

Temporal changes in hamlet communities (*Hypoplectrus* spp., Serranidae) over 17 years

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Transect surveys of hamlet communities (*Hypoplectrus* spp., Serranidae) covering 14 000 m² across 16 reefs off La Parguera, Puerto Rico, are presented and compared with a previous survey conducted in the year 2000. The hamlet community has noticeably changed over 17 years, with a > 30% increase in relative abundance of the yellowtail hamlet *Hypoplectrus chlorurus* on the inner reefs at the expense of the other hamlet species. The data also suggest that the density of *H. chlorurus* has declined and that its distribution has shifted towards shallower depths. Considering that *H. chlorurus* has been previously identified as one of the few fish showing a positive association with seawater turbidity on the inner reefs of La Parguera and that sedimentation of terrestrial origin has increased over recent decades on these reefs, it is proposed that turbidity may constitute an important but so far overlooked ecological driver of hamlet communities.

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Key words: community stability; Parguera; Puerto Rico; sedimentation; turbidity.

INTRODUCTION

The hamlets, simultaneously hermaphroditic sea basses from the tropical western Atlantic Ocean (*Hypoplectrus* spp., Perciformes: Serranidae), have intrigued ichthyologists for decades (Barlow, 1975; Fischer & Petersen, 1987; Domeier, 1994; McCartney *et al.*, 2003; Theodosiou *et al.*, 2016). Seventeen species are now recognized, a third of which have been described in the past few years (Del Moral Flores *et al.*, 2011; Lobel, 2011; Victor, 2012; Tavera & Acero, 2013). The hamlets from the Gulf of Mexico appear to be well-diverged from the Caribbean hamlets at mitochondrial DNA markers (Victor, 2012; Tavera & Acero, 2013), yet hamlets tend to be very closely related genetically within these two regions (McCartney *et al.*, 2003; Barreto & McCartney, 2007; Tavera & Acero, 2013; Puebla *et al.*, 2014). The hamlets are also very similar from an ecomorphological perspective and, to date, colour pattern is the only trait that has been found to consistently differentiate species (Randall, 1968; Lobel, 2011; Tavera & Acero, 2013). Yet colour pattern also varies

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within species, both within and between locations (Thresher, 1978; Aguilar-Perera, 2004), complicating their taxonomy and identification.

Hamlets vary in their distribution (Aguilar-Perera & González-Salas, 2010; Holt *et al.*, 2010), but tend to be highly sympatric, with up to nine species found on a single reef (Puebla *et al.*, 2012a). The hamlets are reef-associated predators that feed on small invertebrates and fishes (Randall, 1967; Holt *et al.*, 2008; G. M. Serviss, unpubl. data). Sympatric species tend to live in the same habitat and have similar diets, except for the indigo hamlet *Hypoplectrus indigo* (Poey 1851) that appears to feed mostly on fishes (Whiteman *et al.*, 2007). Spawning occurs before sunset on a daily basis throughout the year. Sympatric species spawn at the same time and in the same area, often within sight of each other. Yet mating is strongly assortative with respect to colour pattern, with >98% of spawnings occurring among members of the same species (Fischer, 1980a; Barreto & McCartney, 2007; Puebla *et al.*, 2007, 2012a). Apparently, there are no strong intrinsic post-fertilization barriers in the hamlets (Whiteman & Gage, 2007) and in the only case where hybrids were bred in aquaria, they appeared intermediate between parental species in terms of colour pattern (Domeier, 1994).

The hamlets have served as a distinctive model system for the study of a variety of ecological and evolutionary processes including the evolution and maintenance of simultaneous hermaphroditism (Fischer, 1980b), sex allocation (Fischer, 1981), egg trading (Fischer & Petersen, 1987), sexual selection (Puebla *et al.*, 2011), dispersal (Puebla *et al.*, 2009), local adaptation (Picq *et al.*, 2016), speciation (Holt *et al.*, 2011), evolutionary radiation (Puebla *et al.*, 2008) and recombination (Theodosiou *et al.*, 2016). Temporal changes in hamlet communities can potentially affect or be affected by such processes. For example, changes in population densities and relative abundances are expected to affect effective population sizes as well as the potential for hybridization among the different species (Puebla *et al.*, 2012a). Temporal changes in hamlet densities and relative abundances could also provide hints about the ecological factors that shape hamlet communities, which are still eluding ecologists. Yet detailed hamlet surveys are scarce and very little is known about the dynamics of hamlet communities. Data from general fish surveys are to be treated with caution due to extensive colour pattern variation in the group that complicates species identification and typically do not provide a detailed picture of local communities. Hamlet population densities can be relatively low (in the order 10 fish 1000 m⁻² of reef) and several species are rare (in the order 1 fish 1000 m⁻² or less, Puebla *et al.*, 2012a), requiring extensive surveys.

The hamlets from La Parguera, Puerto Rico, constitute a notable exception with a thorough survey available for the year 2000 (Aguilar-Perera, 2003). This survey stands out because it targets the hamlet community specifically, is spread across 16 reefs identified with reef names and GPS coordinates, provides raw fish counts with depth and reef type (inner *v.* outer reefs) and is complemented by a note on colour pattern variation at this location (Aguilar-Perera, 2004). Here, this opportunity is taken to evaluate the temporal dynamics of hamlet communities. Seventeen years later the same reefs were revisited and transect surveys covering 14 000 m² across 16 reefs were conducted. The transect data indicate that hamlet relative abundances have noticeably changed over 17 years, with most notably a 30% increase of the yellowtail hamlet *Hypoplectrus chlorurus* (Cuvier 1828) on the inner reefs at the expense of the other hamlet species. The potential drivers of this change are discussed in light of the literature and it is proposed that recent changes in water

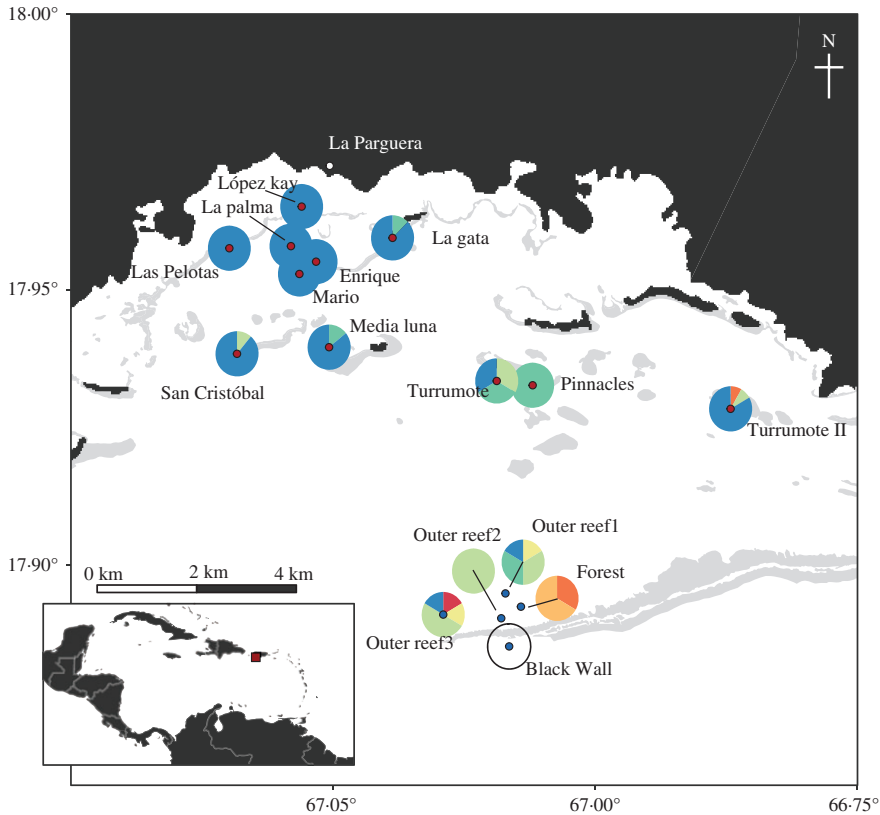


FIG. 1. Pie-chart relative abundance of *Hypoplectrus aberrans* (●), *Hypoplectrus chlorurus* (●), *Hypoplectrus guttavarius* (●), *Hypoplectrus indigo* (●), *Hypoplectrus nigricans* (●) and *Hypoplectrus puella* (●), from 35 survey transects covering a total of 14 000 m² across 16 inner (●) and outer (●) reefs off La Parguera, Puerto Rico. [Reefs (□) from UNEP-WCMC, WorldFish Centre, WRI, TNC (2010), <http://data.unep-wcmc.org/datasets/1>].

turbidity regimes might play an important, but previously overlooked role in this context.

MATERIALS AND METHODS

Fieldwork was conducted under the Institutional Animal Care and Use Committee (IACUC) protocol 2017-0101–2020-2 and the Puerto Rico Departamento de Recursos Naturales y Ambientales research permit #2016-IC-127 (E) between 13 and 24 March 2017 on 16 reefs in the vicinity of La Parguera, Puerto Rico (Fig. 1), targeting the same reefs surveyed by Aguilar-Perera (2003).

TRANSECT SURVEYS

Hamlet population densities and relative abundances were estimated using scuba visual censuses. Belt transects were preferred over the roaming surveys adopted by Aguilar-Perera (2003) since they provide standardized population density estimates (*i.e.* number of individuals per unit of reef area) that can be compared across time and space and also used to estimate population

sizes (Puebla *et al.*, 2009, 2012b). Yet hamlet densities are quite low in La Parguera, resulting in a large proportion of empty 25×2 m transects (Aguilar-Perera, 2003). In order to address this limitation, 100×4 m transects were adopted instead, following the approach used in previous hamlet surveys (Puebla *et al.*, 2007, 2008, 2009, 2012b), resulting in an eightfold increase of the area surveyed per transect (400 m^2 v. 50 m^2 for 25×2 m transects). Briefly, two divers swam in parallel a few feet above the reef with each diver counting all the hamlets observed within 2 m on each side of a 100 m transect tape. Fishes swimming across the transect tape were signalled to avoid counting the same fish twice. Coral-reef habitat was specifically targeted for the transects (*i.e.* avoiding sandy or seagrass areas) and an effort was made to cover a variety of depths and reef zones (*e.g.* reef slope v. reef flat), but the exact location of each transect was randomly chosen. An effort was made to broadly match the sampling effort of Aguilar-Perera (2003) and avoid comparatively under or over-sampling, with also a broadly similar proportion of surveys conducted in the inner v. outer reefs.

DATA ANALYSES

Densities (number of fish 1000 m^{-2} of reef) and hamlet relative abundances (%) were estimated for each species, reef site, reef type (inner v. outer reefs) and overall. Similar data were recompiled from Aguilar-Perera (2003)'s raw species counts (it is noted that some minor numerical errors were found in the total counts in Aguilar-Perera, 2003; (Table I), hence the relative abundances reported here differ slightly from those in the original paper).

Differences in relative abundances were tested with permutational analysis of variance (PERMANOVA; Anderson 2001) with 1999 permutations per test and visualized using non-metric multidimensional scaling as implemented in the vegan package in R (Oksanen *et al.*, 2017; www.r-project.org), using the Bray-Curtis measure of ecological distance in both cases (Bray & Curtis, 1957). This analysis was done at the reef level, *i.e.* considering relative abundances per reef (not per transect). Differences between the inner and outer reefs were first tested and given the significant outcome (see Results) changes in hamlet relative abundances between 2000 (Aguilar-Perera, 2003) and 2017 (this study) were tested for the inner and outer reefs separately. Hamlet diversity in the inner and outer reefs for the years 2000 (Aguilar-Perera, 2003) and 2017 were estimated using the effective number of species of the first order, corresponding to the exponential of the Shannon entropy and referred from here on as the effective number of species (Hill, 1973; Jost, 2006). Differences in diversity between 2000 (Aguilar-Perera, 2003) and 2017 were tested for the inner and outer reefs separately with a Mann-Whitney *U*-test and finally the depth distribution of *H. chlorurus* was tested for significant differences between shallow (<5.5 m) and deep (≥ 5.5 m) sections of the inner reefs using a χ^2 -test following Aguilar-Perera (2003). This test was not repeated for the other species due to the relatively low number of sightings.

RESULTS

TRANSECT SURVEYS

A total of 35 non-overlapping transects were conducted, covering an area of $14\,000 \text{ m}^2$ across 16 reefs at depths ranging between 2 and 18 m (Table I). One hundred and seventeen hamlets from seven species were sighted within the transects, providing an overall hamlet density estimate of 8.4 ± 1.5 fish 1000 m^{-2} of reef (mean \pm S.E.). The most abundant species by far was *H. chlorurus*, representing 80.3% of all hamlets seen, followed by the butter hamlet *Hypoplectrus unicolor* (Walbaum 1792), 7.7% and the barred hamlet *Hypoplectrus puella* (Cuvier 1828), 6.0%. The shy *Hypoplectrus guttavarius* (Poey 1851), *H. indigo*, black *Hypoplectrus nigricans* (Poey 1851) and yellowbelly *Hypoplectrus aberrans* (Poey 1868) hamlets were rare, with only one or two individuals seen over all transects. No other hamlet species were sighted outside of the transects.

TABLE I. Hamlet counts, population densities and relative abundances from 35 survey transects of 400 m² each covering a total of 14 000 m² of reef across 16 reefs off La Parguera, Puerto Rico, in March 2017. Data from 2000 recompiled from Aguilar-Perera (2003)

Reef	Latitude N°	Longitude W°	Depth (m)	<i>H. chlorurus</i>	<i>H. unicolor</i>	<i>H. puella</i>	<i>H. guttavarius</i>	<i>H. indigo</i>	<i>H. nigricans</i>	<i>H. aberrans</i>	Total count	Population density (fish 1000 m ⁻²)	Relative abundance (%)
Inner reefs													
López kay	17-965	-67-056	3-4	10	0	0	0	0	0	0	10	25	8.5
López kay	17-965	-67-056	3-4	6	0	0	0	0	0	0	6	15	5.1
La gata	17-959	-67-039	7-9	3	0	0	0	0	0	0	3	8	2.6
La gata	17-959	-67-039	4-0	4	0	1	0	0	0	0	5	13	4.3
Mario	17-953	-67-056	5-5	0	0	0	0	0	0	0	0	0	0.0
Mario	17-953	-67-056	4-0	2	0	0	0	0	0	0	2	5	1.7
Mario	17-953	-67-056	1-8	0	0	0	0	0	0	0	0	0	0.0
Mario	17-953	-67-056	3-7	15	0	0	0	0	0	0	15	38	12.8
San Cristóbal	17-938	-67-068	6-7	0	1	0	0	0	0	0	1	3	0.9
San Cristóbal	17-938	-67-068	2-1	3	0	0	0	0	0	0	3	8	2.6
San Cristóbal	17-938	-67-068	2-7	5	0	0	0	0	0	0	5	13	4.3
La palma	17-958	-67-058	4-6	10	0	0	0	0	0	0	10	25	8.5
La palma	17-958	-67-058	4-6	7	0	0	0	0	0	0	7	18	6.0
Enrique	17-955	-67-053	4-3	8	0	0	0	0	0	0	8	20	6.8
Media luna	17-940	-67-051	4-6	3	0	1	0	0	0	0	4	10	3.4
Media luna	17-940	-67-051	4-0	3	0	0	0	0	0	0	3	8	2.6
Las Pelotas	17-957	-67-070	6-1	1	0	0	0	0	0	0	1	3	0.9
Las Pelotas	17-957	-67-070	3-0	1	0	0	0	0	0	0	1	3	0.9
Turrumote	17-934	-67-019	9-1	0	1	1	0	0	0	0	2	5	1.7
Turrumote	17-934	-67-019	4-6	0	0	0	0	0	0	0	0	0	0.0
Turrumote	17-934	-67-019	12.8-2.1	1	0	0	0	0	0	0	1	3	0.9
Turrumote II	17-928	-66-974	12.8	5	0	0	0	0	0	0	5	13	4.3
Turrumote II	17-928	-66-974	5-8	5	1	0	0	0	0	0	7	18	6.0
Pinnacles	17-970	-67-046	13-7	0	0	2	0	0	0	0	2	5	1.7
Total count				92	3	5	0	1	0 ^a	0	101	10.5 ± 1.9	
Population density (fish 1000 m ⁻² of reef, mean ± S.E.)				9.6 ± 0.8	0.3 ± 0.1	0.5 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	< 0.1 ^a	0.0 ± 0.0			86.3
Total relative abundance (%)				91.1	3.0	5.0	0.0	1.0	< 1 ^a	0.0			86.9
Total relative abundance Aguilar-Perera (2003) (%)				58.2	5.9	10.5	0.0	7.2	10.5	7.8			

TABLE I. Continued

Reef	Latitude N°	Longitude W°	Depth (m)	<i>H. chlorurus</i>	<i>H. unicolor</i>	<i>H. puella</i>	<i>H. guttavarius</i>	<i>H. indigo</i>	<i>H. nigricans</i>	<i>H. aberrans</i>	Total count	Population density (fish 1000 m ⁻²)	Relative abundance (%)
Outer reefs													
Black Wall	17-885	-67-016	18-0	0	0	0	0	0	0	0	0	0	0-0
Black Wall	17-885	-67-016	18-0	0	0	0	0	0	0	0	0	0	0-0
Forest	17-892	-67-014	13-4	0	0	0	0	1	0	0	1	3	0-9
Forest	17-892	-67-014	13-4	0	0	0	2	0	0	0	2	5	1-7
Outer reef 1	17-895	-67-017	15-8	0	1	0	0	0	1	0	2	5	1-7
Outer reef 1	17-895	-67-017	15-8	1	0	0	0	0	0	0	4	10	3-4
Outer reef 2	17-890	-67-018	15-5	0	1	0	0	0	0	0	1	3	0-9
Outer reef 2	17-890	-67-018	15-5	0	0	0	0	0	0	0	0	0	0-0
Outer reef 3	17-891	-67-029	15-2	0	2	0	0	0	1	0	3	8	2-6
Outer reef 3	17-891	-67-029	15-2	1	0	0	0	0	0	0	1	3	0-9
Outer reef 3	17-891	-67-029	15-2	0	1	0	0	0	0	1	2	5	1-7
Total count				2	6	2	2	1	2	1	16	3.6 ± 1.0	
Density (indiv. 1000 m ⁻² of reef, mean ± S.E.)				0.5 ± 0.1	1.4 ± 0.2	0.5 ± 0.1	0.5 ± 0.2	0.2 ± 0.1	0.5 ± 0.1	0.2 ± 0.1			13-7
Total relative abundance (%)				12-5	37-5	12-5	12-5	6-3	12-5	6-3			13-1
Total relative abundance Aguilar-Perera (2003) (%)				0-0	21-7	60-9	0-0	0-0	0-0	17-4			
Overall													
Total count				94	9	7	2	2	2	1	117	8.4 ± 1.5	
Density (indiv. 1000 m ⁻² of reef, mean ± S.E.)				6.7 ± 0.6	0.6 ± 0.1	0.5 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0			100
Relative abundance (%)				80-3	7-7	6-0	1-7	1-7	0-7	0-9			100
Total relative abundance Aguilar-Perera (2003) (%)				50-6	8-0	17-0	0-0	6-3	9-1	9-1			100

^aSighted outside of the transects on the inner reefs.

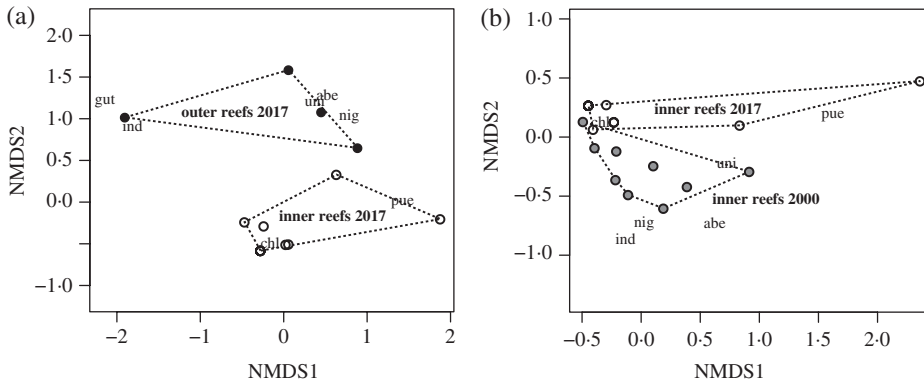


FIG. 2. Non-metric multidimensional scaling (NMDS) of *Hypoplectrus* spp. communities on 16 reefs off La Parguera, Puerto Rico. (a) Comparison between the inner (○) and outer (●) reefs (2017) and (b) comparisons among inner reefs in the years 2000 [Aguilar-Perera, 2003 (●)] and 2017 (○). Each data point represents one reef; species abbreviations indicate the direction (from the centre of the plot) in which each species drives the community: abe, *Hypoplectrus aberrans*; chl, *H. chlorurus*; gut, *H. guttavarius*; ind, *H. indigo*; nig, *H. nigricans*; pue, *H. puella*; uni, *H. unicolor*.

There was a significant difference in relative abundances between the inner and outer reefs [Fig. 2(a); PERMANOVA $P < 0.01$]. The inner reefs were dominated by *H. chlorurus* (91.1% of all hamlets seen) followed by *H. puella* (5.0%) and *H. unicolor* (3.0%) and *H. indigo* was rare (1.0%). No other species was sighted within the transects, but it is noted that *H. nigricans* was observed outside of the transects on the inner reefs, implying presence on these reefs at a density < 0.1 fish 1000 m^{-2} . The outer reefs were dominated by *H. unicolor* (37.5% of all hamlets seen) followed by *H. chlorurus*, *H. puella*, *H. nigricans* and *H. guttavarius* (12.5% each) and finally *H. indigo* and *H. aberrans* (6.3% each). No other species was sighted outside of the transects on these reefs. The difference in community composition between the inner and outer reefs was accompanied by a significant difference in density, with an average of 10.5 ± 1.9 v. 3.6 ± 1.0 fish 1000 m^{-2} of reef in the inner and outer reefs, respectively (mean \pm S.E., Mann–Whitney U -test $P < 0.05$).

There was a significant change in relative abundances between the years 2000 (Aguilar-Perera, 2003) and 2017 on the inner reefs [Fig. 2(b); PERMANOVA $P < 0.05$]. The most notable difference was the relative increase of *H. chlorurus*, from 58.2% in 2000 to 91.1% in 2017 at the expense of *H. nigricans* (10.5% to $< 1\%$), *H. aberrans* (7.8 to 0%) and *H. indigo* (7.2 to 1.0%).

There was a marginally significant change in relative abundances between 2000 and 2017 on the outer reefs (Supporting Information Fig. S1; PERMANOVA $P = 0.05$), but it should be noted that this result is to be interpreted with caution given the low hamlet densities and counts on the outer reefs and the over-dispersion of the 2017 data compared with 2000 (due to the occurrence of both *H. guttavarius* and *H. indigo* in one outer reef in 2017, none of which were observed on the outer reefs in 2000). The most notable change on the outer reefs was a decrease of *H. puella* from 60.9% in 2000 to 12.5% in 2017 and an increase of *H. chlorurus* and *H. nigricans* from 0 to 12.5%. The presence of *H. guttavarius* on the outer reefs is also to be noted since this species was not reported by Aguilar-Perera (2003) in either the inner or outer reefs.

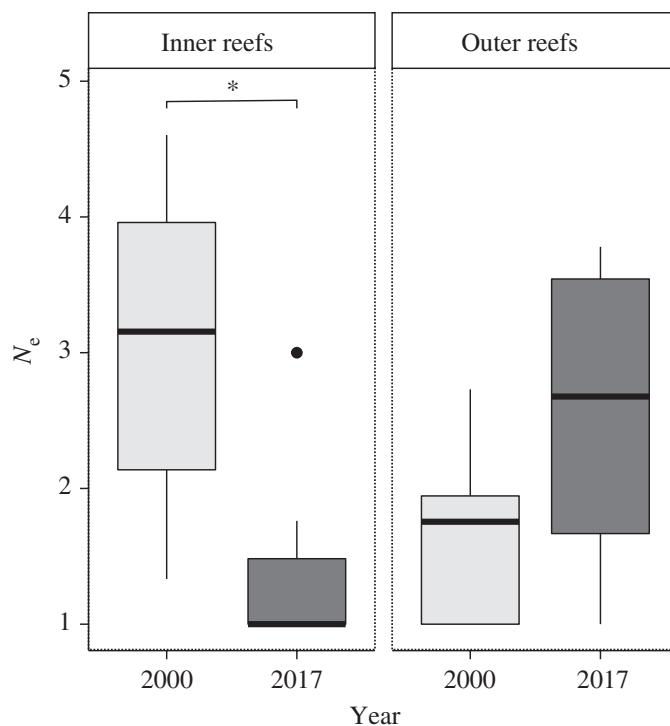


FIG. 3. First-order effective number of *Hypoplectrus* spp. (N_e ; Hill, 1973; Jost, 2006) on the inner v. outer reefs off La Parguera, Puerto Rico, for the year 2000 (Aguilar-Perera, 2003) and 2017. A significant decrease in diversity is observed on the inner reefs between 2000 and 2017 (*, Mann–Whitney U -test $P < 0.001$). —, Median; box, 25th and 75th percentiles; whiskers, largest and smallest value within 1.5 inter-quartile range from box; ●, values larger or smaller than 1.5 inter-quartile range from box.

Effective number of species on the inner and outer reefs from Aguilar-Perera's data and this study are presented in Fig. 3. The increased dominance of *H. chlorurus* on the inner reefs in 2017 compared with 2000 is reflected by a significant decrease in effective number of species, from 3.1 ± 1.1 in 2000 to 1.4 ± 0.6 in 2017 (mean \pm S.D., Mann–Whitney U -test $P < 0.01$). The opposite trend was observed on the outer reefs (1.62 ± 0.25 in 2000 v. 2.53 ± 0.66 in 2017), but this difference was not significant (Mann–Whitney U -test $P > 0.05$) and here again caution is warranted due to the low species densities and counts on the outer reefs.

Overall depth distributions of all hamlets sighted are presented in Fig. 4. *Hypoplectrus chlorurus* was significantly more abundant in the shallow (< 5.5 m) sections of the inner reefs than in the deeper areas (≥ 5.5 m, χ^2 -square test $P < 0.001$).

DISCUSSION

TEMPORAL CHANGES IN THE HAMLET COMMUNITY

Hamlet relative abundances have noticeably changed between the years 2000 and 2017 in La Parguera, with most notably a $> 30\%$ increase of *H. chlorurus* on the inner

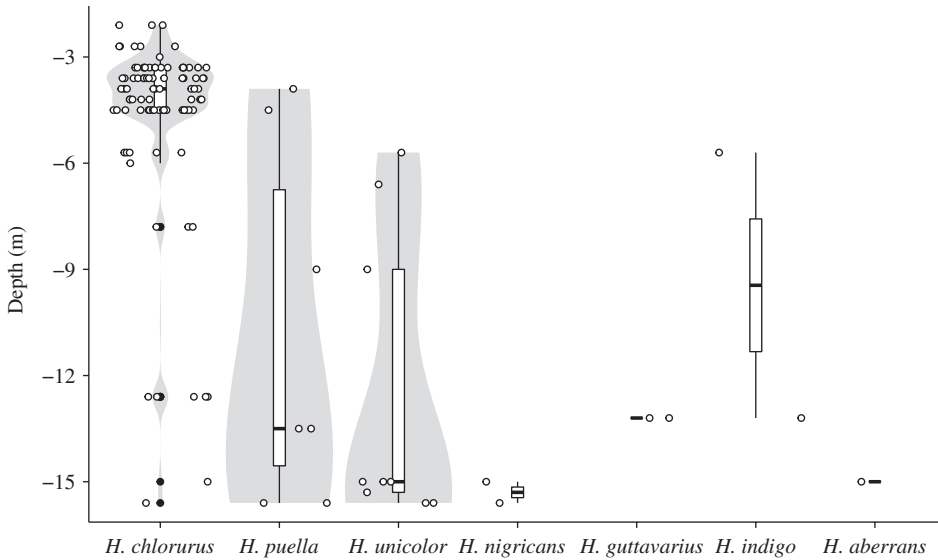


FIG. 4. Depth distribution of all hamlets sighted within 35 transect surveys covering 14 000 m² of across 16 reefs off La Parguera, Puerto Rico. —, Median; box, 25th and 75th percentiles; whiskers, largest and smallest value within 1.5 inter-quartile range from box; ●, values larger or smaller than 1.5 inter-quartile range from box; □, density distribution of the data points (○).

reefs, from 58.2% in 2000 (Aguilar-Perera, 2003) to 91.1% in 2017. Both surveys targeted the hamlets specifically, were extensive and highly replicated at the inner-reef level, conducted on the same reefs and in the same depth range. It is also noteworthy that the hamlets are quite conspicuous. Thus, differences in relative abundance between Aguilar-Perera (2003) and this study are unlikely to be due to methodological biases. The relative increase of *H. chlorurus* on the inner reefs occurred at the expense of the other, less abundant species, resulting in a significant decrease in effective number of species from 2000 to 2017.

While the relative abundance of *H. chlorurus* has increased since the year 2000, it also appears that its density has declined, implying that overall hamlet densities have declined. As mentioned above, Aguilar-Perera (2003) does not provide density estimates, only relative abundances, but densities of *H. chlorurus* in La Parguera have been estimated at 35 fish 1000 m⁻² of reef in 1988–1989 (McGehee, 1994), 18 ± 3.8 in 2005 (Bejarano & Appeldoorn, 2013) and 6.7 ± 0.6 in this study (mean \pm S.E.). These estimates are to be interpreted with caution due to differences in methodologies and reefs surveyed between the three studies, but the magnitude and consistency of the decline suggests that they reflect a real trend.

Hypoplectrus chlorurus was significantly more abundant at shallow depths on the inner reefs in 2017, with a density of 4.5 ± 0.9 fish 1000 m⁻² of reef at <5.5 m v. 2.1 ± 0.6 at ≥ 5.5 m (mean \pm S.E.). Interestingly, Aguilar-Perera (2003) did not find a significant difference in abundance of *H. chlorurus* between shallow (<5.5 m) and deep (>5.5 m) sections of the inner reefs using the same methodology. Further back in time, McGehee (1994) reports the opposite pattern in 1988–1989, with a significant increase in abundance of *H. chlorurus* with depth in La Parguera. Here again, the sequence from

higher abundances of *H. chlorurus* in deeper waters in 1988–1989 (McGehee 1994), no difference with depth in 2000 (Aguilar-Perera 2003) and higher abundances at shallow depths in 2017 suggests that the relative increase of this species on the inner reefs has been accompanied by not only a decrease in density, but also a shift in depth distribution towards shallower depths.

IMPLICATIONS

One implication from these results is that it cannot be assumed that hamlet relative abundances and densities are stable over a temporal scale of <20 years. Retrospectively, this does not come as a surprise given the dynamic nature of the coral reefs with which these fishes are tightly associated and even more so in the face of the large-scale anthropogenic influence on these ecosystems. Thus, data on hamlet relative abundances and densities need to be updated when possible and relevant. Another implication is that given the rarity and uncertain taxonomic status of some species, global databases on hamlet distributions and abundance are to be interpreted with caution [not to mention the pervasive occurrence of errors in such databases (Robertson, 2008)]. Clearly, the distribution of *e.g.* the tan hamlet (*Hypoplectrus randallorum* Lobel 2011) depends on what is considered a tan hamlet in the first place (see below). Extensive surveys are required to capture rare species, which are commonplace in the hamlet as illustrated in the present study; for four species only one or two individuals were sighted over 35 transects covering a total of 14 000 m² across 16 reefs. The hamlets appear to be able to persist at low densities, which might be due to the fact that they are simultaneously hermaphroditic (implying that two individuals can reproduce regardless of their sex). The hamlets are also able to find conspecifics on the reef when present (Puebla *et al.*, 2012a), which is confirmed here by the observation that three of the four rare species were sighted in pairs when found. Finally, given the data presented here, it is also possible that hamlet distributions might be dynamic at the regional scale over a few decades, which could have implications for the understanding of speciation in this group [population-centre hypothesis (Domeier, 1994)].

ECOLOGY

What factors could have driven the observed temporal changes in the hamlet community? The simplest explanation that comes to mind is neutral, stochastic variation. Assuming ecological equivalence among species and individuals, relative species abundances are expected to fluctuate following a process analogous to genetic drift referred to as ecological drift, with the expectation that less abundant species have a higher probability of going extinct (Hubbell, 2001). Since *H. chlorurus* was already the most abundant species on the inner reefs in 2000, it is in principle plausible that stochastic fluctuations in the other, less abundant species led to their relative decline.

Nevertheless, specific patterns in the distribution and abundance of the hamlets from La Parguera suggest that the hamlet community is not behaving neutrally, but is at least in part shaped by ecological factors. The most notable of these patterns is the difference in densities and relative abundances between the inner and outer reefs, despite the fact that these are in close geographic proximity (<12 km). The inner reefs were clearly dominated by *H. chlorurus*, which represented 91.1% of all hamlets sighted. The outer reefs had in contrast a much more even species distribution (resulting in a

higher effective number of species), with the most abundant species, *H. unicolor*, representing 37.5% of the hamlets sighted and *H. chlorurus* only 12.5%. Densities were also three times lower on the outer reefs than on the inner reefs, with an average of 3.6 ± 1.0 (mean \pm S.E.) individual hamlets 1000 m^{-2} of outer reef versus 10.5 ± 1.9 on the inner reefs all hamlet species confounded. This difference between the inner and outer reefs appears to be temporally stable since Aguilar-Perera (2003) also reports differences in relative abundance and densities between the inner and outer reefs (Supporting Information Fig. S2), with lower densities and fewer *H. chlorurus* on the outer reefs. In this context it is noted that the inner reefs are clearly structurally distinct from the outer reefs, justifying the decision to contrast these two types of reefs in both Aguilar-Perera (2003) and this study. The inner reefs are characterized by a shallow reef flat and a reef slope that goes down to c. 14 m while the outer reefs are exclusively deep (13–18 m) and characterized by a spur-and-groove formation. The outer reefs are also clear blue reefs while the inner reefs are more turbid. In addition to differences in hamlet communities between the inner and outer reefs, the non-random depth distribution of *H. chlorurus* also suggests a role for ecology in shaping its distribution.

If ecology drove the observed changes in the hamlet community from La Parguera, what ecological factors in particular might be involved? So far ecologists have failed to identify clear ecological differences among hamlet species. Sympatric species are commonly found in the same habitat, often within sight of each other. The hamlets also have broadly similar diets as revealed by stomach-content and stable-isotope analysis in a variety of locations across the wider Caribbean, including La Parguera, except for *H. indigo* that appears to feed mostly on fishes (Randall, 1967; Whiteman *et al.*, 2007; Holt *et al.*, 2008; G. M. Serviss, unpubl. data). This being said, broad differences in distribution and abundances between reef sections and types have been noted (Thresher, 1978; Fischer, 1980a; McGehee, 1994). Regarding *H. chlorurus* in particular, significant differences have been found in its distribution in Deep Water Cay (Grand Bahama) with higher abundances on the shallow *Acropora cervicornis* zone (G. M. Serviss, unpubl. data). This resonates with the observation that *H. chlorurus* was often (although not exclusively) found in association with *A. cervicornis* in La Parguera.

TURBIDITY

One intriguing point to be noted about *H. chlorurus* is that an extensive study on seawater turbidity and fish communities conducted between February and October 2005 on 21 reefs off La Parguera indicated that it is the only fish together with the sharknose goby *Elacatinus evelynae* (Böhlke & Robins 1968) that shows a positive association with turbidity, with higher abundances on more turbid reefs (Bejarano & Appeldoorn, 2013). In addition, sediment cores indicate that sedimentation of terrestrial origin has significantly increased over recent decades on the inner reefs in La Parguera (Ryan *et al.*, 2008), providing a parallel between changes in turbidity regimes and the relative abundance of *H. chlorurus*. Ryan *et al.*, (2008) also report that sedimentation rates are higher on the inner reefs ($0.47 \pm 0.02 \text{ cm year}^{-1}$) than on the outer reefs ($0.19 \pm 0.01 \text{ cm year}^{-1}$, mean \pm S.D.), once more providing here a parallel between turbidity and relative abundances of *H. chlorurus* on the inner v. outer reefs. This pattern is consistent with the observation that the outer reefs were in clear, open blue waters while the inner reefs were noticeably murkier. It has been noted before that different hamlets tend to associate with different turbidity regimes (Thresher, 1978), but the hypothesis that

water turbidity *per se* could constitute an important ecological factor in shaping hamlet communities has not been evaluated in depth.

If *H. chlorurus* responds positively to turbidity, an increase in turbidity on the inner reefs over recent decades would be expected to result in higher relative abundances of this species on these reefs, as observed here. Water turbidity is also negatively correlated with coral cover ($r^2 = 0.50$; Bejarano & Appeldoorn, 2013). Therefore, a decrease in coral cover associated with the increase in sedimentation rates on the inner reefs would be expected to result in a decrease in hamlet densities, as observed here. One point to consider is seasonality since this survey was conducted during the dry season while Aguilar-Perera's survey as well as Bejarano & Appeldoorn's study on turbidity were conducted over both the dry and rainy seasons. Relative abundances are not expected to vary seasonally at the reef level since the hamlets are reef-associated organisms and as such do not move between reefs after settlement (which would imply swimming over extensive non-reef areas). In addition, transect and tagging data over several seasons at other sites in Panama and Belize (Puebla *et al.*, 2007, 2012a) indicate that hamlet communities do not change substantially at this time scale and that individuals are long-lived (several years) and quite sedentary. This being said, it is possible that the distribution of individuals within reefs might vary seasonally and the data on depth distribution are therefore to be considered with caution.

AGGRESSIVE MIMICRY

Several hamlets, including *H. chlorurus*, have been proposed as aggressive mimics, whereby the predatory hamlets (the putative mimics) gain an advantage in the approach and attack of prey by resembling and sometimes actively associating with other non-predatory fishes (the putative models; Randall & Randall, 1960; Thresher, 1978; Puebla *et al.*, 2007), a hypothesis that is still debated (Robertson, 2013). One prediction generated by this hypothesis is that the distribution of *H. chlorurus* would be expected to match the distribution of its putative model, the yellowtail damselfish *Microspathodon chrysurus* (Cuvier 1830) (Thresher, 1978). This does not appear to be the case in La Parguera since *M. chrysurus* shows a negative association with water turbidity (*i.e.* more abundant on less turbid reefs), the exact opposite of the pattern found for *H. chlorurus* (Bejarano & Appeldoorn, 2013). This lack of association between putative-model and mimic distributions does not necessarily invalidate the aggressive mimicry hypothesis, but it is noted that specific aggressive mimicry behaviours were not observed in the hamlets from La Parguera during this survey.

COLOUR PATTERN VARIATION

The hamlets from La Parguera form discrete phenotypic clusters that correspond to described species, but the taxonomic status of *H. nigricans* is still to be clarified. *Hypoplectrus nigricans* from La Parguera matches the description by Aguilar-Perera (2004) and resembles *H. nigricans* from Barbados (Puebla *et al.*, 2008), but differs from *H. nigricans* from Panama, Belize and Mexico that is smaller, darker, with short and round pelvic fins (Aguilar-Perera, 2004; Puebla *et al.*, 2008). This suggests that this nominal species might in fact constitute a species complex as proposed by Aguilar-Perera (2004); Puebla *et al.*, (2008) and Lobel (2011). It is also noted that

some individuals were tan coloured, but differed from the recently described tan hamlet *H. randallorum* in lacking the spots on the nose, at the base of the pectoral fin and on the upper part of the caudal peduncle that are diagnostic of this species (Lobel, 2011). Additional data from other locations are needed to clarify the taxonomic status of *H. nigricans* and establish whether or not there is another tan hamlet species.

In addition, a few individuals appeared intermediates between species, notably between *H. chlorurus* and *H. nigricans* and *H. chlorurus* and *H. puella*, respectively. Yet it is important to underscore that such individuals were rare, representing <2% of all hamlets sighted within and outside of transects. Considering that hybrid pairings and spawnings have been observed in natural populations (Fischer, 1980a; Barreto & McCartney, 2007; Puebla *et al.*, 2007, 2012a), that there do not appear to be intrinsic post-fertilization barriers between species in the hamlets (Whiteman & Gage 2007) and that in the only case where hybrids were bred in aquaria, they appeared intermediate between parental species (Domeier, 1994), it is plausible that such intermediate individuals might be hybrids.

PERSPECTIVES

The hypothesis that hamlet species might respond differentially to turbidity is intriguing and deserves further evaluation since turbidity correlates with a variety of ecological factors whose effect on hamlet communities need to be disentangled. One possibility is that hamlets might differ in their visual sensitivities, which is currently being investigated using whole-genome analysis with a particular focus on opsin genes. Whole genomes will also allow testing whether individuals of intermediate appearance are actually hybrids and if so what type of hybrids (F_1 , F_2 , backcross, ...) and also clarify the taxonomic status of *H. nigricans*.

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Supporting Information

Supporting Information may be found in the online version of this paper:

FIG. S1. Non-metric multidimensional scaling (NMDS) of hamlet communities on the outer reefs off La Parguera, Puerto Rico, for the years 2000 (Aguilar-Perera, 2003) and 2017. The over-dispersion of the 2017 data compared with 2000 on the first NMDS axis is due to the occurrence of both *H. guttavarius* and *H. indigo* on one outer reef in 2017, none of which were observed in 2000.

FIG. S2. Non-metric multidimensional scaling (NMDS) of hamlet communities on 16 inner (○) and outer (●) reefs off La Parguera, Puerto Rico, for the year 2000 (Aguilar-Perera, 2003). Each circle represents one reef; species abbreviations indicate the direction (from the center of the plot) in which each species drives the community: abe, *Hypoplectrus. aberrans*; chl, *H. chlorurus*; gut, *H. guttavarius*; ind, *H. indigo*; nig, *H. nigricans*; pue, *H. puella*; uni, *H. unicolor*.

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