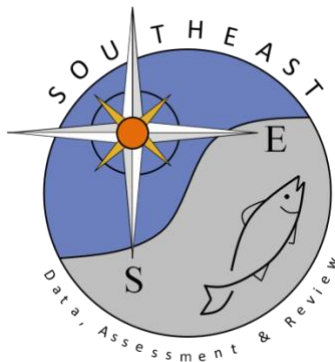


Assigning fates in telemetry studies using hidden Markov models: an application to deepwater groupers released with descender devices

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22 released with descender devices at the continental shelf break (66-120 m depth) to be 0.46 (95%
23 confidence interval 0.33, 0.65). When a combination of HMMs and prior information was
24 utilized, we estimated survival of the same 40 groupers to be 0.61 (0.47, 0.80). Both estimates
25 represent a substantial improvement over survival for surface releases (~zero). Furthermore,
26 HMMs estimated zero survival for an additional five descended groupers at a wreck site in 240
27 m depth, though one analysis using prior information suggests survival may be possible in that
28 depth. These estimates were aided by the objectivity of HMMs and we recommend future
29 survival studies involving acoustic tagging employ similar methodologies. The improved
30 survival of groupers after descending is an important finding for management, as this taxon
31 contains several species of impaired stock status or fishery status.

32

33 Introduction

34 The use and utility of electronic tags in ecology has grown in recent years as such devices
35 have become smaller, cheaper, and more advanced (Kays et al. 2015; Crossin et al. 2017). The
36 incorporation of miniaturized sensors into tags enables scientists to collect a greater variety of
37 information about tagged animals and offers flexibility in study design and objectives (Wilson et
38 al. 2015). For example, sensors for metrics such as temperature (Gorsky et al. 2012), pH
39 (Halfyard et al. 2017), light (Seitz et al. 2019), depth (Bohaboy et al. 2019), and acceleration
40 (Curtis et al. 2015) can provide much insight into biology, movement, and survival (Runde et al.
41 2018). However, the pace of these technological advances has often outstripped the development
42 of methods for the analysis of the data they produce. Novel techniques for processing the vast
43 amounts and diverse types of data created by modern telemetry studies are required to maximize
44 the benefits of electronic tagging.

45 One modern application of electronic tagging is the use of acoustic transmitters to obtain
46 information about post-release (or discard) survival of fishes (e.g., Brill et al. 2002). Studies
47 intending to estimate fish discard survival have become more frequent in recent years as this
48 value has become more important to stock assessments (Breen and Cook 2002; Viana et al.
49 2013). The primary component of most discard survival studies is fate assignment, whereby
50 information about each fish is used to infer its most likely fate (e.g., survival, discard mortality,
51 emigration). Early telemetry studies of fish survival used active tracking to collect data for fate
52 assignment (Bendock and Alexandersdottir 1993), and most assumed any moving tag
53 represented a live fish. However, some authors recognized that transmitters might also move if
54 the study animal had been eaten by a predator (Bacheler et al. 2009), though this was difficult to
55 detect other than by direct observation (e.g., Pepperell and Davis 1999).

56 The incorporation of sensors into transmitters has allowed for more realistic
57 interpretation of fish tagging data, yet some studies using sensor transmitters still rely primarily
58 on subjective inferences to assign fates (Yergey et al. 2012; Baktoft et al. 2013; Curtis et al.
59 2015; Runde and Buckel 2018). This methodology can be accurate when fates are obvious; for
60 example, when a transmitter relays constant depth and zero acceleration, the animal is likely
61 either dead or has shed the tag. However, there are scenarios where fates remain ambiguous. For
62 instance, a tagged animal may reside on the boundary of the detectable area, and therefore may
63 provide only a few intermittent pieces of information making inference difficult. Further, for
64 animals and systems where post-release predation or scavenging may be common, distinguishing
65 between the behaviors (e.g., depth, velocity, acceleration) of a live study animal versus a
66 predator that has ingested the tag may be difficult (Jepsen et al. 1998; Gibson et al. 2015).

67 Resolving uncertainty in fate assignment in survival studies is critical for generating accurate and
68 useful results.

69 More advanced techniques for assigning fates include using a subset of “known-fate”
70 individuals to clarify classification of the remaining subjects. One way to achieve this is to
71 sacrifice some fish prior to tagging and release (i.e., negative control; Muhametsafina et al.
72 2014). The behavior of these transmitters attached to known dead fish can then be scrutinized
73 and any similar patterns among released-alive fish imply discard mortalities (Yergey et al. 2012;
74 Capizzano et al. 2016). A more opportunistic approach to identify a fate involves re-sighting or
75 recapturing a live tagged animal after a period at large, thereby confirming that all data between
76 release and recapture were generated by that individual and allowing for comparisons as above
77 (i.e., a positive control; Capizzano et al. 2019). Even with these approaches, comparing detection
78 information of known-fate and unknown-fate individuals is typically at best a semi-quantitative
79 procedure (Benoît et al. 2012).

80 One method for introducing objectivity into fate assignment is with hidden Markov
81 models (HMMs). HMMs use time series data to detect and classify latent or “hidden” patterns
82 that, when applied to tagging data of animals, are often interpreted as behavioral states
83 (Langrock et al. 2012). To date, the utility of HMMs in ecology has been primarily to expand
84 biological knowledge via descriptive studies. For example, in marine fisheries HMMs have been
85 applied in studies of spawning behaviors (Holan et al. 2009), behavior in sharks (Papastamatiou
86 et al. 2018), migratory phases of Southern Bluefin Tuna *Thunnus maccoyii* (Patterson et al.
87 2009) and Cownose Ray *Rhinoptera bonasus* (Ogburn et al. 2018), movement types in Gray
88 Triggerfish *Balistes capriscus* (Bachelier et al. 2019), and behavioral states in Yellowfin Tuna *T.*
89 *albacares* and Bigeye Tuna *T. obesus* (Vermard et al. 2010). However, instead of identifying and

90 classifying behaviors of the tagged animals themselves, it is possible that HMMs could identify
91 the animal that generated the data and therefore objectively identify likely predation or
92 scavenging within the context of a survival study. To our knowledge, HMMs have never been
93 used in survival studies where changes in movement patterns may imply predation or
94 scavenging.

95 Estimates of discard survival are particularly important for fisheries in which discards
96 comprise a large portion of catch (Runde et al. 2019) and discard survival is likely to be low due
97 to gear interactions or barotrauma (Davis 2002). One group of marine fishes for which discard
98 survival is typically low is deepwater groupers. Many species of deepwater groupers in the
99 southeast United States (SEUS) are imperiled in part because they are naturally rare, aggressive,
100 heavily targeted, and susceptible to extreme barotrauma (Huntsman et al. 1999). In fact,
101 barotrauma of fishes in this group is so severe that discard survival is often assumed to be 0%;
102 this assumption is reflected in regulations for species such as Snowy Grouper *Hyporthodus*
103 *niveatus*, for which the recreational bag limit in the SEUS is currently one per vessel with no
104 minimum size (SAFMC 2016; Runde and Buckel 2018). Further, several species of groupers in
105 the SEUS are listed as overfished (Snowy Grouper; Red Grouper *Epinephelus morio*),
106 undergoing overfishing (Speckled Hind *E. drummondhayi*) or are experiencing a multi-decade
107 decline (Scamp *Mycteroperca phenax*) (Bacheler and Ballenger 2018; NOAA Fisheries 2018).

108 The use of descender devices to recompress barotraumatized fishes has been explored for
109 several species and taxa, including Walleye *Sander vitreus* (Eberts et al. 2018), Red Snapper
110 *Lutjanus campechanus* (Drumhiller et al. 2014; Bohaboy et al. 2019), Pacific rockfishes *Sebastes*
111 spp. (Theberge and Parker 2005), and deepwater groupers (Runde and Buckel 2018). Studies
112 testing this technique have generally found increases in survival of fish released with a descender

113 device as compared to without (reviewed by Eberts and Somers 2017). More challenging has
114 been generating precise estimates of survival that are usable for stock assessments and
115 management strategy evaluations and that could be confidently cited as evidence by managers
116 wishing to encourage or require the use of descender devices in the fishery.

117 Here we use HMMs to quantitatively analyze acoustic telemetry data from several
118 species of deepwater groupers released with descender devices. We build on the findings of
119 Runde and Buckel (2018) by following much of their field methodology but introduce
120 substantial improvements in the approach to analysis and inference. Specifically, we used HMMs
121 to aid in identification of predation or scavenging of the released study animals by examining
122 changes in acceleration and depth. Our results are the first discard survival estimates to be
123 generated with HMMs.

124 Methods

125 *Study area, fish capture, and tagging*

126 We fished for groupers inside the Snowy Wreck Marine Protected Area (33°30'N,
127 76°50'W) off North Carolina, USA, in May-August, 2018 (Figure 1). Fishing was conducted at
128 the continental shelf break in 66-120 m and at a shipwreck (called the Snowy Wreck) in 240 m.
129 Our methods largely followed those of Runde and Buckel (2018). Briefly, we fished using high-
130 low bottom rigs with size-8/0 hooks baited with cut Atlantic Menhaden *Brevoortia tyrannus* and
131 shortfin squid *Illex* sp. Upon capture, grouper total lengths (TL) were measured to the nearest 5
132 mm and groupers > 350 mm TL were affixed with Vemco ultrasonic coded transmitters (V13AP-
133 H; 69 kHz; random delay = 60–180 s; estimated tag life = 158 d) via two nylon dart tags to the
134 dorsal musculature (see Figure 1 in Runde and Buckel 2018). V13AP transmitters contain two

135 sensors: depth (via a converted pressure value) and acceleration, produced as an average value
136 over a 45 sec interval. More description of accelerometer sensors may be found in Curtis et al.
137 (2015). Our external attachment procedure shortened the surface interval, isolated the effects of
138 recompression (instead of venting via an incision), and increased detectability of the transmitters
139 (Johnson et al. 2015; Dance et al. 2016). Transmitters were sterilized in diluted 2% chlorhexidine
140 gluconate prior to attachment, and deck time for each fish was no more than 2 min.

141 At the continental shelf break, grouper were released by one of three methods. Most
142 groupers were descended with a SeaQualizer™ descender device set to 30, 61, or 91 m,
143 depending on the bottom depth. Four groupers in this treatment group were double-tagged
144 (affixed with two V13AP transmitters, one on each side of the dorsum and offset in the anterior-
145 posterior plane) in an effort to estimate tag retention, as is common in conventional tagging
146 studies (Beverton and Holt 1957; Seber 1982). For the second treatment, some groupers were
147 released boat-side into a bottomless surface enclosure (2.5 m square and 1.3 m deep) where their
148 behavior was observed and recorded (*sensu* Hannah et al. 2008). If these groupers floated and
149 appeared moribund, they were assumed to be dead and were recovered, and the transmitter was
150 reused. Finally, a subset of groupers caught at the continental shelf break were sacrificed, tagged
151 as above, and descended to 30, 61, or 91 m with a SeaQualizer™ device. These individuals
152 served as a negative control, because any acceleration and depth changes of their transmitters
153 were known to be from predators or scavengers. At the Snowy Wreck, all grouper were
154 descended to the seafloor with a Blacktip™ descender device in order to promote residency of
155 the transmitter to the site (and detectability on local receivers) as opposed to a mid-water-column
156 release via the SeaQualizer.

157

158 *Submersible receiver mooring deployment and retrieval*

159 We deployed an array of 22 Vemco VR2AR acoustic release receivers in the Snowy
160 Wreck Marine Protected Area on May 1, 2018 (Figure 1). Each mooring was anchored with ~43
161 kg steel sacrificial ballast attached to a receiver lug with 6.4 mm diameter steel cable. Above
162 each receiver was a subsurface trawl float (280 mm diameter, 8.8 kg buoyancy) attached with
163 ultra-high molecular weight polyethylene fiber (Dyneema®) rope and stainless steel shackles.
164 Twenty receivers were deployed at the continental shelf break in likely areas of grouper catch,
165 based on catches by Runde and Buckel (2018) and Rudershausen et al. (2010) in the same
166 region. Two VR2AR receivers were deployed at the Snowy Wreck, approximately 100 m apart.
167 We recovered all receivers on October 2, 2018.

168

169 *Data processing and analysis*

170 Detection data were downloaded to Vemco VUE software and subjected to the False
171 Detection Analyzer to remove likely erroneous detections. We compiled a detection history of
172 depth and acceleration for each transmitter in R (R Core Team 2019) for use in HMM and
173 assignments of fate.

174 A hidden Markov model assumes that each observed variable (in our case, acceleration or
175 depth) can arise from several different probability distributions, called emission distributions
176 (Zucchini et al. 2016). An unobserved state process determines which distribution is active at
177 each time point, and its evolution is modelled with transition probabilities. We fitted a 3-state
178 HMM to the detection data collected from each transmitter. HMMs require data streams to be on
179 a regularized time grid (e.g., one observation every 30 min). Given that our V13AP tags
180 transmitted on a random delay, our detection data were not regularized temporally. Therefore, we

181 binned detections into 30 min time bins for the purpose of regularization. We chose an interval
182 long enough so that most time bins contained one observation or more, and short enough to
183 capture the movement states of interest. From the binned detection data, we generated three data
184 streams that were used as inputs in our HMM. The first data stream was acceleration (m/s^2), for
185 which a single observation from each 30 min time bin was randomly chosen to represent each
186 bin. This acceleration data stream was parameterized as a gamma distribution. The second data
187 stream was depth as a proportion of capture depth (m), where a value of 1.0 represented the fish
188 being detected at exactly the same depth as was recorded during capture. This transformation
189 was necessary as the study animals were released across a range of depths. This data stream was
190 also created using a single random selection from within each time bin and was parameterized as
191 a Gaussian (“normal”) distribution. Finally, the third data stream was the standard deviation of
192 all depth values in each time bin. This final data stream was parameterized as a gamma
193 distribution. We elected not to use summary statistics for the first two data streams (e.g., mean or
194 median values within each time bin) because such values may not appropriately capture the
195 variability in acceleration and depth. In addition, averaging could result in the use of a value that
196 never truly appeared in a given time bin.

197 We used a “bootstrapping” procedure to investigate the sensitivity of our findings to the
198 random selection of values to represent time bins in the acceleration and relative depth data
199 streams. Here we conducted 10 replicate HMMs where each replicate used independent,
200 randomly drawn acceleration and relative depth values. For bins in which no observations
201 occurred, the data frame was filled with a missing value (NA). We calculated the most likely
202 state sequence for each replicate model using the Viterbi algorithm, to infer behavioral states and
203 fate of tagged fish. For each pair of replicate models, we calculated the proportion of time bins in

204 which the predicted state differed, and then closely examined the implications for fate
205 assignment of the state sequences generated by the two least similar models. HMMs and
206 subsequent analyses were performed in the R package ‘momentuHMM’ (McClintock and
207 Michelot 2018).

208 *Fate assignment and survival estimation*

209 Results from the HMM were examined for each individual grouper and used to assign
210 fates. We compared the state sequences of the sacrificed descended individuals (i.e., negative
211 control) to the state sequences of the descended-alive individuals. If descended-alive groupers
212 displayed the same state as the negative controls, they were determined to be deceased and
213 subject to predation or scavenging. The state sequences for groupers displaying other states were
214 scrutinized and used to make informed decisions about their assigned fates. Emigration of a live
215 grouper was determined to have occurred if detections ceased without switching to a state
216 representing predation. Groupers that emigrated from the receiver array or lost their tag were
217 censored from the analysis on the day of emigration or tag loss.

218 We assigned fates using two general scenarios. In Analysis 1, we assigned fates based
219 more strictly on HMM results; we imposed expert knowledge only when the fates suggested by
220 HMMs were illogical. In Analysis 2, we allowed for behaviors and phenomena that have been
221 anecdotally observed in other studies but could not be confirmed here (e.g., vertical movement of
222 live study animals before emigration from the receiver array; N. Wegner, unpublished data).
223 Furthermore, in Analysis 2 we took into account ancillary data that could not be included in the
224 HMM, such any information about a transmitter’s movement through space on different
225 receivers. The fate assignments from Analysis 1 are generally more conservative (i.e., they err on
226 the side of lower survival).

227 Fates for groupers that were released alive were used to inform Kaplan-Meier
228 nonparametric models to estimate post-release survival. We conducted separate Kaplan-Meier
229 procedures for groupers released via descending, released into the surface enclosure, and for
230 releases at the Snowy Wreck; estimates were generated twice for each of these groups (once each
231 for Analysis 1 and Analysis 2). The Kaplan-Meier procedures were conducted in the R package
232 ‘survminer’ (Kassambara and Kosinski 2018).

233 Results

234 At the continental shelf break (depth = 66-120 m), we released 40 groupers via
235 descending, of which four were double tagged. In addition, we released nine groupers into the
236 bottomless surface enclosure. Of these nine surface releases, two groupers swam down and seven
237 floated. The seven groupers that floated were recovered and their tags reused; those reused tags
238 are included in totals below. We sacrificed and descended three tagged groupers for a total of 45
239 individuals released at the shelf break (42 live, three dead). At the Snowy Wreck (depth = 240
240 m), we tagged and released five Snowy Groupers, all of which were descended to the seafloor.
241 Overall, we tagged at least one individual of six grouper species: Gag *M. microlepis* (n = 1), Red
242 Grouper (n = 1), Scamp (n = 11), Snowy Grouper (n = 31 + 5 at the Snowy Wreck), Speckled
243 Hind (n = 4), and Yellowmouth Grouper *M. interstitialis* (n = 4). Total lengths, depths of
244 capture, species identification, and treatments for each individual are shown in Table 1.

245 We obtained over 580,000 detections from telemetered groupers. These detections were
246 from each of the 50 groupers in the study that submerged. Across all individuals, we created
247 60,666 30-min time bins. To investigate the reliability of our method of random selection from
248 each time bin, we first compared the estimated state sequences obtained for the 10 replicates.
249 The largest difference was 1.04% of time bins, which indicates that the estimated states were

250 robust to random selection (Table S1). We also found a high level of agreement between the 10
251 replicates for all emission distribution parameter estimates (Table 2). In the following, we use the
252 average of the parameter estimates of the 10 replicate models.

253 Estimates of the parameters of the emission distributions showed clear distinctions
254 between the three states (Table 2; Figure 2). State 1 was characterized by the lowest mean
255 acceleration (“Acc”) values, the closest relative depth (“RelDepth”) to 1.0, and the lowest mean
256 standard deviation of depth (“DepthSD”). State 2 had similar Acc values to state 1, but had a
257 mean RelDepth of 1.13 (the highest of the three states), and a moderate DepthSD mean. State 3
258 showed the highest mean Acc, the only RelDepth mean less than 1.0 (indicating depths well
259 above tagging depth), and the largest DepthSD value. The estimated probabilities of remaining in
260 the current state were 0.99 for state 1 and 0.96 for state 2, indicating behavioral persistence over
261 multiple time intervals. Comparisons between state sequences generated from the two least
262 similar replicates (HMM 3 and HMM 4) resulted in no differences in fate assignment for any of
263 the groupers in the study.

264 Of the three sacrificed and descended dead groupers, only one provided sufficient data to
265 be included in the HMM (Scamp 3). The other two individuals (Snowy Grouper 11 and Snowy
266 Grouper 5) were detected for approximately 7 and 25 minutes respectively, and each had very
267 few detections. The terminal detection for each of these individuals suggested the transmitter was
268 within a few meters of the surface. Scamp 3 was detected for approximately 26 hours. The HMM
269 classified this individual as exhibiting state 3 throughout the entire time period for which it was
270 detected (Figure 3A). We reviewed the state sequences for the remaining individuals, and those
271 dominated by states 1 and 2 were categorized as survivals (e.g., Figure 3B).

272 For 40 groupers descended alive at the shelf break, Analysis 1 determined 14 had
273 survived the duration of the study, three lost their tags while still alive, one emigrated, and 22
274 experienced discard mortality. For the same fish, fates determined using Analysis 2 differed for
275 11 individuals; in general, this procedure changed fates from mortalities to emigration or tag loss
276 based on previous authors' observations of post-tagging recovery behavior in demersal fishes
277 (e.g., Collins 2014; see *Discussion*). Further, the HMM was not able to distinguish between a
278 dead grouper on the seafloor (with occasional movement caused by scavengers) and a live
279 grouper. These two interpretations of the same general "behavior" is reflected in the differences
280 between the two Analyses. Analysis 2 determined 14 grouper survived the duration of the study,
281 four lost their tags while still alive, seven emigrated, and 15 experienced discard mortality. In
282 Analysis 1, each of the four double-tagged groupers experienced mortality within the first day
283 after release. In Analysis 2, one died, two emigrated in the first two days, and one appeared to
284 lose one tag within hours of release and then emigrate on day 4. We conclude that tag loss is
285 possible given this attachment type, though the sample sizes and durations of observation for
286 double-tagged fish preclude a statistical estimate of that rate. Fates for each individual assigned
287 in both Analyses are shown in Table 1.

288 All mortalities occurred within the first seven days after tagging, therefore our survival
289 estimate at that time represents our estimate for the study overall. For groupers descended alive
290 at the shelf break, the Kaplan-Meier survivorship procedure using Analysis 1 fates generated a
291 survival estimate of 0.46 (95% confidence interval 0.33, 0.65; Figure 4). Using Analysis 2 fates,
292 the survival estimate was 0.61 (0.47, 0.80).

293 Two of nine surface-released groupers swam down; under Analysis 1, both of these fish
294 appeared to experience mortality on the day they were tagged (day zero), resulting in survival of

295 0.00. Under Analysis 2, these two fish could have emigrated on days 1 and 5 respectively. Using
296 these fates, a Kaplan-Meier survivorship procedure estimates survival of 0.22 (0.07, 0.75) for
297 surface-released groupers. Of five groupers released at the Snowy Wreck in 240 m, none
298 survived beyond day zero using Analysis 1 fates, resulting in a survival estimate of 0.00.
299 Analysis 2 interpretations suggest that all five may have emigrated within 9 days based on their
300 disappearance from the receiver array (but see *Discussion*). We therefore estimate survival of
301 0.00-1.00 for groupers released at the Snowy Wreck.

302 Discussion

303 The objectivity for fate assignment provided by hidden Markov models is a major
304 improvement to telemetry-based survival studies. We found that in most cases the HMM could
305 distinguish between known-dead individuals and groupers we believe to have been alive during
306 the study period. However, generating a survival estimate from HMMs still required subjective
307 assignment of fates for some individuals; we describe these procedures and other caveats below.

308 In our study, there were a few groupers for which the HMM identified mortalities that
309 subjective inference would likely have missed. These animals represent one of the major utilities
310 of HMMs. For Scamp 6 (Appendix 2), Snowy Grouper 3 (Figure 3C), and Speckled Hind 4
311 (Appendix 2), initial examination of the acoustic profiles suggested tag loss, and we would likely
312 have considered these fish alive using subjective inference alone. However, the HMM identified
313 clear changes in the states of these three individuals (from states 1 and 2 to state 3) several days
314 prior to flat-lined depth and acceleration. We therefore concluded that these individuals were
315 alive and then eaten by a predator. These three groupers exhibited state 3 for four days, five days,
316 and one day prior to apparent expulsion of the transmitter by the predator. These durations fall
317 within the usual gastric evacuation time of most large elasmobranchs (Wetherbee and Cortés

318 2004). Furthermore, during the period after apparent predation for each of these three fish
319 detections were recorded on several (four or more) receivers, suggesting the transmitter was in
320 an extremely mobile animal.

321 Contrary to the above individuals, where we assigned mortalities based on HMM results,
322 there were several fish for which we used ancillary information to overrule HMM results. For
323 example, Scamp 10 was assigned state 3 for the entirety of its detection history (Figure 3D).
324 Scamp 10 was relatively small (490 mm TL), but was tagged with a transmitter that had been
325 prepared for a larger fish. The wires connecting the tag to the dart tips were therefore longer than
326 necessary. The first author noted that the tag appeared loose upon release. This situation appears
327 to be reflected in the acceleration profile for this fish: there are no observations of zero
328 acceleration until the tag was evidently lost on day six. Because the depth detections for Scamp
329 10 resemble depths for live groupers, we categorized this individual as alive until tag loss in both
330 Analysis 1 and Analysis 2. All other groupers were tagged with transmitters with wire lengths
331 appropriate for their body size.

332 In addition to Scamp 10, there were several individuals that transitioned to state 3 or
333 disappeared after several days of states 1 and 2. Examination of these profiles revealed that some
334 showed almost no changes in depth and few non-zero acceleration detections until their
335 transition to state 3 or disappearance (e.g., Snowy Grouper 20; Figure 3E). This type of detection
336 profile may represent a dead grouper on the seafloor being scavenged by smaller fish and
337 invertebrates with intermittent occurrences of being picked up by a (perhaps larger) scavenger
338 (signaled by a switch to state 3) on (in the case of Snowy Grouper 20) August 30 and again on
339 September 8. These brief, rapid, vertical movements from a near-constant depth of 120m to
340 depths as shallow as 60m are a behavior we never observed in groupers we categorized as alive.

341 Live groupers sometimes exhibited zero acceleration and no changes in depth, but these periods
342 were punctuated with regular movements detected by both sensors. This regular movement was
343 not observed in the several fish we believe may have been dead and experiencing seafloor
344 scavenging. There were nine individuals for which this potential on-seafloor scavenging was
345 observed. The majority of these were categorized by the HMM as states 1 and 2 for much of
346 their observation period but state 3 at the end of their detection history. Contrary to scavenging
347 events during which the predator ingested the transmitter and rose into the water column, on-
348 seafloor scavenging appears to the HMM to be similar to live grouper behavior (i.e., states 1 and
349 2). For Analysis 1, these individuals were considered mortalities on day 0. Under Analysis 2, we
350 considered the possibility that these fish were alive and recovering from the stress associated
351 with capture, tagging, and release, and emigrated after or during this recovery period by first
352 migrating vertically. Collins (2014) and Runde and Buckel (2018) described a post-tagging
353 recovery period during which fish were less active. As none of the descended dead groupers
354 exhibited this type of profile, these individuals were therefore considered alive until the point of
355 emigration in Analysis 2. Recovery followed by emigration behavior has been observed in
356 Pacific rockfishes, some of which were later recaptured, thereby confirming their status as live
357 fish (*N. Wegner, NMFS, pers. comm.*). Unfortunately, we were unable to recapture any
358 telemetered fish in this study; therefore, the interpretation of these animals' behavior remains
359 uncertain. We recommend future telemetry studies tag a larger sample size of sacrificed
360 individuals.

361 We identified some groupers that clearly lost their transmitter (either while still alive or
362 postmortem) prior to the end of the study, as they displayed zero acceleration and constant depth
363 after a certain point. The data file for each of these fish was truncated to remove the detections

364 representing a lost tag, as these tag loss data would not correspond to any of the movement states
365 of the HMM. We considered the possibility of a 4-state HMM, where the additional state would
366 represent these data. However, this was not feasible given our use of relative depth as a
367 datastream for the HMM. Indeed, the distribution of relative depths was not consistent across lost
368 tags, because transmitters were lost at relative depths ranging from approximately 0.56 to 1.95.
369 This wide range is a result of the high relief habitat in which we performed our study; future
370 studies conducted in lower relief areas may have success modeling tag loss as its own HMM
371 state.

372 Choosing the number of states in HMMs is challenging, and often not straightforward
373 (Pohle et al., 2017). In this study, we investigated an HMM with two states in addition to the
374 eventual 3-state model. The 2-state model did not appropriately distinguish the descended-dead
375 grouper from the released-alive fish. We determined that the 3-state model was necessary to
376 capture the complexity of the situation to which we were attempting to apply HMMs. We lacked
377 the data that are perhaps most typical as inputs for HMMs applied to animal movement: turning
378 angle and step length. Instead, we used alternative data streams to characterize movement, e.g.,
379 depth relative to depth at release was chosen as a proxy for distance from the seafloor. We note
380 that some groupers may have consistently occupied seafloor habitat but appear to sometimes be
381 much deeper or much shallower than their release depth (e.g., Red Grouper 1; Figure 3F). This
382 possibly occurred because the shelf break consists of many areas of extreme depth changes over
383 a short linear distance; Red Grouper 1 appeared to prefer seafloor habitat in two primary depths
384 that were ~20 m different yet still within the receiver array. Because of the variation in this and
385 other individuals, the live grouper detection information for all three data streams contained a

386 wide range of values, which resulted from not only a variety of “normal” grouper behaviors but
387 also from the imperfection of the data streams available in this study.

388 Typical HMMs for animal movement result in biological description of the behavioral
389 states identified such as “foraging” or “transiting” (e.g., Bacheler et al. 2019). For our purposes,
390 such description is a dubious exercise given the data streams we had available. States 1 and 2
391 seemed to define animals that accelerate at a relatively low amount, occupy habitat close to the
392 seafloor, and change depths a low to moderate amount. State 3 was described by animals that
393 have higher acceleration, utilize a much wider range of depths, and change depth rapidly. These
394 qualitative descriptions of the states are consistent with our assertion that states 1 and 2 represent
395 live groupers and state 3 represents groupers eaten by predators. In cases where the fate of some
396 of the fish is known, this information can also be included in the HMM to clarify the
397 classification of the other tracks (“semi-supervised learning,” Leos-Barajas et al. 2017). Future
398 work including a greater number and variety of known-fate individuals could attempt this
399 approach.

400 We considered applying a continuous-time model to these data given the irregularity of
401 the detections. However, the implementation of state-switching continuous-time models is much
402 more difficult and computational than using HMMs (Blackwell et al. 2016; Michelot and
403 Blackwell 2019). In particular, it is not clear what continuous-time processes should be used to
404 model the “acceleration” and “depth” variables considered here, given that continuous-time
405 methodology has focused on the analysis of longitude-latitude movement data. Further, there are
406 no accessible software packages to apply those models to telemetry data sets, and the large size
407 of our data set (~60,000 time bins) would make the model fitting infeasible. For all these
408 reasons, we believe that the use of a discrete-time method is defensible here.

409 Our survival estimate from Analysis 1 of 0.46 (0.33, 0.65) and from Analysis 2 of 0.61
410 (0.47, 0.80) fall within the range estimated by Runde and Buckel (2018). Their survival estimate
411 of 0.50 (0.10, 0.91) had extremely broad confidence intervals because many emigrations
412 exacerbated an already-low sample size. Our higher sample size and larger array, paired with
413 more precise fate assignments via HMM, produced much narrower confidence intervals in the
414 present study. Other studies examining the effects of descender devices in this depth range are
415 scarce, though some have been conducted in slightly shallower marine environments. Curtis et
416 al. (2015) worked in 50m and estimated survival of descended Red Snapper as 0.83 (0.68, 0.98).
417 Sumpton et al. (2010) tagged red emperor *L. sebae* in depths predominantly >30 m but found
418 little evidence for descender devices promoting survival in this species. We recommend future
419 descender device studies work in depths and habitats that are most relevant to the fishery.

420 We elected to analyze survival across species for several reasons. First, given the high
421 cost of acoustic telemetry, our sample sizes by species were limited. Second, many of these
422 species cohabitate, and most groupers in the SEUS are managed as an aggregate unit (SAFMC
423 2016), so our findings are applicable to the fishery in general. When analyzed separately, the two
424 species for which we had the highest sample sizes at the shelf break, Snowy Grouper and Scamp,
425 had survival estimates of 0.49 (0.32, 0.76) and 0.38 (0.15, 0.92) respectively in Analysis 1, and
426 the two species had estimates of 0.79 (0.62, 1.00) and 0.31 (0.10, 0.96) respectively in Analysis
427 2. The majority of these mean estimates are near our overall estimates of 0.46 and 0.62, and all
428 of the confidence intervals overlap widely, supporting our choice to pool the species-specific
429 estimates.

430 Current management assumes discard survival of zero for many reef fishes due to
431 extreme barotrauma (SAFMC 2016). In the present study, we made an attempt to gather

432 evidence on this topic by releasing tagged groupers into our bottomless surface enclosure. Since
433 our maximal mean estimate of survival (Analysis 2) for nine groupers released at the surface in
434 this study is 0.22, we are inclined to agree in principle with the current assumption of zero
435 survival for the species examined, though a low level of survival may be possible particularly in
436 the shallower portion of these species' ranges. However, we have demonstrated that survival is
437 significantly higher than zero for groupers released with a descender device. The South Atlantic
438 Fishery Management Council recently approved Regulatory Amendment 29 to the Snapper-
439 Grouper Fishery Management Plan, which requires the presence of descender devices on board
440 vessels fishing for reef fish in the southeast US (approved September 2019; awaiting Formal
441 Secretarial Review). Given our findings, we recommend other management agencies take similar
442 measures to promote widespread use of descender devices in this and other fisheries.

443 Many of our groupers, including all five released at the Snowy Wreck, may have
444 succumbed to predation after release. While Analysis 2 allows for the possibility of emigration
445 for these individuals, we believe that explanation to be unlikely. Three out of five of these fish
446 were detected mid-water-column during their detection history at depths of 22 m, 26 m, and 71
447 m. Ambient pressure at 100 m is 25 atm; the shallower depths where we detected these
448 individuals has ambient pressure of as low as 3 atm. The barotrauma that is likely to be sustained
449 by a Snowy Grouper transitioning between these two depths is probably prohibitive of such
450 movement being voluntary. Therefore, the depth of the Snowy Wreck may be beyond the
451 maximum depth for which groupers can survive the barotraumatic effects of capture, even if
452 released with a descender device. However, the possibly absolute mortality we observed at that
453 site may have partially resulted from a high density of predators in the area.

454 Throughout our study, we detected several acoustically tagged elasmobranchs inside our
455 receiver array; at the shelf break, we detected one Tiger Shark *Galeocerdo cuvier* and five White
456 Sharks *Carcharodon carcharias* over the five month period for which our receivers were
457 deployed. At the Snowy Wreck, receivers were in place for eighteen months, over which we
458 detected one tiger shark and eight white sharks. Total lengths of these predators ranged from 3.1
459 m to 4.2 m for Tiger Sharks (*B. Frazier, pers comm*) and 3.3 m to 4.3 m for White Sharks (*G.*
460 *Skomal and M. Winton, pers comm*). Sharks were detected in every month of the study in both
461 locations, supporting the idea that these species (or others) may have been responsible for the
462 predation of our tagged groupers. It is likely that descended groupers displayed abnormal
463 behavior immediately after release, perhaps during recovery from barotrauma (Collins 2014;
464 Runde and Buckel 2018). This behavior is possibly linked to an increased risk of predation, as
465 elasmobranch predators have been shown to preferentially feed on prey that are struggling or
466 displaying irregular behavior (Kritzler and Wood 1961; Dijkgraaf 1963; Bleckmann and
467 Hofmann 1999). It is conceivable that some of the groupers that died after release might have
468 survived if they were able to avoid predation during their recovery period. Some of the groupers
469 may have been deceased prior to ingestion by a predator though some may have been attacked
470 while alive. This is supported by detection data showing depth and acceleration movements
471 typical of a live grouper prior to switching to state 3 (e.g., Scamp 6). Furthermore, we assume
472 that tagging itself did not increase the risk of predation; if any tagged groupers died as a result of
473 tagging, our estimate of survival after recompression would be lower than when realized in the
474 fishery.

475 External tagging with acoustic transmitters has increased in popularity due to increased
476 detection ranges (Dance et al. 2016) and, for survival studies, the desire to separate the effects of

477 barotrauma with possible relief caused by tagging (Johnson et al. 2015). Attachment methods
478 have ranged from the dart tag style used here and by Runde and Buckel (2018), a method by
479 which the transmitter is glued to a t-bar tag (Yergey et al. 2012), procedures involving “cinch-
480 up” tags used by Curtis et al. (2015), methods using suture material passed through the fish by
481 Bacheler et al. (2019), and attachment via an intramuscular stainless steel bolt by Bohaboy et al.
482 (2019). To our knowledge no attempts have been made to quantify tag loss *in situ* for any of
483 these methods, though some authors used tank holding studies to this end (e.g., Bacheler et al.,
484 2019). Therefore, there is no resolution as to the best tag attachment procedure for such studies.
485 Our attempt to quantify tag loss by double tagging groupers was unsuccessful, as zero of four
486 double-tagged fish survived beyond day zero. This is perhaps because the injury caused by the
487 introduction of four darts was substantially greater than that caused by two darts. Alternatively,
488 the slightly longer surface interval required to tag a fish twice may have resulted in increased
489 mortality risk. It is also possible that these four animals would have experienced mortality if they
490 were tagged only once, and that we simply required a larger sample size to reach a conclusion.
491 As is done for conventional tagging, we recommend studies using external attachment of
492 acoustic transmitters make attempts to quantify tag loss *in situ*, particularly when fate assignment
493 is difficult due to the study animal or habitat. Double tagging with acoustic transmitters, though
494 costly, is likely a sufficient means to that end.

495

496 Conclusions

497 Survival studies often rely on subjectivity when assigning fates of tagged animals. Recent
498 advancements in transmitter technology have resulted in a greater variety of data available to
499 researchers, but methods for quantitative analysis thereof are lacking. We successfully employed

500 hidden Markov models as a means of increasing objectivity of fate assignment in our study.
501 Future researchers should consider HMMs when attempting to determine fates of animals tagged
502 with acoustic transmitters.

503 Our result that all surface-released groupers may have died corroborates the assumed
504 100% discard mortality for many of species in this group when untreated with a descender
505 device. When taken in context with our survival estimates of 0.46 and 0.61 at the shelf break,
506 this information is extremely valuable for reef fish managers. In addition, our result of perhaps
507 zero survival for groupers released in much deeper water suggests that the recent descender
508 device requirement in the South Atlantic region may not achieve the desired effect, even if
509 compliance is high. Given that descender devices may not be effective in very deep water and
510 that grouper survival in shelf break waters is still relatively low even when descended, it may be
511 necessary for managers to take additional measures (such as spatial closures) to protect imperiled
512 species from overfishing.

513

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526

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687

688

689 Tables and Figures

690 Table 1. Information for individual groupers off North Carolina, USA. “Site” identifies whether
691 the fish were tagged at the shelf break (“Shelf”) or at the Snowy Wreck (“Wreck”). Tag names
692 are comprised of the species and a unique identifying number. Tag names including “tag 1” or

693 “tag 2” identify individuals that were double-tagged. Fish were either released alive with a
 694 descender device (“Descend”), descended after sacrifice (“Descend dead”), or released into a
 695 bottomless surface enclosure where they either swam down (“Surface cage, swam”) or floated
 696 (“Surface cage, floated”). “Survival, full” indicates that the fish was still alive at the end of the
 697 study period. Fates were determined mainly by hidden Markov model (HMM); “Analysis 1 fate”
 698 indicates the assigned fate when the HMM results were interpreted more strictly (i.e., lower
 699 subjectivity). “Analysis 2 fate” indicates the assigned fate when we altered fates subjectively and
 700 are only present in this table when they differed from those in Analysis 1. Days alive were used
 701 as inputs for two Kaplan-Meier survivorship procedures.

Site	Tag name	Total length (mm)	Capture depth (m)	Release type	Analysis 1 Fate	Days alive	Analysis 2 Fate	Days alive
Shelf	Gag 1	1085	72	Descend	Mortality	0		
Shelf	Red Grouper 1	850	116	Descend	Survival, full	123		
Shelf	Scamp 1	675	85	Descend	Mortality	3		
Shelf	Scamp 2	630	85	Descend	Mortality	0		
Shelf	Scamp 3	680	85	Descend dead	-			
Shelf	Scamp 4	610	76	Descend	Survival, full	124		
Shelf	Scamp 5	510	82	Surface cage, swam	Mortality	0	Emigration	0
Shelf	Scamp 6	650	88	Descend	Mortality	4		
Shelf	Scamp 7	595	116	Descend	Mortality	0	Mortality	7
Shelf	Scamp 8	550	117	Descend	Mortality	0	Mortality	7
Shelf	Scamp 9	520	91	Descend	Survival, full	34		
Shelf	Scamp 10	490	66	Descend	Tag loss	6		
Shelf	Scamp 11	680	85	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 1	555	119	Descend	Mortality	0	Emigration	0
Shelf	Snowy Grouper 2	410	119	Descend	Mortality	0		
Shelf	Snowy Grouper 3	415	91	Descend	Mortality	2		
Shelf	Snowy Grouper 4	430	79	Descend	Survival, tag loss	9		
Shelf	Snowy Grouper 5	390	118	Descend dead	-			
Shelf	Snowy Grouper 6	600	95	Descend	Survival, full	119		
Shelf	Snowy Grouper 7	470	115	Descend	Mortality	3		
Shelf	Snowy Grouper 8	560	120	Descend	Survival, full	63		
Shelf	Snowy Grouper 9	430	80	Descend	Mortality	1	Tag loss	16

Shelf	Snowy Grouper 10	420	119	Descend	Survival, full	63		
Shelf	Snowy Grouper 11	365	117	Descend dead	-			
Shelf	Snowy Grouper 12	385	117	Descend	Survival, full	63		
Shelf	Snowy Grouper 13	395	117	Descend	Survival, full	63		
Shelf	Snowy Grouper 14	365	117	Descend	Survival, full	63		
Shelf	Snowy Grouper 15	460	82	Descend	Survival, full	63		
Shelf	Snowy Grouper 16	410	91	Descend	Survival, full	63		
Shelf	Snowy Grouper 17	420	108	Descend	Mortality	0	Emigration	11
Shelf	Snowy Grouper 18	390	99	Descend	Survival, full	34		
Shelf	Snowy Grouper 19	590	116	Descend	Emigration	1		
Shelf	Snowy Grouper 20	855	113	Descend	Mortality	0	Emigration	11
Shelf	Snowy Grouper 21 tag 1	645	116	Descend	Mortality	0	Emigration	2
Shelf	Snowy Grouper 21 tag 2	645	116	Descend	Mortality	0	Emigration	2
Shelf	Snowy Grouper 22	710	116	Surface cage, swam	Mortality	0	Emigration	5
Shelf	Snowy Grouper 23 tag 1	870	116	Descend	Mortality	0	Emigration	4
Shelf	Snowy Grouper 23 tag 2	870	116	Descend	Mortality	0	Tag loss	0
Shelf	Snowy Grouper 24	450	113	Descend	Mortality	3		
Shelf	Snowy Grouper 25 tag 1	740	116	Descend	Mortality	0	Emigration	0
Shelf	Snowy Grouper 25 tag 2	740	116	Descend	Mortality	0	Emigration	0
Shelf	Snowy Grouper 26	440	119	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 27	370	116	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 28	725	116	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 29	900	116	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 30	655	116	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 31	390	118	Surface cage, floated	Mortality	0		
Shelf	Speckled Hind 1	770	119	Descend	Mortality	0		
Shelf	Speckled Hind 2	645	117	Descend	Survival, full	63		
Shelf	Speckled Hind 3	540	90	Descend	Tag loss	34		
Shelf	Speckled Hind 4	570	116	Descend	Mortality	3		
Shelf	Yellowmouth Grouper 1 tag 1	730	87	Descend	Mortality	1		
Shelf	Yellowmouth Grouper 1 tag 2	730	87	Descend	Mortality	1		
Shelf	Yellowmouth Grouper 2	620	113	Descend	Mortality	0		
Shelf	Yellowmouth Grouper 3	595	113	Descend	Mortality	0		
Shelf	Yellowmouth Grouper 4	570	119	Descend	Survival, full	64		
Wreck	Snowy Grouper 1 wreck	800	244	Descend	Mortality	0	Emigration	6
Wreck	Snowy Grouper 2 wreck	920	244	Descend	Mortality	0	Emigration	0
Wreck	Snowy Grouper 3 wreck	850	244	Descend	Mortality	0	Emigration	1
Wreck	Snowy Grouper 4 wreck	800	244	Descend	Mortality	0	Emigration	9
Wreck	Snowy Grouper 5 wreck	1020	244	Descend	Mortality	0	Emigration	2

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703

704 Table 2. Mean parameter estimates for the 10 bootstrapped hidden Markov models. Variances
 705 are provided for each estimate parenthetically. The three data streams parameterized were
 706 acceleration (“Acc”), depth relative to the depth of release (“RelDepth”), and standard deviation
 707 of all depth values in each time bin (“DepthSD”). For each data stream, “SD” refers to the
 708 standard deviation parameter. “Zmass” refers to the zero-mass parameter which was estimated
 709 for Acc and DepthSD, as they are described by gamma distributions.

710

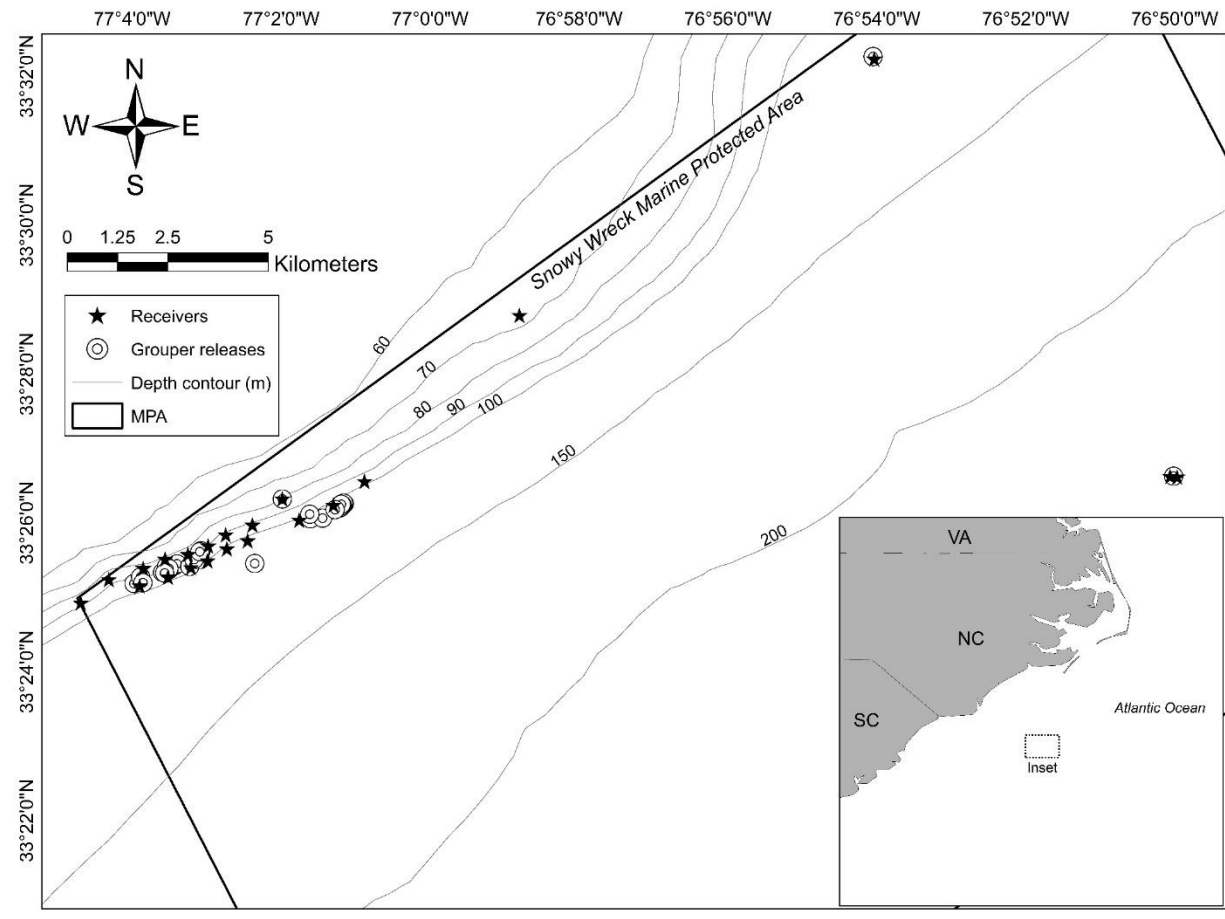
	State 1	State 2	State 3
Acc Mean	0.389 (1.77E-06)	0.388 (7.30E-06)	0.601 (8.00E-05)
Acc SD	0.408 (3.01E-06)	0.395 (1.60E-05)	0.534 (1.06E-04)
Acc Zmass	5.38 E-05 (2.36E-09)	9.09 E-09 (9.88E-18)	5.39 E-04 (5.74E-08)
RelDepth Mean	1.012 (7.05E-09)	1.133 (3.26E-07)	0.880 (9.39E-06)
RelDepth SD	0.023 (1.01E-08)	0.070 (4.85E-08)	0.252 (4.25E-06)
DepthSD Mean	0.587 (1.61E-05)	1.383 (7.62E-05)	4.172 (9.20E-04)
DepthSD SD	0.360 (2.44E-05)	1.187 (1.02E-04)	4.332 (1.60E-03)
DepthSD Zmass	0.461 (1.00E-06)	0.266 (7.69E-07)	0.099 (1.80E-06)

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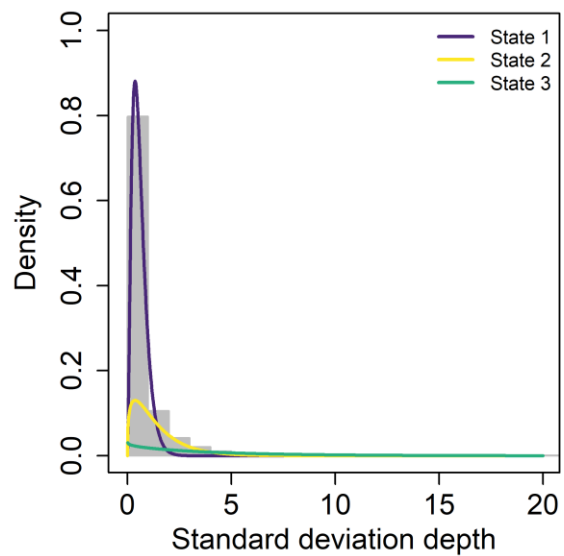
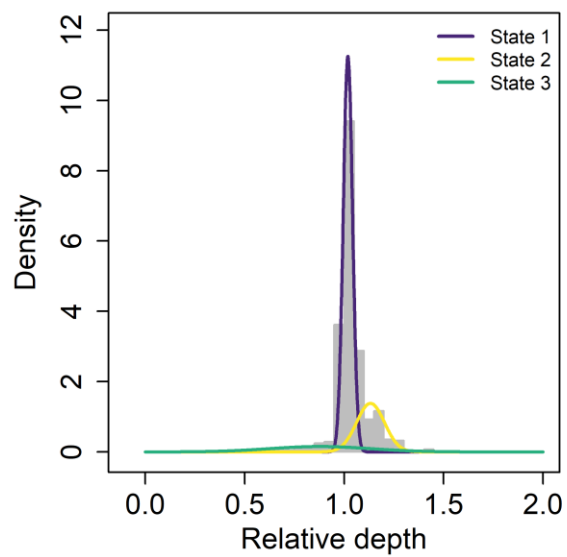
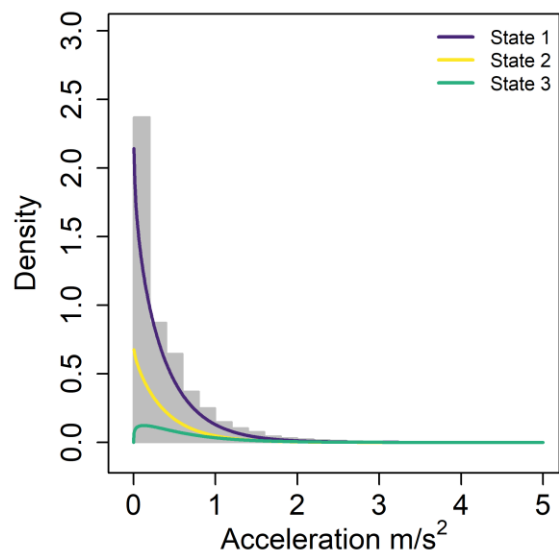
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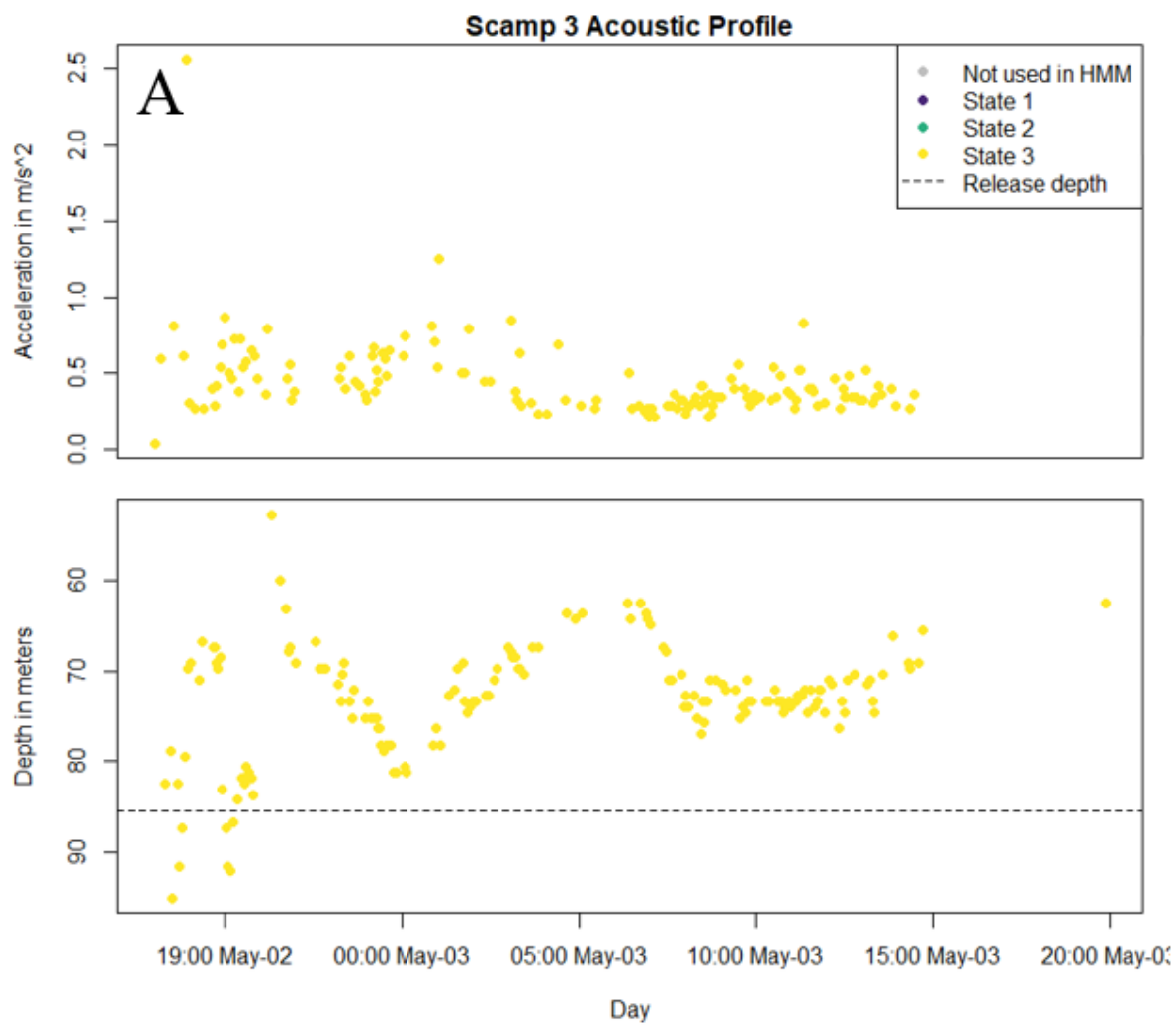


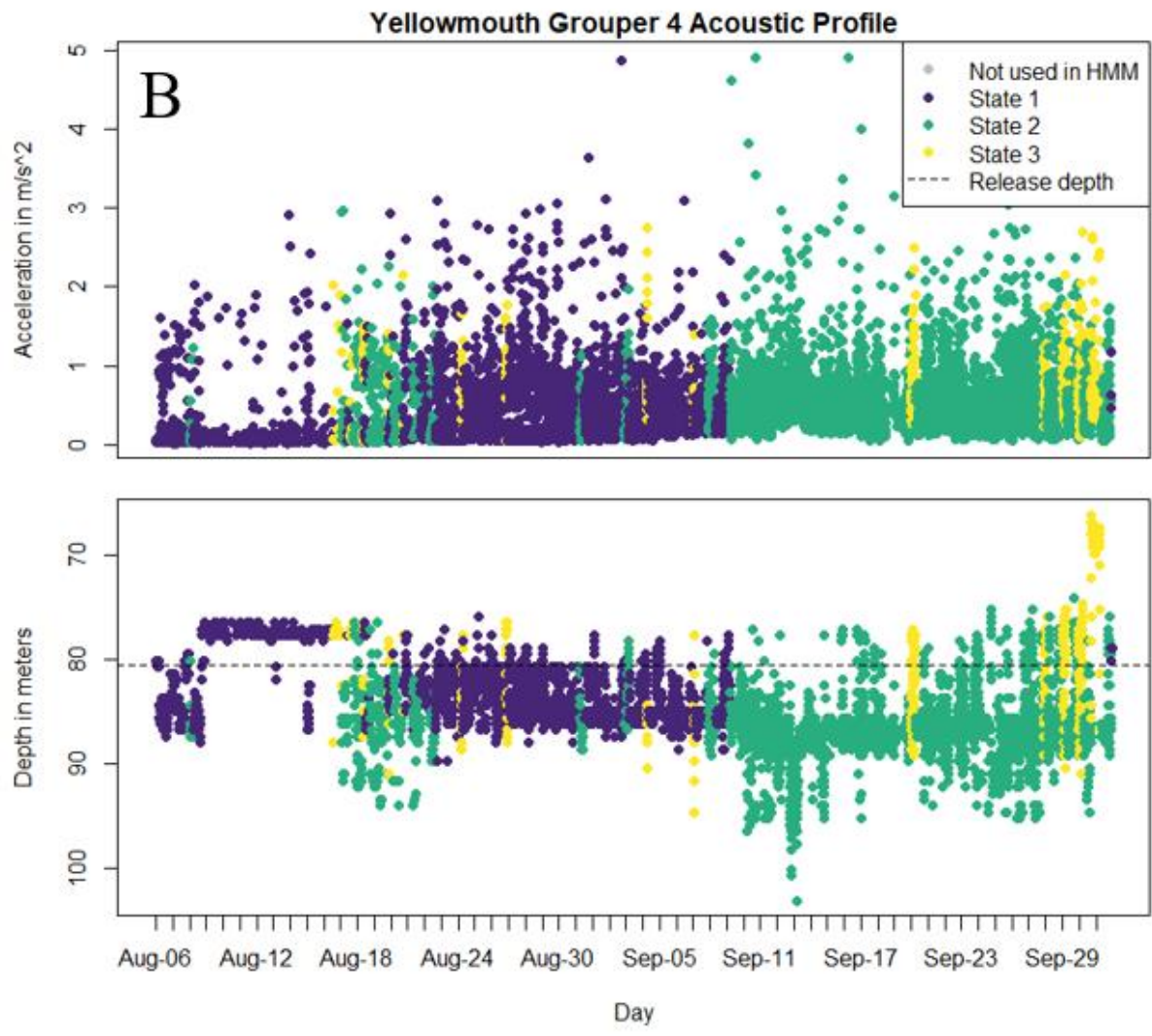
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716 Figure 1. Map showing the region of the Snowy Wreck Marine Protected Area (MPA) off the
717 coast of North Carolina, USA. Grouper releases occurred at the shelf break along the
718 northwestern edge of the MPA and at the Snowy Wreck near the eastern edge of the panel.

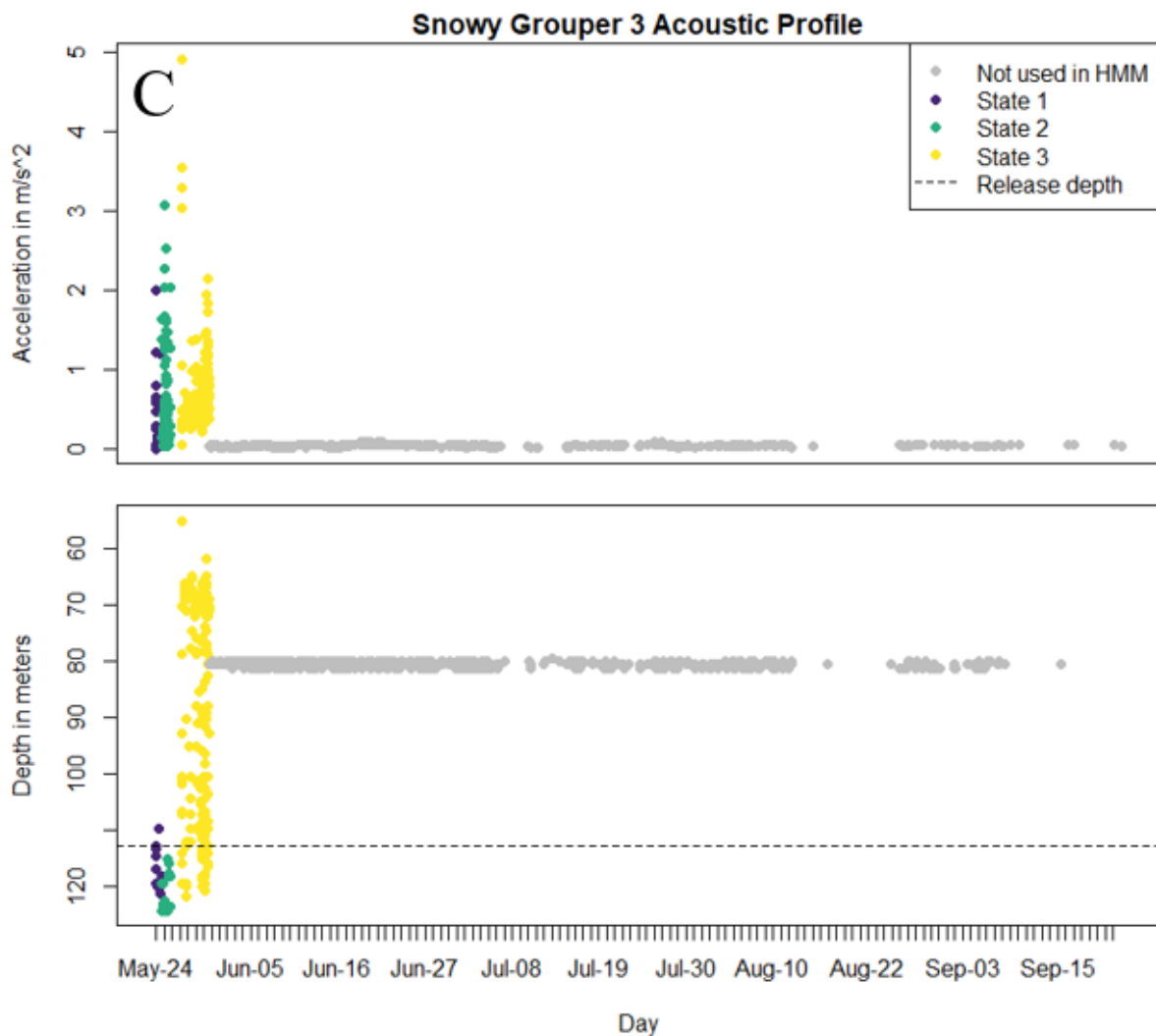


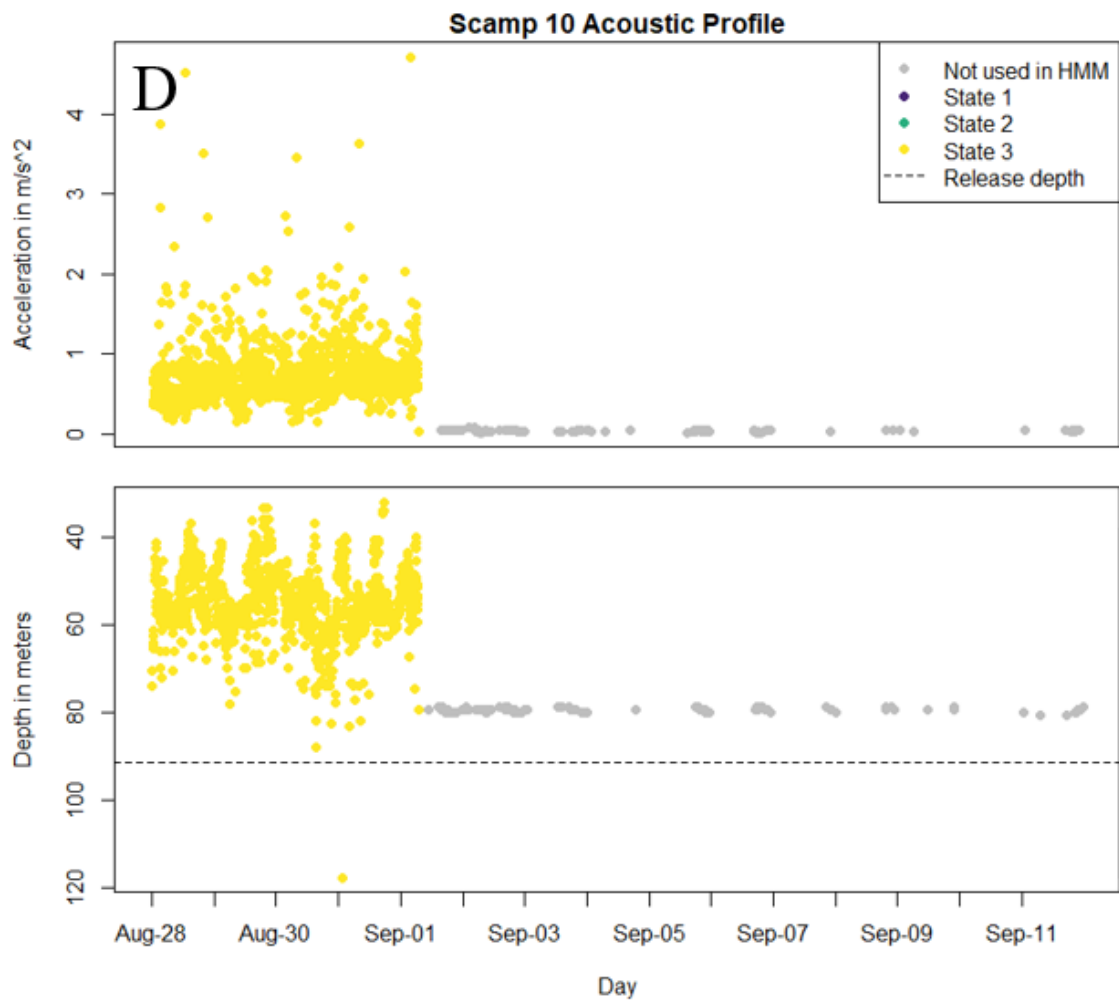
720 Figure 2. Distributions (lines) and histograms (gray bars) of acceleration (m/s^2), relative depth,
721 and depth standard deviation data streams for hidden Markov model (HMM) developed for
722 telemetered six species of deepwater groupers off North Carolina, USA, in 2018. States 1 and 2
723 tended to represent live groupers while state 3 tended to define behavior or predators or
724 scavengers. Histograms were generated from combined observations from all 10 bootstrapped
725 HMM replicates and distributions are drawn from mean maximum likelihood estimates of the 10
726 replicates. Relative depth values are the depth of a given detection divided by the seafloor depth
727 where each fish was released, such that a value of 1.0 represents the animal being detected at the
728 exact depth of release. Standard deviation of depth is the standard deviation of all depth
729 observations within each 30-min time bin.

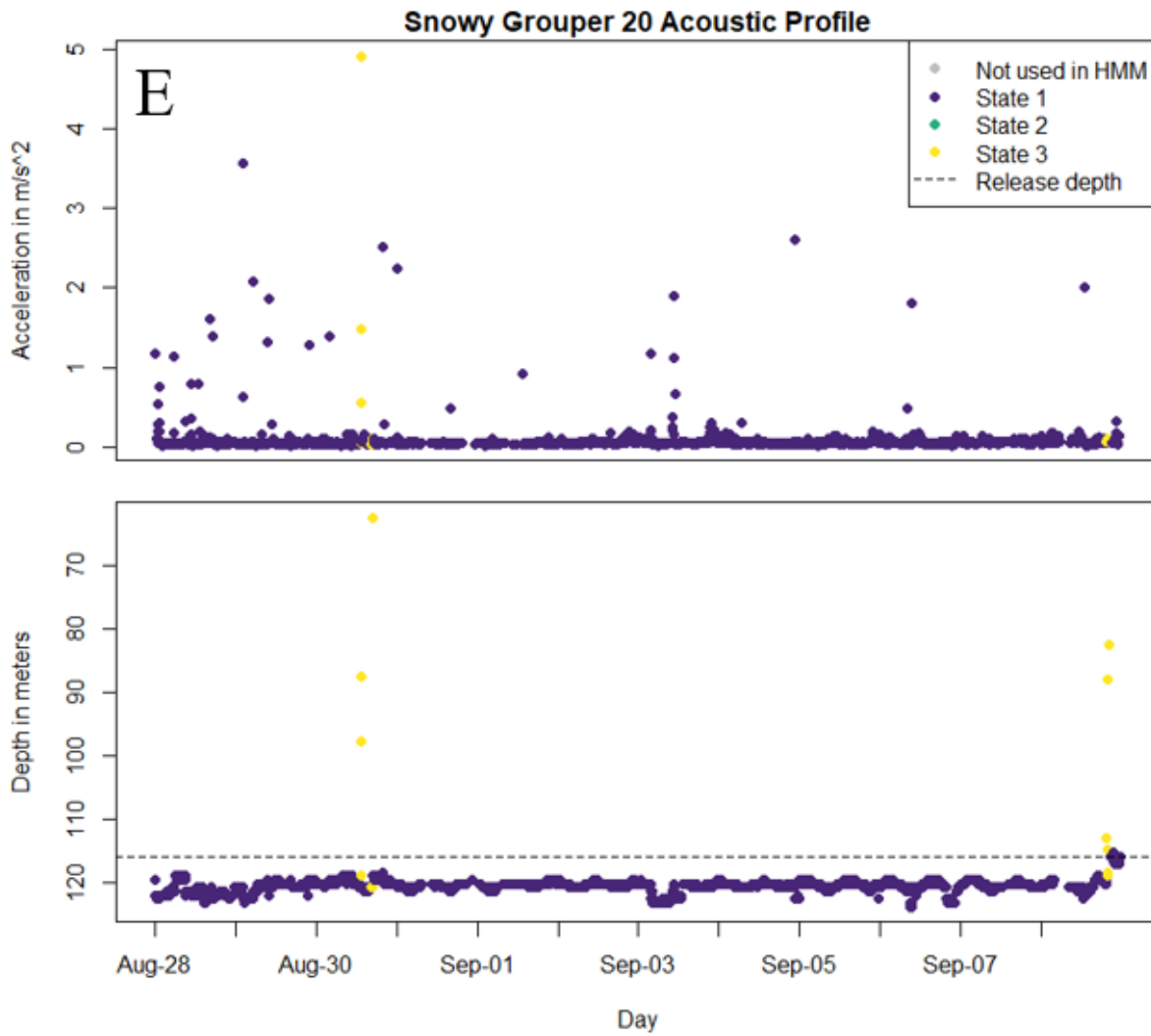




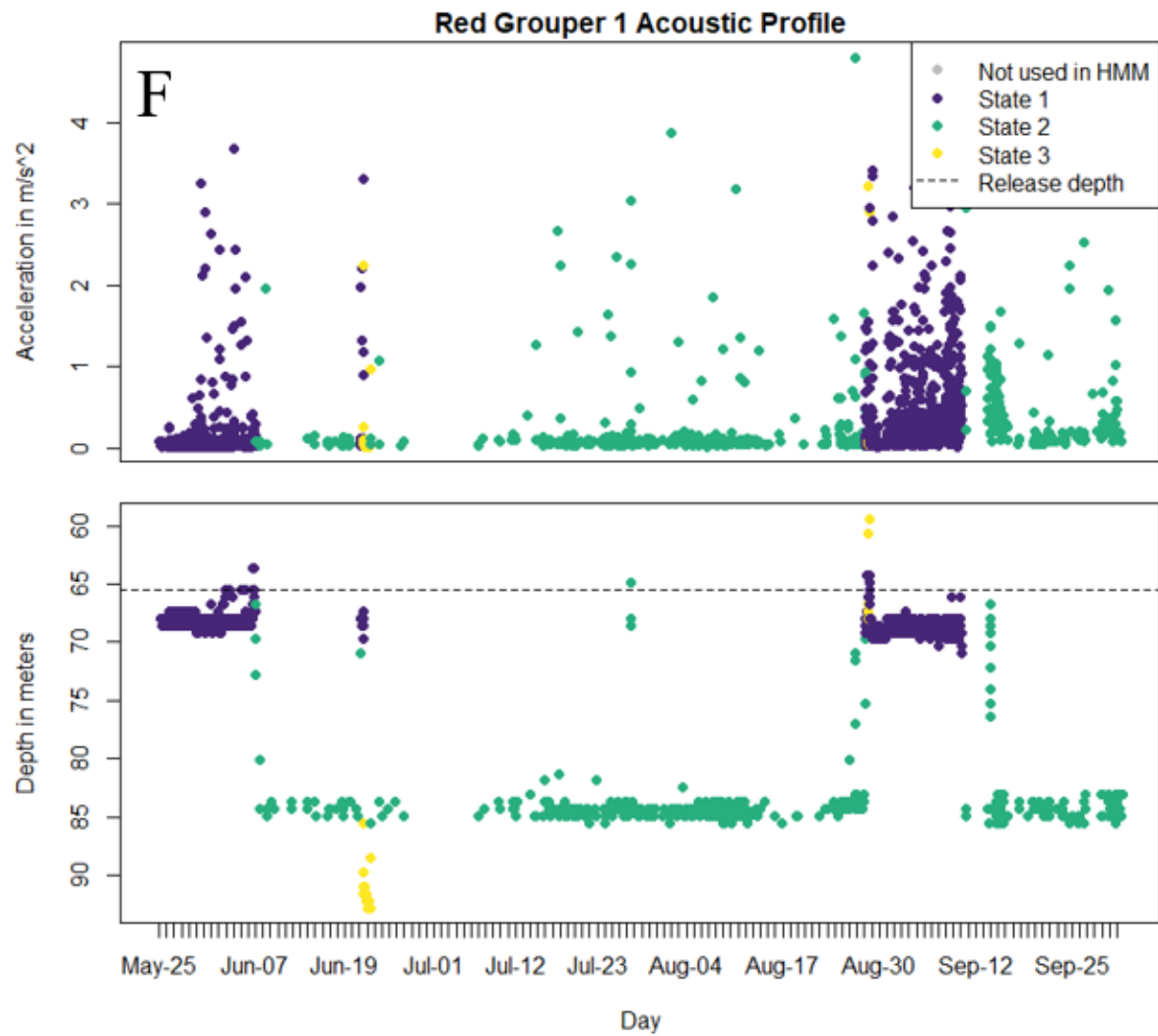
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736 Figure 3. Example acoustic profiles for five telemetry tags, with upper panels indicating
737 acceleration (m/s^2) and lower panels indicating depth (m). Detections are indicated by dots,
738 which are colorized by the state as determined by hidden Markov model. Variations in x-axis
739 scale reflect the duration of detection for each individual. A) Scamp 3 was descended dead and
740 all detections represent movements of the predator by which it was consumed. B) Yellowmouth
741 Grouper 4 appeared alive for the duration of the study. C) Snowy Grouper 3 appeared to be
742 consumed and the tag expelled several days later. D) Scamp 10 was corrected from a mortality to
743 a survival because data suggest its transmitter was loose. E) Snowy Grouper 20 was classified as
744 a mortality on day zero because its profile suggests scavengers interacting with a grouper
745 carcass. F) Red Grouper 1 is an example of a live fish that utilized a range of depths during the
746 study period.

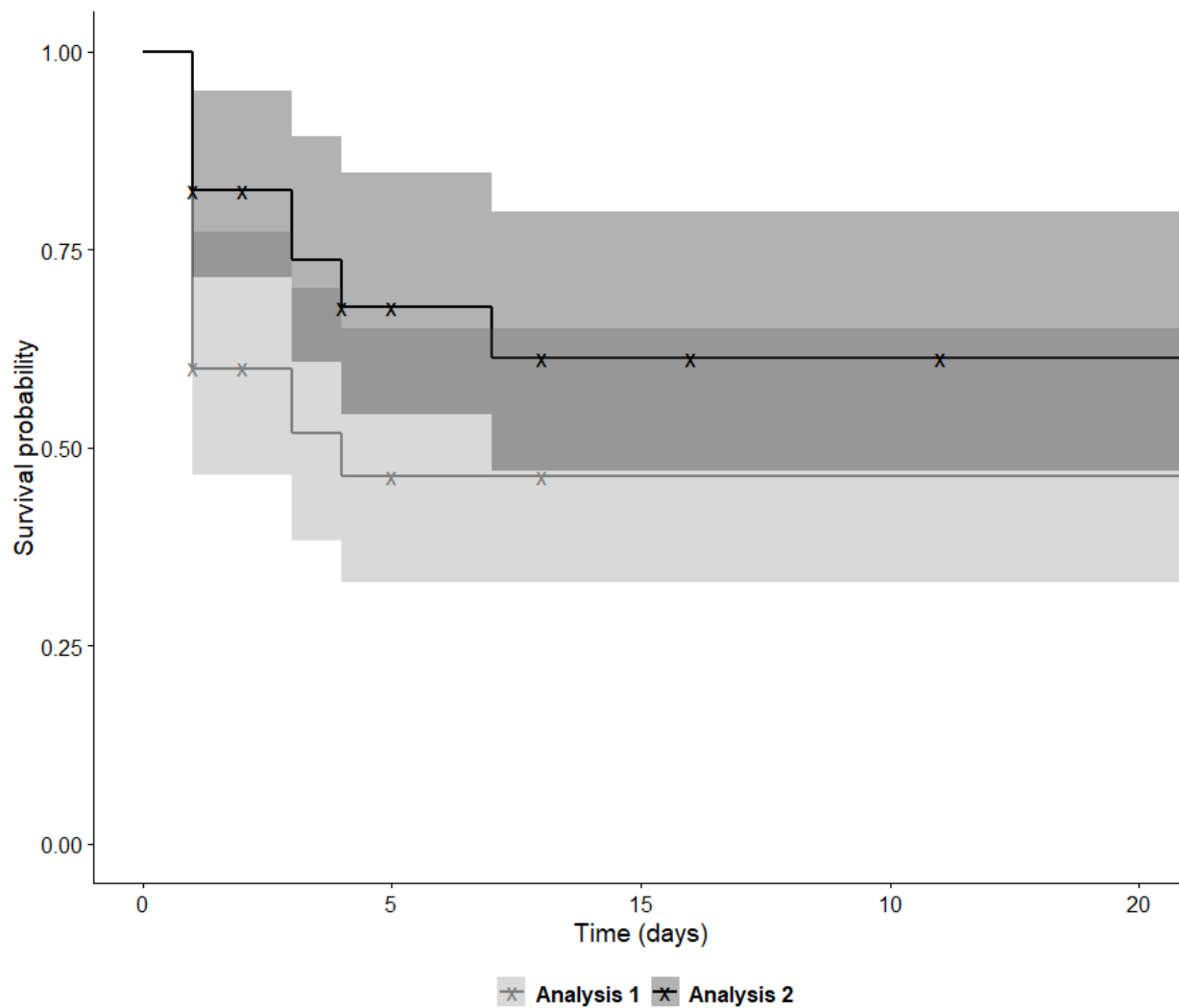
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753 Figure 4. Plot of the Kaplan-Meier survivorship curves for 40 deepwater groupers released via
 754 descender device at the continental shelf break off North Carolina, USA, in 2018. Analysis 1
 755 uses fates that were assigned more strictly with respect to hidden Markov model results. Analysis
 756 2 incorporates more subjectivity. X symbols represent censorships of live groupers that either
 757 were assumed to have lost their tag or emigrated from the array. We show only the first 20 d, as
 758 zero mortalities, emigrations, or tag losses occurred after that point and prior to the end of the
 759 study in either analysis. Shaded regions represent 95% confidence intervals around the mean
 760 estimate (line). Time zero is the day of tagging and release.

761 Supplementary material

762 Table S1. Percentage of time bins identified as being represented by different states between
 763 each pairing of 10 bootstrapped hidden Markov models. The two models that agreed the least
 764 (HMM 3 and HMM 4) differed by 1.04% (indicated in bold).

765

	HMM 1	HMM 2	HMM 3	HMM 4	HMM 5	HMM 6	HMM 7	HMM 8	HMM 9	HMM 10
HMM 1	0.0000	0.0077	0.0080	0.0082	0.0064	0.0086	0.0061	0.0080	0.0067	0.0087
HMM 2	-	0.0000	0.0090	0.0056	0.0076	0.0065	0.0064	0.0075	0.0077	0.0096
HMM 3	-	-	0.0000	0.0104	0.0075	0.0073	0.0076	0.0088	0.0083	0.0083
HMM 4	-	-	-	0.0000	0.0071	0.0075	0.0053	0.0070	0.0081	0.0095
HMM 5	-	-	-	-	0.0000	0.0064	0.0053	0.0082	0.0064	0.0077
HMM 6	-	-	-	-	-	0.0000	0.0081	0.0088	0.0081	0.0096
HMM 7	-	-	-	-	-	-	0.0000	0.0052	0.0073	0.0080
HMM 8	-	-	-	-	-	-	-	0.0000	0.0079	0.0069
HMM 9	-	-	-	-	-	-	-	-	0.0000	0.0082
HMM 10	-	-	-	-	-	-	-	-	-	0.0000

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