

1 Repetitive capture of marine fishes: implications for estimating number and mortality of releases

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24 Abstract

25 In some fisheries, releases are a high percentage of total catch. Recent tagging data of
26 marine fishes have revealed that recapture of the same individual multiple times occurs
27 frequently. We investigated the magnitude of this phenomenon and its effect on survival using
28 previously collected mark-recapture data of four reef-associated species. We used Cox
29 proportional hazard regression models to examine whether survival varied with release number.
30 For three of four species, survival was significantly higher after the second, third, and/or fourth
31 release as compared to the first release, perhaps resulting from selection for robust individuals.
32 Repetitive recapture implies that the estimated number of unique released fish is biased.
33 Increased survival following later releases as compared to the initial release suggests that the
34 number of dead discards may be similarly overestimated. We analyzed sensitivity of stock
35 assessment results to reduced estimates of dead discards using two of our species that had
36 recently been assessed. We found that reduced estimates of dead discards had a modest effect on
37 assessment results, but could nonetheless affect the perception of fishery status. Our findings
38 highlight the need to revise current practices for estimating live and dead discards, either internal
39 or external to stock assessment models.

40 Introduction

41 The practice of releasing part of the catch (discarding) has expanded in some regions in
42 the last half-century. This increase is largely a result of changing angler behavior (Quinn, 1996;
43 Graefe and Ditton, 1997; Allen et al., 2008), and, particularly for marine fisheries, greater fishing
44 effort and stricter regulations (Kelleher, 2005; NMFS, 2016). Cooke and Cowx (2004) used
45 Canadian release statistics to estimate that global annual recreational catch is approximately 47
46 billion fish, of which only 17 billion (36%) are retained. Further, the United States has seen

47 substantial rises in releases in recent decades (Zeller et al., 2018). In the European Union, the
48 landing obligation has banned discarding in certain situations (Guillen et al., 2018), though
49 discarding still occurs in many fisheries for reasons including exemptions and non-compliance
50 (Villasante et al., 2019). Consequently, numbers of live and dead discards (as well as discard
51 mortality estimates) are of growing importance as inputs for many stock assessments (Cooke and
52 Schramm, 2007; Pollock and Pine, 2007; Viana et al., 2013). In general, the total number of dead
53 discards for a fishery is calculated as the assumed rate of discard mortality (i.e., mortality that
54 will occur on live discards) multiplied by the number of live discards, plus any dead discards
55 (i.e., fish that are discarded dead). This methodology implies that each capture is independent; all
56 live discards are treated as unique individuals and the possibility that fish could be caught and
57 released more than once is not accounted for (MRIP, 2018).

58 Many tagging studies have found a high proportion of unique individuals being
59 recaptured multiple times (e.g., Kipling and Le Cren, 1984; Fabrizio et al., 1999). McCormick
60 (2016) described the phenomenon of repetitive recapture in fisheries where a high proportion of
61 individuals are caught and released. In such fisheries, the estimated number of releases may not
62 be equal to the number of unique released fish (or discards), as a single fish captured repeatedly
63 may be incorrectly tabulated as several independent fish. For example, Schill et al. (1986)
64 estimated that Yellowstone cutthroat trout (*Salmo clarkii bouvieri*) were caught an average of 9.7
65 times each during the 1981 fishing season. Moreover, Slavík et al. (2009) monitored fish ladder
66 occupation by brown trout (*Salmo trutta*), and noted high rates of repeated capture and calculated
67 that without individual fish identification (tags) the number of fish in the ladder would have been
68 overestimated by 63.7%. This issue may be particularly important when the number of discards

69 is used in a stock assessment or management context (Crowder and Murawski, 1998; Punt et al.,
70 2006).

71 Despite the possibility of cumulative physiological effects of multiple catch and release
72 events, as suggested by Wydoski (1977), studies of repetitive capture on finfish are scarce.
73 Arlinghaus et al. (2007) speculated that repeated catch-and-release of fishes via angling may
74 result in increased stress and behavioral changes. For example, this additional stress has been
75 shown to increase nest abandonment rates in male smallmouth bass (*Micropterus dolomieu*),
76 (Kieffer et al., 1995; Philipp et al., 1997). Various authors have also recognized that repeated
77 escapement from trawls may result in increased mortality (Suuronen and Erickson, 2010; Caddy
78 and Seijo, 2011; Gilman et al., 2013). Others have documented the occurrence of repeated
79 recaptures for tagged fish and incorporated those data into models for parameters such as
80 movement rates (e.g., Whitlock and McAllister, 2009). However, no studies to our knowledge
81 have empirically investigated the impacts of repetitive hook-and-line capture on the disposition
82 or survival of wild fishes. Estimates of discard survival from tagging data are most often based
83 on the first recapture event only (Hueter et al., 2006; Rudershausen et al., 2014; Sauls, 2014; but
84 see Shertzer et al., 2018). If discard survival varies as a function of how many times an
85 individual is caught and released, stock assessments that use discard survival from only the first
86 capture may be biased and resulting management strategies may be ineffective (Coggins et al.,
87 2007).

88 Our objectives in this study were to examine the impacts of repetitive captures on
89 estimates of (1) the number of independent fish released and (2) survival rates for four reef fish
90 species using previously collected mark-recapture data from the southeast US. The latter
91 objective used tagging data to examine the recapture rate of individual tagged fish that were

92 caught on multiple occasions, which can be interpreted as relative survival. Information obtained
93 from the two objectives was used to simulate the impact on stock assessments under several
94 levels of non-unique releases.

95 Methods

96 Empirical analyses

97 We examined tagging datasets on four species of reef fish: black sea bass (*Centropristis*
98 *striata*), gray triggerfish (*Balistes caprisculus*), red grouper (*Epinephelus morio*), and Warsaw
99 grouper (*Hyporthodus nigritus*). Each of these are demersal, physoclistous reef-associated
100 species that inhabit continental shelf waters of the Atlantic Ocean. Black sea bass are restricted
101 to the US Atlantic and Gulf of Mexico, red grouper and Warsaw grouper are distributed
102 throughout North and South American waters, and gray triggerfish are ubiquitous on both sides
103 of the Atlantic in temperate and tropical latitudes. All four species have current and/or historic
104 value as commercial and recreational targets. The tagging datasets were collected over the last
105 few decades by scientists (in the case of three species) or via a citizen science program (for
106 Warsaw grouper). These datasets have previously been used to estimate discard mortality, as
107 each species is susceptible to barotrauma. Rudershausen et al. (2014) tagged black sea bass with
108 internal anchor tags in a narrow depth range in Onslow Bay, North Carolina. Runde et al. (2019)
109 detail tagging procedures for gray triggerfish with internal anchor tags, and gray triggerfish data
110 included here were from a single site in Raleigh Bay, North Carolina. Sauls (2014) published
111 data on gag (*Mycteroperca microlepis*) but tagged red grouper as part of the same tagging
112 program using identical methodology, involving a plastic dart tag inserted through the anterior
113 dorsal musculature (B. Sauls, unpublished data). For our analysis, we truncated the large red
114 grouper dataset to include only fish from a single region (Tampa Bay, Florida area) to eliminate

115 the confounding effects of variable spatial effort on estimates of relative survival (Royle et al.,
116 2013). Shertzer et al. (2018) and Wiggers (2010) described methods for tagging Warsaw grouper
117 with plastic dart tags, which took place at a single site off the east coast of Florida. All fish in
118 these studies were single-tagged, as estimating tag retention was not a priority for the original
119 investigators.

120 For the purposes of their respective studies, past analyses performed with these tagging
121 datasets only used information up to the first recapture event (with the exception of Shertzer et
122 al. 2018). We reanalyzed versions of each dataset that contained information about subsequent
123 recaptures as well. Our goal was to determine how survival varied by release number. For each
124 dataset, the number and proportion of individuals recaptured from each successive release was
125 determined. A Cox proportional hazards regression model was used to determine whether release
126 number had an effect on survival (Cox, 1972). The formulations associated with this model are
127 detailed elsewhere (Fabrizio et al., 2008; Sauls, 2014), so we summarize them only briefly here.
128 The model is used to estimate the probability that an individual experiences a recapture at a
129 particular time. The hazard function (briefly, the probability of a particular fish experiencing
130 recapture) is explained by a set of covariates in addition to the baseline value for a reference
131 group.

132 For each species, we modeled release survival probability as a function of release number
133 in addition to other covariates when information was available such as release condition, month,
134 year, depth, capture gear, and fish size. Covariate values were changed for each observation of
135 the same fish to reflect each specific release event. Variable selection was conducted using a
136 stepwise selection procedure based on AIC, with iterations between ‘forward’ and ‘backward’
137 selection ($\alpha = 0.05$). Full models from which variables were selected varied by species were:

138 black sea bass, *release number + condition*; gray triggerfish, *release number + condition +*
139 *gear*; red grouper, *release number + condition + size + year + month + depth*; and Warsaw
140 grouper, *release number + size*. Condition categorizations (e.g., deep-hooked, severe
141 barotrauma) were determined by the authors of each study (Rudershausen et al., 2014; Sauls,
142 2014; Runde et al., 2019). The resulting hazard ratio for each variable was interpreted as a factor
143 of survival when all other variables were held constant. Reference variables were *Release*
144 *number 1* (black sea bass, red grouper, Warsaw grouper), *Condition 1* (where higher number
145 indicates worse condition; black sea bass, gray triggerfish, and Warsaw grouper), *Year2009* (red
146 grouper), and *MonthApr* (red grouper). All analyses here and below were performed in R version
147 3.4.1 (R Core Team, 2019) using the R package ‘survival’ (Therneau, 2015).

148 Potential impacts of tag shedding and tagging-induced mortality

149 For some of the species examined, we found increased recapture rate following releases
150 two, three, and four as compared to the initial tag and release event; hereafter, we refer to these
151 subsequent releases as “release numbers 2+”. One explanation for increased recapture rate is that
152 acute (or immediate) tag shedding or tagging-induced mortality (combined rate denoted as Φ ;
153 Beverton and Holt, 1957) reduced the number of alive tagged individuals, thereby reducing the
154 number of tagged fish at large and available for recapture; these rates are assumed to occur after
155 the first release only. Given the information available from these four datasets examined, it was
156 impossible to decompose Φ into its component rates; however, this decomposition was
157 unnecessary, as both acute tag shedding and tagging-induced mortality can be treated as rates
158 that only occur immediately after the first release, therefore their effects on our analyses are
159 identical. Had Φ occurred, the perceived recapture rate would be biased low for the first release

160 only, and not for releases 2+, since Φ does not occur on release 2+ fish because they have the
161 original tag.

162 We used simulations to estimate the level of Φ that would be necessary for the automated
163 variable selection procedure to exclude “release number” from the best model. That is, what
164 level of acute tag loss and tag-induced mortality would it take to increase the recapture rate after
165 release 1 and make it statistically similar to recapture rates for releases 2+? For the three species
166 for which increased recapture rate for release numbers 2+ was found, the Cox proportional
167 hazards models were repeated using bootstrapped variations of the original datasets. We first
168 identified the individuals in each dataset that were never recaptured (in other words, the
169 individuals that may have experienced Φ). Then we removed a randomized portion of these
170 individuals (to represent Φ) and refit the model using the same stepwise variable selection
171 procedure as above, but with the reduced dataset. We varied the proportion of the individuals
172 removed (Φ), and levels of Φ were chosen after preliminary runs to determine the approximate
173 value necessary for exclusion of the variable “release number” for each species. We replicated
174 this bootstrapping procedure 1000 times for each value of Φ to account for differences in
175 covariate values for never-seen individuals. We examined the percentage of the 1000
176 bootstrapped replicates that contained “release number” in the best model. Finally, we
177 graphically determined the value of Φ for which release number was excluded in an appreciable
178 portion (~5%) of replicates. This was considered the threshold value of Φ for each species that
179 would be necessary to explain our finding of increased tag return rate for releases 2+.

180 Furthermore, we considered the possibility that some fish lost their tag and were
181 recaptured later, therefore being incorrectly treated as new individuals (i.e., release number = 1).
182 This phenomenon would artificially increase the number of first releases and decrease the

183 perceived percentage of recaptures of first releases while having the opposite effect for release
184 2+ fish; thus, incorrect assignment of release number could lead to a bias towards higher relative
185 survival of subsequent recaptures. To investigate this, we simulated a population of 1 million fish
186 that were exposed to 5 periods of capture and tagging. We assumed a capture probability of 0.1
187 for each fish in each period, probability of immediate (acute) tag loss of 0.15 (1.5x the highest
188 value published for either tag type examined here; see *Discussion*), and probability of tagging-
189 induced mortality of 0.05 (each time a fish is tagged). We did not include the possibility of
190 discard mortality, as we were only interested in the influence of this phenomenon on *relative*
191 recapture rates. Similarly, we did not include chronic tag shedding in the simulation, as it is
192 assumed constant and likely very small in magnitude when compared to immediate tag shedding.
193 We generated capture histories for each fish, such that we were able to retrospectively identify
194 recaptured individuals that had lost their tag and were incorrectly considered first-time releases.
195 We used these capture histories to tabulate proportions recaptured after the first, second, third,
196 and fourth releases as we had done with empirical tagging data. These proportions were
197 calculated under two scenarios: “Observed,” in which we counted any untagged fish as a first
198 release, and “Reality,” in which we counted untagged recaptures correctly (i.e., if it was
199 untagged but had previously been captured/tagged once before then it was assigned a release
200 number of two). We compared differences in recapture rates between the two scenarios to
201 determine the likely influence of this phenomenon on our empirical results.

202 Magnitude of releases and dead discards

203 We calculated the impacts of two theorized biases in estimates of total releases and dead
204 discards. The first bias was the difference between total releases and total unique released fish.
205 We performed a simulation with several capture and release events assuming an initial release of

206 1000 fish with a constant discard survival of 0.85 after each of three releases. In addition, we
207 assumed all alive fish would be captured in each time bin or period; although this is unlikely in a
208 natural setting, this assumption aids in the illustration of this concept without impacting the
209 conclusions that can be drawn from the results. The total number of releases was calculated as
210 the sum of the releases following each of the three capture events (Figure 1A). The second bias
211 examined was the effect of increased survival for releases 2+ on the estimates of dead discards
212 (Figure 1B). For this analysis, we created another theoretical population of 1000 fish for which
213 we used 0.85 as the discard survival for release 1 but 0.95 as the discard survival for releases 2
214 and 3. For each of these two theoretical populations, we calculated the estimated number of dead
215 discards as the product of the total number of live discards (all releases from three release
216 periods combined) and the discard mortality of 0.15; this is similar to how the number of dead
217 discards are estimated for use in some stock assessments (MRIP, 2018). Next, we calculated the
218 “actual” number of dead discards as the sum of the number of dead fish that occurred as a result
219 of releases 1, 2, and 3. We compared the estimated number of dead discards to the “actual”
220 number of dead discards both within and between the two survival scenarios.

221 Influence on stock assessment

222 We investigated effects of repetitive captures on stock assessments using two case
223 studies: black sea bass and red grouper. We chose these two species because their stock
224 assessments had recently been conducted in the southeast US Atlantic and because we examined
225 tagging data for those species herein. The assessment methods are detailed elsewhere (SEDAR,
226 2017; SEDAR, 2018), and so we summarize them here only briefly. Both assessments applied an
227 integrated, age-structured model and incorporated time-series data on landings, discards, indices
228 of abundance, age and length compositions of these time series, and life-history information such

229 as natural mortality and reproductive capacity (Williams and Shertzer, 2015). To evaluate the
230 importance of repetitive captures on assessment results, we ran the assessment model for each
231 species four times. The first iteration used the base-level estimates of total dead discards as
232 provided in the original time series (100%). Subsequent runs of the assessments reduced the total
233 dead discards to 75%, 50%, or 25% of the original values. These reductions reflect the direction
234 that the estimates would tend if they corrected for repetitive recapture of individuals in the count
235 of total releases or if release mortality were lower (increased survival). All other data inputs and
236 aspects of model configuration remained the same.

237 To quantify the effect of repetitive releases on stock assessment results, we focused on
238 two primary model outputs: estimated stock status and fishery status. Stock status was computed
239 as spawning biomass (S) relative to that at maximum sustainable yield (S_{MSY}), and fishery status
240 was computed as fishing mortality rate (F) relative to its value at maximum sustainable yield
241 (F_{MSY}). For management of these stocks, S_{MSY} serves as a biomass target to be achieved, and
242 F_{MSY} as a fishing limit to be avoided.

243 Results

244 Empirical analyses

245 For three of four species (black sea bass, red grouper, and Warsaw grouper), the
246 proportion of fish recaptured was higher for releases 2+ than for release one (Table 1). The
247 “release number” variable was retained in the best Cox proportional hazards regression model
248 for each of these three species and was positively and significantly correlated with survival
249 (Table 2). For the fourth species, gray triggerfish, release number was not retained. Other
250 retained covariates, which were not of primary interest here, are shown in Table 2.

251 Potential impacts of tag shedding and tagging-induced mortality (Φ)

252 Our first simulation found that it is theoretically possible for Φ to have been the cause of
253 “release number” being significant in our models for two of three species. The first discernable
254 drop in the proportion of bootstrapped models that excluded the release number variable
255 occurred at Φ of ~ 0.396 for black sea bass and ~ 0.125 for Warsaw grouper (Figure 2). For red
256 grouper, “release number” remained significant regardless of the level of Φ (up to the theoretical
257 limit of all never-recaptured fish having experienced Φ), indicating that the change in survival
258 was too great to be a result of any possible value of Φ . Thus, a combined acute tag shedding and
259 tagging mortality rate greater than $\sim 39.6\%$ and $\sim 12.5\%$ would be required to account for the
260 increased survival in the release 2+ fish for black sea bass and Warsaw grouper respectively.

261 Our second simulation, which examined the influence of misidentifying recaptured fish
262 that had lost their tag, found higher recapture rate for first releases in the Reality scenario as
263 compared to the Observed; however, the recapture rates between the two scenarios were similar
264 for 2+ releases. The relative proportions recaptured for releases 2, 3, and 4 were in general
265 slightly lower in the Reality (0.55, 0.29, and 0.12, respectively) scenario as compared to the
266 Observed (0.65, 0.35, and 0.10). Thus, misidentifying recaptured fish would lead to biased high
267 survival of 2+ fish, but the magnitude of this bias is lower than that which we observed in the
268 empirical studies examined herein (Table 1).

269 Magnitude of releases and dead discards

270 Our investigation of two initial releases of 1000 theoretical fish yielded large differences
271 in the metrics we examined. Under both the constant survival and increased survival scenarios,
272 we found the number of total releases to be more than twice the number of unique released fish.

273 We note that this disparity would hold even if not every fish were recaptured in each time period,
274 (as we assumed here for ease of illustration) because such a reduction would impact both the
275 number of total releases and the number of unique released fish. In the constant survival scenario
276 (Figure 1A), we show that the estimate of dead discards produced by using typical stock
277 assessment methods (i.e., number of total releases multiplied by the discard mortality rate) is
278 equivalent to the “actual” number of dead discards. Thus, the estimate of dead discards is not
279 influenced by repeatedly capturing the same fish as long as discard survival is constant across
280 releases. However, for the increased discard survival scenario (Figure 1B), we show that the
281 computed number of dead discards is biased ~70% higher than the actual number of dead
282 discards. Different simulation conditions would lead to different levels of bias (e.g., more
283 releases or a larger difference in initial release survival and survival for releases 2+ would both
284 lead to increased bias (e.g., a value >70%)).

285 Influence on stock assessment

286 The stock assessments of black sea bass and red grouper were affected similarly by
287 reductions in the annual number of dead discards (Figure 3A, D). In general, fewer discards
288 resulted in average selectivity curves that emphasize lower mortality of younger fish. The
289 estimated time series of S relative to its target (S_{MSY}) were relatively insensitive to these
290 reductions (Figure 3B, E), while the estimated time series of F relative to its target were quite
291 sensitive (Figure 3C, F). In general, S/S_{MSY} were marginally higher for model runs with lower
292 amounts of dead discards. This was driven by slight increases in S paired with slight decreases in
293 S_{MSY} . S increased due to more fish being allowed to reach maturity and S_{MSY} decreased slightly
294 as a result of the decline in F attributed to a lower level of dead discards (Table S.1). For black
295 sea bass, the annual number of dead discards influenced the estimate of whether the stock was

296 experiencing overfishing ($F/F_{MSY}>1$) or not ($F/F_{MSY}<1$). The change in F/F_{MSY} resulted from
297 larger changes in F_{MSY} relative to changes in F (Table S.1). For red grouper, the stock status was
298 consistent across scenarios (overfishing); however, the degree to which F exceeded F_{MSY} varied,
299 particularly in the terminal assessment years.

300 Discussion

301 Increased discarding of live fish because of regulations or fishing behavior can result in
302 repetitive captures of individual fish. Given that live releases dominate total catch for many
303 species (Kelleher, 2005; Zeller et al., 2018), that recreational effort is high and has increased
304 through time in many regions (Post et al., 2002; Cooke and Cowx, 2006; Ihde et al., 2011; Hyder
305 et al., 2018; Shertzer et al., 2019), and our finding of repeated captures in the four species
306 examined, it is likely that any fishery with even a low proportion of releases experiences
307 repetitive captures. Our study explored the effects of repetitive captures on important variables
308 that are often used in stock assessments. First, we showed how the estimated number of total live
309 releases using current approaches is higher than the actual number of unique released fish when
310 there are repetitive captures. Second, we found that recapture rate in three of four species
311 increased after the first release and conclude that this represents increased survival for
312 individuals after their second release; thus, estimates of dead discards for these species that use
313 survival rates based on first release are likely biased. Lastly, we found that biased estimates of
314 dead discards have an impact on stock assessment results. We discuss the implications for each
315 of these findings below.

316 Typically, studies using conventional tagging to produce estimates of discard mortality
317 (e.g., Rudershausen et al., 2014; Sauls, 2014) calculate their estimate by using data from the first
318 recapture only and disregard data from subsequent recaptures of those individuals. Published

319 information about the prevalence of repeated recaptures exists for a variety of taxa worldwide,
320 although authors typically make note of this information only in a cursory fashion. (e.g., Springer
321 and McErlean, 1962; Kipling and Le Cren, 1984; Recksiek et al., 1991; Fabrizio et al., 1999;
322 Miller et al., 2001). It is likely that most large-scale tagging datasets contain information about
323 repeated recaptures, although many do not report it. We recommend that future studies explore
324 and report the prevalence of repeated recaptures and their influence on discard survival where
325 possible.

326 We found significantly higher recapture rates for release number 2+ for black sea bass,
327 red grouper, and Warsaw grouper, but not for gray triggerfish. Though theoretically possible, it
328 seems highly unlikely that Φ (acute tag shedding and tagging-induced mortality) caused
329 increased recapture rates for releases 2+ for black sea bass and Warsaw grouper. We searched
330 the literature for empirical estimates of Φ from studies using internal anchor tags and dart tags
331 (the two tag types used in the four datasets we examined), via holding studies and/or double
332 tagging experiments. One hundred percent acute retention and post-tagging survival has been
333 demonstrated for internal anchor tags in striped bass (*Morone saxatilis*), meagre (*Argyrosomus*
334 *regius*), and spotted seatrout (*Cynoscion nebulosus*) (Dunning et al., 1987; del Mar Gil et al.,
335 2017; Ellis et al., 2018). Latour et al. (2001) directly modeled acute tag shedding in red drum
336 (*Sciaenops ocellatus*) for internal anchor tags and stainless steel dart tags (as opposed to plastic,
337 which were used in the Warsaw grouper and red grouper studies examined in the present
338 document). They estimated immediate retention of internal anchor tags to be 0.99 and of
339 stainless steel dart tags to be 1.0. Fonteneau and Hallier (2015) described estimates of acute dart
340 tag shedding for three species of tunas, and stated that while estimates have ranged up to 0.10
341 (Bayliff and Mobernd, 1972) this rate is “widely dependent on the expertise of the tagger”. Other

342 than the single reference of acute shedding of 0.10, all estimates for tunas were below 0.05
343 (Fonteneau and Hallier, 2015). In addition, such rates may vary by taxon and estimates for tunas
344 may not match values for reef fishes. Our literature search yielded no published estimates of Φ
345 that were above 0.10 for either tag type, and most estimates were close to 0. Because no
346 published values of Φ surpassed even our lowest estimated threshold value of 0.125 (for Warsaw
347 grouper; Figure 2), it is unlikely that this is the explanation for our finding of higher recapture
348 rate for releases 2+.

349 Our examination of the effect of recapturing fish that had lost their tag demonstrated that
350 while absolute recapture rates of release 1 fish would be higher if all recaptures were correctly
351 identified, the relative recapture rates between releases 1 and releases 2+ were only marginally
352 impacted. While the directionality of the bias in the Observed scenario was towards our findings,
353 this simulation was conducted with the crucial parameter (acute tag shedding rate) set to an
354 extreme value (0.15). As described above, there are no published estimates of acute tag shedding
355 rates higher than 0.1 for the tag types in the studies we used. Further *ad hoc* simulations revealed
356 that the bias all-but disappeared when tag shedding was set to a more realistic rate, such as 0.05.
357 Given the large magnitude of the difference in relative recapture proportion in our empirical
358 datasets (Table 2) and the marginal influence of incorrect identification of recaptured fish (even
359 in an extreme scenario), we conclude this phenomenon is possible but is unlikely to have caused
360 our finding of significantly higher recapture rates for releases 2+. We note that using tags that
361 cannot be shed, such as electronic transmitters or genetic “tags” would eliminate this potentially
362 confounding phenomenon, and that double tagging would allow for empirical estimation of tag
363 shedding.

364 Time-varying chronic (or continuous) tag shedding could have explained increases in
365 recapture rate as well; however, chronic tag shedding is often assumed to be a constant or near-
366 constant rate, particularly within a few years of tagging (Fabrizio et al., 1996; Latour et al., 2001)
367 and we make that assumption here. A constant tag-shedding rate would not explain our findings
368 of increases in recapture rate of 2+ fish because the same rate would apply after each release.
369 While some authors have modeled chronic tag shedding as a time-varying function (e.g.,
370 Hampton and Kirkwood, 1990; Adam and Kirkwood, 2001), the durations of the tagging studies
371 examined herein were of much shorter timescales than those for which non-constant chronic
372 shedding has been postulated (10 years or more). For our datasets, some individuals were
373 recaptured out to 2,010 days (Table 1); however, the proportion of recaptures occurring within 2
374 years of initial release was 99% for black sea bass, 97% for red grouper, and 100% for gray
375 triggerfish and Warsaw grouper.

376 Another explanation of our findings is a difference in capture probability for previously
377 captured individuals (i.e., heterogeneity of learned behavior). Populations of fish frequently
378 contain individuals with varying vulnerability to angling or aggressiveness (Philipp et al., 2009;
379 Sutter et al., 2012; Villegas-Ríos et al., 2018). Askey et al. (2006) experimentally demonstrated a
380 similar phenomenon with a population of rainbow trout (*Oncorhynchus mykiss*), finding declines
381 in catch per unit effort of tagged fish by dividing the population into two classes based on
382 different intrinsic catchabilities and incorporating a “learned hook avoidance function”. Cox and
383 Walters (2002) modeled catchability dynamics by assuming two pools of fish: available and
384 unavailable to capture (with the possibility of moving from one state to the other due to factors
385 such as learned hook avoidance). If the tagged populations examined in the present study were
386 divided into such pools, it is theoretically possible that rates of learned hook avoidance could

387 differ between groups. This scenario would result in repeated recapture of “bait-happy”
388 individuals, while reducing the probability of encountering educated fish. While it is possible
389 that such heterogeneity influenced our findings, this explanation would require an extremely
390 wide disparity in the catchability between the behavioral phenotypes to account for the
391 magnitude of increases we found in recapture rates (Table 1) and would imply immediate onset
392 of learned behavior following the initial encounter. Given the complexity of this explanation, we
393 consider it less likely to explain increases in recapture rate on releases 2+.

394 The final explanation of the recapture results that we explored was the possibility of
395 heterogeneous movement behavior, i.e., transient and resident fish. After the first release,
396 transient fish would not be available for recapture at the release site but the resident fish would,
397 leading to increase in recapture rate for releases 2+. Given that the fishery returned tags from
398 other locations than tagging sites for most of the species (in particular for black sea bass and red
399 grouper where we saw the strongest effects), we consider this explanation highly unlikely.

400 Due to the lack of evidence for tag loss, tagging-induced mortality, or bait-
401 happy/movement behaviors to fully explain higher recapture rates on releases 2+, we conclude
402 that the higher recapture rates are most likely a result of higher survival. The finding of increased
403 survival was unexpected; intuition suggests that the effects of repeated capture would be
404 cumulative, therefore reducing relative survival with each successive release (as was posited for
405 fishes by Arlinghaus et al. (2007)). The three species for which we observed higher relative
406 survival for release 2+ are in the family Serranidae; the remaining species examined (gray
407 triggerfish) is in Balistidae. The common finding for the three serranids may be associated with
408 their close taxonomic relationship and thus their similar morphology and physiology.
409 Furthermore, it is possible that increased survival after releases 2+ does indeed occur for gray

410 triggerfish (as indicated by the direction of the relative recapture rates; Table 1), but that our
411 methods and/or sample size were not sufficient to detect this phenomenon.

412 Higher survival for release number 2+ may be caused by variability in individual
413 robustness to discard mortality. The species examined in the present study are each susceptible to
414 barotrauma. There may exist phenotypic heterogeneity in these populations resulting in different
415 levels of barotrauma susceptibility. If a subset of the population were substantially more resilient
416 (had higher discard survival), they would be more likely to be recaptured multiple times because
417 they would survive release at a higher rate than less-robust individuals would (assuming constant
418 capture probability). Such a scenario could result in a rapid elimination (via discard mortality) of
419 less-robust fish from the tagged population and persistence of more-robust individuals, and
420 potentially result in increases in tagged population-level relative survival with each successive
421 release event. If we are correct in our assertion that there exists heterogeneity in reef fish stocks
422 with respect to their robustness to discard mortality, there are potential evolutionary implications.
423 The concept of rapid, human-driven evolution of fish populations has been well documented
424 with respect to selection against (i.e., removal of) larger, more aggressive fish (Law, 2000;
425 Stokes and Law, 2000; Conover et al., 2005; Williams and Shertzer, 2005; Heino et al., 2015).
426 We suggest that high rates of discarding may inflict a secondary (yet still substantial) selection
427 pressure on many populations: selection for individuals that are resistant to discard mortality.

428 In light of our findings, improved methodologies for estimating the number of dead
429 discards would strengthen stock assessment results. Kerns et al. (2012) recommended estimating
430 instantaneous rates of discard mortality (e.g., at the population level) through the use of
431 combined telemetry and high-reward conventional tagging; captures are reported via the high-
432 reward tag, and if the fish is released its movements (and survival) are monitored via telemetry.

433 This methodology eliminates the biases discussed in the present document. Another approach is
434 to apply different discard mortality values to the portion of releases that are assumed to be
435 unique and the remaining portion of releases. In the absence of tagging data, it is impossible to
436 determine the proportion of releases that are occurring for the first time so selecting a value by
437 which to decrement current estimates is challenging. For fisheries where releases dominate total
438 catch (e.g., black sea bass in the US southeast; Table 4), it may be appropriate to assume that the
439 proportion of unique releases is low. We suggest that stock assessments test the sensitivity of
440 their results under a range of values for dead discards (treating the estimate produced by the
441 current methodology as the maximum). Alternatively, the capture history of tagged animals
442 could be incorporated into the stock assessment model framework to address the dynamics of
443 repetitive captures.

444 The bias in number of live releases may also be relevant to some stock assessments. For
445 example, any assessment that uses a temporally aggregated form of catch (that includes live
446 releases) to build an index of abundance is at risk for bias. Many assessments use catch per unit
447 effort to index abundance. If catches were aggregated on a per-year or per-season basis, as
448 opposed to per-trip or per-angler, the value would probably include many repeatedly captured
449 fish. If the proportion of live releases to total catch was similar across years in the catch time
450 series, then the bias would not impact the assessment results and total catch would index
451 abundance. However, this proportion has grown (substantially, in many cases) for many species
452 in the last two decades as catch-and-release angling has become more prevalent in the US
453 Atlantic (Table 4) and in many other regions of the world (Kelleher, 2005; Ferter et al., 2013;
454 Zeller et al., 2018). For species where this proportion has increased, total catch would be a biased
455 index of abundance because of the overestimation of the number of unique live releases in recent

456 time periods. We urge assessment scientists to use care when generating time series indices of
457 abundance that include live releases.

458 Our investigation of the sensitivity of fishery status to the number of dead discards
459 demonstrated that F/F_{MSY} was more sensitive than S/S_{MSY} for both black sea bass and red grouper
460 (Figure 3). Differences among F/F_{MSY} were driven primarily by differences in the denominator
461 (F_{MSY}). This resulted from the fact that discards comprised mostly younger fish, and thus a
462 reduction in discard mortality allowed more fish to reach maturity, supporting a higher maximum
463 sustainable fishing rate. We investigated why the variability in F/F_{MSY} for red grouper increased
464 substantially in terminal assessment years. This variation was driven by several years of low
465 recruitment which caused lower estimated abundance of younger ages near the end of the time
466 series. Therefore, estimated abundance of younger age classes for these years is much lower than
467 in prior years; this trend in abundance interacted nonlinearly with estimates of F to account for
468 the number of removals that were observed in these years. For assessments that rely on
469 aggregated catch to index abundance, our findings of inflated catch (as a result of many fish
470 being recaptured multiple times) would likely result in more substantial changes to S/S_{MSY} .
471 Future research could investigate the degree to which this biases such assessments.

472 It is usually unknown whether an untagged fish has been previously caught and released.
473 Therefore, it is likely that a portion of the individuals tagged in the studies examined herein had
474 been captured and released prior to tagging. As a result, for species where discard survival
475 increased after releases 2+, estimates of discard mortality based on the first recapture event
476 (including those used as baselines in this study) probably lie between the true survival after first
477 release and the survival after later releases. Therefore, the difference between these release-

478 number-dependent survival rates is likely larger than we found in this study. Thus, it is probable
479 that our results are conservative in this regard.

480 The degree to which discards (both live and dead) are important to fishery management
481 varies regionally and by stock (Zeller et al., 2018). In fisheries where discards are increasing
482 and/or a large component of catch, accurate estimation is critical to management. We have
483 demonstrated that in such fisheries, repeated captures of unique individuals may lead to large
484 biases in the number of unique live releases that are sometimes used as stock assessment inputs.
485 Further, our examination of tagging datasets yielded evidence that discard survival may increase
486 as fish are repeatedly captured, therefore biasing calculated numbers of dead discards. We
487 propose that phenotypic variation in robustness to the effects of discarding leads to this disparity.
488 We urge researchers conducting tagging studies to report the occurrence and magnitude of
489 repeatedly captured individuals, even as auxiliary data. Finally, we advise stock assessment
490 scientists to consider repetitive captures when performing calculations involving the magnitude
491 of live and dead discards, as determination of fishery status may be impacted.

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714 Table 1. Releases and recaptures from four tagging studies of reef fishes in the southeast US.
 715 Liberty period refers to the range of time (days) fish were at large prior to their terminal
 716 recapture. Relative proportions are the result of scaling the proportion recaptured relative to the
 717 first recapture percentage.

Species	Methods reference	Liberty period (d)	Release number	N released	N recaptured	Proportion recaptured	Relative proportion
Black sea bass	Rudershausen et al. (2014)	0-976	1	3807	933	0.25	1.00
			2	289	130	0.45	1.80
			3	33	18	0.55	2.20
Gray triggerfish	Runde et al. (2019)	0-354	1	273	76	0.28	1.00
			2	59	22	0.37	1.34
			3	19	7	0.37	1.32
			4	6	2	0.33	1.20
Red grouper	Sauls (2014)	0-2010	1	9250	1232	0.13	1.00
			2	281	177	0.63	4.85
			3	16	9	0.56	4.31
Warsaw grouper	Shertzer et al. (2018)	0-542	1	195	80	0.41	1.00
			2	59	38	0.64	1.56
			3	33	16	0.48	1.17

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723 Table 2. Results from Cox proportional hazards regression models for each of four reef fish
 724 species in the southeast US.

Species	Best model	Variable	Hazard ratio	<i>p</i>
Black sea bass	~release number + condition	Release number 2	2.26	<0.01
		Release number 3	2.80	<0.01
		Condition 2	0.89	0.05
		Condition 3	0.14	<0.01
		Condition 4	0.14	<0.01
Gray triggerfish	~gear + condition	Gear: trap	2.14	<0.01
		Condition 2	0.58	0.03
		Condition 3	0.12	0.04
Red grouper	~release number + size + depth + year + month	Release number 2	8.56	<0.01
		Release number 3	6.06	<0.01
		Release number 4	3.64	0.01
		Size (mm)	1.01	<0.01
		Depth (m)	0.97	<0.01
		Year2010	1.04	0.59
		Year2011	1.03	0.74
		Year2012	0.85	0.08
		Year2013	0.88	0.19
		Year2014	1.10	0.62
		Year2015	0.68	<0.01
		Year2016	0.56	<0.01
		MonthJan	0.61	<0.01
		MonthFeb	0.95	0.64
		MonthMar	0.97	0.81
		MonthMay	1.07	0.52
		MonthJun	0.81	0.05
MonthJul	0.59	<0.01		
MonthAug	0.55	<0.01		
MonthSep	0.56	<0.01		
MonthOct	0.82	0.05		
MonthNov	0.82	0.05		
MonthDec	0.69	<0.01		
Warsaw grouper	~release number + size	Release number 2	1.97	<0.01

Release number 3	1.36	0.26
Size (mm)	0.99	<0.01

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726 Table 3. Results from our simulation investigating the possibility that tag shedding can lead to
 727 incorrect identification of recaptured fish. In the “Observed” scenario, recaptured fish that lost
 728 their tag were not able to be identified as such, while the “Reality” scenario accounts for the
 729 phenomenon. Relative proportions are the result of scaling the proportion recaptured relative to
 730 the first recapture proportion.

	Release Number	N tagged	N recaptured	Proportion recaptured	Relative proportion
Observed	1	421735	66719	0.16	<i>1.00</i>
	2	66719	6847	0.10	0.65
	3	6847	384	0.06	0.35
	4	384	6	0.02	0.10
Reality	1	409772	77490	0.19	<i>1.00</i>
	2	77490	7982	0.10	0.55
	3	7982	437	0.06	0.29
	4	437	10	0.02	0.12

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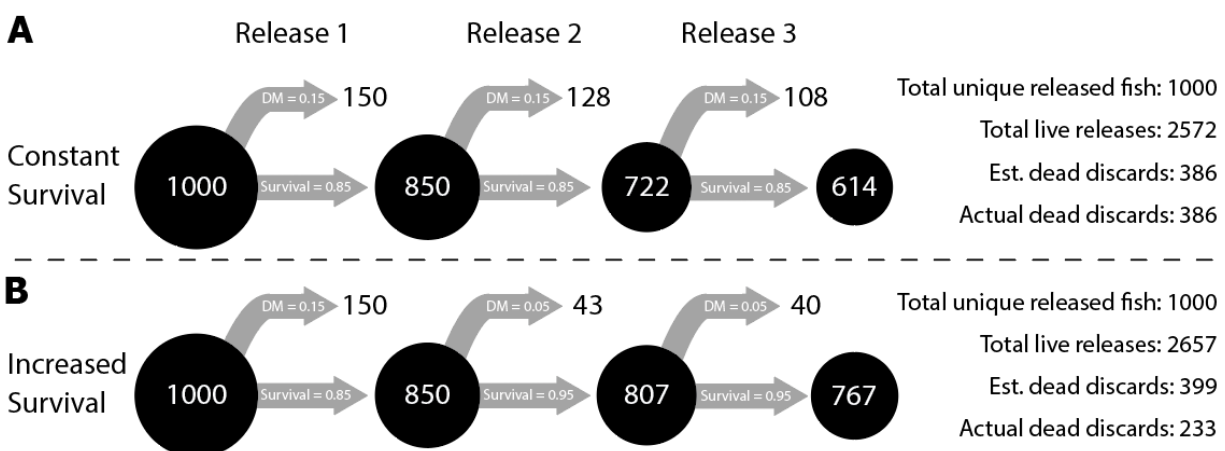
740 Table 4. Proportion of live releases to total catch for a selection of common or popular US
 741 Atlantic recreational demersal or reef-associated species in 1997 and 2017. Total catch was
 742 calculated as observed harvest + reported harvest + released alive. Data are from NOAA Marine
 743 Recreational Information Program (MRIP) for the US Atlantic coast.

Common name	Scientific name	1997	2017	Difference
Atlantic cod	<i>Gadus morhua</i>	0.44	0.91	0.47
Atlantic croaker	<i>Micropogonias undulatus</i>	0.52	0.69	0.17
Black drum	<i>Pogonias cromis</i>	0.55	0.74	0.19
Black sea bass	<i>Centropristis striata</i>	0.60	0.88	0.28
Gag	<i>Mycteroperca microlepis</i>	0.73	0.57	-0.15
Gray triggerfish	<i>Balistes caprisacus</i>	0.21	0.57	0.36
Greater amberjack	<i>Seriola dumerili</i>	0.37	0.64	0.28
Red grouper	<i>Epinephelus morio</i>	0.82	0.69	-0.13
Vermilion snapper	<i>Rhomboplites aurorubens</i>	0.32	0.59	0.27

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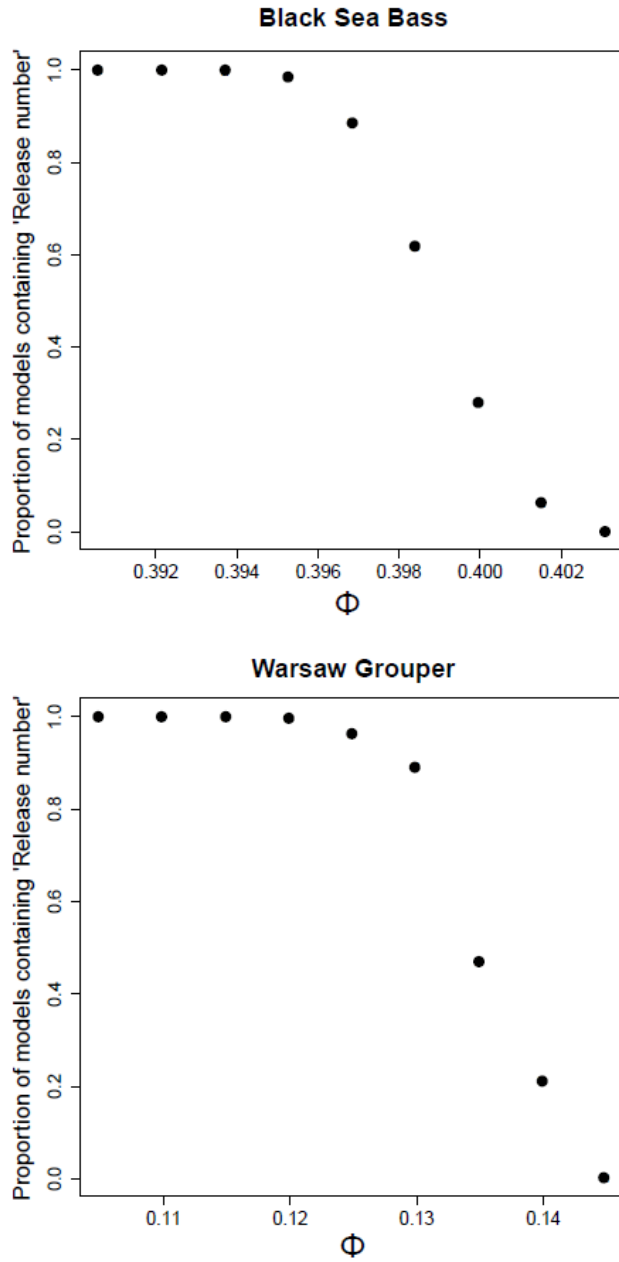


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748 Figure 1. Calculations of total unique released fish, total live releases, estimated (est.) dead
 749 discards, and actual dead discards under (A) constant survival and (B) increased survival. In both
 750 scenarios, we assume all live fish are captured in each period. “Total unique released fish” is
 751 held constant at 1000, and refers to the number of unique fish that are released in time step 1
 752 (first black circle) with those same (and alive) individuals being caught and released in
 753 subsequent time steps (second to fourth black circles). “Total live releases” is calculated as the
 754 sum of the number of releases in each time step (black circles); this value emulates the number
 755 of releases that would be reported by programs such as NOAA Marine Recreational Information
 756 Program (MRIP). “Est. dead discards” represents the sum of dead discards from each release.
 757 Estimated dead discards from all releases are calculated as “Total live releases” multiplied by
 758 [currently assumed constant] discard mortality (DM) of 0.15 for scenarios A and B. Note that
 759 although the same discard mortality rate is used, the number of “Est. dead discards” is slightly
 760 higher in scenario B because the number of live releases is higher. “Actual dead discards” is the
 761 sum of the number of discard mortalities after each of the three release events; in the “Increased
 762 Survival” scenario (B), survival increases from 0.85 for release 1 to 0.95 for releases 2 and 3.

763 This increase corresponds to our findings of increased survival for releases 2+ for three species
764 of reef fish in the southeast US.

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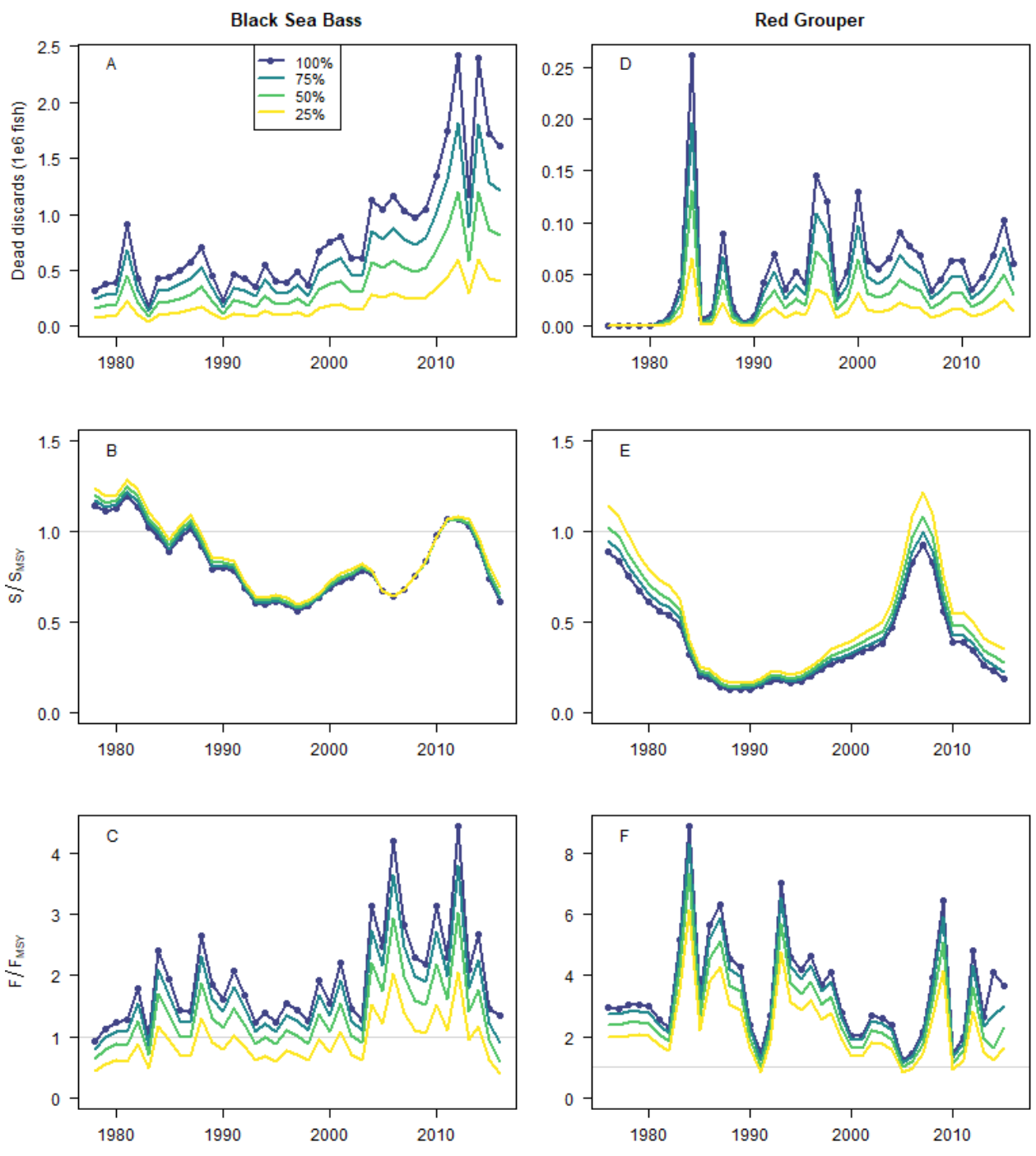
768 Figure 2. Proportion of bootstrapped datasets for which the best model contained Release

769 Number for (A) black sea bass and (B) Warsaw grouper from our examination of the effect of Φ

770 (combined rate of tag shedding and tagging-induced mortality).

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774 Figure 3. Stock assessment results for black sea bass (SEDAR, 2018) and red grouper (SEDAR,
775 2017), given the annual number of dead discards at the base level used in the most recent

776 assessment (100%) or at reduced levels (75%, 50%, or 25% of base-level estimates),
777 representing scenarios with fewer releases of unique fish or higher discard survival. Panels show
778 the annual number of dead discards for each species (A, D), the estimated spawning biomass
779 relative to that at maximum sustainable yield (S/S_{MSY} ; B, E), and the fishing mortality rate
780 relative to its value at maximum sustainable yield (F/F_{MSY} ; C, F). Note different scales on the x-
781 and y-axes among panels.

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795 Supplementary Material

796 Table S.1. Stock assessment output for black sea bass and red grouper under four scenarios for
 797 dead discards. The 100% scenario represents values that are currently used in assessment
 798 models; other scenarios represent model runs using decremented values of the 100% value to
 799 represent our suggestion that repetitive captures imply lower discard mortality than is currently
 800 estimated. S and F represent spawning biomass and fishing mortality rate, respectively. S_{MSY} and
 801 F_{MSY} represent the levels of S and F at MSY. Values shown for S/S_{MSY} are for the terminal years in
 802 the assessments, but values of F (and associated estimates) are averaged from the last two years of the
 803 assessment for black sea bass (SEDAR 2018) and the last three years of the assessment for red grouper
 804 (SEDAR 2017).

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Black sea bass								
Dead discards	N (1000 fish)	S	S_{MSY} (1E10 eggs)	S/S_{MSY}	F	F_{MSY} (y^{-1})	F/F_{MSY}	
100%	55086	288	472	0.61	0.39	0.29	1.34	
75%	53948	289	458	0.63	0.30	0.33	0.90	
50%	52876	293	444	0.66	0.25	0.41	0.60	
25%	51872	295	428	0.69	0.23	0.59	0.39	
Red grouper								
Dead discards	N (1000 fish)	S	S_{MSY} (mt)	S/S_{MSY}	F	F_{MSY} (y^{-1})	F/F_{MSY}	
100%	570	1056	5559	0.19	0.44	0.12	3.69	
75%	619	1141	5188	0.22	0.36	0.12	3.02	
50%	688	1292	4784	0.27	0.32	0.14	2.30	
25%	774	1506	4303	0.35	0.28	0.17	1.66	

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