

ABSTRACT

RUNDE, BRENDAN JAMES. Investigating Challenges and Solutions for Management and Assessment of Reef Fishes off the Southeastern U.S.A. (Under the direction of Dr. Jeffrey A. Buckel).

The southeast US Atlantic supports fisheries for a wide variety of species. Participation in and regulations for these fisheries have both increased in recent decades, causing more fish to be released. Fisheries that release a portion of catch pose challenges for management, particularly if release mortality is high. The complex of reef-associated fishes in the southeast US supports one such fishery. Severe barotrauma experienced by many species in this group leads to levels of release mortality that can impede sustainability. These circumstances have left managers with few options; in order to achieve sustainability in the fishery for fishes like snappers and groupers, either release mortality must be substantially reduced or effort must be eliminated in a portion of habitat. In the first two chapters of this dissertation, I explored these two options via empirical studies. I tagged deep-water groupers and released them with descender devices, and estimated ~60% survival for fish released at depth (a major improvement over the assumed 0% survival for surface releases). In addition, I evaluated the effect of a Marine Protected Area (MPA) that was designated in 2009 off Wilmington, NC. Using scientific sonar and biological sampling, I found limited evidence that the MPA is working as intended, though other analyses were inconclusive. It is possible that more time and stricter enforcement are necessary before the MPA effect is detectable. In the third chapter of this dissertation, I explored the implications of a phenomenon that has long been ignored in most fisheries management: that some individual fish are caught and released multiple times. I modeled tag return data for four species of reef fishes and described the implications for stock assessments. Findings suggest that the proportion of fish that survive release is higher after releases 2 or greater as compared to the first release; this may be a

result of phenotypic heterogeneity with respect to robustness against the stressors of capture and release. Further, values used in some stock assessments may be biased as a result of miscounting unique fish multiple times; assessment scientists should be cautious when using total catch (including releases) as stock assessment input. Overall, this dissertation provides valuable content for stock assessment scientists and fishery managers. Evaluating and refining management approaches is a critical step that must be undertaken if sustainable fisheries are to be attained. The results and insights provided herein have already made a difference in this region's management, and will continue to do so.

© Copyright 2021 by Brendan J. Runde

All Rights Reserved

Investigating Challenges and Solutions for Management and Assessment of Reef Fishes off the
Southeastern U.S.A.

by
Brendan James Runde

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Fisheries, Wildlife, and Conservation Biology

Raleigh, North Carolina
2021

APPROVED BY:

Dr. Jeffrey A. Buckel
Committee Chair

Dr. David B. Eggleston

Dr. Jie Cao

Dr. Kyle W. Shertzer

In itinere virtus

BIOGRAPHY

I grew up in Southern Maryland, a peninsula bordered by tributaries of the Chesapeake Bay and home to a unique cultural cocktail of seafood, Amish-made goods, and misspelled road signs. I spent my first 17 years there, exploring the woods and waters, nurturing a curiosity for the “why” and “how” of nature. Along with my older sister Kristina, I was raised by my parents Chris and Karen Runde to appreciate and respect all living things (mosquitoes notwithstanding). After graduating from Chopticon High School in 2009, I began formal pursuit of my eventual calling (fisheries science) at Virginia Tech. The four years I spent in the mountains of southwest Virginia produced many powerful and enduring friendships and memories. I graduated in 2013 with two Bachelor of Science degrees (Biology and Fisheries Science). After a brief stint reconnecting with Southern Maryland, complacency gave way to ennui; I applied for and was offered a position at NC State University in pursuit of a Master of Science degree in Dr. Jeffrey Buckel’s lab. To that end, I moved first to Raleigh and then to Morehead City, North Carolina. From 2014-2017, I was exposed to the wonders of conducting original biological research on our marine resources. When Jeff offered me an opportunity to stay on for a Doctoral Degree, I accepted without reservation and matriculated in the summer of 2017. The technical aspects of that degree are contained in this document; of the intangible scientific and life experiences that I acquired along the way, there is not sufficient space (nor sufficient words) to explore herein.

ACKNOWLEDGMENTS

This dissertation would not have been possible without the support of quite a few people and organizations; my sincerest thanks to all of them. I begin by thanking my parents, Chris and Karen, and sister Kristina, deceased grandparents Herb and Louise Kraft, extended relatives on both sides (Rundes, Krafts, et al.), as well the Farley and the Mattingly families, for their upbringing, love, and support. I was also shaped into adulthood by some fabulous teachers in grade school – in alphabetical order, I am specifically indebted to Missy Bell, Jennifer Cord, Ann Eichenmueller, Patty Kuzmick, Sarah Lorek (née Vence), Amanda Myatt, Scott Russell, Jessica Yohe, and Cindy Young. During my undergraduate years, several professors and mentors helped me find my footing and passion as a scientist. Thanks to Chris Chambers, Tom Miller, Brian Murphy, Don Orth, and Andrew Rypel for this mentorship.

Thanks of course to Jeff Buckel for his endless tolerance and careful guidance over the course of both of my graduate degrees. I am also grateful for Jie Cao, Dave Eggleston, and Kyle Shertzer for serving on my committee and being ready with guidance whenever asked. I also greatly appreciate Craig Harms for serving as the Graduate School Representative on my committee.

Over my seven years of graduate school, I have benefitted tremendously from friendships and collaborations with other scientists, both inside and outside of the Buckel Lab and NC State. Without question, foremost among these is Paul Rudershausen, who has for the better part of a decade been a sounding board for me on every topic under the sun; I am forever appreciative of him for his roles as my “academic big brother,” teacher, and friend. In addition, it has been an honor and a joy to work (and play) alongside Linnea Andersen, Nate Bacheler, Matt Damiano, Erik Ebert, Riley Gallagher, Christian Kamrath, Jacob Krause, Steve Lombardo, Cori

Lopazanski, Cam Luck, Chloe Mikles, Ray Mroch, Owen Mulvey-McFerron, Avery Paxton, Chris Taylor, and Thom Tears.

For helping me realize my goals for the field components of this research, I am extremely grateful to Tom Burgess, Dale Britt, and Patrick and Jacky Dufour. Their expertise on the water had been invaluable to me.

Thank you to Marlu Bolton, Neal Ciampa, Linda Dunn, Freha Legoas, Dawn Newkirk, and Ernie Yeager for a variety of logistical and administrative support over my time at NC State. Your collective diligence and hard work made graduate life at CMAST a breeze.

I wish to acknowledge the financial support of the NOAA Cooperative Research Program and Saltonstall-Kennedy Program; without their grants, the ideas for the studies discussed in this document would have never taken flight. Finally, I also received several generous scholarships during the course of my PhD. Specifically, the Steven Berkeley Marine Conservation Fellowship, Joe E. and Robin C. Hightower Graduate Student Award, and North Carolina Wildlife Federation Conservation Leadership Grant made a tremendous difference in my quality of life over the last several years.

TABLE OF CONTENTS

LIST OF TABLES	viii
LIST OF FIGURES	x
INTRODUCTION	1
References	5
CHAPTER 1. ASSIGNING FATES IN TELEMTRY STUDIES USING HIDDEN MARKOV MODELS: AN APPLICATION TO DEEPWATER GROUPERS RELEASED WITH DESCENDER DEVICES	8
Abstract	8
Introduction	9
Methods	13
Results	19
Discussion	21
Conclusions	31
Acknowledgements	31
References	32
Tables	40
Figures	44
CHAPTER 2: EVALUATING THE EFFECTS OF A DEEP-WATER MARINE PROTECTED AREA A DECADE AFTER CLOSURE: A MULTIFACTED APPROACH REVEALS EQUIVOCAL BENEFITS TO REEF FISH POPULATIONS	57
Abstract	57
Introduction	58
Methods	64
Results	75
Discussion	80
Conclusions	90
Acknowledgements	90
References	91
Tables	104
Figures	115
CHAPTER 3: REPETITIVE CAPTURE OF MARINE FISHES: IMPLICATIONS FOR ESTIMATING NUMBER AND MORTALITY OF RELEASES	122
Abstract	122
Introduction	123

Methods.....	125
Results.....	132
Discussion.....	134
Acknowledgements.....	143
References.....	144
Tables.....	154
Figures.....	158
CONCLUSION.....	161
References.....	163
APPENDICES.....	164
Appendix A: Chapter 1 Supplementary Material.....	165
Appendix B: Chapter 2 Supplementary Material.....	188
Appendix C: Chapter 3 Supplementary Material.....	196

LIST OF TABLES

CHAPTER 1

Table 1.	Information for individual groupers off North Carolina, USA.....	40
Table 2.	Parameter estimates for our 3-state hidden Markov models.....	43

CHAPTER 2

Table 1.	All reef fish species encountered in the present study and in Rudershausen et al.	106
Table 2.	Linear distance surveyed with hydroacoustics in the Snowy Wreck Marine Protected Area (SWMPA) and an adjacent area (Control) by Rudershausen et al. (2010) before the SWMPA was designated (2007-2009) and in the present study (2018-2020).....	107
Table 3.	Number of aggregations of biomass (fish schools) identified with hydroacoustics in the SWMPA and an adjacent area that is open to fishing (Control) during each survey trip.....	109
Table 4.	Results from the biomass hurdle model with the lowest WAIC: Period + Slope + Season + Trip. Variables containing “hu” pertain to the first stage of the hurdle model. ESS refers to the effective sample size.	110
Table 5.	Results from the biomass model containing the full suite of predictor variables, which was competitive with the best model in terms of WAIC. Variables containing “hu” pertain to the first stage of the hurdle model. ESS refers to the effective sample size...	111
Table 6.	Results from the Area + Trip hurdle model for predicting reef fish CPUE. Variables from the first stage of the hurdle model begin with “Hu,” and coefficient values are provided in untransformed logit terms.....	112
Table 7.	Results from the Period + Trip hurdle model for predicting reef fish CPUE. Variables from the first stage of the hurdle model begin with “Hu,” and coefficient values are provided in untransformed logit terms.....	112
Table 8.	PERMANOVA table relating Area (Snowy Wreck Marine Protected Area or Control),	

Period (before or after closure), and their interaction to the composition of the reef fish community.	113
Table 9.	
Sample sizes for red porgy ages caught with all gear types.	113
Table 10.	
Catch curve estimates of instantaneous total mortality (Z) for red porgy caught with all gear types.	114
Table 11.	
ANOVA table for the model relating Area (Snowy Wreck Marine Protected Area or Control), Period (before or after closure), and their interaction to size distributions of red porgy.	114
 CHAPTER 3	
Table 1.	
Releases and recaptures from four tagging studies of reef fishes in the southeast US...	154
Table 2.	
Results from Cox proportional hazards regression models for each of four reef fish species in the southeast US.	155
Table 3.	
Results from our simulation investigating the possibility that tag shedding can lead to incorrect identification of recaptured fish.	156
Table 4.	
Proportion of live releases to total catch for a selection of common or popular US Atlantic recreational demersal or reef-associated species in 1997 and 2017.	157

LIST OF FIGURES

CHAPTER 1

- Figure 1.
Map showing the region of the Snowy Wreck Marine Protected Area (MPA) off the coast of North Carolina, USA..... 44
- Figure 2.
Distributions (lines) and histograms (gray bars) of mean acceleration (m/s^2), mean relative depth, and depth standard deviation data streams for hidden Markov model (HMM) developed for telemetered six species of deepwater groupers off North Carolina, USA, in 2018..... 46
- Figure 3.
Example acoustic profiles (full time series data) for five telemetry tags, with upper panels indicating acceleration (m/s^2) and lower panels indicating depth (m) 48
- Figure 4.
Plot of the Kaplan-Meier survivorship curves for 40 deepwater groupers released via descender device at the continental shelf break off North Carolina, USA, in 2018. 55

CHAPTER 2

- Figure 1.
Map of the MPA network of the southeast United States Atlantic. Contour lines are 40, 100, and 140 m depth..... 115
- Figure 2.
Map of the central North Carolina (USA) coastline. 116
- Figure 3.
Transect lines for hydroacoustic surveys conducted by Rudershausen et al. (2010) in 2007-2009 (left) and in the present study (right) in the Snowy Wreck Marine Protected Area (below) and an adjacent area that is open to fishing (above)..... 117
- Figure 4.
Results of non-metric multidimensional scaling (NMDS) comparing reef fish communities in the two areas (Snowy Wreck Marine Protected Area and control) and time periods (before and after)..... 118
- Figure 5.
Mean age and Shannon age diversity for red porgy caught in the Snowy Wreck Marine Protected Area and adjacent control area from 2015-2020 by our survey or the Southeast Reef Fish Survey. 119

Figure 6.
Catch curves for red porgy caught in Onslow Bay, North Carolina. 120

Figure 7.
Size (total length) distributions for red porgy caught in the Snowy Wreck Marine
Protected Area..... 121

CHAPTER 3

Figure 1.
Calculations of total unique released fish, total live releases, estimated (est.) dead
discards, and actual dead discards under (a) constant survival and (b) increased
survival. In both scenarios, we assume all live fish are captured in each period..... 158

Figure 2.
Proportion of bootstrapped datasets for which the best model contained Release
Number for (A) black sea bass and (B) Warsaw grouper from our examination of the
effect of Φ (combined rate of tag shedding and tagging-induced mortality)..... 159

Figure 3.
Stock assessment results for black sea bass (SEDAR 2018) and red grouper (SEDAR
2017) 160

INTRODUCTION

The Atlantic Ocean off of the southeast United States supports fisheries for a wide variety of species. This “embarrassment of fishes” has proved a mixed blessing for managers, as increases in fishing effort (Shertzer et al. 2019) and improvements in fishing technology (Glass et al. 2007; Cooke et al. 2021) over the last several decades have given rise to new regulatory challenges. Effort has continued to increase (particularly in the recreational sector; (Ihde et al. 2011; Shertzer et al. 2019)), and managers have often responded with stricter regulations which lead to a greater portion of catch being released (Arlinghaus et al. 2007). Changes in the number and proportion of releases can result in shifts in the suitability of different management strategies. This evolution of fisheries off the southeast United States coast merits innovation and evaluation of new management methods as well as reassessment of previous protocols to ensure their continued applicability.

One fishery in this region that is particularly difficult to manage is that for demersal reef-associated fishes such as snappers and groupers (Lindeman et al. 2000). Several species in this complex are currently listed as overfished or undergoing overfishing (NMFS 2019) despite federal requirements for the prevention of these circumstances via the Magnuson-Stevens Fishery Conservation and Management Act. Dozens of species in this group cohabitate, and the use of unselective gear (such as baited hooks) often results in bycatch of prohibited and/or imperiled species. This frequent bycatch, paired with severe barotrauma experienced by many species in this group, leads to levels of release mortality that can impede sustainability (Huntsman et al. 1999). Even for species that are infrequently encountered, extreme longevity in some species (e.g., >50 years for some groupers) diminishes the possibility of any individual fish escaping capture (and possibly release mortality) over its lifetime.

These circumstances have left managers with few options; in order to achieve sustainability in the fishery for species like snappers and groupers, either release mortality must be substantially reduced or effort must be eliminated in a portion of habitat. In the first two chapters of this dissertation, I explore these two options via empirical studies.

In the last ~15 years, strategies for barotrauma mitigation have emerged and been refined. One such strategy involves recompressing a caught fish by returning it to a depth where expanded gases recompress and it can maintain buoyancy by itself (Bartholomew and Bohnsack 2005; Theberge and Parker 2005). This procedure is accomplished with the use of a descender (or descending) device, and has been tested on several species in the United States Pacific (e.g., Jarvis and Lowe 2008) and Gulf of Mexico (e.g., Curtis et al. 2015). In Chapter 1 of this dissertation, I built upon a previous study of the effectiveness of descender devices in promoting survival in deep-water groupers off North Carolina (Runde and Buckel 2018). With a larger sample size, varied release treatments, and more sophisticated analyses, I generated estimates for post-release survival that are directly usable by fishery managers in this region (Runde et al. 2020a). Partially as a result of this work, the South Atlantic Fishery Management Council (SAFMC) recently adopted new regulations requiring the presence of a descender device on any vessel possessing reef fish species. With increased use, the values of discard mortality for released deepwater grouper (e.g. snowy grouper) might be decreased to values less than 100% in future stock assessments.

In the early 2000s, the SAFMC recognized that one method for eliminating effort in a portion of deep-water habitat was the designation of Marine Protected Areas (MPAs). To that end, in 2009 the SAFMC established a network of eight MPAs along the Atlantic coast from southern Florida to central North Carolina to “protect a portion of the population and habitat of

long-lived, slow growing, deep-water species from directed fishing pressure to achieve a more natural sex ratio, age, and size structure...” (SAFMC 2007). Prior to the establishment of these eight MPAs, Rudershausen et al. (2010) collected biological and fisheries acoustics data in one of the soon-to-be closed areas (off Wilmington, North Carolina) as well as an adjacent area that has remained open to fishing. In the second chapter of this dissertation, I evaluated this MPA by repeating the survey done by Rudershausen et al. (2010). Using the same scientific sonar unit and identical biological sampling protocols, I collected data that were used in a suite of analyses seeking to identify whether the MPA has had a positive effect on the reef fish populations it was intended to protect.

Evaluation of modern management tools such as gear requirements (e.g., descender devices) and spatial closures is extremely valuable. However, at least equally as valuable is the assessment of already-established methods for evaluating fish stocks. In the third and final chapter of this dissertation, I explore the implications of a phenomenon that has long been ignored in fisheries management: that some individual fish are caught and released multiple times. I modeled tag return data from four empirical studies of reef species in the southeast United States and described the implications for stock assessments. Specifically, I examined how the proportion of released fish that survive varies between successive capture events, as well as how changes to the number and mortality of releases could be accounted for in future assessments (Runde et al. 2020b).

Overall, this dissertation provides valuable content for stock assessment scientists and fishery managers. Evaluating and refining management approaches is a critical step that must be undertaken if sustainable fisheries are to be attained. The results and insights provided herein

have already made a difference in this region's management; it is my hope that they will continue to be used as we march forward in an ever-changing world of fisheries science.

References

- Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., and Thorstad, E.B. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science* 15(1-2): 75-167.
- Bartholomew, A. and Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*, 15(1): 129-154.
- Cooke, S.J., Venturelli, P., Twardek, W.M., Lennox, R.J., Brownscombe, J.W., Skov, C., Hyder, K., Suski, C.D., Diggles, B.K., Arlinghaus, R., and Danylchuk, A.J. 2021. Technological innovations in the recreational fishing sector: implications for fisheries management and policy. *Reviews in Fish Biology and Fisheries*. doi:10.1007/s11160-021-09643-1.
- Curtis, J.M., Johnson, M.W., Diamond, S.L., and Stunz, G.W. 2015. Quantifying delayed mortality from barotrauma impairment in discarded red snapper using acoustic telemetry. *Marine and Coastal Fisheries* 7(1): 434-449. doi:10.1080/19425120.2015.1074968.
- Glass, C.W., Walsh, S.J., van Marlen, B., and Amaratunga, T. 2007. Fishing technology in the 21st century: integrating fishing and ecosystem conservation. *ICES J. Mar. Sci* 64(8): 1499-1616.
- Huntsman, G., Potts, J., Mays, R., and Vaughan, D. Groupers (Serranidae, Epinephelinae): Endangered Apex Predators of Reef Communities. *In* American Fisheries Society Symposium. 1999. pp. 217-231.
- Ihde, T.F., Wilberg, M.J., Loewensteiner, D.A., Secor, D.H., and Miller, T.J. 2011. The increasing importance of marine recreational fishing in the US: Challenges for

- management. *Fisheries Research* **108**(2): 268-276.
doi:<https://doi.org/10.1016/j.fishres.2010.12.016>.
- Jarvis, E.T., and Lowe, C.G. 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**(7): 1286-1296. doi:10.1139/F08-071.
- Lindeman, K.C., Pugliese, R., Waugh, G.T., and Ault, J.S. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of marine science* **66**(3): 929-956.
- NMFS. 2019. Status of Stocks 2019 Annual Report to Congress on the Status of US Fisheries. NOAA Fisheries Service.
- Rudershausen, P., Mitchell, W., Buckel, J., Williams, E., and Hazen, E. 2010. Developing a two-step fishery-independent design to estimate the relative abundance of deepwater reef fish: application to a marine protected area off the southeastern United States coast. *Fisheries Research* **105**(3): 254-260.
- Runde, B.J., and Buckel, J.A. 2018. Descender devices are promising tools for increasing survival in deepwater groupers. *Marine and Coastal Fisheries* **10**(2): 100-117.
- Runde, B.J., Michelot, T., Bacheler, N.M., Shertzer, K.W., and Buckel, J.A. 2020a. Assigning fates in telemetry studies using hidden Markov models: an application to deepwater groupers released with descender devices. *North American Journal of Fisheries Management*.

Runde, B.J., Buckel, J.A., Shertzer, K.W., Bacheler, N.M., Rudershausen, P.J., and Sauls, B.

2020b. Repetitive capture of marine fishes: implications for estimating number and mortality of releases. *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsaa166.

SAFMC. 2007. Amendment 14 to the Fishery Management Plan for the Snapper Grouper Fishery of the South Atlantic Region. North Charleston, SC.

Shertzer, K.W., Williams, E.H., Craig, J.K., Fitzpatrick, E.E., Klibansky, N., and Siegfried, K.I.

2019. Recreational sector is the dominant source of fishing mortality for oceanic fishes in the Southeast United States Atlantic Ocean. *Fisheries Management and Ecology* **0**(0). doi:10.1111/fme.12371.

Theberge, S., and Parker, S.J. 2005. Release methods for rockfish. Sea Grant Oregon, Oregon State University.

**CHAPTER 1. ASSIGNING FATES IN TELEMTRY STUDIES USING HIDDEN
MARKOV MODELS: AN APPLICATION TO DEEPWATER GROUPERS RELEASED
WITH DESCENDER DEVICES**

This chapter has been published in North American Journal of Fisheries Management. It is co-authored by Théo Michelot, Nathan Bacheler, Kyle Shertzer, and Jeffrey Buckel.

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 precision, accuracy, and utility of such studies. We released 57 acoustically tagged deepwater groupers of six 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 alive and dead fish (which 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% confidence interval 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 (0.47, 0.80). Both estimates represent a substantial improvement over survival of surface released grouper (~zero). Furthermore, HMMs estimated zero survival for an additional five descended groupers at a wreck site in 240 m depth, though one analysis using prior information suggests survival may be possible in that depth. These

estimates were aided by the objectivity of HMMs and we recommend 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.

Introduction

The use and utility of electronic tags in ecology has 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. 2019), 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 post-release (or discard) survival of fishes (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 to 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 assumed 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), though 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 where 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. Further, for animals and systems where post-release predation or scavenging may be common, distinguishing between the behaviors (e.g., depth, velocity, acceleration) of a live study animal versus 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 released-alive fish imply discard mortalities (Yergey et al. 2012; Capizzano et al. 2016). A more opportunistic approach to identify a fate involves re-sighting 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 detection information of known-fate and unknown-fate individuals 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). HMMs 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, 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, though 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* (Bachelier 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 eaten a tag). To our knowledge, HMMs have never been used in survival studies where 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 catch (Runde et al. 2019) and 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 species of deepwater groupers 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 Snowy Grouper *Hyporthodus niveatus*, for which the recreational bag limit in the SEUS is currently one per vessel with no minimum size (SAFMC 2016; Runde and Buckel 2018). Further, several species of groupers in the SEUS are listed as overfished (Snowy Grouper; Red Grouper *Epinephelus morio*), 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. 2019), 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 without (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 could 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 introduce substantial improvements in the approach to analysis and inference. Specifically, we used 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 total lengths (TL) were measured to the nearest 5 mm and groupers > 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). V13AP transmitters contain two sensors: depth (via a converted pressure value) and acceleration, produced as an average value over a 45 sec interval. More description of accelerometer / pressure sensors may be found in 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 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, grouper 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 m square 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 were 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 grouper 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 ~43

kg steel sacrificial ballast attached to a receiver lug with 6.4 mm diameter 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 HMM and assignments of fate. Examples of full time series information for individual fish are located in Figure 3 and Appendix 1.

A hidden Markov model 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 modelled with transition probabilities. In preliminary analyses, we fitted models with 2, 3, and 4 states, and found that the 3-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 3-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. HMMs 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 regularized temporally. Therefore, we binned detections into 30 min time bins for the purpose of regularization. We chose an interval long enough so that most time bins contained one observation or more, and 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-minute bin, denoted by Z_{1t} , and was parameterized as a gamma distribution. Acceleration is a proxy for the level of activity of the animal, and we expect the levels of activity of groupers and their predators to be different. Therefore, we would expect the distributions of accelerations from a live grouper and a dead grouper to be different. The second data stream was mean depth as a proportion of release depth (m), denoted by Z_{2t} , where a value of 1.0 represented the fish being detected at exactly the same depth as was recorded during capture. This transformation was necessary as the study animals were released across a range of depths and therefore serves as a proxy for distance from the seafloor. For example, two surviving grouper 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 HMM model 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), we expected different depth utilizations. This data stream was also parameterized as a gamma distribution. Finally, the third data stream was the standard

deviation of all depth values in each time bin, denoted by Z_{3t} . Standard deviation 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/down movements, though 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 standard deviation of depth for each time bin offer 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

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

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

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

in state $S_t = j = \in(1, 2, 3)$ where the θ_{ij} are state-dependent observation parameters. HMMs 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 descended-alive individuals. If descended-alive groupers displayed the same state as the negative controls, they were determined to be 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 tag 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, 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 post-release survival. We conducted separate Kaplan-Meier procedures for groupers released via descending, released into the surface enclosure, and for releases at the Snowy Wreck; estimates were generated twice for each of these groups (once each for Analysis 1 and Analysis 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 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 descended alive, two surface released that swam down, and three dead). 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). Total lengths, 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 estimates for the emission distributions for each data stream were estimated (Table 2). Estimates of the parameters of the emission distributions showed clear distinctions between the three states (Table 2; Figure 2). State 1 was characterized by the lowest mean acceleration (“Acc”) values, the closest relative depth (“RelDepth”) to 1.0, and the lowest mean standard deviation of depth (“DepthSD”). State 2 had similar Acc values to 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

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

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 minutes respectively, and each had very few detections. The terminal detection for each of these individuals suggested the transmitter was within a few meters of the surface. Scamp 3 was detected for approximately 26 hours. The HMM classified this individual as exhibiting state 3 throughout the entire time period for which it was detected (Figure 3A). We reviewed the state sequences for the remaining individuals, and those dominated by states 1 and 2 were categorized as survivals (e.g., Figure 3B).

For 40 groupers descended alive at the shelf break, Analysis 1 determined 14 had survived the duration of the study, three lost their tags while still alive, one 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 post-tagging recovery behavior in demersal fishes (e.g., Collins 2014; see *Discussion*). Further, 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" is reflected in the differences between the two Analyses. Analysis 2 determined 14 grouper survived the duration of the study, four lost their tags while still alive, seven 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 died, two emigrated in the first two days, and one appeared to lose one tag within hours of release and then emigrate on day 4. We conclude that tag loss is possible given this attachment type, though 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 seven days after tagging, therefore our survival estimate at that time represents our estimate for the study overall. For groupers descended alive at the shelf break, the Kaplan-Meier survivorship procedure using Analysis 1 fates generated a survival estimate of 0.46 (95% confidence interval 0.33, 0.65; Figure 4). Using Analysis 2 fates, the survival estimate was 0.61 (0.47, 0.80).

Two of nine surface-released groupers swam down; under Analysis 1, both of these fish appeared to experience mortality on the day they were tagged (day zero), 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 estimates survival of 0.22 (0.07, 0.75) for surface-released groupers. Of five groupers released at the Snowy Wreck in 240 m, none survived beyond day zero using Analysis 1 fates, resulting in a survival estimate of 0.00. Analysis 2 interpretations suggest that all five may have emigrated within 9 days 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 to 1.00) from Analysis 1 and 2.

Discussion

The objectivity for fate assignment provided by hidden Markov models is a major improvement to telemetry-based survival studies. We found that in most cases the HMM could distinguish between known-dead individuals and 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 (Appendix 1; figures are ordered by species and individual), Snowy Grouper 3 (Figure 3C), and Speckled Hind 4 (Appendix 1), initial examination of the acoustic profiles suggested tag loss, and we would likely have considered these fish alive using subjective inference alone. 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 four days, five days, and one day 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 the transmitter was in 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 3D). 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 six. Because the depth detections for Scamp 10 resemble depths for live groupers, we categorized this individual as alive until tag loss in both

Analysis 1 and Analysis 2. All other groupers were tagged with transmitters with 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 non-zero acceleration detections until their transition to state 3 or disappearance (e.g., Snowy Grouper 20; Figure 3E). 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 (in the case of Snowy Grouper 20) August 30 and again on September 8. These brief, rapid, vertical movements from a near-constant depth of 120m to depths as shallow as 60m are a behavior we never observed in groupers 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 experiencing seafloor scavenging. There were nine individuals for which this potential on-seafloor scavenging was observed. The majority of these were categorized by the HMM as states 1 and 2 for much of their observation period but state 3 at the end of their detection history. 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 were alive and recovering from the stress associated with capture, tagging, and release, and emigrated after or during this recovery period by first migrating vertically. Collins (2014) and Runde and Buckel (2018) described a post-tagging

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 (*N. Wegner, NMFS, pers. comm.*). Unfortunately, we were unable to recapture any telemetered fish in this study; therefore, the interpretation of these animals' behavior remains uncertain. We recommend future telemetry studies tag a larger sample size of sacrificed individuals.

We identified some groupers that clearly lost their transmitter (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 these tag loss data would not correspond to any of the movement states of the HMM. We considered the possibility of a 4-state HMM, where the additional state would represent these data. However, this was not feasible given our use of relative depth as a datastream for the HMM. Indeed, the distribution of relative depths was not consistent across lost tags, because transmitters were lost at relative depths 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 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 3-state model. The 2-state model did not appropriately distinguish the descended-dead grouper from the released-alive fish. In the 4-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 3-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, e.g., depth relative to depth at release was chosen as a proxy for distance from the seafloor. We note that some groupers may have consistently occupied seafloor habitat but appear to sometimes be much deeper or much shallower than their release depth (e.g., Red Grouper 1; Figure 3F). 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 ~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 from the imperfection of the data streams available in this study.

Typical HMMs for animal movement result in biological description of the behavioral states identified such as “foraging” or “transiting” (e.g., Bacheler et al. 2019). For our purposes, such description is a dubious exercise given the data streams we had available. States 1 and 2 seemed to define animals that accelerate at a relatively low amount, occupy habitat close to the seafloor, and change depths a low to moderate amount. State 3 was described by animals that have higher acceleration, utilize a much wider range of depths, and change 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, though

without recapture of tagged groupers or of predators containing grouper tags, confirmation of these assertions is impossible. In cases where the fate of some of the fish is 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. Further, there are no accessible software packages to apply those models to telemetry data sets, and the large size of our data set (~60,000 time bins) would make the model fitting time-consuming. For these reasons, we opted for a more standard discrete-time approach, and recommend that continuous-time methods could be explored in future research.

The duration of time bins for discrete-time models can influence results. In addition to 30-minute bins, we investigated the use of 15- and 60-minute intervals. Neither of these models resulted in different fate assignments than the 30-minute version. We elected to use 30 minutes because the proportion of bins with no data was much lower than the 15-minute 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 estimate from Analysis 1 of 0.46 (0.33, 0.65) and from Analysis 2 of 0.61 (0.47, 0.80) fall within the range estimated by Runde and Buckel (2018). Their survival estimate of 0.50 (0.10, 0.91) had extremely broad confidence intervals 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 confidence intervals in the present study. However, uncertainty in state determination from the HMM was not propagated into our final fate assignment and 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, though some have been conducted in slightly shallower marine environments. Curtis et al. (2015) worked in 50m and estimated survival of descended Red Snapper as 0.83 (0.68, 0.98). Sumpton et al. (2010) tagged red emperor *L. sebae* in depths predominantly >30 m but found little evidence for descender devices promoting survival in this species. We recommend 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 (0.32, 0.76) and 0.38 (0.15, 0.92) respectively in Analysis 1, and

the two species had estimates of 0.79 (0.62, 1.00) and 0.31 (0.10, 0.96) respectively in Analysis 2. The majority of these mean estimates are near our overall estimates of 0.46 and 0.62, and all of the confidence intervals overlap widely, supporting our choice to pool the species-specific estimates.

Current management assumes discard survival of zero for many 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 is 0.22, we are inclined to agree in principle with the current assumption of zero survival for the species examined, though a low level of survival may be possible particularly in the shallower portion of these species' ranges. However, we have demonstrated that survival is significantly higher than zero for groupers 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 southeast US (implemented June 2020). Given our findings, we recommend other management agencies take similar measures to promote widespread use of descender devices in this and other fisheries.

Many of our groupers, including all five 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 out of five of these fish were detected mid-water-column during their detection history at depths of 22 m, 26 m, and 71 m. Ambient pressure at 100 m is 25 atm; the shallower depths where we detected these individuals has ambient pressure of 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 for 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 five month period for which our receivers were deployed. At the Snowy Wreck, receivers were in place for eighteen months, over which we detected one tiger shark and eight white sharks. Total lengths of these predators ranged from 3.1 m to 4.2 m for Tiger Sharks (*B. Frazier, pers comm*) and 3.3 m to 4.3 m for White Sharks (*G. Skomal and M. Winton, pers comm*). Sharks were detected in 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 were able to avoid predation during their recovery period. Some of the groupers may have been deceased prior to ingestion by a predator though some may have been attacked while alive. This is supported by detection data showing 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 when 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 with possible relief caused by tagging (Johnson et al. 2015). Attachment methods have ranged from 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 used by Curtis et al. (2015), methods using suture material passed through the fish by Bachelier et al. (2019), and attachment via an intramuscular stainless steel bolt by Bohaboy et al. (2019). To our knowledge no attempts have been made to quantify tag loss *in situ* for any of these methods, though some authors used tank holding studies to this end (e.g., Bachelier et al., 2019). Therefore, there is no resolution as to the best tag attachment procedure for such studies. Our attempt to quantify tag loss by double tagging groupers was unsuccessful, as zero of four double-tagged fish survived beyond day zero. 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 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, though 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 hidden Markov models as a means of increasing objectivity of fate assignment in our study. While 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 that all surface-released groupers may have died corroborates the assumed 100% discard mortality for many of 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 descended, it may be necessary for managers to take additional measures (such as spatial closures) to protect imperiled species from overfishing.

Acknowledgements

Funding for this work was provided by the NOAA Saltonstall-Kennedy Program (#NA17NMF4270204). For assistance in the field, we thank P. Rudershausen, J. Styron, D. Wells, K. Johns, D. Berrane, D. Britt, P. Dufour, E. Scheeler, E. Ebert, R. Gallagher, C. Mikles,

J. Fader, O. Mulvey-Mcferron, K. Erickson, A. Matthews, and T. Burgess. We gratefully acknowledge J. Locascio for the extended use of two receivers and N. Wegner for his thoughts on fate assignment. We thank J. Cao for reviewing an early draft of this paper. Scholarship support for B. Runde was provided by the Steven Berkeley Marine Conservation Fellowship, the Joseph E. and Robin C. Hightower Graduate Student Award in Fisheries and Wildlife Sciences, and the North Carolina Wildlife Federation. The scientific results and conclusions, as well as any views and opinions expressed herein, are those of the authors and do not necessarily reflect those of any government agency or institution. There is no conflict of interest declared in this article.

References

- Bacheler, N. M., and J. C. Ballenger. 2018. Decadal-scale decline of Scamp (*Mycteroperca phenax*) along the southeast United States Atlantic coast. *Fisheries Research* 204: 74-87.
- Bacheler, N. M., J. A. Buckel, J. E. Hightower, L. M. Paramore, and K. H. Pollock. 2009. A combined telemetry–tag return approach to estimate fishing and natural mortality rates of an estuarine fish. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1230-1244.
- Bacheler, N. M., T. Michelot, R. T. Cheshire, and K. W. Shertzer. 2019. Fine-scale movement patterns and behavioral states of Gray Triggerfish *Balistes capriscus* determined from acoustic telemetry and hidden Markov models. *Fisheries Research* 215:76-89.
- Baktoft, H., K. Aarestrup, S. Berg, M. Boel, L. Jacobsen, A. Koed, M. W. Pedersen, J. C. Svendsen, and C. Skov. 2013. Effects of angling and manual handling on pike behaviour investigated by high-resolution positional telemetry. *Fisheries Management and Ecology* 20:518-525.
- Bendock, T., and M. Alexandersdottir. 1993. Hooking mortality of Chinook Salmon released in the Kenai River, Alaska. *North American Journal of Fisheries Management* 13:540-549.

- Benoît, H. P., T. Hurlbut, J. Chassé, and I. D. Jonsen. 2012. Estimating fishery-scale rates of discard mortality using conditional reasoning. *Fisheries Research* 125:318-330.
- Beverton, R., and S. J. Holt. 1957. On the Dynamics of Exploited Fish Populations, Vol. II of *Fishery Investigations*, Ministry of Agriculture. Fisheries and Food.
- Blackwell, P. G., M. Niu, M. S. Lambert, and S. D. LaPoint. 2016. Exact Bayesian inference for animal movement in continuous time. *Methods in Ecology and Evolution*, 7: 184-195.
- Bleckmann, H., and M. H. Hofmann. 1999. Special senses. *Sharks, Skates and Rays: the Biology of Elasmobranchs*:300-328.
- Bohaboy, E. C., T. L. Guttridge, N. Hammerschlag, M. P. M. Van Zinnicq Bergmann, and W. F. Patterson, III. 2019. Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. *ICES Journal of Marine Science*.
- Breen, M., and R. Cook. 2002. Inclusion of discard and escape mortality estimates in stock assessment models and its likely impact on fisheries management. *ICES CM* 27:15.
- Brill, R., M. Lutcavage, G. Metzger, P. Bushnell, M. Arendt, and J. Lucy. 2002. Survival of juvenile Northern Bluefin Tuna following catch and release, using ultrasonic telemetry. Pages 180-183 in *American Fisheries Society Symposium*. American Fisheries Society.
- Capizzano, C. W., J. W. Mandelman, W. S. Hoffman, M. J. Dean, D. R. Zemeckis, H. P. Benoît, J. Kneebone, E. Jones, M. J. Stettner, and N. J. Buchan. 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.
- Capizzano, C. W., D. R. Zemeckis, W. S. Hoffman, H. P. Benoît, E. Jones, M. J. Dean, N. Ribblett, J. A. Sulikowski, and J. W. Mandelman. 2019. Fishery-scale discard mortality

- rate estimate for Haddock in the Gulf of Maine recreational fishery. *North American Journal of Fisheries Management* 0.
- 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, Florida.
- Crossin, G. T., M. R. Heupel, C. M. Holbrook, N. E. Hussey, S. K. Lowerre-Barbieri, V. M. Nguyen, G. D. Raby, and S. J. Cooke. 2017. Acoustic telemetry and fisheries management. *Ecological Applications* 27:1031-1049.
- 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* 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. W. 2002. Key principles for understanding fish bycatch discard mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1834-1843.
- Dijkgraaf, S. 1963. The functioning and significance of the lateral-line organs. *Biological reviews* 38:51-105.
- 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* 6:190-199.

- Eberts, R. L., and C. M. Somers. 2017. Venting and descending provide equivocal benefits for catch-and-release survival: study design influences effectiveness more than barotrauma Relief Method. *North American Journal of Fisheries Management* 37:612-623.
- Eberts, R. L., M. A. Zak, R. G. Manzon, and C. M. Somers. 2018. Walleye responses to barotrauma relief treatments for catch-and-release angling: short-term changes to condition and behavior. *Journal of Fish and Wildlife Management* 9:415-430.
- Gibson, A. J. F., E. A. Halfyard, R. G. Bradford, M. J. Stokesbury, and A. M. Redden. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic Salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 72:728-741.
- Gorsky, D., J. Zydlewski, and D. Basley. 2012. Characterizing seasonal habitat use and diel vertical activity of Lake Whitefish in Clear Lake, Maine, as determined with acoustic telemetry. *Transactions of the American Fisheries Society* 141:761-771.
- Halfyard, E. A., D. Webber, J. Del Papa, T. Leadley, S. Kessel, S. Colborne, and A. Fisk. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods in Ecology and Evolution* 8:1063-1071.
- Hannah, R. W., S. J. Parker, and K. M. Matteson. 2008. Escaping the surface: the effect of capture depth on submergence success of surface-released Pacific rockfish. *North American Journal of Fisheries Management* 28:694-700.
- Holan, S. H., G. M. Davis, M. L. Wildhaber, A. J. DeLonay, and D. M. Papoulias. 2009. Hierarchical Bayesian Markov switching models with application to predicting spawning success of Shovelnose Sturgeon. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 58:47-64.

- Huntsman, G., J. Potts, R. Mays, and D. Vaughan. 1999. Groupers (Serranidae, Epinephelinae): endangered apex predators of reef communities. Pages 217-231 in American Fisheries Society Symposium.
- Jepsen, N., K. Aarestrup, F. Økland, and G. Rasmussen. 1998. Survival of radiotagged Atlantic Salmon (*Salmo salar*)—and trout (*Salmo trutta*) smolts passing a reservoir during seaward migration. *Hydrobiologia* 371:347.
- 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.
- Kassambara, A., and M. Kosinski. 2018. survminer: Drawing Survival Curves using 'ggplot2'. R package version 0.4.3. <https://CRAN.R-project.org/package=survminer>
- Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348:aaa2478.
- Kritzler, H., and L. Wood. 1961. Provisional audiogram for the shark, *Carcharhinus leucas*. *Science* 133:1480-1482.
- Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J. M. Morales. 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* 93:2336-2342.
- Leos-Barajas, V., T. Photopoulou, R. Langrock, T. A. Patterson, Y. Y. Watanabe, M. Murgatroyd, and Y. P. Papastamatiou. 2017. Analysis of animal accelerometer data using hidden Markov models. *Methods in Ecology and Evolution* 8:161-173.
- McClintock, B. T., and T. Michelot. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution* 9:1518-1530.

- Michelot, T., and P. G. Blackwell. 2019. State-switching continuous-time correlated random walks. *Methods in Ecology and Evolution*, 10: 637-649.
- Muhametsafina, A., J. Midwood, S. Bliss, K. Stampelcoskie, and S. Cooke. 2014. The fate of dead fish tagged with biotelemetry transmitters in an urban stream. *Aquatic ecology* 48:23-33.
- NOAA Fisheries. 2018. 2018 Report to Congress on the Status of U.S. Fisheries
- Ogburn, M. B., C. W. Bangley, R. Aguilar, R. A. Fisher, M. C. Curran, S. F. Webb, and A. H. Hines. 2018. Migratory connectivity and philopatry of Cownose Rays *Rhinoptera bonasus* along the Atlantic coast, USA. *Marine Ecology Progress Series* 602:197-211.
- Papastamatiou, Y. P., Y. Y. Watanabe, U. Demšar, V. Leos-Barajas, D. Bradley, R. Langrock, K. Weng, C. G. Lowe, A. M. Friedlander, and J. E. Caselle. 2018. Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. *Movement ecology* 6:9.
- Patterson, T. A., M. Basson, M. V. Bravington, and J. S. Gunn. 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology* 78:1113-1123.
- Pepperell, J., and T. Davis. 1999. Post-release behaviour of Black Marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. *Marine Biology* 135:369-380.
- R Core Team. 2019. R: a language and environment for statistical computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rudershausen, P., W. Mitchell, J. Buckel, E. Williams, and E. Hazen. 2010. Developing a two-step fishery-independent design to estimate the relative abundance of deepwater reef fish:

- application to a marine protected area off the southeastern United States coast. *Fisheries Research* 105:254-260.
- Rudershausen, P. J., B. J. Runde, and J. A. Buckel. 2020. Effectiveness of Venting and Descender Devices at Increasing Rates of Postrelease Survival of Black Sea Bass. *North American Journal of Fisheries Management* 40:125-132.
- Runde, B. J., and J. A. Buckel. 2018. Descender devices are promising tools for increasing survival in deepwater groupers. *Marine and Coastal Fisheries* 10:100-117.
- Runde, B. J., J. E. Harris, and J. A. Buckel. 2018. Symposium review: using electronic tags to estimate vital rates in fishes. *Fisheries* 43:268-270.
- Runde, B. J., P. J. Rudershausen, B. Sauls, C. S. Mikles, and J. A. Buckel. 2019. Low discard survival of Gray Triggerfish in the southeastern US hook-and-line fishery. *Fisheries Research* 219:105313.
- SAFMC. 2016. Snapper Grouper Fishery Management Plan. South Atlantic Fishery Management Council.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, Volume 8. Blackburn press Caldwell, New Jersey.
- Seitz, A. C., M. B. Courtney, M. D. Evans, and K. Manishin. 2019. Pop-up satellite archival tags reveal evidence of intense predation on large immature Chinook Salmon (*Oncorhynchus tshawytscha*) in the North Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*:1-8.
- Theberge, S., and S. J. Parker. 2005. Release methods for rockfish. Sea Grant Oregon, Oregon State University.

- Vermard, Y., E. Rivot, S. Mahévas, P. Marchal, and D. Gascuel. 2010. Identifying fishing trip behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov Models. *Ecological Modelling* 221:1757-1769.
- Viana, M., L. McNally, N. Graham, D. G. Reid, and A. L. Jackson. 2013. Ignoring discards biases the assessment of fisheries' ecological fingerprint. *Biology Letters* 9:20130812.
- Wetherbee, B. M., and E. Cortés. 2004. Food consumption and feeding habits. Pages 232-253 *in* *Biology of Sharks and their Relatives*. CRC press.
- Wilson, A. D., M. Wikelski, R. P. Wilson, and S. J. Cooke. 2015. Utility of biological sensor tags in animal conservation. *Conservation Biology* 29:1065-1075.
- Yergey, M. E., T. M. Grothues, K. W. Able, C. Crawford, and K. DeCristofer. 2012. Evaluating discard mortality of Summer Flounder (*Paralichthys dentatus*) in the commercial trawl fishery: developing acoustic telemetry techniques. *Fisheries Research* 115:72-81.
- Zucchini, W., I. L. MacDonald, and R. Langrock. 2016. Hidden Markov models for time series: an introduction using R. Chapman and Hall/CRC.

Tables

Table 1. Information for individual groupers off North Carolina, USA. “Site” identifies whether the fish were tagged at the shelf break (“Shelf”) or at the Snowy Wreck (“Wreck”). Tag names are comprised 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”). “Survival, full” indicates that the fish was still alive at the end of the study period. Fates were determined mainly by 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 are only present in this table when they differed from those in Analysis 1. Days alive were used as inputs for two Kaplan-Meier survivorship procedures.

Site	Tag name	Total length (mm)	Capture depth (m)	Release type	Analysis 1 Fate	Days alive	Analysis 2 Fate	Days alive
Shelf	Gag 1	1085	72	Descend	Mortality	0		
Shelf	Red Grouper 1	850	116	Descend	Survival, full	123		
Shelf	Scamp 1	675	85	Descend	Mortality	3		
Shelf	Scamp 2	630	85	Descend	Mortality	0		
Shelf	Scamp 3	680	85	Descend dead	-			
Shelf	Scamp 4	610	76	Descend	Survival, full	124		
Shelf	Scamp 5	510	82	Surface cage, swam	Mortality	0	Emigration	0
Shelf	Scamp 6	650	88	Descend	Mortality	4		
Shelf	Scamp 7	595	116	Descend	Mortality	0	Mortality	7
Shelf	Scamp 8	550	117	Descend	Mortality	0	Mortality	7
Shelf	Scamp 9	520	91	Descend	Survival, full	34		
Shelf	Scamp 10	490	66	Descend	Tag loss	6		
Shelf	Scamp 11	680	85	Surface cage, floated	Mortality	0		
Shelf	Snowy Grouper 1	555	119	Descend	Mortality	0	Emigration	0
Shelf	Snowy Grouper 2	410	119	Descend	Mortality	0		
Shelf	Snowy Grouper 3	415	91	Descend	Mortality	2		
Shelf	Snowy Grouper 4	430	79	Descend	Survival, tag loss	9		
Shelf	Snowy Grouper 5	390	118	Descend dead	-			
Shelf	Snowy Grouper 6	600	95	Descend	Survival, full	119		
Shelf	Snowy Grouper 7	470	115	Descend	Mortality	3		
Shelf	Snowy Grouper 8	560	120	Descend	Survival, full	63		
Shelf	Snowy Grouper 9	430	80	Descend	Mortality	1	Tag loss	16
Shelf	Snowy Grouper 10	420	119	Descend	Survival, full	63		
Shelf	Snowy Grouper 11	365	117	Descend dead	-			
Shelf	Snowy Grouper 12	385	117	Descend	Survival, full	63		
Shelf	Snowy Grouper 13	395	117	Descend	Survival, full	63		
Shelf	Snowy Grouper 14	365	117	Descend	Survival, full	63		
Shelf	Snowy Grouper 15	460	82	Descend	Survival, full	63		
Shelf	Snowy Grouper 16	410	91	Descend	Survival, full	63		

Table 1 (continued)

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

Table 1 (continued).

Wreck	Snowy Grouper 4 wreck	800	244	Descend	Mortality	0	Emigration	9
Wreck	Snowy Grouper 5 wreck	1020	244	Descend	Mortality	0	Emigration	2

Table 2. Parameter estimates for our 3-state hidden Markov models. The three data streams parameterized were mean acceleration (“Acc”), mean depth relative to the depth of release (“RelDepth”), and standard deviation 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.

	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 E-05	9.99 E-09	4.56 E-04
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

Figures

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.

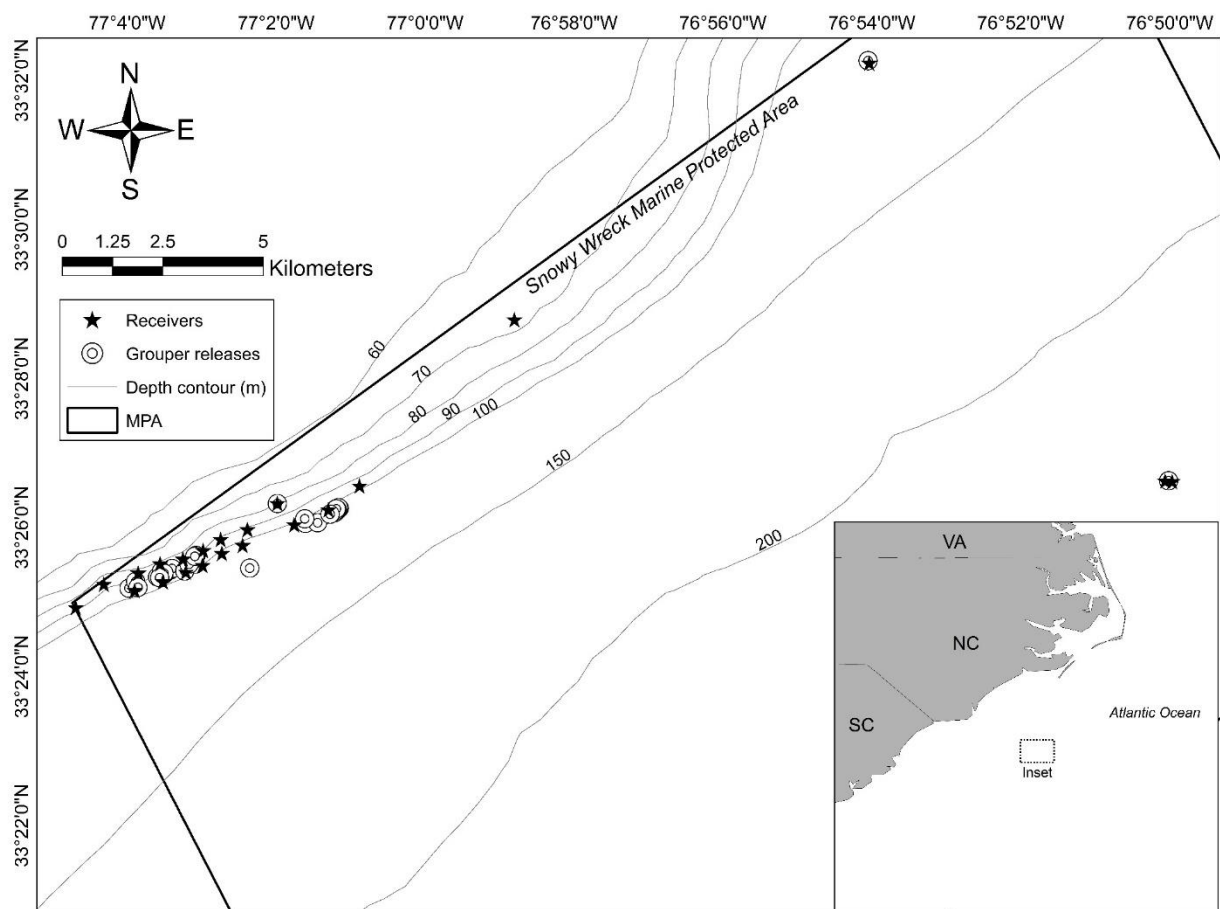


Figure 2. Distributions (lines) and histograms (gray bars) of mean acceleration (m/s²), mean relative depth, and depth standard deviation data streams for hidden Markov model (HMM) developed for telemetered six species of deepwater groupers off North Carolina, USA, in 2018.

States 1 and 2 tended to represent live groupers while state 3 tended to define behavior or predators or scavengers. Relative depth values are 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. Standard deviation of depth is the standard deviation of all depth observations within each 30-min time bin.

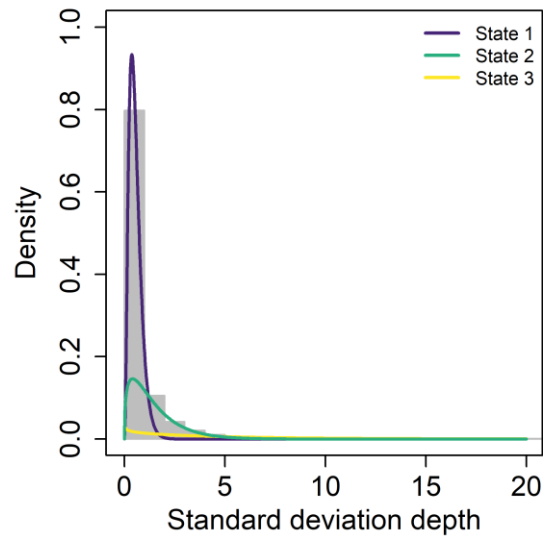
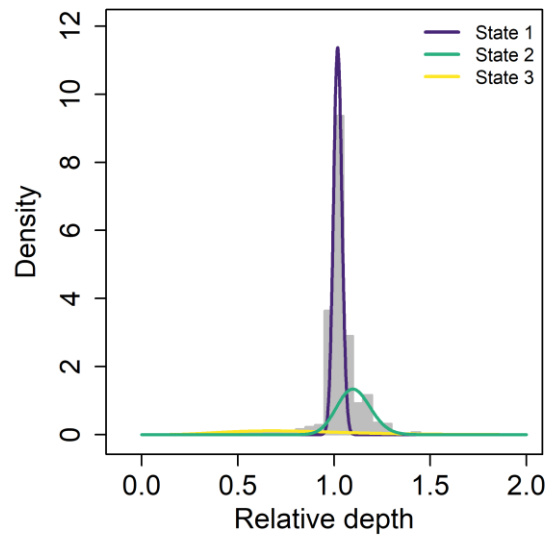
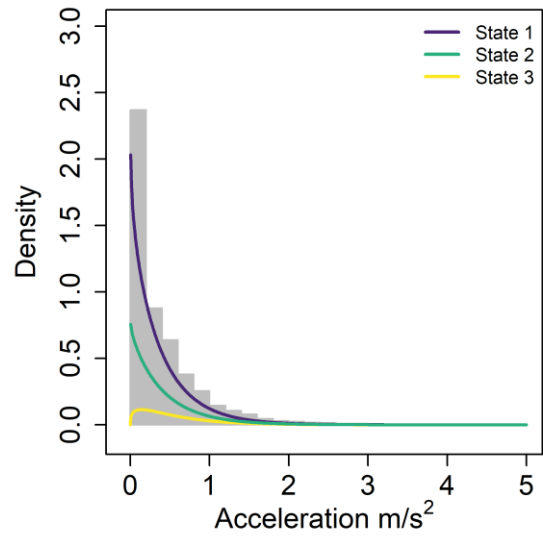
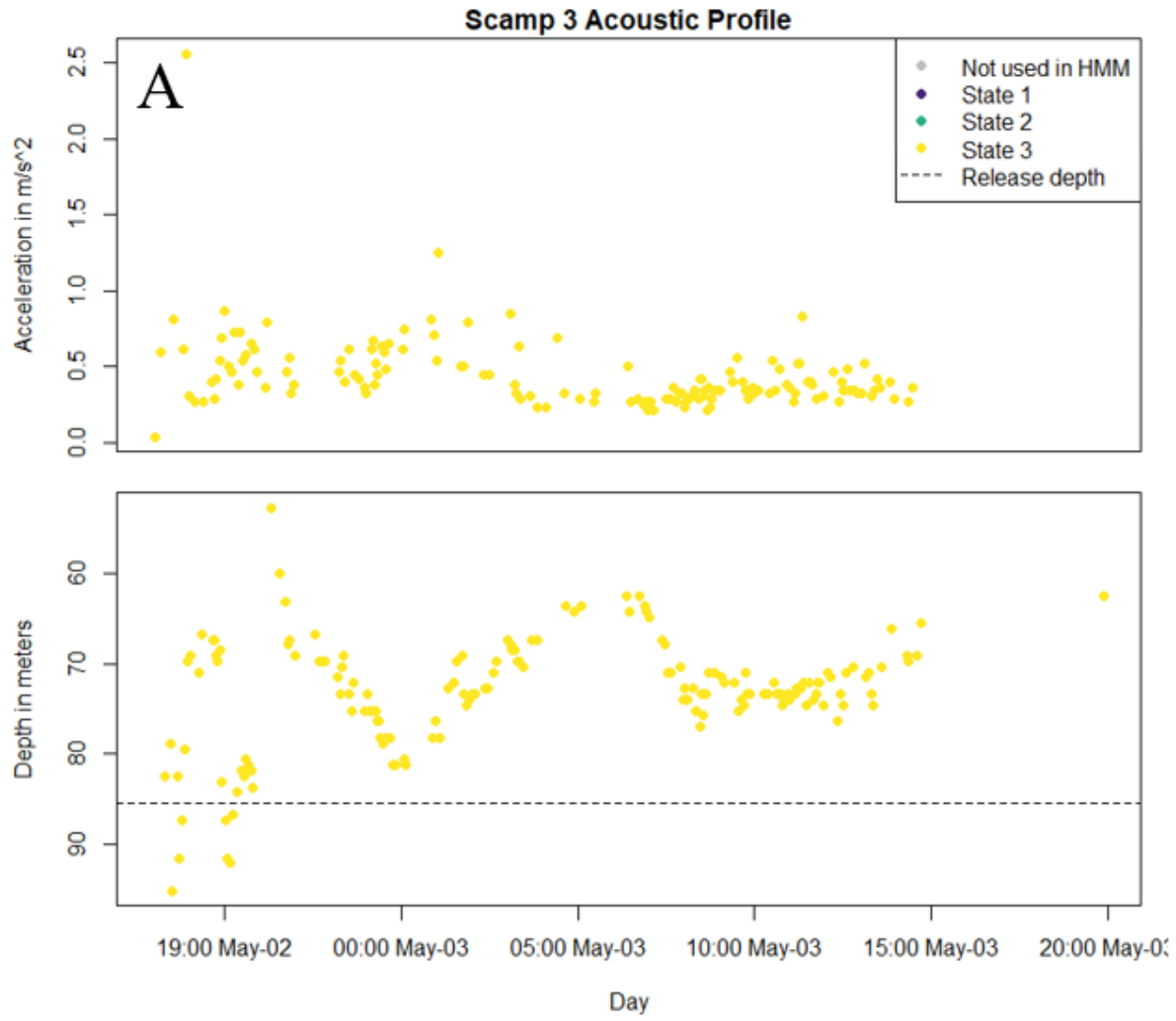
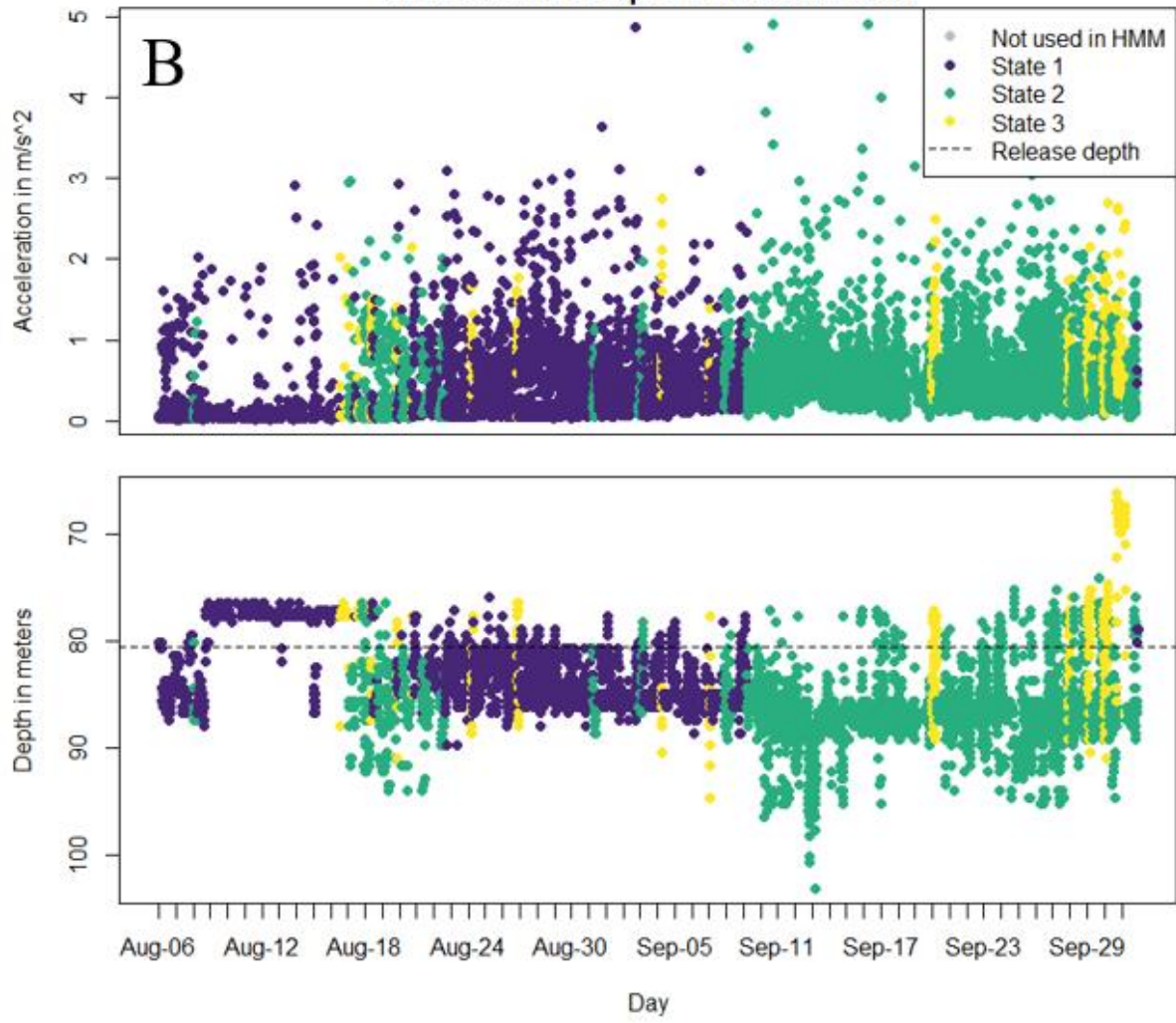


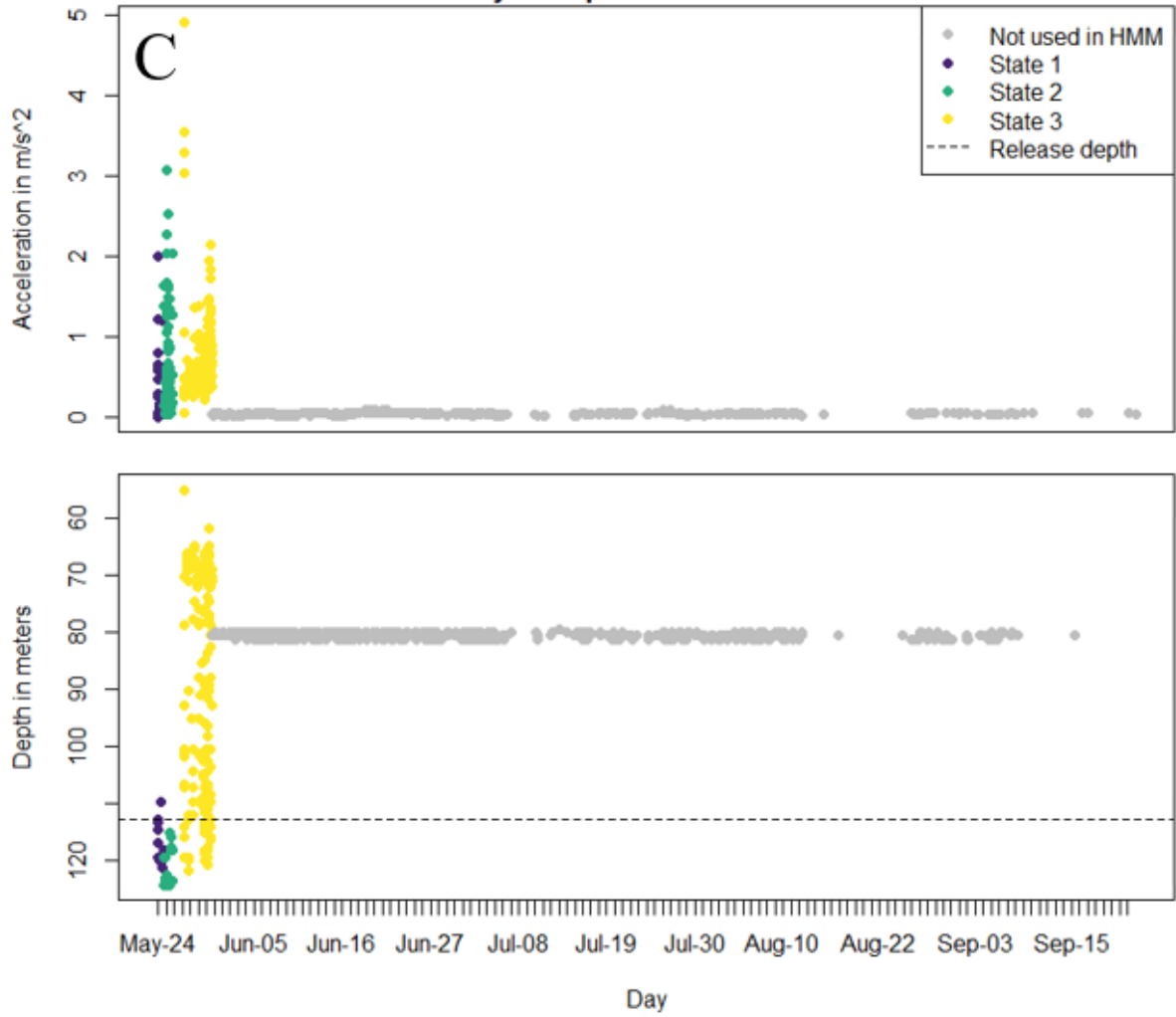
Figure 3. Example acoustic profiles (full time series data) for five telemetry tags, with upper panels indicating acceleration (m/s^2) and lower panels indicating depth (m). Detections are indicated by dots, which are colorized by the state as determined by a hidden Markov model. Variations in x-axis 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 expelled several days later. D) Scamp 10 was corrected from a mortality to a survival because data suggest its transmitter was loose. E) Snowy Grouper 20 was classified as a mortality on day zero because its profile suggests scavengers interacting with a grouper carcass. F) Red Grouper 1 is an example of a live fish that utilized a range of depths during the study period.

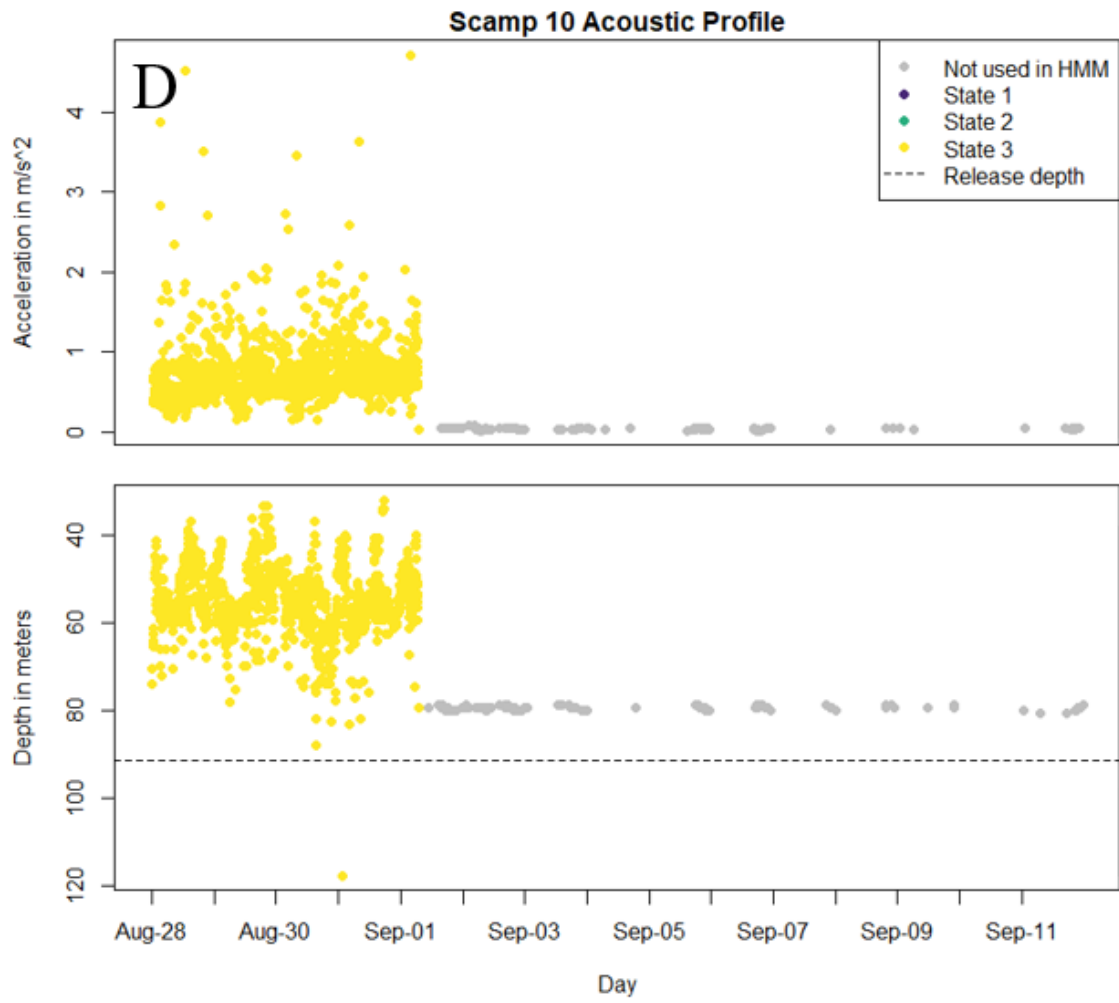


Yellowmouth Grouper 4 Acoustic Profile

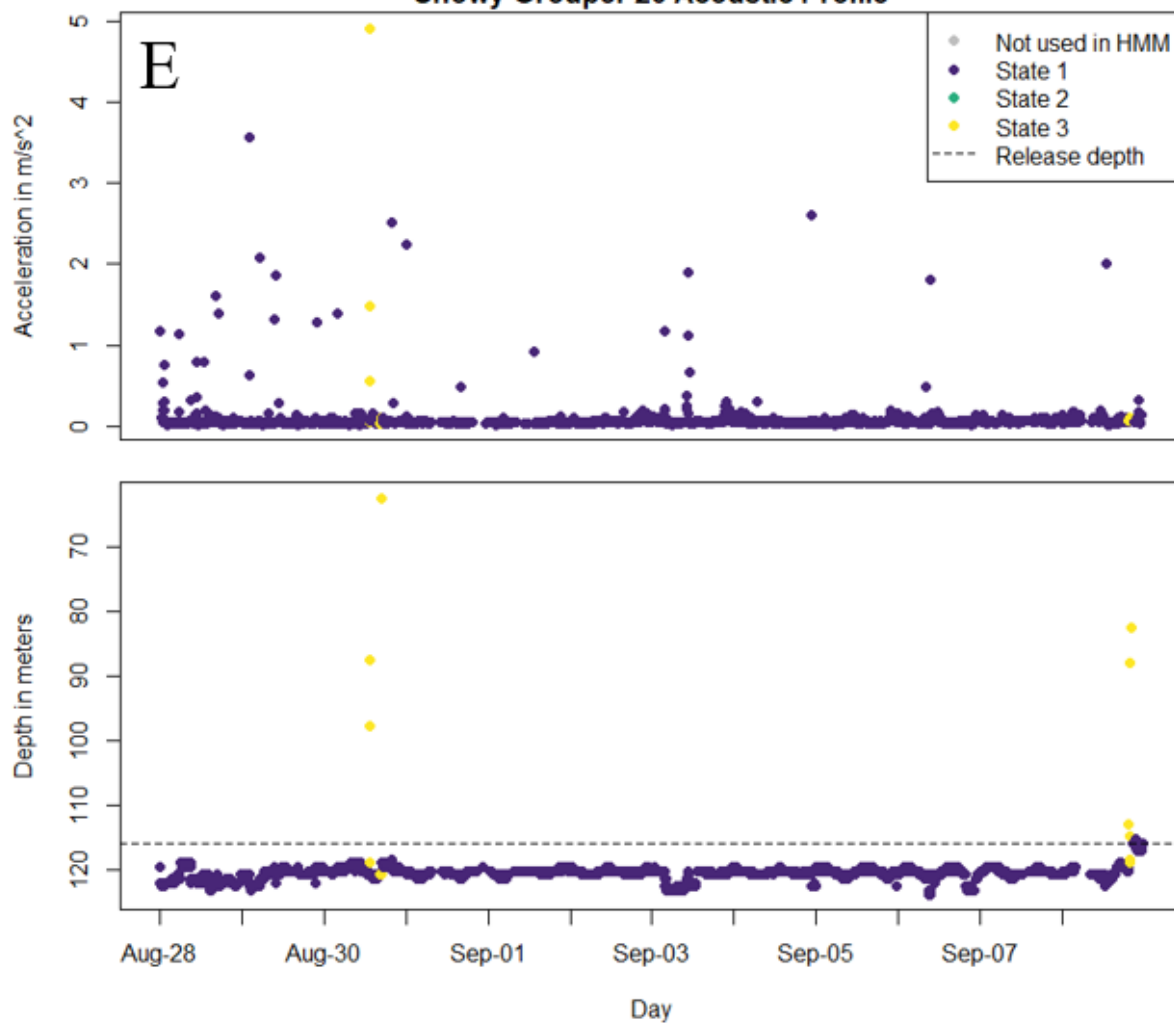


Snowy Grouper 3 Acoustic Profile





Snowy Grouper 20 Acoustic Profile



Red Grouper 1 Acoustic Profile

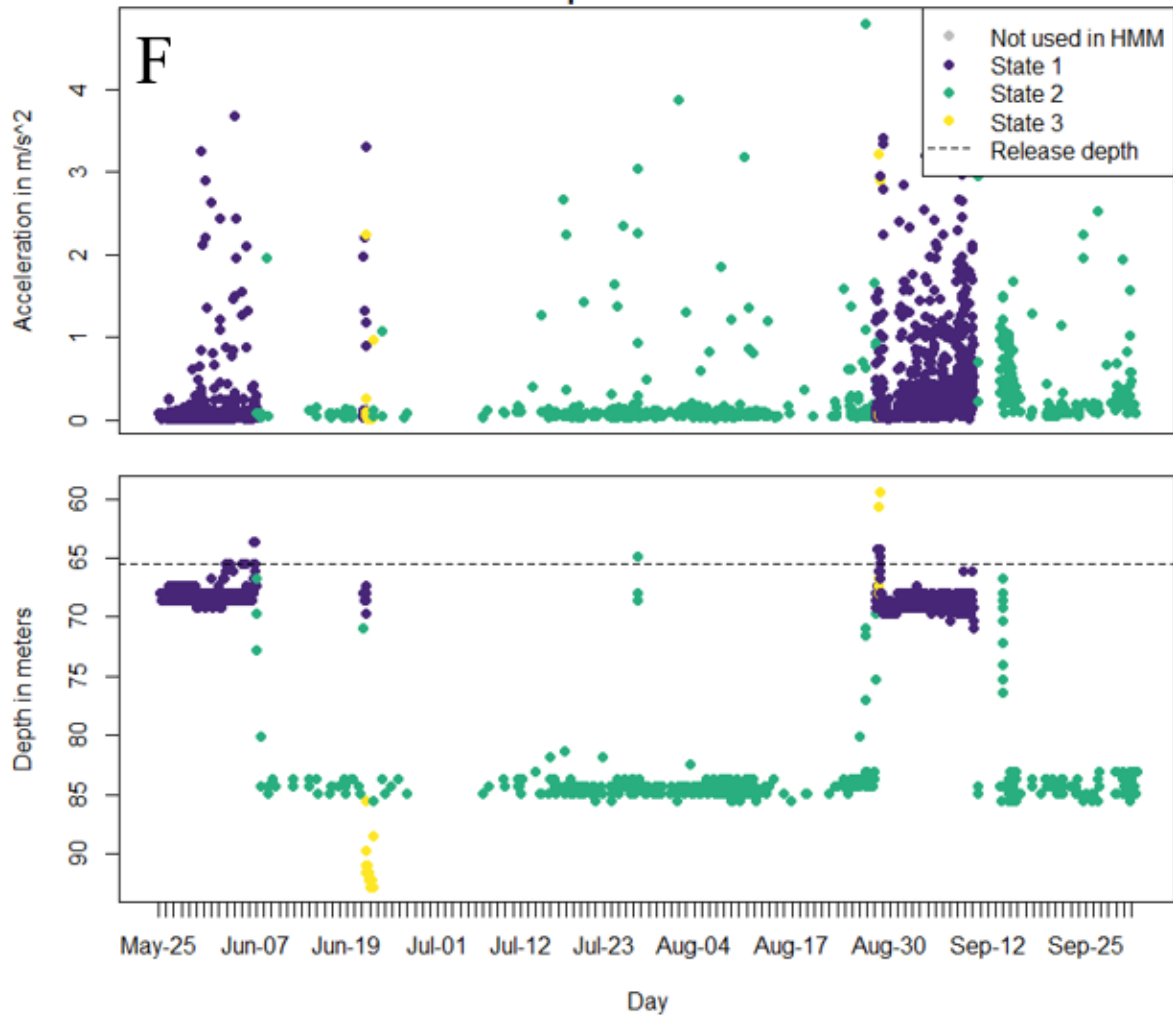
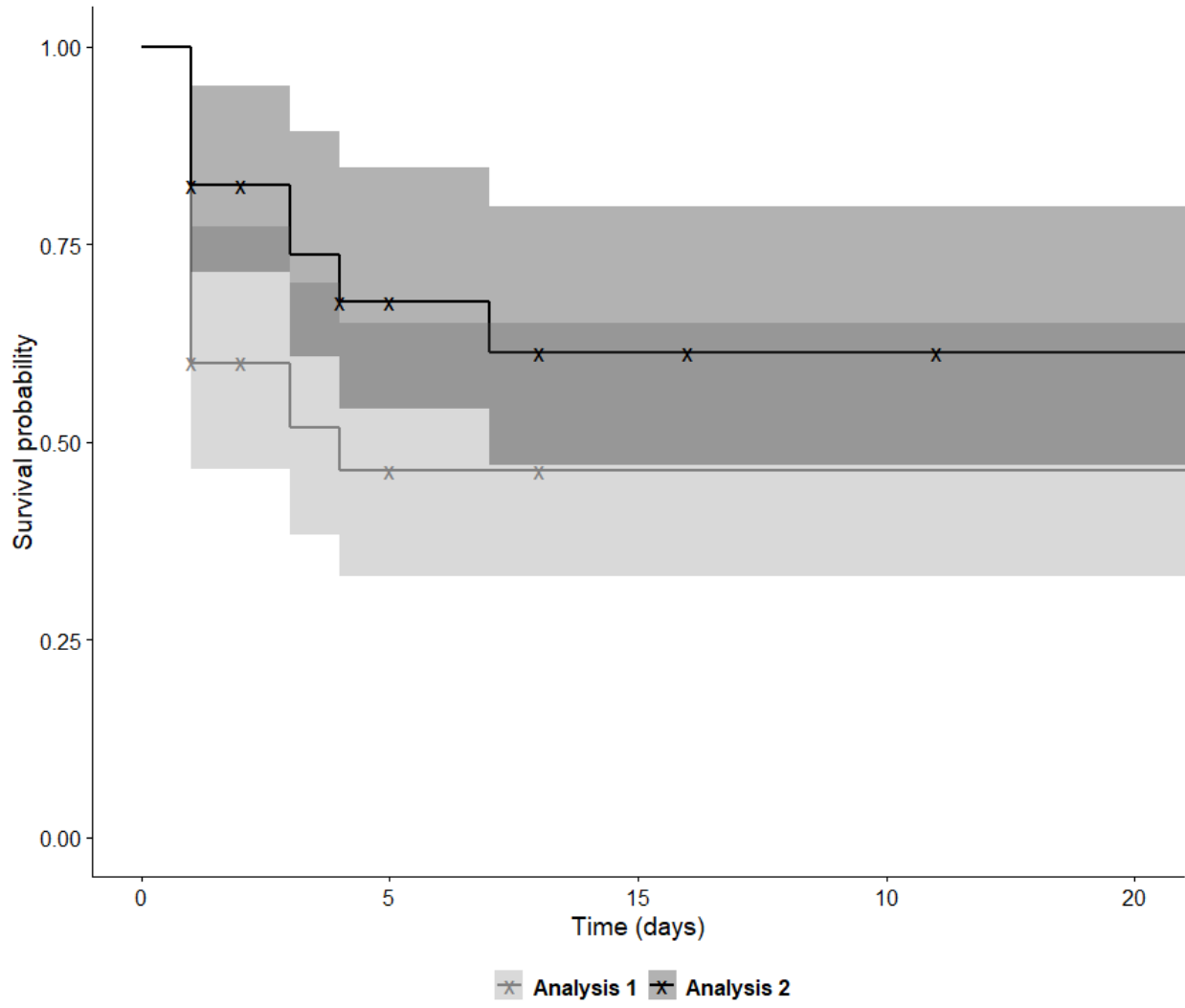


Figure 4. Plot of the Kaplan-Meier survivorship curves for 40 deepwater groupers released via descender device at the continental shelf break off North Carolina, USA, in 2018. Analysis 1 uses fates that were assigned more strictly with respect to hidden Markov model results. Analysis 2 incorporates more subjectivity. X symbols represent censorships of live groupers that either were assumed to have lost their tag 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% confidence intervals around the mean estimate (line). Time zero is the day of tagging and release.



**CHAPTER 2: EVALUATING THE EFFECTS OF A DEEP-WATER MARINE
PROTECTED AREA A DECADE AFTER CLOSURE: A MULTIFACTED APPROACH
REVEALS EQUIVOCAL BENEFITS TO REEF FISH POPULATIONS**

*This chapter has been prepared for publication. Coauthors are Jeffrey Buckel, Paul
Rudershausen, Warren Mitchell, Erik Ebert, and J. Chris Taylor*

Abstract

Marine protected areas (MPAs) are increasingly used as a tool for rebuilding fish populations. In 2009, a network of eight MPAs was designated in the southeast United States Atlantic with the goal of protecting and rebuilding populations of deep-water reef fishes. We used several analyses to test whether the largest of these MPAs, the Snowy Wreck Marine Protected Area (SWMPA), has had the desired effect. A previous study by several of the current authors collected hydroacoustic and biological data in the SWMPA and an adjacent control area prior to closure. We collected data in the same areas using matching methodology. Bayesian hurdle models of reef fish biomass using scientific sonar data collected in 2007-2009 and 2018-2020 yielded no evidence of a positive MPA effect. Investigations of catch-per-unit-effort of reef fishes with hook-and-line sampling had a similar result. However, we did identify significant positive changes in size structure for red porgy (*Pagrus pagrus*) inside the SWMPA; no such changes occurred in the control area, indicating a positive MPA effect. Further, we found changes in community composition in both areas through time, though we did not identify an MPA effect with this analysis. Given the life history of some of the species the SWMPA was intended to protect, more time since closure may be necessary before an effect occurs and/or is detectable. Finally, stricter enforcement of the MPA boundaries could eliminate illegal fishing that may depress any positive effect of closure.

Introduction

The restriction of consumptive activities in a portion of the world's oceans has become increasingly popular as a management tool in the last few decades. These restricted areas, variously called marine reserves, no-take zones, marine sanctuaries, and marine protected areas (MPAs), are used to meet a range of social, political, and biological goals (Halpern, 2003). In 2010, the Convention on Biological Diversity (CBD) called for drastically increasing global coverage of MPAs to 10% of the ocean (CBD, 2010). Though that goal has not been reached, MPA coverage has increased from approximately 0.9% in 2000 (Lubchenco and Grorud-Colvert, 2015) to 6.4% currently, with 2.7% designated as “fully or highly protected” (MPA Atlas, 2021).

Part of the reason for the lag in MPA creation as compared to the CBD target is the failure to reach a global consensus about the effectiveness of protection. Hundreds of studies have empirically examined individual MPAs or local MPA networks (Caveen et al., 2012), and many reviews and meta-analyses have sought to synthesize the findings thereof (e.g., Lester et al., 2009; Babcock et al., 2010; Sciberras et al., 2013). Further, Woodcock et al. (2017) examined 24 available review articles in a meta-review intended to characterize the existing literature in terms of scope, reliability, and knowledge gaps. While the preponderance of studies have demonstrated that MPAs are useful tools for meeting some goals, there is uncertainty surrounding their most efficient and effective use (Woodcock et al., 2017).

One of the most common purposes of designating MPAs is to rebuild, conserve, or otherwise positively influence fish populations (Sale et al., 2005). While ample literature exists on the topic, the debate about whether MPAs are an appropriate tool for fisheries management continues (Hilborn, 2018; Pendleton et al., 2018; Sala and Giakoumi, 2018). Despite the lack of universal agreement, the majority of syntheses have reported that restricting or banning fishing

activities results in increased biological metrics (e.g., biomass, density, species richness) within MPA boundaries (Halpern and Warner, 2002; Claudet et al., 2008; Egerton et al., 2018) and/or outside their borders due to beneficial spillover effects of adults or larvae (Quinn et al., 1993; Murray et al., 1999; Gell and Roberts, 2003). Botsford et al. (2003) described the theory behind MPAs as a fisheries management tool and noted that properly designating MPAs is tantamount to a reduction in fishing mortality. Lester et al. (2009) estimated that MPAs that completely prohibit extractive activities resulted in a 446% increase in fish biomass on average, though these findings were not standardized by duration of protection. More recently, Ojeda-Martínez et al. (2011) reviewed MPA literature and showed that a majority of peer-reviewed articles found significant differences in some biological metric between protected and unprotected areas, though publication bias may have influenced this result (Woodcock et al., 2017). Others argue that while closed areas can generate positive responses within their boundaries, they can displace fishing effort and concentrate it elsewhere (Dinmore et al., 2003; Branch et al., 2006; Hoos et al., 2019) which may negate any positive effects inside the closure by creating detrimental effects outside the borders (Greenstreet et al., 2009). Robust methodologies for detecting MPA effects on fish populations must be employed if the debate is ever to be settled (Woodcock et al., 2017).

Many empirical studies seeking to assess MPAs as a fisheries management tool have compared post-closure biota inside and outside the closed area (Ojeda-Martínez et al., 2011; Osenberg et al., 2011). However, some studies have tested for an effect of MPAs using Before-After-Control-Impact (BACI) studies. BACI studies measure one or more variables in a location that has experienced a major alteration (or “Impact”), such as a disturbance or management change, and in one or more areas that sustained no such impact (Green, 1979). Crucially, data from both before and after the impact in both areas are utilized to control for the effects of

ecosystem-wide shifts that may occur independent of the interference of interest (Stewart-Oaten et al., 1986; Underwood, 1992). For MPAs, BACI and similar designs are considered robust approaches to assessing effects (Sciberras et al., 2013; Kerr et al., 2019), but have been infrequently used for this purpose. Mateos-Molina et al. (2014) employed underwater visual surveys in a BACI framework to examine for the effects of an MPA in Puerto Rico. Moland et al. (2013) also used a BACI study to evaluate changes in abundance of European lobster (*Homarus gammarus*) and Atlantic cod (*Gadus morhua*) in MPAs off the coast of Norway. Similarly, Francini-Filho and Moura (2008) measured reef spillover from an MPA in Brazil by estimating fish biomass and body size in replicate sites inside and outside MPA boundaries, both before and after closure. BACI designs have also been used to examine the effects of MPAs on rebuilding groundfish stocks in Europe (Frank et al., 2000; Fisher and Frank, 2002). Kerr et al. (2019) wrote an extensive review of the use of BACI designs for evaluating MPAs, in which the authors characterized possible BACI outcomes and listed potential limitations and pitfalls. They also demonstrated the use of BACI for evaluating the response of two groundfish species to two MPAs on Georges Bank, USA. Overall, Kerr et al. (2019) urged researchers to carefully consider response variables and analytical design (including replication) when intending to use BACI for MPA evaluation, and to combine BACI with other methodologies to assess MPA performance in several ways.

The variables of interest used in MPA studies have been diverse, as have methodologies for measuring them. For instance, some studies have used underwater visual census via divers to evaluate fish biomass, size, abundance, or species richness in pursuit of quantifying MPA effects (Russ et al., 2005; Seytre and Francour, 2008; Prato et al., 2017). Others have employed similar methods, such as remotely operated vehicles, to meet this goal (Harter et al., 2009; Bachelier et

al., 2016; Huvenne et al., 2016). Furthermore, some have collected hydroacoustic data to estimate biomass (Kracker, 2007), noting that this methodology is faster and therefore cheaper (in the long-run) than visual surveys and allows for sampling of almost the entire water column (Egerton et al., 2018), though species-level data are difficult or impossible to obtain with acoustics. Beyond remote or visual methods, empirical biological data (such as size, age, fecundity, and abundance indices) have been gathered in studies of MPAs using trawls (Kerr et al., 2019), traps (Moland et al., 2013), and baited hooks (Alós et al., 2015). Species-level data have been used in MPA studies not only to analyze changes in size or biomass but also in multivariate analyses of community composition (e.g., Claudet et al., 2006; Alemany et al., 2013; Bacheler et al., 2016). In general, researchers have sought metrics that would aptly depict whether or not the intended MPA effect is occurring.

In the southeast United States Atlantic (hereafter: SEUSA), a rich assemblage of reef fishes (such as snappers and groupers) comprise a multispecies fishery (Lindeman et al., 2000); some component species are currently overfished or undergoing overfishing (NMFS, 2019). Several of these, including speckled hind (*Epinephelus drummondhayi*) and Warsaw grouper (*Hyporthodus nigritus*), are deep-water (>60 m) species that are predisposed to imperilment due to a combination of aggressiveness, natural rarity, extreme maximum longevity, and susceptibility to severe barotrauma when brought to the surface (Huntsman et al., 1999; Coleman et al., 2000; Andrews et al., 2013; Sanchez et al., 2019). Even when harvest is prohibited, bycatch of these species still occurs; because barotrauma-induced post-release mortality is extremely high, fishing mortality will not reach zero unless effort is eliminated. In the early 2000s, the South Atlantic Fishery Management Council (SAFMC) recognized that one method for eliminating effort in a portion of deep-water habitat was the designation of MPAs. To that

end, in 2009 the SAFMC established a network of eight MPAs along the Atlantic coast from southern Florida to central North Carolina to “protect a portion of the population and habitat of long-lived, slow growing, deep-water species from directed fishing pressure to achieve a more natural sex ratio, age, and size structure...” (SAFMC, 2007). These MPAs range in area from approximately 24 km² to 501 km² and each contains biologically productive continental shelf edge habitat; they collectively cover approximately 3.2% of the total area between 40 and 400 m deep in the SEUSA (Figure 1; Bacheler et al., 2016). Within these areas, targeting or possessing reef fish species is prohibited, but other activities including pelagic trolling are permitted (SAFMC, 2007).

The largest of the eight MPAs in the SEUSA is the Snowy Wreck Marine Protected Area (hereafter: SWMPA) off North Carolina. The SWMPA is approximately rectangular (18.52 x 27.78 km) and was designated in this area in part to protect a shipwreck, called the “Snowy Wreck,” from continued exploitation (Figure 2). The Snowy Wreck is a metal-hulled shipwreck about 100 m long that lies in approximately 250 m depth and was discovered around the mid-1980s. The site supported large quantities of snowy grouper (*H. niveatus*) and other large groupers and was fished heavily until closure in 2009 (Quattrini and Ross, 2006; Paxton et al., 2021). In addition to protecting the Snowy Wreck, the SWMPA was intended to protect a portion of high-relief shelf-edge known to be biologically productive habitat that supports many species of reef fishes (Quattrini and Ross, 2006).

Since the eight SEUSA deep-water MPAs were created in 2009, only two studies to our knowledge have investigated their effectiveness. Bacheler et al. (2016) used video transects to examine species richness, density of all fished (i.e., targeted by a fishery) species, and density of one common fished species (vermillion snapper; *Rhomboplites aurorubens*) inside five of the

eight MPAs (including the SWMPA) for data up to 2014. In addition, they used non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) to compare fish communities inside and outside MPAs. None of the analyses performed in Bachelier et al. (2016) produced indications that the SEUSA MPA network was effectively rebuilding reef fish populations. Most recently, (Pickens et al., 2021) evaluated three of the MPAs (Northern South Carolina, Edisto, and North Florida) using video and trap catch information from 2011 to 2017 and reported no significant increases within MPAs relative to outside areas for any metric examined. There are several circumstances under which MPAs might not appear effective when they actually are, including low statistical power, masking source-sink dynamics, and that population- or community-level changes often take more than a few years to occur (Claudet, 2018). Accordingly, both Bachelier et al. (2016) and Pickens et al. (2021) concluded that while no positive MPA effects were found in their studies, further research was warranted.

Aware of the impending designation of the SWMPA, Rudershausen et al. (2010) collected hydroacoustic and biological catch data in 2007-2009 in the soon-to-be-closed area as well as an adjacent area with the same depth and habitat characteristics. In the present study, we re-analyze data collected by Rudershausen et al. (2010) and offer the third (to our knowledge) evaluation of the effects of any SEUSA MPA on rebuilding reef fish stocks. More than a decade after closure, some positive effects of the SWMPA should be detectable if present. In pursuit of determining whether these effects exist, we take a multifaceted approach and analyze hydroacoustic data, catch data, and biological data with several different methodologies in a BACI design where possible.

Methods

Study site and data collection

We replicated the sampling methods of Rudershausen et al. (2010). Accordingly, we collected data inside the SWMPA along the continental shelf break in 47 to 150 m water depths. Besides the eponymous shipwreck near the offshore edge of the area, the only known biologically productive habitat resides along the inshore edge of the SWMPA (Rudershausen et al., 2010). Therefore, our sampling was restricted to a 4.63 x 27.78 km rectangle inside the SWMPA, as well as an adjacent comparison area of equal dimensions that has never been closed to bottom fishing (hereafter: “control” or “control area”; Figure 2) that was also sampled in Rudershausen et al. (2010). For the purposes of consistency, all data collection trips in the present study were attended by at least one author of Rudershausen et al. (2010) and/or the collaborating boat captain from that study.

Within each area, we collected hydroacoustic backscatter and biological data. Hydroacoustic backscatter data were collected along tracks that formed a ‘zig-zag’ pattern by transecting through points that alternated along the inshore and offshore long edge of each box (Figure 3). Points along the edges of the box through which we transected were spaced 4.63 km apart and specific paths were varied between trips so that we sampled new habitat each day. This followed the sampling protocol for the majority of the Rudershausen et al. (2010) data collection, though in 2007 the authors of that study conducted some transects in the SWMPA both parallel and perpendicular to the long edge of the area (Figure 3A). For a given day of sampling, data were collected in either the SWMPA or the control area. In addition, on a single day in 2019, we acoustically surveyed the Snowy Wreck itself; Rudershausen et al. (2010) acoustically surveyed the Snowy Wreck on a single day in 2007.

Fisheries acoustics gear consisted of a Simrad ES60 transceiver outfitted with a single-beam transducer that operated at 38 kHz. We elected to use this gear because it was the exact unit used in Rudershausen et al. (2010). The transducer emitted an elliptical beam; longitudinal (i.e., bow/stern) and transverse (i.e., port/starboard) beam angles were 13° and 21°, respectively. Acoustic data were collected from the *R/V Cape Fear* (20-m diesel-powered former fishing vessel) in 2018-2019 and from the *R/V Regulator* (8-m center-console vessel) in 2020. On both acoustic data collection vessels, the transducer was mounted to the base of an aluminum pole and deployed off the port side so that the face of the transducer was approximately 0.5 m below the water surface. Boat speed ranged from three to five knots during acoustic data collection. The Simrad transceiver was connected to a laptop computer which was also connected to an on-board GPS plotter for positioning. During sampling, we noted the presence of any schools of on- or near-bottom biomass (within 10 m of the seafloor) and recorded these locations as acoustic events. Raw ES60 files were saved for subsequent processing. These methodologies are consistent with those of (Rudershausen et al., 2010).

A subset of acoustic events were biologically sampled with either hook-and-line or chevron traps. We determined *ad hoc* which events would be sampled with which gear based on a combination of the observed size of each school (we wished to sample a range of sizes) and their geographic proximity to our location (for logistical reasons). Hook-and-line sampling gear matched the methods of Rudershausen et al. (2010) and consisted of conventional rods with electric reels and 59 kg braided line. Terminal tackle was a high-low bottom rig made of 68 kg monofilament line and two 8/0 J-style hooks and lead weight ranging from 0.68 to 1.36 kg. Hooks were baited with cut squid (*Illex* or *Loligo* spp.). Hook-and-line sampling was conducted on the *R/V Cape Fear*, the *R/V Ocellatus* (8-m center-console vessel), the *F/V Merry Marlin* (9-

m center-console vessel), the *F/V Sensation* (16-m diesel sportfisher), and the *F/V Wide Open* (11-m diesel sportfisher). Chevron traps were constructed of 35-mm square vinyl coated wire, with one funnel entrance and one release panel, and had maximum dimensions of 1.5×1.7×0.6 m (0.91 m³). Each trap was baited with 24 whole Atlantic menhaden (*Brevoortia tyrannus*); 16 were hung on four stringers and eight were scattered inside. All chevron trap sampling was conducted on the *R/V Cape Fear*. Biological sampling usually took place within 24 hours of acoustic data collection, though in one instance a hook-and-line trip took place 23 days after acoustic data collection.

Biological sampling protocols matched those of Rudershausen et al. (2010). When hook-and-line fishing, captains were permitted to keep vessels in gear (i.e., hover over events) or out of gear (i.e., drift over events) depending on sea conditions. Gear was deployed within 50 m of an acoustic event. Hook-and-line sampling was terminated when the boat drifted greater than 50 m from the event, whereupon the captain repositioned the boat. Hook-and-line sampling continued at an event until at least four drops of baited rigs had been conducted. Chevron traps were soaked on acoustic events for approximately 90 minutes. Depending on the conventional gear type, catch per unit effort (CPUE) was measured as fish-per-drop for each baited two-hook rig or fish-per-trap. Caught reef fish were identified, measured (fork and total length; mm), and released. In 2019-2020, red porgy (*Pagrus pagrus*) were retained for otolith removal and aging.

Acoustic data processing

Acoustic data were processed using Myriax Echoview software (v. 10.0.275). We processed data that were collected during the present study (2018-2020). In addition, raw acoustic data were available from the Rudershausen et al. (2010) study (collected in 2007-2009); we obtained and reprocessed these data as well. For each data file, seafloor definitions were

edited by one or two authors (BR and/or EE) and an impulse noise removal filter was applied to all files to reduce systematic non-biomass backscatter. Data were limited to backscatter stronger than -60 dB. For one analysis, we imposed a 100 m linear grid on each data file. Grid cells were bounded vertically by the seafloor and a line 10 m above it. This analysis yielded a total biomass value for each 100 m x 10 m cell as the Nautical Area Scattering Coefficient (NASC; also called S_A ; units m^2nmi^{-2}). The Echoview software inherently scaled NASC values depending on depth (and therefore beam width) so output data were standardized by water volume. Additionally, we expected that biomass would be correlated with habitat quality; the continental shelf break inside the SWMPA and control area consists of stretches of low-slope sand punctuated by high-relief drop-offs and ledges (Rudershausen et al., 2010). High vertical relief habitat is known to result in greater fish production (Randall and Minns, 2000; Claisse et al., 2014), therefore we wished to include this metric in our statistical model. We generated an estimate of seafloor slope for each 100 m grid cell in our survey. This metric was not available in the Echoview software. However, Echoview natively exports mean depth for each 100 m cell, so we estimated slope by generating a raster image for the inshore edge of the SWMPA and the control area using all mean depth observations from all acoustic sampling trips. Point values for mean depth were used to interpolate full coverage of each area using inverse distance weighting. Slope in degrees for each cell was then calculated using a 3x3 cell moving window of mean depth. Because this methodology relies on depth information from adjacent locations, we could not use it to estimate slope for some grid cells around the edge of each area. For these locations, we applied the slope from the nearest (linear distance) grid cell in which it was estimable. These analyses were conducted in R (R Core Team, 2020) and Esri ArcPro (v 2.7).

For a separate analysis, individual acoustic events (schools of fish) were defined and their acoustic backscatter was measured (again in terms of NASC). Only acoustic events that were sampled biologically (with either hook-and-line or chevron traps) in our study or during Rudershausen et al. (2010) were measured for this second analysis. Definitions of what was considered a single fish school were determined *ad hoc* by a single author (EE), and were consistent across data files (and thus between areas and time periods).

Hurdle model for predicting biomass

We fitted a series of hurdle models in a Bayesian framework to the data consisting of all hydroacoustic backscatter (total biomass) per 100 m grid cell using the R package ‘brms’ (Bürkner, 2017). The first stage of the hurdle model estimated the probability of a given cell containing zero biomass and the second stage estimated the distribution of biomass given that it was non-zero. We fitted a range of candidate models to the data. The full model included *Area* (SWMPA or control), *Period* (before or after), and their interaction as main effects. In a BACI design such as our own, an *Area:Period* interaction tests for an MPA effect; if the directionality and/or magnitude of change through time differs between the two areas, we are able to infer whether the designation of the MPA (or “impact”) is the cause. In addition to these main effects, we included a fixed effect for seafloor slope (*Slope*; continuous), a fixed effect for season (*Season*; factor; winter, spring, summer, and fall), and a random effect for trip (*Trip*; intended to account for stochasticity in environmental conditions that we were unable to measure). The full model was specified as:

$$p(Y_i = 0) \sim \text{Binom}(1, p_i)$$

$$\begin{aligned} \text{logit}(p_i) = & hu_beta_0 + hu_beta_1 Period_i + hu_beta_2 Area_i + hu_beta_3 Period_i * Area_i + hu_beta_4 Season_i \\ & + hu_beta_5 Slope_i + hu_alpha_{Trip_i} \end{aligned}$$

With priors:

$$hu_{\beta_0} \sim Normal(0,10)$$

$$hu_{\beta_1} \sim Normal(0,10)$$

$$hu_{\beta_2} \sim Normal(0,10)$$

$$hu_{\beta_3} \sim Normal(0,10)$$

$$hu_{\beta_4} \sim Normal(0,10)$$

$$hu_{\beta_5} \sim Normal(0,10)$$

$$hu_{\alpha_j} \sim Normal(0, hu_{\sigma_{Trip}}) \text{ where } j = 1 \dots 22$$

$$hu_{\sigma_{Trip}} \sim HalfCauchy(10)$$

And

$$(\log(Y_i) | Y_i > 0) \sim Normal(\mu_i, \sigma)$$

$$\mu_i = \beta_0 + \beta_1 Period_i + \beta_2 Area_i + \beta_3 Period_i * Area_i + \beta_4 Season_i + \beta_5 Slope_i + \alpha_{Trip_i}$$

With priors:

$$\beta_0 \sim Normal(0,10)$$

$$\beta_1 \sim Normal(0,10)$$

$$\beta_2 \sim Normal(0,10)$$

$$\beta_3 \sim Normal(0,10)$$

$$\beta_4 \sim Normal(0,10)$$

$$\beta_5 \sim Normal(0,10)$$

$$\alpha_j \sim Normal(0, \sigma_{Trip}) \text{ where } j = 1 \dots 22$$

$$\sigma_{Trip} \sim HalfCauchy(10)$$

Where Y_i is the amount of biomass (NASC) per 100-m grid cell in the sonar survey, β terms describe coefficients for each variable, α_j is a random intercept for trip j , and σ_j is a random standard deviation for the intercept term for trip j . Coefficients preceded by hu are for the first stage of the model. Other candidate models included different combinations of these variables, starting with the most basic model (intercept only) and working up to the full model. Candidate models were examined only if they were deemed biologically plausible and no three-way interaction terms were included in any model (Table 1). All models used the same effects for both model stages. Each model was fitted assuming a lognormal distribution for positive observations and using four sampling chains, each with 2000 iterations (which was sufficient for convergence), a burn-in period of 1000 iterations, and thinning of every other sample to reduce the possibility of autocorrelation. We used Widely Applicable Information Criterion (WAIC) to compare our candidate models and select the model of best fit; WAIC is useful for comparing complex Bayesian models and often outperforms other metrics such as AIC or DIC (Watanabe and Opper, 2010; Gelman et al., 2014). Significance of individual variables was evaluated by examining 95% credible intervals and checking whether they contained zero.

We considered including depth as a variable in these models, however *ad hoc* investigations revealed that depth and slope were highly correlated. This was unsurprising considering the most extreme drop-off of the continental shelf tends to occur around the same depth regardless of latitude. The correlation between these two variables was non-linear (Figure S1), and a generalized additive model (GAM) revealed that the relationship was highly significant (Figure S2; edf = 8.5; $p < 0.001$). We therefore excluded depth as a predictor variable in all models. Generalized additive modeling was conducted in the R package ‘mgcv’ (Wood, 2011).

Hurdle model for predicting CPUE

We also fitted hurdle models to the data consisting of CPUE (fish per drop) at sites that were biologically sampled. For this analysis, we excluded chevron trap data due to low effort in both time periods; models were fit exclusively to hook-and-line data. In this procedure, the first stage of the hurdle model estimated the probability of a given site producing zero CPUE (no fish caught) and the second stage estimated the distribution of CPUE given that it was non-zero. We again fitted a range of candidate models to the data, beginning with an intercept only model and working up to various combinations of the main effects (*Area*, *Period* and the *Area:Period* interaction) along with a fixed effect of biomass (*NASC*) calculated at each individual site (Table 2). Finally, we included a random effect of *Trip* in some candidate models, intended to account for between-day variability in environmental conditions and fish catchability. All models used the same effects for both model stages, and all models were fit assuming a lognormal family for observations of positive CPUE. Candidate models were evaluated in terms of WAIC (Watanabe and Opper, 2010; Gelman et al., 2014) and models were fitted in the R package ‘brms’ (Bürkner, 2017). Significance of individual variables was evaluated by examining 95% credible intervals and checking whether they contained zero.

Multivariate analysis of community composition

We examined reef fish community composition in both periods and areas using non-metric multidimensional scaling (NMDS), analysis of similarities (ANOSIM), and permutational multivariate analysis of variance (PERMANOVA) using distance matrices. NMDS and ANOSIM have been used previously to investigate differences in fish community composition in impacted areas as compared to control sites (Shepherd et al., 1992; Bacheler et al., 2016). For NMDS and ANOSIM, we treated each area/period cross as an independent community of reef

fish. Given that gear was standardized between time periods, we assume that any changes in catch reflect real changes in the fish community rather than an effect of sampling. For this analysis, we used reef fish that were caught with hook-and-line only, given assumed variability in selectivity-by-species of these two gear types paired with lower chevron trap sampling effort. Our sampling unit was each trip during which fish were caught. We binned reef fish into six groups based on taxonomy; the groups were groupers, jacks, porgies, snappers, tilefish, and triggerfish (Table 3). Observations of species that did not fit into these groups were rare (< 5% of all catch) and were therefore excluded from the community analyses. Catch data were standardized by effort (number of drops) for a given trip, yielding a CPUE value for each trip and species group; relative rather than absolute values are required for NMDS when sampling effort is variable (Clarke, 1993). CPUE data were fourth-root transformed to down-weight the dominance of highly abundant species groups (Clarke and Warwick, 2001). Relationships between crosses of area and period were visualized by plotting NMDS results based on zero-adjusted Bray-Curtis similarity; this adjustment controls for erratic behavior that sometimes occurs for zero-rich data (Clarke et al., 2006). We conducted a one-way ANOSIM using the same zero-adjusted Bray-Curtis similarities as in the NMDS analysis. The ANOSIM was used to calculate an R statistic and differences between the four communities were evaluated for significance at $\alpha = 0.05$. Finally, we used PERMANOVA to examine statistical differences in community structure in the four crosses of period and area. This procedure is akin to a traditional ANOVA, but it uses F -tests based on sequential sums of squares from permutations of raw data. Using this procedure, we tested for the effect of *Area*, *Period*, and their interaction. Significance was evaluated at $\alpha = 0.05$. All three multivariate analyses were performed in the R package ‘vegan’ (Oksanen et al., 2020).

Red porgy age analyses and catch curves

We conducted single-species analyses with red porgy for several reasons. First, they were the most frequently caught species in both areas and time periods; other species lacked appropriate sample sizes in one or more areas or periods (see Results). Moreover, red porgy have fairly narrow home ranges relative to the size of the SWMPA; short term ranges are generally $\sim 0.5 \text{ km}^2$ (Afonso et al., 2009) while the entire SWMPA is $>500 \text{ km}^2$. Red porgy reach reproductive maturity quickly, with most spawning by age 2 or 3 (Manooch and Huntsman, 1977; Wyanski et al., 2019). Given the size and age of the SWMPA relative to these biological characteristics of red porgy, we felt this species represented an ideal candidate for testing for the presence of an MPA effect. Moreover, for similar reasons Pickens et al. (2021) conducted single-species analyses for red porgy caught in three of the other SEUSA MPAs; by singling out this species, we can add to the scope of their work.

For red porgy collected in 2019-2020, fish were weighed (whole weight; g) and sagittal otoliths were removed. Otoliths were processed and analyzed at the NOAA Fisheries Laboratory in Beaufort, North Carolina, using the methods described by Burton et al. (2017). Calendar ages were assigned to each specimen based on the number of opaque annuli and the month of capture (J. Potts, NOAA Fisheries, personal communication). In addition to red porgy collected by our survey, we obtained age information for red porgy caught by the Southeast Reef Fish Survey (SERFS) in the SWMPA and the surrounding region of Onslow Bay, NC, including the control area, from 2015-2019 (T. Smart, SC DNR, personal communication). There were ages available prior to 2015 in the region; however, sample sizes in the SWMPA were insufficient for comparison until 2015. Similarly, no red porgy ages were available from Rudershausen et al. (2010), which precluded a BACI framework for this analysis. Red porgy in the present study

were collected with hook-and-line and chevron traps; red porgy from SERFS were collected with chevron traps and short bottom longlines. We assume that the selectivity of these gears is equivalent because a recent stock assessment of this species used logistic selectivity curves for hook-based gear as well as traps, and both curves used age 6 as the youngest age of full recruitment to the gear (SEDAR, 2020). We examined age frequencies of red porgy by area (SWMPA or control) and year (2015-2020). We calculated mean age by area and year and compared yearly means using a Wilcoxon rank-sum test. Significance was assessed at the $\alpha = 0.05$ level. In addition to mean age, we compared yearly age diversity between the SWMPA and control sites using the Shannon diversity index. Age diversity is an important metric of fish stock health, with higher diversity implying greater health (Marteinsdottir and Thorarinsson, 1998). Diversity values were calculated using the R package ‘vegan’ (Oksanen et al., 2020).

In addition to comparing age distributions, we calculated yearly catch curves from red porgy ages. For each year from which sufficient data were available (2015-2019), we constructed catch curves from red porgy caught 1) inside the SWMPA and 2) in the vicinity of but outside the SWMPA, including the control area. Low sample sizes in the control area precluded specific investigations of red porgy caught therein; expanding across the region allowed a larger sample size (see Results). As with the prior red porgy analyses, we examined catch for all gears combined as we assume selectivity follows the same pattern for this species regardless of gear type. Catch curves use catch-at-age to estimate total mortality (Z) (Chapman and Robson, 1960; Thorson and Prager, 2011). Theoretically, Z should be lower for a given species inside MPAs due to a lack of F (Pradervand and Hiseman, 2006). We examined annual catch curves inside and outside the SWMPA for trends in Z that may be indicative of this effect. Catch curve analyses were performed in the R package ‘FSA’ (Ogle et al., 2021).

Red porgy size distributions

We compared size distributions (TL, mm) of red porgy caught by the authors of Rudershausen et al. (2010) with those caught in 2018-2020 in both areas. Red porgy were the only species with sufficient sample sizes in both areas and periods for analysis. To augment our dataset in the latter period, we obtained length information for red porgy caught by SERFS in these two areas (T. Smart, personal communication). As in the age analysis, we assume selectivity of gears used in these surveys was equivalent for red porgy. For the size analysis, we did not use red porgy data from elsewhere in the region; analyses were restricted to individuals that were caught in either the SWMPA or the control. We did not expand our dataset to include fish from outside the control area because data were not available from SERFS in the “before” period. We used a two-way ANOVA to compare the four size distributions and tested for the effect of *Area*, *Period*, and their interaction. Significance was evaluated at $\alpha = 0.05$ and analyses were performed in base R (R Core Team, 2020).

Results

Data collection

We made five trips each to the SWMPA and the control area for sonar data collection. In total, we collected hydroacoustic data for 422.40 km and 356.50 km of linear seafloor in the SWMPA and control, respectively (Table 4). In the SWMPA, we identified 163 aggregations of biomass in total, of which 41 were fished with 250 total hook-and-line drops and 15 sites were fished with chevron traps. In the control area, we identified 207 total aggregations of biomass of which 72 were fished with 382 total hook-and-line drops and 16 were fished with chevron traps. Sonar collection and hook-and-line sampling occurred in 2018, 2019, and 2020 (Table 5).

Chevron trapping occurred in 2018 and 2019; no chevron trapping occurred in 2020 due to the unavailability of the *R/V Cape Fear*.

We caught at least one individual of 31 fish species with hook-and-line and/or chevron traps. In the SWMPA, per-species CPUE values ranged from 0.001 to 0.166 fish per drop for hook-and-line and 0.067 to 0.467 fish per chevron trap. In the control area, CPUE values ranged from 0.002 to 0.074 for hook and line and 0.063 to 1.750 for chevron traps; many of these CPUE values are similar to values from Rudershausen et al. (2010) (Table 3). Our most numerous caught species with both gear types in both areas was red porgy. We caught 12 species that were not observed by Rudershausen et al. (2010): blackfin snapper *Lutjanus buccanella*, goldface tilefish *Caulolatilus chrysops*, marbled grouper *Dermatolepis inermis*, sand tilefish *Malacanthus plumieri*, silk snapper *Lutjanus vivanus*, spotfin butterflyfish *Chaetodon ocellatus*, squirrelfish *Holocentrus adscensionis*, white grunt *Haemulon plumierii*, whitebone porgy *Calamus leucosteus*, whitespotted soapfish *Rypticus maculatus*, yellowmouth grouper *Mycteroperca interstitialis* and a hybrid snapper *Lutjanus* sp., most likely a cross between a blackfin snapper and a silk snapper (N. Bacheler, NOAA Fisheries, personal communication). In comparison, Rudershausen et al. (2010) observed seven species that were absent from our survey: graysby *Cephalopholis cruentata*, lionfish *Pterosis* sp., lesser amberjack *Seriola fasciata*, red cornetfish *Fistularia petimba*, rock hind *Epinephelus adscensionis*, hogfish *Lachnolaimus maximus*, and tomtate *Haemulon aurolineatum*.

Sonar and catch data from the Snowy Wreck

Hydroacoustic surveys were conducted over the Snowy Wreck on June 6 2007 and August 2 2019. A total of three transects were completed (one in 2007 and two in 2019) and we estimated biomass in NASC for each transect. The NASC showed a slightly higher fish

density at the Snowy Wreck in 2007 ($1142.9 \text{ m}^2\text{nmi}^{-2}$) compared to both the 2019 transects (841.5 and $680.5 \text{ m}^2\text{nmi}^{-2}$). Hook-and-line CPUE at the Snowy Wreck was 1.75 (four drops; six snowy grouper and one wreckfish *Polyprion americanus*) in 2007 and 1.25 (four drops; five snowy grouper) in 2019.

Hurdle model for predicting biomass

Across both areas and periods, sonar data collection resulted in 10,951 grid cells of 100 m length. The distribution of non-zero biomass (NASC) observations in these cells was approximately lognormal (Figure S3). We compared a range of candidate Bayesian hurdle models testing different combinations of variables for predicting biomass and compare the fit of ten candidate models (Table 1). The best model (lowest WAIC) was *Period + Slope + Season + Trip*. There were several additional models that were competitive in terms of WAIC; each of these models contained *Slope* and *Trip*. Results from the best model indicated significant effects of *Slope* in both stages of the model; cells with higher slope were less likely to contain zero biomass, and given non-zero biomass, cells with higher slope had higher biomass (Table 6; Figure S4). In this model, the only other variable whose credible interval did not include zero was *Period*, for which the before timeframe had significantly less biomass than the After timeframe (Figure S5). We also investigated results from the full model (*Area*Period + Slope + Season + Trip*) given that it was competitive in terms of WAIC (Table 2). The only significant variable in either stage of this model was *Slope* (Table 7). The MPA effect (*Area:Period* interaction) was not significant in either stage. As an *ad hoc* investigation, we generated a conditional effect plot of the *Area*Period* interaction term for biomass; though its credible interval widely overlapped with zero indicating no difference across combinations of *Area* and

Period, the trend (larger increase of biomass in MPA relative to control) was in the direction of our hypothesized effect (Figure S6).

Hurdle model for predicting CPUE

We explored a range of candidate models for predicting CPUE and compared the fit of ten candidate models (Table 2). The best model based on WAIC was *Area + Trip*. However, the model *Period + Trip* was also competitive in terms of WAIC, with a difference of only 0.2. In neither of the top two models did the 95% credible intervals for any predictor variable contain zero in either stage of the model (Tables 8 and 9). Marginal effects plots for these two models show widely overlapping intervals between Areas and Periods respectively (Figures S7 and S8). Two candidate models contained the *Area*Period* interaction (i.e., MPA effect); neither was competitive with the best model. Despite this non-competitiveness, we explored the results of the *Area*Period + Trip* model as an *ad hoc* procedure. None of the 95% credible intervals for the predictor variables in this model contained zero or were close to containing zero.

Multivariate analysis of community composition

The four crosses of *Area* and *Period* each had distinct community composition. NMDS indicated four groupings with very minimal overlap and had an estimated stress value of 0.131, indicating a fair or good fit (Figure 4). NMDS results suggest that in both areas, communities have shifted away from being dominated by groupers and moved toward being dominated by snappers and tilefish. From the ANOSIM procedure, the *R* statistic was 0.454 with an associated *P* value of 0.001, both of which indicate significant separation between the four fish communities. PERMANOVA was similarly conclusive, with a significant effect of *Area* ($F = 4.06$; $p = 0.001$) and *Period* ($F = 8.19$; $p = 0.004$) but not their interaction, though the *P* value for

the interaction term was fairly low ($F = 1.561$; $p = 0.166$; Table 10). The results from these multivariate analyses indicate that fish communities in both the SWMPA and the Control area have changed in the decade since the SWMPA was closed, but there is no evidence from these procedures that the directionality of those changes varied between the two areas.

Red porgy age analyses and catch curves

Per-year sample sizes for red porgy ages from 2015-2020 ranged from 14 to 67 inside the SWMPA and from 8 to 73 inside the control area (Table 11). For all red porgy from outside the SWMPA, yearly sample sizes ranged from 386 to 546; SERFS data were only available through 2019, so red porgy encountered in 2020 for both *inside control* and *outside SWMPA* were all from our collections in the control area. Mean annual ages ranged from 4.9 to 7.1 inside the SWMPA and from 4.8 to 5.3 in the control area, and were higher in the SWMPA for each of the six years examined. Wilcoxon rank sum tests found that mean age was significantly higher in the SWMPA than the control in 2016 and 2018 (Figure 5). Age diversity values ranged from 1.7 to 2.0 inside the SWMPA and from 0.9 to 2.0 in the control. Diversity values were higher inside the SWMPA for five out of six years examined (Figure 5).

Catch curves on red porgy ages from inside the SWMPA resulted in a mean estimated Z across years of 0.39 (range 0.22 – 0.69). For regional data from outside the SWMPA, mean estimated Z was 0.38 (range 0.33 – 0.44) (Figure 6; Table 12). For the most recent three years in this analysis, estimates of Z from inside the SWMPA were below estimates of Z outside the SWMPA.

Red porgy size distributions

Rudershausen et al. (2010) collected lengths for 26 red porgy in the control area and 41 red porgy in the SWMPA in 2007-2009. Between data from the present study and SERFS data,

lengths were available for 89 red porgy in the control area and 181 red porgy in the SWMPA from 2018-2020. Size distributions showed an increase in red porgy total lengths in the SWMPA from the before to the after period but no shift was evident in the control area (Figure 7). ANOVA results determined that neither the effect of *Area* nor *Period* were significant predictors of length as standalone variables, but their interaction was highly significant ($F = 13.208$; $p < 0.001$; Table 13). This result indicates a positive effect of MPA designation on the size structure of red porgy inside the closed area.

Discussion

Our results are equivocal, though in most ways they indicate that the designation of the Snowy Wreck Marine Protected Area has not yet had the desired effect. BACI-style analyses of CPUE and sonar data showed no evidence of a positive change inside the SWMPA that did not also occur in the control area. Evidence suggests that the reef fish populations in the SWMPA and control have both undergone similar community-level changes over the last decade. However, single-species analyses with red porgy indicate a possible positive MPA effect. For each of our analyses, we provide explanations for the results we observed.

Red porgy size was the only metric that indicated the presence of an MPA effect. It is clear that the size structure for red porgy has shifted in the last decade to larger individuals within the SWMPA but has not changed inside the control area. Red porgy were the only species for which we had a sufficient sample size to make this comparison, but it remains possible that other species have experienced a similar effect. Even marginal increases in body length can have substantial benefits to fish stocks - Barneche et al. (2018) found that for 95% of fish species examined, reproductive energy output increases disproportionately with body size (hyperallometric growth). In our study, the median TL for red porgy in the SWMPA was 390

mm before closure and 420 mm after closure (7.7% increase). Using the previously published length-weight relationship for red porgy (Manooch and Huntsman, 1977), this length increase corresponds to a biomass increase from 795 to 985 g (23.9% increase). Finally, assuming a reproductive scaling component of 1.24 (the average for three porgy species from Barneche et al. 2018), a 23.9% biomass increase corresponds to a 30.6% increase in reproductive capacity. Such an increase is especially important considering red porgy are currently overfished and undergoing overfishing in the SEUSA (NOAA Fisheries, 2019). The phenomenon of minor increases in length corresponding to substantial increases in reproductive capacity has often been overlooked when studying the effects of MPAs on fish populations (Marshall et al., 2019). This phenomenon may hold true for other species in the SWMPA (now or in the future).

For all six years examined, mean red porgy age in the SWMPA was higher than that in the control area; for two of the six years, we detected a statistically significant difference. Similarly, for five of six years, age diversity was higher in the SWMPA than in the control (Figure 6). Yearly differences in these metrics were generally not substantial, and sample sizes were low (Table 11). Higher sample sizes and thus greater statistical power may have resulted in more significant differences in mean annual age and wider gaps in diversity values. Even with our low sample sizes, these trends suggest the age structure for red porgy differs between the two areas. However, because ages of this species from the SWMPA and control were not available from before closure, we were unable to determine whether this finding implies an MPA effect. Nevertheless, given our finding of a significant MPA effect on red porgy length (and the positive correlation between length and age), evidence suggests that the SWMPA has also positively influenced mean and diversity of red porgy ages. Fishing tends to remove older, larger individuals which typically reduces spawning stock biomass and can cause stock fluctuations

(Berkeley et al., 2004b; Rouyer et al., 2011). Management measures (such as spatial closures) can shift age structures towards older and more age-diverse populations therefore increasing the reproductive potential of a stock (Marteinsdottir and Thorarinsson, 1998; Berkeley et al., 2004a). Taken in context with the above length analysis, it is possible that this phenomenon is occurring with red porgy in the SWMPA and may be occurring with other species, including those with longer generation times for which the effect may not yet be detectable.

Catch curve analyses for red porgy produced variable estimates for Z for fish caught inside the SWMPA, probably due to low sample sizes. Estimates for Z from red porgy caught outside the SWMPA were much more consistent between years (Figure 7). However, low Z estimates from in the SWMPA in the most recent years examined (2017-2019) indicate a possible positive influence of the prohibition of fishing on the annual survival of red porgy. Increasing sampling of red porgy and other reef species inside the SWMPA and other SEUSA MPAs would be beneficial for monitoring MPA effects.

Pickens et al. (2021) examined red porgy size and age distributions for three other SEUSA MPAs in comparison to control areas. For the Northern South Carolina MPAs, they did not report an MPA effect on red porgy size. However, for the Edisto and North Florida MPAs, Pickens et al. (2021) showed a significant positive MPA effect on size. Furthermore, in the North Florida MPA, they reported a positive MPA effect on red porgy age. Their findings support our assertion of a positive effect of closure on the SEUSA red porgy population.

Using our models of the SWMPA effect on acoustic biomass, we were unable to reject the null hypothesis of no effect. It is possible that there has truly been no effect of the SWMPA on biomass, or that our survey was not comprehensive enough to detect it. However, other possibilities exist as well. Biomass is an imperfect variable to measure the effect of a spatial

closure, particularly over highly productive offshore reef habitat that comprises a relatively small portion of our survey area. It is possible that in the “before” period, available niche space was occupied by more, younger, smaller fish than in the “after” period. Therefore, the overall volume of biomass may not have changed since the designation of the SWMPA (and therefore we would be unable to detect a difference using sonar data), but the component animals of that biomass may be different now than they were when the SWMPA was closed to fishing. This hypothesis, that overall fish biomass may not have increased in the SWMPA but that it now consists of *higher quality* individuals, is supported by the red porgy size comparison discussed above. Furthermore, the community shift away from groupers and towards tilefish and snappers may inherently affect total reef fish biomass, as tilefish and snappers are generally smaller-bodied than are groupers. It is unsurprising that *Slope* was a significant predictor of biomass in our hurdle models, since greater vertical relief tends to aggregate reef fishes (Randall and Minns, 2000). The importance of *Trip* as a random effect is similarly unsurprising since a variety of stochastic factors, such as sea surface conditions, upwelling, and simply whether or not we encountered fish schools along sonar transects might have influenced our hydroacoustic data collection. Future surveys could be improved by measuring environmental variables wherever possible. Furthermore, our biomass analysis focused on the lowest 10 m of the water column. Though reef fish sometimes occur higher in the water than 10 m off of the seafloor, we assume that the proportion of reef fish excluded from our survey due to this truncation was equivalent between both periods and areas. If this assumption was not met, our results from this analysis may be biased.

Models for predicting CPUE showed no sign of a positive MPA effect. Ad hoc examination of a model that contained the interaction of *Area* and *Period* indicated no significant

trend in the direction of (or away from) a positive effect of the fishing prohibition. Though the best two models contained *Area* and *Period* respectively, the estimated CPUE values at the two levels of each of these variables overlapped widely and do not suggest any difference between levels. The results of biological sampling (in our case, hook-and-line fishing) are highly stochastic. Here we used a random effect of *Trip* in an attempt to account for much of the environmental and biological variability that can influence fishing success. However, it is likely that some of these variables were non-constant even within a single trip; for example, current direction and magnitude can influence the success of bottom fishing, and can also vary over small spatial scales particularly in proximity to the Gulf Stream. We considered using *Site* as a random effect (nested within *Trip*), but given that each site was only sampled once we elected to use *Trip*, though it is an imperfect variable for this purpose. Future surveys could consider attempting to sample each site multiple times and/or to quantify environmental variables such as current, though these efforts would likely come at a high opportunity cost.

From our NMDS analysis, it is evident that the fish communities in the two areas were not similar before the SWMPA was designated, as the centroid ellipses for the two “before” communities do not overlap (Figure 4). This may be because the SWMPA was intentionally designated in this location to protect the highest quality reef fish habitat, as is often the case when spatial closures are created (Lester et al., 2009). Similarly, though both fish communities changed significantly over time, they were not similar to each other in the “after” period (though there was slight overlap; Figure 5). The temporal difference was driven by several key species. First, red grouper were commonly caught in the before period but were scarce a decade later. In the before period, red grouper was the 6th and 4th most commonly caught species with hook-and-line in the SWMPA and control respectively. In the after period, red grouper was the 16th most

commonly caught species in the SWMPA and was never observed in the control. These observations are consistent with the region-wide decline of red grouper documented in the most recent stock assessment for that species (SEDAR, 2017). Other groupers, such as snowy grouper, scamp, and speckled hind, were also more commonly caught in the before period than the after period in both areas; these species are similarly imperiled (Bacheler and Ballenger, 2018; NOAA Fisheries, 2019). Contrary to the observed decline in groupers was an increase in observations for species such as silk snapper and sand tilefish. Neither species was observed with either gear in the before period, but both were observed with medium-to-high frequency in the after period in both areas (Table 3). These changes in community composition are evident in the movement in NMDS centroid ellipses away from “Groupers” and towards “Snappers” and “Tilefish” (Figure 4). Moreover, the results of our ANOSIM and PERMANOVA (and the non-significant *Area*Period* interaction term thereof) support the idea that the community-level changes we observed were ecosystem-wide and not a result of MPA designation (Table 10). However, it is possible that an MPA effect on the fish community did occur and that the ecosystem-wide changes were greater in magnitude; this could have resulted in a masking effect and an inability to detect the positive influence of the MPA alone (Claudet, 2018). It is unclear what may be driving ecosystem-wide changes to the reef fish community, though recent findings in stock assessments and analyses of survey data have also identified broad changes to this assemblage. For example, over the last few years decadal recruitment declines have been documented across this region for species such as red porgy (SEDAR, 2020), red grouper (SEDAR, 2017), black sea bass (*Centropristis striata*) (SEDAR, 2018), and scamp (Bacheler and Ballenger, 2018). The community changes we document here merit further investigation, especially when taken in context with the concerning findings for recruitment for some species.

Though several of the above analyses offer no explicit evidence for a positive MPA effect, there are several reasons why an effect may still be present. Claudet (2018) described six conditions by which an MPA may not seem effective when it actually is. One of these is that a spillover effect may be occurring into the surrounding (fished) areas, which masks the effects of continued fishing pressure outside the MPA. It is possible that this scenario is occurring in the SEUSA: changes in both the SWMPA and control area from the community analysis and the CPUE-to-biomass analysis had the same directionality and similar magnitude. While these changes may be a result of ecosystem-wide measures such as shifts in management regimes (Stewart-Oaten et al., 1986; Kerr et al., 2019), it is also possible that they are restricted to the general vicinity of the SWMPA (including our control area). Ideal control areas in BACI studies are far enough away from the MPA that they are not impacted by it (Kerr et al., 2019) but are close enough that they have similar biotic and abiotic characteristics. Approximately 14 km separate the north edge of the SWMPA from the south edge of the control area in our study, which may result in non-independence between the areas. Furthermore, the control area is “downstream” of the SWMPA, and may therefore be more likely to absorb spillover of adult or larval fish produced in the SWMPA than would an upstream area (Halpern, 2003). We therefore conclude that the control area in our study was imperfect. Having replication of control sites has been recommended (e.g., Kerr et al., 2019) and may have resulted in different conclusions for our analyses. However, given that Rudershausen et al. (2010) sampled only one control site, a true BACI comparison with multiple controls was not possible here. Our study is therefore limited in this respect.

Even if the control in this study was adequate, we still may not have detected a strong MPA effect; there are several reasons why the SWMPA may not be working as intended. Edgar

et al. (2014) listed five key features of MPAs that, if present, often result in the desired effect of closure; those features are: 1) the MPA is old (has been closed for 10 or more years), 2) the MPA is large ($>100 \text{ km}^2$), 3) harvests are prohibited in the MPA, 4) the MPA is isolated by deep water or sand, and 5) the area is well enforced. The SWMPA is now over a decade old, is over 500 km^2 , is closed to reef fish harvest, and is isolated by deep water and sand. However, there is evidence to suggest that the SWMPA is not well enforced. Bacheler et al. (2016) commented that non-compliance with MPA closures may be prevalent in the SEUSA and reported witnessing illegal bottom fishing in the SEUSA MPA network during their study. Indeed, during the course of the present study, suspected illegal bottom fishing was observed on approximately 50% of trips to the SWMPA including once at the Snowy Wreck itself; a United States Coast Guard vessel was observed on a single day out of approximately 15 in the area since 2015 (B. Runde, personal observation). Any amount of illegal fishing could depress an MPA effect, particularly since the largest, most aggressive individuals (such as large groupers) would likely be caught first (Huntsman et al., 1999). Some instances of noncompliance may be malicious; however it is also possible that some (perhaps many) anglers are unaware of the presence of the SWMPA. To our knowledge, no digital nautical charting databases (e.g., Garmin) currently include polygons or other indications of the MPAs in the SEUSA. In lieu of (or in addition to) greater enforcement, we recommend managers seek to raise awareness of the SEUSA MPA network by working with the US Coast Guard and private companies to delineate closed areas on digital nautical charts that are ubiquitous on offshore fishing vessels.

Though the SWMPA is large and old by the definitions of Edgar et al. (2014), their recommendations are generalizations and may not apply to our study. The minimum size and age of an MPA that are necessary in order to detect an effect depends on the effect being measured

and on the system in question (Halpern and Warner, 2003). The choice of reserve size should reflect the dispersal patterns of the species targeted for protection (Halpern, 2003; Halpern and Warner, 2003) and even small MPAs can be adequate for protection of sedentary stocks (Orensanz and Jamieson, 1998). The MPA network in the SEUSA was intended to protect deepwater reef fishes, such as speckled hind and Warsaw grouper. Little is known of the movement patterns of these fishes, though Runde et al. (2020) documented individual acoustically tagged speckled hind persisting in the SWMPA for at least 63 days. Likewise, Shertzer et al. (2018) used mark-and-recapture data for Warsaw grouper that showed repeated capture of some individual fish on a single site over the span of several years. These reports, though isolated, suggest that these species have fairly high site fidelity or at least exhibit homing. Therefore, for these deepwater groupers and likely other reef fishes, the size of the SWMPA is probably adequate for protecting a portion of these stocks. However, the age of the SWMPA may not yet be great enough for the full effects of closure to be observed. At present (2021), the SWMPA has been closed to bottom fishing for over 12 years; while this may be long enough for a noticeable effect to appear in the age structure of species like red porgy, it is a fraction of the maximum longevity of some of the species targeted for protection. Sanchez et al. (2019) found that the maximum age of both snowy and Warsaw groupers is at least 56 years (and perhaps several decades longer). Similarly, Andrews et al. (2013) showed that longevity for speckled hind may approach 60-80 years. It is therefore unreasonable to expect a decipherable effect of the SWMPA on, for instance, speckled hind a mere 12 years post-closure. Though our models did not find statistical significance of an MPA effect, models containing the *Area*Period* interaction were competitive in terms of WAIC and showed trends in the direction of a positive

MPA effect. Continued monitoring of the fish populations inside the SWMPA as it ages may clarify some of the null results we found in this study.

Other studies examining the effects of MPAs with a BACI framework have found significant positive effects more often than not (e.g., Moland et al., 2013; Mateos-Molina et al., 2014; Kerr et al., 2019). However, this trend in the literature may be a result of publication bias (Woodcock et al., 2017). That our BACI analyses failed to detect a positive effect may be a relic of sampling design (as discussed above). We urge future MPA researchers to use BACI designs wherever possible. Further, we suggest that whenever new MPAs are designated, an explicit plan for monitoring their biological effects (including in the period prior to or immediately following designation) and that of at least one control area (but preferably several) should also be defined.

The only two (to our knowledge) previous studies of the SEUSA MPA network demonstrated mostly null effects of spatial closure (Bacheler et al., 2016; Pickens et al., 2021). Our results are in line with their findings: most of our analyses did not show an effect, although single-species evaluations indicated positive effects. Overall, the amount and quality of available data on this network of MPAs is poor. While monitoring the effect of MPAs is difficult (particular when they are far from shore) we recommend directed efforts to gather time-series data on demersal fishes inside the eight SEUSA MPAs. The addition of sites within MPA boundaries to existing surveys such as SERFS could result in a greater ability to detect positive MPA effects, if present. To this same end, we recommend *ad hoc* designation of control areas (e.g., north and south of each of the eight MPAs) and increased sampling therein.

Conclusions

In this paper, we provide indications that the system of deep-water MPAs in the SEUSA is having a positive effect on some shorter-lived reef fish stocks, though no evidence of an effect was found for longer-lived fishes or for reef fish biomass in general. Though limited to a single MPA and corresponding control area, our multifaceted approach included several analyses conducted in a BACI framework, which is a robust method for analyzing MPA effects (Kerr et al., 2019). We recommend the following measures to enhance the effectiveness of this MPA network and the detection thereof:

1. Increased enforcement of the MPAs by federal and state agencies;
2. Promotion of awareness of the MPA network, including by designation of polygons on digital GPS chartplotter databases;
3. Increased fishery independent monitoring of the SWMPA and other MPAs (e.g., by SERFS) with the specific goal of accumulating larger reef fish sample sizes for diverse analyses.

If these measures are adhered to, the SEUSA MPA network may indeed prove to be an effective long-term means of protecting and restoring portions of imperiled reef fish stocks.

Acknowledgements

We are indebted to the decades of collaboration and expertise provided by Capt. T. Burgess, who participated in nearly every data collection trip of the previous and present studies. We thank J. Styron, D. Wells, K. Johns, and the support staff of the *R/V Cape Fear* for providing a platform for the bulk of the data collection in this study. Further, thanks to D. Britt, J. Dufour, P. Dufour, E. Scheeler, B. Love, C. Mikles, O. Mulvey-McFerron, R. Gallagher, J. Fader, and R. Tharp for assistance in the field. We thank J. Potts and W. Rogers for expeditious aging of reef fish and T.

Smart and SERFS for providing red porgy size and age data. J. Cao provided immense assistance with model development. The literature review in this paper benefitted from discussions with C. Lopazanski. M. Damiano offered advice on analysis of age data. Thanks to C. Schobernd for clarification and interpretation of community analyses. N. Bacheler reviewed an earlier version of this paper. Funding for data collected from 2007-2009 was provided by North Carolina Sea Grant projects 07-FEG-15 and 08-FEG-10. Funding for data collected in 2018-2020 was provided by the National Oceanic and Atmospheric Administration's Cooperative Research Program (NA17NMF4540138). Scholarship support for B. Runde was provided by the Steven Berkeley Marine Conservation Fellowship, the Joe E. and Robin C. Hightower Graduate Student Award, and the North Carolina Wildlife Federation Conservation Leadership Grant. The scientific results and conclusions, as well as any views and opinions expressed herein, are those of the authors and do not necessarily reflect those of any government agency or institution. There is no conflict of interest declared in this article.

References

- Afonso, P., Fontes, J., Guedes, R., Tempera, F., Holland, K. N., and Santos, R. S. 2009. A multi-scale study of red porgy movements and habitat use, and its application to the design of marine reserve networks. *In* Tagging and tracking of marine animals with electronic devices, pp. 423-443. Springer.
- Aleman, D., Iribarne, O. O., and Acha, E. M. 2013. Effects of a large-scale and offshore marine protected area on the demersal fish assemblage in the Southwest Atlantic. *ICES Journal of Marine Science*, 70: 123-134.

- Alós, J., Puiggrós, A., Díaz-Gil, C., Palmer, M., Rosselló, R., and Arlinghaus, R. 2015. Empirical evidence for species-specific export of fish naïveté from a no-take marine protected area in a coastal recreational hook and line fishery. *PLoS ONE*, 10: e0135348.
- Andrews, A. H., Barnett, B. K., Allman, R. J., Moyer, R. P., and Trowbridge, H. D. 2013. Great longevity of speckled hind (*Epinephelus drummondhayi*), a deep-water grouper, with novel use of postbomb radiocarbon dating in the Gulf of Mexico. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 1131-1140.
- Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K., Mcclanahan, T. R., and Russ, G. R. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences*, 107: 18256-18261.
- Bacheler, N. M., and Ballenger, J. C. 2018. Decadal-scale decline of scamp (*Mycteroperca phenax*) abundance along the southeast United States Atlantic coast. *Fisheries Research*, 204: 74-87.
- Bacheler, N. M., Schobernd, C. M., Harter, S. L., David, A. W., Sedberry, G. R., and Todd Kellison, G. 2016. No evidence of increased demersal fish abundance six years after creation of marine protected areas along the southeast United States Atlantic coast. *Bulletin of marine science*, 92: 447-471.
- Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science*, 360: 642-645.
- Berkeley, S. A., Chapman, C., and Sogard, S. M. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, 85: 1258-1264.

- Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29: 23-32.
- Botsford, L. W., Micheli, F., and Hastings, A. 2003. Principles for the design of marine reserves. *Ecological Applications*, 13: 25-31.
- Branch, T. A., Hilborn, R., Haynie, A. C., Fay, G., Flynn, L., Griffiths, J., Marshall, K. N., Randall, J. K., Scheuerell, J. M., and Ward, E. J. 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 1647-1668.
- Bürkner, P.-C. 2017. brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software*, 80: 1-28.
- Burton, M. L., Potts, J. C., Page, J., and Poholek, A. 2017. Age, growth, mortality and reproductive seasonality of jolthead porgy, *Calamus bajonado*, from Florida waters. *PeerJ*, 5: e3774.
- Caveen, A., Sweeting, C., Willis, T. J., and Polunin, N. 2012. Are the scientific foundations of temperate marine reserves too warm and hard? *Environmental Conservation*, 39: 199-203.
- CBD 2010. Strategic Plan for Biodiversity 2011-2020. *In* Tenth Conference of Parties to the Convention on Biological Diversity. Nagoya, Japan.
- Chapman, D., and Robson, D. 1960. The analysis of a catch curve. *Biometrics*: 354-368.
- Claissé, J. T., Pondella, D. J., Love, M., Zahn, L. A., Williams, C. M., Williams, J. P., and Bull, A. S. 2014. Oil platforms off California are among the most productive marine fish habitats globally. *Proceedings of the National Academy of Sciences*, 111: 15462-15467.

- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian journal of ecology*, 18: 117-143.
- Clarke, K. R., Somerfield, P. J., and Chapman, M. G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330: 55-80.
- Clarke, K. R., and Warwick, R. 2001. *Change in marine communities. An approach to statistical analysis and interpretation*, 2.
- Claudet, J. 2018. Six conditions under which MPAs might not appear effective (when they are). *ICES Journal of Marine Science*, 75: 1172-1174.
- Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J. A., Pérez-Ruzafa, Á., Badalamenti, F., Bayle-Sempere, J., Brito, A., and Bulleri, F. 2008. Marine reserves: size and age do matter. *Ecology letters*, 11: 481-489.
- Claudet, J., Pelletier, D., Jouvenel, J.-Y., Bachet, F., and Galzin, R. 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation*, 130: 349-369.
- Coleman, F. C., Koenig, C. C., Huntsman, G. R., Musick, J. A., Eklund, A. M., McGovern, J. C., Sedberry, G. R., Chapman, R. W., and Grimes, C. B. 2000. Long-lived Reef Fishes: The Grouper-Snapper Complex. *Fisheries*, 25: 14-21.
- Dinmore, T., Duplisea, D., Rackham, B., Maxwell, D., and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES Journal of Marine Science*, 60: 371-380.

- Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T., and Berkhout, J. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506: 216-220.
- Egerton, J. P., Johnson, A. F., Turner, J., LeVay, L., Mascareñas-Osorio, I., and Aburto-Oropeza, O. 2018. Hydroacoustics as a tool to examine the effects of Marine Protected Areas and habitat type on marine fish communities. *Scientific Reports*, 8: 47.
- Fisher, J. A., and Frank, K. T. 2002. Changes in finfish community structure associated with an offshore fishery closed area on the Scotian Shelf. *Marine Ecology Progress Series*, 240: 249-265.
- Francini-Filho, R., and Moura, R. L. d. 2008. Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fisheries Research*, 93: 346-356.
- Frank, K. T., Shackell, N. L., and Simon, J. E. 2000. An evaluation of the Emerald/Western Bank juvenile haddock closed area. *ICES Journal of Marine Science*, 57: 1023-1034.
- Gell, F. R., and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in ecology & evolution*, 18: 448-455.
- Gelman, A., Hwang, J., and Vehtari, A. 2014. Understanding predictive information criteria for Bayesian models. *Statistics and computing*, 24: 997-1016.
- Green, R. H. 1979. *Sampling design and statistical methods for environmental biologists*, John Wiley & Sons.
- Greenstreet, S. P., Fraser, H. M., and Piet, G. J. 2009. Using MPAs to address regional-scale ecological objectives in the North Sea: modelling the effects of fishing effort displacement. *ICES Journal of Marine Science*, 66: 90-100.

- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications*, S117-S137.
- Halpern, B. S., and Warner, R. R. 2002. Marine reserves have rapid and lasting effects. *Ecology letters*, 5: 361-366.
- Halpern, B. S., and Warner, R. R. 2003. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270: 1871-1878.
- Harter, S. L., Ribera, M. M., Shepard, A. N., and Reed, J. K. 2009. Assessment of fish populations and habitat on Oculina Bank, a deep-sea coral marine protected area off eastern Florida. *Fishery Bulletin*, 107: 195-206.
- Hilborn, R. 2018. Are MPAs effective? *ICES Journal of Marine Science*, 75: 1160-1162.
- Hoos, L. A., Buckel, J. A., Boyd, J. B., Loeffler, M. S., and Lee, L. M. 2019. Fisheries management in the face of uncertainty: Designing time-area closures that are effective under multiple spatial patterns of fishing effort displacement in an estuarine gill net fishery. *PLoS ONE*, 14: e0211103.
- Huntsman, G., Potts, J., Mays, R., and Vaughan, D. 1999. Groupers (Serranidae, Epinephelinae): Endangered Apex Predators of Reef Communities. *In American Fisheries Society Symposium*, pp. 217-231.
- Huvenne, V., Bett, B., Masson, D., Le Bas, T., and Wheeler, A. J. 2016. Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. *Biological Conservation*, 200: 60-69.

- Kerr, L. A., Kritzer, J. P., and Cadrin, S. X. 2019. Strengths and limitations of before–after–control–impact analysis for testing the effects of marine protected areas on managed populations. *ICES Journal of Marine Science*, 76: 1039-1051.
- Kracker, L. M. 2007. Hydroacoustic surveys: A non-destructive approach to monitoring fish distributions at National Marine Sanctuaries.
- Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airamé, S., and Warner, R. R. 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, 384: 33-46.
- Lindeman, K. C., Pugliese, R., Waugh, G. T., and Ault, J. S. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of marine science*, 66: 929-956.
- Lubchenco, J., and Grorud-Colvert, K. 2015. Making waves: The science and politics of ocean protection. *Science*, 350: 382-383.
- Manooch, C. S., and Huntsman, G. R. 1977. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. *Transactions of the American Fisheries Society*, 106: 26-33.
- Marshall, D. J., Gaines, S., Warner, R., Barneche, D. R., and Bode, M. 2019. Underestimating the benefits of marine protected areas for the replenishment of fished populations. *Frontiers in Ecology and the Environment*, 17: 407-413.
- Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1372-1377.

- Mateos-Molina, D., Schärer-Umpierre, M., Appeldoorn, R., and García-Charton, J. 2014. Measuring the effectiveness of a Caribbean oceanic island no-take zone with an asymmetrical BACI approach. *Fisheries Research*, 150: 1-10.
- Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., André, C., and Knutsen, J. A. 2013. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study. *In Proc. R. Soc. B*, p. 20122679. The Royal Society.
- MPA Atlas 2021. Atlas of Marine Protection.
- Murray, S. N., Ambrose, R. F., Bohnsack, J. A., Botsford, L. W., Carr, M. H., Davis, G. E., Dayton, P. K., Gotshall, D., Gunderson, D. R., and Hixon, M. A. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries*, 24: 11-25.
- NMFS 2019. Status of Stocks 2019 Annual Report to Congress on the Status of US Fisheries. NOAA Fisheries Service.
- NOAA Fisheries 2019. 2019 Report to Congress on the Status of U.S. Fisheries
- Ogle, D. H., Wheeler, P., and Dinno, A. 2021. FSA: Fisheries Stock Analysis. R package version 0.8.32 edn.
- Ojeda-Martínez, C., Bayle-Sempere, J. T., Sanchez-Jerez, P., Salas, F., Stobart, B., Goñi, R., Falcón, J. M., Graziano, M., Guala, I., and Higgins, R. 2011. Review of the effects of protection in marine protected areas: current knowledge and gaps. *Animal Biodiversity and Conservation*, 34: 191-203.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., and Wagner, H. 2020. vegan: Community Ecology Package. 2.5-7 edn.

- Orensanz, J., and Jamieson, G. S. 1998. The assessment and management of spatially structured stocks: an overview of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Canadian Special Publication of Fisheries and Aquatic Sciences: 441-459.
- Osenberg, C. W., Shima, J. S., Miller, S. L., and Stier, A. C. 2011. Ecology: assessing effects of marine protected areas: confounding in space and possible solutions. Marine protected areas: a multidisciplinary approach: 143-167.
- Paxton, A. B., Harter, S. L., Ross, S. W., Schobernd, C. M., Runde, B. J., Rudershausen, P. J., Johnson, K. H., Shertzer, K. W., Bacheler, N. M., Buckel, J. A., Kellison, G. T., and Taylor, C. J. 2021. Five decades of reef observations illuminate deep-water grouper hotspots. Fish and Fisheries.
- Pendleton, L. H., Ahmadi, G. N., Browman, H. I., Thurstan, R. H., Kaplan, D. M., and Bartolino, V. 2018. Debating the effectiveness of marine protected areas. ICES Journal of Marine Science, 75: 1156-1159.
- Pickens, C., Smart, T., Reichert, M., Sedberry, G. R., and McGlenn, D. 2021. No effect of marine protected areas on managed reef fish species in the southeastern United States Atlantic Ocean. Regional Studies in Marine Science: 101711.
- Pradervand, P., and Hiseman, R. 2006. An analysis of the recreational shore fishery in the Goukamma Marine Protected Area. African Zoology, 41: 275-289.
- Prato, G., Thiriet, P., Di Franco, A., and Francour, P. 2017. Enhancing fish Underwater Visual Census to move forward assessment of fish assemblages: An application in three Mediterranean Marine Protected Areas. PLoS ONE, 12: e0178511.

- Quattrini, A. M., and Ross, S. W. 2006. Fishes associated with North Carolina shelf-edge hardbottoms and initial assessment of a proposed marine protected area. *Bulletin of marine science*, 79: 137-163.
- Quinn, J. F., Wing, S. R., and Botsford, L. W. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist*, 33: 537-550.
- R Core Team 2020. R: a language and environment for statistical computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Randall, R., and Minns, C. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 1657-1667.
- Rouyer, T., Ottersen, G., Durant, J. M., Hidalgo, M., Hjermann, D. Ø., Persson, J., Stige, L. C., and Stenseth, N. C. 2011. Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology*, 17: 3046-3057.
- Rudershausen, P., Mitchell, W., Buckel, J., Williams, E., and Hazen, E. 2010. Developing a two-step fishery-independent design to estimate the relative abundance of deepwater reef fish: application to a marine protected area off the southeastern United States coast. *Fisheries Research*, 105: 254-260.
- Runde, B. J., Michelot, T., Bacheler, N. M., Shertzer, K. W., and Buckel, J. A. 2020. Assigning fates in telemetry studies using hidden Markov models: an application to deepwater groupers released with descender devices. *North American Journal of Fisheries Management*.

- Russ, G. R., Stockwell, B., and Alcala, A. C. 2005. Inferring versus measuring rates of recovery in no-take marine reserves. *Marine Ecology Progress Series*, 292: 1-12.
- SAFMC. 2007. Amendment 14 to the Fishery Management Plan for the Snapper Grouper Fishery of the South Atlantic Region.
- Sala, E., and Giakoumi, S. 2018. No-take marine reserves are the most effective protected areas in the ocean. *ICES Journal of Marine Science*, 75: 1166-1168.
- Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., Polunin, N. V., Russ, G. R., and Sadovy, Y. J. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in ecology & evolution*, 20: 74-80.
- Sanchez, P. J., Pinsky, J. P., and Rooker, J. R. 2019. Bomb radiocarbon age validation of Warsaw grouper and snowy grouper. *Fisheries*, 44: 524-533.
- Sciberras, M., Jenkins, S. R., Kaiser, M. J., Hawkins, S. J., and Pullin, A. S. 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. *Environmental Evidence*, 2: 1-31.
- SEDAR. 2017. SEDAR 53 – South Atlantic Red Grouper Assessment Report. 159 pp.
- SEDAR. 2018. SEDAR 56 - South Atlantic Black Seabass Assessment Report. 164 pp.
- SEDAR. 2020. SEDAR 60 - South Atlantic Red Porgy Stock Assessment Report. 181 pp.
- Seytre, C., and Francour, P. 2008. Is the Cape Roux marine protected area (Saint-Raphaël, Mediterranean Sea) an efficient tool to sustain artisanal fisheries? First indications from visual censuses and trammel net sampling. *Aquatic Living Resources*, 21: 297-305.
- Shepherd, A. R. D., Warwick, R. M., Clarke, K. R., and Brown, B. E. 1992. An analysis of fish community responses to coral mining in the Maldives. *Environmental biology of fishes*, 33: 367-380.

- Shertzer, K. W., Bacheler, N. M., Kellison, G. T., Fieberg, J., and Wiggers, R. K. 2018. Release mortality of endangered Warsaw grouper *Hyporthodus nigrurus*: a state-space model applied to capture-recapture data. *Endangered Species Research*, 35: 15-22.
- Stewart-Oaten, A., Murdoch, W. W., and Parker, K. R. 1986. Environmental impact assessment: "Pseudoreplication" in time? *Ecology*, 67: 929-940.
- Thorson, J. T., and Prager, M. H. 2011. Better catch curves: incorporating age-specific natural mortality and logistic selectivity. *Transactions of the American Fisheries Society*, 140: 356-366.
- Underwood, A. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology*, 161: 145-178.
- Watanabe, S., and Opper, M. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of machine learning research*, 11.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73: 3-36.
- Woodcock, P., O'Leary, B. C., Kaiser, M. J., and Pullin, A. S. 2017. Your evidence or mine? Systematic evaluation of reviews of marine protected area effectiveness. *Fish and Fisheries*, 18: 668-681.
- Wyanski, D. M., Kolmos, K. J., and Buble, W. J. 2019. Update of Red Porgy, *Pagrus pagrus*, reproductive life history from the MARMAP/SERFS program. SEDAR60-WP02.

Southeast Data, Assessment, and Review, SEDAR60-WP02, North Charleston, South
Carolina.

Tables

Table 1. Candidate models examined for their fit to the data consisting of biomass (NASC) in each 100 m grid cell in our sonar survey in both areas (SWMPA or Control) and periods (Before and After). An asterisk (*) between two terms indicates that both effects were examined individually as was the two-way interaction between them. Where it was included, Trip was modeled as a random effect. Widely Applicable Information Criterion (WAIC) is presented for each model, and the model with the lowest WAIC is considered to be the best fit.

Model variables	WAIC	Δ WAIC
<i>~ Period + Slope + Season + Trip</i>	52211.2	0
<i>~ Area + Period + Slope + Trip</i>	52212.4	0.2
<i>~ Area * Period + Slope + Trip</i>	52212.7	0.5
<i>~ Area * Period + Slope + Season + Trip</i>	52212.7	0.5
<i>~ Slope + Trip</i>	52212.7	0.5
<i>~ Slope + Season + Trip</i>	52212.8	0.6
<i>~ Area + Slope + Season + Trip</i>	52212.8	0.6
<i>~ Period + Slope + Trip</i>	52213.0	1.8
<i>~ Area + Slope + Trip</i>	52213.4	2.6
<i>~ 1</i>	56263.6	4052.4

Table 2. Candidate models examined for their fit to the data consisting of CPUE at each site sampled with hook-and-line in both areas (SWMPA or Control) and periods (Before and After). NASC is the amount of acoustic backscatter (i.e., fish biomass) at each site. An asterisk (*) between two terms indicates that both effects were examined individually as was the two-way interaction between them. Where it was included, Trip was modeled as a random effect. The model with no variables (i.e., “1”) is the intercept-only model, included for comparison. Widely Applicable Information Criterion (WAIC) is presented for each model, and the model with the lowest WAIC is considered to be the best fit.

Model variables	WAIC	Δ WAIC
~ <i>Area</i> + <i>Trip</i>	228.6	0
~ <i>Period</i> + <i>Trip</i>	228.8	0.2
~ <i>Area</i> + <i>Period</i> + <i>Trip</i>	230.4	1.8
~ <i>Area</i> + <i>Period</i>	231.9	3.3
~ <i>Area</i> + <i>Period</i> + <i>NASC</i> + <i>Trip</i>	232.4	3.8
~ <i>Area</i> * <i>Period</i> + <i>Trip</i>	232.8	4.2
~ <i>Area</i> + <i>Period</i> + <i>NASC</i>	234.4	5.8
~ <i>Area</i>	234.8	6.2
~ <i>Area</i> * <i>Period</i> + <i>NASC</i> + <i>Trip</i>	235.8	7.2
~ <i>1</i>	240.2	11.6

Table 3. All reef fish species encountered in the present study (After) and in (Rudershausen et al., 2010; Before). Catch per unit effort (CPUE) values are fish/drop for hook-and-line and fish/trap for chevron trap. MPA refers to the Snowy Wreck Marine Protected Area, and Control refers to an adjacent area that is open to bottom fishing. Community grouping is the taxonomic group in which each species was included for multivariate analyses.

Species	Community grouping	CPUE - Hook-and-line				CPUE - Chevron Trap			
		MPA-Before	Control-Before	MPA-After	Control-After	MPA-Before	Control-Before	MPA-After	Control-After
Almaco jack <i>Seriola rivoliana</i>	Jacks	0.005	0	0.036	0.014	0	0	0	0
Atlantic creolefish <i>Paranthias furcifer</i>	-	0.003	0	0.001	0.002	0	0	0	0
Blackfin snapper <i>Lutjanus buccanella</i>	Snappers	0	0	0.006	0	0	0	0	0
Blueline tilefish <i>Caulolatilus microps</i>	Tilefish	0.005	0	0.011	0	0	0.037	0.067	0.063
Coney <i>Cephalopholis fulva</i>	Groupers	0	0.020	0.001	0	0	0	0	0
Gag <i>Mycteroperca microlepis</i>	Groupers	0.003	0	0.001	0	0	0	0	0
Goldface tilefish <i>Caulolatilus chrysops</i>	Tilefish	0	0	0.003	0	0	0	0	0.063
Gray triggerfish <i>Balistes capriscus</i>	Triggerfish	0.005	0	0.017	0.009	0.500	0.037	0	0
Graysby <i>Cephalopholis cruentata</i>	Groupers	0.011	0	0	0	0	0	0	0
Greater amberjack <i>Seriola dumerili</i>	Jacks	0.008	0	0.006	0	0	0.037	0.067	0
Hogfish <i>Lachnolaimus maximus</i>	-	0.003	0	0	0	0	0	0	0
Hybrid snapper <i>Lutjanus</i> sp.	Snappers	0	0	0.001	0	0	0	0	0
Jolthead porgy <i>Calamus bajonado</i>	Porgies	0.003	0.010	0	0.007	0.050	0	0	0
Knobbed porgy <i>Calamus nodosus</i>	Porgies	0.016	0.070	0.010	0.019	0	0	0	0.063
Lesser amberjack <i>Seriola fasciata</i>	Jacks	0.003	0	0	0	0	0	0	0
Lionfish <i>Pterosis</i> sp.	-	0	0	0	0	0.050	0.074	0	0
Marbled grouper <i>Dermatolepis inermis</i>	Groupers	0	0	0.001	0	0	0	0	0
Moray <i>Gymnothorax</i> sp.	-	0	0	0.001	0	0	0.074	0	0.125
Red cornetfish <i>Fistularia petimba</i>	-	0.003	0	0	0	0	0	0	0
Red grouper <i>Epinephelus morio</i>	Groupers	0.016	0.020	0.003	0	0.200	0.222	0.133	0
Red porgy <i>Pagrus pagrus</i>	Porgies	0.109	0.220	0.166	0.074	0.050	0.148	0.667	1.750
Rock hind <i>Epinephelus adscensionis</i>	Groupers	0.005	0	0	0	0	0	0	0
Sand tilefish <i>Malacanthus plumieri</i>	Tilefish	0	0	0.005	0.037	0	0	0	0
Scamp <i>Mycteroperca phenax</i>	Groupers	0.033	0	0.014	0.007	0	0.111	0	0.063
Short bigeye <i>Pristigenys alta</i>	-	0.005	0	0.004	0	0	0	0	0
Silk snapper <i>Lutjanus vivanus</i>	Snappers	0	0	0.032	0.058	0	0	0.267	0.375
Snowy grouper <i>Hyporthodus niveatus</i>	Groupers	0.057	0.030	0.060	0.009	0.200	0.074	0.467	0
Spotfin butterflyfish <i>Chaetodon ocellatus</i>	-	0	0	0	0	0	0	0	0.063
Speckled hind <i>Epinephelus drummondhayi</i>	Groupers	0.022	0	0.006	0	0.100	0.037	0	0
Spinycheek scorpionfish <i>Neomerinthe hemingwayi</i>	-	0.003	0	0.001	0	0	0	0	0
Squirrelfish <i>Holocentrus adscensionis</i>	-	0	0	0.001	0.002	0	0	0	0
Tattler <i>Serranus phoebe</i>	-	0.005	0.010	0.010	0.007	0.050	0	0	0

Table 3 (continued).

Tomtate <i>Haemulon aurolineatum</i>	-	0.022	0	0	0	0	0	0	0
Vermilion snapper <i>Rhomboplites aurorubens</i>	Snappers	0.003	0	0.068	0.035	0	0.037	0	1.125
White grunt <i>Haemulon plumierii</i>	-	0	0	0.001	0	0	0	0	0
Whitebone porgy <i>Calamus leucosteus</i>	Porgies	0	0	0.004	0	0	0	0	0
Whitespotted soapfish <i>Rypticus maculatus</i>	-	0	0	0	0.002	0	0	0.067	0
Yellowmouth grouper <i>Mycteroperca interstitialis</i>	Groupers	0	0	0.005	0	0	0	0	0

Table 4. Linear distance surveyed with hydroacoustics in the Snowy Wreck Marine Protected Area (SWMPA) and an adjacent area (Control) by Rudershausen et al. (2010) before the SWMPA was designated (2007-2009) and in the present study (2018-2020).

Area	Period	Linear distance surveyed (km)
SWMPA	2007-2009	404.43
Control	2008-2009	144.06
SWMPA	2018-2020	422.40
Control	2018-2020	356.50

Table 5. Number of aggregations of biomass (fish schools) identified with hydroacoustics in the SWMPA and an adjacent area that is open to fishing (Control) during each survey trip, as well as the number that were sampled with hook-and-line (HL) and chevron traps (Trap).

Area	Date	Aggregations	Fished HL	Fished Trap
SWMPA	5/1/2018	24	8	3
	8/27/2018	74	11	6
	8/2/2019	32	6	6
	7/6/2020	25	13	-
	9/24/2020	8	3	-
Control	6/5/2018	55	10	6
	4/30/2019	63	15	10
	2/23/2020	27	18	-
	7/17/2020	37	14	-
	11/20/2020	25	15	-

Table 6. Results from the biomass hurdle model with the lowest WAIC: Period + Slope + Season + Trip. Variables containing “hu” pertain to the first stage of the hurdle model. ESS refers to the effective sample size.

Variable	Estimate	Est. Error	2.5% CI	97.5% CI	Rhat	ESS
<i>Trip Sd(Intercept)</i>	0.60	0.13	0.41	0.91	1.00	1622
<i>Trip Sd(Hu_Intercept)</i>	1.32	0.25	0.93	1.90	1.00	1687
<i>Intercept</i>	1.16	0.33	0.49	1.82	1.00	2810
<i>Hu_Intercept</i>	-0.46	0.70	-1.88	0.89	1.00	2915
<i>PeriodBefore</i>	-0.62	0.29	-1.17	-0.03	1.00	3118
<i>Slope</i>	0.45	0.03	0.39	0.51	1.00	7612
<i>SeasonSpring</i>	-0.46	0.47	-1.39	0.46	1.00	3220
<i>SeasonSummer</i>	-0.56	0.36	-1.27	0.16	1.00	2711
<i>SeasonWinter</i>	-0.46	0.43	-1.31	0.37	1.00	3214
<i>Hu_PeriodBefore</i>	-1.18	0.61	-2.36	0.03	1.00	2530
<i>Hu_slope</i>	-0.35	0.03	-0.41	-0.29	1.00	7250
<i>Hu_SeasonSpring</i>	1.03	0.99	-0.91	2.99	1.00	3156
<i>Hu_SeasonSummer</i>	0.77	0.77	-0.69	2.31	1.00	2612
<i>Hu_SeasonWinter</i>	0.98	0.92	-0.85	2.79	1.00	2866

Table 7. Results from the biomass model containing the full suite of predictor variables, which was competitive with the best model in terms of WAIC. Variables containing “hu” pertain to the first stage of the hurdle model. ESS refers to the effective sample size.

Variable	Estimate	Est. Error	2.5% CI	97.5% CI	Rhat	ESS
<i>Trip Sd(Intercept)</i>	0.61	0.14	0.41	0.95	1.00	1968
<i>Trip Sd(Hu_Intercept)</i>	1.42	0.29	0.98	2.10	1.00	1845
<i>Intercept</i>	1.36	0.41	0.55	2.17	1.00	3907
<i>Hu_Intercept</i>	-0.42	0.91	-2.20	1.43	1.00	2795
<i>PeriodBefore</i>	-0.38	0.53	-1.42	0.70	1.00	3548
<i>AreaMPA</i>	-0.28	0.43	-1.14	0.59	1.00	3705
<i>SeasonSpring</i>	-0.66	0.53	-1.71	0.35	1.00	4113
<i>SeasonSummer</i>	-0.55	0.36	-1.29	0.13	1.00	3427
<i>SeasonWinter</i>	-0.72	0.50	-1.70	0.30	1.00	3812
<i>Slope</i>	0.45	0.03	0.39	0.51	1.00	7609
<i>AreaMPA:PeriodBefore</i>	-0.21	0.64	-1.48	1.10	1.00	3204
<i>Hu_PeriodBefore</i>	-1.24	1.17	-3.54	1.00	1.00	3216
<i>Hu_AreaMPA</i>	-0.06	0.96	-1.90	1.86	1.00	2863
<i>Hu_SeasonSpring</i>	1.04	1.15	-1.30	3.31	1.00	3333
<i>Hu_SeasonSummer</i>	0.77	0.80	-0.85	2.38	1.00	2648
<i>Hu_SeasonWinter</i>	0.98	1.13	-1.29	3.19	1.00	3093
<i>Hu_Slope</i>	-0.35	0.03	-0.41	-0.29	1.00	6900
<i>Hu_AreaMPA:PeriodBefore</i>	0.10	1.44	-2.65	3.03	1.00	2827

Table 8. Results from the Area + Trip hurdle model for predicting reef fish CPUE. Variables from the first stage of the hurdle model begin with “Hu,” and coefficient values are provided in untransformed logit terms.

Variable	Estimate	Est. Error	2.5% CI	97.5% CI	Rhat	ESS
<i>Trip Sd(Intercept)</i>	0.28	0.11	0.09	0.52	1.00	1061
<i>Trip Sd(Hu_Intercept)</i>	0.30	0.22	0.01	0.83	1.00	1335
<i>Intercept</i>	-1.21	0.14	-1.49	-0.94	1.00	2095
<i>Hu_Intercept</i>	-0.32	0.27	-0.84	0.18	1.00	3774
<i>AreaMPA</i>	0.30	0.19	-0.09	0.66	1.00	2245
<i>Hu_AreaMPA</i>	0.42	0.36	-0.27	1.13	1.00	3866

Table 9. Results from the Period + Trip hurdle model for predicting reef fish CPUE. Variables from the first stage of the hurdle model begin with “Hu,” and coefficient values are provided in untransformed logit terms.

Variable	Estimate	Est. Error	2.5% CI	97.5% CI	Rhat	ESS
<i>Trip Sd(Intercept)</i>	0.33	0.10	0.15	0.56	1.00	1475
<i>Trip Sd(Hu_Intercept)</i>	0.28	0.21	0.01	0.78	1.00	1257
<i>Intercept</i>	-0.99	0.13	-1.26	-0.73	1.00	1760
<i>Hu_Intercept</i>	-0.25	0.23	-0.69	0.21	1.00	4485
<i>PeriodBefore</i>	-0.15	0.20	-0.53	0.25	1.00	2390
<i>Hu_PeriodBefore</i>	0.38	0.35	-0.34	1.08	1.00	4999

Table 10. PERMANOVA table relating Area (Snowy Wreck Marine Protected Area or Control), Period (before or after closure), and their interaction to the composition of the reef fish community.

	Sum of squares	Df	R2	F	Pr > F
Area	0.414	1	0.117	4.061	0.004
Period	0.835	1	0.235	8.195	0.001
Area:Period	0.159	1	0.045	1.559	0.166
Residual	2.140	21	0.603		

Table 11. Sample sizes for red porgy ages caught with all gear types. “Inside SWMPA” indicates that only fish caught within the boundaries of the Snowy Wreck Marine Protected Area are included. “Outside SWMPA” includes all ages for red porgy caught anywhere in Onslow Bay other than the Snowy Wreck Marine Protected Area, and “Inside Control” includes only red porgy caught in the specific control area used for other analyses in this study.

	Inside SWMPA	Outside SWMPA	Inside Control
2015	55	546	33
2016	67	495	57
2017	45	386	73
2018	27	480	24
2019	34	435	8
2020	14	23	23

Table 12. Catch curve estimates of instantaneous total mortality (Z) for red porgy caught with all gear types. “Inside SWMPA” indicates that only fish caught within the boundaries of the Snowy Wreck Marine Protected Area are included. “Outside SWMPA” includes all ages for red porgy caught anywhere in Onslow Bay other than the Snowy Wreck Marine Protected Area.

	Z Inside SWMPA	Z Outside SWMPA
2015	0.687	0.326
2016	0.477	0.437
2017	0.224	0.366
2018	0.347	0.388
2019	0.218	0.366

Table 13. ANOVA table for the model relating Area (Snowy Wreck Marine Protected Area or Control), Period (before or after closure), and their interaction to size distributions of red porgy.

	Sum of squares	Df	Mean square error	F	Pr > F
Area	10495	1	10495	3.599	0.059
Period	860	1	860	0.295	0.588
Area:Period	38513	1	38513	13.208	< 0.001
Residual	959330	329	2916		

Figures

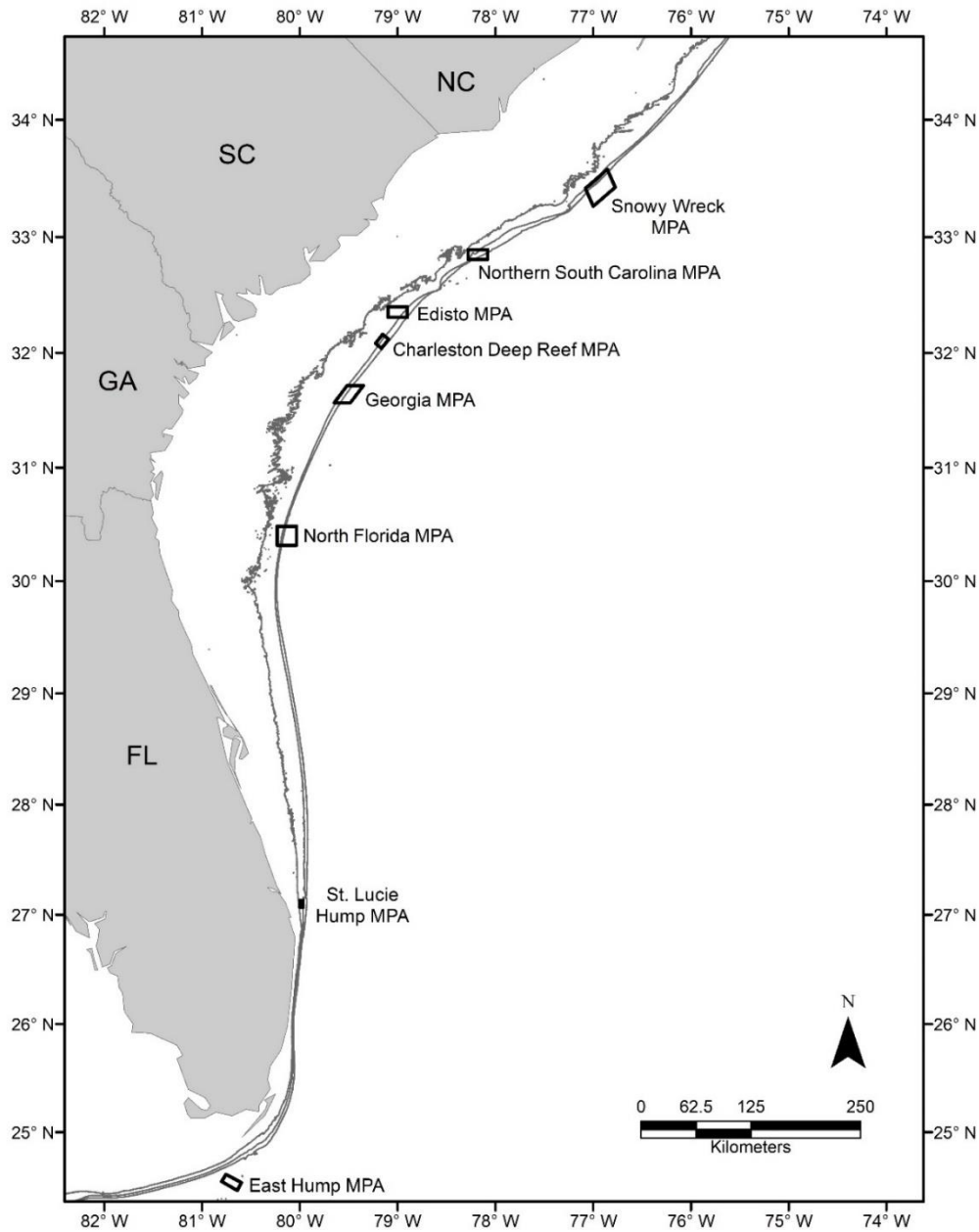


Figure 1. Map of the MPA network of the southeast United States Atlantic. Contour lines are 40, 100, and 140 m depth.

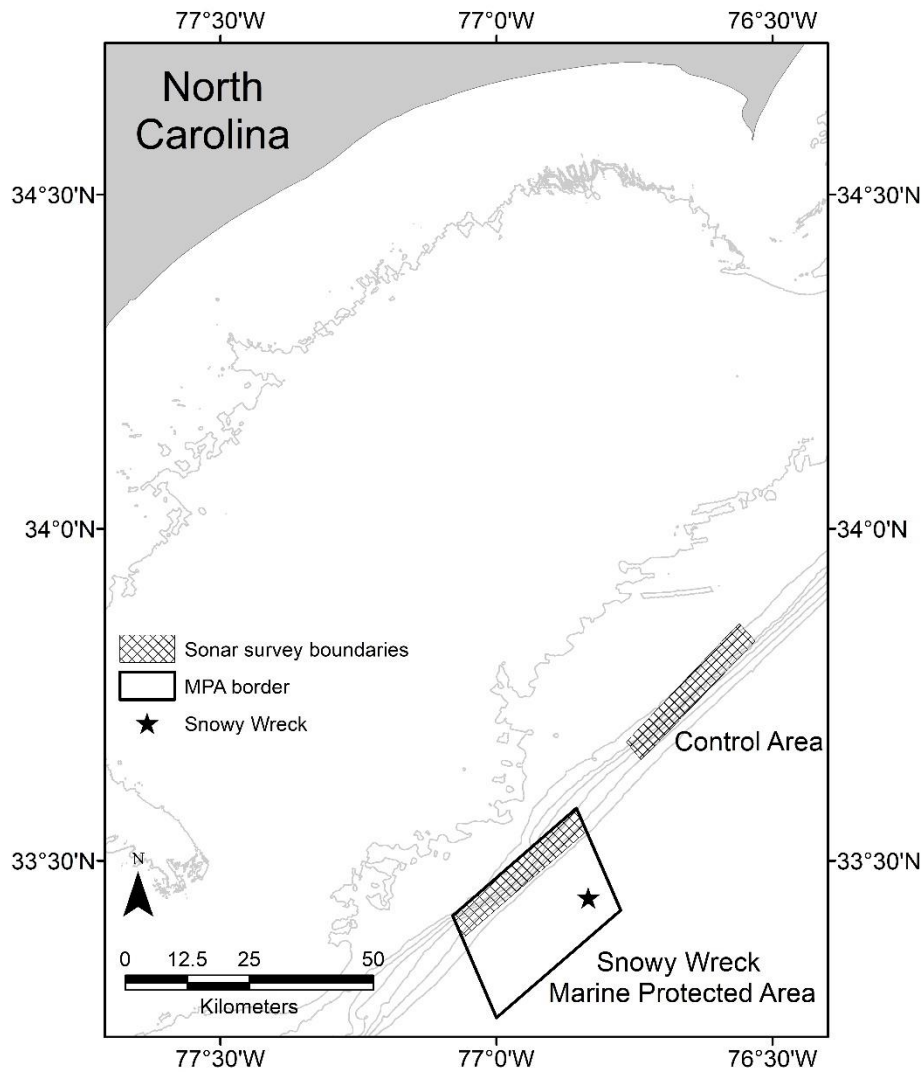


Figure 2. Map of the central North Carolina (USA) coastline. Checkered boxes delineate the survey extent within the Snowy Wreck Marine Protected Area and the control area for the present study and from Rudershausen et al. (2010). The Snowy Wreck location is indicated with a star. Contour lines are 20, 40, 60, 80, 100, 120, 140, and 160 m depth.

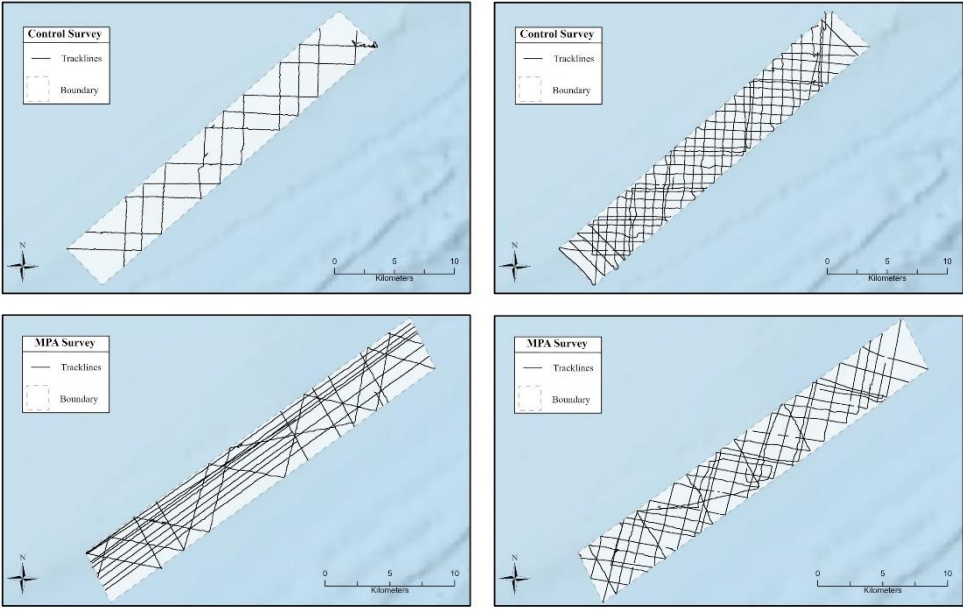


Figure 3. Transect lines for hydroacoustic surveys conducted by Rudershausen et al. (2010) in 2007-2009 (left) and in the present study (right) in the Snowy Wreck Marine Protected Area (below) and an adjacent area that is open to fishing (above).

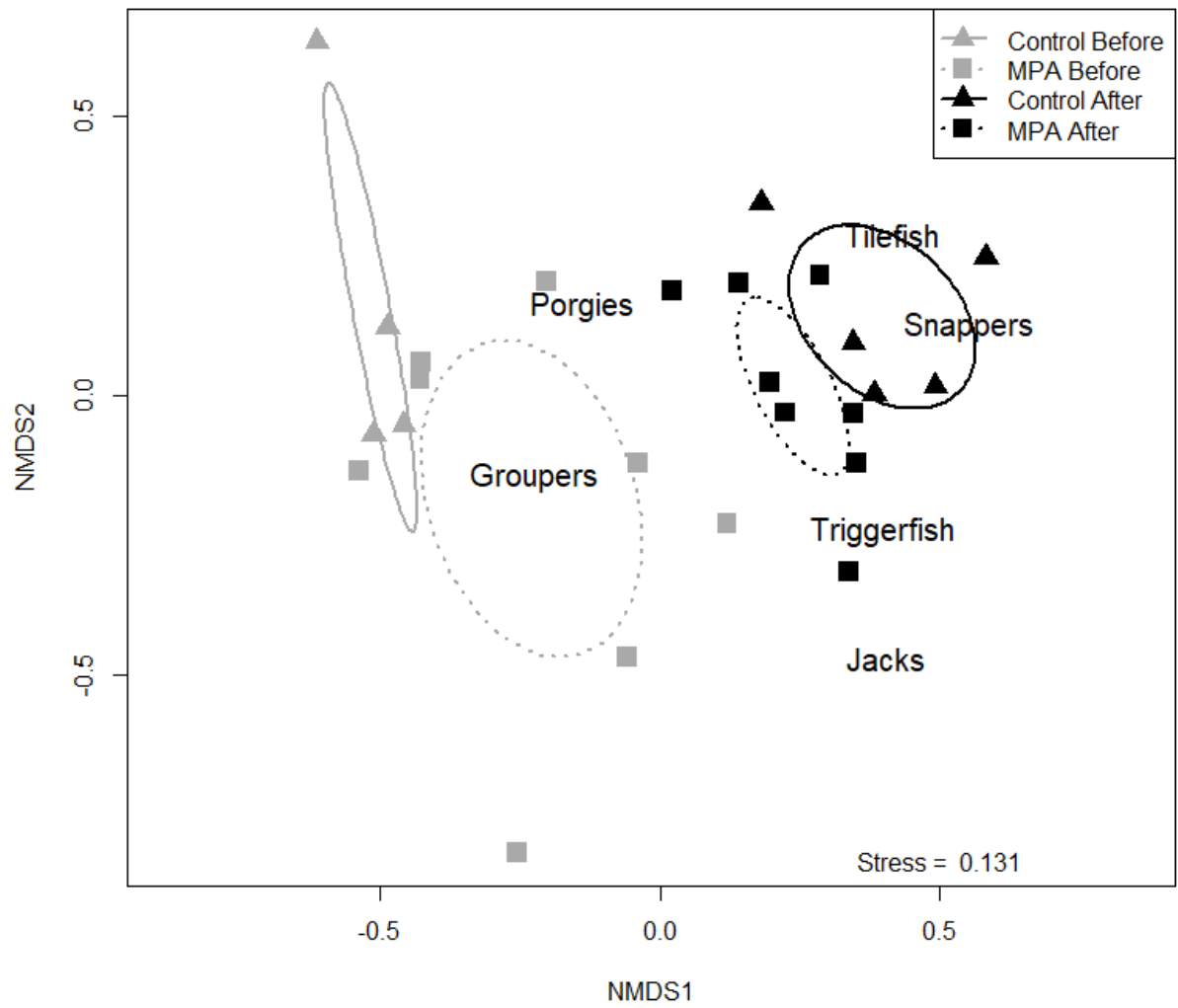


Figure 4. Results of non-metric multidimensional scaling (NMDS) comparing reef fish communities in the two areas (Snowy Wreck Marine Protected Area and control) and time periods (before and after).

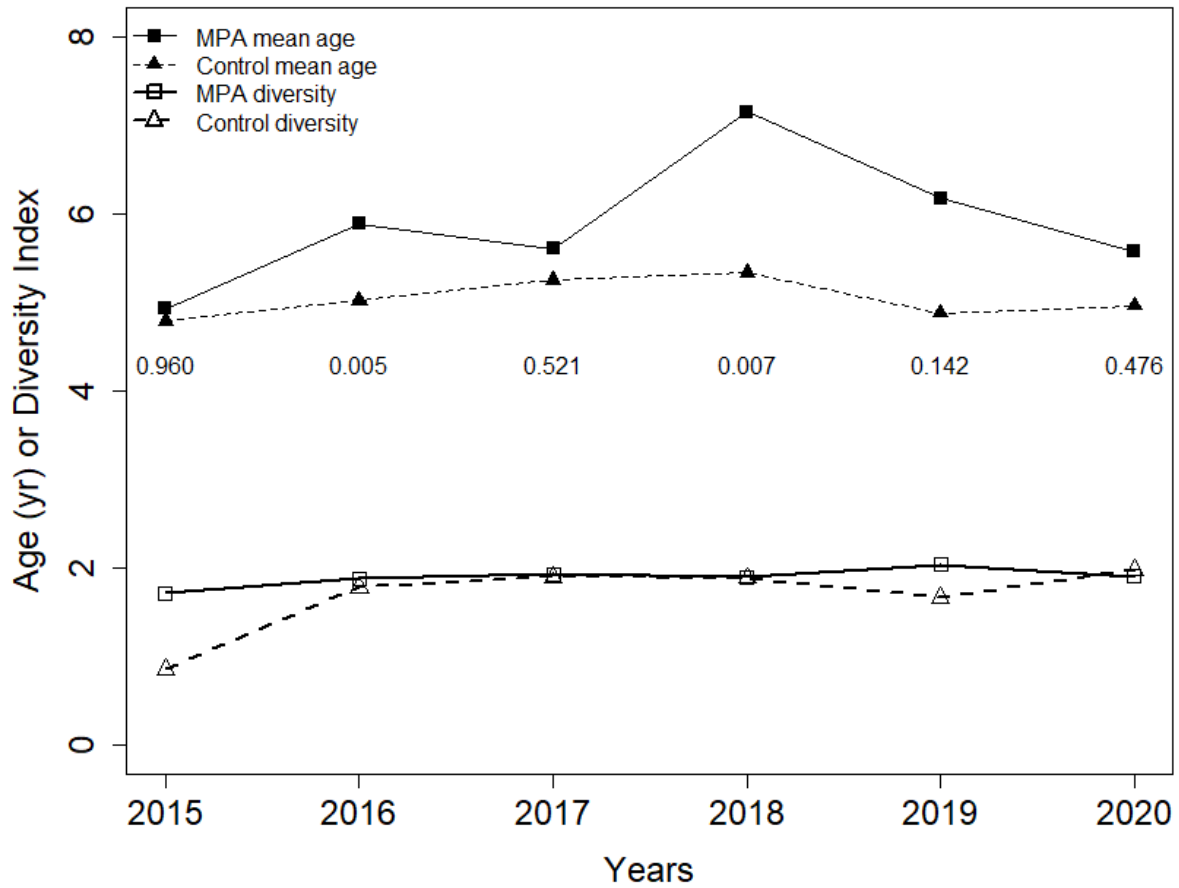


Figure 5. Mean age and Shannon age diversity for red porgy caught in the Snowy Wreck Marine Protected Area and adjacent control area from 2015-2020 by our survey or the Southeast Reef Fish Survey. Numbers displayed below mean ages are p-values resulting from annual between-area Wilcoxon rank sum tests.

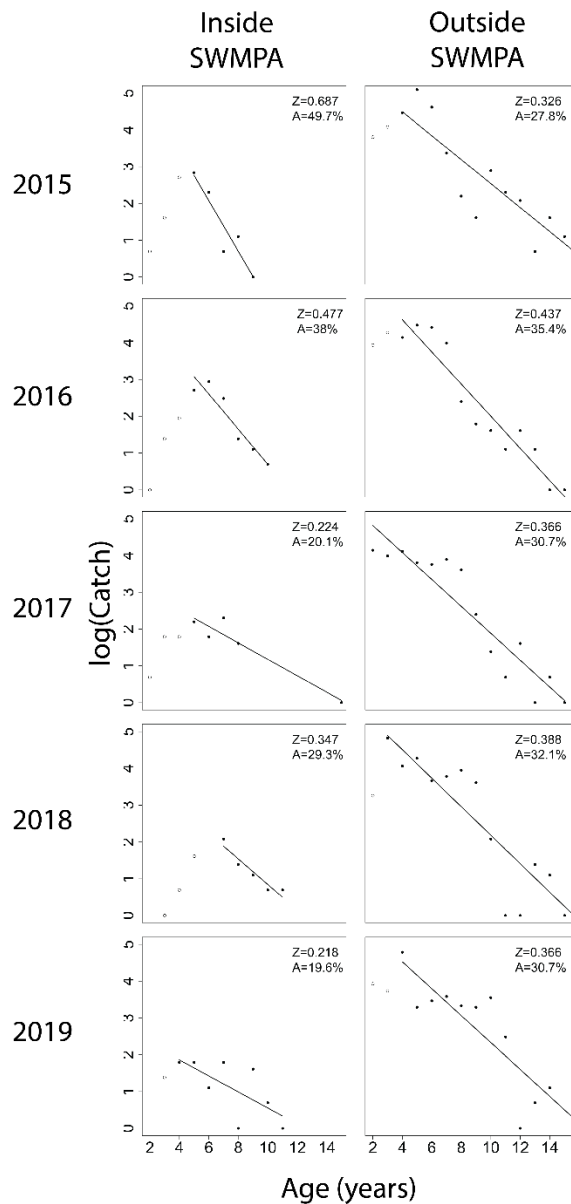


Figure 6. Catch curves for red porgy caught in Onslow Bay, North Carolina. “Inside SWMPA” indicates that only fish caught within the boundaries of the Snowy Wreck Marine Protected Area are included. “Outside SWMPA” includes all ages for red porgy caught anywhere in Onslow Bay other than the Snowy Wreck Marine Protected Area. Z represents total annual mortality (instantaneous) and A represents total annual mortality (discrete).

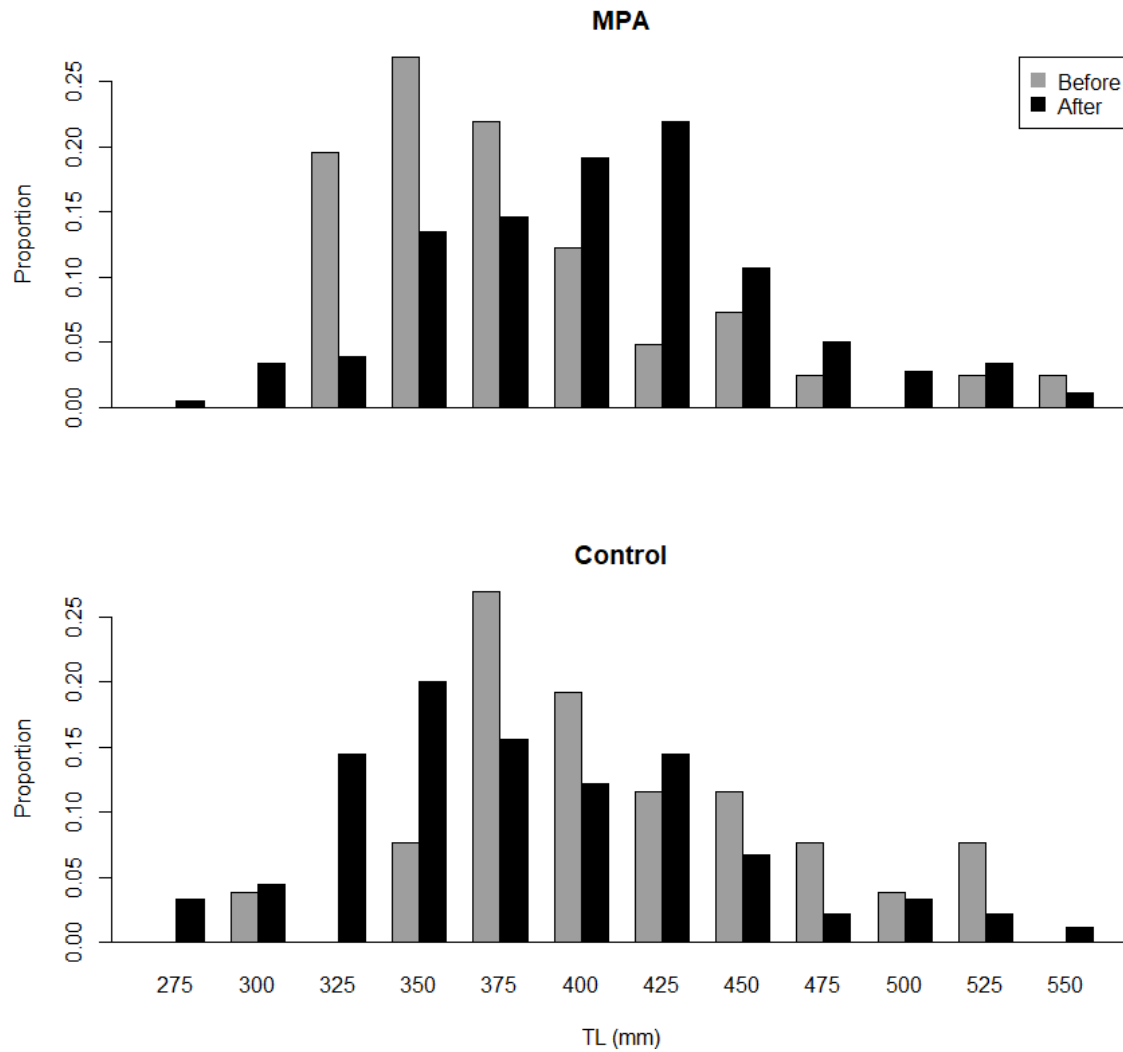


Figure 7. Size (total length) distributions for red porgy caught in the Snowy Wreck Marine Protected Area (SWMPA) and the adjacent control area in the before period (2007-2009) by Rudershausen et al. (2010) and in the present study (after; 2018-2020).

CHAPTER 3: REPETITIVE CAPTURE OF MARINE FISHES: IMPLICATIONS FOR ESTIMATING NUMBER AND MORTALITY OF RELEASES

This chapter has been published in ICES Journal of Marine Science. Coauthors are Jeffrey Buckel, Kyle Shertzer, Nathan Bacheler, Paul Rudershausen, and Beverly Sauls.

Abstract

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

Introduction

The practice of releasing part of the catch (discarding) has expanded in some regions in the last half-century. This increase is largely a result of changing angler behavior (Quinn, 1996; Graefe and Ditton, 1997; Allen et al., 2008), and, particularly for marine fisheries, greater fishing effort and stricter regulations (Kelleher, 2005; NMFS, 2016). Cooke and Cowx (2004) used Canadian release statistics to estimate that global annual recreational catch is approximately 47 billion fish, of which only 17 billion (36%) are retained. Further, the United States has seen substantial rises in releases in recent decades (Zeller et al., 2018). In the European Union, the landing obligation has banned discarding in certain situations (Guillen et al., 2018), though discarding still occurs in many fisheries for reasons including exemptions and non-compliance (Villasante et al., 2019). Consequently, numbers of live and dead discards (as well as discard mortality estimates) are of growing importance as inputs for many stock assessments (Cooke and Schramm, 2007; Pollock and Pine, 2007; Viana et al., 2013). In general, the total number of dead discards for a fishery is calculated as the assumed rate of discard mortality (i.e., mortality that will occur on live discards) multiplied by the number of live discards, plus any dead discards (i.e., fish that are discarded dead). This methodology implies that each capture is independent; all live discards are treated as unique individuals and the possibility that fish could be caught and released more than once is not accounted for (MRIP, 2018).

Many tagging studies have found a high proportion of unique individuals being recaptured multiple times (e.g., Kipling and Le Cren, 1984; Fabrizio et al., 1999). McCormick (2016) described the phenomenon of repetitive recapture in fisheries where a high proportion of individuals are caught and released. In such fisheries, the estimated number of releases may not be equal to the number of unique released fish (or discards), as a single fish captured repeatedly

may be incorrectly tabulated as several independent fish. For example, Schill et al. (1986) estimated that Yellowstone cutthroat trout (*Salmo clarkii bouvieri*) were caught an average of 9.7 times each during the 1981 fishing season. Moreover, Slavík et al. (2009) monitored fish ladder occupation by brown trout (*Salmo trutta*), and noted high rates of repeated capture and calculated that without individual fish identification (tags) the number of fish in the ladder would have been overestimated by 63.7%. This issue may be particularly important when the number of discards is used in a stock assessment or management context (Crowder and Murawski, 1998; Punt et al., 2006).

Despite the possibility of cumulative physiological effects of multiple catch and release events, as suggested by Wydoski (1977), studies of repetitive capture on finfish are scarce. Bartholomew and Bohnsack (2005) posited that multiple capture events would result in cumulative mortality and recognized the importance of this phenomenon to stocks that experience high fishing pressure. Arlinghaus et al. (2007) speculated that repeated catch-and-release of fishes via angling may result in increased stress and behavioral changes. For example, this additional stress has been shown to increase nest abandonment rates in male smallmouth bass (*Micropterus dolomieu*), (Kieffer et al., 1995; Philipp et al., 1997). Various authors have also recognized that repeated escapement from trawls may result in increased mortality (Suuronen and Erickson, 2010; Caddy and Seijo, 2011; Gilman et al., 2013). Others have documented the occurrence of repeated recaptures for tagged fish and incorporated those data into models for parameters such as movement rates (e.g., Whitlock and McAllister, 2009). However, no studies to our knowledge have empirically investigated the impacts of repetitive hook-and-line capture on the disposition or survival of wild fishes. Estimates of discard survival from tagging data are most often based on the first recapture event only (Hueter et al., 2006;

Rudershausen et al., 2014; Sauls, 2014; but see Shertzer et al., 2018). If discard survival varies as a function of how many times an individual is caught and released, stock assessments that use discard survival from only the first capture may be biased and resulting management strategies may be ineffective (Coggins et al., 2007).

Our objectives in this study were to examine the impacts of repetitive captures on estimates of (1) the number of independent fish released and (2) survival rates for four reef fish species using previously collected mark-recapture data from the southeast US. The latter objective used tagging data to examine the recapture rate of individual tagged fish that were caught on multiple occasions, which can be interpreted as relative survival. Information obtained from the two objectives was used to simulate the impact on stock assessments under several levels of non-unique releases.

Methods

Empirical analyses

We examined tagging datasets on four species of reef fish: black sea bass (*Centropristis striata*), gray triggerfish (*Balistes capriscus*), red grouper (*Epinephelus morio*), and Warsaw grouper (*Hyporthodus nigritus*). Each of these are demersal, physoclistous reef-associated species that inhabit continental shelf waters of the Atlantic Ocean. Black sea bass are restricted to the US Atlantic and Gulf of Mexico, red grouper and Warsaw grouper are distributed throughout North and South American waters, and gray triggerfish are ubiquitous on both sides of the Atlantic in temperate and tropical latitudes. All four species have current and/or historic value as commercial and recreational targets. The tagging datasets were collected over the last few decades by scientists (in the case of three species) or via a citizen science program (for Warsaw grouper). These datasets have previously been used to estimate discard mortality, as

each species is susceptible to barotrauma. Rudershausen et al. (2014) tagged black sea bass with internal anchor tags in a narrow depth range in Onslow Bay, North Carolina. Runde et al. (2019) detail tagging procedures for gray triggerfish with internal anchor tags, and gray triggerfish data included here were from a single site in Raleigh Bay, North Carolina. Sauls (2014) published data on gag (*Mycteroperca microlepis*) but tagged red grouper as part of the same tagging program using identical methodology, involving a plastic dart tag inserted through the anterior dorsal musculature (B. Sauls, unpublished data). For our analysis, we truncated the large red grouper dataset to include only fish from a single region (Tampa Bay, Florida area) to eliminate the confounding effects of variable spatial effort on estimates of relative survival (Royle et al., 2013). Shertzer et al. (2018) and Wiggers (2010) described methods for tagging Warsaw grouper with plastic dart tags, which took place at a single site off the east coast of Florida. All fish in these studies were single-tagged, as estimating tag retention was not a priority for the original investigators.

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

recapture) is explained by a set of covariates in addition to the baseline value for a reference group.

For each species, we modeled release survival probability as a function of release number in addition to other covariates when information was available such as release condition, month, year, depth, capture gear, and fish size. Covariate values were changed for each observation of the same fish to reflect each specific release event. Variable selection was conducted using a stepwise selection procedure based on AIC, with iterations between ‘forward’ and ‘backward’ selection ($\alpha = 0.05$). Full models from which variables were selected varied by species were: black sea bass, *release number + condition*; gray triggerfish, *release number + condition + gear*; red grouper, *release number + condition + size + year + month + depth*; and Warsaw grouper, *release number + size*. Condition categorizations (e.g., deep-hooked, severe barotrauma) were determined by the authors of each study (Rudershausen et al., 2014; Sauls, 2014; Runde et al., 2019). The resulting hazard ratio for each variable was interpreted as a factor of survival when all other variables were held constant. Reference variables were *Release number 1* (black sea bass, red grouper, Warsaw grouper), *Condition 1* (where higher number indicates worse condition; black sea bass, gray triggerfish, and Warsaw grouper), *Year2009* (red grouper), and *MonthApr* (red grouper). All analyses here and below were performed in R version 3.4.1 (R Core Team, 2019) using the R package ‘survival’ (Therneau, 2015).

Potential impacts of tag shedding and tagging-induced mortality

For some of the species examined, we found increased recapture rate following releases two, three, and four as compared to the initial tag and release event; hereafter, we refer to these subsequent releases as “release numbers 2+”. One explanation for increased recapture rate is that acute (or immediate) tag shedding or tagging-induced mortality (combined rate denoted as Φ ;

Beverton and Holt, 1957) reduced the number of alive tagged individuals, thereby reducing the number of tagged fish at large and available for recapture; these rates are assumed to occur after the first release only. Given the information available from these four datasets examined, it was impossible to decompose Φ into its component rates; however, this decomposition was unnecessary, as both acute tag shedding and tagging-induced mortality can be treated as rates that only occur immediately after the first release, therefore their effects on our analyses are identical. Had Φ occurred, the perceived recapture rate would be biased low for the first release only, and not for releases 2+, since Φ does not occur on release 2+ fish because they have the original tag.

We used simulations to estimate the level of Φ that would be necessary for the automated variable selection procedure to exclude “release number” from the best model. That is, what level of acute tag loss and tag-induced mortality would it take to increase the recapture rate after release 1 and make it statistically similar to recapture rates for releases 2+? For the three species for which increased recapture rate for release numbers 2+ was found, the Cox proportional hazards models were repeated using bootstrapped variations of the original datasets. We first identified the individuals in each dataset that were never recaptured (in other words, the individuals that may have experienced Φ). Then we removed a randomized portion of these individuals (to represent Φ) and refit the model using the same stepwise variable selection procedure as above, but with the reduced dataset. We varied the proportion of the individuals removed (Φ), and levels of Φ were chosen after preliminary runs to determine the approximate value necessary for exclusion of the variable “release number” for each species. We replicated this bootstrapping procedure 1000 times for each value of Φ to account for differences in covariate values for never-seen individuals. We examined the percentage of the 1000

bootstrapped replicates that contained “release number” in the best model. Finally, we graphically determined the value of Φ for which release number was excluded in an appreciable portion (~5%) of replicates. This was considered the threshold value of Φ for each species that would be necessary to explain our finding of increased tag return rate for releases 2+.

Furthermore, we considered the possibility that some fish lost their tag and were recaptured later, therefore being incorrectly treated as new individuals (i.e., release number = 1). This phenomenon would artificially increase the number of first releases and decrease the perceived percentage of recaptures of first releases while having the opposite effect for release 2+ fish; thus, incorrect assignment of release number could lead to a bias towards higher relative survival of subsequent recaptures. To investigate this, we simulated a population of 1 million fish that were exposed to 5 periods of capture and tagging. We assumed a capture probability of 0.1 for each fish in each period, probability of immediate (acute) tag loss of 0.15 (1.5x the highest value published for either tag type examined here; see *Discussion*), and probability of tagging-induced mortality of 0.05 (each time a fish is tagged). We did not include the possibility of discard mortality, as we were only interested in the influence of this phenomenon on *relative* recapture rates. Similarly, we did not include chronic tag shedding in the simulation, as it is assumed constant and likely very small in magnitude when compared to immediate tag shedding. We generated capture histories for each fish, such that we were able to retrospectively identify recaptured individuals that had lost their tag and were incorrectly considered first-time releases. We used these capture histories to tabulate proportions recaptured after the first, second, third, and fourth releases as we had done with empirical tagging data. These proportions were calculated under two scenarios: “Observed,” in which we counted any untagged fish as a first release, and “Reality,” in which we counted untagged recaptures correctly (i.e., if it was

untagged but had previously been captured/tagged once before then it was assigned a release number of two). We compared differences in recapture rates between the two scenarios to determine the likely influence of this phenomenon on our empirical results.

Magnitude of releases and dead discards

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

Influence on stock assessment

We investigated effects of repetitive captures on stock assessments using two case studies: black sea bass and red grouper. We chose these two species because their stock assessments had recently been conducted in the southeast US Atlantic and because we examined tagging data for those species herein. The assessment methods are detailed elsewhere (SEDAR, 2017; SEDAR, 2018), and so we summarize them here only briefly. Both assessments applied an integrated, age-structured model and incorporated time-series data on landings, discards, indices of abundance, age and length compositions of these time series, and life-history information such as natural mortality and reproductive capacity (Williams and Shertzer, 2015). To evaluate the importance of repetitive captures on assessment results, we ran the assessment model for each species four times. The first iteration used the base-level estimates of total dead discards as provided in the original time series (100%). Subsequent runs of the assessments reduced the total dead discards to 75%, 50%, or 25% of the original values. These reductions reflect the direction that the estimates would tend if they corrected for repetitive recapture of individuals in the count of total releases or if release mortality were lower (increased survival). All other data inputs and aspects of model configuration remained the same.

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

Results

Empirical analyses

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

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

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

Our second simulation, which examined the influence of misidentifying recaptured fish that had lost their tag, found higher recapture rate for first releases in the Reality scenario as compared to the Observed; however, the recapture rates between the two scenarios were similar for 2+ releases (Table 3). The relative proportions recaptured for releases 2, 3, and 4 were in general slightly lower in the Reality (0.55, 0.29, and 0.12, respectively) scenario as compared to

the Observed (0.65, 0.35, and 0.10). Thus, misidentifying recaptured fish would lead to biased high survival of 2+ fish, but the magnitude of this bias is lower than that which we observed in the empirical studies examined herein (Table 1).

Magnitude of releases and dead discards

Our investigation of two initial releases of 1000 theoretical fish yielded large differences in the metrics we examined. Under both the constant survival and increased survival scenarios, we found the number of total releases to be more than twice the number of unique released fish. We note that this disparity would hold even if not every fish were recaptured in each time period, (as we assumed here for ease of illustration) because such a reduction would impact both the number of total releases and the number of unique released fish. In the constant survival scenario (Figure 1A), we show that the estimate of dead discards produced by using typical stock assessment methods (i.e., number of total releases multiplied by the discard mortality rate) is equivalent to the “actual” number of dead discards. Thus, the estimate of dead discards is not influenced by repeatedly capturing the same fish as long as discard survival is constant across releases. However, for the increased discard survival scenario (Figure 1B), we show that the computed number of dead discards is biased ~70% higher than the actual number of dead discards. Different simulation conditions would lead to different levels of bias (e.g., more releases or a larger difference in initial release survival and survival for releases 2+ would both lead to increased bias (e.g., a value >70%)).

Influence on stock assessment

The stock assessments of black sea bass and red grouper were affected similarly by reductions in the annual number of dead discards (Figure 3A, D). In general, fewer discards resulted in average selectivity curves that emphasize lower mortality of younger fish. The

estimated time series of S relative to its target (S_{MSY}) were relatively insensitive to these reductions (Figure 3B, E), while the estimated time series of F relative to its target were quite sensitive (Figure 3C, F). In general, S/S_{MSY} were marginally higher for model runs with lower amounts of dead discards. This was driven by slight increases in S paired with slight decreases in S_{MSY} . S increased due to more fish being allowed to reach maturity and S_{MSY} decreased slightly as a result of the decline in F attributed to a lower level of dead discards (Table S.1). For black sea bass, the annual number of dead discards influenced the estimate of whether the stock was experiencing overfishing ($F/F_{MSY}>1$) or not ($F/F_{MSY}<1$). The change in F/F_{MSY} resulted from larger changes in F_{MSY} relative to changes in F (Table S.1). For red grouper, the stock status was consistent across scenarios (overfishing); however, the degree to which F exceeded F_{MSY} varied, particularly in the terminal assessment years.

Discussion

Increased discarding of live fish because of regulations or fishing behavior can result in repetitive captures of individual fish. Given that live releases dominate total catch for many species (Kelleher, 2005; Zeller et al., 2018), that recreational effort is high and has increased through time in many regions (Post et al., 2002; Cooke and Cowx, 2006; Ihde et al., 2011; Hyder et al., 2018; Shertzer et al., 2019), and our finding of repeated captures in the four species examined, it is likely that any fishery with even a low proportion of releases experiences repetitive captures. Our study explored the effects of repetitive captures on important variables that are often used in stock assessments. First, we showed how the estimated number of total live releases using current approaches is higher than the actual number of unique released fish when there are repetitive captures. Second, we found that recapture rate in three of four species increased after the first release and conclude that this represents increased survival for

individuals after their second release; thus, estimates of dead discards for these species that use survival rates based on first release are likely biased. Lastly, we found that biased estimates of dead discards have an impact on stock assessment results. We discuss the implications for each of these findings below.

Typically, studies using conventional tagging to produce estimates of discard mortality (e.g., Rudershausen et al., 2014; Sauls, 2014) calculate their estimate by using data from the first recapture only and disregard data from subsequent recaptures of those individuals. Published information about the prevalence of repeated recaptures exists for a variety of taxa worldwide, although authors typically make note of this information only in a cursory fashion. (e.g., Springer and McErlean, 1962; Kipling and Le Cren, 1984; Recksiek et al., 1991; Fabrizio et al., 1999; Miller et al., 2001). It is likely that most large-scale tagging datasets contain information about repeated recaptures, although many do not report it. We recommend that future studies explore and report the prevalence of repeated recaptures and their influence on discard survival where possible.

We found significantly higher recapture rates for release number 2+ for black sea bass, red grouper, and Warsaw grouper, but not for gray triggerfish. Though theoretically possible, it seems highly unlikely that Φ (acute tag shedding and tagging-induced mortality) caused increased recapture rates for releases 2+ for black sea bass and Warsaw grouper. We searched the literature for empirical estimates of Φ from studies using internal anchor tags and dart tags (the two tag types used in the four datasets we examined), via holding studies and/or double tagging experiments. One hundred percent acute retention and post-tagging survival has been demonstrated for internal anchor tags in striped bass (*Morone saxatilis*), meagre (*Argyrosomus regius*), and spotted seatrout (*Cynoscion nebulosus*) (Dunning et al., 1987; del Mar Gil et al.,

2017; Ellis et al., 2018). Latour et al. (2001) directly modeled acute tag shedding in red drum (*Sciaenops ocellatus*) for internal anchor tags and stainless steel dart tags (as opposed to plastic, which were used in the Warsaw grouper and red grouper studies examined in the present document). They estimated immediate retention of internal anchor tags to be 0.99 and of stainless steel dart tags to be 1.0. Fonteneau and Hallier (2015) described estimates of acute dart tag shedding for three species of tunas, and stated that while estimates have ranged up to 0.10 (Bayliff and Mobernd, 1972) this rate is “widely dependent on the expertise of the tagger”. Other than the single reference of acute shedding of 0.10, all estimates for tunas were below 0.05 (Fonteneau and Hallier, 2015). In addition, such rates may vary by taxon and estimates for tunas may not match values for reef fishes. Our literature search yielded no published estimates of Φ that were above 0.10 for either tag type, and most estimates were close to 0. Because no published values of Φ surpassed even our lowest estimated threshold value of 0.125 (for Warsaw grouper; Figure 2), it is unlikely that this is the explanation for our finding of higher recapture rate for releases 2+.

Our examination of the effect of recapturing fish that had lost their tag demonstrated that while absolute recapture rates of release 1 fish would be higher if all recaptures were correctly identified, the relative recapture rates between releases 1 and releases 2+ were only marginally impacted. While the directionality of the bias in the Observed scenario was towards our findings, this simulation was conducted with the crucial parameter (acute tag shedding rate) set to an extreme value (0.15). As described above, there are no published estimates of acute tag shedding rates higher than 0.1 for the tag types in the studies we used. Further *ad hoc* simulations revealed that the bias all-but disappeared when tag shedding was set to a more realistic rate, such as 0.05. Given the large magnitude of the difference in relative recapture proportion in our empirical

datasets (Table 2) and the marginal influence of incorrect identification of recaptured fish (even in an extreme scenario), we conclude this phenomenon is possible but is unlikely to have caused our finding of significantly higher recapture rates for releases 2+. We note that using tags that cannot be shed, such as electronic transmitters or genetic “tags” would eliminate this potentially confounding phenomenon, and that double tagging would allow for empirical estimation of tag shedding.

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

Another explanation of our findings is a difference in capture probability for previously captured individuals (i.e., heterogeneity of learned behavior). Populations of fish frequently contain individuals with varying vulnerability to angling or aggressiveness (Philipp et al., 2009; Sutter et al., 2012; Villegas-Ríos et al., 2018). Askey et al. (2006) experimentally demonstrated a similar phenomenon with a population of rainbow trout (*Oncorhynchus mykiss*), finding declines

in catch per unit effort of tagged fish by dividing the population into two classes based on different intrinsic catchabilities and incorporating a “learned hook avoidance function”. Cox and Walters (2002) modeled catchability dynamics by assuming two pools of fish: available and unavailable to capture (with the possibility of moving from one state to the other due to factors such as learned hook avoidance). If the tagged populations examined in the present study were divided into such pools, it is theoretically possible that rates of learned hook avoidance could differ between groups. This scenario would result in repeated recapture of “bait-happy” individuals, while reducing the probability of encountering educated fish. While it is possible that such heterogeneity influenced our findings, this explanation would require an extremely wide disparity in the catchability between the behavioral phenotypes to account for the magnitude of increases we found in recapture rates (Table 1) and would imply immediate onset of learned behavior following the initial encounter. Given the complexity of this explanation, we consider it less likely to explain increases in recapture rate on releases 2+.

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

Due to the lack of evidence for tag loss, tagging-induced mortality, or bait-happy/movement behaviors to fully explain higher recapture rates on releases 2+, we conclude that the higher recapture rates are most likely a result of higher survival. The finding of increased survival was unexpected; intuition suggests that the effects of repeated capture would be

cumulative, therefore reducing relative survival with each successive release (as was posited for fishes by Arlinghaus et al. (2007)). The three species for which we observed higher relative survival for release 2+ are in the family Serranidae; the remaining species examined (gray triggerfish) is in Balistidae. The common finding for the three serranids may be associated with their close taxonomic relationship and thus their similar morphology and physiology. Furthermore, it is possible that increased survival after releases 2+ does indeed occur for gray triggerfish (as indicated by the direction of the relative recapture rates; Table 1), but that our methods and/or sample size were not sufficient to detect this phenomenon.

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

We suggest that high rates of discarding may inflict a secondary (yet still substantial) selection pressure on many populations: selection for individuals that are resistant to discard mortality.

In light of our findings, improved methodologies for estimating the number of dead discards would strengthen stock assessment results. Kerns et al. (2012) recommended estimating instantaneous rates of discard mortality (e.g., at the population level) through the use of combined telemetry and high-reward conventional tagging; captures are reported via the high-reward tag, and if the fish is released its movements (and survival) are monitored via telemetry. This methodology eliminates the biases discussed in the present document. Another approach is to apply different discard mortality values to the portion of releases that are assumed to be unique and the remaining portion of releases. In the absence of tagging data, it is impossible to determine the proportion of releases that are occurring for the first time so selecting a value by which to decrement current estimates is challenging. For fisheries where releases dominate total catch (e.g., black sea bass in the US southeast; Table 4), it may be appropriate to assume that the proportion of unique releases is low. We suggest that stock assessments test the sensitivity of their results under a range of values for dead discards (treating the estimate produced by the current methodology as the maximum). Alternatively, the capture history of tagged animals could be incorporated into the stock assessment model framework to address the dynamics of repetitive captures.

The bias in number of live releases may also be relevant to some stock assessments. For example, any assessment that uses a temporally aggregated form of catch (that includes live releases) to build an index of abundance is at risk for bias. Many assessments use catch per unit effort to index abundance. If catches were aggregated on a per-year or per-season basis, as opposed to per-trip or per-angler, the value would probably include many repeatedly captured

fish. If the proportion of live releases to total catch was similar across years in the catch time series, then the bias would not impact the assessment results and total catch would index abundance. However, this proportion has grown (substantially, in many cases) for many species in the last two decades as catch-and-release angling has become more prevalent in the US Atlantic (Table 4) and in many other regions of the world (Kelleher, 2005; Ferter et al., 2013; Zeller et al., 2018). For species where this proportion has increased, total catch would be a biased index of abundance because of the overestimation of the number of unique live releases in recent time periods. We urge assessment scientists to use care when generating time series indices of abundance that include live releases.

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

It is usually unknown whether an untagged fish has been previously caught and released. Therefore, it is likely that a portion of the individuals tagged in the studies examined herein had been captured and released prior to tagging. As a result, for species where discard survival increased after releases 2+, estimates of discard mortality based on the first recapture event (including those used as baselines in this study) probably lie between the true survival after first release and the survival after later releases. Therefore, the difference between these release-number-dependent survival rates is likely larger than we found in this study. Thus, it is probable that our results are conservative in this regard.

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

Acknowledgements

Funding for the tagging studies was provided by NOAA grants NA14NMF4540061, NA09NMF4720265, NA09NMF4540140, and North Carolina Sea Grant Fishery Resource Grant projects 07-FEG-01 and 11-FEG-04. We thank Gary Shepherd from the NMFS Northeast Fisheries Science Center for his initial idea to examine the effects of repetitive capture on survival and a review on an earlier version of this manuscript. None of the studies examined herein would have been possible without the work of numerous taggers, tag returners, and scientists (in particular, R. Rincones and R. Wiggers); we are grateful for their efforts. We thank Jie Cao and three anonymous reviewers for reviewing early drafts of this paper and improving it greatly. The scientific results and conclusions, as well as any views and opinions expressed herein, are those of the authors and do not necessarily reflect those of any government agency or institution.

References

- Adam, M. S., and Kirkwood, G. P. 2001. Estimating tag-shedding rates for skipjack tuna, *Katsuwonus pelamis*, off the Maldives. *Fishery Bulletin*, 99: 193-196.
- Allen, M. S., Walters, C. J., and Myers, R. 2008. Temporal trends in largemouth bass mortality, with fishery implications. *North American Journal of Fisheries Management*, 28: 418-427.
- Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S. G., and Thorstad, E. B. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science*, 15: 75-167.
- Askey, P. J., Richards, S. A., Post, J. R., and Parkinson, E. A. 2006. Linking angling catch rates and fish learning under catch-and-release regulations. *North American Journal of Fisheries Management*, 26: 1020-1029.
- Bartholomew, A. and Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*, 15(1): 129-154.
- Bayliff, W. H., and Mobrand, L. M. 1972. Estimates of the rates of shedding of dart tags from yellowfin tuna. *Inter-American Tropical Tuna Commission Bulletin*, 15: 439-462.
- Beverton, R., and Holt, S. J. 1957. *On the Dynamics of Exploited Fish Populations*, Vol. II of *Fishery Investigations*, Ministry of Agriculture. Fisheries and Food.
- Caddy, J., and Seijo, J. 2011. Destructive fishing practices by bottom gears: a broad review of research and practice. *Ciencia Pesquera*, 19: 5-58.

- Coggins, L. G., Catalano, M. J., Allen, M. S., Pine, W. E., and Walters, C. J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries*, 8: 196-210.
- Conover, D. O., Arnott, S. A., Walsh, M. R., and Munch, S. B. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 730-737.
- Cooke, S., and Schramm, H. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology*, 14: 73-79.
- Cooke, S. J., and Cowx, I. G. 2004. The Role of Recreational Fishing in Global Fish Crises. *BioScience*, 54: 857-859.
- Cooke, S. J., and Cowx, I. G. 2006. Contrasting recreational and commercial fishing: Searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biological Conservation*, 128: 93-108.
- Cox, D. R. 1972. Regression models and life-tables. *In* *Breakthroughs in statistics*, pp. 527-541. Springer.
- Cox, S. P., and Walters, C. 2002. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. *North American Journal of Fisheries Management*, 22: 21-34.
- Crowder, L. B., and Murawski, S. A. 1998. Fisheries Bycatch: Implications for Management. *Fisheries*, 23: 8-17.
- del Mar Gil, M., Palmer, M., Grau, A., Massutí, E., and Pastor, E. 2017. Comparing tagging strategies: Effects of tags on retention rate, mortality rate and growth in hatchery-reared juvenile meagre, *Argyrosomus regius* (Pisces: Sciaenidae). *Scientia Marina*, 81: 171-178.

- Dunning, D. J., Ross, Q. E., Waldman, J. R., and Mattson, M. T. 1987. Tag retention by, and tagging mortality of, Hudson River striped bass. *North American Journal of Fisheries Management*, 7: 535-538.
- Ellis, T. A., Hightower, J. E., and Buckel, J. A. 2018. Relative importance of fishing and natural mortality for spotted seatrout (*Cynoscion nebulosus*) estimated from a tag-return model and corroborated with survey data. *Fisheries Research*, 199: 81-93.
- Fabrizio, M. C., Nichols, J. D., Hines, J. E., Swanson, B. L., and Schram, S. T. 1999. Modeling data from double-tagging experiments to estimate heterogeneous rates of tag shedding in lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1409-1419.
- Fabrizio, M. C., Scharf, F. S., Shepherd, G. R., and Rosendale, J. E. 2008. Factors affecting catch-and-release mortality of bluefish. *North American Journal of Fisheries Management*, 28: 533-546.
- Fabrizio, M. C., Swanson, B. L., Schram, S. T., and Hoff, M. H. 1996. Comparison of three nonlinear models to describe long-term tag shedding by lake trout. *Transactions of the American Fisheries Society*, 125: 261-273.
- Ferter, K., Weltersbach, M. S., Strehlow, H. V., Vølstad, J. H., Alós, J., Arlinghaus, R., Armstrong, M., Dorow, M., de Graaf, M., van der Hammen, T., Hyder, K., Levrel, H., Paulrud, A., Radtke, K., Rocklin, D., Sparrevohn, C. R., and Veiga, P. 2013. Unexpectedly high catch-and-release rates in European marine recreational fisheries: implications for science and management. *ICES Journal of Marine Science*, 70: 1319-1329.

- Fonteneau, A., and Hallier, J.-P. 2015. Fifty years of dart tag recoveries for tropical tuna: A global comparison of results for the western Pacific, eastern Pacific, Atlantic, and Indian Oceans. *Fisheries Research*, 163: 7-22.
- Gilman, E., Suuronen, P., Hall, M., and Kennelly, S. 2013. Causes and methods to estimate cryptic sources of fishing mortality. *Journal of Fish Biology*, 83: 766-803.
- Graefe, A. R., and Ditton, R. B. 1997. Understanding catch and release behavior among billfish anglers. *Proceedings of the 49th Annual Gulf and Caribbean Fisheries Institute*, 49: 430-455.
- Guillen, J., Holmes, S., Carvalho, N., Casey, J., Dörner, H., Gibin, M., Mannini, A., Vasilakopoulos, P., and Zanzi, A. 2018. A review of the European Union landing obligation focusing on its implications for fisheries and the environment. *Sustainability*, 10: 900.
- Hampton, J., and Kirkwood, G. P. 1990. Tag shedding by southern bluefin tuna *Thunnus maccoyii*. *Fishery Bulletin*, 88: 313-321.
- Heino, M., Pauli, B. D., and Dieckmann, U. 2015. Fisheries-induced evolution. *Annual review of ecology, evolution, and systematics*, 46.
- Hueter, R. E., Manire, C. A., Tyminski, J. P., Hoenig, J. M., and Hepworth, D. A. 2006. Assessing mortality of released or discarded fish using a logistic model of relative survival derived from tagging data. *Transactions of the American Fisheries Society*, 135: 500-508.
- Hyder, K., Weltersbach, M. S., Armstrong, M., Ferter, K., Townhill, B., Ahvonen, A., Arlinghaus, R., Baikov, A., Bellanger, M., Birzaks, J., Borch, T., Cambie, G., de Graaf, M., Diogo, H. M. C., Dziemian, Ł., Gordo, A., Grzebielec, R., Hartill, B., Kagervall, A.,

- Kapiris, K., Karlsson, M., Kleiven, A. R., Lejk, A. M., Levrel, H., Lovell, S., Lyle, J., Moilanen, P., Monkman, G., Morales-Nin, B., Mugerza, E., Martinez, R., O'Reilly, P., Olesen, H. J., Papadopoulos, A., Pita, P., Radford, Z., Radtke, K., Roche, W., Rocklin, D., Ruiz, J., Scougal, C., Silvestri, R., Skov, C., Steinback, S., Sundelöf, A., Svagzdys, A., Turnbull, D., van der Hammen, T., van Voorhees, D., van Winsen, F., Verleye, T., Veiga, P., Vølstad, J.-H., Zarauz, L., Zolubas, T., and Strehlow, H. V. 2018. Recreational sea fishing in Europe in a global context—Participation rates, fishing effort, expenditure, and implications for monitoring and assessment. *Fish and Fisheries*, 19: 225-243.
- Ihde, T. F., Wilberg, M. J., Loewensteiner, D. A., Secor, D. H., and Miller, T. J. 2011. The increasing importance of marine recreational fishing in the US: Challenges for management. *Fisheries Research*, 108: 268-276.
- Kelleher, K. 2005. Discards in the world's marine fisheries: an update, Food & Agriculture Org.
- Kerns, J. A., Allen, M. S., and Harris, J. E. 2012. Importance of assessing population-level impact of catch-and-release mortality. *Fisheries*, 37: 502-503.
- Kieffer, J. D., Kubacki, M. R., Phelan, F. J. S., Philipp, D. P., and Tufts, B. L. 1995. Effects of Catch-and-Release Angling on Nesting Male Smallmouth Bass. *Transactions of the American Fisheries Society*, 124: 70-76.
- Kipling, C., and Le Cren, E. 1984. Mark-recapture experiments on fish in Windermere, 1943–1982. *Journal of Fish Biology*, 24: 395-414.
- Latour, R. J., Pollock, K. H., Wenner, C. A., and Hoenig, J. M. 2001. Estimates of fishing and natural mortality for subadult red drum in South Carolina waters. *North American Journal of Fisheries Management*, 21: 733-744.

- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57: 659-668.
- McCormick, J. L. 2016. Using Tag-Return Models to Estimate the Number of Times Fish Are Captured in Fisheries with High Catch-and-Release Rates. *North American Journal of Fisheries Management*, 36: 584-589.
- Miller, L. M., Kallemeyn, L., and Senanan, W. 2001. Spawning-site and natal-site fidelity by northern pike in a large lake: mark-recapture and genetic evidence. *Transactions of the American Fisheries Society*, 130: 307-316.
- MRIP. 2018. *Marine Recreational Information Program Data User Handbook*
- NMFS. 2016. *U.S. National Bycatch Report First Edition Update 2*. 90 pp.
- Philipp, D. P., Cooke, S. J., Claussen, J. E., Koppelman, J. B., Suski, C. D., and Burkett, D. P. 2009. Selection for vulnerability to angling in largemouth bass. *Transactions of the American Fisheries Society*, 138: 189-199.
- Philipp, D. P., Toline, C. A., Kubacki, M. F., Philipp, D. B. F., and Phelan, F. J. S. 1997. The Impact of Catch-and-Release Angling on the Reproductive Success of Smallmouth Bass and Largemouth Bass. *North American Journal of Fisheries Management*, 17: 557-567.
- Pollock, K., and Pine, W. 2007. The design and analysis of field studies to estimate catch-and-release mortality. *Fisheries Management and Ecology*, 14: 123-130.
- Post, J. R., Sullivan, M., Cox, S., Lester, N. P., Walters, C. J., Parkinson, E. A., Paul, A. J., Jackson, L., and Shuter, B. J. 2002. Canada's Recreational Fisheries: The Invisible Collapse? *Fisheries*, 27: 6-17.

- Punt, A. E., Smith, D. C., Tuck, G. N., and Methot, R. D. 2006. Including discard data in fisheries stock assessments: Two case studies from south-eastern Australia. *Fisheries Research*, 79: 239-250.
- Quinn, S. 1996. Trends in regulatory and voluntary catch-and-release fishing. *In* Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium, pp. 152-162.
- R Core Team 2019. R: a language and environment for statistical computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Recksiek, C. W., Appeldoorn, R. S., and Turingan, R. G. 1991. Studies of fish traps as stock assessment devices on a shallow reef in south-western Puerto Rico. *Fisheries Research*, 10: 177-197.
- Royle, J. A., Chandler, R. B., Sollmann, R., and Gardner, B. 2013. Spatial capture-recapture, Academic Press.
- Rudershausen, P. J., Buckel, J. A., and Hightower, J. E. 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.
- Runde, B. J., Rudershausen, P. J., Sauls, B., Mikles, C. S., and Buckel, J. A. 2019. Low discard survival of gray triggerfish in the southeastern US hook-and-line fishery. *Fisheries Research*, 219: 105313.
- Sauls, B. 2014. Relative survival of gags *Mycteroperca microlepis* released within a recreational hook-and-line fishery: Application of the Cox Regression Model to control for heterogeneity in a large-scale mark-recapture study. *Fisheries Research*, 150: 18-27.

- Schill, D. J., Griffith, J., and Gresswell, R. E. 1986. Hooking mortality of cutthroat trout in a catch-and-release segment of the Yellowstone River, Yellowstone National Park. *North American Journal of Fisheries Management*, 6: 226-232.
- SEDAR. 2017. SEDAR 53 – South Atlantic Red Grouper Assessment Report. 159 pp.
- SEDAR. 2018. SEDAR 56 – South Atlantic Black Seabass Assessment Report. 164 pp.
- Shertzer, K. W., Bacheler, N. M., Kellison, G. T., Fieberg, J., and Wiggers, R. K. 2018. Release mortality of endangered Warsaw grouper *Hyporthodus nigrurus*: a state-space model applied to capture-recapture data. *Endangered Species Research*, 35: 15-22.
- Shertzer, K. W., Williams, E. H., Craig, J. K., Fitzpatrick, E. E., Klibansky, N., and Siegfried, K. I. 2019. Recreational sector is the dominant source of fishing mortality for oceanic fishes in the Southeast United States Atlantic Ocean. *Fisheries Management and Ecology*, 0.
- Slavík, O., Bartoš, L., and Horký, P. 2009. Effect of river fragmentation and flow regulation on occurrence of landlocked brown trout in a fish ladder. *Journal of Applied Ichthyology*, 25: 67-72.
- Springer, V. G., and McErlean, A. J. 1962. A study of the behavior of some tagged south Florida coral reef fishes. *American Midland Naturalist*: 386-397.
- Stokes, K., and Law, R. 2000. Fishing as an evolutionary force. *Marine Ecology Progress Series*, 208: 307-309.
- Sutter, D. A., Suski, C. D., Philipp, D. P., Klefoth, T., Wahl, D. H., Kersten, P., Cooke, S. J., and Arlinghaus, R. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences*, 109: 20960-20965.

- Suuronen, P., and Erickson, D. L. 2010. Mortality of animals that escape fishing gears or are discarded after capture: approaches to reduce mortality. *Behavior of marine fishes: capture processes and conservation challenges*: 265-293.
- Therneau, T. 2015. *A Package for Survival Analysis in S*. Version 2.38.
- Viana, M., McNally, L., Graham, N., Reid, D. G., and Jackson, A. L. 2013. Ignoring discards biases the assessment of fisheries' ecological fingerprint. *Biology letters*, 9: 20130812.
- Villasante, S., Antelo, M., Christou, M., Fauconnet, L., Frangoudes, K., Maynou, F., Morato, T., Pita, C., Pita, P., and Stergiou, K. I. 2019. The Implementation of the Landing Obligation in Small-Scale Fisheries of Southern European Union Countries. *In The European Landing Obligation*, pp. 89-108. Springer.
- Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., and Olsen, E. M. 2018. Personalities influence spatial responses to environmental fluctuations in wild fish. *Journal of Animal Ecology*.
- Whitlock, R., and McAllister, M. 2009. A Bayesian mark–recapture model for multiple-recapture data in a catch-and-release fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 1554-1568.
- Wiggers, R. K. 2010. South Carolina marine game fish tagging program 1978-2009. South Carolina Department of Marine Resources Division
- Williams, E. H., and Shertzer, K. W. 2005. Effects of fishing on growth traits: a simulation analysis. *Fishery Bulletin*, 103: 392-403.
- Williams, E. H., and Shertzer, K. W. 2015. Technical documentation of the Beaufort Assessment Model (BAM), US Department of Commerce, National Oceanic and Atmospheric

Administration, National Marine Fisheries Service, Southeast Fisheries Science Center,
NOAA Beaufort Laboratory.

Wydoski, R. S. 1977. Relation of hooking mortality and sublethal hooking stress to quality
fishery management. Catch-and-release fishing as a management tool. Humboldt State
University, Arcata, California: 43-87.

Zeller, D., Cashion, T., Palomares, M., and Pauly, D. 2018. Global marine fisheries discards: a
synthesis of reconstructed data. *Fish and Fisheries*, 19: 30-39.

Tables

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

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

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

Species	Best model	Variable	Hazard ratio	<i>p</i>
Black sea bass	~release number + condition	Release number 2	2.26	<0.01
		Release number 3	2.80	<0.01
		Condition 2	0.89	0.05
		Condition 3	0.14	<0.01
		Condition 4	0.14	<0.01
Gray triggerfish	~gear + condition	Gear: trap	2.14	<0.01
		Condition 2	0.58	0.03
		Condition 3	0.12	0.04
Red grouper	~release number + size + depth + year + month	Release number 2	8.56	<0.01
		Release number 3	6.06	<0.01
		Release number 4	3.64	0.01
		Size (mm)	1.01	<0.01
		Depth (m)	0.97	<0.01
		Year2010	1.04	0.59
		Year2011	1.03	0.74
		Year2012	0.85	0.08
		Year2013	0.88	0.19
		Year2014	1.10	0.62
		Year2015	0.68	<0.01
		Year2016	0.56	<0.01
		MonthJan	0.61	<0.01
		MonthFeb	0.95	0.64
		MonthMar	0.97	0.81
		MonthMay	1.07	0.52
		MonthJun	0.81	0.05
		MonthJul	0.59	<0.01
		MonthAug	0.55	<0.01
		MonthSep	0.56	<0.01
MonthOct	0.82	0.05		
MonthNov	0.82	0.05		
MonthDec	0.69	<0.01		
Warsaw grouper	~release number + size	Release number 2	1.97	<0.01
		Release number 3	1.36	0.26
		Size (mm)	0.99	<0.01

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

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

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

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

Figures

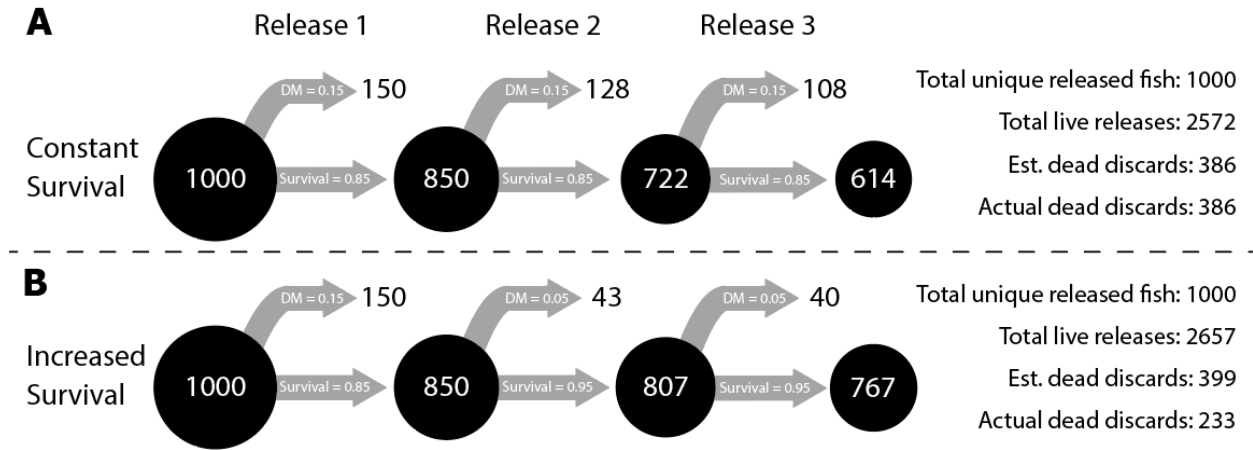


Figure 1. Calculations of total unique released fish, total live releases, estimated (est.) dead discards, and actual dead discards under (a) constant survival and (b) increased survival. In both scenarios, we assume all live fish are captured in each period. “Total unique released fish” is held constant at 1000 and refers to the number of unique fish that are released in time step 1 (first black circle) with those same (and alive) individuals being caught and released in subsequent time steps (second to fourth black circles). “Total live releases” is calculated as the sum of the number of releases in each time step (black circles); this value emulates the number of releases that would be reported by programs such as NOAA Marine Recreational Information Program. “Est. dead discards” represents the sum of dead discards from each release. Estimated dead discards from all releases are calculated as “Total live releases” multiplied by (currently assumed constant) discard mortality of 0.15 for scenarios (a) and (b). Note that although the same discard mortality rate is used, the number of “Est. dead discards” is slightly higher in scenario (b) because the number of live releases is higher. “Actual dead discards” is the sum of the number of discard mortalities after each of the three release events; in the “Increased Survival” scenario (b), survival increases from 0.85 for release 1 to 0.95 for releases 2 and 3. This increase corresponds to our findings of increased survival for releases 2p for three species of reef fish in the southeast United States.

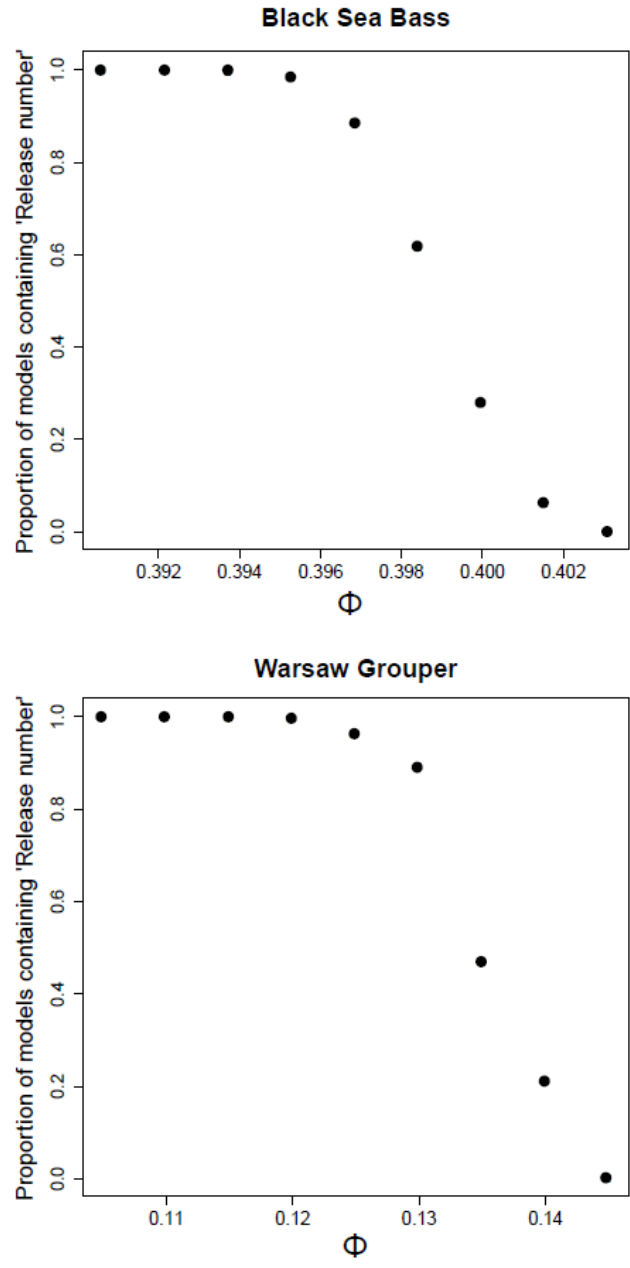


Figure 2. Proportion of bootstrapped datasets for which the best model contained Release Number for (A) black sea bass and (B) Warsaw grouper from our examination of the effect of Φ (combined rate of tag shedding and tagging-induced mortality).

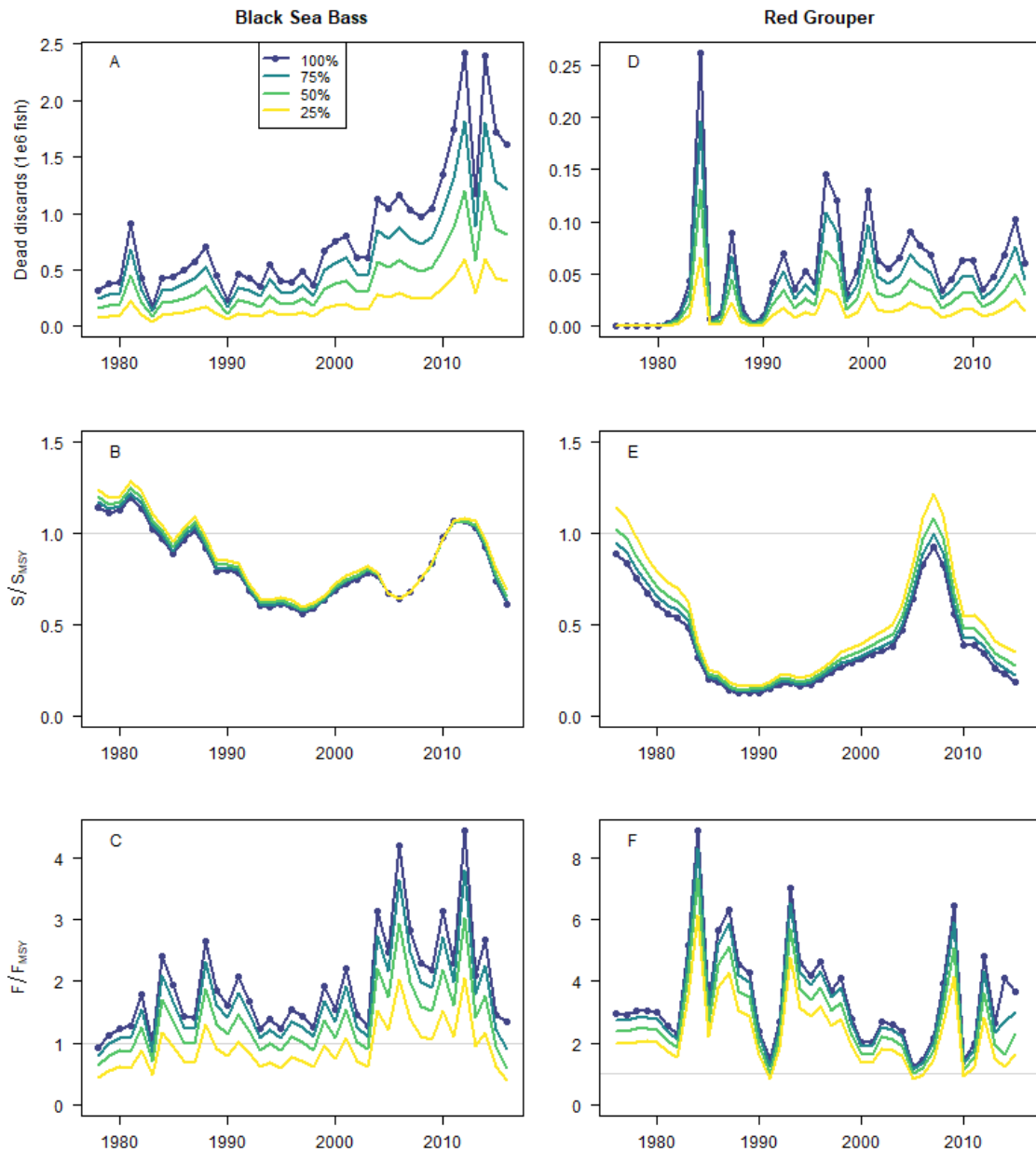


Figure 3. Stock assessment results for black sea bass (SEDAR 2018) and red grouper (SEDAR 2017), given the annual number of dead discards at the base level used in the most recent assessment (100%) or at reduced levels (75%, 50%, or 25% of base-level estimates), representing scenarios with fewer releases of unique fish or higher discard survival. Panels show the annual number of dead discards for each species (A, D), the estimated spawning biomass relative to that at maximum sustainable yield (S/S_{MSY} ; B, E), and the fishing mortality rate relative to its value at maximum sustainable yield (F/F_{MSY} ; C, F). Note different scales on the x- and y-axes among panels.

CONCLUSION

Combating unsustainable levels of release mortality is possible through the use of descender devices and spatial closures. For descender devices, education and outreach are of paramount importance (Crandall et al., 2018; Bellquist et al., 2019; Runde, 2019) and can result in substantial increases in survival when applied appropriately (Eberts and Somers, 2017; Runde et al., 2020b). Our finding for deep-water groupers of survival of ~60% suggests that with widespread use, some overfished stocks such as speckled hind and snowy grouper could be rebuilt much more quickly than if all releases occurred at the surface. The use of hidden Markov models to improve fate assignment, as well as the varied release treatments and controls we used, could be emulated and improved upon by future researchers. For spatial closures, it seems clear that the Snowy Wreck MPA has the potential to bolster populations of the reef species it was intended to protect. Indeed, some evidence is already present that the MPA is working as intended, though the most imperiled longer-lived species probably require more time to show an effect. Furthermore, we found that enforcement of the MPA is lax; increased enforcement and widespread information campaigns could prevent illegal fishing and promote positive effects on fish populations (Edgar et al., 2014).

Fisheries management could further be improved by a greater understanding of the effects of repeated capture of individual fish (Runde et al., 2020a). Our findings on this topic have potentially broad implications. First, some assessment methods could be modified to account for double- and triple-counting some released fish. Second, we posited that increased levels of releasing could inflict a selection pressure on fish populations and may result in human-induced adaptation. Future research could examine this concept more in depth and perhaps experimentally to determine the potential magnitude of this effect.

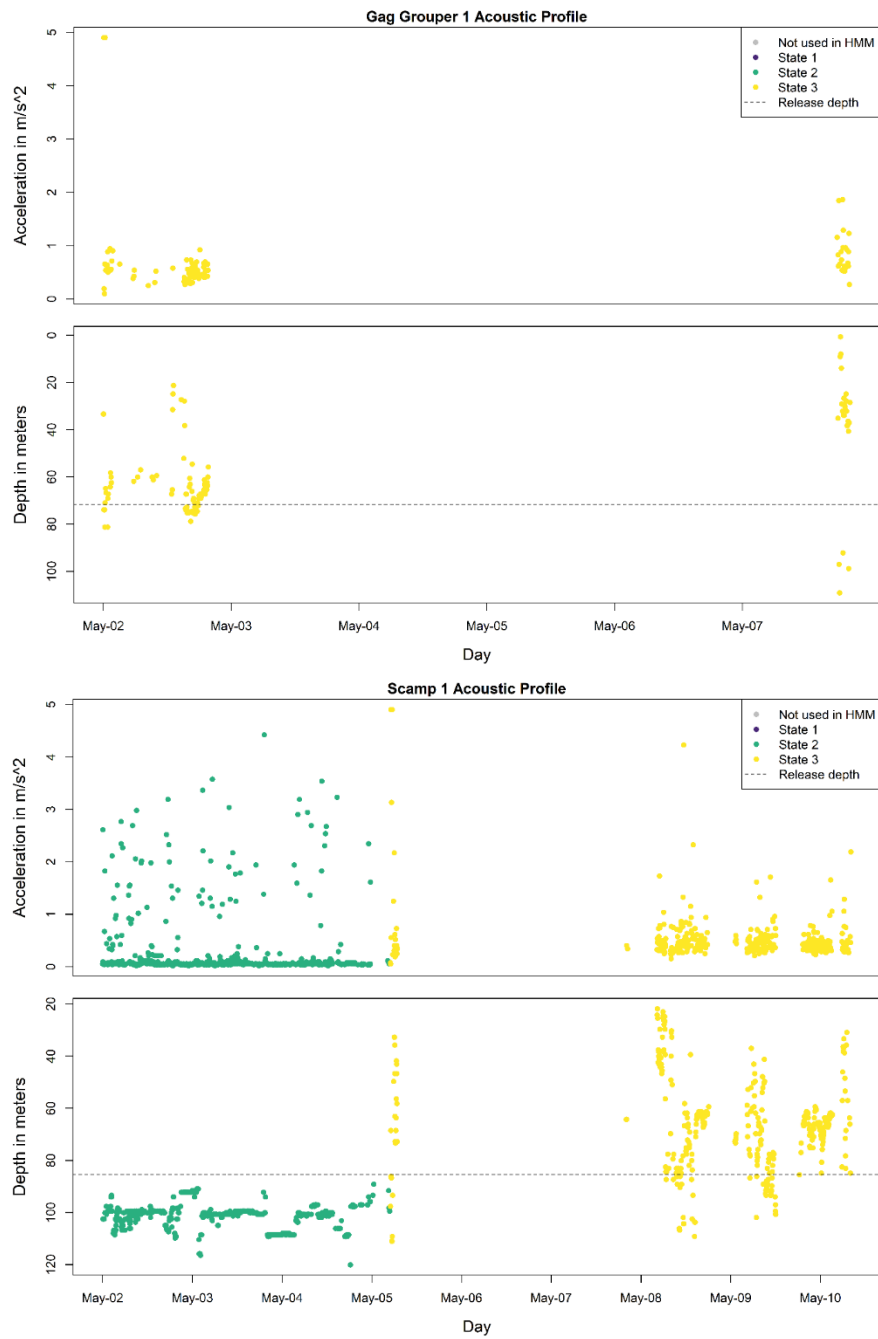
Overall, my conclusion is that assessing and managing reef fish species is challenging but innovative strategies, paired with revisions of existing methods, offer a promising path forward. As fisheries for these and other species continue to evolve, researchers must try to keep pace by implementing and (crucially) evaluating regulations as we work towards rebuilding and conserving fish stocks.

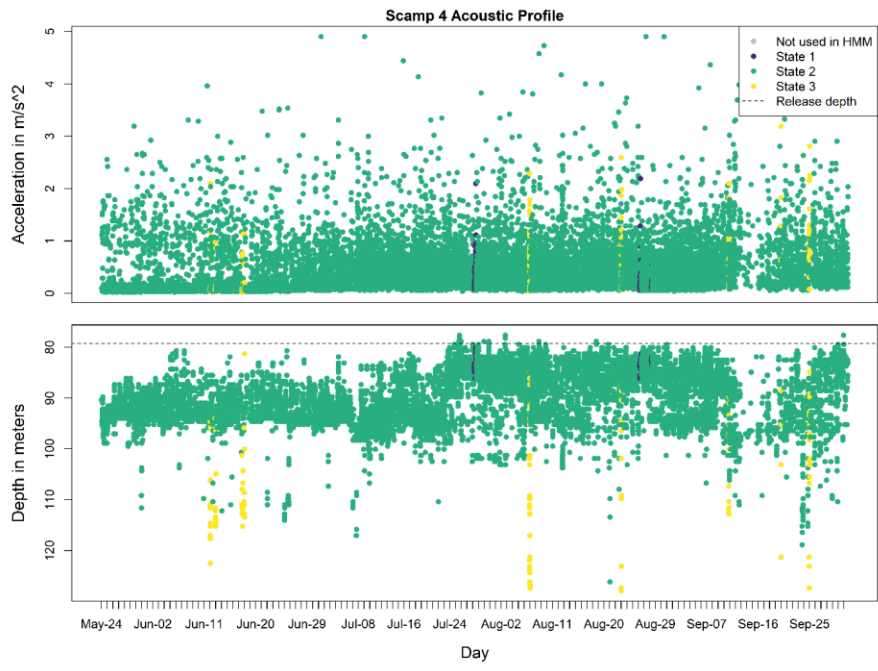
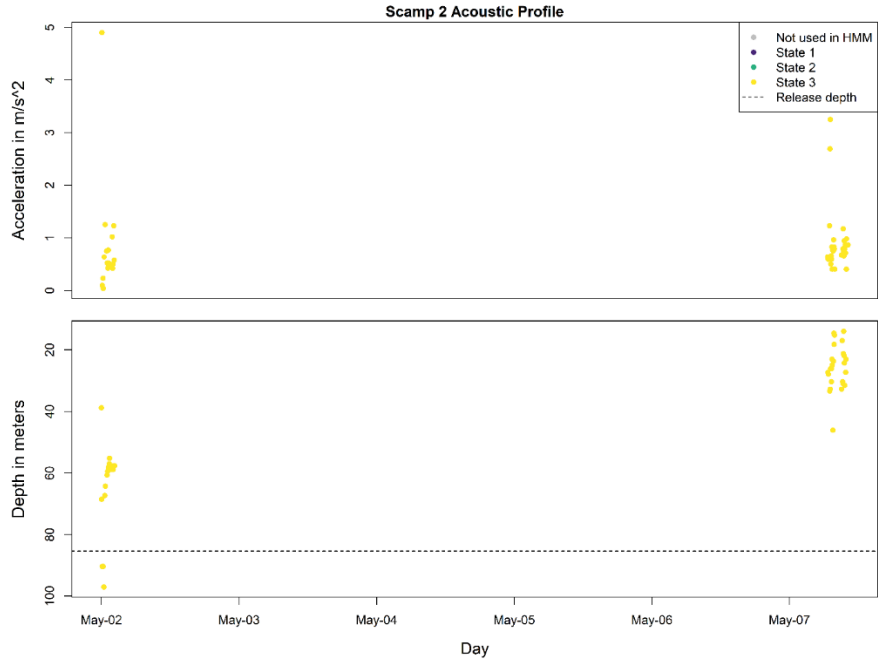
References

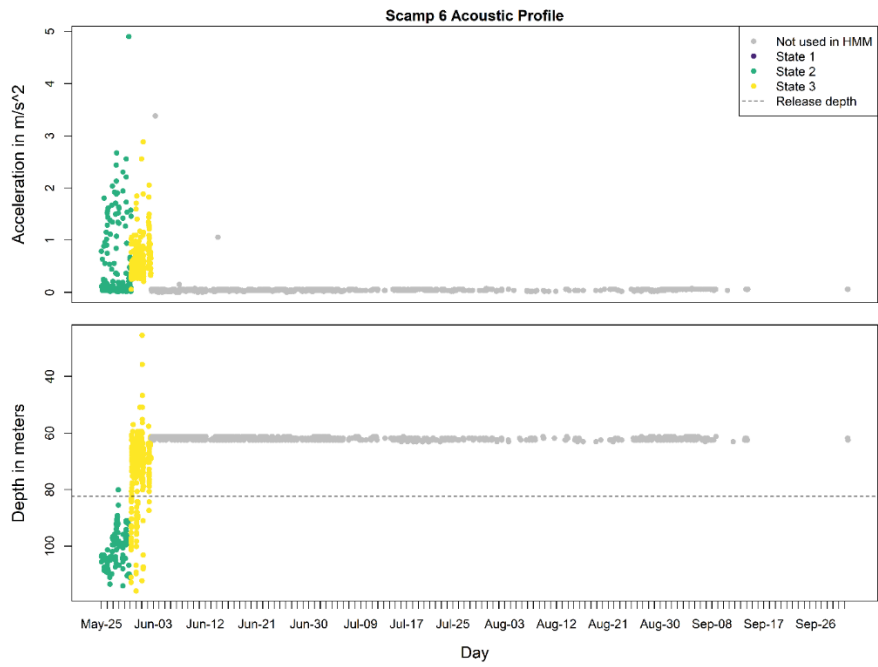
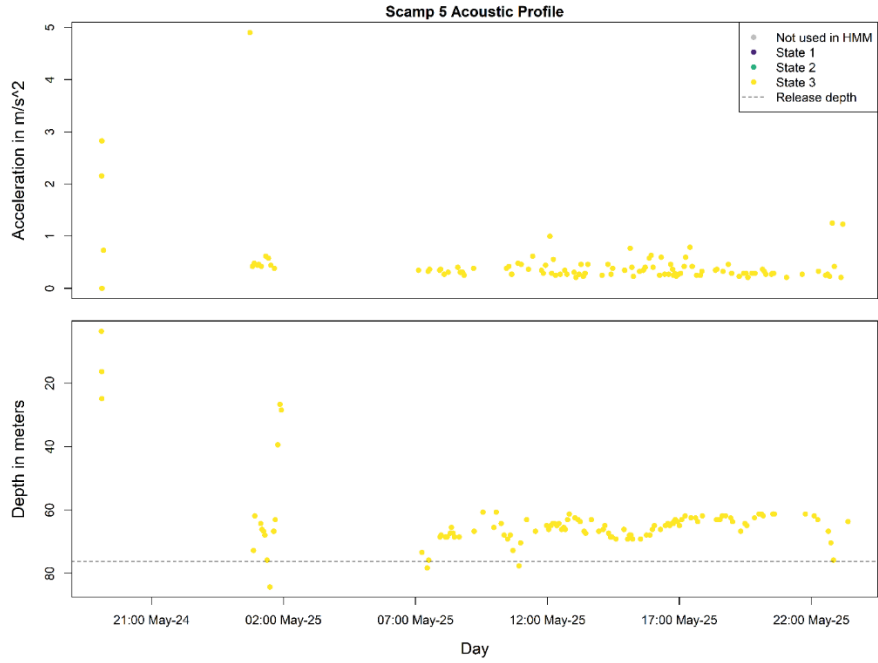
- Bellquist, L., Beyer, S., Arrington, M., Maeding, J., Siddall, A., Fischer, P., Hyde, J., and Wegner, N. C. 2019. Effectiveness of descending devices to mitigate the effects of barotrauma among rockfishes (*Sebastes* spp.) in California recreational fisheries. *Fisheries Research*, 215: 44-52.
- Crandall, C. A., Garlock, T. M., and Lorenzen, K. 2018. Understanding Resource-Conserving Behaviors Among Fishers: Barotrauma Mitigation and the Power of Subjective Norms in Florida's Reef Fisheries. *North American Journal of Fisheries Management*, 38: 271-280.
- Eberts, R. L., and Somers, C. M. 2017. Venting and Descending Provide Equivocal Benefits for Catch-and-Release Survival: Study Design Influences Effectiveness More than Barotrauma Relief Method. *North American Journal of Fisheries Management*, 37: 612-623.
- Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T., and Berkhout, J. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506: 216-220.
- Runde, B. J. 2019. Stakeholder engagement is the path to successful management. *Fisheries*, 44: 209-211.
- Runde, B. J., Buckel, J. A., Shertzer, K. W., Bacheler, N. M., Rudershausen, P. J., and Sauls, B. 2020a. Repetitive capture of marine fishes: implications for estimating number and mortality of releases. *ICES Journal of Marine Science*.
- Runde, B. J., Michelot, T., Bacheler, N. M., Shertzer, K. W., and Buckel, J. A. 2020b. Assigning fates in telemetry studies using hidden Markov models: an application to deepwater groupers released with descender devices. *North American Journal of Fisheries Management*.

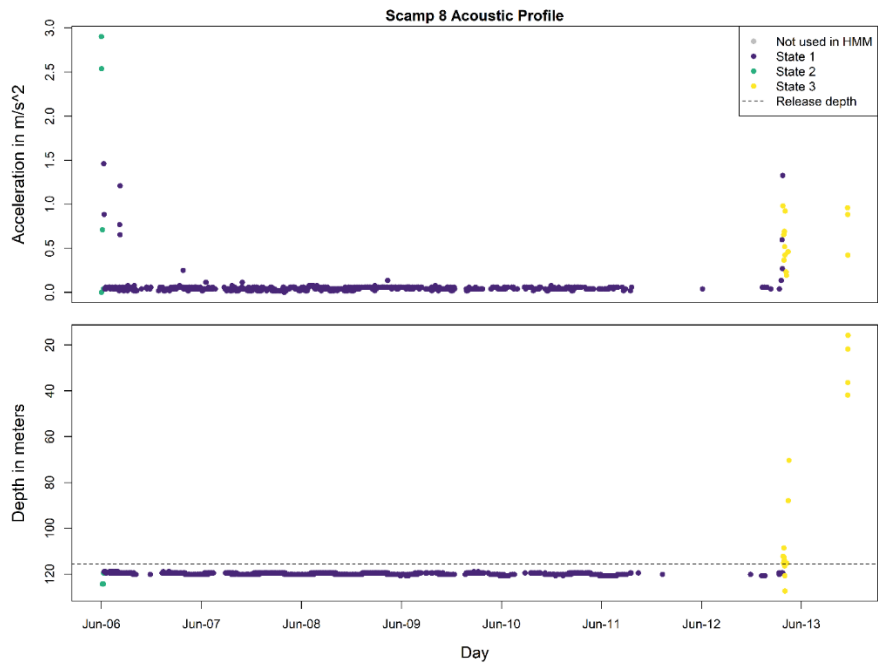
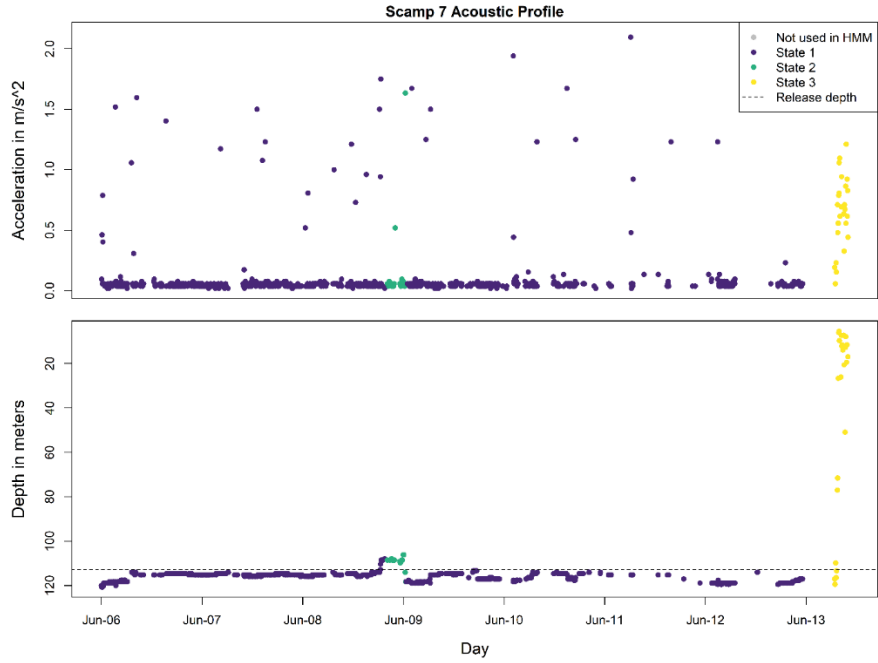
APPENDICES

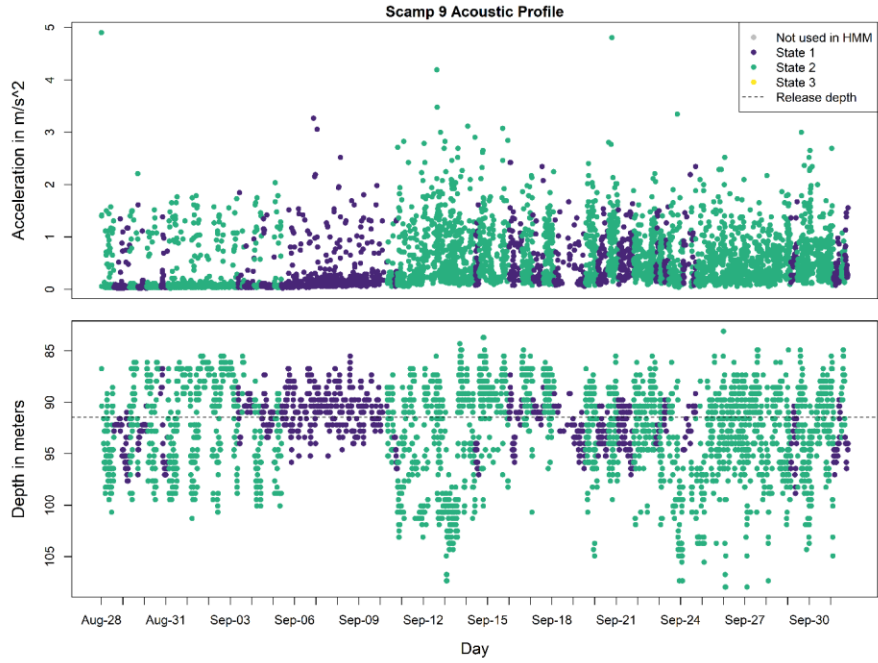
Appendix A: Chapter 1 Supplementary Material

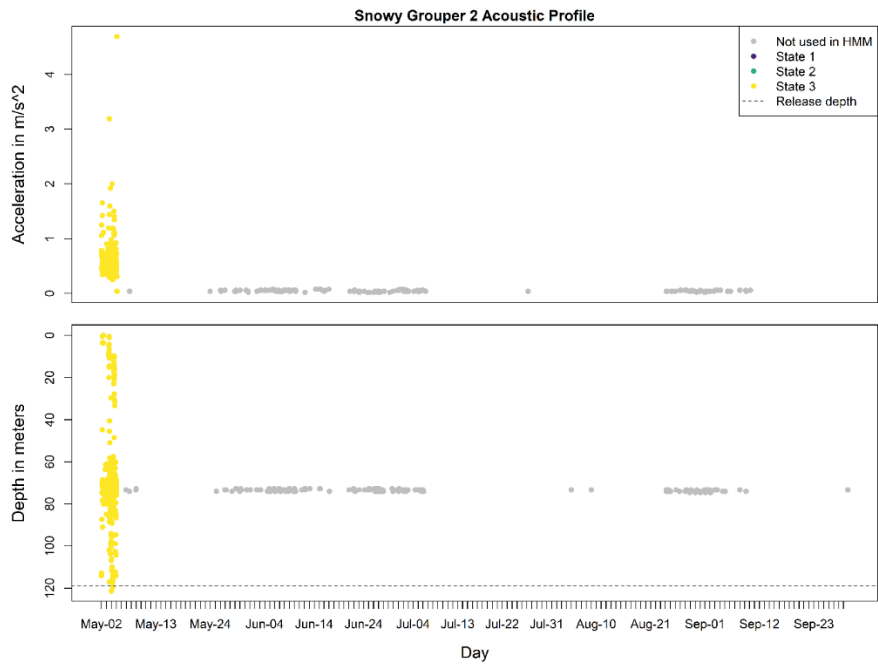
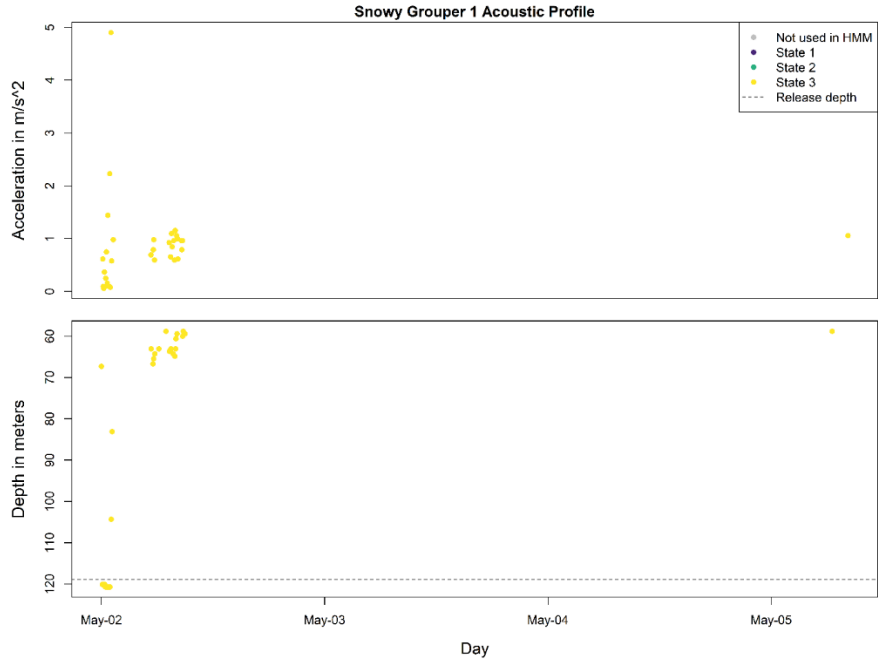


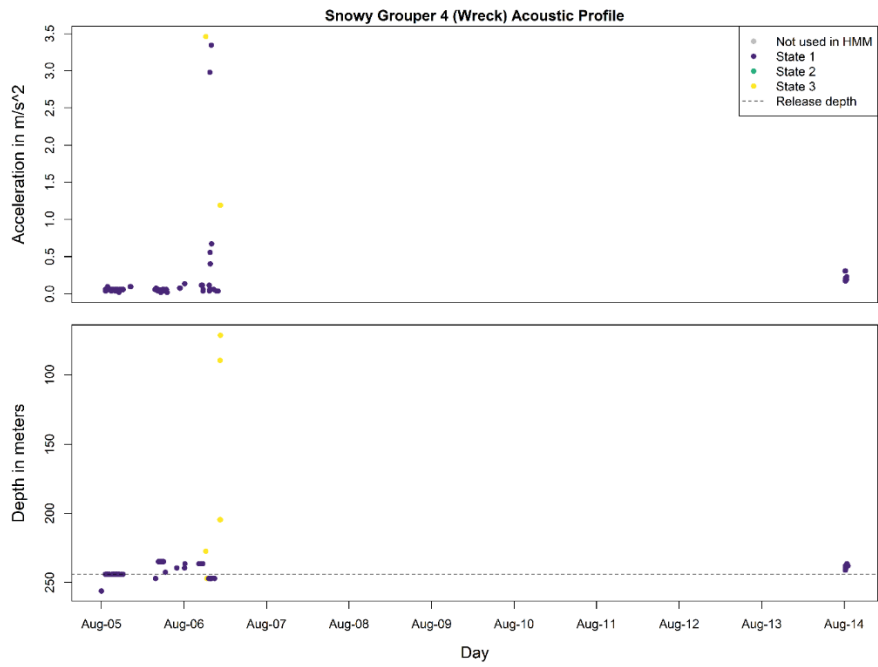
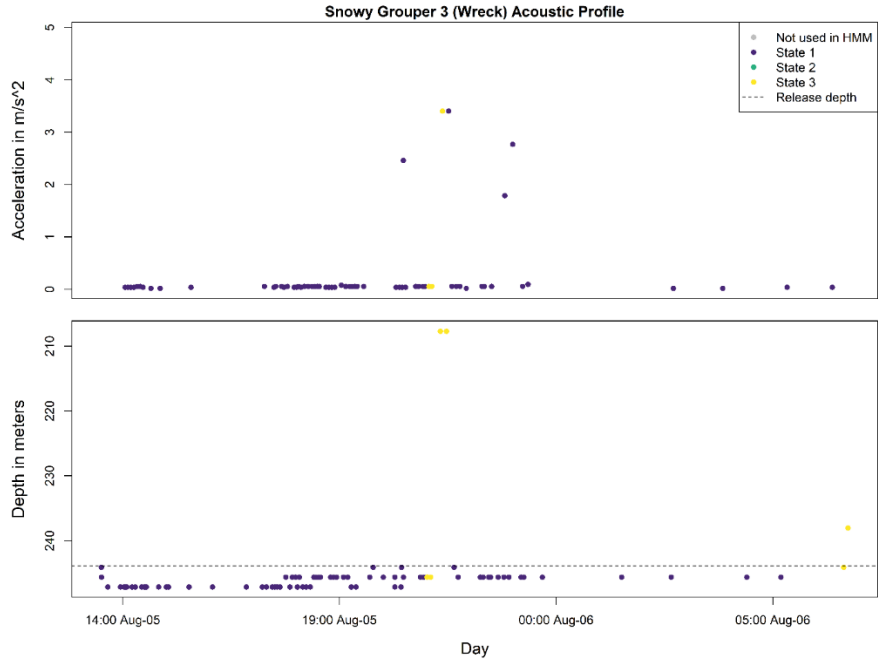


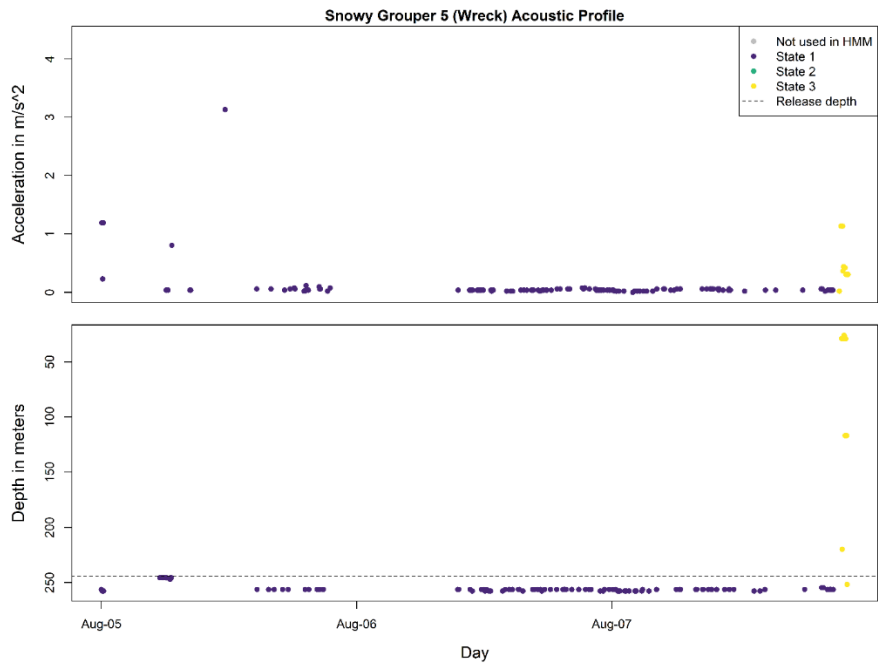
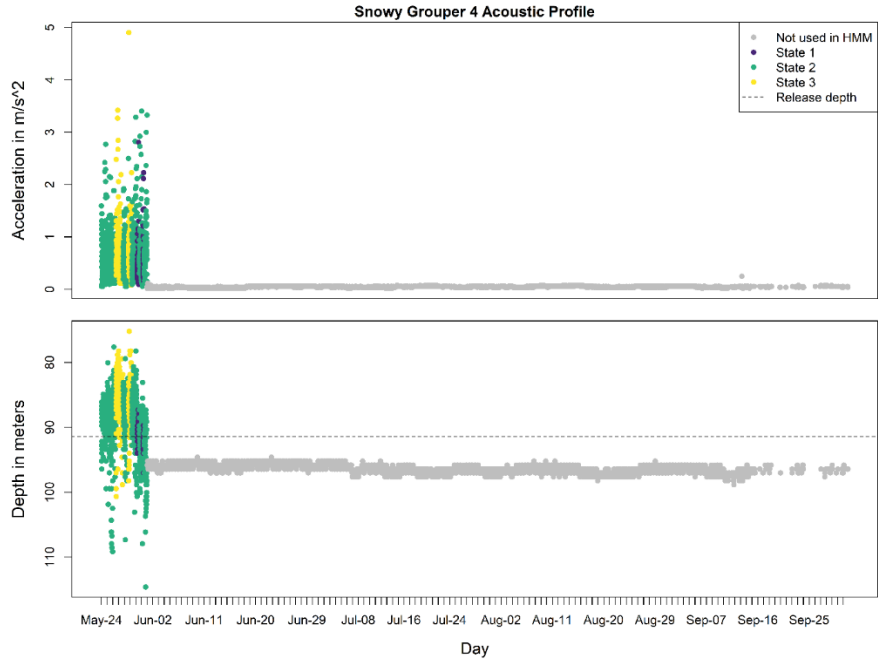


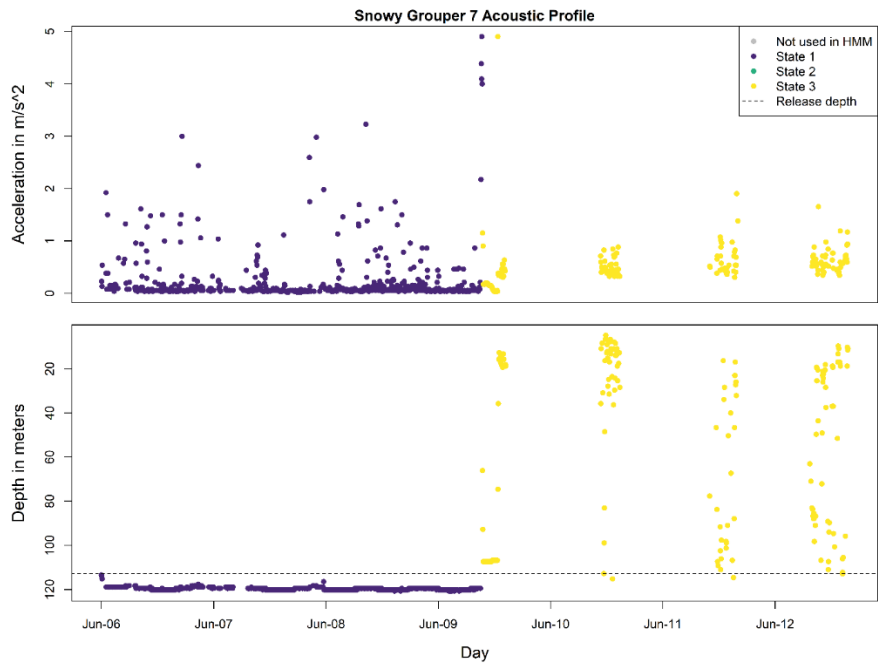
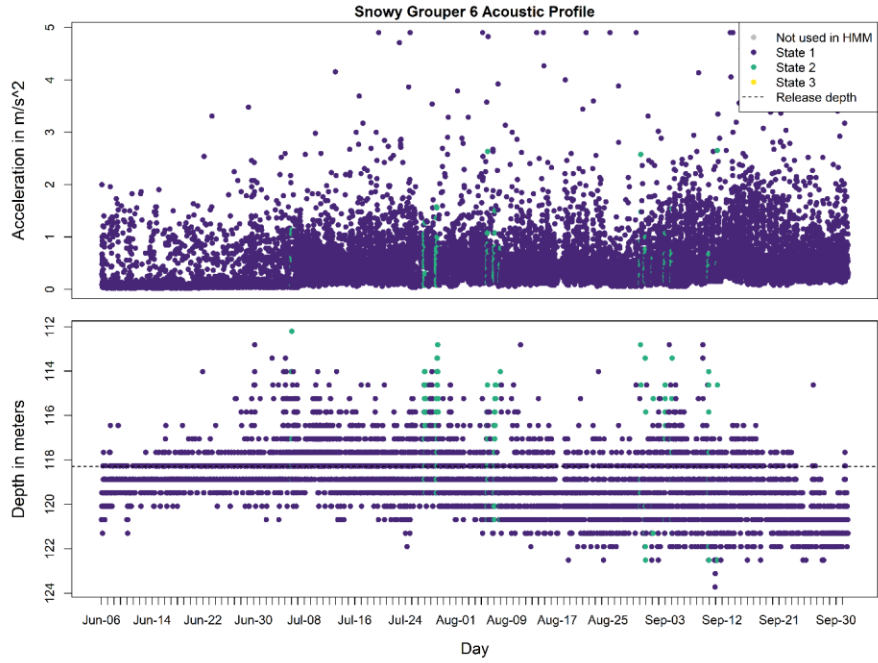


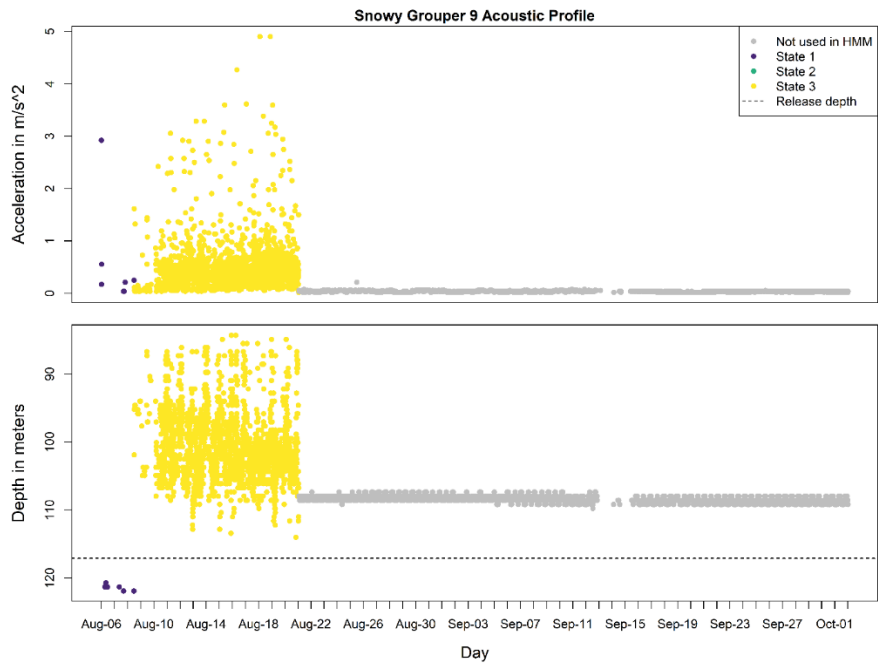


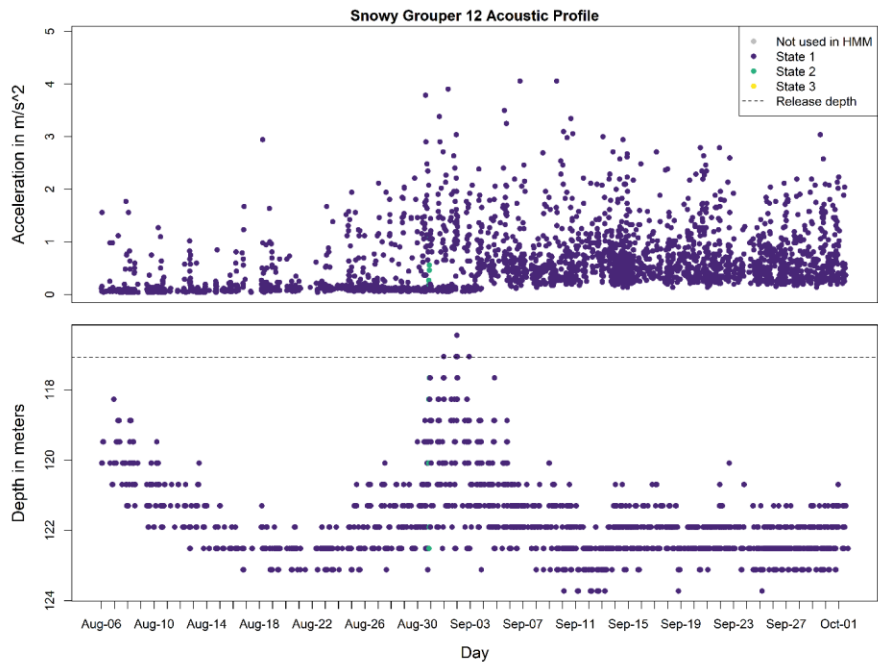
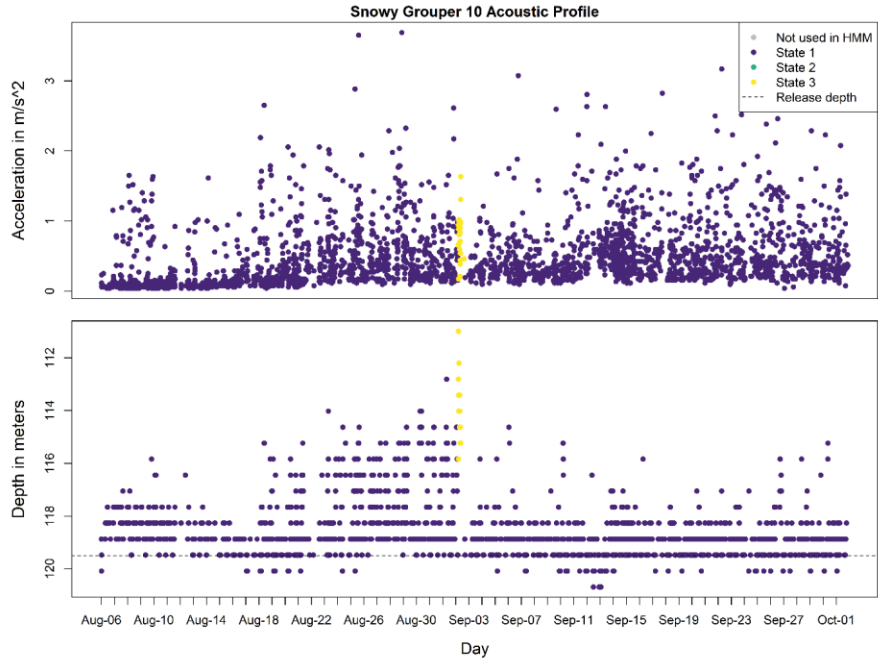


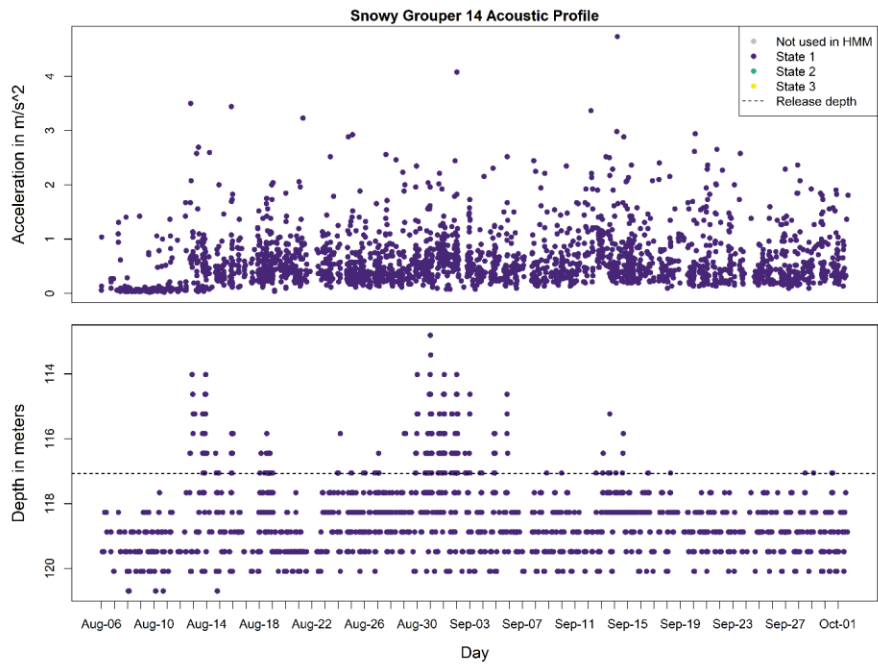


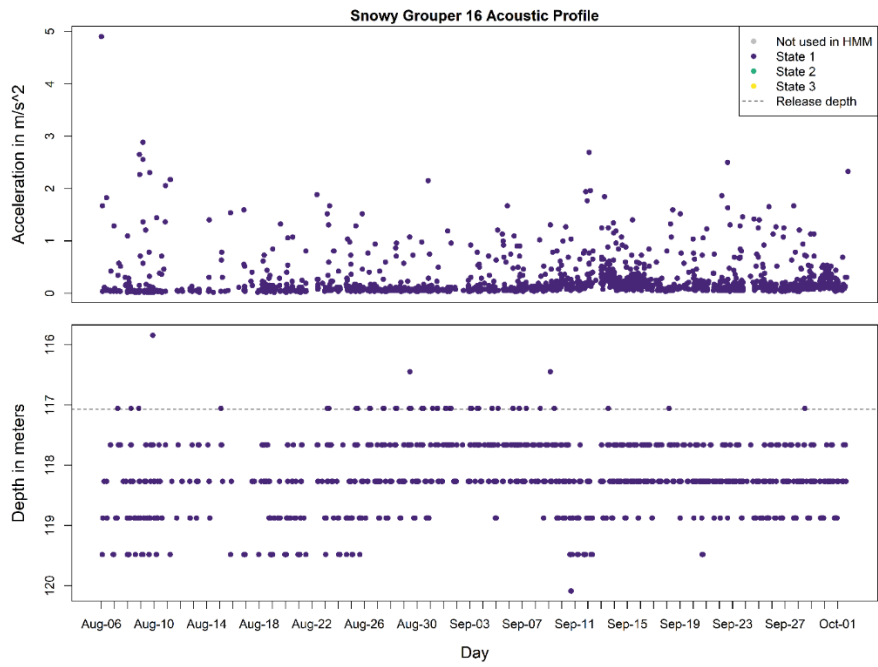
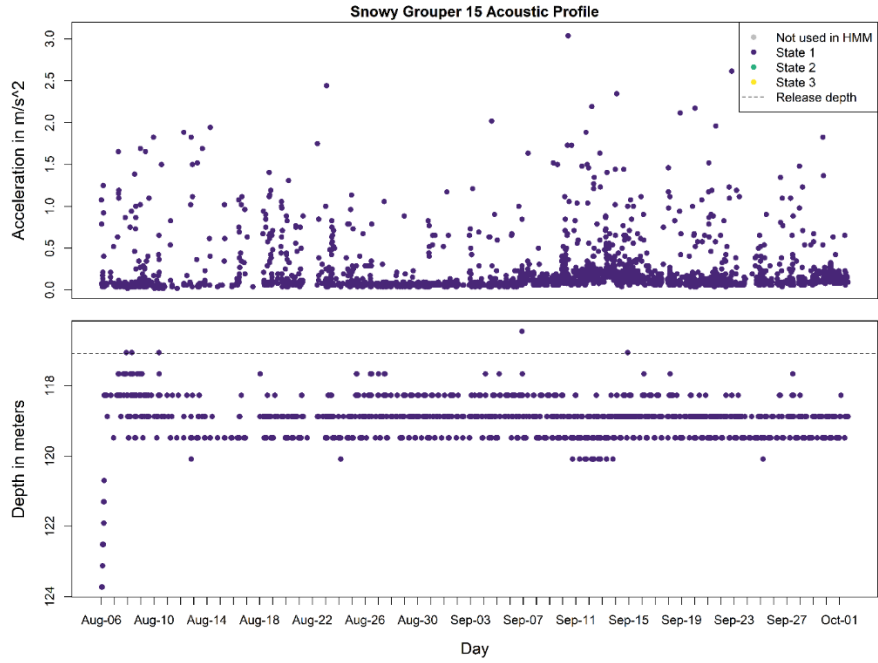


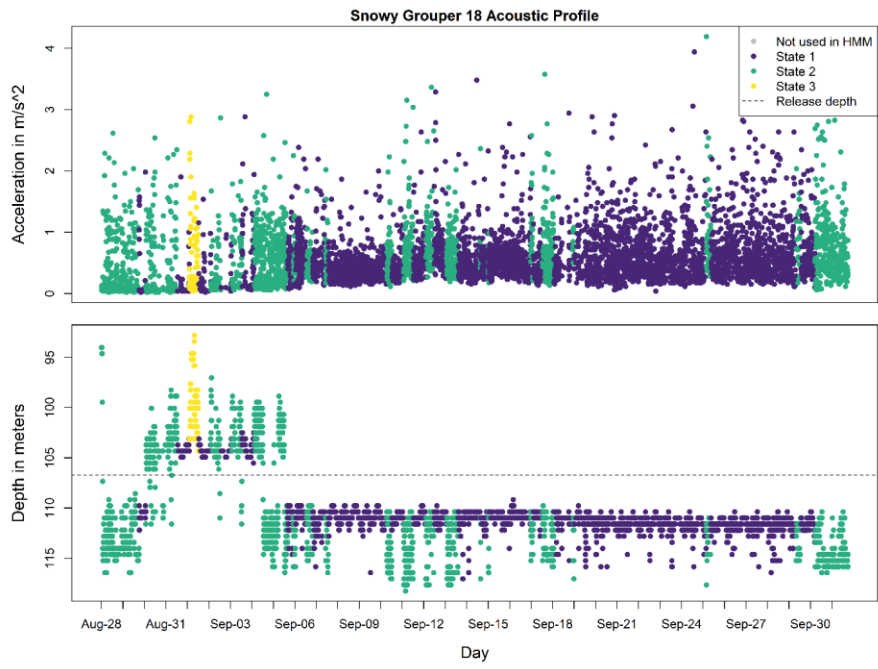
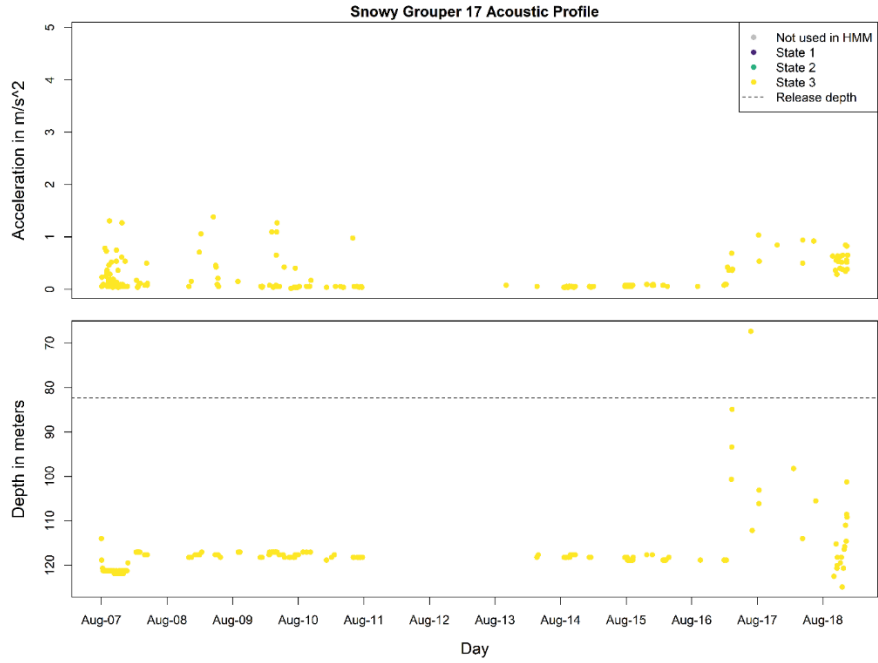


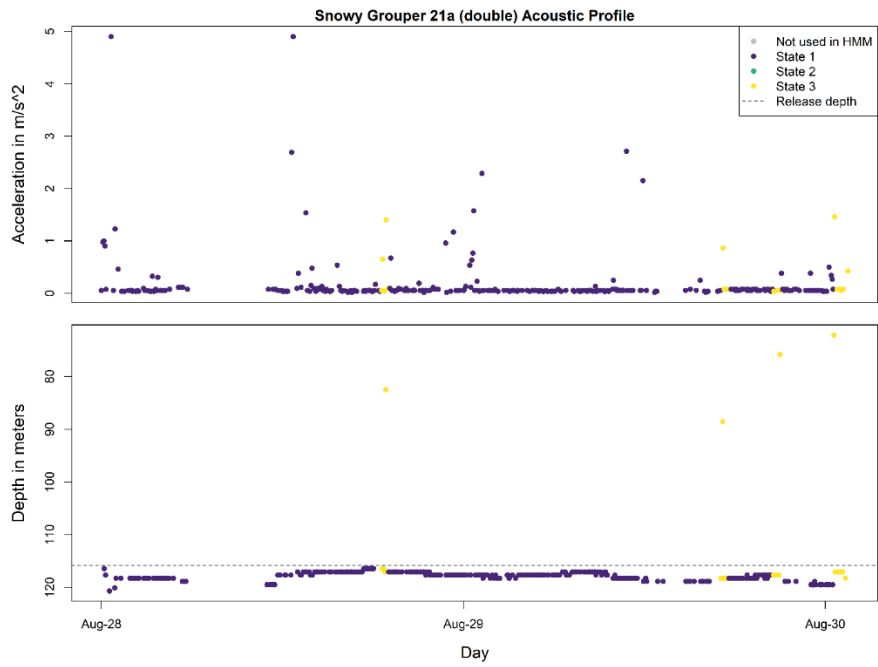
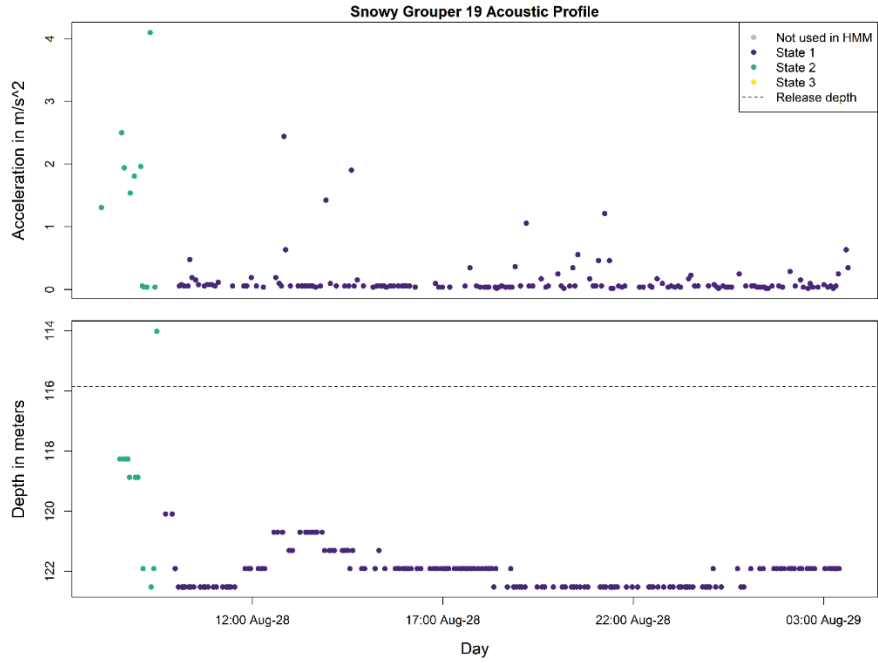


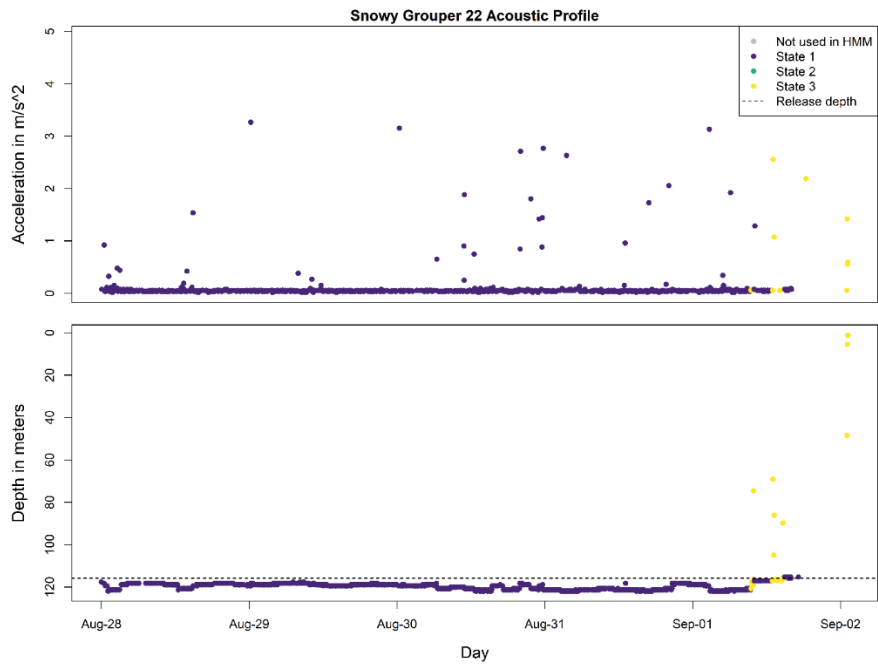


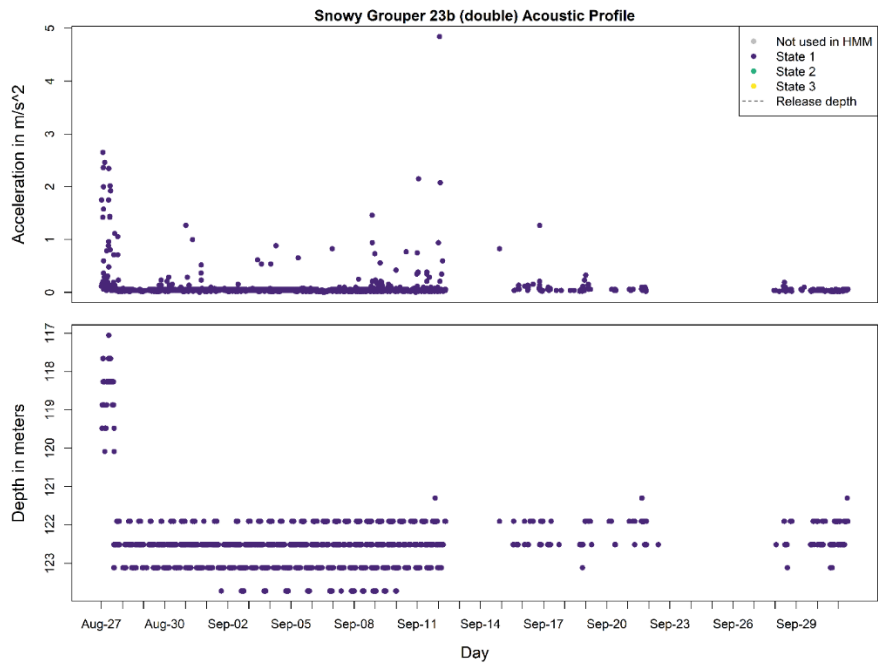
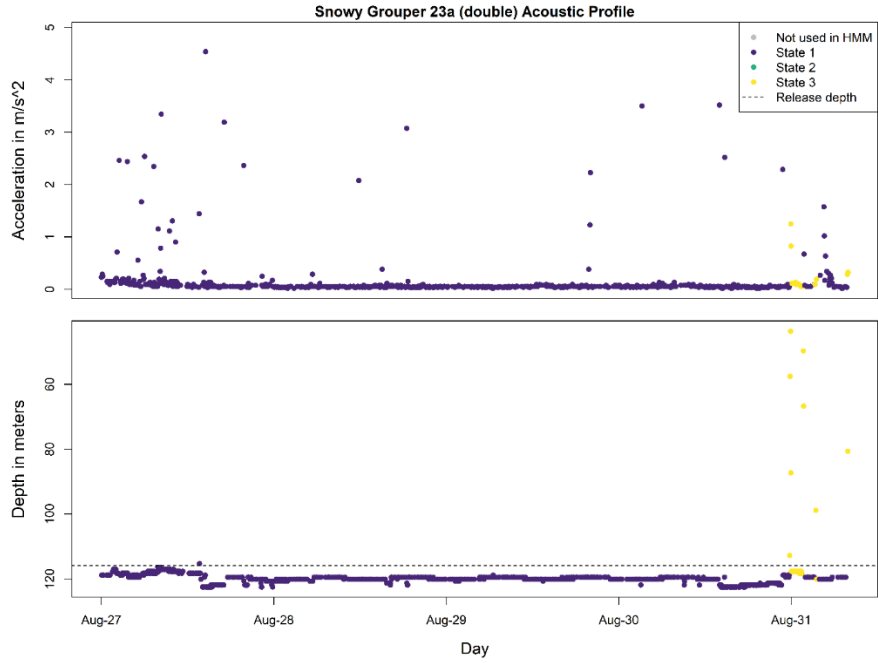


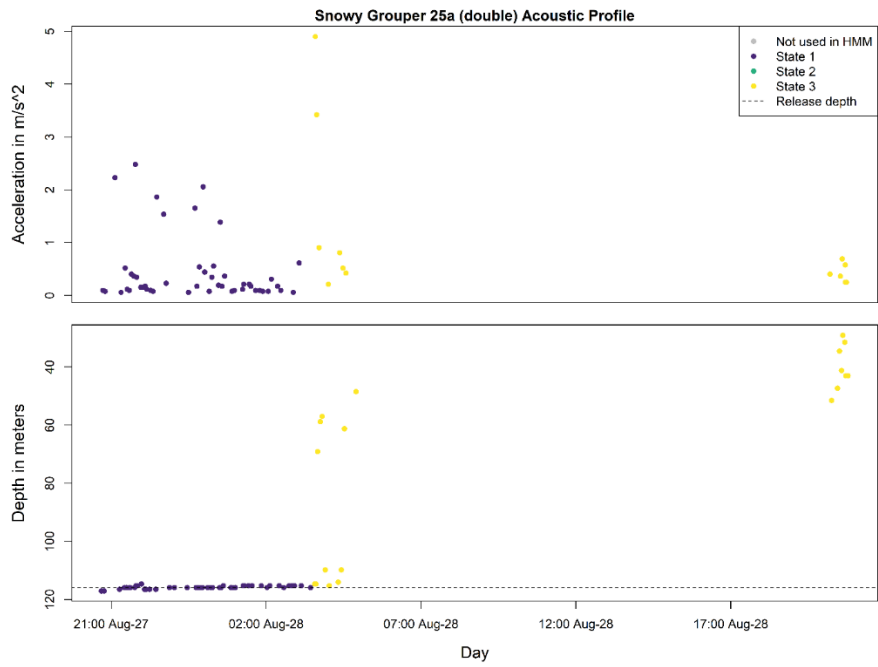
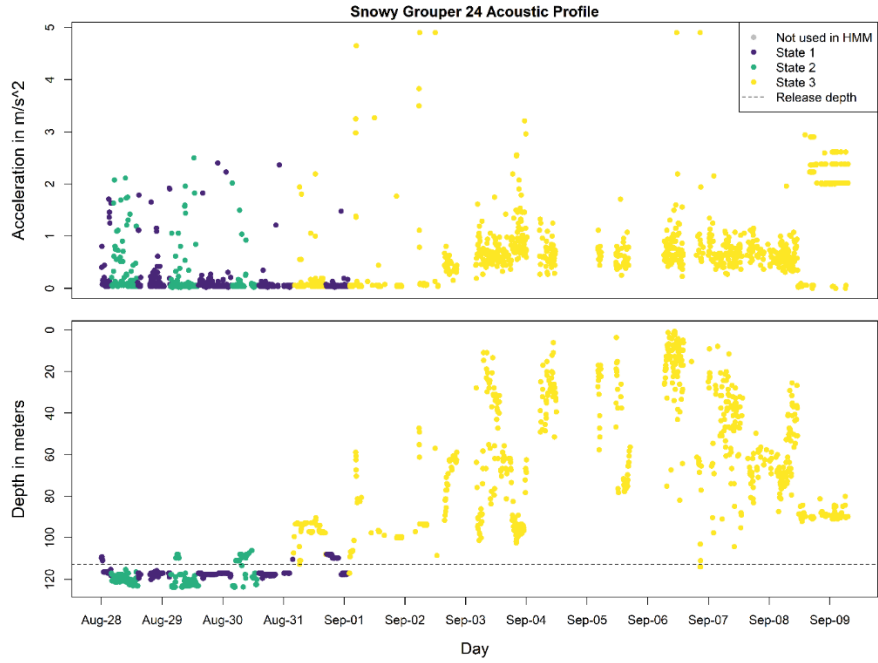


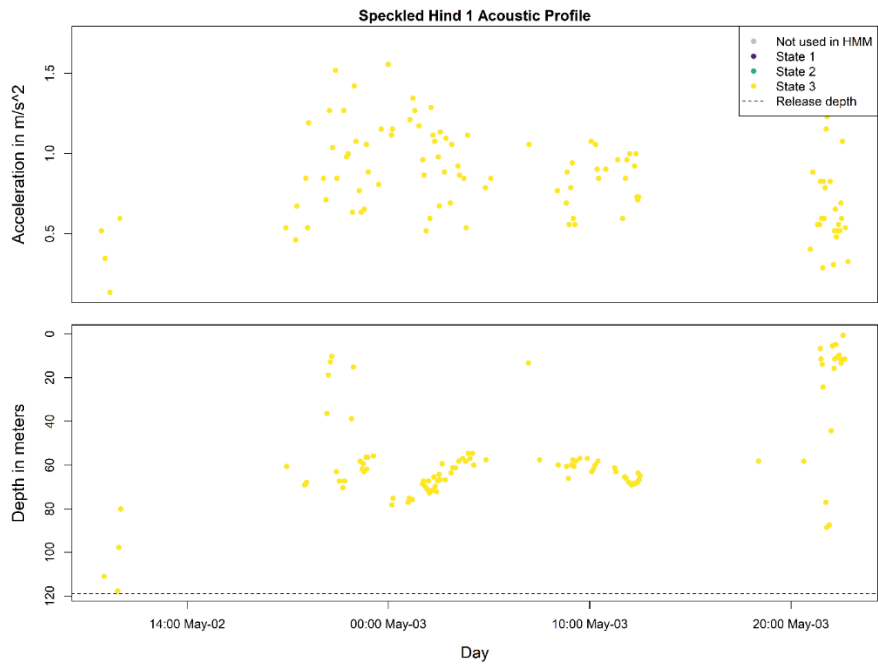
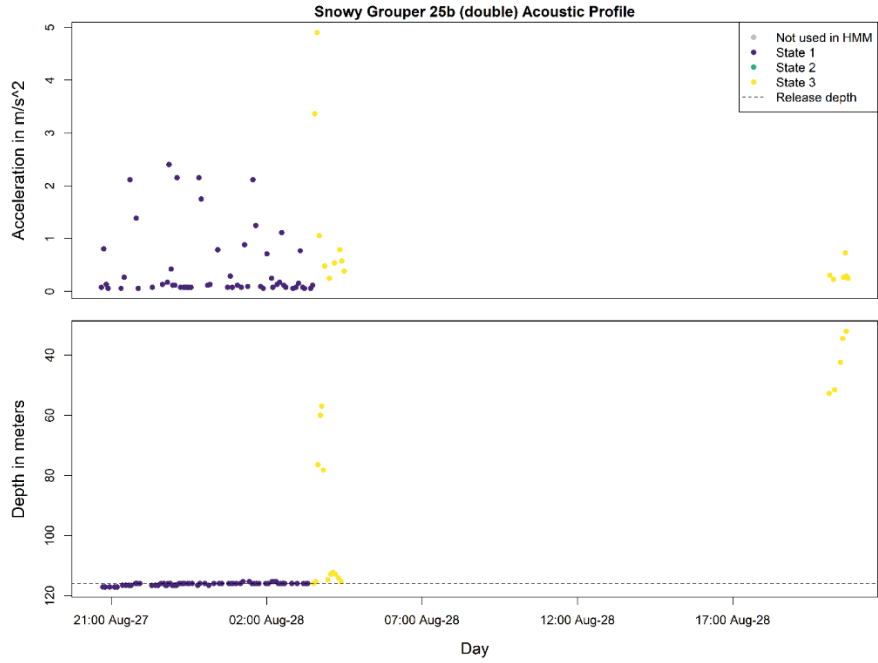


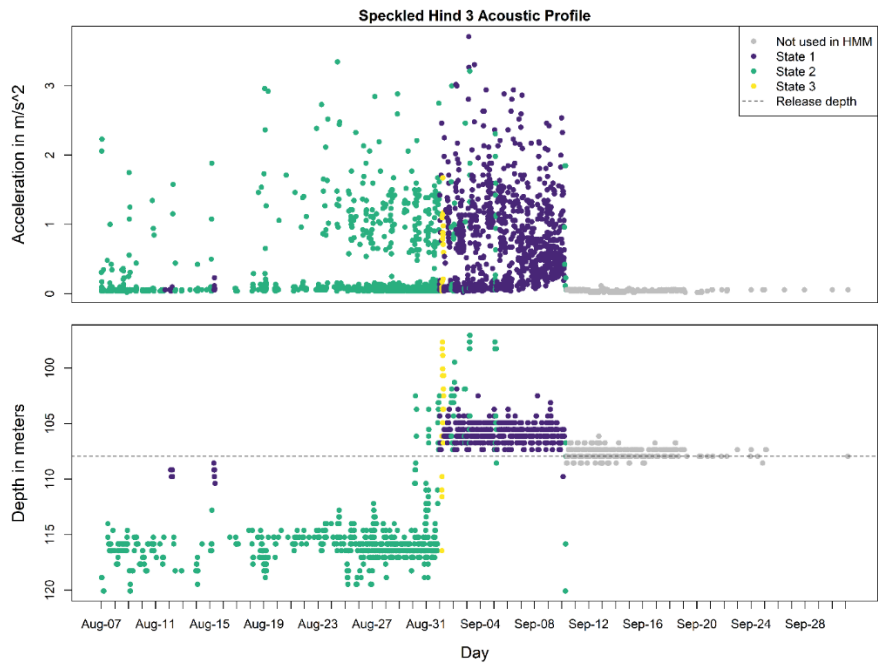
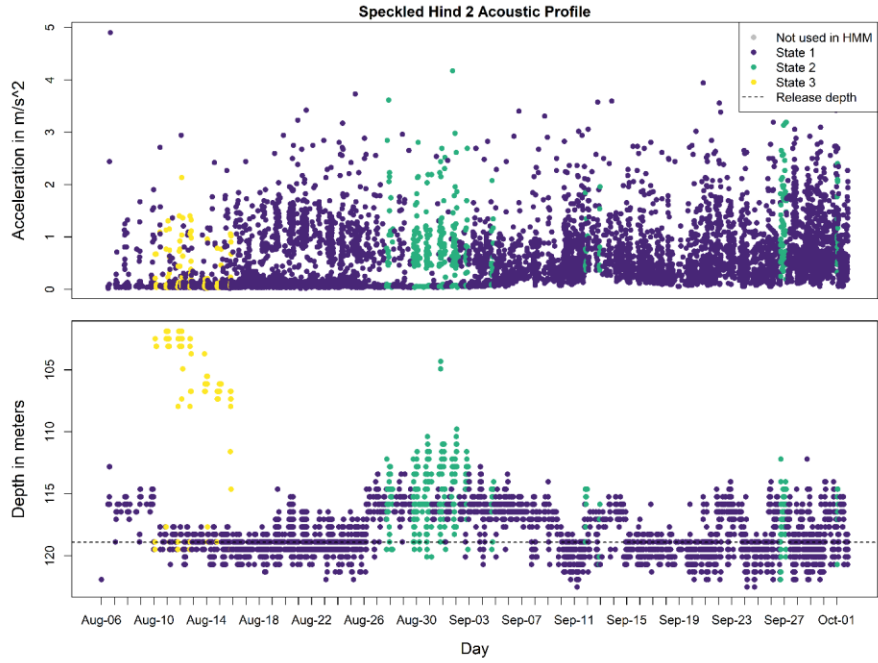


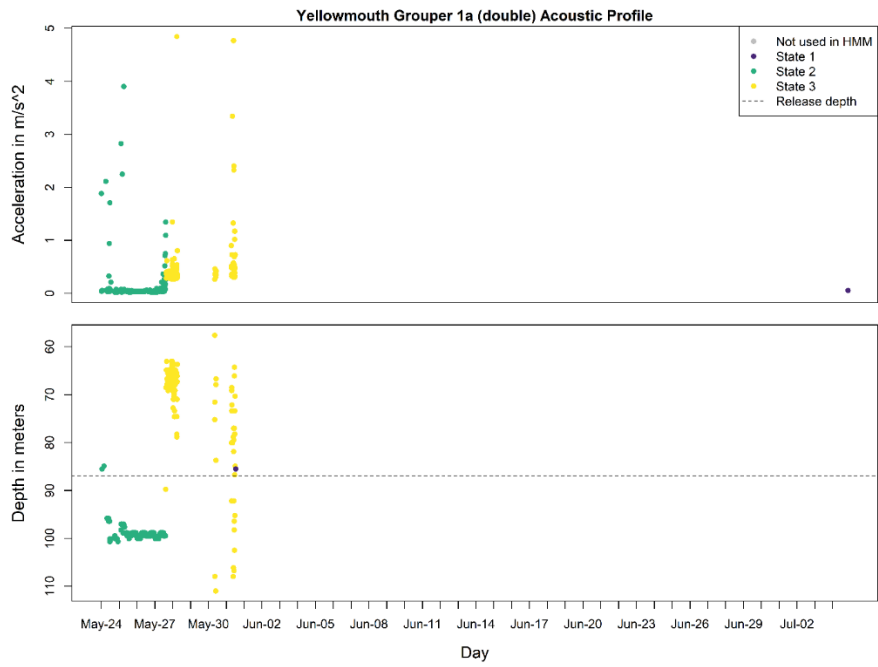
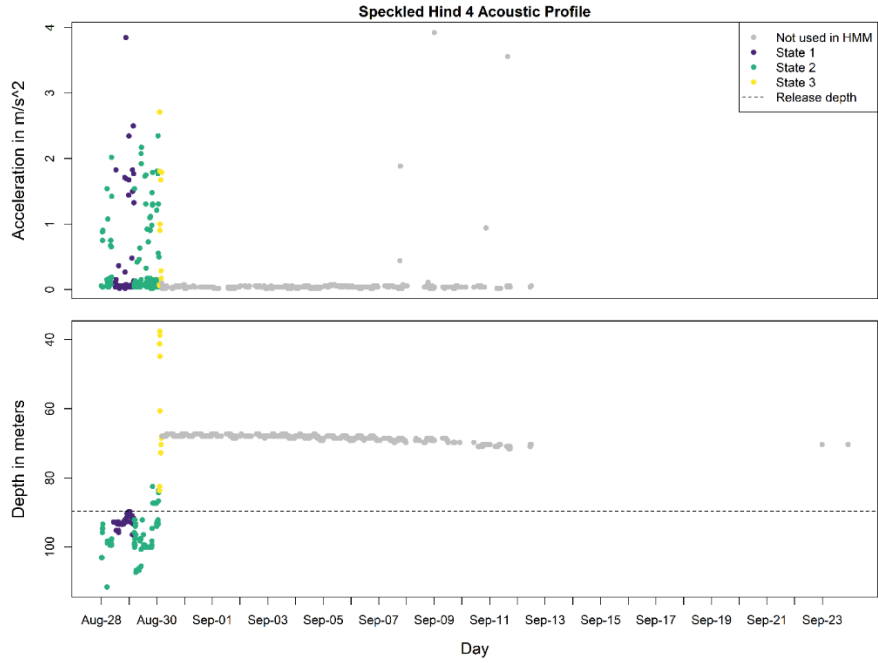


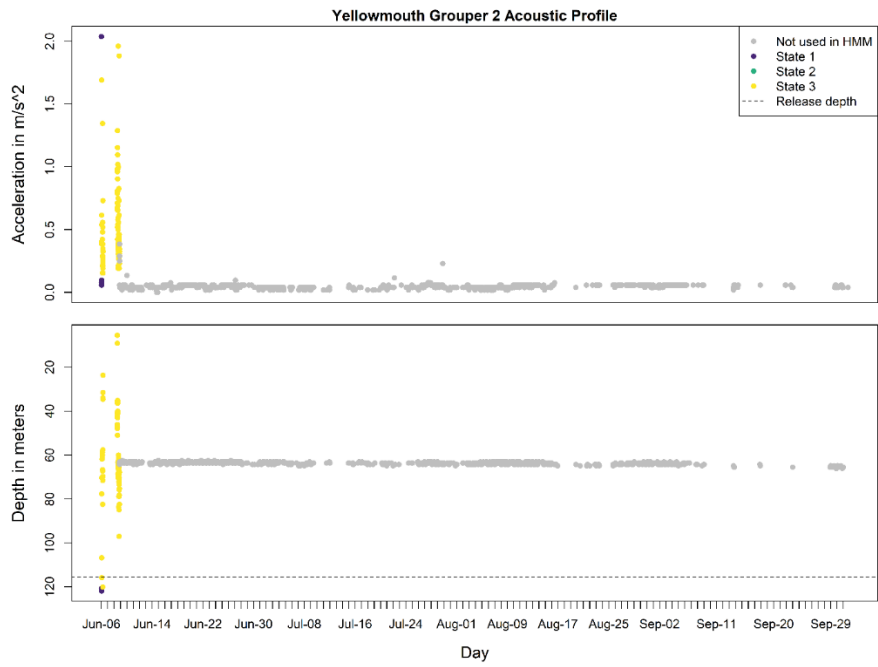
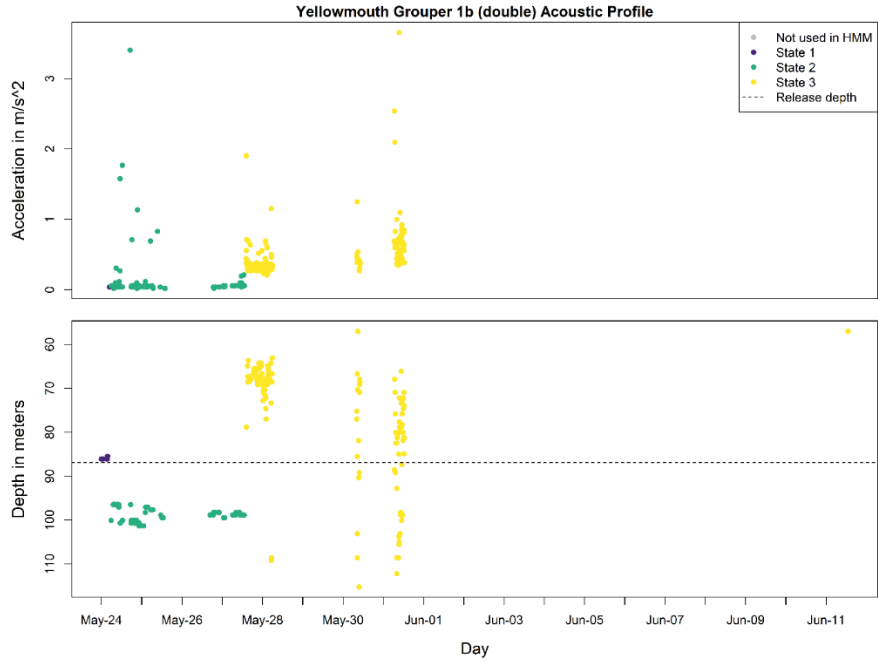












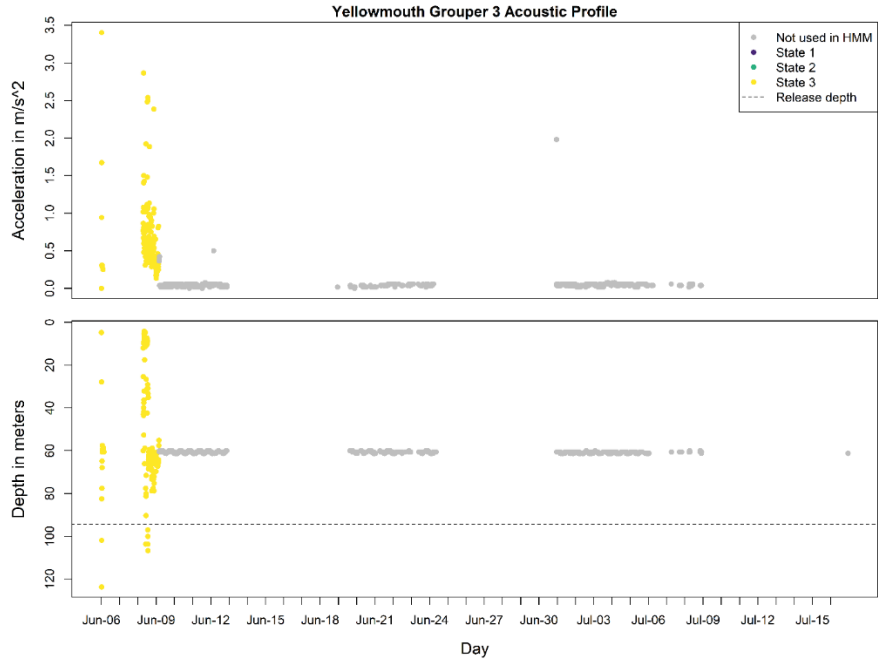


Figure S1. Acceleration and depth profiles for deepwater groupers tagged off southeastern NC in 2018.

Appendix B: Chapter 2 Supplementary Material

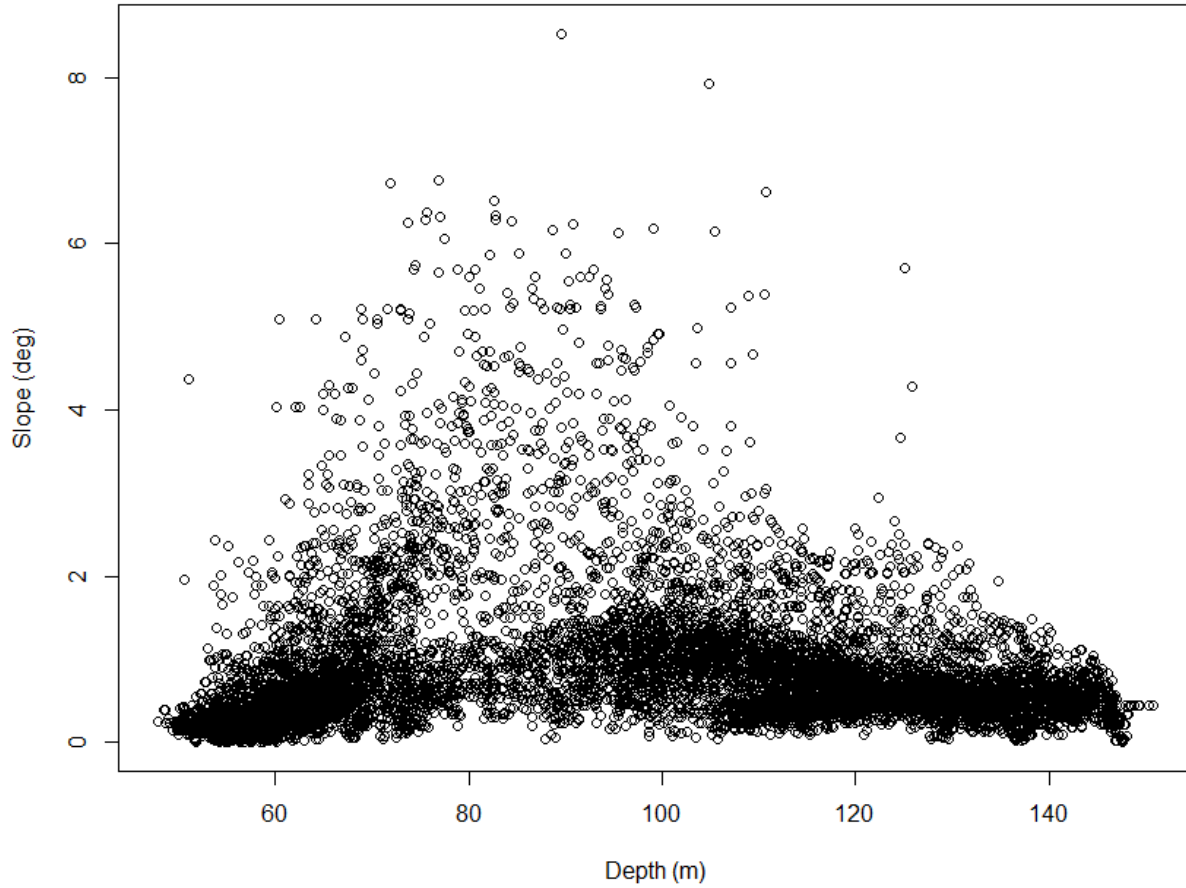


Figure S1. Mean depth (m) versus slope (degrees) for all 100 m grid cells in the sonar survey (both areas and both periods included).

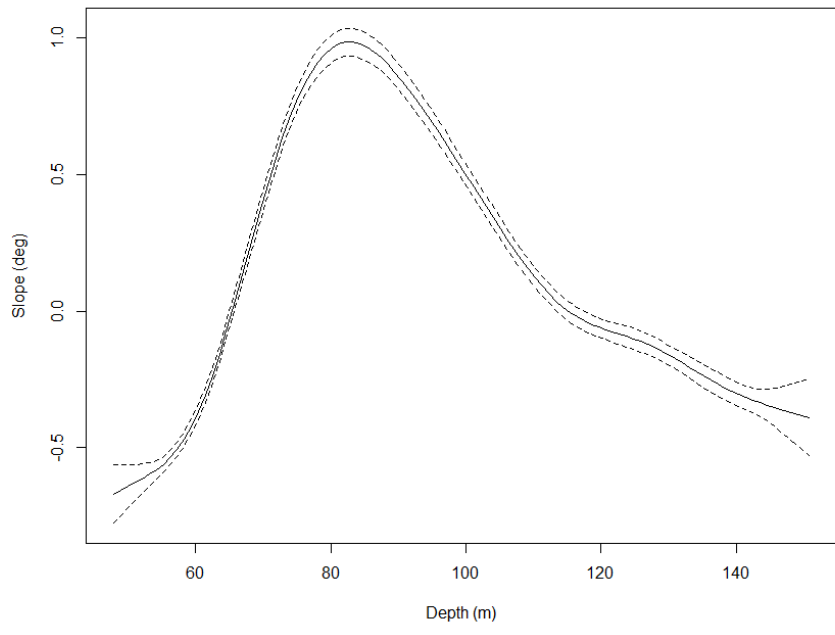


Figure S2. Results of a generalized additive model relating mean depth (m) and seafloor slope (degrees) for all 100 m grid cells in the sonar survey (both areas and both periods included).

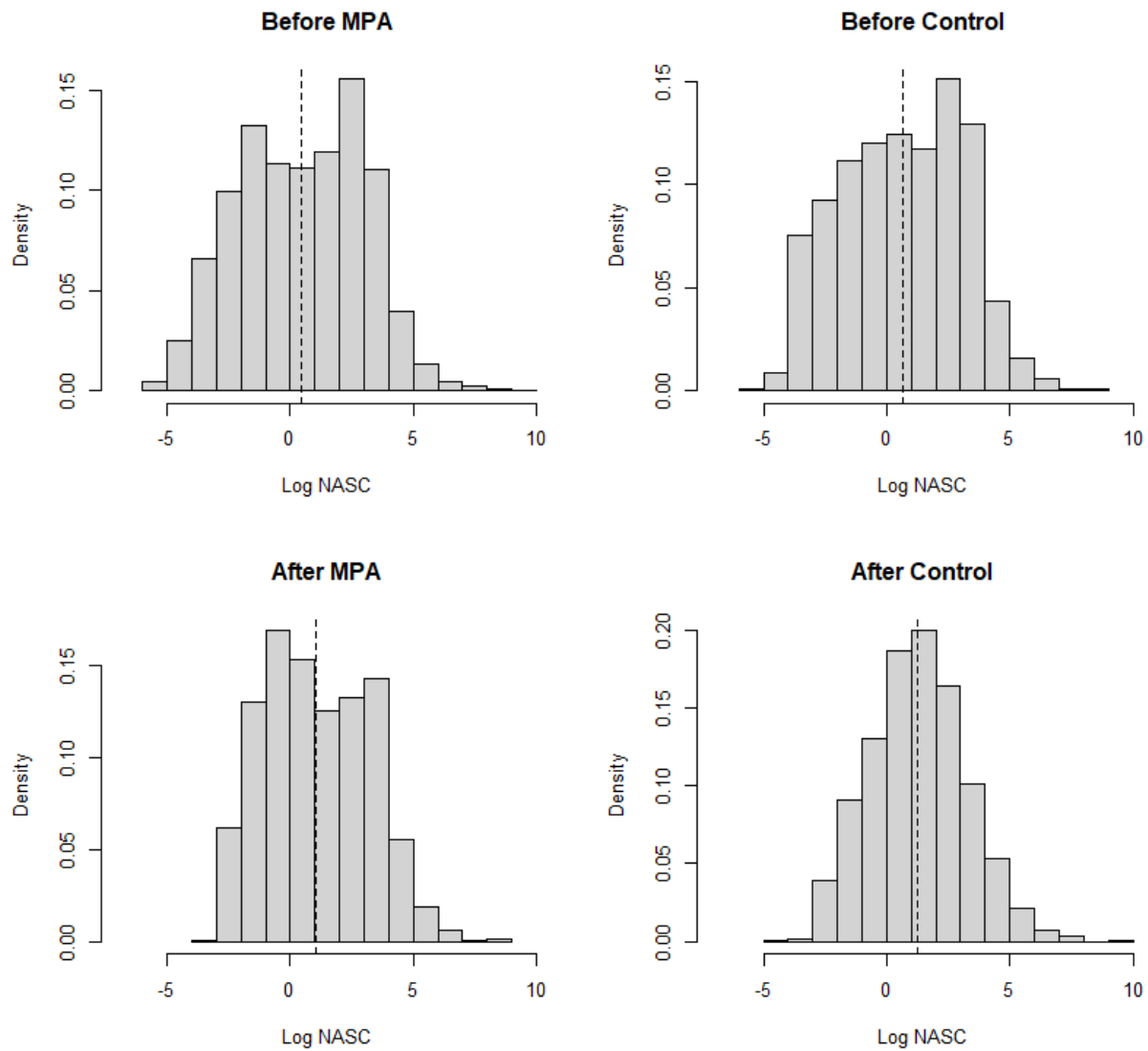


Figure S3. Distributions of the natural logarithm of all non-zero biomass observations from our sonar analysis, broken down by Area and Period. Each observation represents the total biomass volume (NASC) per 100 m grid cell. Vertical dashed lines are the mean of the distributions.

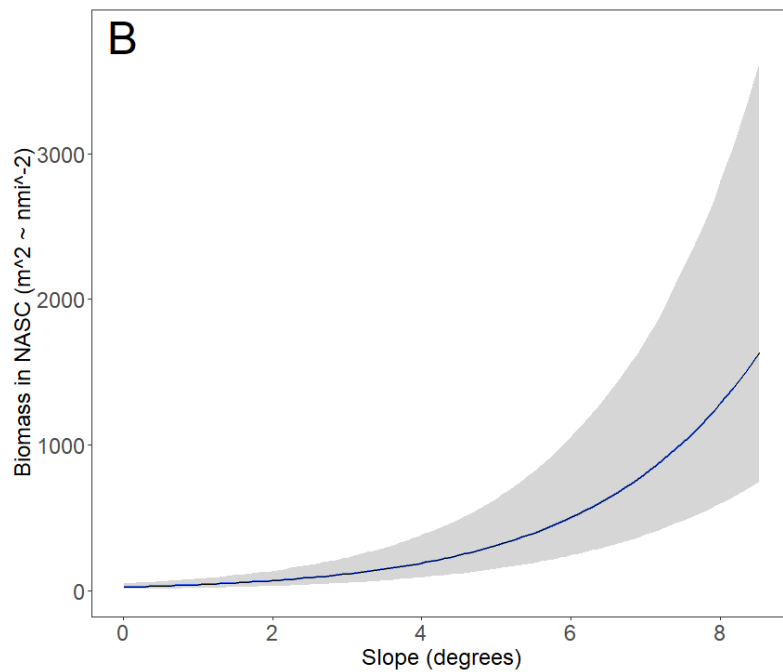
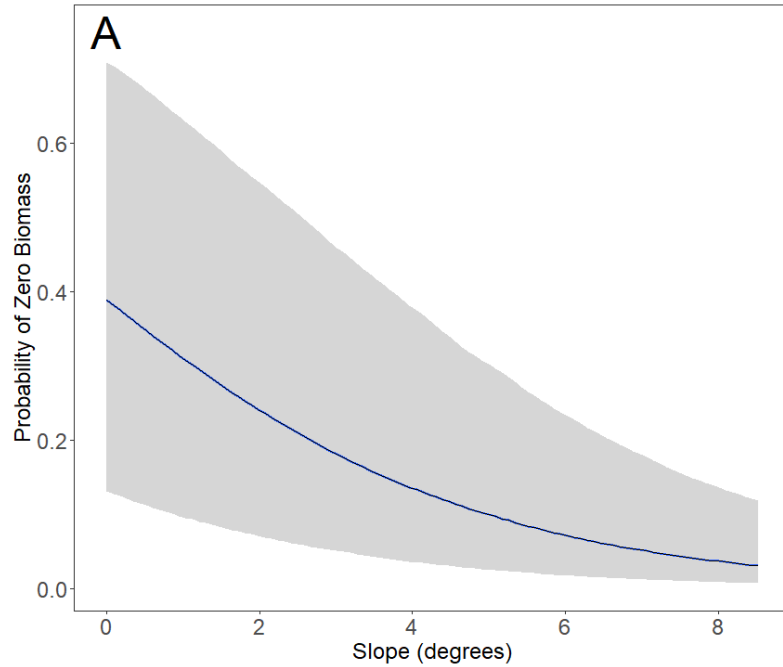


Figure S4. Marginal effect plots from the best model of biomass showing the effect of seafloor slope (degrees) on A) the probability of observing zero biomass in a given 100 m grid cell and B) the amount of biomass observed in terms of NASC (Nautical Area Scattering Coefficient; units m^2nmi^{-2}).

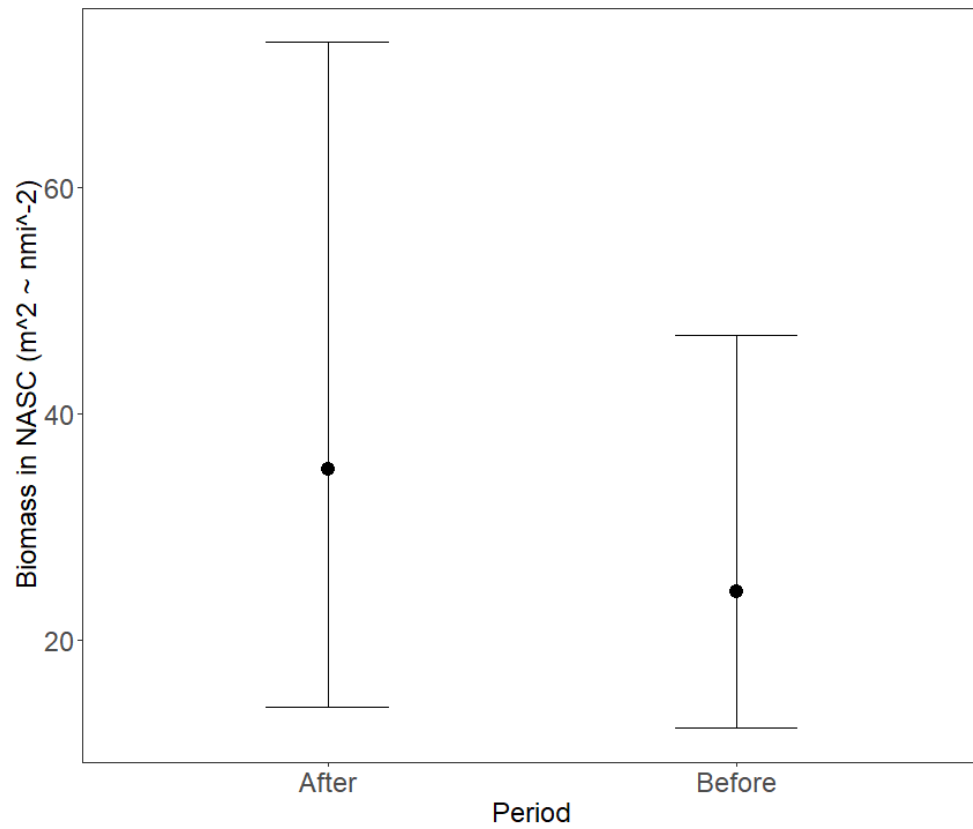


Figure S5. Marginal effect of *Period* on biomass (reported as Nautical Area Scattering Coefficient; units m^2nmi^{-2}) resulting from the best model of biomass from our sonar survey. Levels of *Period* are before (2007-2009) and after (2018-2020) the SWMPA was closed to bottom fishing.

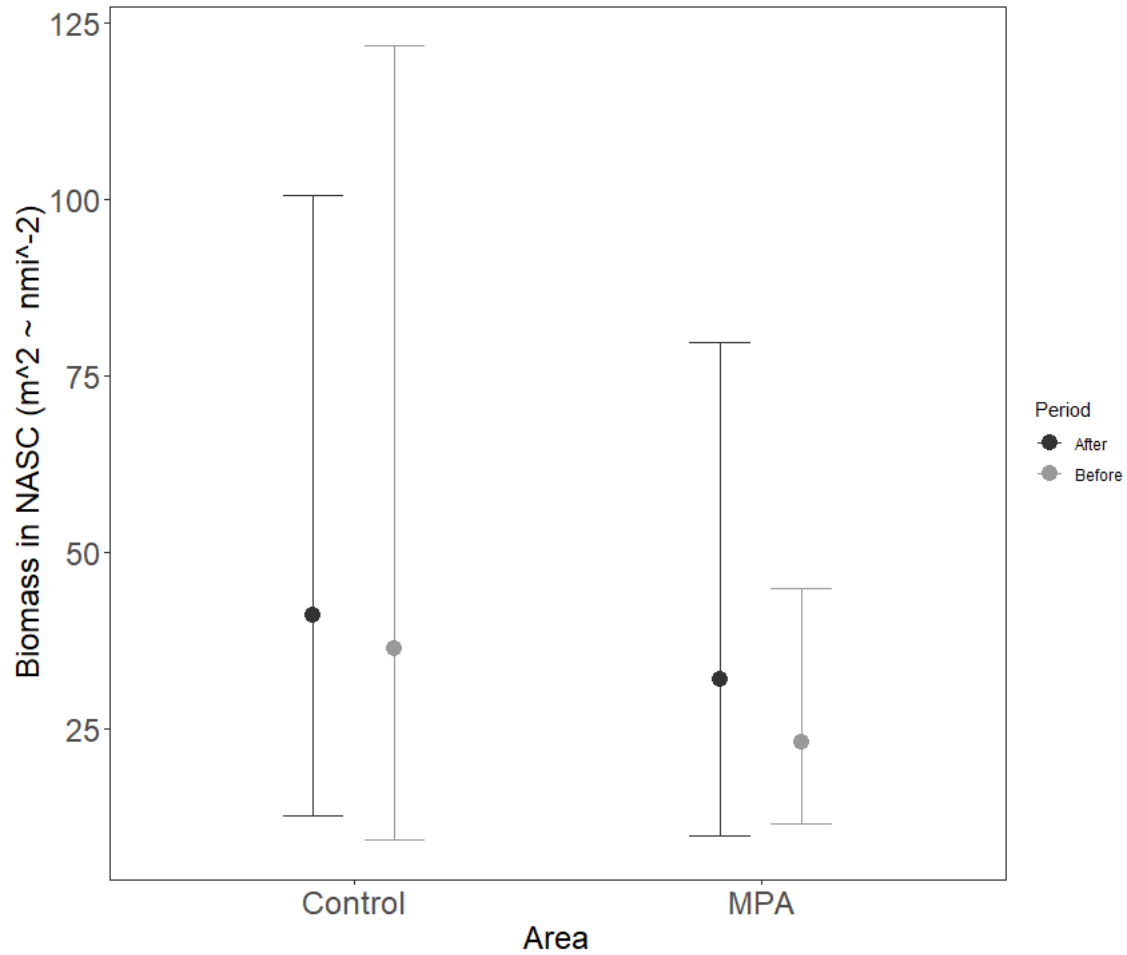


Figure S6. Conditional effect of the *Area:Period* interaction on biomass (reported as Nautical Area Scattering Coefficient; units m^2nmi^{-2}) resulting from the full model which contained all tested predictor variables. Levels of *Area* are the SWMPA and control area. Levels of *Period* are before (2007-2009) and after (2018-2020) the SWMPA was closed to bottom fishing.

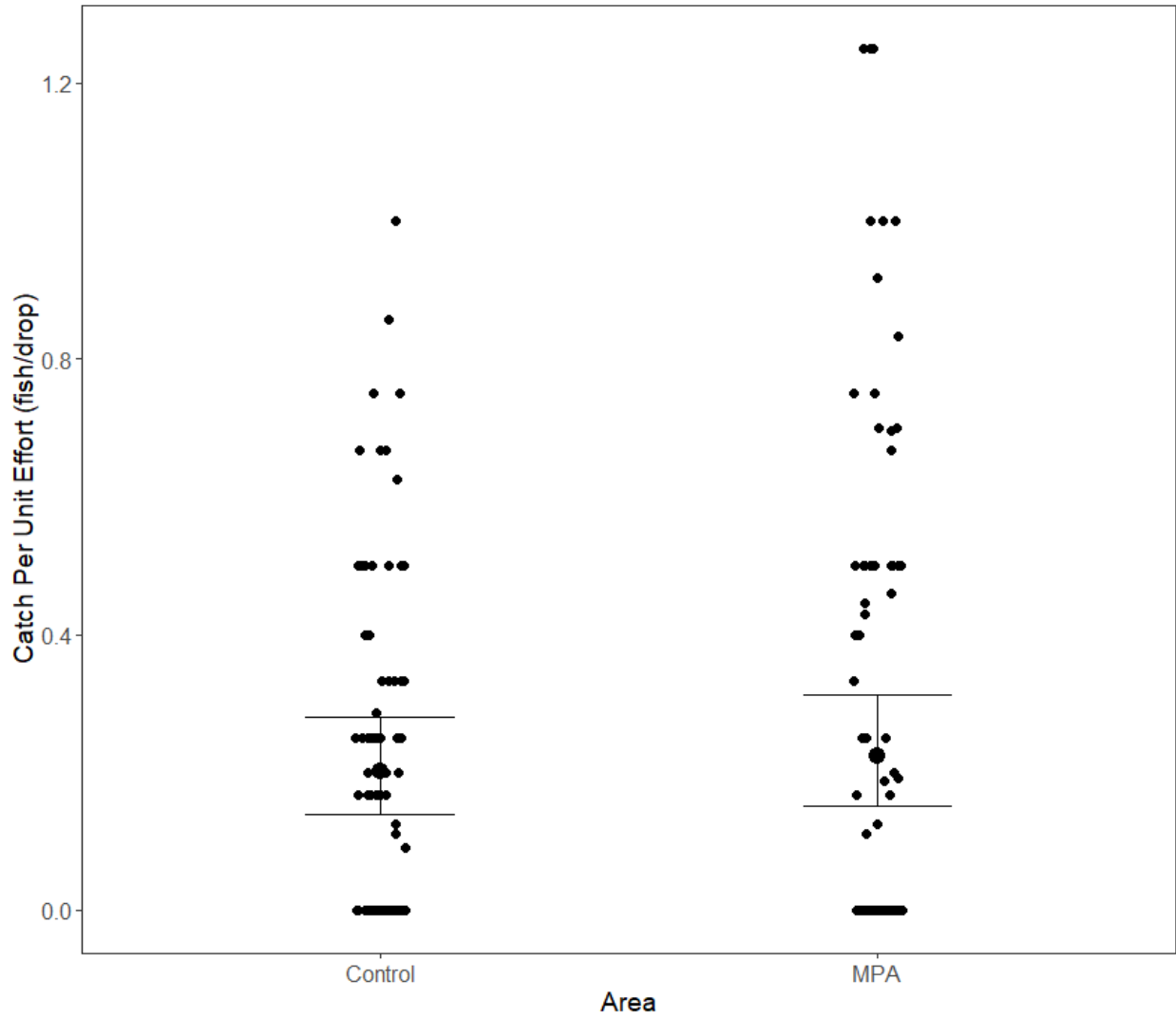


Figure S7. Marginal effects plot of the effect of Area on CPUE, from the best CPUE model selected with WAIC. Each point represents a hook-and-line sampling event, and points are adjusted with a random horizontal offset for clarity.

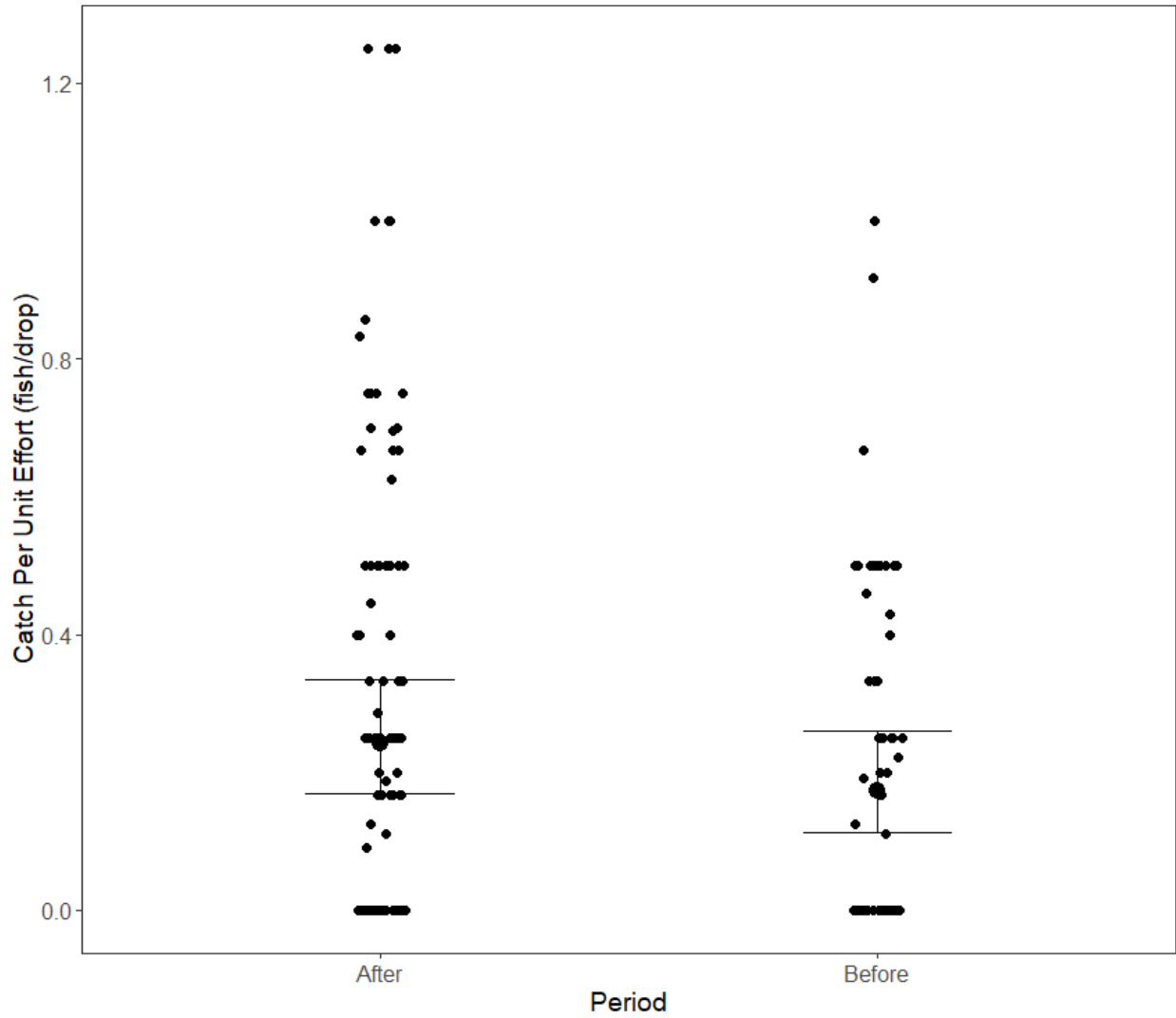


Figure S8. Marginal effects plot of the effect of Period on CPUE, from the second best CPUE model selected with WAIC. Each point represents a hook-and-line sampling event, and points are adjusted with a random horizontal offset for clarity.

Appendix C: Chapter 3 Supplementary Material

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

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