



Effects of Hurricane Maria in hamlet communities (Serranidae: *Hypoplectrus* spp.) in Puerto Rico

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ABSTRACT

Hamlets (*Hypoplectrus* spp.) are hermaphroditic, carnivorous, and highly territorial fishes in the family Serranidae that are endemic to the Western Atlantic. We studied 10 reefs located in the La Parguera Natural Reserve in Puerto Rico and report differences in hamlet communities after the passage of Hurricane Maria. Our results were compared to surveys conducted in the years 2000 and 2017, before the reefs were hit by Hurricane Maria in 2017. Non-metric multidimensional analyses revealed a “boomerang pattern” in species composition and abundance, with high diversity in 2000, low diversity in 2017, and a subsequent return to high diversity levels in 2018. By and large, the study reveals a positive effect on the diversity of hamlet communities in the aftermath of Hurricane Maria. The reemergence of diversity patterns, including the recording of previously unobserved species in the study site serves as indicator of the underlying and often underestimated benefits of major disturbance events.

1. Introduction

Among the diversity in Caribbean coral reef fishes lies a group of simultaneously small hermaphroditic and carnivorous sea basses in the genus *Hypoplectrus* (Perciformes: Serranidae). *Hypoplectrus* spp. or hamlets are restricted to the Western Atlantic (WA), including all of the Caribbean and the Gulf of Mexico (Victor, 2012). The genus comprises about 17 recognized species. Hamlets use mimicry coloration of non-predatory coral reef fishes (e.g., damselfishes) to attack preys, preying mainly small crustaceans and fishes (Randall, 1967; Whiteman et al., 2007; Holt et al., 2008). All species of hamlets are morphologically similar but have a strong differentiation of color patterns (Haldane, 2016; Hench et al., 2019) including hybrids with mixed color arrangements (Barreto & McCartney, 2008).

A substantial portion of the native habitat of hamlets throughout the WA include overfished, eutrophicated coral reefs with disrupted reef communities, a situation that can be further aggravated by the effect of natural disasters. On 20 September 2017, Hurricane Maria (category 4–5) made landfall on Puerto Rico, severely affecting the island, causing floods, runoff, landslides and thousands of direct and indirect deaths (Kishore et al., 2018). Before Hurricane Maria, surveys

performed in 2000 by Aguilar-Perera (2003) and in March 2017 by Hench et al. (2017) estimated the diversity of the hamlet communities of La Parguera Natural Reserve (LPNR) in Puerto Rico, providing a unique opportunity to assess the effects of this violent disturbance in the community composition of hamlets in the reserve.

According to the Emergency Support Function 10 (ESF-10) response teams, in LPNR, a total of 377 sunken or beached vessels were identified and more than 18,150 gallons of oily water were removed (Coastguardnews.com, 2018). Natural disturbances have the potential to affect fish assemblage structures due to high wave movement, habitat destruction (coral reefs) and even oil spills. By applying the same survey techniques used by previous studies (Aguilar-Perera, 2003; Hench et al., 2017), the goal of this study is to determine whether the community composition and diversity of hamlets in LPNR changed in the aftermath of Hurricane Maria.

2. Materials and methods

The studies were conducted in La Parguera Natural Reserve (LPNR), which is located on the southwest coast of Puerto Rico between Cabo Rojo and Guanica. LPNR is a dry and warm area with annual mean

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surface water temperature of 28.4 °C and average surface salinity is 35.2 ppt (García Sais et al., 1998). The insular shelf of LPNR extends 8–10 km offshore divided into inner, middle and shelf edge reefs (aligned east to west) (García Sais et al., 1998). LPNR contains abundant coral reefs and adjacent marine ecosystems such as seagrass beds (dominated by *Thalassia testudinum*) and mangrove forests (dominated by *Rhizophora mangle*) (Soto-Santiago and Irizarry Soto, 2013).

The surveys consisted of 100 × 4 m belt transects. In each site, two nearly parallel transect belts were set at different depths, ranging from 2 to 13 m. Transects consisted of two shoulder-to-shoulder scuba divers, where each diver assessed 2 m on their respective sides. The surveyed areas in the study sites were focused on coral reef patches, backreefs, reef edges and gorgonian forests. Sand patches were avoided as much as possible, as those are not representative habitats of the hamlet's diversity. Each reef was surveyed two times (20 surveys in total), with all the surveys performed during morning hours (7:00 a.m.–11:00 a.m.) and lasting about 30 min each. The studied sites at LPNR were restricted to the inner reefs, resurveying the same locations surveyed by previous studies (Aguilar-Perera, 2003), including a total of ten cays: Enrique, Mario, San Cristobal, Pelotas, López, La Palma, Turrumote, La Gata, Pinnacles, and Media Luna. Note that previous studies also surveyed outer reefs. During the belt transects the two divers were always communicating and pointing the sighted hamlets to avoid double recording of the same individual. This was practical because hamlet species are not typically skittish, and usually remain in their crevices, or between gorgonians. Data collected included abundance (fish counts) and diversity (differentiating between the different species of hamlets) exclusively inside the belt transects.

3. Results and discussion

Supplementary figures and tables can be accessed via the Figshare repository (DOI: <https://doi.org/10.6084/m9.figshare.8251430>). To visualize the similarities between the 10 sites surveyed, we performed a non-metric multidimensional scaling (nMDS) analysis in PRIMER v7 (Anderson et al. 2008), using a Bray Curtis resemblance matrix transformed to the 4th root for each of the survey years (2000, 2017, and 2018). Abundance and diversity of hamlets observed after Hurricane Maria (Supplementary Table 1, Fig. 1) differed relative to those reported in pre-hurricane surveys (Aguilar-Perera, 2003; Hench et al., 2017). We recorded five species of Hamlets at the inner reefs of LPNR, contrasting with the six species reported in 2000 by Aguilar-Perera (2003) and only four species reported by Hench et al. (2017; Fig. 1). Compared to the 2000 survey (Aguilar-Perera, 2003), the total relative abundance was lower for *H. nigricans* (2.4% vs. 10.5%, respectively) and *H. unicolor* (5.61% vs. 5.9%, respectively), but higher for *H. chlorurus* (78.4% vs. 58.2%, respectively) and *H. puella* (11.2% vs. 10.5%, respectively). Two species, *H. indigo* and *H. aberrans*, were recorded in 2000 but not in 2018 (Fig. 1). The surveys performed by Hench et al. (2017) reflect a higher relative abundance of *H. chlorurus* in 2017 compared to 2018 (91.1% vs. 78.4%), but a lower relative abundance for *H. unicolor* (3.0% vs. 5.61%) and *H. puella* (5.0% vs. 11.2%). The overdominance of *H. chlorurus* reported in 2017 (Hench et al., 2017), but not in 2000 (Aguilar-Perera, 2003), was still observed after the impact of the hurricane but to a lesser degree relative to levels reported in 2017 (78.4% in 2018 vs. 91.1% in 2017).

The nMDS analysis of the inner reefs after Hurricane Maria (Supplementary Fig. 1) shows similarities in *Hypoplectrus* spp. community compositions between La Palma and Lopez (both had *H. chlorurus*, *H. puella*, *H. randallorum* and *H. unicolor*). The cays Pelotas and Pinnacles were found to be the least diverse of the study sites, where only one species (*H. chlorurus*) was observed. Notably, higher visual sedimentation was observed in Pelotas compared to other reefs, thus providing a possible explanation for the higher abundance of *H. chlorurus* on this site (Supplementary Table 1; see also Hench et al., 2017).

The nMDS analyses also allow temporal comparisons of hamlet

communities from the two previous surveys in 2000 and 2017 (Aguilar-Perera, 2003; Hench et al. 2017). Hamlet communities before Hurricane Maria in 2017 (Supplementary Fig. 2) exhibited low species diversity with only three species (*H. chlorurus*, *H. puella*, and *H. unicolor*) present on the same reefs surveyed. Contrary to the high species diversity of *Hypoplectrus* we report (Supplementary Fig. 1), Hench et al. (2017) found substantially fewer species and more homogeneity in the reef communities of cays Mario, Lopez, and La Palma, where only *H. chlorurus* was observed. The most diverse inner reef sites (San Cristobal, Turrumote, La Gata, and Media Luna) recorded in 2017 were represented by only two species in our study.

The nMDS analyses for the year 2000 (Supplementary Fig. 3) contrasts markedly with the results obtained in recent surveys. For instance, Mario's hamlet communities were more similar to Media Luna's, with five species reported at each location (*H. chlorurus*, *H. puella*, *H. aberrans*, *H. nigricans*, and *H. unicolor*). Other reefs also showed high diversity of *Hypoplectrus* spp. Considerably less anthropogenic effects (e.g., lower sedimentation) and other environmental factors (e.g., lower water temperatures) during 2000 could be offered as a possible explanation of the differences observed more than a decade after (see also Hench et al., 2017).

For a more comprehensive analysis on the differences in *Hypoplectrus* spp. communities, we merged all previous nMDS and analyzed them on a temporal scale (Fig. 2), including three time points: Time 1, 2000; Time 2, 2017 (pre-Maria); Time 3, 2018 (post-Maria). The major trends of hamlet communities over the years can be described as a 'boomerang pattern' (Fig. 2). On all study sites, we observed the same distribution pattern for hamlet communities, where the year 2000 had the greatest diversity, followed by a steep decline in the year 2017 before Maria, and an increase in diversity post-Maria. Interestingly, two species that were not recorded the year before Hurricane Maria in inner reef cays (*H. nigricans* and *H. randallorum*) were observed after the climatic event. Because *H. randallorum* was first described in the year 2011 (Lobel, 2011), it is possible that Aguilar-Perera (2003) observed the species in 2000 but counted it as *H. nigricans*, the most similar color morph (Fig. 1). If that were the case, the distances between points in Time 1 (2000) and Time 3 (2018) on the nMDS (Fig. 2) would be smaller, making the 'boomerang pattern' even more apparent.

This trend was to some extent expected and serves as another instance supporting the intermediate disturbance hypothesis, which establishes that species diversity will be maximized when an ecological disturbance (e.g., a hurricane) occurs sporadically (Grime, 1973; Connell, 1978; Huston, 1979; Dial and Roughgarden, 1998; Rogers, 1993; Roxburgh et al., 2004). Another possible explanation for the increase in diversity could be the gradual reduction of water temperatures (ca. 2 °C) recorded by the National Weather Service in the aftermath of the hurricane. This decrease in temperature could serve as a facilitator for hamlets to move to the colder and shallower parts of the reef. Note that the diversity of hamlets in the outer reefs (not assessed here), at found at greater depths and lower temperatures, was substantially higher than that in the inner reefs (Hench et al., 2017).

A positive correlation was established between the passage of Hurricane Maria and *Hypoplectrus* spp. communities located on the studied sites in LPNR. The dominance of *H. chlorurus* reported in 2017 but not in 2000, was still observed in all surveyed reefs. A possible correlation between an increase in sedimentation and the dominance of *H. chlorurus* was confirmed in the study sites (particularly in Pelotas), but further analyses are required to test this relationship. It also remains to be assessed whether an increase in the diversity of hamlet communities will take place as time progresses (e.g., reaching similar levels to those recorded in 2000). It is also possible, however, that once the pre-disturbance conditions are restored, the diversity of the hamlet communities may return to the pre-hurricane (2017) levels as a result of the continuation of human activities that were halted due to the effects of Hurricane Maria (e.g., farming, fishing, and tourism). It can be implied

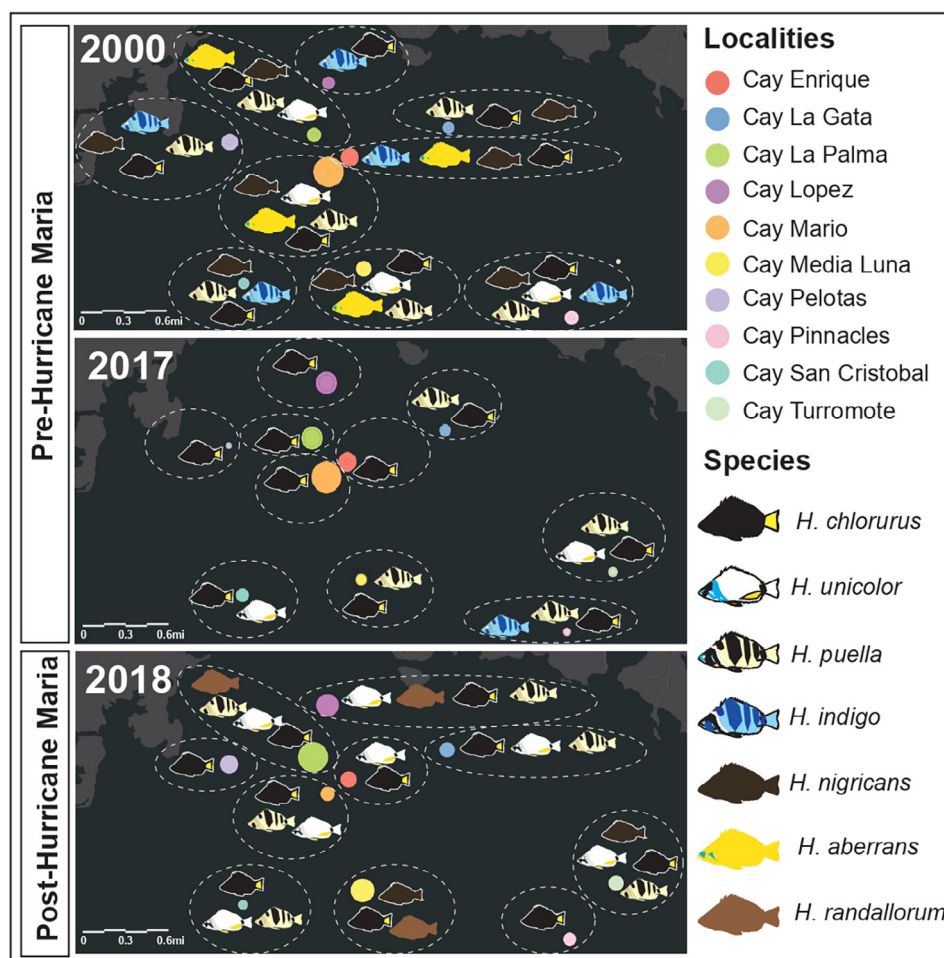


Fig. 1. Hamlet (*Hypoplectrus* spp.) abundance, diversity, and distribution at the La Parguera Natural Reserve in Puerto Rico during the years before Hurricane Maria (2000 and 2017) and after Hurricane Maria. Each colored circle indicates a different cay; size of circle indicates total abundance at each site. Fish symbols inside the dashed circle indicate the species recorded at each particular cay.

that the passage of Hurricane Maria had both a direct effect (lowering of water temperature, shifting sedimentation rates, and the triggering of breeding events) and an indirect effect (prolonged interruption of the anthropogenic activities mentioned above) in the increased richness and abundance observed on hamlet communities after Hurricane Maria. The resurgence of anthropogenic activity compounded by the time

lapse without another major hurricane event will probably play a role in determining the fate of the diversity dynamics of these communities.

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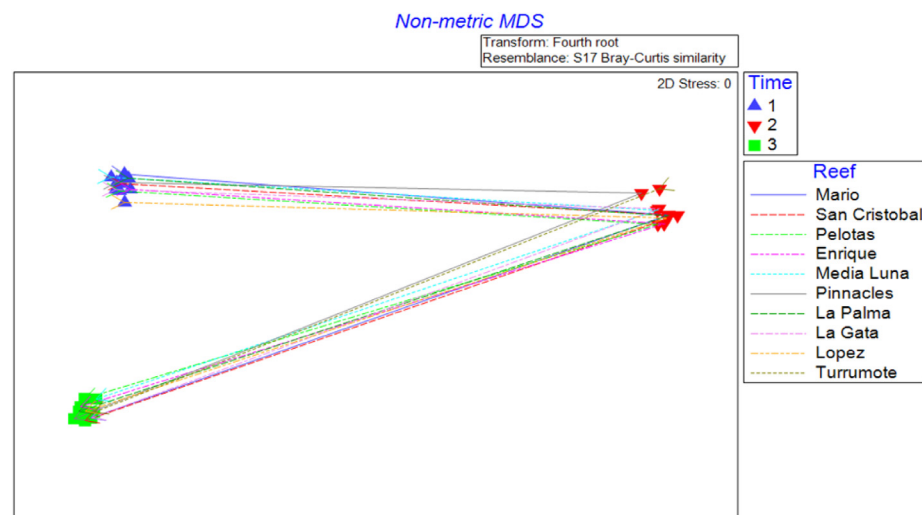


Fig. 2. Merged non-metric multidimensional scaling (nMDS) for 10 reefs off La Parguera Natural Reserve for Time 1 (year 2000), Time 2 (year 2017 before Hurricane Maria), and Time 3 (year 2018 after Hurricane Maria). Temporal *Hypoplectrus* spp. community comparisons for the study sites. Data from 2000 and 2017 were compiled from Aguilar-Perera (2003) and Hench et al. (2017), respectively.

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Conflict of Interest Statement

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105591>.

References

- Aguilar-Perera, A., 2003. Abundance and distribution of hamlets (Teleostei: Hypoplectrus) in coral reefs off Southwestern Puerto Rico: support for the multiple-species hypothesis. *Carib. J. Sci.* 39, 147–151.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd.
- Barreto, F.S., McCartney, M.A., 2008. Extraordinary AFLP fingerprint similarity despite strong assortative mating between reef fish color morphospecies. *Evolution* 62, 226–233.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Dial, R., Roughgarden, J., 1998. Theory of marine communities: the intermediate disturbance hypothesis. *Ecology* 79, 1412–1424.
- García Sais, J.R., C. S., et al., 1998. Caribbean coral reefs, seagrass and mangrove sites. *CARICOMP* 3, 195–213.
- Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Haldane, J.B.S., 2016. Recombination in the Eggs and Sperm Ina Simultaneously Hermaphroditic Vertebrate. The Royal Society Publishing.
- Hench, K., Mcmillan, W.O., Betancur-R, R., Puebla, O., 2017. Temporal changes in hamlet communities (Hypoplectrus Spp., Serranidae) over 17 Years. *J. Fish Biol.* 91, 1475–1490.
- Hench, K., Vargas, M., Höppner, M.P., Owen, McMillan W., Puebla, O., 2019. Inter-Chromosomal coupling between vision and pigmentation genes during genomic divergence. *Nat. Ecol. Evol.* 657–667.
- Holt, B.G., Emerson, B.C., Newton, J., Gage, M.J.G., Côté, I.M., 2008. Stable isotope analysis of the hypoplectrus species complex reveals no evidence for dietary niche divergence. *Mar. Ecol. Prog. Ser.* 357, 283–289.
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–101.
- Kishore, N., Marqués, D., Mahmud, A., Kiang, M.V., Rodriguez, I., Fuller, A., Ebner, P., Sorensen, C., Racy, F., Lemery, J., et al., 2018. Mortality in Puerto Rico after hurricane maria. *N. Engl. J. Med.* 379, 162–170.
- Lobel, P.S., 2011. A review of the Caribbean Hamlets (Serranidae, Hypoplectrus) with description of two new species. *Zootaxa* 3096, 1.
- Randall, J.E., 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5, 665–847.
- Rogers, C.S., 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12, 127–137.
- Roxburgh, S.H., Shea, K., Wilson, J.B., 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85, 359–371.
- Soto-Santiago, F.J., Irizarry Soto, E., 2013. The sea urchin diadema antillarum (Echinodermata, Equinoidea), algal cover and juvenile coral densities in La Parguera Puerto Rico. *UNED Res. J.* 5 (1), 33–40.
- Victor, B.C., 2012. Hypoplectrus floridiae n. sp. and Hypoplectrus ecosur n. sp., two new barred hamlets from the Gulf of Mexico (Pisces: Serranidae): more than 3% Divergent in COI mtDNA sequence from the caribbean hypoplectrus species flock. *J. Ocean Sci. Found.* 5, 1–19.
- Whiteman, E.A., Côté, I.M., Reynolds, J.D., 2007. Ecological differences between Hamlet (Hypoplectrus: Serranidae) colour morphs: between-morph variation in diet. *J. Fish Biol.* 71, 235–244.

Electronic Reference

Coastguardnews.com, 2018. Hurricane Maria Response Team Assesses Distressed Vessels in La Parguera, Puerto Rico <https://coastguardnews.com/hurricane-maria-response-team-assesses-distressed-vessels-in-la-parguera-puerto-rico/2018/02/13/>.