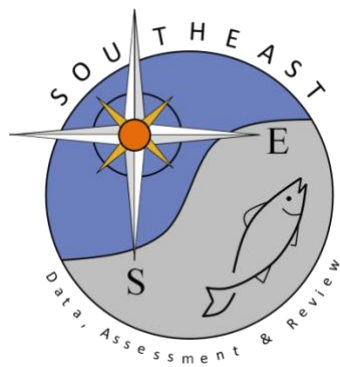


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ABSTRACT

We estimated condition-specific survival rates of gray triggerfish (*Balistes capriscus*) using a tag-recapture approach and extrapolated these values to produce an overall discard survival estimate for the US South Atlantic recreational hook-and-line fishery. Tag return rates of fish tagged at the seafloor using SCUBA served as a reference for return rates of fish tagged at the surface. We examined the validity of gross necropsy as a proxy for survival by identifying likely causes of discard mortality. Best-condition surface-released fish (no external trauma) had an estimated mean proportional survival of 0.39 (95% confidence interval 0.28, 0.55). For gray triggerfish exhibiting visible trauma, estimated survival was 0.24 (0.10, 0.60). Floating fish had a survival rate of zero. The necropsy-based estimate of gray triggerfish lacking organ displacement closely matched the tag-based estimate of survival. Mean estimated discard survival across all depths for North Carolina was 0.35 (0.10, 0.59) and for Florida was 0.34 (0.08, 0.59). These results have implications for gray triggerfish management because our estimate of discard survival is substantially lower than previously assumed and for future discard survival research given our findings with gross necropsies.

1. Introduction

For many fisheries, discarded fish make up a large and increasing proportion of total catch (NMFS, 2016). This trend has resulted from changing angler behavior (Quinn, 1996; Graefe and Ditton, 1997; Allen et al., 2008) and more restrictive management (Kelleher, 2005). Substantial effort has been spent assessing the magnitude of discards (e.g., Bartholomew and Bohnsack, 2005; Kelleher, 2005; Zeller et al., 2018) and estimating survival rates of discarded fishes (e.g. Davis, 2002), as these figures remain crucial components of modern stock assessments (Alverson et al., 1994; Breen and Cook, 2002; Punt et al., 2006; Viana et al., 2010, 2013; Dapp et al., 2017).

Methodologies for estimating discard survival have varied, largely due to the difficulty and expense associated with quantifying delayed mortality that may result from latent trauma. Electronic tagging is expensive, and the effects of such tagging may confound the estimate of discard survival for species prone to barotrauma (Curtis et al., 2015). Further, tank holding studies may exclude the effects of discard-related predation and therefore may not produce a realistic survival estimates (Pollock and Pine, 2007). Mark-recapture methods with conventional tags have frequently been employed to account for delayed mortality;

however, many mark-recapture studies lack a control group and instead rely on assumptions about fish in the best observable condition based on swimming ability or physical injury (e.g. Wilson and Burns, 1996; Patterson et al., 2002). Most discard survival studies of physoclistous reef fishes have reported barotrauma as a contributor to mortality. The pressure differential between the seafloor and the surface leads to internal gas expansion when fish are retrieved, often resulting in positive buoyancy and an inability to resubmerge when released at the surface (Davis, 2002). Severe physical effects, such as organ displacement and internal injuries, have also been documented for many reef fishes, particularly when retrieved from deeper depths (Davis, 2002; Rummer and Bennett, 2005; Jarvis and Lowe, 2008).

In general, authors have argued that fish with mild or no visible barotrauma are likely to survive discarding if they resubmerge (e.g., Beverton et al., 1959; Kaimmer and Trumble, 1998; Hannah et al., 2008) and have deemed these individuals a control group to which fish in compromised conditions may be compared (Hueter et al., 2006). Such proxies may be ineffective because internal and latent injuries may impact survival. Furthermore, condition classification is often subjective between observers, which may make results between studies incomparable. More recent studies have addressed the issue of latent

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trauma by applying a range of survival estimates to the reference group (e.g. Sauls, 2014). While this approach is likely more realistic than the former, studies that have an adequate control remain the most robust (Pollock and Pine, 2007) because they estimate absolute survival (e.g., Rudershausen et al., 2014).

One technique to estimate absolute survival of demersal fish while having a suitable control group is to tag a group of fish at depth using SCUBA divers. This approach was originally used by Hislop and Hemmings (1971) to estimate haddock (*Melanogrammus aeglefinus*) discard survival and was recently used by Rudershausen et al. (2014) for black sea bass (*Centropristis striata*). The group of fish tagged by divers is not subjected to barotrauma or other sources of mortality associated with surface release, such as hooking injury, air exposure, and water column predators, and any handling stress from tagging (though likely negligible) is the same at the surface and the seafloor. Furthermore, attrition of tagged fish due to processes such as tag shedding, predation, and movement occur at the same rate for fish in the surface-tagged group and the diver-tagged group, and thus do not need to be estimated or accounted for in this type of study. Therefore, all diver-tagged fish are assumed to survive and absolute survival rates of surface-tagged fish with injuries can be estimated by comparing recapture rates of surface- and diver-tagged fish. Survival estimates from this approach include immediate and delayed mortality.

Mark-recapture methodologies including SCUBA are costly and time-consuming, and a validated proxy for estimating absolute mortality would be valuable to researchers. Laboratory examination of sacrificed individuals may be an inexpensive means of elucidating the extent of latent trauma and informing mortality estimates (Mikles et al., 2019). Gross necropsy has rarely been used in studies of discard survival of barotraumatized fishes (but see Burns and Restrepo, 2002; Neufeld and Spence, 2004; Rummer and Bennett, 2005) and has never to our knowledge been employed to directly compare prevalence of severe internal injuries to robust estimates of discard survival.

Increased regulations have led to higher rates of discarding in many regions (Kelleher, 2005; NMFS, 2016) but robust estimates of discard survival are scarce. One of the species for which regulations have recently changed in the southeast United States (SEUS) is gray triggerfish (*Balistes capriscus*), a commercially and recreationally important demersal reef fish in the SEUS and Gulf of Mexico. Gray triggerfish and other *Balistes* spp. are also important to fisheries in other coastal regions of the North and South Atlantic (Floeter et al., 2006; Aggrey-Fynn, 2009; Gamito et al., 2016). Numbers of recreationally discarded gray triggerfish in the SEUS have frequently exceeded harvests by a factor of ~2–3 (Fig. 1; MRIP, 2017). Increased discarding in the Atlantic recreational fishery coincided with recent changes to minimum size requirements for gray triggerfish with a 305 mm fork-length (FL) limit established for federal waters in North Carolina, South Carolina, and Georgia and 356 mm FL limit established in Florida (SAFMC, 2014; effective July 1, 2015).

These recent regulatory changes highlight the growing importance of this species in the SEUS. There are several studies that estimated discard survival for gray triggerfish (Table 1), but none used a control. In this study we estimate discard survival of gray triggerfish using SCUBA diver-tagged fish as a control group. We then apply condition-specific estimates of discard survival to fishery-dependent observer data to estimate overall discard survival for the gray triggerfish recreational fishery in the SEUS. Additionally, we compare our survival estimates to the prevalence of external injury or severe internal injury observed using gross necropsies to validate the latter as a less expensive proxy for discard survival.

2. Methods

2.1. Study area and fish tagging

Gray triggerfish were caught in Onslow and Raleigh Bays, North

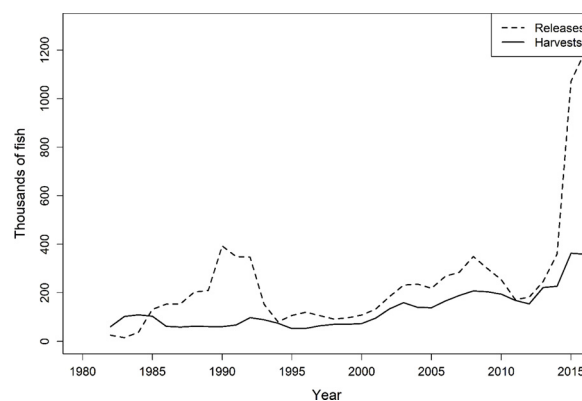


Fig. 1. Gray triggerfish *Balistes capriscus* releases and harvests (3-year moving average; e.g., 1982 value is average of 1981, 1982, and 1983) in the southeast US from National Oceanic and Atmospheric Administration Marine Recreational Information Program, 1981–2017 (MRIP, 2017). Input variables for query were: 1981–2017, all modes (e.g. charter boats, private boats) combined, all areas combined, South Atlantic, and all catch types. Query performed 2 November, 2018. In mid-2015, a 305 mm minimum size requirement was established for North Carolina, South Carolina, and Georgia and an existing 305 mm fork-length requirement was increased to 356 mm for Florida. MRIP query can be accessed at: <https://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index>.

Carolina, USA using hook-and-line (with conventional reels; maximum drag 12.7 kg) and on-bottom fish traps. Terminal tackle for hook-and-line sampling consisted of a three-hook bottom rig with circle hooks (Gamakatsu #42410 size 1 or Gamakatsu #42411 size 1/0) or ‘J’ hooks (Gamakatsu #81411 size 1; Gamakatsu USA, Inc., Tacoma, Washington, USA) and 0.2–0.7 kg lead weight connected by 59 kg monofilament line. Hooks were baited with cut squid (*Dosidicus* spp.). Traps were approximately cubical with side lengths 0.6 m, and were constructed of 12-ga vinyl-coated wire with square mesh size 38 mm and baited with approximately 2 kg Atlantic menhaden (*Brevoortia tyrannus*). Traps had two funnel-type entrances with elongated openings approximately 250 mm long and 75 mm wide when stretched. Bait wells were cylindrical (diameter = 120 mm), were positioned vertically in the middle of the traps, and extended the entire height of the traps. Traps were sometimes set in a string of 5–10 and sometimes set as a single trap per float line, depending on the capabilities of the vessel. Traps were retrieved both by pot haulers and by hand, depending on vessel capabilities and sea conditions. Tagging occurred in three distinct regions: Onslow Bay and two subsets of Raleigh Bay which we term “Atlas” (after a prominent shipwreck) and Chicken Rock. Gray triggerfish were angled from depths of 30–40 m (May–December 2015; February–September 2016; October 2017), which is a common depth of capture of this species in the recreational fishery in this region (Fig. 2A).

Gray triggerfish caught with hook-and-line gear were retrieved to the research vessel where they were measured (FL, mm), marked with a FM-95W wire-core tag (15 mm × 4 mm ovular disc; 73 mm streamer; Floy, Inc., Seattle, WA, USA) that was inserted into the abdomen, and released at the surface. Each tag displayed the unique identification number and a statement of “CUT TAG. REWARD.” Tags also provided the toll-free phone number for reporting recaptures. Fish were evaluated upon release with respect to their behavior and observable trauma and each was assigned one of three conditions: condition 1 (no trauma; swam down), condition 2 (trauma; swam down), and condition 3 (floated). Trauma was defined as obvious external injury related to capture, such as prolapsed intestine or visceral extrusion through the mouth or gill operculum, and also included possible stressors such as moderate to severe bleeding or abrasions that were a result of capture. Condition categorizations were made for every surface-released fish in the study by the first author (B. Runde) and did not depend on the

Table 1

Discard survival estimates from studies used in the 2016 South Atlantic Fishery Management Council gray triggerfish *Balistes capriscus* stock assessment. Reproduced and adapted from SEDAR (2016). Gear identifies whether the study methods included hook-and-line (HL) or trap-caught fish.

Source	Depths	Methods	n fish	Gear	Est. survival
Sauls et al. (2013)	Broad; mean = 29 m	Observer data, condition proxy	797	HL	0.88
McCarthy (2013)	Unreported	Logbooks, condition proxy	N/A	HL, trap	0.88
Rudershausen et al. (2010)	29–37 m	Tagging, condition proxy	332	HL, trap	0.85
Collins (1996)	21 m, 46–54 m	Condition proxy	6	HL	0.83
Stephen and Harris (2010)	20–80 m	Condition proxy	25	HL	0.07
Patterson et al. (2002)	21–32 m	Tagging, condition proxy	842	HL	1.00

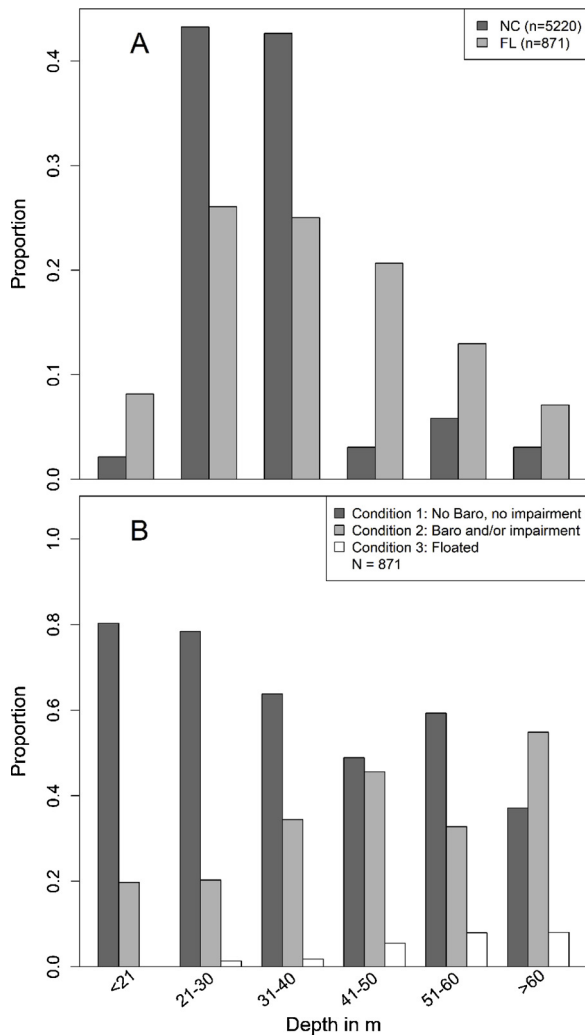


Fig. 2. A) Proportion of gray triggerfish *Balistes capriscus* released in each depth bin off North Carolina and Florida, 2013–2017. Data for North Carolina are from NOAA Fisheries Southeast Region Headboat Survey and data from Florida are from the Florida Fish and Wildlife Conservation Commission (Sauls et al., 2015).

B) Proportion of gray triggerfish released in conditions 1, 2, and 3 by depth off Florida (Sauls et al., 2015). Condition 1 fish showed no external trauma, condition 2 fish showed external trauma but swam down, and condition 3 fish floated.

length of time it took gray triggerfish to submerge once released, provided that they did submerge. Almost all (99+) gray caught with hook-and-line are jaw-hooked (Sauls et al., 2015), therefore we elected to tag only jaw-hooked individuals. Depths of capture were recorded as the depth measured by the on-board sonar unit of the vessel.

In order to establish a control group, gray triggerfish caught with fish traps were tagged at the seafloor using SCUBA (*sensu* Rudershausen

et al., 2014). Two divers removed gray triggerfish from traps on the seafloor one at a time and tagged them at depth with the methods described above. If more gray triggerfish were captured in the traps than could be tagged by divers, the remainder were retrieved to the research vessel where they were measured, tagged, and released at the surface. Survival estimates of these individuals was modeled separately from those tagged with hook-and-line.

2.2. Estimation of discard survival of tagged fish

We used a Cox proportional hazards regression model to estimate survival of gray triggerfish (Cox, 1972). Sauls (2014) took this approach when using mark-recapture data to estimate discard survival of gag (*Mycteroperca microlepis*). The response variable for this model is the time-at-large for an individual tagged fish prior to recapture (coded as 1) or censorship (coded as 0). For censored fish that were not recaptured, time-at-large was the amount of days between when an individual was tagged and October 1, 2018, which we defined as the end of the study period for this analysis. In addition to condition (our variable of interest) we tested covariates that may have had a significant influence on the recapture rates for gray triggerfish, including size (FL), season, year, and region, as well as interaction terms. For each model, covariates for inclusion were selected through alternate forward and backward selection using the function *stepAIC* in R (R Core Team, 2017), which uses AIC to determine the most parsimonious model. The hazard for each individual is defined as the probability that it is recaptured at time *t* given the particular set of covariate values for that fish. The resulting hazard ratios for each treatment can be interpreted as relative survival when all other variables are held constant. If the reference group also serves as a control (as in this case, since diver-tagged fish experienced no trauma from retrieval to the surface), then the hazard ratio is a measure of absolute survival for fish in the same treatment group. Further mathematical details on using this model may be found in Cox (1972), Sauls (2014), and the R package “survival” (Therneau, 2015; R Core Team, 2017).

We conducted separate models for trap-caught surface released fish and hook-and-line-caught surface released fish, each relative to the seafloor control group. This was necessary because all seafloor control fish were assigned to both the reference gear and the reference condition, resulting in perfect correlation between these two variables. We also had an interest in evaluating survival values for hook-and-line-caught gray triggerfish separately, because the vast majority of releases in the fishery are from this gear.

Proportionality of the underlying hazard function is a critical assumption of the Cox proportional hazards model (Peduzzi et al., 1995). We tested this assumption by examining our hook-and-line and trap results graphically in the form of “survival” curves (where “survival” equals “not recaptured”), generated with the function *ggadjustedcurves* in the R package ‘survminer’ (Kassambara and Kosinski, 2018). If the curves appeared parallel and did not cross, we could accept that the assumption of proportionality was not violated (Kumar and Klefsjö, 1994).

2.3. Effect of tagging on condition

We tested for an effect of tagging on release condition. Making incisions through the body cavity of physoclistous fish may relieve pressure from barotrauma (Rudershausen et al., 2014; Johnson et al., 2015) and result in a tagging-induced improvement in observed condition (i.e., more fish swim down because they were effectively vented). We examined whether tagging influenced release condition by performing a Fisher's exact test of independence to compare the frequencies of floating between tagged and untagged groups of gray triggerfish. We caught gray triggerfish by hook-and-line with the gear described above. Some fish were tagged as part of the tagging study while others were released untagged for unbiased condition observation. This portion of the study took place at a single site over 4 days, with similar numbers of tagged and untagged individuals released each day. If there was no effect of tagging on condition then it would be possible to extrapolate the numbers by condition in our study to the fishery without, or in addition to, fishery-dependent condition data. Any significant effect of tagging on condition assignment would require fishery-dependent data alone to make accurate inferences about discard survival in the fishery.

2.4. Estimation of fishery-dependent discard survival

We categorized gray triggerfish from a Florida fishery-dependent dataset into depth bins based on the bottom depths recorded by fishery observers aboard recreational for-hire fishing vessels. Proportional condition-by-depth was determined for each of six depth bins (< 21 m, 21–30 m, 31–40 m, 41–50 m, 51–60 m, and > 60 m; Fig. 2B). The Florida Fish and Wildlife Conservation Commission has collected information on the quantity and disposition of discarded hook-and-line-caught gray triggerfish observed from headboats since 2011, and fish were also observed from smaller charter vessels during a three-year period from 2013 to 2015 (Sauls et al., 2015). While observer datasets exist for other states in the US southeast, to our knowledge only the Florida program records sufficient detail (i.e., they recorded injury from barotrauma, release disposition, and hooking location for each fish) to allow *post hoc* categorization into our condition categories (1, 2, and 3). The fish included in the Florida program were not tagged. We assumed survival-by-condition for tagged fish and untagged fish was the same.

We calculated fishery-dependent discard survival by using our survival-by-condition as estimated from the tagging study and applying them to each depth zone as:

$$Survival_j = \frac{\sum_{i=1}^3 S_i n_{ij}}{n_j}$$

where i is the condition category (1–3), j is the depth zone, S_i is the survival of condition i fish as determined from our tagging study (hook-and-line-caught fish only), and n_{ij} is the number of released fish in condition i at depth j as determined from the Florida fishery dependent dataset (Fig. 2B). Survival probability for condition 3 fish (S_3 ; floating fish) was fixed at zero (Burns and Restrepo, 2002).

In order to estimate a rate of fishery-wide discard survival across all depths, we calculated proportions of released gray triggerfish for Florida using the fishery-dependent dataset described above and for North Carolina using a similar less-detailed dataset. The North Carolina dataset was from the NOAA Fisheries Southeast Region Headboat Survey and contained numbers of gray triggerfish released from headboats in North Carolina from 2013 to 2017, as well as “primary depth fished” on the day of observation (J. Hackney, National Marine Fisheries Service, Beaufort, North Carolina, personal communication, 2017). We calculated the proportion of releases for North Carolina in each depth zone based on primary depth fished for that day (Fig. 2A). For each state (North Carolina and Florida), we simulated a population of 10 million fish. Each individual was assigned a depth bin of release

based on the proportions of releases in each state (Fig. 2A). Based on the assigned depth bin, each simulated individual was assigned a release condition with the probabilities determined from the observer data (Fig. 2B) and an associated “chance of survival.” Chances of survival were random draws from an untransformed (i.e., normal) distribution with means and standard deviations taken from the condition-specific Cox proportional hazards output. The resulting 10 million chances of survival were then back-transformed through exponentiation, and means and standard deviations were calculated for each state based on these matrices.

2.5. Post-mortem examination of gray triggerfish and comparison to tagging results

We performed necropsies on gray triggerfish captured with hook-and-line and traps from 30 to 40 m. After capture, individuals were placed directly into an ice-water mixture and remained on ice for 5–72 h prior to necropsy. We examined individual gray triggerfish for external and internal gross signs of barotrauma, including organ damage and displacement. Gray triggerfish were classified into condition categories as they would have been if tagged and released (conditions 1 and 2 only, as it was impossible to determine if retained fish would have floated). We measured the amount of any organ displacement (e.g., intestinal prolapse) in the un-stretched state. Where applicable, we also qualitatively assessed the severity of internal injuries. We considered injuries not survivable if they appeared likely to result in inhibition of feeding or respiration. We did not consider a ruptured swim bladder to be lethal, given that reef fish have been shown to heal this organ in as little as 4 days (Burns and Restrepo, 2002). Necropsies were performed in consultation with Dr. Craig Harms, NC State University College of Veterinary Medicine, Raleigh, NC, USA under the auspices of IACUC #16-205. We compared the proportion of gray triggerfish with severe internal or external injury to our mean estimates of discard survival.

3. Results

3.1. Estimation of discard survival of tagged fish

For gray triggerfish tagged at the seafloor from traps by SCUBA divers, 121 of 215 (56%) individuals were recaptured. Of individuals tagged at the surface, we recaptured 67 of 242 (28%) captured with hook-and-line and 58 of 192 (30%) captured with traps. The majority of recaptures (80%) were by our research team during tagging operations at sites where fish were previously tagged. Remaining recaptures were from recreational, commercial, and charter anglers. Breakdowns of recaptures by condition are provided in Table 2. Liberty periods for recaptured fish ranged from 2 d to 470 d, with a mean of 72 d.

The Cox proportional hazards model of gray triggerfish caught with hook-and-line produced a survival estimate for condition 1 individuals of 0.39 (95% CI 0.28, 0.55; $z = -5.42$; $p < 0.01$; Table 2). Gray triggerfish in condition 2 caught with hook-and-line had an estimated survival of 0.24 (0.10, 0.60; $z = -3.06$; $p < 0.01$). While confidence intervals for conditions 1 and 2 overlap, indicating that survival is not significantly different among these two treatments, survival for both groups is reduced relative to the control group since neither confidence interval contains 1.0 (which would indicate 100% survival). Condition 1 fish caught with traps had an estimated survival of 0.49 (0.37, 0.67; $z = -4.63$; $p < 0.01$). Condition 2 fish caught with traps had an estimated survival of 0.24 (0.13, 0.45; $z = -4.59$; $p < 0.01$). Zero floating gray triggerfish were recaptured, therefore condition 3 individuals caught with both gear types had survival estimates of 0.00 with infinite confidence intervals, which can be interpreted as a survival of exactly zero. Covariates retained in the best models for hook-and-line were condition, season, year, region, and depth and for traps were condition, region, and depth. Test statistics and p-values are

Table 2

Mean and confidence intervals for discard survival of conventionally tagged gray triggerfish *Balistes capricus* estimated from fitting two Cox proportional hazards models to data collected in the southeast US reef fishery. Fish were tagged between May 2015 and December 2017 and tags were returned between June 2015 and July 2018. Condition 0 fish were tagged by SCUBA divers at the seafloor and had an assumed survival of 1.0 (italicized below). Condition 1 fish had no visible trauma, condition 2 fish had visible trauma but swam down, and condition 3 fish floated. Model results are separated by the two gear types used in the fishery. For each model run, mean survival estimates for conditions 1–3 are relative to assumed survival for condition 0 fish.

Condition	Capture gear	n tagged	n recaptured	Proportion recaptured	2.5% CI	Mean est. survival	97.5% CI	Liberty period range (days)
0	SCUBA Control	215	121	0.56	–	<i>1.0</i>	–	0–324
1	Hook-and-line	200	61	0.31	0.28	0.39	0.55	5–470
2	Hook-and-line	37	6	0.16	0.10	0.24	0.60	11–255
3	Hook-and-line	5	0	0.00	–	–	–	–
1	Trap	120	46	0.38	0.37	0.49	0.67	8–210
2	Trap	62	12	0.19	0.13	0.24	0.45	7–465
3	Trap	10	0	0.00	–	–	–	–

Table 3

Summary of the independent variables retained in two Cox hazard models of gray triggerfish *Balistes capricus* caught with A) hook-and-line and B) traps. Variable selection was conducted alternately forward and backward using the R procedure *step()*. Reference variables were Condition = 0, Season = winter, Year = 2015, and Region = Onslow Bay.

A.			
Variable	df	χ^2	$p(> \chi^2)$
Condition	3	61.97	< 0.01
Season	3	14.16	< 0.01
Year	2	1.75	0.42
Region	2	11.83	< 0.01
Depth	1	2.72	0.10
B.			
Variable	df	χ^2	$p(> \chi^2)$
Condition	3	51.88	< 0.01
Region	2	15.52	< 0.01
Depth	1	2.20	0.14

provided in Table 3 and further statistics for each retained variable, including coefficients and confidence intervals, are provided in Table S1. Confidence intervals in Table S1 are for the odds ratio, which can be interpreted as the proportional relationship between the effects of each variable on survival (relative to an effect of 1.0). Graphical examination of the survival curves for each condition in both models (traps and hook-and-line) suggested that the assumption of proportionality was not violated (Fig. 3).

3.2. Effect of tagging on condition

We found that a higher proportion of untagged fish floated (40/256, 15.6%) versus tagged fish (14/393; 3.6%) caught with hook-and-line. A Fisher's exact test of independence of these values was significant ($p < 0.01$, sample odds ratio: 0.20; 95% CI for odds ratio: 0.10, 0.39). Because the confidence interval for the odds ratio does not contain 1.0, we conclude that untagged gray triggerfish have a significantly higher chance of floating as compared to tagged gray triggerfish.

3.3. Estimation of fishery-dependent discard survival

Discard survival values for each of the six depth bins, calculated based on the proportions of each condition in each depth bin (Fig. 2B), ranged from 0.29 to 0.37 (Table 4). Using our simulated populations of 10 million fish for each state, we estimated overall discard survival for the recreational hook-and-line fishery in North Carolina as 0.35 (0.10, 0.59) and for Florida as 0.34 (0.08, 0.59).

3.4. Post-mortem examination of gray triggerfish and comparison to tagging results

We performed necropsies on a total of 68 gray triggerfish. The most common severe internal injury was a prolapsed intestine into the buccal cavity ($n = 37$), likely as a result of pressure from the expanded (often to the point of rupture) swim bladder (Fig. 4). We also observed related trauma in some individuals, such as liver prolapse into the buccal cavity ($n = 2$) and visceral protrusion between gill arches ($n = 4$), but these traumas always co-occurred with buccal intestinal prolapse. Lengths of prolapsed intestine into the buccal cavity ranged from 20 to 240 mm (mean = 102 mm). For gray triggerfish classified as condition 1 (no obvious external injuries) caught with hook-and-line, we observed severe internal injury in 24 of 32 fish (75%). For gray triggerfish caught with traps in condition 1, 12 of 24 fish (50%) had sustained severe internal injury. Lower percentages of gray triggerfish in condition 2 had sustained severe internal injuries: 1 of 4 fish (25%) caught with hook-and-line and 0 of 8 fish (0%) caught with traps. Overall, 31% of necropsied gray triggerfish caught with hook-and-line had experienced neither external nor severe internal injury, which is extremely close to our survival estimate for this depth range (33%; Table 4).

4. Discussion

We found that discard survival of gray triggerfish was much lower than estimated in previous studies. Our study accounted for delayed mortality by using a mark-recapture approach and we employed a robust control group through the use of SCUBA divers. None of the previous studies of this species (Table 1) used a control, and their survival

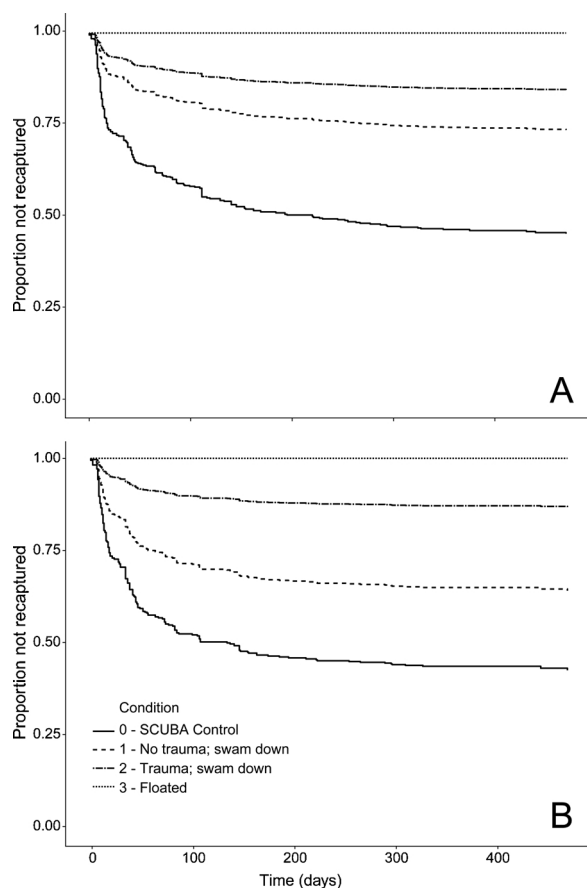


Fig. 3. Adjusted “proportion not recaptured” curves from the Cox proportional hazards model for each release condition group for A) hook-and-line and B) traps. The y-axis refers to the probability (or proportion) at time *t* that an individual tagged fish remained at-large without being recaptured. The probability was 100% at time zero (the day of tagging), and declined with increasing time.

Table 4

Depth-specific mean survival estimates for gray triggerfish *Balistes capriscus* in the southeast US hook and line fishery. Survival estimates were calculated as a weighted average using survival-by-condition estimates (Table 2) and proportion of releases in each condition for each depth bin (Fig. 2B).

Depth	< 21 m	21–30 m	31–40 m	41–50 m	51–60 m	> 60 m
Estimated Survival	0.37	0.37	0.33	0.32	0.33	0.29

estimates varied widely (0.07–1.0; mean = 0.75). A discard survival of 0.875 was used for all gears, depths, conditions, and fishing sectors in a 2016 gray triggerfish stock assessment (SEDAR, 2016). Based on our estimates, 0.875 is an overestimate of the discard survival in the hook-and-line fishery. Our estimates of discard survival for hook-and-line fisheries in North Carolina of 0.35 (0.10, 0.59) and in Florida of 0.34 (0.08, 0.59) are likely more accurate because they account for delayed mortality and used a control group that did not undergo traumas associated with a surface release.

The estimates of survival by condition were similar for surfaced-released gray triggerfish from hook-and-line and trap gear. The overwhelming majority of gray triggerfish landings across sectors are from the hook-and-line fishery (approximately 99.4% from 2006 to 2013; SEDAR, 2016; MRIP, 2017). Therefore, discard survival by condition data for gray triggerfish caught with hook-and-line are most relevant to the stock assessment and were used to estimate overall discard survival in the fishery.

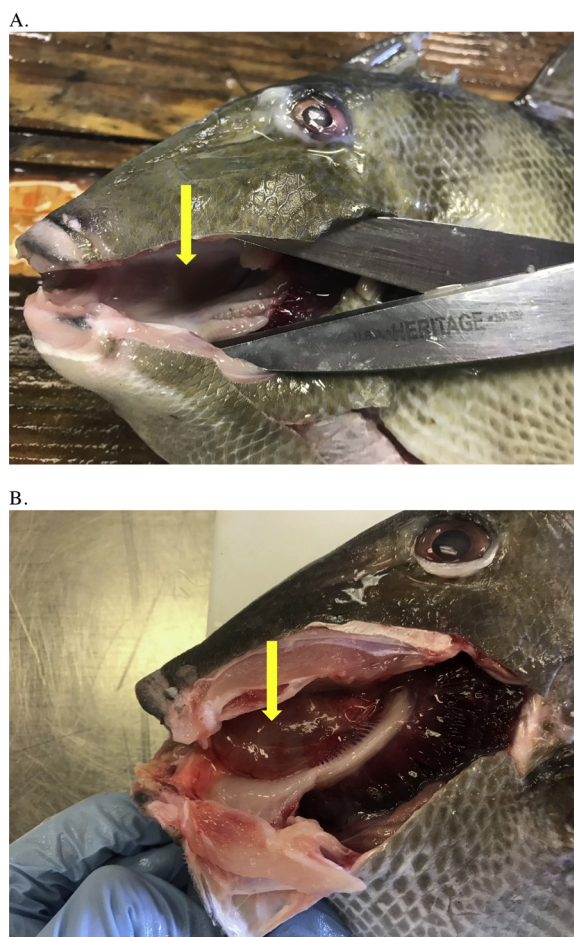


Fig. 4. Image of gray triggerfish *Balistes capriscus* with a clear buccal cavity (A) and of gray triggerfish with a buccal cavity blocked by intestine (B). Yellow arrows indicate the buccal cavity, and in B, prolapsed intestine in the buccal cavity and caught in the first gill arch. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We considered the possibility that our finding of low survival for surface-released gray triggerfish was a result of spatial displacement of fish in this category. In theory, surface-released fish could have drifted some horizontal distance away from the tagging location during their descent. To examine whether this was likely, we reanalyzed the data after omitting all recaptures that occurred within the first 30 d, a period we deemed sufficient to allow for “re-mixing” of the surface- and sea-floor-released groups. The results of this analysis were extremely similar to the results when the full dataset was used; we therefore conclude that displacement of surface-released gray triggerfish was not the of low discard survival.

We estimated depth-specific discard survival for gray triggerfish (Table 4) because releases-by-depth for this species vary between states (Fig. 2A). Such information is valuable to managers who may consider management strategies such as varying minimum length limits based on depth (Stewart, 2008) or implementing spatial closures in deeper water (Roberts, 2002). The utility of this information could be increased by adapting recreational fisheries data collection (e.g., NOAA MRIP) to include information about depth of capture.

Our estimate of discard survival takes into account any proportional increase in impaired conditions with depth, but assumes survival-by-condition remains constant regardless of depth of capture. It is likely that survival within condition differs with changing depth and we describe the direction of bias for our study below. We collected empirical data only in 30–40 m. While relatively narrow, this depth range does

represent an increase in seafloor pressure from approximately 4–5 atm. Our tagging effort within this range was concentrated in two depths: of 649 total tagged gray triggerfish, 152 were tagged at a single site in 30 m and 390 were tagged at a single site in 38 m. In the Cox proportional hazards model for gray triggerfish caught with hook-and-line, the variable for depth was retained. However, depth was not significant ($p = 0.10$) and its correlation with survival was positive (i.e., the model predicts higher survival in deeper depths) which is contrary to the expectation (Table S1). Therefore, the evidence at hand suggests survival-by-condition is constant across depths from 30 to 40 m. If survival-by-condition in depths other than 30–40 m differed from the estimates we present here, we would predict higher survival in shallower depths and lower survival in deeper depths. Based on the distribution of releases-by-depth in NC and FL (Fig. 2A) we suggest that overall survival estimates would decrease if survival-by-condition were not constant across depths.

Most published estimates of discard survival of reef fish (including those cited above) are for Perciform fishes. The paucity of estimates for species of other taxonomic orders is probably due to the dominance of perciform fishes in many reef fish communities and their associated popularity as food/sport fish. Colotelo et al. (2012) commented on the dramatic effect of morphological differences on the impacts of decompression and barotrauma. It is possible that the different biology and physiology of tetraodontiform fishes (including gray triggerfish) contributes to their lower discard survival. Swim bladder expansion may be more traumatic in triggerfish than in perciforms as a result of these anatomical differences. For example, the rigid body wall in gray triggerfish might result in organ compression where fish such as black sea bass may only experience body expansion and stomach eversion, the effects of which may be reversible.

Anatomical characteristics of the gastrointestinal tract may also contribute to low survival we observed in gray triggerfish relative to other species. Gray triggerfish have a relatively long intestinal tract (Al-Hussaini, 1947) perhaps as a result of their largely durophagous diet (Durie and Turingan, 2001). Through necropsy, we found intestinal prolapse into the buccal cavity in a high percentage (69%) of fish caught with hook-and-line. Given the low discard survival we estimated in this study, this injury may result in permanent damage to the gastrointestinal tract and adjacent organs, or perhaps temporary disability that increases predation risk. Because this injury is cryptic, it was not accounted for in categorizing tagged gray triggerfish release condition.

We used obvious external injuries (most commonly, intestinal prolapse through the cloaca) to classify released gray triggerfish by condition. Some studies have shown that such metrics are not good predictors of mortality (Jarvis and Lowe, 2008; Hochhalter and Reed, 2011). Our finding of latent injuries in gray triggerfish is further evidence that external condition alone may be a poor predictor of survival: based on our necropsy results, many fish that we classified as condition 1 likely experienced internal injuries. This is probably reflected in the overlapping confidence intervals around estimated rates of mean survival for conditions 1 and 2 (Table 2).

The preponderance of past discard survival studies of reef fishes have relied on external proxies to inform mortality estimates (e.g., Wilson and Burns, 1996; Hueter et al., 2006). A comparison of our results to studies employing this methodology for gray triggerfish (e.g., studies in Table 1) demonstrates the magnitude of inaccuracy that may occur when certain proxies (such as swimming ability) are used. Our use of gross necropsy demonstrated that examination of internal traumas can be valuable when combined with traditional external condition assessment of reef fishes. The proportions of gray triggerfish with either external or internal injury matched our mean survival estimates closely.

Sampling design (including sample size) and analytical methodology are crucial to the success of survival studies in fisheries and other disciplines (Goodyear, 2002; Ryan, 2013). Simulations can be valuable when considering the sample size necessary to attain a desired

level of statistical power in survival studies (Horodysky and Graves, 2005). However, fisheries researchers often do not have the luxury of performing realistic simulations due to a lack of pilot data and/or broad uncertainty in necessary input values (e.g., tag recovery rate, survival rate). Therefore choosing an analytical method that produces relatively precise estimates is even more valuable in these situations than otherwise. The Cox proportional hazards model is one such method because it incorporates temporal information and covariates (Sauls, 2014). Earlier methodologies such as the “relative-risk” model (Hueter et al., 2006; Rudershausen et al., 2014) require a larger sample size to obtain similar precision. In the absence of covariates, the Cox model reduces to the relative risk model; we therefore suggest that future authors performing similar analyses to those shown here employ the Cox proportional hazards regression model, especially when data are unavailable for simulations.

Many authors have explored methods to increase post-release survival of reef fish by mitigating the effects of barotrauma (e.g. Theberge and Parker, 2005; Curtis et al., 2015; Runde and Buckel, 2018). Two techniques include venting and forced recompression via the use of a descender device (reviewed by Eberts and Somers, 2017). However, these efforts are most often used when there is a high likelihood of fish being unable to re-submerge after release (Crandall et al., 2018). For gray triggerfish, a low percentage (< 10%) floated regardless of depth (Fig. 2B) so venting or forced recompression devices are unlikely to be useful for many released individuals of this species, although some may protect recompressed fish from water column predation. Even if the survival for floating gray triggerfish was greater than 0, overall discard survival for this species would still be low.

Our findings could be used to refine management for gray triggerfish, perhaps by reconsidering the 2015 size requirement. Minimum size requirements may be ineffective for short-lived highly productive fish (such as gray triggerfish) if the discard survival rate is below 0.80 and effort is high (Coggins et al., 2007). Indeed, if discard survival is relatively low (as found here), length-based management strategies may not be effective for long-term conservation of a stock even under moderate ($\text{fishing mortality} = 0.8 \times \text{natural mortality}$) levels of exploitation (Gwinn et al., 2015). While gray triggerfish are not overfished in the US South Atlantic region (SEDAR, 2016), this species is considered overfished in the US Gulf of Mexico (SEDAR, 2015). Given the low discard survival estimated here, management strategies that result in gray triggerfish discards will not reduce rates of fishing mortality to the extent estimated in previous assessments. Low discard survival should also be considered for management of other balistids and related fishes worldwide.

The importance of accurate estimates of discard survival in assessing fish stocks has been recognized (Davis, 2002; Coggins et al., 2007) and improvements to study design (Pollock and Pine, 2007) have increased in recent years (e.g., Rudershausen et al., 2014; Curtis et al., 2015; Capizzano et al., 2016). Our research demonstrates how tag-recapture techniques and the use of an adequate control group can lead to markedly different estimates of discard survival for an important reef species in the US South Atlantic region. In addition, we demonstrate the utility of gross necropsy in identifying severe internal injuries in fish that would otherwise have been considered best-condition. The technique lends itself to incorporation in future studies of discard survival of reef fishes given its ease and low cost. The approach we have taken to estimate discard survival of gray triggerfish is warranted for other reef species where barotrauma and high rates of discarding are issues facing fisheries managers.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2019.105313>.

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