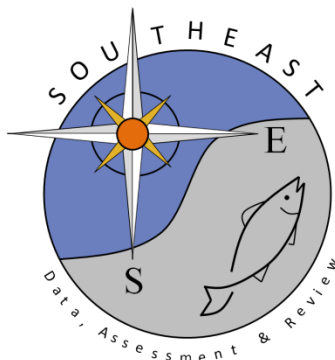


# Descender Devices are Promising Tools for Increasing Survival in Deepwater Groupers

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ARTICLE

## Descender Devices are Promising Tools for Increasing Survival in Deepwater Groupers

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### Abstract

Discard survival of deepwater (>60 m) groupers (Serranidae; Epinephelinae) is often assumed to be 0% given the severity of barotrauma and the inability of fish to submerge. We used acoustic telemetry to study the activity of 19 deepwater grouper after a recompressed release with a descender device, achieved by rapidly returning fish to a depth where expanded gases can contract. The species tested were the Scamp *Mycteroperca phenax* ( $n = 8$ ), Snowy Grouper *Hyporthodus niveatus* ( $n = 7$ ), and Speckled Hind *Epinephelus drummondhayi* ( $n = 4$ ). Individuals of all three species showed post-recompression variation in water depth and acceleration indicative of survival, whereas information from other tags indicated discard mortality. Nonparametric Kaplan–Meier survivorship procedures yielded a 14-d survival estimate of 0.50 (95% confidence interval = 0.10–0.91); although low, this estimate is higher than the currently assumed 0% survival. Additionally, our estimate of discard survival is likely biased low because we assumed that no individuals shed their tag, which is unlikely for our attachment method. A technique to increase discard survival of deepwater groupers may lead to better-constructed regulations for reef fishes in the southeastern USA and in other areas where these species are caught and released.

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The management of reef fishes has for several decades been recognized as a challenge. Many economically important reef-associated species have life history traits that render them vulnerable to overfishing (Coleman et al. 2000). Exploitation of slow-growing, long-lived piscivorous reef fishes, such as deepwater groupers (Serranidae; Epinephelinae), has led to diminished abundances around the world (Huntsman et al. 1999; Musick et al. 2000; Sumpton et al. 2010). Managers have used a variety of tools, such as size limits, seasonal closures, annual catch limits, and total fishery closures (moratoria), in an attempt to reduce

fishing mortality for such species. However, these regulations generally result in increased levels of discards and are only effective if released fish have a high probability of survival.

Indeed, for many fisheries, discarded fish make up a large and increasing proportion of the total catch (Kelleher 2005; NMFS 2016). Because of this trend, research has focused not only on ways to estimate discard survival but also on methods to increase its magnitude (Davis 2002; Benaka et al. 2016). For example, authors have tested approaches such as modifications to fishing gear

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(e.g., the use of circle hooks; Bacheler and Buckel 2004; Patterson et al. 2012) and release procedures (Wilde 2009; Burns and Froeschke 2012; Curtis et al. 2015). Many of these studies have focused on vulnerable reef fishes (e.g., groupers).

Grouper often sustain pressure-related injuries (barotrauma) upon being hooked and brought to the surface (Huntsman et al. 1999). For many taxa, the severity of barotrauma and associated rates of discard mortality are positively correlated with depth of capture (Gitschlag and Renaud 1994; Wilson and Burns 1996). Thus, species that inhabit deeper water are probably more susceptible to discard mortality than are their shallow-water counterparts (St John and Syers 2005; Rudershausen et al. 2007). One common type of barotrauma in deepwater (>60 m) groupers is swim bladder distention or rupture, which results in abdominal bloating; this bloating may render a fish unable to submerge (Huntsman et al. 1999; Burns et al. 2002). Floating, barotraumatized reef fish may suffer near 100% mortality (Burns and Restrepo 2002; Rudershausen et al. 2014).

There are two common techniques intended to mitigate barotrauma. Puncturing the swim bladder to relieve pressure (venting) has been explored for many reef fish species (e.g., Burns et al. 2002; Drumhiller et al. 2014). However, the conclusion of a review of 17 studies was that the practice of venting may adversely affect survival rather than promote it (Wilde 2009). An alternative to venting is forced recompression, achieved by rapidly returning traumatized fish to a depth where expanded gases can contract. Studies have shown that recompressing deepwater Pacific rockfishes *Sebastes* spp. increases their postrelease survival as compared to surface release (e.g., Theberge and Parker 2005; Pribyl et al. 2012). This technique also appears to increase survival in Red Snapper *Lutjanus campechanus* (Drumhiller et al. 2014). However, to our knowledge, there have been no studies that have tested the efficacy of recompressing deepwater groupers (or any closely related species) to increase survival.

Deepwater grouper are discarded in the southeastern USA for a variety of reasons. Speckled Hind *Epinephelus drummondhayi*, Snowy Grouper *Hyporhamphus niveatus*, and Scamp *Mycteroperca phenax* are groupers whose current regulations represent a range of scenarios by which discards might occur. Because these fish often share habitat, the bycatch and discarding of one species may occur when another species is targeted. Even in fisheries that have a harvest moratorium (e.g., Speckled Hind), this bycatch and associated mortality could hinder population rebuilding. For example, Coggins et al. (2007) showed that population-level discard mortality rates as low as 0.05 would prevent length limit regulations from achieving sustainability in fish such as groupers; this is because the number of discarded undersized fish that ultimately perish is high

enough to result in recruitment overfishing. Reductions in the discard mortality rate for these species could result in more rapid rebuilding of stocks.

Methods for estimating discard mortality in serranids and other fishes have included the use of observable symptoms (e.g., floating, bleeding, and hook trauma) as proxies for mortality (Davis 2007; Rudershausen et al. 2007), but this method does not account for subclinical injuries that may result in delayed mortality (Davis 2002). One method of assessing delayed mortality is through the use of ultrasonic acoustic telemetry (Hightower et al. 2001; Heupel and Simpfendorfer 2002). The incorporation of accelerometers and/or depth sensors into acoustic transmitters allows for monitoring of fish behavior after release; such transmitters have recently been used to evaluate discard mortality rates in Red Snapper (Curtis et al. 2015), Atlantic Cod *Gadus morhua* (Capizzano et al. 2016), and several species of Pacific rockfish (N. Wegner, National Marine Fisheries Service, personal communication). In this study, we evaluated whether forced recompression with a descender device can increase postrelease survival to above 0% in three deepwater grouper species: the Speckled Hind, Snowy Grouper, and Scamp. We used acoustic telemetry to monitor changes in depth and acceleration of fish after tagging as indicators of survival. Our results will inform fishery managers of the potential for increasing postrelease survival among grouper, which have an assumed 0% survival rate when caught and released in this deepwater fishery.

## METHODS

**Fish capture and tagging.**—All grouper were captured at the continental shelf break inside the Snowy Wreck Marine Protected Area (33°30'N, 76°50'W; Figure 1) off North Carolina, USA, on August 17–18, 2015. We fished in depths of 60–120 m using high-low bottom rigs with size-8/0 J-hooks baited with cut Atlantic Menhaden *Brevoortia tyrannus* and shortfin squid *Illex* sp. For each grouper, we recorded TL (mm) and any visible barotrauma signs, including stomach eversion and exophthalmia. Upon capture, grouper larger than 350 mm TL were tagged with Vemco V13AP ultrasonic coded transmitters (V13AP-H; 69 kHz; random delay = 60–180 s; estimated tag life = 158 d) with incorporated acceleration and pressure (depth) sensors. The transmitters calculated depth by using a converted pressure value (maximum = 136 m). Overall acceleration ( $\text{m/s}^2$ ) was calculated by a preprogrammed activity algorithm. For a fixed interval (45 s for our transmitters), the tag produced an average acceleration value ( $\text{m/s}^2$ ) from three component acceleration measurements (each in  $\text{m/s}^2$ ) along X-, Y-, and Z-axes (see Curtis et al. 2015) as

$$\sqrt{X^2 + Y^2 + Z^2}.$$

Surgical implantation of transmitter tags requires anesthesia and a long surface interval, and it may relieve abdominal gas pressure that would otherwise prevent fish from swimming down (i.e., effectively venting the fish; Johnson et al. 2015). Because we wished to isolate the efficacy of recompression (with no venting) and to apply surface intervals similar to those of normal fishing operations, we chose to attach the transmitters externally. In addition, external attachment results in greater detection ranges for this type of transmitter (Dance et al. 2016). Transmitters were attached to a short length of 20-gauge, galvanized-steel wire with polyolefin heat shrink tubing (1.27-cm diameter). A plastic dart tag tip (Floy Tag, Inc., Model FIM-96) was attached to each end of the wire by looping through a double-barrel brass crimp (size 1.0). Crimps were covered with polyolefin heat shrink tubing (0.32-cm diameter) to reduce friction (Figure 1). Prior to tagging, the prepared transmitters and metal applicator tools were soaked in diluted 2% chlorhexidine gluconate antiseptic solution. Fish were tagged by simultaneously inserting the two dart tips through the dorsal pterygiophores so that the long axis of the transmitter was fixed parallel to the lateral line of the fish. Deck time for each fish was no more than 4 min. Grouper were descended by using a SeaQualizer tool set to release the fish at either 46 or 61 m. One transmitter, prepared as above, was affixed to a submersible receiver mooring to serve as a control.

*Submersible receiver mooring deployment and retrieval.*—Vemco VR2W submersible receivers were attached to rigging consisting of a subsurface trawl float, sacrificial ballast, and an acoustic release (SubSeaSonics, LLC, Model AR-50-AA). We deployed six moorings on August 17 and

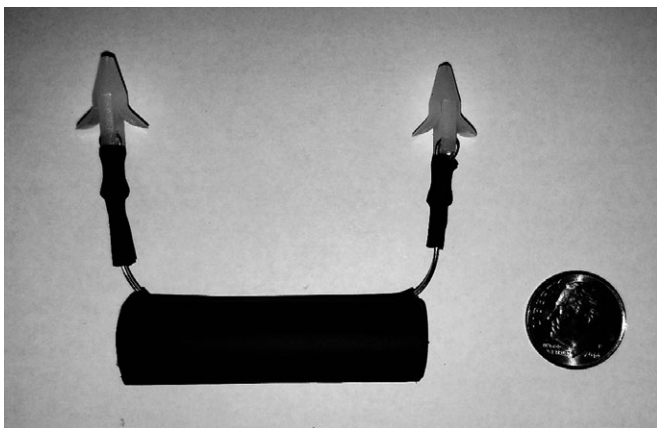


FIGURE 1. A Vemco V13AP transmitter prepared for external attachment.

18, 2015, in locations determined ad hoc based on the spatial arrangement of grouper releases (Figure 2). When grouper were released in a location not within 400 m of a previously deployed receiver, we deployed a mooring at that location. Therefore, all grouper release locations were within 400 m of a submersible receiver mooring. On September 30, 2015, we recovered the moorings by signaling the acoustic releases to separate from the sacrificial ballast.

*Data processing, fate assignment, and analysis.*—Acoustic detection data were downloaded using Vemco VUE software. Overall survival of grouper was estimated with a non-parametric Kaplan–Meier survivorship procedure (Cox and Oakes 1984; Pollock et al. 1989). The Kaplan–Meier procedure allows for the censorship of individuals from the survival analysis. All analyses were performed by using the “survival” package in R version 3.3.0.

Fates were assigned to grouper by qualitatively evaluating their individual acceleration and depth profiles (Curtis et al. 2015). Activity for the first 14 d postrelease was used to determine fates. Possible fate assignments were (1) discard mortality, (2) censorship due to a lack of data, and (3) survival. Fishing mortality was not considered possible because we released fish in an area that was closed to all bottom fishing. Individuals were considered to have emigrated from the study area if they displayed lifelike changes in depth and acceleration until their final detection. In the Kaplan–Meier survivorship procedure, emigrants were censored from the analysis on the day during which emigration occurred. Tags that showed a cessation of movement (i.e., exhibited typical movement patterns followed by constant depth and zero acceleration) within the 14-d period of analysis were assumed to have suffered discard mortality, although we could not rule out the possibility of tag shedding.

To test the effects of covariates such as species, TL, and depth of capture, we conducted a logistic regression in R version 3.3.0. These analyses were conducted using fate as a binomial variable (mortality = 0; nonmortality = 1). Variables were examined for significance at the  $\alpha$  level of 0.05.

## RESULTS

In total, 19 grouper belonging to the three target species were tagged with acoustic transmitters (Table 1). From the transmitters on these 19 fish, we accumulated approximately 60,000 detections throughout the 44-d study period (Appendix Figure A.1). The control tag showed that depth was constant and acceleration was minimal for a tag moored to one of our receivers (Figure 3A). Durations of detection histories ranged from 0 to 44 d (i.e., the entire study period; Figure 4). One grouper was never detected, and two grouper were detected for less than 4 h; these

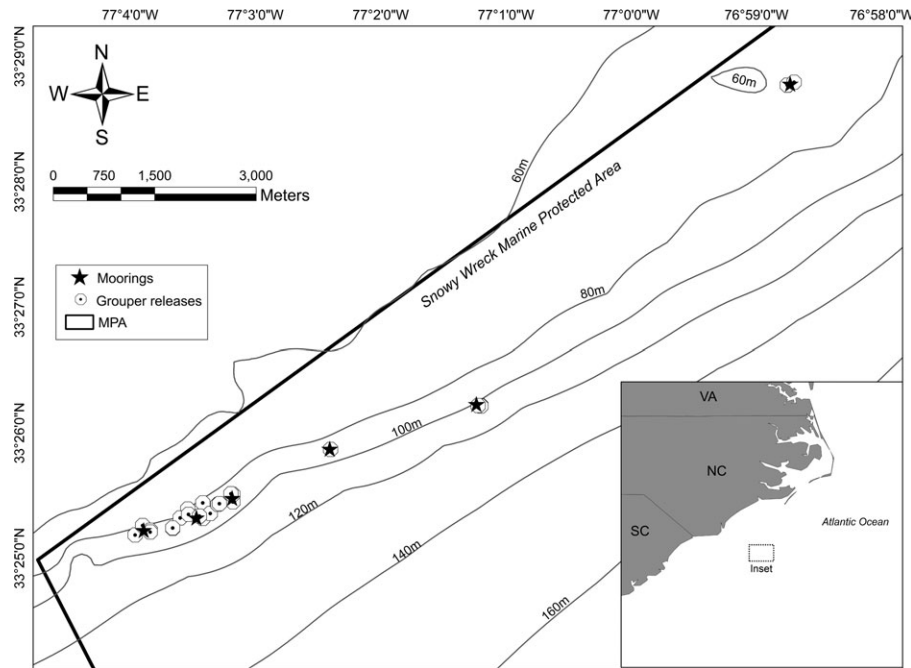


FIGURE 2. Map showing the western corner of the Snowy Wreck Marine Protected Area (MPA) off the North Carolina coast. All grouper releases occurred along the continental shelf break (i.e., the northwestern edge of the MPA).

three fish were assigned a fate classification of “unknown” and were excluded from the Kaplan–Meier analysis. Six additional fish showed movements indicating survival up to their date of emigration from the array before day 14; these fish were censored on the day they emigrated. One grouper had a few initial detections on receivers local to the release site and then was next detected 24 h later on a receiver approximately 4 km away at a shallow depth (Scamp 8; Figure 3B). We assumed that the transmitter from this grouper was in the stomach of a large predator or scavenger that moved away from the tagging study area at a shallow depth; this tag was never detected again, and the fish was classified as a discard mortality on day 1. Six fish were classified as discard mortalities due to a cessation of tag movement (e.g., Figure 3C). Three fish survived and remained within detection range beyond day 14. One of these was still detected alive at the end of the study and is denoted by an “S” in Figure 4. One fish emigrated on day 16 of the study, and one fish showed a cessation of tag movement 34 d after release. Because these latter two events occurred outside of our 14-d period of analysis, both fish were assigned the fate of survival. The Kaplan–Meier survival estimate on day 14 was 0.50 (95% confidence interval = 0.10–0.91); discard survival ranged from about 0.60 at 8 d after release to about 0.90 at 4 d after release (Figure 5).

We found no evidence of covariates having an influence on discard survival in grouper. A logistic regression model

including three variables found no significant effect of the depth of capture ( $z = 0.62$ ,  $P = 0.54$ ), TL ( $z = 0.76$ ,  $P = 0.45$ ), or species ( $z = 1.28$ ,  $P = 0.20$ ) on grouper discard survival.

## DISCUSSION

Our study examined survival of deepwater grouper to 14 d postrelease. There has been little consistency in the literature as to an appropriate period of analysis for such studies. Curtis et al. (2015) used field methods similar to ours but chose a 3-d period of analysis for Red Snapper. As justification, the authors of that study assumed 0% tag loss and reported that no individuals displayed a cessation of tag movement after 3 d. Hochhalter and Reed (2011) used mark–recapture to estimate relative delayed mortality of Pacific rockfish under a variety of treatments. They chose 17 d as their period of analysis and were aided in their work by high densities and high site fidelities of their target species. Sumpton et al. (2010) also used mark–recapture but in a large-scale, long-term (4-year) study involving angler participation. Other studies of discard mortality (particularly those that have employed caging or other enclosures) have varied widely in their period of analysis: from 2 d (Jarvis and Lowe 2008) to 10–15 d (Gitschlag and Renaud 1994) in situ and up to 31 d in a controlled setting (Pribyl et al. 2012).

TABLE 1. Summary description of the 19 total deepwater grouper that were tagged with Vemco V13AP transmitters. Size ranges, depth ranges of capture, and current recreational harvest regulations in the southeastern USA varied among species.

Species	Number tagged with V13AP transmitters	Size range of released fish (mm TL)	Depth range of capture (m)	Current recreational regulations in southeastern USA
Scamp	8	514–690	60–115	508-mm (20-in) minimum length; 3 fish per individual per day; open May 1–December 31
Snowy Grouper	7	359–434	81–103	1 fish per vessel per day; open May 1–December 31
Speckled Hind	4	437–752	84–119	Harvest prohibited

In many of the above studies, an abbreviated observation period was deemed necessary to avoid confounding effects of caging (e.g., protection from predation; physical damage from contact with the cage) with discard mortality. For example, Jarvis and Lowe (2008) considered all fish that were still alive at 2 d postcapture to have survived the release event. Our work shows that a 2-d observation period would not have been long enough for deepwater groupers. Only one fish was classified as a mortality up to the end of day 2; if we had limited our analysis to discard mortalities to day 2, our survival estimate would have been approximately 95% and biased high because it would not have included subsequent discard mortalities.

All fish that showed a cessation of tag movement did so within the 14-d period of analysis, with the exception of Scamp 5, which stopped moving 34 d after release. Given the high level of activity observed until that time, we consider tag shedding the most parsimonious explanation for cessation of movement by this fish. The six grouper that were classified as discard mortalities (and not eaten by a predator) displayed similar activity patterns until the moment when they stopped moving. One or more of these fish could have shed their tag rather than suffered mortality. Musyl et al. (2011) provided estimates of tag shedding for pop-up satellite archival tags (PSATs) that were attached to billfishes by using the same style of nylon dart tip used in this study. Those authors showed that retention of PSATs attached with nylon dart tips was significantly worse than the retention of PSATs attached via any of four other methods examined (although they used a single dart tip rather than two). In fact, approximately 50% of PSATs attached with nylon dart tips had been shed by day 10 of their study. Although PSATs differ from acoustic transmitters in terms of size and shape, the low retention rates from Musyl et al. (2011) substantiate the possibility that some of our grouper may have lost their tags. Furthermore, given the abundance of hard structure in our study area, it is conceivable that some of the individuals in our study could have removed their

transmitters by intentionally abrading them on an available environmental object. In addition, while we intended to insert the dart tips through the pterygiophores, it is possible that some were not placed properly. Particularly for larger individuals, the inter-ptyerygiophore distance may exceed the width of the dart tip including the two barbs. If this was the case, the dart would have only been held by skin, membrane, and muscle and would have been more likely to be easily removed. If tag shedding occurred on or before day 14, then our estimates of discard survival would be biased low.

Although our estimate of survival is low, 50% represents a substantial increase over the previous assumption of 0% survival. Our findings of increased survival through recompression corroborate the results of many of the studies cited above. However, those studies (with few exceptions) have been limited to Pacific rockfishes (e.g., Parker et al. 2006; Hannah and Matteson 2007; Hochhalter and Reed 2011) or Red Snapper (e.g., Gitschlag and Renaud 1994; Curtis et al. 2015) and do not represent the diversity of reef fishes that are susceptible to barotrauma. To our knowledge, this study is the first to test the effects of recompression on any member of Serranidae, despite their current and historical value as food fish in the United States and in other countries. Further work on serranids and other under-explored taxa would be useful in elucidating the effects of recompression on survival.

We did not include a control group in this study because it is well known that non-treated grouper (i.e., those not vented or descended) float after being captured and released at these water depths. Indeed, the most recent stock assessment for Snowy Grouper used 0% discard survival for this species regardless of capture depth (SEDAR 2013). The behavior of Snowy Grouper released as part of two other unpublished studies corroborates the stock assessment assumption: after capture in depths of 129–153 m ( $n = 8$ ) and 195–246 m ( $n = 12$ ), 100% of untreated fish floated (B. Runde, unpublished data; J. Facendola, North Carolina Division of Marine Fisheries, unpublished

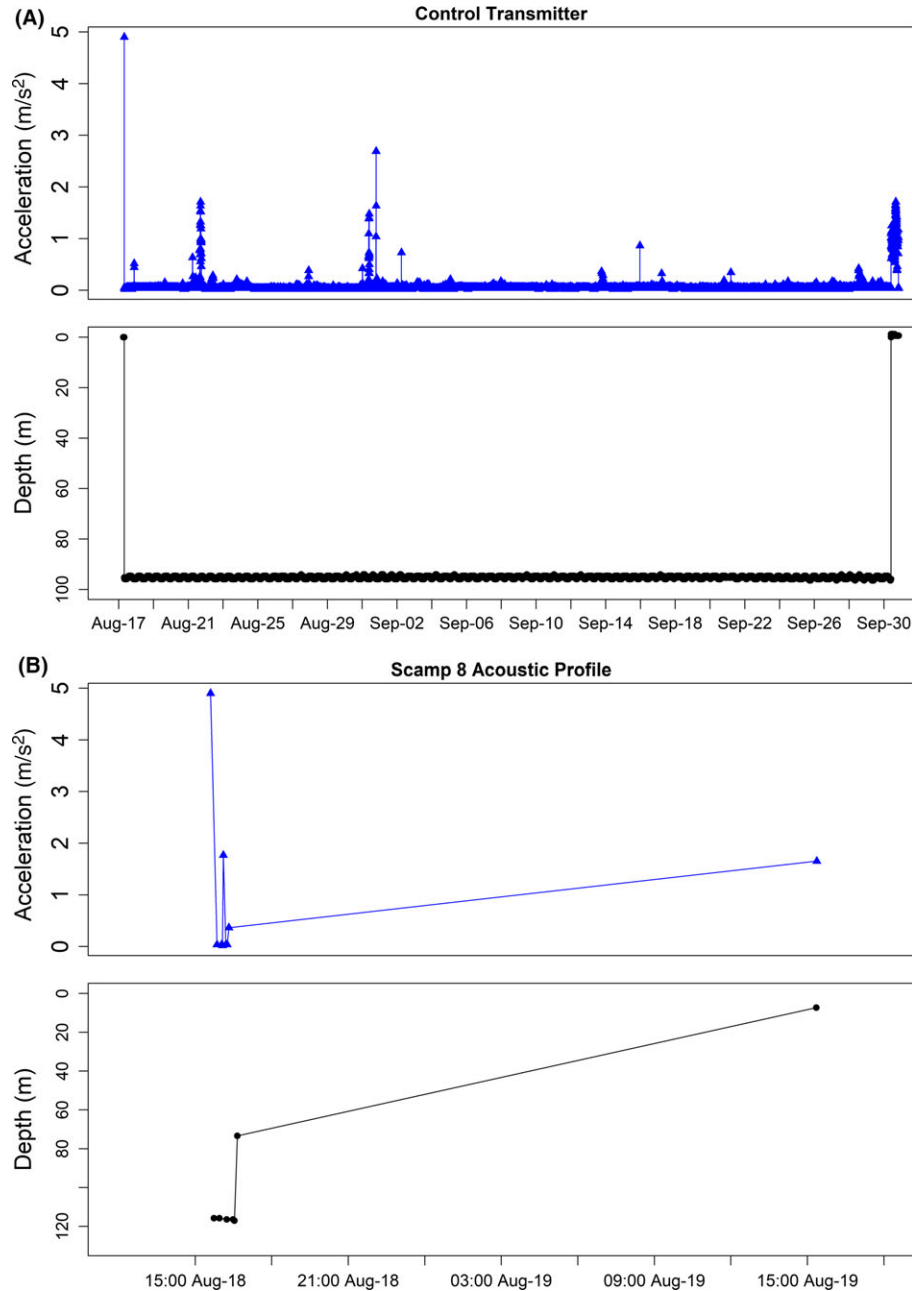


FIGURE 3. Example activity plots for three telemetry tags, with upper panels indicating acceleration ( $m/s^2$ ) and lower panels indicating depth (m). Variations in x-axis scale reflect the duration of detection for each individual. (A) The control transmitter was fixed on a receiver mooring for the duration of the study. (B) Scamp 8 was detected a few times immediately after release, followed by a single detection 24 h later. This final detection took place on a receiver about 4 km from the release site, indicating that this fish probably was the victim of predation or scavenging resulting from the trauma associated with being caught and released. (C) Snowy Grouper 6 displayed an approximately 2-d recovery period with little movement before returning to a state of higher activity. Around August 27 (10 d after release), this individual's tag ceased movement. (D) Speckled Hind 3 is an example of a fish that appears to have emigrated from the study area. Because the last detections of this fish were on day 3 after release, this individual was censored from the analysis on that day.

data). Empirical data for surface-released Speckled Hind and Scamp for this depth range are unavailable. However, it is very likely that their disposition would be comparable to that of Snowy Grouper given their close taxonomic

relationship and our observations of universal severe barotrauma.

Injuries suffered by reef fishes as a result of rapid decompression may appear lethal (Rummer and Bennett

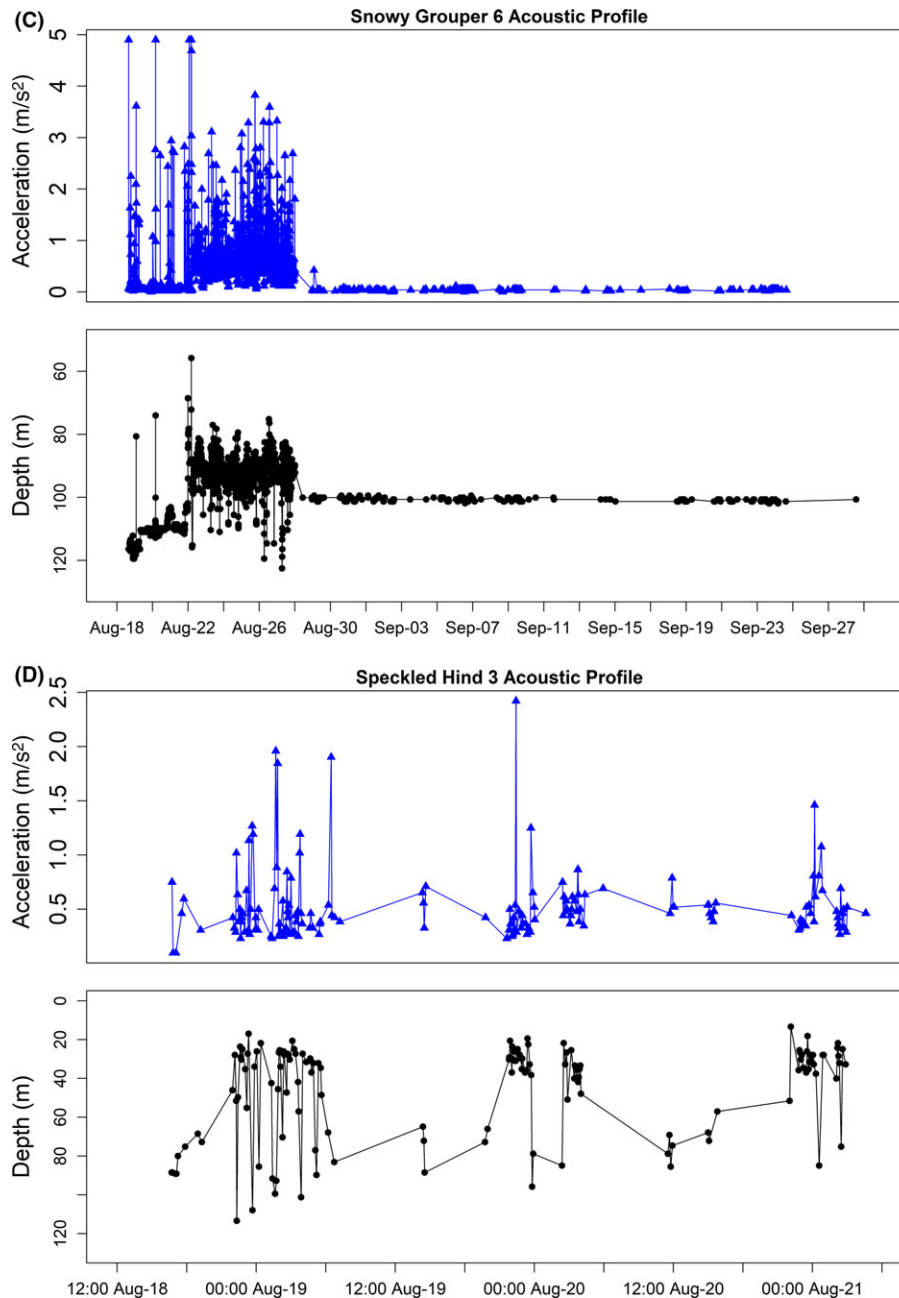


FIGURE 3. Continued.

2005); however, there is evidence to suggest that rapid physical and physiological recovery is possible. Using transmitters almost identical to those used here (Vemco V13P), Collins (2014) tagged Atlantic Goliath Grouper *E. itajara* that were captured from 12 to 39-m depths. The author documented a discard survival rate of 100% even though there was a high occurrence of barotrauma in fish captured from the deeper portion of that range (traumatized fish were vented). In addition, Collins (2014) observed that the majority of tagged fish were temporarily

inactive (for up to 24 h) immediately after tagging, a phenomenon we observed with several of our tagged grouper (e.g., Figure 3C). This period of inactivity may be related to the healing process. Indeed, Burns and Restrepo (2002) experimentally demonstrated that Red Grouper *E. morio* could heal a ruptured swim bladder in as little as 4 d. Such recovery is likely also possible in our three closely related subject species, provided that they are able to submerge and return to the bottom (e.g., through the use of a descender device).

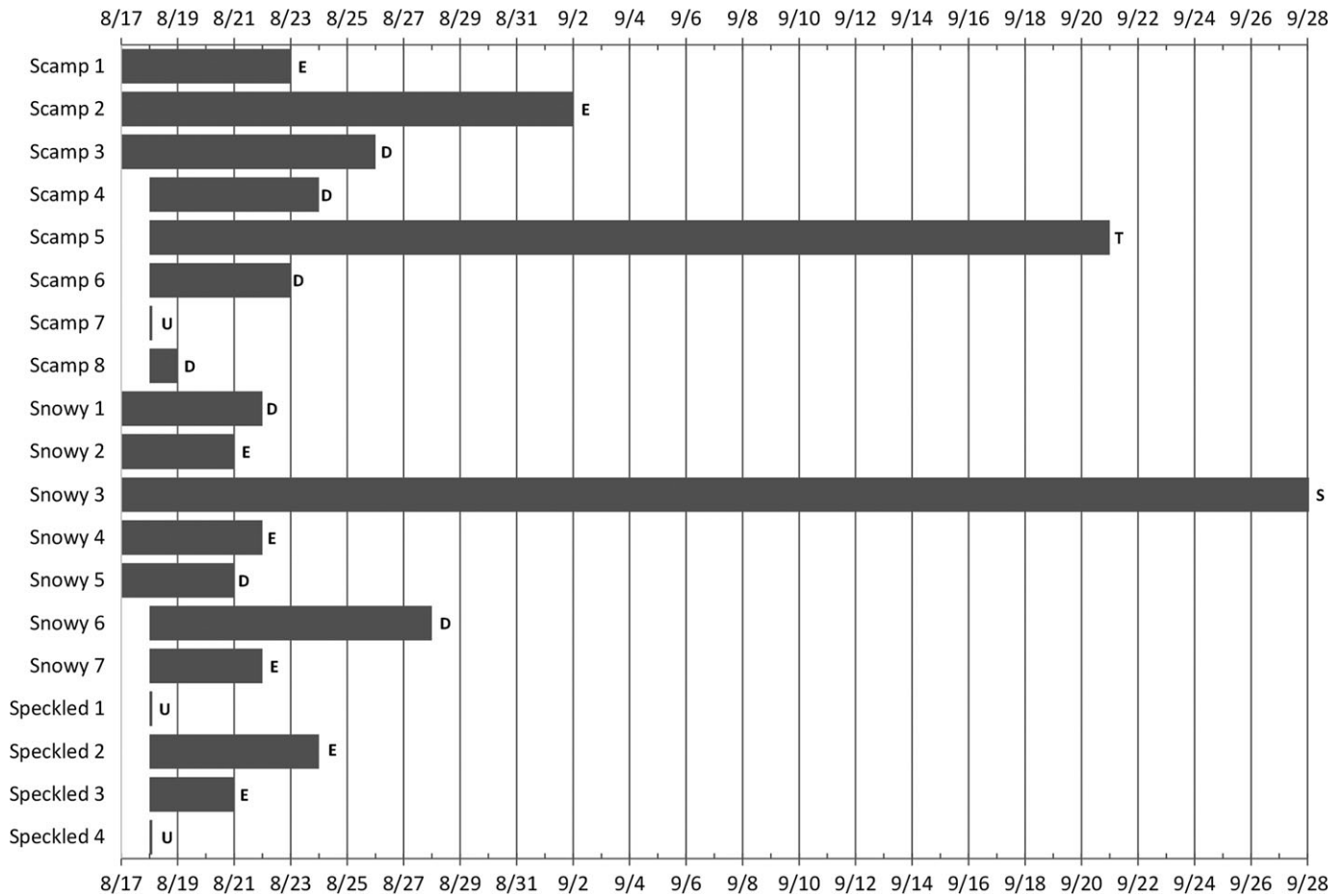


FIGURE 4. Detection histories for 19 telemetered individuals representing three deepwater grouper species, which were tagged at the Snowy Wreck Marine Protected Area on August 17–18, 2015. Each row indicates the detection history and fate of an individual. Letters at the end of each bar identify emigration (E;  $n = 7$ ) before the end of the study period, assumed discard mortality (D;  $n = 7$ ), assumed tag loss (T;  $n = 1$ ), or survival to the end of the study period (S;  $n = 1$ ). Individuals with fewer than 24 h of detections were assigned a fate of “unknown” (U;  $n = 3$ ).

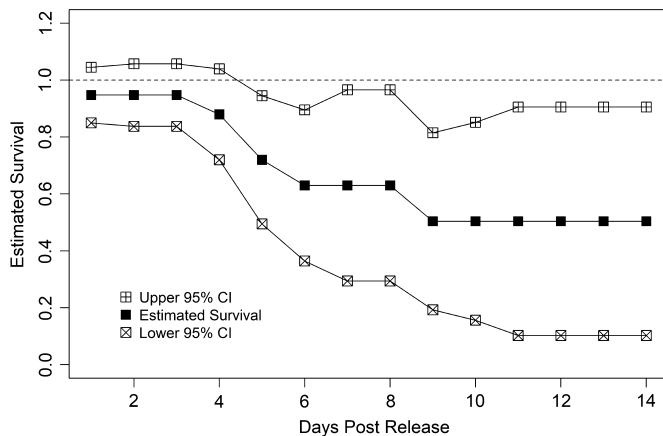


FIGURE 5. Kaplan–Meier survival estimates (with 95% confidence interval [CI]) for 19 telemetered deepwater grouper (three species: Scamp, Snowy Grouper, and Speckled Hind) caught at 60–120-m water depth and then released with a descender device.

We censored grouper from our analysis on the day that they permanently emigrated from the receiver detection area. This resulted in a smaller pool of remaining or “at-risk” individuals that could die from discard mortality. As a result, mortalities that occurred later in our period of analysis had a correspondingly larger effect on the overall estimate of survival. Furthermore, censorships lead to wider confidence intervals because overall sample sizes are lower. Thus, our results would not be comparable to studies where survival is estimated only at the completion of the study (i.e., [number of survivors]/[total number of fish tagged]) and emigrants are counted as survivors.

Because of the type of descender devices used, many recompression studies release fish at the seafloor (e.g., Brown et al. 2010; Butcher et al. 2012; Curtis et al. 2015), although Hannah and Matteson (2007) used variable release depths for two rockfish species depending on depth of capture and severity of visible barotrauma. The SeaQualizer tool used in this study allows fishers to choose

the depth of release (triggered by an internal pressure sensor). Our intended release depth for all fish was 46 m; however, due to equipment loss during field work, we had to employ the use of a second SeaQualizer that did not allow release at 46 m. As such, some individuals were descended to 46 m and others to 61 m before release. Release depth may be of little consequence provided that it is at least a few meters below the surface, as the greatest pressure differential occurs closest to the surface (Theberge and Parker 2005). However, a secondary benefit of descender devices that attach to the jaw of the fish (e.g., SeaQualizer or Shelton Fish Descender) is that by pulling the fish down headfirst, oxygenated water is forced over the gills. This may aid the fish in overcoming the oxygen debt resulting from capture-related fatigue and removal from the water (Ferguson and Tufts 1992). Additionally, release at depths closer to the bottom may assist the recovering fish in evading larger predators. Thus, deeper release depths using a descender device may provide benefits beyond recompression. In our study, there was no evidence of an effect of varied released depth on survival.

Fishery managers have struggled to set regulations for relatively abundant species that cohabitate with at-risk or rare species, such as those studied here, and for species whose discard survival is thought to be extremely low. A method of increasing discard survival of deepwater groupers would be extremely useful for grouper management. For example, there are no size limits for Snowy Grouper in the southeastern USA because of the assumed 0% discard survival. This regulation might be amended if discarded fish were known to have a reasonable chance of survival through the use of a descender device. Gear requirements for fisheries are not without precedent: circle hooks, dehooking tools, and venting tools have all (at times) been mandated equipment (GMFMC 2007; SAFMC 2009, 2010). Descender tools, with a variety of designs, generally require little skill to operate, and even the most advanced are modestly priced (e.g., SeaQualizer; US\$55). We have demonstrated that forced recompression through the use of a descender device has the potential to be an effective approach to increase discard survival for deepwater groupers.

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## REFERENCES

- Bacheler, N. M., and J. A. Buckel. 2004. Does hook type influence the catch rate, size, and injury of grouper in a North Carolina commercial fishery? *Fisheries Research* 69:303–311.
- Benaka, L. R., L. Sharpe, K. Abrams, M. Campbell, J. Cope, F. Darby, E. J. Dick, J. Hyde, B. Linton, C. Lunsford, D. Rioux, and Y. Swimmer. 2016. Action plan for fish release mortality science. National Marine Fisheries Service, Silver Spring, Maryland.
- Brown, I., W. Sumpton, M. McLennan, D. Mayer, M. Campbell, J. Kirkwood, A. Butcher, I. Halliday, A. Mapleston, and D. Welch. 2010. An improved technique for estimating short-term survival of released line-caught fish, and an application comparing barotrauma-relief methods in Red Emperor (*Lutjanus sebae* Cuvier 1816). *Journal of Experimental Marine Biology and Ecology* 385:1–7.
- Burns, K. M., and J. T. Froeschke. 2012. Survival of Red Grouper (*Epinephelus morio*) and Red Snapper (*Lutjanus campechanus*) caught on J-hooks and circle hooks in the Florida recreational and recreational-for-hire fisheries. *Bulletin of Marine Science* 88:633–646.
- Burns, K. M., C. C. Koenig, and F. C. Coleman. 2002. Evaluation of multiple factors involved in release mortality of undersized Red Grouper, Gag, Red Snapper and Vermilion Snapper. Mote Marine Laboratory, Technical Report 790, Sarasota, Florida.
- Burns, K. M., and V. Restrepo. 2002. Survival of reef fish after rapid depressurization: field and laboratory studies. Pages 148–151 in J. A. Lucy and A. L. Studholme, editors. *Catch and release in marine recreational fisheries*. American Fisheries Society, Bethesda, Maryland.
- Butcher, P. A., M. K. Broadhurst, K. C. Hall, B. R. Cullis, and S. R. Raidal. 2012. Assessing barotrauma among angled snapper (*Pagrus auratus*) and the utility of release methods. *Fisheries Research* 127:49–55.
- Capizzano, C. W., J. W. Mandelman, W. S. Hoffman, M. J. Dean, D. R. Zemeckis, H. P. Benoit, J. Kneebone, E. Jones, M. J. Stettner, N. J. Buchan, J. A. Langan, and J. A. Sulikowski. 2016. Estimating and mitigating the discard mortality of Atlantic Cod (*Gadus morhua*) in the Gulf of Maine recreational rod-and-reel fishery. *ICES Journal of Marine Science* 73:2342–2355.
- Coggins, L. G., M. J. Catalano, M. S. Allen, W. E. Pine, and C. J. Walters. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* 8:196–210.
- Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, G. R. Sedberry, R. W. Chapman, and C. B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries* 25(3):14–21.
- Collins, A. 2014. An investigation into the habitat, behavior and opportunistic feeding strategies of the protected Goliath Grouper (*Epinephelus itajara*). Doctoral dissertation. University of South Florida, Tampa.
- Cox, D. R., and D. Oakes. 1984. Analysis of survival data, volume 21. CRC Press, Boca Raton, Florida.
- Curtis, J. M., M. W. Johnson, S. L. Diamond, and G. W. Stunz. 2015. Quantifying delayed mortality from barotrauma impairment in discarded Red Snapper using acoustic telemetry. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 7:434–449.
- Dance, M. A., D. L. Moulton, N. B. Furey, and J. R. Rooker. 2016. Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? *Fisheries Research* 183:80–85.

- Davis, M. 2007. Simulated fishing experiments for predicting delayed mortality rates using reflex impairment in restrained fish. *ICES Journal of Marine Science* 64:1535–1542.
- Davis, M. W. 2002. Key principles for understanding fish bycatch discard mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1834–1843.
- Drumhiller, K. L., M. W. Johnson, S. L. Diamond, M. M. Reese Robillard, and G. W. Stunz. 2014. Venting or rapid recompression increase survival and improve recovery of Red Snapper with barotrauma. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 6:190–199.
- Ferguson, R., and B. Tufts. 1992. Physiological effects of brief air exposure in exhaustively exercised Rainbow Trout (*Oncorhynchus mykiss*): implications for “catch and release” fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1157–1162.
- Gitschlag, G. R., and M. L. Renaud. 1994. Field experiments on survival rates of caged and released Red Snapper. *North American Journal of Fisheries Management* 14:131–136.
- GMFMC (Gulf of Mexico Fishery Management Council). 2007. Amendment 27 to the Reef Fish Fishery Management Plan. GMFMC, Tampa, Florida.
- Hannah, R. W., and K. M. Matteson. 2007. Behavior of nine species of Pacific rockfish after hook-and-line capture, recompression, and release. *Transactions of the American Fisheries Society* 136:24–33.
- Heupel, M., and C. Simpfendorfer. 2002. Estimation of mortality of juvenile Blacktip Sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:624–632.
- Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Use of telemetry methods to estimate natural and fishing mortality of Striped Bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society* 130:557–567.
- Hochhalter, S. J., and D. J. Reed. 2011. The effectiveness of deepwater release at improving the survival of discarded Yelloweye Rockfish. *North American Journal of Fisheries Management* 31:852–860.
- Huntsman, G., J. Potts, R. Mays, and D. Vaughan. 1999. Groupers (Serranidae, Epinephelinae): endangered apex predators of reef communities. Pages 217–231 in J. A. Musick, editor. *Life in the slow lane: ecology and conservation of long-lived marine animals*. American Fisheries Society, Bethesda, Maryland.
- Jarvis, E. T., and C. G. Lowe. 2008. The effects of barotrauma on the catch-and-release survival of southern California nearshore and shelf rockfish (Scorpaenidae, *Sebastes* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 65:1286–1296.
- Johnson, M. W., S. L. Diamond, and G. W. Stunz. 2015. External attachment of acoustic tags to deepwater reef fishes: an alternate approach when internal implantation affects experimental design. *Transactions of the American Fisheries Society* 144:851–859.
- Kelleher, K. 2005. Discards in the world’s marine fisheries: an update. Food and Agriculture Organization of the United Nations Fisheries Technical Paper 470.
- Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, G. R. Sedberry, S. J. Parker, S. G. Poss, E. Sala, T. W. Schmidt, H. Weeks, and S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25(11):6–30.
- Musyl, M., M. Domeier, N. Nasby-Lucas, R. Brill, L. McNaughton, J. Swimmer, M. Lutcavage, S. Wilson, B. Galuardi, and J. Liddle. 2011. Performance of pop-up satellite archival tags. *Marine Ecology Progress Series* 433:1–28.
- NMFS (National Marine Fisheries Service). 2016. U.S. national bycatch report, first edition, update 2. U.S. Department of Commerce. Available: <https://www.st.nmfs.noaa.gov/observer-home/first-edition-update-2>. (February 2018).
- Parker, S. J., H. I. McElderry, P. S. Rankin, and R. W. Hannah. 2006. Buoyancy regulation and barotrauma in two species of nearshore rockfish. *Transactions of the American Fisheries Society* 135:1213–1223.
- Patterson, W. F., C. E. Porch, J. H. Tarnecki, and A. J. Strelcheck. 2012. Effect of circle hook size on reef fish catch rates, species composition, and selectivity in the northern Gulf of Mexico recreational fishery. *Bulletin of Marine Science* 88:647–665.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Pribyl, A., C. Schreck, M. Kent, K. Kelley, and S. Parker. 2012. Recovery potential of Black Rockfish, *Sebastes melanops* Girard, recompressed following barotrauma. *Journal of Fish Diseases* 35:275–286.
- Rudershausen, P. J., J. A. Buckel, and J. E. Hightower. 2014. Estimating reef fish discard mortality using surface and bottom tagging: effects of hook injury and barotrauma. *Canadian Journal of Fisheries and Aquatic Sciences* 71:514–520.
- Rudershausen, P. J., J. A. Buckel, and E. H. Williams. 2007. Discard composition and release fate in the snapper and grouper commercial hook-and-line fishery in North Carolina, USA. *Fisheries Management and Ecology* 14:103–113.
- Rummer, J. L., and W. A. Bennett. 2005. Physiological effects of swim bladder overexpansion and catastrophic decompression on Red Snapper. *Transactions of the American Fisheries Society* 134:1457–1470.
- SAFMC (South Atlantic Fishery Management Council). 2009. Amendment 16 to the Fishery Management Plan for the snapper grouper fishery of the South Atlantic region. SAFMC, North Charleston, South Carolina.
- SAFMC (South Atlantic Fishery Management Council). 2010. Amendment 17A to the Fishery Management Plan for the snapper grouper fishery of the South Atlantic region. SAFMC, North Charleston, South Carolina.
- SEDAR (Southeast Data, Assessment, and Review). 2013. SEDAR 36: South Atlantic Snowy Grouper stock assessment report. SEDAR, North Charleston, South Carolina.
- St John, J., and C. J. Syers. 2005. Mortality of the demersal West Australian Dhufish, *Glaucosoma hebraicum* (Richardson 1845) following catch and release: the influence of capture depth, venting and hook type. *Fisheries Research* 76:106–116.
- Sumpton, W., I. Brown, D. Mayer, M. McLennan, A. Mapleston, A. Butcher, D. Welch, J. Kirkwood, B. Sawynok, and G. Begg. 2010. Assessing the effects of line capture and barotrauma relief procedures on post-release survival of key tropical reef fish species in Australia using recreational tagging clubs. *Fisheries Management and Ecology* 17:77–88.
- Theberge, S., and S. J. Parker. 2005. Release methods for rockfish. Oregon State University, Sea Grant Oregon, Corvallis.
- Wilde, G. R. 2009. Does venting promote survival of released fish? *Fisheries* 34:20–28.
- Wilson, R. R., and K. M. Burns. 1996. Potential survival of released groupers caught deeper than 40 m based on shipboard and in-situ observations, and tag-recapture data. *Bulletin of Marine Science* 58:234–247.

### Appendix: Additional Plots of Grouper Behavior

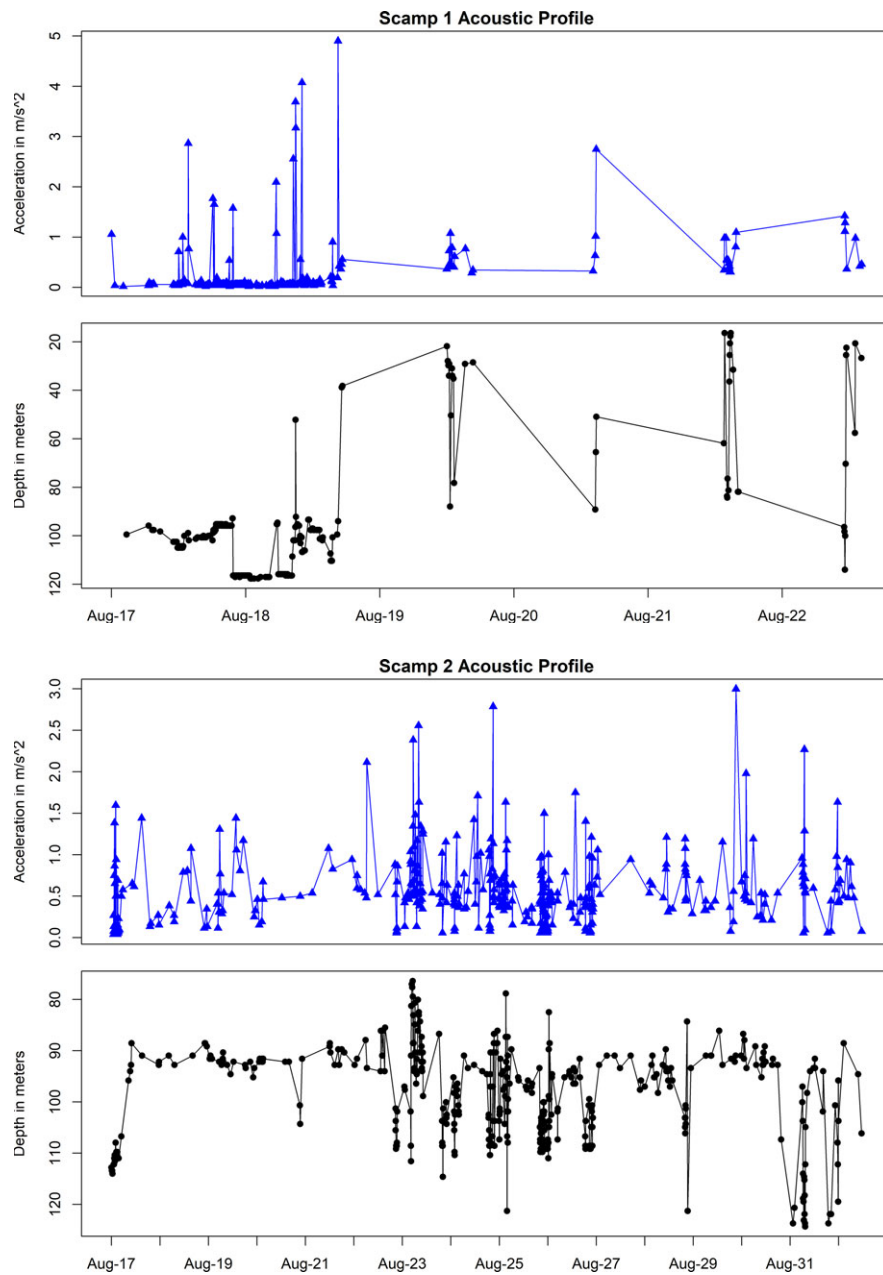


FIGURE A.1. Detection histories for 15 deepwater grouper (three species: Scamp, Snowy Grouper, and Speckled Hind) that were tagged with Vemco V13AP telemetry tags and not shown in Figure 3. Scamp 7 is not depicted here or in Figure 3 because there were no detections for that individual. Note the differences in the range of y- and x-axes among individual grouper. Upper panels indicate acceleration ( $\text{m/s}^2$ ) and lower panels indicate depth (m).

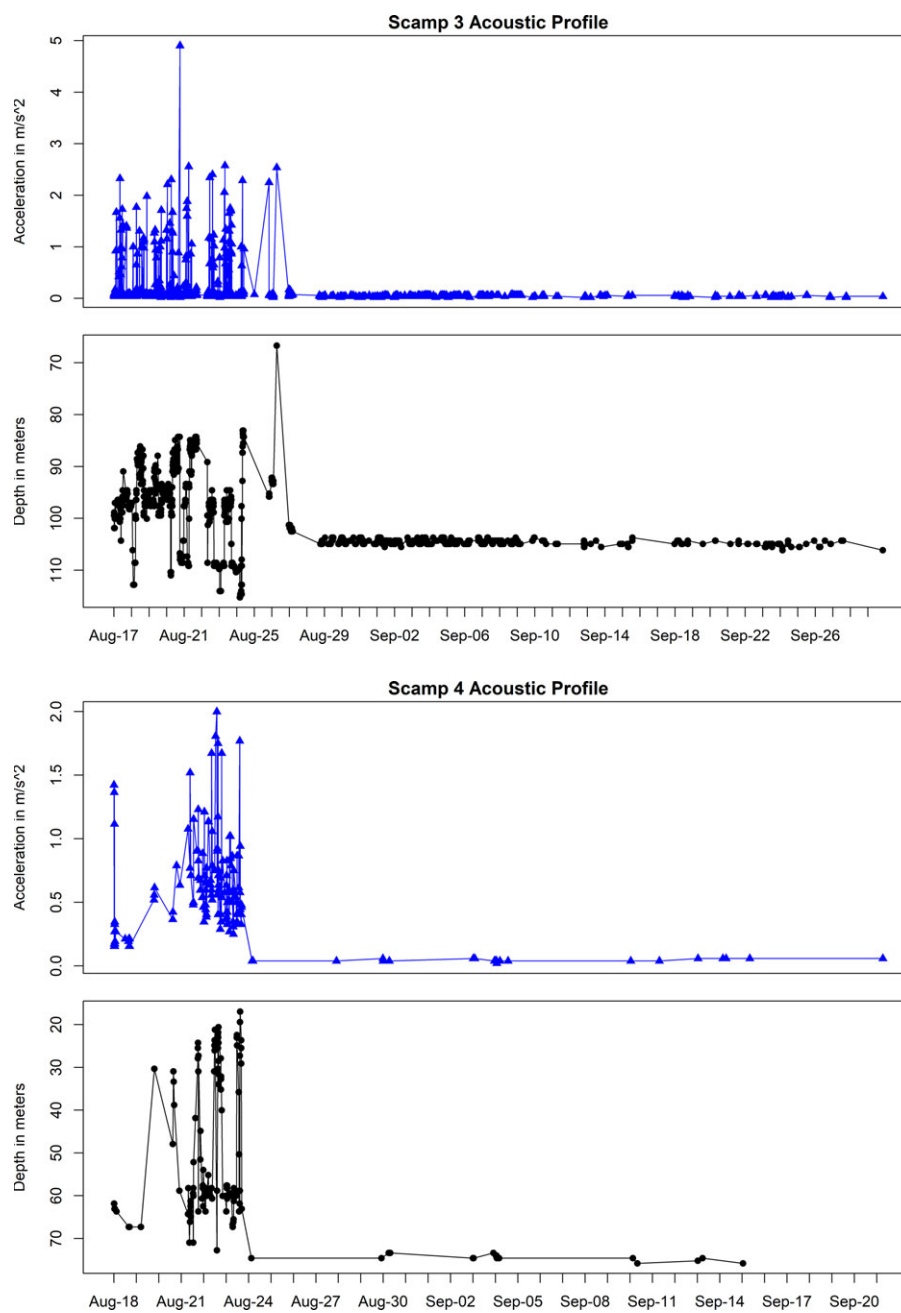


FIGURE A.1. Continued.

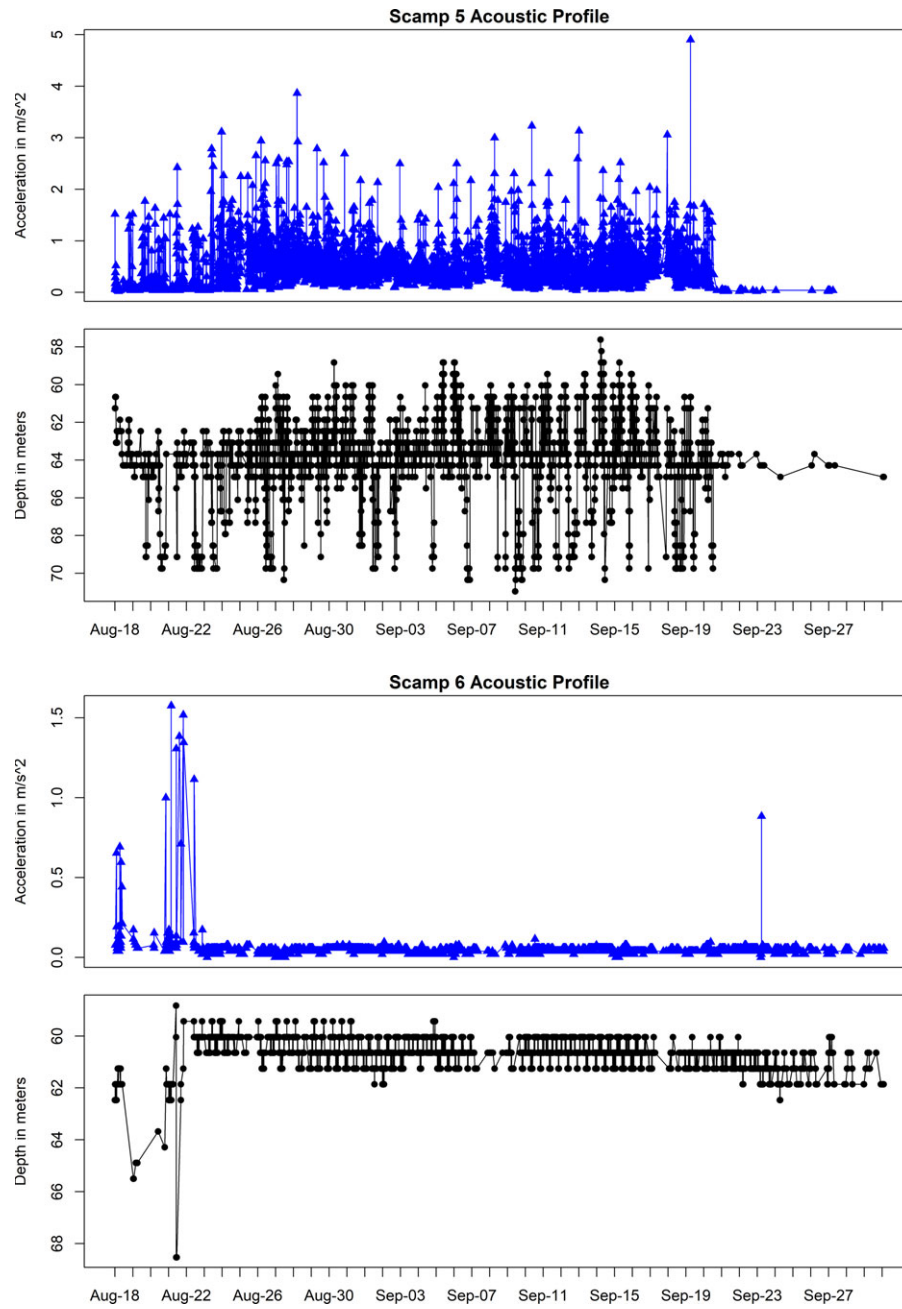


FIGURE A.1. Continued.

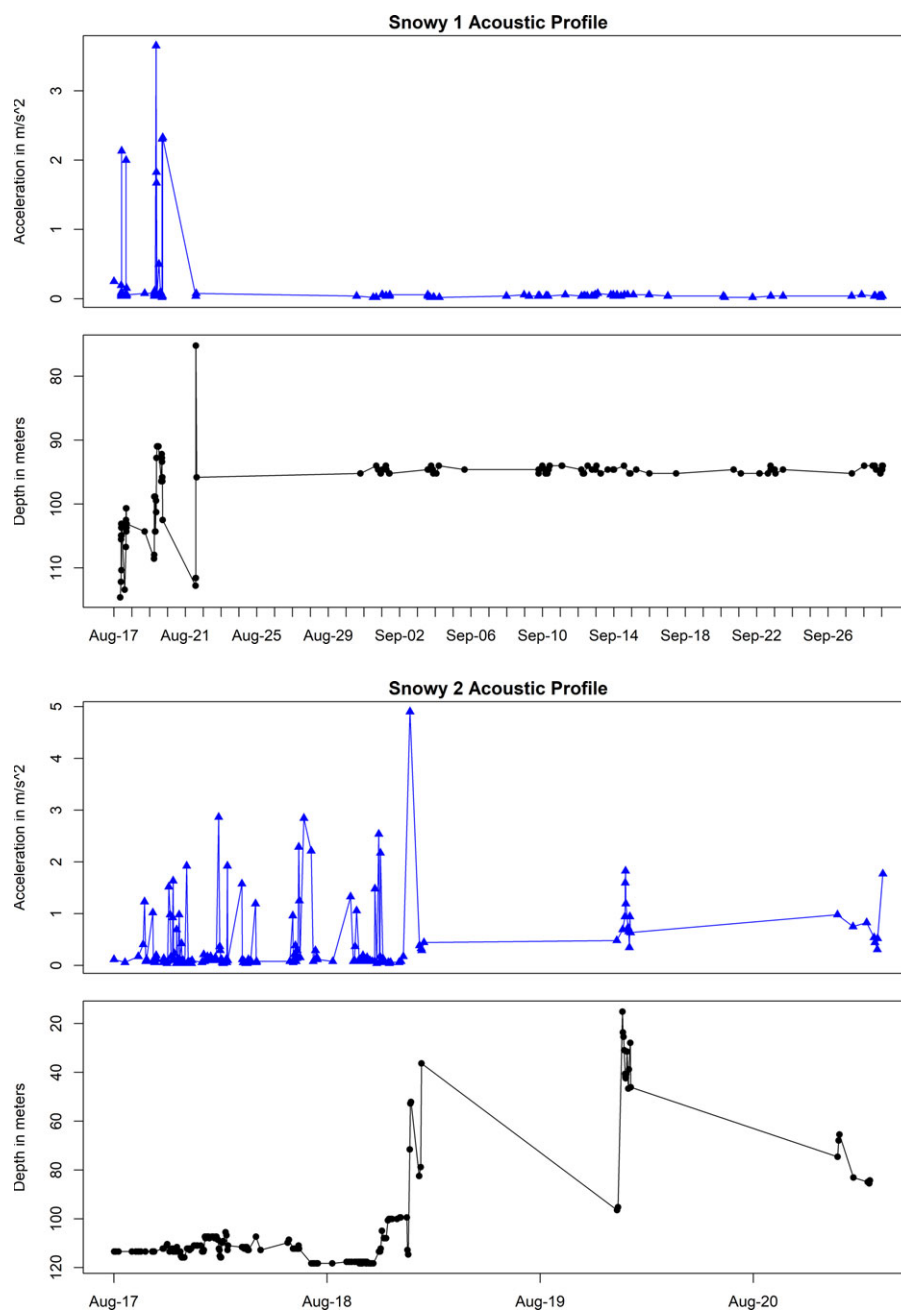


FIGURE A.1. Continued.

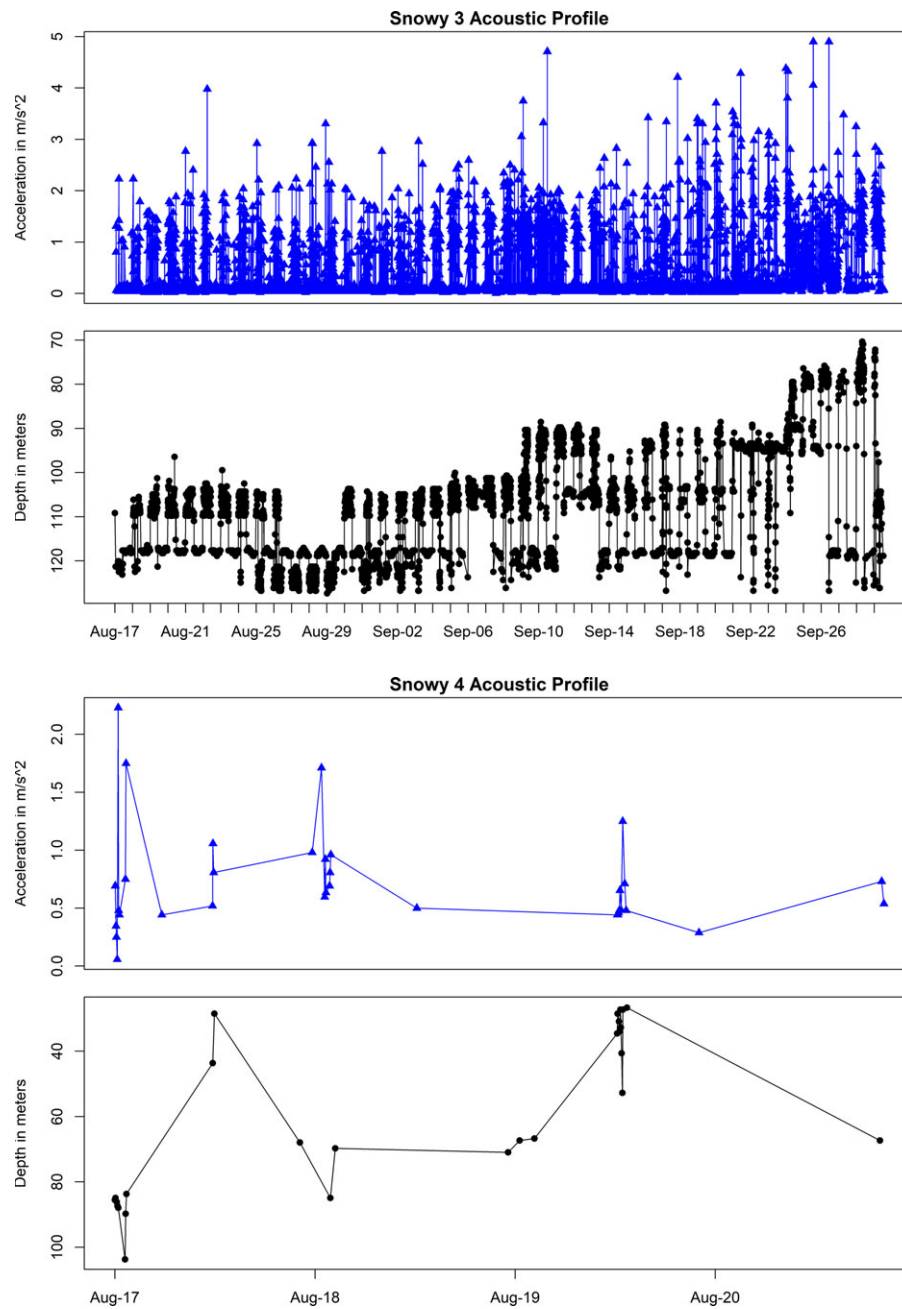


FIGURE A.1. Continued.

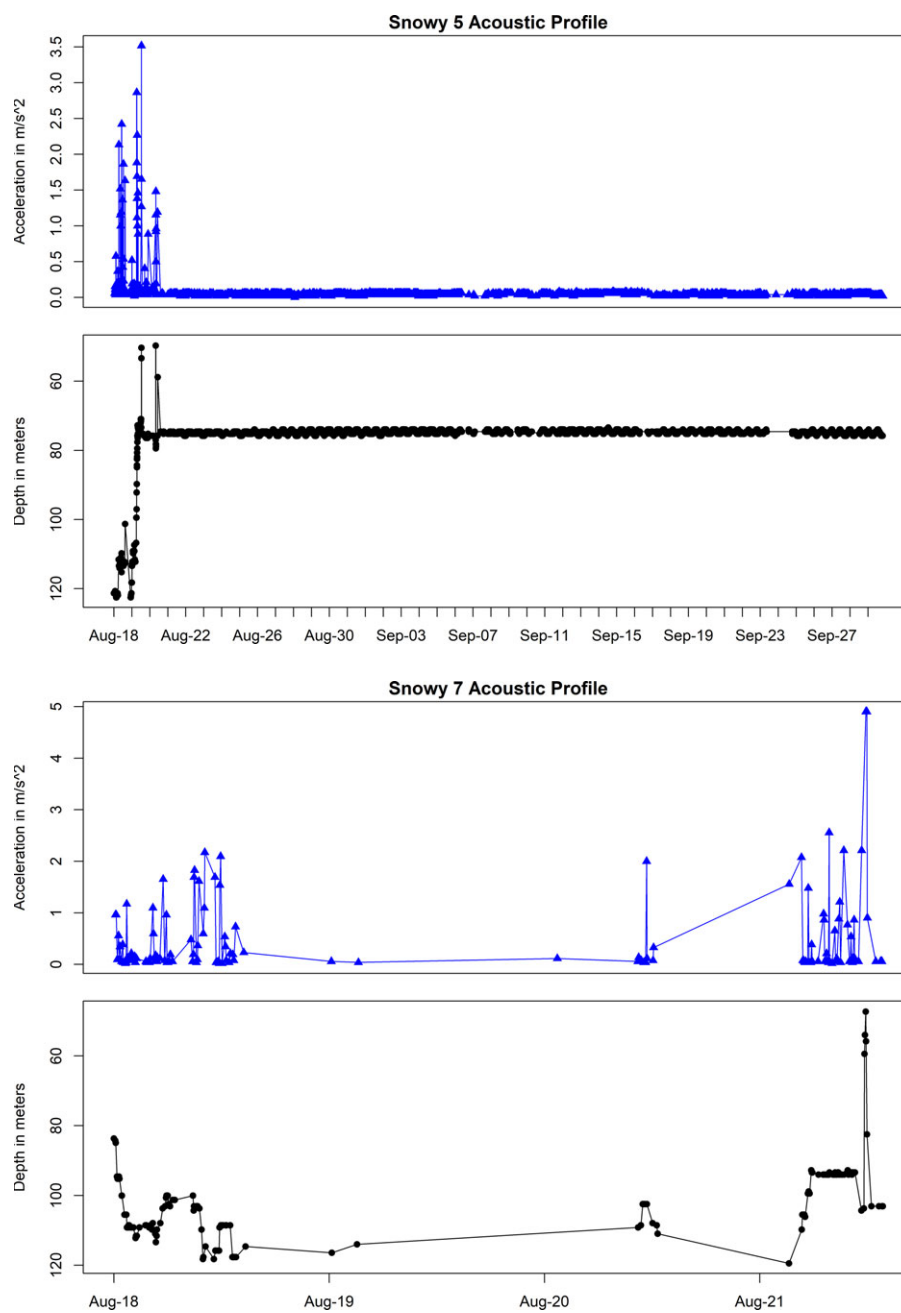


FIGURE A.1. Continued.

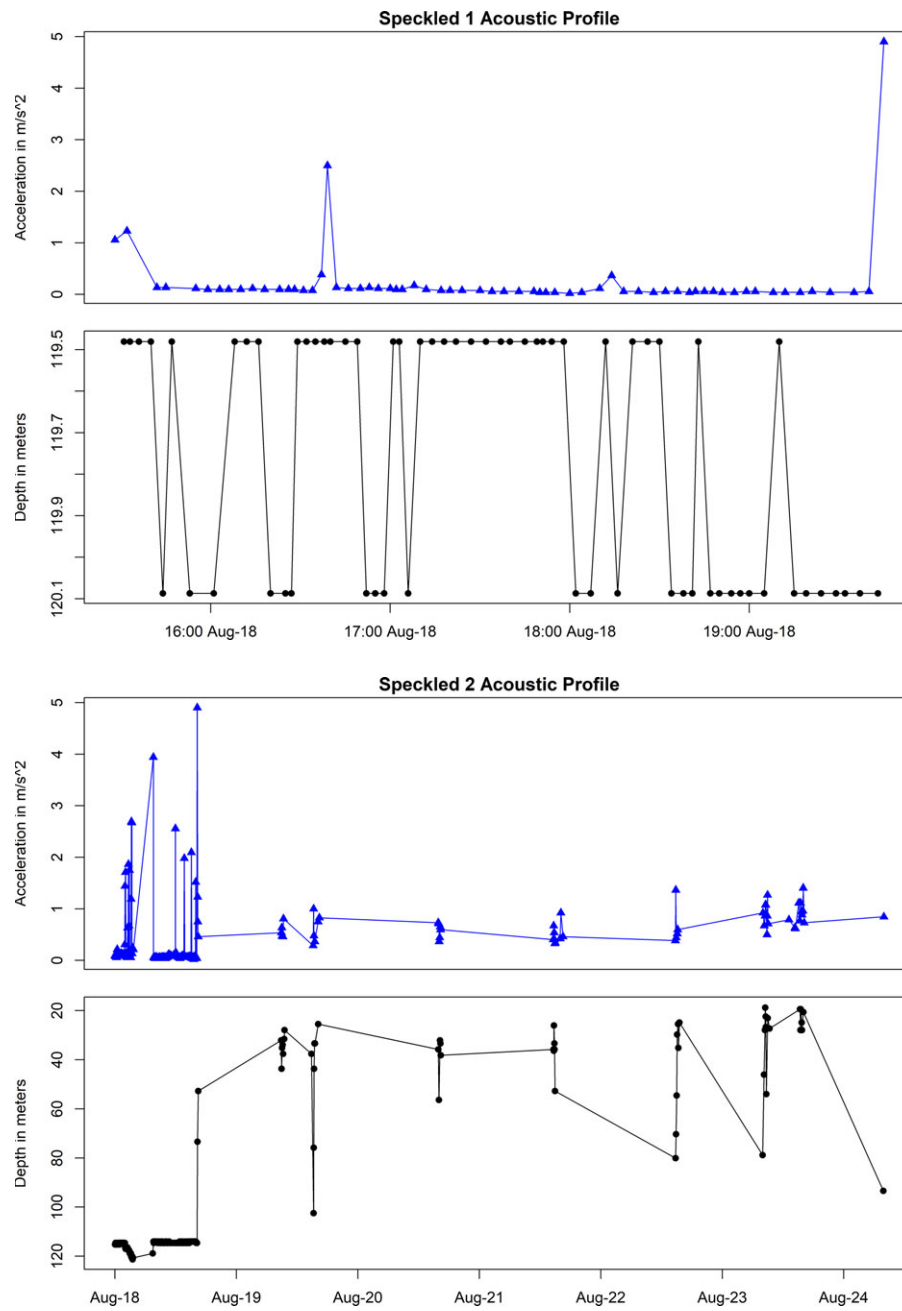


FIGURE A.1. Continued.

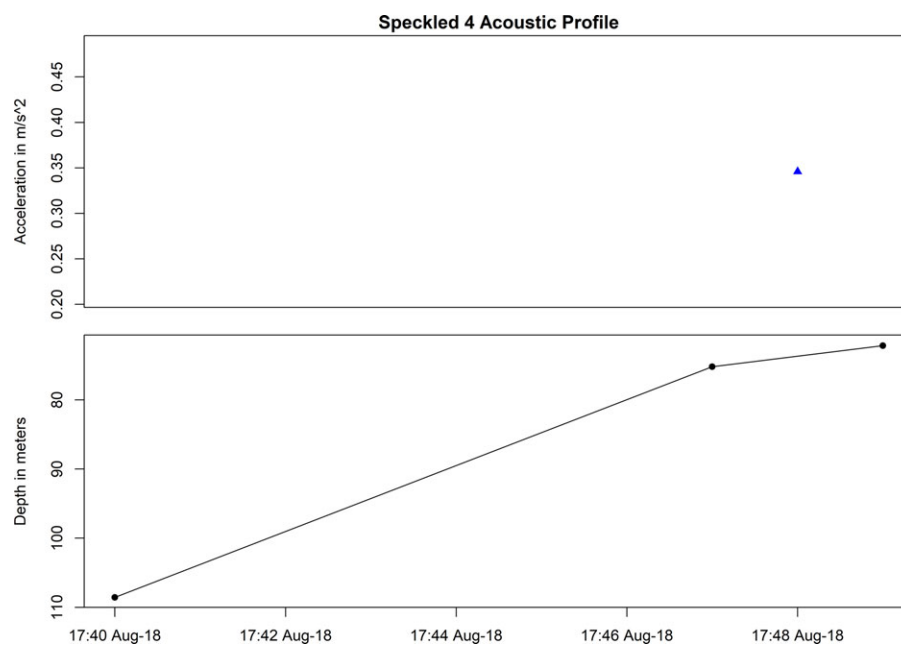


FIGURE A.1. Continued.