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Original Article

Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality

Erin Collings Bohaboy [1*], Tristan L. Guttridge[2,3], Neil Hammerschlag[4], Maurits P. M. Van Zinnicq Bergmann [2,5], and William F. Patterson III[1‡]

[1]*School of Forest Resources and Conservation, Fisheries and Aquatic Sciences, University of Florida, 7922 Northwest 71st Street, Gainesville, FL 32653, USA*
[2]*Bimini Biological Field Station Foundation, South Bimini, The Bahamas*
[3]*Saving the Blue, Miami, FL, 33186, USA*
[4]*Department of Marine Ecosystems and Society, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA*
[5]*Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA*

Corresponding author: tel: (352) 273-3610; e-mail: erin.bohaboy@ufl.edu.
[‡]*Present address: School of Forest Resources and Conservation, Fisheries and Aquatic Sciences, University of Florida, 7922 Northwest 71st Street, Gainesville, FL 32653, USA.*

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Geopositioning underwater acoustic telemetry was used to test whether rapid recompression with weighted return-to-depth (descender) devices reduced discard mortality of red snapper ($n = 141$) and gray triggerfish ($n = 26$) captured and released at 30–60 m depths at two 15 km^2 study sites in the northern Gulf of Mexico. Cox proportional hazards modelling indicated red snapper released with descender devices had significantly lower discard mortality within the first 2 d (95% CI = 18.8–41.8% for descender-released vs. 44.0–72.4% for surface-released, unvented fish), while there was no significant effect of descender devices on discard mortality of gray triggerfish. Predation by large pelagic predators was estimated to account 83% of red snapper and 100% of gray triggerfish discard mortality. Discard mortality due to predation has likely been overlooked in previous mark-recapture, laboratory, and enclosure studies, suggesting cryptic population losses due to predation on discards may be underestimated for red snapper and gray triggerfish. Large-area three-dimensional positioning acoustic telemetry arrays combined with collaboration and data sharing among acoustic telemetry researchers have the potential to advance our knowledge of the processes affecting discard mortality in reef fishes and other taxa.

Keywords: acoustic telemetry, descender device, discard mortality, predation, rapid recompression, recreational fisheries, red snapper

Introduction

Marine recreational fishing is an important economic activity and source of non-monetary benefits for people around the world (Arlinghaus *et al.*, 2007; Lovell et al., 2013). In addition to fish they harvest, recreational fishers often release (discard) a large portion of their catch. In the US, Canada, and Europe, marine recreational discarding rates often exceed 50% of the total catch and approach 100% for some species (Ferter *et al.*, 2013; National Marine Fisheries Service, 2017; Fisheries and Oceans Canada, 2019). Catch-and-release fishing has historically been practiced in recreational fisheries as a conservation and management strategy (Radonski, 2002). However, discarded fish that die as a result of being captured and released are still removed from the population, reducing the intended conservation benefits of release

(Bartholomew and Bohnsack, 2005). The proportion of live discards that die following release (discard mortality) may approach 100% in some recreational fisheries and is influenced by multiple factors including environmental conditions (e.g. depth of capture and water temperature), fish condition (e.g. species, size, and presence of hook-related injuries), and handling (e.g. time out of water and time required for an angler to land a fish once hooked) (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Brownscombe *et al.*, 2017). In fisheries where recreational catches, discarding rates, or discard mortality are high, dead discards can represent a significant portion of stock removals. In these cases, reducing uncertainty of discard mortality estimates, improving understanding of the factors that affect discard mortality, and developing methods to minimize discard mortality may be instrumental in successful management.

Estimating discard mortality and quantifying the factors affecting it are particularly challenging for marine fish species, largely due to the difficulty of monitoring the fate of released fish. Traditional approaches to studying discard mortality, such as mark-recapture, enclosure, and inferences from physiological studies, often require numerous assumptions (including emigration/immigration rates of fish, angler reporting rates, and natural and fishing mortality), expose fish to the deleterious effects of prolonged captivity, or fail to account for the effects of predation. Ultrasonic underwater acoustic telemetry can provide estimates of three-dimensional positions of tagged fish, and is a reliable means to track the movement, behaviour, and survival of tagged fish for months to years in their natural environment. In particular, predation may be a greatly underestimated contributor to discard mortality because predation events are rarely observed using approaches traditionally applied in post-release mortality studies (Raby *et al.*, 2014). Acoustic transmitter tags often are surgically implanted in the abdominal cavity of fish, requiring sedation, extended handling, and may rupture over-inflated swim bladders of fish suffering from barotrauma, or otherwise add extraneous variables to the process of estimating release mortality. Alternatively, external attachment of acoustic transmitter tags (e.g. Curtis *et al.*, 2015; Dance *et al.*, 2016; Runde and Buckel, 2018) reduces handling trauma and preserves barotrauma symptoms, thus improving estimates of barotrauma-related mortality.

Red snapper (*Lutjanus campechanus*) are highly sought-after by recreational fishers in the US Gulf of Mexico (GOM) who annually discard more than 70% of red snapper they catch (SEDAR, 2018). Discard mortality estimates for recreationally caught red snapper vary from near zero to greater than 80% depending on factors such as release method, handling, season, capture depth, and fish condition (Campbell *et al.*, 2014; Drumhiller *et al.*, 2014; Curtis *et al.*, 2015). Gray triggerfish (*Balistes capriscus*) are another popular recreational reef fish species in the northern GOM that are targeted by recreational fishers with hook and line over artificial reefs where they are also caught incidentally to red snapper. GOM gray triggerfish have experienced long-term stock declines concurrent with reductions in recreational fishing seasons and increased discards; 70% of recreationally caught gray triggerfish in the eastern GOM are discarded annually (SEDAR, 2015). Discard mortality of recreationally caught and released gray triggerfish is rarely studied and most estimates are fairly low based on recapture rates of tagged fish and observations of fish behaviour at release (0–15%, Patterson *et al.*, 2002; Rudershausen *et al.*, 2013). Discard mortality was assumed to be 5% in the most recent GOM gray triggerfish stock assessment (SEDAR, 2015). However, Runde *et al.* (2019) used underwater tagging to control for the effects of barotrauma and estimated that discard mortality of gray triggerfish in the southeastern US recreational fishery was much higher (65–66%) and could account for extensive stock removals when considered together with the magnitude of annual discards.

Fish experience a rapid drop in pressure as they are brought to the surface by anglers, leading to barotrauma which can be a significant contributor to post-release mortality of discarded fish (Bartholomew and Bohnsack, 2005). Venting (the practice of releasing gas from a fish's swim bladder with a large gauge hypodermic needle) has been proposed as a means to improve post-release survival of marine fish suffering from barotrauma, but results are equivocal regarding the benefits of venting and some investigators suggest that improperly venting fish can damage organs and increase discard mortality (Wilde, 2009; Scyphers *et al.*, 2013; Eberts and Somers, 2017). Releasing fish with weighted return-to-depth tools, also known as descender devices, is an alternative means to alleviate barotrauma symptoms and potentially improve post-release survival. Descender devices include several different designs of weighted hooks, clamps, or cages. Forcing fish that would otherwise be too positively buoyant at the surface to resubmerge may reduce predation by delivering reef fishes as closely as possible to the relative safety of the reef structure from which they were captured while avoiding the internal trauma of venting. Evidence supporting the efficacy of descender devices in reducing discard mortality is largely based on studies which show fish recompressed in the laboratory or in cages (absent predation) have increased survival (Parker *et al.*, 2006; Pribyl *et al.*, 2012). In very few studies, the effect of cage-less descender devices on discard mortality of marine fish has been examined (Sumpton *et al.*, 2010; Hochhalter and Reed, 2011; Curtis *et al.*, 2015). In contrast to the US recreational West Coast rockfish fishery, where the use of descender devices has been widely advocated (Chen, 2012; California Sea Grant et al., 2014), descender devices have yet to gain widespread usage among GOM recreational reef fish anglers (Crandall *et al.*, 2018), and no management regulations exist to require or encourage their usage.

The goals of this study were to investigate whether descender devices reduce discard mortality in recreationally caught red snapper and gray triggerfish, and to evaluate the effects of other variables that might affect survival, including season (air/water temperature), capture depth, handling time, and fish condition. A large-area (>15 km^2) three-dimensional geopositioning acoustic telemetry array was used to monitor fine-scale movement and behaviour of tagged fish for up to 1 year, providing insight into the importance of predation on post-release survival, which has traditionally been overlooked in studies of discard mortality (Raby *et al.*, 2014). During this study, techniques for quickly applying external acoustic transmitter tags to red snapper and gray triggerfish were developed, thus eliminating the need for sedation and surgery to more closely approximate the handling of recreationally caught-and-released fish.

Methods

Acoustic telemetry array

An array of 60 Vemco (Bedford, Nova Scotia, Canada) VR2 acoustic receivers was deployed 28 km south of Pensacola Beach, Florida from February 2016 to March 2017 at 28–35 m depth (hereafter "30-m array"). In September 2016, the array was shifted approximately 0.5 km to the south and expanded in the southeast corner to include additional artificial reefs (Figure 1). The array was reduced to 46 receivers and moved to a deeper location (48–55 m) approximately 80 km south of Orange Beach, Alabama from August 2017 to July 2018 (hereafter "55-m" array). Habitat within the study areas of each array deployment consisted of open sand bottom interspersed with numerous artificial reef structures (cement pyramids, reef balls, and chicken coops) and likely also included some natural low-relief limestone hard-bottom habitat in the 55-m array. Acoustic receivers were placed in a grid that provided geopositioning capability of tagged fish in an area >15 km^2 at each array. A range test was done prior to the start of the study to evaluate detection efficiency at distances from 100 to 1000 m. Results of the range test showed that detection efficiency decreased to 50% at 700 m, so we conservatively used a maximum distance between receivers of 600 m, allowing for >50% probability that acoustic tag transmissions within the array could be detected by at least three receivers simultaneously. Receivers within each array were a mix of Vemco model VR2Tx and VR2W receivers. Model VR2Tx receivers were deployed with the internal synchronization (sync) transmitters set to very high output (160 dB), while each model VR2W receiver was deployed with a Vemco V16-5x sync transmitter (set to output 162 dB) suspended 2 m above the receiver on a line attached to a foam buoy. Each receiver was attached to the top of a 2-m tall PVC support pipe that was set in a 36-kg cement base. Grab lines were attached between the cement base and the support pipe that could be used as hoist points during deployment or retrieval. Most receiver bases had a line attached to a floating buoy approximately 2 m above the receiver to increase visibility or suspend a V16-5x sync transmitter (for model VR2W receivers). Each receiver-base unit was lowered to the sea floor on a hook and line from the side of the boat and then located using the boat's sonar depth sounder to measure the GPS coordinates and ensure the acoustic receiver was properly deployed in an upright position.

Acoustic receivers were retrieved midway through each array deployment in September 2016 and March 2018, respectively, to clean any fouling from the acoustic hydrophone and offload the logged acoustic transmission data from each receiver. During retrieval, the vessel's captain would locate the receiver-base unit using the boat's sonar depth sounder. A heavy retrieval line connected to a large mooring hook was attached to a VideoRay (Pottstown, PA, USA) Pro4 mini remotely operated vehicle (ROV). The pilot manoeuvred the ROV to attach the retrieval hook to one of the base's grab lines. The mooring hook was mounted on the ROV so that it would easily detach when the ROV was flown away from the receiver base, thus leaving the retrieval line and hook attached to the base. After ensuring the ROV was free from the retrieval line, the receiver base was raised to the surface and brought onboard the boat with the assistance of a stainless steel davit and an electric winch. Using the ROV enabled the retrieval of 20–30 receiver-base units in a single day, and retrieving the cement base in addition to the receiver avoided leaving marine debris at study sites.

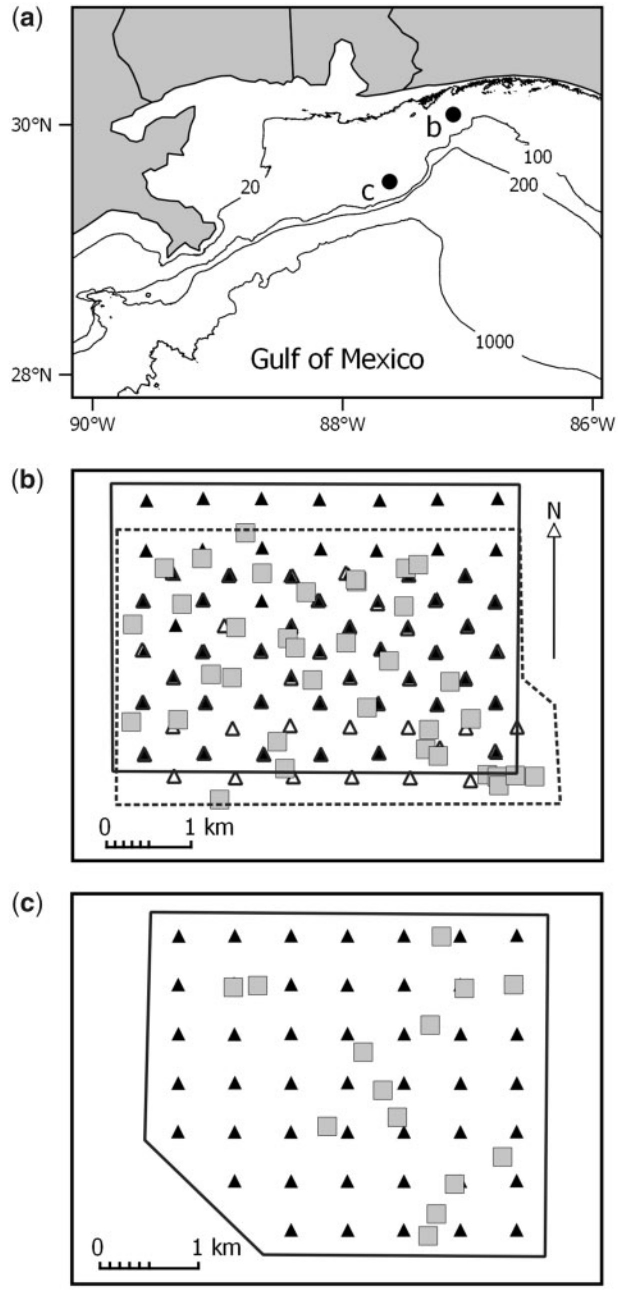

Figure 1. (a) Map of the study area in the northern Gulf of Mexico indicating acoustic array locations. (b) The 60-receiver shallow acoustic array was deployed at 28–35 m depth from February 2016 to March 2017. Receiver locations and the approximate extent of the array from February 2016 to September 2016 are shown as solid triangles (▲) and a solid line (—), while receiver locations and array extent from September 2016 to March 2017 are shown as open triangles (△) and a broken line (- - -). (c) The deep array was deployed at 48–55 m depth from August 2017 to July 2018. Receivers and array extent are shown by solid triangles (▲) and a solid line (—). Artificial reef locations are denoted by squares (■) in both panels (b) and (c).

Tagging

Fish were tagged with Vemco V13P-1x acoustic transmitter tags which transmitted a 153 dB unique acoustic ID code and pressure value at random intervals between 1 and 3 min (expected battery life = 468 d). Tags were attached to fish externally to minimize handling time and avoid rupturing the swim bladder which often occurs when fish suffering from barotrauma are subjected to tag implantation in the abdominal cavity. There were two different

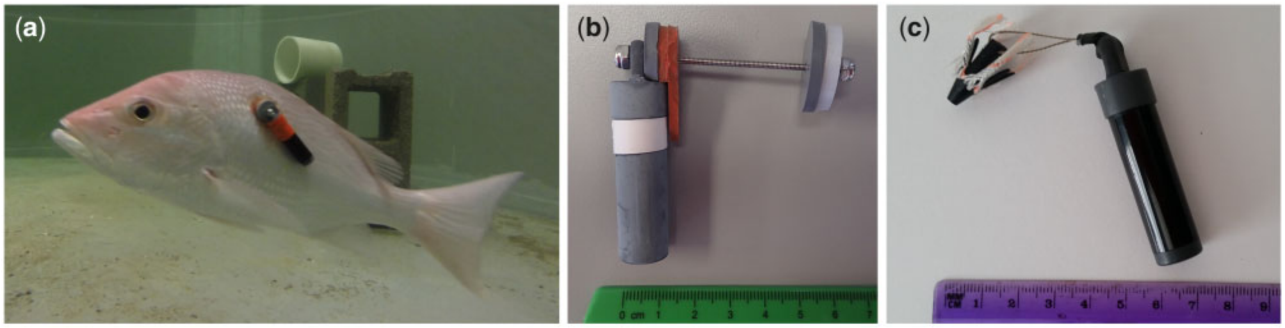

Figure 2. Digital images of (a) a 43-cm TL red snapper held in captivity with an external acoustic tag attached with the stainless steel bar method, (b) an acoustic tag with the stainless steel bar external attachment device, and (c) an acoustic tag with a Domeier dart attachment device.

tag attachment methods used in this study. For the majority of tagged fish, the tag was secured to a 2-mm diameter threaded stainless steel bar with a 6.35-mm nylon-lined locking stainless steel hex nut. The stainless steel bar was sharpened on one end and inserted through the fish's dorsal pterygiophores and secured with a second 6.35-mm stainless steel hex nut behind a 3.2-mm thick polyethylene disk. Silicon disks (2.4–3.2 mm thick) were placed under the tag and under the polyethylene disk to minimize abrasion (Figure 2a and b).

This stainless steel bar acoustic tag attachment device was tested on wild-caught red snapper ($n = 3$) that were held in captivity at Dauphin Island Sea Lab (Dauphin Island, AL, USA), with the goal of achieving greater than 2-week tag retention. These tagging trials were performed with "dummy" V13P tags, which had the same dimensions, weight, and buoyancy as regular V13P tags but did not transmit acoustic signals. One fish shed its tag at 39 d which was the result of becoming tangled in the net cover of the aquaculture tank, causing the entire tag attachment to tear dorsally through the fish's back. Another fish lost its tag at 54 d when the stainless steel hex nut unscrewed from the threaded bar. This potential issue was controlled for in the field by using only new hex nuts where the nylon liner was not compressed from previous use or by slightly bending the ends of the stainless steel rod after affixing tags to fish such that nuts could not spin off the end of the threaded bar. The tag retention trial was terminated after 220 d and the remaining fish which had retained its tag for the duration was euthanized.

An alternate tag attachment method was used to attach acoustic tags to red snapper during late summer 2017 in the deep array. Tags were attached with this second method to a medium-sized (20 mm length × 10 mm width) Domeier dart head (Domeier *et al.*, 2005) with approximately 3 cm of polymer-coated braided stainless steel fishing line. Marine heat-shrink tubing was applied over the tag cap to reduce movement and friction against the side of the fish (Figure 2c). Domeier dart heads are constructed of soft polymer and polyethylene terephthalate surgical fibres and are designed to heal into the muscle tissue of tagged fish. These dart heads have been used to quickly attach acoustic and satellite tags to tunas (Domeier *et al.*, 2005), sharks (Rogers *et al.*, 2013), and groupers (A. Collins, pers. comm.), minimizing handling time and producing high tag retention estimates. However, after examining the acoustic detection data from fish tagged with the Domeier tag attachment device, it was apparent that red snapper tag retention, while adequate to estimate release mortality, did not always allow us to track fish for longer (>1 month) time periods. Therefore, we returned to the initial tagging method for the final tagging event in spring 2018.

Red snapper and other reef fishes were captured from artificial reefs within the study area using hook and line baited with cut squid or herring. Red snapper were the primary species tagged in this study ($n = 141$); however, several gray triggerfish ($n = 26$) were also tagged. Fish were tagged during four events: (i) spring 2016 in the 30-m array, (ii) late summer 2016 in the 30-m array, (iii) late summer 2017 in the 55-m array, and (iv) spring 2018 in the 55-m array. Each fish was held in a damp V-shaped silicone-covered measuring board, measured to the nearest mm fork or total length (FL or TL) and tagged externally with a V13P acoustic transmitter tag using either of the methods described above. Acoustically tagged fish were also tagged with a Floy (Seattle, WA, USA) dart tag that advertised a $50 reward and toll-free phone number to report tagged fish. The presence/absence of traumatic hooking injury, any signs of barotrauma (exophthalmia, pronounced bloating, prolapsed intestine or gonads, protruding scales, or everted stomach), and handling time (total time out of water for dehooking and tagging) were recorded for each tagged fish. The fight time (time between when a fish was hooked and reached the surface) was recorded for most fish based on verbal indication of the hooking event by the angler. During the final tagging event in spring 2018, a Reefnet (Mississauga, Ontario, Canada) Sensus Ultra depth logger was attached to the terminal fishing tackle used to capture fish (Murie and Parkyn, 2013). Depth profiles were examined to identify when a fish was hooked and subsequently reached the surface to determine hooking depth and fight time. Bottom water temperature at each artificial reef where fish were captured was taken from the average daily logged temperature by the closest VR2Tx receiver. Air temperature on each day when fish were tagged was acquired from the National Data Buoy Center at Station 42012 (approximately 48 km west of the 30-m array; National Oceanic and Atmospheric Administration and National Weather Service, 2017) and Station 42040 (approximately 77 km west/southwest of the 55-m array; National Oceanic and Atmospheric Administration and National Weather Service, 2019).

Each tagged fish was released either at the surface or with a descender device over the reef where it was captured. A SeaQualizer (Davie, FL, USA) descender device was primarily used to release fish at depth. However, a second type of descender device was also used to return seven red snapper to depth in spring 2016, but its use was discontinued when some fish prematurely detached from the device at the surface. A downward looking GoPro (San Mateo, CA, USA) Hero3 camera was mounted above each descender device to record fish descent and release to evaluate the performance of the descender device, behaviour of released fish, and possible predator interactions. Fish released at the surface were observed and assessed for release condition following Patterson *et al.* (2001): condition-1 = fish immediately oriented to the bottom and swam down rapidly; condition-2 = fish oriented to the bottom and swam down slowly or erratically; condition-3 = fish remained on the surface; and condition-4 = fish was apparently dead at the surface, including from predation.

Data analyses

Detection data were offloaded from acoustic receivers in September 2016, March 2017, April 2018, and July 2018 and sent to Vemco for Vemco Positioning System (VPS) geolocation estimation. Position estimates with horizontal position error (Smith, 2013) in the upper 5th percentile for each of the four datasets were excluded from further analyses. This level of data filtering eliminated position estimates that were highly uncertain and those that resulted from false detections (i.e. an acoustic tag was recorded by a receiver erroneously due to interference from other tags or background noise). Successive geoposition estimates separated by less than 10 min (600 s) were used to calculate swim speeds of tagged fish. The average swim speed (v) in metres per second of a tagged fish as it moved from position 1 with coordinates (Lat_1, Lon_1) at time t_1 to position 2 with coordinates (Lat_2, Lon_2) at time t_2, where coordinates are in radians, was calculated as

$$v = \frac{2r * arcsin\sqrt{sin^2\left(\frac{Lat_2 - Lat_1}{2}\right) + cos\,(Lat_1)cos(Lat_2)\,sin^2\left(\frac{Lon_2 - Lon_1}{2}\right)}}{(t_2 - t_1)}$$

where $r = 6.371 \times 10^6$ m is the assumed mean radius of the Earth.

Tagged fish were assigned a fate based on estimated swim speeds, geographical movements, and depth below the surface. The days to each fate were calculated and fish fates were binned for some analyses over each of three time periods: immediate (within 48 h of release), short-term (48 h to 14 d after release), and long-term (greater than 14 d after release). The possible assigned fates were predation, emigration, tag loss, surface mortality, harvest, survival, and unknown. Predation and tag loss were indicated by an abrupt change in tag movement or depth. Tags from fish that were preyed upon moved faster than 0.5 m s^{-1} through the array and displayed no affinity for reef structure (see below for rationale). Tags that were stationary on the bottom were assumed to have detached from fish and were classified as tag loss. Fish that were classified as surface mortalities were either observed dead after release or were detected only at the surface as the fish drifted from the array. Harvested fish disappeared from within the centre of the array and were reported by fishers, while emigrating fish moved toward and then disappeared from the edge of the array. Tagged fish that were still alive at the end of each time period were classified as alive and present within the array. In instances when position and depth data of tagged fish were insufficient to differentiate among potential fates, the fate was classified as unknown.

Mortality (predation or surface mortality) was attributed to capture and release (i.e. discard mortality) if it occurred within 48 h of release. Point estimates and SEs of discard mortality were estimated assuming a binomial error distribution (as by Pollock and Pine, 2007). The point estimate of mortality is $\hat{M} = d/n$ where known mortalities (d = number of fish assigned to either predation or surface mortality fates) divided by the total number of "at-risk" tagged fish (n = number of tagged fish with known fates excluding individuals assigned the fate of harvest or emigration). The standard error of estimated mortality is $SE_{\hat{M}} = \sqrt{\hat{M}(1-\hat{M})/n}$.

The influence of release method (surface versus at depth with a descender device), season, reef depth, fish length, presence/absence of trauma to the mouth or gills from hooking or handling, presence/absence of barotrauma symptoms, handling time, fight time, difference between water and air temperature (ΔT where $\Delta T = T_{bottom} - T_{air}$), and inadvertent venting (caused by insertion of the anchor tag or a fish's everted oesophagus or stomach being punctured by its teeth) on an individual's probability of mortality in the immediate time period was explored with nonlinear regression. The predicted probability of mortality for each individual ($\hat{M}_i$ for $i = 1 \ldots n$) was modelled as a function of potential explanatory variables ($X_1, X_2, \ldots, X_k$) and model parameters ($\beta_1, \beta_2, \ldots, \beta_k$), where $\hat{M}_i = \frac{e^{\beta_0+\beta_1X_1+\beta_2X_2+\ldots+\beta_kX_k}}{1+e^{\beta_0+\beta_1X_1+\beta_2X_2+\ldots+\beta_kX_k}}$, with the total binomial log-likelihood being $\sum_{i=1}^{n} \hat{M}_i^{M_i}(1-\hat{M}_i)^{(1-M_i)}$. Categorical variables such as release method, season, capture depth, presence/absence of hooking trauma, and presence/absence of barotrauma were coded as binary variables {0, 1} and M_i was the assigned fate of each tagged fish from the telemetry data (where mortality = 1, survival to next time period = 0). Continuous variables (length, time out of water, fight time, and ΔT) were scaled to have mean = 0 and variance = 1. For red snapper where only FL was measured, FL was converted to TL following $TL = 1.0812 * FL - 0.950$ (in mm; SEDAR, 2018). Candidate models were evaluated for parsimony with the small-sample Akaike Information Criterion (AIC_c).

The risk of mortality over time for fish released with a descender device relative to fish released at the surface was evaluated using Cox proportional hazards models (Cox and Oakes, 1984). Cox proportional hazards models describe the risk of mortality as a function of elapsed time (i.e. are well suited to staggered-entry designs such as this study where individuals are tagged and released during multiple events). Proportional hazards models are also well suited to describe the relative risk of mortality between two different treatments (e.g. fish released at the surface or at depth with a descender device) and can accommodate datasets where individuals leave the study and must be censored from the model. Fish that were assigned fates of emigration, harvest, tag loss, or were still alive when the acoustic array was retrieved were censored at the date of the event. Fish reported harvested or recaptured either outside the array or after having lost the acoustic tag were censored from the model on the date of harvest or recapture, not on the earlier date of tag loss or emigration. We included the maximum number of covariables (thus minimizing risk of falsely rejecting variables) found to be informative in the nonlinear regression models of discard mortality (were within 2 AIC_c from the lowest AICc models; Burnham and Anderson, 2002). Cox proportional hazards models were fit and model performance evaluated with the "survival" package in R (Therneau and Lumley, 2019; R Core Team, 2016). We described goodness of fit (pseudo-r^2) of the

Cox proportional hazards models as the proportional reduction in the sum of squared residuals from the null (intercept only) to the final (with covariables) model.

Results

In total, 141 red snapper ranging from 30.5 to 89.0 cm TL (mean ± *SD*: 52.1 ± 14.1 cm) and 26 gray triggerfish ranging from 32.1 to 50.0 cm FL (mean ± *SD*: 41.5 ± 5.5 cm) were tagged with acoustic transmitter tags and released into the acoustic array (Table 1). Fight times were mistakenly not recorded for the majority ($n = 30$) of red snapper tagged in late summer 2017. A total of 13 red snapper showed signs of traumatic hooking (i.e. the fish hook was removed from the fish's throat, gills, or gut, or bleeding from the mouth or gills was observed). Approximately half of red snapper ($n = 74$) and gray triggerfish ($n = 10$) were released at depth using a descender device. There were no observed instances of a predator removing a tagged fish from the descender device, although 3 red snapper of 71 descended fish successfully recorded on video were observed being consumed by a shark ($n = 2$) or dolphin ($n = 1$) shortly after release from the descender. Sharks or dolphins were present in 25 observed descender releases (35%).

Offloaded detection data from acoustic receivers yielded position estimates for 154 tagged fish. Fish were tracked within the acoustic array up to 330 d following release. Fate and time to fate (days post-release) were assigned to each tagged fish by comparing the individual's movement, swim speed, and depth to known or inferred behaviour patterns indicating a unique fate. Movement, swim speed, and depth data available for large sharks present within our arrays were provided by serendipitous detection of two large (2.50 and 2.55 m TL) female bull sharks (*Carcharhinus leucas*) tagged elsewhere. The calculated mean swim speed of these two tagged bull sharks within the array was 0.95 m s^{-1} (range 0.10–1.54 m s^{-1}; Figure 3a). There are no depth data for these sharks as neither fish's tag contained a pressure sensor. In addition, movement and depth of feeding sharks were provided from tags attached to red snapper (45.2 and 46.0 cm TL) that were observed being preyed upon by large sharks (species uncertain, estimated length 1.5–2.5 m TL). Both acoustic tags continued transmitting for several days following consumption by sharks and provided position estimates up to 50 h following release. The estimated mean speed of these two consumed tags, hence sharks, within the array was 0.57 m s^{-1} (range 0.00–1.44 m s^{-1}; Figure 3b). Two tagged red snapper (65.7 and 54.9 cm TL) were also observed being consumed by bottlenose dolphins, *Tursiops truncatus*, following release. The 65.7 cm TL red snapper was observed by the tagging crew being taken by a dolphin at the surface and the transmitter tag was detected on the bottom immediately following consumption, suggesting the dolphin did not consume the tag together with the fish. The 54.9 cm TL red snapper was visible on the GoPro video footage being taken into the mouth of a dolphin at depth following release from the descender device. That acoustic tag transmitted from depths above the bottom 4 times within approximately 2 min following release, after which no acoustic transmissions were detected. Although there were no instances where tagged fish were observed being preyed upon by dolphins that yielded sufficient detection data to draw inferences on dolphin movement or behaviour, depth data for a 34.0 cm TL red snapper released at the surface show the tag moving frequently (several times per hour) from the bottom to within several metres of the surface for approximately 4 d following release, suggesting the tag may have been moving with a dolphin as it travelled frequently to the surface to breathe.

Normal behaviour indicative of living red snapper and gray triggerfish was inferred from fish that were harvested or recaptured after spending time at liberty within the array. Ten tagged red snapper were recaptured or harvested after being at large between 30 and 844 d, providing confirmation that these fish were alive within the array. Although eight of ten red snapper had lost their acoustic tags prior to being recaptured, review of the VPS position data revealed that prior to tag loss, harvest, or emigration from the array, median calculated swim speed was 0.02 m s^{-1} (range 0.00–0.75 m s^{-1}, based on 95 000 positions; Figure 3c). The frequency distribution of swim speeds was roughly negative exponential with a mode between 0.0 and 0.1 m s^{-1}. Two gray triggerfish were harvested by spearfishers after 16 and 20 d at large, respectively. Prior to being harvested, median calculated swim speed was 0.02 m s^{-1} (range 0.00–0.40 m s^{-1}, based on 8100 positions; Figure 3d). The frequency distribution of swim speeds for these two gray triggerfish was similar to the ten recaptured red snapper with a mode between 0.0 and 0.1 m s^{-1}.

A sudden shift in depth or position over time indicated predation, tag loss, or emigration from the array. For example, a 33.5 cm TL red snapper was tagged and released in the shallow array on 14 September 2016. After approximately 8 h, the fish moved 600 m to an adjacent reef where it remained at depths greater than 25 m until 19 September 2016 03:00 UTC. A sudden shift in depth (ranging from the surface to the bottom) and movement (exiting and entering the array and moving several kilometers in a single direction) indicated the occurrence of a predation event (Figure 4a). Tag loss was apparent by a shift from variable to constant depth and position (Figure 4b). Emigration events were often assumed to occur when tagged fish left the acoustic array without first displaying the abrupt shift in speed, depth, or movement patterns indicative of a predation event (Figure 4c).

Point estimates of red snapper discard mortality (0–48 h following release) were lowest for descender-released fish in the 30-m array in late summer (22.7%, SE = 8.9%) and highest for surface-released fish in the 55-m array in late summer (80%, SE = 12.6%) (Figure 5). Overall, red snapper discard mortality for all tagging events combined was 56.6% (SE = 6.8%) for surface released fish and 36.1% (SE = 6.1%) for descender released fish. Predation accounted for 77% of all red snapper mortalities and 83% of discard mortalities. Our estimates of discard mortality are within the upper range of estimates by depth from previous acoustic telemetry and discard mortality studies of red snapper (Figure 6; Campbell *et al.*, 2014; Piraino and Szedlmayer, 2014; Curtis *et al.*, 2015; Williams *et al.*, 2015; Williams-Grove and Szedlmayer, 2016).

Release method (surface or descender), presence/absence of traumatic hooking injury, fish length, time out of water, and ΔT were all informative variables in regression models of red snapper discard mortality (Table 2). The Cox proportional hazards model including these variables (pseudo-$r^2 = 0.73$) indicated using a descender device to release red snapper significantly reduced discard mortality by a ratio of 0.40 (95% *CI* = 0.23–0.71; Figure 7a) and red snapper suffering from traumatic hooking were five times

Table 1. Summary table of red snapper (RS) and gray triggerfish (GT) that were tagged and released during four tagging events over the course of this study.

	Conditions			**Fish tagged**						
Tagging event	**Depth (m)**	**Air temperature (°C)**	**Bottom temperature (°C)**	**Species**	**Release method**	**Length (cm, mean ± *SD*)**	**Fight time (s, mean ± *SD*)**	**Time out of water (s, mean ± *SD*)**	**% with barotrauma symptoms**	***n***
Spring 2016 26 April–3 May	28 – 31	22.7 – 24.3	20.0 – 21.4	RS	S	45 ± 17	75 ± 61	78 ± 28	30	10
				RS	D	55 ± 17	63 ± 29	118 ± 39	0	10
				GT	S	41 ± 5	67 ± 42	100 ± 35	8	13
				GT	D	41 ± 6	68 ± 44	126 ± 27	0	9
Summer 2016 14 September	28 – 31	26.6	28.8 – 29.9	RS	S	39 ± 5	57 ± 32	80 ± 17	11	18
				RS	D	45 ± 12	81 ± 60	95 ± 32	23	22
				GT	S	45	51	90	0	2
Summer 2017 2 September	51 – 57	28.5	20.4 – 21.7	RS	S	57 ± 78	ND	74 ± 20	53	15
				RS	D	59 ± 14	ND	117 ± 74	61	18
Spring 2018 11 – 24 April	51 – 57	19.8 – 20.3	21.0 – 21.8	RS	S	56 ± 12	146 ± 39	94 ± 26	48	23
				RS	D	58 ± 13	134 ± 36	114 ± 25	83	24
				GT	S	50	177	85	100	1
				GT	D	45	168	131	100	1

Length for red snapper is total length and gray triggerfish is fork length.

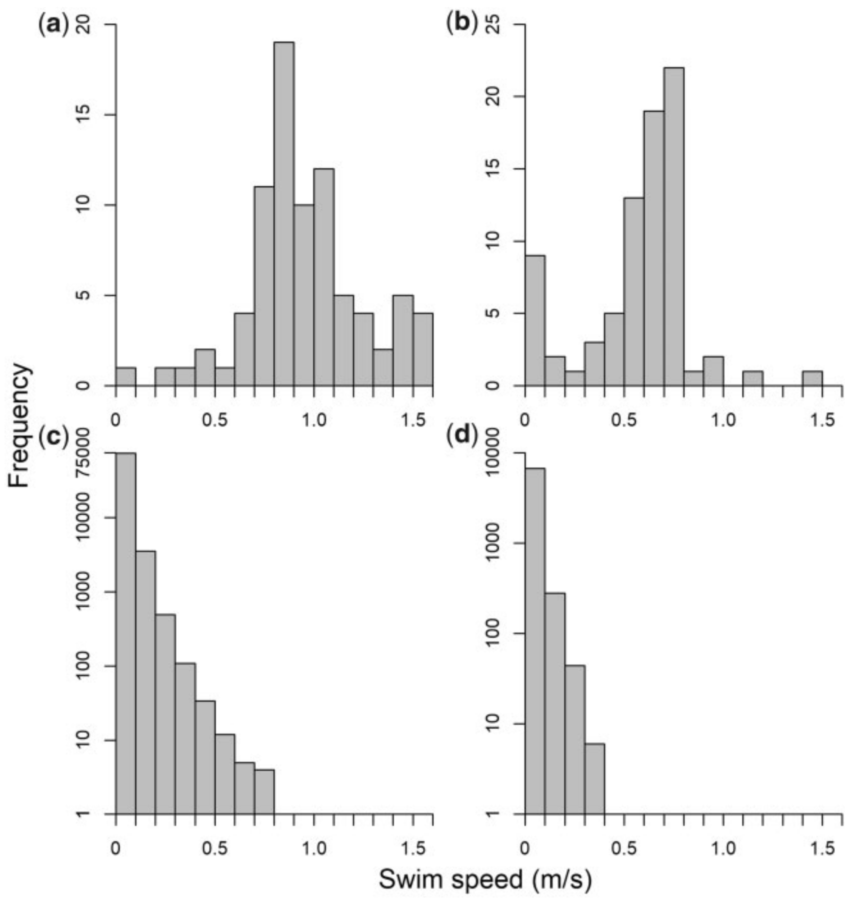

Figure 3. Calculated swim speeds of (a) tagged bull sharks ($n = 2$), (b) red snapper that were observed being preyed upon by large sharks in September 2017 ($n = 2$), (c) red snapper prior to recapture ($n = 10$), and (d) gray triggerfish prior to harvest ($n = 2$).

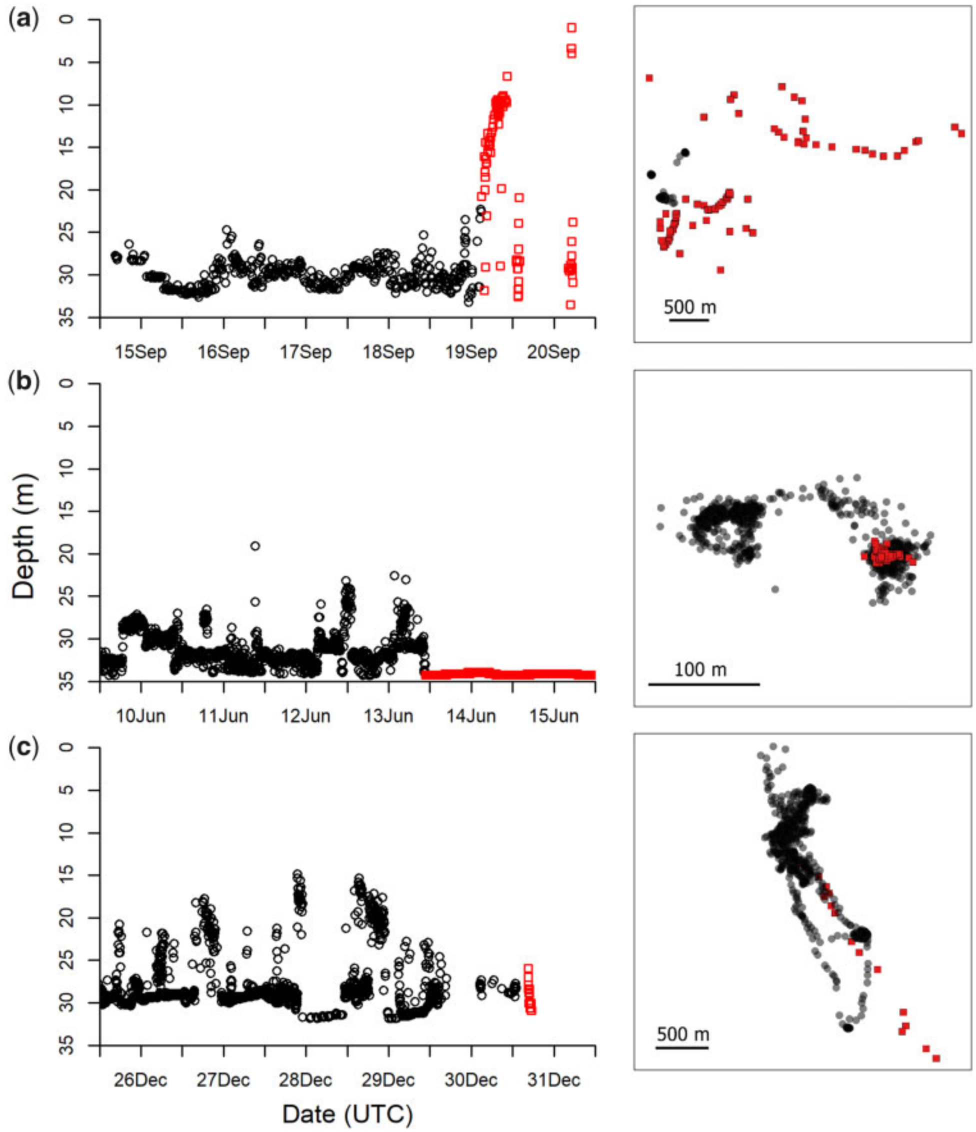

Figure 4. Depth (left) and position (right) of (a) 33.5-cm TL red snapper released 14 September 2016 and consumed by a predator 19 September 2016, (b) 37.6-cm TL red snapper released 26 April 2016 and lost the acoustic transmitter tag 13 June 2016, and (c) 43.8-cm FL gray triggerfish released 14 September 2016 and emigrated from the array 30 December 2016. Normal behaviour of each tagged fish is noted with dark symbols (●) whereas squares (■) indicate the shifted depths and movements associated with each fate (predation, tag loss, and emigration, respectively). Depth is in m and dates are UTC.

more likely to experience discard mortality (95% $CI = 2.2–11.2$). Fish length, time out of water, and ΔT did not significantly affect probability of mortality in the Cox proportional hazards model at alpha = 0.05 ($p = 0.054$, 0.283, and 0.630, respectively). However, the full parameter set chosen *a priori* based on regression model selection was retained. When presence/absence of traumatic hooking injury, fish length, time out of water, and ΔT were controlled, estimated discard mortality of surface-released red snapper was 60.7% (95% CI = 44.0–72.4%) and for descender-released red snapper was 31.2% (95% $CI = 18.8–41.8\%$).

Gray triggerfish ($n = 26$) were tagged primarily in spring 2016 in the 30-m array ($n = 22$). Point estimates of discard mortality were higher (60.0%; SE = 15.5%) for descender-released fish than for surface-released fish (26.7%; SE = 11.4%). Predation accounted for 85% of total gray triggerfish mortalities and 100% of discard mortality. Our dataset did not include enough tagged gray triggerfish to evaluate the effects of depth, season, barotrauma symptoms, traumatic hooking, or accidental venting on gray triggerfish discard mortality. Of the remaining variables, we selected the nonlinear regression model for gray triggerfish discard mortality that included fight time, time out of the water, and fish length, while additional variables such as ΔT or release method did not inform the model sufficiently to warrant inclusion (Table 2). The Cox proportional hazards model did not indicate that fight time, time out of water, fish length, or release method had a significant effect on gray triggerfish survival at the alpha = 0.05 level ($p = 0.0516$, 0.828, 0.098, and 0.339, respectively). When all three covariates were included (pseudo-r^2 = 0.77), 95% *CIs* based on the Cox proportional hazards modelling of predicted gray triggerfish survival overlapped for surface (95%

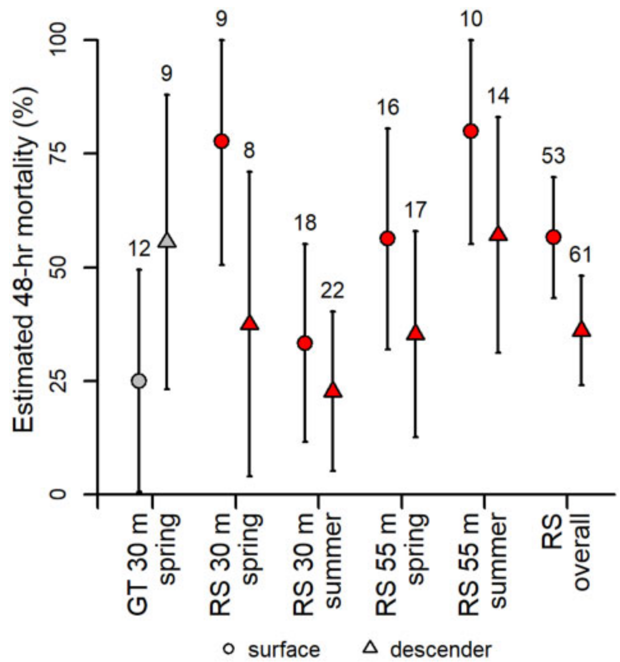

Figure 5. Estimated 48-h % mortality for red snapper (RS) and gray triggerfish (GT) released at the surface versus at depth with descender devices. Error bars represent 95% *CIs* as 1.96*SE following Pollock and Pine (2007). Sample size (number of fish with known fates at the end of 48 h post-release) is above each point estimate.

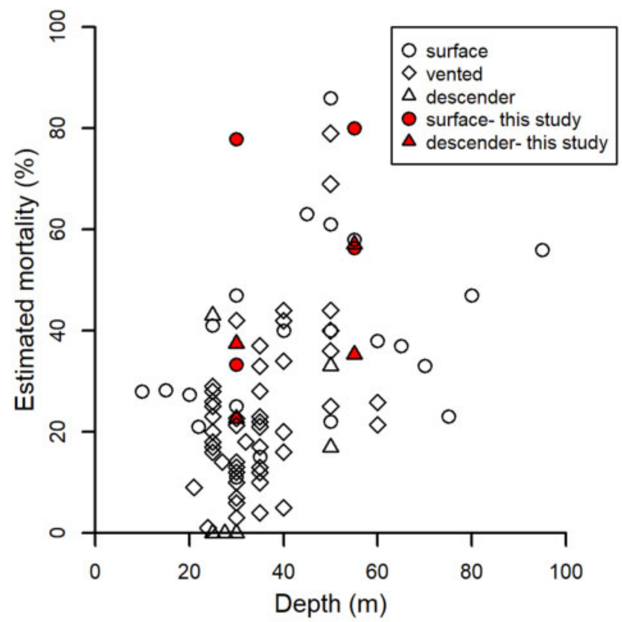

Figure 6. Estimated red snapper discard mortality (%) by release method. Data from prior studies (open symbols) were compiled in Campbell *et al.* (2014), with more recent estimates from Piraino and Szedlmayer (2014), Curtis *et al.* (2015), Williams *et al.* (2015), and Williams-Grove and Szedlmayer (2016).

CI = 55–100%) and descender (*CI* = 22–100%) released fish (Figure 7b).

Few mortalities of red snapper (seven predation and six reported harvests of fish after tag loss or emigration from the array) or gray triggerfish (one predation, two harvest) were observed beyond the first 48 h following release (Table 3). Emigration of tagged fish from an array within 14 d following release was rare, as only 4 red snapper were inferred to have emigrated from an array within 48 h following release, but there were an additional four red snapper and two gray triggerfish that emigrated from an array within 14 d. Ultimately, 14 red snapper and 7 gray triggerfish (25 and 54% of at-risk fish for each species) emigrated from an array 14–269 d following release. The mean time to emigration was 44 d (± *SD*: 46 d) for red snapper and 118 d (± *SD*: 99 d) for gray triggerfish. Acoustic tag losses were highest for the Domeier dart attachment used in late summer 2017 (13.8% tag loss within 48 h, 20.7% within 14 d). Otherwise, the highest 14-d cumulative tag loss using the threaded bar attachment was 5.1% for red snapper tagged in spring 2018. The threaded bar attachment for gray triggerfish also had low tag loss rates. Of 26 gray triggerfish that were tagged in 2016, only one was estimated to have lost its acoustic tag (330 d after release).

Discussion

Predation by highly mobile predators within several hours of release was the dominant source of discard mortality for acoustically tagged red snapper (83%) and gray triggerfish (100%). Traditional mark-recapture, laboratory, and enclosure approaches utilized to estimate discard mortality do not explicitly account for predation, although authors of several studies have drawn inferences of fish behaviour or included observations indicating that predation may be an important contributor to discard mortality, at least in the case of red snapper (Campbell *et al.*, 2010; Drumhiller *et al.*, 2014). Authors of most discard mortality studies using acoustic telemetry methods identified mortality events by lack of movement (freshwater/estuarine: Hightower *et al.*, 2001; Bacheler *et al.*, 2009, marine: Curtis *et al.*, 2015; Runde and Buckel, 2018), implying that following release fish succumbed directly to handling injury, starvation, cold-kill, or disease. Data from the current study suggest, at least in the marine environment where large predators may be present or abundant, fish that are compromised following capture and release may be more likely to be consumed by predators before they die and settle to the bottom. The large spatial coverage and positioning accuracy of our acoustic telemetry arrays, combined with observations of large tagged sharks moving within the arrays or of sharks consuming tagged fish, provided the unique ability to explicitly identify predation events. Researchers using acoustic telemetry to estimate mortality of tagged fish have inferred the occurrence of predation events from movement, depth, or acceleration data (Heupel and Simpfendorfer, 2002; Runde and Buckel, 2018); however, data in our study indicate predation accounted for the majority of discard mortality observed in acoustically tagged red snapper and gray triggerfish. This result may be location-specific, with an abundance of large coastal sharks or dolphins occurring in our region, or it may indicate that the large spatial coverage of our study and the inclusion of depth sensors on tags enabled us to identify predation events that otherwise would have gone undetected.

Our large-area acoustic arrays enabled us to differentiate between tagged fish which emigrated from an array under their own volition and transmitters which moved out of an array with a predator that had consumed a tagged fish. We observed that following predation by a large shark, transmitters moved away from

Table 2. Nonlinear regression models testing factors affecting discard mortality for red snapper and gray triggerfish.

Model	*n*	k	-LL	ΔAIC_c
Red snapper				
$\hat{M} \approx \beta_0 + \Delta T + descender + trauma + length$	140	5	65.9	0
$\hat{M} \approx \beta_0 + \Delta T + descender + trauma + length + time_{out}$	139	6	65.7	1.7
$\hat{M} \approx \beta_0 + \Delta T + descender + trauma$	140	4	68.3	2.6
$\hat{M} \approx \beta_0 + \Delta T + descender + trauma + length + time_{out} + season$	139	7	65.5	3.6
$\hat{M} \approx \beta_0 + \Delta T + descender$	140	3	71.4	6.7
$\hat{M} \approx \beta_0 + \Delta T$	141	2	74.5	10.8
$\hat{M} \approx \beta_0$	141	1	79.2	18.1
Gray triggerfish[a]				
$\hat{M} \approx \beta_0 + time_{fight} + time_{out} + length$	21	4	8.5	0
$\hat{M} \approx \beta_0 + time_{fight} + time_{out}$	21	3	10.1	0.2
$\hat{M} \approx \beta_0 + time_{fight} + time_{out} + length + \Delta T$	21	5	8.3	3.1
$\hat{M} \approx \beta_0 + time_{fight}$	22	2	13.6	4.4
$\hat{M} \approx \beta_0 + time_{fight} + time_{out} + length + \Delta T + descender$	21	6	7.9	6.4
$\hat{M} \approx \beta_0$	26	1	16.8	8.3

ΔAIC_c values are shown relative to the model with the lowest AIC_c.

[a]For gray triggerfish, not all levels of some variables contained samples, thus effects of depth, barotrauma symptoms, accidental venting, traumatic hooking, ΔT, and season on discard mortality could not be explored.

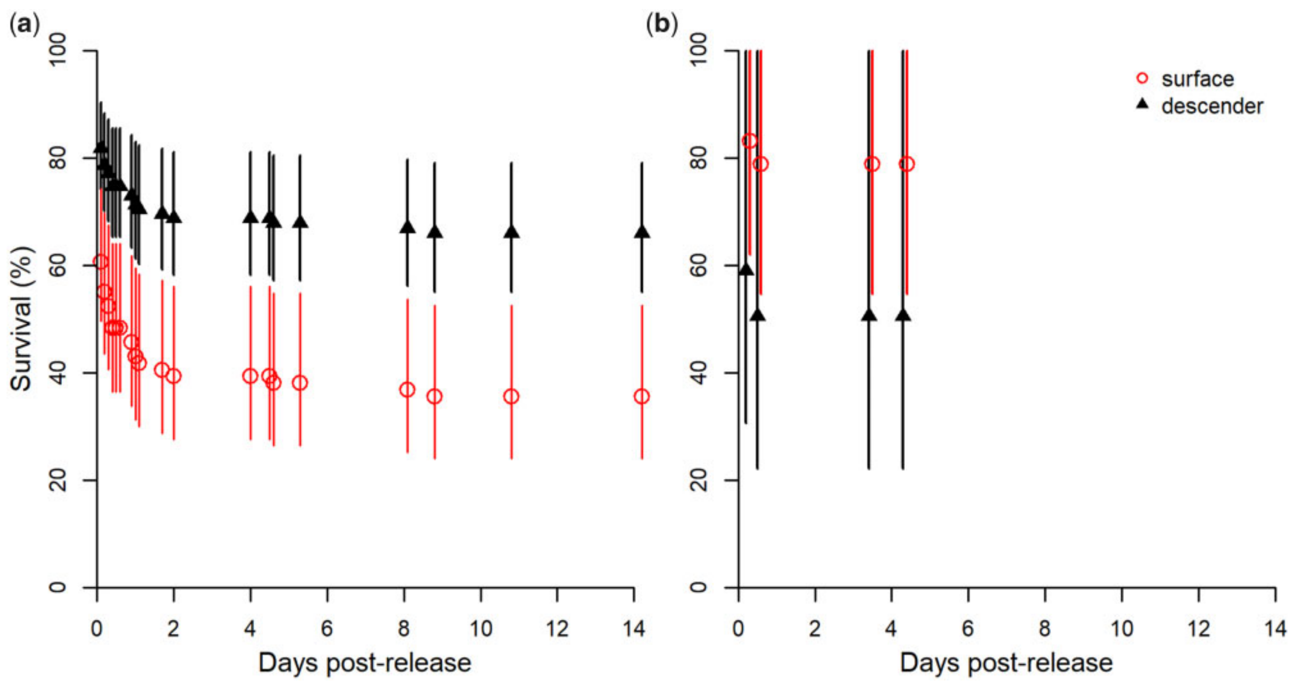

Figure 7. Cox proportional hazards model-estimated survival (±95% *CIs*) for surface-released (○) and descender-released (▲) fish. (a) Red snapper models included presence/absence of traumatic hooking injury, fish length, time out of water, and the change in temperature from the bottom water to the air as covariables (pseudo-$r^2 = 0.73$) and (b) gray triggerfish models included fight time, time out of the water, and fish length as covariables (pseudo-$r^2 = 0.77$).

the tagging site immediately, and often moved out of the detection area of the array within several hours. Surviving fish, in contrast, rarely moved away from the reef within hours of being tagged. Results of several acoustic telemetry studies have indicated a large number of tagged red snapper and gray triggerfish apparently leave the detection area surrounding tagging reefs within 2–6 d post-tagging (Szedlmayer and Schroepfer, 2005; Piraino and Szedlmayer, 2014; Herbig and Szedlmayer, 2016). These individuals, which can be >30% of all tagged animals, typically have been classified as tagging-induced emigrations and censored from further analyses when the objective of a study was to examine fish behaviour or survival separate from discard or tagging mortality. However, when the primary objective is to estimate discard mortality with acoustic telemetry data, it is vital to accurately distinguish between emigration from the tagging site and predation, as censoring these individuals from the post-release survival data may greatly underestimate discard mortality.

Our overall red snapper discard mortality estimates are within the range of discard mortality estimates reported by other authors but also generally higher than most previous estimates at

Table 3. Number of tagged fish in each fate assignment category by time period following release.

	Time post-release		
Fate	**0–48 h**	**2–14 d**	**14+d**
Red snapper: surface released			
Predation mortality	21	2	4
Surface mortality	9	0	0
Harvest mortality	0	0	0
Emigration	3	1	3
Tag lost	3	0	11
Unknown	7	0	0
Alive and present	23	20	2
Red snapper: descender released			
Predation mortality	22	1	0
Surface mortality	0	0	0
Harvest mortality	0	0	1
Emigration	1	3	12
Tag lost	3	3	13
Unknown	9	0	0
Alive and present	39	32	6
Gray triggerfish: surface released			
Predation mortality	4	0	1
Surface mortality	0	0	0
Harvest mortality	0	0	1
Emigration	0	2	6
Tag lost	0	0	0
Unknown	1	0	0
Alive and present	11	9	1
Gray triggerfish: descender			
Predation mortality	6	0	0
Surface mortality	0	0	0
Harvest mortality	0	0	1
Emigration	0	0	1
Tag lost	0	0	1
Unknown	0	0	1
Alive and present	4	4	0

"Alive and present" includes tagged fish that were identified as alive with acoustic tag attached and within a study array at the end of each time period (the end of the 14^{+} d time period was the retrieval of the acoustic array).

comparable depths. This may be because our approach to estimating discard mortality, with large-scale three-dimensional tracking of reef fish over weeks to years, was better able to detect predation events than existed in previous studies. If we exclude predation from discard mortality (by censoring all tagged fish that were identified as predation mortalities), estimated red snapper overall discard mortality in the 30-m array (regardless of release method or season) would drop from 36.8% (including predation) to 5.3% (excluding predation), corresponding to a reduction from approximately the 90th percentile to the 10th percentile of estimates from previous studies at depths from 25 to 35 m (Figure 6). For red snapper released in the 55-m array, excluding predation as a source of mortality reduced estimated discard mortality from 54.4% (70th percentile of previous studies at depths from 50 to 60 m) to 21.2% (lower estimate than previous studies at comparable depths; Figure 6). Many coastal and offshore shark populations in the southeast US and GOM have begun to recover in recent years, with positive trends expected to persist (Peterson *et al.*, 2017; SEDAR, 2017). Increased shark abundance, including bull sharks (Froeschke *et al.*, 2013), could lead to higher predation rates on recreationally released fish, explaining the high estimates in this study and suggesting that predation may be an increasingly important driver of discard mortality of reef fish in coming years as shark populations continue to recover.

Descender devices approximately halved estimated red snapper discard mortality in this study. There have been very few comparable studies of descender devices where released fish were at risk of predation. In several of these investigations, the authors concluded that releasing fish with descender devices substantially decreased discard mortality (e.g. by 67% for red snapper, Curtis *et al.*, 2015; by 98% for yelloweye rockfish *Sebastes ruberrimus*, Hochhalter and Reed, 2011). However, there was no significant benefit of releasing fish with descender devices for six additional species investigated in mark-recapture and acoustic telemetry studies (Sumpton *et al.*, 2010; Eberts *et al.*, 2018). Laboratory and enclosure studies that exclude predation are much more numerous and are more likely to conclude little or no effect of descender devices on discard mortality (e.g. Roach *et al.*, 2011; Butcher *et al.*, 2012; Ng *et al.*, 2015), with Drumhiller *et al.* (2014) being a notable exception (red snapper survival was estimated to be 17% for surface-released and 83% for experimentally recompressed fish). We found the effect of descender devices on discard mortality of gray triggerfish was not statistically significant, largely due to small sample size. Increased handling (fight time and time out of water) and decreased fish size appeared to have a positive effect on discard mortality; however, none of the variables investigated were deemed to have a significant effect on gray triggerfish discard mortality. All gray triggerfish tagged in this study were captured from shallow (30 m) depth and none were observed to be suffering from barotrauma, so it is possible that confounding effects of additional handling and delayed return to depth obscured any benefits of being returned to depth with the descender device.

Aside from release method, the presence of traumatic hooking injury greatly affected discard mortality of red snapper, which is widely supported by results of previous investigations that suggest throat-, gut-, or gill-hooked fish have low survival probability (Muoneke and Childress, 1994; Murphy *et al.*, 1995). Reef depth, presence/absence of barotrauma symptoms, fish size, and season did not have an apparent effect on discard mortality of red snapper or gray triggerfish. This was somewhat surprising given barotrauma is a primary contributor to discard mortality and fish size is expected to influence physiological stress and the degree of barotrauma that fish experience. However, many barotrauma symptoms may be cryptic and not detectable without internal examination of fish tissues and organ systems (Rummer and Bennett, 2005). Fishing depth profiles from spring 2018 tagging also indicated fish were rarely captured near the bottom and instead were hooked and retrieved from a range of mid-water depths. The absence of a depth effect may be due to this observation error because we had to rely on reef depth in our discard mortality models since we did not have capture depth data for most of our tagged fish. Similarly, the categorical variable season may not have adequately described the physiological stressors that fish were exposed to during each of the four tagging events. It is possible that seasonal variation in predation pressure obscured any apparent effect of temperature-induced physiological stress that tagged fish experienced. For example, fish tagged and released in the early spring may have experienced less temperature-induced physiological stress but were exposed to more actively feeding sharks. Instead of season, we chose to use the change in temperature between bottom water and air temperature to reflect the amount of temperature stress that fish experienced, which was significant in the red snapper discard mortality nonlinear regression model (a larger increase in temperature from the bottom water to the air increased mortality). The overall lowest red snapper discard mortality occurred in late summer 2016 when the bottom water temperature was greater than the air temperature (i.e. fish experienced a 2–3°C temperature drop when they were brought to the surface and removed from the water for tagging). The highest overall discard mortality occurred in late summer 2017 when air temperature was comparable to late summer 2016 but the bottom water temperature was 7°C colder than the air temperature on the day of tagging.

We believe our estimates of discard mortality reduction due to descender devices may be conservative since seasoned fishers, in particular crew on for-hire fishing vessels, could streamline the rigging of the descender device (reducing the amount of weight and excluding the video cameras to reduce drag and increase retrieval speed) while also reducing handling time relative to fishes tagged in this study. We did not examine the effect of venting fish on discard mortality and chose instead to evaluate the efficacy of descender devices compared with unvented surface-released fish. Results are equivocal regarding the benefits of venting and some investigators suggest that many fishers improperly vent fish, which can damage organs and increase discard mortality (Wilde, 2009; Scyphers *et al.*, 2013; Eberts and Somers, 2017). In contrast, neither we nor previous researchers to our knowledge have presented evidence that descender devices cause harm to fish. Recreational fishers will undoubtedly play the primary role in efforts to reduce discard mortality, and although venting may continue to be the preferred method of discard mortality reduction among fishers in many instances (Crandall *et al.*, 2018), further evidence supporting the efficacy of descender devices could facilitate acceptance among GOM reef fish fishers.

Continuing advances in geopositioning acoustic technology, including reduced costs, enable researchers to deploy more receivers covering larger areas. Greater spatial coverage within studies, combined with the proliferation of cooperative networks that foster equipment sharing and information exchange among researchers (Hussey *et al.*, 2015), will be instrumental to improving studies of discard mortality of marine fishes. Future investigations in the marine environment should be designed to measure the effects of predation on the survival of discarded fish or else risk ignoring this potentially significant driver of mortality. The quantification of dead discards and efforts to reduce discard mortality will be increasingly vital considerations in recreational fisheries around the world where recovering population abundances, harvest prohibitions, or non-consumptive attitudes of fishers results in large numbers of discarded fish.

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