessarily translate to actual use. Education and outreach, including demonstrations and presentations detailing findings such as those of the present study, are crucial to increasing the use of descender devices (Crandall et al. 2018; Curtis et al. 2019; Runde 2019). Vecchio et al. (2020) surveyed 801 boat parties on the east coast of Florida during recent recreational Red Snapper seasons and found that only 1.5% reported using descender devices, although venting is used more commonly (Scyphers et al. 2013). However, Curtis et al. (2019) determined that once introduced to descender devices, 76% of anglers reported that they would continue using them. This information has been taken into account for the most recent stock assessment in the SEUSA (SEDAR 2021). We suggest that managers continue to

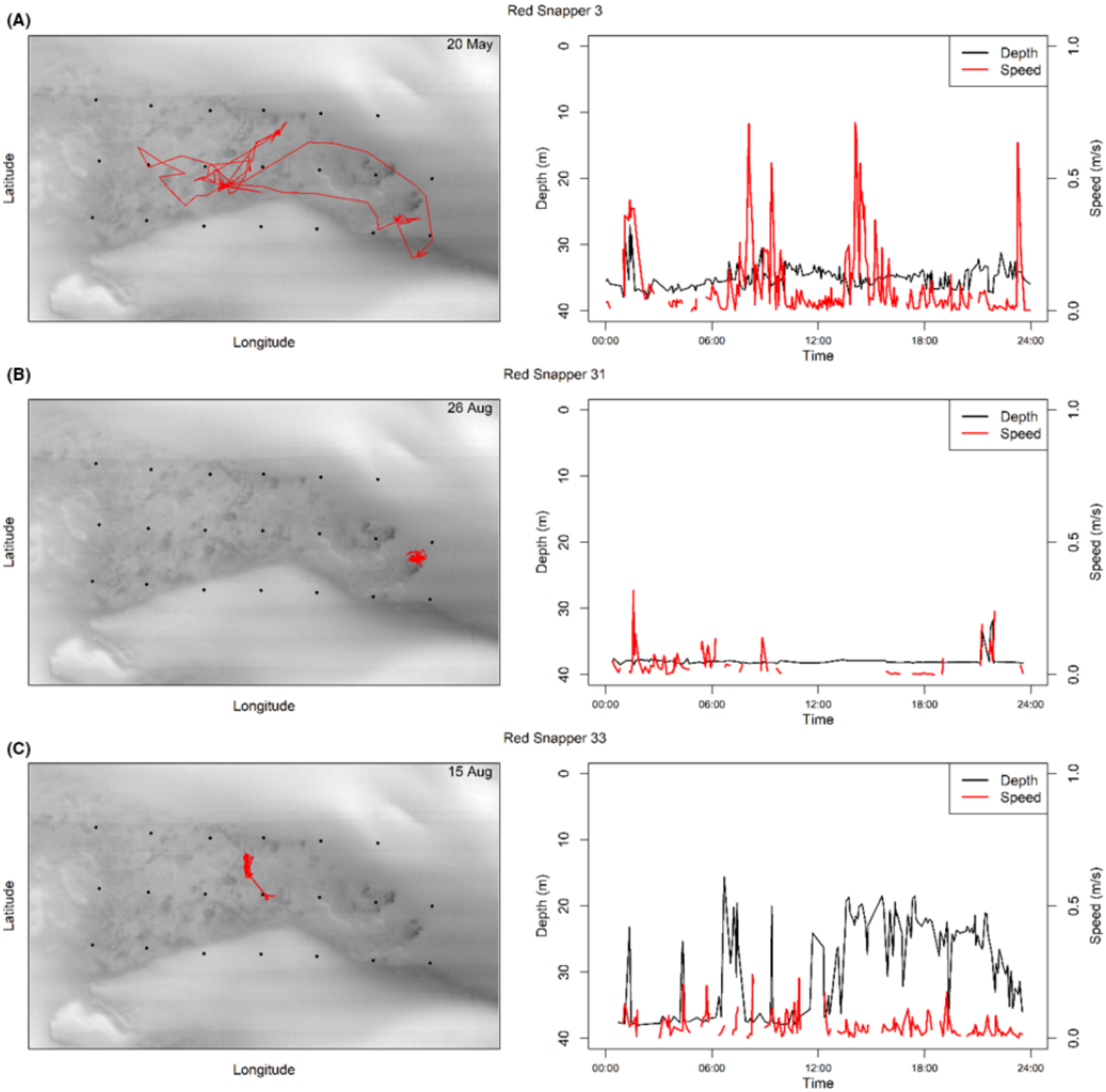

FIGURE 6. Three different movement profiles of live Red Snapper that were positive controls (recaptured or resighted). Left panels show acoustic receivers (black dots) and a single day of GPS movement track (red line) of the individual transmitter in question, with bathymetry overlaid (darker color represents deeper water). Right panels show transmitter depth and speed over the same day. Gaps in speed data occur because speed was only calculated when consecutive detections occurred within 20 min of each other.

estimate descender device use regionally so that mortality estimates used in future stock assessments could be similarly calibrated to trends in angler behavior; efforts such as the MyFishCount mobile application are already making recreational data collection more feasible (Errigo and Collier 2020). Additionally, our estimates could be used in stock assessment projections as a sensitivity analysis for the best-case scenario; the results of this analysis could also be used as an educational and outreach tool. Higher descender device use—and, therefore, lower discard

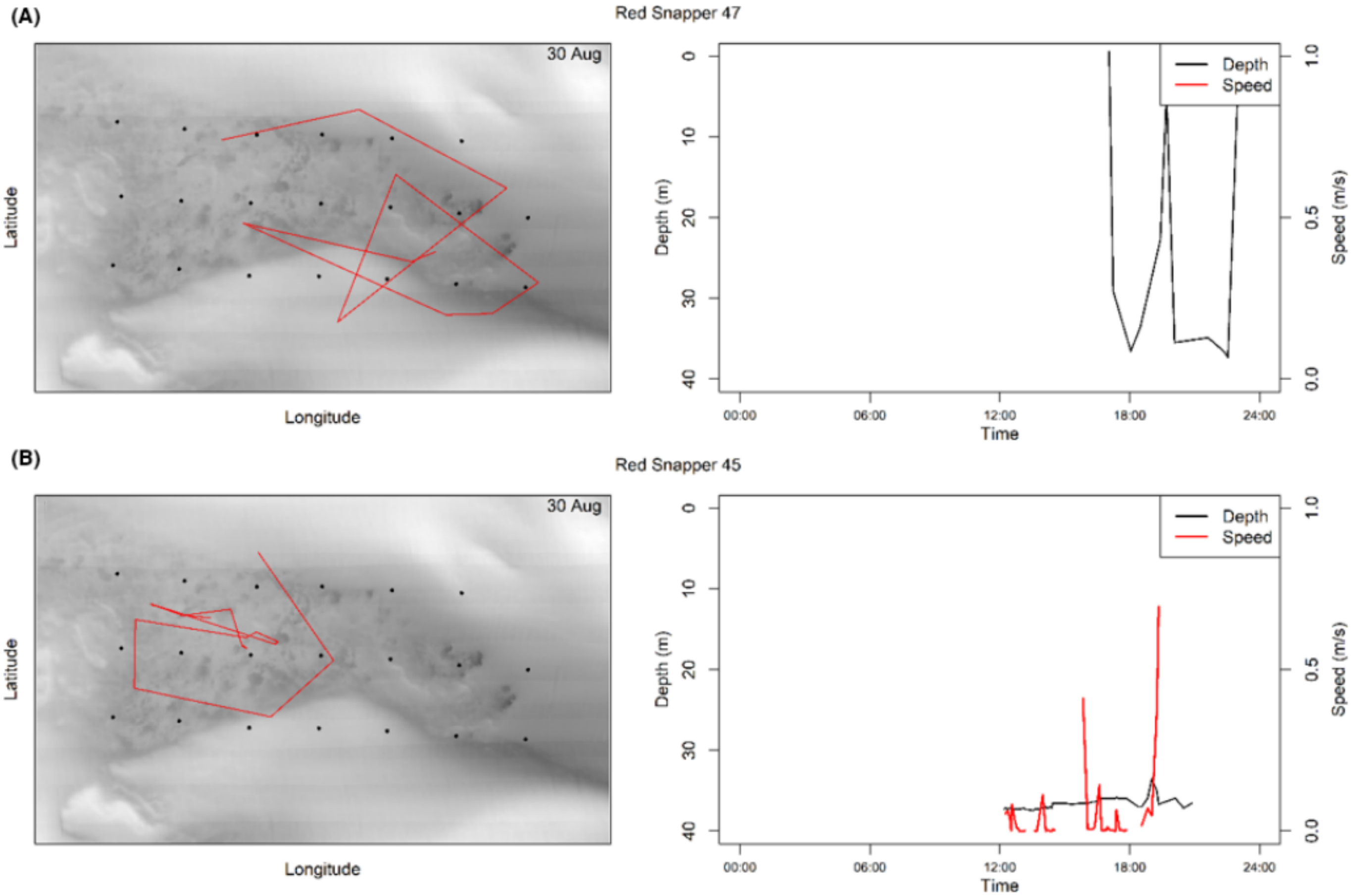

FIGURE 7. Two different movement profiles of dead Red Snapper (i.e., of their scavengers) that were negative controls (i.e., descended dead). Left panels show acoustic receivers (black dots) and a single day of GPS movement track (red line) of the individual transmitter in question, with bathymetry overlaid (darker color represents deeper water). Right panels show depth and speed for the same day and same transmitter. Gaps in speed data occur because speed was only calculated when consecutive detections occurred within 20 min of each other.

mortality—would contribute to rebuilding the Red Snapper stock in this region.

It is not physiologically necessary to descend every reef fish that is brought to the surface. For example, a study in the eastern Gulf of Mexico found that 78% of surface-released Gag *Mycteroperca microlepis* observed within the recreational hook-and-line fishery displayed no swimming impairment, re-submerged without barotrauma mitigation, and exhibited a higher survival rate compared to fish that were vented (Sauls 2014). In this study, we unintentionally allowed three Red Snapper to swim down under their own power, and all three survived. Several other individuals escaped the device at the surface and floated, allowing us to corral and eventually descend them. It may be possible for fishers to determine boat-side whether each individual fish will require descending by observing the extent of their barotrauma (Brownscombe et al. 2017). One of the three Red Snapper that swam on their own showed signs of barotrauma (stomach eversion), while the other two did not. Even so, it is probable that ad hoc determination of whether fish are likely to float would not be 100% accurate: some undescended individuals would inevitably float. The only cost to descending fish (besides the gear itself) is additional time and effort, but the benefits may be substantial. Claims that depredation of Red Snapper from descenders is a frequent occurrence have recently been refuted in a Gulf of Mexico study (Drymon et al. 2020); such depredation did not occur in our study. Therefore, we recommend that even experienced fishers err on the side of caution and descend all Red Snapper for which there is any indication of barotrauma. In situations when multiple Red Snapper are brought to the boat simultaneously, priority for descending should be given to larger fish, since they must overcome greater buoyancy due to the larger volume of air in their swim bladders. For the nondescended fish in this scenario, venting could be used to increase the chance of submergence, as venting has been shown to have similar effectiveness in increasing

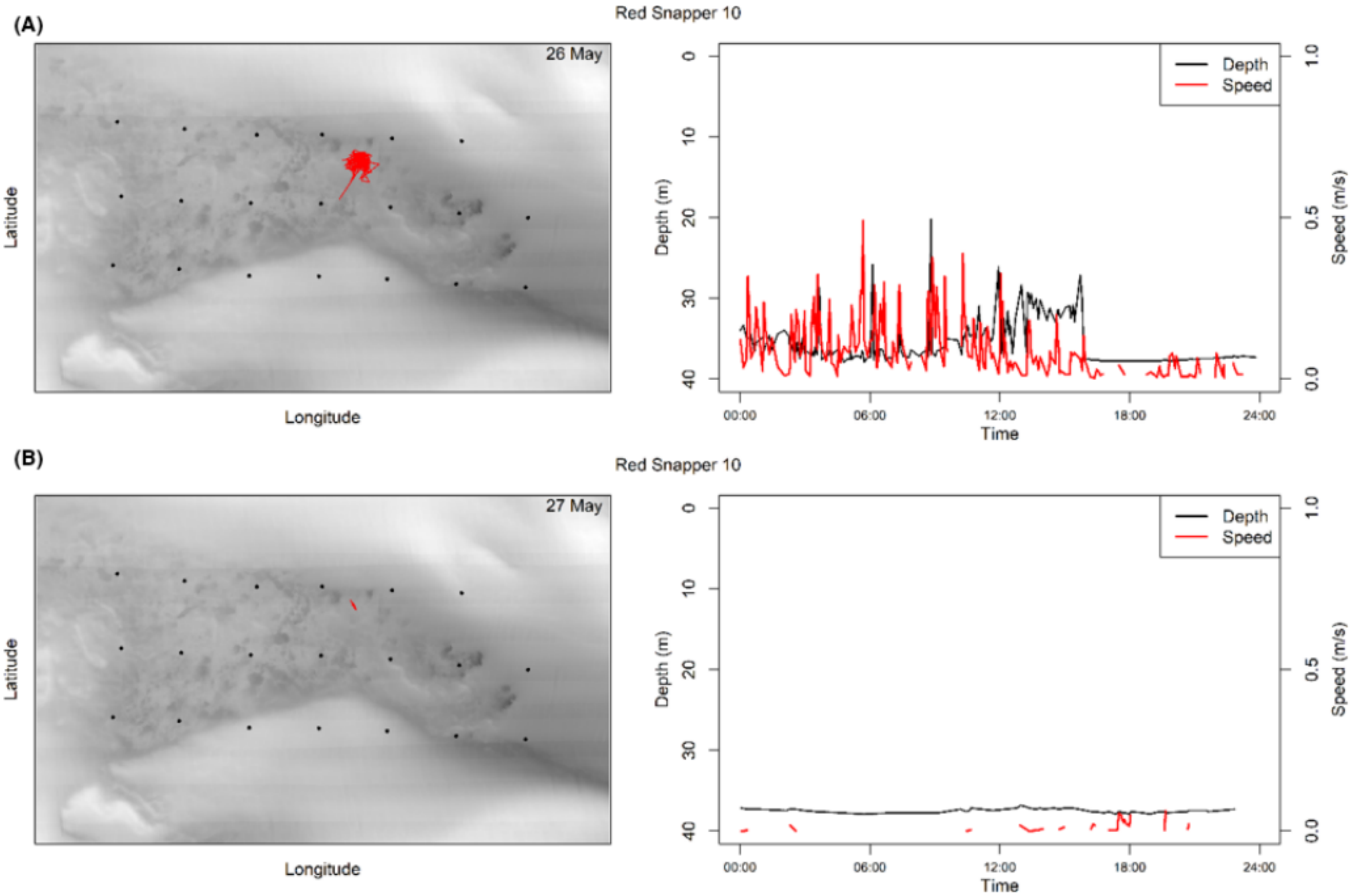

FIGURE 8. Movement profiles over two consecutive days (May 26 and 27, 2019) for a live Red Snapper that lost its tag at approximately 1600 hours on May 26. Left panels show acoustic receivers (black dots) and a single day of GPS movement track (red line) of the individual transmitter in question, with bathymetry overlaid (darker color represents deeper water). Right panels show depth and speed for the same day and same transmitter. Gaps in speed data occur because speed was only calculated when consecutive detections occurred within 20 min of each other.

discard survival as descending tools when properly administered (Eberts and Somers 2017; Rudershausen et al. 2020). However, we note that the consequences of improper administration are greater for venting than for descender devices (Scyphers et al. 2013).

Even when descended, fish may resurface and float; this occurred with three Red Snapper in our study. Video evidence confirmed that each of these fish became detached from the descender device prematurely. Two of these three individuals experienced discard mortality on the day they were tagged, and the third survived for several months before tag loss. It is unclear whether the condition of these fish (and, therefore, their chance of survival) was worsened by repeated handling and two descents, whether their barotrauma was initially so severe that they had a higher propensity to resurface, or whether these factors had any bearing on their survival at all. We elected to exclude them from our estimate because of this uncertainty and because of our uncertainty about the rate at which this occurs in the fishery; however, fishery participants are likely to experience some device failure, and our estimate is a “best-case” value.

It is conceivable that our tagging procedure increased mortality in this study. Considering the effects of tagging on behavior and disposition is critical to generating unbiased estimates of fish survival (Hondorp et al. 2015; Klinard et al. 2018; Brownscombe et al. 2019). While no estimates of tagging-induced mortality currently exist for our external transmitter attachment method, it is possible that some such mortalities occurred here either as a result of transmitter-related trauma or extended deck time for the purpose of tagging. If any of the Red Snapper that we inferred to have experienced discard mortality actually died as a result of tagging (and not discarding), then our mortality estimates would be biased high. The mortality estimates we report here are thus conservative in this regard and if anything would be lower for untagged fish.

Depth of capture can influence discard survival, as retrieving a fish from greater depth can result in more

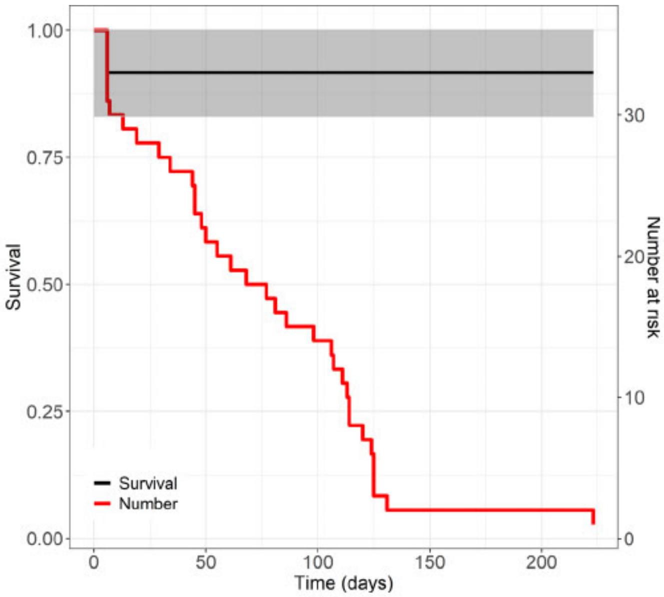

FIGURE 9. Kaplan–Meier curve (black line) demonstrating survival rate (1 − mortality) for non-deep-hooked, descended Red Snapper off North Carolina and the number of at-risk Red Snapper (red line) throughout the 223-d study. No fish experienced discard mortality after the day of release.

extreme barotrauma (Campbell et al. 2014). The precise distribution of Red Snapper releases across depths in the SEUSA is currently unclear, but Sauls et al. (2017) reported that over 90% of discards observed in the for-hire recreational hook-and-line fishery off the east coast of Florida occurred in depths shallower than 40 m. The Southeast Reef Fish Survey currently samples natural bottom habitat from Florida to North Carolina in depths of approximately 10–100 m. From 2010 to 2018, 77% of Red Snapper observations by the Southeast Reef Fish Survey were shallower than 40-m depth (N. M. Bacheler, unpublished data). Furthermore, Red Snapper abundance is known to be highest at 35–40 m in this region (Bacheler et al. 2016). These observations support the assertion that our estimate is representative of the fishery, though uncertainty remains. Such uncertainty could contribute to error in our fishery-wide estimates of mortality when descender devices are used.

Discard survival of Red Snapper in the Gulf of Mexico has been demonstrated to vary seasonally, perhaps as a result of changes in surface temperatures (Campbell et al. 2010; Curtis et al. 2015). If survival is similarly variable in the SEUSA, we anticipate that warm summertime temperatures would lead to the lowest seasonal survival due to the increased risk of homeostatic imbalances and oxygen debt upon capture (Gale et al. 2013). Of the three jaw-hooked, descended-once fish that experienced discard mortality in this study, two were tagged on August 13 and one was tagged on May 7. It is possible that the mortalities we observed were in part due to the seasonal effect. While recreational discarding in this region occurs year-round, recreational fishing effort in offshore waters of the Exclusive Economic Zone peaks during May–August (National Marine Fisheries Service, Fisheries Statistics Division, personal communication), and the recreational Red Snapper harvest season typically has occurred during July in recent years; thus, our results are reflective of the period when the majority of Red Snapper discarding takes place.

CONCLUSIONS

The body of evidence continues to build for the benefits of descending barotraumatized fish. In virtually every study for which descender devices have been formally evaluated, survival is higher for descended individuals than for those that are released at the surface (Eberts and Somers 2017). Although we did not examine survival for surface-released Red Snapper here, our overall discard mortality estimate when descenders were used is lower than estimates used in either of the recent stock assessments for this species (SEDAR 2017, 2021), which accounted for surface releases. Mitigating the effects of barotrauma is increasingly important in the SEUSA as the proportion of caught fish that are released increases for many species (Zeller et al. 2018; Runde et al. 2020a), as fishing effort grows, particularly in the recreational sector (Shertzer et al. 2019), and as several key species of reef fish show concerning population trends (NOAA Fisheries 2020). The presence of descender devices is currently required on vessels possessing or targeting reef fish in the SEUSA; however, the use of descender devices is only encouraged, not required, and it is certain that many impaired fish are still being released without assistance. Because a portion of these fish float (Campbell et al. 2010), barotrauma mitigation is necessary to reduce discard mortality; here, we have shown that the vast majority of descended Red Snapper survive release. We therefore recommend that fishery managers devote additional resources to education and outreach to inspire fishery participants across sectors to use descender devices. Some stakeholders across sectors have already shown their dedication to reducing discard mortality by using barotrauma mitigation devices when releasing reef fish (B. J. Runde, personal observation). Our findings for Red Snapper, perhaps the most high-profile reef species in the SEUSA, should serve as a target that could be reached by motivating continued change in the behavior of anglers.

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