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ARTICLE

Assigning Fates in Telemetry Studies Using Hidden Markov Models: an Application to Deepwater Groupers Released with Descender Devices

Brendan J. Runde*
Center for Marine Sciences and Technology, Department of Applied Ecology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

Théo Michelot
School of Mathematics and Statistics, Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, St. Andrews KY16 9LZ, UK

Nathan M. Bacheler and Kyle W. Shertzer
National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, North Carolina 28516, USA

Jeffrey A. Buckel
Center for Marine Sciences and Technology, Department of Applied Ecology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

Abstract

Fate assignment is crucial to the results of survival studies, particularly those that utilize acoustic tagging. Most current methodologies are at least partially subjective; thus, having a means of objectively assigning fates would improve the precision, accuracy, and utility of such studies. We released 57 acoustically tagged fish belonging to six deepwater grouper species off North Carolina, USA, via surface release and recompressed release with descender devices. We applied a three-state hidden Markov model (HMM) in a novel way: to distinguish movement patterns between fish that were alive and fish that were dead (and might have been eaten by predators). We assigned fates using two approaches that differed in their reliance on HMMs. When HMMs were the predominant source of fate assignment, we estimated survival of 40 deepwater groupers released with descender devices at the continental shelf break (66–120-m depth) to be 0.46 (95% CI = 0.33–0.65). When a combination of HMMs and prior information was utilized, we estimated survival of the same 40 groupers to be 0.61 (95% CI = 0.47–0.80). Both estimates represented a substantial improvement over the survival of surface-released groupers (*n* = 9; survival ~0.0). Furthermore, HMMs estimated zero survival for an additional five descended groupers at a wreck site in 240-m depth, although one analysis using prior information suggested that survival was possible in that depth. These estimates were aided by the objectivity of HMMs, and we recommend that future survival studies involving acoustic tagging employ similar methodologies. The improved survival of groupers after descending is an important finding for management, as this taxon contains several species of impaired stock status or fishery status.

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*Corresponding author: bjrunde@ncsu.edu
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The use and utility of electronic tags in ecology have grown in recent years as such devices have become smaller, cheaper, and more advanced (Kays et al. 2015; Crossin et al. 2017). The incorporation of miniaturized sensors into tags enables scientists to collect a greater variety of information about tagged animals and offers flexibility in study design and objectives (Wilson et al. 2015). For example, sensors for metrics such as temperature (Gorsky et al. 2012), pH (Halfyard et al. 2017), light (Seitz et al. 2019), depth (Bohaboy et al. 2020), and acceleration (Curtis et al. 2015) can provide much insight into biology, movement, and survival (Runde et al. 2018). However, the pace of these technological advances has often outstripped the development of methods for the analysis of the data they produce. Novel techniques for processing the vast amounts and diverse types of data created by modern telemetry studies are required to maximize the benefits of electronic tagging.

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

The incorporation of sensors into transmitters has allowed for more realistic interpretation of fish tagging data, yet some studies using sensor transmitters still rely primarily on subjective inferences to assign fates (Yergey et al. 2012; Baktoft et al. 2013; Curtis et al. 2015; Runde and Buckel 2018). This methodology can be accurate when fates are obvious; for example, when a transmitter relays constant depth and zero acceleration, the animal is likely either dead or has shed the tag. However, there are scenarios in which fates remain ambiguous. For instance, a tagged animal may reside on the boundary of the detectable area and therefore may provide only a few intermittent pieces of information, making inference difficult. Furthermore, for animals and systems where postrelease predation or scavenging may be common, distinguishing between the behaviors (e.g., depth, velocity, and acceleration) of a live study animal and those of a predator that has ingested the tag may be difficult (Jepsen et al. 1998; Gibson et al. 2015). Resolving uncertainty in fate assignment in survival studies is critical for generating accurate and useful results.

More advanced techniques for assigning fates include using a subset of "known-fate" individuals to clarify classification of the remaining subjects. One way to achieve this is to sacrifice some fish prior to tagging and release (i.e., negative control; Muhametsafina et al. 2014). The behavior of these transmitters attached to known-dead fish can then be scrutinized, and any similar patterns among fish released alive imply discard mortalities (Yergey et al. 2012; Capizzano et al. 2016; Zemeckis et al. 2020). A more opportunistic approach to identifying fate involves resighting or recapturing a live, tagged animal after a period at large, thereby confirming that all data between release and recapture were generated by that individual and allowing for comparisons as above (i.e., a positive control; Capizzano et al. 2019). Even with these approaches, comparing the detection information of individuals with known and unknown fates is typically at best a semi-quantitative procedure (Benoît et al. 2012).

One method for introducing objectivity into fate assignment is with hidden Markov models (HMMs). Hidden Markov models are statistical models comprising two processes: an unobserved state process, which represents the underlying dynamics of the observed system, and an observation process. In telemetry studies, the state process has been used as a proxy for the behavior of an animal (e.g., foraging and resting), and it can be inferred from observed movement patterns (Langrock et al. 2012). To date, the utility of HMMs in ecology has been primarily to expand biological knowledge via descriptive studies, although authors have also used HMMs for other purposes (e.g., McClintock et al. 2020). In marine fisheries, HMMs have been applied in studies of spawning behaviors (Holan et al. 2009), behavior in sharks (Papastamatiou et al. 2018), migratory phases of Southern Bluefin Tuna *Thunnus maccoyii* (Patterson et al. 2009) and Cownose Ray *Rhinoptera bonasus* (Ogburn et al. 2018), movement types in Gray Triggerfish *Balistes capriscus* (Bacheler et al. 2019), and behavioral states in Yellowfin Tuna *T. albacares* and Bigeye Tuna *T. obesus* (Vermard et al. 2010). However, instead of identifying and classifying behaviors of the tagged animals, it is possible that HMMs could identify changes in movement patterns of the tags, which may in fact relate to different animals (e.g., a predator that has ingested a tag). To our knowledge, HMMs have never been applied to survival studies in which changes in movement patterns may imply predation or scavenging.

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

The use of descender devices to recompress barotraumatized fishes has been explored for several species and taxa, including Walleye *Sander vitreus* (Eberts et al. 2018), Red Snapper *Lutjanus campechanus* (Drumhiller et al. 2014; Bohaboy et al. 2020), Pacific rockfishes *Sebastes* spp. (Theberge and Parker 2005), Black Sea Bass *Centropristis striata* (Rudershausen et al. 2020), and deepwater groupers (Runde and Buckel 2018). Studies testing this technique have generally found increases in survival of fish released with a descender device as compared to fish released without a descender (reviewed by Eberts and Somers 2017). More challenging has been generating precise estimates of survival that are usable for stock assessments and management strategy evaluations and that can be confidently cited as evidence by managers wishing to encourage or require the use of descender devices in the fishery.

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

METHODS

Study area, fish capture, and tagging.— We fished for groupers inside the Snowy Wreck Marine Protected Area (33°30′N, 76°50′W) off North Carolina, USA, in May–August 2018 (Figure 1). Fishing was conducted at the continental shelf break in 66–120 m and at a shipwreck (called the Snowy Wreck) in 240 m. Our methods largely followed those of Runde and Buckel (2018). Briefly, we fished using high–low bottom rigs with size-8/0 hooks baited with cut Atlantic Menhaden *Brevoortia tyrannus* and shortfin squid *Illex* sp. Upon capture, grouper TLs were measured to the nearest 5 mm and groupers larger than 350 mm TL were affixed with Vemco ultrasonic coded transmitters (V13AP-H; 69 kHz; random delay = 60–180 s; estimated tag life = 158 d) via two nylon dart tags to the dorsal musculature (see Figure 1 in Runde and Buckel 2018). Vemco V13AP transmitters contain two sensors: depth (via a converted pressure value) and acceleration, produced as an average value over a 45-s interval. A more detailed description of accelerometer/pressure sensors was given by Curtis et al. (2015). Our external attachment procedure shortened the surface interval, isolated the effects of recompression (instead of venting via an incision), and increased the detectability of the transmitters (Johnson et al. 2015; Dance et al. 2016). Transmitters were sterilized in diluted 2% chlorhexidine gluconate prior to attachment, and deck time for each fish was no more than 2 min.

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

Submersible receiver mooring deployment and retrieval.— We deployed an array of 22 Vemco VR2AR acoustic release receivers in the Snowy Wreck Marine Protected Area on May 1, 2018 (Figure 1). Each mooring was anchored with an approximately 43-kg, steel sacrificial ballast attached to a receiver lug with 6.4-mm-diameter

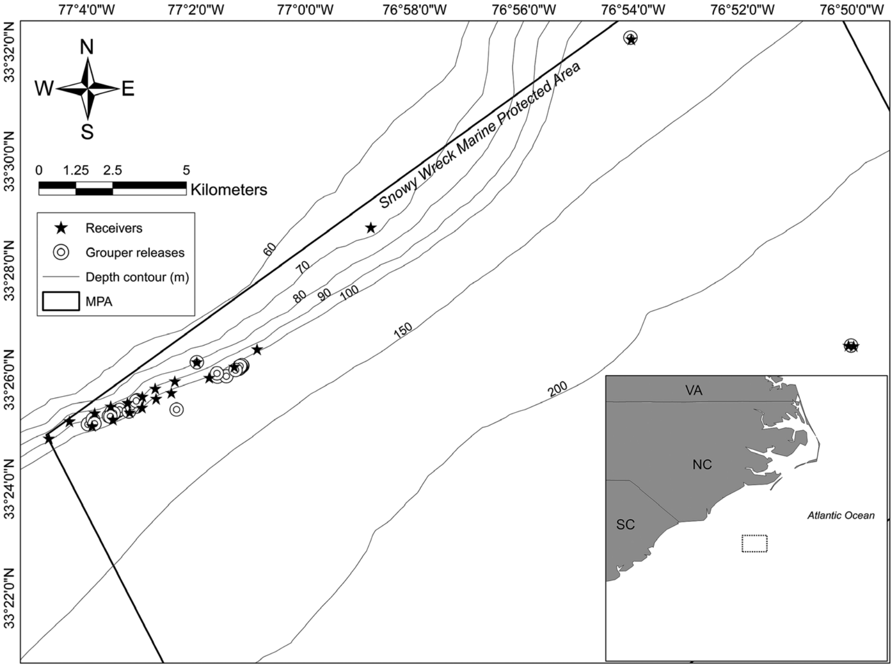

FIGURE 1. Map showing the region of the Snowy Wreck Marine Protected Area (MPA) off the coast of North Carolina, USA. Grouper releases occurred at the shelf break along the northwestern edge of the MPA and at the Snowy Wreck near the eastern edge of the panel.

steel cable. Above each receiver was a subsurface trawl float (280-mm diameter; 8.8-kg buoyancy) attached with ultra-high molecular weight polyethylene fiber (Dyneema) rope and stainless-steel shackles. Twenty receivers were deployed at the continental shelf break in likely areas of grouper catch, based on catches by Runde and Buckel (2018) and Rudershausen et al. (2010) in the same region. Two VR2AR receivers were deployed at the Snowy Wreck, approximately 100 m apart. We recovered all receivers on October 2, 2018.

Data processing and analysis.— Detection data were downloaded to Vemco VUE software and subjected to the False Detection Analyzer to remove likely erroneous detections. We compiled a detection history of depth and acceleration for each transmitter in R (R Core Team 2019) for use in the HMM and assignments of fate. Examples of full time series information for individual fish are located in Figure 2 and Figure S.1 (available in the Supplement in the online version of this article).

An HMM assumes that each observed variable (in our case, acceleration or depth) can arise from several different probability distributions, called “emission distributions” (Zucchini et al. 2016). An unobserved state process S_t determines which distribution is active at each time t, and its evolution is modeled with transition probabilities. In preliminary analyses, we fitted models with two, three, and four states and we found that the three-state model was a good compromise to obtain biologically interpretable states. Two of these states appeared to capture the behavioral heterogeneity in the movement of live groupers (we do not attempt to assign a more specific description in this paper), and the third state served as a proxy for the movement of groupers' predators. Our three-state HMM resulted in nine transition probabilities:

$$\begin{pmatrix} \gamma_{11} & \gamma_{12} & \gamma_{13} \\ \gamma_{21} & \gamma_{22} & \gamma_{23} \\ \gamma_{31} & \gamma_{32} & \gamma_{33} \end{pmatrix},$$

where $\gamma_{ij} = \Pr(S_{t+1} = j | S_t = i)$ is the probability of a transition from state i to state j over one time interval. Hidden Markov models require data streams to be on a regularized time grid (e.g., one observation every 30 min). Given that our V13AP tags transmitted on a random delay, our detection data were not temporally regularized. Therefore, we binned detections into 30-min time bins for the purpose of regularization. We chose an interval that was (1) long enough so that most time bins contained one observation or more and (2) short enough to capture the movement states of interest (see Discussion). Based on qualitative examination of the binned detection data, we generated three informative data streams that were used as inputs in our HMM. The first data stream was mean acceleration (m/s^2) for the 30-min bin, denoted by Z_{1t},

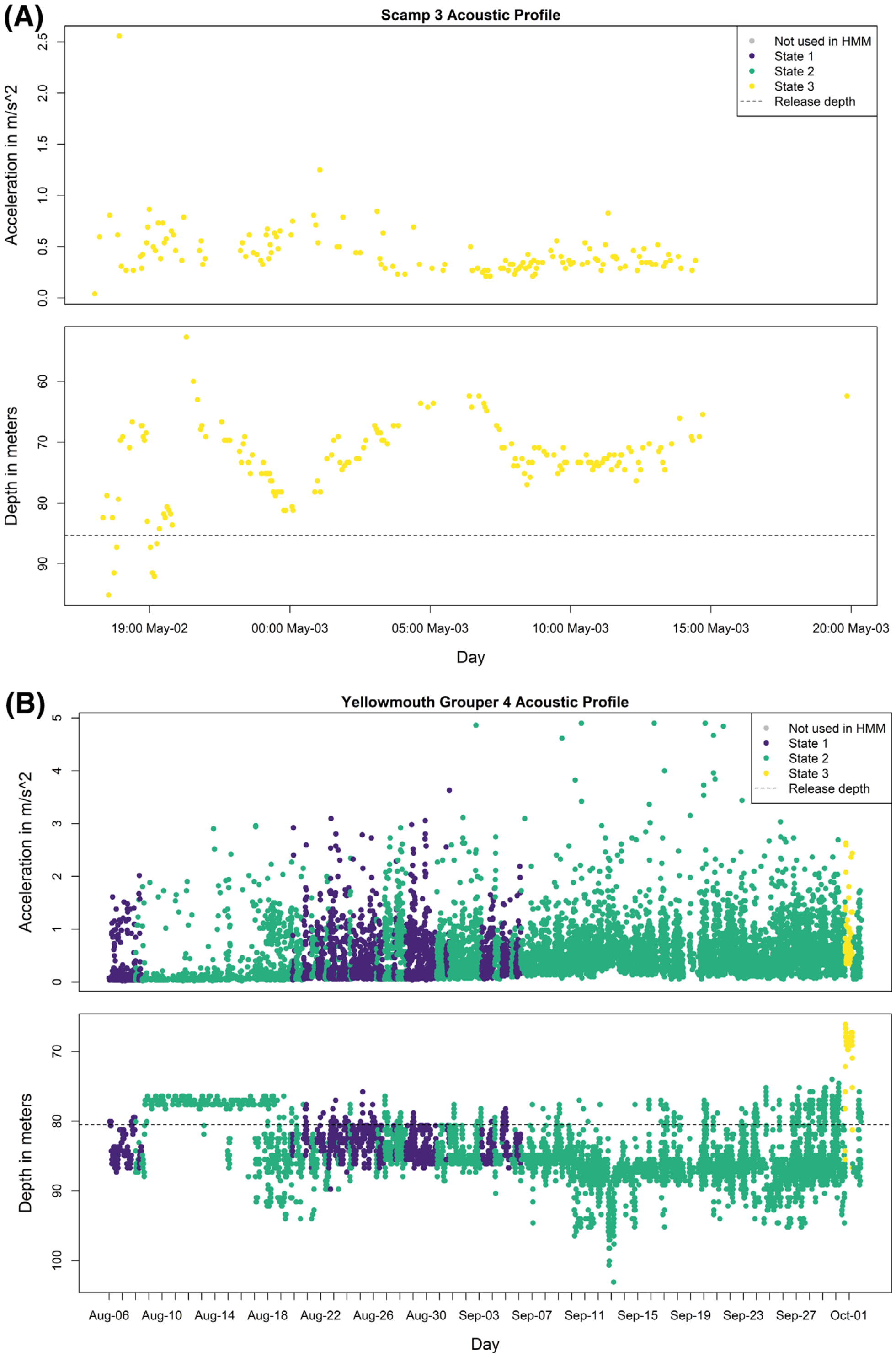

FIGURE 2. Example acoustic profiles for five telemetry tags, with upper panels indicating acceleration (m/s^2) and lower panels indicating depth (m). Detections are indicated by dots, which are colorized according to state as determined by the hidden Markov model (HMM). Variations in the *x*-axis scale reflect the duration of detection for each individual. **(A)** Scamp 3 was descended dead, and all detections represent movements of the predator by which it was consumed. **(B)** Yellowmouth Grouper 4 appeared alive for the duration of the study. **(C)** Snowy Grouper 3 appeared to be consumed, and the tag was expelled several days later. **(D)** Scamp 10 was corrected from a mortality to a survival because data suggested that its transmitter was loose. **(E)** Snowy Grouper 20 was classified as a mortality on day 0 in analysis 1 because its profile suggested scavengers interacting with the grouper's carcass. In analysis 2, Snowy Grouper 20 was classified as having emigrated on day 11 after a period of relative inactivity. **(F)** Red Grouper 1 is an example of a live fish that utilized a range of depths during the study period.

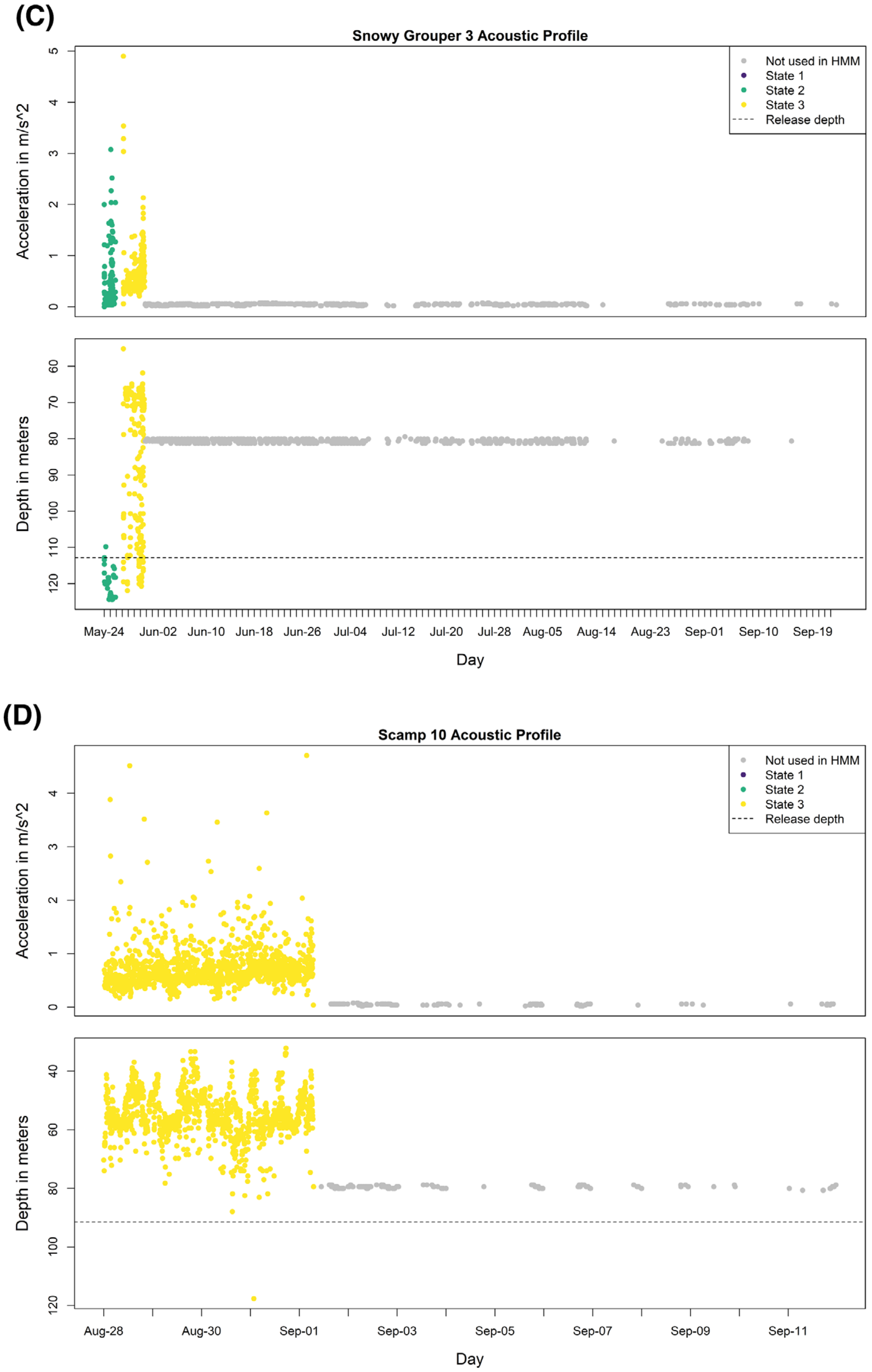

FIGURE 2. Continued.

and was parameterized as a gamma distribution. Acceleration is a proxy for the level of activity of the animal, and we expect the activity levels of groupers and their predators to be different. Therefore, we would expect the distribution of accelerations from a live grouper to differ from that of a dead grouper. The second data stream was mean depth as a proportion of release depth (m), denoted by Z_{2t}, where a value of 1.0 represents the fish being

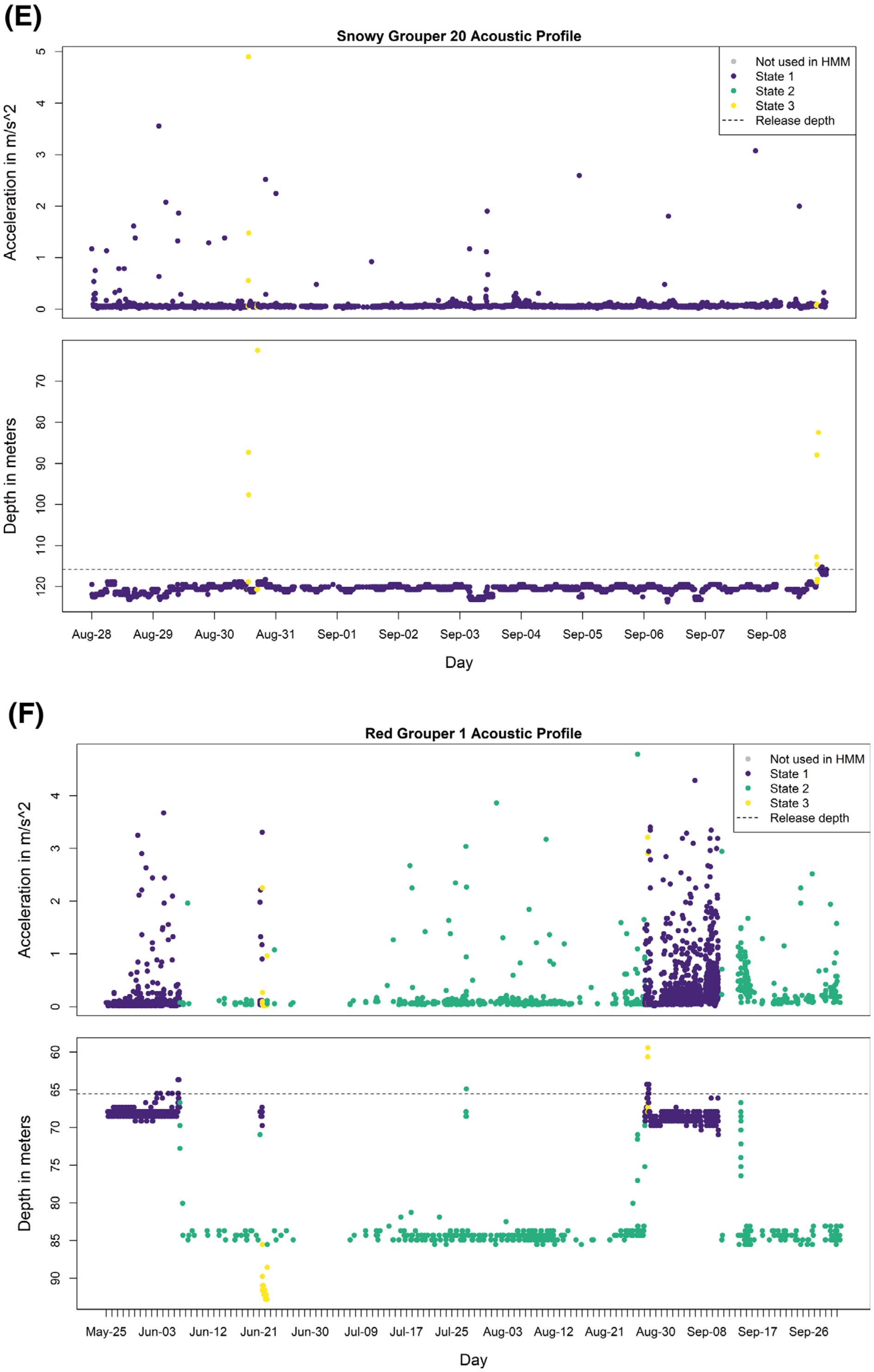

FIGURE 2. Continued.

detected at exactly the same depth as was recorded during capture. This transformation was necessary because the study animals were released across a range of depths; therefore, it serves as a proxy for distance from the seafloor. For example, two surviving groupers released in areas where the seafloor was 60 and 120 m, respectively, would have drastically different absolute depth values and erroneously have different states in the HMM when their survival is the same; normalizing by release depth allows for a comparison of relative depth movements. Given the different biology of demersal fishes and their likely predators (for large groupers, elasmobranchs, or large transient teleosts), we expected different depth utilizations. This data stream was also parameterized as a gamma distribution. Finally, the third data stream was the SD of all depth values in each time bin, denoted by Z_{3t}. The SD in depth is a proxy for the rate of movement of the fish in the vertical dimension. We did not expect normal grouper behavior to involve rapid up or down movements, although this type of behavior is likely in elasmobranchs. This final data stream was again parameterized as a gamma distribution. Using both a value for relative depth and a value for the SD of depth for each time bin offers a more adequate characterization of the vertical movements of each fish in each bin than would one of these variables alone. Both are needed to determine whether a fish was shallow or deep (relatively) as well as changing depth regularly or at a stationary depth. The observation model can therefore be written

$$Z_{1t} \sim \text{gamma}\left(\theta_{1j}, \theta_{2j}\right),$$
$$Z_{2t} \sim \text{gamma}\left(\theta_{3j}, \theta_{4j}\right),$$

and

$$Z_{3t} \sim \text{gamma}\left(\theta_{5j}, \theta_{6j}\right)$$

in state $S_t = \; j = \in \{1,\ 2,\ 3\}$, where the θ_{ij} are state-dependent observation parameters. Hidden Markov models and subsequent analyses were performed in the R package “momentuHMM” (McClintock and Michelot 2018).

Fate assignment and survival estimation.— Results from the HMM were examined, and data for each individual grouper were used to assign fates. We compared the state sequences of the sacrificed descended individuals (i.e., negative control) to the state sequences of the individuals that were descended alive. If groupers that were descended alive displayed the same state as the negative controls, they were designated as deceased and subject to predation or scavenging. The state sequences for groupers displaying other states were scrutinized and used to make informed decisions about their assigned fates. Emigration of a live grouper was determined to have occurred if detections ceased without switching to a state representing predation. Tag loss was determined to have occurred if depth became near constant and acceleration became zero simultaneously and remained in those conditions until the terminal detection. Groupers that emigrated from the receiver array or lost their tags were censored from the analysis on the day of emigration or tag loss.

We assigned fates using two general scenarios. In analysis 1, we assigned fates based more strictly on HMM results; we imposed expert knowledge only when the fates suggested by HMMs were illogical (e.g., a grouper displaying brief periods of a predator-like state surrounded by months of grouper-like states was not considered to have been temporarily dead). In analysis 2, we allowed for behaviors and phenomena that have been anecdotally observed in other studies but could not be confirmed here (e.g., vertical movement of live study animals before emigration from the receiver array; N. Wegner, National Marine Fisheries Service, unpublished data). Furthermore, in analysis 2 we took into account ancillary data that could not be included in the HMM, such as any information about a transmitter’s movement through space on different receivers. For example, if a transmitter was detected twice in a very short period of time on receivers that were several kilometers apart, we considered this to be evidence of possible predation. The fate assignments from analysis 1 are generally more conservative (i.e., they err on the side of lower survival).

Fates for groupers that were released alive were used to inform Kaplan–Meier nonparametric models to estimate postrelease survival. We conducted separate Kaplan–Meier procedures for groupers released via descending, released into the surface enclosure, and released at the Snowy Wreck; estimates were generated twice for each of these groups (once each for analyses 1 and 2). The Kaplan–Meier procedures were conducted in the R package “survminer” (Kassambara and Kosinski 2018).

RESULTS

At the continental shelf break (depth = 66–120 m), we released 40 groupers via descending, of which four were double tagged. In addition, we released nine groupers into the bottomless surface enclosure. Of these nine surface releases, two groupers swam down and seven floated. The seven groupers that floated were recovered, and their tags were reused; those reused tags are included in totals below. We sacrificed and descended three tagged groupers for a total of 45 individuals released at the shelf break (40 fish that were descended alive, 2 surface-released fish that swam down, and 3 dead fish). At the Snowy Wreck (depth = 240 m), we tagged and released five Snowy Groupers, all of which were descended to the seafloor. Overall, we tagged at least one individual of six grouper species: Gag *M. microlepis* ($n = 1$), Red Grouper ($n = 1$), Scamp ($n = 11$), Snowy Grouper ($n = 31 + 5$ at the Snowy Wreck), Speckled Hind ($n = 4$), and Yellowmouth Grouper *M. interstitialis* ($n = 4$). The TLs, depths of capture, species identification, and treatments for each individual are shown in Table 1.

We obtained over 580,000 detections from telemetered groupers. These detections were from each of the 50 groupers in the study that submerged. Across all individuals, we created 60,666 30-min time bins. Parameter

TABLE 1. Information for individual groupers off North Carolina. "Site" identifies whether the fish were tagged at the shelf break or at the Snowy Wreck. Tag names consist of the species and a unique identifying number; tag names including "tag 1" or "tag 2" identify individuals that were double tagged. Fish were either released alive with a descender device (Descend), descended after sacrifice (Descend dead), or released into a bottomless surface enclosure where they either swam down (Surface cage, swam) or floated (Surface cage, floated). Fates were determined mainly by a hidden Markov model (HMM). "Analysis 1 fate" indicates the assigned fate when the HMM results were interpreted more strictly (i.e., lower subjectivity). "Analysis 2 fate" indicates the assigned fate when we altered fates subjectively and is only presented in this table when it differs from the fate in analysis 1. "Survival, full" indicates that the fish was still alive at the end of the study period. Days alive were used as inputs for two Kaplan–Meier survivorship procedures.

Site	Tag name	TL (mm)	Capture depth (m)	Release type	Analysis 1 fate	Days alive	Analysis 2 fate	Days alive
Shelf	Gag 1	1,085	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		

TABLE 1. Continued.

Site	Tag name	TL (mm)	Capture depth (m)	Release type	Analysis 1 fate	Days alive	Analysis 2 fate	Days alive
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	1,020	244	Descend	Mortality	0	Emigration	2

estimates for the emission distributions for each data stream were generated (Table 2). Estimates of the emission distribution parameters showed clear distinctions between the three states (Table 2; Figure 3). State 1 was characterized by the lowest mean acceleration (Acc) values, the closest relative depth (RelDepth) to 1.0, and the lowest mean SD of depth (DepthSD). State 2 had Acc values similar to those of state 1 but had a mean RelDepth of 1.10 (the highest of the three states) and a moderate DepthSD mean. State 3 showed the highest mean Acc, the only RelDepth mean less than 1.0 (indicating depths well above tagging depth), and the largest DepthSD value. State transition probabilities were

$$\begin{pmatrix} 0.994 & 0.004 & 0.001 \\ 0.009 & 0.990 & 0.001 \\ 0.007 & 0.004 & 0.989 \end{pmatrix}.$$

TABLE 2. Parameter estimates for our three-state hidden Markov models. The three data streams parameterized were mean acceleration (Acc), mean depth relative to the depth of release (RelDepth), and the SD of all depth values in each time bin (DepthSD). For each data stream, "SD" refers to the standard deviation parameter; "Zmass" refers to the zero-mass parameter, which was estimated for Acc and DepthSD.

Parameter	State 1	State 2	State 3
Acc mean	0.386	0.420	0.574
Acc SD	0.405	0.428	0.498
Acc Zmass	4.30×10^{-5}	9.99×10^{-9}	4.56×10^{-4}
RelDepth mean	1.019	1.105	0.815
RelDepth SD	0.022	0.087	0.339
DepthSD mean	0.543	1.462	5.173
DepthSD SD	0.310	1.240	5.605
DepthSD Zmass	0.472	0.249	0.104

Of the three sacrificed and descended dead groupers, only one provided sufficient data to be included in the HMM (Scamp 3). The other two individuals (Snowy Grouper 11 and Snowy Grouper 5) were detected for approximately 7 and 25 min, respectively, and each had very few detections. The terminal detection for each of these individuals suggested that the transmitter was within a few meters of the surface. Scamp 3 was detected for approximately 26 h. The HMM classified this individual as exhibiting state 3

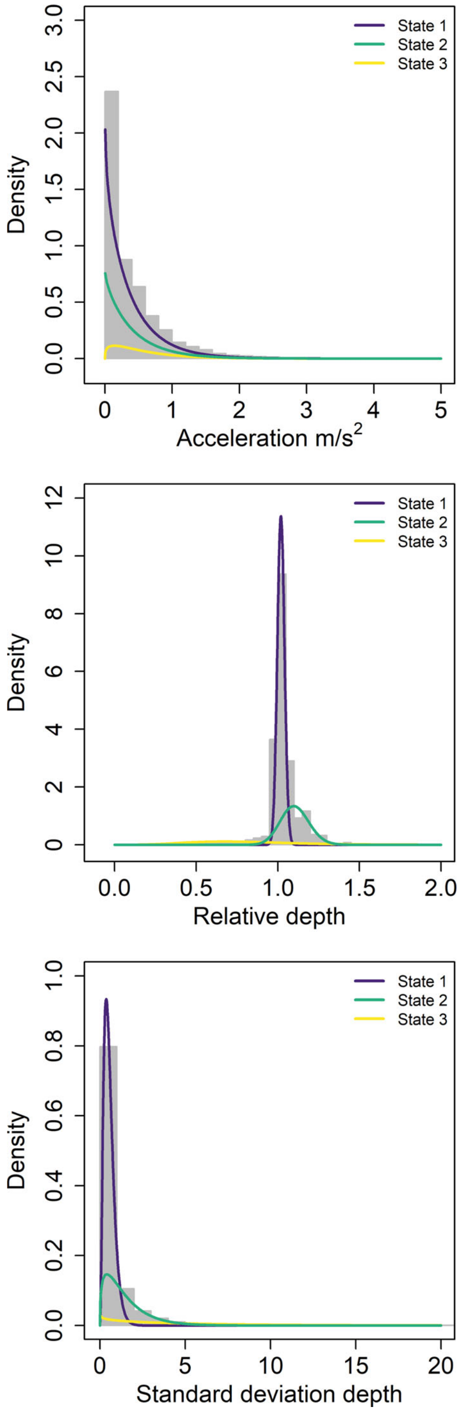

FIGURE 3. Distributions (lines) and histograms (gray bars) of mean acceleration (m/s^2), mean relative depth, and depth SD data streams for the hidden Markov model developed for six telemetered species of deepwater groupers off North Carolina in 2018. States 1 and 2 tended to represent live groupers, while state 3 tended to define the behavior of predators or scavengers. Relative depth values represent the depth of a given detection divided by the seafloor depth where each fish was released, such that a value of 1.0 represents the animal being detected at the exact depth of release. The SD of depth is the SD of all depth observations within each 30-min time bin.

throughout the entire time period for which it was detected (Figure 2A). We reviewed the state sequences for the remaining individuals, and those dominated by states 1 and 2 were categorized as survivals (e.g., Figure 2B).

For the 40 groupers that were descended alive at the shelf break, analysis 1 determined that 14 had survived the duration of the study, 3 lost their tags while still alive, 1 emigrated, and 22 experienced discard mortality. For the same fish, fates determined using analysis 2 differed for 11 individuals; in general, this procedure changed fates from mortalities to emigration or tag loss based on previous authors' observations of posttagging recovery behavior in demersal fishes (e.g., Collins 2014; see Discussion). Furthermore, the HMM was not able to distinguish between a dead grouper on the seafloor (with occasional movement caused by scavengers) and a live grouper. These two interpretations of the same general "behavior" are reflected in the differences between the two analyses. Analysis 2 determined that 14 groupers survived the duration of the study, 4 lost their tags while still alive, 7 emigrated, and 15 experienced discard mortality. In analysis 1, each of the four double-tagged groupers experienced mortality within the first day after release. In analysis 2, one grouper died, two emigrated in the first 2 d, and one appeared to lose one of its tags within hours of release and then to emigrate on day 4. We conclude that tag loss is possible given this attachment type, although the sample sizes and durations of observation for double-tagged fish preclude a statistical estimate of that rate. Fates for each individual assigned in both analyses are shown in Table 1.

All mortalities occurred within the first 7 d after tagging; therefore, our survival estimate at that time represents our estimate for the study overall. For groupers that were descended alive at the shelf break, the Kaplan–Meier survivorship procedure using analysis 1 fates generated a survival estimate of 0.46 (95% CI = 0.33–0.65; Figure 4). Using analysis 2 fates, the survival estimate was 0.61 (95% CI = 0.47–0.80).

Two of the nine surface-released groupers swam down; under analysis 1, both of these fish appeared to experience mortality on the day they were tagged (day 0), resulting in survival of 0.00. Under analysis 2, these two fish could have emigrated on days 1 and 5, respectively. Using these fates, a Kaplan–Meier survivorship procedure estimated survival of 0.22 (95% CI = 0.07–0.75) for surface-released groupers. Of the five groupers released at the Snowy Wreck in 240 m, none survived beyond day 0 based on analysis 1 fates, resulting in a survival estimate of 0.00. Analysis 2 interpretations suggested that all five may have emigrated within 9 d based on their disappearance from the receiver array (but see Discussion). Thus, no conclusions can be robustly drawn for groupers released at the Snowy Wreck given the survival estimates (0.00–1.00) from analyses 1 and 2.

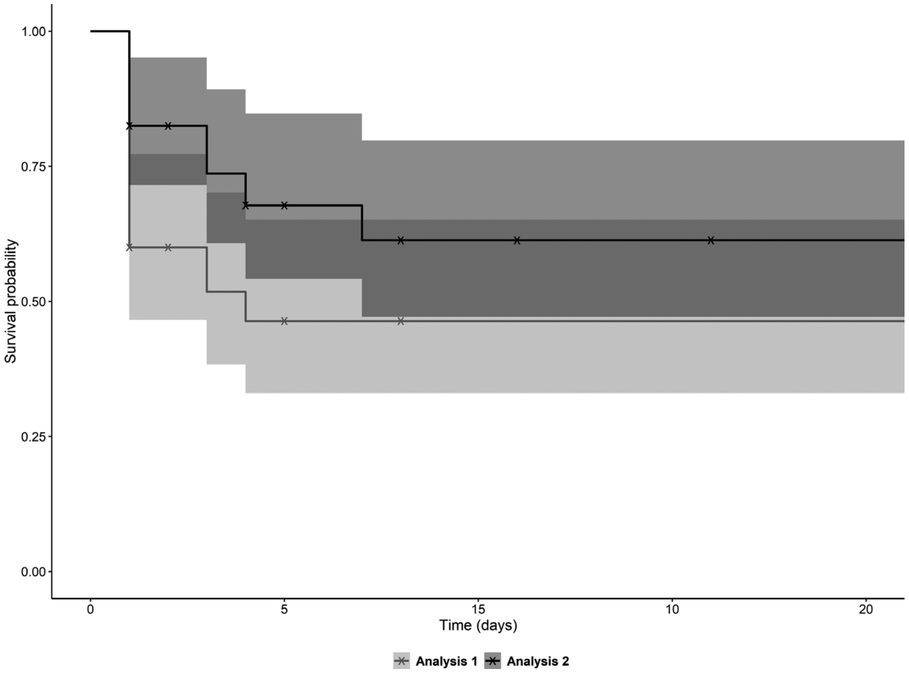

FIGURE 4. Plot of the Kaplan–Meier survivorship curves for 40 deepwater groupers released by use of a descender device at the continental shelf break off North Carolina in 2018. Analysis 1 used fates that were assigned more strictly with respect to hidden Markov model results. Analysis 2 incorporated more subjectivity. The "×"symbols represent censorships of live groupers that either were assumed to have lost their tags or emigrated from the array. We show only the first 20 d, as zero mortalities, emigrations, or tag losses occurred after that point and prior to the end of the study in either analysis. Shaded regions represent 95% CIs around the mean estimate (line). Time zero is the day of tagging and release.

DISCUSSION

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

In our study, there were a few groupers for which the HMM identified mortalities that subjective inference would likely have missed. These animals represent one of the major utilities of HMMs. For Scamp 6 (Figure S.1; figure panels are ordered by species and individual), Snowy Grouper 3 (Figure 2C), and Speckled Hind 4 (Figure S.1), initial examination of the acoustic profiles suggested tag loss; using subjective inference alone, we would likely have considered these fish to be alive. However, the HMM identified clear changes in the states of these three individuals (from states 1 and 2 to state 3) several days prior to flat-lined depth and acceleration. We therefore concluded that these individuals were alive and then eaten by a predator. These three groupers exhibited state 3 for 4, 5, and 1 d prior to apparent expulsion of the transmitter by the predator. These durations fall within the usual gastric evacuation time of most large elasmobranchs (Wetherbee and Cortés 2004). Furthermore, during the period after apparent predation for each of these three fish, detections were recorded on several (four or more) receivers, suggesting that the transmitter was consumed by an extremely mobile animal.

Contrary to the above individuals, where we assigned mortalities based on HMM results, there were several fish for which we used ancillary information to overrule HMM results. For example, Scamp 10 was assigned state 3 for the entirety of its detection history (Figure 2D). Scamp 10 was relatively small (490 mm TL) but was tagged with a transmitter that had been prepared for a larger fish. The wires connecting the tag to the dart tips were therefore longer than necessary. The first author noted that the tag appeared loose upon release. This situation appears to be reflected in the acceleration profile for this fish: there are no observations of zero acceleration until the tag was evidently lost on day 6. Because the depth detections for Scamp 10 resembled depths for live groupers, we categorized this individual as alive until tag loss in analyses 1 and 2. All other groupers were tagged with transmitters having wire lengths appropriate for their body size.

In addition to Scamp 10, there were several individuals that transitioned to state 3 or disappeared after several days of states 1 and 2. Examination of these profiles revealed that some showed almost no changes in depth and few nonzero acceleration detections until their transition to state 3 or disappearance (e.g., Snowy Grouper 20; Figure 2E). This type of detection profile may represent a dead grouper on the seafloor being scavenged by smaller fish and invertebrates, with intermittent occurrences of being picked up by a (perhaps larger) scavenger (signaled by a switch to state 3) on August 30 (in the case of Snowy Grouper 20) and again on September 8. These brief, rapid vertical movements from a near-constant depth of 120 m to depths as shallow as 60 m constitute a behavior we never observed in groupers that we categorized as alive. Live groupers sometimes exhibited zero acceleration and no changes in depth, but these periods were punctuated with regular movements detected by both sensors. This regular movement was not observed in the several fish we believe may have been dead and subject to seafloor scavenging. There were nine individuals for which this potential on-seafloor scavenging was observed. The majority of these groupers were categorized by the HMM as being in states 1 and 2 for much of their observation periods but were in state 3 at the end of their detection histories. Contrary to scavenging events during which the predator ingested the transmitter and rose into the water column, on-seafloor scavenging appears to the HMM to be similar to live grouper behavior (i.e., states 1 and 2). For analysis 1, these individuals were considered mortalities on day 0. Under analysis 2, we considered the possibility that these fish (1) were alive and recovering from the stress associated with capture, tagging, and release; and (2) emigrated after or during this recovery period by first migrating vertically. Collins (2014) and Runde and Buckel (2018) described a posttagging recovery period during which fish were less active. As none of the descended dead groupers exhibited this type of profile, these individuals were therefore considered alive until the point of emigration in analysis 2. Recovery followed by emigration behavior has been observed in Pacific rockfishes, some of which were later recaptured, thereby confirming their status as live fish (Wegner, personal communication). Unfortunately, we were unable to recapture any telemetered fish in this study; therefore, the interpretation of these animals' behavior remains uncertain. We recommend that future telemetry studies tag a larger sample size of sacrificed individuals.

We identified some groupers that had clearly lost their transmitters (either while still alive or postmortem) prior to the end of the study, as they displayed zero acceleration and constant depth after a certain point. The data file for each of these fish was truncated to remove the detections representing a lost tag, as such tag loss data would not correspond to any of the movement states of the HMM. We considered the possibility of a four-state HMM, where the additional state would represent these data. However, this was not feasible given our use of RelDepth as a data stream for the HMM. Indeed, the distribution of RelDepth values was not consistent across lost tags because transmitters were lost at RelDepth ranging from approximately 0.56 to 1.95. This wide range is a result of the high-relief habitat in which we performed our study; future studies conducted in lower-relief areas may have success in modeling tag loss as its own HMM state.

Choosing the number of states in HMMs is challenging and often not straightforward (Pohle et al. 2017). In this study, we investigated HMMs with two and four states in addition to the eventual three-state model. The two-state model did not appropriately distinguish the groupers that were descended dead from the fish that were released alive. In the four-state model, the additional state emerged as something of a midpoint between states 2 and 3, which obfuscated the results rather than clarifying them. We determined that the three-state model was necessary to capture the complexity of the situation to which we were attempting to apply HMMs but not so state-heavy that the results were difficult or impossible to glean. We lacked the data that are perhaps most typical as inputs for HMMs applied to animal movement: turning angle and step length. Instead, we used alternative data streams to characterize movement—for example, depth relative to depth at release (RelDepth) was chosen as a proxy for distance from the seafloor. We note that some groupers may have consistently occupied seafloor habitat but appeared to sometimes be much deeper or much shallower than their release depth (e.g., Red Grouper 1; Figure 2F). This possibly occurred because the shelf break consists of many areas of extreme depth changes over a short linear distance; Red Grouper 1 appeared to prefer seafloor habitat in two primary depths that were about 20 m different yet still within the receiver array. Because of the variation in this and other individuals, the live-grouper detection information for all three data streams contained a wide range of values, which resulted from not only a variety of "normal" grouper behaviors but also the imperfection of the data streams available in this study.

Typical HMMs for animal movement result in biological descriptions of the behavioral states identified, such as "foraging" or "transiting" (e.g., Bacheler et al. 2019). For our purposes, such descriptions were a dubious exercise given the data streams we had available. States 1 and 2 seemed to define animals with relatively low acceleration, that occupied habitat close to the seafloor, and that exhibited low to moderate changes in depth. State 3 was typified by animals that had higher acceleration, utilized a much wider range of depths, and changed depth rapidly. These qualitative descriptions of the states are consistent with our assertion that states 1 and 2 represent live groupers and state 3 serves as a reasonable proxy for groupers eaten by predators—although without the recapture of tagged groupers or of predators containing grouper tags, confirmation of these assertions is impossible. For cases in which the fates of some fish are known, this information can also be included in the HMM to clarify the classification of the other tracks ("semi-supervised learning"; Leos-Barajas et al. 2017). Future work including a greater number and variety of known-fate individuals could attempt this approach.

The mathematical formulation of discrete-time models (like the HMMs used here) is tied to a particular time interval of observation, necessitating the regularization of the data. We considered applying a continuous-time model to these data given the irregularity of the detections. Indeed, continuous-time models make no assumption about the time resolution of the data and offer a more natural description of the continuous movement of animals. However, the implementation of state-switching continuous-time models is much more difficult and computational than using HMMs (Blackwell et al. 2016; Michelot and Blackwell 2019). In particular, continuous-time methodology has focused on the analysis of longitude–latitude movement data, and it may not be straightforward to adapt it to the acceleration and depth variables used in this study. Furthermore, there are no accessible software packages with which to apply those models to telemetry data sets, and the large size of our data set (~60,000 time bins) would make it time consuming to fit the model. For these reasons, we opted for a more standard discrete-time approach, but we recommend that continuous-time methods be explored in future research.

The duration of time bins for discrete-time models can influence results. In addition to 30-min bins, we investigated the use of 15- and 60-min intervals. Neither of those models resulted in different fate assignments than the 30-min version. We elected to use 30 min because the proportion of bins with no data was much lower than the proportion for the 15-min version. In addition, we wished to use a fine enough temporal resolution that our model would not obscure the biological reality of behavioral changes. Thirty-minute bins seemed a good compromise for this purpose.

Our survival estimates of 0.46 (95% CI = 0.33–0.65) from analysis 1 and 0.61 (95% CI = 0.47–0.80) from analysis 2 fell within the range estimated by Runde and Buckel (2018). Their survival estimate of 0.50 (95% CI = 0.10–0.91) had an extremely broad CI because many emigrations exacerbated an already-low sample size. Our higher sample size and larger array, paired with more precise fate assignments via HMM, produced much narrower CIs in the present study. However, uncertainty in state determination from the HMM was not propagated into our final fate assignment; therefore, variance may be underestimated. When discard survival is used as a stock assessment input, we recommend examining its effect via sensitivity analysis or other means to quantify uncertainty in model output. Other studies examining the effects of descender devices in this depth range are scarce, although some have been conducted in slightly shallower marine environments. Curtis et al. (2015) worked in 50 m and estimated the survival of descended Red Snapper as 0.83 (95% CI = 0.68–0.98). Sumpton et al. (2010) tagged Red Emperor *L. sebae* in depths predominantly greater than 30 m but found little evidence that descender devices promoted survival in this species. We recommend that future descender device studies work in depths and habitats that are most relevant to the fishery.

We elected to analyze survival across species for several reasons. First, given the high cost of acoustic telemetry, our sample sizes by species were limited. Second, many of these species cohabitate, and most groupers in the SEUS are managed as an aggregate unit (SAFMC 2016), so our findings are applicable to the fishery in general. When analyzed separately, the two species for which we had the highest sample sizes at the shelf break—Snowy Grouper and Scamp—had survival estimates of 0.49 (95% CI = 0.32–0.76) and 0.38 (95% CI = 0.15–0.92), respectively, in analysis 1 and estimates of 0.79 (95% CI = 0.62–1.00) and 0.31 (95% CI = 0.10–0.96), respectively, in analysis 2. The majority of these mean estimates were near our overall estimates of 0.46 and 0.62, and all of the CIs overlapped widely, supporting our choice to pool the species-specific estimates.

Current management assumes discard survival of zero for some reef fishes due to extreme barotrauma (SAFMC 2016). In the present study, we made an attempt to gather evidence on this topic by releasing tagged groupers into our bottomless surface enclosure. Since our maximal mean estimate of survival (analysis 2) for nine groupers released at the surface in this study was 0.22, we are inclined to agree in principle with the current assumption of zero survival for the species examined, although a low level of survival is possible, particularly in the shallower portion of these species' ranges. However, we have demonstrated that survival is significantly higher than zero for groupers that are released with a descender device. The South Atlantic Fishery Management Council recently approved Regulatory Amendment 29 to the Snapper–Grouper Fishery Management Plan, which requires the presence of descender devices on-board vessels fishing for reef fish in the SEUS (implemented in June 2020). Given our findings, we recommend that other management agencies take similar measures to promote widespread use of descender devices in this fishery and other fisheries.

Many of our groupers, including all five individuals that were released at the Snowy Wreck, may have succumbed to predation after release. While analysis 2 allows for the possibility of emigration for these individuals, we believe that explanation to be unlikely. Three of the five fish were detected mid-water column during their detection history at depths of 22, 26, and 71 m. Ambient pressure at 240 m is 25 standard atmospheres (atm); the shallower depths where we detected these individuals have ambient pressure as low as

3 atm. The barotrauma that is likely to be sustained by a Snowy Grouper transitioning between these two depths is probably prohibitive of such movement being voluntary. Therefore, the depth of the Snowy Wreck may be beyond the maximum depth at which groupers can survive the barotraumatic effects of capture, even if released with a descender device. However, the possibly absolute mortality we observed at that site may have partially resulted from a high density of predators in the area.

Throughout our study, we detected several acoustically tagged elasmobranchs inside our receiver array; at the shelf break, we detected one Tiger Shark *Galeocerdo cuvier* and five White Sharks *Carcharodon carcharias* over the 5-month period for which our receivers were deployed. At the Snowy Wreck, receivers were in place for 18 months, over which we detected one Tiger Shark and eight White Sharks. Total lengths of these predators ranged from 3.1 to 4.2 m for Tiger Sharks (B. Frazier, South Carolina Department of Natural Resources, personal communication) and from 3.3 to 4.3 m for White Sharks (G. Skomal, Massachusetts Division of Marine Fisheries, and M. Winton, Atlantic White Shark Conservancy, personal communication). Sharks were detected during every month of the study in both locations, supporting the idea that these species (or others) may have been responsible for the predation of our tagged groupers. It is likely that descended groupers displayed abnormal behavior immediately after release, perhaps during recovery from barotrauma (Collins 2014; Runde and Buckel 2018). This behavior is possibly linked to an increased risk of predation, as elasmobranch predators have been shown to preferentially feed on prey that are struggling or displaying irregular behavior (Kritzler and Wood 1961; Dijkgraaf 1963; Bleckmann and Hofmann 1999). It is conceivable that some of the groupers that died after release might have survived if they had been able to avoid predation during their recovery period. Some of the groupers may have been deceased prior to ingestion by a predator, although some may have been attacked while alive. This is supported by detection data, which showed depth and acceleration movements typical of a live grouper prior to switching to state 3 (e.g., Scamp 6). Furthermore, we assume that tagging itself did not increase the risk of predation; if any tagged groupers died as a result of tagging, our estimate of survival after recompression would be lower than survival realized in the fishery.

External tagging with acoustic transmitters has increased in popularity due to increased detection ranges (Dance et al. 2016) and, for survival studies, the desire to separate the effects of barotrauma from the possible relief caused by tagging (Johnson et al. 2015). Attachment methods include the dart tag style used here and by Runde and Buckel (2018), a method by which the transmitter is glued to a T-bar tag (Yergey et al. 2012), procedures involving “cinch-up” tags (Curtis et al. 2015), methods using suture material passed through the fish (Bacheler et al. 2019), and attachment via an intramuscular stainless-steel bolt (Bohaboy et al. 2020). To our knowledge, no attempts have been made to quantify tag loss in situ for any of these methods, although some authors used tank holding studies to this end (e.g., Bacheler et al. 2019). Therefore, the best tag attachment procedure for such studies has not been resolved. Our attempt to quantify tag loss by double tagging of groupers was unsuccessful, as none of the four double-tagged fish survived beyond day 0. This is perhaps because the injury caused by the introduction of four darts was substantially greater than that caused by two darts. Alternatively, the slightly longer surface interval required to tag a fish twice may have resulted in increased mortality risk. It is also possible that these four animals would have experienced mortality if they were tagged only once and that we simply required a larger sample size to reach a conclusion. As is done for conventional tagging, we recommend that studies using external attachment of acoustic transmitters make attempts to quantify tag loss in situ, particularly when fate assignment is difficult due to the study animal or habitat. Double tagging with acoustic transmitters, although costly, is likely a sufficient means to that end.

Conclusions

Survival studies often rely on subjectivity when assigning fates of tagged animals. Recent advancements in transmitter technology have resulted in a greater variety of data available to researchers, but methods for quantitative analysis thereof are lacking. We successfully employed HMMs as a means of increasing the objectivity of fate assignment in our study. Although our methods and results are imperfect and still included some subjectivity and additional information (e.g., detection on different receivers in a short time period), future researchers should consider HMMs when attempting to determine fates of animals tagged with acoustic transmitters.

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

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ORCID

Brendan J. Runde https://orcid.org/0000-0002-2125-4486
Nathan M. Bacheler https://orcid.org/0000-0003-1955-6044

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.