Received: 30 March 2016 | Revised: 21 January 2017 | Accepted: 14 February 2017
DOI: 10.1002/aqc.2770

WILEY

RESEARCH ARTICLE

Archipelago Los Roques: A potential baseline for reef fish assemblages in the southern Caribbean

Simon Elise[1,2] | Isabel Urbina-Barreto[1] | Hazael Boadas-Gil[3] | Miguel Galindo-Vivas[4] | Jesús Ernesto Arias-González[5] | Sergio Ricardo Floeter[6] | Alan Marc Friedlander[7,8] | Michael Nemeth[9] | Michel Kulbicki[10]

[1] UMR 9220 ENTROPIE - Université de la Réunion, La Réunion, France
[2] NortekMed, Toulon, France
[3] Fundación de Investigaciones Marinas Francisco de Miranda, Archipiélago Los Roques, Venezuela
[4] Independent, Dominican Republic
[5] Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México
[6] Federal University of Santa Catarina, Florianópolis, Brazil
[7] Pristine Seas, National Geographic Society, Washington, DC, USA
[8] Fisheries Ecology Research Lab, University of Hawai'i at Mānoa, Honolulu, Hawai'i, USA
[9] University of Puerto Rico, Mayagüez, Puerto Rico
[10] UMR 9220 ENTROPIE - IRD - Labex Corail - Université de Perpignan, France

Correspondence
Simon Elise, NortekMed – 67, avenue Irène et Frédéric Joliot-Curie - 83078 Toulon Cedex 9, France.
Email: simon_elise@hotmail.com

Abstract

1. Despite increasing policies of protection, few localities in the Caribbean remain spared from human impacts. These lightly affected areas can better reflect the past composition of reef fish assemblages and provide baseline information about the natural factors driving fish distributions in the region.
2. Reef fish assemblage structures were analysed in 21 Caribbean fished areas and marine protected areas (MPAs) along a gradient of distance to the nearest major market place. Assemblage structures by size and by trophic group were significantly related to the distance to market.
3. Relationships of reef fish life-history traits, families, and vulnerability indicators were examined with the seascape and the benthic composition at Los Roques Archipelago, the most isolated MPA in the analysis. Factors linked to seascape features were more important than benthic composition or human activities in explaining fish assemblage structure.
4. Wave exposure was the most influential seascape metric. Exposed habitats were dominated by octocorals and sponges. More sheltered habitats were characterized by high coral cover, while leeward sites were characterized by steep slopes with close proximity to deeper water.
5. Exposed habitats were mostly occupied by unspecialized fish species. Piscivore densities were high at south and south-west sites, and were likely related to the large concentrations of planktivorous fishes found there. South and south-west sites experience full oceanic conditions, and supported the highest species richness and densities within the archipelago.
6. Los Roques National Park is one of the oldest and most remote Caribbean MPAs. Its fish assemblage structure is healthier than other fished or protected areas, with higher species richness, higher density of piscivores, and an abundance of large species. Predator–prey relationships provided additional evidence that Los Roques reef fish assemblage presented specific characteristics.
7. The main patterns observed in this study represent a baseline for assessing reef fish assemblages elsewhere in the southern Caribbean.

KEYWORDS

benthos, coral, ecological status, fishes, life-history traits, marine protected area, overfishing, reef, Venezuela, vulnerability indicators

1 | INTRODUCTION

Understanding the spatial distribution of fishes on coral reefs is a fundamental step in adopting effective conservation policies (Bellwood & Hughes, 2001; Gaston, 2000), and requires information from complementary studies spanning a wide range of scales, from a few metres to thousands of kilometres. At broad spatial scales, studies on species distributions have delineated biogeographical entities around the world (Floeter et al., 2008; Kulbicki et al., 2013). A number of researchers have tried to identify the factors involved in variations in species richness and/or abundances at large spatial scales and have identified latitude and longitude (Bellwood & Hughes, 2001; Bouchon-Navaro, Bouchon, Louis, & Legendre, 2005), connectivity (McArthur & Wilson, 1967; Parravicini et al., 2013), pelagic larval duration (Luiz et al., 2013; Mora et al., 2012), potential habitat availability (Bellwood & Hughes, 2001; Parravicini et al., 2013; Sandin et al., 2008), coastal length and sea surface temperature (Parravicini et al., 2013) as factors driving these variations. These mostly geographical factors can provide predictions of species richness at broad spatial scales but are not helpful in predicting local fish assemblage composition (Mellin, Bradshaw, Meekan, & Caley, 2010).

Bio-physical characteristics (particularly reef type, reef area, water motion, depth, substrate cover, and complexity) are generally considered the most important factors structuring reef fish assemblages at smaller spatial scales (Arias-González, Núñez-Lara, Rodríguez-Zaragoza, & Legendre, 2011; Floeter, Krohling, Gasparini, Ferreira, & Zalmon, 2007; Friedlander & Parrish, 1998; Gratwicke & Speight, 2005; McGehee, 1994; Mejía & Garzón-Ferreira, 2000; Rousseau, 2010). In the western Atlantic, these bio-physical characteristics are known to influence the presence or absence of certain fish species (Bouchon-Navaro et al., 2005), species richness and abundance (Arias-González et al., 2011; Floeter et al., 2007; Gratwicke & Speight, 2005; Luckhurst & Luckhurst, 1978) and beta diversity (Arias-González, Legendre, & Rodríguez-Zaragoza, 2008; Acosta-González et al., 2013). The influence of environmental conditions on fish functional structures (considering the life-history traits that determine trophic, mobility, and schooling guilds, among others) is less documented. Mejía and Garzón-Ferreira (2000) highlighted significant relationships between trophic categories and habitats (i.e. geomorphological zones), and found greater differences in the structure of the fish assemblages between habitats within four atolls of the San Andrés Archipelago than between distant islands. In the same way, Arias-González et al. (2008) showed greater differences between habitats within the same reef than for the same habitat among distant reefs for fishes and benthic community composition along the Mesoamerican reef system. Several authors (Dominici-Arosemena & Wolff, 2005; Floeter et al., 2007) have shown that wave exposure was an important factor in explaining differences in the trophic structure and distribution of particular mobility classes of reef fishes. Bradbury and Young (1981) defined exposure as the main driver of the benthic assemblage on the Great Barrier Reef. Relationships between reef fish assemblage characteristics and benthic factors have been widely studied, and live coral cover, topographic complexity/habitability, macroalgal cover, octocoral cover, sponge cover have been shown to influence fish assemblage structure (Friedlander, Nowlis et al., 2003; Rousseau, 2010).

Anthropogenic factors may, however, locally prevail over environmental factors and affect the relative composition of fish assemblages, especially in areas close to the coast where human presence has been important in the Caribbean for decades and even centuries (Jackson et al., 2001; Núñez-Lara, Arias-González, & Legendre, 2005). Caribbean reefs have been suffering direct anthropogenic disturbances, including: overfishing (Hughes, 1994; Jackson et al., 2001), pollution (Bozec, Acosta-González, Núñez-Lara, & Arias-González, 2008; DeGeorges, Goreau, & Reilly, 2010; Mora, 2008), coastal development, and climate change. These perturbations have certainly contributed to the region-wide decline in Caribbean coral reef fish density shown by Paddack et al. (2009), with a particularly significant effect on carnivores, invertebrate feeders, and herbivores. These findings were partially confirmed by Stallings (2009) who demonstrated that large predatory reef fishes are nearly absent from most Caribbean locations with high human population densities.

In response to these impacts, the implementation of marine protected areas (MPAs), especially on coral reefs, has greatly increased over the past 20 years (Knowles et al., 2015; Toropova, Meliane, Laffoley, Matthews, & Spalding, 2010). While a number of factors controlling the effectiveness of MPAs have been identified (e.g. size, level of protection; Edgar et al., 2014; Kaplan et al., 2015; Mesnildrey, Gascuel, & Le Pape, 2013), it has only been recently that remoteness has been identified as a factor enhancing coral reef condition and functioning in MPAs (D'agata et al., 2016; MacNeil et al., 2015; Maire et al., 2016). Mora et al. (2006) considered MPA management performance particularly low in the Caribbean. Conversely, in a study including several Caribbean MPAs, Halpern (2003) showed that marine reserves led to significant increases in density, biomass, individual size, and diversity for the overall assemblages and for each functional group within these assemblages. Some important factors influencing the effectiveness of MPAs in the Caribbean have been identified, notably the magnitude and connectivity of coral reefs with nursery habitats (mangroves and seagrass beds; Nagelkerken, Grol, & Mumby, 2012) and the age and the size of the MPA (Edgar et al., 2014; Halpern, 2003).

Los Roques National Park is the largest coral reef MPA in Venezuela (221 120 ha) and it has been in existence since 1972, making it one of the oldest MPAs in the Caribbean. Los Roques NP contains large areas of seagrass, macroalgal beds, and mangroves distributed throughout the archipelago (Méndez-Baamonde, 1978). For these reasons, this MPA presents an interesting case for establishing a baseline on the distribution of species and functions among habitats, in terms of richness and density, for the southern Caribbean.

This study proposes the evaluation of the relative importance of local anthropogenic, seascape, and environmental factors on the functional structure of the reef fish assemblages within Archipelago Los Roques. A focus on the spatial distribution of vulnerability indicators (abundance of rare species, abundance of monospecific functional entities, and abundance of species with reduced geographical range) complements this approach and provides valuable information about the effectiveness of this MPA. This work also provides a comparison of the functional structure of reef fish assemblages over a wide range of fished and protected Caribbean localities. The aims of the present study are to:

1. determine the best characteristics for a baseline of Caribbean reef fishes;
2. identify the main reef fish assemblages and associated habitats in Archipelago Los Roques, and evaluate the major patterns explaining their distribution;
3. compare the structure of Los Roques fish assemblage to fished areas and other MPAs of the Caribbean to evaluate its quality and assess its potential in defining a baseline.

The results of this study should provide for a better understanding of the relation between the functional structure of reef fish assemblages and their environmental conditions, as well as contributing to a baseline on what a lightly impacted reef fish assemblage may look like in the southern Caribbean.

2 | METHODS

2.1 | Study system

Archipelago Los Roques National Park was established in 1972 and comprises 221 120 ha, approximately 10 000 ha of which consist of coral reef habitat. The park is located at the southern edge of the Caribbean Sea (11°44′ – 11°58′ N, 66°32′ – 66°57′ W), 135 km north of the Venezuelan coast (Figure 1). The archipelago is spread over a wide volcanic platform, covered by a thick sedimentary layer (Méndez-Baamonde, 1978). On this oceanic platform, two narrow barrier reefs, the east reef and south reef (~ 20 and 30 km long, respectively) partially enclose a shallow lagoon with a mean depth of 4 m. By protecting the interior of the archipelago from the direct influence of oceanic waves and currents (dominant winds blow from east and north-east), the eastern barrier facilitated the formation of 42 cays with fringing reefs, multiple sand and coral banks, and important areas of mangroves, spread around the lagoon (Méndez-Baamonde, 1978; Figure 1). The lagoon floor is predominantly composed of bare sand with large expanses of seagrass and/or macroalgal beds, with numerous patch reefs. Archipelago Los Roques is considered to be among the least affected coral reef systems in the Caribbean (Kramer, 2003; Posada, Villamizar, & Alvarado, 2003). In fact, the archipelago lies outside the path of most hurricanes and benefits from its remote location from the continental coast, far from land runoff, sewage, and major anthropogenic disturbances. In spite of increasing development in the past 20 years, tourism and fishing (especially for spiny lobsters, which yields 90% of Venezuela's production) are restricted by the park authorities. Spearfishing was banned in 1972 and the use of nets in 1994. The archipelago supports a small human population of around 1500 inhabitants (~ 0.7 inhabitants km^{-2} of MPA), mostly concentrated on the north-eastern island of Gran Roque and on the nearest surrounding cays.

2.2 | Background

The fish fauna of Los Roques comprises about 370 species, including 21 species of sharks (Cervigón & Ramírez-Nahím, 2003; Tavares, 2005). Only one other study of the reef fish assemblages has been conducted at the scale of the archipelago (Posada et al., 2003). These authors followed the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Version 2.2 fish protocol (underwater visual censuses along transects of 2 m wide × 30 m long; see Kramer & Lang, 2003). They observed 59 of the 70 fish species listed by this protocol for the entire Caribbean and concluded that the reef fish assemblages in the archipelago were in a ‘healthy state’, with highly diverse and abundant populations, some large-sized species, and a good balance between herbivores and carnivores (Posada et al., 2003). Nevertheless, they found fewer commercially important carnivorous fishes close to Gran Roque and the eastern barrier where most of the human population of the archipelago lives. The authors speculated that the decline in carnivorous fishes was related to natural differences associated with

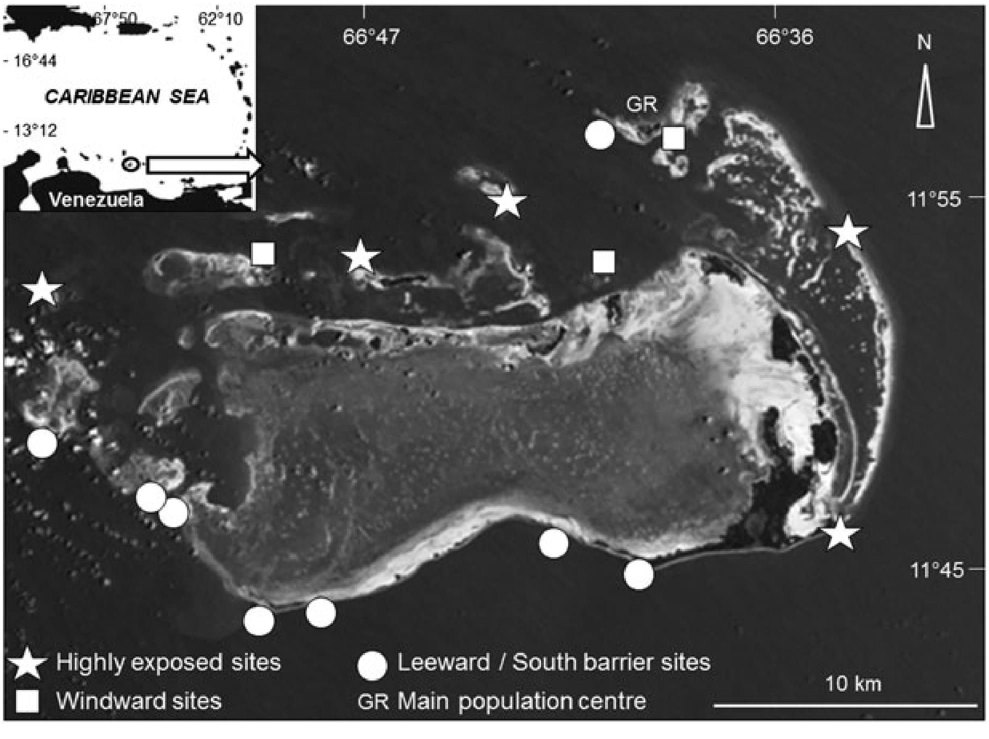


FIGURE 1 Archipelago Los Roques National Park (adapted from a satellite photography by Landsat 7 with a resolution of 30 m); GR: gran Roque, main population Centre; stars highly exposed sites; squares – more sheltered windward fringing reef sites; circles – leeward fringing reef and southern barrier sites

geographic location or depth, or, alternatively, the result of human activities (Posada et al., 2003).

In the corresponding benthic AGRRA assessment, Villamizar, Posada, and Gomez, (2003) considered that coral reefs were globally healthy in 1999, but diseases (Cróquer, Weil, Zubillaga, & Pauls, 2005; Villamizar, pers. com.) and a mass bleaching event in 2010 (Bastidas et al., 2012) have strongly affected coral communities during the past decade. In 1999, benthic shallow water assemblages (< 6.5 m) were dominated by partially dead colonies of *Acropora palmata*, *Porites astreoides*, and *Diploria strigosa*, whereas deeper assemblages (7.5–13.5 m) were healthier and dominated by *Oribicella faveolata*, *O. annularis*, and *Montastraea cavernosa*, except on the eastern barrier, which was dominated by partially dead colonies of *A. palmata* (Villamizar et al., 2003).

2.3 | Reef fish assemblage and benthic community sampling

The surveys were conducted in March and April 2013 and focused on coral reef formations at 10 m depth. As no detailed map of the benthic substratum was available for the archipelago, manta tows were performed around numerous cays to identify areas with ≥50% of hard bottom cover and a sufficient spatial extent to allow the deployment of three transects. Sixteen sites were selected across the archipelago (Figure 1) in each of which three transects were sampled. The mean depth (± SD) of the transects evaluated was 10.3 ± 0.8 m.

Underwater visual censuses were conducted at each site along triplicate belt transects of 2 m × 30 m laid out at 10 m depth and at least 30 m apart. Transects encompassed the entire water column from the sea floor to surface. During each census, a diver swam over the transect line identifying and counting all fishes within 1 m on either side of the central line. Highly mobile and wary species were enumerated on the first pass as the transect line was laid and all the remaining species during the second pass. All detected fishes were recorded. For reasons of dive time limitations, fish lengths could not be evaluated and biomasses were thus not calculated in this study. Although the absence of biomass data penalizes the analysis of the effectiveness of this MPA, relevant results were obtained from richness and density data.

Benthic composition was assessed along the same transects using the medium scale approach (MSA) of Clua et al. (2006). Six 5 × 5 m quadrats were evaluated on each side of the three transects (12 × 25 m^2 described for each transect). Two divers started their sampling once the fish census was completed, so as to minimize the impact of the presence of divers on the fish assemblage. Depth was measured in the centre of each of the 12 quadrats along the transect. Habitability was evaluated in each quadrat on a 1–6 scale, with 1 indicating the absence of any refuges (i.e. holes providing shelter for fishes or any other reef organisms) and 6 being the most complex reef matrix, with numerous refuges of diverse sizes. Several substrate covers (see Methods S1, Supporting information) were evaluated on each quadrat on a 1–5 scale (1: cover comprised between 1 and 10%; 2: between 11 and 30%; 3: between 31 and 50%; 4: between 51 and 75%; 5: between 76 and 100%) as defined by Clua et al. (2006).

2.4 | Los Roques reef fish data

In order to characterize the structure of the fish assemblages at Los Roques, life-history traits were compiled for each species according to the classification used in recent articles (Kulbicki, Parravicini, & Mouillot, 2015; Mellin et al., 2016; Mouillot et al., 2014; Parravicini et al., 2013). Six major traits were considered: diet, species size class, schooling, daily activity, adult home range, and height in the water column (Methods S2 and Table S1). Functional entities were defined as the combination of diet and size classes, resulting in 36 possible entities, of which 24 were represented by at least one species (Table S1). Geographic range was defined for each species, with an index based on the number of checklists where the species is known in the Atlantic (Kulbicki et al., 2013). For each of the 48 transects sampled, overall fish species richness and density, as well as relative species richness and density of each group of life-history traits, functional entity and dominant family were calculated. In addition, three vulnerability indicators were defined: abundance of rare species (species present on 1 or 2 transect(s) out of 48), abundance of monospecific functional entities (functional entities represented by only one species), and abundance of species with limited geographical range (in some sense endemic species).

2.5 | Environmental and anthropogenic influences on Los Roques reef fish assemblages

In total, 16 explanatory factors were considered in the analyses (details in Methods S1): four seascape factors (reef type, exposure, distance to shore, and distance to the nearest mangrove), two factors for the impact of human presence (distance to the main population centre (Advani, Rix, Aherne, Alwany, & Bailey, 2015) and anthropogenic pressure), along with 10 benthic factors.

Given the number of factors, their unbalanced patterns and the multiple potential interactions between them, linear models or mixed-effect models were not employed. Instead, multivariate regression trees (MRT) and cascade MRTs offer the possibility to explore relationships between multispecies fish data and environmental characteristics, with the advantage of dealing with nonlinearity of relationships between species composition and the environmental variables (De'ath, 2002). MRTs form clusters of sites chosen to minimize the dissimilarity of sites within clusters. The clusters and their dependence on the environmental data are represented graphically by a tree (De'ath, 2002).

First, two multivariate regression trees were constructed to identify the clusters representing the main reef fish assemblages and associated environments present at Los Roques, using the function ‘mvpart’ within the ‘MVPART’ package from R (R Core Team, 2014). The number of splits of the trees was limited so as to keep in the same cluster the three replicate transects corresponding to each site. The best (most accurate) MRT was selected with the minimum cross-validated relative error (De'ath, 2002). A Hellinger transformation was applied to a matrix of the abundances of all fish species by transect (Table S2), and to a second matrix of the abundances of functional entities by transect, before their use in the MRT. The Hellinger distance is calculated as a Euclidean distance on transect vectors, where the abundance values are first divided by the transect total abundance and the result is square-root transformed (Borcard, Gillet, & Legendre, 2011). Legendre and Gallagher (2001) consider that the Hellinger transformation, which gives low weights to rare species, is an appropriate transformation for community composition data when the aim is to explore the relationship between species composition and a set of explanatory factors.

Indicator species analyses (IndVal; Dufrêne & Legendre, 1997) were then used on the global MRT model to identify the most characteristic species of each assemblage identified in the first step of the analysis. The function 'MRT' within the 'MVPARTwrap' package in R (Ouellette, Legendre, & Borcard, 2012) was used in this step. Indicator species analysis takes into account species mean abundance and frequency of occurrence on the transects within each cluster. A high indicator value results when a species is both abundant and occurs in most transects within a cluster. The indicator value ranges from 0 to 1, with 1 referring to a perfect indicator species, which would be present exclusively in a single cluster, and abundant on each of its transects. A species with a high indicator value is thus characteristic of a given assemblage and associated habitat (i.e. a cluster).

The next step was to characterize the main features of the different assemblages and associated habitats (i.e. the clusters) identified. The fish assemblage structure and benthic composition were compared among clusters. Overall fish species richness and numerical density, the values of benthic factors, as well as the species richness and density of the groups of life-history traits and dominant families were calculated for each transect. These metrics were averaged by cluster and represented (± confidence intervals at $\alpha = 0.05$) on barplots. The significance of the observed differences was tested using either one-way ANOVAs or Kruskal–Wallis rank sum tests (using 'aov' or 'kruskal.test' within the 'STATS' package in R), after examining normality and homogeneity of variance for each metric. Normality was tested using a Shapiro–Wilk W test ($P = 0.05$) while a Bartlett's test ($P = 0.05$) was used to examine homogeneity of variance. Post hoc tests were also performed using either Tukey's Honestly Significant Difference (HSD) tests after ANOVAs (using 'TukeyHSD' within the 'STATS' package in R) or Dunn's multiple comparison tests after Kruskal–Wallis tests (using 'Kruskalmc' within the 'pgirmess' package in R).

Finally, the factors explaining the most significant patterns were highlighted. Among the metrics tested in the previous step, only those with the most significant variations between clusters ($P < 0.001$) were considered for the final step. For example, if the numerical density of a given group of life-history traits varied very significantly between clusters ($P < 0.001$), the abundances matrix of the species representing this group was analysed with a cascade MRT in order to identify the factors involved in these variations (Table 1). The function 'CascadeMRT' within the 'MVPARTwrap' package in R (Ouellette et al., 2012) was used. Cascade MRTs were chosen instead of standard MRTs because it was assumed that the effect of the set of benthic factors is nested within the effect of the set of seascape and anthropogenic factors (Ouellette et al., 2012). Cascade MRTs separate the explanatory power of each partition (using 'CasMRTR2' within the 'MVPARTwrap' package in R). By running trees with increasing parameter complexity (Ouellette et al., 2012), the main factors (seascape, anthropogenic, and benthic factors) responsible for the variations in the species distribution were identified. The percentage of variation explained by each of these factors in each tree was also calculated, quantifying the relative effects of local anthropogenic and environmental factors.

The same analyses were run on the vulnerability indicators abundances matrices so as to identify a potential influence of human presence. All the matrices received a Hellinger transformation before their use in the cascade MRT.

2.6 | Comparison with other Caribbean MPAs and fished areas

Similar reef fish assemblages sampling was conducted by the authors between 1998 and 2013 across the Caribbean. To homogenize these data with Los Roques data, only the transects evaluated at depths between 8 and 12 m were included in this comparison (mean ± SD = 10.0 ± 1.1 m). The dataset included 196 transects from six fished areas and 218 transects from 14 MPAs throughout the Caribbean (see Table S3). Relative species richness and density of trophic groups, size class groups, and geographic range groups (see details above in 'Los Roques reef fish data') were analysed by transect.

First, correlations between these metrics and the distance of each sampled locality to the nearest market place were examined. The distance to the nearest major market place has been highlighted as an important structuring factor for reef fish assemblages (Cinner, Graham, Huchery, & MacNeil, 2013; Maire et al., 2016) and should be considered a fundamental criterion in defining baselines. Major markets were identified as population centres with a density > 100 inhabitants km^{-2} and a total population > 100 000 inhabitants (supplementary material in Maire et al., 2016). Distances were measured on the global map of human density (available at http://sedac.ciesin.columbia.edu/data/collection/gpw-v4) using the Quantum GIS program version 2.4. Pearson's correlations values and their significance were calculated (using the function 'cor.test' within the 'STATS' package in R) for fished areas and MPAs. To estimate the protection status, spatial information on MPAs were collected from the WDPA (World Database on Protected Areas, available at http://protectedplanet.net/). Both fished areas and MPAs were homogeneously distributed along the distance gradient, from 4 to 135 km (Figure 2).

In a second step, Los Roques reef fish assemblage structure was compared with the mean structure by transect observed in MPAs and fished areas. As no variables were normally distributed, Kruskal–Wallis rank sum tests (using 'kruskal.test' within the 'STATS' package in R) and unplanned Dunn's post hoc multiple comparison tests were used to look for significant differences between assemblages structures of Los Roques, MPAs, and fished areas. Since the number of transects was different for the three groups (48, 218 and 196, respectively), Dunn's test (at $P < 0.001$) was chosen as it is appropriate for groups with unequal numbers of observations (Zar, 2010).

In a third step, the distribution of prey and predators was examined across an extended selection of Caribbean localities. Species richness and mean density of prey and predators were calculated for 10 fished localities and 21 MPAs (see localities in Table S3).

TABLE 1 Results of the cascade multivariate regression trees performed on different matrices of species abundances at Los Roques Archipelago (all species, species belonging to several groups of life-history traits, species from three dominant families and vulnerable species): percentages of variation of these matrices explained by seascape, human presence and environmental factors. Relative contributions exceeding 40% of the total of variation explained are in bold. DIST.SHORE: distance to shore; DIST.MANG: distance to mangrove; DIST.POP: distance to population center; ANTHROP.P: anthropogenic pressure; HETEROGENEITY: index of heterogeneity of the hard bottom; COSD: hard bottom cover; COCM: dead coral cover; COCV: live coral cover; OCTOCORALS: index of octocorals cover; SPONGES: index of sponges cover; MACROALGAE: index of macroalgae cover. In a few case, the analysis could not separate the percentage of variation explained by the combination of 2 factors: (a) SLOPE VALUE and HETEROGENEITY (b) OCTOCORALS and SPONGES (c) SPONGES and OCTOCORALS

	Exposure	Reef type	Dist. Shore	Dist. Mang	Dist. Pop	Anthrop. p	Habitability	Topography	Slope value	Heterogeneity	Cosd	Cocm	Cocv	Octocorals	Sponges	Macroalgae	Total explained
All species	**18.5**	10.7						4.5	4			5.7					43.4
Herbivores				11.1			1.3	0.8				**13.8**					27
Omnivores	**23.1**				11.3			9.4				8.8		3.3			55.9
Plankton feeders		11.8	13.6					6.3	11.5 (a)	3.9		13.6				6.9	67.6
Size class 1	**41**										22.4			14.1 (b)			77.5
Size class 2				**35.9**	11.9				1.1					12.6			61.5
Size class 3	17.5			11.3					12.9			7.2					48.9
Mobile species	13.9			11.5					11.4			4.9					41.7
Species schooling in large groups				9.9				**15.4**					7.8				33.1
Species schooling in medium groups	**23.6**		11.9				5.3		6.5		1.4			11			59.7
Solitary species				**26.4**			14.5										40.9
Pelagic species		10.4	13.8							5.8			8	4.2		6.3	48.5
Pomacentridae	27	17.9								6.5		2	5	6		8.2	72.6
Gobiidae	**41**										22.4			14.1 (b)			77.5
Scaridae				**18.3**	3.8								5.8	9			36.9
Rare species						2.9	**6.8**	4.2									13.9
Monospecific functional entities	**36.5**							5					1.7	17.4	14.2 (c)		74.8
Species of reduced geographical range	**23.8**		12.2						6.1		2.7			8.1			52.9

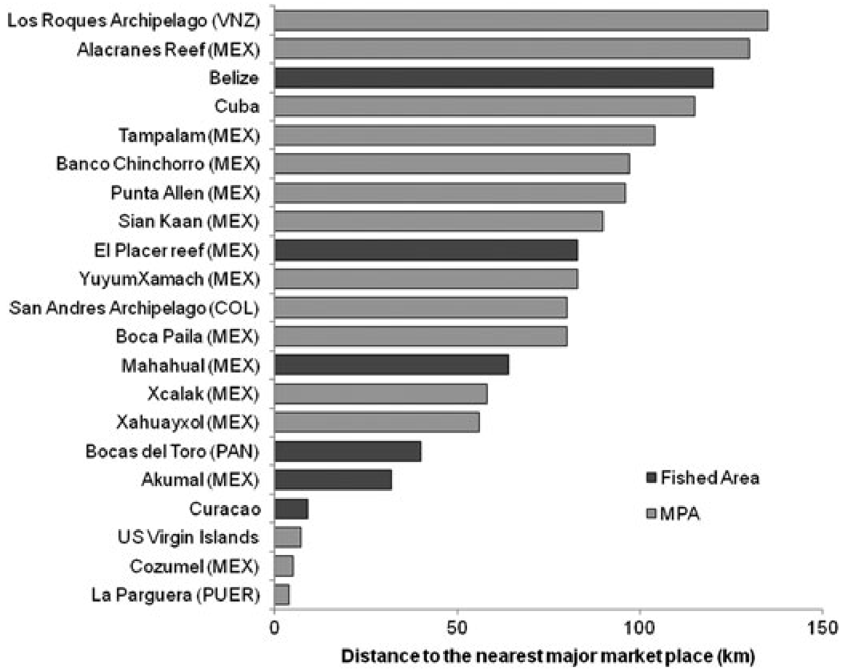


FIGURE 2 Distance to the nearest market place (in km) for 21 Caribbean localities. Marine protected areas are in light grey, fished areas are in dark grey

3 | RESULTS

3.1 | Los Roques reef fish assemblage

In total, 12 315 individuals from 114 fish species (Table S2) belonging to 33 families were recorded throughout the study area. Four families accounted for 80% of the individuals censused: Pomacentridae (damselfishes), Labridae (wrasses), Gobiidae (gobies), and Scaridae (parrotfishes). The next four families in order of importance represented mainly carnivorous species (Haemulidae [grunts], Lutjanidae [snappers], Carangidae [jacks], and Serranidae [groupers]) and accounted for 9.7% of the individuals censused. The ten most abundant species in decreasing order were *Chromis multilineata*, *Stegastes partitus*, *Coryphopterus personatus*, *Chromis cyanea*, *Thalassoma bifasciatum*, *Clepticus parrae*, *Halichoeres garnoti*, *Ocyurus chrysurus*, *Scarus taeniopterus*, and *Haemulon vittatum*. These species accounted for 75.6% of all fishes censused. Mean species richness per 60 m^2 transect (mean ± SE) was 29.29 ± 0.99 species, with a minimum of 14 and a maximum of 40 species. The mean density (mean ± SE) was 4.28 ± 0.26 ind m^{-2}, with a minimum of 1.30 and a maximum of 9.30 ind m^{-2}.

3.2 | Global MRT models

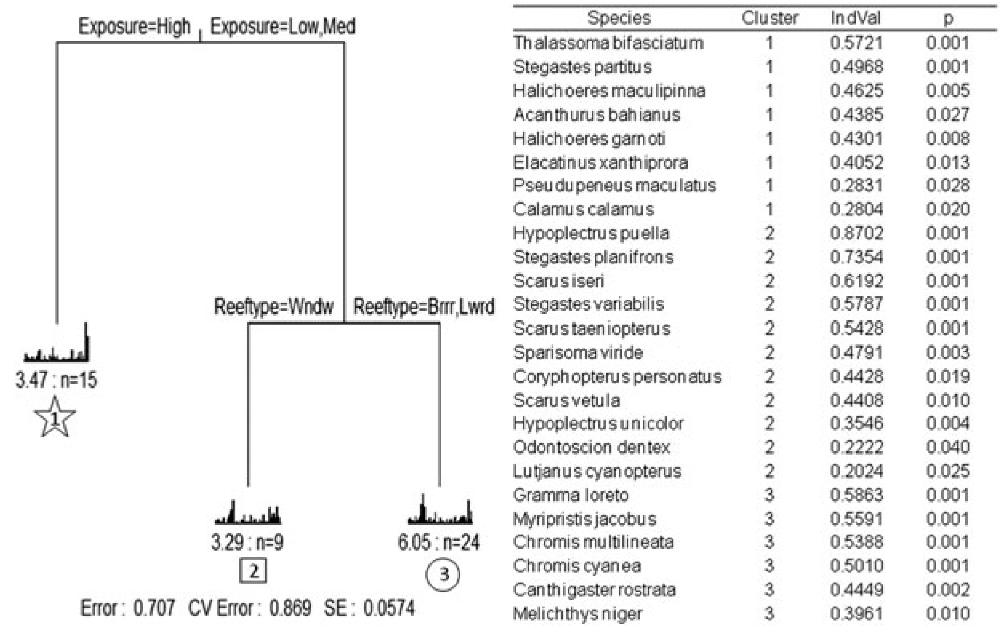
Three main clusters of transects were identified using the global MRT models (Figure 3) representing three distinct fish assemblages with their associated habitats. The same clusters were identified whether the model was constructed with fish abundance data or functional entity abundance data. In both models, exposure was the first splitting factor, followed by reef type. The first cluster corresponded to five sites (stars on Figure 1; 15 transects), which were exposed to wind, waves, and current and located on the northern and eastern outermost portions of the archipelago. The second cluster consisted of three sites (squares on Figure 1; nine transects) located on the windward fringing reefs of northern cays, but less exposed than the sites of the previous cluster. The third cluster corresponded to eight sites (circles on Figure 1; 24 transects) located on the southern barrier and on the leeward fringing reefs of south-western cays. Gran Roque leeward fringing reef also belonged to this cluster (Figure 1).

Based on Indicator value, characteristic species for each of the three assemblages were identified (IndVal >0.5 and $P < 0.001$; Figure 3). *Thalassoma bifasciatum* was characteristic of exposed sites. *Hypoplectrus puella*, *Stegastes planifrons*, *Scarus iseri*, *Stegastes variabilis*, and *Scarus taeniopterus* characterized windward sheltered sites. *Gramma loreto*, *Myripristis jacobus*, *Chromis multilineata*, and *Chromis cyanea* were characteristic of leeward and south barrier reef sites. Some of these species were among the most abundant in Los Roques (e.g. *C. multilineata*,) whereas others were much rarer (e.g. *H. puella*).

3.3 | Spatial variations of the benthic assemblage

The three main reef fish assemblages were associated with habitats that differed significantly in benthic composition (Figure 4). Highly exposed sites had lower coral cover (ANOVAs, $P < 0.001$ and Tukey's HSD post hoc test, $P < 0.05$). On these sites, hard bottom was characterized by a high cover of carbonate slabs, providing significantly lower habitability (Kruskal–Wallis test, $P < 0.001$ and Dunn's unplanned multiple comparison test, $P < 0.05$). These slabs supported higher cover of octocorals (Kruskal-Wallis test, $P < 0.001$ and Dunn's unplanned multiple comparison test, $P < 0.05$) and sponges (ANOVA, $P = 0.007$ and Tukey's HSD post hoc tests, $P < 0.05$). The increase of macroalgae cover with exposure was marginally significant (Kruskal–Wallis test, $P = 0.014$ and Dunn's unplanned multiple comparison test, $P < 0.05$).

Less exposed windward sites and leeward/south barrier sites had similar benthic compositions, except for live coral cover, which was significantly higher on windward sites (ANOVA, $P < 0.001$ and Tukey's HSD post hoc tests, $P < 0.05$). The slope and topography were significantly higher on leeward and south barrier sites (Kruskal–Wallis tests, $P < 0.001$ and Dunn's unplanned multiple comparison test, $P < 0.05$).



Species	Cluster	IndVal	p
Thalassoma bifasciatum	1	0.5721	0.001
Stegastes partitus	1	0.4968	0.001
Halichoeres maculipinna	1	0.4625	0.005
Acanthurus bahianus	1	0.4385	0.027
Halichoeres garnoti	1	0.4301	0.008
Elacatinus xanthiprora	1	0.4052	0.013
Pseudupeneus maculatus	1	0.2831	0.028
Calamus calamus	1	0.2804	0.020
Hypoplectrus puella	2	0.8702	0.001
Stegastes planifrons	2	0.7354	0.001
Scarus iseri	2	0.6192	0.001
Stegastes variabilis	2	0.5787	0.001
Scarus taeniopterus	2	0.5428	0.001
Sparisoma viride	2	0.4791	0.003
Coryphopterus personatus	2	0.4428	0.019
Scarus vetula	2	0.4408	0.010
Hypoplectrus unicolor	2	0.3546	0.004
Odontoscion dentex	2	0.2222	0.040
Lutjanus cyanopterus	2	0.2024	0.025
Gramma loreto	3	0.5863	0.001
Myripristis jacobus	3	0.5591	0.001
Chromis multilineata	3	0.5388	0.001
Chromis cyanea	3	0.5010	0.001
Canthigaster rostrata	3	0.4449	0.002
Melichthys niger	3	0.3961	0.010

FIGURE 3 A summary tree of the MRT analysis performed on the matrix of all fish species' abundances. The best model accounts for 29.3% of variation in assemblage structure (error of 0.707 corresponds to R^2 of 0.293). There are two nodes and three leaves in the 'best' regression tree. At the first node, assemblages are divided by the exposure to wind, waves and currents. At the second node, they are divided by the reeftype. CV Error = cross-validated mean error; SE = standard error. The table presents the most characteristic species of each cluster. The associated Indicator Value ('IndVal') provides a measure of the specificity and fidelity of each species to a cluster, with 1 referring to a perfect indicator species (only present in one cluster, on all its transects)

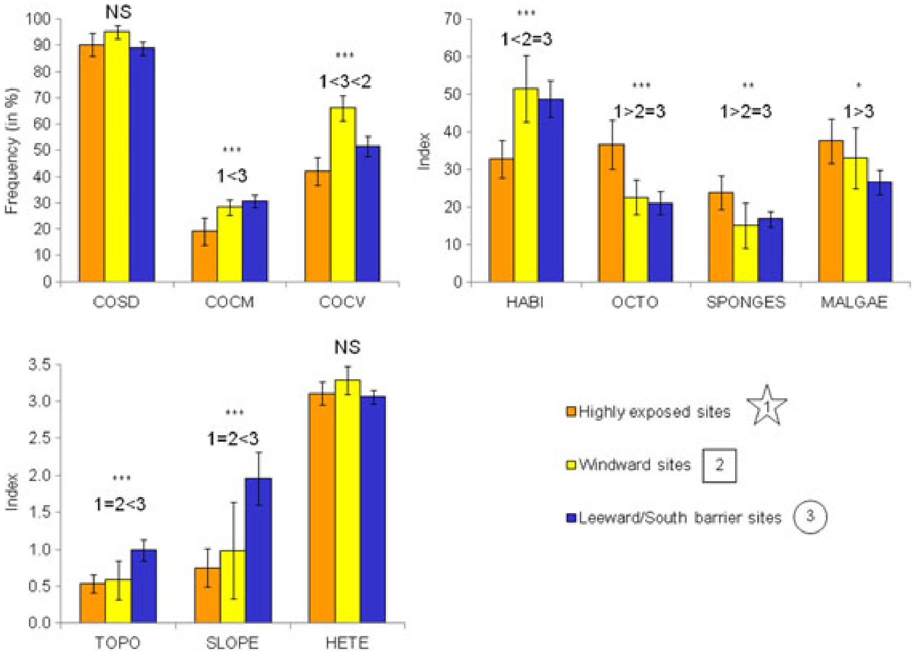


FIGURE 4 Mean values of the benthic factors in the three clusters of sites (± confidence intervals at α = 0.05). COSD: hard bottom cover; COCM: dead coral cover; COCV: live coral cover; HABI: habitability index; OCTO: index of octocorals cover; SPONGES: index of sponges cover; MALGAE: index of macroalgae cover; TOPO: index of topography; SLOPE: index of slope value; HETE: index of heterogeneity of the hard bottom (see methods S1 for details on the calculation of these factors). Results of the ANOVAs or kruskal–Wallis tests are indicated, with the results of the associated post hoc tests below

3.4 | Spatial patterns of the reef fish assemblages

Species richness was significantly higher (Kruskal–Wallis test, $P = 0.0022$ and Dunn's unplanned multiple comparison test, $P < 0.05$) on leeward/South barrier sites ($\bar{X}$ = 32.9 ± 4.3 species per 60 m^2) than on highly exposed sites (24.8 ± 8.5 species per 60 m^2) but differences were not significant between windward sites (27.1 ± 4.2 species per 60 m^2) and highly exposed sites, or between windward sites and leeward/south barrier sites. Mean density was significantly higher (Kruskal-Wallis test, $P < 0.001$ and Dunn's unplanned multiple comparison test, $P < 0.05$) on leeward/south barrier sites (5.53 ± 1.55ind m^{-2}) than on windward sites (3.16 ± 1.22 ind m^{-2}) and highly exposed sites (2.94 ± 0.80 ind m^{-2}). Exposure and reef type explained 18.52% and 10.74%, respectively, of the variation in composition of fish assemblages, along with dead coral cover (5.65%), index of topography (4.53%) and slope value (4.04%) (Table 1).

Mean species richness (Figure 5) and numerical density (Figure 6) of several groups of life-history traits were significantly different among the three assemblages. These variations were mostly explained by exposure and distance to mangroves (Table 1). Octocoral cover, dead coral cover, slope value, and index of topography also explained part of these variations (Table 1).

The densities of Pomacentridae, Gobiidae and Scaridae were significantly different between the three assemblages (Kruskal–Wallis tests, $P < 0.001$). Their distributions were respectively driven by exposure (27.01%) and reef type (17.93%), exposure (41.03%) and hard bottom cover (22.41%), and distance to the nearest mangrove (18.26%) (Table 1).

Anthropogenic pressure did not explain much of the variability in any of the groups or dominant families tested. However, distance to the population centre explained 11.3% of the variations in the distribution of omnivores, 11.8% of the variations in the distribution of small-bodied species (size class 2), and 3.8% of the variations in the distribution of Scaridae (Table 1).

Distance to the population centre did not explain variations of any of the three defined vulnerability indicators (Table 1). Anthropogenic pressure was marginally useful in explaining the variation (2.9%) in the distribution of rare species, and was not informative in explaining the variation in the other two vulnerability indicators (Table 1).

3.5 | The influence of distance to the nearest major market place in Caribbean localities

Distance to the nearest major market place appeared as a significant structuring factor for Caribbean reef fish assemblages, whether they are fished or located in MPAs. Relative species richness and densities of large size classes (max species length > 30 cm) were positively correlated with increasing distance to the market place in both fished areas and MPAs (Table 2). Relative species richness of herbivores, as well as relative densities of herbivores, mobile and sessile invertebrate feeders, and piscivores were also positively correlated with increasing distance to market in fished areas. Only species having large geographic ranges showed significant positive correlations with increasing distance to market (Table 2).

3.6 | Comparison of Los Roques fish assemblages with Caribbean fished areas and MPAs

Los Roques fish assemblage structure was significantly different from the mean structures found in Caribbean fished areas and MPAs for various metrics (Figure 7). Relative species richness and densities of plankton feeders, piscivores, and the largest species (max species length > 80 cm) were significantly higher in Los Roques, as well as density of species of size class 3 (16–30 cm) (Kruskal–Wallis test, $P < 0.001$ and Dunn's test, $P < 0.001$). Relative species richness and

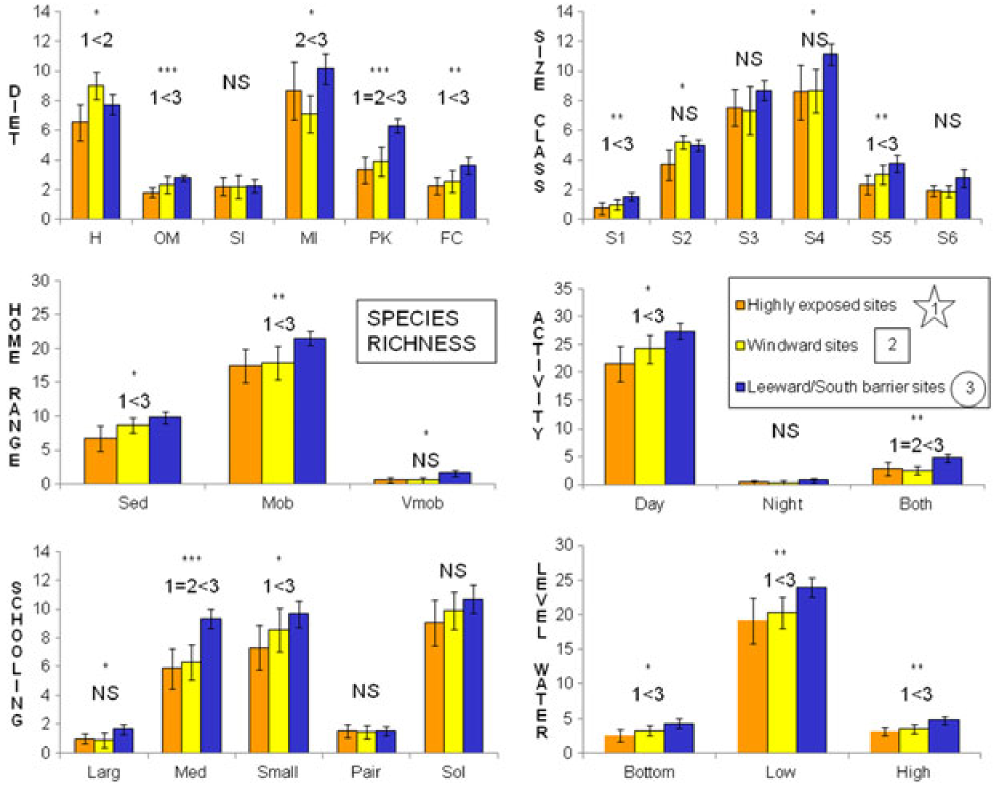


FIGURE 5 Mean species richness on a 60 m^2 transect (± confidence intervals at $\alpha = 0.05$) by group of life-history traits in the three clusters of sites. DIET: trophic group; SIZE: size class; HRANG: adult home range; ACT: diurnal activity; SCH: schooling; LWATER: level in the water column (see methods S2 for the significance of the groups of life-history traits). Results of the ANOVAs or kruskal–Wallis tests are indicated, with the results of the associated post hoc tests

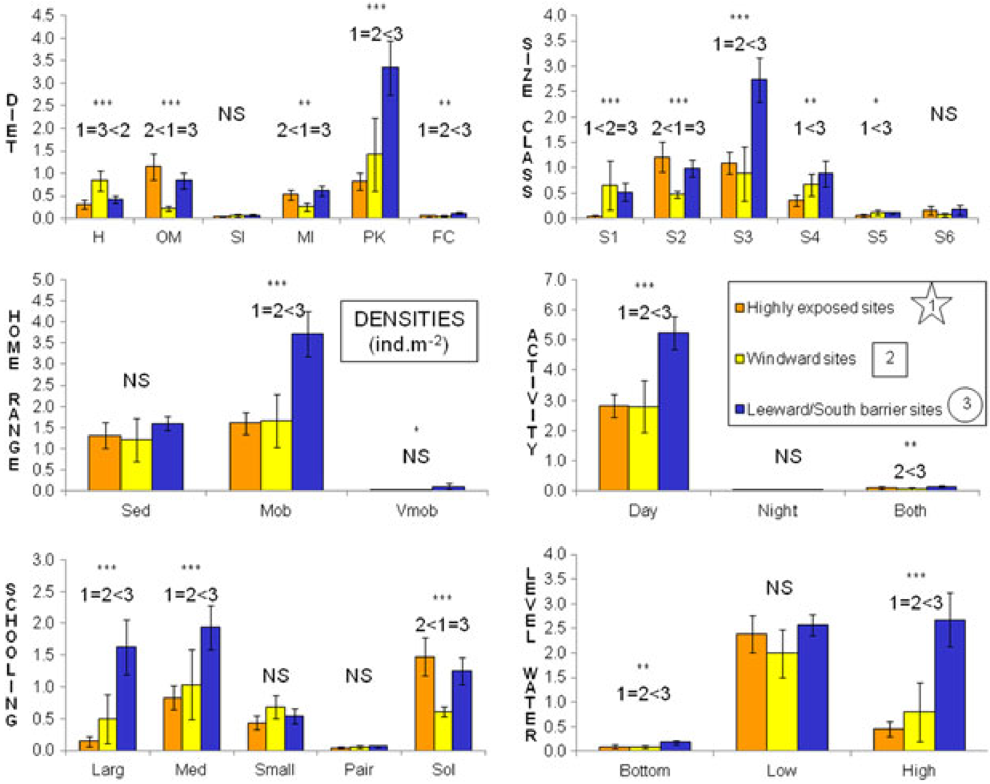


FIGURE 6 Mean fish densities (ind m^{-2}) (± confidence intervals at $\alpha = 0.05$) by group of life-history traits in the three clusters of sites. DIET: trophic group; SIZE: size class; HRANG: adult home range; ACT: diurnal activity; SCH: schooling; LWATER: level in the water column (see methods S2 for the significance of the groups of life-history traits). Results of the ANOVAs or kruskal–Wallis tests are indicated, with the results of the associated post hoc tests

density of herbivores were significantly lower in Los Roques, as well as relative species richness of species of size class 2 (7–15 cm) (Kruskal–Wallis test, $P < 0.001$ and Dunn's test, $P < 0.001$). Relative species richness and numerical density of large geographic range species were significantly higher in Los Roques (Kruskal–Wallis test, $P < 0.001$ and Dunn's test, $P < 0.001$).

4 | DISCUSSION

Recent studies on coral reefs have highlighted that unique ecological values are supported by wilderness areas, with no equivalency closer to human settlements, even in large and well-managed marine reserves (Graham & McClanahan, 2013; D'agata et al., 2016). Indeed, local human density (Bellwood, Hoey, & Hughes, 2012; Williams et al., 2015), linear distance to human population centres (Advani et al., 2015), and linear distance and travel time from the nearest major market place (D'agata et al., 2016; Maire et al., 2016) have been identified as important predictors of coral reef conditions (biomass or biodiversity) and functioning (e.g. herbivory). Although D'agata et al. (2016) recommend the use of wilderness areas (i.e. located at more than 20 h travel time from the main market) as benchmarks for management effectiveness in the Indo-Pacific, such areas do not exist in the Caribbean. In fact the most isolated reef is located at ‘only’ 13 h travel time to the main market in this region (Maire et al., 2016), making Caribbean reefs much more accessible from markets than their Indo-Pacific counterparts (Maire et al., 2016). This raises the question of what a good baseline for the Caribbean should look like.

4.1 | The influence of distance to the nearest major market place: the Caribbean case

Even if distances from the nearest major market are reduced in the Caribbean compared to the Indo-Pacific (Maire et al., 2016), the results of the present study suggest that it still represents an important factor for structuring reef fish assemblages in this region. Within the 21 fished areas and MPAs compared in this paper, both species richness and density of the largest reef fishes (max species length > 50 cm for MPAs, between 30 and 80 cm for fished areas) were positively correlated with increasing distance to the nearest market (Table 2). As these species are generally the most targeted by fishermen, the distance to the nearest major market likely provides a good measure of fishing pressure (Maire et al., 2016). These results are consistent with a previous study by Stallings (2009) who highlighted the increase of large-bodied predators with decreasing human population density in Caribbean localities. Fishing in the Caribbean is characterized by over-harvesting reef species from all trophic levels simultaneously (Jackson et al., 2001; Pandolfi et al., 2005). Indeed, relative densities of piscivores, invertivores, sessile invertebrate feeders, and herbivores in the fished localities were all positively correlated with the distance to the major market (Table 2). In contrast, no trends were detectable for these trophic groups in the MPAs (Table 2), which could signal a certain effectiveness of the MPAs included in this comparison.

Isolation per se could also be an important driver explaining the differences in the reef fish assemblage structures observed in this study, but its influence is likely weak along the small gradient of isolation found in the Caribbean (Jacquet, Mouillot, Kulbicki, & Gravel, 2016). Instead, distance to the nearest market seems to influence reef fish assemblages structure at much smaller scales (Advani et al., 2015; D'agata et al., 2016; Maire et al., 2016).

Given these results and the absence of real wilderness areas in the Caribbean (Maire et al., 2016), remote MPAs (MacNeil et al., 2015) may potentially provide the best baselines available for the region as they benefit from the natural protection offered by their isolation (Devillers et al., 2014). A world map of travel time to the nearest market place (D'agata et al., 2016) highlights that Los Roques is one of the least accessible reefs in the southern Caribbean, and it is indeed the most remote locality among the sites compared in the present study (Figure 2).

In addition, the overall distribution of reef fishes within Los Roques was not strongly influenced by anthropogenic factors. Only the distribution of omnivores and species of intermediate size (7–15 cm) were related to the distance to the population centre, but it seems unlikely that human presence could have a direct effect on these two groups. The same trend was observed at the Caribbean scale (Table 2). Most importantly, the distribution of vulnerable groups (defined as rare species, monospecific functional entities, and species of reduced geographical range) were influenced neither by anthropogenic pressure nor by the distance to the population centre, highlighting the low human influence on Los Roques fish assemblages (Advani et al., 2015).

Thus, Archipelago Los Roques combines important conditions for establishing a baseline: it is far from the nearest major market, among the oldest and largest Caribbean MPAs, and the structure of its reef fish assemblages do not seem to be influenced by local anthropogenic factors such as land-based pollution. This provides an excellent opportunity to examine the natural factors influencing the distribution of reef fishes, the patterns identified being likely valid for a majority of localities in the southern Caribbean.

TABLE 2 Significance of the Pearson's correlations between distance to the nearest major market place and relative species richness or density of groups of life-history traits in both fished areas and MPAs of the Caribbean. Value of the Pearson's correlation is given for the most significant correlations (*P* value <0.01). Positive correlations are in bold, negative correlations are in italic

		DIET						Size class						GEOGR. Range		
		H	OM	IS	IM	PK	FC	S1	S2	S3	S4	S5	S6	Small	Med	Large
Relative species richness	Fished areas	*** **0.24**	*** *−0.47*	*	NS	*	NS	*** *−0.45*	** *−0.21*	NS	*** **0.47**	*	NS	*	NS	** **0.21**
	MPA	NS	*** *−0.33*	NS	NS	*** **0.35**	NS	*** *−0.26*	** *−0.21*	NS	NS	** **0.18**	** **0.18**	NS	NS	NS
Relative density	Fished areas	*** **0.25**	*** *−0.39*	*** **0.34**	*** **0.50**	NS	** **0.21**	*** *−0.41*	NS	*	*** **0.52**	*** **0.27**	NS	NS	NS	** **0.23**
	MPA	NS	*** *−0.33*	NS	*	*** **0.30**	NS	*** *−0.29*	NS	NS	*	NS	** **0.20**	NS	NS	** **0.21**

4.2 | Contrasted reef habitats support different fish assemblages in archipelago Los Roques

Limiting the surveys to a similar depth reduced the variance in fish assemblage structure, since depth plays an important role in structuring reef fish assemblages (Arias-González et al., 2008; Friedlander & Parrish, 1998; Luiz et al., 2015; McGehee, 1994). Exposure (18.5%) and reef type (10.7%) were the most important factors in explaining the overall distribution of reef fishes in the archipelago. As reef type is strongly influenced by the degree of wave exposure (Bradbury & Young, 1981; Dominici-Arosemena & Wolff, 2005; Floeter et al., 2007; Friedlander, Brown, Jokiel, Smith, & Rodgers, 2003; Friedlander, Nowlis et al., 2003; Mejía & Garzón-Ferreira, 2000;), the global influence of exposure explained nearly 30% of the overall variation in the distribution of reef fishes. As has been documented in other insular oceanic systems (Friedlander, Brown et al., 2003; Friedlander, Nowlis et al., 2003; Mejía & Garzón-Ferreira, 2000), species richness and density decreased with exposure. Three main reef fish assemblages were identified in Archipelago Los Roques, corresponding to three different kinds of habitat along a gradient of exposure.

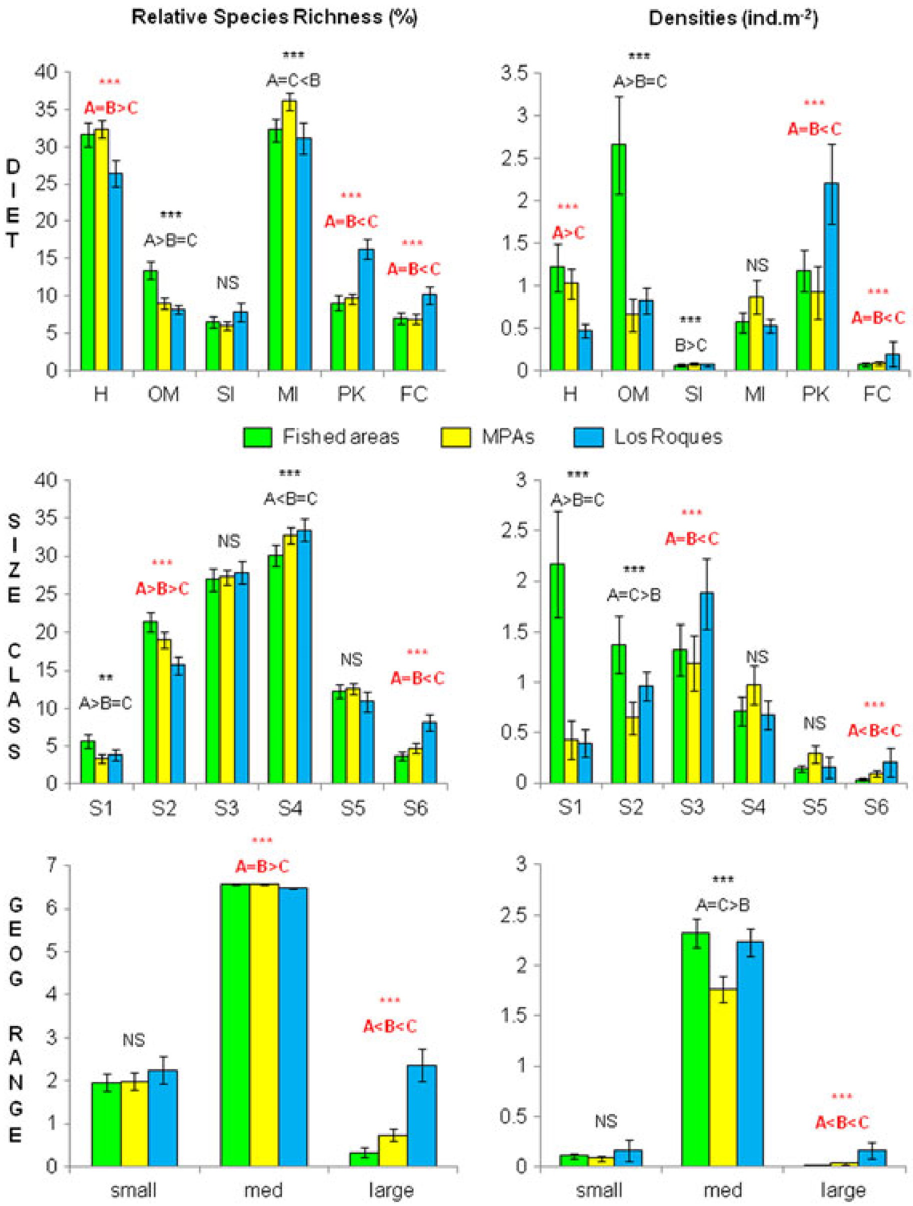


FIGURE 7 Mean relative species richness and fish densities (ind m^{-2}) (± confidence intervals at $\alpha = 0.05$) calculated by transect for several groups of life-history traits in Caribbean fished areas (green), marine protected areas (yellow) and in archipelago Los Roques (blue). DIET: trophic group; SIZE CLASS: size class group; GEOG RANGE: geographical range group (see methods S2 for the significance of the groups of life-history traits). Results of the Kruskal–Wallis tests are indicated, with the results of the associated post-hoc tests below. Results for which Los Roques is significantly different from other localities are indicated in red.

The first habitat type (highly exposed areas, with major current and/or wave forcing) was dominated by small demersal species *Stegastes partitus* and *Thalassoma bifasciatum* that find refuges in the little holes and crevices of the rock slabs. Although these slabs were largely colonized by octocorals and sponges, which create some multi-dimensional complexity, the habitability potential was reduced in this habitat and cannot be compared with the high availability of refuges found in the other habitats. Generally described as opportunistic in terms of food, *S. partitus* and *T. bifasciatum* are commonly observed over a wide range of habitats in the Caribbean (Dominici-Arosemena & Wolff, 2005; Mejía & Garzón-Ferreira, 2000; Rousseau, 2010; Toller, Debrot, Vermeij, & Hoetjes, 2010), and certainly take advantage of the lack of competition in their respective niche to settle under these unfavorable conditions. *Thalassoma bifasciatum* presents a high pectoral fin aspect ratio among the labrids and high swimming abilities which are likely to be a significant advantage in exposed habitat with strong water motion (Bellwood, Wainwright, Fulton, & Hoey, 2002). *Stegastes partitus* was very abundant in this highly exposed habitat and, as it is considered as an omnivorous species (it feeds primarily on algae but also on polychaetes, hydroids, copepods and ascidians; Froese & Pauly, 2014), the overall distribution of this trophic guild was strongly influenced by exposure at the archipelago scale (*Stegastes partitus* represent 90% of the omnivores in the study). Small-sized species (<7 cm), exclusively represented by Gobiidae in this study, were almost absent from the exposed habitat. Only a few individuals of the genus *Elacatinus* were observed hiding in the crevices of large sponges, whereas in the rest of the archipelago, *Coryphopterus personatus* was found hovering in medium size groups just above large refuges. Both strong hydrodynamic conditions (Longo et al., 2015) and the lack of refuges may explain the absence of this species from the exposed habitat. Patterns of distribution for small-sized species (<7 cm)/Gobiidae were well explained in the archipelago by exposure (41%), hard bottom cover (22%), and the combination of octocoral and sponge cover (14%).

In the second habitat type (moderately exposed areas with a dominance of hard corals, mainly massive or submassive growth forms), two herbivores species of Pomacentridae, *Stegastes planifrons* and *Stegastes variabilis*, were likely in competition with the ubiquitous *Stegastes partitus* for the territorial occupancy of the bottom and seemed to limit the densities of the latter species. Calmer hydrodynamic conditions and/or higher habitat complexity may explain the dominance of *S. planifrons* and *S. variabilis* in this habitat (Dominici-Arosemena & Wolff, 2005; Floeter et al., 2007; Mejía & Garzón-Ferreira, 2000). In contrast to highly exposed areas, the higher complexity, habitability, and live coral cover at the moderately exposed areas did not enhance species richness nor numerical density of the overall fish assemblage, despite relations commonly observed on other coral reefs (Komyakova, Munday, & Jones, 2013; Messmer et al., 2011). Scarids (*Scarus iseri*, *S. taeniopterus*, and to a lesser extent, *Sparisoma viride*) were also characteristic of this moderately exposed habitat. The high abundances of these different herbivorous fishes suggest that they prefer abundant algae (dead corals supporting turf matrix and macroalgae), but also somewhat sheltered habitats (Dominici-Arosemena & Wolff, 2005; Floeter et al., 2007; Friedlander, Nowlis et al., 2003; Longo et al., 2015). Moreover, the abundance of Scaridae (and to a lesser extent the abundance of overall herbivores) was positively influenced by the proximity to mangroves, which they may use as nursery habitat as suggested by Cocheret de la Morinière, Pollux, Nagelkerken, and Van der Velde (2002) and Nagelkerken et al. (2002). *Hypoplectrus puella* was strongly associated with this bio-constructed habitat, as in Martinique (Rousseau, 2010), but was almost absent from the third habitat type (similar in benthic composition but more sheltered) whereas Dominici-Arosemena and Wolff (2005) found this species in the most sheltered zones of their study. This suggests either a distinct behaviour of certain species with localities or more probably the involvement of other abiotic or biotic factors.

The third habitat type (sheltered areas dominated by hard corals, creating complex structures on steep slopes) was mostly characterized by *Gramma loreto*, which was found almost exclusively in this habitat. This species was also characteristic of the sheltered leeward areas of the oceanic atolls of San Andrés and Providencia (Mejía & Garzón-Ferreira, 2000). The other three indicator species for this habitat, *Myripristis jacobus*, *Chromis multilineata*, and *Chromis cyanea*, were plankton feeders. Plankton feeder distribution at the archipelago scale was mainly explained by distance to shore (13.6%), dead coral cover (13.6%), reef type (11.8%), and the combination of slope and habitat heterogeneity (11.5%), reflecting the affinity of this trophic group for this sheltered habitat, which consisted of leeward and barrier reefs with important slope values, and thus short distances to shore. Plankton feeders such as *Chromis multilineata* and *Chromis cyanea* are usually associated with exposed windward habitats (Dominici-Arosemena & Wolff, 2005; Floeter et al., 2007; Luiz et al., 2015; Mejía & Garzón-Ferreira, 2000), but their high abundances along sheltered leeward steep slopes has also been reported for oceanic islands such as Bonaire and Curaçao (Sandin, Sampayo, & Vermeij, 2007) and Old Providence and Santa Catalina reef complex (Friedlander, Nowlis et al., 2003). Plankton feeders were most numerous along reef edges adjacent to deeper water, probably because their major prey is most accessible (Hobson, 1991). Steep slopes and the proximity to deeper areas, along with consistent trade winds (from the east and north east), are likely to create upwellings on the southern barrier and leeward fringing reef edges and may provide abundant plankton (Casanova, Zoppi de Roa, & Montiel, 2007). The high percentage of plankton feeders in the Los Roques fish assemblage seem to be a characteristic of Caribbean assemblages with similar oceanic settings (Friedlander Nowlis et al., 2003; Mejía & Garzón-Ferreira, 2000; Sandin et al., 2007; see also Martinique, Guadeloupe, Banco Chinchorro in Table S4).

The three main reef fish assemblages found in Los Roques may represent references for other Caribbean sites with similar habitat characteristics. Despite these significant variations inside the archipelago, fish assemblage structure differed significantly between Los Roques and other Caribbean localities for several important metrics.

4.3 | The effectiveness of Los Roques' Marine protected area and its potential as a baseline

The comparison of trophic and size structures between Caribbean fished areas, MPAs, and Los Roques highlighted that fish assemblages at Los Roques may represent a reference of relatively natural state. Relative species richness of plankton feeders, piscivores, and very large species (max length > 80 cm) were higher at Los Roques compared with other locations in the Caribbean. Most importantly, the mean numerical densities of these three groups were two times higher than the average densities observed in fished areas and MPAs of the region (Figure 7). The high richness and densities of large piscivores, particularly targeted by fishing, can be interpreted as a major sign of the effectiveness of Los Roques MPA (Lamb & Johnson, 2010; Mosqueira, Côté, Jennings, & Reynolds, 2000; Newman, Paredes, Sala, & Jackson, 2006). Predators likely benefit from the low human density in the area (Stallings, 2009) and from the large size and long existence of this national park (Newman et al., 2006). Although the lack of biomass data for Los Roques assemblage is a limitation to our comparative analysis, it is very likely that the high densities of plankton feeders, piscivores, and especially very large species are supported by large biomass. High biomass, and in particular those of large predators, are one of the best indicators of lightly impacted and healthy coral reefs (D'agata et al., 2016; Friedlander & DeMartini, 2002; Maire et al., 2016; Sandin et al., 2008), which provide an appropriate measure of the effectiveness of a MPA. Indeed, large mobile predators support unique roles in the functioning of marine ecosystems through trophic regulation and nutrient transfer across habitats (Ferretti, Worm, Britten, Heithaus, & Lotze, 2010). Further studies will have to include biomass evaluation of reef fishes to highlight the levels of biomass in Los Roques and validate its importance as a baseline for the region.

Richness and numerical density of herbivores were particularly low in Los Roques (Figure 7). This result cannot be interpreted as a consequence of fishing as these species are not targeted in the area (pers. comm.). On the contrary, the densities of large bodied Scarids in Los Roques are among the highest in the Caribbean (Debrot, Choat, Posada, & Robertson, 2007), suggesting that the low abundance of herbivores could be due to natural predator-induced mortality, particularly focused on small herbivorous species (e.g. *Scarus iseri*) as shown by Mumby et al. (2006). Despite this likely predator-induced mortality for small grazers, macroalgal cover is scarce in comparison with live coral cover on the reefs of Los Roques (Villamizar et al., 2003; present study). The role of herbivores, in particular fishes, in the coral–algae relationship on reefs is at the centre of much debate (Adam, Burkepile, Ruttenberg, & Paddack, 2015; Carassou, Léopold, Guillemot, Wantiez, & Kulbicki, 2013; Cheal, Emslie, MacNeil, Miller, & Sweatman, 2013). Our results are somewhat opposite to the mainstream hypothesis, i.e. high cover of macroalgae is expected when herbivore densities are low (Hughes et al., 2007; Poore et al., 2012; Roff & Mumby, 2012). In the absence of biomass data we cannot conclude, but our data suggest a major role for the larger herbivorous fishes in regulating macroalgal abundance.

Plankton feeders between 15 and 30 cm max length (mostly *Chromis*) exhibited very high densities in Los Roques (Figure 7) and may represent an important prey source that could explain the high abundance of predators (Newman et al., 2006). In a comparison extended to other fished areas and MPAs (31 localities; Table S3), predator richness increased as prey richness increased, irrespective of whether the localities were fished or not (Figure 8a), in agreement with the results found by Stier, Heinz, Parravicini, and Kulbicki (2014) in the Pacific. In Los Roques archipelago, prey richness was within the average of the other localities whereas predator richness was greatly above average. Moreover, predator density increased as prey density increased in the Caribbean MPAs, and Los Roques archipelago exhibited very high densities of predators when compared with other localities (Figure 8b). Hein and Gillooly (2011) found predator density was mostly driven by resource availability, suggesting that Caribbean prey and predator densities should be related. In contrast, there was no significant relationship between predator and prey densities in fished areas where fishing could limit predator densities. In fished areas, predator densities could be represented mainly either by non-target species or by those only slightly vulnerable to fishing pressure, such as moray eels (Gilbert, Rasmussen, & Kramer, 2005).

D'agata et al. (2016) expressed some reservations about the potential for a marine reserve to preserve viable populations of large mobile predators. Nevertheless, large groups of hundreds of such predators (e.g. jacks and barracudas) are regularly observed within Archipelago Los Roques National Park, which is probably presently a rare feature for the Caribbean.

4.4 | Conclusion: archipelago Los Roques National Park reveals interesting characteristics for establishing a baseline

In view of the marginal effects of human presence and considering the healthy state of this reef fish assemblage in the regional context, Archipelago Los Roques National Park appears to be an effective MPA, which can be explained by: (1) its remoteness from nearest markets and large population centres (Advani et al., 2015; Maire et al., 2016); (2) its low human population, with a low fishing impact, particularly on piscivores (Micheli, 1999; Stallings, 2009); (3) its old age (created in 1972) and large size (Edgar et al., 2014; Halpern, 2003; Newman et al., 2006); (4) the presence of extensive areas of mangroves and seagrass beds, which are important nursery habitats for numerous species, highly connected to coral reefs (Nagelkerken et al., 2012); 5) its location far (~ 130 km) from terrestrial run-off sources which can affect more specifically lower trophic levels (Micheli, 1999). These characteristics indicate that Los Roques Archipelago can be considered a relatively unimpaired area that provides a rare opportunity to study the influence of natural seascape and environmental factors involved in reef fish distribution patterns in the southern Caribbean.

Exposure appeared to be the most important factor structuring reef fish assemblages at Los Roques through a complex interrelationship of particular habitats, availability of food, and ecological requirements of each species. We assume that the patterns observed in this study could be those that existed in the past in a large part of the Caribbean. Additional information on biomass levels and the production of the major reef fish species and functional groups are needed to complement these first results. Connectivity and, in particular, the role of adjacent habitats such as seagrass beds and mangroves, which are abundant in this MPA, should also be assessed in greater

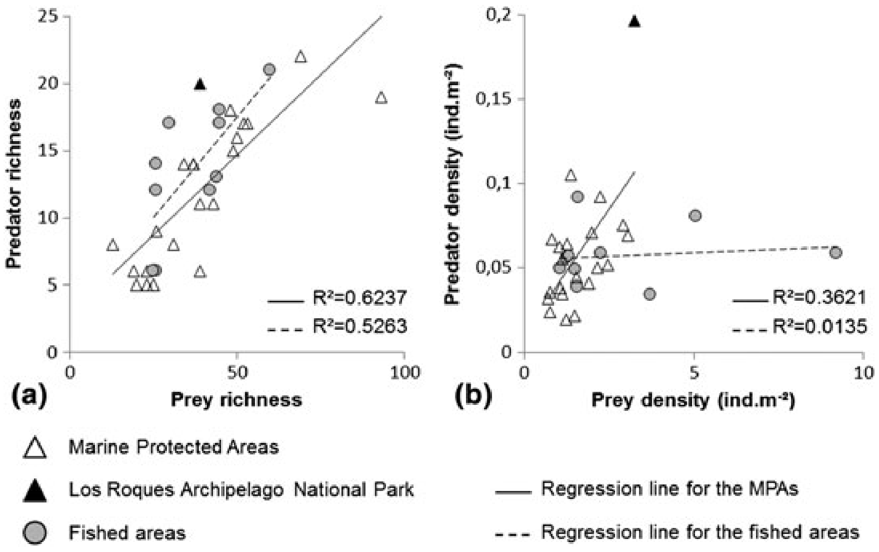


FIGURE 8 Relationships between predator and prey richness (a) and density (ind m^{-2}) (b) in 31 localities of the Caribbean (details are given in Table S3). Predators correspond to the piscivores (category FC in methods) and prey to the small species (i.E. adult size <30 cm: categories S1, S2 and S3 in methods S2). Empty triangles marine protected areas; black triangle Los Roques archipelago National Park; grey circles fished areas; solid lines regression lines for the MPAs; dashed lines regression lines for the fished areas

detail. This study points to the need for regional databases as accessing detailed information on the species composition, density, and biomass of reef fish of verifiable quality is still difficult. Finally, Archipelago Los Roques National Park appears to be a regional priority for the conservation of reef fishes as it contains unique features for the Caribbean. In fact the potential for creating other large coral reef MPAs in the region is reduced because of the paucity of large reef complexes and the high human densities. As a consequence it should be of international concern to maintain Los Roques relatively unimpacted.

ACKNOWLEDGEMENTS

This work was made possible thanks to the gracious collaboration of Fundacion Cientifica Los Roques (FCLR) which provided free access to their installations on Dos Mosquises island and invaluable logistical support. Thank you and congratulations for the whole support offered to local investigation all along the past forty years. The authors are grateful to Juan Carlos Bastidas from Arrecifes Divers for providing diving equipment in Gran Roque, to the National Parks Institute of Venezuela (INPARQUES)'s office in Gran Roque for their logistical support and to Phecda Marquez-Lossada for the accomodation. We would like to thank L.T.A. and Albatros airline for carrying us and the National Parks Institute of Venezuela (INPARQUES) for issuing the permits to work in the park. We are also grateful to Henrich Bruggemann for its helpful comments and to an anonymous reviewer who greatly helped in structuring and improving this manuscript.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

REFERENCES

Acosta-González, G., Rodríguez-Zaragoza, F. A., Hernández-Landa, R. C., & Arias-González, J. E. (2013). Additive diversity partitioning of fish in a Caribbean coral reef undergoing shift transition. *PLoS ONE*, *8*, e65665. https://doi.org/10.1371/journal.pone.0065665

Adam, T. C., Burkepile, D. E., Ruttenberg, B. I., & Paddack, M. J. (2015). Herbivory and the resilience of Caribbean coral reefs: Knowledge gaps and implications for management. *Marine Ecology Progress Series*, *520*, 1–20.

Advani, S., Rix, L. N., Aherne, D. M., Alwany, M. A., & Bailey, D. M. (2015). Distance to a fishing community explains fish abundance in a no-take zone with weak compliance. *PLoS ONE*, *10*, e0126098. https://doi.org/10.1371/journal.pone.0126098

Arias-González, J. E., Legendre, P., & Rodríguez-Zaragoza, F. A. (2008). Scaling up beta diversity on Caribbean coral reefs. *Journal of Experimental Marine Biology and Ecology*, *366*, 28–36.

Arias-González, J. E., Núñez-Lara, E., Rodríguez-Zaragoza, F. A., & Legendre, P. (2011). Indicadores del paisaje arrecifal para la conservación de la biodiversidad de los arrecifes de coral del Caribe. *Ciencias Marinas*, *37*, 87–96.

Bastidas, C., Bone, D., Cróquer, A., Debrot, D., Garcia, E., Humanes, A., … Rodríguez, S. (2012). Massive hard coral loss after a severe bleaching event in 2010 at Los Roques, Venezuela. *Revista de Biología Tropical*, *60*, 29–37.

Bellwood, D. R., & Hughes, T. P. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science*, *292*, 1532–1534.

Bellwood, D. R., Hoey, A. S., & Hughes, T. P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1621–1629.

Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. (2002). Assembly rules and functional groups at global biogeographical scales. *Functional Ecology*, *16*, 557–562.

Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R*. New York, NY: Springer.

Bouchon-Navaro, Y., Bouchon, C., Louis, M., & Legendre, P. (2005). Biogeographic patterns of coastal fish assemblages in the West Indies. *Journal of Experimental Marine Biology and Ecology*, *315*, 31–47.

Bozec, Y. M., Acosta-González, G., Núñez-Lara, E., & Arias-González, J. E. (2008). Impacts of coastal development on ecosystem structure and function of Yucatan coral reefs, Mexico. In *Proceedings of the 11th International Coral Reef Symposium*: Fort Lauderdale, Florida, pp. 691–695.

Bradbury, R. H., & Young, P. C. (1981). The effects of major forcing function, wave energy, on a coral reef ecosystem. *Marine Ecology Progress Series*, *5*, 229–241.

Carassou, L., Léopold, M., Guillemot, N., Wantiez, L., & Kulbicki, M. (2013). Does herbivorous fish protection really improve coral reef resilience? A case study from New Caledonia (South Pacific). *PLoS ONE*, *8*, e60564.

Casanova, E., Zoppi de Roa, E., & Montiel, E. (2007). Caracterización espacial y temporal del zooplancton en el archipiélago Los Roques, Venezuela. *Boletín del Instituto Oceanográfico de Venezuela*, *46*, 51–65.

Cervigón, F., & Ramírez-Nahím, H. (2003). *Peces del Archipiélago Los Roques*. Caracas, Venezuela: Agencia Española de Cooperación Internacional.

Cheal, A. J., Emslie, M., MacNeil, M. A., Miller, I., & Sweatman, H. (2013). Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecological Applications*, *23*, 174–188.

Cinner, J. E., Graham, N. A. J., Huchery, C., & MacNeil, M. A. (2013). Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conservation Biology*, *27*, 453–458.

Clua, E., Legendre, P., Vigliola, L., Magron, F., Kulbicki, M., Sarramegna, S., … Galzin, R. (2006). Medium scale approach (MSA) for improved assessment of coral reef fish habitat. *Journal of Experimental Marine Biology and Ecology*, *333*, 219–230.

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., & Van der Velde, G. (2002). Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine, Coastal and Shelf Science*, *55*, 309–321.

Cróquer, A., Weil, E., Zubillaga, A. L., & Pauls, S. M. (2005). Impact of a white plague-II outbreak on a coral reef in the archipelago Los Roques National Park, Venezuela. *Caribbean Journal of Science*, *41*, 815–823.

D'agata, S., Vigliola, L., Graham, N. A., Wantiez, L., Parravicini, V., Villéger, S., … Mouillot, D. (2016). Unexpected high vulnerability of functions in wilderness areas: evidence from coral reef fishes. *Proceedings of the Royal Society B*, *283*(1844). https://doi.org/10.1098/rspb.2016.0128

De'ath, G. (2002). Multivariate regression trees: A new technique for modeling species-environment relationships. *Ecology*, *83*, 1105–1117.

Debrot, D., Choat, J. H., Posada, J. M., & Robertson, D. R. (2007). High densities of the large bodied parrotfishes (Scaridae) at two Venezuelan offshore reefs: Comparison among four localities in the Caribbean. In Proceedings of the 60th Gulf and Caribbean Fisheries Institute: Punta Cana, Dominican Republic, pp. 335–337.

DeGeorges, A., Goreau, T. J., & Reilly, B. (2010). Land-sourced pollution with an emphasis on domestic sewage: Lessons from the Caribbean and implications for coastal development on Indian Ocean and Pacific coral reefs. *Sustainability*, *2*, 2919–2949.

Devillers, R., Pressey, R., Grech, A., Kittinger, J. N., Edgar, G. J., Ward, T., & Watson, R. (2014). Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*, 480–504.

Dominici-Arosemena, A., & Wolff, M. (2005). Reef fish community structure in Bocas del Toro (Caribbean, Panama): Gradients in habitat complexity and exposure. *Caribbean Journal of Science*, *41*, 613–637.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, *67*, 345–366.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., … Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, *506*, 216–220.

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, *13*, 1055–1071.

Froese, R., & Pauly, D. (Eds.). (2014). FishBase. http://www.fishbase.org/ (06/2014)

Floeter, S. R., Krohling, W., Gasparini, J. L., Ferreira, C. E. L., & Zalmon, I. R. (2007). Reef fish community structure on coastal islands of the southeastern Brazil: The influence of exposure and benthic cover. *Environmental Biology of Fishes*, *78*, 147–160.

Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., … Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, *35*, 22–47.

Friedlander, A. M., Brown, E. K., Jokiel, P. L., Smith, W. R., & Rodgers, K. S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, *22*, 291–305.

Friedlander, A. M., & DeMartini, E. E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. *Marine Ecology Progress Series*, *230*, 253–264.

Friedlander, A. M., Nowlis, J. S., Sanchez, J. A., Appeldoorn, R., Usseglio, P., McCormick, C., … Mitchell-Chui, A. (2003). Designing effective marine protected areas in Seaflower biosphere reserve, Colombia, based on biological and sociological information. *Conservation Biology*, *17*, 1769–1784.

Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, *224*, 1–30.

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, *405*, 220–227.

Gilbert, M., Rasmussen, J. B., & Kramer, D. L. (2005). Estimating the density and biomass of moray eels (Muraenidae) using a modified visual census method for hole-dwelling reef fauna. *Environmental Biology of Fishes*, *73*, 415–426.

Graham, N. A., & McClanahan, T. R. (2013). The last call for marine wilderness? *Bioscience*, *63*, 397–402.

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*, 650–667.

Halpern, B. S. (2003). The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications*, *13*, S117–S137.

Hein, A. M., & Gillooly, J. F. (2011). Predators, prey, and transient states in the assembly of spatially structured communities. *Ecology*, *92*, 549–555.

Hobson, E. S. (1991). Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In P. F. Sale (Ed.), *The ecology of fishes on coral reefs* (pp. 69–95). San Diego, CA: Academic Press.

Hughes, T. P. (1994). Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science*, *265*, 1547–1551.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., … Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, *17*, 360–365.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., … Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, *293*, 629–638.

Jacquet, C., Mouillot, D., Kulbicki, M., & Gravel, D. (2016). Extensions of island biogeography theory predict the scaling of functional trait composition with habitat area and isolation. *Ecology Letters*, *20*(2), 135–146. https://doi.org/10.1111/ele.12716

Kaplan, K. A., Ahmadia, G. N., Fox, H., Glew, L., Pomeranz, E. F., & Sullivan, P. (2015). Linking ecological condition to enforcement of marine protected area regulations in the greater Caribbean region. *Marine Policy*, *62*, 186–195.

Knowles, J. E., Doyle, E., Schill, S. R., Roth, L. M., Milam, A., & Raber, G. T. (2015). Establishing a marine conservation baseline for the insular Caribbean. *Marine Policy*, *60*, 84–97.

Komyakova, V., Munday, P. L., & Jones, G. P. (2013). Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, *8*, e83178.

Kramer, P. A. (2003). Synthesis of coral reef health indicators for the western Atlantic: Results of the AGRRA program (1997-2000). *Atoll Research Bulletin*, *496*, 1–55.

Kramer, P. A., & Lang, J. C. (2003). The Atlantic and gulf rapid reef assessment (AGRRA) protocols: Former version 2.2. *Atoll Research Bulletin*, *496*, 611–624.

Kulbicki, M., Parravicini, V., Bellwood, D. R., Arias-González, E., Chabanet, P., Floeter, S. R., … Mouillot, D. (2013). Global biogeography of reef fishes: A hierarchical quantitative delineation of regions. *PLoS ONE*, *8*, e81847.

Kulbicki, M., Parravicini, V., & Mouillot, D. (2015). Patterns and processes in reef fish body size. In C. Mora (Ed.), *Ecology of fishes on coral reefs* (pp. 104–105). Cambridge, UK: Cambridge University Press.

Lamb, R. W., & Johnson, D. W. (2010). Trophic restructuring of coral reef fish communities in a large marine reserve. *Marine Ecology Progress Series*, *408*, 169–180.

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280.

Longo, G. O., Morais, R. A., Martins, C. D. L., Mendes, T. C., Aued, A. W., Cândido, D. V., … Floeter, S. R. (2015). Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: Rocas atoll, NE Brazil. *PLoS ONE*, *10*, e0127176.

Luckhurst, B. E., & Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, *49*, 317–323.

Luiz, O. J., Allen, A. P., Robertson, D. R., Floeter, S. R., Kulbicki, M., Vigliola, L., … Madin, J. S. (2013). Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 16498–16502.

Luiz, O. J., Mendes, T. C., Barneche, D. R., Ferreira, C. G. W., Noguchi, R., Villaça, R. C., … Ferreira, C. E. L. (2015). Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's archipelago, equatorial Atlantic): The relative influence of abiotic and biotic variables. *Marine and Freshwater Research*, *66*(8), 739–749. https://doi.org/10.1071/MF14150

MacNeil, M. A., Graham, N. A., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., … McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, *520*(7547), 341–344.

Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., … Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters*, *19*, 351–360.

McArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

McGehee, M. A. (1994). Correspondence between assemblages of coral reef fishes and gradients of water motion, depth and substrate size off Puerto Rico. *Marine Ecology Progress Series*, *105*, 243–255.

Mejía, L. S., & Garzón-Ferreira, J. (2000). Estructura de comunidades de peces arrecifales en cuatro atolones del Archipiélago de San Andrés y Providencia (Caribe Sur occidental). *Revista de Biología Tropical*, *48*, 883–896.

Mellin, C., Bradshaw, C. J. A., Meekan, M. G., & Caley, M. J. (2010). Environmental and spatial predictors of species richness and abundance in coral reef fishes. *Global Ecology and Biogeography*, *19*, 212–222.

Mellin, C., Mouillot, D., Kulbicki, M., McClanahan, T. R., Vigliola, L., Bradshaw, C. J. A., … Caley, M. J. (2016). Humans and seasonal climate variability threaten large-bodied coral reef fish with small ranges. *Nature Communications*, *7*, 10491. https://doi.org/10.1038/ncomms10491

Méndez-Baamonde, J. (1978). *Archipiélago Los Roques/Islas de Aves*. Caracas, Venezuela: Cuadernos Lagoven.

Mesnildrey, L., Gascuel, D., & Le Pape, O. (2013). Integrating marine protected areas in fisheries management systems: Some criteria for ecological efficiency. *Aquatic Living Resources*, *26*, 159–170.

Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2011). Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, *92*, 2285–2298.

Micheli, F. (1999). Eutrophication, fisheries, and consumer resource dynamics in marine pelagic ecosystems. *Science*, *285*, 1396–1398.

Mora, C. (2008). A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*, 767–773.

Mora, C., Andréfouët, S., Costello, M., Kranenburg, S., Rollo, A., Veron, J., … Myers, R. A. (2006). Coral reefs and the global network of marine protected areas. *Science*, *312*, 1750–1751.

Mora, C., Treml, E. A., Roberts, J., Crosby, K., Roy, D., & Tittensor, D. P. (2012). High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography*, *35*, 89–96.

Mosqueira, I., Côté, I. M., Jennings, S., & Reynolds, J. D. (2000). Conservation benefits of marine reserves for fish populations. *Animal Conservation*, *3*, 321–332.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M., … Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13757–13762.

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., … Gill, A. B. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, *311*, 98–101.

Nagelkerken, I., Grol, M. G., & Mumby, P. J. (2012). Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. *PLoS ONE*, *7*, e36906.

Nagelkerken, I., Roberts, C. M., Van Der Velde, G., Dorenbosch, M., Van Riel, M. C., Cocheret de La Moriniere, E., & Nienhuis, P. H. (2002). How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series*, *244*, 299–305.

Newman, M. J. H., Paredes, G. A., Sala, E., & Jackson, J. B. C. (2006). Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters*, *9*, 1216–1227.

Núñez-Lara, E., Arias-González, J. E., & Legendre, P. (2005). Spatial patterns of Yucatan reef fish communities: Testing models using a multi-scale survey design. *Journal of Experimental Marine Biology and Ecology*, *324*, 157–169.

Ouellette, M. H., Legendre, P., & Borcard, D. (2012). Cascade multivariate regression tree: A novel approach for modelling nested explanatory sets. *Methods in Ecology and Evolution*, *3*, 234–244.

Paddack, M. J., Reynolds, J. D., Aguilar, C., Appeldoorn, R. S., Beets, J., Burkett, E. W., … Côté, I. (2009). Recent region-wide declines in Caribbean reef fish abundance. *Current Biology*, *19*, 590–595.

Pandolfi, J. M., Jackson, J. B. C., Baron, N., Bradbury, R. H., Guzman, H. M., Hughes, T. P., … Sala, E. (2005). Are US coral reefs on the slippery slope to slime? *Science*, *307*, 1725–1726.

Parravicini, V., Kulbicki, M., Bellwood, D. R., Friedlander, A. M., Arias-Gonzalez, J. E., Chabanet, P., … Mouillot, D. (2013). Global patterns and predictors of tropical reef fish species richness. *Ecography*, *36*, 1254–1262.

Poore, A. G., Campbell, A. H., Coleman, R. A., Edgar, G. J., Jormalainen, V., Reynolds, P. L., … Duffy, J. E. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, *15*, 912–922.

Posada, J. M., Villamizar, E., & Alvarado, D. (2003). Rapid assessment of coral reefs in the Archipiélago Los Roques National Park, Venezuela (part 2: Fishes). *Atoll Research Bulletin*, *496*, 530–543.

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Roff, G., & Mumby, P. J. (2012). Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution*, *27*, 404–413.

Rousseau, Y. (2010). Structure des peuplements ichtyologiques des récifs coralliens de la Martinique en relation avec la qualité de l'habitat (PhD thesis). Ecole Pratique des Hautes Etudes, La Sorbonne, Paris, France.

Sandin, S. A., Sampayo, E. M., & Vermeij, M. J. (2007). Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles. *Caribbean Journal of Science*, *44*, 137–144.

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., … Sala, E. (2008). Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*, *3*, e1548.

Stallings, C. D. (2009). Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. *PLoS ONE*, *4*, e5333.

Stier, A., Heinz, A., Parravicini, V., & Kulbicki, M. (2014). Larval dispersal drives trophic structure across Pacific coral reefs. *Nature Communications*, *5*, 5575.

Tavares, R. (2005). Abundance and distribution of sharks in Los Roques archipelago national and other Venezuelan oceanic islands, 1997-1998. *Ciencias Marinas*, *32*, 441–454.

Toller, W., Debrot, A. O., Vermeij, M. J., & Hoetjes, P. C. (2010). Reef fishes of Saba Bank, Netherlands Antilles: Assemblage structure across a gradient of habitat types. *PLoS ONE*, *5*, e9207.

Toropova, C., Meliane, I., Laffoley, D., Matthews, E., & Spalding, M. (Eds.). (2010). Global Ocean protection: Present status and future possibilities. Brest, France: Agence des aires marines protégées, Gland, Switzerland, Washington, DC and New York, USA: IUCN WCPA, Cambridge, UK : UNEP-WCMC, Arlington, USA: TNC, Tokyo, Japan: UNU, New York, USA: WCS.

Villamizar, E., Posada, J. M., & Gomez, S. (2003). Rapid assessment of coral reefs in the Archipiélago Los Roques National Park, Venezuela (part 1: Stony corals and algae). *Atoll Research Bulletin*, *496*, 512–529.

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015). Human, oceanographic and habitat drivers of central and western pacific coral reef fish assemblages. *PLoS ONE*, *10*, e0120516.

Zar, J. H. (2010). *Biostatistical analysis* (5th ed.). Upper Saddle River, NJ: Pearson Prentice Hall.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Elise S, Urbina-Barreto I, Boadas-Gil H, et al. Archipelago Los Roques: A potential baseline for reef fish assemblages in the southern Caribbean. *Aquatic Conserv: Mar Freshw Ecosyst*. 2017;27:1116–1132. https://doi.org/10.1002/aqc.2770