

Winners and losers of reef flattening: a trait-based assessment of Florida coral reef fishes

Ganadores y perdedores del aplanamiento de arrecifes: una evaluación basada en rasgos de los peces de los arrecifes de coral de Florida

Gagnants et perdants de l'aplatissement des récifs : une évaluation basée sur les traits des poissons des récifs coralliens de Floride

DAVID P. KOCHAN¹, MATTHEW D. MITCHELL^{1,2}, RACHEL ZUERCHER^{1,3}, PETER F. COWMAN^{4,5}, AND ALASTAIR R. HARBORNE⁶

¹*Institute of Environment and Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA, dkoch010@fiu.edu, ²New York University, Abu Dhabi, UAE, mdm18@nyu.edu*

³*The National Socio-Environmental Synthesis Center, Annapolis, MD 21401, USA, rachel.zuercher@gmail.com*

⁴*School of Marine and Tropical Biology, James Cook University, Townsville, Qld. 4811, Australia, peter.cowman@jcu.edu.au, ⁵Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld. 4811, Australia, ⁶Institute of Environment and Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA, aharborn@fiu.edu*

EXTENDED ABSTRACT

Anthropogenic stressors are causing widespread coral mortality in the Caribbean, leading to negative carbonate budgets and decreased structural complexity which ultimately threatens reef functioning and ecosystem services (Graham and Nash, 2013, Perry et al, 2013). Species are not equally affected by disturbances, often causing reshuffling of ecosystem assemblages and communities (McKinney, 1997). Trait-based analysis can build generic frameworks of how species respond to environmental change (McGill, et al, 2006), and we use this approach to better understand implications of reef flattening on fishes. Coral reef fish assemblages depend on three-dimensional structure provided by stony coral (Graham and Nash, 2013), and coral reef fishes are well-suited to trait-based analysis with well parameterized traits and phylogeny in databases and literature (Hadj-Hammou, et al 2021, Rabosky, et al 2018). Reef structural complexity is critical for fish community dynamics, providing spatial refuges from predation and water flow, creating niche space, increasing food availability, and supplying nesting sites (Binning and Roche, 2015, Hixon, 1991, Johansen, et al, 2008, Robertson and Sheldon, 1979). The Florida reef tract stretches more than 550 km along the Atlantic coast of southeastern Florida and the Florida Keys and is subject to a wide range of stressors leading to degradation of reefs and loss of reef structure (Alvarez-Filip, et al 2015, Alvarez-Filip, et al 2019, Schutte, et al 2010). The combination of pre-anthropogenic large-scale climatic changes with recent acceleration of anthropogenic disturbances has led to the marked decline of structure on Florida coral reefs (Toth, et al, 2019, Burman, et al, 2012). Despite their decline, Florida's coral reefs still support reef fish assemblages that drive fisheries and ecotourism (Ault, et al 2013). Using a trait-based framework, we aim to predict the winners and losers of reef flattening on Florida coral reefs and identify the traits which govern fish responses to both loss of coral cover and complexity.

Using surveys from 3,999 Florida reef and hardbottom sites, we used boosted regression trees to model biophysical and anthropogenic factors correlated with the abundance of 109 fish species. Reef fish and benthic survey data were sourced from NOAA fishery-independent coral reef fish and benthic surveys across southeast Florida since 1979 as part of the Reef Visual Census and National Coral Reef Monitoring Program (Bohnsack, et al 1999, Smith, et al 2011). First, we used the NOAA survey data to model common reef species' densities against 21 biophysical and anthropogenic drivers using boosted regression trees, which are capable of handling large numbers of interacting predictors and fixing non-linear relationships (Elith, et al 2008). We isolated the relative importance of structural complexity and coral cover for each species, categorizing species as 'losers' (more abundant on complex reefs) or negative associations as 'winners' (more abundant on flat reefs). We tested those species' associations with complexity and coral cover for phylogenetic relationships using the Fish Tree of Life and Blomberg's K. We then modeled if 13 morphological, behavioral, and functional traits mediate species' responses to reef degradation.

The species density models predicted 52 species as losers of flattening and 10 of coral cover and only 17 and 7 winners of each respectively. We determined phylogeny did not explain relationships with complexity or coral cover. Instead, eight traits explained 65% of variation of species' association with complexity, and seven traits explained 38% of association with coral cover. Tail shape, body roundness, size, and swim mode make up half of the traits linked to complexity. These findings indicate that smaller, streamlined generalists are more likely to be ecological winners on flattened reefs. The species better at maneuvering on complex reefs seemed to have traded off some ability to persist in flat habitats with higher flow. Habitat generalists able to persist on habitats other than coral reefs and those with a wider depth range were more successful on flattened reefs. Degraded reefs will likely have decreased predation, thus hindering resilience and recovery. Identifying these important traits provides a better understanding of how fishes interact with complexity and allows us to predict general assemblage-wide responses to flattening. The trait-based analysis provides information to build predictive models for rarer species, such as goliath and Nassau grouper, two iconic Caribbean species heavily fished and thus rare

throughout the Florida reef tract. In addition to provide a generic understanding of which species will be most affected by loss of structure, trait responses to loss of complexity and coral cover provide important predictions for how assemblage shifts and the potential loss of some traits will affect ecosystem functions. Additionally, these results suggest that ecosystem services like fisheries and ecotourism will be diminished as reefs continue to degrade. This research has provided critical information identifying species- and trait-specific responses to reef flattening and loss of coral cover to assist with the management and conservation of biodiversity on coral reefs.

KEYWORDS: Florida, structural complexity, trait analysis, community assemblage, habitat degradation

LITERATURE CITED

- Alvarez-Filip, L., M.J. Paddock, B. Collen, D.R. Robertson, and I.M. Côté. 2015. Simplification of Caribbean reef-fish assemblages over decades of coral reef degradation. *PLoS ONE* 10(4):1-14
- Alvarez-Filip, L., N.K. Dulvy, J.A. Gill, I.M. Côté, and A.R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* 276(1669):3019–3025.
- Ault, J.S. S.G. Smith, J.A. Bohnsack, J. Luo, N. Zurcher, D.B. McClellan, T.A. Ziegler, D.E. Hallac, M. Patterson, M.W. Feeley, B.I. Ruttenberg, J. Hunt, D. Kimball, and B. Causey. 2013. Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. *Fisheries Research* 144:28–37.
- Binning, S.A. and D.G. Roche. 2015. Water flow and fin shape polymorphism in coral reef fishes. *Ecology* 96(3):828–839.
- Bohnsack, J.A., D.B. McClellan, D.E. Harper, G.S. Davenport, G.J. Konoval, A. Eklund, J.P. Contillo, S.K. Bolden, P.C. Fischel, G.S. Sandort, J.C. Javech, M.W. White, M.H. Pickett, M.W. Hulsbeck, J.L. Tobias, J.S. Ault, G.A. Meester, S.G. Smith, and J. Luo. 1999. Baseline data for evaluating reef fish populations in the Florida Keys, 1979-1998. NOAA Technical Memorandum NMFS-SEFSC:1–61.
- Burman, S., R. Aronson, & R. van Woesik. 2012. Biotic homogenization of coral assemblages along the Florida reef tract. *Marine Ecology Progress Series* 467:89–96.
- Elith, J., J.R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77(4):802–813.
- Graham, N.A.J. and K.L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32(2):315–326.
- Hadj-Hammou, J., D. Mouillot, and N.A.J. Graham. 2021. Response and Effect Traits of Coral Reef Fish. *Frontiers in Marine Science* 8:1-14.
- Hixon, M.A. 1991. Predation as a Process Structuring Coral Reef Fish Communities. Pages 475-508 in P.F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*. Academic Press.
- Johansen, J., D. Bellwood. and C. Fulton. 2008. Coral reef fishes exploit flow refuges in high-flow habitats. *Marine Ecology Progress Series* 360:219–226.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21(4):178–185.
- McKinney, M. L. 1997. Extinction Vulnerability and Selectivity: Combining Ecological and Paleontological Views. *Annual Review of Ecology and Systematics* 28(1):495–516.
- Perry, C. T., G.N. Murphy, P.S. Kench, S.G. Smithers, E.N. Edinger, R.S. Steneck, and P.J. Mumby. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature Communications* 4(1):1402
- Rabosky, D. L., J. Chang, P.O. Title, P.F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T.J. Near, M. Coll, and M.E. Alfaro. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* 559(7714):392–395.
- Robertson, D.R. and J.M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *Journal of Experimental Marine Biology and Ecology* 40(3):285–298.
- Schutte, V.G.W., E.R. Selig, and J.F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series* 402:115–122.
- Smith, S.G., J.S. Ault, J.A. Bohnsack, D.E. Harper, J. Luo, and D.B. McClellan. 2011. Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. *Fisheries Research* 109:25–41.
- Toth, L.T., A. Stathakopoulos, I.B. Kuffner, M.A. Colella, and E.A. Shinn. 2019. The unprecedented loss of Florida's reef-building corals and the emergence of a novel coral-reef assemblage. *Ecology* 100, 1–14.