

Unusual reef fish biomass and functional richness at Malpelo, a remote island in the Tropical Eastern Pacific

Juan P. Quimbayo  · Thiago C. Mendes ·
Michel Kulbicki · Sergio R. Floeter ·
Fernando A. Zapata

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Abstract Fish assemblages can vary across temporal and spatial scales due to changes in habitat structure and the influence of local factors such as wave exposure, depth and anthropogenic influence. This study presents a description of species richness, functional richness, density and biomass of fish assemblages of Malpelo Island, a Marine Protected Area located in the Tropical

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S. R. Floeter
Programa de Pós-graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, SC 88010-970, Brazil
e-mail: quimbayo.j.p@gmail.com

J. P. Quimbayo · S. R. Floeter
Laboratório de Biogeografia e Macroecologia Marinha,
Departamento de Ecologia e Zoologia, Centro de Ciências
Biológicas, Universidade Federal de Santa Catarina,
Florianópolis, SC 88010-970, Brazil

J. P. Quimbayo · F. A. Zapata
Grupo de Investigación en Ecología de Arrecifes Coralinos,
Universidad del Valle, Apartado Aéreo, 25360 Cali, Colombia

T. C. Mendes · M. Kulbicki
Institute de Recherche pour le Développement (IRD), UMR
“Entropie”, Labex Corail, Université de Perpignan,
66000 Perpignan, France

Present Address:

J. P. Quimbayo (✉)
Programa de Pós-graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, SC 88010-970, Brazil
e-mail: quimbayo.j.p@gmail.com

Eastern Pacific (TEP) region and considered a World Heritage site. Underwater visual censuses ($n = 103$) from two years and a local checklist were used to characterize the reef fish assemblage of Malpelo Island. Our results show a numerical dominance, during both sampling years, by the planktivore species *Chromis atrilobata* and *Apogon atradorsatus*, which are regional TEP endemic species. Among the most striking results found were the high biomass values ($706.2 \text{ g/m}^2 \pm 73.2$ in 2010 and $879 \text{ g/m}^2 \pm 116.2$ in 2015) of large-bodied TEP endemic piscivorous species and the high functional diversity represented mainly by vulnerable species. The dominance in density and biomass of regional endemic species exemplifies the high endemism level within the TEP. High levels of fish biomass and functional richness suggest that Malpelo is one of the most pristine and vulnerable sites within the TEP region. Thus, Malpelo island represents a baseline for untouched assemblages in this marine province, as well as a priority area for conservation at the national and international level.

Keywords Marine protected area · Endemism · Biomass · Reef fish · Malpelo Island · Colombia

Introduction

Understanding temporal and spatial variations of assemblages and the influence of biotic and abiotic factors on communities are among the most important goals in community ecology (Jones and Syms 1998; Ricklefs 2006). This interest arises due to the fact that each

species perceives the environment on a unique range of scales and thus responds individually to environmental variability (Levin 1992). Species often show a patchy distribution over a range of temporal and spatial scales as a result of different evolutionary (dispersal, speciation and extinction) and ecological (environmental tolerances, habitat choice and species interactions) processes operating at those scales (Ricklefs 2004). Although several studies have been key to understanding these questions on tropical reefs (Mora et al. 2003; Connolly et al. 2005; Parravicini et al. 2013), our knowledge on the influence of these processes in structuring reef fish communities in the Tropical Eastern Pacific (TEP) is still scarce. Few studies in this region have examined the regional reef fish assemblage, but they have primarily focused on range size distribution (Mora and Robertson 2005a), latitudinal variation in species richness (Mora and Robertson 2005b), and the delineation of biogeographic provinces based on species composition (Robertson and Cramer 2009). One aspect of reef fish ecology that is receiving increasing attention in other regions is that of functional diversity (Stuart-Smith et al. 2013). While this topic has begun to be studied in the TEP (Alvarez-Filip and Reyes-Bonilla 2006; Aguilar-Medrano and Calderón-Aguilera 2015), these studies have been carried out mostly on coastal locations of the northern portion of the region (Gulf of California and Mexican Pacific), whereas no study has examined functional diversity on an oceanic island of the TEP. The study of functional aspects of communities, especially in areas with little or no local human influence, such as isolated oceanic islands, has only recently been receiving increased attention (Sandin et al. 2008; Mora et al. 2011; Williams et al. 2015). These studies point to specific characteristics shared by oceanic islands, such as high productivity (Gove et al. 2016), high levels of endemism, reduced gene flow among populations (Hachich et al. 2015), and high density of top predators (Sandin et al. 2008), all of which convert these islands into important natural laboratories to studies of marine communities. Additionally, these islands because of their isolation are often nearly untouched by humans, and may exhibit features, such as “inverted biomass pyramids”, typical of pristine places (Trebilco et al. 2013).

Despite the importance of remote oceanic islands as the last pristine marine sites, the number of studies focused on their marine communities is low (Friedlander and DeMartini 2002; Sandin et al. 2008; Williams et al. 2015). This is in part linked to logistical constraints imposed by the remote location of these

islands, which increase the costs and difficulties of acquiring quantitative data of the marine communities and local factors that influence the species composition (Dawson 2015; Luiz et al. 2015), such as wave exposure, depth, and anthropogenic influence, among others. This lack of information is most evident in regions with high geographic isolation, such as the TEP, whose isolation from the central Pacific by the Eastern Pacific Barrier (EPB) and from the Caribbean by the closure of the Isthmus of Panama, has led to high endemism but low richness at the species level (Zapata and Robertson 2007; Robertson and Cramer 2009).

Malpelo Island is a small remote island located in the TEP region, which has low reef fish species richness compared to oceanic islands in the Indo-Pacific and Caribbean Regions (Kulbicki et al. 2013). Malpelo, together with the Revillagigedos, Clipperton, Cocos and Galapagos islands define a biogeographical sub-province distinct from the coastal adjacent regions, due to the presence of a small number of island endemics and a high number of transpacific species (Robertson and Cramer 2009). Currently, this island is the only Marine Protected Area (MPA) in the Colombian Pacific recognized as a World Heritage site since 2006 owing to its unique characteristics and importance as a stepping-stone for marine wildlife between the continent and other oceanic islands of the TEP (McCosker and Rosenblatt 1974). Additionally this island has a high endemism and a high concentration of sharks and mega-fauna (Bessudo et al. 2011). Malpelo Island is also part of “Eastern Tropical Pacific Marine Conservation Corridor”, an international marine conservation initiative that additionally include the Galápagos, Gorgona, Coiba and Cocos Islands. Despite its status as a World Heritage Site and MPA, populations of large fishes have drastically decreased around Malpelo due to illegal fishing activities (Soler et al. 2013). This type of impact has never been locally evaluated despite the increasing human population and its continuing appetite for natural resources.

Our objective here is to describe the temporal and spatial variation in species richness, functional richness, density and biomass of the Malpelo Islands reef fish assemblages based on data obtained in two years. More specifically, this study aims to answer the following questions: 1) How did the species richness, functional richness, density and biomass of the fish assemblages vary between 2010 and 2015? 2) How do these same attributes vary spatially across the island? 3) What is the relative importance of endemic species vs widely

distributed species in terms of total density and biomass? 4) How do wave exposure and depth influence the species richness, functional richness, density and biomass of fishes concentrated in different trophic groups, size classes and geographic distribution classes across the island? 5) How does the functional structure of the fish assemblage vary across three different scales (i.e. regional species pool, local species pool, and species observed in underwater visual censuses)? 6) Are the fish assemblages in Malpelo more redundant or vulnerable when compared to the TEP regional species pool, given their isolation level and small habitat area?

Materials and methods

Study area

This study was carried out at Malpelo Island (4°00'05" N, 81°36'30" W; Fig. 1), a protected Sanctuary of Marine Fauna and Flora, located 377 km from the nearest reef habitat (Gorgona Island) and 395 km off the coast of Colombia (Fig. 1). The oceanic waters surrounding Malpelo are seasonally influenced by four currents: the North Equatorial Countercurrent, the South Equatorial Countercurrent, the Colombia Current, and the Panama Cyclonic Current (Rodríguez-Rubio et al. 2007). The annual mixing period of these currents depends on the variation of the Intertropical Convergence Zone, with the degree of mixing depending on long-term cycles such as the El-Niño Southern Oscillation (Rodríguez-Rubio and Schneider 2003). This island is of volcanic origin and is subjected to constant erosion of its coastal cliffs. The seabed around the island is dominated by steep walls and mostly covered by loose boulders resulting from landslides, though there are some small terraces with underdeveloped coral formations (Zapata and Vargas-Ángel 2003).

Fieldwork was conducted during two SCUBA diving expeditions, one in 2010 and another in 2015. During these expeditions, we sampled four sites around the island (one site in 2010 and four sites in 2015), which were classified into 'sheltered' and 'exposed' according to wave exposure and prevailing winds. The 'sheltered sites' of "El Arrecife" (AR) and "La Nevera" (LN) are unique sites in Malpelo in the sense that they are characterized by coral development and structural complexity (Zapata and Vargas-Ángel 2003; Chasqui and Zapata 2007). On the other hand, the 'exposed' sites of "Bajo de Junior" (BJ) and "Pared del Náufrago" (PN) are mainly

rocky reefs with low structural complexity, formed by large boulders and vertical walls, with comparatively lower coral cover (*personal observations*: Fig. 1).

Reef fish assemblages

We estimated reef fish species, density and biomass for 103 underwater visual censuses (UVCs) along transects of 40 m² (20 × 2 m). This sampling involved identifying, counting and estimating the size (total length in cm) of all fishes observed both in the water column and on the bottom along the 20 m-long transect (see Floeter et al. 2007). We had two sampling schemes, one for comparing temporal and the other for testing spatial variation in reef fish assemblages. For the temporal analysis, we carried out 50 UVCs at El Arrecife location in 2010 and repeated the sampling at the same location in 2015, but made only seven UVCs. To compare spatial variation in reef fish assemblages, we sampled three more locations (totaling four locations) in 2015. Therefore, our spatial analysis was restricted to the 2015 sampling whereas temporal changes in reef fish assemblages are specific to El Arrecife location.

Multiple UVCs were performed in each location in shallow (7–17 m) and deep (17–30 m) area, and allowed the estimation of species richness, as well as density and biomass for each species (Fig. 1). We estimated the weight of each fish using the allometric length-weight conversion $W = a \times TL^b$, where parameters a and b are species-specific constants, TL is the estimated total length in cm, and W is weight in grams. Length-weight parameters (a and b) were obtained for each species from FishBase (Froese and Pauly 2016). All shark and ray species were excluded from the analysis since they may disproportionately increase the biomass values, especially in transects with small areas (Ward-Paige et al. 2010). Finally, based on Rubio et al. (1992) and Robertson and Allen (2016), we also compiled a reef fish checklist (i.e. all species that are reported in a place) for Malpelo to compare the characteristics of the local and regional species pools.

Geographic distribution

All reef fish recorded during the UVCs and from the checklists were classified into six classes according to their geographic distribution (Robertson and Allen 2016): (1) Species endemic to Malpelo (LOC); (2) species that occur only in one or more of the TEP oceanic

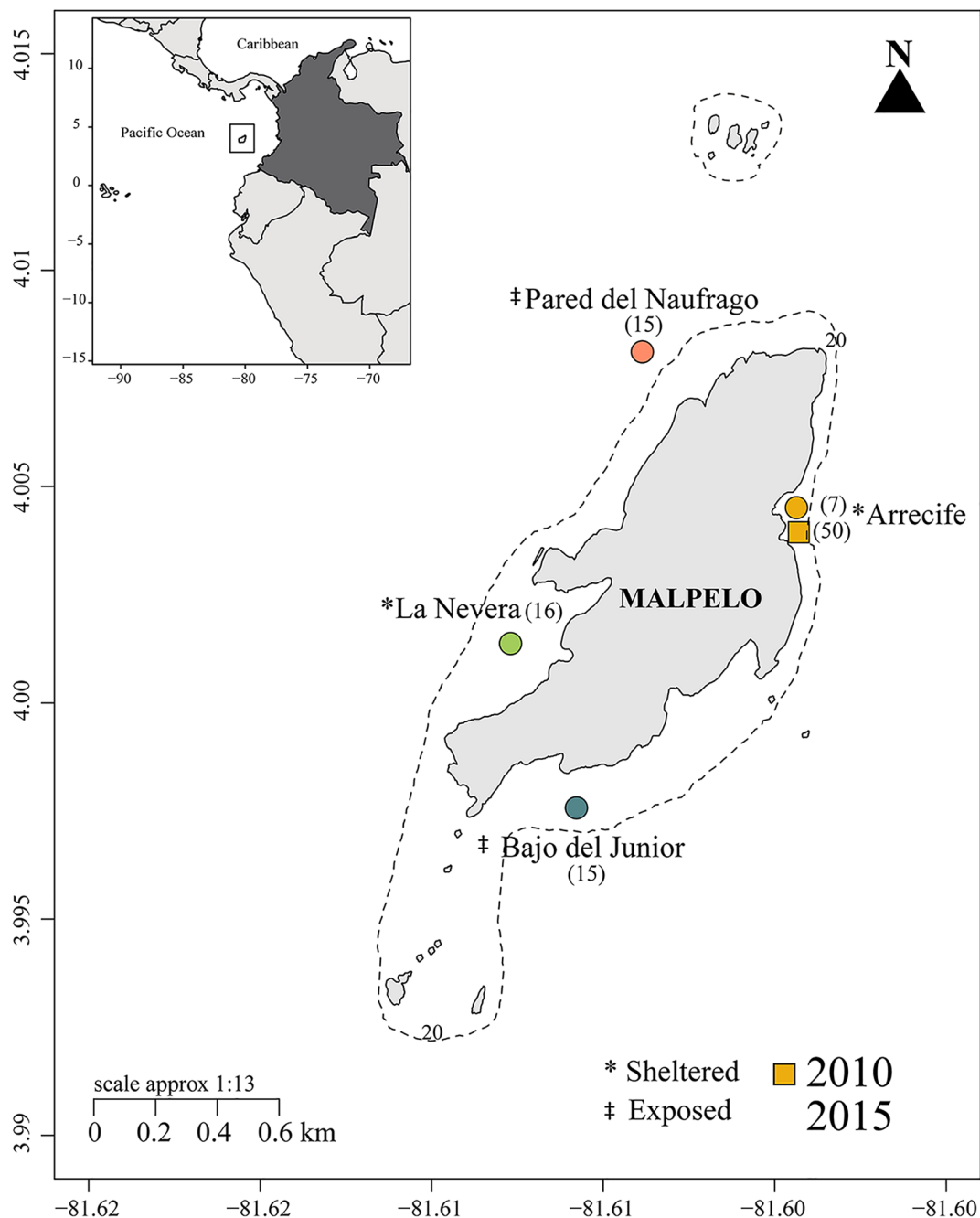


Fig. 1 Map of Malpelo Island showing the four sampling sites. The map also indicates the location El Arrecife, which was visited both 2010 and 2015, as well as exposed and sheltered sites.

Numbers within parenthesis represent the total number of underwater visual censuses. The dashed line represents the 20-m isobath

islands (ITEP); (3) species restricted to the TEP (on both continental coast and islands: CTEP); (4) species shared with the Central Pacific (CP); (5) species with occurrence in the TEP and Atlantic Ocean (AT); and (6) species with circumglobal distribution (CG).

Fish functional richness

All species were classified according to six different life-history traits using functional properties defined by Moullot et al. (2014): (1) Species maximum body size:

<7 cm, 8–15 cm, 16–30 cm, 31–50 cm, 51–80 cm or >80 cm; (2) Mobility: sedentary (including territorial species), mobile or very mobile; (3) Period of activity: diurnal, nocturnal, or both; (4) Schooling: solitary, pairing, small groups (3–20 individuals), medium groups (20–50 individuals) or large groups (>50 individuals); (5) Position in the water column: benthic (species associated with the bottom), benthopelagic, or pelagic and (6) Trophic group: herbivores-detritivores (feed upon turf and filamentous algae and/or detritus), macroalgae-feeders (large fleshy algae and/or seagrass), sessile invertebrate feeders (e.g., corals, sponges, ascidians), mobile invertebrate feeders (benthic prey, such as crabs and mobile mollusks), planktivores (small organism in the water column), piscivores (fish and cephalopods) or omnivores (both vegetal and animal material). Functional Entities (FEs) were defined as a combination of the six life history traits. We used the number of FEs as a proxy for the functional richness of each fish census.

Statistical analysis

Temporal analysis

To quantify temporal changes in fish assemblages, we compared UVCs from El Arrecife between 2010 and 2015. As the number of UVCs sampled varied between these periods (50 in 2010 and seven in 2015; AR: Fig. 1), we randomly sampled seven UVCs from 2010 and repeated this procedure 999 times to estimate mean differences in richness, density, biomass, and FEs richness of comparable sample sizes. This procedure simulates a sample-based rarefaction procedure that enables temporal comparisons of reef fish assemblage parameters while controlling for sample size differences (Gotelli and Colwell 2001). We explored the temporal variations of fish density and biomass using GLM with Gamma distribution since these data are positive and continuous and tend to have a log-normal distribution (Zuur et al. 2009).

Spatial analysis

We explored the spatial variations in fish assemblages among the four sampling sites in the 2015 survey using rarefaction curves (species richness and functional richness) and generalized linear mixed model –GLMM – (fish density and biomass) with a Gamma distribution.

We considered depth classes (shallow and deep) and sites as fixed factors, while transect were defined as a random factor to attempt to account for spatial autocorrelation. We used a Gamma distribution in all of the above models as density and biomass are overdispersed, positive and continuous response variables (Zuur et al. 2009). We used a Tukey test for testing the difference observed in the GLMMs, using the function “*glht*” within the package *multcomp* (Hothorn et al. 2008). Finally, we compared the contribution of local endemic species vs non-endemic species within the same family to density and biomass per transect using Mann-Whitney *U*-tests.

We evaluated the effect of wave exposure and depth on species richness, functional richness, density and biomass classified into different (1) trophic groups, (2) size classes and (3) geographic distribution levels, with permutational Multivariate Analyses of Variance (PERMANOVA) using wave exposure (2 levels: sheltered and exposed) and depth (2 levels: shallow and deep) as factors (Anderson 2001). The PERMANOVAs were performed using a Bray-Curtis dissimilarity distance matrix. The statistical significance of the PERMANOVA was tested with 999 permutations under a reduced model and type II (conditional) sums of squares (Anderson et al. 2008). PERMANOVA analyses were made using the function “*adonis*” within the package *vegan* (Oksanen et al. 2015). To explore the multivariate patterns observed in the PERMANOVA test, we used a Redundancy Analysis (RDA) to graphically display the influence of the above factors (wave exposure and depth class) on the species richness, functional richness, density and biomass of the reef-associated fish assemblages.

We used the six life history traits assigned to each species observed in 2015 to compare the multidimensional functional space occupied by the regional species pool (species with occurrence in the TEP), the local species pool (species registered in local checklist), and species detected in UVCs. The multidimensional functional space was built from a Principal Coordinates Analysis (PCoA) using a Gower’s distance dissimilarity matrix, which allows mixing qualitative and quantitative data (Villéger et al. 2008; Mouillot et al. 2014). The intent was to understand potential links between three levels of spatial organization and the decrease in functional richness according to isolation level (Bender et al. 2016). Finally, we analyzed the redundancy within functional entities for both the local checklist and the

assemblages determined by UVCs and the proportion of vulnerability (functional entities with only one species). To test whether the functional richness observed at each scale (TEP pool, checklist and UVCs) was significantly different from the functional richness of a random subset of species, we used null models based on randomization of species pools. To simulate a realistic pool of species in each realm, the number of species per taxonomic order was kept constant in the random choice process (999 iterations). Random matrices were generated through the “oecosimu” function available in the *vegan* R package (Oksanen et al. 2015). All statistical analyses were performed in R software version 3.2.4 (R Core Team 2016).

Results

Temporal analysis

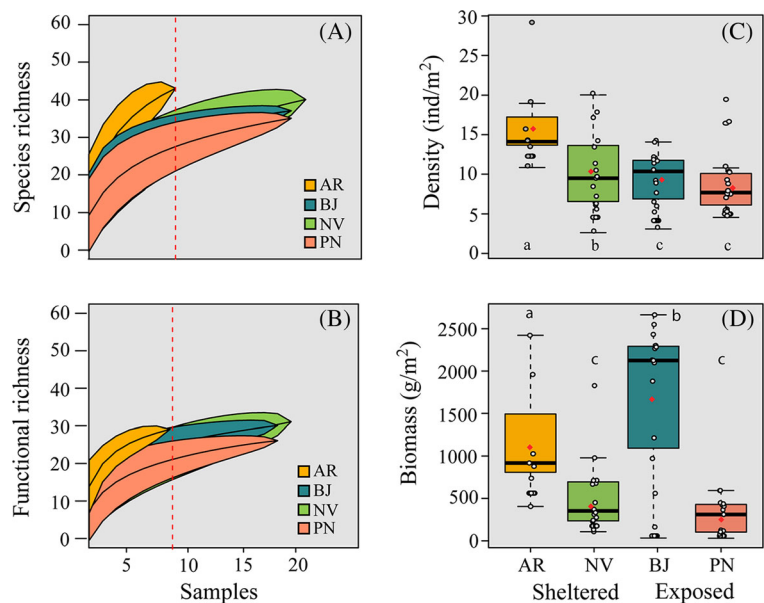
A total of 87 species (37 families) was recorded during the two surveys. We found during the 2010 survey, 70 species (35 families), whereas in 2015 we found 65 species (29 families). Richness ranged from five to 30 species per transect. We detected higher species richness and functional richness in 2015 compared to 2010 (Fig. S1 A, B). We also observed some exclusive species for each year, 22 species in 2010 and 16

in 2015 (Table S1). Species exclusive to 2010 were mainly piscivores and mobile invertebrate feeders (41% each), planktivores (13.6%) and omnivores (4.4%) (Table S1). On the other hand, the exclusive species in 2015 were mainly mobile invertebrate feeders (43.7%), planktivores (31.3%), piscivores (12.5%), herbivores-detritivores and omnivores (6.3% each) (Table S1). We found differences in density (2010: $9.30 \text{ ind/m}^2 \pm 0.68 \text{ s.e.}$; 2015: $9.77 \text{ ind/m}^2 \pm 0.7 \text{ s.e.}$) and biomass (2010: $706.2 \text{ g/m}^2 \pm 73.2 \text{ s.e.}$; 2015: $879 \text{ g/m}^2 \pm 116.2 \text{ s.e.}$) between sampling years (GLM: $p\text{-value} < 0.05$; Fig. S1 C, D). The species that most contributed to the total density for both years were the regional endemics: *Chromis atrilobata*, *Apogon atradorsatus*, *Cirrhitichthys oxycephalus* and *Paranthias colonus* (Table S1). In terms of biomass, the dominant species were the regional endemic *Lutjanus viridis*, *L. jordani*, *Gymnothorax dovii*, *Paranthias colonus*, and the circumglobal *Seriola rivoliana* (Table S1).

Spatial analysis

We found a higher species richness in “El Arrecife” (AR), followed by “La Nevera” (NV), “Bajo de Junior” (BJ) and “Pared del Náufrago (PN) (Fig. 2a), but no difference was detected for functional richness (Fig. 2b). The mean density found in 2015 was 5.95 ind/m^2 and varied from 0.02 to 140.4 ind/m^2 (Table S1). There was

Fig. 2 Comparison among the four sampling sites in 2015. **(a)** Species richness, **(b)** Functional richness, **(c)** Density and **(d)** Biomass. Each color represents a different site. Boxplots show medians (black line), mean (red diamond), upper and lower quartiles, and 95% confidence intervals. Letters show statistical groupings (Tukey post hoc) with boxplot having different letters being significantly different. Boxplot with the same letter are not significantly different. Red lines in **a** and **b**, represent the standardized number of surveys. Each point represents an underwater visual census



a significant difference in mean density among sampling sites, but not between the two depth classes (GLMM: p -value < 0.05 ; Fig. 2c). AR and NV were the most different sites (Tukey test: p -value < 0.05 ; Fig. 2c), and were also the sites that presented the highest mean densities (15.1 ind/m² and 10.2 ind/m², respectively), whereas PN and BJ had a lower mean density (9.01 ind/m² and 7.58 ind/m², respectively; Fig. 2c). The mean biomass in 2015 was 872 g/m² and varied from 5.03 to 2683.0 g/m² (Table S1). There was a significant difference in mean biomass among sampling sites, but not between the two deep sites (GLMM: p -value < 0.05 ; Fig. 2d). BJ and AR presented significantly higher

biomass values (Tukey test, p -value < 0.05 ; 1730 g/m² and 1212 g/m²; Fig. 2d), whereas NV and PN had lower mean biomass values (474 g/m² and 229 g/m²; Fig. 2d).

Planktivores accounted for 64.8% of all individuals recorded, followed by mobile invertebrate feeders (22.6%), piscivores (8.96%), herbivores-detritivores (2.63%), macroalgae-feeders, sessile invertebrate feeders and omnivores ($<1\%$ each; Fig. 3a). The most common size class among the fish assemblages was 8–15 cm (47.64%) followed by the classes of 31–50 cm (35%), 16–30 cm (10.5%), 51–80 cm (5.06%), >80 cm (1.56%) and 0–7 ($<1\%$; Fig. 3b). Species present in one or more of the TEP oceanic islands (ITEP) were the

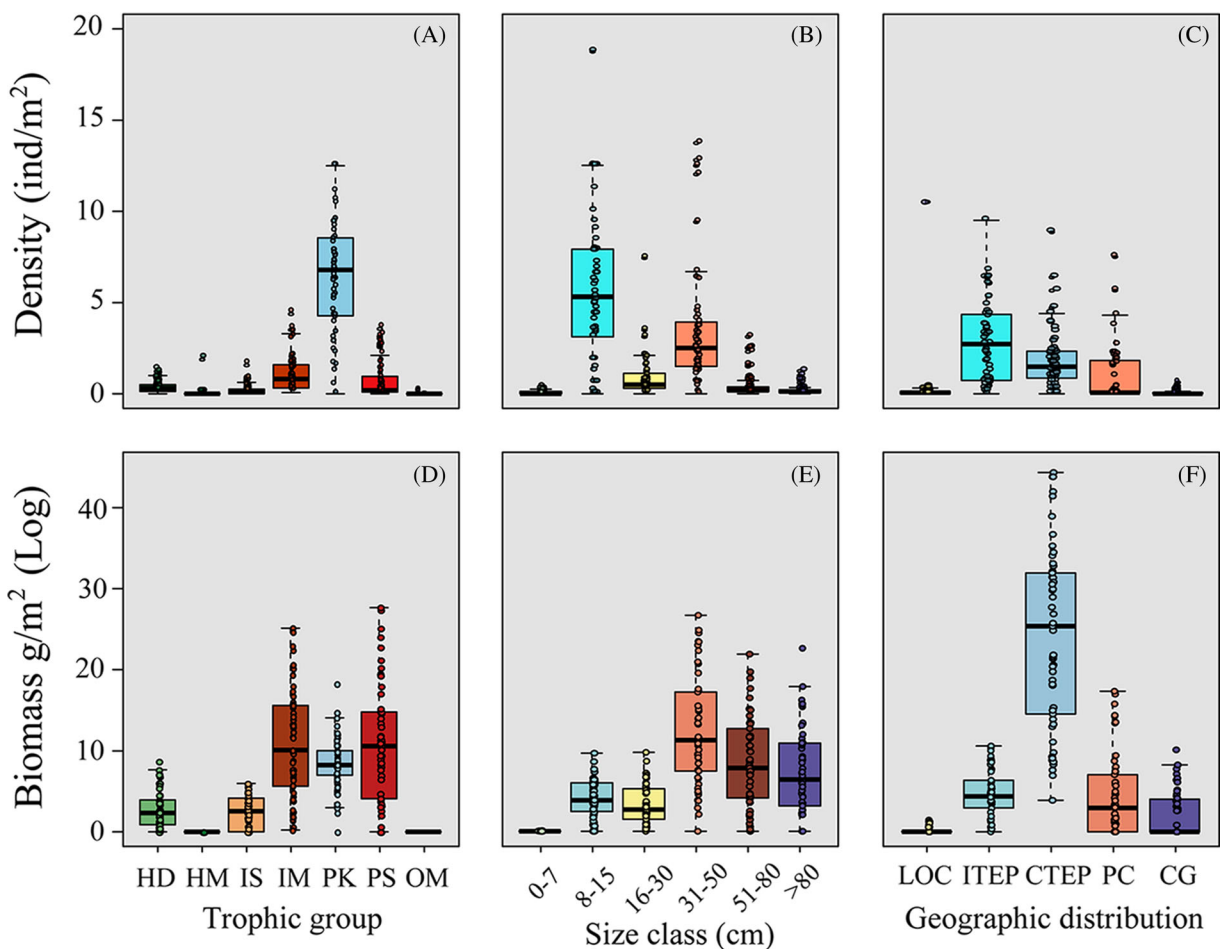


Fig. 3 Comparison of density and biomass during the 2015 sampling in Malpelo Island. (a) Density per trophic groups. (b) Density per size classes. (c) Density per geographic distribution classes. (d) Biomass per trophic groups. (e) Biomass per size classes. (f) Biomass per geographic distribution classes. Each color represents a different a class. Boxplots show medians (black line), upper and lower quartiles, and 95% confidence intervals. Each

point represents an UVC. Trophic groups: herbivores-detritivores (HD), macroalgae-feeder (HM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK), piscivores (PS) and omnivores (OM). Geographic distribution: Circum-global (CG), Pacific (PC), Coastal Tropical Eastern Pacific (CTEP), restricted to oceanic islands in Tropical Eastern Pacific (ITEP) and local endemic (LOC)

most important for density (59.4%; Fig. 3c), followed by species with wide distribution in the TEP (CTEP; 29.6%), species shared with the central Pacific (PC; 10.33%), endemics (LOC), and circumglobally distributed species (CG; <1%). Species shared with the Atlantic Ocean were not observed during the 2015 sampling (Table S1). In terms of biomass, piscivores were the most important (54.6%), followed by planktivores (23.3%), mobile invertebrate feeders (16.7%), sessile invertebrate feeders (3.3%), herbivores-detritivores (1.9%), macroalgae-feeders, and omnivores (<1%; Fig. 3d). The size class with the highest biomass was 31–50 cm (48.7%), followed by the class of 51–80 cm (26.6%), >80 cm (21.3%), 8–15 cm (2.2%), 16–30 cm (1.2%), and 0–7 cm (<1%; Fig. 3e). Species considered as CTEP had the largest contribution to biomass (82%), followed by CG species (10.5%), PC (4.3%), ITEP (3.1%) and LOC (<1%; Fig. 3f).

During the UVCs we observed 80% (four out of five) of all endemic species reported from Malpelo: *Axoclinus rubinoffi*, *Acanthemblemaria stephensi*, *Lepidonectes bimaculatus* and *Halichoeres malpelo* (the fifth endemic, the gobiid *Chriolepis lepidota*, has never been observed after its initial collection of two individuals with rotenone in 1972; Findley 1974). Local endemic species and non-endemic species differed in their contribution to density (Wilcoxon's test, $W = 320$, $p < 0.01$) and biomass (Wilcoxon's test, $W = 107$, $p < 0.01$), being lower for local endemic than for those

non-endemic species within the same families (Fig. S2 A B). Among endemic species, the most important in terms of density was *A. rubinoffi* (0.013 ind/m²), followed by *H. malpelo* (0.011 ind/m²), *L. bimaculatus* (0.008 ind/m²) and *A. stephensi* (0.001 ind/m²). For biomass, the most important endemic species was *H. malpelo* (0.27 g/m²), followed by *L. bimaculatus* (0.004 g/m²), *A. rubinoffi* (0.003 g/m²) and *A. stephensi* (0.0004 g/m²) (Table S1). Among the endemic species observed during the sampling, three are mobile invertebrate feeders (75%) and one is planktivore (25%). Three of these endemic species are in the 0–7 cm size class (*A. rubinoffi*, *A. stephensi*, and *L. bimaculatus*), whereas *H. malpelo* is in the 8–15 cm size class.

Our results show that both wave exposure and depth influenced the fish assemblages of Malpelo (PERMANOVA: p -value <0.05; Table 1). However, the magnitude and direction of these effects varied. For instance, wave exposure was the unique factor that influenced species richness of several trophic groups, size classes and geographic distribution classes (Table 1). Species richness was concentrated in sheltered places (Fig. 4a, b, c). Functional richness observed for different trophic groups, size and geographic distribution classes was influenced exclusively by wave exposure, which was concentrated in sheltered and shallow places (Fig. 4d, e, f; Table 1). Density observed for the different trophic groups, size and geographic distribution classes was influenced by depth and interaction of depth and wave

Table 1 The influence of depth and exposure on species richness, functional richness, density and biomass of reef fishes for each trophic group, size and geographic distribution classes in 2015. Significant values ($p < 0.05$) in bold

Source	Species richness				Functional richness				Density				Biomass			
	df	SS	F	P	df	SS	F	P	df	SS	F	P	df	SS	F	P
Trophic group																
Depth	1	0.22	2.29	0.08	1	0.09	2.01	0.11	1	0.36	3.12	0.02	1	1.18	6.02	0.001
Exposure	1	0.02	0.45	0.03	1	0.25	5.2	0.002	1	0.25	2.19	0.06	1	1.02	5.23	0.002
Depth:Exposure	1	0.02	0.37	0.8	1	0.11	2.24	0.07	1	0.26	2.27	0.06	1	0.38	1.93	0.08
Size classes																
Depth	1	0.14	2.53	0.52	1	0.16	3.09	0.06	1	0.37	3.23	0.01	1	1.08	5.35	0.01
Exposure	1	0.32	6.01	0.001	1	0.27	5.23	0.003	1	0.25	2.12	0.07	1	1.11	5.48	0.01
Depth:Exposure	1	0.08	1.54	0.19	1	0.07	1.45	0.22	1	0.46	3.92	0.01	1	0.31	1.52	0.16
Geographic distribution classes																
Depth	1	0.1	2.17	0.1	1	0.11	2.45	0.08	1	0.51	4.48	0.03	1	1.3	7.41	0.01
Exposure	1	0.32	6.76	0.02	1	0.24	5.15	0.003	1	0.19	0.16	0.16	1	0.99	5.64	0.01
Depth:Exposure	1	0.01	0.33	0.79	1	0.01	0.31	0.81	1	0.24	2.11	0.1	1	0.33	1.89	0.11

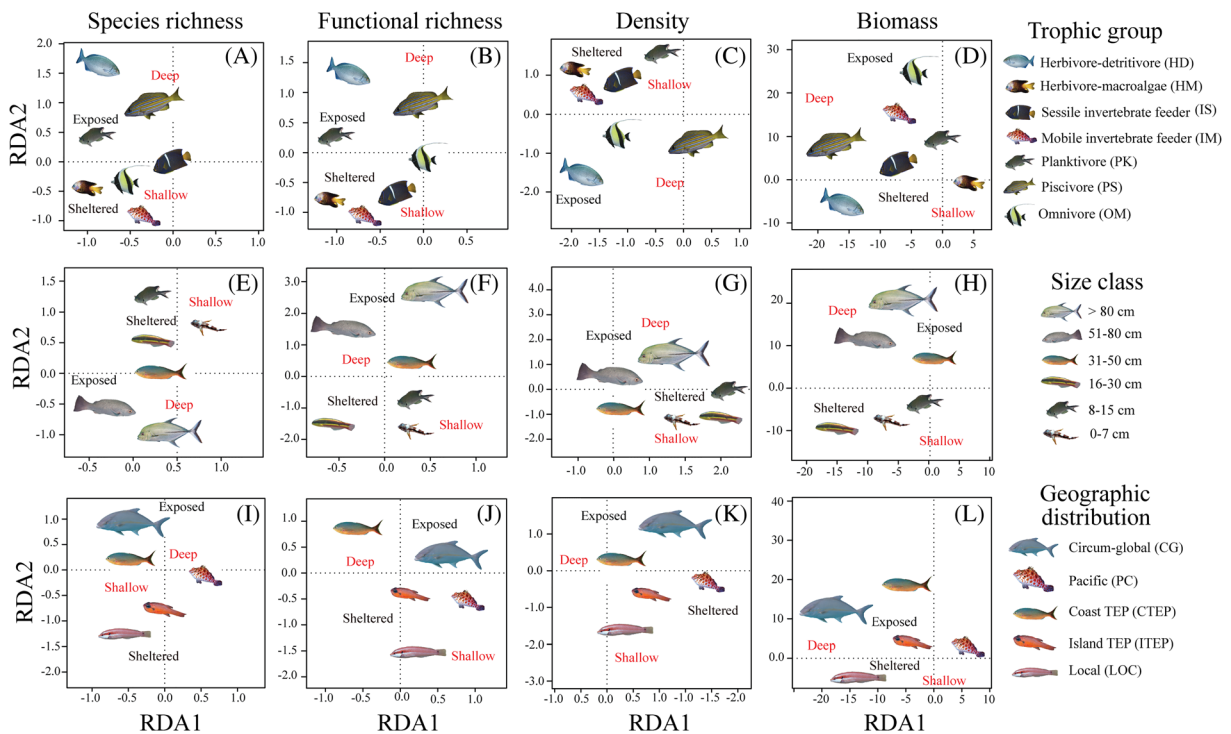


Fig. 4 Redundancy analysis biplots representing the influence of environmental factors wave exposure (Exposed and Sheltered: Black labels) and depth classes (Shallow and Deep: Red labels) on the species richness (a, e, i), functional richness (b, f, j), density

(c, g, k) and biomass (d, h, l) for each trophic group, size class and geographic distribution class. Each fish figure represents the most common species observed in each level

exposure (Table 1), and was also concentrated in sheltered and shallow places (Fig. 5g, h, i). Finally, the biomass observed for the different trophic groups, size and geographic distribution classes were influenced by both wave exposure and depth, and was concentrated in exposed and deep places (Fig. 5j, k, l; Table 1).

The Malpelo fish checklist represented 35% of the reef-associated species in the TEP, and the species recorded during our UVCs represented 15% of those TEP species (Fig. 5a). The proportion of functional entities (FEs) present in the TEP was respectively 60% for the Malpelo checklist (121 FEs) and 30% for the UVCs (62 FEs: Fig. 5a). The high number of FEs found in the species checklist of Malpelo occupied a large proportion of the functional volume calculated for the TEP region, while the functional volume calculated for UVCs occupied the central part of the total TEP volume (Fig. 5b). The most common species trait combination reported in the checklist of Malpelo was: sedentary species, diurnal, solitary, bottom-dweller, 8–15 cm and mobile invertebrate feeder, such as *Cirrhitichthys oxycephalus*, whereas for the UVCs the most frequent trait combination was:

mobile species, diurnal, solitary, bottom-dweller, size class 51–80 cm and mobile invertebrate feeder, such as *Bodianus diplotaenia*. The proportion of FEs with at least two species changed with scale: 60% of FEs from the regional pool, 22% from the local checklist and only 10% from the species observed in the UVCs (Fig. 6a). Finally, we observed that the fish assemblage registered in local checklist and observed in UVCs at Malpelo was disproportionally represented by vulnerable FEs (Null model p -value <0.01; Fig. 6b).

Discussion

The composition of reef fish assemblages at Malpelo was different between the two years sampled (48 species in common: 55.2%), which can be associated with changes in oceanographic features, such as upwelling (Luiz et al. 2015; Gove et al. 2016). This factor probably increased primary production thus favoring planktivores (McClanahan and Branch 2008), which presented a high density and the highest richness in 2015. These

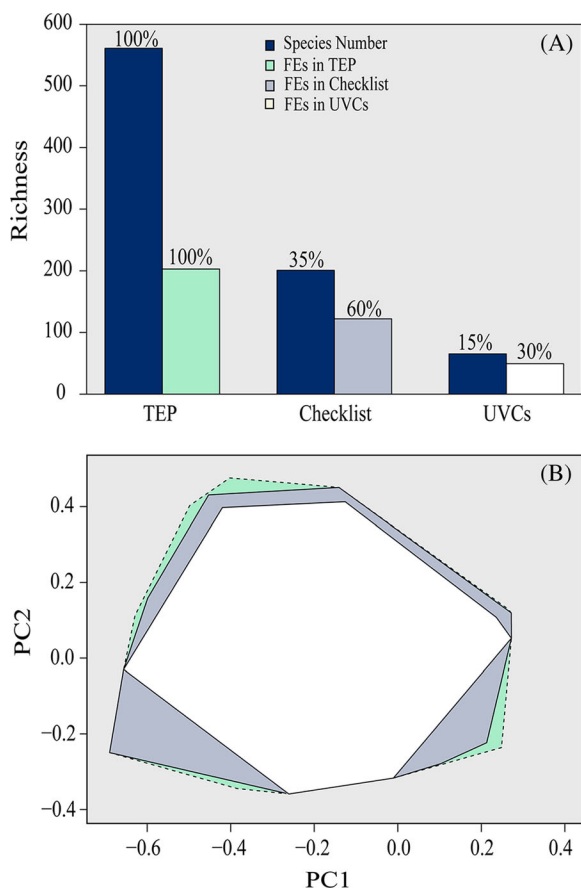


Fig. 5 Comparison of the functional richness of Malpelo Island in relation to the regional species pool and the local pool (Checklist and UVCs). **(a)** Number of species (dark blue bars) and number of functional entities (FEs) found in the regional pool (light green bar), in the Malpelo checklist (gray bar), and in the UVCs (white bar). **(b)** Representation of the first and second, component axes of the functional volume across the three levels with the corresponding convex hull. Dashed lines in light green represent the FEs occurring in the entire TEP, gray color represents FEs observed in Malpelo checklists and white represents FEs observed during the UVCs

differences could also be associated with natural variations in species abundance (McGill et al. 2007; Locey and White 2013), which may have affected the detectability of species during the UVCs (i.e. the common and abundant species being the most observed during surveys). However, our findings showed that such turnover was among different trophic groups, which could suggest a change in the trophic structure of the assemblage over time. The number of species detected during our UVCs (87 species in two years) is lower than for nearby oceanic islands, such as Galapagos (171 species of reef fish excluding elasmobranchs; Edgar et al. 2004) and

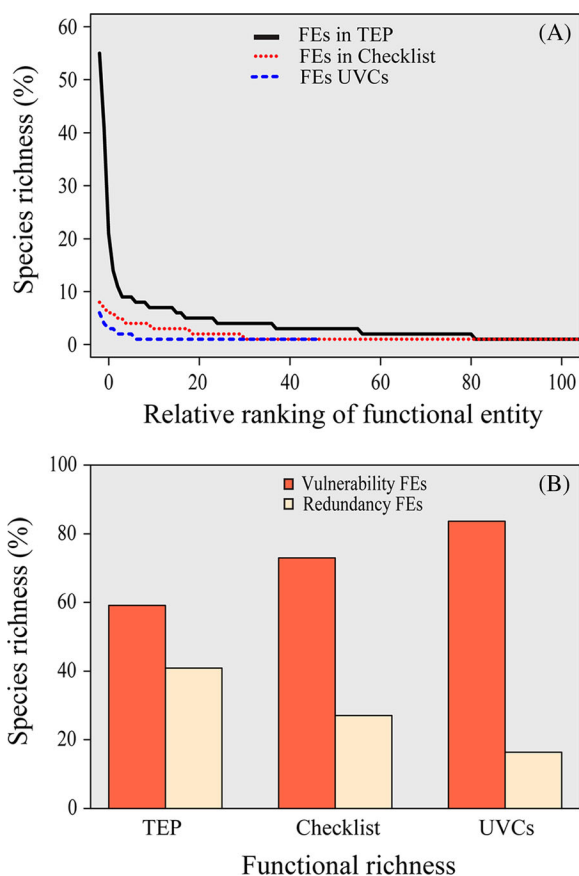


Fig. 6 Species richness related to the number of functional entities in different scales. **(a)** Perceptual species richness related to relative ranking of functional entities (FEs), representing across the TEP region (black solid line), Malpelo checklists (red line), and UVCs (dashed blue line). **(b)** Proportion of vulnerable FEs for each scale: regional species pool, Malpelo checklist and UVCs

Cocos Island (102 species of reef fish excluding elasmobranchs; Friedlander et al. 2012). These differences are likely to be associated with the local species pool, which is smaller in Malpelo (202 species) compared to these islands (Galapagos: 291 species and Cocos: 236 species; Robertson and Allen 2016), as well as differences in sampling protocols (i.e. our transects were smaller and less numerous than those in other studies). The dominance of a small number of species in density and biomass during the two sampling years is consistent with general patterns observed for diversified assemblages, where abundance or biomass are dominated by a restricted number of species, most other species being uncommon to rare (Gaston et al. 1997; Hubbell 2001; Mouillot et al. 2013).

Our results showed a variation in species richness, density and biomass across four sampling sites in 2015,

which could be associated with particular features at each site. For instance, “El Arrecife” and “La Nevera” are unique sites in Malpelo with sheltered areas that allow the development of high coral cover and great structural complexity (Zapata and Vargas-Ángel 2003; Chasqui and Zapata 2007). Such features tend to favor small species (e.g., *A. atradorsatus*, *C. oxycephalus* and *T. lucasanum*) that can more easily find shelter and food within coral branches. The two other sites, “El Bajo de Junior” and “Pared del Náufrago”, are mainly rocky reefs with low structural complexity, formed by large boulders and vertical walls, with comparatively low coral cover (personal observations). These types of reefs tend to favor the presence of medium and large-bodied species, usually in high densities. On the other hand, the lack of difference in the functional richness observed among sites reflects the functional homogenization despite taxonomic differences and the lack of influence from environmental factors on the functional structure of fish assemblages at such a small spatial scale. Moreover, it can be related to the wide home range of a number of species which travel around the island, mainly schooling and large species in search of food, cleaning service or refuge (Quimbayo et al. 2014, 2016).

Despite the differences observed among sites, density and biomass were dominated by planktivores and piscivores respectively, which is consistent with other MPAs on oceanic islands. These places often support local upwellings, which may bring nutrients favorable to plankton and therefore favor plankton feeders (Gove et al. 2016). In addition, these islands are under little human influence, which allows the concentration of large species (Sandin et al. 2008; Aburto-Oropeza et al. 2011; Edgar et al. 2011; Longo et al. 2015). The low contribution of mobile invertebrate feeders to biomass could be related to the fact that all these species were mainly small and presented low densities in Malpelo. The low density and biomass values for species classified as herbivores-detritivores, macroalgae-feeders, sessile invertebrate feeders and omnivores could be associated both with the low number of these species within the TEP species pool as well as with local conditions (bottom dominance by calcareous algae) which may not favor the presence of these groups at Malpelo. A comparison of the biomass values found in Malpelo with those from other oceanic islands considered as pristine (Fig. S3), indicates that Malpelo even when excluding elasmobranchs, is remarkable for its high concentration of large species such as groupers,

jacks, moray eels and snappers. The proportion of piscivores on Malpelo is comparable to what is found on other islands, which are considered as pristine such as Chagos and Cocos Island (Fig. S3). On the other hand, Malpelo differs from these islands because of the low contribution of herbivores and the high contribution of plankton feeders to its total biomass.

The considerable contribution of regional endemics (CTEP) to density and biomass could be associated with the high level of endemism observed in the TEP (Zapata and Robertson 2007; Robertson and Cramer 2009; Kulbicki et al. 2013). Species belonging to the CTEP group are rather large. Large species tend to be found in higher proportions on small isolated islands (Kulbicki et al. 2015), which may in part explain the contribution of CTEP species to density or biomass on Malpelo. On the other hand, the high contribution to density of species endemic to TEP islands (ITEP) could be related to the importance of endemics in systems such as the Hawaiian islands (DeMartini and Friedlander 2004), Easter Island (Friedlander et al. 2013), and Kermadec (Cole et al. 1992). The low density values observed for endemic species in Malpelo (four species: LOC) are opposite to those patterns observed for the ITEP species. The reasons for this difference are unknown, but a comparative analysis of their phylogeny may reveal major differences in their evolutionary history. In Malpelo, the density of the LOC endemic species reported here is 0.034 ind/m². However, when performing censuses focused on these LOC endemic species, Chasqui et al. (2011) registered an average of 0.27 ind/m², almost eight times higher than ours. These differences are likely to be associated with the type of census used by Chasqui et al. (2011), which focused exclusively on these endemic species and was adapted for the analysis of populations of small-bodied species. The contribution in density of transpacific species in the fish assemblages of Malpelo (9.3%), supports the findings of Robertson and Cramer (2009), who highlighted that these species form a sizeable part of the total reef fish assemblages in TEP oceanic islands. The presence and importance of species with circumglobal distribution in biomass reflects the specific traits of these species, such as large body size, unspecialized diet, high reproductive capacity and long pelagic larval duration (Luiz et al. 2012), which favor their dispersal and colonization of isolated areas.

Wave exposure and depth played an important role in the fish distribution at Malpelo. Shallow sheltered areas presented high species richness, functional richness and

abundance, whereas exposed and deep sites were dominated by large-bodied species. These results support those found by Dominici-Arosemena and Wolff (2006), who observed a decrease in abundance of planktivorous species such as *Chromis atrilobata*, territorial herbivores such as *Stegastes arcifrons* and small species as depth increases. According to them, such a relationship would be due to a decrease in both food (plankton, algae) and refuge. Similar patterns have been observed in other oceanic islands of the Pacific (Friedlander and Parrish 1998; Friedlander et al. 2016) and Atlantic Oceans (Pinheiro et al. 2011; Luiz et al. 2015). The increase in biomass in exposed or deep places is related to space requirements of large species, which use mostly areas of high spatial relief with strong hydrodynamics (Friedlander and Parrish 1998; Schultz et al. 2014).

The large number of FEs found in both species checklist and UVCs are evidence of a high functional richness, despite the fact that only 35% and 15% of the regional species pool were registered in the local checklist and the UVCs, respectively. These results suggest that the relatively high functional richness observed at Malpelo is not related to taxonomic richness, but to the high endemism of the TEP (Mora and Robertson 2005a). These results also support the idea that functional richness is different from taxonomic richness regarding the theory of island biogeography (which considers the effects of area and isolation), since, despite its small area and long distance from the coast, Malpelo harbors a high proportion of the regional FEs. This result supports the findings of Bender et al. (2016) who observed that isolated places possess a subset of functional richness of the regional functional pool, which is independent of taxonomic richness. The high overlap found among the functional spaces of the TEP, the local species checklist and UVCs, is related to similar overlaps found at a much wider scale by Mouillot et al. (2014) who compared the functional volume across realms for reef fish assemblages. This suggests a high conservatism of ecological functions across scales and calls attention to the vulnerability of the fish assemblages of Malpelo as they have a high proportion of vulnerable FEs. When a species that constitutes a vulnerable FEs disappears or becomes so rare that it no longer fulfills its ecological role, there is a loss in function that may have larger consequences than the same fate for a species belonging to a redundant FEs as the latter may be replaced by another species within its FEs.

Finally, our study presents for the first time an assessment of the density, biomass, taxonomic and functional structure of fish assemblages at Malpelo Island a World Heritage site. The high biomass values composed mainly by piscivorous species endemic to the TEP, as well as a high functional vulnerability, suggests that this island is still in a very pristine state and represents a baseline for untouched assemblages in this marine province, as well as a priority area for conservation. Additionally, our study provides new information about the density and biomass of local and regional endemic species, which confirms that regional endemics may constitute a large share in isolated systems of the TEP region.

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