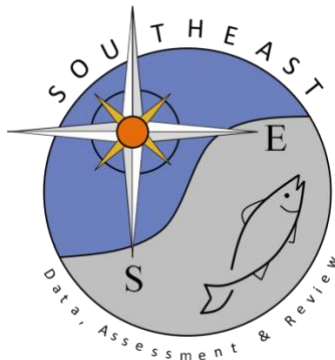


Low discard survival of gray triggerfish in the southeastern US hook-and-line fishery

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23

24 **Abstract**

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

39

40 **Keywords:** *Balistes capriscus*, catch-and-release, mortality, reef fisheries, tagging

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45 **1. Introduction**

46 For many fisheries, discarded fish make up a large and increasing proportion of total
47 catch (NMFS 2016). This trend has resulted from changing angler behavior (Quinn 1996; Graefe
48 and Ditton 1997; Allen et al. 2008) and more restrictive management (Kelleher 2005).
49 Substantial effort has been spent assessing the magnitude of discards (e.g., Bartholomew and
50 Bohnsack 2005; Kelleher 2005; Zeller et al. 2017) and estimating survival rates of discarded
51 fishes (e.g. Davis 2002), as these figures remain crucial components of modern stock
52 assessments (Alverson et al. 1994; Breen and Cook 2002; Punt et al. 2006; Viana et al. 2011,
53 2013; Dapp et al. 2017).

54 Methodologies for estimating discard survival have varied, largely due to the difficulty
55 and expense associated with quantifying delayed mortality that may result from latent trauma.
56 Electronic tagging is expensive, and the effects of such tagging may confound the estimate of
57 discard survival for species prone to barotrauma (Curtis et al. 2015). Further, tank holding
58 studies may exclude the effects of discard-related predation and therefore may not produce a
59 realistic survival estimates (Pollock and Pine 2007). Mark-recapture methods with conventional
60 tags have frequently been employed to account for delayed mortality; however, many mark-
61 recapture studies lack a control group and instead rely on assumptions about fish in the best
62 observable condition based on swimming ability or physical injury (e.g. Wilson and Burns 1996;
63 Patterson et al. 2002). Most discard survival studies of physoclistous reef fishes have reported
64 barotrauma as a contributor to mortality. The pressure differential between the seafloor and the
65 surface leads to internal gas expansion when fish are retrieved, often resulting in positive
66 buoyancy and an inability to resubmerge when released at the surface (Davis 2002). Severe
67 physical effects, such as organ displacement and internal injuries, have also been documented for

68 many reef fishes, particularly when retrieved from deeper depths (Davis 2002; Rummer and
69 Bennett 2005; Jarvis and Lowe 2008).

70 In general, authors have argued that fish with mild or no visible barotrauma are likely to
71 survive discarding if they resubmerge (e.g., Beverton et al. 1959; Kaimmer and Trumble 1998;
72 Hannah et al. 2008) and have deemed these individuals a control group to which fish in
73 compromised conditions may be compared (Hueter et al. 2006). Such proxies may be ineffective
74 because internal and latent injuries may impact survival. Furthermore, condition classification is
75 often subjective between observers, which may make results between studies incomparable.
76 More recent studies have addressed the issue of latent trauma by applying a range of survival
77 estimates to the reference group (e.g. Sauls 2014). While this approach is likely more realistic
78 than the former, studies that have an adequate control remain the most robust (Pollock and Pine
79 2007) because they estimate absolute survival (e.g., Rudershausen et al. 2014).

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

91 of surface-tagged fish with injuries can be estimated by comparing recapture rates of surface-
92 and diver-tagged fish. Survival estimates from this approach include immediate and delayed
93 mortality.

94 Mark-recapture methodologies including SCUBA are costly and time-consuming, and a
95 validated proxy for estimating absolute mortality would be valuable to researchers. Laboratory
96 examination of sacrificed individuals may be an inexpensive means of elucidating the extent of
97 latent trauma and informing mortality estimates (Mikles et al. 2019). Gross necropsy has rarely
98 been used in studies of discard survival of barotraumatized fishes (but see Burns and Restrepo
99 2002; Neufeld and Spence 2004; Rummer and Bennett 2005) and has never to our knowledge
100 been employed to directly compare prevalence of severe internal injuries to robust estimates of
101 discard survival.

102 Increased regulations have led to higher rates of discarding in many regions (Kelleher
103 2005; NMFS 2016) but robust estimates of discard survival are scarce. One of the species for
104 which regulations have recently changed in the southeast United States (SEUS) is gray
105 triggerfish (*Balistes capriscus*), a commercially and recreationally important demersal reef fish
106 in the SEUS and Gulf of Mexico. Gray triggerfish and other *Balistes* spp. are also important to
107 fisheries in other coastal regions of the North and South Atlantic (Floeter et al. 2006; Aggrey-
108 Fynn 2009; Gamito et al. 2016). Numbers of recreationally discarded gray triggerfish in the
109 SEUS have frequently exceeded harvests by a factor of ~2-3 (Figure 1; MRIP 2017). Increased
110 discarding in the Atlantic recreational fishery coincided with recent changes to minimum size
111 requirements for gray triggerfish with a 305 mm fork-length (FL) limit established for federal
112 waters in North Carolina, South Carolina, and Georgia and 356 mm FL limit established in
113 Florida (SAFMC 2014; effective July 1, 2015).

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

122 **2. Methods**

123 *2.1. Study area and fish tagging*

124 Gray triggerfish were caught in Onslow and Raleigh Bays, North Carolina, USA using
125 hook-and-line (with conventional reels; maximum drag 12.7 kg) and on-bottom fish traps.
126 Terminal tackle for hook-and-line sampling consisted of a three-hook bottom rig with circle
127 hooks (Gamakatsu #42410 size 1 or Gamakatsu #42411 size 1/0) or ‘J’ hooks (Gamakatsu
128 #81411 size 1; Gamakatsu USA, Inc., Tacoma, Washington, USA) and 0.2-0.7 kg lead weight
129 connected by 59 kg monofilament line. Hooks were baited with cut squid (*Dosidicus* spp.). Traps
130 were approximately cubical with side lengths 0.6 m, and were constructed of 12-ga vinyl-coated
131 wire with square mesh size 38 mm and baited with approximately 2 kg Atlantic menhaden
132 (*Brevoortia tyrannus*). Traps had two funnel-type entrances with elongated openings
133 approximately 250 mm long and 75 mm wide when stretched. Bait wells were cylindrical
134 (diameter = 120 mm), were central to the horizontal plane of the traps, and extended the entire
135 height of the traps. Traps were sometimes set in a string of 5-10 and sometimes set as a single
136 trap per float line, depending on the capabilities of the vessel. Traps were retrieved both by pot

137 haulers and by hand, depending on vessel capabilities and sea conditions. Tagging occurred in
138 three distinct regions: Onslow Bay and two subsets of Raleigh Bay which we term “Atlas” (after
139 a prominent shipwreck) and Chicken Rock. Gray triggerfish were angled from depths of 30-40 m
140 (May-December 2015; February-September 2016; October 2017), which is a common depth of
141 release of this species in the recreational fishery in this region (Figure 2A).

142 Gray triggerfish caught with hook-and-line gear were retrieved to the research vessel
143 where they were measured (FL, mm), marked with a FM-95W wire-core tag (15 mm x 4 mm
144 ovular disc; 73 mm streamer; Floy, Inc., Seattle, WA, USA) that was inserted into the abdomen,
145 and released at the surface. Each tag displayed the unique identification number and a statement
146 of “CUT TAG. REWARD.” Tags also provided the toll-free phone number for reporting
147 recaptures. Fish were evaluated upon release with respect to their behavior and observable
148 trauma and each was assigned one of three conditions: condition 1 (swam down; no visible
149 trauma), condition 2 (swam down; visible trauma), and condition 3 (floated). Trauma was
150 defined as obvious external injury related to capture, such as prolapsed intestine or visceral
151 extrusion through the mouth or gill operculum, and also included possible stressors such as
152 moderate to severe bleeding or abrasions that were obviously as a result of capture. Condition
153 categorizations were made for every surface-released fish in the study by the first author (B.
154 Runde). Condition categorization did not depend on the length of time it took gray triggerfish to
155 submerge once released, provided that they did submerge. Almost all (99+%) gray caught with
156 hook-and-line are jaw-hooked (Sauls et al. 2015), therefore we elected to tag only jaw-hooked
157 individuals. Depths of capture were recorded as the depth measured by the on-board sonar unit of
158 the vessel.

159 In order to establish a control group, gray triggerfish caught with fish traps were tagged at
160 the seafloor using SCUBA (*sensu* Rudershausen et al. 2014). Two divers removed gray
161 triggerfish from traps on the seafloor one at a time and tagged them at depth with the methods
162 described above. If more gray triggerfish were captured in the traps than could be tagged by
163 divers, the remainder were retrieved to the research vessel where they were measured, tagged,
164 and released at the surface. Survival estimates of these individuals was modeled separately from
165 those tagged with hook-and-line, and are of less consequence to the fishery (see below).

166 2.2. Estimation of discard survival of tagged fish

167 We used a Cox proportional hazards regression model to estimate survival of gray
168 triggerfish (Cox 1972). Sauls (2014) took this approach when using mark-recapture data to
169 estimate discard survival of gag (*Mycteroperca microlepis*). The response variable for this model
170 is the time-at-large for an individual tagged fish prior to recapture (coded as 1) or censorship
171 (coded as 0). For censored fish that were not recaptured, time-at-large was the amount of days
172 between when an individual was tagged and October 1, 2018, which we defined as the end of the
173 study period for this analysis. In addition to condition (our variable of interest) we tested
174 covariates that may have had a significant influence on the recapture rates for gray triggerfish,
175 including size (FL), season, year, and region, as well as interaction terms thereof. For each
176 model, covariates for inclusion were selected through alternate forward and backward selection
177 using the function *step()* in R (R Core Team 2017), which uses AIC to determine the most
178 parsimonious model. The hazard for each individual is defined as the probability that an
179 individual tagged fish is recaptured at time t given the particular set of covariate values for that
180 fish. The resulting hazard ratios for each treatment can be interpreted as relative survival when
181 all other variables are held constant. If the reference group also serves as a control (as in this

182 case, since diver-tagged fish experienced no trauma from retrieval to the surface), then the
183 hazard ratio is a measure of absolute survival for fish in the same treatment group. Further
184 mathematical details on using this model may be found in Cox (1972), Sauls (2014), and the R
185 package “survival” (Therneau 2015; R Core Team 2017).

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

192 2.3. *Effect of tagging on condition*

193 We tested for an effect of tagging on release condition. Making incisions through the
194 body cavity of physoclistous fish may relieve pressure from barotrauma (Rudershausen et al.
195 2014; Johnson et al. 2015) and result in a tagging-induced improvement in observed condition
196 (i.e., more fish swim down because they were effectively vented). We examined whether tagging
197 influenced release condition by performing a Fisher’s exact test of independence to compare the
198 frequencies of floating between tagged and untagged groups of gray triggerfish. We caught gray
199 triggerfish by hook-and-line with the gear described above. Some fish were tagged as part of the
200 tagging study while others were released untagged for unbiased condition observation. This
201 portion of the study took place at a single site on a series of 4 days, with similar numbers of
202 tagged and untagged individuals released each day. If there was no effect of tagging on condition
203 then it would be possible to extrapolate the numbers by condition in our study to the fishery
204 without, or in addition to, fishery-dependent condition data. Any significant effect of tagging on

205 condition assignment would require fishery-dependent data alone to make accurate inferences
206 about discard survival in the fishery.

207 2.4. Estimation of fishery-dependent discard survival

208 We categorized gray triggerfish from a Florida fishery-dependent dataset into depth bins
209 based on the bottom depths recorded by fishery observers aboard recreational for-hire fishing
210 vessels. Proportional condition-by-depth was determined for each of six depth bins (< 21 m, 21-
211 30 m, 31-40 m, 41-50 m, 51-60 m, and >60 m; Figure 2B). The Florida Fish and Wildlife
212 Conservation Commission has collected information on the quantity and disposition of discarded
213 hook-and-line-caught gray triggerfish observed from headboats since 2011, and fish were also
214 observed from smaller charter vessels during a three-year period from 2013-2015 (Sauls et al.
215 2015). While observer datasets exist for other states in the US southeast, to our knowledge only
216 the Florida program records sufficient detail (i.e., they recorded injury from barotrauma, release
217 disposition, and hooking location for each fish) to allow *post hoc* categorization into our
218 condition categories (1, 2, and 3). The fish included in the Florida program are not tagged. We
219 assumed survival-by-condition for tagged fish and untagged fish was the same.

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

$$222 \text{Survival}_j = \frac{\sum_{i=1}^3 S_i n_{ij}}{n_j}$$

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

228 In order to estimate a rate of fishery-wide discard survival across all depths, we
229 calculated proportions of released gray triggerfish for Florida using the fishery-dependent dataset
230 described above and for North Carolina using a similar less-detailed dataset. The North Carolina
231 dataset was from the NOAA Fisheries Southeast Region Headboat Survey and contained
232 numbers of gray triggerfish released from headboats in North Carolina from 2013-2017, as well
233 as “primary depth fished” on the day of observation. (J. Hackney, National Marine Fisheries
234 Service, Beaufort, North Carolina, personal communication, 2017). We calculated the proportion
235 of releases for North Carolina in each depth zone based on primary depth fished for that day
236 (Figure 2A). For each state (North Carolina and Florida), we simulated a population of 10
237 million fish. Each individual was assigned a depth bin of release based on the proportions of
238 releases in each state (Figure 2A). Based on the assigned depth bin, each simulated individual
239 was assigned a release condition with the probabilities determined from the observer data (Figure
240 2B) and an associated “chance of survival.” Chances of survival were random draws from an
241 untransformed (i.e., normal) distribution with means and standard deviations taken from the
242 condition-specific Cox proportional hazards output. The resulting 10 million chances of survival
243 were then back-transformed through exponentiation, and means and standard deviations were
244 calculated for each state based on these matrices.

245 *2.5. Post-mortem examination of gray triggerfish and comparison to tagging results*

246 We performed necropsies on gray triggerfish captured with hook-and-line and traps from
247 30-40 m. After capture, individuals were placed directly into an ice-water mixture and remained
248 on ice for 5-72 h prior to necropsy. We examined individual gray triggerfish for external and
249 internal gross signs of barotrauma, including organ damage and displacement. Gray triggerfish
250 were classified into condition categories as they would have been if tagged and released

251 (conditions 1 and 2 only, as it was impossible to determine if retained fish would have floated).
252 We measured the amount of any organ displacement (e.g., intestinal prolapse) in the un-stretched
253 state. . Where applicable, we also qualitatively assessed the severity of internal injuries. We
254 considered injuries not survivable if they appeared likely to result in inhibition of feeding or
255 respiration. We did not consider a ruptured swim bladder to be lethal, given that reef fish have
256 been shown to heal this organ in as little as 4 days (Burns and Restrepo 2002). Necropsies were
257 performed in consultation with Dr. Craig Harms, NC State University College of Veterinary
258 Medicine, Raleigh, NC, USA under the auspices of IACUC #16-205. We compared the
259 proportion of gray triggerfish with severe internal or external injury to our mean estimates of
260 discard survival.

261 **3. Results**

262 *3.1. Estimation of discard survival of tagged fish*

263 For gray triggerfish tagged at the seafloor from traps by SCUBA divers, 121 of 215
264 (56%) individuals were recaptured. Of individuals tagged at the surface, we recaptured 67 of 242
265 (28%) captured with hook-and-line and 58 of 192 (30%) captured with traps. The majority of
266 recaptures (80%) were by our research team during tagging operations at sites where fish were
267 previously tagged. Remaining recaptures were from recreational, commercial, and charter
268 anglers. Breakdowns of recaptures by condition are provided in Table 2. Liberty periods for
269 recaptured fish ranged from 2 d to 470 d, with a mean of 72 d.

270 The Cox proportional hazards model of gray triggerfish caught with hook-and-line
271 produced a survival estimate for condition 1 individuals of 0.39 (95% CI 0.28, 0.55; $z = -5.42$; p
272 < 0.01 ; Table 2). Gray triggerfish in condition 2 caught with hook-and-line had an estimated
273 survival of 0.24 (0.10, 0.60; $z = -3.06$; $p < 0.01$). While confidence intervals for conditions 1 and

274 2 overlap, indicating that survival is not significantly different among these two treatments,
275 survival for both groups is reduced relative to the control group since neither confidence interval
276 contains 1.0 (which would indicate 100% survival). Condition 1 fish caught with traps had an
277 estimated survival of 0.49 (0.37, 0.67; $z = -4.63$; $p < 0.01$). Condition 2 fish caught with traps
278 had an estimated survival of 0.24 (0.13, 0.45; $z = -4.59$; $p < 0.01$). Zero floating gray triggerfish
279 were recaptured, therefore condition 3 individuals caught with both gear types had survival
280 estimates of 0.00 with infinite confidence intervals, which can be interpreted as a survival of
281 exactly zero. Covariates retained in the best models for hook-and-line were condition, season,
282 year, region, and depth and for traps were condition, region, and depth. Test statistics and p-
283 values are provided in Table 3 and further statistics for each retained variable, including
284 coefficients and confidence intervals, are provided in Table S1. Confidence intervals in Table S1
285 are for the odds ratio, which can be interpreted as the proportional relationship between the
286 effects of each variable on survival (relative to an effect of 1.0).

287 *3.2. Effect of tagging on condition*

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

294 *3.3. Estimation of fishery-dependent discard survival*

295 Discard survival values for each of the six depth bins, calculated based on the proportions
296 of each condition in each depth bin (Figure 2B), ranged from 0.29 to 0.37 (Table 4). Using our

297 simulated populations of 10 million fish for each state, we estimated overall discard survival for
298 the recreational hook-and-line fishery in North Carolina as 0.35 (0.10, 0.59) and for Florida as
299 0.34 (0.08, 0.59).

300 *3.4. Post-mortem examination of gray triggerfish and comparison to tagging results*

301 We performed necropsies on a total of 68 gray triggerfish. The most common severe
302 internal injury was a prolapsed intestine into the buccal cavity (n=37), likely as a result of
303 pressure from the expanded (often to the point of rupture) swim bladder (Figure 3). We also
304 observed related trauma in some individuals, such as liver prolapse into the buccal cavity (n=2)
305 and visceral protrusion between gill arches (n=4), but these traumas always co-occurred with
306 buccal intestinal prolapse. Lengths of prolapsed intestine into the buccal cavity ranged from 20-
307 240 mm (mean = 102 mm). For gray triggerfish classified as condition 1 (no obvious external
308 injuries) caught with hook-and-line, we observed severe internal injury in 24 of 32 fish (75%).
309 For gray triggerfish caught with traps in condition 1, 12 of 24 fish (50%) had sustained severe
310 internal injury. Lower percentages of gray triggerfish in condition 2 had sustained severe internal
311 injuries: 1 of 4 fish (25%) caught with hook-and-line and 0 of 8 fish (0%) caught with traps.
312 Overall, 31% of necropsied gray triggerfish caught with hook-and-line had experienced neither
313 external nor severe internal injury, which is extremely close to our survival estimate for this
314 depth range (33%; Table 4).

315 **4. Discussion**

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

320 widely (0.07 to 1.0; mean = 0.75). The differences in survival estimates between previous studies
321 can likely be attributed to variations in methodology (e.g., survival proxy used instead of
322 control). After reviewing these studies, the individuals involved in the 2016 gray triggerfish
323 stock assessment chose 0.875 as the mean discard survival value for all gears, depths, conditions,
324 and fishing sectors (SEDAR 2016). Based on our estimates, 0.875 is an overestimate of the
325 discard survival in the hook-and-line fishery. Our estimates of discard survival for hook-and-line
326 fisheries in North Carolina of 0.35 (0.10, 0.59) and in Florida of 0.34 (0.08, 0.59) are likely more
327 accurate because they account for delayed mortality and used a control group that did not
328 undergo traumas associated with a surface release.

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

335 Our estimate of discard survival takes into account any proportional increase in impaired
336 conditions with depth, but assumes survival-by-condition remains constant regardless of depth of
337 capture. It is likely that survival within condition differs with changing depth and we describe the
338 direction of bias for our study below. We collected empirical data only in 30-40 m. While
339 relatively narrow, this depth range does represent an increase in seafloor pressure from
340 approximately 4 to 5 atm. Our tagging effort within this range was concentrated in two depths: of
341 649 total tagged gray triggerfish, 152 were tagged at a single site in 30 m and 390 were tagged at
342 a single site in 38 m. In the Cox proportional hazards model for gray triggerfish caught with

343 hook-and-line, the variable for depth was retained. However, depth was not significant ($p = 0.10$)
344 and its correlation with survival was positive (i.e., the model predicts higher survival in deeper
345 depths) which is contrary to the expectation (Table S1). Therefore, the evidence at hand suggests
346 survival-by-condition is constant across depths from 30-40 m. If survival-by-condition in depths
347 other than 30-40 m differed from the estimates we present here, we would predict higher survival
348 in shallower depths and lower survival in deeper depths. Based on the distribution of releases-by-
349 depth in NC and FL (Figure 2A) we suggest that overall survival estimates would decrease if
350 survival-by-condition were not constant across depths.

351 The overwhelming majority of gray triggerfish landings across sectors are from the hook-
352 and-line fishery (approximately 99.4% from 2006-2013; SEDAR 2016; MRIP 2017). Therefore,
353 discard survival values for gray triggerfish caught with hook-and-line are most relevant to the
354 stock assessment of the species.

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

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

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

381 The preponderance of past discard survival studies of reef fishes have relied on external
382 proxies to inform mortality estimates (e.g., Wilson and Burns 2002; Hueter et al. 2006). A
383 comparison of our results to studies employing this methodology for gray triggerfish (e.g.,
384 studies in Table 1) demonstrates the magnitude of inaccuracy that may occur when certain
385 proxies (such as swimming ability) are used. Our use of gross necropsy demonstrated that
386 examination of internal traumas can be valuable when combined with traditional external
387 condition assessment of reef fishes. The proportions of gray triggerfish with either external or
388 internal injury matched our mean survival estimates closely.

389 Many authors have explored methods to increase post-release survival of reef fish by
390 mitigating the effects of barotrauma (e.g. Theberge and Parker 2005; Curtis et al. 2015; Runde
391 and Buckel 2018). Two techniques include venting and forced recompression via the use of a
392 descender device (reviewed by Eberts and Somers 2017). However, these efforts are most often
393 used when there is a high likelihood of fish being unable to re-submerge after release (Crandall
394 et al. 2018). For gray triggerfish, a low percentage (< 10%) floated regardless of depth (Figure
395 2B) so venting or forced recompression devices are unlikely to be useful for many released
396 individuals of this species, although some may protect recompressed fish from water column
397 predation. Even if the survival for floating gray triggerfish was greater than 0, overall discard
398 survival for this species would still be low.

399 Our findings could be used to refine management for gray triggerfish, perhaps by
400 reconsidering the 2015 size requirement. Minimum size requirements may be ineffective for
401 short-lived highly productive fish (such as gray triggerfish) if the discard survival rate is below
402 0.80 and effort is high (Coggins et al. 2007). Indeed, if discard survival is relatively low (as
403 found here), length-based management strategies may not be effective for long-term
404 conservation of a stock even under moderate (*fishing mortality* = $0.8 * \textit{natural mortality}$) levels of
405 exploitation (Gwinn et al. 2013). While gray triggerfish are not overfished in the US South
406 Atlantic region (SEDAR 2016), this species is considered overfished in the US Gulf of Mexico
407 (SEDAR 2015). Given the low discard survival estimated here, management strategies that result
408 in gray triggerfish discards will not reduce rates of fishing mortality to the extent estimated in
409 previous assessments. Low discard survival should also be considered for management of other
410 Balistids and related fishes worldwide.

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

422

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435

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638 **Tables**

639

640 Table 1. Discard survival estimates from studies used in the 2016 South Atlantic Fishery
 641 Management Council gray triggerfish *Balistes capriscus* stock assessment. Reproduced and
 642 adapted from SEDAR (2016). Gear identifies whether the study methods included hook-and-line
 643 (HL) or trap-caught fish.

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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

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649 Table 2. Mean and confidence intervals for discard survival of conventionally tagged gray
650 triggerfish *Balistes capriscus* estimated from fitting two Cox proportional hazards models to data
651 collected in the southeast US reef fishery. Fish were tagged between May 2015 and December
652 2017 and tags were returned between June 2015 and July 2018. Condition 0 fish were tagged by
653 SCUBA divers at the seafloor and had an assumed survival of 1.0 (italicized below). Condition 1
654 fish had no visible trauma, condition 2 fish had visible trauma but swam down, and condition 3
655 fish floated. Model results are separated by the two gear types used in the fishery. For each
656 model run, mean survival estimates for conditions 1-3 are relative to assumed survival for
657 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	-	-	-	-

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667 Table 3. Summary of the independent variables retained in two Cox hazard models of gray
 668 triggerfish *Balistes capriscus* caught with A) hook-and-line and B) traps. Variable selection was
 669 conducted alternately forward and backward using the R procedure *step()*. Reference variables
 670 were Condition = 0, Season = winter, Year = 2015, and Region = Onslow Bay.

671 A.

Variable	df	X^2	$p(> X^2)$
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

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673 B.

Variable	df	X^2	$p(> X^2)$
Condition	3	51.88	<0.01
Region	2	15.52	<0.01
Depth	1	2.20	0.14

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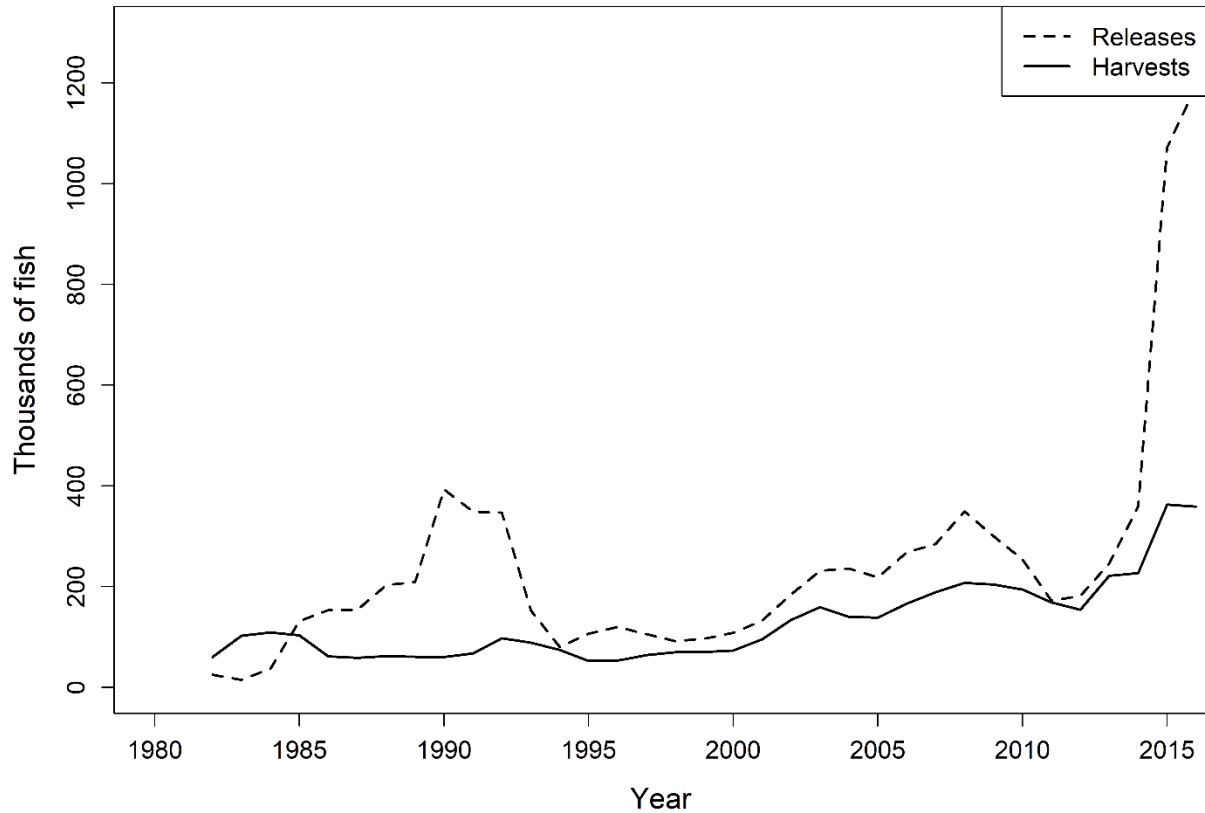
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680 Table 4. Depth-specific mean survival estimates for gray triggerfish *Balistes capriscus* in the
 681 southeast US hook and line fishery. Survival estimates were calculated as a weighted average
 682 using survival-by-condition estimates (Table 2) and proportion of releases in each condition for
 683 each depth bin (Figure 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

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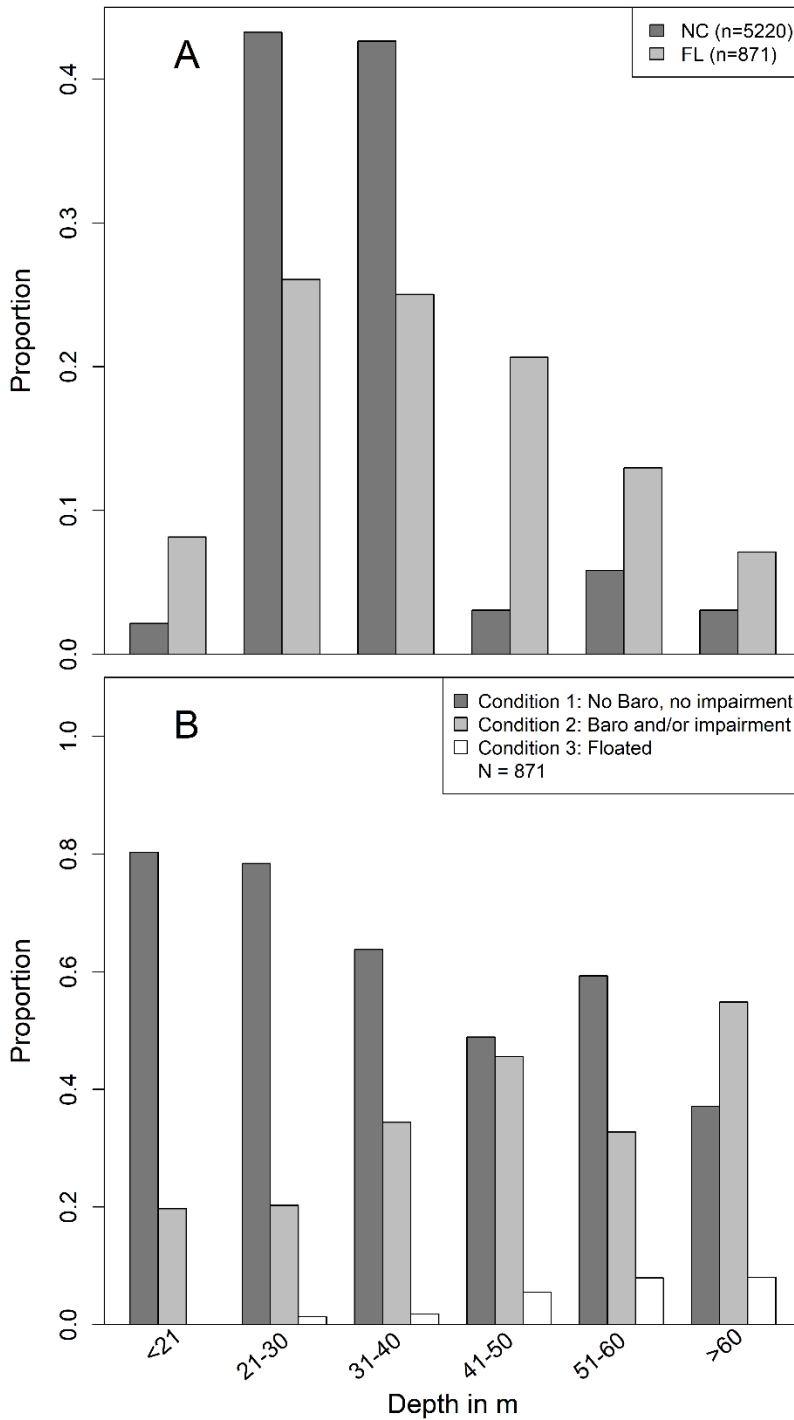
689 **Figures**



690

691 Figure 1. Gray triggerfish *Balistes capriscus* releases and harvests (3-year moving average; e.g.,
692 1982 value is average of 1981, 1982, and 1983) in the southeast US from National Oceanic and
693 Atmospheric Administration Marine Recreational Information Program, 1981-2017 (MRIP
694 2017). Input variables for query were: 1981-2017, all modes (e.g. charter boats, private boats)
695 combined, all areas combined, South Atlantic, and All Catch Types. Query performed 2
696 November, 2018. In mid-2015, a 305 mm minimum size requirement was established for North
697 Carolina, South Carolina, and Georgia and an existing 305 mm fork-length requirement was
698 increased to 356 mm for Florida. MRIP query can be accessed at:

699 <https://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index>.



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701 Figure 2. A) Proportion of gray triggerfish *Balistes caprisicus* released in each depth bin off

702 North Carolina and Florida, 2013-2017. Data for North Carolina are from NOAA Fisheries

703 Southeast Region Headboat Survey and data from Florida are from the Florida Fish and Wildlife
704 Conservation Commission (Sauls et al. 2015).
705 B) Proportion of gray triggerfish released in conditions 1, 2, and 3 by depth off Florida (Sauls et
706 al. 2015). Condition 1 fish showed no external trauma, condition 2 fish showed external trauma
707 but swam down, and condition 3 fish floated.
708

709 A.



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711
712 B.



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714
715 Figure 3. Image of gray triggerfish *Balistes capriscus* with a clear buccal cavity (A) and of gray
716 triggerfish with a buccal cavity blocked by intestine (B). Yellow arrows indicate the buccal
717 cavity, and in B, prolapsed intestine in the buccal cavity and caught in the first gill arch.

718 Supplementary Tables

719 Table S1. Variables retained in the best Cox proportional hazards model for gray triggerfish
 720 caught with A. hook-and-line and B. traps. Reference variables were Condition = 0, Season =
 721 winter, Year = 2015, and Region = Onslow Bay.

722 A.

Variable	Exp(coef)	Se(coef)	z	Pr(> z)	Lower 95%	Upper 95%
Condition1	3.89E-01	1.74E-01	-5.416	6.09E-08	0.27638	0.5474
Condition2	2.42E-01	4.63E-01	-3.064	0.002186	0.09751	0.5996
Condition3	7.17E-08	2.07E+03	-0.008	0.993651	0	Inf
SeasonFall	2.99E+00	4.83E-01	2.273	0.023049	1.16282	7.7065
SeasonSpring	8.23E+00	6.16E-01	3.422	0.000621	2.46114	27.5227
SeasonSummer	3.80E+00	5.86E-01	2.276	0.022862	1.20336	11.9792
Year2016	4.59E-01	4.05E-01	-1.921	0.054736	0.20759	1.0159
Year2017	5.15E+01	1.87E+00	2.112	0.034655	1.32895	1996.883
RegionAtlas	3.99E-01	6.78E-01	-1.355	0.175529	0.1056	1.5076
RegionChickenRock	2.43E+00	5.69E-01	1.562	0.118347	0.79722	7.4205
Depth	1.13E+00	7.82E-02	1.56	0.118789	0.96918	1.317

723

724 B.

Variable	Exp(coef)	Se(coef)	z	Pr(> z)	Lower 95%	Upper 95%
Condition1	4.94E-01	1.53E-01	-4.627	3.70E-06	0.3661	0.6657
Condition2	2.44E-01	3.08E-01	-4.587	4.49E-06	0.1335	0.4457
Condition3	2.25E-08	2.17E+03	-0.008	0.994	0	Inf
RegionAtlas	2.89E-01	2.55E-01	0.007	0.995	0	Inf
RegionChickenRock	4.47E-01	2.55E-01	0.007	0.994	0	Inf
Depth	1.84E-08	2.55E+03	-1.495	0.135	0.9797	1.0028

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