Post-release survival of red snapper (*Lutjanus campechanus*) and red grouper (*Epinephelus morio*) using different barotrauma mitigation methods

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SEDAR90-RD-20

April 2025

Fisheries Research 264 (2023) 106717

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

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A R T I C L E I N F O

Handled by A.E. Punt

Keywords:
Discards
Field experiment
Fisheries management
Snapper-grouper complex
Stock assessment

A B S T R A C T

Captured fish that are released due to fishing regulations, catch-and-release efforts, or nontargeted bycatch are susceptible to mortality, particularly for species that are subject to barotrauma when retrieved from deep depths. To mitigate the effects of barotrauma, venting tools are commonly used to release air trapped in the gas bladder and enable fish released at the surface to return to their depth of capture. Recently, fishery managers have begun to promote an alternative method that involves recompression via the rapid descent of fish to their depth of capture or to a depth at which they can swim on their own. For some economically important species in the Gulf of Mexico, such as red snapper (*Lutjanus campechanus*) and red grouper (*Epinephelus morio*), discards account for more than 75% of total recreational catch. Because these two species are particularly susceptible to barotrauma, it is imperative to determine best practices for barotrauma mitigation. Here, we used mark-recapture to compare relative survival of both red snapper and red grouper after release using venting and recompression methods. We found that vented red snapper had similar tag return rates compared to those that were recompressed to a depth of 10 m. However, red snapper recompressed to 20 m or deeper had significantly higher return rates (up to 2.5 times higher) compared to those that were vented, indicating a lower discard mortality for individuals that were released using descender devices. The patterns were qualitatively similar for red grouper, with tag return rates 2 times higher for fish recompressed deeper than 20 m compared to vented fish. However, these results for red grouper were not statistically significant, potentially due to insufficient power (Type II error), a reduced relative tolerance to barotrauma compared to red snapper, or a combination of both. For both red snapper and red grouper, tag return rates were higher when fish were recompressed to deeper depths, but descending them all the way to the bottom was not necessary. Indeed, video observations further indicated that both species regained swimming abilities at depths shallower than depths of capture, although red grouper needed to be descended deeper than red snapper. The combined results of this study can inform fishery managers and anglers in the region on the apparent benefits of using recompression as a barotrauma mitigation method to improve post-release survival, and the species-specific needs of red snapper and red grouper.

1. Introduction

Discard mortality is a global problem that has represented between 10-20% of the total annual catch (removals via landings and discards) over the past half century (Zeller et al., 2018). In addition to landings and illegal catch, fish that die as a consequence of discarding represent an additional source of fishing mortality (Davis, 2002; Harrington et al., 2005) that is often unaccounted for and difficult to estimate (Pollock and Pine, 2007; Capizzano et al., 2019). Recreational fishing commonly involves a substantial portion of captured fish that are returned to the water (Ferter et al., 2013; Bohaboy et al., 2020) due to strict fishing regulations (e.g., minimum sizes, bag limits, closed seasons), elective catch-and-release efforts, and species that are nontargeted bycatch. For physoclistous species, barotrauma is a significant source of mortality for fish discarded in recreational fisheries. Injuries from barotrauma can cause immediate and latent mortality, and make discarded fish more susceptible to predation (Raby et al., 2014; Wegner et al., 2021). Determining how to reduce mortality of discarded fish is therefore an important goal in fisheries science, and there have been a number of methods and tools developed to help fish overcome issues of

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https://doi.org/10.1016/j.fishres.2023.106717
Received 28 October 2022; Received in revised form 11 April 2023; Accepted 12 April 2023
Available online 18 April 2023

barotrauma. However, the emerging picture from this work over the past decade suggests there to be strong variation in the magnitude of discard mortality among species (e.g., Hannah et al., 2014), and even within-species across different regions, requiring research and management policies on a case-by-case basis (e.g., Eberts and Somers, 2017; Drymon et al., 2020). We therefore have an incomplete understanding of how best to improve survival of discarded fish for many recreational fisheries and regions. Filling this research gap will help us to improve estimates of discard mortality for stock assessments (Cook, 2019), and guide management and conservation policies for best practices to reduce mortality of discarded fish that experience barotrauma.

The Gulf of Mexico supports large recreational fisheries with landings for some species that exceed that of the commercial sector (Coleman et al., 2004). Much of the recreational fishing effort is focused on reef fishes, especially species in the snapper-grouper complex (Keithly and Roberts, 2017; Cross et al., 2018). In the eastern GOM (eGOM), red snapper (*Lutjanus campechanus*; Lutjanidae) and red grouper (*Epinephelus morio*; Serranidae) are among the most highly targeted and captured species of reef fish, with high and increasing proportions allocated to the recreational sector (SEDAR, 2018; SEDAR, 2019). Thus, it is imperative to understand the effects of recreational discarding for these two economically important species. Recreational fishing regulations for these two species differ, and include a combination of minimum legal sizes, bag limits, and varied season lengths. For most of the year, recreational harvest is currently closed for red snapper and open for red grouper (Fig. 1a). These species may also be captured as bycatch since they are part of a broader, multispecies recreational reef-fish fishery (Chagaris et al., 2019). The combined effects of strict regulations, high potential for bycatch, and year-round angler activity (Simard et al., 2016) have resulted in discard rates that far exceed harvest of both red snapper and red grouper (Fig. 1b). Because many species within the snapper-grouper complex co-occur and most species have year-round open harvest seasons, red snapper can have high discard rates when their harvest season is closed. Indeed, for every harvested red snapper and red grouper during the period between 2000 and 2017, there were on average 2.8 (annual range: 2.0–4.6) and 11.4 (annual range: 5.4–32.5) discarded fish, respectively (SEDAR, 2018; SEDAR, 2019). Both species are commonly captured in water deep enough to cause barotrauma (Wilson and Burns, 1996; Campbell et al., 2014), making the discards vulnerable to mortality and necessitating the need to determine best practices to improve their post-release survival.

Two different release methods have been promoted by fishery managers to mitigate barotrauma in reef fishes. The first is venting, which involves puncturing the inflated gas bladder with a hollow needle (venting tool) to allow gases to escape. This technique reduces buoyancy and enables fish to return to their depth of capture, and is the most common method used by anglers in the eGOM to mitigate barotrauma (FWC unpublished at-sea observer data). However, studies on venting have found various levels of efficacy (reviewed by Wilde, 2009) and fish may be exposed to additional internal injuries if vented improperly (Collins et al., 1999; Wilde, 2009; Scyphers et al., 2013). As an alternative to venting, weighted descender devices rapidly return the fish back to depth of capture, which has been shown to effectively recompress gas trapped in the gas bladder and enable discards to overcome excessive buoyancy (Eberts and Somers, 2017; Jarvis and Lowe, 2008; Hannah and Matteson, 2007). Fish that are returned to depth with recompression gear may expend less energy during descent through the water column and may experience reduced predation both at the surface and during the return to protective bottom habitats (Bohaboy et al., 2020; Drymon et al., 2020). Recompression of red snapper has been shown to improve survival compared to release at the surface without venting (Stunz et al., 2017; Bohaboy et al., 2020; Runde et al., 2021). Laboratory experiments (Drumhiller et al., 2014) and field studies (e.g., Curtis et al., 2015) have found survival of red snapper was similar between those vented and recompressed, and both methods performed better than releasing fish at the surface without venting. However, venting was associated with delayed mortality of red snapper, even when the method appeared to improve immediate survival (Tompkins, 2017). Much of the previous work on survival of red snapper released with descender devices was conducted in the western Gulf of Mexico, where seasonal thermoclines are an additional stressor for fish retrieved to the surface from deep depths (Campbell et al., 2010; Campbell et al., 2014). Less work has focused on the fate of discarded red grouper, but Burns et al. (2002) found survival was higher for unvented fish compared to those that were vented when captured at depths from 20 to 60 m. In addition, Runde et al. (2020) reported one red grouper off North Carolina, USA (western Atlantic) captured at a depth of 116 m survived after it was descended; however, no published studies have comprehensively evaluated the relative benefits of descending over surface release for this species. Therefore, comparisons of these two barotrauma mitigation methods have yet to be conducted in the eGOM, where habitat types, temperature profiles, depths of capture, and predator communities can be different from that in the other regions of the Gulf of Mexico (Buster and Holmes, 2011; Drymon et al., 2020 and references therein).

In addition to determining whether survival of discarded fish varies with release method (e.g., venting versus rapid recompression), implementation of best practices with angler buy-in may be challenging, especially if it requires adoption of using descender devices over the more widely used venting method. In a recent survey of recreational anglers in the southern U.S. Atlantic and Gulf of Mexico regions, nearly three quarters of respondents had little prior knowledge of descender

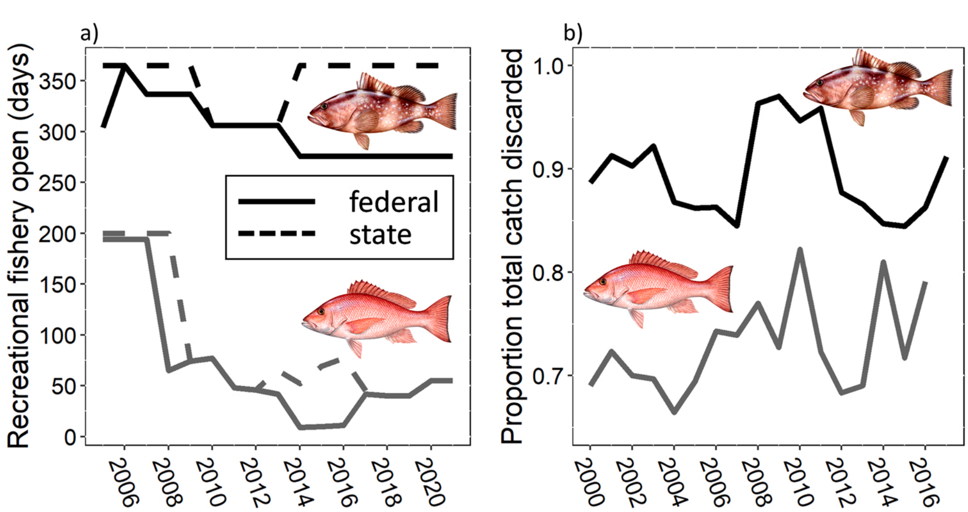

Fig. 1. Lengths of open harvest seasons for recreational fisheries of red snapper (gray lines) and red grouper (black lines) from 2005 to 2021 in the eGOM (a). State waters on the Gulf coast of Florida extend nine miles from the coast. Estimated proportions of discards for the focal species by recreational fisheries in the eGOM from 2000 to 2016 (b).
Data sources: red snapper (SEDAR, 2018); red grouper (SEDAR, 2019). Fish illustrations in Figs. 1, 3, 4, and 5 were provided with permission courtesy of Diane Rome Peebles.

devices, but a near equal amount reported they preferred the method over venting after they were provided the tools and instructions for their use (Curtis et al., 2019). However, despite having positive experiences using descender devices, Florida anglers perceived venting to be as effective as rapid recompression (Crouch, 2018). Similarly, anglers in the region reported their intention to continue to use venting over rapid recompression, since they thought the methods had similar efficacies for improving discard survival but that descender devices were more difficult to use and time consuming (Crandall et al., 2018). More recently, a survey reported that less than one third of Gulf of Mexico anglers were aware of fish descending devices as an alternative to venting, and almost half that were familiar with them do not use them (Southwick Associates, 2022). Recompression to a midwater depth shallower than that of capture has been shown to improve survival compared to surface-released fish (e.g., Tompkins, 2017; Bellquist et al., 2019). The benefits of midwater release include reduced time required to release individual fish, reduced time of potential interference between descender devices and fishing gear, and increased number of fish that can be recompressed. Midwater release also alleviates angler concern that descending a fish to the bottom may disturb other fish and disrupt catch (*pers. comms.* with anglers). Determining whether recompression to depths less than that of capture improves survival of red snapper and red grouper may therefore increase the willingness of anglers in the region to use the method. Furthermore, determining the depths at which each species is able to regain swimming ability, and factors that may influence it (e.g., depth of capture, size of fish), is critical to being able to prescribe minimum depths for anglers to recompress fish.

In the current study, we compared venting and recompression methods used to release reef fishes captured from depths that typically induce barotrauma. Specifically, we addressed the following questions, each for red snapper and red grouper: 1) Does survival differ between fish that are vented and released at the surface compared to those that are recompressed?, 2) Does survival differ between fish recompressed to different depths?, and 3) At what depths do released fish regain sustained swimming behaviors and is this affected by either depth of capture or size of fish? This work was a cooperative study with the charter boat fishing industry in the eGOM, and provides guidance on best practices for improving survival of discarded red snapper and red grouper in the region.

2. Materials and methods

2.1. Fishing methods

We conducted fourteen research trips on chartered fishing vessels in the eastern Gulf of Mexico off the west coast of Florida (Fig. 2). Two regions were chosen based on the distribution and anticipated catch of the target species: 1) the panhandle and peninsula for red snapper, and 2) the peninsula for red grouper. We conducted seven one-day trips (12-hours each) in the panhandle region in 2014. In the peninsular region, we conducted a total of seven two-day trips (40-hours each), three in 2014 and four in 2016. The additional trips in 2016 were made to supplement low numbers of red grouper sampled and tagged in 2014. Longer trips were necessary in the peninsular region due to the long travel times (12 h roundtrip) to reach the target water depths. Fishing locations were chosen by the boat captains, not the researchers. We caught all fish at depths ranging from 30 m to 50 m where barotrauma was expected to result in impairments and affect post-release survival. All research trips were conducted during months of high recreational fishing effort for reef fishes in the eGOM (July to October; Cross et al., 2018). This period also coincides with the highest annual water temperatures, which can potentially increase post-release stress on reef fishes (Gale et al., 2013; Curtis et al., 2015). Fishery observer data collected in the GOM for red snapper and red grouper have shown that immediate discard mortality was positively correlated with increased depths, seasons associated with warmer temperatures, and external

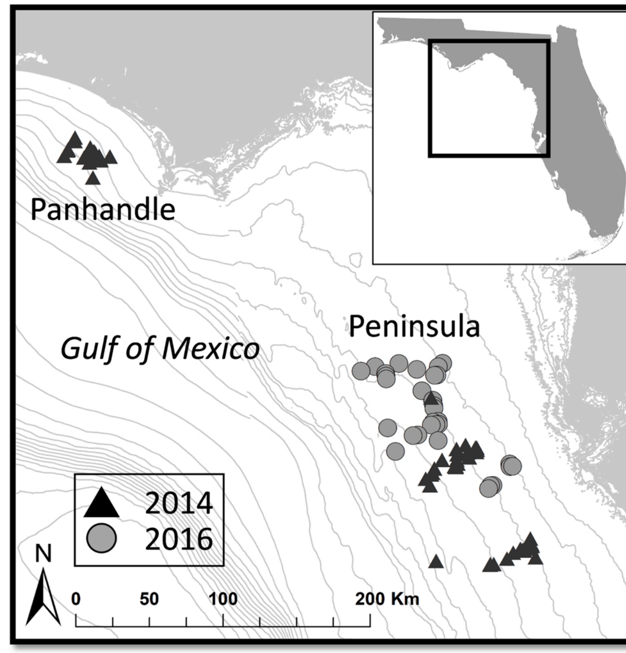

Fig. 2. Map of sampling locations where we targeted red snapper (panhandle and peninsula) and red grouper (peninsula) in 2014 and 2016.

evidence of barotrauma (Pulver, 2017).

On each trip, four research personnel used recreational hook-and-line gear provided by the for-hire vessel operator that complied with current gear requirements for reef fishes (circle hooks) in the eGOM. We processed all fish immediately upon capture to minimize the duration of time they spent out of water. Upon capture, we recorded the species and fork length (in mm), and assessed the fish for all visual signs of barotrauma (e.g., swollen abdomen, stomach eversion into the buccal cavity, anal prolapse, extrusion of intestines through the anal opening, bleeding, exophthalmia) and hooking injuries (e.g., fish that were hooked in the gills, inside the mouth, in the throat, or in the gut if the fish had completely swallowed the hook). Finally, we recorded the release method (see Section 2.2). We tagged all fish prior to release with a conventional 100 mm Hallprint™ PDS dart tag inserted into the dorsal muscle tissue and in between adjacent pterygiophores per manufacturer instructions, such that the act of tagging did not inadvertently vent the fish. The tag had a ~1.6 mm diameter and was applied with a ~3.3 mm outside diameter applicator needle suited for fish approximately 350–550 mm in length.

A reward incentive program was used to encourage the public to report recaptured fish. Each dart tag was printed with a unique alphanumeric tag number, an email address, a toll-free telephone number maintained by the Florida Fish and Wildlife Conservation Commission (FWC), and the word "REWARD" in bold. We distributed catch cards with pre-paid postage to the captains of the charter vessels so they could easily record information for recaptured fish and return the information to FWC. We also distributed catch cards to other vessel operators in the area and displayed reward posters in the regions to encourage tag returns from recreational anglers. Anglers that reported recaptured fish received a screen-printed t-shirt via mail.

2.2. Study design and experimental release methods

Our study design allowed us to compare realistic scenarios in recreational fisheries, where fish that do not exhibit any visible signs of barotrauma are typically released at the surface without mitigation treatment, and those that do may be vented or rapidly recompressed and returned to depth without venting. Only fish that were lip hooked without injury were included in the study. We excluded any fish that had a hooking injury, which might have affected its survival rate. For fish that did not have hooking injuries, we determined whether they displayed any signs of barotrauma (described in Section 2.1). If we did not observe signs of barotrauma, the fish was tagged and released at the surface without being vented. This allowed us to test the relative effects of angler decisions to vent or descend fish when the need for barotrauma mitigation was apparent. Although we report the tag return rates for fish that did not display signs of barotrauma, we did not test whether they differed from fish in the vented or descended treatments since such comparisons would be confounded by the varied condition of fish included in different treatment groups. For fish that experienced barotrauma, we employed one of the two release methods used by recreational anglers to mitigate it: 1) surface release after being vented (VT), or 2) recompressed to depth without being vented. We recompressed fish to one of four depths with a SeaQualizer© descender device that released automatically at pre-set depths: 1) 10 m (R1), 2) 20 m (R2), 3) 30 m (R3), or 4) 40 m (R4). Assignment of the first release method of each fishing trip was random, after which we attempted to assign fish sequentially among treatment levels to ensure relatively even sample sizes (e.g., VT, then R1, R2, R3, R4). However, there were inherent differences in the time required to execute each treatment. For example, if a recompression tool was not available because all were being used to return fish to depth, we released the fish at the surface after being vented (VT) to minimize the time it was held out of water. As a result, sample sizes among treatments were not even. However, the distribution of assigned treatments did not differ by depth for either red snapper ($F_{4,1022} = 1.15$, $p = 0.33$) or red grouper ($F_{3153} = 2.37$, $p = 0.07$), based on an analysis of variance. A total of 1030 red snapper (mean (se) fork length = 385 (2.2) mm; range: 205–712 mm) and 190 red grouper (mean (se) fork length = 500 (8.4) mm; range: 257–780 mm) were tagged, released, and included in our study (Table 1).

For fish that were surface-released (both vented and those that did not display sign of barotrauma), we constructed a bottomless cage with floats attached to the top so it would remain on the surface next to the boat (Hannah et al., 2008; Runde et al., 2020). Releasing the fish inside the bottomless cage kept them from floating away, but allowed them to swim back down on their own. The surface cage was circular with a 60 cm diameter, 110 cm height, and constructed with 12-gauge plastic-coated wire mesh (3.5 cm) to minimize abrasion and harm to the fish.

For the recompression treatments, we used two separate devices: 1) SeaQualizer© descender devices commonly used by recreational anglers, and 2) a cage constructed to allow video-recorded observations of fish behavior as they were recompressed (see Section 2.3 for description of fish behavior methods). The SeaQualizer© descender devices were attached to a weighted 75 m line (1.4 kg weight). Per manufacturer instructions, we attached the fish directly to the device and rapidly recompressed it to the assigned depth for the treatment. The recompression cage was designed similarly to that described by Hannah and Matteson (2007). It was 80 cm square x 60 cm in height and constructed with 12-gauge plastic-coated wire mesh (3.5 cm) to minimize harm to the fish. The cage bottom consisted of two outward swinging doors secured in the closed position with a SeaQualizer© descender device that released automatically at pre-set depths according to the assigned treatment. When the descender device released, the doors opened to allow the fish to exit through the bottom of the cage. We used a winch and pulley system with 12-volt power so the cage could be easily lowered and raised in the water column. We attached a HOBO® water level data logger (model U20–001–03) inside the cage to record atmospheric pressure (psi) as a proxy for depth at three-second intervals during the experimental trials. Additionally, inside the top of the cage we mounted a DeepSea Wide-i SeaCam® camera with a wide-angle view (125 degrees horizontal by 89 degrees vertical field of view) in a downward-facing position to view the behavioral response of fish during descent. The camera was connected via video cables to monitors onboard the fishing vessel to allow real-time viewing of the recompression cage treatment.

Table 1
Sample sizes of red snapper and red grouper that were captured, tagged, and released using different methods (VT = vented and surface release; NV = not-vented and surface release; RC = recompressed; R1 = recompressed to 10 m; R2 = recompressed to 20 m; R3 = recompressed to 30 m; R4 = recompressed to 40 m). Note that the sum of the R1-R4 equals RC for each species. *Statistical comparisons were not made with the R4 groups for either species due to the small sample size, nor with the R1 group for red grouper due to a lack of spatial balance in sampling locations (see Section 2.4).

Release method	Red snapper	Red grouper
VT	344	38
NV	44	6
RC	642	146
R1	262	* 22
R2	202	67
R3	175	46
R4	* 3	* 11
Total	1030	190

2.3. *Depth of sustained swimming behavior*

In addition to comparing tag returns of fish recompressed to different depths, we also measured the depth at which the focal species were able to regain sustained swimming behavior. We recorded recompression cage descents with a GPS-enabled four-channel mobile DVR SD video recorder. The DVR system recorded date and time-stamped video footage at five-minute intervals to minimize any loss of video footage.

We used video from the recompression cage to quantify the depth at which sustained swimming behavior was initiated. To do this, we matched the elapsed time from the video to the corresponding pressure data from the HOBO® water depth logger, and converted pressure to depth in meters. Since the data logger was set to record every three seconds, it was often necessary to calculate the median swimming depth from the two readings immediately before and after the elapsed swimming time.

2.4. *Statistical analyses*

We used tag return data to evaluate relative survival. To compare tag returns among treatments for each species, we used Fisher's Exact Tests. This method has broad applications for comparing tag returns as a measure of relative survival to determine whether the odds ratio differed from 1 between any two experimental release treatments (Hueter et al., 2006). Exact methods are recommended when small counts make maximum likelihood estimation inappropriate. There were no differences in recapture rates between the descender device and the cage for either red snapper (odds ratio = 1.47 (0.87, 2.46), p = 0.15) or red grouper (odds ratio = 1.17 (0.29, 4.67, p = 1.0). We therefore pooled the data between devices according to their recompression depths for each species. To determine whether survival of fish differed between those that were vented compared to those that were recompressed (question 1), we conducted multiple comparisons for each species. For red snapper, we compared tag returns of fish that were vented against those recompressed to: 1) 10 m, 2) 20 m, and 3) 30 m. We were unable to make comparisons for red snapper recompressed to 40 m due to an extremely low sample size (n = 3). For red grouper, we compared tag returns of fish that were vented against those recompressed to: 1) 20 m and 2) 30 m. Again, we were unable to make comparisons for red grouper recompressed to 40 m due to sample size (n = 11). In addition, we sought to distribute all release treatments equally across the spatial domain of the study area to prevent unequal effort in the recreational fishery from confounding recapture rates with treatments. We were unable to accomplish spatial balance in the release of red grouper recompressed to 10 m. These fish were confined to a small area that did not meet our requirement of spatial balance.

To determine whether survival differed among release depths for recompressed fish (question 2), we conducted additional analyses for each species. First, we conducted logistic regressions for each species with the binary response of tag return (0,1) as a function of the depth of recompression. We then conducted Fisher's Exact Tests between each of the recompression depths for each species.

Finally, to determine the depths at which each species regained sustained swimming behaviors (question 3), we analyzed data collected from videos taken in the recompression cage. We used a linear model (Gaussian distribution) to determine whether depth of sustained swimming (response) varied with depth of capture (continuous variable, fixed effect), fish size (continuous variable, fixed effect), and species (categorical variable, fixed effect). We first determined there were no interactions between species and either depth of capture ($t = 0.86$, $p = 0.39$) or fish size ($t = 0.97$, $p = 0.33$), so we dropped these interaction terms and focused on the main effects. All analyses were performed in the *base* package for the *R* statistical environment (R Core Team, 2022) and outputs were plotted using the *ggplot2* package (Wickham, 2016).

3. Results

Anglers reported tagged fish for 103 red snapper and 15 red grouper. The time between tagging and recapture was highly variable for both species. Tagged red snapper remained at large from 2 to 1453 days (mean (se) = 304 (31)) and tagged red grouper from 31 to 1754 days (mean (se) = 270 (79)). For the fish that showed no signs of barotrauma, tag return rates were 11.4% for red snapper and 16.7% for red grouper.

Among fish that required a treatment for barotrauma, tag return rates for both species were highest for fish that were recompressed, especially to depths at or deeper than 20 m, and lowest for those that were vented. For red snapper (Fig. 3), tag returns for vented fish (6.4%) did not differ from those recompressed to 10 m (6.9%; odds ratio = 1.08 (0.53, 2.16), $p = 0.87$). In contrast, tag returns were higher for fish recompressed to 20 m (16.5%; odds ratio = 2.88 (1.56, 5.41), $p = 0.0004$) and 30 m (15.5%; odds ratio = 2.68 (1.42, 5.12), $p = 0.001$) compared to those that were vented. Among recompressed red snapper, tag returns were higher for fish descended to deeper depths. The logistic regression indicated a significant, positive relationship between tag returns and depth of recompression (coefficient (se) = 0.040 (0.015), $z = 2.72$, $p = 0.007$). Thus, tag returns increased by approximately 4% for each one-meter increase in depth of recompression between 10 and 40 m. Compared to those released at 10 m, tag returns were higher for both the 20 m (odds ratio = 2.67 (1.39, 5.26), $p = 0.002$) and 30 m treatments (odds ratio = 2.48 (1.27, 4.97), $p = 0.006$). Tag return rates did not differ for red snapper recompressed to 20 m compared to 30 m (odds ratio = 0.93 (0.51, 1.70), $p = 0.89$). Recompressing red snapper to depths of 20–30 m resulted in tag returns that were over two times (143–158%) greater than those that were vented (Fig. 3).

For red grouper (Fig. 4), the results were qualitatively similar to red snapper, although none of the tests were statistically significant. Tag returns of vented red grouper (5.3%) did not differ from those recompressed to either 20 m (7.9%; odds ratio = 1.54 (0.24, 17.05), $p = 0.71$) or 30 m (11.9%; odds ratio = 2.41 (0.37, 26.82), $p = 0.44$). The logistic regression indicated a positive relationship between tag returns and depth of recompression, but it was not significant (coefficient (se) = 0.036 (0.043), $z = 0.84$, $p = 0.40$). Tag returns did not differ between the two recompression depths for red grouper (11.9%; odds ratio = 1.56 (0.33, 7.29), $p = 0.52$). Recompressing red grouper to depths at or below 20 m resulted in tag returns that were 51–126% greater than those that were vented (Fig. 4).

The mean ($\pm$ se) depth at which red snapper regained sustained swimming ability (5.7 $\pm$ 0.5 m) was less than that for red grouper (13.7 $\pm$ 2.0 m; $t = 4.84$, $p < 0.001$, Fig. 5a). There was also substantial variability in the depths at which each species regained sustained swimming ability. Depths ranged from 1 to 35 m for red snapper and 1–44 m for red grouper. There was no relationship between depth of swimming ability with either depth of capture ($t = 0.63$, $p = 0.53$) or fish size ($t = 0.13$, $p = 0.89$; Fig. 5b and 5c).

4. Discussion

In this study, we have experimentally demonstrated that recompressing two of the most highly targeted reef fishes in the eGOM can result in tag return rates over 2 times higher than venting them, which is indicative of increased survival. Moreover, our results also suggest that tag returns tended to be higher when fish were recompressed to deeper depths, but that descending them all the way to the bottom was not necessary. Our work represents one of the first efforts to examine the potential benefits of recompression in the open-access recreational fishery for red snapper and red grouper in the eGOM.

Qualitatively, the responses to the different mitigation techniques were similar between species. Indeed, tag returns were highest for fish

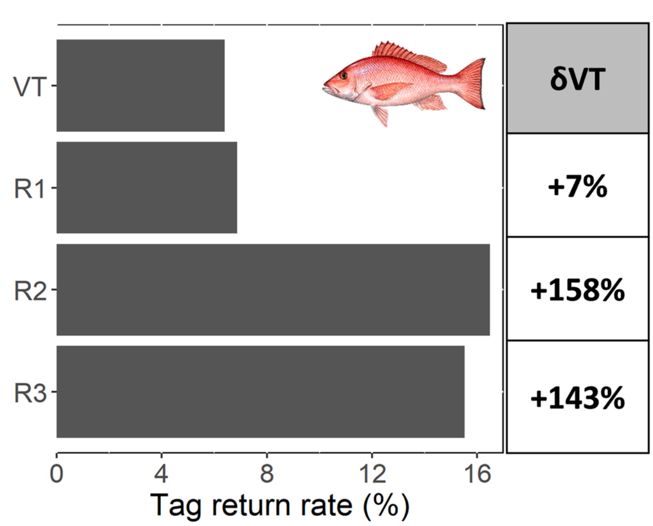

Fig. 3. Tag return rates of red snapper across release methods for vented fish (VT), and those recompressed to 10 m (R1), 20 m (R2), and 30 m (R3). The difference in tag return rate of red snapper between the treatment and venting (δVT) is provided. For example, a δVT = +100% would mean the release method resulted in 2x the number of tag returns compared to venting.

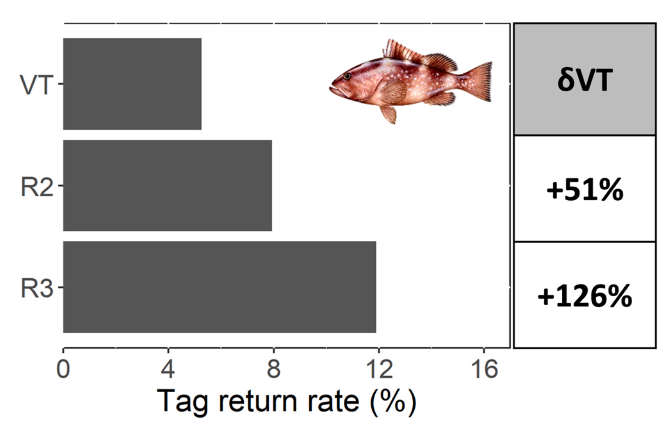

Fig. 4. Tag return rates of red grouper across release methods for vented fish (VT), and those recompressed to 20 m (R2) and 30 m (R3). The difference in tag return rate of red grouper between the treatment and venting (δVT) is provided. For example, a δVT = +100% would mean the release method resulted in 2x the number of tag returns compared to venting.

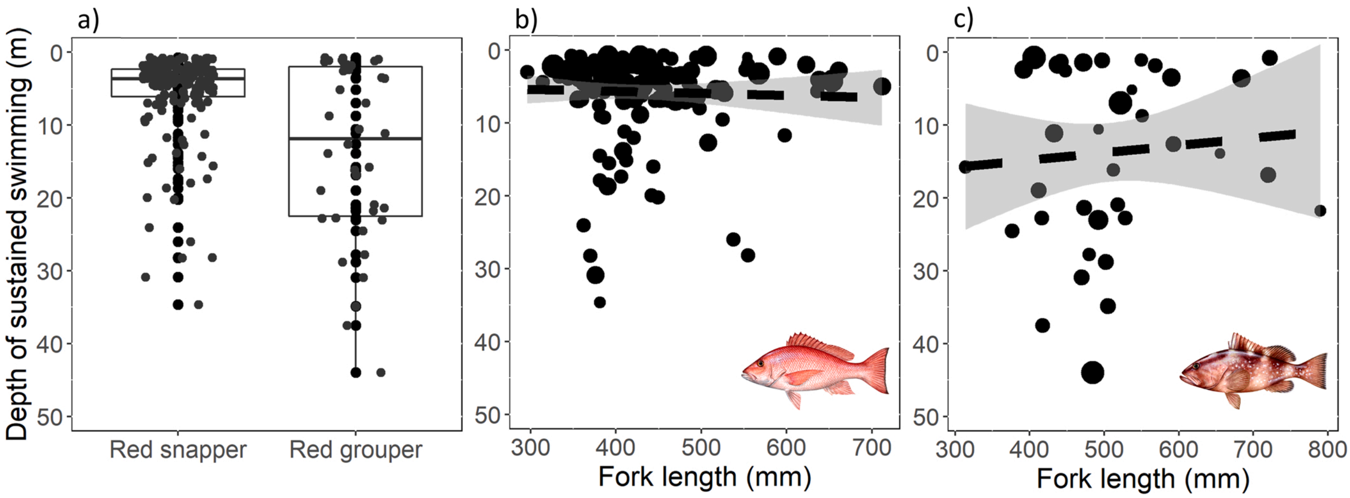

Fig. 5. Boxplots of depths at which sustained swimming occurred for the focal species (a). The boxplots display the 25% (lower hinge of box) and 75% quantiles (upper hinge of box), the median (middle lines), and 95% confidence intervals (lower and upper whiskers). Relationships between fork length and depth at which sustained swimming occurred for red snapper (a) and red grouper (b), with point size corresponding to depth of capture (fish with larger points were captured at deeper depths). The dashed trendlines reflect the non-significant relationships and gray envelopes are the 95% confidence intervals.

recompressed to at least 20 m and were higher the deeper the fish were descended. Although these differences were statistically significant for red snapper, low sample size for red grouper potentially limited our ability to detect differences in tag return rates among treatments. Indeed, a post hoc power analysis ($\alpha = 0.05$, $\beta = 0.2$, power $= 0.8$) indicated we needed a sample size an order of magnitude larger than the one we had (VT = 306, RC = 1071) in order to conclude the observed return rates were statistically different. However, red grouper also required deeper recompression depths than red snapper to resume normal swimming capabilities, thus there does appear to be real differences between the two species in their ability to recover following rapid retrieval to the surface. Red grouper have larger gas bladders in relation to body size (thus have larger volumes of gas) composed of thinner tissue compared to red snapper, which makes them more susceptible to gas bladder ruptures and hemorrhaging (Burns, 2009). Similarly, sympatric Pacific rockfishes (*Sebastes* spp.) exhibited variable responses to recompression, possibly due to anatomical and physiological differences in the severity of barotrauma experienced by the different species (Hannah and Matteson, 2007; Jarvis and Lowe, 2008; Pribyl et al., 2009).

The physiological disadvantages of higher susceptibility to barotrauma by red grouper appear to be offset by the combined effects of how the fishery is currently managed and where the species occurs at various stages of their life history. The harvest season for red grouper is open nearly the entire year, whereas it is much shorter for red snapper (Fig. 1). Red grouper are most abundant in the eGOM across the shallow slope of the West Florida Shelf (Sagarese et al., 2014; SEDAR, 2019) and the majority discarded in the recreational fishery are sub-legal sized fish caught at depths less than 21 m (Sauls et al., 2014). Although both species can overcome barotrauma at depths up to 21 m, particularly for smaller sized fish (Burns, 2009), red snapper of all sizes must be released throughout most of the year, due to the short harvest season, and the majority of discarding in the eGOM takes place at somewhat deeper depths (21–40 m; Sauls et al., 2014). Given how the fishery operates and the two species are currently managed, as well as physiological differences that likely played a role in the results of this study, encouraging anglers to practice recompression may provide more measurable conservation benefits for red snapper. Further, our data suggest that anglers would not need to recompress fish all the way to the bottom when fishing in depths between 30 and 50 m, and may not be required at all when fish do not exhibit signs of barotrauma. If the recommended practices for mitigating barotrauma can be less burdensome, such as recompression to midwater depths instead of all the way to the bottom, anglers may be more willing to adopt descending devices as their method for releasing fish. Our tag return data and observations of swimming behaviors suggested that recompression to depths at or deeper than 20 m will improve survival of red snapper and possibly red grouper compared to surface release with venting. In addition, the depths at which both species regained swimming ability were not related to either depth of capture or fish size, so the positive effects of recompression to 20 m or deeper appear consistent across broad circumstances the anglers could encounter. It is important to note, however, that we fished at a relatively narrow range of depths (30–50 m) and cannot extend this conclusion to depths of capture beyond 50 m. We also did not include a treatment for surface release of unvented fish that displayed signs of barotrauma, which would be needed to test the absolute efficacy of mitigation techniques (e.g., Curtis et al., 2015; Zemeckis et al., 2020).

The comparisons of tag return rates among fish released with different methods is an effective method to evaluate latent mortality under true environmental conditions present within a fishery (Campbell et al., 2014; Hueter et al., 2006; Rudershausen et al., 2020; Sauls, 2014). Although pressure-controlled lab studies provide a highly tractable approach to isolate the effects of individual stressors, they are often unable to account for the multiple, highly variable stressors present in real-world fisheries that influence survival of released fish. For example, Campbell et al. (2010) found that red snapper suffered greater impairment when the additional effect of temperature increase (to simulate fish retrieved from beneath the thermocline to the surface) was included in experimental trials. Our study was conducted in the field during months when water temperatures in the eGOM reach their peak. Indeed, the cage-mounted HOBO® loggers used in our study measured a mean temperature of 29 °C and maximum over 34 °C during the research trips. In contrast, Drumhiller et al. (2014) used controlled conditions in the lab to simulate different catch-and-release methods, had lower water temperatures (mean ± SD = 25 ± 2 °C), and did not find differences in survival of red snapper between those that were recompressed versus vented. Future work in the eGOM can explore whether the strong differences we observed between recompression and venting may be realized when fish are captured and released during months with cooler water temperatures. Many reef fishes in the region are open for harvest during the summer months, coinciding with the highest levels of recreational angling activities (Simard et al., 2016). In their review, Gale et al. (2013) concluded that thermal stressors increase the likelihood for mortality of discarded fish, even when exposure was within the optimum physiological range for the species. Increased thermal gradients during summer months between the bottom and the surface represent an added stressor for red snapper released at the surface (Diamond and Campbell, 2009). In this regard, use of a recompression tool may help to reduce exposure time in higher temperatures.

In addition to higher temperatures, predation might be higher in the upper water column. Recompression tools can rapidly descend released fish past these predators in the upper water column (e.g., dolphins, sharks). Our red snapper data indicated that survival was similar between surface-released vented fish and those recompressed to 10 m. These red snapper from both release techniques would have had to swim on their own through most or all of the water column to reach bottom habitat, and likely had higher predation risk. In contrast, fish that were recompressed to the deeper parts of the water column were released closer to bottom refuge and past predators that foraged near surface waters. This finding is consistent with others who have found that predation is low for fish attached to descenders (Drymon et al., 2020).

Although anglers in the US GOM have not widely adopted recompression tools for discarding fish (Crandall et al., 2018), this study suggests that there is a potential conservation benefit for red snapper if anglers were to increase their use of this method to mitigate the effects of barotrauma. Similar benefits may be realized for red grouper, but additional work is required to determine whether the qualitative similarities with red snapper result in statistical significance. However, this message should be properly outreached to anglers to avoid unnecessary handling for fish that may survive better if returned quickly to the water. Barotrauma is less severe in shallow depths, and a large-scale, mark--recapture study of recreational discards in the GOM found that a high proportion of surface-released red snapper, red grouper, and gag (*Mycteroperca microlepis*) descended on their own and survived better than fish that required venting (Sauls et al., 2014; Sauls, 2014). The Gulf of Mexico Fisheries Management Council currently recommends minimizing handling time and only using barotrauma mitigation methods when a fish displays visible signs of stress (https://gulfcouncil.org/fishing-for-our-future). For fish without severe barotrauma, quickly releasing them as opposed to holding them on deck or in warm surface waters until a descender device is available, is particularly important when discard rates are high, as is frequently the case in the red snapper and similar fisheries. While reef fishes retrieved from shallow depths are frequently able to descend without mitigation, they still require assistance more often in deeper depths (Burns and Restrepo, 1999; Collins et al., 1999). Managed stocks in the region may benefit from adoption of the recompression method, particularly given the magnitude of recreational discards. Implementing measures that target particular species or fisheries where recompression methods have been proven successful will provide the greatest conservation benefits, and anglers may also be more willing to adopt methods that are less burdensome.

CRediT authorship contribution statement

Christopher D. Stallings: Conceptualization, Formal analysis, Writing – original draft, Visualization, Data curation, Writing – review & editing, Funding acquisition. **Oscar Ayala:** Conceptualization, Methodology, Writing – original draft, Data curation, Writing – review & editing, Funding acquisition. **Tiffanie A. Cross:** Methodology, Data curation, Writing – review & editing. **Beverly Sauls:** Conceptualization, Project administration, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christopher Stallings reports financial support was provided by National Oceanic and Atmospheric Administration.

Data Availability

Data will be made available on request.

Acknowledgments

We are incredibly grateful for the collaboration with the charter boat industry that assisted us, especially Captains Brad Gorst on the FV Gulfstream, Chris Padilla on the FV Lady S, and Jesse Zuban on the FV Paladin. This work was supported by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI), including Fisheries Dependent Monitoring (FWRI-FDM) which directed the project and coordinated with the FWRI Tag Return Hotline. Anglers were provided by the FWRI Fish Health staff and volunteers from the USF Fish Ecology Lab. Numerous staff at FWRI contributed important work on this project, including but not limited to Chris Berry, Bridget Cermak, Chris Bradshaw, Rachel Germeroth. In addition, Richard Cody and Ernst Peebles provided valuable feedback on various aspects of the study design and on early versions of the manuscript. This work was funded by a grant (contract number NA13NMF4720270) from the National Marine Fisheries Service Bycatch Reduction Engineering Program (NOAA-BREP).

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