

## ABSTRACT

SIMMONS, KAYELYN REGINA. Evaluating the Efficacy of Management Zones in the Florida Keys National Marine Sanctuary: Integrative Visual and Photogrammetric Surveys, and Passive Acoustics to Characterize Reef Fish Assemblages and Habitat Associations across Coral Reef Management Regimes (Under the direction of Dr. David B. Eggleston).

Comparisons between spatial management zones and regulated fishing sites in The Florida Keys National Marine Sanctuary (FKNMS), a network of marine reserves varying in level of protection, Sanctuary Preservation Area (SPAs), Ecological Reserve (ER), and Special/Research-Use Only Areas (SUAs), allows for the exploration of fundamental questions about drivers in reef fish biodiversity across space and time, habitat complexity, and the influence of human interactions (i.e., management, tourism, recreation, fishing pressure). In 2017, category 4 Hurricane Irma directly passed over FKNMS in the lower Florida Keys resulting in heavy sedimentation and moderate to severe structural impacts to the coral reef framework. As the Florida Keys reef community endures chronic and acute stressors, resource managers require up-to-date, high-resolution data on reef fish biodiversity, coral species conditions, impact responses, and resiliency indicators to guide decision-making and prioritize actions that support resiliency. Therefore, this dissertation conducted a comprehensive study examining reef fish biodiversity and habitat associations as a function of management zone using traditional reef visual census (RVC) surveys, passive acoustic monitoring, and structure-from-motion (SfM) photogrammetry across eight shallow fore-reef sites representing three management zones in the FKNMS before, during, and after the impact of hurricane Irma between 2017 and 2018.

In Chapter 1, I investigated the acoustic energy exposure and temporal patterns in the coral reef soundscape via a high frequency band (7-20kHz) representative of snapping shrimp activity and two partitioned low frequency bands (< 3kHz) representative of reef fish

vocalizations before, during, and after hurricane Irma at fished site WDR and research-only area ESB. Temporal patterns in the coral reef soundscape by sound producing reef fish and snapping shrimp were relatively resilient to the acoustic energy exposure during the hurricane and recovered within a few weeks to pre-disturbance sound pressure levels despite experiencing detrimental damage to reef habitats and harsh environmental conditions. In Chapter 2, I characterized the spatiotemporal variation in habitat complexity and coral morphology using traditional reef visual census (RVC) surveys at eight sites and SfM photogrammetry at five sites across the FKNMS's three management zones. Digital elevation models showed high within site variation of seabed topography and physical features while orthoimage image analysis identified differences in dominant coral morphology among sites.

Building upon the previous chapters, Chapter 3 used a multidisciplinary approach combining RVC surveys and coral reef soundscapes to investigate the response of reef fish biodiversity indices (i.e., mean density, biomass, species richness, species diversity, and evenness) and its associated L1 low frequency band (<3kHz) as well as a target group, comprised of Haemulidae and Lutjanidae, indices (mean density and biomass) and their associated L2 low frequency band (1.2 – 2kHz) to habitat features (i.e., depth, vertical hard relief, surface hard relief) before and after the hurricane at eight sites across three management zones. Although total reef fish density decreased by >60% at most sites after Irma, species diversity, richness, and evenness increased during the sampling periods following the disturbance; and there were no major relationships with temporal patterns in the L1 low frequency band. However, the target group did show seasonal trends in mean L2 sound pressure levels and increases in mean biomass were more prevalent at protected sites or sites with complex reef structures (i.e., vertical hard relief, surface hard relief).

This dissertation provides baseline, fine-scale spatiotemporal reef biodiversity, habitat, and soundscape data for several spur-and -groove reef sites in the FKNMS and highlights the combined use of traditional (i.e., RVC) and novel (i.e., soundscapes, photogrammetry) monitoring methods to observe trends and habitat associations of ecologically and commercially important marine fauna in the FKNMS, and aids in evaluating the efficacy of a network of marine reserves.

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Evaluating the Efficacy of Management Zones in the Florida Keys National Marine Sanctuary:  
Integrative Visual and Photogrammetric Surveys, and Passive Acoustics to Characterize Reef  
Fish Assemblages and Habitat Associations across Coral Reef Management Regimes

by  
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## **DEDICATION**

This dissertation is dedicated to my late father Reginald Simmons, my mother Sharon LaCour, and two sisters Lyn Wilson and Tenielle Peterson in remembrance of our family vacations to the coastal beaches of South Carolina and Florida, including my life changing family vacation to St. Thomas, USVI where I taught myself how to swim. Thank you for instilling in me the joys of traveling, being courageous by standing out, and taking wild, unexpected adventures in nature. I would also like to dedicate this dissertation to all the mermaids of color, in particular to the “cocoamermaids” who are only yet to be discovered.

## BIOGRAPHY

Kayelyn Simmons was born in Atlanta, Georgia and was raised in the suburbs of Stone Mountain, Georgia. She was a “wild child” who loved the outdoors and many of her earliest memories are taking family trips to Hilton Head and Myrtle Beach, South Carolina. Her fondest childhood memory was a family vacation to hilly island of St. Thomas, US Virgin Islands. While there, she learned how to swim and remembers eating mangos every morning – a small glimpse into the island life. Throughout her adolescent, she continued to gain an affinity toward the natural environment and the many animals who thrived there, especially those animals who thrived in the ocean! She also enjoyed staying active by running track and being the shortest person on her high jump team, and she even did a couple back handsprings at the historical Georgia Dome as a cheerleader for her high school football team.

Kayelyn embarked on her undergraduate education at Historically Black College or University (HBCU) Hampton University and enrolled in a bachelor’s degree in Marine Environmental and Science at her “home by the sea”. During her undergraduate tenure, she became part of NOAA’s Living Marine Resources Cooperative Science Center (LMRCSC) program which opened the doors for research experiences for undergraduates at several institutions. She began her first internship at the Monterey Bay Aquarium Research Institute in Moss Landing, California studying the distribution of egg cases from the deep-sea worm polychaete *Tomopteris* spp. using AUV/ROV video footage. She also became open water SCUBA certified during this internship where she took her first open water dive to the cold waters of Monterey’s Metridium Fields, fields of white plume-like sea anemones. She was captivated and knew she wanted SCUBA diving to be part of her adventurous life. Her next internship took her the Florida Keys coral reefs near University of Miami’s Rosenstiel School of

Marine and Atmospheric Science where she investigated spatial and temporal patterns in the life history of the coral reef bicolor damselfish *Stegastes partitus*. This internship was pivotal in Kayelyn's interest in reef fish ecology, marine biology, and ocean conservation.

In 2011, Kayelyn graduated with her bachelors and moved to sunshine state of Florida to begin a master's program in Marine Biology at Nova Southeastern University. Her thesis on the endoparasite fauna of the invasive lionfish, *Pterois volitans/miles* allowed her dive in warmer waters all over Fort Lauderdale and the upper Florida Keys. She also participated in lionfish derbies by spreading awareness about the detrimental impacts they have on native reef fish. Her love of dissections was not only applied to her reef fish research, but she also regularly volunteered for South Florida's Marine Animal Rescue Society helping with necropsies on pygmy sperm whales *Kogia breviceps* and pilot whales *Globicephala sp.* In the latter years of her higher education, Kayelyn studied abroad down under at James Cook University furthering her education in fisheries science, conservation biology, and marine wildlife management. While there, she continued her training in capoeira, a Brazilian jiu-jitsu, enjoyed biking every day and took a chance cage-diving with eight great white sharks, *Carcharodon carcharias*, in their natural habitat off the coast of Port Lincoln, South Australia.

After completing her masters, Kayelyn embarked on her next adventure in marine research at North Carolina State University by enrolling in a PhD program for Marine, Earth, and Atmospheric Science. Her research exploring the relationship between reef fish biodiversity and coral reef habitats took her to the beautiful and tropical area of the Florida Keys National Marine Sanctuary off the coast of Key West, Florida. She put her passion for SCUBA diving and conservation research to work by teaming up with state and federal partners to answer critical questions related to restoration and marine reserve management. She even threw a "soundscape

block party” with a local DJ at a dive shop to raise awareness about hurricane impacts to reefs while boosting moral for the Key West community following the devastation of Hurricane Irma. Her favorite times top side at sea include seeing dolphins, huge loggerhead turtles, and eating slim jim in the ocean spray. Underwater, Kayelyn not only learned more about several fish species, but enhanced her understanding of the importance of the habitat created by living corals. Her research provided pivotal baseline information on coral assemblages and the coral reef soundscape using two non-invasive, novel tools to assess ecosystem recovery and resiliency for coral reefs.

Toward the end of her doctoral program, Kayelyn was awarded the prestigious National Sea Grant’s John A. Knauss Marine Policy Fellowship and began working for NOAA’s Coral Reef Conservation Program. She enjoyed collaborating with several state and federal partners aiming to bring resources to on-the-ground coral managers across all US coral jurisdictions ranging from the Marianas Islands to the US Virgin Islands via the US Coral Reef Task Force. Currently, Kayelyn is the first author on two publications and has accepted a federal position as an Oceanographer at NOAA's Atlantic Oceanographic & Meteorological Laboratory in Miami, Florida. She will lead benthic habitat characterization studies for several efforts with their Ocean Chemistry & Ecosystems Division, including the National Coral Reef Monitoring Program and the Port Everglades Dredging Expansion project. Kayelyn is excited to continue her career and passion in coral reef ecology and conservation while exploring new dive destinations in the vast ocean realm.

## ACKNOWLEDGMENTS

Thank you to my mother, Sharon LaCour, who raised me most of my life as a single parent but was still able to come support me at my cheerleading competitions and even go kayaking with me in saltwater crocodile territory. Thank you to my sisters Lyn Wilson and Tenielle Peterson who always makes me stop and appreciate all the little important things in life as well as how crazy some of my adventures actually are to non-scientists. They never know what I will do next!

Thank you to the Marine, Earth, and Atmospheric Sciences Department, as well as my lab family, the Marine Ecology and Conservation Lab: Erin Voigt, Olivia Caretti, Pat Lyon, Dan Bowling, Ian Grace, and Melissa LaCroce for all the literal blood, sweat, and beer it took conducting my field research. Special thanks to my besties in science Cindy Meyepa, Ph.D., Jacob Rudolph, and Enie Hensel, Ph.D. for supporting me with painstaking stats, lots of MATLAB coding and reviewer edits. My deepest gratitude to my committee members Dave Eggleston (NCSU/CMASST), Del Bohnenstiehl (NCSU), Kar Castillo (UNC Chapel Hill), and Jeff Buckel (NCSU/CMASST) and my long-term mentor Su Sponaugle (OSU). I also would like to thank my funding and permitting agencies for the opportunity to collaborate on such a fun and fulfilling project in the beautiful setting of Lower Florida Keys: NOAA Coral Reef Conservation Program, Office of National Marine Sanctuaries (ONMS), FL Fish & Wildlife Conservation Commission (FWCC). Moreover, I appreciate the support of Mote's Elizabeth Moore International Center for Coral Reef Research and Restoration in Summerland Key for accommodations and a grill with the best view for post-dive cookouts.

Finally, I would like to thank several individuals and groups who provided key checks and balances in my drive to success while recognizing that even a graduate student is still

human. Thank you to the NC State Black Alumni Society for providing me with financial support and scholarships for several years along with three wonderful mentors to represent people of color in the sciences. I would like to thank my cousin sports medicine professional Ryan Hubbard, M.D. and brother-in-law mechanical engineer Jamal Wilson, Ph.D. for their countless reviews of scientific papers that were not in their field, and for agreeing with me that “it is hard”. We overcame the odds. Additionally, I would love to thank my brother-in-law Deonte Peterson for all the last minute “little sister” IT support. Finally, thank you to my entire extended Smalls family in Georgia, the Carolinas and beyond, including my “A1’s since Day1” childhood best friends Kristen Ticar Woodard, Anna Marie Bennett, and Brittini Johnson for their immense social media support, reality checks, and encouragement.

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## DISSERTATION INTRODUCTION

Coral reefs support about one-third of the world's marine fish populations and are vital for global economic and ecological services (1). Global pressures on coral reefs extend to marine resource overexploitation, sediment runoff, coastal development, climate change, and chronic tourism activities (2–4). Consequently, direct and indirect effects of climatic and anthropogenic stressors are key causes for large-scale declines in the biodiversity of coral reef ecosystems and their resilience to multiple stressors (5–8; and references therein). In the absence of anthropogenic stressors, coral reefs can restore to natural health conditions following episodic environmental events (i.e., hurricanes) that cause major fluctuations in coral communities (9–11). However, as these combined threats to coral reefs and associated ecosystems (i.e., coastlines, mangroves, seagrass beds) increase, management action is necessary to better understand and monitor coral reef resiliency, and discern which factors support the ecosystem's ability to absorb chronic disturbances, resist phase shifts and recover after natural and human-induced disturbances (5,12,13).

Modern coral reef management objectives have shifted beyond achieving sustainability for individual target species to broader impacts related to community interactions and food web dynamics (14–16). Maintaining ecosystem function across multiple spatial scales also requires managers to first detect changes in a time-effective manner and then to adequately intervene (i.e., implement closures, habitat restoration) at relevant spatial scales, such as the organism level to community level, with the goal to further protect the current and future status and/or resilience of reef ecosystem functions (17–20). No-take marine reserves (NTMRs) were established to both decrease the exploitation of target and non-target species and rebuild depleted stocks, while protecting the integrity of biodiversity within marine ecosystems (21–24). Since first establishing

NTMRs, they have produced several potential benefits such as increasing target fish species density, increasing spawning stock biomass, supplying source populations for neighboring habitats (i.e., spill-over), preserving trophic interactions and protecting essential reef habitat from structural damage (25–29). Generally, species diversity is enhanced inside marine reserves (26), yet the variable processes that influence diversity within and around reserves still needs further investigation (28).

New technological approaches in marine ecology, such as (i) passive acoustics to characterize underwater soundscapes, and (ii) habitat photogrammetry, which provides high-resolution, 3D images of habitats, can facilitate efficient and accurate assessments of coral reefs across varying spatial and temporal scales, providing a transformative way to characterize reef fish biodiversity as well as the ecological function of essential, hard-bottom habitats. The Florida Keys National Marine Sanctuary (FKNMS) is an ideal network of marine protected areas and fished areas to characterize coral reef soundscapes, in addition to furthering our understanding of how soundscapes reflect changes in reef fish distribution and habitat use.

Coral reef soundscape results generally show significant site-specific spectral patterns in sound pressure levels (SPLs), such that protected sites displayed higher average spectra in low frequencies than fished sites (30–33). Given that passive acoustic monitoring is a non-destructive sampling tool when compared to traditional sampling (visual surveys, gill nets, traps), soundscape monitoring is a relatively low-cost tool that can be implemented with high spatial and temporal fidelity even at night and in adverse weather conditions. Previous soundscape research conducted in the Florida Keys characterized ambient reef sounds and observed spatial and temporal acoustic patterns, creating a baseline for understanding reef soundscapes in this region (34). If metrics characterizing the soundscape reflect species composition and diversity, or

habitat complexity, this approach could provide an important and transformative tool for understanding the efficacy of the various management zones in the FKNMS, as well as coral reef resiliency.

The spur-and-groove coral reef habitats in the lower Florida Keys, for example, are subject to multiple impacts to the overall structural framework and have been under pressure, over both space and time, by (i) anthropogenic stressors (i.e., fishing pressure, recreational use, dredging/port expansion), (ii) direct impacts from severe climatic disturbances (e.g., Hurricane Irma in 2017), and (iii) the rapid expansion of highly detrimental stony coral tissue loss disease (SCTLD) (35–38). Additionally, more fine-scale questions aimed at identifying within-site variations in structural complexity (i.e., relief, rugosity, depth) and diversity in reef-building corals also provides insight into habitat selection for reef fish aggregations, spawning sites, and foraging activity. The use of *in-situ* photogrammetry surveys to produce 3D elevation and photomosaic models is an emerging and important conservation and restoration monitoring tool (39–42). Moreover, photogrammetry aids in characterizing and documenting differences in coral composition that contribute to the overall reef framework and how habitat quality can vary across a network of management zones.

In this collaborative study with the Florida Fish and Wildlife Conservation Commission (FWCC) and NOAA Office of National Marine Sanctuaries (ONMS), this dissertation builds on previous work across the FKNMS to evaluate the efficacy of a network of reserves (~0.5 – 30 km<sup>2</sup>) varying in size and level of protection (43–46) by quantifying reef fish density, diversity, and size across a range of management zones from highly fished to research only, with an emphasis on three objectives: (i) characterize the biological soundscape reef fish and snapping shrimp sound production at each reef site using passive acoustic monitoring, (ii) quantify biotic

(e.g., % live coral cover, dominant coral morphologies) and abiotic (e.g., vertical relief, depth, vector terrain ruggedness) characteristics of reefs using structure-from-motion photogrammetry, and (iii) quantify reef fish species composition, density, size, and habitat associations among the various management zones (fished, no-take but with public access, no-take and no public access) in the lower FKNMS (i.e., Zone D of the FKNMS) using a two-stage, point count survey method by divers (45,47,48).

Collectively, these multidisciplinary objectives were addressed in the following dissertation chapters using data collected from several shallow fore-reef sites within the FKNMS from 2017-2018. In September 2017, Hurricane Irma (Category 4) traveled directly across the lower Florida Keys with sustained hurricane force winds ( $> 64$ kts) making landfall near Cudjoe Key, Florida approximately 15 km away from this study's most northern reef site Looe Key (49,50). In Chapter 1, this dissertation focused on passive acoustic data collected before, during, and after Hurricane Irma at two spur-and-groove sites, Western Dry Rocks (WDR) a fished site, and a special-use-only area named Eastern Sambo (ESB). We observed changes in temporal patterns in sound pressure levels (SPLs) produced by snapping shrimp in the high-frequency band (7–20 kHz) during crepuscular hours, and daily daytime reef fish sound production in the low-frequency band ( $< 2$  kHz) to better understand how changes in the biophony or biological soundscape reflect patterns of resilience and recovery. Chapter 2 characterized spatiotemporal variation of several habitat metrics at eight fore-reef sites using visual habitat surveys and further investigated fine-scale abiotic and biotic structural features using structure-from-motion photogrammetry and three-dimensional models at five mapped reef sites representative of each management zone type in the FKNMS. Finally, Chapter 3 explored the response of reef fish biodiversity indicators (i.e., density, biomass, diversity, evenness) and associated low-frequency

SPLs according to sample location, time of sampling, reef habitat characteristics from data collected using passive acoustics and reef visual census (RVC) surveys.

In each chapter, the special sanctuary areas (SUA's, SPA's, ER's etc.) and fishing zones in nearby geographical areas will serve as experimental treatments. Reef fish and soundscape metrics will serve as response variables, and habitat characteristics and abiotic measures as explanatory variables. The collection of biological, habitat and environmental data provides a framework for addressing a diverse array of scientific questions and management goals, and further informs policy makers engaged in the design of marine reserve networks. These data provide critical baseline evaluations for Post- Hurricane Irma impacts and may assist in monitoring the recovery of coral reefs as well as provide examples of long-term monitoring methods useful at multiple spatial and temporal scales.

## REFERENCES

1. Reaka-Kudla ML. Biodiversity II: Understanding and Protecting Our Biological Resources. In: Reaka-Kudla ML, Wilson DE, Wilson EO, editors. Washington D.C.: Joseph Henry Press; 1996 [cited 2022 Sep 7]. p. 1454–7. Available from: <https://books.google.com/books?hl=en&lr=&id=-X5OAgAAQBAJ&oi=fnd&pg=PR1&ots=f3VjqE5Ybw&sig=9YNC2yHELJ1ziOm-49yniNfelhA#v=onepage&q&f=false>
2. Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, et al. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* (1979) [Internet]. 2001 Jul 27 [cited 2022 Sep 7];293(5530):629–37. Available from: <https://www.science.org/doi/10.1126/science.1059199>
2. Fabricius KE. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Pollut Bull.* 2005 Feb 1;50(2):125–46.
4. Halpern BS, Walbridge S, Selkoe KA, Kappel C v., Micheli F, D’Agrosa C, et al. A global map of human impact on marine ecosystems. *Science* (1979) [Internet]. 2008 Feb 15 [cited 2022 Sep 7];319(5865):948–52. Available from: <https://www.science.org/doi/10.1126/science.1149345>
5. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, et al. Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* (1979) [Internet]. 2003 Aug 15 [cited 2022 Sep 7];301(5635):929–33. Available from: <https://www.science.org/doi/10.1126/science.1085046>
6. Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, et al. Are U.S. coral reefs on the slippery slope to slime? Vol. 307, *Science*. 2005. p. 1725–6.
7. Bozec YM, O’Farrell S, Bruggemann JH, Luckhurst BE, Mumby PJ. Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proc Natl Acad Sci U S A* [Internet]. 2016 Apr 19 [cited 2022 Sep 7];113(16):4536–41. Available from: <https://www.pnas.org/doi/abs/10.1073/pnas.1601529113>
8. Zaneveld JR, Burkepille DE, Shantz AA, Pritchard CE, McMinds R, Payet JP, et al. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun* [Internet]. 2016 Sep 7 [cited 2019 Jun 13];7(1):11833. Available from: <http://www.nature.com/articles/ncomms11833>
9. Brown BE. Disturbances to Reefs in Recent Times. In: Birkeland C, editor. *Life and Death of Coral Reefs*. New York NY: Chapman and Hall; 1997.

10. Bruno JF, Selig ER. Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLoS One* [Internet]. 2007 Aug 8 [cited 2022 Sep 7];2(8):e711. Available from: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0000711>
11. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. Coral reefs under rapid climate change and ocean acidification. *Science* (1979). 2007;318(5857):1737–42.
12. Nyström M, Folke C, Moberg F. Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol*. 2000 Oct 1;15(10):413–7.
13. Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, et al. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology*. 2007 Feb 20;17(4):360–5.
14. Pauly D, Froese R, Palomares ML. Fishing Down Aquatic Food Webs: Industrial fishing over the past half-century has noticeably depleted the topmost links in aquatic food chains. *Am Sci*. 2000;88(1):46–51.
15. Walters CJ, Martell JD. *Fisheries Ecology & Management* [Internet]. Princeton, New Jersey: Princeton University Press; 2004 [cited 2022 Sep 7]. Available from: [https://scholar.google.com/scholar?hl=en&as\\_sdt=0%2C10&q=Fisheries+Ecology+%26+Management.+Princeton+University+Press.+&btnG=](https://scholar.google.com/scholar?hl=en&as_sdt=0%2C10&q=Fisheries+Ecology+%26+Management.+Princeton+University+Press.+&btnG=)
16. Levin PS, Fogarty MJ, Murawski SA, Fluharty D. Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean. *PLoS Biol* [Internet]. 2009 Jan [cited 2022 Sep 7];7(1):e1000014. Available from: <https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1000014>
17. Nyström M, Folke C. Spatial resilience of coral reefs. *Ecosystems*. 2001;4(5):406–17.
18. Aston EA, Williams GJ, Green JAM, Davies AJ, Wedding LM, Gove JM, et al. Scale-dependent spatial patterns in benthic communities around a tropical island seascape. *Ecography* [Internet]. 2019 Mar 1 [cited 2020 May 16];42(3):578–90. Available from: <http://doi.wiley.com/10.1111/ecog.04097>
19. Hughes TP, Kerry JT, Connolly SR. Ecological memory modifies the cumulative impact of recurrent climate extremes. *Bioscience* [Internet]. 2020 [cited 2021 Nov 28];70(10):854–70. Available from: <https://doi.org/10.1038/s41558-018-0351-2>
20. Lustic C, Maxwell K, Bartels E, Reckenbeil B, Utset E, Schopmeyer S, et al. The impacts of competitive interactions on coral colonies after transplantation: A multispecies experiment from the Florida Keys, US. *Bull Mar Sci*. 2020 Mar 6;

21. Roberts CM, Polunin NVC. Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* 1991 1:1 [Internet]. 1991 Sep [cited 2022 Sep 7];1(1):65–91. Available from: <https://link.springer.com/article/10.1007/BF00042662>
22. Bohnsack JA,, Ault JS. Management strategies to conserve marine biodiversity. *Oceanography* [Internet]. 1996 [cited 2022 Aug 16];9(1):73–82. Available from: <https://www.jstor.org/stable/43925544>
23. Allison GW, Lubchenco J, Carr MH. Marine reserves are necessary but not sufficient for marine conservation [Internet]. Vol. 8, *Ecological Applications*. 1998 [cited 2022 Aug 16]. Available from: [https://doi.org/10.1890/1051-0761\(1998\)8\[S79:MRANBN\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)8[S79:MRANBN]2.0.CO;2)
24. Lubchenco J, Palumbi S, SD Gaines. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* [Internet]. 2003 [cited 2022 Aug 16];13(1):S3–7. Available from: <https://www.jstor.org/stable/3099993>
25. Côté I, Mosqueira I, biology JRJ of F, 2001 undefined. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Wiley Online Library* [Internet]. 2001 [cited 2022 Sep 7];178–89. Available from: [https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1095-8649.2001.tb01385.x?casa\\_token=yVGooyLfwWcAAAAA:3jUSHXB15IUMx-I\\_CkgnHfQpl5JzmPYJ\\_eDlm8Q\\_DUUn1U4zF7LyCDVzW2zrG992HQAkSqKpNt-is2g](https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1095-8649.2001.tb01385.x?casa_token=yVGooyLfwWcAAAAA:3jUSHXB15IUMx-I_CkgnHfQpl5JzmPYJ_eDlm8Q_DUUn1U4zF7LyCDVzW2zrG992HQAkSqKpNt-is2g)
26. Halpern BS. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* [Internet]. 2003 [cited 2022 Aug 16];13(1):117–37. Available from: <http://www.wcmc.org.uk:80/marine/data/>
27. Sale PF. Connectivity, recruitment variation, and the structure of reef fish communities. In: *Integrative and Comparative Biology* [Internet]. 2004. p. 390–9. Available from: <https://academic.oup.com/icb/article/44/5/390/799582>
28. Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, et al. Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol*. 2005 Feb 1;20(2):74–80.
29. Gårdmark A, Jonzén N, Mangel M. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *Journal of Applied Ecology* [Internet]. 2006 Feb 1 [cited 2022 Sep 7];43(1):61–9. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2664.2005.01104.x>
30. Radford C, Stanley J, Tindle C, Montgomery J, Jeffs A. Localised coastal habitats have distinct underwater sound signatures. *Mar Ecol Prog Ser* [Internet]. 2010

Feb 22 [cited 2020 May 12];401:21–9. Available from: <http://www.int-res.com/abstracts/meps/v401/p21-29/>

31. Nedelec SL, Simpson SD, Holderied M, Radford AN, Lecellier G, Radford C, et al. Soundscapes and living communities in coral reefs: Temporal and spatial variation. *Mar Ecol Prog Ser.* 2015;524.
32. Bertucci F, Parmentier E, Lecellier G, Hawkins AD, Lecchini D. Acoustic indices provide information on the status of coral reefs: An example from Moorea Island in the South Pacific. *Sci Rep [Internet].* 2016 Sep 15 [cited 2020 Aug 30];6(1):1–9. Available from: [www.nature.com/scientificreports/](http://www.nature.com/scientificreports/)
33. Freeman LA, Freeman SE. Rapidly obtained ecosystem indicators from coral reef soundscapes. *Mar Ecol Prog Ser.* 2016 Dec 15;561:69–82.
34. Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D’Alessandro EK. Celestial patterns in marine soundscapes. *Mar Ecol Prog Ser.* 2014 Aug 4;508:17–32.
35. Precht WF, Gintert BE, Robbart ML, Fura R, van Woesik R. Unprecedented Disease-Related Coral Mortality in Southeastern Florida. *Sci Rep [Internet].* 2016 [cited 2021 Nov 28];6:31374. Available from: [www.nature.com/scientificreports/](http://www.nature.com/scientificreports/)
36. Walton CJ, Hayes NK, Gilliam DS. Impacts of a regional, multi-year, multi-species coral disease outbreak in Southeast Florida. *Front Mar Sci.* 2018 Sep 13;5(SEP):323.
37. Aeby GS, Ushijima B, Campbell JE, Jones S, Williams GJ, Meyer JL, et al. Pathogenesis of a Tissue Loss Disease Affecting Multiple Species of Corals Along the Florida Reef Tract. *Front Mar Sci.* 2019 Nov 1;6.
38. Muller EM, Sartor C, Alcaraz NI, van Woesik R. Spatial Epidemiology of the Stony-Coral-Tissue-Loss Disease in Florida. *Front Mar Sci.* 2020;7(March).
39. Burns J, Delparte D, Gates R, Takabayashi M. Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ.* 2015;
40. Ferrari R, McKinnon D, He H, Smith RN, Corke P, González-Rivero M, et al. Quantifying multiscale habitat structural complexity: A cost-effective framework for underwater 3D modelling. *Remote Sens (Basel) [Internet].* 2016 Feb 1 [cited 2021 May 10];8(2):113. Available from: <https://doi.org>
41. Fukunaga A, Burns JHR, Craig BK, Kosaki RK. Integrating three-dimensional benthic habitat characterization techniques into ecological monitoring of coral

- reefs. *J Mar Sci Eng* [Internet]. 2019 [cited 2019 Aug 18];7(2). Available from: <https://www.mdpi.com/2077-1312/7/2/27>
42. Fukunaga A, Burns JHR, Pascoe KH, Kosaki RK. Associations between benthic cover and habitat complexity metrics obtained from 3D reconstruction of coral reefs at different resolutions. *Remote Sens* (Basel). 2020;12(6).
  43. NOAA, ONMS (Office of National Marine Sanctuary), Florida Keys National Marine Sanctuary. Florida Keys National Marine Sanctuary Revised Management Plan. 2007.
  44. Bartholomew A, Bohnsack JA, Smith SG, Ault JS, Harper DE, McClellan DB. Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. *Landsc Ecol*. 2008 Jan;23(SUPPL. 1):55–65.
  45. Brandt M, Zurcher N, Acosta A, Ault JS. A cooperative multi-agency reef fish monitoring protocol for the Florida Keys coral reef ecosystem Interest on Ecosystem based management View project Nutrient addition and herbivore exclusion controlling the growth of *Dictyota* spp. View project [Internet]. 2009. Available from: <https://www.researchgate.net/publication/265682772>
  46. Medina M, Estes C, Best B, Stallings C, Montes E, McEachron L, et al. Reef-Fish Abundance, Biomass, and Biodiversity Inside and Outside No-Take Marine Zones in the Florida Keys National Marine Sanctuary: 1999–2018. *Oceanography*. 2021 Jun 1;34(2).
  47. Bohnsack JA, Bannerot SP. A Stationary Visual Census Technique for Quantitatively Assessing Community Structure of Coral Reef Fishes. 1986.
  48. Simmons KR, Bohnenstiehl DR, Eggleston DB. Spatiotemporal Variation in Coral Assemblages and Reef Habitat Complexity among Shallow Fore-Reef Sites in the Florida Keys National Marine Sanctuary. *Diversity* (Basel) [Internet]. 2022;14:153. Available from: <https://doi.org/10.3390/d14030153>
  49. Cangialosi JP, Latta AS, Berg R. Tropical Cyclone Report: Hurricane Irma (AL112017): 30 August–12 September 2017. National Center Tropical Cyclone Report. 2018;111.
  50. Viehman S, Gittings S, Groves S, Moore J, Moore T, Stein J. NCCOS Assessment: Coral Disturbance Response Monitoring (DRM) along the Florida Reef Tract following Hurricane Irma from 2017-10-09 to 2017-10-18 (NCEI Accession 0179071).[indicate subset used]. NOAA National Centers for Environmental Information Dataset doi. 2018;10.

## CHAPTER 1: Hurricane impacts on a coral reef soundscape

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## RESEARCH ARTICLE

## Hurricane impacts on a coral reef soundscape

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## Abstract

Soundscape ecology is an emerging field in both terrestrial and aquatic ecosystems, and provides a powerful approach for assessing habitat quality and the ecological response of sound-producing species to natural and anthropogenic perturbations. Little is known of how underwater soundscapes respond during and after severe episodic disturbances, such as hurricanes. This study addresses the impacts of Hurricane Irma on the coral reef soundscape at two spur-and-groove fore-reef sites within the Florida Keys USA, using passive acoustic data collected before and during the storm at Western Dry Rocks (WDR) and before, during and after the storm at Eastern Sambo (ESB). As the storm passed, the cumulative acoustic exposure near the seabed at these sites was comparable to a small vessel operating continuously overhead for 1–2 weeks. Before the storm, sound pressure levels (SPLs) showed a distinct pattern of low frequency diel variation and increased high frequency sound during crepuscular periods. The low frequency band was partitioned in two groups representative of soniferous reef fish, whereas the high frequency band represented snapping shrimp sound production. Daily daytime patterns in low-frequency sound production largely persisted in the weeks following the hurricane. Crepuscular sound production by snapping shrimp was maintained post-hurricane with only a small shift (~1.5dB) in the level of daytime vs nighttime sound production for this high frequency band. This study suggests that on short time scales, temporal patterns in the coral reef soundscape were relatively resilient to acoustic energy exposure during the storm, as well as changes in the benthic habitat and environmental conditions resulting from hurricane damage.

## OPEN ACCESS

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## Introduction

Ecosystems throughout the world are increasingly threatened by multiple natural and anthropogenic stressors, often leading to ecosystem shifts from desirable to less desirable states [1–4]. Coral reefs are some of the most diverse ecosystems on Earth, and the transition between disturbance states is often observed through changes in coral reef community composition and ecosystem function [5–7]. The desired state is an environment that supports critical ecological processes and resulting patterns across space and time, such as overall system production, key predator-prey (or grazer) interactions, and reproduction across multiple functional

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groups [8, 9]. Disturbance states in coral reef ecosystems are often described as a shift from the desired, structurally complex coral dominated reef, to a less desirable macroalgal dominated state [10–12], as well as reductions in major functional groups such as herbivorous grazers, prey fish stocks, and apex predators [13, 14].

Natural disturbance impacts to coral reef ecosystems vary from chronic events such as coral predation, bioerosion, and intermittent disease, to pulsed catastrophic events such as mass bleaching and hurricanes [15–17]. In certain geographic regions such as the Caribbean, Bahamas and Florida, coral reefs are prone to hurricanes that can cause massive structural damage [18, 19]. Hurricanes can disrupt and reduce ecosystem functions and services [20–24]. Long-term habitat degradation and the persistent decline in the three-dimensional structure of coral reefs can have cascading consequences for reef fish diversity, fisheries, and ecosystem services [25–27]. The response of reef fauna to disturbed benthic habitats can lead to a shift in their spatial distribution as changes in prey densities or habitat specialists compete for sufficient refuge space [28]. Conversely, large-bodied, transient reef fish are more likely to survive an immediate decline in benthic cover because of their ability to relocate to a presumably more desirable habitat [29]. Hurricane impacts have been widely assessed in coral reef ecosystems as catastrophic events that not only promote long-term declines in habitat quality (e.g. algal regime shifts, sedimentation), but further hinder recovery processes from other chronic stressors such as coral disease, overfishing, pollution, and sedimentation [18, 24, 30, 31]. Nevertheless, we know little about how extreme episodic impacts, such as hurricanes, alter the behavior of biological sound production, or biophony, of soniferous (sound-producing) species.

One of the most common quantitative methods to assess the magnitude of change within a population or community pre- and post-disturbance is to assess the temporal response of species composition using abundance or biomass indices [22, 32, 33]. Recent application of passive and active acoustic sampling techniques now allow studies of hurricane impacts to marine organisms using a before, during, and after impact approach [34–36]. For example, acoustic telemetry (active acoustic techniques) of tagged fish characterized the success or failure of nocturnal foraging reef fish (e.g. grunts, snapper) to find refugia, as well as their vulnerability to predation, following a severe disturbance [37]. A recent study on juvenile bull shark (*Carcharchinus leucas*) movements before and after hurricane Irma also described predatory behavioral responses related to shifting prey densities [38]. Although active acoustic studies provide information on individual animal movements, passive acoustic monitoring provides information on soniferous species assemblages that use sounds to communicate, and thereby can be sampled to reflect potential deviations in behavior in response to disturbances such as hurricanes [39–41].

### Soundscape ecology

Soundscapes, the collection of biological, environmental, and anthropogenic sound sources within an ecosystem, can provide high resolution spatiotemporal information about ecosystem patterns and processes [42–44]. Critical information about habitat-specific biodiversity and environmental conditions can be derived from passive acoustic monitoring [44, 45]. Additionally, soundscape analysis allows for the passive acquisition of species assemblage patterns without the influence of human interactions [46–48]. The presence of divers can alter fish distribution and behavior as a negative (i.e. avoidance) or positive (i.e. aggregate) association with human presence [49–51]. Soundscapes provide a collection of empirical data in a natural state without disrupting critical biological or ecological interactions, and allows for visualization of various temporal patterns in acoustic activity and inferred behavior (e.g. hourly, daily, annually, seasonally) for soniferous species. The ecological application of soundscapes is

becoming more widely accepted as an indicator of species presence/absence, habitat associations, and complex biological interactions (e.g. territorial behavior, spawning aggregations, migratory patterns) with applications across a wide range of terrestrial (e.g. woodland forest, desert) [52–54] and aquatic (e.g. coral reefs, oyster reefs, seagrass beds, kelp forest) [55–59] ecosystems.

### Application of soundscape ecology to disturbance impacts

Soundscape methods have been useful in distinguishing between healthy and degraded ecosystems largely by recording the presence and absence, as well as behavior of key soniferous taxa [44]. For example, distinct changes in important ecological behavior (e.g. foraging, mating) or daily activities across space and time can reflect noise avoidance or acoustic masking [60–62], with the former resulting in quieter areas due to a decrease in soniferous species abundance and diversity [63, 64]. Landscape ecology studies are increasingly relying on bioacoustic monitoring to assess deleterious impacts resulting from human land use activities (e.g. clear cutting, forest fire, habitat destruction, noise pollution etc.), and to assess changes in biodiversity, spatial distribution, and animal behavior [65–67]. In a broader context, soundscape studies in terrestrial systems are proving to be instrumental in rapidly assessing biodiversity and informing management recommendations for ecological conservation in the aftermath of detrimental anthropogenic and natural disturbances [68, 69]. Thus, understanding the interaction between disturbance states due to natural or anthropogenic impacts and changes in a soundscape are becoming increasingly relevant to management in terrestrial [70, 71] and aquatic ecosystems [72, 73].

Underwater soundscape monitoring is unique in its access to sound-producing invertebrates and resident reef fish assemblages. In underwater environments, sound is an important indicator of habitat quality [74–76], where relatively high densities of soniferous species may indicate high ecosystem health or structural complexity via an abundance of refugia [77]. For example, Freeman & Freeman [78] used coral reef soundscapes to quantitatively assess the correlation between dominant biological frequencies and habitat quality, in which macroalgal dominated reefs are an indicator of reef degradation and were dominated by high frequency sounds produced by benthic invertebrates. Underwater soundscape studies have been successful in characterizing critical spawning habitats, estimating soniferous species abundance, and characterizing community-level interactions [79–81] by collecting semi-continuous, non-invasive information when traditional sampling methods, such as use of nets or diver surveys, are logistically not feasible (e.g. at night, during extreme storm events). Recent work on coral reef soundscapes have provided baseline data on spatiotemporal variation of coral reef soundscapes across various disturbance states such as dead coral cover, high crustose coralline algae cover, and other degraded habitats [82–85].

The presence of rainfall, wind and wave activity on the ocean's ambient soundscape is well established [86, 87]; however, few studies have focused specifically on modification in the soundscape during extreme weather events, such as hurricanes. Weather and climate may also indirectly influence abiotic sound production by controlling the distribution of ice at high latitudes [88], with the collapse of large ice sheets in Antarctica elevating sound levels throughout the southern Pacific and Indian Oceans [89]. In some ocean basins, the soundscape may be disrupted by large earthquakes that generate high amplitude sounds over time scales of minutes, or by intense episodes of submarine volcanism, which may extend for periods of days-to-weeks [90–93]. The potential ecological significance of these transient natural sound sources is not well understood; however, like hurricanes, they dominant the low-frequency portions of the acoustic spectrum that can be critical in the communication of many marine fauna.

## Hurricane Irma and objectives

On September 2017, Hurricane Irma (Category 4) traveled across the Lower Florida Keys with sustained hurricane force winds (>64kts) extending 130 km from the center [94]. Hurricane Irma passed directly over the Florida Keys National Marine Sanctuary (FKNMS) nearshore marine habitats before making landfall near Cudjoe Key, Florida (USA) [94, 95]. Short-term impacts by large freshwater inflows resulted in changes in the phytoplankton community in nearby coastal canals, with phytoplankton communities returning to normal seasonal patterns within 3 months after the hurricane [96]. The impacts to the Lower Florida Keys seagrass communities from Irma were generally localized, with species-specific beds of seagrass uprooted, and loss of seagrass from storm water runoff resulting in low dissolved oxygen and persistent hyposalinity, similar to historical datasets [97, 98]. Coral reefs in the Middle and Upper Keys showed a significant decline in abundance of the keystone urchin grazer *Diadema antillarum*, as well as loss of sponges and hydrocorals due to high sedimentation [99].

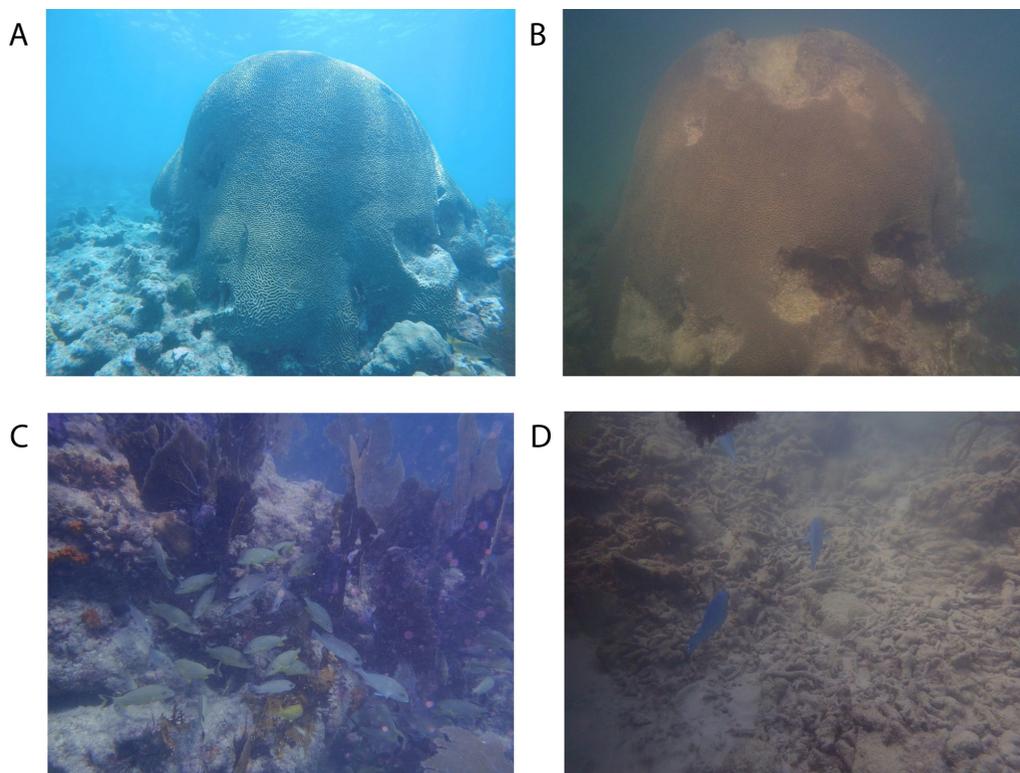
During October 2017, NOAA science divers and partners surveyed more than 50 coral reef sites from Biscayne Bay (near Miami) to the Marquesas (southwest of Key West) and described severe damage in the Middle and Lower Florida Keys sponge and coral communities from storm force waves, fast-moving debris, and heavy sediment deposits [100]. Sedimentation was the most common impact among sites, resulting in poor visibility and high amounts of marine debris [100]. In December 2017, NC State science divers surveyed eight fore-reef sites, including ESB and WDR, and observed poor visibility (<3m), loose rubble, collapsed reef ledges with a mix of schooling species, as well as sedimented and fragmented sub-massive reef-building corals (Fig 1, personal observation K. Simmons). The short-term disturbance in environmental conditions and the remaining fractured reef habitat structure likely impacted marine faunal interactions and behavior; however, little is known about how these changes in the coral reef habitat are reflected in the sound production of coral reef animals that are mobile.

Passive acoustic recordings were used to characterize the underwater soundscape of the coral reef tract in the lower Florida Keys, USA before, during and after Hurricane Irma. In the weeks following the storm, the biological sounds produced by fish exhibited similar pre-disturbance temporal patterns, and the high frequency noise associated with snapping shrimp showed only a small shift in its diurnal patterns. This opportunistic study investigates the utility of soundscapes in assessing disturbance impacts to the coral reef soundscape generated by soniferous reef fishes and snapping shrimp within a track of the Florida Keys reef system impacted by Hurricane Irma. The main objectives of this study were to (i) quantify the cumulative acoustic exposure associated with the passage of hurricane Irma, and (ii) identify and quantify temporal changes within the biophony in response to Irma with emphasis on daily and diurnal soundscape patterns.

## Materials and methods

### Study system

Underwater soundscape characterization was conducted within the lower (Zone D) FKNMS, which comprises a network of marine reserve types and regulated fishing habitats designated in 1990 [101] (Fig 2). This region is part of the Florida Keys Coral Reef Tract, a large bank-barrier reef system that extends 350 km from the Florida Straits northward to St. Lucie Inlet, Martin County [102]. The lower FKNMS habitat includes a mosaic of shallow, marginal reef systems with spur-and-groove reef formations, reef rubble and a diverse array of hardbottom habitat (e.g. stony corals, soft corals, sponges, macroalgae, adjacent seagrass beds). No-take, marine reserves within the FKNMS vary in size, yet most are relatively small (~0.2 to 0.5km<sup>2</sup>).

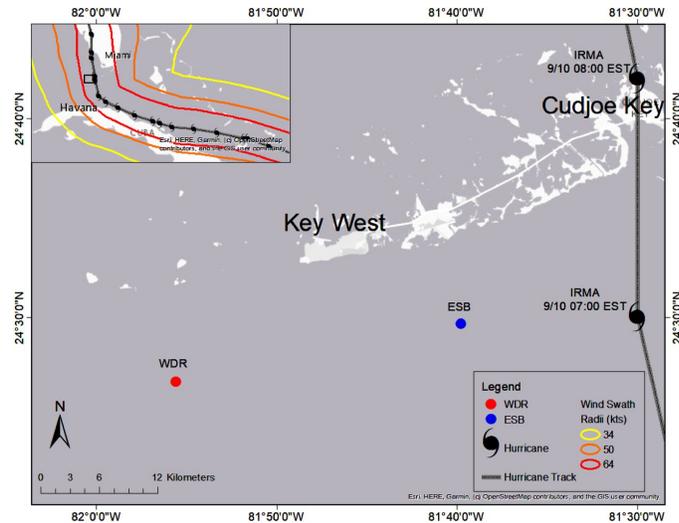


**Fig 1. Before-and-after impacts of hurricane Irma on coral reefs in the Florida Keys, with before images taken in August 2017 and after images taken in December 2017.** (A) Brain coral at Eastern Sambo study site taken in August 2017 and (B) its structural damage after Irma in December 2017. (C) Divers observed fish aggregations near and underneath collapsed reef ledges at Looe Key reef (~26 km northeast of Eastern Sambo study site), and the (D) same site with high amounts of reef rubble after Irma. Photo credit K. Simmons.

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The Lower Keys often have higher salinity and turbidity relative to the Middle and Upper Keys region due to nearshore transport of nutrient-rich deep water [103] facilitated by the Florida Current, gyre system [104, 105].

As a part of a larger study by our research group, eight hydrophones were deployed in July 2017 across several marine reserve zones. The research was permitted by the Florida Keys National Marine Sanctuary Program (FKNMS-2016-111-A1) and the National Wildlife Service (NW5-SAJ-2016-02423). After the passage of Hurricane Irma (Category 4) in the lower Florida Keys on September 2017, only 2 of 8 hydrophones were recovered: (1) Eastern Sambo, a no-entry reserve, and (2) Western Dry Rocks, which is open to fishing (Fig 2). The other hydrophones were lost, presumably due to wave action and surge from the hurricane. The hydrophone at Western Dry Rocks was recovered after the hurricane lying in sand near the mooring, which removed our ability to use these data to quantitatively assess the post-disturbance soundscape. Western Dry Rocks (WDR—24.445°N, 81.926°W) is a regulated fishing site ~22 km southeast of Key West, FL within the FKNMS. This reef is characterized by wide



**Fig 2. Study site—FKNMS Zone D.** Sites are denoted by initials: Western Dry Rocks (WDR) is shown in red and Eastern Sambo (ESB) is shown in blue. NOAA wind swath data are shown as contour lines for maximum sustained wind speeds for 2mins/10meters at 34kts (yellow), 50kts (orange), and 64kts (red). Credit: NOAA NHC Best Track Data updated 06/30/2018.

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spur-and-groove sand channels with high relief ledges and a mean depth of 6m. Although live coral cover is relatively low compared to protected reefs, the benthos consists of gorgonians, coral rubble, and hard-bottom substrate. Eastern Sambo (ESB—24.491°N, 81.664°W) is one of four Special-Use Areas (SUA) or no-entry/no-take zones within the FKNMS, and is no-access except for permitted scientific research, restoration, monitoring, or educational purposes. This reef is characterized as a spur-and-groove bank reef with a mean depth of 5m comprised of massive reef building corals, sponges, and gorgonians.

### Environmental data collection

Hurricane Irma's track, wind swath and landfall data were accessed from NOAA's National Hurricane Center report on Irma ([https://www.nhc.noaa.gov/data/tcr/AL112017\\_Irma.pdf](https://www.nhc.noaa.gov/data/tcr/AL112017_Irma.pdf)). Hurricane Irma made landfall near Cudjoe Key in the lower Florida Keys at 08:00 Eastern Standard Time (EST) on September 10, 2017 (Fig 2) before continuing north toward central Florida. Maximum wind speeds reached 115kts with a minimum barometric pressure of 931 hPa at landfall. Wind swath radii were defined as maximum sustained 1-minute wind speed values for tropical storm force winds (34kts), storm force winds (50kts) and hurricane force winds (64kts).

Barometric pressure data were used, independent of the acoustic time series, to delineate the passage of the storm over the reef. Storm duration was defined as the time window over which the pressure fell and remained below its 2.5% quantile level for data collected between July and October 2017. Barometric pressure data were obtained from the Sand Key Lighthouse, Buoy Station ID SANF1 (24.456°N, 81.877°W), located ~ 5km from WDR. These data were recorded hourly with a standard barometer elevation at 14.6 m above the mean sea level.

Because underwater acoustic time series are non-stationary (i.e., have time dependent mean and variance), soundscape changes must be evaluated within time windows before and after the storm that minimize the effect of processes, such as lunar phase (e.g., [85, 106, 107]), that are likely to influence biological sound production on relevant timescales. To account for this potential influence, 18-day and 24-day periods spanning the same portion of the lunar cycle around the New Moon were identified before (New Moon on August 21st) and after (New Moon on September 20th) the hurricane. These time periods were constrained by the timing of the storm and length of our acoustic time series. Astronomical data were obtained from the US Naval Observatory Portal ([www.usno.navy.mil/USNO](http://www.usno.navy.mil/USNO)).

### Acoustic data collection and analysis

The coral reef soundscape was monitored via bottom-mounted hydrophones (Soundtrap ST300, Ocean Instruments NZ) suspended ~0.15m above the sandy bottom of the fore-reef at each reef site. Both hydrophones began recording on 14 July 2017 and ended on 01 October 2017 (WDR) and 17 October 2017 (ESB). Both recorders were recovered by a dive team on December 2017. The WDR hydrophone was found lying flat in the sand and detached from the mooring. A spectrogram of the WDR data (Fig 5) indicates a change in acoustic coupling after the hydrophone came into contact with the seabed. Although fish chorusing and snapping shrimp activity are still evident in the time series, the post-storm WDR data were excluded from our quantitative before-after comparisons of the soundscape.

The hydrophone recorders were calibrated with a flat frequency response over the ~0.02–40kHz band. Hydrophones were programmed to record 2 minutes of acoustic data every 20 minutes (72 files/day) with 16-bit A/D conversion and at a sample rate of 48kHz. Acoustic recordings were processed in MATLAB using purpose-written code. The mean spectrum of the acoustic data was calculated for each 2-minute recording using the fast Fourier transform, with a window length (NFFT) of  $2^{14}$  samples and a frequency resolution ( $\Delta f$ ) of 2.93 Hz. Hydrophones were also equipped with a temperature sensor that recorded once during each acoustic sampling period.

Fish sounds occupy the low-frequency spectrum (<50Hz to several kHz), often competing with background environmental noise (i.e. wind, wave action) in similar frequency bands [86, 108]. Sound Pressure Levels (SPLs) were calculated at several frequency bands of ecological interest: (1) a low frequency band L1 (50–300Hz) representative of the fish families Serranidae [109–111], Holocentridae [112], and Pomacentridae [113], (2) a low frequency band L2 (1.2–1.8kHz) representative of Haemulidae [114, 115], Lutjanidae [116], Scaridae [81], Sciaenidae [116, 117], and (3) a high frequency band H (7–20kHz) representative of snapping shrimp (Alpheidae), which are a dominant sound producer in coral reef habitats [82, 83, 118, 119]. See S1 Fig for examples of fish calls in each representative band.

To minimize the potential influence of anthropogenic noise and “fish bump” signals in the acoustic time series, SPL data before and after the storm were trimmed to exclude files constituting the loudest 2% of the data over these combined intervals (S2A Fig). Incidental fish bumps are transient signals caused by the physical interaction of an animal with the hydrophone or hydrophone mooring, generating artifacts in the acoustic data [120–122]. Trimming excludes those files containing large amplitude fish bumps (S2B and S2C Fig), as well as files with anomalously large SPLs due to transient boat noise (S2D Fig). For a given recording window (i.e. 00:00, 00:20, . . . 23:40), the trimmed mean SPLs before and after the storm were calculated for each band (L1, L2, and H). Uncertainty (68% confidence interval) was estimated using a bootstrap resampling procedure (see below).

Generally, for reefs in the South Atlantic and Caribbean, as well as in other coral reef systems, biologic sound production varies diurnally. These patterns often reflect the abundance or acoustic behavior of multiple species, with times of peak acoustic activity in a given frequency band varying between reef systems [e.g., 57, 83, 106, 123, 124]. Because these daily acoustic patterns tend to persist, even as average SPLs may rise and fall, the disruption of this pattern following a disturbance event may indicate changes in the abundance or acoustic behavior of the impacted species. We therefore investigated the daily SPL patterns (over the 72 recordings made each day), as well as the diurnal (daytime vs. nighttime) differences in SPLs within each of the ecologically relevant frequency bands. The decibel difference between daytime and nighttime SPL provides way to normalize for the non-stationarity of the acoustic time series on longer time scales—as opposed to making inferences based on small changes in the absolute SPL before and after the storm. Daily and diurnal patterns are absent or masked during the storm, and therefore not discussed.

For each 24-hour period, daytime and nighttime mean SPLs were also calculated from the trimmed SPL time series. Daytime was defined as the period between local sunrise (05:48–06:19 EST) and sunset (18:15–19:18 EST), whereas nighttime was defined as the period between sunset and sunrise. Uncertainties (68% confidence interval) in the means were estimated using a bootstrap resampling (5000 draws). The probability that the mean daytime SPL was higher than the mean nighttime SPL on each day was estimated from the portion of resampled outcomes with  $\overline{SPL}_{day} > \overline{SPL}_{night}$ . Values of  $p \approx 1$  indicate significantly higher daytime sound levels, and values of  $p \approx 0$  indicate significantly higher nighttime sound levels on a given day.

For the 18- and 24-day windows assessed before and after the hurricane, the mean difference between daytime and nighttime SPLs, and the confidence intervals for this difference, were estimated using a paired resampling (5000 draws) of the nighttime and daytime means for each 24-hour period. The probability that daytime SPL was greater than nighttime SPL was calculated from the resampled differences, where  $p \approx 1$  indicates significantly higher daytime sound levels, and  $p \approx 0$  indicates significantly higher nighttime sound levels over the assessment window.

### Hurricane acoustic energy exposure

Hurricanes represent broadly distributed acoustic sources, with the sounds recorded at each hydrophone arriving from a range of azimuths and incidence angles. However, to place the acoustic exposure at these reef sites in context and make comparisons with other sound sources, we quantified the acoustic exposure by representing all storm related noise as being sourced from a point at the sea surface directly above each hydrophone and calculating the equivalent energy.

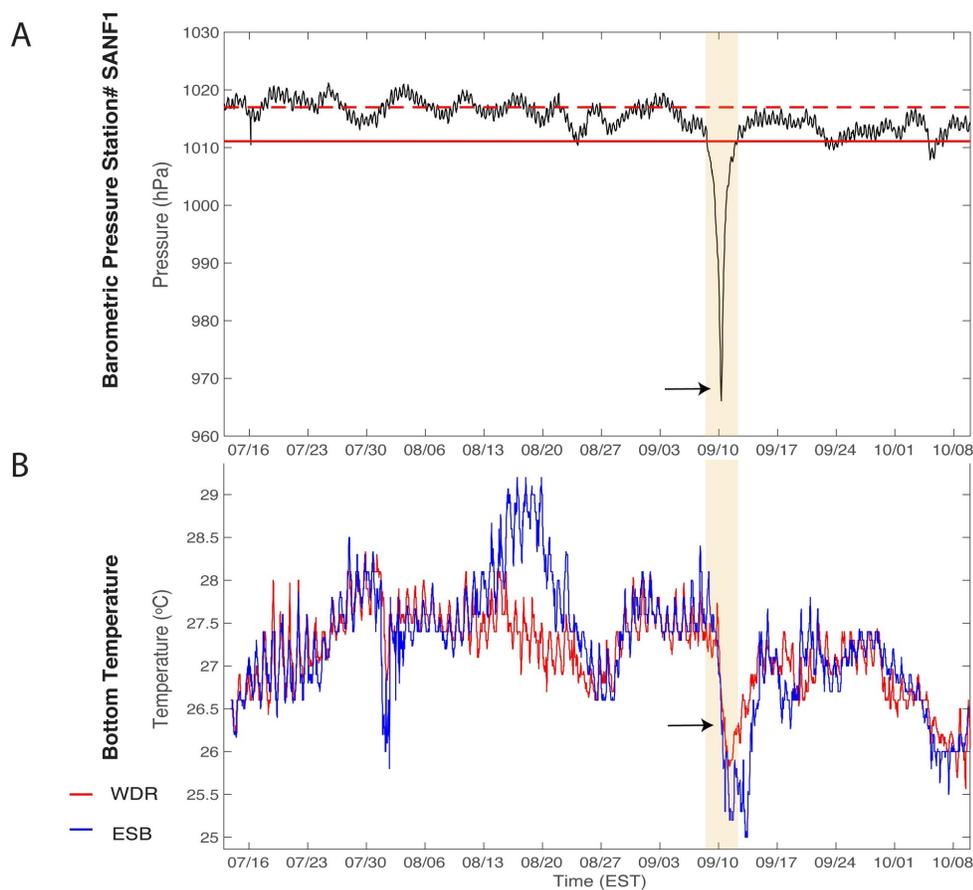
Over the four-day duration of the storm, the received root mean square SPLs calculated for each file were corrected to acoustic source levels (referenced @ 1m) assuming spherical spreading loss between the sea surface and seafloor. The equivalent acoustic power (J/s) that radiated into the water column (i.e., across a 1 m radius hemisphere with surface area  $2\pi$ ) was then estimated assuming a constant water density ( $1030 \text{ kg/m}^3$ ) and sound velocity (1485 m/s) [125]. The acoustic energy was determined by integrating these power values over the duration of the storm, assuming each two minute file is representative of a surrounding 20 minute time window, and then subtracting the energy that would be calculated if the procedure was repeated using the mean background (pre-storm) noise levels. This energy exposure value can then be compared to the equivalent energy that would be associated with common natural and anthropogenic sources (e.g. fishing vessels) operating over a set duration (e.g., [126, 127]) if these

sources were fixed in position at the sea surface directly above the hydrophone. This value, however, does not represent the total acoustic energy imparted by the storm.

## Results

### Environmental conditions

Barometric pressure data exhibited semidiurnal oscillations characteristic of the Florida Keys region (Fig 3A). The passage of the storm is marked by a period of low (< 1011 hPa) barometric pressure, which extends from ~12:00 on September 8, 2017 to ~12:00 September 12, 2017 (4 days), reaching a trough at 966 hPa on September 10, 2017 at 06:50 (all times EST). In



**Fig 3. Environmental data.** (A) Barometric pressure data from Sand Key Lighthouse, FL (Station ID SANF1 24.456°N, 81.877°W) NOAA-National Data Buoy Center is shown as a black line with the median (dashed red) and the lower 2.5% confidence interval (solid red). (B) Mean hourly bottom temperature (°C) from hydrophone sensor for Western Dry Rocks (red) and Eastern Sambo (blue). The orange bar represents Hurricane Irma duration and the black arrow indicates the times of landfall at Cudjoe Key FL on September 10, 2017 08:00 EST.

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analyzing the soundscape during the pre- and post-storm windows, a 1-day buffer was applied on either side of the hurricane, such that the pre-storm period ends on September 7<sup>th</sup> at 12:00 and the post-storm period begins on September 13<sup>th</sup> at 12:00.

Before and after the storm, daily bottom temperatures at WDR and ESB varied between 26–28°C, except for a short period of slightly increased temperatures at ESB between August 15 to August 19, 2017, which was likely influenced by the lunar spring tide. Both sites exhibited a sharp decline in bottom temperature reaching 25°C shortly after the hurricane made landfall (Fig 3B). Post-hurricane, cooler water temperatures remained a few days longer at ESB than WDR before returning to pre-disturbance daily temperature oscillations.

### Acoustic spectra

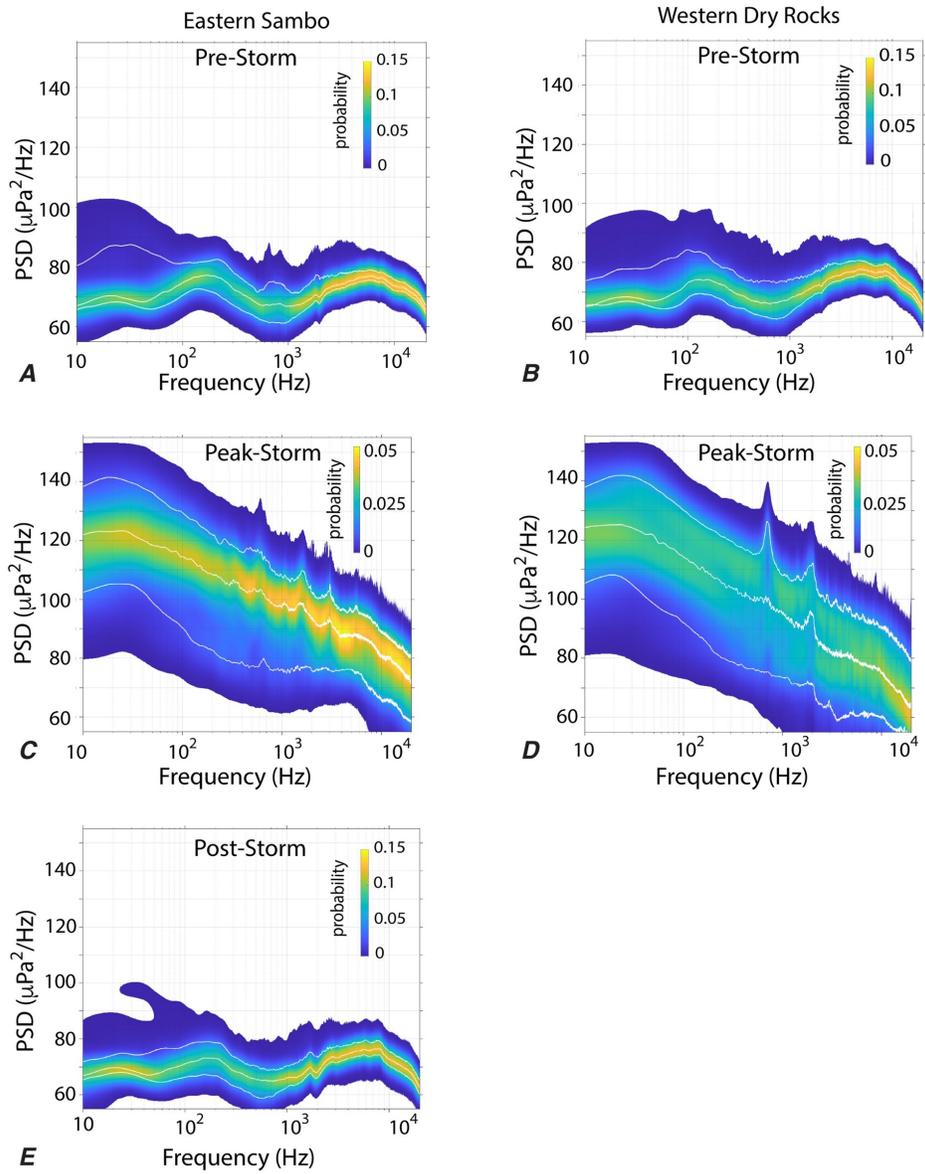
The acoustic spectra were assessed over the peak of the storm period (September 9<sup>th</sup>–10<sup>th</sup>) and compared with the spectra over four-day periods immediately before (September 3<sup>rd</sup>–7<sup>th</sup>) and after (September 13<sup>th</sup>–17<sup>th</sup>) the storm (Fig 3). Over the four days before the hurricane, the spectra at each site was elevated broadly across the 50–300 Hz frequency range, with additional low amplitude spectral peaks in the frequency ranges of 600–900Hz and 1600–1900Hz being observed most clearly at ESB (Fig 4A). During the peak of the hurricane, the low frequency component of the soundscape was impacted most dramatically and median spectral power increased by 40–50 dB over pre-storm levels in the ~10–100 Hz frequency range, and with multiple narrow band spectral peaks at frequencies of 100's to 1000's Hz observed at both sites (Fig 4C and 4D). Within the four-day window after the hurricane, spectra at ESB remained elevated in the 50–300 Hz and 1600–1900Hz frequencies (Fig 4E), yet the pre-storm peak between 600–900Hz was absent.

### Acoustic energy exposure

WDR experienced a higher cumulative energy exposure than ESB estimated at  $9.9 \times 10^3$  J and  $4.8 \times 10^3$  J, respectively. In comparison to other acoustic energy disturbances commonly experienced in the lower Florida Keys region, the exposure over the duration of Hurricane Irma was comparable to small vessel (SL = 153 dB re 1 $\mu$ Pa @ 1m) operating continuously [128–130] directly overhead for 1 week (ESB) to 2 weeks (WDR). The WDR hydrophone presumably detached from its mooring at some point during the storm; however, the exact timing of this event was not readily identifiable, and no corrections were made to account for potential changes in sensitivity of the instrument. Estimates of acoustic exposure also do not account for the signals produced by debris impacting the hydrophone and mooring, since this effect is not easily disentangled from the acoustic wavefield.

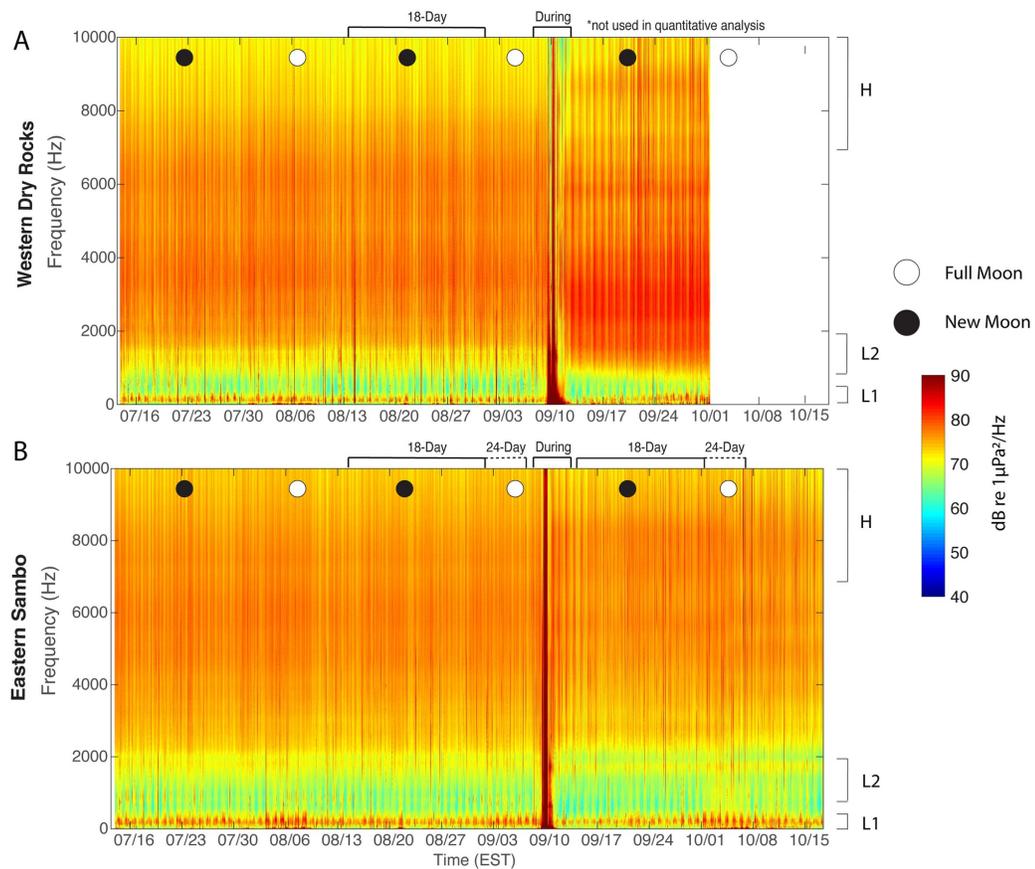
### Biophony

Both sites showed temporal patterns in the biophony evident with their long-term spectrograms (Figs 5 and 6). A daily pattern of fish vocalizations within the L1 frequency band was apparent at WDR and ESB over the ~2 month recording period before the hurricane, with increased sound levels around the full moons in August and September (Fig 5). Fish calls within both low frequency bands were masked or absent during the storm, before reappearing immediately after the storm (Figs 5 and 6). The apparent post-storm shift in high-frequency sound levels at WDR likely reflected a change in sensitivity of the hydrophone after it became detached from the mooring (Fig 5A). The low frequency bands at ESB diminished in intensity during the waning part of the lunar cycle and became more pronounced approaching the October full moon (Fig 5B). Additionally, the less pronounced, yet persistent fish calling evident in the L2 band was observed before and after the storm at ESB (Figs 5B and 6). The L2



**Fig 4. Power Spectral Density (PSD) plot.** Power spectral density plot of Eastern Sambo (left) and Western Dry Rocks (right) pre-storm (A, B), peak-storm (C, D), and post-storm (E). The colors show the probability distribution of the spectral amplitudes, and white lines show the 5, 50, and 95% quantiles of power spectral density as a function of frequency.

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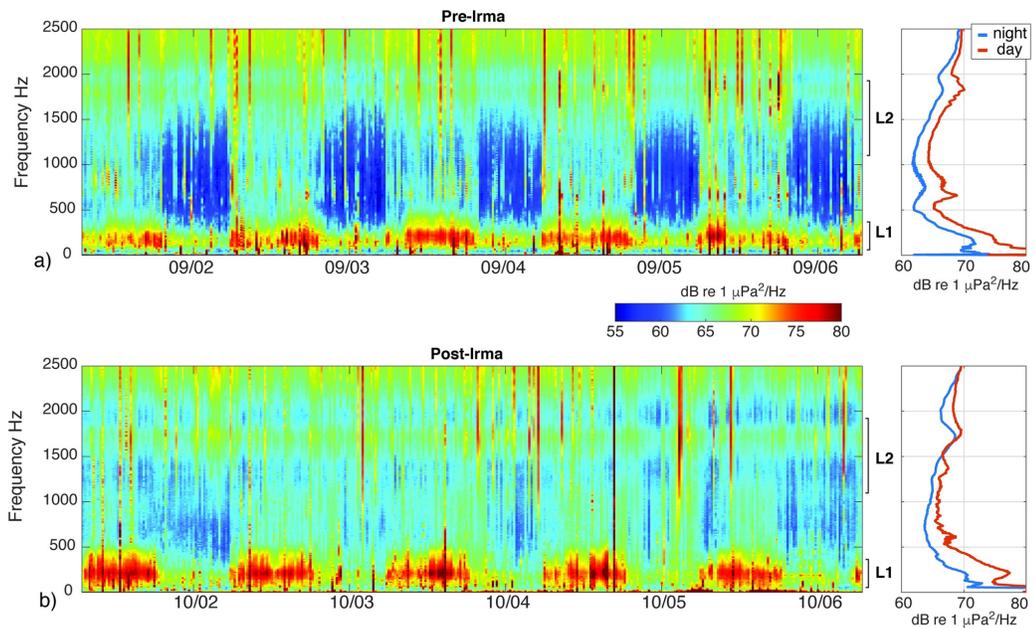
**Fig 5. Deployment period spectrogram.** Spectrogram displaying the power spectral density (PSD in dB re  $1\mu\text{Pa}^2/\text{Hz}$ ) for Western Dry Rocks (A) and Eastern Sambo (B). Frequency bands are denoted as follows: H, high frequency (7,000–20,000Hz); L1 low frequency (50–300Hz); L2 low frequency (1,200–1,800Hz). Open and filled circles indicate the full and new moons respectively. Hurricane Irma made landfall on September 10, 2017. Data within the WDR post-window was not valid or used for quantitative analysis. Spectrogram was generated from the average spectra within each two-minute recording (NFFT =  $2^{14}$ ,  $\Delta f$ ) = 2.93 Hz).

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band captured broadband fish calls, including the upper range of pulsated “grunts” (>1000Hz) and aggregated “knocks” between 1200–2500Hz, as well as including the lower range of snapping shrimp sound production in the high frequency band. Snapping shrimp activity within the H band persisted before and after the storm at both sites (Fig 5).

### Temporal soundscape patterns

The daily patterns in SPLs before and after the storm were examined for the ESB site. Within the three frequency bands, trimmed means were calculated for each recording interval (00:00, 00:20 . . . 23:40) over the 18- and 24-day windows capturing the same portion of the lunar cycle

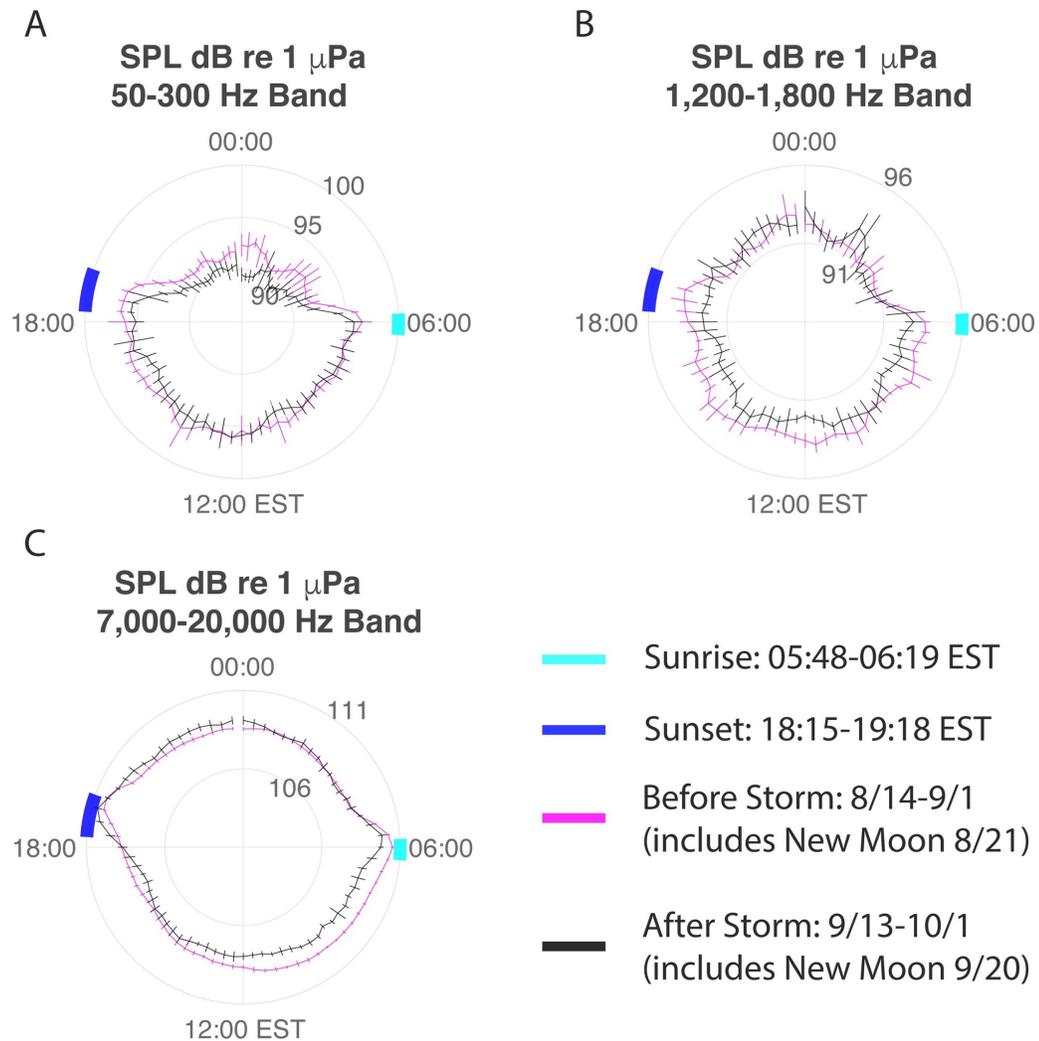


**Fig 6. Short-duration spectrograms from Eastern Sambo.** Spectrograms displaying the low frequency patterns of sound production during 5-day windows around the full moons that occurred (a) before and (b) after the passage of Hurricane Irma. Spectrograms are derived using the average spectra with each two minute recording. Time-axis ticks indicate midnight EST. Sound pressure levels are elevated during daytime hours, relative to the nighttime hours. The diurnal pattern of sound production reflects the acoustic activity and/or presence of multiple species (see call example in S1 Fig). The diurnal pattern in low-frequency (L1) sound production is present before and after the storm. The diurnal pattern of mid-frequency (L2) sound production is a less pronounced, and appears to weaken after the passage of the storm. Panels on the right show average sound pressure levels during daytime and nighttime recordings averaged over the 5-day windows.

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before and after the storm. The results for the 18-day windows are displayed in Fig 7, along with their bootstrapped confidence intervals. The dominant temporal pattern was a diurnal rhythm (day vs. night) in sound production, along with a small increase in high frequency noise during crepuscular periods. The daily pattern of low and high frequency sound production was largely maintained after the storm, with only small shifts in the average loudness. Within the L1 band, a small decrease in the average SPL is observed during the nighttime hours, with little change in the average level during the daytime hours. For the L2 band, a small decrease in the average SPL is observed during the daytime hours, with little change observed at night.

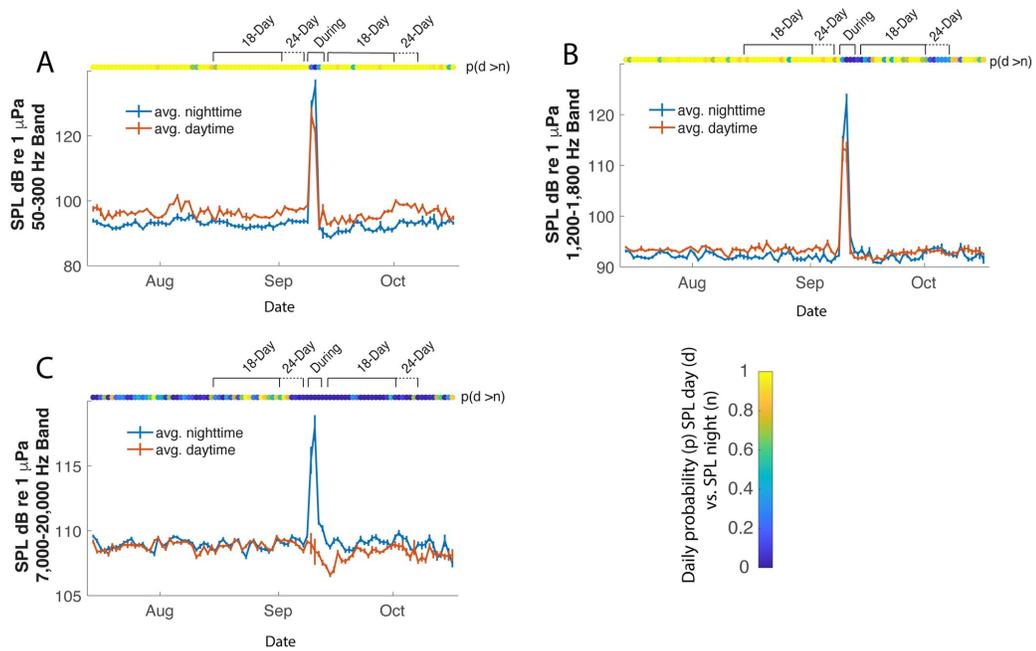
To investigate the diurnal patterns in more detail, the mean daytime and nighttime SPLs, along with their bootstrapped confidence intervals, were calculated daily for each frequency band (Fig 8). For each 24-hour period, the probability that the mean daytime SPL is greater than the mean nighttime SPL was estimated from the resampled means. Within the L1 frequency band, daytime SPL was consistently higher than nighttime SPL ( $p \approx 1$ ), except for the time window when the storm passed over the reef (Fig 8A). Within the L2 frequency band, daytime SPL was consistently higher than nighttime SPL ( $p \approx 1$ ) before the storm; however, there was no consistent diurnal pattern after the storm (Fig 8B). Within the H frequency band,



**Fig 7. Polar diagram for Eastern Sambo.** Polar diagram of Sound Pressure Levels (SPLs) for ESB for the 18-day observation window before (magenta) and after (black) the hurricane. Means for each recording interval are shown with 3-point moving average. Error bars represent the 68% confidence interval of mean. Data are displayed for A) L1 frequency band (50-300Hz); B) L2 frequency band (1,200–1,800Hz); and C) H frequency band (7,000–20,000Hz). Local sunrise (05:48–06:19 EST) and sunset (18:15–19:18 EST) times during the deployment are shown in cyan and blue, respectively.

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there was no persistent diurnal pattern before the storm, yet daytime sound production decreased slightly after the storm creating a persistent pattern of higher nighttime SPL relative to daytime SPL ( $p \approx 0$ ) (Fig 8C).

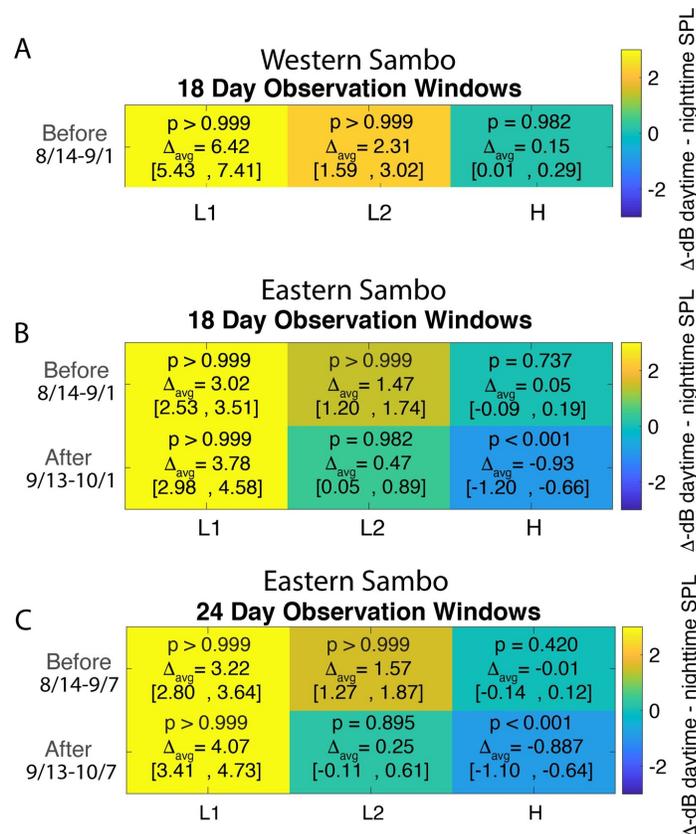


**Fig 8. Eastern Sambo diurnal patterns.** Mean daytime (red) and nighttime (blue) SPL during the deployment period July 14<sup>th</sup>–October 15<sup>th</sup>. Error bars represent the 68% confidence interval for the mean daytime and nighttime SPL within each 24-hour period. Data are displayed for the A) L1 frequency band (50–300Hz); B) L2 frequency band (1,200–1,800Hz); and C) H frequency band (7,000–20,000Hz). The color bar shows probability that daytime SPL is greater than nighttime SPL,  $p \approx 1$  indicates significantly higher daytime sound levels, and  $p \approx 0$  indicates significantly higher nighttime sound levels on a given day. Test periods are within an 18-day lunar cycle before the hurricane August 14<sup>th</sup>–September 1<sup>st</sup> (includes August 21<sup>st</sup> new moon) and after the hurricane September 13<sup>th</sup>–October 1<sup>st</sup> (includes September 20<sup>th</sup> new moon).

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The magnitude and significance of these diurnal patterns in SPLs were quantified further by resampling the paired daytime and nighttime means over the 18- and 24-day windows before and after the storm. Fig 9 summarizes these results, reporting the mean diurnal difference ( $\Delta_{avg}$ ) and its 95% confidence interval. Time windows with  $p \approx 1$ , and positive confidence intervals, exhibited significantly higher daytime SPL, relative to nighttime SPL; or conversely, time windows with  $p \approx 0$ , and negative confidence intervals, exhibited significantly higher nighttime SPL, relative to daytime SPL.

Before the hurricane, daytime SPL over the 18-day window was higher than nighttime SPL in the L1 band at both WDR ( $\Delta_{avg} = 6.42dB$ ) and ESB ( $\Delta_{avg} = 3.02dB$ ), with  $p \approx 1$ . This diurnal difference was maintained with similar amplitude at ESB after the storm ( $\Delta_{avg} = 3.78dB$ ,  $p \approx 1$ ). The same pattern of higher daytime SPL than nighttime SPL was observed over the 24-day windows. Within the L2 band, before the storm daytime SPL also was higher than nighttime SPL at both WDR ( $\Delta_{avg} = 2.31dB$ ) and ESB ( $\Delta_{avg} = 1.47dB$ ), with  $p \approx 1$ . This pattern weakened slightly at ESB after the storm, within both the 18- ( $\Delta_{avg} = 0.47dB$ ) and 24-day ( $\Delta_{avg} = 0.25dB$ ) windows,  $p = -0.98$ . Within the H band prior to the storm, a small diurnal difference was observed only at WDR ( $\Delta_{avg} = 0.15dB$ ,  $p = 0.98$ ). After the storm, however, the nighttime SPLs



**Fig 9. Pairwise bootstrap analysis results.** Pairwise bootstrap ( $n = 5000$ ) of mean differences, 95% confidence, and probabilities ( $p$ ) daytime mean SPL > nighttime mean SPL for 18-day observation window at Western Dry Rocks (A) and Eastern Sambo (B). An additional pairwise analysis is given for Eastern Sambo for 24-day observation window (C). Frequency bands are denoted as follows: L1 low frequency (50–300Hz); L2 low frequency (1,200–1,800Hz); H, high frequency (7,000–20,000Hz). The color-bar represents the change in SPL (dB) between daytime-nighttime paired SPLs, with the 95% confidence range for decibel differences given in brackets. High  $p$  values and positive changes in decibel levels indicate periods when the average daytime SPL was higher than average nighttime SPL. Low  $p$  values and negative changes in decibel levels indicate periods when the average nighttime SPL was higher than average daytime SPL.

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were elevated slightly relative to daytime SPL within both the 18- ( $\Delta_{avg} = -0.93dB$ ) and 24-day ( $\Delta_{avg} = -0.89dB$ ) windows,  $p \approx 0$  at ESB.

## Discussion

This study used passive acoustics to characterize the impacts of a major hurricane on a coral reef soundscape and the underlying temporal changes within the biophony that reflect biological behavior and activity. Observing changes in temporal patterns at hourly and daily scales for both the high and low frequency band, representative of ecologically important soniferous

taxa, provided evidence that coral reef soundscapes may be resilient to a natural, acute disturbance despite experiencing physically destructive conditions. The extent to which a coral reef soundscape recovers to pre-disturbance patterns in sound pressure levels may depend on known characteristics of resilience in coral reef ecosystems, such as structural complexity or relative abundance of herbivorous species [131 and references therein], as well as characteristics of the storm itself, such as wind-speed, direction and duration.

### The influence of abiotic factors on the underwater soundscape during a disturbance

The expanse of the hurricane wind swath (64kt radius) exposed both sites (WDR and ESB) to high levels of acoustic energy, yet the potential of inflated exposure estimates from WDR's hydrophone as it detached and presumably came into contact with fast moving sediment and debris did not allow for uncertainty estimates. Spectral densities during the hurricane did increase and produced narrow, wave-like peaks at high frequencies that may be explained by hydrodynamic processes. For example, previous studies indicate air-sea interactions can generate bubble formations that vary with wind speed intensity [132, 133], and bubble formation and dissipation can be produced via wave action [134, 135]. Moreover, air-sea interactions and the resulting swell of waves can vary depending on water depth and the structural complexity of the reef as current velocities can change when interacting with physical features. As previously described, WDR is characterized by relatively wide spur-and-groove channels, whereas ESB is dominated by a matrix of massive reef building corals and micro-patch reefs with relatively low sloping sand channels. Down-welling current velocities can intensify along the reef slope (spur) and increase vertically over the grooves of spur-and-groove reef formations [136]. Physical attributes of reef formations also drive other hydrodynamic processes such as refraction, dissipation, and shoaling—attributes that dictate the force and momentum of flow within the water column [137]. Therefore, the difference in sound spectral densities at each site during the storm passage may relate to stronger circulatory flows of wave action funneling into deep groove channels at WDR compared to ESB. Environmental changes during the hurricane, such as a decrease in bottom temperature and barometric pressure, may have had minimal impacts on the biophony as the presence of resident soniferous species immediately following the storm provides an alternative perspective on pre-storm migration patterns of fish and sharks seen in related studies [138, 139].

### Hurricane impacts to coral reef soundscapes

There are very few examples of how coral reef soundscapes respond to hurricane impacts, and of those, there is little quantitative information on specific impacts to soniferous reef fish groups. In contrast with previous coral reef soundscape studies that observe temporal patterns in the low frequency band across a wide frequency range (e.g. 0–3kHz), our results partitioned the low band to distinguish between reef fish families such Serranidae, Holocentridae, and Pomacentridae (represented by the L1 frequency band), and Haemulidae, Lutjanidae, Scariidae, and Sciaenidae (represented by the L2 frequency band). Nonetheless, the increased SPL at low frequencies during the daytime, relative to the nighttime, can likely be viewed as the integrated signature of multiple soniferous species with varying abundances and acoustic behaviors.

Reef fish chorusing around lunar phases were more prominent at ESB than WDR, and the presence of both the L1 and L2 frequency bands suggest the presence of a range of fish families during the same lunar phase despite impacts from Hurricane Irma. Fish chorusing was sometimes indicative of spawning behavior, and essential spawning locations are commonly

populated by multiple species [140–143]. In a related study, Hurricane Charley (category 4) passed directly over Charlotte Harbor, Florida, USA yet nightly fish chorusing during spawning events yielded louder SPLs during and a few days after the hurricane than before, suggesting fish distribution patterns or behavior may not have been impacted by the hurricane [144]. Although the magnitude of change in low frequency-band sound pressure levels within the Irma observation windows (18- and 24-days) tested in this study were not significant, increased spatial coverage of soundscape characterization within a site using multiple hydrophones may have revealed different results.

The magnitude of change in diurnal sound pressure levels varied for each frequency band across the observation windows in this study. The L1 band at ESB was most resilient to change as average daytime sound levels maintained louder sound levels than paired nighttime sound levels during both observation windows. The L2 band also followed a similar diurnal trend as the L1 band at both sites; however, diurnal patterns in ESB's L2 band weakened post-hurricane due to a decrease in daytime SPLs. This result differs from observations within the coral reefs Puerto Rico, where nighttime chorusing is reported to have increased following the passage of Hurricanes Irma and Maria [145, 146].

Diel migrations and nocturnal activity documented by acoustic tagging (telemetry), represented by the L2 band in this study, has been observed for grunts [147] and snappers [148, 149]. These species typically form mixed-species schools in refuge space underneath reef outcroppings or ledges during daylight hours before migrating to forage on adjacent seagrass beds around dusk [150–153]. The reductions in habitat quality (e.g. habitat degradation, turbidity) following a hurricane may have provided enhanced opportunities for cryptic or nocturnal species to forage or find mates during low visibility conditions and presumably low predation risk, which could promote a relatively broad range of vocalizations among reef fish [146, 154].

Diurnal snapping shrimp activity, as characterized by the H-frequency band, appeared resilient to the hurricane disturbance, with little change in snapping shrimp activity in the weeks following the storm. The H band at ESB did not show any significant difference between day-night SPLs before Irma, with only a small (~0.2 dB) difference developed in the weeks after the storms as daytime SPL decreased slightly. Recent studies in Puerto Rico revealed snapping shrimp inhabiting a shallow reef were silenced or masked during Hurricane Maria and did not return to crepuscular peaks in sound production until several days after hurricane passage [145, 146].

In this study, the coral reef soundscape post-Irma reflected the response of both fish and invertebrate behavior (e.g. daily, diurnal chorusing patterns) to a large-episodic disturbance in the form of a Category 4 Hurricane. Temporal patterns in the biophony at ESB appeared resilient to the acoustic energy exposure, change in environmental variables, and physical damage caused by Hurricane Irma. There are very few studies of how the soundscape of an ecosystem responds to a major environmental disturbance. Gasc et al. [52] highlighted changes in acoustic composition of an isolated desert after a wildfire event in which not only was acoustic activity diminished at burned sites, but the soundscape also reflected a change in taxonomic species distribution (e.g. insects, birds) and vegetative response (e.g. floral regeneration) post-disturbance. Their results are supported by traditional disturbance ecology studies where the resulting ecosystem reflected the severity of the disturbance and revealed which biological legacies (i.e. taxa-specific traits of survivors, remaining habitat structure) contribute to the re-establishment of an ecosystem [15, 155, 156].

In conclusion, this study characterized environmental variables associated with the passage of a Category 4 hurricane on a coral reef, and the associated temporal patterns in the biophony before, during, and after a natural disturbance. The short-term response of Eastern Sambo's coral reef soundscape appeared resilient to the acoustic energy exposure, change in

environmental variables, and physical damage caused by Hurricane Irma. Underwater soundscapes can be a complimentary ecological tool useful in characterizing small, yet important shifts in ecological communities during disturbances with localized impacts.

### Supporting information

**S1 Fig. Fish call spectrograms.** Representative waveforms (top) and spectrograms (bottom) for the L1 low frequency band 50-300Hz: (A) Serranid growl, (B) fish “chirps”; and the L2 low frequency band 1200-1800Hz: (C) Haemulid “grunts”, (D) rapid aggregated “knocks”. Mean amplitudes were calculated using a bandpass filter 30-3000Hz and a steepness of 0.65. Spectrograms were calculated using a window length of 2048Hz with 50% overlap.  
(TIF)

**S2 Fig. Illustration of trimmed sound pressure level time series.** S1 Illustration of the trimmed sound pressure level time series applied to a section of the pre-storm storm data from Eastern Sambo site. The red line in panel A) shows the original broadband time series generated by calculating the root-mean-square (rms) sound pressure level in each 2-minute recording collected every 20 minutes. The blue line shows the time series after eliminating those files with the largest 2% of the amplitudes during the combined pre- and post-storm window. These trimmed data were used in calculating daytime and nighttime means. The largest amplitude spikes removed by this process are associated with files that contain one or more fish bumps. These signals do not represent sound, but can have a major influence on the calculated sound pressure levels. For example, the sound pressure level of the file shown in panel B) has a value of 113 dB rms re 1  $\mu$ Pa when averaged over the first 90 seconds of the file; this is consistent with expected background noise levels. However, when the series of fish bumps are included in the calculation, the amplitude rises by more than 30 decibels. Panel C) shows an individual bump signal. These signals are often clustered temporally, but typically occur in no more than 1 or 2 files per day. The trimming of the time series also removes a handful of files (3–4 per week) containing the sounds of a nearby small boat, as shown in panel D). The resulting trimmed time series better represents the underlying diurnal pattern of acoustic noise with the environment and is used to assess patterns of biophony.  
(TIF)

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## References

1. Swindles GT, Morris PJ, Whitney B, Galloway JM, Galka M, Gallego-Sala A, et al. Ecosystem shifts during long-term development of an Amazonia peatland. *Global Change Biology*. 2018; 24(2):738–757. <https://doi.org/10.1111/gcb.13950> PMID: 29055083
2. Hempton TN, Graham NAJ, MacNeil MA, Hoey AS, Wilson SK. Ecosystem regime shifts disrupt trophic structure. *Ecological Applications*. 2018; 28(1):191–200. <https://doi.org/10.1002/eap.1639> PMID: 29035010
3. Lercari D, Defeo O, Ortega L, Orlando L, Gianelli I, Celentano E. Long-term structural and functional changes driven by climate variability and fishery regimes in a sandy beach ecosystem. *Ecological Modelling*. 2018; 368:41–51. <https://doi.org/10.1016/j.ecolmodel.2017.11.007>
4. Bevilacqua S, Savonitto G, Lipizer M, Mancuso P, Ciriaco S, Srijemsi M, et al. Climatic anomalies may create a long-lasting ecological phase shift by altering the reproduction of a foundation species. *Ecology*. 2019; 100(12):e02838. <https://doi.org/10.1002/ecy.2838> PMID: 31330045
5. Graham NAJ, Chong-Seng K, Huchery C, Januchowski-Hartley F, Nash KL. Coral Reef Community Composition in the Context of Disturbance History on the Great Barrier Reef, Australia. *PLoS One* 2014; 9(7):e101204. <https://doi.org/10.1371/journal.pone.0101204> PMID: 24983747
6. Mellin C, Bradshaw CJ, Fordham DA, Caley MJ. Strong but opposing  $\beta$ -diversity–stability relationships in coral reef fish communities. *Proceedings of the Royal Society B: Biological Sciences*. 2014; 281(1777):20131993. <https://doi.org/10.1098/rspb.2013.1993> PMID: 24403321
7. Courtney TA, Barnes BB, Chollett I, Elahi R, Gross K, Guest JR, et al. Disturbances drive changes in coral community assemblages and coral calcification capacity. *Ecosphere*. 2020; 11(4):e03066. <https://doi.org/10.1002/ecs2.3066>
8. Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, et al. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*. 2004; 35(2004):557–581. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105711>
9. Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences*. 2006; 273(1582):101–7. <https://doi.org/10.1098/rspb.2005.3276> PMID: 16519241
10. Hughes TP. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*. 1994; 265(5178):1547–51. <https://doi.org/10.1126/science.265.5178.1547> PMID: 17801530
11. Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. Long-term region-wide declines in Caribbean corals. *Science*. 2003; 301(5635):958–60. <https://doi.org/10.1126/science.1086050> PMID: 12869698
12. Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, et al. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current biology*. 2007; 17(4):360–5. <https://doi.org/10.1016/j.cub.2006.12.049> PMID: 17291763
13. Duffy JE. Biodiversity and ecosystem function: the consumer connection. *Oikos*. 2002; 99(2):201–19. <https://doi.org/10.1034/j.1600-0706.2002.990201.x>

14. Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, et al. Global trajectories of the long-term decline of coral reef ecosystems. *Science*. 2003; 301(5635):955–8. <https://doi.org/10.1126/science.1085706> PMID: 12920296
15. Connell J. Disturbance and recovery of coral assemblages. *Coral Reefs*. 1997; 16:S101–S113. <https://doi.org/10.1007/s003380050246>
16. Hatcher BG. Coral reef ecosystems: how much greater is the whole than the sum of the parts?. *Coral Reefs*. 1997; 16(1):S77–91.
17. Nyström M, Folke C, Moberg F. Coral reef disturbance and resilience in a human-dominated environment. *Trends in ecology & evolution*. 2000; 15(10):413–7. [https://doi.org/10.106/S0169-5347\(00\)01948-0](https://doi.org/10.106/S0169-5347(00)01948-0)
18. Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. Hurricanes and Caribbean coral reefs: Impacts, recovery, patterns, and role in long-term decline. *Ecology*. 2005; 86(1):174–184. <https://doi.org/10.1890/04-0141>
19. Fuhrmann CM, Wood KM, Rodgers JC. Assessment of storm surge and structural damage on San Salvador, Bahamas, associated with Hurricane Joaquin (2015). *Natural Hazards*. 2019; 99:913–930. <https://doi.org/10.1007/s11069-019-03782-2>
20. Rogers CS. Hurricanes and coral reefs: The intermediate disturbance hypothesis revisited. *Coral Reefs*. 1993; 12:127–137. <https://doi.org/10.1007/BF00334471>
21. Mallin MA, Posey MH, Shank GC, McIver MR, Ensign SH, Alphin TD. Hurricane effects on water quality and benthos in the Cape Fear watershed: Natural and anthropogenic impacts. *Ecological Applications*. 1999; 9(1):350–362. [https://doi.org/10.1890/1051-0761\(1999\)009\[0350:HEOWQA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0350:HEOWQA]2.0.CO;2)
22. Burkholder J, Eggleston D, Glasgow H, Brownie H, Brownie C, Reed R, et al. Comparative impacts of two major hurricane seasons on the Neuse River and western Pamlico Sound ecosystems. *Proceedings of the National Academy of Sciences*. 2004; 101(25):9291–9296. <https://doi.org/10.1073/pnas.0306842101> PMID: 15199179
23. Hughes TP, Anderson KR, Connolly SR, Heron SF, Kerry JT, Lough JM, et al. Spatial and temporal patterns of mass bleaching of corals in Anthropocene. *Science*. 2018; 359(6371): 80–83. <https://doi.org/10.1126/science.aan8048> PMID: 29302011
24. Steneck RS, Arnold SN, Boenish R, de León R, Mumby PJ, Rasher DB, et al. Managing recovery resilience in coral reefs against climate-induced bleaching and hurricanes: A 15-year cast study from Bonaire, Dutch Caribbean. *Frontiers in Marine Science*. 2019; 6:265. <https://doi.org/10.3389/fmars.2019.00265>
25. Moberg F, Folke C. Ecological goods and services of coral reef ecosystems. *Ecological economics*. 1999; 29(2):215–33. [https://doi.org/10.1016/S0921-8009\(99\)00009-9](https://doi.org/10.1016/S0921-8009(99)00009-9)
26. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. Coral reefs under rapid climate change and ocean acidification. *science*. 2007 Dec 14; 318(5857):173–42. <https://doi.org/10.1126/science.1152509> PMID: 18079392
27. Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific reports*. 2013; 3:3486. <https://doi.org/10.1038/srep03486> PMID: 24336631
28. Wilson SK, Graham NA, Pratchett MS, Jones GP, Polunin NV. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*. 2006; 12(11):2220–2234. <https://doi.org/10.1111/j.1365-2486.2006.01252.x>
29. Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NA. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity*. 2011; 3(3):424–452. <https://doi.org/10.3390/d3030424>
30. Hughes TP. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*. 1994; 265(5178):1547–1551. <https://doi.org/10.1126/science.265.5178.1547> PMID: 17801530
31. Edmunds PJ, Tsounis G, Boulon R, Bramanti L. Acute effects of back-to-back hurricanes on the underwater light regime of a coral reef. *Marine Biology*. 2019; 166:20. <https://doi.org/10.1007/s00227-018-3459-z>
32. Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, et al. Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecology Letters*. 2011; 14(1): 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x> PMID: 21070562
33. Lamy T, Legendre P, Chancerelle Y, Siu G, Claudet J. Understanding the spatio-temporal response of coral reef fish communities to natural disturbances: Insights from beta-diversity decomposition. *PLoS ONE*. 2015; 10(9):e0138696. <https://doi.org/10.1371/journal.pone.0138696> PMID: 26393511
34. Watterson JC, Patterson WF III, Shipp RL, Cowan JH. Movement of red snapper, *Lutjanus campechanus*, in the Gulf of Mexico: potential effects of hurricanes. *Gulf of Mexico Science*. 1998; 16(1):19–104. <https://doi.org/10.18785/goms.1601.13>

35. Bailey H, Secor DH. Coastal evacuations by fish during extreme weather events. *Scientific Reports*. 2016; 6:30280. <https://doi.org/10.1038/srep30280> PMID: 27455872
36. Bacheler NM, Shertzer KW, Cheshire RT, MacMahan JH. Tropical storms influence the movement behavior of a demersal oceanic fish species. *Scientific Reports*. 2019; 9:1481. <https://doi.org/10.1038/s41598-018-37527-1> PMID: 30728378
37. Khan JA, Goatley CHR, Brandl SJ, Tebbett SB, Bellwood DR. Shelter use by large reef fishes: long-term occupancy and the impacts of disturbance. *Coral Reefs*. 2017; 36:1123–1132. <https://doi.org/10.1007/s00338-017-1604-7>
38. Strickland BA, Massie JA, Viadero N, Santos R, Gastrich KR, Paz V, et al. Movements of juvenile bull sharks in response to a major hurricane within a tropical estuarine nursery area. *Estuaries and Coasts*. 2019; <https://doi.org/10.1007/s12237-019-00600-7>
39. Di Iorio L, Gervaise C, Jaud V, Robson AA, Chauvaud L. Hydrophone detects cracking sounds: Non-intrusive monitoring of bivalve movement. *Journal of Experimental Marine Biology and Ecology*. 2012; 432:9–16. <https://doi.org/10.1016/j.jembe.2012.07.010>
40. Coquereau L, Grall J, Chauvaud L, Gervaise C, Clavier J, Jolivet A, et al. Sound production and associated behaviours of benthic invertebrates from a coastal habitat in the north-east Atlantic. *Marine Biology*. 2016; 163(5):127. <https://doi.org/10.1007/s00227-016-2902-2>
41. Van Opzeeland I, Hillebrand H. Year-round passive acoustic data reveal spatio-temporal patterns in marine mammal community composition in the Weddell Sea, Antarctica. *Marine Ecology Progress Series*. 2020; 638:191–206. <https://doi.org/10.3354/meps13258>
42. Radford CA, Stanley JA, Tindle CT, Montgomery JC, Jeffs AG. Localised coastal habitats have distinct underwater sound signatures. *Marine Ecology Progress Series*. 2010; 401:21–29. <https://doi.org/10.3354/meps08451>
43. Kennedy EV, Holderied MW, Mair JM, Guzman HM, Simpson SD. Spatial patterns in reef-generated noise relate to habitats and communities: evidence from a Panamanian case study. *Journal of Experimental Marine Biology and Ecology*. 2010; 395(1–2):85–92. <https://doi.org/10.1016/j.jembe.2010.08.017>
44. Pijanowski BC, Farina A, Gage SH, Dumyahn SL, Krause BL. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*. 2011; 26(9):1213–1232. <https://doi.org/10.1007/s10980-011-9600-8>
45. Bormpoudakis D, Sueur J, Pantis JD. Spatial heterogeneity of ambient sound at the habitat type level: ecological implications and applications. *Landscape Ecology*. 2013; 28:495–506. <https://doi.org/10.1007/s10980-013-9849-1>
46. Sueur J, Pavoine S, Hamerlynck O, Duvail S. Rapid acoustic survey for biodiversity appraisal. *PLoS ONE*. 2008; 3(12): e4065. <https://doi.org/10.1371/journal.pone.0004065> PMID: 19115006
47. Sueur J, Farina A. Ecoacoustics: the ecological investigation and interpretation of environmental sound. *Biosemiotics*. 2015; 8:493–502.
48. MacLaren AR, Crump PS, Royle JA, Forstner MRJ. Observer-free experimental evaluation of habitat and distance effects on the detection of anuran and bird vocalizations. *Ecology and Evolution*. 2018; 8:12991–13003. <https://doi.org/10.1002/ece3.4752> PMID: 30619599
49. Chapman CJ, Johnstone AD, Dunn JR, Creasey DJ. Reactions of fish to sound generated by divers' open-circuit underwater breathing apparatus. *Marine Biology*. 1974; 27(4):357–66. <https://doi.org/10.1007/BF00394372>
50. Schmidt MB, Gassner H. Influence of scuba divers on the avoidance reaction of a dense vendace (*Coregonus albula* L.) population monitored by hydroacoustics. *Fisheries research*. 2006; 82(1–3):131–9. <https://doi.org/10.1016/j.fishres.2006.08.014>
51. Dickens LC, Goatley CH, Tanner JK, Bellwood DR. Quantifying relative diver effects in underwater visual censuses. *PloS one*. 2011; 6(4):e18965. <https://doi.org/10.1371/journal.pone.0018965> PMID: 21533039
52. Gasc A, Gottesman BL, Francomano D, Jinha Jung, Durham M, Mateljak J, et al. Soundscapes reveal disturbance impacts: biophonic response to wildfire in the Sonoran Desert Sky Islands. *Landscape Ecology*. 2018; 33:1399–1415. <https://doi.org/10.1007/s10980-018-0675-3>
53. Turner A, Fischer M, Tzanopoulos J. Sound-mapping a coniferous forest- perspectives for biodiversity monitoring and noise mitigation. *PLoS ONE*. 2018; 13(1):e0189843. <https://doi.org/10.1371/journal.pone.0189843> PMID: 29320514
54. Moreno-Gómez FN, Bartheld J, Silva-Escobar AA, Briones R, Márquez R, Penna M. Evaluating acoustic indices in the Valdivian rainforest, a biodiversity hotspot in South America. *Ecological Indicators*. 2019; 103:1–8. <https://doi.org/10.1016/j.ecolind.2019.03.024>
55. Urlick RJ. Principles of underwater sound. McGraw-Hill, New York, NY. 1983

56. Lillis A, Eggleston DB, Bohnenstiehl DR. Estuarine soundscapes: distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. *Marine Ecology Progress Series*. 2014; 505:1–17. <https://doi.org/10.3354/meps10805>
57. Kaplan MB, Mooney TA, Partan J, Solow AR. Coral reef species assemblages are associated with ambient soundscapes. *Marine Ecology Progress Series*. 2015; 533:93–107. <https://doi.org/10.3354/meps11382>
58. Pine M, Radford C, Jeffs A. Eavesdropping on the Kaipara Harbour: characterizing underwater soundscapes within a seagrass bed and a subtidal mudflat. *New Zealand Journal of Marine and Freshwater Research*. 2015; 49(2):247–258. <https://doi.org/10.1080/00288330.2015.1009916>
59. Pagniello C, Butler J, D'Spain G, Jaffe J, Parnell E, Širović A. Soundscape fishing: Spatial variability in a low-frequency fish chorus in the southern California kelp forest. *The Journal of the Acoustical Society of America*. 2017; 142(4):2503. <https://doi.org/10.1121/1.5014140>
60. Sun JWC, Narins PM. Anthropogenic sounds differentially affect amphibian all rate. *Biological Conservation*. 2005; 121(3):419–427. <https://doi.org/10.1016/j.biocon.2004.05.017>
61. Francis CD, Ortega CP, Cruz A. Vocal frequency change reflects different responses to anthropogenic noise in two subsocial tyrant flycatchers. *Proceedings of the Royal Society B: Biological Sciences*. 2011; 278(1714):2025–2031. <https://doi.org/10.1098/rspb.2010.1847> PMID: 21123268
62. Schroeder J, Nakagawa S, Cleasby IR, Burke T. Passerine birds feeding under chronic noise experience reduced fitness. *PLoS ONE*. 2012; 7(7):e39200. <https://doi.org/10.1371/journal.pone.0039200> PMID: 22808028
63. Bayne EM, Habib L, Boutin S. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*. 2008; 22:1186–1193. <https://doi.org/10.1111/j.1523-1739.2008.00973.x> PMID: 18616740
64. Proppe DS, Sturdy CB, St. Clair CC. Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. *Global Change Biology*. 2013; 19:1075–1084. <https://doi.org/10.1111/gcb.12098> PMID: 23504885
65. Francis CD, Ortega CP, Cruz A. Noise pollution filters bird communities based on acoustics. *PLoS ONE*. 2011; 6(11):e27052. <https://doi.org/10.1371/journal.pone.0027052> PMID: 22096517
66. Saha DC, Padhy PK. 2011 Effect of air and noise pollution on species diversity and population density of forest birds at Lalpahari, West Bengal, India. *Science of the Total Environment*. 2011; 409(24):5328–5336. <https://doi.org/10.1016/j.scitotenv.2011.08.062> PMID: 21962592
67. Tucker D, Gage SH, Williamson I, Fuller S. Linking ecological condition and the soundscape in fragmented Australian forests. *Landscape Ecology*. 2014; 29:745–758. <https://doi.org/10.1007/s10980-014-0015-1>
68. Bobryk CW, Rega-Brodsky CC, Bardhan S, Farina A, He HS, Jose S. A rapid soundscape analysis to quantify conservation benefits of temperate agroforestry systems using low-cost technology. *Agroforestry Systems*. 2016; 90:997–1008. <https://doi.org/10.1007/s10457-015-9879-6>
69. Furumo PR, Aide TM. Using soundscapes to assess biodiversity in Neotropical oil palm landscapes. *Landscape Ecology*. 2019; 34:911–923. <https://doi.org/10.1007/s10980-019-00815-w>
70. Farina A, Pieretti N. Sonic environment and vegetation structure: a methodological approach for a soundscape analysis of a Mediterranean maqui. *Ecological Informatics*. 2014; 21:120–132. <https://doi.org/10.1016/j.ecoinf.2013.10.008>
71. Gasc A, Gottesman BL, Francomano D, Jung J, Durham M, Mateljak J, et al. Soundscapes reveal disturbance impacts: biophonic response to wildfire in the Sonoran Desert Sky Islands. *Landscape Ecology*. 2018; 33:1399–1415. <https://doi.org/10.1007/s10980-018-0675-3>
72. Butler J, Stanley J, Butler MJ IV. Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. *Journal of Experimental Marine Biology and Ecology*. 2016; 479:89–96. <https://doi.org/10.1016/j.jembe.2016.03.006>
73. Stimpert AK, Madrigal BC, Wakefield WW, Yoklavich MM. Acoustic influence of underwater mobile survey vehicles on the soundscape of Pacific rockfish habitat. *The Journal of the Acoustical Society of America*. 2019; 146(1):EL45–EL51. <https://doi.org/10.1121/1.5109914> PMID: 31370646
74. Radford CA, Stanley JA, Tindle CT, Montgomery JC, Jeffs AG. Localised coastal habitats have distinct underwater sound signatures. *Marine Ecology Progress Series*. 2010; 401:21–29. <https://doi.org/10.3354/meps08451>
75. Parmentier E, Berten L, Rigo P, Auburn F, Nedelec SL, Simpson SD, et al. The influence of various reef sounds on coral-fish larvae behaviour. *Journal of Fish Biology*. 2015; 86(5):1507–1518. <https://doi.org/10.1111/jfb.12651> PMID: 25786340
76. Coquereau L, Lossent J, Grall J, Chauvaud L. Marine soundscape shaped by fishing activity. *Royal Society of Open Science*. 2017; 4:160606. <https://doi.org/10.1098/rsos.160606> PMID: 28280559

77. Bertucci F, Parmentier E, Lecellier G, Hawkins AD, Lecchini D. Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. *Scientific Reports* (Nature Publisher Group). 2016; 6:33326. <https://doi.org/10.1038/srep33326> PMID: 27629650
78. Freeman LA, Freeman SE. Rapidly obtained ecosystem indicators from coral reef soundscapes. *Marine Ecology Progress Series*. 2016; 561:69–82. <https://doi.org/10.3354/meps11938>
79. Rountree RA, Gilmore RG, Goudey CA, Hawkins AD, Luczkovich JJ, Mann DA. Listening to Fish. *Fisheries*. 2006; 31:433–446. [https://doi.org/10.1577/1548-8446\(2006\)31\[433:LTF\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2006)31[433:LTF]2.0.CO;2)
80. Locascio JV, Burton ML. A passive acoustic survey of fish sound production at Riley's Hump within Tortugas South Ecological Reserve: implications regarding spawning and habitat use. *Fishery Bulletin*. 2016; 114:103–116. <https://doi.org/10.7755/FB.114.1.9>
81. Tricas C, Boyle KS. Acoustic behaviors in Hawaiian coral reef fish communities. *Marine Ecology Progress Series*. 2014; 511:1–16. <https://doi.org/10.3354/meps10930>
82. Radford CA, Jeffs AG, Tindle CT, Montgomery JC. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia*. 2008; 156:921–929. <https://doi.org/10.1007/s00442-008-1041-y> PMID: 18461369
83. Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D'Alessandro EK. Celestial patterns in marine soundscapes. *Marine Ecology Progress Series*. 2014; 508:17–32. <https://doi.org/10.3354/meps10911>
84. Nedelec S, Simpson S, Holderied M, Radford A, Lecellier G, Radford C, et al. Soundscapes and living communities in coral reefs: Temporal and spatial variation. *Marine Ecology Progress Series*. 2015; 524:125–135. <https://doi.org/10.3354/meps11175>
85. Lillis A, Mooney TA. Snapping shrimp sound production patterns on Caribbean coral reefs: relationships with celestial cycles and environmental variables. *Coral Reefs*. 2018; 37:597–607. <https://doi.org/10.1007/s00338-018-1684-z>
86. Wenz GM. Acoustic ambient noise in the ocean: Spectra and sources. *The Journal of the Acoustical Society of America*. 1962; 34:1936. <https://doi.org/10.1121/1.1909155>
87. Knudsen VO, Alford RS, Emling JW. Underwater ambient noise. *Journal of Marine Research* 1948; 7(3):410–29.
88. Pettit EC, Lee KM, Brann JP, Nystuen JA, Wilson PS, O'Neil S. Unusually loud ambient noise in tide-water glacier fjords: A signal of ice melt. *Geophysical Research Letters*. 2015; 42(7):2309–2316. <https://doi.org/10.1002/2014GL062950>
89. Matsumoto H, Bohnenstiehl DR, Tournadre J, Dziak RP, Haxel JH, Lau TK, et al. Antarctic icebergs: A significant natural ocean sound source in the Southern Hemisphere. *Geochemistry, Geophysics, Geo-systems*. 2014; 15(8):3448–58. <https://doi.org/10.1002/2014GC005454>
90. Fox CG, Dziak RP. Hydroacoustic detection of volcanic activity on the Gorda Ridge, February–March 1996. *Deep Sea Research Part II: Topical Studies in Oceanography*. 1998; 45(12):2513–30. [https://doi.org/10.106/S0967-0645\(98\)00081-2](https://doi.org/10.106/S0967-0645(98)00081-2)
91. Dziak RP, Fox CG. Evidence of harmonic tremor from a submarine volcano detected across the Pacific Ocean basin. *Journal of Geophysical Research: Solid Earth*. 2002 May; 107(B5):E5E–1. <https://doi.org/10.1029/2001JB000177>
92. Hildebrand JA. Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*. 2009; 395:5–20. <https://doi.org/10.3354/meps08353>
93. Bohnenstiehl DR, Dziak RP, Matsumoto H, Lau TK. Underwater acoustic records from the March 2009 eruption of Hunga Ha'apai-Hunga Tonga volcano in the Kingdom of Tonga. *Journal of Volcanology and Geothermal Research*. 2013; 249:12–24. <https://doi.org/10.106/j.jvolgeores.2012.08.014>
94. Cangialosi JP, Latto AS, Berg R. Tropical Cyclone Report: Hurricane Irma (AL112017): 30 August–12 September 2017. National Center Tropical Cyclone Report. 2018;111.
95. RAMMB N. Aircraft-based tropical cyclone surface wind analysis. In AL112017-major hurricane Irma: Regional and mesoscale meteorology branch. National Oceanic and Atmospheric Administration. 2017.
96. Wachnicka A, Browder J, Jackson T, Louda W, Kelbe C, Abdelrahman O, et al. Hurricane Irma's impact on water quality and phytoplankton communities in Biscayne Bay (Florida, USA). *Estuaries and Coasts*. <https://doi.org/10.1007/s12237-019-00592-4>
97. Fourqurean JW, Rutten LM. The impact of Hurricane Georges on soft-bottom, back reef communities: site- and species-specific effects in south Florida seagrass beds. *Bulletin of Marine Science*. 2004; 75(2):239–257.
98. Wilson SS, Furman BT, Hall MO, Fourqurean JW. Assessment of Hurricane Irma impacts on south Florida seagrass communities using long-term monitoring programs. *Estuaries and Coasts*. 2019; Jan:1–4. <https://doi.org/10.1007/s12237-019-00623-0>

99. Kobelt JN, Sharp WC, Miles TN, Feehan CJ. Localized impacts of Hurricane Irma on *Diadema antillarum* and coral reef community structure. *Estuaries and Coasts*. 2019. Nov 15:1–1. <https://doi.org/10.1007/s12237-019-00665-4>
100. Viehman, Shay; Gittings, Steve; Groves, Sarah; Moore, Jennifer; Moore, Tom; Stein, Jennifer (2018). NCCOS Assessment: Coral Disturbance Response Monitoring (DRM) along the Florida Reef Tract following Hurricane Irma from 2017-10-09 to 2017-10-18 (NCEI Accession 0179071). [indicate subset used]. NOAA National Centers for Environmental Information. Dataset. <https://doi.org/10.25921/sscd-6h41>
101. Keller BD, Donahue S. 03 sanctuary science report: An ecosystem report card after five years of marine zoning. US Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service. OYce of National Marine Sanctuaries, Florida Keys National Marine Sanctuary, Marathon. 2002.
102. Stephenson TA, Stephenson A. Life between tide-marks in North America: The Florida Keys. *The Journal of Ecology*. 1950; 1:354–402. <https://doi.org/10.2307/2256451>
103. Leichter JJ, Stewart HL, Miller SL. Episodic nutrient transport to Florida coral reefs. *Limnology and Oceanography*. 2003; 48(4):1394–1407.
104. Szmant AM, Forrester A. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Cora Reefs*. 1996; 15:21–41. <https://doi.org/10.1007/BF01626075>
105. Boyer JN, Jones RD. A view from the bridge: external and internal forces affecting the ambient water quality of the Florida National Marine Sanctuary (FKNMS). *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*. CRC Press, Boca Raton, FL. 2002:609–28.
106. McWilliam JN, McCauley RD, Erbe C, Parson MJG. Patterns of biophonic periodicity on coral reefs in the Great Barrier Reef. *Scientific Reports*. 2017; 7:17459. <https://doi.org/10.1038/s41598-017-15838-z> PMID: 29234024
107. Monczak A, Mueller C, Miller ME, Ji Y, Borgianini SA, Montie EW. Sound patterns of snapping shrimp, fish, and dolphins in an estuarine soundscape of the southeastern USA. *Marine Ecology Progress Series*. 2019; 609:49–68. <https://doi.org/10.3354/meps12813>
108. Cato DH. Some unusual sounds of apparent biological origin responsible for sustained background noise in the Timor Sea. *The Journal of the Acoustical Society of America*. 1980; 68(4):1056–1060. <https://doi.org/10.1121/1.384989>
109. Mann DA, Locascio JV, Coleman FC, Koenig CC. Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. *Endangered Species Research*. 2009; 7:229–236. <https://doi.org/10.3354/esr00109>
110. Mann DA, Locascio JV, Schärer MT, Nemeth MI, Appeldoorn RS. Sound production by red hind *Epinephelus guttatus* in spatially segregated spawning aggregations. *Aquatic Biology*. 2010; 10(2):149–154. <https://doi.org/10.3354/ab0072>
111. Schärer MT, Nemeth MI, Rowell TJ, Appeldoorn RS. Sounds associated with reproductive behavior of the black grouper (*Mycteroperca bonaci*). *Marine Biology*. 2014; 161:141–147. <https://doi.org/10.1007/s00227-013-2324-3>
112. Horch K, Salmon M. Adaptations to the acoustic environment by the squirrelfishes *Myripristis violaceus* and *M. pralinus*. *Marine Behaviour and Physiology*. 1973; 2:1–4. <https://doi.org/10.1080/10236247309386920>
113. Mann DA, Lobel PS. Passive acoustic detection of sounds produced by the damselfish *Dascyllus albisella* (Pomacentridae). *Bioacoustics*. 1995; 6(3):199–213. <https://doi.org/10.1080/09524622.1995.9753290>
114. Burkenroad MD. Sound production in the Haemulidae. *Copeia*. 1930; 1930(1):17–18.
115. Bertucci F, Ruppé L, Van Wassenbergh S, Compère Parmentier E. New insights into the role of the pharyngeal jaw apparatus in the sound-producing mechanism of *Haemulon flavolineatum* (Haemulidae). *Journal of Experimental Biology*. 2014; 217:3862–3869. <https://doi.org/10.1242/jeb.109025> PMID: 25355850
116. Fish MP, Mowbray WH. Sounds of western North Atlantic fishes. A reference file for biological underwater sounds. John Hopkins Press; 1970. pp.1–231
117. Monczak A, Ji Y, Soueidan J, Montie EW. Automatic detection, classification, and quantification of sciaenid fish calls in an estuarine soundscape in the southeast United States. *PLoS ONE*. 2019; 14(1). <https://doi.org/10.1371/journal.pone.0209914> PMID: 30650120
118. Au WW, Banks K. The acoustics of the snapping shrimp *Synalpheus parneomeris* in Kaneohe Bay. *The Journal of the Acoustical Society of America*. 1998; 103(1):41–47. <https://doi.org/10.1121/1.423234>

119. Lyon RP, Eggleston DB, Bohnenstiehl DR, Layman CA, Ricci SW, Allgeier JE. Fish community structure, habitat complexity, and soundscape characteristics of patch reefs in a tropical, back-reef system. *Marine Ecology Progress Series*. 2019; 609:33–48. <https://doi.org/10.3354/meps12829>
120. Buskirk RE, Frohlich C, Latham GV, Chen AT, Lawton J. Evidence that biological activity affects ocean bottom seismograph recordings. *Marine Geophysical Researches*. 1981; 5(2):189–205. <https://doi.org/10.1007/BF00163479>
121. Bowman DC, Wilcock WS. Unusual signals recorded by ocean bottom seismometers in the flooded caldera of Deception Island volcano: volcanic gases or biological activity?. *Antarctic Science*. 2014; 26(3):267. <https://doi.org/10.1017/S095410203000758>
122. Van Hoek RV, Paxton AB, Bohnenstiehl DR, Taylor JC, Fodrie FJ, Nowacek DP, et al. Soundscapes of natural and artificial temperate reefs: similar temporal patterns but distinct spectral content. *Marine Ecology Progress Series*. 2020; 649:35–51. <https://doi.org/10.3354/meps13434>
123. Ruppé L, Clément G, Herrel A, Ballesta L, Décamps T, Kéver L, et al. Environmental constraints drive the partitioning of the soundscape in fishes. *Proceedings of the National Academy of Sciences*. 2015; 112:6092–7. <https://doi.org/10.1073/pnas.1424667112> PMID: 25848025
124. McWilliam JN, McCauley RD, Erbe C, Parsons MJ. Soundscape diversity in the Great Barrier Reef: Lizard Island, a case study. *Bioacoustics*. 2018; 27(3):295–311. <https://doi.org/10.1080/09524622.2017.1344930>
125. Davis TM, Countryman KA, Carron MJ. Tailored acoustic products utilizing the NAVOCEANO GDEM (a generalized digital environmental model). In *Proceedings, 36th Naval Symposium on Underwater Acoustics 1986 Apr*. San Diego, CA: Naval Ocean Systems Center.
126. Hildebrand J. Sources of anthropogenic sound in the marine environment. In *Report to the policy on sound and marine mammals: an international workshop*. US Marine Mammal Commission and Joint Nature Conservation Committee UK London England. 2004.
127. Hildebrand JA. Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*. 2009; 395:5–20. <https://doi.org/10.3354/meps08353>
128. Kipple BM, Gabriele CM. Glacier Bay watercraft noise: report to Glacier Bay National Park by the Naval Surface Warfare Cent-Detachment Bremerton. Technical Report NSWCDD-71-TR-2003/522; 2003.
129. Hatch L, Clark C, Merrick R, Van Parijs S, Ponirakis D, Schwehr K, et al. 2008. Characterizing the relative contributions of large vessels to total ocean noise fields: A case study using the Gerry E. Studds Stellwagen Bank National Marine Sanctuary. *Environmental Management*. 2008; 42:735–752. <https://doi.org/10.1007/s00267-008-9169-4> PMID: 18626686
130. Bassett C, Polagye B, Holt M, Thomson J. A vessel noise budget for Admiralty Inlet, Puget Sound, Washington (USA). *The Journal of Acoustical Society of America*. 2012; 132:3706. <https://doi.org/10.1121/1.4763548> PMID: 23231102
131. Steneck RS, Arnold SN, Boenish de León R, Mumby PJ, Rasher DB, et al. Managing recovery resilience in coral reefs against climate-induced bleaching and hurricanes: a 15 year case study from Bonaire, Dutch Caribbean. *Frontiers in Marine Science*. 2019; 6:265. <https://doi.org/10.3389/fmars.2019.00265>
132. Emanuel K. Tropical cyclones. *Annual Review of Earth and Planetary Sciences*. 2003. 31(1):75–104. <https://doi.org/10.1146/annurev.earth.31.100901.141259>
133. Zhao Z, D'Asaro EA, Nystuen JA. The sound of tropical cyclones. *Journal of Physical Oceanography*. 2014; 44(10):2763–2778. <https://doi.org/10.1175/JPO-D-14-0040.1>
134. Carey WM, Bradley MP. Low-frequency ocean surface noise sources. *The Journal of the Acoustical Society of America*. 1985; 78(S1):S1–S2. <https://doi.org/10.1121/1.2022686>
135. Prosperetti A. Bubble-related ambient noise in the ocean. *The Journal of the Acoustical Society of America*. 1985; 78(S1):S2. <https://doi.org/10.1121/1.2022741>
136. Wolanski E, Delesalle B. Upwelling by internal waves, Tahiti, French Polynesia. *Continental Shelf Research*. 1995; 15(2–3):357–368. [https://doi.org/10.1016/0278-4343\(93\)E0004-R](https://doi.org/10.1016/0278-4343(93)E0004-R)
137. Longuet-Higgins MS, Stewart RW. Radiation stresses in water waves; a physical discussion, with applications. *Deep-Sea Research*. 1964; 11(4):529–562.
138. Heupel MR, Simpfendorfer CA, Hueter RE. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *Journal of Fish Biology*. 2003; 64(5): 1357–1363. <https://doi.org/10.1046/j.1095-8649-2003.00250.x>
139. Secor DH, Zhang F, O'Brien MH, Li M. Ocean destratification and fish evacuation caused by a Mid-Atlantic tropical storm. *ICES Journal of Marine Science*. 2019; 76(2):573–584. <https://doi.org/10.1093/icesjms/tsx241>

140. Johannes RE. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*. 1978; 3:65–84. <https://doi.org/10.1007/BF00006309>
141. Kobara S, Heyman WD. Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series*. 2010; 405:243–254. <https://doi.org/10.3354/meps08512>
142. Habrun CA, Sancho G. Spawning ascent durations of pelagic spawning reef fishes. *Current Zoology*. 2012; 58(1):95–102. <https://doi.org/10.1093/czoolo/58.1.95>
143. Claydon JAB, McCormick MI, Jones GP. Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns. *Journal of Fish Biology*. 2014; 84(4):1–28. <https://doi.org/10.1111/jfb.12355> PMID: 24665915
144. Locascio JV, Mann DA. Effects of Hurricane Charley on fish chorusing. *Biology Letters*. 2005; 1:362–365. <https://doi.org/10.1098/rsbl.2005.0309> PMID: 17148207
145. American Geophysical Union. Hurricanes Irma, Maria temporarily altered choruses of land, sea animals. Laboratory Equipment. 2018. Available from: <https://news.agu.org/press-release/hurricanes-irma-and-maria-temporarily-altered-choruses-of-land-and-sea-animals/>
146. Gross M. Listening to the sounds of the biosphere. *Current Biology*. 2018; 28(16):R847–R850. <https://doi.org/10.1016/j.cub.2018.08.002>
147. Tulevech SM, Recksiek CW. Acoustic tracking of adult white grunt, *Haemulon plumieri*, in Puerto Rico and Florida. *Fisheries Research*. 1994; 19(3–4):301–319. [https://doi.org/10.1016/0165-7836\(94\)90046-9](https://doi.org/10.1016/0165-7836(94)90046-9)
148. Hitt S, Pittman SJ, Brown KA. Tracking and mapping sun-synchronous migrations and diel space use patterns of *Haemulon sciurus* and *Lutjanus apodus* in the US Virgin Islands. *Environmental Biology of Fishes*. 2011; 92:525–538. <https://doi.org/10.1007/s10641-011-9875-2>
149. Herbig JL, Keller J, Morley D, Kristen W, Barbera P, Acosta A. Examining movement patterns of yellowtail snapper, *Ocyurus chrysurus*, in the Dry Tortugas, Florida. *Bulletin of Marine Science*. 2019; 95(1):45–67. <https://doi.org/10.5343/bms.2018.0003>
150. Rooker JR, Dennis GD. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science*. 1991; 49(3):684–698.
151. Burke NC. Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. *Environmental Biology of Fishes*. 1995; 42:365–374. <https://doi.org/10.1007/BF00001467>
152. Nagelkerken I, van der Velde G, Gorissen MW, Van't Hof T, den Hartog C. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science*. 2000; 51(1):31–44. <https://doi.org/10.1006/ecss.2000.0617>
153. Pereira PHC, Ferreira BP. Effects of life phase and schooling patterns on the foraging behavior of coral-reef fishes from the genus *Haemulon*. *Fish Biology*. 2013; 83(4):1226–1238. <https://doi.org/10.1111/jfb.12054> PMID: 23557301
154. Leahy SM, McCormick MI, Mitchell MD, Ferrari MCO. To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biology Letters*. 2011; 7(6):811–813. <https://doi.org/10.1098/rsbl.2011.0645> PMID: 21849308
155. White PS. Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS, editors. *The ecology of natural disturbance and patch dynamics*; Academic Press: Orlando, Florida; 1985. pp. 3–13.
156. Platt WJ, Connell JH. Natural disturbances and directional replacement of species. *Ecological Monographs*. 2003; 73(4):507–522. <https://doi.org/10.1890/01-0552>

**CHAPTER 2: Spatiotemporal variation in coral assemblages and reef habitat complexity  
among shallow fore-reef sites in the Florida Keys National Marine Sanctuary**

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Article

# Spatiotemporal Variation in Coral Assemblages and Reef Habitat Complexity among Shallow Fore-Reef Sites in the Florida Keys National Marine Sanctuary

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**Abstract:** With the unprecedented degradation and loss of coral reefs at multiple scales, the underlying changes in abiotic and biotic features relevant to the three-dimensional architecture of coral reefs are critical to conservation and restoration. This study characterized the spatiotemporal variation of habitat metrics at eight fore-reef sites representing three management zones in the Florida Keys, USA using visual habitat surveys (2017–2018) acquired before and after Hurricane Irma. Post-hurricane, five of those sites were surveyed using structure-from-motion photogrammetry to further investigate coral morphology on structural complexity. Multivariate results for visual surveys identified moderate separation among sites, with fished sites characterized by complex physical features such as depth and vertical hard relief while protected sites generally harbored high abundances of live coral cover. Three-dimensional models of mapped sites showed within site variation as another driver in site separation. Additionally, fine-scale orthoimage analyses identified significant differences in dominant coral morphologies at each mapped site. This study suggests protected reef sites generally harbor higher live coral cover despite some fished sites being structurally similar in seabed topography. Our work provides fine-scale spatial data on several managed sites within a marine sanctuary and highlights the contribution of diverse coral assemblages to the coral reef framework.

**Keywords:** structure-from-motion; underwater photogrammetry; coral reef; habitat complexity; coral morphology; reef monitoring; Hurricane Irma



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## 1. Introduction

Coral reefs are highly productive, biologically rich, and structurally complex ecosystems supporting 25% of marine life in the world's oceans [1]. They also support a broad range of ecosystem services [2–4] with recreational and cultural benefits [5–7], as well as resources that support the economically important pharmaceutical, fisheries, aquarium trade, and construction industries [8–10]. Coral reefs are also increasingly threatened by a broad array of chronic and acute stressors. Chronic stressors range from destructive fishing practices to eutrophication and sedimentation from land-use practices and sewage-runoff [11–14]. Additive effects of acute but highly destructive impacts such as the spread of invasive species [15–17] and aggressive coral diseases [18,19], thermal stress [20,21] and vessel grounding incidents [22,23] are causing unprecedented mortality rates for reef-building corals. Although not as detrimental as large-sale anthropogenic stressors, the residual effects of long-term recreational SCUBA diving on coral reefs can decrease structural complexity from broken and abraded benthos [24].

Persistent declines in the three-dimensional structure of coral reefs will have cascading consequences for reef fish diversity, fisheries, and the ecosystem services that coastal human societies rely on [8,25–27]. Marine protected areas (MPAs) are increasingly used to support

ecosystem-based management, mitigate damage from fishing interactions, conserve species at risk, and are often successful when designed as a network connected by larval dispersal and migration by mobile species [28–31]. However, coral reef restoration methods and long-term monitoring in protected areas can vary across local to regional scales, and can address multiple restoration goals [32,33].

Defining ecological units to assess impacts for local and regional management plans can be difficult when spatiotemporal differences occur at complex scales. For example, seascape-level metrics relevant to ecological resilience, such as coral cover and diversity or herbivorous fish biomass, are often important at local spatial scales [34–37]. Efforts to understand and monitor spatiotemporal variations across reef habitats recognize the need for spatially relevant metrics and biological data at multiple scales (e.g., organism level to community level) [38]. Modern coral reef monitoring and restoration efforts are implementing photomosaics as tools to study reef resilience indicators at the community level in the face of hurricanes, coral disease, and overall decline [37,39,40]. The use of fine-scale mapping tools such as Structure-from-Motion (SfM) photogrammetry is becoming widely used to monitor and quantify differences among sites that vary in three-dimensions [41–43]. Moreover, fine-scale reef mapping approaches at the colony scale (1 mm–1 cm pixel) highlight the local variability in biotic cover and relevant physical features appropriate for local management priorities [44,45].

Established in 1990, the Florida Keys National Marine Sanctuary (FKNMS) includes ~9500 km<sup>2</sup> of the Florida Reef Tract (FRT), a large bank-barrier reef system comprised of fringing mangroves, seagrass beds, near-shore patch reefs, and the off-shore reef tract across a network of marine zones and regulated fishing habitats [46,47]. The FKNMS is one of the largest MPAs in the United States and provides a mosaic of critical habitats along the Florida Keys archipelago for over 6000 species of invertebrates, fishes, and coastal flora [47]. The main causes for coral decline within the FKNMS are related to disease, thermal mass bleaching, fragmentation, and predation [48,49]. Several prominent massive, reef-building corals in the Florida Keys are listed on The Endangered Species Act (50 CFR 402) as threatened, such as the pillar coral *Dendrogyra cylindrus* [48,50,51] and three star corals *Orbicella* sp., as well as the branching staghorn coral *Acropora cervicornis* and elkhorn coral *A. palmata* [49,52]. The average benthic cover of scleractinian (stony) corals in the FKNMS were estimated to have declined from ~13% in 1996 to 8 % in 2009 [53]. More recently, the aggressive stony coral tissue loss disease (SCTLD) epidemic in the Florida Keys, first reported in 2014, has impacted at least 23 coral species, leading to reductions in coral density by 30%, with differential susceptibility factors for specific coral families and morphologies [54–56].

Long-term regional coral surveys from 2007–2016 in the Southeast FRT, the three parallel liner reefs within the FRT extending from Biscayne Bay to St. Lucie Inlet, observed spatiotemporal variations in the negative response to thermal stress for key reef building coral taxa (e.g., Acroporidae, Montastraeidae, Siderastreidae), and also observed minimal or positive impacts for weedy or small coral taxa (e.g., Poritidae) [57]. As the threats to coral reefs progress, fine-scale baseline data on reef habitats and benthic cover is necessary to document how changes in coral communities and their contribution to reef structure complexity will impact future ecological productivity [19,58,59].

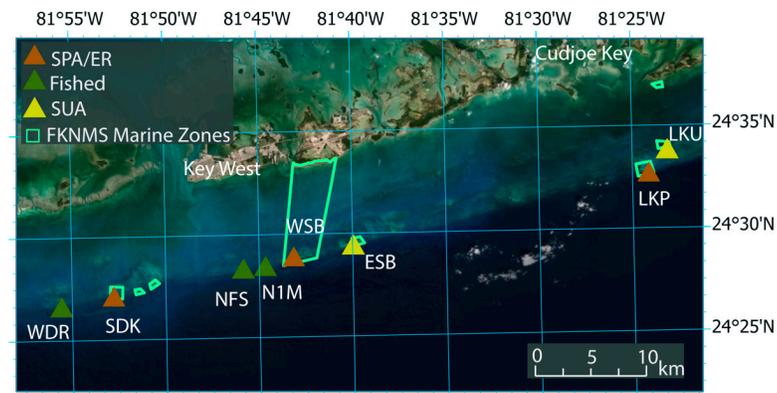
The goal of this study was to characterize spatiotemporal variation in coral reef habitat features using visual habitat surveys and high-resolution benthic maps produced by SfM photogrammetry of coral reefs located in different management zones within the FKNMS. A secondary goal was to compare changes in habitat characteristics before versus after the passage of Hurricane Irma (September 2017) in the Lower Keys section of the FKNMS. Large-scale benthic mapping in the Florida Keys region has occurred since 1996 [60,61]. However, the results from the present study may serve as a baseline for a more fine-scale approach to long-term monitoring and restoration efforts by characterizing the relationship between management zones, coral reef assemblages and habitat characteristics on a local scale.

## 2. Materials and Methods

Reef Visual Census (RVC) surveys were conducted seasonally by scuba divers at eight fore-reef study sites in the lower Florida Keys between February 2017 and December 2018. In 2018, SfM habitat photogrammetry was conducted within a subset of 5 of the 8 sites. The general statistical approach included generating a suite of habitat metrics from each survey dataset to test for differences in habitat characteristics among sites and over time. These datasets were also used to observe differences in metrics derived from each data source.

### 2.1. Study System

There are five marine zone types in the FKNMS to protect reef habitats while allowing adequate access for fishing and recreation—these include: (i) sanctuary preservation areas (SPAs), (ii) ecological reserves (ERs), (iii) wildlife management areas (WMAs), (iv) special use, research only areas (SUAs), and (v) existing management areas (EMAs). The five focal reef sites mapped within this study included four marine zones [Figure 1. Site Map]: (i) one regulated fished site subject to hook-and-line, trolling, and the harvest of state/federally regulated species; (ii) two SPAs with open access to recreational divers/snorkelers and boats yet prohibits the harvest of species (no-take) and anchoring; (iii) one ER, and (iv) one SUA that is permit accessible only for scientific research and restoration efforts.



**Figure 1.** Study site map of zone D in the FKNMS and survey sites Western Dry Rocks (WDR), Sand Key SPA (SDK), Nine Foot Stake (NFS), Number 1 Marker (N1M), Western Sambo ER (WSB), Eastern Sambo SUA (ESB), Looe Key SPA (LKP), and Looe Key SUA (LKU).

Nine Foot Stake (NFS) is a regulated, fished site comprised of shallow hardbottom spur and sand grooves and is frequently visited by recreational charter boats for fishing and scuba diving. This site contains mooring buoys for vessels to minimize anchor damage. Sand Key SPA (SDK) is roughly 11 km southeast of Key West, Florida. It has a spur-and-groove formation but contains several channels of reef rubble due to wind and wave action. Located offshore of Cudjoe Key, Looe Key SPA (LKP) is one the most iconic reefs in the lower Florida Keys due to the abundance and diversity of coral species, large barrel sponges, schooling reef fishes, large predatory fishes (e.g., *Carcharhinus* spp., *Epinephelus itajara*) and deep spur-and-groove formations greater than 7 m in depth. LKP is also a sentinel site for coral restoration and coral outplant studies for endangered coral species impacted by coral disease and long-term decline [62,63]. Western Sambo ER (WSB) is one of the largest marine zones protecting 30 km<sup>2</sup> of a broad range of habitats from nearshore patch reefs to the offshore shallow bank reef and is relatively shallow (~4 m) [64]. Additionally, WSB has historically harbored a large abundance of branching and boulder corals. Eastern Sambo SUA (ESB) lies adjacent to WSB and is widely recognized as a pristine site home to

healthy massive star (e.g., *Montastraea cavernosa*, *Siderastrea siderea*) and brain corals (e.g., *Colpophyllia natans*, *Diploria* spp.), as well as serving as a control site for resource managers evaluating the efficacy of marine zone types [64].

On September 10th 2017, before making landfall at Cudjoe Key, Florida, category 4 Hurricane Irma traveled directly over the lower Florida Keys with maximum wind speeds reaching 115 kts and sustained hurricane force winds extending across all reef sites [65]. One month later, science divers with the National Oceanographic and Atmospheric Administration (NOAA), as well as other stakeholders surveyed over 50 coral reef sites for damage by identifying evidence of heavy sedimentation, long-lasting turbidity, reef erosion, and fast-moving marine debris [66]. Reefs closer to the where the hurricane made landfall, such as LKP, suffered >26% prevalence of hurricane-impacted corals while sites farther south along the archipelago, such as WSB and SDK, showed <20% of coral impacts [67]. To document impacted reef sites and observe variation in habitat characteristics after hurricane Irma, habitat characteristics at all eight sites were assessed via the visual surveys by divers (RVC protocol), and five of eight sites were digitally mapped by NC State science divers using SfM photogrammetry methods in September 2018 (Table 1).

**Table 1.** Summary of the number of RVC and structure-from-motion (SfM) photogrammetry surveys conducted at each site between 2017 and 2018. Post-Irma surveys were conducted starting in December 2018. SfM models that were not successful in the AgiSoft Metashape reconstruction workflow are denoted (\*). Not sampled = NS.

Method	RVC									SfM	
	Site	Feb-17	May-17	Jul-17	Dec-17	Feb-18	Jun-18	Sep-18	Dec-18	Sum	Sep-18
Fished		2	3	3	3	1	3	2	2	19	2
N1M			1	1	1		1			4	NS
NFS		1	1	1	1		1	1	1	7	1
WDR		1	1	1	1	1	1	1	1	8	*
SPA		1	3	3	2	1	3	3	3	19	3
LKP			1	1		1	1	1	1	6	1
SDK			1	1	1		1	1	1	6	1
WSB		1	1	1	1		1	1	1	7	1
SUA		1	2	2	2	1	2	2	2	14	1
ESB		1	1	1	1		1	1	1	7	1
LKU			1	1	1	1	1	1	1	7	*
<b>Grand Total</b>		4	8	8	7	3	8	7	7	52	5

## 2.2. RVC Habitat Surveys

Reef Visual Census (RVC) surveys followed modified Bohnsack-Bannerot visual survey methods and standardized protocols developed by a cooperative multi-agency network of the Florida Fish and Wildlife Conservation Commission (FWCC), NOAA, National Park Service, and the University of Miami [68–70]. Primary sampling units (100 m × 100 m cells) within in each reef site were generated and as a part of a larger study by our research group bottom-mounted soundscape moorings were deployed on the sandy bottom in sand channels at a randomly selected GPS coordinate near the seaward side of each fore-reef site. The primary sampling units were further subdivided into a two-stage stratified random design in which two divers each conducted a stationary point-count RVC survey inside individual 15 m diameter cylinders extending from the seafloor vertically to the surface (depending on visibility) at randomly selected points along the spur-and-groove habitat [69]. RVC surveys allowed for the simultaneous collection of reef fish density and distribution features as well as information on biotic and abiotic habitat features; however, for the purpose of this study, data results will only reflect habitat data acquired from the two divers (see below and Table 2). Depending on the habitat type and visibility, the time required for each survey ranged from 15–20 min to record both fish and habitat data. PVC-pipes constructed as a “T” (1 m length with 0.1 m increments × 0.3 m width) were

used as reference measurements for estimating substrate slope and maximum vertical hard and soft relief. The surveys from the two divers were non-overlapping (~10–30 m apart), and the data from the divers combined to produce mean values for many of the habitat characteristics within a given monthly survey at a given site. There were three Pre-Irma (Feb., May, July 2017) and five post-Irma surveys (Dec. 2017, Feb., Jan., Sept., Dec. 2018), however not all sites were surveyed during each sampling period due to unfavorable weather conditions limiting site visitation (Table 1).

**Table 2.** Summary and descriptions of RVC habitat variables collected Pre-Irma and Post-Irma 2017–2018. N = 3 Pre-Irma and N = 5 Post-Irma.

Group	Habitat Metric	Description	Variable Name
Environmental Data	Depth (m)	Maximum depth	<i>depth</i>
	Visibility (m)	Horizontal visibility at depth	<i>viz</i>
Structural Complexity	Max. hard vertical relief (m)	Maximum height of hard relief (coral, coralline spur, hardbottom ledge)	<i>v-hard</i>
	Max. soft vertical relief (m)	Maximum height of soft relief (e.g., octocorals, sponges, macroalgae)	<i>v-soft</i>
Surface Relief Cover	Hard relief surface cover (%)	Percentage of hard relief <0.2, 0.2–0.5, 0.5–1.0, 1.0–1.5, and >1.5 m in height.	<i>s-hard</i>
	Soft relief surface cover (%)	Percentage of soft relief <0.2, 0.2–0.5, 0.5–1.0, 1.0–1.5, and >1.5 in height.	<i>s-soft</i>
Abiotic Footprint	Abiotic sand	Percentage cover of coarse or biogenic sand	<i>a-sand</i>
	Abiotic rubble	Percentage cover of coarse gravel to unconsolidated rock or dislodged coral fragments	<i>a-rubble</i>
	Abiotic hardbottom	Percentage of consolidated lithogenic/biogenic substratum including dead coral	<i>a-hard</i>
Biotic Cover	Biotic algae <1 cm	Percentage of hardbottom covered in algae <1 cm height (e.g., turf algae)	<i>b-algae1</i>
	Biotic algae >1 cm	Percentage of hardbottom covered in algae >1 cm height (e.g., Halimeda, Dictyota)	<i>b-algae2</i>
	Biotic live coral	Percentage of live coral cover	<i>b-coral</i>
	Biotic octocoral	Percentage of octocoral cover	<i>b-octo</i>
	Biotic sponge	Percentage sponge cover	<i>b-sponge</i>

In the Florida Keys, spur-and-groove reefs are comprised of coalesced coral fragments cemented into hardbottom substrate that has undergone generations of coral growth in the direction of dominant wave energy and sediment accretion [71–73]. Therefore, habitat type was classified according to four types: (i) contiguous spur-and-groove, (ii) rubble dominated, (iii) isolated reef structure, or (iv) a matrix of habitat types. Visual surveys by divers generated information on (i) depth, (ii) hard relief of stony corals, (iii) soft relief of soft corals, (iv) abiotic footprint (percent cover sand, hardbottom, rubble), and (v) the dominant biological cover of the hardbottom (percent cover algae, live stony corals, octocorals, sponges) (Table 2). Additionally, divers recorded the presence of submerged debris such as derelict lobster traps, fishing gear, and rope.

### 2.3. SfM Image Acquisition

Two divers used transect tape to create a rectangular 30 m × 15 m area covering the spur-and-groove reef formation. This grid was positioned to span the area where the RVC

surveys (15 m diameter cylinders) were randomly sited by the divers. Ground control points were set along the transect tape at 15 m increments and six weighted, polyvinyl disks (Frisbees) were deployed as ground control points (GCPs) for each corner and long-axis mid-points. Four to five PVC-pipes shaped as a “T” (1 m length) were placed randomly on the seabed as a known reference distance to further constrain the scale of the model. Next, a diver swam back and forth in a grid pattern, with transects oriented perpendicular to the spur-and-groove structure and separated by ~2–3 m. A PVC-pipe frame housed three GoPro Hero3/Hero4 cameras operating at an aperture of f2.8, shutter speed 1/120 s, ISO 120–157-, and 12-megapixels capturing images on Time Lapse Intervals of two seconds to ensure adequate image overlapping for post-processing. The number of images per site ranged from ~6000–12,000, and each mapping survey was completed over a period of a few hours to minimize variability in visibility and lighting.

#### 2.4. D Habitat Reconstruction Workflow

Agisoft Metashape (v 1.5.2.7838) software was used to reconstruct three-dimensional models from the digital photographs (Figure 2; Table 3). We adopted data workflows from related studies such as Burns et al. [74] and Fukunaga et al. [43,75] (Table S1) to create coral reef photogrammetry models. Initial image alignment settings used a key point limit and tie point limit of 40,000 and 10,000, respectively with the level of accuracy set as ‘high’ and generic preselection enabled. If the initial alignment was unsuccessful, then alignment settings were modified to a key point limit and tie point limit of 70,000 and 8000, respectively, in addition to re-aligning free floating points [75]. The model scale was constrained based on the GPC and pvc-T-stick markers. Dense (100’s millions of points) elevation point clouds were gridded using MB-System (Caress et al., 1995) to generate 0.5 cm × 0.5 cm-resolution digital elevation models (DEMs). These data were saved as GeoTIFF files with both local and UTM coordinates. The area and dimensions of the 3D models vary between sites based on image quality and spatial coverage obtained by the divers. Imagery from Western Dry Rocks and Looe Key SUAs were not successful in the image alignment process due to poor water quality, poor camera adjustments, and/or lack of sufficient overlapping images.

**Table 3.** Summary of SfM model statistics by site. Average point density is the average number of dense cloud points per cell in the DEM. Each DEM cell is 0.005 m × 0.005 m.

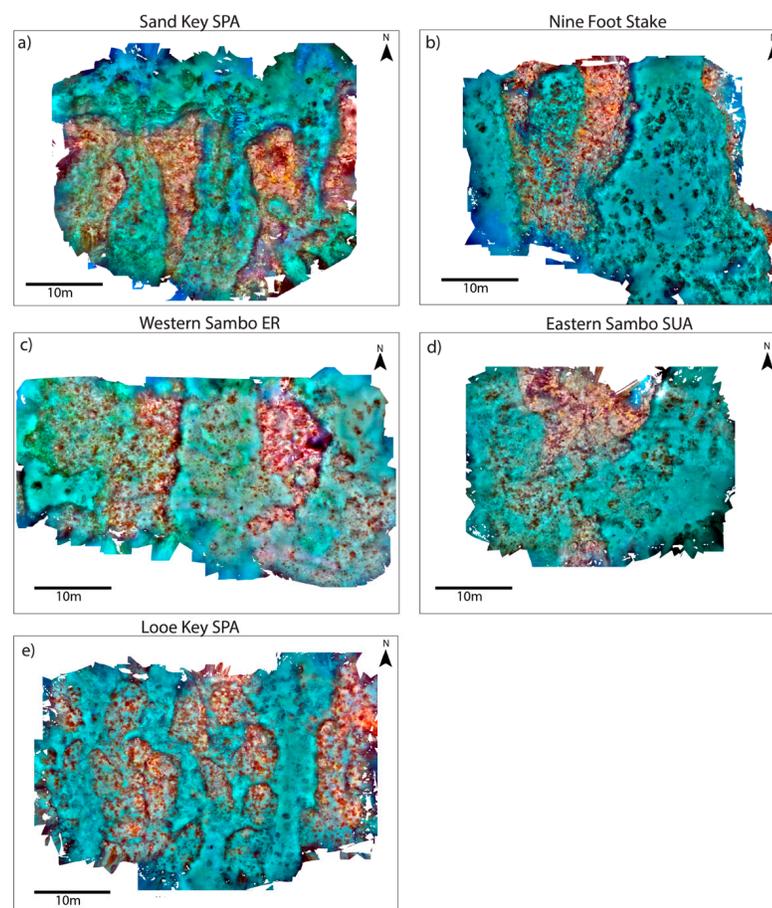
Site	Camera Images	Map area (m <sup>2</sup> )	Avg. Point Density/Cell	Depth (m)			
				Mean	SD	Median	Min–Max
Sand Key (SPA)	6258	1092	38	5.3	0.90	5.4	1.9–7.1
Nine Foot Stake	9569	1037	50	6.7	0.77	7.0	3.8–7.7
Western Sambo (ER)	7074	1005	49	4.3	0.62	4.4	2.0–5.8
Eastern Sambo (SUA)	4815	765	17	5.1	0.81	5.2	1.7–6.4
Looe Key (SPA)	12,809	1079	6	7.3	0.75	7.4	4.3–8.9

#### 2.5. Quantifying Habitat Complexity Metrics

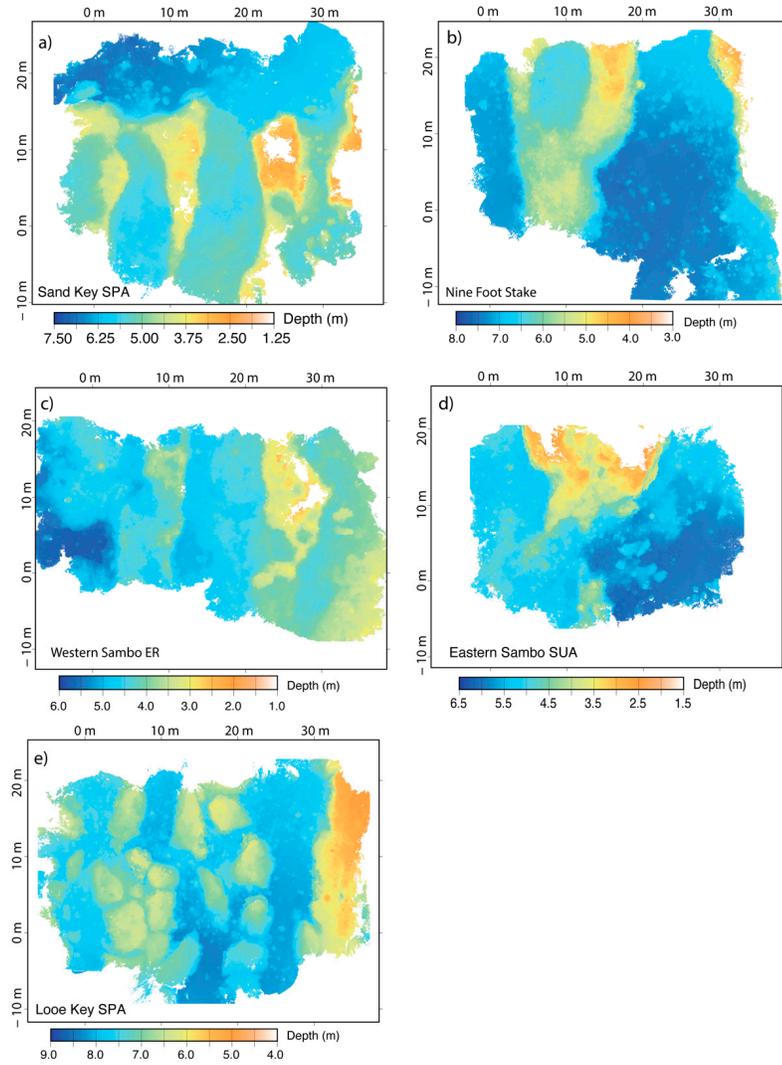
The DEMs were imported into ArcGIS Pro (Figure 3) to quantify habitat complexity metrics using the 3D Analyst and Spatial Analyst and Benthic Terrain Modeler (BTM) v3.0, which generated habitat metrics such as neighborhood depth, slope, vector ruggedness measure (VRM), and surface area-to-planar area ratio [76] (See Table 4). To calculate the VRM, a unit vector normal to each grid cell is resolved into its x-y-z components. The normalized resultant vector (R) is then calculated within a 3 m × 3 m neighborhood using a moving window centered on each grid cell. The VRM is defined as 1-R, where the value of 0 indicates a planar surface and 1 indicates a surface maximum roughness [77,78]. The surface area to planar area (SAPA) ratio, or rugosity, was also calculated using 3 × 3 neighborhood windows. Eight triangular surfaces were created by linking the center point

of the central grid cell with the adjoining cells. The summed area of these surfaces was normalized by the planar surface area [79].

To quantify variability in digital terrain metrics within each site, these raster layers were sampled along a series of transects, and average metric values were reported for each profile. These transects extended 30 m orthogonal to the spur-and-groove structures (oriented approximately west-to-east) with 3 m spacing in between lines, resulting between 6 and 7 profiles per site (Figure S1). The maximum relief and *rms* roughness were also calculated from these same depth profiles [80,81]. Coral reef rugosity was digitally calculated measuring the ratio of the digital contour line along the three-dimensional surface and the straight horizontal distance.



**Figure 2.** SfM orthomosaics for (a) Sand Key SPA, (b) Nine Foot Stake, (c) Western Sambo ER, (d) Eastern Sambo SUA, and (e) Looe Key SPA. Imagery collected post-Hurricane Irma in September 2018.



**Figure 3.** SfM-derived bathymetry for sites (a) Sand Key SPA (SDK), (b) Nine Foot Stake (NFS), (c) Western Sambo ER (WSB), (d) Eastern Sambo SUA (ESB), and (e) Looe Key SPA (LKP).

**Table 4.** Summary and descriptions of photogrammetry habitat variables collected for benthic composition analysis. Software utilized are also listed. Hard live coral cover was the sum of percent cover for the three trait-based coral groups (\*).

Group	Habitat Metric	Description	Software/License	Variable Name
Habitat complexity—Digital Elevation Model (0.5 cm res.)	Depth (m)	Depth of water relative to MLW	ArcMap/BTM	<i>depth</i>
	Slope (°)	Angle of seabed relative to a horizontal surface	ArcMap/BTM	<i>slope</i>
	Vector terrain ruggedness	Dispersion of surface normal vectors over a 3 × 3 cell neighborhood.	ArcMap/BTM	<i>vrn</i>
	Surface area to planar area ratio (SAPA)	Rugosity evaluated across each 3 × 3 cell neighborhood	ArcMap/BTM	<i>sapa</i>
	Root mean square roughness	Standard deviation of depths along transect line	MATLAB	<i>rms</i>
	Digital relief	Range of depths along transect line	MATLAB	<i>relief</i>
	Coral reef rugosity	Ratio of contour line to straight horizontal distance	MATLAB	<i>crrug</i>
Habitat Composition—Orthomosaic (1 mm res.)	Hard live coral * cover (%)	Percentage of live hard/stony coral cover	MATLAB Image Labeler	<i>live coral</i>
	Sponge cover (%)	Percentage of sponge cover	MATLAB Image Labeler	<i>sponge</i>
	Macroalgal cover (%)	Percentage of macroalgal turfs on the sandy bottom/grooves	MATLAB Image Labeler	<i>macroalgae</i>
	Rubble cover (%)	Percentage of coarse gravel, unconsolidated rock, or dislodged coral fragments cover	MATLAB Image Labeler	<i>rubble</i>
	Density of octocorals	Number of octocorals per sq. m	MATLAB Image Labeler	<i>den-octo</i>
	Encrusting Zoanthid cover (%)	encrusting zoanthid <i>Palythoa caribaeorum</i>	MATLAB Image Labeler	<i>zoan</i>
Trait-Based Coral Groups *	submassive boulder (%)	Starlet Coral ( <i>Sideraster sidera</i> , <i>S. radians</i> ), Star Coral ( <i>Montastrea cavernosa</i> , <i>Orbicella annularis</i> , <i>O. faveolata</i> , <i>O. franksi</i> ) Mustard Hill Coral ( <i>Porites astreoides</i> ), Brain Coral ( <i>Colpophyllia natans</i> , <i>Pseudodiploria clivosa</i> , <i>Diploria labyrinthiformis</i> ) Staghorn Coral ( <i>Acropora cervicornis</i> , <i>A. palmata</i> ), Finger Coral ( <i>Porites porites</i> ), Yellow pencil coral ( <i>Madracis auretenra</i> )	MATLAB Image Labeler	<i>submassive</i>
	encrusting dome (%)		MATLAB Image Labeler	<i>encdome</i>
	branching (%)		MATLAB Image Labeler	<i>branch</i>

## 2.6. Characterizing Coral Assemblages

To further characterize benthic cover and coral assemblages, orthomosaics from the SfM data were exported at 1 mm<sup>2</sup> resolution and then tiled into 3 m × 3 m images for labeling (Table 4). Classification of coral morphologies were based on colony size and growth trait from related studies [82–85] as follows: (A) submassive boulder (e.g., *Siderastrea* spp., *M. cavernosa*, *Orbicella* spp.); (B) encrusting dome (e.g., *Porites astreoides*, *C. natans*, *D. labyrinthiformis*, *Pseudodiploria clivosa*); (C) branching (e.g., *Acropora* spp., *Porites* spp.); (D) encrusting zoanthid (*Palythoa caribaeorum*); and (E) sponges (e.g., *Callyspongia plicifera*, *Xestospongia muta*). Reef rubble generally occurred within sandy grooves of the spur-and-groove systems and were mapped using ROI polygons. Soft corals such as sea fans, sea plumes and other octocorals were often moving in response to underwater currents, and therefore were too distorted to accurately assign pixel labels. Thus, soft corals were labeled as Rectangle ROIs.

### 2.7. Statistical Analyses RVC Data

Potential differences in mean habitat characteristics among sites for each grouped sampling period (e.g., before vs after Irma) were tested using multivariate analyses of variance (MANOVA) models. When necessary, arcsine-square root transformation was applied to the RVC data percent cover estimates to meet assumptions of normality and homogeneity of variances prior to analysis. Canonical discriminant analysis (CDA) was used to observe variation in the benthic community composition among sites using the linear combination of each habitat variable. The coefficients of the linear combinations were plotted as eigenvectors in a two-dimensional space corresponding to the ratio of the between-group variance and within-group variance for each variable combination to show the largest separation between site group means. The direction and length of each eigenvector identifies which combination of habitat variables contribute significantly to the separation of site group means. Post-hoc tests included one-way analysis of variance (ANOVA) models and pairwise multiple comparisons tests (95% confidence level).

### 2.8. Statistical Analyses of Orthoimage Analysis and Mapping

The summed area of each habitat class (trait-based coral groups, sponge, rubble, etc.) within each tile was normalized by the tile area (9 m<sup>2</sup>) to calculate percent cover. Potential differences in mean habitat characteristics among sites that were mapped post-Irma were tested with MANOVA models. Post-hoc tests included one-way analysis of variance (ANOVA) models and pairwise multiple comparisons tests (95% confidence level).

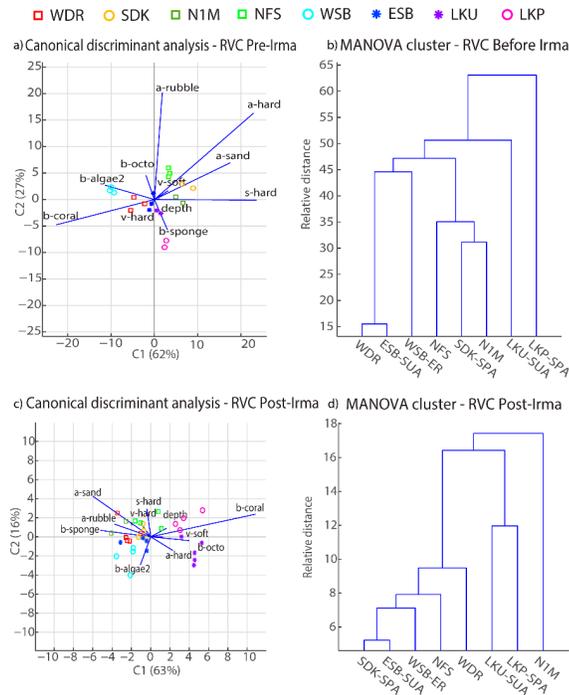
## 3. Results

In general, protected reefs sites had higher mean live coral cover than fished sites yet differed in dominant corals contributing to their overall structural complexity. In contrast, fished sites were more characterized by physical structures related to hardbottom habitat (e.g., vertical relief, percent rubble, rugosity). Despite the hurricane impacts, RVC surveys did not show a drastic change in site characteristics and consistently described sample sites as contiguous spur-and-groove or a matrix of patchy hardbottom structures with reef rubble. Depth and surface hard relief were the most robust habitat metrics across pre- versus post-Hurricane sample periods. The subset of sites surveyed using SfM photogrammetry provided evidence for more site-specific variation in habitat characteristics related to coral composition, local abiotic footprint, and small-scale variations in benthic features.

### 3.1. RVC Survey Results

Visual surveys identified small variations in the balance between live coral and other biotic habitat characteristics among sites, as well as abiotic physical features such as depth and surface hard relief across both pre- versus post-Irma. Before hurricane Irma, site separation was driven by structural features such as *a-rubble*, *a-hard*, and *s-hard* and the presence of live coral cover, *b-coral*. Sites characterized by physical seabed features with low presence in coral cover were grouped together along the first canonical axis such as sample sites SDK, N1M, and NFS (Figure 4a), whereas sites with high percentages in biotic cover (*b-coral*, *b-sponge*) such as WSB, LKP, and LKU generally resulted in more distinct separations among sites (Figure 4b). ANOVA post-hoc analysis identified significant differences in depth ( $p < 0.01$ ), surface hard relief ( $p = 0.05$ ) and rubble ( $p = 0.03$ ) (Table 5). Spur-and-groove sites NFS and LKP were similar in depth (>7 m); however, there was a significant difference in percent rubble ( $p = 0.02$ ) as LKP had the lowest percentage of rubble cover at 16% (Figure 5a). Live coral cover was not a significant driver in site characterization due to high variations in percent cover across the seabed for all sites. However, live coral cover did have a moderate influence in site characterization by scoring sites with higher percentages in coral cover lower in the second canonical axis. For example, LKP and LKU did not cluster with other sites (Figure 4b) and had the highest median percent coral cover at 63% and 66% respectively (Figure 5i). Given the recent sharp declines in percent coral cover within the FKNMS noted above [56–58], it is important to note that the percentage

results in this case are specific to the area (15 m<sup>2</sup>) surveyed and the RVC method in which each percentage in a given habitat category has to add to 100%. WSB also did not closely cluster with other sites due to the combination of a relatively low median depth of 4.6 m and an overall low percent cover in surface hard relief (Figure 5d).



**Figure 4.** Canonical discriminant analyses (left) and MANOVA-based clusters (right) for RVC data pre-Irma (a,b) versus post-Irma (c,d). Site symbols indicate level of protection: fished (squares), ER (circles), SPA (open circles), and SUA (stars). See Table 2 for data source and habitat variable definitions.

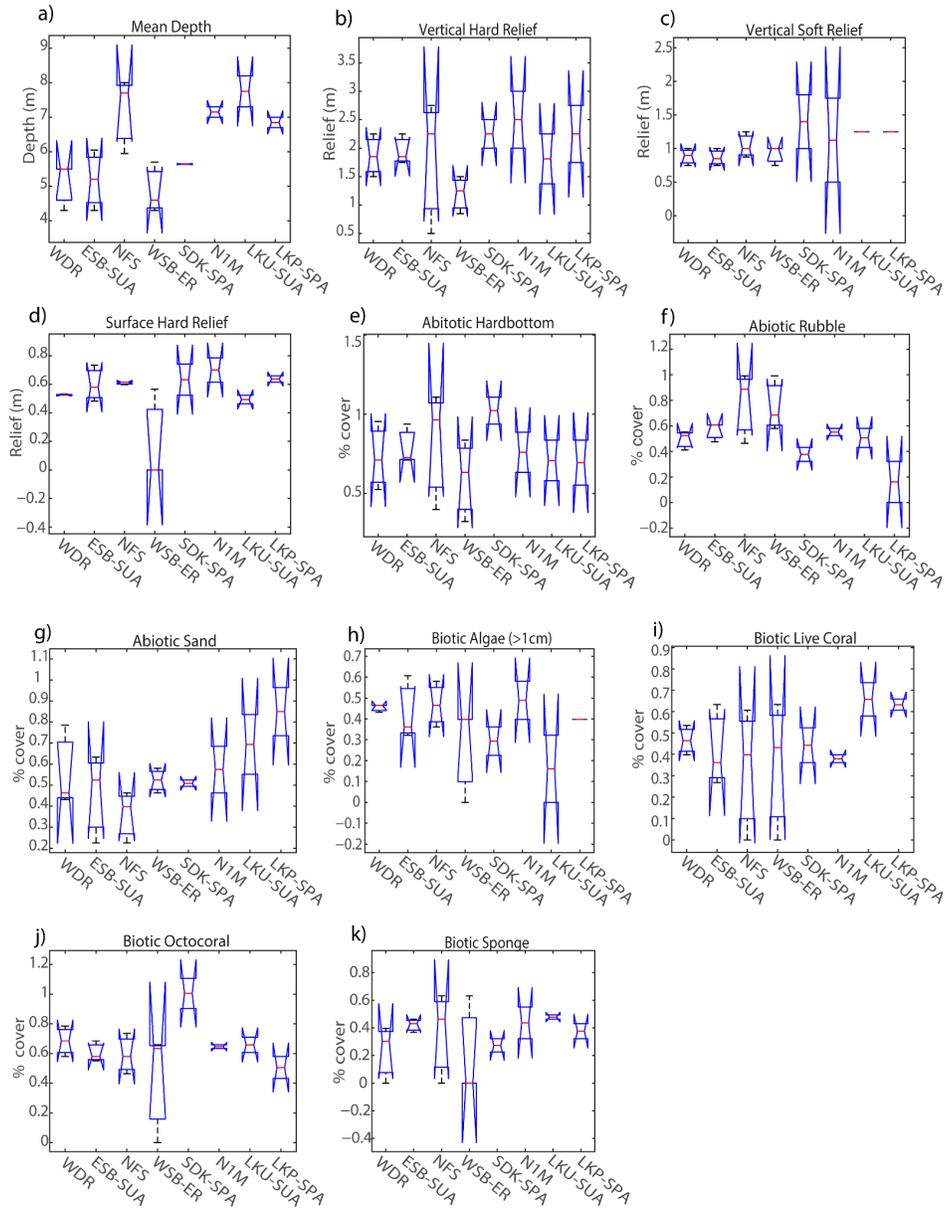
**Table 5.** ANOVA results for RVC surveys before and after Irma.

		Before Irma		
Source	df	Source	F	Prob > F
Sites	7	depth	6.05	<0.01
Error	12	v-hard relief	0.94	0.51
'Total'	19	v-soft relief	0.87	0.55
		s-hard relief	2.91	0.05
		a-hardbottom	0.65	0.71
		a-rubble	3.31	0.03
		a-sand	2.09	0.13
		b-algae	1.49	0.26
		b-coral	0.79	0.61
		b-octo	2.00	0.14
		b-sponge	0.49	0.83

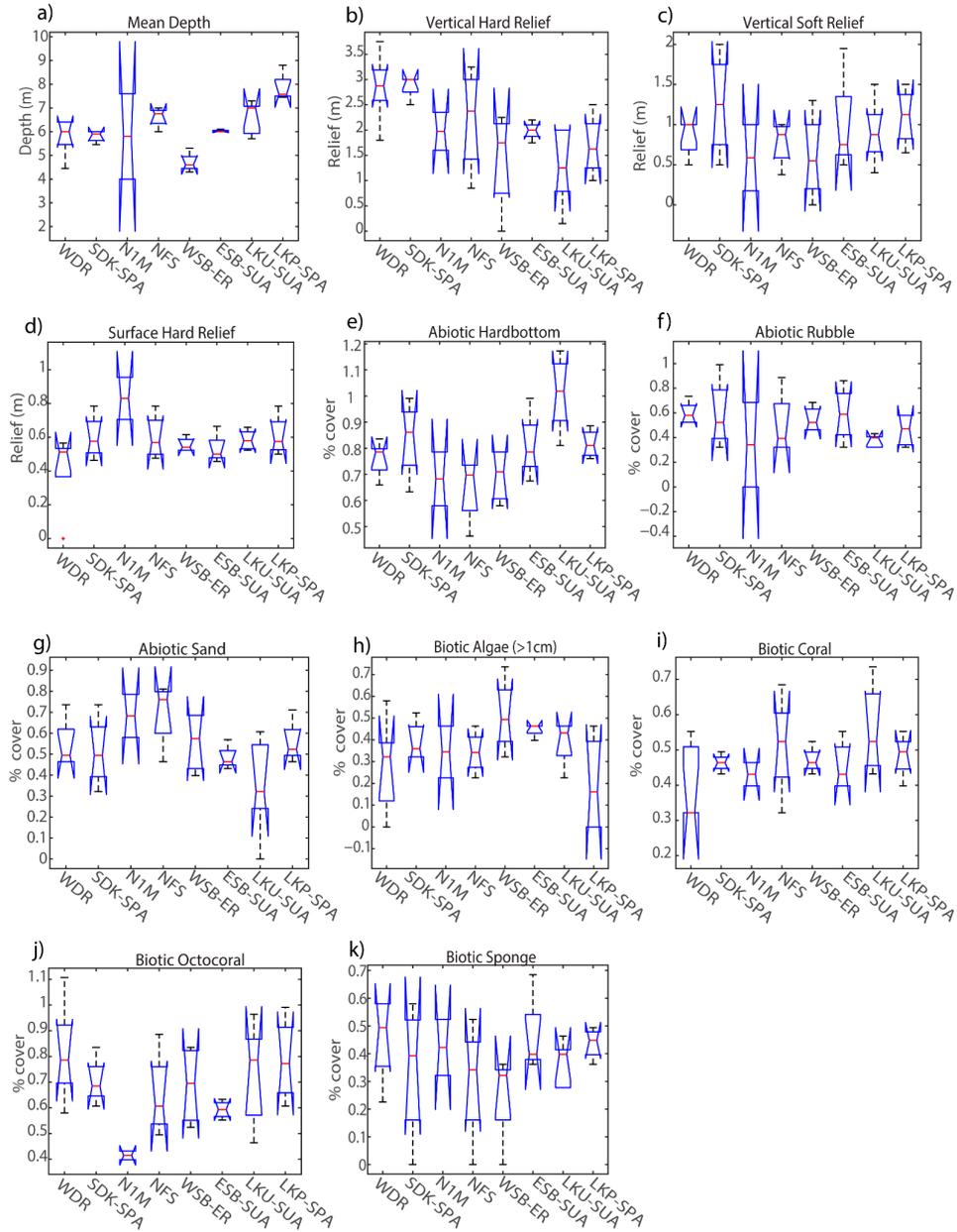
Table 5. Cont.

		After Irma		
Source	df	Source	F	Prob > F
Sites	7	<i>depth</i>	5.86	<0.01
Error	24	<i>v-hard relief</i>	3.07	0.02
'Total'	31	<i>v-soft relief</i>	0.85	0.56
		<i>s-hard relief</i>	2.06	0.09
		<i>a-hardbottom</i>	4.09	<0.01
		<i>a-rubble</i>	0.89	0.53
		<i>a-sand</i>	1.99	0.10
		<i>b-algae</i>	1.65	0.17
		<i>b-coral</i>	1.16	0.36
		<i>b-octo</i>	1.88	0.12
		<i>b-sponge</i>	0.92	0.51

Habitat separations among sites were diminished after the hurricane; however, there was more separation in site characterization between protected and fished sites post-Irma than pre-Irma. Discriminant analysis identified *b-coral* and *a-sand* as strong variables in distinguishing among sites (Figure 4c) and displayed a small inverse response between sites strongly characterized by biotic cover of corals, macroalgae, or sponges such as protected sites in contrast to fished sites with generally higher percentages of bare sand channels and rubble (Figure 6). Deeper sites with physical traits that contribute to spur-and-groove structures (e.g., *a-sand*, *v-hard*, *b-coral*) were scored more positively on the second canonical axis than the first axis, while shallow sites characterized by other non-coral biotic variables, such as the presence of octocorals or macroalgae, generally separated in the opposite direction (Figure 4c). MANOVA clustering grouped protected sites SDK, ESB and WSB together and did not closely group any fished sites together (Figure 4d). Post-hoc ANOVA results identified significant differences in depth ( $p < 0.01$ ), vertical hard relief ( $p = 0.02$ ), and abiotic hardbottom ( $p < 0.01$ ) (Table 5). Multiple comparison tests resulted in three groups where LKP's (median depth = 7.6 m) group means were significantly different from all sites whose median depths were below 6.5 m, except N1M ( $p = 0.07$ ). The next group distinguished WSB as the shallowest site (median depth = 4.6 m) and was significantly different than sites where the shallowest depth did not exceed 5 m (Figure 6a). Variation in percent cover for each biotic variable increased post-Irma at all sites and resulted in no significant differences among sites. Macroalgae percent cover revealed major changes at both Looe Key sites via a ~30% decrease in macroalgae at LKP and ~30% increase at LKU, while all other survey sites relatively remained the same or showed minor decreases in percent macroalgae cover. Although live coral cover was not a significant habitat variable in site characterization, there were changes in live coral cover post-Irma at sites with higher percent cover than pre-Irma. For example, SDK, N1M, NFS, and ESB showed similar ranges in percent live coral cover post-Irma with NFS resulting in the highest percent cover at 52%. In contrast, WDR, WSB, LKP, and LKU recorded minor decreases of up to 10% in live coral cover post-Irma, and overall, there were no strong distinctions between level of protection and live coral cover. Octocoral percent cover showed either no change or small decreases at all sites post-Irma except for LKP and LKU, which both showed an ~20% increase. Minor changes in sponge percent cover post-Irma were present at all sites except for WSB, where percent cover increased from 0 to 35% post-Irma.



**Figure 5.** Percent cover of habitat variables collected among sites in the lower Florida Keys during RVC surveys (15 m diameter) before Hurricane Irma: (a) mean depth, (b) vertical hard relief, (c) vertical soft relief, (d) surface hard relief, (e) abiotic hardbottom, (f) abiotic rubble, (g) abiotic sand, (h) biotic algae > 1 cm, (i) biotic coral, (j) biotic octocoral, (k) biotic sponge. The central red line represents the median, and the 25th and 75th percentiles are shown as the upper and lower limits respectively.



**Figure 6.** Percent cover of habitat variables collected among sites in the lower Florida Keys during RVC surveys (15 m diameter) after Hurricane Irma: (a) mean depth, (b) vertical hard relief, (c) vertical soft relief, (d) surface hard relief, (e) abiotic hardbottom, (f) abiotic rubble, (g) abiotic sand, (h) biotic algae > 1 cm, (i) biotic coral, (j) biotic octocoral, (k) biotic sponge. The central red line represents the median, and the 25th and 75th percentiles are shown as the upper and lower limits respectively.

### 3.2. Digital Elevation Model (DEM) Topographic Results

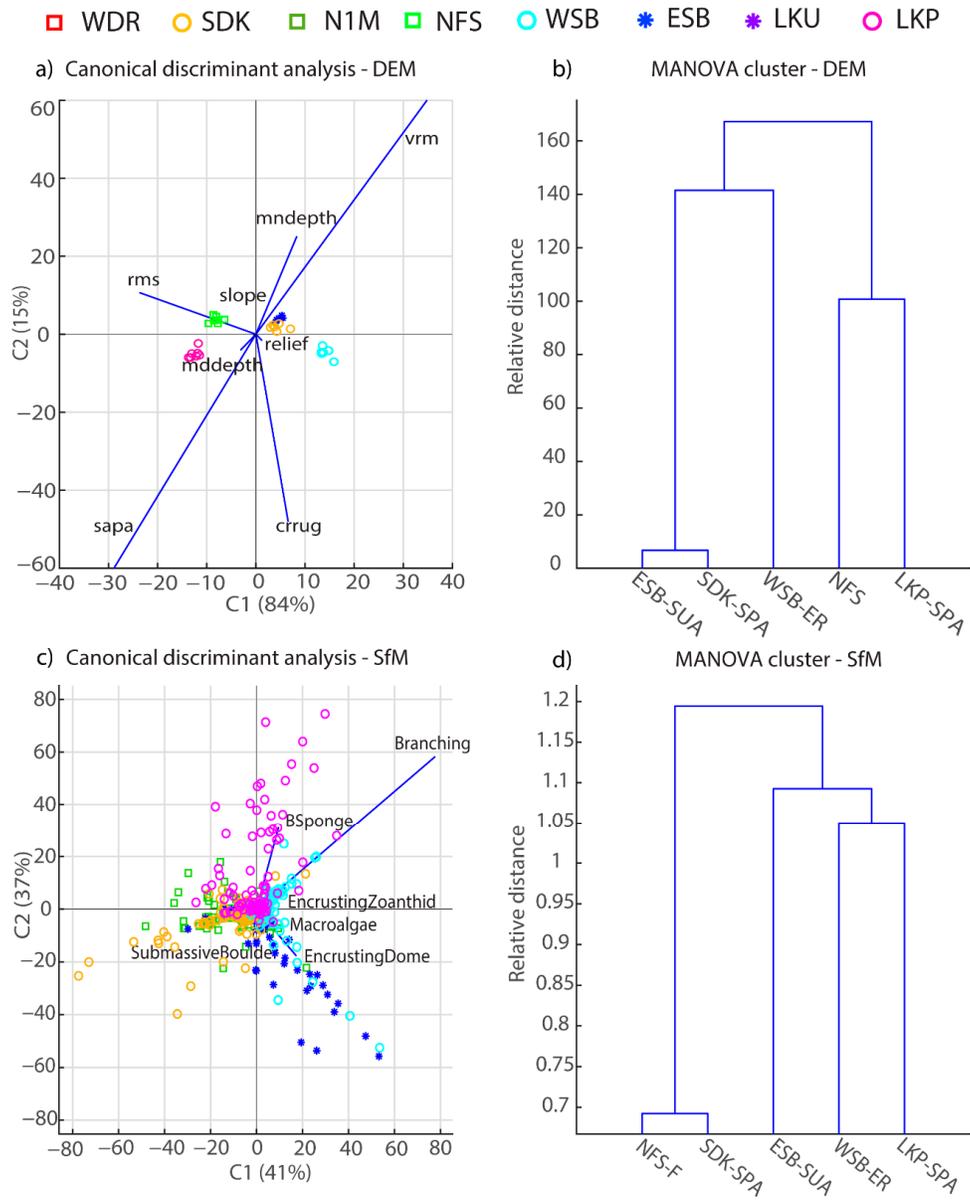
The DEM metrics captured more fine-scale changes in habitat metrics than the RVC surveys and highlight the influence of within site variation in benthic topography driving the separations among sites. For example, the surface area to planar area ratio (*sapa*), which evaluates rugosity across neighboring cells within a site, was the most influential metric separating sites, followed by vector terrain ruggedness (*vrms*) (Figure 7a). RVC metrics related to physical structures (*a-hard*, *depth*, *s-hard*) generally clustered LKP and NFS as sites with relatively high structural complexity, and the DEM MANOVA results also clustered these two sites (Figure 7b) based on *sapa* and *rms*. The second canonical axis separated sites based on metrics related to coral cover such as *crug*, in which coral-dominated sites were positioned on the lower axis (Figure 7b). WSB was the only site not grouped with other sites because of its low structural complexity and relatively high coral cover.

Post-hoc ANOVA results indicated all DEM habitat metrics being significantly different among sites except for *rms* roughness ( $p = 0.21$ ) and *relief* ( $p = 0.22$ ) (Table 6). WSB yielded the highest median coral reef rugosity index of 3.23 and was a relatively shallow site (~4.3 m in depth) with small variations in surface relief ( $2.5 \text{ m} \pm 0.18$ ) (Figure 8e). In contrast, NFS and LKP were grouped together (Figure 7b) due to being relatively deep sites, 6.7 m and 7.3 m respectively, and showed more variation in relief than other sites due to their distinct spur-and-groove formations. MANOVA cluster analysis closely grouped ESB and SDK and showed a large separation from the other mapped sites. Additionally, ANOVA results found no significant difference in all tested DEM metrics between ESB and SDK. However, it is important to recognize the specific reef-area analyzed using depth-transect profiles for both sites were structurally different, such that SDK had several spur-and-groove formations included in the analysis (Figure 2a), whereas the area mapped at ESB mainly consisted of one large spur (Figure 2d).

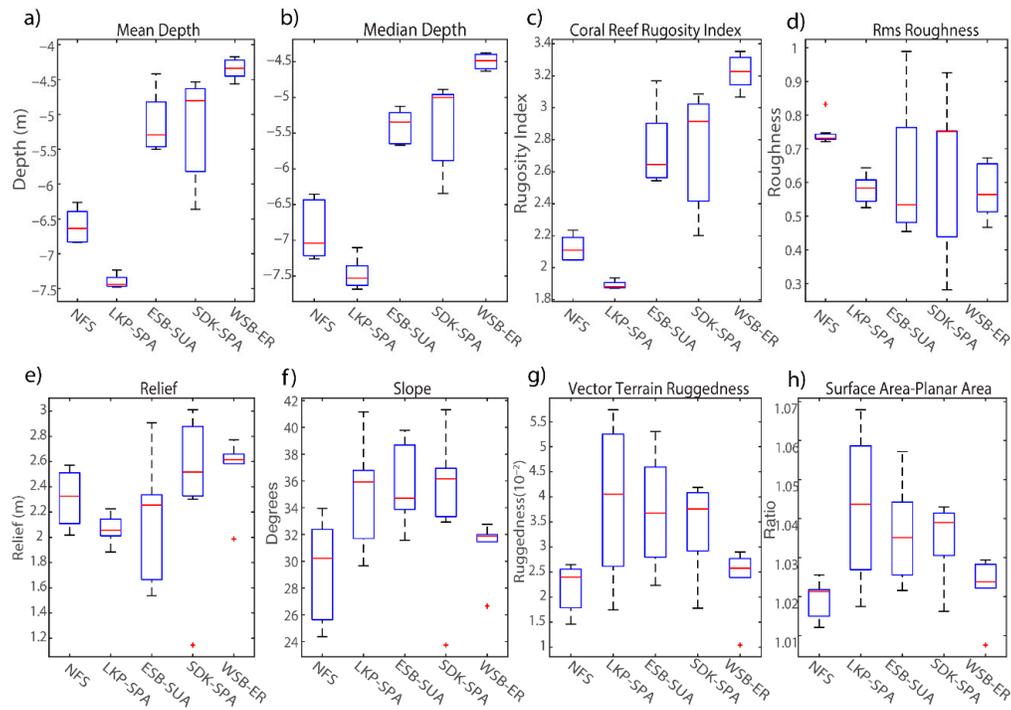
### 3.3. Orthomosaic Analysis Benthic Composition Results

Results from the orthomosaic image analysis provide insight into the biological reef surface characteristics contributing to the reef framework, including trade-offs between coral assemblages and other benthic organisms typically found colonizing hardbottom substrates. The density of octocorals was  $\sim 2/\text{m}^2$  for all sites and therefore was not included in the following site characterization analysis due to its low encounter rate in the mapping process. Canonical discriminant analysis and MANOVA clusters showed relatively small separations among sites, with the presence of branching corals being a strong driver in site characterization. The first canonical axis generally separated less biologically diverse sites (SDK, NFS) from sites presumably with high coral or sponge cover (LKP, ESB, WSB) (Figure 7c). Variation in presence or absence of habitat characteristics across each sampled tile within a site highlights relatively fine-scale differences in coral assemblages and associated benthos, such as encrusting zoanthids and sponges, leading to minimal relative distances in site separation (Figure 7d).

Further distinction between coral-dominated sites was dependent on the relative presence of encrusting zoanthids and abundance of both the trait-based corals shown by post hoc ANOVA results, where all fine-scale habitat metrics were significantly different ( $p < 0.01$ ) for each mapped site (Table 7). For example, WSB had small patches of branching staghorn (*A. cervicornis*) and finger corals (*Porites* spp.) on the seabed surface, while LKP had several staghorn and elkhorn (*A. palmata*) coral outplants at various growth stages within the mapped area. Additionally, several brain corals (*C. natans*, *P. clivosa*, *D. labyrinthiformis*) were observed at LKP, yet had been impacted by coral disease diminishing the area characterized as live coral cover. Although all sites were dominated by encrusting zoanthids (*P. caribaeorum*), the relative percent cover was lowest at WSB (<3.7%) and was highest at NFS (<24%) followed by LKP (<20%) (Figure 9g). Percent cover of encrusting zoanthids at NFS was significantly higher at all sites except LKP ( $p = 0.54$ ).



**Figure 7.** Canonical discriminant analyses (left) and MANOVA-based clusters (right) for digital elevation model (DEM) variables (a,b) and structure-from-motion (SfM) orthomosaic variables (c,d). Site symbols indicate level of protection: fished (squares), ER (circles), SPA (open circles), and SUA (stars). See Table 3 for data source and habitat variable definitions.



**Figure 8.** Percent cover of habitat variables collected from the digital elevation models of mapped sites after Hurricane Irma and 30-m scan line analysis: (a) mean depth, (b) median depth, (c) coral reef rugosity index, (d) *rms* roughness, (e) relief, (f) slope, (g) vector terrain ruggedness, (h) surface area to planar area ratio. The central red line represents the median, and the 25th and 75th percentiles are shown as the upper and lower limits respectively. Outliers are denoted as red '+' symbols.

**Table 6.** ANOVA results for DEM habitat variables.

		DEM		
Source	df	Source	F	Prob > F
Sites	4	<i>mean depth</i>	60.97	<0.01
Error	28	<i>median depth</i>	73.28	<0.01
'Total'	32	<i>crrug</i>	45.25	<0.01
		<i>rms</i>	1.56	0.17
		<i>relief</i>	1.53	0.10
		<i>slope</i>	3.11	0.02
		<i>vrm</i>	3.85	<0.01
		<i>sapa</i>	4.56	<0.01

Table 7. ANOVA results for SfM habitat variables.

Source	df	SfM		
		Source	F	Prob > F
Sites	4	submassive boulder	6.66	<0.01
Error	745	encrusting dome	24.15	<0.01
Total	749	branching	8.32	<0.01
		sponge	23.86	<0.01
		macroalgae	10.53	<0.01
		rubble	14.57	<0.01
		encrusting zoanthid	12.64	<0.01

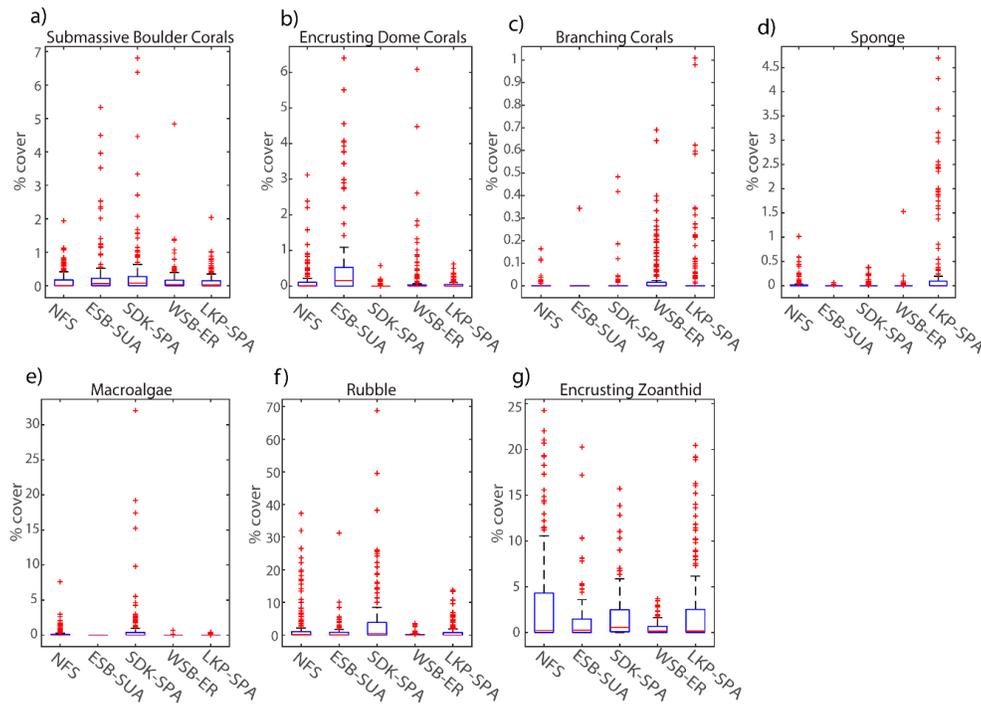


Figure 9. Percent cover of habitat variables collected from each mapped site’s orthomosaic tiles annotated in MATLAB ImageLabeler: (a) submassive boulder corals, (b) encrusting dome corals, (c) branching corals, (d) sponge, (e) macroalgae, (f) rubble, (g) encrusting zoanthid. The central red line represents the median and the 25th and 75th percentiles are shown as the upper and lower limits respectively. Outliers are denoted as red ‘+’ symbols.

The relative percent cover of encrusting dome corals (*C. natans*, *Pseudodiploria* sp.) was highest at ESB (<6%) and significantly different from all sites ( $p < 0.01$ ) (Table 7). Percent cover of sub-massive corals at ESB was significantly different than all sites except SDK ( $p = 0.99$ ), as both sites showed outliers greater than 5% (Table 7 and Figure 9a respectively). ESB’s coral composition was dominated by mustard hill (*P. astreoides*) corals characterized

as encrusting dome corals, and their spatial distribution varied from patches on reef rubble to relatively dense colonies on shallow ridges. ESB also had several large boulder star coral colonies characterized as sub-massive corals, such as the mountainous star coral (*O. faveolata*) and the massive starlet coral (*S. siderea*). The percent cover of large barrel sponges (*X. muta*) (4.7%) was significantly higher at LKP than other sites (Table 6; Figure 9d). Percent cover of rubble was generally higher at sites previously characterized as having distinct sand channels and ridges (e.g., SDK) at 70%, compared to WSB with 3.5% rubble cover.

#### 3.4. Comparison of RVC and SfM Methods

The combination of visual surveys and mapping using photogrammetry demonstrates how observational scale and methods influence site-specific habitat characterization. Both methods suggest that depth and features that contribute to bottom topography (e.g., surface hard relief, rubble, coral assemblages) are important components in describing habitat complexity among these shallow coral reef sites. Also, the difference in habitat variables that describe hard-bottom seabed surfaces (e.g., *a-rubble*, *a-hard*, *sapa*) that provide structure for biotic variables (e.g., *b-coral*, *b-sponge*, *branching corals*) colonizing the three-dimensional surface for both sampling methods provided critical thresholds for site separation within each cluster analysis. RVC survey site characterization was limited to larger spatial scale differences among sites and did not provide fine-scale descriptions of within-site variation. Conversely, SfM photogrammetry was more robust in not only separating among sites beyond the variables of depth and vertical relief, but also further distinguished sites using more fine-scale variables such as vector terrain ruggedness and specific coral morphologies as key drivers in site characterization. For example, live coral cover was not a significant variable in site characterization for the RVC surveys, yet the SfM mapping approach showed significant differences in the dominance of coral morphologies, as well as the related topographical metrics such as the coral reef rugosity index among sites. RVC surveys were able to capture site variation over space and time relevant to important broad-scale habitat impacts, such as impacts from recreational use (i.e., vessel anchoring, scuba divers) and environmental disturbances (i.e., hurricanes). The one sampling period for SfM mapping was robust in observing within site variations across the three-dimensional surface of the seabed, and captured localized topographical features not generally captured by visual surveys, such as local depressions, patchy coral heads, and the matrix of benthos on sand (e.g., rubble, boulder corals, macroalgal turfs).

#### 4. Discussion

This study provides baseline fine-scale spatial data for several spur-and-groove reef sites in the FKNMS and highlights the combined use of reef visual census surveys and SfM photogrammetry to assess the physical and biological contributions to reef structural complexity relevant to coral reef management and conservation. Characterizing reef habitat complexity using a combination of visual surveys, photogrammetry, and orthoimage analysis provided new insights into understanding both the physical and biological benthic characteristics contributing to the coral reef framework at several fore-reef sites in the FKNMS. Our results from RVC surveys and photogrammetry suggest that shallow reef sites existing within research-only areas and public access sites with mooring buoys generally harbor more reef-building corals than fished sites, but each site may be unique in their combined framework of physical features (i.e., abiotic cover, relief) and dominant coral assemblages. RVC surveys were robust in differentiating among shallow sites and deeper fore-reef sites based on habitat characteristics, as well as describing hard structures that contribute to hardbottom complexity. Depth and seabed surface hard relief cover were key habitat characteristics separating all sites over time, however this separation among sites was diminished after hurricane Irma. In characterizing each site's site-specific habitat traits, including the presence of varying coral assemblages using orthoimage analysis, our study suggests that colony-scale seabed features, as well as the spatial placement of marine reserves and coral taxa post hurricanes may also play a role in driving habitat complexity.

In characterizing habitat complexity at the site level, our results on the type of coral dominating an area and the amount of seabed surface attributed to hard features (e.g., rubble, dead corals, sponges) may be more important factors in site characterization than percent live coral cover. As hard seabed surfaces essentially include hardbottom substrate, living and non-living corals, and reef rubble, our SfM habitat mapping approach at a high resolution supports previously identified variations in coral assemblages and shows that within site variation in benthic cover may drive structural complexity [26,86,87].

The combination of abiotic and biotic habitat metrics was also useful in characterizing the potential impact of reef management zones on habitat characteristics, as well as providing baseline information on the coral taxa historically present within the reef system, and new taxa [88,89]. For example, WSB is one of the oldest marine reserve sites in the FKNMS, designated as the first ecological reserve in 1997, and lies adjacent to Middle Sambo (not sampled) and ESB. WSB and ESB were not significantly different based on RVC surveys; however, orthoimage analysis found that WSB and ESB differed in dominant coral assemblages present and digital elevation models also found key structural differences in metrics utilized in both survey methods such as median depth, relief, and slope. WSB yielded high coral reef rugosity values comparable to other studies in which high rugosity values (i.e., >2.5) indicate coral richness [90–92]. Both sites yielded the lowest coverage in the encrusting zoanthid (*P. caribaeorum*), yet differed in dominant coral taxa and protection level, suggesting that these sites may possess strong fine-scale habitat traits or biological legacies from previous disturbance impacts for certain coral taxa [93–96]. For example, following Hurricane Irma's direct impact on the study sites, the coral reef soundscape at ESB during the same sampling periods (2017–2018) showed signs of recovery within weeks to months following the disturbance through the return of periodic fish chorusing and snapping shrimp activity [97]. NOAA's National Weather Service has recorded ten tropical storms and nine hurricanes either passing over or making landfall in the Florida Keys and the Dry Tortugas between 2000 and 2020 [98]. The next prior storm to Hurricane Irma was Hurricane Isaac (category 1) in 2012; however, the storm track from Cuba to the southern tip of the Florida Keys was positioned ~40 km away from this study's southern most site WDR, and there was no major damage reported for reef habitats [99]. The frequent physical destruction in the Lower Florida Keys reef habitats may retain physical complexity; however, the biotic characteristics such as corals, sponges, and gorgonians may shift to reflect a less complex surface cover on hardbottom substrates over time [81,100,101]. Long-term reduced coral diversity can cause a decline in the ecological function of coral reefs and hinder ecosystem recovery as the combined effects of habitat loss and dampening of complex food web dynamics become exacerbated over time [102,103]. For example, many three-dimensional branching, corymbose, plating, and other complex coral morphologies serve as microhabitats for habitat specialists, refugia for ontogenetic niche shifts between size classes or life history stages [102,104,105]. The legacy of the biotic and abiotic features that remain will determine the successive traits and survivorship of future generations at coral reef habitats [106,107].

The relationship between specific habitat metrics, live coral cover or colony size, reef slope, and overall ecosystem health metrics for coral reefs remains unclear. For example, slope serves as a robust indicator of the proportion of hardbottom substrates at a site and provides information on gradual two-dimensional changes in abiotic reef structures (i.e., reef ledge, crest) [43]. In contrast, ruggedness strongly correlates with traditional reef rugosity and trait-based coral cover, and considers the full spatial area for model reconstruction [75,108]. The spatial resolution in estimating VRM or ruggedness varies with coral morphology, yet can also aid in identifying coral assemblages. At high-resolution scales where the raster cell size is less than 4 cm, complex three-dimensional corals such as branching corals, positively correlate with ruggedness while other growth forms, including encrusting and mound-building corals, generally correlate at larger spatial scales between 8–16 cm resolution [43]. Additionally, shallow-water coral reefs often reflect scale-dependent rugosity [109,110], which depends on the abundance and diversity of

coral growth forms [74,108] and the presence of intra-species growth plasticity [111]. For example, high relief fished sites such as WDR, NFS, and N1M were essentially physically complex, yet lacked the biological cover present at similarly structured protected sites such as LKP and LKU. Although ESB was a moderately shallow and less complex site than both Looe Key sites, ESB's variation in surface relief and slope shown in the depth profile was comparable to LKP and reflects the high abundance of *P. astreoides* that forms dome-shaped colonies. Recent three-dimensional reconstruction of a hurricane impacting a Hawaiian reef atoll showed that mean rugosity and slope decreased as the benthic cover of tabular corals decreased after reef destruction, yet ruggedness varied depending on raster resolution due to the presence of reef rubble, fallen ledges, and depressions [112].

## 5. Conclusions

As coral reef habitat assessments and restoration efforts evolve to include 3D mapping at scales relevant to management priorities, more research will be needed to understand the relationship between changes in living coral taxa and morphologies, reef structural complexity, and the processes underlying these changes. Additionally, adaptive management frameworks aiming to monitor and promote coral reef resilience in the face of multiple complex stressors calls for knowledge of the magnitude of disturbances and ecosystem vulnerability at finer spatial scales [113]. The use of orthoimage analysis and SfM habitat mapping can provide critical information on changes in the three-dimensional reef structure and biotic surface cover over time to track reef degradation or recovery [112,114]. Furthermore, our coral-trait based approach enhances the understanding of severe disturbances (i.e., hurricanes, SCTLD, ocean warming) on the composition of coral assemblages and the subsequent shifts in benthic communities [85,115,116]. Monitoring fine-scale habitat variables through high-resolution mapping is beneficial in assessing the outcomes of MPAs [117–120] and coral restoration efforts [121,122] as well as understanding the biological benthic structure of reefs [123] that can help guide place-based coral restoration efforts [124,125]. The combined approach of SfM photogrammetry with traditional monitoring methods, such as visual surveys at multiple spatial and temporal scales, can enhance the ability to find niche habitats or coral taxa that promote resilience against regional stressors prominent in ecologically and economically important coral reef ecosystem such as the Florida Keys.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14030153/s1>, Table S1: Example settings used to generate 3D models of Sand Key in Agisoft Metashape Professional. (\*) Low settings were used if image alignment was not immediately successful; however, all models were aligned on high before generating the dense cloud or mesh building. Figure S1: Depth-transect profiles based on the DEM raster are shown for (a) Sand Key SPA (SDK), (b) Nine Foot Stake (NFS), (c) Western Sambo ER (WSB), (d) Eastern Sambo SUA (ESB), and (e) Looe Key SPA (LKP). Transect profiles are 30 m in length (west-east) with 3 m spacing between transects heading in a northerly direction.

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## References

- Spalding, M.; Spalding, M.D.; Ravilious, C.; Green, E.P. *World Atlas of Coral Reefs*; University of California Press: Oakland, CA, USA, 2001.
- Brander, L.M.; Van Beukering, P.; Cesar, H.S.J. The Recreational Value of Coral Reefs: A Meta-Analysis. *Ecol. Econ.* **2007**, *63*, 209–218. [[CrossRef](#)]
- Spalding, M.; Burke, L.; Wood, S.A.; Ashpole, J.; Hutchison, J.; zu Ermgassen, P. Mapping the Global Value and Distribution of Coral Reef Tourism. *Mar. Policy* **2017**, *82*, 104–113. [[CrossRef](#)]
- Ferrario, F.; Beck, M.W.; Storlazzi, C.D.; Micheli, F.; Shepard, C.C.; Airoidi, L. The Effectiveness of Coral Reefs for Coastal Hazard Risk Reduction and Adaptation. *Nat. Commun.* **2014**, *5*, 3794. [[CrossRef](#)] [[PubMed](#)]
- Cinner, J. Coral Reef Livelihoods. *Curr. Opin. Environ. Sustain.* **2014**, *7*, 65–71. [[CrossRef](#)]
- Hicks, C.C.; Cinner, J.E. Social, Institutional, and Knowledge Mechanisms Mediate Diverse Ecosystem Service Benefits from Coral Reefs. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 17791–17796. [[CrossRef](#)] [[PubMed](#)]
- Woodhead, A.J.; Hicks, C.C.; Norström, A.V.; Williams, G.J.; Graham, N.A.J. Coral Reef Ecosystem Services in the Anthropocene. *Funct. Ecol.* **2019**, *33*, 1023–1034. [[CrossRef](#)]
- Hoegh-Guldberg, O.; Mumby, P.J.; Hooten, A.J.; Steneck, R.S.; Greenfield, P.; Gomez, E.; Harvell, C.D.; Sale, P.F.; Edwards, A.J.; Caldeira, K.; et al. Coral Reefs under Rapid Climate Change and Ocean Acidification. *Science* **2007**, *318*, 1737–1742. [[CrossRef](#)]
- Albert, J.A.; Olds, A.D.; Albert, S.; Cruz-Trinidad, A.; Schwarz, A.M. Reaping the Reef: Provisioning Services from Coral Reefs in Solomon Islands. *Mar. Policy* **2015**, *62*, 244–251. [[CrossRef](#)]
- Grafeld, S.; Oleson, K.L.L.; Teneva, L.; Kittinger, J.N. Follow That Fish: Uncovering the Hidden Blue Economy in Coral Reef Fisheries. *PLoS ONE* **2017**, *12*, e0182194. [[CrossRef](#)]
- Haapkylä, J.; Unsworth, R.K.F.; Flavell, M.; Bourne, D.G.; Schaffelke, B.; Willis, B.L. Seasonal Rainfall and Runoff Promote Coral Disease on an Inshore Reef. *PLoS ONE* **2011**, *6*, e16893. [[CrossRef](#)]
- Staley, C.; Kaiser, T.; Gidley, M.L.; Enochs, I.C.; Jones, P.R.; Goodwin, K.D.; Sinigalliano, C.D.; Sadowsky, M.J.; Chun, C.L. Differential Impacts of Land-Based Sources of Pollution on the Microbiota of Southeast Florida Coral Reefs. *Appl. Environ. Microbiol.* **2017**, *83*, e03378-16. [[CrossRef](#)] [[PubMed](#)]
- Cunning, R.; Silverstein, R.N.; Barnes, B.B.; Baker, A.C. Extensive Coral Mortality and Critical Habitat Loss Following Dredging and Their Association with Remotely-Sensed Sediment Plumes. *Mar. Pollut. Bull.* **2019**, *145*, 185–199. [[CrossRef](#)] [[PubMed](#)]
- Gintert, B.E.; Precht, W.F.; Fura, R.; Rogers, K.; Rice, M.; Precht, L.L.; D'Alessandro, M.; Croop, J.; Vilmar, C.; Robbart, M.L. Regional Coral Disease Outbreak Overwhelms Impacts from a Local Dredge Project. *Environ. Monit. Assess.* **2019**, *191*, 630. [[CrossRef](#)] [[PubMed](#)]
- Carter, A.L.; Edwards, C.B.; Fox, M.D.; Amir, C.G.; Eynaud, Y.; Johnson, M.D.; Lewis, L.S.; Sandin, S.A.; Smith, J.E. Changes in Benthic Community Composition Associated with the Outbreak of the Corallimorph, *Rhodactis Howesii*, at Palmyra Atoll. *Coral Reefs* **2019**, *38*, 1267–1279. [[CrossRef](#)]
- Figueroa, D.F.; McClure, A.; Figueroa, N.J.; Hicks, D.W. Hiding in Plain Sight: Invasive Coral *Tubastraea Tagusensis* (Scleractinia:Hexacorallia) in the Gulf of Mexico. *Coral Reefs* **2019**, *38*, 395–403. [[CrossRef](#)]
- Crivellaro, M.S.; Silveira, T.C.L.; Custódio, F.Y.; Battaglin, L.C.; de Sá Dechoum, M.; Fonseca, A.C.; Segal, B. Fighting on the Edge: Reproductive Effort and Population Structure of the Invasive Coral *Tubastraea Coccinea* in its Southern Atlantic Limit of Distribution Following Control Activities. *Biol. Invasions* **2021**, *23*, 811–823. [[CrossRef](#)]
- Alvarez-Filip, L.; Estrada-Saldivar, N.; Pérez-Cervantes, E.; Molina-Hernández, A.; González-Barrios, F.J. A Rapid Spread of the Stony Coral Tissue Loss Disease Outbreak in the Mexican Caribbean. *PeerJ* **2019**, *7*, e8069. [[CrossRef](#)]
- Estrada-Saldivar, N.; Molina-Hernández, A.; Pérez-Cervantes, E.; Medellín-Maldonado, F.; González-Barrios, F.J.; Alvarez-Filip, L. Reef-Scale Impacts of the Stony Coral Tissue Loss Disease Outbreak. *Coral Reefs* **2020**, *39*, 861–866. [[CrossRef](#)]

20. Kaufman, M.L.; Watkins, E.; van Hooidonk, R.; Baker, A.C.; Lirman, D. Thermal History Influences Lesion Recovery of the Threatened Caribbean Staghorn Coral *Acropora Cervicornis* under Heat Stress. *Coral Reefs* **2021**, *40*, 289–293. [[CrossRef](#)]
21. Studivan, M.S.; Shatters, A.; Dodge, D.L.; Beal, J.L.; Voss, J.D. Synergistic Effects of Thermal Stress and Estuarine Discharge on Transcriptomic Variation of *Montastraea cavernosa* Corals in Southeast Florida. *Front. Mar. Sci.* **2021**, *8*, 662220. [[CrossRef](#)]
22. Riegl, B. Degradation of Reef Structure, Coral and Fish Communities in the Red Sea by Ship Groundings and Dynamite Fisheries. *Bull. Mar. Sci.* **2001**, *69*, 595–611. Available online: <https://www-ingentaconnect-com.prox.lib.ncsu.edu/content/umrsmas/bullmar/2001/00000069/00000002/art00031#> (accessed on 26 December 2021).
23. Raymundo, L.J.; Licuanan, W.L.; Kerr, A.M. Adding Insult to Injury: Ship Groundings Are Associated with Coral Disease in a Pristine Reef. *PLoS ONE* **2018**, *13*, e0207078. [[CrossRef](#)] [[PubMed](#)]
24. Lyons, P.J.; Arboleda, E.; Benkwitt, C.E.; Davis, B.; Gleason, M.; Howe, C.; Mathe, J.; Middleton, J.; Sikowitz, N.; Untersteiggaber, L.; et al. The Effect of Recreational SCUBA Divers on the Structural Complexity and Benthic Assemblage of a Caribbean Coral Reef. *Biodivers. Conserv.* **2015**, *24*, 3491–3504. [[CrossRef](#)]
25. Moberg, F.; Folke, C. Ecological Goods and Services of Coral Reef Ecosystems. *Ecol. Econ.* **1999**, *29*, 215–233. [[CrossRef](#)]
26. Alvarez-Filip, L.; Carricart-Ganivet, J.P.; Horta-Puga, G.; Iglesias-Prieto, R. Shifts in Coral-Assemblage Composition Do Not Ensure Persistence of Reef Functionality. *Sci. Rep.* **2013**, *3*, 3486. [[CrossRef](#)]
27. Rogers, A.; Blanchard, J.L.; Mumby, P.J. Vulnerability of Coral Reef Fisheries to a Loss of Structural Complexity. *Curr. Biol.* **2014**, *24*, 1000–1005. [[CrossRef](#)]
28. Lester, S.E.; Halpern, B.S.; Grorud-Colvert, K.; Lubchenco, J.; Ruttenberg, B.I.; Gaines, S.D.; Airamé, S.; Warner, R.R. Biological Effects within No-Take Marine Reserves: A Global Synthesis. *Mar. Ecol. Prog. Ser.* **2009**, *384*, 33–46. [[CrossRef](#)]
29. 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.F.; Berkhout, J.; et al. Global Conservation Outcomes Depend on Marine Protected Areas with Five Key Features. *Nature* **2014**, *6000*, 216–220. [[CrossRef](#)]
30. Manel, S.; Loiseau, N.; Andrello, M.; Fietz, K.; Goñi, R.; Forcada, A.; Lenfant, P.; Kininmonth, S.; Marcos, C.; Marques, V.; et al. Long-Distance Benefits of Marine Reserves: Myth or Reality? *Trends Ecol. Evol.* **2019**, *34*, 342–354. [[CrossRef](#)]
31. Sponaugle, S.; Cowen, R.K. Coral Ecosystem Connectivity Between Pulley Ridge and the Florida Keys. In *Mesophotic Coral Ecosystems. Coral Reefs of the World*; Loya, Y., Puglise, K., Bridge, T., Eds.; Springer: Cham, Switzerland, 2019; Volume 3, pp. 897–907. [[CrossRef](#)]
32. Boström-Einarsson, L.; Babcock, R.C.; Bayraktarov, E.; Ceccarelli, D.; Cook, N.; Ferse, S.C.A.; Hancock, B.; Harrison, P.; Hein, M.; Shaver, E.; et al. Coral Restoration—A Systematic Review of Current Methods, Successes, Failures and Future Directions. *PLoS ONE* **2020**, *15*, e0226631. [[CrossRef](#)]
33. Gouezo, M.; Fabricius, K.; Harrison, P.; Golbuu, Y.; Doropoulos, C. Optimizing Coral Reef Recovery with Context-Specific Management Actions at Prioritized Reefs. *J. Environ. Manage.* **2021**, *295*, 113209. [[CrossRef](#)] [[PubMed](#)]
34. Cheal, A.J.; Emslie, M.; MacNeil, M.A.; Miller, I.; Sweatman, H. Spatial Variation in the Functional Characteristics of Herbivorous Fish Communities and the Resilience of Coral Reefs. *Ecol. Appl.* **2013**, *23*, 174–188. [[CrossRef](#)] [[PubMed](#)]
35. Zaneveld, J.R.; Burkepile, D.E.; Shantz, A.A.; Pritchard, C.E.; McMinds, R.; Payet, J.P.; Welsh, R.; Correa, A.M.S.; Lemoine, N.P.; Rosales, S.; et al. Overfishing and Nutrient Pollution Interact with Temperature to Disrupt Coral Reefs down to Microbial Scales. *Nat. Commun.* **2016**, *7*, 11833. [[CrossRef](#)] [[PubMed](#)]
36. Ruttenberg, B.I.; Adam, T.C.; Duran, A.; Burkepile, D.E. Identity of Coral Reef Herbivores Drives Variation in Ecological Processes over Multiple Spatial Scales. *Ecol. Appl.* **2019**, *29*, e01893. [[CrossRef](#)]
37. Goergen, E.A.; Schopmeyer, S.; Moulding, A.L.; Moura, A.; Kramer, P.; Viehman, T.S. Coral Reef Restoration Monitoring Guide: Methods to Evaluate Restoration Success from Local to Ecosystem Scales. In *NOAA Technical Memorandum NOS NCCOS 279*; NOAA: Silver Spring, MD, USA, 2020; p. 145. [[CrossRef](#)]
38. Pittman, S.; Yates, K.; Bouchet, P.; Alvarez-Berastegui, D.; Andréfouët, S.; Bell, S.; Berkström, C.; Boström, C.; Brown, C.; Connolly, R.; et al. Seascape Ecology: Identifying Research Priorities for an Emerging Ocean Sustainability Science. *Mar. Ecol. Prog. Ser.* **2021**, *663*, 1–29. [[CrossRef](#)]
39. Miller, M.W.; Bourque, A.S.; Bohnsack, J.A. An Analysis of the Loss of Acroporid Corals at Looe Key, Florida, USA: 1983–2000. *Coral Reefs* **2002**, *21*, 179–182. [[CrossRef](#)]
40. Palandro, D.A.; Andréfouët, S.; Hu, C.; Hallock, P.; Müller-Karger, F.E.; Dustan, P.; Callahan, M.K.; Kranenburg, C.; Beaver, C.R. Quantification of Two Decades of Shallow-Water Coral Reef Habitat Decline in the Florida Keys National Marine Sanctuary Using Landsat Data (1984–2002). *Remote Sens. Environ.* **2008**, *112*, 3388–3399. [[CrossRef](#)]
41. Figueira, W.; Ferrari, R.; Weatherby, E.; Porter, A.; Hawes, S.; Byrne, M. Accuracy and Precision of Habitat Structural Complexity Metrics Derived from Underwater Photogrammetry. *Remote Sens.* **2015**, *7*, 16883–16900. [[CrossRef](#)]
42. Ferrari, R.; McKinnon, D.; He, H.; Smith, R.N.; Corke, P.; González-Rivero, M.; Mumby, P.J.; Upcroft, B. Quantifying Multiscale Habitat Structural Complexity: A Cost-Effective Framework for Underwater 3D Modelling. *Remote Sens.* **2016**, *8*, 113. [[CrossRef](#)]
43. Fukunaga, A.; Burns, J.H.R.; Pascoe, K.H.; Kosaki, R.K. Associations between Benthic Cover and Habitat Complexity Metrics Obtained from 3D Reconstruction of Coral Reefs at Different Resolutions. *Remote Sens.* **2020**, *12*, 1011. [[CrossRef](#)]
44. Phinn, S.R.; Roelfsema, C.M.; Mumby, P.J. Multi-Scale, Object-Based Image Analysis for Mapping Geomorphic and Ecological Zones on Coral Reefs. *Int. J. Remote Sens.* **2012**, *33*, 3768–3797. [[CrossRef](#)]

45. Royer, J.P.; Nawaf, M.M.; Merad, D.; Saccone, M.; Bianchimani, O.; Garrabou, J.; Ledoux, J.B.; Lopez-Sanz, A.; Drap, P. Photogrammetric Surveys and Geometric Processes to Analyse and Monitor Red Coral Colonies. *J. Mar. Sci. Eng.* **2018**, *6*, 42. [CrossRef]
46. Suman, D.; Shivlani, M.; Walter Milon, J. Perceptions and Attitudes Regarding Marine Reserves: A Comparison of Stakeholder Groups in the Florida Keys National Marine Sanctuary. *Ocean Coast Manag.* **1999**, *42*, 1019–1040. [CrossRef]
47. Keller, B.; Donahue, S. Florida Keys National Marine Sanctuary U.S. Environmental Protection Agency State of Florida 2002–03 Sanctuary Science Report: An Ecosystem Report Card. In *U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Office of National Marine Sanctuaries, Florida Keys National Marine Sanctuary, Marathon, FL*; 2006. Available online: <http://sanctuaries.noaa.gov/science/conservation/pdfs/Keller1.pdf> (accessed on 28 November 2021).
48. Bruckner, A.W. Proceedings of the Caribbean *Acropora* Workshop: Potential Application of the U.S. Endangered Species Act as a Conservation Strategy. In *NOAA Technical Memorandum NMFS-OPR-24*; NOAA: Silver Springs, MD, USA, 2002; p. 199. Available online: <https://repository.library.noaa.gov/view/noaa/435> (accessed on 28 November 2021).
49. Hogarth, W.T. Endangered and Threatened Species: Final Listing Determinations for Elkhorn Coral and Staghorn Coral. *Fed. Regist.* **2006**, *71*, 26852–26861. Available online: <https://www.federalregister.gov/documents/2006/05/09/06-4321/endangered-and-threatened-species-final-listing-determinations-for-elkhorn-coral-and-staghorn-coral> (accessed on 28 January 2022).
50. Miller, J.; Muller, E.; Rogers, C.; Waara, R.; Atkinson, A.; Whelan, K.R.T.; Patterson, M.; Witcher, B. Coral Disease Following Massive Bleaching in 2005 Causes 60% Decline in Coral Cover on Reefs in the US Virgin Islands. *Coral Reefs* **2009**, *28*, 925–937. [CrossRef]
51. Lewis, C.L.; Neely, K.L.; Richardson, L.L.; Rodriguez-Lanetty, M. Temporal Dynamics of Black Band Disease Affecting Pillar Coral (*Dendrogyra cylindrus*) Following Two Consecutive Hyperthermal Events on the Florida Reef Tract. *Coral Reefs* **2017**, *36*, 427–431. [CrossRef]
52. Florida Fish and Wildlife Conservation Commission. A Species Action Plan for the Pillar Coral *Dendrogyra cylindrus* Final Draft. 2013. Available online: <https://myfwc.com/wildlifehabitats/wildlife/species-action-plans/> (accessed on 28 November 2021).
53. Ruzicka, R.R.; Colella, M.A.; Porter, J.W.; Morrison, J.M.; Kidney, J.A.; Brinkhuis, V.; Lunz, K.S.; MacAulay, K.A.; Bartlett, L.A.; Meyers, M.K.; et al. Temporal Changes in Benthic Assemblages on Florida Keys Reefs 11 Years after the 1997/1998 El Niño. *Mar. Ecol. Prog. Ser.* **2013**, *489*, 125–141. [CrossRef]
54. Precht, W.F.; Gintert, B.E.; Robbart, M.L.; Fura, R.; van Woesik, R. Unprecedented Disease-Related Coral Mortality in Southeastern Florida. *Sci. Rep.* **2016**, *6*, 31374. [CrossRef]
55. Walton, C.J.; Hayes, N.K.; Gilliam, D.S. Impacts of a Regional, Multi-Year, Multi-Species Coral Disease Outbreak in Southeast Florida. *Front. Mar. Sci.* **2018**, *5*, 323. [CrossRef]
56. Aeby, G.S.; Ushijima, B.; Campbell, J.E.; Jones, S.; Williams, G.J.; Meyer, J.L.; Häse, C.; Paul, V.J. Pathogenesis of a Tissue Loss Disease Affecting Multiple Species of Corals Along the Florida Reef Tract. *Front. Mar. Sci.* **2019**, *6*, 678. [CrossRef]
57. Jones, N.P.; Figueiredo, J.; Gilliam, D.S. Thermal Stress-Related Spatiotemporal Variations in High-Latitude Coral Reef Benthic Communities. *Coral Reefs* **2020**, *39*, 1661–1673. [CrossRef]
58. Rippe, J.P.; Kriefall, N.G.; Davies, S.W.; Castillo, K.D. Differential Disease Incidence and Mortality of Inner and Outer Reef Corals of the Upper Florida Keys in Association with a White Syndrome Outbreak. *Bull. Mar. Sci.* **2019**, *95*, 305–316. [CrossRef]
59. Courtney, T.A.; Andersson, A.J. Evaluating Measurements of Coral Reef Net Ecosystem Calcification Rates. *Coral Reefs* **2019**, *38*, 997–1006. [CrossRef]
60. Bohnsack, J.A.; Cantillo, A.Y.; Bello, M.J. Resource Survey of Looe Key National Marine Sanctuary 1983. United States Department of Commerce. In *NOAA Technical Memorandum NMFS-SEFSC*; 2002; Volume 478, p. 267. Available online: [https://www.aoml.noaa.gov/general/lib/CEDAR\\_files/cedar106.pdf](https://www.aoml.noaa.gov/general/lib/CEDAR_files/cedar106.pdf) (accessed on 26 December 2021).
61. Somerfield, P.J.; Jaap, W.C.; Clarke, K.R.; Callahan, M.; Hackett, K.; Porter, J.; Lybolt, M.; Tsokos, C.; Yanev, G. Changes in Coral Reef Communities among the Florida Keys, 1996–2003. *Coral Reefs* **2008**, *27*, 951–965. [CrossRef]
62. Page, C.A.; Muller, E.M.; Vaughan, D.E. Microfragmenting for the Successful Restoration of Slow Growing Massive Corals. *Ecol. Eng.* **2018**, *123*, 86–94. [CrossRef]
63. Lustic, C.; Maxwell, K.; Bartels, E.; Reckenbeil, B.; Utset, E.; Schopmeyer, S.; Zink, I.; Lirman, D. The Impacts of Competitive Interactions on Coral Colonies after Transplantation: A Multispecies Experiment from the Florida Keys, US. *Bull. Mar. Sci.* **2020**, *96*, 805–818. [CrossRef]
64. Baker, B. First Aid for an Ailing Reef: Research in the Florida Keys National Marine Sanctuary. *BioScience* **1999**, *49*, 173–178. [CrossRef]
65. Cangialosi, J.P.; Latta, A.S.; Berg, R. Tropical Cyclone Report: Hurricane Irma (AL112017): 30 August–12 September 2017. In *National Center Tropical Cyclone Report*; 2018; Volume 111. Available online: [https://www.nhc.noaa.gov/data/tcr/AL112017\\_Irma.pdf](https://www.nhc.noaa.gov/data/tcr/AL112017_Irma.pdf) (accessed on 28 January 2022).
66. Viehman, S.; Gittings, S.; Groves, S.; Moore, J.; Moore, T.; Stein, J. NCCOS Assessment: Coral Disturbance Response Monitoring (DRM) along the Florida Reef Tract Following Hurricane Irma from 2017-10-09 to 2017-10-18 (NCEI Accession 0179071). [Hurricane Impacts]. NOAA National Centers for Environmental Information. Dataset. 2018. Available online: <https://doi.org/10.25921/sscd-6h41> (accessed on 17 February 2022).

67. Florida Reef Resilience Program. In *Florida Reef Resilience Program Disturbance Response Monitoring and Hurricane Irma Rapid Reef Assessment Quick Look Report: Summer 2017*; 2017. Available online: <https://repository.library.noaa.gov/view/noaa/15575> (accessed on 28 November 2021).
68. Bohnsack, J.A.; Bannerot, S.P. *A Stationary Visual Census Technique for Quantitatively Assessing Community Structure of Coral Reef Fishes*; 1986; Volume 33, pp. 291–303. Available online: <https://www.st.nmfs.noaa.gov/spo/SPO/tr41opt.pdf> (accessed on 28 November 2021).
69. Ault, J.S.; Smith, S.G.; Meester, G.A.; Luo, J.; Bohnsack, J.A. *Site Characterization for Biscayne National Park: Assessment of Fisheries Resources and Habitats*; NOAA Technical Memorandum NMFS-SEFSC-468; 2001; p. 156. Available online: <https://repository.library.noaa.gov/view/noaa/8519> (accessed on 28 November 2021).
70. Brandt, M.; Zurcher, N.; Acosta, A.; Ault, J.S. *A Cooperative Multi-Agency Reef Fish Monitoring Protocol for the Florida Keys Coral Reef Ecosystem*; Natural Resources Report NPS/SFCN/NRR-2009/150; National Park Service: Fort Collins, CO, USA, 2009. Available online: <https://www.researchgate.net/publication/265682772> (accessed on 28 January 2022).
71. Shinn, E. Spur-and-groove Formation on the Florida Reef Tract. *J. Sediment. Res.* **1963**, *33*, 291–303. [[CrossRef](#)]
72. Shinn, E.; Hudson, J.; Robbin, D.; Lidz, B. Spurs and Grooves Revisited: Construction versus Erosion, Looe Key Reef, Florida. 1982. Available online: <https://pubs.er.usgs.gov/publication/70122248> (accessed on 7 June 2020).
73. Duce, S.; Dechnik, B.; Webster, J.M.; Hua, Q.; Sadler, J.; Webb, G.E.; Nothdurft, L.; Salas-Saavedra, M.; Vila-Concejo, A. Mechanisms of Spur-and-groove Development and Implications for Reef Platform Evolution. *Quat. Sci. Rev.* **2019**, *231*, 106155. [[CrossRef](#)]
74. Burns, J.; Delparte, D.; Gates, R.; Takabayashi, M. Integrating Structure-from-Motion Photogrammetry with Geospatial Software as a Novel Technique for Quantifying 3D Ecological Characteristics of Coral Reefs. *PeerJ* **2015**, *3*, e1077. [[CrossRef](#)] [[PubMed](#)]
75. Fukunaga, A.; Burns, J.H.R.; Craig, B.K.; Kosaki, R.K. Integrating Three-Dimensional Benthic Habitat Characterization Techniques into Ecological Monitoring of Coral Reefs. *J. Mar. Sci. Eng.* **2019**, *7*, 27. [[CrossRef](#)]
76. Walbridge, S.; Slocum, N.; Pobuda, M.; Wright, D.J. Unified Geomorphological Analysis Workflows with Benthic Terrain Modeler. *Geosciences* **2018**, *8*, 94. [[CrossRef](#)]
77. Hobson, R.D. Surface Roughness in Topography: Quantitative Approach. In *Spatial Analysis in Geomorphology*; Chorley, R.J., Ed.; Harper and Row: New York, NY, USA, 1972; pp. 221–246.
78. Sappington, J.M.; Longshore, K.M.; Thompson, D.B. Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. *J. Wildl. Manage.* **2007**, *71*, 1419–1426. [[CrossRef](#)]
79. Jenness, J.S. Calculating Landscape Surface Area from Digital Elevation Models. *Wildl. Soc.* **2004**, *32*, 829–839. [[CrossRef](#)]
80. Nunes, V.; Pawlak, G. Observations of Bed Roughness of a Coral Reef. *J. Coast. Res.* **2008**, *24*, 39–50. [[CrossRef](#)]
81. Bozec, Y.M.; Alvarez-Filip, L.; Mumby, P.J. The Dynamics of Architectural Complexity on Coral Reefs under Climate Change. *Glob. Chang. Biol.* **2015**, *21*, 223–235. [[CrossRef](#)]
82. González-Rivero, M.; Beijbom, O.; Rodríguez-Ramírez, A.; Holtrop, T.; González-Marrero, Y.; Ganase, A.; Roelfsema, C.; Phinn, S.; Hoegh-Guldberg, O. Scaling up Ecological Measurements of Coral Reefs Using Semi-Automated Field Image Collection and Analysis. *Remote Sens.* **2016**, *8*, 30. [[CrossRef](#)]
83. De Clippele, L.H.; Huvenne, V.A.L.; Orejas, C.; Lundäl, T.; Fox, A.; Hennige, S.J.; Roberts, J.M. The Effect of Local Hydrodynamics on the Spatial Extent and Morphology of Cold-Water Coral Habitats at Tisler Reef, Norway. *Coral Reefs* **2018**, *37*, 253–266. [[CrossRef](#)]
84. Conti, L.A.; Lim, A.; Wheeler, A.J. High Resolution Mapping of a Cold Water Coral Mound. *Sci. Rep.* **2019**, *9*, 1016. [[CrossRef](#)]
85. Zawada, K.J.A.; Madin, J.S.; Baird, A.H.; Bridge, T.C.L.; Dornelas, M. Morphological Traits Can Track Coral Reef Responses to the Anthropocene. *Funct. Ecol.* **2019**, *33*, 962–975. [[CrossRef](#)]
86. Darling, E.S.; Alvarez-Filip, L.; Oliver, T.A.; Mcclanahan, T.R.; Côté, I.M. Evaluating Life-History Strategies of Reef Corals from Species Traits. *Ecol. Lett.* **2012**, *15*, 1378–1386. [[CrossRef](#)] [[PubMed](#)]
87. Darling, E.S.; Graham, N.A.J.; Januchowski-Hartley, F.A.; Nash, K.L.; Pratchett, M.S.; Wilson, S.K. Relationships between Structural Complexity, Coral Traits, and Reef Fish Assemblages. *Coral Reefs* **2017**, *36*, 561–575. [[CrossRef](#)]
88. Connell, J.H.; Hughes, T.P.; Wallace, C.C.; Tanner, J.E.; Harms, K.E.; Kerr, A.M. A Long-Term Study of Competition and Diversity of Corals. *Ecol. Monogr.* **2004**, *74*, 179–210. [[CrossRef](#)]
89. McWilliam, M.; Hoogenboom, M.O.; Baird, A.H.; Kuo, C.-Y.; Madin, J.S.; Hughes, T.P. Biogeographical Disparity in the Functional Diversity and Redundancy of Corals. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 3084–3089. [[CrossRef](#)] [[PubMed](#)]
90. Aronson, R.B.; Precht, W.F. Landscape Patterns of Reef Coral Diversity: A Test of the Intermediate Disturbance Hypothesis. *J. Exp. Mar. Biol. Ecol.* **1995**, *192*, 1–14. [[CrossRef](#)]
91. Alvarez-Filip, L.; Dulvy, N.K.; Côté, I.M.; Watkinson, A.R.; Gill, J.A. Coral Identity Underpins Architectural Complexity on Caribbean Reefs. *Ecol. Appl.* **2011**, *21*, 2223–2231. [[CrossRef](#)]
92. Young, G.C.; Dey, S.; Rogers, A.D.; Extton, D. Cost and Time-Effective Method for Multiscale Measures of Rugosity, Fractal Dimension, and Vector Dispersion from Coral Reef 3D Models. *PLoS ONE* **2017**, *12*, e0201847. [[CrossRef](#)]
93. Peterson, G.D. Contagious Disturbance, Ecological Memory, and the Emergence of Landscape Pattern. *Ecosystems* **2002**, *5*, 329–338. [[CrossRef](#)]
94. Hughes, T.P.; Kerry, J.T.; Connolly, S.R.; Baird, A.H.; Eakin, C.M.; Heron, S.F.; Hoey, A.S.; Hoogenboom, M.O.; Jacobson, M.; Liu, G.; et al. Ecological Memory Modifies the Cumulative Impact of Recurrent Climate Extremes. *BioScience* **2020**, *70*, 854–870. [[CrossRef](#)]

95. Burton, P.J.; Jentsch, A.; Walker, L.R. The Ecology of Disturbance Interactions. *BioScience* **2020**, *70*, 854–870. [[CrossRef](#)]
96. Wall, C.B.; Ricci, C.A.; Wen, A.D.; Ledbetter, B.E.; Klinger, D.E.; Mydlarz, L.D.; Gates, R.D.; Putnam, H.M. Shifting Baselines: Physiological Legacies Contribute to the Response of Reef Corals to Frequent Heatwaves. *Funct. Ecol.* **2021**, *35*, 1366–1378. [[CrossRef](#)]
97. Simmons, K.R.; Eggleston, D.B.; Bohnenstiehl, D.R. Hurricane Impacts on a Coral Reef Soundscape. *PLoS ONE* **2021**, *16*, e0244599. [[CrossRef](#)] [[PubMed](#)]
98. NOAA National Weather Service. Tropical Cyclones of the 2000s. Available online: <https://www.weather.gov/key/2000SHurricanes> (accessed on 26 January 2022).
99. Berg, R. Tropical Cyclone Report: Hurricane Isaac (AL092012): 21 August—1 September 2012. In *National Hurricane Center*; 2013; pp. 1–78. Available online: <https://nhc.noaa.gov/data/tcr/index.php?season=2012&basin=atl> (accessed on 28 January 2019).
100. Rogers, C.S. Hurricanes and Coral Reefs: The Intermediate Disturbance Hypothesis Revisited. *Coral Reefs* **1993**, *12*, 127–137. [[CrossRef](#)]
101. Alvarez-Filip, L.; Dulvy, N.K.; Gill, J.A.; Côté, I.M.; Watkinson, A.R. Flattening of Caribbean Coral Reefs: Region-Wide Declines in Architectural Complexity. *Proc. Royal Soc. B* **2009**, *276*, 3019–3025. [[CrossRef](#)]
102. Rogers, A.; Blanchard, J.L.; Mumby, P.J. Fisheries Productivity under Progressive Coral Reef Degradation. *J. Appl. Ecol.* **2018**, *55*, 1041–1049. [[CrossRef](#)]
103. Dubois, M.; Gascuel, D.; Coll, M.; Claudet, J. Recovery Debts Can Be Revealed by Ecosystem Network-Based Approaches. *Ecosystems* **2019**, *22*, 658–676. [[CrossRef](#)]
104. Wilson, S.K.; Burgess, S.C.; Cheal, A.J.; Emslie, M.; Fisher, R.; Miller, I.; Polunin, N.V.C.; Sweatman, H.P.A. Habitat Utilization by Coral Reef Fish: Implications for Specialists vs. Generalists in a Changing Environment. *J. Anim. Ecol.* **2008**, *77*, 220–228. [[CrossRef](#)]
105. Pratchett, M.S.; Coker, D.J.; Jones, G.P.; Munday, P.L. Specialization in Habitat Use by Coral Reef Damselfishes and Their Susceptibility to Habitat Loss. *Ecol. Evol.* **2012**, *2*, 2168–2180. [[CrossRef](#)]
106. Gardner, T.A.; Côté, I.M.; Gill, J.A.; Grant, A.; Watkinson, A.R. Hurricanes and Caribbean Coral Reefs: Impacts, Recovery Patterns, and Role in Long-Term Decline. *Ecology* **2005**, *86*, 174–184. [[CrossRef](#)]
107. McWilliam, M.; Pratchett, M.S.; Hoogenboom, M.O.; Hughes, T.P. Deficits in Functional Trait Diversity Following Recovery on Coral Reefs. *Proc. Royal Soc. B* **2020**, *287*, 20192628. [[CrossRef](#)] [[PubMed](#)]
108. Price, D.M.; Robert, K.; Callaway, A.; Lo Iacono, C.; Hall, R.A.; Huvenne, V.A.I. Using 3D Photogrammetry from ROV Video to Quantify Cold-Water Coral Reef Structural Complexity and Investigate Its Influence on Biodiversity and Community Assemblage. *Coral Reefs* **2019**, *38*, 1007–1021. [[CrossRef](#)]
109. Knudby, A.; Ledrew, E.; Newman, C. Progress in the Use of Remote Sensing for Coral Reef Biodiversity Studies. *Prog. Phys. Geogr.* **2007**, *31*, 421–434. [[CrossRef](#)]
110. Richardson, L.E.; Graham, N.A.; Hoey, A.S. Cross-Scale Habitat Structure Driven by Coral Species Composition on Tropical Reefs OPEN. *Sci. Rep.* **2017**, *7*, 7557. [[CrossRef](#)] [[PubMed](#)]
111. Todd, P.A. Morphological Plasticity in Scleractinian Corals. *Biol. Rev.* **2008**, *83*, 315–337. [[CrossRef](#)] [[PubMed](#)]
112. Pascoe, K.H.; Fukunaga, A.; Kosaki, R.K.; Burns, J.H.R. 3D Assessment of a Coral Reef at Lalo Atoll Reveals Varying Responses of Habitat Metrics Following a Catastrophic Hurricane. *Sci. Rep.* **2021**, *11*, 12050. [[CrossRef](#)]
113. Anthony, K.R.N.; Marshall, P.A.; Abdulla, A.; Beeden, R.; Bergh, C.; Black, R.; Eakin, C.M.; Game, E.T.; Gooch, M.; Graham, N.A.J.; et al. Operationalizing Resilience for Adaptive Coral Reef Management under Global Environmental Change. *Glob. Chang. Biol.* **2015**, *21*, 48–61. [[CrossRef](#)]
114. Gleason, A.C.R.; Lirman, D.; Williams, D.; Gracias, N.R.; Gintert, B.E.; Madjidi, H.; Pamela Reid, R.; Boynton, G.C.; Negahdaripour, S.; Miller, M.; et al. Documenting Hurricane Impacts on Coral Reefs Using Two-Dimensional Video-Mosaic Technology. *Mar. Ecol.* **2007**, *28*, 254–258. [[CrossRef](#)]
115. Hughes, T.P.; Kerry, J.T.; Baird, A.H.; Connolly, S.R.; Dietzel, A.; Eakin, C.M.; Heron, S.F.; Hoey, A.S.; Hoogenboom, M.O.; Liu, G.; et al. Global Warming Transforms Coral Reef Assemblages. *Nature* **2018**, *556*, 492–496. [[CrossRef](#)]
116. Fukunaga, A.; Pascoe, K.H.; Pugh, A.R.; Kosaki, R.K.; Burns, J.H. Underwater Photogrammetry Captures the Initial Recovery of a Coral Reef at Lalo Atoll. *Divers* **2022**, *14*, 39. [[CrossRef](#)]
117. Roelfsema, C.; Thurstan, R.; Beget, M.; Dudgeon, C.; Loder, J.; Kovacs, E.; Gallo, M.; Flower, J.; Cabrera, K.L.G.; Ortiz, J.; et al. A Citizen Science Approach: A Detailed Ecological Assessment of Subtropical Reefs at Point Lookout, Australia. *PLoS ONE* **2016**, *11*, e0163407. [[CrossRef](#)] [[PubMed](#)]
118. Bayley, D.T.I.; Mogg, A.O.M.; Purvis, A.; Koldewey, H.J. Evaluating the Efficacy of Small-Scale Marine Protected Areas for Preserving Reef Health: A Case Study Applying Emerging Monitoring Technology. *Aquat. Conserv.* **2019**, *29*, 2026–2044. [[CrossRef](#)]
119. Chen, G.K.; Dai, C.F. Using 3D Photogrammetry to Quantify the Subtle Differences of Coral Reefs under the Impacts of Marine Activities. *Mar. Pollut. Bull.* **2021**, *173*, 113032. [[CrossRef](#)] [[PubMed](#)]
120. Richaume, J.; Cheminée, A.; Drap, P.; Bonhomme, P.; Cadene, F.; Ferrari, B.; Hartmann, V.; Michez, N.; Bianchimani, O. 3D Photogrammetry Modeling Highlights Efficient Reserve Effect Apparition After 5 Years and Stillness After 40 for Red Coral (*Corallium Rubrum*) Conservation in French MPAs. *Front. Mar. Sci.* **2021**, *8*, 1174. [[CrossRef](#)]

121. Torres-Pulliza, D.; Wilson, J.R.; Darmawan, A.; Campbell, S.J.; Andréfouët, S. Ecoregional Scale Seagrass Mapping: A Tool to Support Resilient MPA Network Design in the Coral Triangle. *Ocean Coast Manag.* **2013**, *80*, 55–64. [[CrossRef](#)]
122. Lawrence, A.; Heenan, A.; Levine, A.; Haddaway, N.R.; Powell, F.; Wedding, L.; Roche, R.; Lawrence, P.; Szostek, C.; Ford, H.; et al. Spatial and Temporal Scales of Coral Reef Fish Ecological Research and Management: A Systematic Map Protocol. *Environ. Evid.* **2021**, *10*, 3. [[CrossRef](#)]
123. Sierra-Escrigas, S.L.; Peluffo, D.R.P.; García-Urueña, R. Shallow Coral Reef Community Mapping and Update on Its Ecological Units Using Aerial Images at Isla Arena, Colombian Caribbean. *Int. J. Remote Sens.* **2020**, *41*, 8198–8215. [[CrossRef](#)]
124. Roelvink, F.E.; Storlazzi, C.D.; van Dongeren, A.R.; Pearson, S.G. Coral Reef Restorations Can Be Optimized to Reduce Coastal Flooding Hazards. *Front. Mar. Sci.* **2021**, *8*, 1–11. [[CrossRef](#)]
125. Storlazzi, C.D.; Reguero, B.G.; Cumming, K.A.; Cole, A.D.; Shope, J.B.; Gaido, L.C.; Viehman, T.S.; Nickel, B.A.; Beck, M.W. Rigorously Valuing the Coastal Hazard Risks Reduction Provided by Potential Coral Reef Restoration in Florida and Puerto Rico. Geological Surveys (U.S.). 2021. Available online: <https://doi.org/10.3133/ofr20211054> (accessed on 28 November 2021).

**CHAPTER 3: Spatiotemporal patterns in reef fish biodiversity and habitat utilization  
using reef visual census surveys and underwater soundscapes**

## ABSTRACT

Spatiotemporal changes in reef fish biodiversity, fish density and biomass of target group fish families, Haemulidae and Lutjanidae, and their associated low frequency (< 3kHz) mean sound pressure levels (SPLs) were investigated across three reserve types in the Florida Keys National Marine Sanctuary before and after hurricane Irma between 2017 and 2018. A multidisciplinary approach combining traditional reef fish visual census (RVC) surveys and underwater soundscapes explored the response of reef fish biodiversity indices and the target group fish families to habitat characteristics, reserve location, and time of sampling. Prior to the hurricane, reef fish biodiversity indices were relatively similar among sites and sampling period, although sites varied in depth and reef structure. The sampling period after the hurricane resulted in a > 60% decrease in fish density for all sites except one research-only area. Species diversity, richness, and evenness increased after the disturbance with the greatest increase occurring at protected sites. The target group's density and biomass response to variations in habitat feature strongly reflected site-specific preferences related to the presence of complex reef structures (i.e., vertical hard relief, surface hard relief) and protection status. Mean low-frequency band sound pressure levels (SPLs) associated with reef fish sounds (L1 0.1-3kHz) were site-specific and ANCOVA models found all reef fish biodiversity metrics to be significant predictors except evenness. A narrower low-frequency band (1.2 – 2kHz) associated the target group fish families pooled by sample date responded strongly with habitat covariates depth and vertical hard relief and dominant biomass varied by reserve type. The network of reserves varying in protection status is beneficial for displaced reef fish after a severe disturbance and supports efforts in understanding the effectiveness of marine reserves to protect the integrity of coral reef ecosystems.

## Introduction

Coral reefs provide structurally complex habitats that support a range of ecosystem services, including high biodiversity, fisheries production, and recreational opportunities for humans, as well as buffer coastal societies from climatic impacts (1–3). Coral reefs, however, are in decline globally and are becoming more susceptible to environmental stressors, climatic disturbances (i.e., hurricanes, ocean warming), diseases and anthropogenic impacts (4–7). Decreased reef structural complexity and habitat diversity can lead to reduced fish diversity and fisheries productivity and, in extreme cases, lead to extirpation of local fish species (8–10). Conservation and restoration efforts for coral reefs include multiple spatial management strategies such as networks of no-take marine reserves (NTMRs) adjacent to open fishing areas (11–14), coral restoration via artificial propagation or cryopreservation (15,16), and stock enhancement of herbivores that balance the growth of macroalgae on corals and help clear space for coral larvae to settle (17–19).

NTMRs were established to decrease the exploitation of target and non-target species and rebuild depleted stocks while protecting the integrity of biodiversity within marine ecosystems (20–24). NTMRs have produced several benefits, such as increasing target fish species density, increasing spawning stock biomass, supplying source populations for neighboring habitats (i.e., spill-over), preserving trophic interactions, and protecting essential reef habitats from structural damage (25–28). In contrast, some studies indicate a decline in these biological measures, no apparent difference between NTMRs and fished habitats, or changes in the efficacy of the NTMRs in response to reef degradation (29–32). For example, a recent study assessed ecological responses to NTMRs over two decades, spanning a major climate-driven coral bleaching event (23). Before the bleaching event, the reef fish responses to NTMRs were consistent with the

general literature, with relatively high coral cover, more species of fish, and greater fish biomass, particularly of upper trophic levels. However, in the 16 years following coral mortality due to bleaching, reserve effects were absent for the reef benthos, and greatly diminished for fish species richness (23).

In this unprecedented, current decline of coral reef habitats and its cascading impacts on reef fish biodiversity, new methods for long-term monitoring at the ecosystem level, including collecting biological data and related physical reef metrics, is critical. Reef structure composition and spatial distribution of habitat types (i.e., coral-dominated, patch reef) can influence reef fish assemblages, recruitment, and population connectivity (33–36). Underwater soundscapes are an emerging, non-invasive technology that can reflect biological and physical sources of sound in the environment, including vocalizations by soniferous species (e.g., whales, fish), the sounds associated with animal behavior (e.g., spawning, foraging, burrowing) (37–39), as well as physical sources from air-sea interactions such as rain, wind, and wave action (40,41). Therefore, characteristics of the soundscape can be used to infer habitat quality and biodiversity, identify important spawning habitats, and estimate the density of soniferous fish species (42–46).

The Florida Keys is home to a diverse community of sound-producing reef fish and invertebrate species. For example, studies have found higher snapping shrimp sound pressure levels (SPLs), presumably from higher densities, in more structurally complex, healthy habitats than degraded reefs (53) and have observed that spatiotemporal changes in snapping shrimp may be a good indicator of habitat quality due to their dependence on living in three-dimensional structures and burrows (54–57). Mixed-species schools of grunts (*Haemulidae*) and snapper (*Lutjanidae*) are prominent in shallow reef communities and play an important ecological role in schooling associations for protective mimicry and facilitate multiple trophic interactions (58–61).

These species also demonstrate a high affinity for complex reef sites with moderate to high relief structures such as reef outcroppings or ledges, high relief coral spurs, and microhabitats that serve as refugia against predation, while allowing for opportunistic feeding behavior (i.e., ambush) before migrating at night to forage neighboring habitats (e.g., seagrass beds, mangroves) (62–65).

Grunts also aggregate for spawning (66,67) yet have not been documented to emit sound related to interspecific communication (68). Grunts generally express “grunting” noises in response to stress or perceived threats (68–71). This unique grunting noise is a stridulatory sound produced by the pharyngeal jaws first described in the white grunt *Haemulon plumieri* (69). During an experimental study on the French grunt *H. flavolineatum*, sounds emitted during food processing occurred dominantly at ~700Hz (68). As Haemulids are known to be receptive to low frequencies (>300-400Hz), sounds may aid in the location of foraging schools at night (72). A recent study by Simmons et al. (41) in the lower Florida Keys found differences between mean daytime and nighttime sound pressure levels (SPL) for a targeted frequency band 1.2-1.8kHz representative of schooling snapper and grunts before and after Hurricane Irma in 2017, such that mean sound production during the daytime weakened indicating that the disturbance may have impacted foraging behavior or diel activity due to low visibility conditions. Thus, biological acoustic patterns may be applicable to monitoring social behavior, foraging activity, or spawning success for sound-producing schooling species (68,73–75).

### *Study Area*

The Florida Keys National Marine Sanctuary (FKNMS) provides a unique study system to observe comparisons between varying management levels, including NTMRs. The diverse spatial management zones and non-regulated sites comprise a network of 18 “no-take” Sanctuary

Preservation Areas (SPAs), one “no-take” Ecological Reserve (ER), four Special-Use Areas (SUAs), and reef tracts without special management status can be used as controls to address fundamental questions regarding some of the drivers of biodiversity and habitat complexity. Field studies employing visual surveys by divers have compared changes in reef fish and spiny lobster among management zones and fished areas within the FKNMS. Within one year of NTMRs being established, there was evidence of a higher annual mean density of economically important exploited species such as yellowtail snapper (*Ocyurus chrysurus*), grouper species (*Epinephelus* sp., *Mycteroperca* sp.), and hogfish (*Lachnolaimus maximus*) within NTMRs compared to fished areas; however, non-economically important species such as striped parrotfish (*Scarus iseri*) and stoplight parrotfish (*Sparisoma viride*) exhibited no uniform difference in density across fished and non-fished sites (76–78). Interestingly, fish densities were generally higher in NTMRs before being protected in 1997 than in fished sites (77), suggesting that habitat is an important explanatory variable.

For the period 1996-2002, exploited species within the FKNMS such as gray snapper (*Lutjanus griseus*), black grouper (*Mycteroperca bonaci*), and yellowtail snapper densities were highest in NTMRs, while both striped parrotfish and stoplight parrotfish continued to show similar mean densities at fished and non-fished sites (79). For the period 1994-2001, changes in the relative rates of density for several important fish groups, including Haemulidae, Lutjanidae, and Serranidae were found across 22 reserve types (i.e., SPAs, SUAs, ERs) in FKNMS, and reflected an overall increased density of exploitable fishes inside reserves (78). For the period 1999-2018, protected areas in the FKNMS had higher reef-fish biomass compared to unprotected areas at the beginning of the observation period; however, metrics such as fish abundance, biomass, and diversity throughout the FKNMS decreased over time (80). Although high-relief

reefs are important for biodiversity conservation and restoration, policies should address the decline in fish abundance, biomass, and diversity observed throughout the FKNMS (80).

The diver surveys that generated the fish metrics used by Medina et al (80) were conducted annually between May and October by trained scuba divers from 1999 to 2012, and then every two years through 2018. Data were obtained from the NOAA National Marine Fisheries Service Southeast Fisheries Science Center (NOAA, 2021). The present study applied the same standardized visual survey techniques for reef fish and habitat characteristics used in the previous studies in the FKNMS (see detailed Methods below); however, the temporal resolution was increased to four times per year (as opposed to once every year or two), and visual surveys were paired with underwater soundscape measures using hydrophones at each site.

### *Research Objectives*

According to the FKNMS Science Plan 2002 and the NOAA-CORIS Florida Reef Resilience report, resource managers require up-to-date, high-resolution data on reef fish biodiversity, coral species conditions, impact responses, and resiliency indicators to guide decision-making and prioritize actions that support resiliency. A comprehensive study examining reef fish biodiversity and habitat associations as a function of management, however, has not been conducted in the FKNMS since 2004. Moreover, there is limited information on the relationship between reef fish, habitat characteristics and the underwater soundscape (81–83). Therefore, we addressed three overarching questions in the lower Florida Keys fore-reef tract: (1) How does reef fish biodiversity and the target group families, Haemulidae and Lutjanidae, vary according to sampling location, time of sampling and reef habitat characteristics? (2) How does the underwater soundscape at relatively low frequencies (<3kHz) that correspond to dominant fish families vary according to sampling location, time of sampling and reef habitat

characteristics? (3) Do spatiotemporal patterns in the underwater soundscape correspond to patterns of reef fish measured by diver surveys? Throughout these research questions, we also investigated changes in reef fish biodiversity metrics and mean sound pressure levels (SPLs) before and after the impact of hurricane Irma on our research sites. Using a multidisciplinary approach that combines traditional visual surveys with underwater soundscape measurements provides a more robust understanding of spatiotemporal relationships between reef fish, habitat characteristics and management zones than would be achieved by either visual surveys or soundscape measurements alone.

## **Materials and Methods**

### *Visual Surveys of Reef Fish*

Reef fish visual (RVC) and habitat surveys were conducted seasonally between February 2017- December 2018 at eight sites in the FKNMS (Figure 1) using a modified Bohnsack-Bannerot point count method developed by a cooperative multi-agency network of the Florida Fish and Wildlife Conservation Commission (FWCC), NOAA, and the National Park Service (84–86). Primary sampling units (PSU) of 100 m x 100 m (10,000 m<sup>2</sup>) at each reef site were further subdivided into a two-stratified design randomly applied among the spur-and-groove portions of each reef in which two divers identified and sized all reef fish within a 177m<sup>2</sup> cylinder area inclusive of the seafloor vertically to the surface of the reef structure (86,87). Immediately following the initial fish surveys, observers examined any crevices or visually obstructed areas within the survey radius to record any cryptic species. Each diver used a PVC pipe constructed in a “T” shape (1 m length with 0.1 increments x 0.3 m width) as reference measurements for fish total length (to the nearest centimeter) and habitat metrics such as

maximum vertical relief (m) and surface coverage relief (m). RVC surveys allowed for additional time to collect data on biotic and abiotic habitat features in a standardized manner according to FWCC protocols. Each diver survey did not exceed 20 min (88). Fish density is defined as the average number of individuals per cylindrical area surveyed and scaled to numbers per m<sup>2</sup> for comparisons with related studies. (47,87).

### *Visual Surveys of Habitat Characteristics*

In this study, we focused on pre- and post-Irma RVC surveys between 2017 and 2018 to observe the relationship between total reef fish density, biomass, diversity indices (i.e., species richness, diversity), and habitat metrics at each site. On average, each sample period contained 16 surveys (2 divers/ site x 8 sites). Habitat metrics such as depth, vertical hard relief (m), and hard surface relief coverage (m) were previously identified as drivers in site separation and characterization among the sampled reefs using an RVC and structure-from-motion approach (9) and were therefore used in our current study. Surface hard relief coverage was calculated as a weighted mean in meters based on each percentage allocated to each height category: <0.5m, 0.5 – 1.0m, 1.0 – 1.5m, > 1.6m.

### *Hypothesis Testing: RVC Surveys*

We tested two hypotheses using fish and habitat data collected from RVC surveys conducted in 2017-2018. The first set of hypotheses tested the mean fish response of density, biomass, species diversity, and evenness as a function of location, sample period and habitat characteristics. The second set of hypotheses tested whether the mean fish response of the target group density and biomass as a function of location, sampling period, and habitat characteristics. Each fish response and explanatory habitat variable are described in detail below.

Fish Response Variables. – Mean fish density per m<sup>2</sup> was generated for each PSU during four sampling periods at each site, in which the total fish counts collected from 2-3 divers (sub-samples) were averaged to create a single data point. Reef fish biomass was calculated using the length-weight relationship  $W=aL^b$  where  $W$  is the estimated weight (g),  $L$  is the observed fish total length,  $a$  and  $b$  are the constants for allometric growth rates and body shape (87,89,90) and species richness was the total number of species observed during an individual survey. The Shannon diversity ( $H'$ ) index (12) for each diver survey at each site and sampling period was also calculated. This sampling design, implemented by FWCC, optimizes density and biomass indices for several commercially and recreationally important species (84,86); however, for this study, a separate target group comprised of grunts (Haemulidae) and snapper (Lutjanidae) (herein “target group”) was also used as a fish response variable. Target group density and biomass were calculated as the sum of observations of both target fish families, Haemulidae and Lutjanidae, per diver for each site and sampling period.

Habitat Explanatory Variables. – During each RVC survey at a given site, divers would start their surveys in the vicinity of the moored hydrophone (typically 15-30 m away), such that the sites were not necessarily the same from one sampling period to the next. Given that the habitat characteristics were relatively fixed from one sampling period to the next, we treated each diver survey as an independent replicate for RVC habitat surveys to capture variation in such features as depth, vertical relief, and rugosity associated with a given site.

### *Passive Acoustic Monitoring*

Coral reef soundscape monitoring was conducted seasonally using bottom-mounted hydrophones (Soundtrap ST300, Ocean Instruments NZ) deployed and retrieved before or after

RVC surveys at each site. The bottom-mounted moorings were suspended ~0.15m from the bottom of a sand channel near the seaward side of the spur-and-groove habitat. All hydrophones were programmed to a sound recording schedule of 2 minutes every 20 minutes (72 files/day) at a sample rate of 48kHz. The mean spectrum for each 2-minute recording was post-processed using a fast Fourier transform with a window length (NFFT) of  $2^{14}$  at a frequency resolution ( $\Delta f$ ) of 2.93 Hz by purpose-written code in MATLAB.

To ensure the analyses focused on biological sound sources, targeted acoustic frequencies encompassed the low-frequency spectrum (<50Hz to several kHz) often associated with reef fish bioacoustics (92–94). Specifically for this study, daily averages of mean sound pressure levels (SPLs) were calculated at two frequency bands: (1) L1 0.1-3kHz to encompass the acoustic spectrum of all fish-associated low-frequency sounds and, (2) L2 1.2-2kHz representative of the target reef fish group consisting of Haemulidae (68,69) and Lutjanidae (92) vocalizations. Several reef sites are within mixed-use (recreational diving, boating, and fishing) areas. Thus, SPL data from all sites were trimmed to exclude files creating the loudest 2% of the sound data over the sampling period to avoid anomalously large amplitudes from transient vessel noise impacting daily hour SPL calculations.

#### *Hypothesis Testing: Passive Acoustic Monitoring*

The RVC and soundscape data collected in 2018 were used to explore the relationships between reef fish biodiversity, underwater soundscapes, and habitat characteristics. The first set of hypotheses tested the response of mean SPLs from the L1 frequency band (0.1-3kHz) as a function of mean fish density, mean fish biomass, location, sampling period, and habitat characteristics. The second set of hypotheses tested the response of mean SPLs from the L2

frequency band (1.2-2kHz) associated with the target group as a function of the target group's mean density, mean biomass, location, sample period, and habitat characteristics.

Temporal patterns in the biological coral reef soundscape vary diurnally for South Atlantic and Caribbean reefs. In general, these temporal patterns reflect the density, distribution, and acoustic behavior of multiple soniferous species and can vary in the range of SPLs and frequencies based on the reef site (e.g., (38,95,96)). For each 24-hour period, day-hour-frequency SPLs were calculated to produce mean daily, mean daytime, mean nighttime, mean crepuscular, mean morning twilight, and mean evening twilight hours defined in Table 1. Uncertainties (95% confidence interval) in each sampling period mean were estimated using bootstrap sampling (500 draws). During the daylight hours, SPLs increased and were more likely to be impacted by boat noise, especially at fished sites or SPAs that are open access for recreational use (97) (Figure S1-S2). Therefore, comparisons between the FKNMS study sites focused on analyzing differences in SPLs during crepuscular hours (e.g., sunrise and sunset).

A series of 7-day temporal windows of mean SPLs the week after each RVC survey were generated to add variation in the samples used to correlate the reef fish and habitat data from RVC surveys, which were tested against the reef fish acoustic data (Table 2). In general, the mean SPLs for the L2 band were highest during crepuscular hours compared to the mean daily, daytime, and nighttime SPLs at all sites (Figure S3-S4). Analysis of SPLs represented by the L2 low-frequency band (1.2-2 kHz) during crepuscular hours also allowed for inferences to be made about the exchange of schooling grunts and snappers on and off the sampled fore-reef sites.

### *Statistical Approach*

Statistical analyses were completed in R Studio (version 2022.07.01) to address each hypothesis related to the response variables of total fish data (i.e., density, biomass, H', S', J' )

and the target group (i.e., density, biomass). Several analyses of covariance (ANCOVA) models tested the significance of fish response variables as a function of each habitat metric interactions with location and sampling period. The coefficient estimates and variable interaction produced from each ANCOVA model were plotted to observe overall main and interaction effects. When site (Model 1) or sampling period (Model 2) was insignificant, these metrics were removed from the model and not reported. For the RVC only data, a total of 14 statistical models were applied, ten tested overall fish response variables, and four models tested the target fish group (see below).

### **Total Fish Data ANCOVA model**

Model notation is interpreted as the *dependent variable's statistical relationship* ' ~ ' to the *independent variable and covariate interactions* '\*'

*Model 1 Fish response variable (density, biomass, H', S',J) ~ Site \* depth \* surface hard relief \* vertical hard relief*

*Model 2 Fish response variable (density, biomass, H', S',J) ~ Date \* depth \* surface hard relief \* vertical hard relief*

### **Target Group Fish Data ANCOVA model**

*Model 1: Target group response variable (density, biomass) ~ Site \* depth \* surface hard relief \* vertical hard relief*

*Model 2: Target group response variable (density, biomass) ~ Date \* depth \* surface hard relief \* vertical hard relief*

Since each SPL corresponded to both diver surveys at each location, site was not a significant variable used in the soundscape model for the L1 frequency band. Therefore,

ANCOVA models were used to observe the response of mean SPLs for the L1(0.1-3kHz) and L2 (1.2-2kHz) frequency bands as a function of date with habitat metrics (Model 1) and fish response variables (Model 2) used as covariates. The models used to explore the relationship between the soundscape, RVC fish and habitat data were built as follows:

### **L1 (0.1-3kHz) frequency band ANCOVA model**

*Model 1: mean L1 SPLs ~ Date \* depth \* surface hard relief \* vertical hard relief*

*Model 2: mean L1 SPLs ~ Date \* fish biomass \* fish density \* species richness \* species diversity*

### **L2 (1.2-2kHz) frequency band ANCOVA model**

*Model 1: 1 mean L2 SPLs ~ Date \* depth \* surface hard relief \* vertical hard relief*

*Model 2: 1 mean L2 SPLs ~ Date \* target group density \* target group biomass*

## **Results**

*The Response of reef fish biodiversity to sampling location, time of sampling and reef habitat characteristics*

Reef fish biodiversity and time of sampling. – A total abundance of 14,143 reef fish were observed during RVC surveys between 2017 and 2018 across three management zones in the FKNMS: 7,852 in 2017 (37 families, 103 species) and 6,291 in 2018 (29 families, 95 species). Mean reef fish density ( $\pm$  SE) was highly variable within and among sites across each seasonal sample period, ranging from 0.20 ( $\pm$  0.05) m<sup>-2</sup> to 1.75 ( $\pm$  0.03) m<sup>-2</sup>, although there was minimal difference between annual mean reef densities of 0.72 ( $\pm$  0.01) m<sup>-2</sup> and 0.71 ( $\pm$  0.02) m<sup>-2</sup> in 2017 and 2018 respectively (Table 3). In 2017, the highest mean reef fish density ( $\pm$  SE) was observed at fished site NFS with a mean reef fish density of 1.45 ( $\pm$  0.07) m<sup>-2</sup> in July followed by ecological reserve WSB's mean reef fish density of 1.38 ( $\pm$  0) m<sup>-2</sup> (Figure 2A). Following the

passage of Hurricane Irma in September 2017, most sites surveyed in December 2017 decreased in mean reef fish density with the largest decrease, > 60% occurring at protected site LKP and fished sites N1M, NFS, and WDR. Research-only area LKU was the only site to increase by > 80%, but also had the lowest overall mean reef fish densities ( $< 0.06 \text{ m}^{-2}$ ) for each sample period in for 2017. Although three sites, LKU, LKP, and WDR were successfully surveyed in February 2018, this sample period resulted in the highest mean reef fish densities of  $1.75 (\pm 0.03) \text{ m}^{-2}$  at LKU and  $1.61 (\pm 0.13) \text{ m}^{-2}$  at WDR.

Mean reef fish biomass ( $\pm$  SE) varied within sites across each sample period, and despite the occurrence of the hurricane, all sites mean reef fish biomass generally ranged from  $10 (\pm 4.48) \text{ g}\cdot\text{m}^{-2}$  to  $209.14 (\pm 193.82) \text{ g}\cdot\text{m}^{-2}$  between 2017 and 2018 (Figure 2B). The highest mean fish biomass recorded during our sampling periods occurred at two sites during December 2018, LKU  $363.86 (\pm 354.05) \text{ g}\cdot\text{m}^{-2}$  and NFS  $359.19 (\pm 248.13) \text{ g}\cdot\text{m}^{-2}$ . Prior to hurricane Irma, mean species richness (number of species per  $\text{m}^{-2}$ ;  $\pm$  SE) was similar among sites ranging from  $16 (\pm 2.04)$  to  $24 (\pm 2.89)$  with minimal variation in mean species richness within sites, except for WDR which had the highest mean species richness of  $30 (\pm 8.54)$  (Figure 2C). Following the hurricane, mean species richness at WDR and LKP decreased by 50%, and NFS decreased by 30%. In 2018, within site variation increased in mean species richness for all sites and several sites showed a slight trend where mean species richness gradually increases in late winter (February) and late summer (September) while decreasing during the spring-summer season (May/June/July).

Mean species diversity ( $\pm$  SE) was higher in 2017 than 2018 with mean values of  $2.16 (\pm 0.18)$  and  $1.99 (\pm 0.21)$  respectively (Figure 2D). All sites sampled in December 2017 after the hurricane increased in species diversity and the largest increase occurred at research only

area ESB which had a mean species diversity of 1.51 ( $\pm$  0.15) in July and increase to 2.13 ( $\pm$  0.01) in December. ESB mean species diversity gradually increased in 2018 peaking at 2.52 ( $\pm$  0.15) in September 2018. In contrast, all other sites drastically decreased in 2018 and showed a similar trend to mean species richness in which mean species diversity gradually increased and peaks in late summer before decreasing in winter. There was little difference in annual mean evenness ( $\pm$  SE) between 2017 and 2018 which was 0.73 ( $\pm$  0.05) and 0.72 ( $\pm$  0.08) respectively (Figure 2E). There was high variation in mean evenness within and among sites across each sampling period, but generally the highest scores were at protected site LKP and the two research only areas LKU and ESB. In December 2017, all sites increased in mean evenness except research only area LKU which slightly decreased from 0.81 ( $\pm$  0) to 0.79 ( $\pm$  0.01). WSB had the highest overall mean evenness of 0.9 ( $\pm$  0.03) recorded in September 2018 followed by ESB with a mean evenness of 0.87 ( $\pm$  0.02) in June 2018. The lowest mean evenness of 0.52 ( $\pm$  0.06) was recorded at LKU in February 2018 followed by WDR with a mean evenness of 0.53 ( $\pm$  0.05) recorded in December 2018.

All sites observed species of the concern within the target group during RVC surveys but varied in presence/absence throughout the seasonal sampling periods. The total abundance of the target group was 263 in 2017 (18 species) and 236 in 2018 (16 species). Haemulidae were more abundant species during both years with a total abundance of 155 (11 species) in 2017 and 140 (10 species) in 2018. Lutjanidae had a total abundance of 108 (7 species) in 2017 and decreased to a total abundance of 96 (6 species) in 2018. Mean fish density and mean fish biomass drastically increased in between 2017 and 2018 for both families, but Haemulidae had the highest annual mean fish density of 0.19 m<sup>-2</sup> and mean fish biomass of 38.93 ( $\pm$  2.24) in 2018 (Table 4). LKU had the highest mean fish density for Haemulidae at 1.43 ( $\pm$  0.15) m<sup>-2</sup> in

February 2018 followed by NFS with a mean fish density of  $0.62 (\pm 0.07) \text{ m}^{-2}$  in December 2018. The highest mean fish biomass for Haemulidae was observed at fished sites NFS and WDR in December 2018 at  $177.12 (\pm 42.97) \text{ g}\cdot\text{m}^{-2}$  and  $117.81 (\pm 19.84) \text{ g}\cdot\text{m}^{-2}$ , respectively. Lutjanidae had the highest mean fish density at SDK reaching  $0.61 (\pm 0.13) \text{ m}^{-2}$  in September 2018 at protected site SDK while the highest mean fish biomass of  $195.19 (\pm 122.29) \text{ g}\cdot\text{m}^{-2}$  was observed at LKP in June 2018.

Predicting reef fish biodiversity. – In general, water depth was the main driver separating sites based on habitat features (S5). LKP was the deepest site ( $>7 \text{ m}$ ) and WSB was the shallowest site ( $\sim 4 \text{ m}$ ); however, all sites showed high within-site variation in vertical hard relief and surface hard relief providing little site separation based solely on the latter habitat features. In support of the site-specific habitat features and seasonal trends in the reef fish biodiversity indices, the reef fish response metrics varied in significance between Model 1 (pooled by site) and Model (pooled by date) and did reflect the overall importance of within and among site variation in data collected by RVC surveys. Reef fish biomass varied significantly among sites when pooled by sampled date ( $F = 4.82, p = 0.03, \alpha = 0.05$ ). In contrast, species richness did vary significantly among sample date when pooled by site ( $F = 3.61, p = 0.02, \alpha = 0.05$ ), and increased with increasing depth ( $F = 3.46, p = 0.02, \alpha = 0.05$ ). Additionally, species richness increased significantly at sites with deeper depths ( $> 6 \text{ m}$ ) and higher ranges in surface hard relief ( $> 2.5 \text{ m}$ ) ( $F = 12.66, p < 0.01, \alpha = 0.01$ ). Species richness showed the most the variation among sample date ( $F = 16.79, p < 0.001, \alpha = 0.001$ ) and several sites showed seasonal trends with increasing species richness in late winter and early fall, while decreasing during summer months (Figure 2C). This relationship was strengthened when sample date interacted with surface hard

relief ( $F = 10.59$ ,  $p < 0.01$ ,  $\alpha = 0.01$ ) and was the most significant when depth was added an additional covariate to the overall interactions ( $F = 13.42$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ). This was supported by higher estimates of species richness at deeper sites such as LKP and NFS due to more variation in habitat features reminiscent to deep spur and groove channels (Figure 3A). Additionally, surface hard relief over time yielded a larger coefficient estimate than vertical hard relief and causing a stronger relationship between species richness and sample date (Figure 3B), therefore more significant interactions occurred when including surface hard relief in Model 2. Variations in vertical hard relief were significantly related to increases in species richness ( $F = 5.49$ ,  $p = 0.02$ ,  $\alpha = 0.05$ ) but was not as strong as an indicator as other habitat metrics. Species diversity also varied significantly with sample date ( $F = 4.42$ ,  $p = 0.04$ ,  $\alpha = 0.05$ ), but showed more significant relationships when interacting with both depth and vertical hard relief ( $F = 10.15$ ,  $p = 0.01$ ,  $\alpha = 0.01$ ) due to high within-site variations for these habitat features. For example, SDK had higher fish densities and biomass at deeper depths than other sites yet had similar results to most sites in terms of species richness and species diversity. Evenness was not significantly different among sites, but was significantly different among sample dates ( $F = 5.01$ ,  $p = 0.04$ ,  $\alpha = 0.05$ ) and showed the strongest relationship with variations in depth and vertical hard relief ( $F = 7.93$ ,  $p = 0.01$ ,  $\alpha = 0.01$ ) over time.

WDR was also variable in terms of depth and had higher vertical hard relief ( $>3$ ) than most sites.

The target group, Haemulidae and Lutjanidae reef fish, density and biomass showed several strong relationships with habitat metrics when pooled by site or sample date (Table 5). Target group density ( $N\ m^{-2}$ ) did vary among sites, although site alone as a factor was not a strong predictor. Target group density among sites increased significantly with higher vertical hard relief values ranging from 2 – 4m ( $F = 4.04$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ). This interaction slightly

increased in significance when interacting with covariates surface hard relief and depth ( $F = 6.48, p < 0.001, \alpha = 0.001$ ) as most species were recorded at sites depths greater than 4m and when surface hard relief ranged from 0.5-1m (S6). Target group density showed stronger relationships with variations among sample date ( $F = 11, p < 0.001, \alpha = 0.001$ ) and weakened relationships with changes in depth and vertical hard relief ( $F = 4.69, p = 0.03, \alpha = 0.05$ ) over time. For example, the site-specific coefficient estimates for LKP and LKU target group density had strong effects when interacting with surface hard relief, yet negatively impacted sites with lower values in surface hard relief such as NFS and SDK (Figure 4A). However, significant interaction effects that included sample date, depth, and vertical hard relief essentially weakened the effects of surface hard relief over time (Figure 4B). In general, all habitat features were important predictors for target group biomass ( $\text{g m}^{-2}$ ) within both models, but varied in significance when observing changes in biomass across sites and over time. Target group biomass did vary significantly among sites with the strongest relationship occurring when depth interacted with surface hard relief ( $F = 14.9, p < 0.001, \alpha = 0.001$ ). Although depth was site specific, depth's interaction with variations in vertical hard relief demonstrated a strong relationship with increases in target group biomass ( $F = 10.9, p = 0.001, \alpha = 0.01$ ). Like the site-based target group density model coefficients, the target group biomass coefficient estimates also highlighted site-based effects for LKU, WDR WSB as these sites differed in depth but were similar in both surface hard and vertical relief structures (Figure 4C). Sample date was an important predictor for increases in target group biomass and complemented similar seasonal patterns in greater species presence at sites with deeper depths and high variations in vertical hard relief. However, the coefficient estimate for surface hard relief was relatively large as this metric showed high within site variation and in general negatively affected the strength of habitat

features in the predicting target group biomass over time (Figure 4D). This is supported by the strongest interaction effect between depth and vertical hard relief ( $F = 12.3$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ) when predicting target group biomass when compared to depth interacting with surface hard relief ( $F = 7.22$ ,  $p = 0.01$ ,  $\alpha = 0.01$ ).

*The response of the reef fish biophony to sampling location, time of sampling and reef habitat characteristics*

Mean SPLs were site-specific and fish biomass was highly variable across each sampling period. The highest mean SPLs of  $\sim 104$  dB were recorded at WDR in December 2018 (Figure 5A) and ESB in September 2018 (Figure 5F). LKP was the quietest site in comparison to all sampled sites with a mean maximum SPL of 99 dB during the September 2018 sample period (Figure 5G). The December 2018 sample period had the highest mean fish biomass for all sample sites with LKU having the highest mean biomass  $363.86 \text{ g}\cdot\text{m}^{-2}$  (Figure 5H) followed by NFS with a mean fish biomass of  $359.19 \text{ g}\cdot\text{m}^{-2}$  (Figure 5C). Overall, WDR and SDK were the only sites to show a slight trend in increasing mean SPLs as reef fish biomass increased, while other sites such as NFS, WSB, LKP, and LKU had site-specific mean SPLs during sample periods when reef fish biomass was relatively low. No sound data was collected for N1M and the site was only sampled once in June 2018 recording a mean biomass of  $67.22 \text{ g}\cdot\text{m}^{-2}$ .

Mean SPLs for the L1 frequency band (0.1 – 3kHz) associated with reef fish sound production during crepuscular hours did not show a distinct relationship with the fish or habitat metrics as mean SPLs were site-dependent (Figure S7). ANCOVA results for the mean L1 SPLs pooled by sample date showed stronger interaction effects with fish metrics (Model 2) than the habitat metrics (Model 1) (Table 7). Depth was the only significant predictor in Model 1 ( $F =$

19.04,  $p < 0.001$ ,  $\alpha = 0.001$ ) supporting previous results highlighting site separation based on differences in mean depth. Reef fish biomass ( $F = 16.9$ ,  $p < 0.01$ ,  $\alpha = 0.01$ ) was a significant predictor in mean L1 SPLs and mean SPLs were highest when there also increases demonstrated by the significant interaction of reef biomass, fish density and species richness ( $F = 53.2$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ).

*The response of the target group reef fish biophony to sampling location, time of sampling and reef habitat characteristics*

In general, there were no trends between RVC metrics used for the target fish group L2 frequency band (1.2 – 2 kHz) SPLs during crepuscular hours; however, mean SPLs and target group biomass did have site-specific patterns in loudness as well as fish biomass (Figure S6). Most sites ranged in mean L2 SPLs between 95 – 98 dB with protected sites SDK, ESB, and WSB recording the highest mean variations in SPLs > 96 dB, while LKP and NFS had quieter ranges of mean L2 SPLs well below 93 dB (Figure 6). In general, two distinct temporal patterns in mean L2 SPLs either reflected seasonal variations or gradual increases in mean SPLs in 2018, but differences in target group biomass and the dominant reef fish family (Haemulidae vs Lutjanidae) were site dependent. For example, WDR, SDK, LKP, and LKU showed a seasonal trend where mean SPLs decreased in late winter (February) and early fall (September) and increased during the summer (June) and peak winter (December). However, WDR and LKU were consistently dominated by Haemulidae mean biomass across all sampling periods, while SDK was dominated by Lutjanidae until December surveys, and LKP was dominated by Lutjanidae mean biomass across all sampling periods (Figure 6B). NFS, WSB, and ESB showed a gradual increase in mean L2 SPLs between June and December 2018, but also differed in

dominance of species of concern. NFS was dominated by Haemulidae mean biomass across all sample periods (Figure 6C), while WSB was dominated by Lutjanidae mean fish biomass (Figure 6E). ESB was dominated by Haemulidae mean biomass for all sampling periods except for June 2018 (Figure 6F).

ANCOVA models for the L2 frequency band (1.2-2 kHz) associated with mean crepuscular SPLs produced by the target group identified more significant interactions between habitat metrics (Model 1) than target fish group metrics (Model 2) when pooled by sample date ( $F=28.3$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ) (Table 8). In Model 1, depth ( $F = 134.7$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ) was a stronger significant main effect than vertical hard relief ( $F = 10.8$ ,  $p = 0.001$ ,  $\alpha = 0.01$ ) in predicting L2 mean SPLs. However, the interaction of sample date and vertical hard relief yielded a stronger effect ( $F = 40.3$ ,  $p < 0.001$ ,  $\alpha = 0.001$ ) than the interaction sample date and depth ( $F = 9.26$ ,  $p = 0.002$ ,  $\alpha = 0.01$ ). Like the target group biomass models, surface hard relief was a less impactful covariate predictor and was only significant when interacting with sample date ( $F = 6.64$ ,  $p = 0.01$ ,  $\alpha = 0.01$ ) and depth ( $F = 4.07$ ,  $p = 0.04$ ,  $\alpha = 0.05$ ). Target group biomass was significant predictor for mean 2 SPLs ( $F = 4.52$ ,  $p = 0.04$ ,  $\alpha = 0.05$ ), but the strongest predictors resulted from the interaction of sample date, reef fish family (Lutjanidae vs Haemulidae), and target group density ( $F = 8.73$ ,  $p = 0.01$ ,  $\alpha = 0.01$ ) supporting the importance of changing dominance of reef fish families within the target group over time.

## Discussion

*Spatiotemporal patterns in reef fish biodiversity, target group species, habitat complexity, and reserve type using reef visual census (RVC) surveys*

Although the coral reef sites within this study exist in the same region of the lower Florida Keys, localized coral reefs can vary at small spatial scales (83) in addition to large scale impacts from human interactions (i.e., reserve type, recreational use, restoration, fishing pressure), and extrinsic environmental factors such as proximity to deeper reef sites that also facilitate changes in species distribution and metapopulation dynamics (98). In the aftermath of Hurricane Irma, a rapid reconnaissance team of science divers from federal and state partners reported moderate to severe physical and environmental damage such as broken and abraded corals, and collapsed reef ledges at 51 sites in the FKNMS (99,100). In our two-year study, reef fish density decreased immediately following Hurricane Irma, but essentially recovered over time to similar mean annual densities while annual mean reef fish biomass relatively increased between 2017 and 2018. However, there were localized impacts demonstrated by the differences in site-specific mean fish densities and biomass in response to the disturbance. Most sites surveyed immediately following hurricane Irma suffered a substantial loss in reef fish density, except for research only LKU, which despite being in relatively close proximity (<16 km) to where Irma made landfall had a major increase in fish density. Mean species diversity and evenness was higher at research only area sites LKU and ESB, as well as the ecological reserve WSB and remained relatively resilient to changes in reef fish density and biomass. Although fished sites were structurally complex and supported relatively high densities and biomass of species in a manner similar to protected sites, protected sites that were also structurally complex served as an important factor in predicting reef fish biodiversity. Increases in reef fish biomass and species diversity and

evenness after hurricane Irma suggests this fish community is relatively resilient to hurricane impacts.

Historically, the FKNMS has been susceptible to episodic extreme weather events including tropical cyclones and hurricanes, therefore it is important to observe trends in reef fish communities and habitat quality over long temporal scales. A 14-year study in the FKNMS showed no significant difference in mean live coral cover between NTMRs and fished sites, yet trends in overall percent cover gradually declined from combined impacts of hurricane damage and disease outbreak with greater impacts at NTMRs than non-protected sites (101). A more recent, 19-year study observed that NTMR and high relief sites generally had higher reef fish abundance, biomass, and species diversity, yet also exhibited a decline in reef fish metrics after 2008 from multiple stressors such as diminished habitat quality from coral disease outbreaks and varying fishing pressure (87). Variation in reef fish biodiversity across space and time may serve as an important buffer mechanism against ecosystem collapse and can enhance resilience processes such as promoting species diversity and recruitment/dispersal (102–105). Additionally, a 9-year monitoring study investigating spatiotemporal trends in reef fish biodiversity recovery following two severe natural disturbances, a crown-of-thorns outbreak and a hurricane at Moorea Island reef sites, found no impacts in total reef fish biomass, yet observed evidence of species-specific compensatory changes in spatial distribution driven by responses to fluctuations in predator-prey interactions and habitat quality across sites (106).

Target group abundance in this study decreased after hurricane Irma, yet mean target group density and biomass increased for both Lutjanidae and Haemulidae over the two-year study period. Both family groups also showed a slight trend in increasing mean density and biomass during the fall and winter months, with little to no impacts resulting from the passage of the

hurricane. Mean fish biomass corresponded more with site-specific habitat features than sampling period, and remained fairly consistent from pre- to post-hurricane impacts disturbance. Haemulidae were more abundant at several sites, which may be due to their schooling behavior and the occurrence of more diverse species or conspecifics within this reef fish family. Haemulids were also more prevalent at deeper depth sites with moderate to high relief such as LKU, NFS, and WDR, than more shallow sites such as WSB. In contrast, Lutjanids generally had higher mean densities and mean biomass at protected sites with high relief such as SDK. As Lutjanids are important to commercial and recreational fishing, level of protection may be an important status for habitat utilization, site fidelity and foraging patterns across the FKNMS reserve network. Collectively, target group density and biomass did not show any major changes attributed to the impacts of the hurricane, but instead may reflect changes in habitat use and species distribution because of direct impacts to reef refugia and diminished environmental qualities such as heavy sedimentation and turbidity.

Spatial heterogeneity in biodiversity can be weakened by frequent and severe disturbances resulting in spatial homogeneity as species composition at the community-level tends to reflect the survival of biological legacies (i.e., remaining coral structures, extirpation of local species, loss of specialists) after long-term impacts (107–109). Relevant studies on the behavioral response of schooling white grunts (*H. plumieri*) following a storm in the Bahamas recorded migrations up to 2 km from turbid waters to more suitable reef habitats (110–112). A more recent study used acoustic telemetry to investigate movement patterns of yellowtail snapper in Dry Tortugas network of marine reserves and found that yellowtail snapper migrated relatively short distances from home reefs (< 1.2 km), and site fidelity was size dependent (50).

Additionally, several studies support that the notion that crevice dwelling species can redistribute themselves after a hurricane disturbance (113,114).

*The relationship between reef fish biodiversity and the low frequency coral reef soundscape*

In our study, within-site mean SPLs within the low frequency (L1) band (0.1-3kHz) during crepuscular hours are site-specific and may not correspond to mean reef fish biomass. Rather, this SPL band may be a good indicator of seasonal changes in the local biological soundscape. However, mean L1 SPLs did correlate significantly with the interaction of mean reef fish density and species richness, and may provide insight into how changes in species presence and distribution are reflected by variations within underwater soundscape over time (46). Target group mean SPLs were generally not site-specific in this study, and there was a small change in loudness ( $\Delta 2$  dB) with depth when comparing among shallow sites with depths ranging from 4–6m (i.e., ESB, WSB) to deeper reef sites with depths greater than 7m (i.e., LKP, NFS). Mean L2 SPLs during crepuscular hours displayed seasonal trends of increased loudness in summer (June) and peak winter (December), or gradual increases in loudness leading to a peak in winter. Temporal patterns in the mean L2 frequency band did not reflect changes in relative abundance of reef fish families for the target group. However, mean biomass of Haemulidae and Lutjanidae was site dependent. Mean L2 SPLs were loudest during the same sampling period when mean fish biomass was highest for all sites except LKU. However, these sites differed in dominance between reef families such that LKP had higher mean fish biomass for Haemulidae while, Lutjanidae dominated mean fish biomass at LKU at lower. LKP and LKU are two neighboring marine zones (< 3 km) that differ in level of protection and are ~ 26 km northeast from the next nearest site, ESB.

Mixed schools of this study's target group species and other cryptic reef species (i.e., Sciaenidae) that occupy a similar sound producing spectrum, habitat preference for complex reef structures (i.e., reef spurs, microhabitat, shelter), and actively forage at night may share the L2 frequency band during crepuscular hours. A recent study found that the relationship between reef fish sound production via passive acoustic monitoring and remote sensing environmental data reflected temporal trends in the distribution of ecologically similar reef fish (i.e., behavior, diet, foraging patterns) (83). Similar passive acoustic monitoring studies have also recorded nighttime patterns in SPLs during multispecies spawning aggregations for several nocturnally active coastal fish species (115–117). In our study, WDR and SDK are adjacent, spur-and-groove reef sites that had seasonal trends in increased mean biomass and mean L2 SPLs associated with target group, yet Lutjanidae were distinctly more dominant at the protected site. In 2021, FWCC enforced a seasonal fishing closure at fished site WDR, located ~ 16 km from Key West, prohibiting fishing from April to late July to better protect spawning aggregations and recruitment for Mutton Snapper (*Lutjanus analis*), Gray Snapper (*L. griseus*), and Yellowtail Snapper (*O. chrysurus*) and Carangid species permit (*Trachinotus falcatus*) (118). Therefore, temporal patterns in the mean SPLs within the L2 frequency band associated with migratory crevice dwelling reef species that are also commercially or recreationally important may depend on the spatial scale, placement, and level of protection of the marine reserve. Future work may consider a three-way factorial ANOVA using marine zone type (fished, SPA, SUA) as a factor in observing how the biomass of species of concern and SPLs vary depending on habitat characteristics and relevant environmental data such as turbidity.

## **Conclusion**

Relatively small marine reserves (0.3-0.5 km<sup>2</sup>) can be pivotal in protecting reef building corals and resident reef fish species against local stressors (28,119) yet may be more susceptible or less resilient than larger marine reserves when impacted by extreme climatic changes or storms (120,121). Prior to hurricane Irma, reef fish biodiversity indices were relatively similar among sites and sampling periods. After Irma, there was a > 60% decrease in fish density for all sites except one research-only area. Conversely, reef fish species diversity, richness, and evenness increased after Irma with the greatest increase occurring at protected sites. Thus, although site-specific habitat and reef fish characteristics vary among different sites within the FKNMS, the network of relatively small reserves varying in level of protection may be beneficial for the emigration and redistribution of displaced marine fauna after severe disturbances such as hurricanes. Ultimately, the persistence of reef fish biodiversity and seasonal use of essential habitats for spawning provides a way to assess ecosystem recovery and overall resilience from acute, but severe ecosystem impacts unlike long-term chronic climatic impacts such as coral disease or thermal stress. The combined approach of traditional visual surveys with emerging tools such as photogrammetric habit mapping and underwater soundscape measurements can provide a relatively comprehensive assessment of reef health among varying levels of protection.

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## References

1. Bellwood DR, Streit RP, Brandl SJ, Tebbett SB. The meaning of the term ‘function’ in ecology: A coral reef perspective. *Funct Ecol* [Internet]. 2019 Jun 1 [cited 2022 Aug 11];33(6):948–61. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/1365-2435.13265>
2. Brandl SJ, Rasher DB, Côté IM, Casey JM, Darling ES, Lefcheck JS, et al. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Vol. 17, *Frontiers in Ecology and the Environment*. Wiley Blackwell; 2019. p. 445–54.
3. Woodhead AJ, Hicks CC, Norström A v., Williams GJ, Graham NAJ. Coral reef ecosystem services in the Anthropocene. *Funct Ecol*. 2019;33(6):1023–34.
4. Walton CJ, Hayes NK, Gilliam DS. Impacts of a regional, multi-year, multi-species coral disease outbreak in Southeast Florida. *Front Mar Sci*. 2018 Sep 13;5(SEP):323.
5. Perry CT, Alvarez-Filip L. Changing geo-ecological functions of coral reefs in the Anthropocene. *Funct Ecol* [Internet]. 2019 Jun 1 [cited 2022 Aug 11];33(6):976–88. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/1365-2435.13247>
5. Dove SG, Brown KT, van den Heuvel A, Chai A, Hoegh-Guldberg O. Ocean warming and acidification uncouple calcification from calcifier biomass which accelerates coral reef decline. *Commun Earth Environ*. 2020 Dec 1;1(1).
7. Tsai CH, Sweatman HPA, Thibaut LM, Connolly SR. Volatility in coral cover erodes niche structure, but not diversity, in reef fish assemblages. *Sci Adv* [Internet]. 2022 Jun 17;8(24):6858. Available from: <https://www.science.org/doi/10.1126/sciadv.abm6858>
8. Newman SP, Meesters EH, Dryden CS, Williams SM, Sanchez C, Mumby PJ, et al. Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology*. 2015;84(6).
9. Rogers A, Blanchard JL, Mumby PJ. Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology*. 2018;55(3).
10. Komyakova V, Jones GP, Munday PL. Strong effects of coral species on the diversity and structure of reef fish communities: A multi-scale analysis. *PLoS One* [Internet]. 2018 Aug 1 [cited 2022 Aug 8];13(8):e0202206. Available from: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0202206>

11. Williamson DH, Russ GR, Ayling AM. No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ Conserv*. 2004 Jun;31(2):149–59.
12. Friedlander A, Brown E, Monaco M. Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Mar Ecol Prog Ser* [Internet]. 2007 Dec 6;351:221–33. Available from: <http://www.int-res.com/abstracts/meps/v351/p221-233/>
13. Vandeperre F, Higgins RM, Sánchez-Meca J, Maynou F, Goñi R, Martín-Sosa P, et al. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. *Fish and Fisheries* [Internet]. 2011 Dec 1 [cited 2022 Aug 13];12(4):412–26. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/j.1467-2979.2010.00401.x>
14. Tong C, Hock K, Krueck NC, Tyazhelnikov V, Mumby PJ. An MPA Design Approach to Benefit Fisheries: Maximising Larval Export and Minimising Redundancy. *Diversity 2021, Vol 13, Page 586* [Internet]. 2021 Nov 17 [cited 2022 Aug 16];13(11):586. Available from: <https://www.mdpi.com/1424-2818/13/11/586/htm>
15. Hagedorn M, Spindler R, Daly J. Cryopreservation as a tool for reef restoration: 2019. *Adv Exp Med Biol* [Internet]. 2019 [cited 2022 Aug 11];1200:489–505. Available from: [https://link.springer.com/chapter/10.1007/978-3-030-23633-5\\_16](https://link.springer.com/chapter/10.1007/978-3-030-23633-5_16)
16. Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SCA, et al. Coral restoration – A systematic review of current methods, successes, failures and future directions. *PLoS One* [Internet]. 2020 Jan 1 [cited 2022 Aug 11];15(1):e0226631. Available from: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0226631>
17. Houk P, Cuetos-Bueno J, Kerr AM, McCann K. Linking fishing pressure with ecosystem thresholds and food web stability on coral reefs. *Ecol Monogr* [Internet]. 2018 Feb 1 [cited 2022 Aug 16];88(1):109–19. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1002/ecm.1278>
18. Chung AE, Wedding LM, Green AL, Friedlander AM, Goldberg G, Meadows A, et al. Building Coral reef resilience through spatial herbivore management. *Front Mar Sci*. 2019;6(MAR):98.
19. Williams ID, Kindinger TL, Couch CS, Walsh WJ, Minton D, Oliver TA. Can Herbivore Management Increase the Persistence of Indo-Pacific Coral Reefs? *Front Mar Sci*. 2019 Sep 10;6:557.

20. Bohnsack JA, Ault JS. Management strategies to conserve marine biodiversity. *Oceanography* [Internet]. 1996 [cited 2022 Aug 16];9(1):73–82. Available from: <https://www.jstor.org/stable/43925544>
21. Allison GW, Lubchenco J, Carr MH. Marine reserves are necessary but not sufficient for marine conservation [Internet]. Vol. 8, *Ecological Applications*. 1998 [cited 2022 Aug 16]. Available from: [https://doi.org/10.1890/1051-0761\(1998\)8\[S79:MRANBN\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)8[S79:MRANBN]2.0.CO;2)
22. Lubchenco J, Palumbi S, SD Gaines. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* [Internet]. 2003 [cited 2022 Aug 16];13(1):S3–7. Available from: <https://www.jstor.org/stable/3099993>
23. Graham NAJ, Robinson JPW, Smith SE, Govinden R, Gendron G, Wilson SK. Changing role of coral reef marine reserves in a warming climate. *Nature Communications* 2020 11:1 [Internet]. 2020 Apr 24 [cited 2022 Aug 16];11(1):1–8. Available from: <https://www.nature.com/articles/s41467-020-15863-z>
24. Wilson JR, Bradley D, Phipps K, Gleason MG. Beyond protection: Fisheries co-benefits of no-take marine reserves. *Mar Policy*. 2020 Dec 1;122:104224.
25. Halpern BS. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* [Internet]. 2003 [cited 2022 Aug 16];13(1):117–37. Available from: <http://www.wcmc.org.uk:80/marine/data/>
26. Gårdmark A, Jonzén N, Mangel M. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *Journal of Applied Ecology* [Internet]. 2006 Feb 1 [cited 2022 Aug 16];43(1):61–9. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2664.2005.01104.x>
27. Hopf JK, Jones GP, Williamson DH, Connolly SR. Marine reserves stabilize fish populations and fisheries yields in disturbed coral reef systems. *Ecological Applications* [Internet]. 2019 Jul 1 [cited 2022 Aug 16];29(5):e01905. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1002/eap.1905>
28. Wright LS. Small no-take areas benefit hard corals more than regulation through fishing permits. *Aquat Conserv* [Internet]. 2022 Jul 1 [cited 2022 Aug 16];32(7):1209–16. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1002/aqc.3814>
29. Valles H, Sponaugle S, Oxenford HA. Larval supply to a marine reserve and adjacent fished area in the Soufriere Marine Management Area, St Lucia, West Indies. *J Fish Biol* [Internet]. 2001 Dec [cited 2022 Aug 16];59(sa):152–77. Available from: <http://doi.wiley.com/10.1006/jfbi.2001.1763>
30. Tupper M, Conservation MRE, 2002 undefined. Species-specific impacts of a small marine reserve on reef fish production and fishing productivity in the Turks

and Caicos Islands. [cambridge.org](http://www.cambridge.org) [Internet]. 2002 [cited 2022 Aug 16]; Available from: <https://www.cambridge.org/core/journals/environmental-conservation/article/speciesspecific-impacts-of-a-small-marine-reserve-on-reef-fish-production-and-fishing-productivity-in-the-turks-and-caicos-islands/0FFEF4C7E0DC22F46C312916474CCB96>

31. Forcada A, Valle C, Bonhomme P, Criquet G, Cadiou G, Lenfant P, et al. Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar Ecol Prog Ser* [Internet]. 2009 Mar 30 [cited 2022 Aug 16];379:197–211. Available from: <https://www.int-res.com/abstracts/meps/v379/p197-211/>
32. Buxton CD, Hartmann K, Kearney R, Gardner C. When Is Spillover from Marine Reserves Likely to Benefit Fisheries? *PLoS One* [Internet]. 2014 [cited 2022 Aug 16];9(9):e107032. Available from: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0107032>
33. Holbrook SJ, Brooks AJ, Schmitt RJ. Variation in structural attributes of patch-forming corals and in patterns of abundance of associated fishes. *Mar Freshw Res* [Internet]. 2002 [cited 2022 Aug 12];53(7):1045. Available from: <http://www.publish.csiro.au/?paper=MF02063>
34. Sale PF. Connectivity, recruitment variation, and the structure of reef fish communities. In: *Integrative and Comparative Biology* [Internet]. 2004. p. 390–9. Available from: <https://academic.oup.com/icb/article/44/5/390/799582>
35. Kane CN, Brooks AJ, Holbrook SJ, Schmitt RJ. The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. *Environ Biol Fishes* [Internet]. 2009 Jan 25 [cited 2022 Aug 16];84(1):1–10. Available from: <http://link.springer.com/10.1007/s10641-008-9377-z>
36. Agudo-Adriani EA, Cappelletto J, Cavada-Blanco F, Cróquer A. Structural Complexity and Benthic Cover Explain Reef-Scale Variability of Fish Assemblages in Los Roques National Park, Venezuela. *Front Mar Sci*. 2019 Nov 12;6:690.
37. Rowell T, Schärer M, Appeldoorn R, Nemeth M, Mann D, Rivera J. Sound production as an indicator of red hind density at a spawning aggregation. *Mar Ecol Prog Ser* [Internet]. 2012 Aug 21 [cited 2022 Aug 16];462:241–50. Available from: <http://www.int-res.com/abstracts/meps/v462/p241-250/>
38. Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D’Alessandro EK. Celestial patterns in marine soundscapes. *Mar Ecol Prog Ser*. 2014 Aug 4;508:17–32.

39. Harris SA, Shears NT, Radford CA. Ecoacoustic indices as proxies for biodiversity on temperate reefs. Reynolds J, editor. *Methods Ecol Evol* [Internet]. 2016 Jun 1 [cited 2020 May 12];7(6):713–24. Available from: <http://doi.wiley.com/10.1111/2041-210X.12527>
40. Freeman SE, Freeman LA, Giorli G, Haas AF. Photosynthesis by marine algae produces sound, contributing to the daytime soundscape on coral reefs. *PLoS One* [Internet]. 2018 Oct 1 [cited 2022 Aug 16];13(10):e0201766. Available from: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0201766>
41. Simmons KR, Eggleston DB, Bohnenstiehl DR. Hurricane impacts on a coral reef soundscape. *PLoS One*. 2021;16(2 February 2021).
42. Bolgan M, O'Brien J, Chorazyczewska E, Winfield IJ, McCullough P, Gammell M. The soundscape of Arctic Charr spawning grounds in lotic and lentic environments: can passive acoustic monitoring be used to detect spawning activities? <http://dx.doi.org/10.1080/0952462220171286262> [Internet]. 2017 Jan 2 [cited 2022 Aug 16];27(1):57–85. Available from: <https://www.tandfonline.com/doi/abs/10.1080/09524622.2017.1286262>
43. McWilliam JN, McCauley RD, Erbe C, Parsons MJG. Soundscape diversity in the Great Barrier Reef: Lizard Island, a case study. <https://doi.org/10.1080/0952462220171344930> [Internet]. 2017 Jul 3 [cited 2022 Aug 16];27(3):295–311. Available from: <https://www.tandfonline.com/doi/abs/10.1080/09524622.2017.1344930>
44. Rowell TJ, Demer DA, Aburto-Oropeza O, Cota-Nieto JJ, Hyde JR, Erisman BE. Estimating fish abundance at spawning aggregations from courtship sound levels. *Scientific Reports* 2017 7:1 [Internet]. 2017 Jun 13 [cited 2022 Aug 16];7(1):1–14. Available from: <https://www.nature.com/articles/s41598-017-03383-8>
45. Lindseth A v., Lobel PS. Underwater Soundscape Monitoring and Fish Bioacoustics: A Review. *Fishes* 2018, Vol 3, Page 36 [Internet]. 2018 Sep 12 [cited 2022 Aug 16];3(3):36. Available from: <https://www.mdpi.com/2410-3888/3/3/36/htm>
46. Elise S, Urbina-Barreto I, Pinel R, Mahamadaly V, Bureau S, Penin L, et al. Assessing key ecosystem functions through soundscapes: A new perspective from coral reefs. *Ecol Indic*. 2019 Dec 1;107:105623.
47. Ault JS, Smith SG, Bohnsack JA, Luo J, Zurcher N, McClellan DB, et al. Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. *Fish Res*. 2013 Jul 1;144:28–37.

48. Locascio J v., Burton ML. A passive acoustic survey of fish sound production at Riley's hump within tortugas south ecological reserve; implications regarding spawning and habitat use. *Fishery Bulletin*. 2015 Dec 10;114(1):103–16.
49. Feeley MW, Morley D, Acosta A, Barbera P, Hunt J, Switzer T, et al. Spawning migration movements of Mutton Snapper in Tortugas, Florida: Spatial dynamics within a marine reserve network. *Fish Res*. 2018 Aug 1;204:209–23.
50. Herbig JL, Keller JA, Morley D, Walter K, Barbera P, Acosta A. Examining movement patterns of yellowtail snapper, *Ocyurus chrysurus*, in the Dry Tortugas, Florida. *Bull Mar Sci*. 2019 Jan 1;95(1):45–67.
51. Keller JA, Herbig JL, Morley D, Wile A, Barbera P, Acosta A. Grouper Tales: Use of Acoustic Telemetry to Evaluate Grouper Movements at Western Dry Rocks in the Florida Keys. *Marine and Coastal Fisheries*. 2020 Oct 1;12(5):290–307.
52. Butler J, Anderson ER, Butler MJ. Habitat Restoration Restores Underwater Soundscapes and Larval Recruitment. *Front Ecol Evol* [Internet]. 2022 Mar 1 [cited 2022 Aug 16];10. Available from: [https://digitalcommons.odu.edu/biology\\_fac\\_pubs/483](https://digitalcommons.odu.edu/biology_fac_pubs/483)
53. Butler J, Butler MJ, Gaff H. Snap, crackle, and pop: Acoustic-based model estimation of snapping shrimp populations in healthy and degraded hard-bottom habitats. *Ecol Indic*. 2017 Jun 1;77:377–85.
54. Piercy JJB, Codling EA, Hill AJ, Smith DJ, Simpson SD. Habitat quality affects sound production and likely distance of detection on coral reefs. *Mar Ecol Prog Ser*. 2014 Dec 3;516:35–47.
55. Gross M. Listening to the sounds of the biosphere. *Current Biology* [Internet]. 2018 [cited 2019 Jan 7];28(16):R847–50. Available from: [https://ac-els-cdn-com.prox.lib.ncsu.edu/S0960982218310479/1-s2.0-S0960982218310479-main.pdf?\\_tid=77c9a286-4b43-4c39-964d-6109db1d0eb0&acdnat=1547004276\\_306c7a5cbc96fbff63a0542652dc3d9e](https://ac-els-cdn-com.prox.lib.ncsu.edu/S0960982218310479/1-s2.0-S0960982218310479-main.pdf?_tid=77c9a286-4b43-4c39-964d-6109db1d0eb0&acdnat=1547004276_306c7a5cbc96fbff63a0542652dc3d9e)
56. Lyon R, Eggleston D, Bohnenstiehl D, Layman C, Ricci S, Allgeier J. Fish community structure, habitat complexity, and soundscape characteristics of patch reefs in a tropical, back-reef system. *Mar Ecol Prog Ser* [Internet]. 2019 Jan 17 [cited 2022 Aug 16];609:33–48. Available from: <https://www.int-res.com/abstracts/meps/v609/p33-48/>
57. Gottesman BL. USING SOUNDSCAPES TO MEASURE BIODIVERSITY, HABITAT CONDITION, AND ENVIRONMENTAL CHANGE IN AQUATIC ECOSYSTEMS. 2019.

58. Ehrlich PR, Ehrlich AH. Coevolution: Heterotypic Schooling in Caribbean Reef Fishes. *Am Nat* [Internet]. 1973 [cited 2022 Aug 16];107(953):157–60. Available from: <https://www.jstor.org/stable/2459572>
59. Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC. Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* [Internet]. 2004 Jul 1 [cited 2022 Aug 13];31(7):1093–106. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/j.1365-2699.2004.01044.x>
60. Pereira PHC, Ferreira BP. Effects of life phase and schooling patterns on the foraging behaviour of coral-reef fishes from the genus *Haemulon*. *J Fish Biol* [Internet]. 2013 Apr 1 [cited 2022 Aug 13];82(4):1226–38. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/jfb.12054>
61. Alevizon WS, Porter JW. Coral loss and fish guild stability on a Caribbean coral reef: 1974–2000. *Environ Biol Fishes* [Internet]. 2015 Apr 1 [cited 2022 Aug 13];98(4):1035–45. Available from: <https://link-springer-com.prox.lib.ncsu.edu/article/10.1007/s10641-014-0337-5>
62. Randall JE, Bishop Museum BP. Food habits of reef fishes of the West Indies [Internet]. Vol. 5. Coral Gables: Institute of Marine Sciences, University of Miami; 1967 [cited 2022 Aug 16]. 665–847 p. Available from: [https://teatrzo.ru/wp-content/uploads/2019/11/ryba-s-zelenymi-kostyami\\_34.pdf](https://teatrzo.ru/wp-content/uploads/2019/11/ryba-s-zelenymi-kostyami_34.pdf)
63. Hammerschlag N, Serafy JE. Nocturnal fish utilization of a subtropical mangrove-seagrass ecotone. *Marine Ecology* [Internet]. 2010 Jun 1 [cited 2022 Aug 13];31(2):364–74. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/j.1439-0485.2009.00337.x>
64. Kerry JT, Bellwood DR. The functional role of tabular structures for large reef fishes: avoiding predators or solar irradiance? *Coral Reefs* 2015 34:2 [Internet]. 2015 Feb 27 [cited 2022 Aug 16];34(2):693–702. Available from: <https://link.springer.com/article/10.1007/s00338-015-1275-1>
65. Arias-Godínez G, Jiménez C, Gamboa C, Cortés J, Espinoza M, Alvarado JJ. Spatial and temporal changes in reef fish assemblages on disturbed coral reefs, north Pacific coast of Costa Rica. *Marine Ecology* [Internet]. 2019 Feb 1 [cited 2022 Aug 12];40(1):e12532. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/maec.12532>
66. Heyman W, Kjerfve B. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bull Mar Sci* [Internet]. 2008 [cited 2022 Sep 11];83(3):531–51. Available from: <https://www.ingentaconnect.com/content/umrsmas/bullmar/2008/00000083/00000003/art00006>

67. Trott TM, Luckhurst BE, Pitt JM. Occurrence and Management of a Spawning Aggregation of Bluestriped Grunt (*Haemulon sciurus*) in Bermuda. *Proceedings of Gulf and Caribbean Fisheries Institute* [Internet]. 2010;62:260–6. Available from: <https://www.researchgate.net/publication/277890791>
68. Bertucci F, Ruppé L, van Wassenbergh S, Compère P, Parmentier E. New insights into the role of the pharyngeal jaw apparatus in the sound-producing mechanism of *Haemulon flavolineatum* (Haemulidae). *Journal of Experimental Biology*. 2014 Nov 1;217(21):3862–9.
69. Burkenroad MD. Sound production in the Haemulidae. *Copeia*. 1930;1930(1):17–8.
70. Moulton JM. The Acoustical Behavior of Some Fishes in the Bimini Area. *Biological Bulletin* [Internet]. 1958 [cited 2022 Sep 12];114(3):357–74. Available from: [www.jstor.org/stable/1538991](http://www.jstor.org/stable/1538991)
71. Millot M, Bertucci F, Lecchini D, Smeets S, René-Trouillefou M, Parmentier E. Characteristics of sound production and associated pharyngeal jaws in the tomtate grunt *Haemulon aurolineatum* (Cuvier, 1830) in Caribbean reefs. *Belg J Zool* [Internet]. 2021 Feb 25 [cited 2022 Sep 11];151(0):43–56. Available from: <https://www.belgianjournalofzoology.eu/BJZ/article/view/84>
72. Mcfarland WN, Hillis ZM. OBSERVATIONS ON AGONISTIC BEHAVIOR BETWEEN MEMBERS OF JUVENILE FRENCH AND WHITE GRUNTS-FAMILY HAEMULIDAE. Vol. 32, *BULLETIN OF MARINE SCIENCE*. 1982.
73. Tricas T, Boyle K. Acoustic behaviors in Hawaiian coral reef fish communities. *Mar Ecol Prog Ser* [Internet]. 2014 Sep 24 [cited 2020 May 12];511:1–16. Available from: <http://www.int-res.com/abstracts/meps/v511/p1-16/>
74. Parmentier E, Diogo R, Fine ML. Multiple exaptations leading to fish sound production. *Fish and Fisheries* [Internet]. 2017 Sep 1 [cited 2022 Sep 13];18(5):958–66. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/faf.12217>
75. Spence HR. Passive acoustic monitoring of nocturnal fish sounds in Quintana Roo, Mexico. Vol. 93, *Bulletin of Marine Science*. Rosenstiel School of Marine and Atmospheric Science; 2017. p. 641–52.
76. Ault JS, Smith SG, Bohnsack JA, Luo J, Harper DE, McClellan DB. BUILDING SUSTAINABLE FISHERIES IN FLORIDA’S CORAL REEF ECOSYSTEM: POSITIVE SIGNS IN THE DRY TORTUGAS [Internet]. Vol. 78, *BULLETIN OF MARINE SCIENCE*. 2006. Available from: <http://floridakeys.noaa.gov>

77. Keller BD, Donahue S. 2002-03 Florida Keys National Marine Sanctuary science report: An ecosystem report card after five years of marine zoning [Internet]. <http://aquaticcommons.org/id/eprint/2285>. NOAA/National Ocean Service/National Marine Sanctuary Program; 2007 [cited 2022 Sep 13]. Available from: <https://aquadocs.org/handle/1834/20090>
78. Bartholomew A, Bohnsack JA, Smith SG, Ault JS, Harper DE, McClellan DB. Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. *Landsc Ecol*. 2008 Jan;23(SUPPL. 1):55–65.
79. Keller B, Donahue S. Florida Keys National Marine Sanctuary U . S . Environmental Protection Agency State of Florida 2002-03 Sanctuary Science Report : An Ecosystem Report Card. US Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Office of National Marine Sanctuaries, Florida Keys National Marine Sanctuary, Marathon, FL. 2006;(October).
80. Medina M, Estes C, Best B, Stallings CD, Montes E, McEachron LG, et al. REEF-FISH ABUNDANCE, BIOMASS, AND BIODIVERSITY INSIDE AND OUTSIDE NO-TAKE MARINE ZONES IN THE FLORIDA KEYS NATIONAL MARINE SANCTUARY: 1999–2018 on JSTOR. In: *Oceanography* [Internet]. Oceanography Society; 2021 [cited 2022 Aug 31]. p. 52–61. Available from: [https://www.jstor.org/stable/27085038#metadata\\_info\\_tab\\_contents](https://www.jstor.org/stable/27085038#metadata_info_tab_contents)
81. Nedelec SL, Simpson SD, Holderied M, Radford AN, Lecellier G, Radford C, et al. Soundscapes and living communities in coral reefs: Temporal and spatial variation. *Mar Ecol Prog Ser*. 2015;524.
82. Kaplan MB, Lammers MO, Zang E, Aran Mooney T. Acoustic and biological trends on coral reefs off Maui, Hawaii. *Coral Reefs* [Internet]. 2018 Mar 1 [cited 2022 May 26];37(1):121–33. Available from: <https://link-springer-com.prox.lib.ncsu.edu/article/10.1007/s00338-017-1638-x>
83. Elise S, Guilhaumon F, Mou-Tham G, Urbina-Barreto I, Vigliola L, Kulbicki M, et al. Combining Passive Acoustics and Environmental Data for Scaling Up Ecosystem Monitoring: A Test on Coral Reef Fishes. *Remote Sens (Basel)*. 2022 May 16;14(10):2394.
84. Bohnsack JA, Bannerot SP. A Stationary Visual Census Technique for Quantitatively Assessing Community Structure of Coral Reef Fishes. 1986.
85. Ault JS, Smith SG, Meester GA, Luo J, Bohnsack JA. Site Characterization for Biscayne National Park: Assessment of Fisheries Resources and Habitats. NOAA Technical Memorandum. 2001.

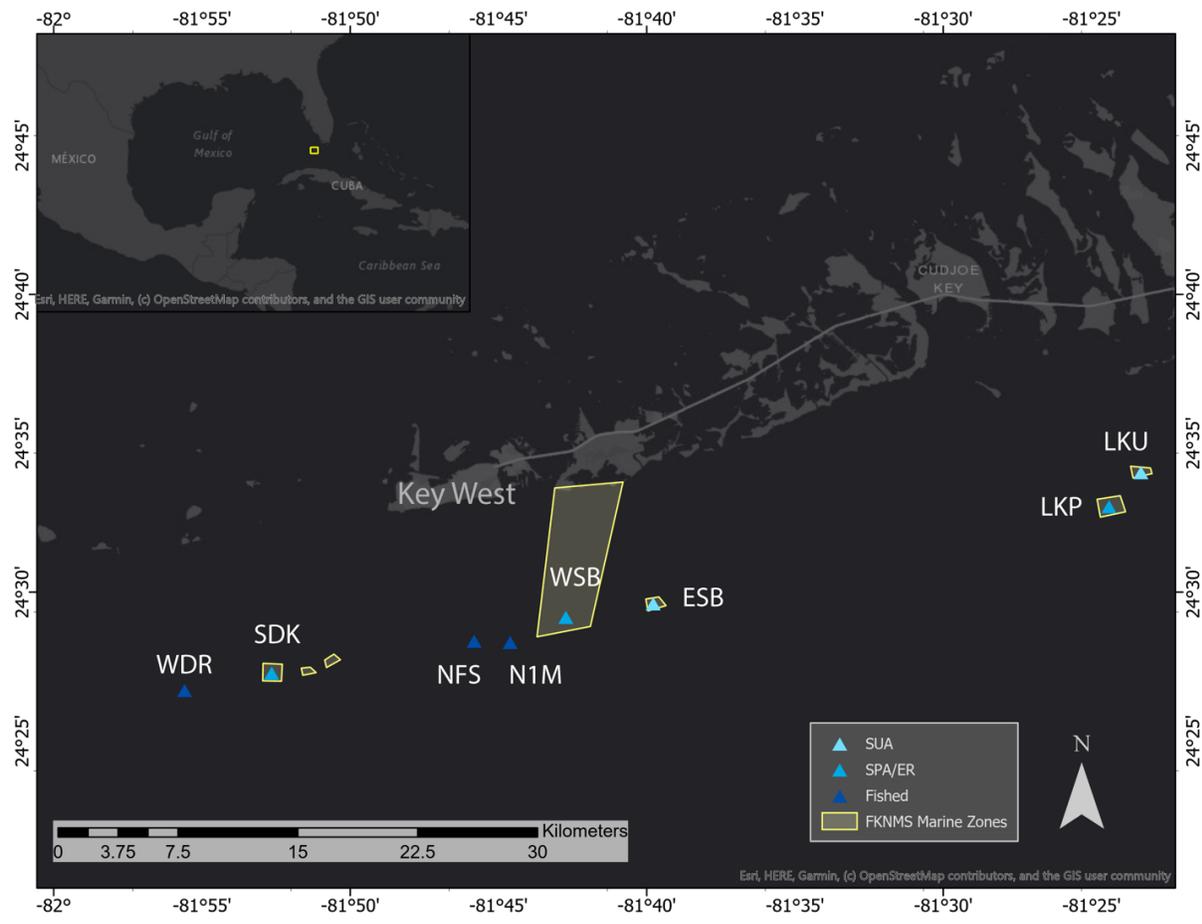
86. Brandt ME, Zurcher N, Acosta A, Ault JS, Bohnsack J a, Feeley MW, et al. A cooperative multi-agency reef fish monitoring protocol for the Florida Keys coral reef ecosystem. Natural resource report NPS/SFCN/NRR ; 2009/150 [Internet]. 2009;Electronic text document (128 p.). Available from: [http://femar.rsmas.miami.edu/Research/FLKeys%7B\\_%7Drvc/FLKeys%7B\\_%7DReef%7B\\_%7DFish%7B\\_%7Dmonitoring%7B\\_%7Dprotocol%7B\\_%7DFinal2009.pdf](http://femar.rsmas.miami.edu/Research/FLKeys%7B_%7Drvc/FLKeys%7B_%7DReef%7B_%7DFish%7B_%7Dmonitoring%7B_%7Dprotocol%7B_%7DFinal2009.pdf)
87. Medina M, Estes C, Best B, Stallings C, Montes E, McEachron L, et al. Reef-Fish Abundance, Biomass, and Biodiversity Inside and Outside No-Take Marine Zones in the Florida Keys National Marine Sanctuary: 1999–2018. *Oceanography* [Internet]. 2021 Jun 1 [cited 2022 Sep 7];34(2). Available from: <https://tos.org/oceanography/article/reef-fish-abundance-biomass-and-biodiversity-inside-and-outside-no-take-marine-zones-in-the-florida-keys-national-marine-sanctuary-1999-2018>
88. Simmons KR, Bohnenstiehl DR, Eggleston DB. Spatiotemporal Variation in Coral Assemblages and Reef Habitat Complexity among Shallow Fore-Reef Sites in the Florida Keys National Marine Sanctuary. *Diversity (Basel)* [Internet]. 2022;14:153. Available from: <https://doi.org/10.3390/d14030153>
89. Froese R. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* [Internet]. 2006 Aug 1 [cited 2022 Jun 5];22(4):241–53. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/j.1439-0426.2006.00805.x>
90. Froese R, Thorson JT, Reyes RB. A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology* [Internet]. 2014 Feb 1 [cited 2022 Jun 5];30(1):78–85. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/jai.12299>
91. Hutcheson K. A test for comparing diversities based on the shannon formula. *J Theor Biol.* 1970 Oct 1;29(1):151–4.
92. Fish MP, Mowbray WH. *Sounds of Western North Atlantic Fishes: A Reference File of Biological Underwater Sounds* [Internet]. Johns Hopkins Press; 1970. Available from: <https://books.google.com/books?id=kdaFtAEACAAJ>
93. Mann DA, Lobel PS. Passive acoustic detection of sounds produced by the damselfish, *Dascyllus albisella* (Pomacentridae). *Bioacoustics.* 1995;6(3):199–213.
94. Rountree RA, Gilmore RG, Goudey CA, Hawkins AD, Luczkovich JJ, Mann DA. Listening to Fish. *Fisheries (Bethesda).* 2006 Sep 1;31(9):433–46.

95. Kaplan MB, Mooney TA, Partan J, Solow AR. Coral reef species assemblages are associated with ambient soundscapes. *Mar Ecol Prog Ser* [Internet]. 2015 Aug 6 [cited 2022 Jun 5];533:93–107. Available from: <https://www.int-res.com/abstracts/meps/v533/p93-107/>
96. McWilliam JN, McCauley RD, Erbe C, Parsons MJG. Patterns of biophonic periodicity on coral reefs in the Great Barrier Reef. *Sci Rep* [Internet]. 2017 Dec 12 [cited 2019 Jun 24];7(1):17459. Available from: <http://www.nature.com/articles/s41598-017-15838-z>
97. Kaplan MB, Lammers MO, Zang E, Aran Mooney T. Acoustic and biological trends on coral reefs off Maui, Hawaii. *Coral Reefs*. 2018 Mar 1;37(1):121–33.
98. Barneche DR, Kulbicki M, Floeter SR, Friedlander AM, Maina J, Allen AP. Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecol Lett* [Internet]. 2014 Sep 1 [cited 2022 Aug 30];17(9):1067–76. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1111/ele.12309>
99. Florida Reef Resilience Program. Florida Reef Resilience Program Disturbance Response Monitoring and Hurricane Irma Rapid Reef Assessment Quick Look Report: Summer 2017 [Internet]. 2017 [cited 2021 Nov 28]. Available from: <http://frp.org/wp-content/uploads/2018/01/2017-Summer-DRM-Quick-Look-Report.pdf>
100. Viehman S, Gittings S, Groves S, Moore J, Moore T, Stein J. NCCOS Assessment: Coral Disturbance Response Monitoring (DRM) along the Florida Reef Tract following Hurricane Irma from 2017-10-09 to 2017-10-18 (NCEI Accession 0179071).[indicate subset used]. NOAA National Centers for Environmental Information Dataset doi [Internet]. 2018 [cited 2022 Oct 6];10. Available from: [https://coastalscience.noaa.gov/data\\_reports/nccos-assessment-coral-disturbance-response-monitoring-drm-along-the-florida-reef-tract-following-hurricane-irma-from-2017-10-09-to-2017-10-18-ncei-accession-0179071/](https://coastalscience.noaa.gov/data_reports/nccos-assessment-coral-disturbance-response-monitoring-drm-along-the-florida-reef-tract-following-hurricane-irma-from-2017-10-09-to-2017-10-18-ncei-accession-0179071/)
101. Toth LT, van Woesik R, Murdoch TJT, Smith SR, Ogden JC, Precht WF, et al. Do no-take reserves benefit Florida’s corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. *Coral Reefs*. 2014;33(3):565–77.
102. Schindler D, Hilborn R, Chasco B, Nature CB, 2010 undefined. Population diversity and the portfolio effect in an exploited species. *nature.com* [Internet]. 2010 Jun 3 [cited 2022 Aug 31];465(7298):609–12. Available from: [https://www.nature.com/articles/nature09060?source=your\\_stories\\_page](https://www.nature.com/articles/nature09060?source=your_stories_page)

103. Pasari JR, Levi T, Zavaleta ES, Tilman D. Several scales of biodiversity affect ecosystem multifunctionality. *Proc Natl Acad Sci U S A*. 2013 Jun 18;110(25):10219–22.
104. Thorson JT, Scheuerell MD, Buhle ER, Copeland T. Spatial variation buffers temporal fluctuations in early juvenile survival for an endangered Pacific salmon. *Journal of Animal Ecology*. 2014 Jan;83(1):157–67.
105. Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, et al. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* [Internet]. 2015 Nov 1 [cited 2022 Aug 31];90(4):1215–47. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/brv.12155>
106. Lamy T, Legendre P, Chancerelle Y, Siu G, Claudet J. Understanding the Spatio-Temporal Response of Coral Reef Fish Communities to Natural Disturbances: Insights from Beta-Diversity Decomposition. Chen CA, editor. *PLoS One* [Internet]. 2015 Sep 22 [cited 2019 Jan 7];10(9):e0138696. Available from: <https://dx.plos.org/10.1371/journal.pone.0138696>
107. Clavel J, Julliard R, Devictor V. Worldwide decline of specialist species: toward a global functional homogenization? *Front Ecol Environ* [Internet]. 2011 May 1 [cited 2022 Aug 31];9(4):222–8. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1890/080216>
108. Richardson LE, Graham NAJ, Pratchett MS, Eurich JG, Hoey AS. Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Glob Chang Biol* [Internet]. 2018 Jul 1 [cited 2022 Aug 31];24(7):3117–29. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.14119>
109. McDevitt-Irwin JM, Garren M, McMinds R, Vega Thurber R, Baum JK. Variable interaction outcomes of local disturbance and El Niño-induced heat stress on coral microbiome alpha and beta diversity. *Coral Reefs* 2019 38:2 [Internet]. 2019 Mar 14 [cited 2022 Aug 31];38(2):331–45. Available from: <https://link.springer.com/article/10.1007/s00338-019-01779-8>
110. McLean R, Herrnkind WF. Compact Schooling during a Mass Movement by Grunts. *Copeia*. 1971 Jun 1;1971(2):328.
111. Mcfarland WN, Hillis ZM. OBSERVATIONS ON AGONISTIC BEHAVIOR BETWEEN MEMBERS OF JUVENILE FRENCH AND WHITE GRUNTS-FAMILY HAEMULIDAE. Vol. 32, *BULLETIN OF MARINE SCIENCE*. 1982.
112. Appeldoorn RS, Aguilar-Perera A, Bouwmeester BLK, Dennis GD, Hill RL, Merten W, et al. Movement of fishes (Grunts: Haemulidae) across the coral reef

seascape: A review of scales, patterns and processes. *Caribb J Sci* [Internet]. 2009 Jan 1 [cited 2022 Oct 6];45(2–3):304–16. Available from: <http://www.bioone.org/doi/10.18475/cjos.v45i2.a16>

113. Huijbers CM, Nagelkerken I, Govers LL, van de Kerk M, Oldenburger JJ, de Brouwer JHF. Habitat type and schooling interactively determine refuge-seeking behavior in a coral reef fish throughout ontogeny. *Mar Ecol Prog Ser* [Internet]. 2011 Sep 15 [cited 2022 Oct 6];437:241–51. Available from: <https://www-int-res-com.prox.lib.ncsu.edu/abstracts/meps/v437/p241-251/>
114. Khan JA, Goatley CHR, Brandl SJ, Tebbett SB, Bellwood DR. Shelter use by large reef fishes: long-term occupancy and the impacts of disturbance. *Coral Reefs* [Internet]. 2017 Dec 1 [cited 2022 Oct 6];36(4):1123–32. Available from: <https://link-springer-com.prox.lib.ncsu.edu/article/10.1007/s00338-017-1604-7>
115. Locascio J v., Mann DA. Effects of Hurricane Charley on fish chorusing. *Biol Lett* [Internet]. 2005 Sep 9 [cited 2022 Oct 6];1(3):362. Available from: </pmc/articles/PMC1617161/>
116. Locascio J v., Mann DA. Diel Periodicity of Fish Sound Production in Charlotte Harbor, Florida. *Trans Am Fish Soc* [Internet]. 2008 Feb 1 [cited 2022 Oct 6];137(2):606–15. Available from: <https://onlinelibrary-wiley-com.prox.lib.ncsu.edu/doi/full/10.1577/T06-069.1>
117. Rice AN, Soldevilla MS, Quinlan JA. Nocturnal patterns in fish chorusing off the coasts of Georgia and eastern Florida. *Bull Mar Sci*. 2017 Apr 1;93(2):455–74.
118. Florida Fish and Wildlife Conservation Commission D of MF. 68B-6.004 Western Dry Rocks Seasonal Closure [Internet]. Apr 1, 2021. Available from: <https://www.flrules.org/gateway/RuleNo.asp?title=FLORIDA%20KEYS%20NATIONAL%20MARINE%20SANCTUARY&ID=68B-6.004>
119. Magdaong ET, Fujii M, Yamano H, Licuanan WY, Maypa A, Campos WL, et al. Long-term change in coral cover and the effectiveness of marine protected areas in the Philippines: a meta-analysis. *Hydrobiologia* 2013 733:1 [Internet]. 2013 Oct 30 [cited 2022 Aug 30];733(1):5–17. Available from: <https://link.springer.com/article/10.1007/s10750-013-1720-5>
120. Panga FM, Anticamara JA, Quibilan MCC, Atrigenio MP, Aliño PM. Through the Boundaries: Environmental Factors Affecting Reef Benthic Cover in Marine Protected Areas in the Philippines. *Front Mar Sci*. 2021 Aug 18;8:1069.
121. Russ GR, Rizzari JR, Abesamis RA, Alcala AC. Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications* [Internet]. 2021 Jan 1 [cited 2022 Aug 30];31(1):e02224. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1002/eap.2224>



**Figure 1.** Study site map of zone D in the FKNMS and survey sites Western Dry Rocks (WDR), Sand Key SPA (SDK), Nine Foot Stake (NFS), Number 1 Marker (N1M), Western Sambo ER SPA (WSB), Eastern Sambo SUA (ESB), Looe Key SPA (LKP), and Looe Key SUA (LKU).

**Table 1.** Time periods used to compare acoustic sound pressure levels (SPLs) across sites. Time periods were based on archived astronomical data on local sunrise and sunset times (accessed via the US Naval Observatory Portal ([www.usno.navy.mil/USNO](http://www.usno.navy.mil/USNO))).

<b>Category</b>	<b>Time period</b>
daily	24-hour period
day	only daylight hours
night	only nighttime hours
crepuscular	sunrise and sunset
morning twilight	before sunrise
evening twilight	after sunset

**Table 2.** Reef Visual Census (RVC) dates in Feb., June, Sept., and Dec. of 2018 and the associated 7-day window of soundscape data used to calculate the mean SPLs specific time periods outlined in Table 1.

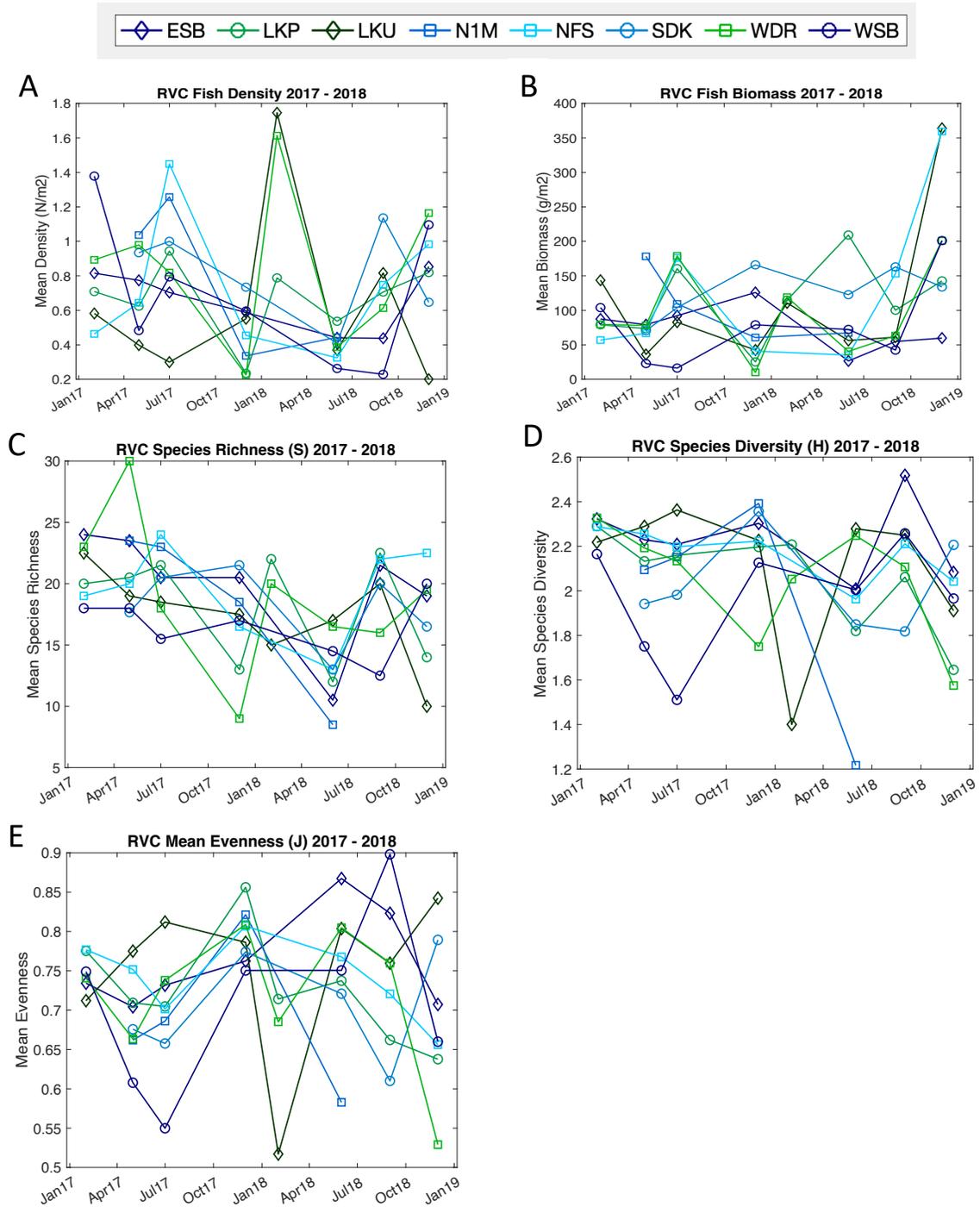
<b>RVC</b>	<b>Date</b>	<b>Sound Window</b>	<b>7-day Window</b>
1	2/26/18	1	3/5-3/12
2	6/3/18	2	6/13-6/20
3	9/25/18	3	10/2-10/9
4	12/18/18	4	12/25-1/1

**Table 3.** Summary Table of RVC mean fish metrics density, biomass (g), species diversity ( $H'$ ), species richness (S), and evenness ( $J'$ ) pooled by year and month for each site Eastern Sambo SUA (ESB), Looe Key SPA (LKP), Looe Key SUA (LKU), Number 1 Marker (N1M), Nine Foot Stake (NFS), Sand Key SPA (SDK), Western Dry Rocks (WDR), and Western Sambo ER (WSB) 2017-2018. Mean density is the number of individuals per primary sampling unit divided by the number of divers. Mean biomass is in units of grams per meter squared. Standard error is denoted in parentheses.

Site	Mean Density (N m <sup>-2</sup> )	Mean Biomass (g m <sup>-2</sup> )	Mean Species Diversity ( $H'$ )	Mean Species Richness (S)	Mean Evenness (J)
<b>2017</b>	0.72 (0/01)	106.67 (6)	2.16 (0.18)	20 (3.28)	0.73 (0.05)
<b>Feb</b>	0.81 (0.02)	92.28 (15.57)	2.28 (0.16)	22 (2.49)	0.74 (0.04)
ESB	0.82 (0.02)	87.42 (28.83)	2.32 (0.1)	24 (2.89)	0.73 (0.02)
LKP	0.71 (0.06)	79.02 (27.33)	2.29 (0.08)	20 (3.27)	0.78 (0.07)
LKU	0.58 (0.09)	143.63 (111.90)	2.22 (0.1)	23 (0.41)	0.71 (0.03)
NFS	0.46 (0)	56.87 (0)	2.29 (0)	19 (0)	0.78 (0)
WDR	0.89 (0.07)	79.65 (45.49)	2.33 (0.34)	23 (3.51)	0.74 (0.07)
WSB	1.38 (0)	103.96 (0)	2.16 (0)	18 (0)	0.75 (0)
<b>May</b>	0.73 (0.04)	104.55 (12.77)	2.11 (0.22)	22 (4.05)	0.69 (0.05)
ESB	0.77 (0.05)	79.26 (39.66)	2.23 (0.32)	24 (1.22)	0.70 (0.09)
LKP	0.62 (0.06)	73.60 (40.91)	2.13 (0.11)	21 (2.86)	0.71 (0)
LKU	0.40 (0.09)	36.02 (10.66)	2.29 (0.35)	19 (2.45)	0.78 (0.09)
N1M	1.04 (0.12)	178.23 (109.87)	2.09 (0.25)	24 (2.04)	0.66 (0.06)
NFS	0.64 (0.06)	66.77 (27.13)	2.25 (0.21)	20 (0.82)	0.75 (0.06)
SDK	0.93 (0.16)	70.52 (46.11)	1.94 (0.24)	18 (1.2)	0.68 (0.08)
WDR	0.98 (0.11)	78.04 (28.91)	2.19 (0.31)	30 (8.54)	0.66 (0.04)
WSB	0.48 (0.07)	22.84 (5.08)	1.75 (0)	18 (1.63)	0.61 (0.02)
<b>Jul</b>	0.91 (0.02)	138.38 (9.5)	2.08 (0.18)	20 (2.37)	0.69 (0.05)
ESB	0.70 (0.02)	92.25 (8.6)	2.21 (0.15)	21 (0.41)	0.73 (0.03)
LKP	0.94 (0.05)	160.40 (25.02)	2.16 (0.11)	22 (2.04)	0.70 (0.05)
LKU	0.30 (0.01)	82.77 (29.15)	2.36 (0.10)	19 (2.04)	0.81 (0)
N1M	1.26 (0.04)	109.37 (15.06)	2.15 (0.18)	23 (2.45)	0.69 (0.03)
NFS	1.45 (0.07)	175.91 (68.88)	2.20 (0.05)	24 (4.9)	0.70 (0.02)
SDK	1.00 (0.14)	103.89 (3.16)	1.98 (0.05)	21 (1.22)	0.66 (0.03)
WDR	0.82 (0)	178.87 (0)	2.13 (0)	18 (0)	0.74 (0)
WSB	0.79 (0.07)	16.24 (1.84)	1.51 (0.22)	16 (2.04)	0.55 (0.05)
<b>Dec</b>	0.47 (0.02)	91.64 (9)	2.20 (0.15)	17 (2.92)	0.80 (0.03)
ESB	0.59 (0.08)	125.87 (18.98)	2.30 (0.01)	21 (0.41)	0.76 (0.01)
LKP	0.23 (0.05)	25.22 (3.28)	2.20 (0.14)	13 (0)	0.86 (0.05)
LKU	0.55 (0.15)	42.46 (18.04)	2.23 (0.19)	18 (3.67)	0.79 (0.01)
N1M	0.34 (0.02)	60.56 (32.2)	2.39 (0)	19 (1.22)	0.82 (0.02)
NFS	0.45 (0.12)	40.85 (3.37)	2.22 (0.28)	17 (4.49)	0.81 (0.02)
SDK	0.73 (0.10)	165.88 (64.4)	2.36 (0.11)	22 (3.67)	0.77 (0.01)
WDR	0.23 (0.07)	9.99 (4.8)	1.75 (0.09)	9 (1.63)	0.81 (0.03)

**Table 3** (continued)

WSB	0.60 (0.02)	78.98 (44.48)	2.13 (0)	17 (0)	0.75 (0)
<b>2018</b>	0.71 (0.02)	146.38 (19.49)	1.99 (0.21)	17 (2.69)	0.72 (0.08)
<b>Feb</b>	1.38 (0.03)	114.91 (8.62)	1.89 (0.27)	19 (2.16)	0.64 (0.07)
LKP	0.79 (0.14)	114.85 (8.59)	2.21 (0.22)	22 (0)	0.71 (0.07)
LKU	1.75 (0.03)	110.74 (8.11)	1.40 (0.17)	15 (0)	0.52 (0.06)
WDR	1.61 (0.13)	119.15 (34.20)	2.05 (0.21)	20 (2.45)	0.69 (0.04)
<b>Jun</b>	0.40 (0.03)	104.98 (27.11)	1.92 (0.22)	13 (1.91)	0.75 (0.07)
ESB	0.44 (0.16)	26.60 (4.28)	2.01 (0.12)	11 (2.04)	0.87 (0.02)
LKP	0.54 (0.19)	209.14 (193.82)	1.82 (0.2)	12 (0.82)	0.74 (0.1)
LKU	0.37 (0.02)	56.28 (1.26)	2.28 (0.3)	17 (2.45)	0.80 (0.60)
NIM	0.44 (0.01)	67.22 (27.97)	1.22 (0.12)	9 (1.22)	0.58 (0.1)
NFS	0.32 (0.03)	35.10 (2.05)	1.96 (0.07)	13 (0.82)	0.77 (0.05)
SDK	0.41 (0.05)	122.68 (47.83)	1.85 (0.16)	13 (0)	0.72 (0.06)
WDR	0.39 (0.07)	40.51 (1.26)	2.25 (0.08)	17 (1.22)	0.80 (0.05)
WSB	0.26 (0.01)	72.33 (1.39)	2.00 (0.09)	15 (1.22)	0.75 (0.03)
<b>Sep</b>	0.67 (0.02)	106.31 (8.44)	2.17 (0.19)	19 (2.48)	0.75 (0.08)
ESB	0.44 (0.09)	54.82 (17.89)	2.52 (0.15)	22 (1.22)	0.82 (0.06)
LKP	0.71 (0.04)	100.17 (4.54)	2.06 (0.02)	23 (0.41)	0.66 (0)
LKU	0.82 (0.16)	61.10 (33.43)	2.25 (0.2)	20 (2.45)	0.76 (0.1)
NFS	0.75 (0.10)	153.21 (0.7)	2.21 (0.16)	22 (4.08)	0.72 (0.01)
SDK	1.14 (0.15)	162.99 (58.29)	1.82 (0.41)	20 (0.82)	0.61 (0.14)
WDR	0.61 (0.01)	63.23 (11.4)	2.11 (0.11)	16 (0)	0.76 (0.04)
WSB	0.23 (0.04)	42.37 (4.56)	2.26 (0.01)	13 (1.22)	0.90 (0.03)
<b>Dec</b>	0.82 (0.02)	243.56 (51.38)	1.92 (0.18)	17 (2.57)	0.69 (0.08)
ESB	0.85 (0.19)	59.75 (20.81)	2.08 (0.12)	19 (0)	0.71 (0.04)
LKP	0.82 (0.23)	142.71 (90.24)	1.65 (0.39)	14 (1.63)	0.64 (0.18)
LKU	0.20 (0.05)	363.86 (354.05)	1.91 (0.03)	10 (1.63)	0.84 (0.05)
NFS	0.98 (0.14)	359.19 (248.13)	2.04 (0.11)	23 (0.41)	0.66 (0.04)
SDK	0.65 (0.19)	133.86 (100.63)	2.21 (0.03)	17 (1.22)	0.79 (0.03)
WDR	1.16 (0.2)	200.93 (0.76)	1.57 (0.19)	20 (1.22)	0.53 (0.05)
WSB	1.10 (0.12)	201.09 (137.25)	1.97 (0.02)	20 (2.45)	0.66 (0.02)
<b>Grand Total</b>	<b>0.72 (0)</b>	<b>103.62 (6.20)</b>	<b>2.08 (0.2)</b>	<b>19 (3.17)</b>	<b>0.73 (0.06)</b>



**Figure 2.** RVC fish metrics for mean density, biomass (g), species diversity ( $H'$ ), species richness (S), and evenness ( $J'$ ) for each site Eastern Sambo SUA (ESB), Looe Key SPA (LKP), Looe Key SUA (LKU), Number 1 Marker (N1M), Nine Foot Stake (NFS), Sand Key SPA (SDK), Western Dry Rocks (WDR), Western Dry Rocks (WDR), and Western Sambo ER (WSB) 2017-2018. Mean density is the number of individuals per meter squared. Mean biomass is in units of grams per meter squared. Site symbols indicate level of protection: fished (squares), ER/SPA (circles), and SUA (diamonds). See Table 3 for data source.

**Table 4.** Summary Table of RVC 2018 mean fish metrics for the Target group fish families Haemulidae and Lutjanidae pooled by year and month for each site: Eastern Sambo SUA (ESB), Looe Key SPA (LKP), Looe Key SUA (LKU), Nine Foot Stake (NFS), Sand Key SPA (SDK), Western Dry Rocks (WDR), and Western Sambo ER (WSB). Mean density is the number of individuals per primary sampling unit divided by the number of divers. Mean biomass is in units of grams per meter squared. Standard error is denoted in paratheses ( ).

Site	Haemulidae		Lutjanidae		Target Group	
	Mean Density (N m <sup>-2</sup> )	Mean Biomass (g m <sup>-2</sup> )	Mean Density (N m <sup>-2</sup> )	Mean Biomass (g m <sup>-2</sup> )	Mean Density (N m <sup>-2</sup> )	Mean Biomass (g m <sup>-2</sup> )
<b>2017</b>	0.05 (0)	17.47 (0.95)	0.08 (0)	17.09 (1.06)	0.13 (0)	34.56 (0.96)
<b>Feb</b>	0.04 (0)	9.06 (1.25)	0.09 (0)	15.26 (6.39)	0.13 (0.01)	24.32 (1.24)
ESB	0.07 (0)	12.55 (1.82)	0.13 (0.01)	19.78 (4.04)	0.21 (0.01)	32.33 (3.1)
LKP	0.01 (0)	1.29 (0)	0.10 (0.01)	16.62 (12.99)	0.12 (0.02)	17.91 (10.83)
LKU	0.03 (0)	11.73 (2.34)	0.06 (0.02)	16.76 (3.43)	0.13 (0.01)	28.49 (2.91)
NFS	0.05 (0)	20.70 (11.85)	0.07 (0.02)	18.03 (5.09)	0.10 (0.02)	38.73 (7.33)
WDR	0.03 (0)	3.78 (0.6)	0.07 (0.01)	9.41 (6.71)	0.10 (0.01)	13.19 (4.02)
WSB	0.03 (0)	12.98 (1.07)	0.06 (0.07)	10.78 (0)	0.10 (0.03)	23.76 (3.49)
<b>May</b>	0.04 (0)	10.37 (1.08)	0.06 (0.01)	10.96 (2.71)	0.10 (0)	21.33 (1.71)
ESB	0.04 (0)	7.77 (1.82)	0.06 (0.01)	6.10 (2.47)	0.10 (0.01)	13.87 (1.95)
LKP	0.01 (0)	1.08 (0)	0.03 (0)	2.88 (0.31)	0.03 (0)	3.95 (0.04)
LKU	0.03 (0)	5.63 (0.51)	0.01 (0)	1.58 (1.1)	0.04 (0)	7.21 (0.59)
NIM	0.11 (0.02)	16.42 (6.17)	0.01 (0)	0.46 (0.28)	0.11 (0.02)	16.88 (5.56)
NFS	0.01 (0)	1.01 (0.3)	0.16 (0.06)	23.64 (21.28)	0.16 (0.04)	24.65 (13.87)
SDK	0.08 (0.01)	6.88 (2.03)	0.11 (0.01)	8.80 (4.28)	0.18 (0.01)	15.67 (3.06)
WDR	0.03 (0)	16.67 (5.79)	0.09 (0.01)	12.93 (4.1)	0.12 (0.01)	29.6 (5.02)
WSB	0.00 (0)	0.19 (0)	0.03 (0.01)	3.99 (3.19)	0.03 (0.01)	4.18 (2.7)
<b>Jul</b>	0.05 (0)	23.13 (2.23)	0.07 (0.01)	23.28 (1.89)	0.12 (0.01)	46.41 (2.35)
ESB	0.05 (0)	6.63 (0.58)	0.04 (0.01)	9.85 (5.08)	0.09 (0.01)	16.48 (3.02)
LKP	0.01 (0)	2.01 (0.48)	0.21 (0.06)	59.02 (7.42)	0.22 (0.05)	61.04 (15.45)
LKU	0.01 (0)	5.19 (1.69)	0.04 (0.01)	16.07 (5.02)	0.05 (0)	21.25 (4.05)

**Table 4.** (continued)

NIM	0.14 (0.02)	51.87 (12.47)	0.06 (0.01)	9.21 (2.09)	0.19 (0.01)	61.07 (0)
NFS	0.09 (0.01)	46.25 (10.86)	0.04 (0.01)	18.04 (13.36)	0.13 (0.01)	64.29 (10.88)
SDK	0.08 (0.02)	25.02 (9.48)	0.10 (0.02)	24.54 (9.86)	0.18 (0.02)	49.56 (9.19)
WDR	0.01 (0)	0.75 (0.01)	0.06 (0.04)	2.95 (0.16)	0.07 (0.03)	3.7 (0.64)
WSB	0.01 (0)	1.44 (0.02)	0.02 (0.01)	1.47 (0.58)	0.03 (0)	2.91 (0.35)
<b>Dec</b>	0.08 (0)	27.91 (2.69)	0.09 (0.01)	19.36 (2.18)	0.17 (0.02)	47.27 (2.39)
ESB	0.17 (0.01)	64.37 (16.82)	0.12(0.03)	13.54 (4.12)	0.29 (0.02)	77.9 (14.43)
LKP	0.02 (0)	4.21 (0.58)	0.03 (0)	5.57 (0.8)	0.05 (0)	9.78 (0.7)
LKU	0.21 (0.03)	21.18 (3.53)	0.12 (0.01)	12.63 (4.03)	0.33 (0.02)	33.82 (3.56)
NIM	0.06 (0)	17.06 (1.96)	0.03 (0)	5.22 (1.53)	0.09 (0)	22.28 (1.78)
NFS	0.01 (0)	2.94 (0.51)	0.04 (0)	7.02 (1.16)	0.05 (0)	9.96 (1.01)
SDK	0.16 (0.02)	55.13 (13.07)	0.17 (0.02)	55.73 (16.85)	0.33 (0.02)	110.85 (14.48)
WDR	0.00 (0)	0.00 (0)	0.03 (0.01)	1.88 (1.38)	0.03 (0.03)	1.88 (1.38)
WSB	0.00 (0)	2.55 (0)	0.18 (0.03)	14.59 (2.41)	0.18 (0.04)	17.14 (4.23)
<b>(4.23)</b>			0.17			
<b>2018</b>	0.19 (0)	38.93 (2.24)	0.17 (0.01)	34.60 (6.23)	0.36 (0.01)	73.53 (4.44)
<b>Feb</b>	0.57 (0.04)	41.73 (2.2)	0.17 (0.01)	14.80 (1.48)	0.74 (0.04)	56.53 (2.42)
LKP	0.05 (0.01)	28.28 (6.52)	0.31 (0.04)	32.22 (5.57)	0.36 (0.01)	60.5 (5.93)
LKU	1.43 (0.15)	75.94 (13.03)	0.14 (0.03)	4.31 (1.18)	1.57 (0.13)	80.25 (12.45)
WDR	0.24 (0.04)	20.98 (6.37)	0.06 (0.01)	7.86 (1.10)	0.3 (0.03)	28.84 (4.6)
<b>Jun</b>	0.05 (0)	12.48 (0.95)	0.10 (0.01)	43.38 (16.26)	0.15 (0.01)	55.87 (12.74)
ESB	0.01 (0)	1.82 (0.72)	0.09 (0.02)	7.12 (4)	0.10 (0.02)	8.94 (3.07)
LKP	0.01 (0)	1.72 (0.62)	0.27 (0.05)	195.19 (122.29)	0.28 (0.04)	196.91 (92.08)
LKU	0.18 (0.02)	27.45 (5.86)	0.05 (0.01)	9.05 (2.25)	0.23 (0.01)	36.5 (4.84)
NIM	0.01 (0)	3.69 (1.96)	0.21 (0.05)	26.16 (7.03)	0.23 (0.05)	29.85 (9.92)

**Table 4** (continued)

NFS	0.14 (0.02)	24.02 (5.09)	0.05 (0.01)	6.43 (2.71)	0.19 (0.02)	30.45 (4.44)
SDK	0.01 (0)	1.09 (0)	0.03 (0)	6.55 (4.11)	0.04 (0.01)	7.64 (3.41)
WDR	0.07 (0.01)	14.83 (3.49)	0.07 (0.01)	8.66 (3.45)	0.14 (0.01)	23.48 (3.22)
WSB	0.00 (0)	0.29 (0)	0.02 (0)	1.16 (0.07)	0.03 (0)	1.45 (0.09)
<b>Sep</b>	0.07 (0)	20.12 (2.59)	0.24 (0.02)	31.36 (3.13)	0.3 (0.01)	51.48 (3.19)
ESB	0.06 (0)	16.14 (2.03)	0.11 (0.03)	13.32 (5.12)	0.17 (0.02)	29.46 (3.37)
LKP	0.03 (0)	5.12 (0.83)	0.31 (0.05)	35.72 (8.34)	0.34 (0.04)	40.84 (6.48)
LKU	0.12 (0.01)	25.93 (3.96)	0.31 (0.07)	20.06 (6.32)	0.43 (0.04)	45.99 (4.76)
NFS	0.22 (0.02)	70.39 (17.64)	0.26 (0.03)	39.81 (4.36)	0.48 (0.03)	110.2 (13.89)
SDK	0.03 (0)	0.07 (0)	0.61 (0.13)	75.54 (23.13)	0.64 (0.12)	75.61 (22.07)
WDR	0.01 (0)	1.89 (0.58)	0.00 (0)	0.13 (0)	0.01 (0)	2.02 (0.59)
WSB	0.00 (0)	1.18 (0)	0.04 (0.01)	3.57 (1.6)	0.04 (0.01)	4.74 (1.23)
<b>Dec</b>	0.31 (0.01)	82.77 (5.76)	0.17 (0.02)	38.96 (12.02)	0.48 (0.02)	121.73 (6.76)
ESB	0.25 (0.03)	33.54 (10.25)	0.03 (0)	4.10 (0.85)	0.28 (0.03)	37.63 (8.58)
LKP	0.02 (0)	3.16 (0.83)	0.48 (0.21)	90.62 (81.6)	0.50 (0.14)	93.78 (53.29)
LKU	0.08 (0.02)	17.24 (4.5)	0.05 (0.01)	13.73 (6.38)	0.13 (0.01)	30.98 (5.04)
NFS	0.62 (0.07)	177.12 (42.97)	0.05(0.01)	10.50 (3.55)	0.67 (0.06)	187.62 (35.88)
SDK	0.39 (0.04)	78.92 (20.91)	0.08 (0.01)	16.85 (6.02)	0.47 (0.04)	95.77 (17.92)
WDR	0.57 (0.06)	117.81 (19.84)	0.01 (0)	1.87 (1.4)	0.58 (0.06)	119.68 (20.77)
WSB	0.26 (0.03)	68.85 (22.96)	0.48 (0.06)	96.08 (27.77)	0.74 (0.05)	164.93 (24.94)
<b>Grand Total</b>	<b>0.12 (0)</b>	<b>27.37 (1.88)</b>	<b>0.12 (0.02)</b>	<b>2290.57 (17.01)</b>	<b>0.23(0.03)</b>	<b>4781.49</b>

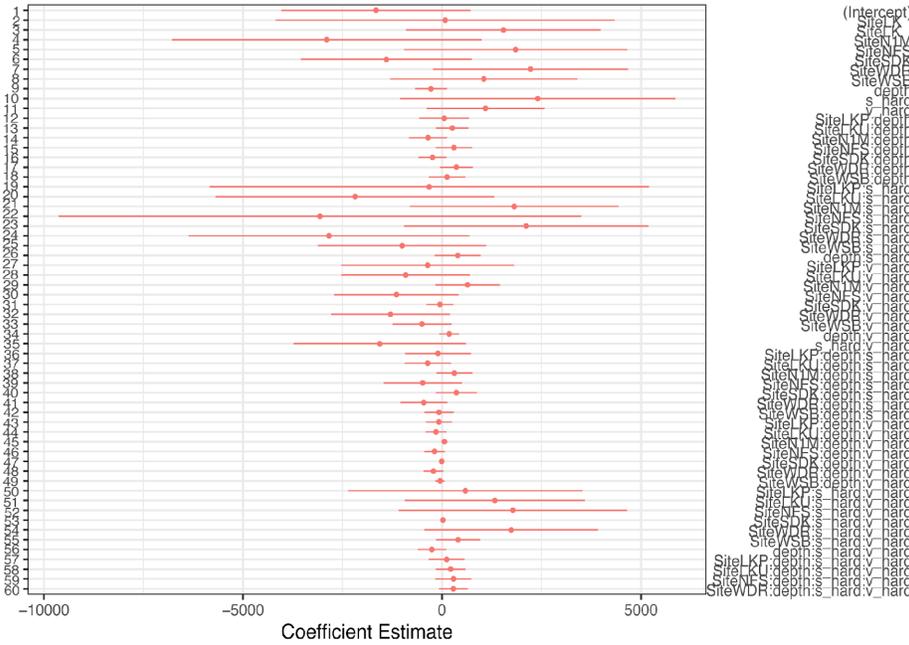
**Table 5.** Results of ANCOVA model 1 (function of site) and model 2 (function of date) on reef fish biodiversity and habitat metrics were obtained by visual surveys between sites and sample date, and their interactions denoted by (\*). The default significance level is 0.05 ‘\*’; ‘\*\*’ denotes 0.01 significance; ‘\*\*\*’ denotes 0.001 significance.

<b>Factor</b>	<b>Interaction</b>	<b>Df</b>	<b>SS</b>	<b>F</b>	<b>P-value</b>
Fish Biomass (Model 2)	Date	1	2.6e+09	4.82	0.03*
Species Richness (Model 1)	Site	7	452.8	3.61	0.02*
	Site * depth	7	433.9	3.46	0.02*
	Depth * surface hard relief	1	226.7	12.66	<0.01**
Species Richness (Model 2)	Date	1	341.9	16.79	<0.001***
	Vertical hard relief	1	111.8	5.49	0.02*
	Date * depth	1	82.4	4.05	0.05*
	Date * surface hard relief	1	215.5	10.59	<0.01**
	Date * depth * surface hard relief	1	273.2	13.42	<0.001***
Species Diversity (Model 2)	Date	1	0.42	4.42	0.04*
	Surface hard relief	1	0.64	6.78	0.01*
	Date * depth * surface hard relief	1	0.66	6.96	0.01*
	Date * depth * vertical hard relief	1	0.96	10.15	<0.01**
Evenness (Model 1)	Depth	1	0.06	5.01	0.04*
Evenness (Model 2)	Date * depth * vertical hard relief	1	0.95	7.93	0.01**

**Table 6.** Results of ANCOVA models 1 (function of site) and models 2 (function of date) on Target reef fish Haemulidae and Lutjanidae and habitat metrics obtained by visual surveys between sites and sample date and their interactions denoted by (\*). The default significance level is 0.05 ‘\*’; ‘\*\*’ denotes 0.01 significance; ‘\*\*\*’ denotes 0.001 significance.

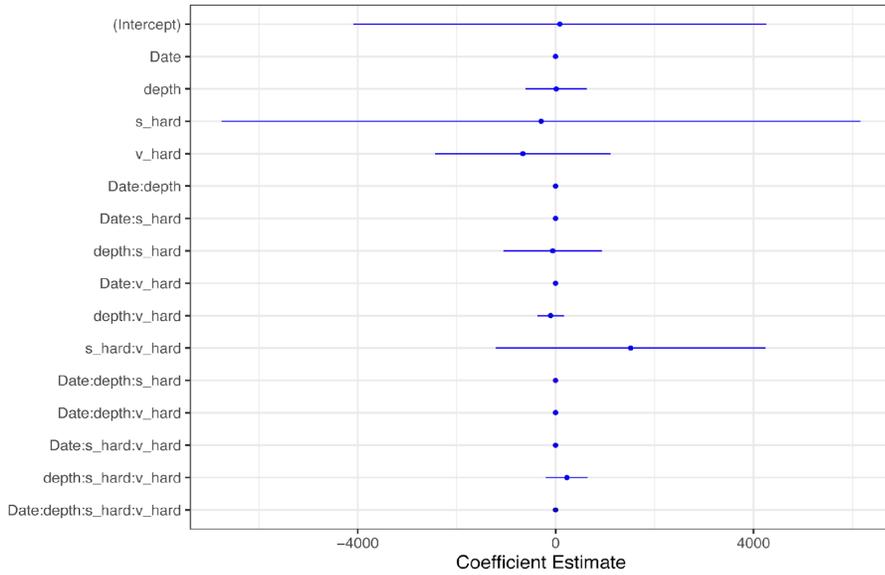
<b>Factor</b>	<b>Interaction</b>	<b>Df</b>	<b>SS</b>	<b>F</b>	<b>P-value</b>
Target Fish Density (Model 1)	Vertical hard relief	1	1444	3.9	0.05*
	Site * vertical hard relief	7	10473	4.04	<0.001***
	Site * depth * surface hard relief * vertical hard relief	4	9601	6.487	<0.001***
Target Fish Density (Model 2)	Date	1	4609	11.07	<0.001***
	Depth * vertical hard relief	1	1804	4.33	0.04*
	Date * depth * vertical hard relief	1	1950	4.69	0.03*
Target Fish Biomass (Model 1)	Site	7	2.81e+08	2.35	0.02*
	Depth * surface hard relief	1	2.55e+08	14.95	<0.001***
	Site * vertical hard relief	7	3.10e+08	2.59	0.01*
	Depth * vertical hard relief	1	1.87e+08	10.97	0.001**
	Site * depth * surface hard relief	7	5.77e+08	4.83	<0.001***
Target Fish Biomass (Model 2)	Date	1	1.95e+08	10.16	0.001**
	Depth * surface hard relief	1	1.39e+08	7.22	0.01**
	Depth * vertical hard relief	1	2.36e+08	12.3	<0.001***
	Date * depth * vertical hard relief	1	7.94e+07	4.13	0.04*
	Date * depth * surface hard relief	1	8.71e+07	4.53	0.03*

A) Predicting Species Richness by Site 2017–2018

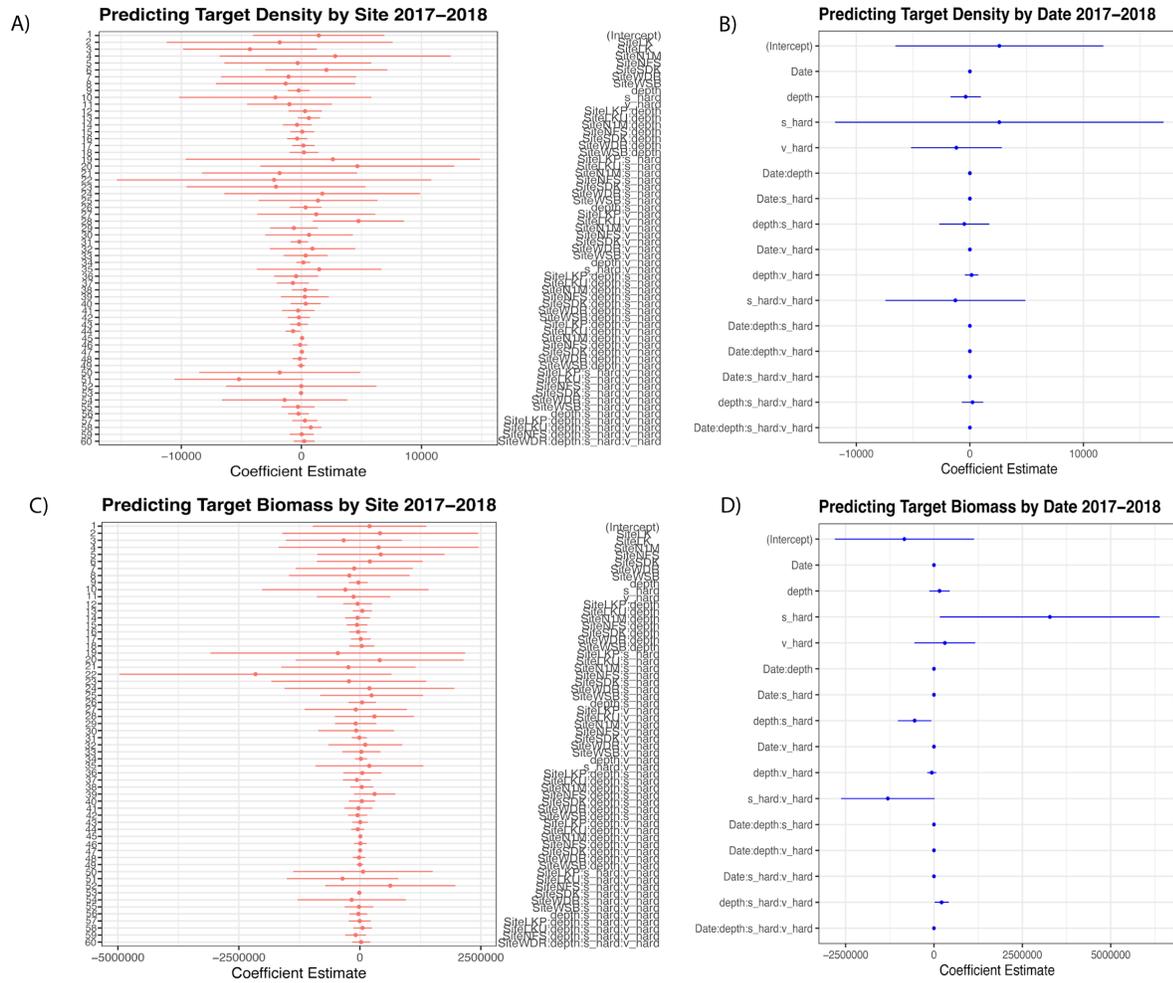


B)

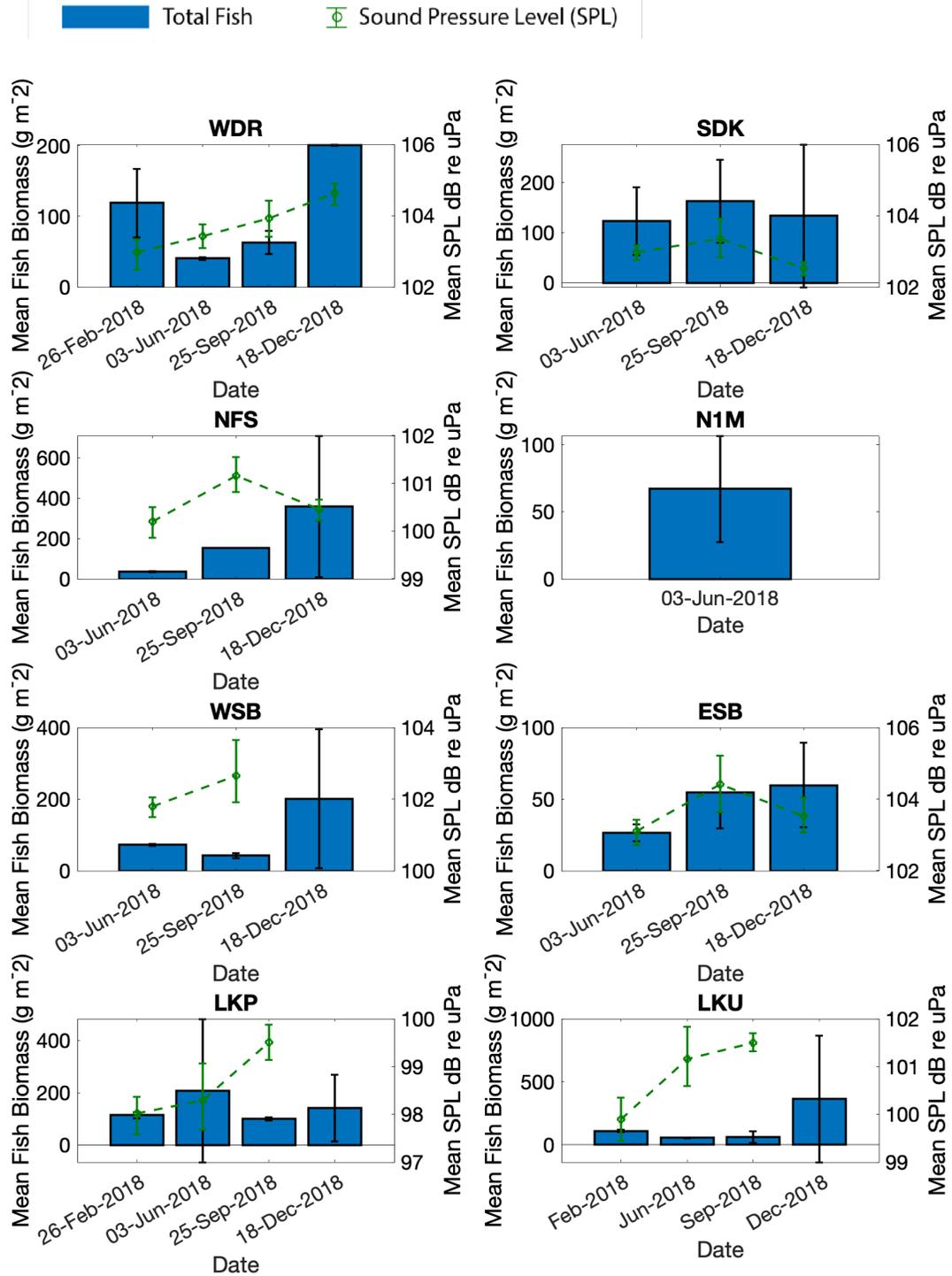
Predicting Species Richness by Date 2017–2018



**Figure 3.** Model plots of coefficient estimates 95% confidence level from habitat interactions for predicting species richness categorized by site (A) and sample date (B) for 2017-2018 RVC surveys. See Table 5 for description of site interactions listed on the y-axis for Fig 3A.



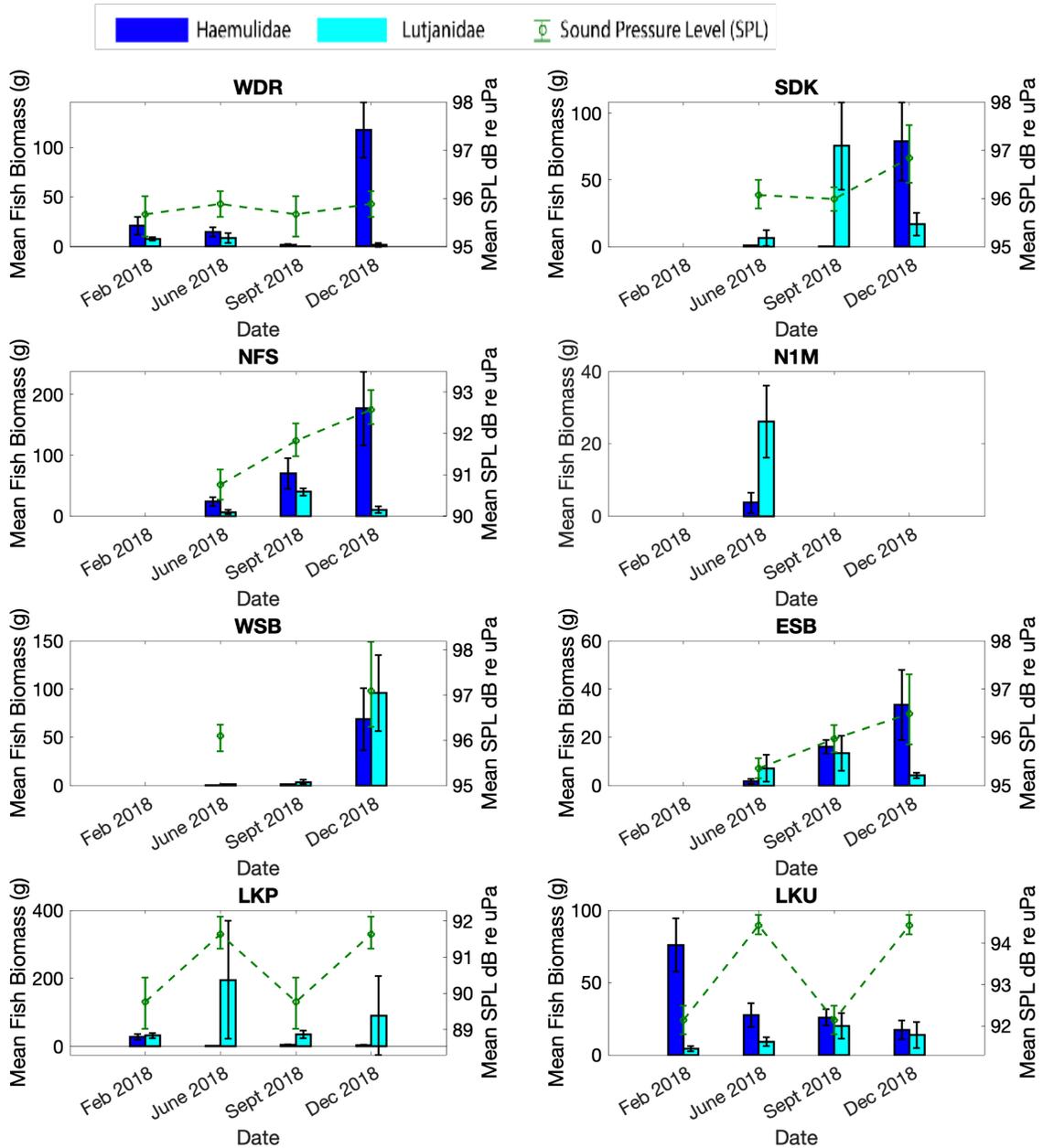
**Figure 4.** Model plots of coefficient estimates at the 95% confidence level from habitat interactions for predicting target group density categorized by site (A) and sample date (B) and target group biomass categorized by sites (C) and sample date (D) for 2018 RVC surveys. See Table 6 for description of site interactions listed on the y-axis for Fig 4A and 4C.



**Figure 5.** Box plots of mean fish biomass and line graph of mean SPLs crepuscular hours for the L1 frequency band (0.1-3kHz) for each sample period at sites: Western Dry Rocks (A), Sand Key SPA (B), Nine Foot Stake (C), Number 1 Marker (D), Western Sambo ER (E), Eastern Sambo SUA (F), Looe Key SPA (G), and Looe Key SUA (H). Error bars for mean biomass represent 1 standard deviation and error bars for SPL represent the upper and lower quartiles. Note the change in y-axis values for each site.

**Table 7.** Results of ANCOVA models 1 (habitat metric interactions) and models 2 (fish metric interactions) on L1 (0.1-3kHz) frequency band SPLs produced during crepuscular hours between sites and sample date, and their interactions denoted by (\*). The default significance level is 0.05 ‘\*’; ‘\*\*’ denotes 0.01 significance; ‘\*\*\*’ denotes 0.001 significance.

<b>Factor</b>	<b>Interaction</b>	<b>D</b>	<b>SS</b>	<b>F</b>	<b>P-value</b>
L1 Frequency Band 0.1-3kHz (Model 1)	Date	1	18.4	8.59	<0.01**
	Depth	1	40.8	19.0	<0.001* **
L1 Frequency Band 0.1-3kHz (Model 2)	Date	1	24.7	37.5	<0.001* **
	Fish biomass	1	11.2	16.9	<0.01**
	Fish density	1	3.93	5.95	0.03*
	Species richness	1	4.49	6.81	0.03*
	Fish biomass : species richness	1	7.28	11.0	0.01**
	Fish biomass : species diversity	1	4.56	6.91	0.03*
	Fish biomass : fish density : species richness	1	35.1	53.2	<0.001* **
	Date : species richness : species diversity	1	23.2	35.1	<0.001* **
	Fish density : species richness : species diversity	1	9.09	13.8	<0.01**



**Figure 6.** Box plots of mean fish biomass for Haemulids (blue) and Lutjanids (cyan), and line graph of mean SPLs during crepuscular hours for the L2 frequency band (1.2-2kHz) for each sample period at sites: Western Dry Rocks (A), Sand Key SPA (B), Nine Foot Stake (C), Number 1 Marker (D), Western Sambo ER (E), Eastern Sambo SUA (F), Looe Key SPA (G), and Looe Key SUA (H). Error bars for mean biomass represent 1 standard deviation and error bars for SPL represent the upper and lower quantiles.

**Table 8.** Results of ANCOVA models 1 (habitat metric interactions) and models 2 (fish metric interactions) on L2 (1.2-2kHz) frequency band SPLs produced during crepuscular hours between sites and sample date, and their interactions with 0.05 significance. The default significance level is 0.05 ‘\*’; ‘\*\*’ denotes 0.01 significance; ‘\*\*\*’ denotes 0.001 significance.

<b>Factor</b>	<b>Interaction</b>	<b>df</b>	<b>SS</b>	<b>F</b>	<b>P-value</b>
L2 Frequency Band 1.2-2kHz (Model 1)	Date	1	99.9	43.02	<0.001***
	Depth	1	312.9	134.7	<0.001***
	Vertical hard relief	1	25.1	10.8	0.001**
	Date * depth	1	21.5	9.26	0.002**
	Date * surface hard relief	1	15.4	6.64	0.01**
	Depth * surface hard relief	1	9.4	4.07	0.04*
	Date * vertical hard relief	1	93.5	40.3	<0.001***
	Date * depth * surface hard relief * vertical hard relief	1	12.2	5.26	0.02*
L2 Frequency Band 1.2-2kHz (Model 2)	Date	1	143.5	28.3	<0.001***
	Biomass	1	22.9	4.52	0.04*
	Date * Family * Density	1	44.3	8.73	<0.01**

## DISSERTATION CONCLUSION

The global decline in coral reefs continues to increase in the face of intensifying anthropogenic and climatic stressors (1, 2). In traditional disturbance ecology, the resulting ecosystem is a product of the biological legacies (i.e., remaining habitat structure, survival of species) shaping post-disturbance recovery processes and re-establishment of an ecologically functional ecosystem (3). This dissertation contributes to our understanding of the relationship between reef fish biodiversity, habitat complexity, and diverse spatial management zones (including non-regulated sites) within the Florida Keys National Marine Sanctuary (FKNMS). Data collected between 2017 and 2018 provided baseline data on several shallow fore-reef sites before versus after this system was impacted by a category 4 Hurricane (Irma). Additionally, this dissertation combined traditional reef visual census (RVC) surveys, coral reef soundscapes and structure-from-motion photogrammetry to provide fine-scale spatiotemporal data that will inform management and restoration efforts. Moreover, this dissertation also addresses fundamental questions regarding some of the drivers of biodiversity and habitat complexity, and the implications of such features on resilience of coral reef systems to human interactions (i.e., fishing pressure, coral intervention, recreational use) and hurricanes.

In Chapter 1, underwater soundscapes at two sites were used to characterize the impacts of Hurricane Irma on the biological coral reef soundscape, specifically the high-frequency band representative of snapping shrimp (7-20 kHz) and the low-frequency band associated with sound-producing reef fish (<3 kHz), and the underlying temporal patterns that reflect changes in species behavior and activity. Temporal patterns in reef fish chorusing during the daytime hour and snapping shrimp activity during crepuscular hours at a research-only area (ESB) appeared resilient to the acoustic energy exposure, change in environmental variables, and physical

damage caused by Hurricane Irma. There is limited quantitative research on specific impacts to soniferous reef fish groups by hurricanes, however this study helped fill this knowledge gap by partitioning the low-frequency band to distinguish between reef fish families that are similar in foraging behavior, habitat preference, hours of chorusing. Additionally, this study supports that notion that underwater soundscape work can be a complimentary ecological tool in characterizing small, yet important shifts in ecological communities during disturbances with localized impacts (4-6).

In Chapter 2, we characterized spatiotemporal variation of habitat metrics at eight fore-reef sites representing three management zones in the FKNMS using visual habitat surveys (2017–2018) acquired before and after Hurricane Irma. Post-hurricane, five of those sites were surveyed using structure-from-motion photogrammetry to further investigate the effects of coral morphology on structural complexity. In general, protected reef sites harbored more mean live coral cover than fished sites, yet sites differed in the dominant coral taxa contributing to reef structural complexity. At the site level, the type of coral dominating an area and its morphology (i.e., encrusting dome, boulder, branching) may be more important factors in characterizing habitat complexity than mean live coral cover. Conversely, fished sites were structurally complex and were more characterized by hard-bottom habitat (i.e., ruggedness, percent rubble, vertical relief). Monitoring fine-scale habitat variations through high-resolution mapping methods (i.e., photogrammetry, digital elevation models) is beneficial in (i) assessing the effectiveness of marine protected areas (7-8), (ii) understanding the biological legacies that may preserve habitat complexity (i.e., survival of reef building coral taxa) (9), and (iii) in guiding place-based coral restoration efforts (10, 11). Combining traditional spatiotemporal monitoring methods such as visual habitat surveys with underwater photogrammetry across marine reserves

of varying levels of protection may enhance the ability of managers to monitor and promote resiliency (12).

In Chapter 3, we used a multidisciplinary approach combining RVC surveys and underwater soundscapes to explore the response of reef fish biodiversity indices (i.e., density, biomass, species richness, diversity, evenness) and two target group reef fish families, Haemulidae and Lutjanidae, to habitat characteristics, reserve location, and time of sampling before and after Hurricane Irma. Mean SPLs during crepuscular hours for the reef fish associated low frequency band were site-specific and correlated with site and complex habitat features such depth and vertical hard relief. The sampling period after the hurricane resulted in a > 60% decrease in fish density for most sites despite increases in species diversity, richness, and evenness after the hurricane. Mean fish density and mean fish biomass increased between 2017 and 2018. The distribution and biomass of the target group largely depended on presence of complex reef structures (i.e., vertical hard relief, surface hard relief) and protection status. Although the reef sites exist in the same region of the lower Florida Keys, localized reefs can vary in habitat features at small spatial scales and can reflect site-specific variation in reef fish biodiversity. Relatively small marine reserves (0.3-0.5 km<sup>2</sup>) can be pivotal in protecting reef building corals and resident reef fish species against local stressors such as fishing and recreational use (13-14). This dissertation identified important site-specific spatiotemporal changes in reef fish biodiversity that vary in magnitude due to protection status, and supports efforts in further understanding the effectiveness of a network of marine reserves

## References

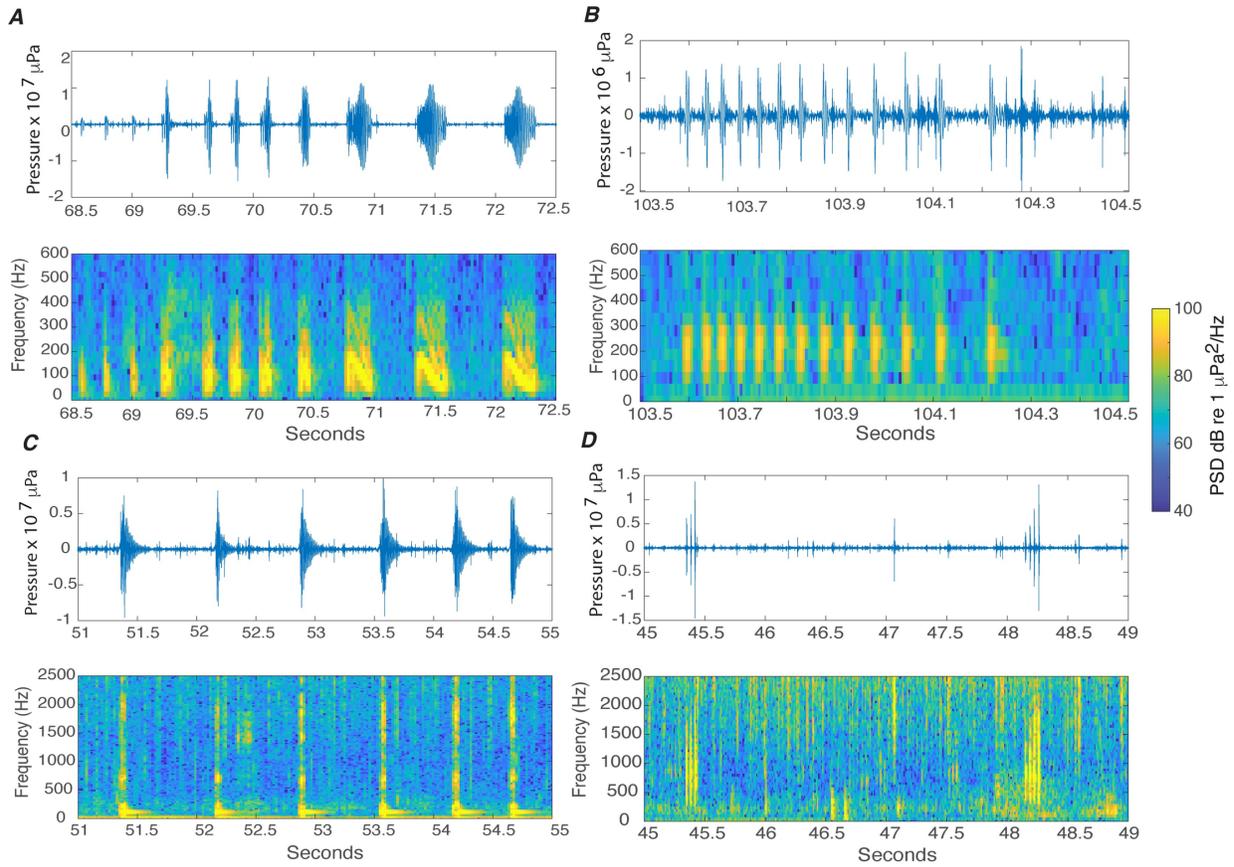
1. Fox, M. D., Carter, A. L., Edwards, C. B., Takeshita, Y., Johnson, M. D., Petrovic, V., Amir, C. G., Sala, E., Sandin, S. A., & Smith, J. E. (2019). Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. *Coral Reefs*, 38(4), 701–712. <https://doi.org/10.1007/s00338-019-01796-7>
2. Cornwall, C. E., Comeau, S., Kornder, N. A., Perry, C. T., van Hooidonk, R., DeCarlo, T. M., Pratchett, M. S., Anderson, K. D., Browne, N., Carpenter, R., Diaz-Pulido, G., D'Olivo, J. P., Doo, S. S., Figueiredo, J., Fortunato, S. A. V., Kennedy, E., Lantz, C. A., McCulloch, M. T., González-Rivero, M., ... Lowe, R. J. (2021). Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proceedings of the National Academy of Sciences of the United States of America*, 118(21), e2015265118. [https://doi.org/10.1073/PNAS.2015265118/SUPPL\\_FILE/PNAS.2015265118.SD02.XLSX](https://doi.org/10.1073/PNAS.2015265118/SUPPL_FILE/PNAS.2015265118.SD02.XLSX)
3. Platt, W. J., & Connell, J. H. (2003). Natural disturbances and directional replacement of species. *Ecological Monographs*, 73(4), 507–522. <https://doi.org/10.1890/01-0552>
4. Locascio, J. v., & Mann, D. A. (2005). Effects of Hurricane Charley on fish chorusing. *Biol. Lett*, 1, 362–365. <https://doi.org/10.1098/rsbl.2005.0309>
5. Gottesman, B. L., Olson, J. C., Yang, S., Acevedo-Charry, O., Francomano, D., Martinez, F. A., Appeldoorn, R. S., Mason, D. M., Weil, E., & Pijanowski, B. C. (2021). What does resilience sound like? Coral reef and dry forest acoustic communities respond differently to Hurricane Maria. *Ecological Indicators*, 126, 107635. <https://doi.org/10.1016/J.ECOLIND.2021.107635>
6. Simmons, K. R., Eggleston, D. B., & Bohnenstiehl, D. R. (2021). Hurricane impacts on a coral reef soundscape. *PLoS ONE*, 16(2 February 2021). <https://doi.org/10.1371/journal.pone.0244599>
7. Chen, G. K., & Dai, C. F. (2021). Using 3D photogrammetry to quantify the subtle differences of coral reefs under the impacts of marine activities. *Marine Pollution Bulletin*, 173(Pt B), 113032. <https://doi.org/10.1016/j.marpolbul.2021.113032>
8. Richaume, J., Cheminée, A., Drap, P., Bonhomme, P., Cadene, F., Ferrari, B., Hartmann, V., Michez, N., & Bianchimani, O. (2021). 3D Photogrammetry Modeling Highlights Efficient Reserve Effect Apparition After 5 Years and Stillness After 40 for Red Coral (*Corallium rubrum*) Conservation in French MPAs. *Frontiers in Marine Science*, 8. <https://doi.org/10.3389/FMARS.2021.639334/FULL>
9. Sierra-Escrigas, S. L., Peluffo, D. R. P., & García-Urueña, R. (2020). Shallow coral reef community mapping and update on its ecological units using aerial images at Isla Arena,

Colombian Caribbean. *International Journal of Remote Sensing*, 41(21), 8198–8215.  
<https://doi.org/10.1080/01431161.2020.1763495>

10. Ferrari, R., Lachs, L., Pygas, D. R., Humanes, A., Sommer, B., Figueira, W. F., Edwards, A. J., Bythell, J. C., & Guest, J. R. (2021). Photogrammetry as a tool to improve ecosystem restoration. *Trends in Ecology & Evolution*, 36(12), 1093–1101.  
<https://doi.org/10.1016/J.TREE.2021.07.004>
11. Roelvink, F. E., Storlazzi, C. D., van Dongeren, A. R., & Pearson, S. G. (2021). Coral Reef Restorations Can Be Optimized to Reduce Coastal Flooding Hazards. *Frontiers in Marine Science*, 8(May), 1–11. <https://doi.org/10.3389/fmars.2021.653945>
12. Simmons, K. R., Bohnenstiehl, D. R., & Eggleston, D. B. (2022). Spatiotemporal Variation in Coral Assemblages and Reef Habitat Complexity among Shallow Fore-Reef Sites in the Florida Keys National Marine Sanctuary. *Diversity*, 14, 153.  
<https://doi.org/10.3390/d14030153>
13. Magdaong ET, Fujii M, Yamano H, Licuanan WY, Maypa A, Campos WL, et al. Long-term change in coral cover and the effectiveness of marine protected areas in the Philippines: a meta-analysis. *Hydrobiologia* 2013 733:1 [Internet]. 2013 Oct 30 [cited 2022 Aug 30];733(1):5–17. Available from:  
<https://link.springer.com/article/10.1007/s10750-013-1720-5>
14. Wright LS. Small no-take areas benefit hard corals more than regulation through fishing permits. *Aquat Conserv* [Internet]. 2022 Jul 1 [cited 2022 Aug 16];32(7):1209–16. Available from: <https://onlinelibrary.wiley.com/doi/full/10.1002/aqc.3814>

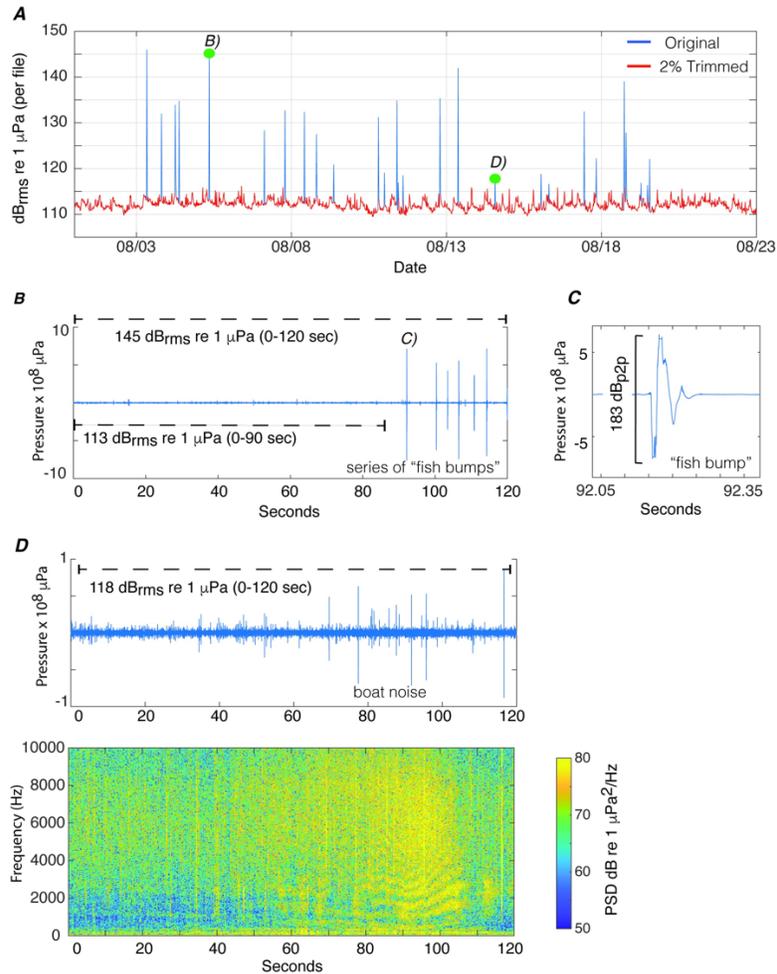
## APPENDICES

**APPENDIX A: SUPPLEMENTARY MATERIALS ACCOMPANYING CHAPTER 1:  
HURRICANE IMPACTS ON A CORAL REEF SOUNDSCAPE**



**S1 Fig. Fish call spectrograms.**

Representative waveforms (top) and spectrograms (bottom) for the L1 low frequency band 50-300Hz: (A) Serranid growl, (B) fish “chirps”; and the L2 low frequency band 1200-1800Hz: (C) Haemulid “grunts”, (D) rapid aggregated “knocks”. Mean amplitudes were calculated using a bandpass filter 30-3000Hz and a steepness of 0.65. Spectrograms were calculated using a window length of 2048Hz with 50% overlap



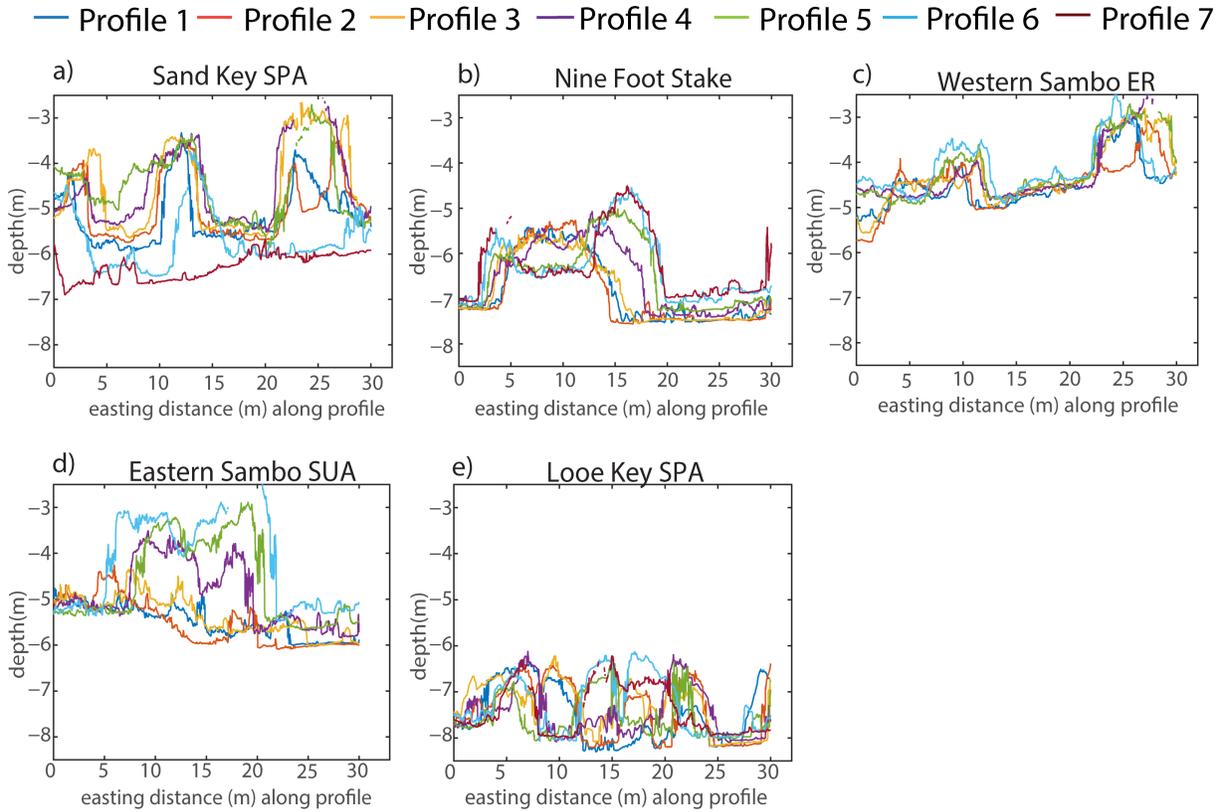
## S2 Fig. Illustration of trimmed sound pressure level time series.

S1 Illustration of the trimmed sound pressure level time series applied to a section of the pre-storm storm data from Eastern Sambo site. The red line in panel A) shows the original broadband time series generated by calculating the root-mean-square (rms) sound pressure level in each 2-minute recording collected every 20 minutes. The blue line shows the time series after eliminating those files with the largest 2% of the amplitudes during the combined pre- and post-storm window. These trimmed data were used in calculating daytime and nighttime means. The largest amplitude spikes removed by this process are associated with files that contain one or more fish bumps. These signals do not represent sound but can have a major influence on the calculated sound pressure levels. For example, the sound pressure level of the file shown in panel B) has a value of 113 dB rms re 1  $\mu\text{Pa}$  when averaged over the first 90 seconds of the file; this is consistent with expected background noise levels. However, when the series of fish bumps are included in the calculation, the amplitude rises by more than 30 decibels. Panel C) shows an individual bump signal. These signals are often clustered temporally, but typically occur in no more than 1 or 2 files per day. The trimming of the time series also removes a handful of files (3–4 per week) containing the sounds of a nearby small boat, as shown in panel D). The resulting trimmed time series better represents the underlying diurnal pattern of acoustic noise with the environment and is used to assess patterns of biophony.

**APPENDIX B: SPATIOTEMPORAL VARIATION IN CORAL ASSEMBLAGES AND REEF HABITAT COMPLEXITY AMONG SHALLOW FORE-REEF SITES IN THE FLORIDA KEYS NATIONAL MARINE SANCTUARY**

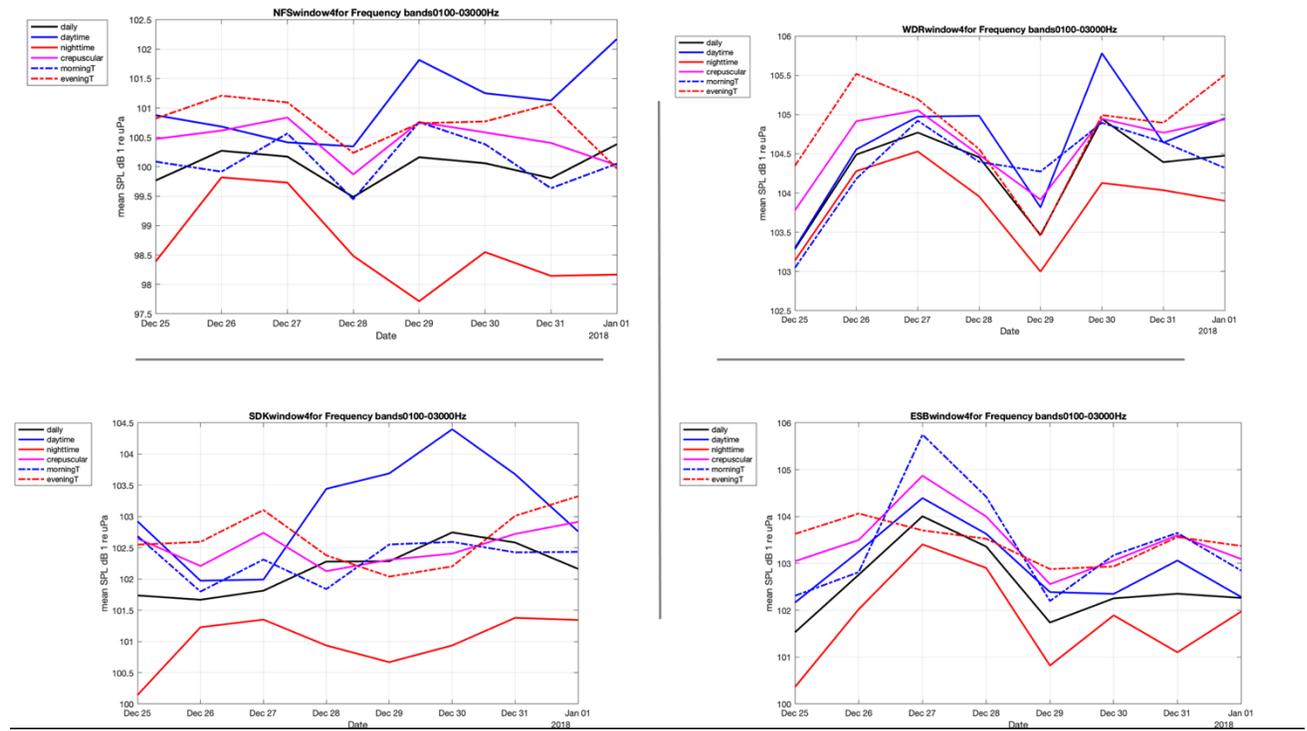
<b>Stage of Data Processing</b>	<b>GoPro Hero4 Black/Silver (7168 cameras)</b>
Accuracy	High/ Low*
Key Point Limit	40,000 points
Tie Point Limit	10,000 points
Photo Alignment	6090/6574 (93%) cameras
Est Image Quality (>0.50)	Total tie points – 3,123,260
Dense Cloud: Quality and Depth Filtering	High Aggressive Depth Maps (6066)
Mesh Building	ST: Height Field SD: Dense Cloud (1,037,228,326 FaceCount: High (207,445,665) Interpolation enabled
Build Texture	Mapping Mode: adaptive Orthophoto Blending Mode: Mosaic (default) Texture size/count: 4096 Enable color correction

**Table S1.** Example settings used to generate 3D models of Sand Key in Agisoft Metashape Professional. (\*) Low settings were used if image alignment was not immediately successful; however, all models were aligned on high before generating the dense cloud or mesh building

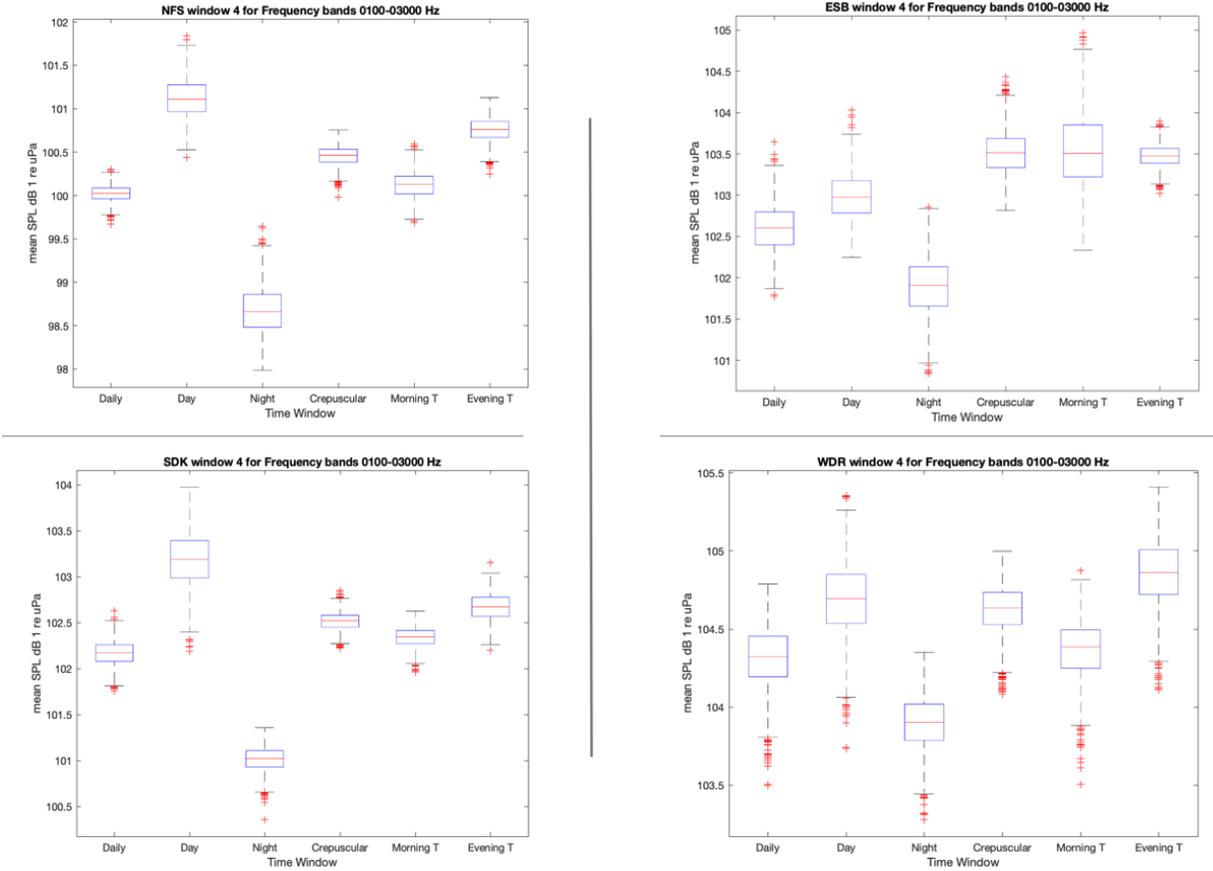


**Figure S1:** Depth-transect profiles based on the DEM raster are shown for (a) Sand Key SPA (SDK), (b) Nine Foot Stake (NFS), (c) Western Sambo ER (WSB), (d) Eastern Sambo SUA (ESB), and (e) Looe Key SPA (LKP). Transect profiles are 30 m in length (west-east) with 3 m spacing between transects heading in a northerly direction

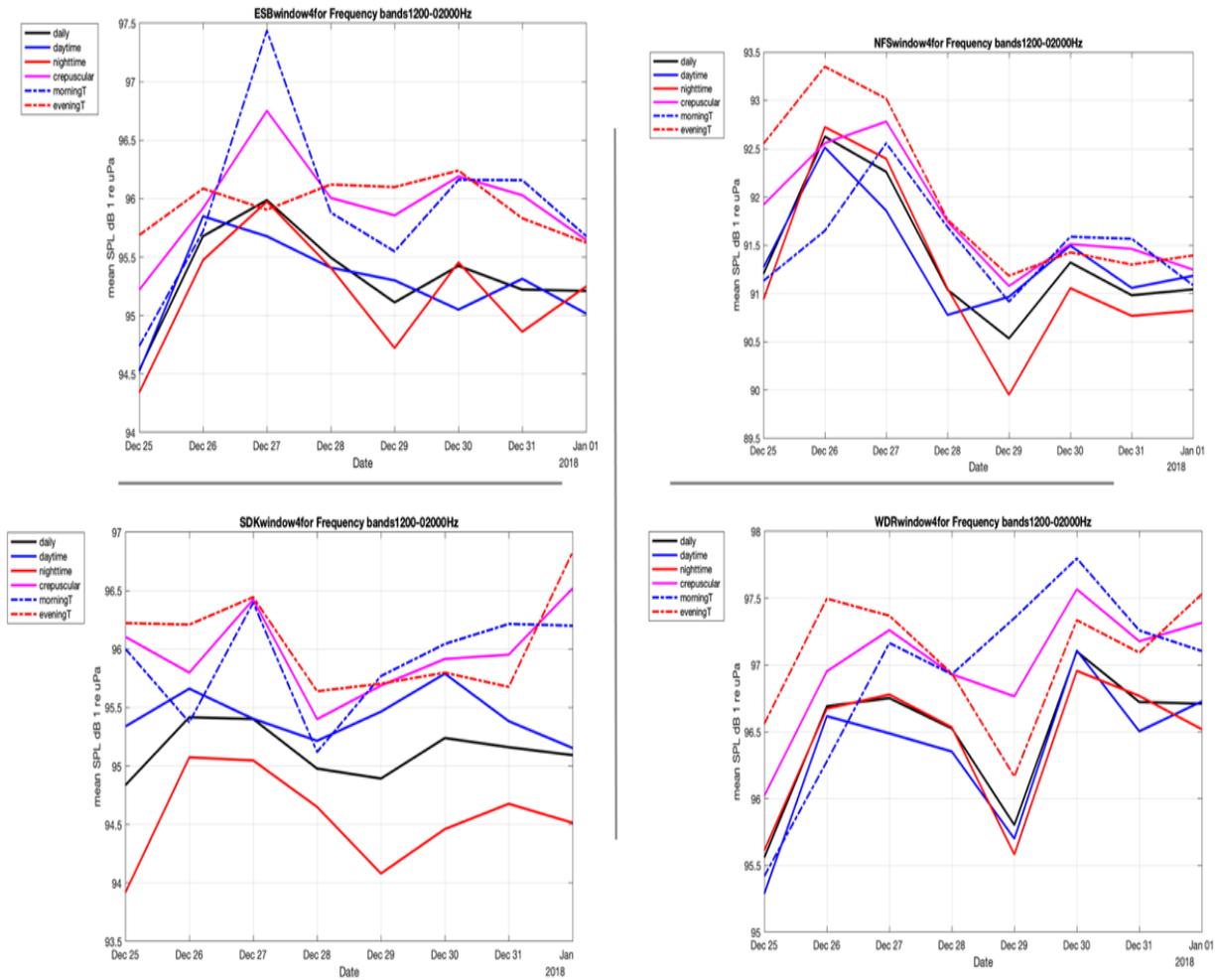
## APPENDIX C: SUPPLEMENTARY MATERIALS ACCOMPANYING CHAPTER 3: SPATIOTEMPORAL PATTERNS IN REEF FISH BIODIVERSITY AND HABITAT UTILIZATION USING REEF VISUAL CENSUS SURVEYS AND UNDERWATER SOUNDSCAPES



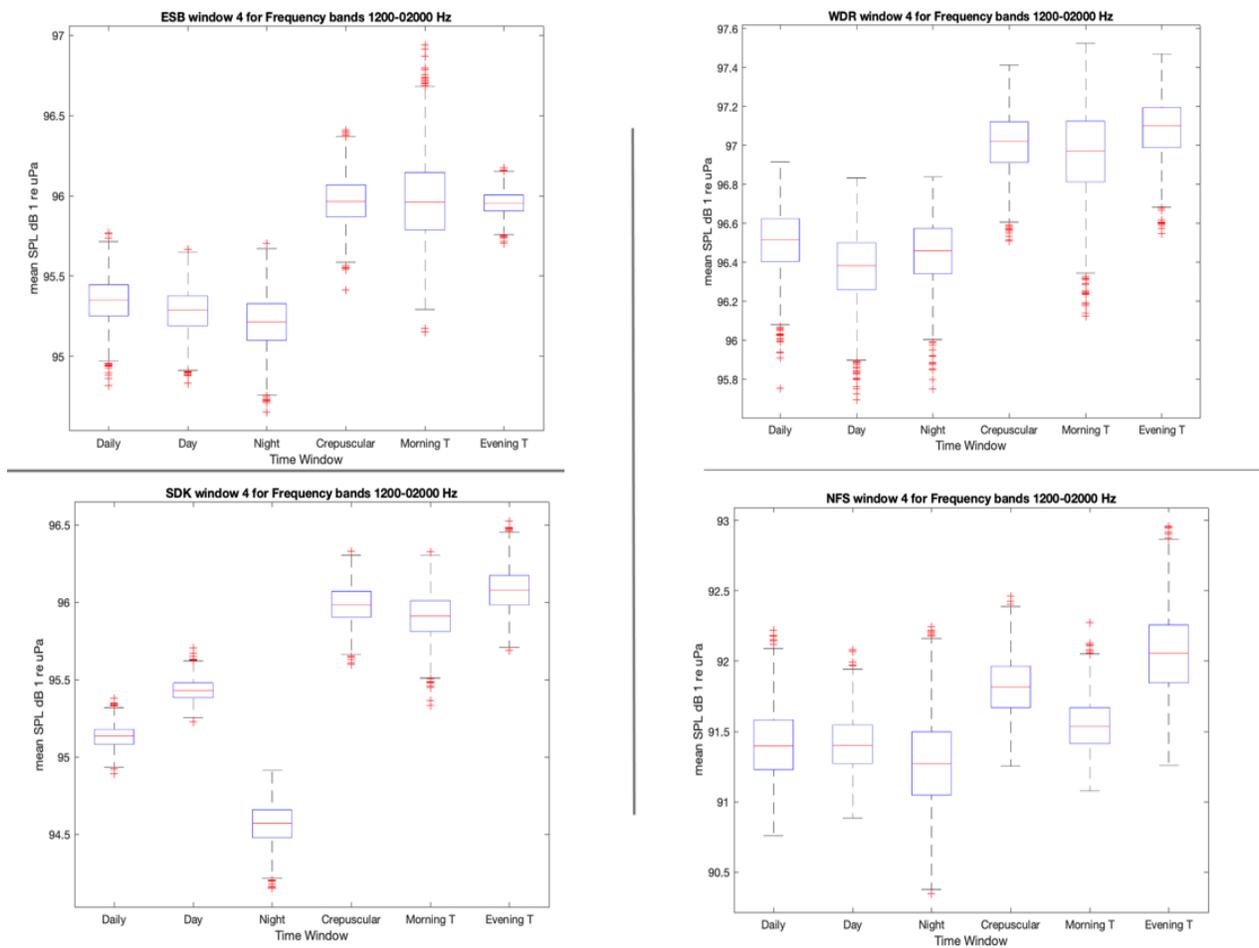
**Figure S1.** An example of a 7-day window of the mean SPLs in the L1 low frequency band (0.1-3kHz) associated with soniferous reef fish activity. Each color line represents the mean SPL for specific time periods: daily/24hr (black), daytime hours (blue), nighttime hours (red), crepuscular hours (pink), morning twilight (blue dash), and evening twilight (red dash).



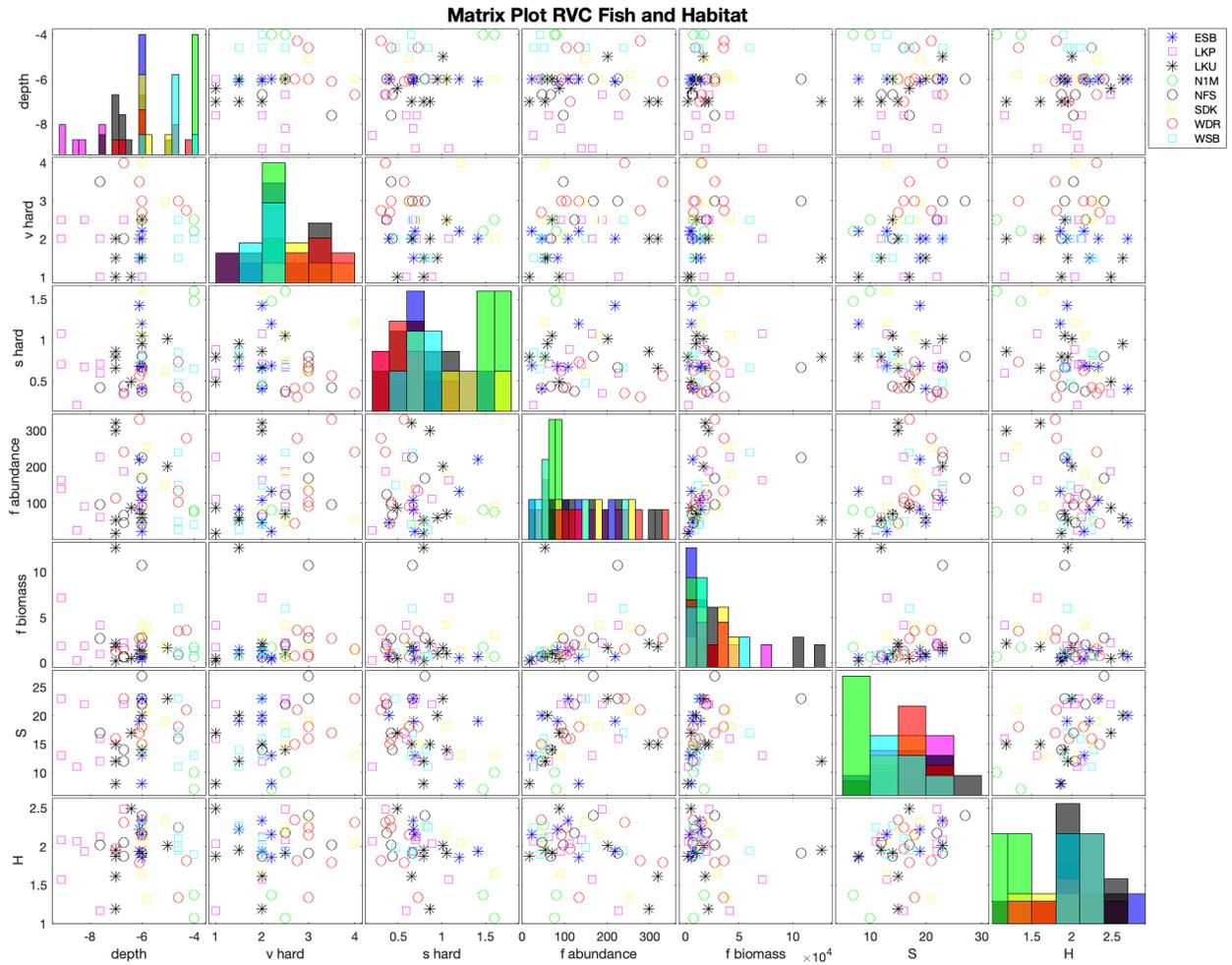
**Figure S2.** An example boxplot the mean SPLs in the L1 low frequency band (0.1-3kHz) for each sampling period over the 7-day window in Figure S1. The central red line represents the median and the 25<sup>th</sup> and 75<sup>th</sup> percentiles are shown as the upper and lower limits respectively. Outliers are denoted as red '+' symbols.



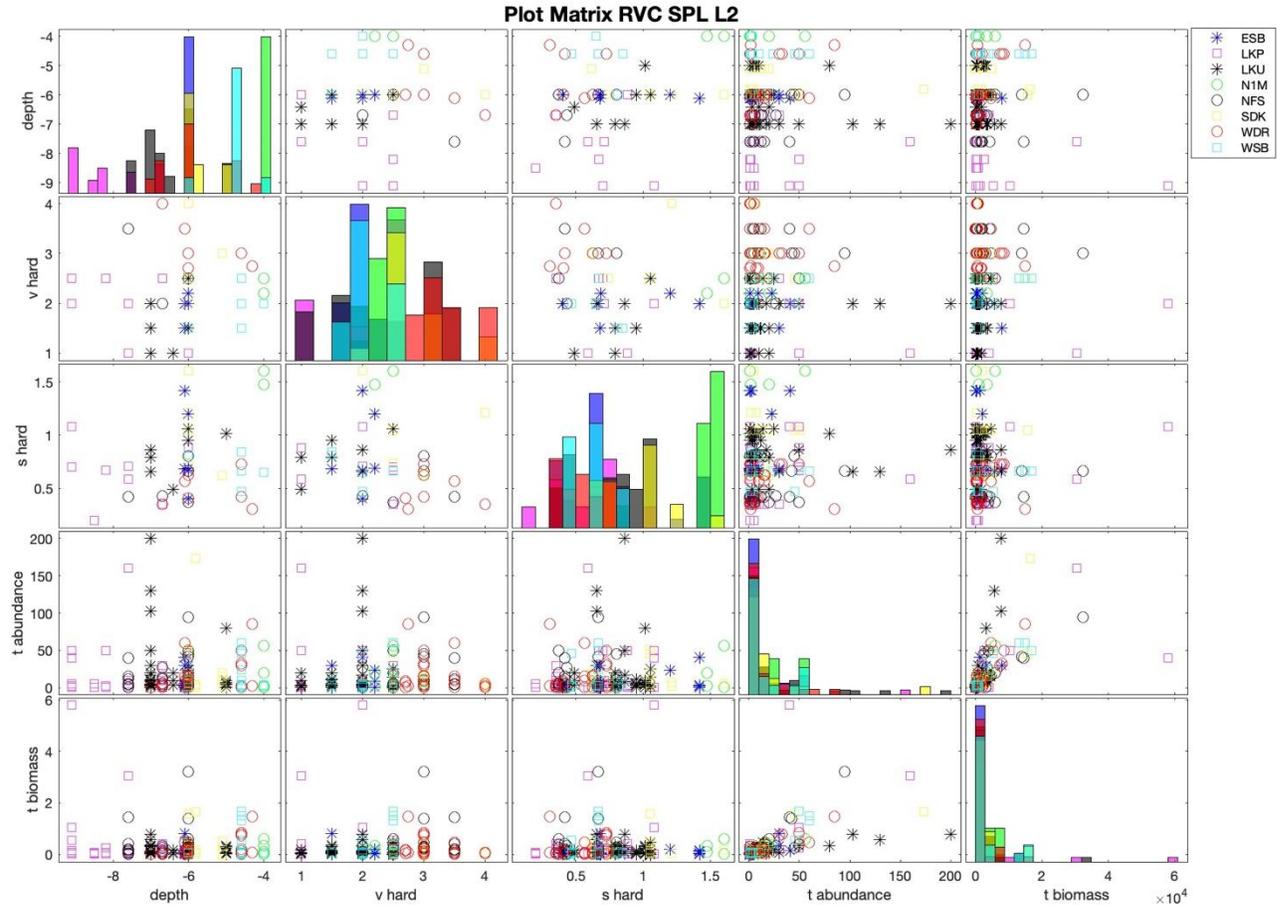
**Figure S3.** An example of a 7-day window of the mean SPLs in the L2 low frequency band (1.2-2kHz) associated with soniferous Haemulids and Lutjanids activity. Each color line represents the mean SPL for specific time periods: daily/24hr (black), daytime hours (blue), nighttime hours (red), crepuscular hours (pink), morning twilight (blue dash), and evening twilight (red dash).



**Figure S4.** An example boxplot the mean SPLs in the L2 low frequency band (1.2-2kHz) for each sampling period over the 7-day window in Figure S3. The central red line represents the median and the 25<sup>th</sup> and 75<sup>th</sup> percentiles are shown as the upper and lower limits respectively. Outliers are denoted as red '+' symbols.



**Figure S5.** Relationships between RVC habitat metrics (depth, vertical hard relief ‘v hard’, surface hard relief ‘s hard’) and RVC fish metrics (fish density ‘f abundance’, fish biomass ‘f biomass’, species richness ‘S’, species diversity ‘H’) nested by sample date for each reef site. Height of group bars indicates the weight of that bin for each site. Site symbols indicate level of protection: fished (circles), ER/SPA (squares), SUA (stars).



**Figure S6.** RVC habitat metrics associated with target (Haemulidae and Lutjanidae) density and biomass pooled by sample date. Height of group bars indicates the weight of that bin for each site. Site symbols indicate level of protection: fish (squares), ER/SPA (circles), SUA (stars).