



Local benthic assemblages in shallow rocky reefs find refuge in a marine protected area at Madeira Island

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Abstract

The patterns of variability in the composition and structure of benthic communities along two depth strata (5 and 10 m) and the presence of sea urchins in structuring the subtidal rocky reefs were quantified in a long-established coastal marine protected area (Garajau MPA) and in two size equivalent and contiguous impacted areas (one highly urbanized and other with high fishing pressure) at Madeira Island (northeast Atlantic). Results suggest i) the MPA could be acting as a refuge for local biodiversity, ii) communities from the highly fished area could be suffering an impoverishment of local biodiversity, and iii) communities from the highly urbanized area would be enriched by the establishment of opportunistic species. These findings support that the level of human-pressure likely plays an important role in the composition of benthic communities in this insular ecosystem, although this was more relevant at the shallower stratum where the key grazer *Diadema africanum* explained 65% of the variance of benthic assemblages. It is suggested that this MPA small dimension and proximity to human impacted areas are limiting the survival of predators of the *D. africanum*.

Keywords Community structure · *Diadema africanum* · Macroalgae · Human pressure · Madeira Island · Sessile macrofauna

Introduction

Marine coastal ecosystems are highly exposed to human-induced pressures, and as a consequence are particularly vulnerable to changes in the biotic structure and composition of ecological communities (Kappel 2005; Jiao et al. 2015; Aucelli et al. 2018). These human-induced pressures cover a wide range of activities including overfishing, urbanization, coastal development or habitat transformations, which have been increasing globally in most coastal areas (Halpern et al. 2008; Elliot 2011, 2014). For example, the removal of natural predators may indirectly influence the entire community

through trophic cascades (Paine 1980; Tegner and Dayton 2000), human population density in coastal perimeter can be positively correlated with benthic grazers' abundance (Micheli et al. 2005; Hernández et al. 2008a), or the construction of urban infrastructures (e.g., harbours, marinas) can cause dramatic decreases in the cover of dominant space occupiers and promote bare space for the settlement of non-indigenous species (Stachowicz et al. 2002; Airoldi and Bulleri 2011; Canning-Clode et al. 2013).

A useful strategy to address and minimize the disturbance of human activities in coastal areas has been throughout the establishment of no-take or marine protected areas (MPAs,

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revised by Day et al. 2012). The designation of MPAs is a potential and rising tool to achieve conservation goals, and therefore has been suggested as an important step for the protection of natural habitats and marine biodiversity (Salm et al. 2000; McCay and Jones 2011; Foster et al. 2017). However, MPAs are vulnerable to development and exploitation occurring outside those areas, especially when considering small coastlines that cannot be integrated into spatial development strategies for larger areas (Roberts et al. 2005; Castrejón and Charles 2013). This is particularly common with small MPAs located in the vicinities of non-protected and/or urbanized areas, where it is more challenging to successfully linkage the ecological, social and economic roles (Cicin-Sain and Belfiore 2005), as in many insular ecosystems (Hernández et al. 2008b; Abecasis et al. 2013; Friedlander et al. 2013, 2017).

Madeira is the main island of the archipelago bearing the same name, and is among the most isolated temperate regions of the Atlantic. This small island has become an important offshore tourism and business center, with rapid economic and demographic development (Oliveira and Pereira 2008; Baioni 2011). The rapid urbanization processes in the coastal areas of Madeira has affected several adjacent natural marine habitats throughout direct destruction (e.g. seawalls; Baioni 2011) or overfishing (Hermida and Delgado 2016). Especially the latter, was responsible for the removal of most natural predators of sea urchins, which are the most important grazers in temperate reefs (Sala et al. 1998; Guidetti 2006). Consequently, it caused an ecosystem disequilibrium and the formation of extensive barrens (i.e., bare rocks with encrusting algae) in most of the island's subtidal hard bottoms (Bianchi et al. 1998; Alves et al. 2001; Friedlander et al. 2017). In order to promote the recovery and protection of the natural habitats and biodiversity, several MPAs were created along the archipelago during the last decades (Batista and Cabral 2016; Gestoso et al. 2017). The Garajau MPA was established in 1986 at Madeira Island and lies between human-impacted areas of different pressures that distances only few kilometers apart; at two kilometers from the islands' capital and harbour (that is visited by approximately 300 large ferries per year, DREM 2017) in one side, and at close to a highly fished area on the other. Yet, benthic assemblages of this long-established and small coastal MPA (ca. 5 km long, 3.8 km²) has not been quantified in relation to its contiguous human-impacted areas.

In the present study, the composition and structure of sessile benthic communities (macroalgae and invertebrates) in the rocky reefs of a small MPA and two nearby areas with different levels of human pressure at Madeira Island were quantified. This allowed i) assessing the patterns of variability in benthic communities at two depth strata, ii) identifying the species responsible for differences within distinct areas and depths, and iii) quantifying the importance of key grazer species (i.e., sea urchins) in structuring the subtidal assemblages.

Finally, the importance of the MPA for the local benthic assemblages is also discussed.

Material and methods

Study area

The Madeira Archipelago (Portugal) is located in the Lusitanian province of the Macaronesia ecoregion, together with the Azores and the Canaries (Spalding et al. 2007), in the warm-temperate waters of the northeast Atlantic (Fig. 1). Of volcanic origin from the Miocene (Klügel et al. 2009), the archipelago lies at approximately 1000 km of the European continent and 500 km of the West African coast. Surrounded by oceanic waters, Madeira is characterized by an absence (or reduced) continental shelf and its subtidal substrates (from the coastline to approximately 20 m isobath) are dominated by rocky reefs. The archipelago is influenced by the Portuguese, Azores, and Canary Currents, all part of the eastern anticyclonic North Atlantic subtropical gyre (Sala et al. 2013), resulting in high salinity, high temperature and low-nutrient regime waters (Johnson and Stevens 2000; New et al. 2001).

The archipelago comprises two inhabited islands - Madeira and Porto Santo (resident population of 262,302 and 5483, respectively; INE 2012) - and the smaller uninhabited islands (Desertas and Selvagens). Madeira is the largest of the group, with a coastline of 157 km comprising heterogeneous levels of anthropogenic pressure and of MPAs. For example, the Garajau MPA offers the highest level of protection to marine life in Madeira Island, where any type of fishery and boat traffic within the 50 m isobath is not permitted. This exclusively marine reserve was created to protect local biodiversity, and covers 4.4% of the island's coastline. No resident population inhabits the coastline of the Garajau MPA, and its human pressure comes from SCUBA activities and two small land stations supporting swimmers mainly during summer. On the other hand, Santa Cruz and Machico coastlines (Fig. 1) are not subjected to any type of protection, are open to local fisheries (e.g. fish traps, line fishing, spearfishing, and purse seine), and have a population density of 528 and 320 hab./km², respectively (INE 2012). In contrast, Funchal is the most urbanized area of Madeira due to i) being the largest city and capital of the island, with a population density of 1470 hab./km² (INE 2012), ii) hosting most of the hotels of an island that relies on tourism as its main source of economic income, with ≈6 million annual overnight stays (DREM 2017), and iii) bearing the principal harbour for ferry ships, fishing vessels, and cruiser/sailing boats, thus resulting in a coastline with a severe human pressure. Although Funchal coastline is open to fishing, its pressure remains at low levels (Roi Martínez-

Fig. 1 Map of the study area with the sampling locations within the three areas with different levels of human-pressure: Protected (Garajau MPA), Non-protected (Santa Cruz and Machico, with 528 and 320 hab./km², respectively), and Urbanized (Funchal, with 1470 hab./km²). Locations: 1 - Clube Naval, 2 - Lido, 3 - Barreirinha, 4 - Lazareto, 5 - Pináculo, 6 - Garajau, 7 - Reis Magos, 8 - Santa Cruz, 9 - Machico. © Google Earth Images



Escauriaza, Unpublished results), mainly by line fishing, occasional spearfishing, and occasional purse seine fishing (toward small coastal pelagic species) (Fig. 1).

The three areas mentioned above were used as references to a MPA with residual human pressure (MPA hereafter mentioned as ‘Protected’), to a non-protected coastal area exposed to low/intermediate human density and to high fishing activity (Santa Cruz and Machico coastlines hereafter referred as ‘Non-protected’), and to an urbanized coastal area exposed to high levels of human density and low/intermediate fishing activity (Funchal, island’s capital and hereafter referred as ‘Urbanized’). These areas were chosen due to being contiguous (Fig. 1) and thus considered equivalent. This facilitates interpretation of data analysis by reducing the influence of potential variations in the benthic assemblages caused by the geographic distance between areas. Finally, similar criteria have been used in other studies to provide a useful depiction of human pressure (e.g. Hawkins and Roberts 2004; Hernández et al. 2008a).

Sampling design

Three locations were sampled within each of the three selected areas (Protected, Non-protected, and Urbanized) (Fig. 1). In each location, 12 random replicates separated by approximately 10 m were collected from the rocky substrates at 5 m depth, and another 12 replicates at 10 m depth. Each replicate consisted of a digital photographic-quadrat of 25 × 25 cm for a posteriori quantitative image analysis of the sessile benthic

communities. In addition, at each location and depth, six random 1 m² quadrat replicates were used to survey in situ the abundances of sea urchins (*Diadema africanum*, *Arbacia lixula*, *Sphaerechinus granularis*, and *Paracentrotus lividus*, according to Alves et al. 2001). These abundances were used as predictors in order to help explaining the variability of sessile benthic communities. The selection of this group of marine organisms was based on the fact that sea urchins are known as voracious grazers that, when at high densities, are often keystone species responsible for the ecosystem functioning (Sala et al. 1998; Pinnegar et al. 2000; Sala 2004), as it is the case in Madeira (Alves et al. 2001; Friedlander et al. 2017). All surveys were carried out with SCUBA divers in August 2008, minimizing any potential seasonal effects.

For each digital photographic-quadrat we determined species richness, total cover and bare space by recording species identity from the photographs by employing the image analysis software CPCe (Kohler and Gill 2006). To reduce the risk of any sampling artifacts, no data was considered from a 1 cm wide margin around the 25 × 25 cm photographic-quadrat, originating a 23 × 23 cm image. Each image was then sub-divided into a grid of 9 cells in CPCe, with 11 random points in each cell, resulting in 99 points analyzed per image. We opted for this stratified random sampling technique as it ensures points are sampled in each region of the image (Kohler and Gill 2006). Finally, sessile macro-invertebrates and macroalgae were identified to the lowest possible taxonomic group based on existing literature and by consulting taxonomic experts.

Data analysis

Multivariate and univariate analyses of variance were used to evaluate the ecological effects of areas with distinct levels of human pressure on subtidal sessile benthic communities. Non-parametric permutation-based multivariate analyses of variance (PERMANOVA) on a Bray-Curtis similarity matrix calculated from data of percentage cover of sessile species was performed to evaluate the variability of benthic communities in composition and structure of species. For that, we employed a mixed model design with three orthogonal factors: Human-pressure (P, 3 levels: Protected, Non-Protected, and Urbanized; fixed; orthogonal), Location (L, 3 levels; random; nested within Human-pressure, i.e. three locations per area), and Depth (D, 2 levels: 5 and 10 m; fixed; orthogonal) ($n = 12$). P -values for the pseudo- F ratios were calculated by permutation of raw data through 999 permutations. Significant effects ($P < 0.05$) were further investigated through a posteriori pairwise comparisons between treatments. A non-metric multidimensional scaling (nMDS) was used to produce an ordination in two dimensions and graphically visualize multivariate patterns of variation and explain the responses of communities to the different human-pressure levels and depths. To understand community changes, the taxa that contributed most to the similarity of the sessile benthic communities between areas of different human-pressure levels and depth strata were identified using similarity percentages (SIMPER) analysis (Clarke 1993). Then, differences in percent cover, species richness, and Shannon diversity index were compared using univariate analysis of variance (ANOVA) following the same model used in the PERMANOVA analysis ($n = 12$). Homogeneity of variances was examined using Cochran's C -test and when significant differences among main factors or their interactions were found, Student-Newman-Keuls (SNK) tests were used as post-hoc comparisons among factors (Zar 2010).

To assess the grazers influence, the abundance of each sea urchin species was used as a predictor to explain the variability in composition and structure of the whole sessile benthic community along the different human-pressure levels, locations, and depths. For that, distance-based linear models (DISTLM) were run using the step-wise selection procedure and the R^2 selection criterion (McArdle and Anderson 2001). Benthic communities created with DISTLM were performed by calculating centroids for communities sampled at both depths along the three locations within each human-pressure level. Euclidean distances matrix among these centroids was then constructed to compare with a single vector of predictor variables produced with abundance data of sea urchin species.

Multivariate analyses were performed in PRIMER v6 (Anderson et al. 2008; Clarke and Gorley 2006,) with the PERMANOVA+ for PRIMER (PRIMER-E Ltd., UK). Univariate analyses were performed in R platform (R Core

Team 2017) using the statistical GAD package (Sandrini-Neto and Camargo 2010) and GMAV5 software (Institute of Marine Ecology, University of Sydney).

Results

Sessile benthic communities

A total of 26 sessile benthic species were identified, of which 14 were macrofauna and 12 were macroalgae (Table 1). The former group included anemones (one species), barnacles (three), bryozoan (two), gastropods (one), hydroids (one), sponges (four), and tubeworms (two). The latter included green (three), brown (four), and red (five) algae, comprising erect turfs and encrusting coralline species. The most abundant groups were crustose coralline algae (mainly calcareous red encrusting and rhodoliths) and erect algal turfs (Table 1). Macro-invertebrates dominated all areas at Depth 10 m and the Non-protected area at Depth 5 m, whereas macroalgae dominated the Protected and Urbanized areas at Depth 5 m. The average abundance of each taxon per area and depth stratum is presented in Table 1.

The multivariate analysis showed that the composition of sessile benthic communities was especially affected by human-pressure (P) and depth (D) factors. Additionally, it also showed spatial variability across locations (L), with significant interactions between P x D and L(P) x D (Table 2A, Fig. 2). The pairwise comparison revealed significant differences between communities from Depth 5 and 10 m in the Non-protected ($P = 0.021$) and Urbanized areas ($P = 0.024$), and only marginally significant in the Protected area ($P = 0.071$) (Table 2B, Fig. 2). The comparison between depths within each of the nine locations showed significant differences among all communities, except at one location in the Protected area and one in the Non-protected area (Locations 5 and 8, respectively, Fig. 1, Electronic supplementary material A.1). On the other hand, the pairwise comparisons of the horizontal structure, i.e., between areas within the same depth, showed that communities of the Protected, Non-protected, and Urbanized areas, did not differ significantly within Depth 5 m, nor within Depth 10 m (Table 2B, Fig. 2).

The SIMPER analysis showed that average similarity was higher in the Urbanized area, at both depth strata ($> 53\%$), than in the Protected (30.19% and 27.44% at Depths 5 and 10 m, respectively) and Non-protected areas (35.88% and 24.38%) (Table 1). It also showed that the communities from the Protected area at Depth 10 m and from the Urbanized area at Depth 5 m presented species not found in any other area or depth (Table 1), and that the average dissimilarity was highest (90.23%) between those two groups (Electronic supplementary material A.2).

Table 1 Results from analyses of similarities and species contributions (SIMPER) of sessile benthic communities for each area with different level of human-pressure and depth stratum

Species	Av. Abund.	Sim./ SD	Contr. %	Cum. %
Protected Depth 5 m (Av. Sim. = 30.19)				
Erect algal turfs	42.45	0.57	63.91	63.91
Calcar. red encrusting	17.51	0.58	34.20	98.11
<i>Serpula vermicularis</i>	0.20	0.07	0.81	98.92
<i>Vermetus triqueter</i>	1.66	0.20	0.66	99.58
<i>Liagora</i> sp.	0.08	0.04	0.15	99.73
<i>Asparagopsis taxiformis</i>	0.81	0.05	0.08	99.81
<i>Schizoporella</i> sp.	0.20	0.06	0.07	99.88
<i>Chthamalus stellatus</i>	0.22	0.10	0.05	99.93
Orange sponge	0.39	0.04	0.04	99.97
<i>Aglaophenia pluma</i>	0.25	0.04	0.03	100
Non-protected Depth 5 m (Av. Sim. = 35.88)				
Calcar. red encrusting	47.70	0.90	92.07	92.07
Erect algal turfs	14.37	0.23	7.35	99.43
<i>Vermetus triqueter</i>	1.04	0.21	0.56	99.98
<i>Serpula vermicularis</i>	0.08	0.04	0.02	100
Urbanized Depth 5 m (Av. Sim. = 53.27)				
Erect algal turfs	63.08	1.62	90.39	90.39
Calcar. red encrusting	7.88	0.54	6.73	97.12
<i>Anemonia viridis</i>	3.51	0.17	1.20	98.32
<i>Asparagopsis taxiformis</i>	5.33	0.10	0.63	98.95
<i>Padina pavonica</i>	0.73	0.34	0.36	99.31
<i>Dictyota</i> spp.	2.27	0.15	0.28	99.59
Crustose brown (cf. <i>Ralfsia</i>)	1.74	0.06	0.14	99.73
<i>Aglaophenia pluma</i>	1.23	0.10	0.14	99.86
Red sponge	0.34	0.08	0.04	99.90
<i>Valonia utricularis</i>	0.42	0.09	0.03	99.93
cf. <i>Parvocaulis</i>	0.20	0.09	0.02	99.95
<i>Liagora</i> sp.	0.48	0.07	0.01	99.96
<i>Corallina</i> sp.	0.25	0.07	0.01	99.97
<i>Ulva</i> cf. <i>rigida</i>	0.17	0.04	0.01	99.98
<i>Colpomenia sinuosa</i>	0.11	0.04	0.01	99.99
Serpulidae	0.06	0.04	0.00	100
Protected Depth 10 m (Av. Sim. = 27.44)				
Calcar. red encrusting	27.27	0.91	82.53	82.53
<i>Balanus trigonus</i>	3.00	0.26	4.25	86.77
<i>Chthamalus stellatus</i>	3.11	0.32	3.88	90.66
<i>Schizoporella</i> sp.	1.99	0.44	3.55	94.21
Rhodoliths	5.11	0.19	2.34	96.56
<i>Vermetus triqueter</i>	0.90	0.20	1.13	97.69
Erect algal turfs	0.93	0.15	1.02	98.71
Black sponge	1.01	0.14	0.56	99.27
<i>Serpula vermicularis</i>	0.31	0.18	0.25	99.52
<i>Aglaophenia pluma</i>	0.42	0.09	0.16	99.68
<i>Megabalanus azoricus</i>	0.25	0.07	0.10	99.77
<i>Reptadeonella</i> cf. <i>violacea</i>	0.42	0.06	0.08	99.85
Orange sponge	0.22	0.09	0.08	99.93
<i>Callyspongia simplex</i>	0.56	0.07	0.07	100

Table 1 (continued)

Species	Av. Abund.	Sim./ SD	Contr. %	Cum. %
Non-protected Depth 10 m (Av. Sim. = 24.38)				
Rhodoliths	8.67	0.57	49.47	49.47
Calcar. red encrusting	14.73	0.56	37.34	86.81
Erect algal turfs	16.08	0.18	10.00	96.81
<i>Chthamalus stellatus</i>	2.24	0.26	2.77	99.58
Orange sponge	0.42	0.09	0.21	99.80
<i>Schizoporella</i> sp.	0.45	0.07	0.16	99.96
<i>Vermetus triqueter</i>	0.08	0.07	0.03	99.99
<i>Serpula vermicularis</i>	0.08	0.04	0.01	100
Urbanized Depth 10 m (Av. Sim. = 54.50)				
Calcar. red encrusting	35.69	2.50	86.91	86.91
<i>Chthamalus stellatus</i>	5.53	0.74	8.81	95.73
<i>Balanus trigonus</i>	1.60	0.42	1.83	97.55
<i>Schizoporella</i> sp.	1.77	0.31	1.32	98.87
Rhodoliths	2.08	0.20	0.71	99.59
Red sponge	0.45	0.15	0.28	99.87
<i>Vermetus triqueter</i>	0.20	0.05	0.07	99.94
Erect algal turfs	0.22	0.07	0.02	99.97
Orange sponge	0.17	0.04	0.02	99.98
<i>Serpula vermicularis</i>	0.11	0.07	0.02	100

Exclusive species/taxon of each group are indicated in bold. Av. - Average, Sim. - Similarity, Abund. - Abundance, SD - Standard Deviation, Contr. - Contribution, Cum. - Cumulative

The univariate analysis indicated significant spatial variability along the different locations included within levels of human-pressure and depth for the three univariate

Table 2 A Summary of multivariate analyses of variance (PERMANOVA) to test for changes in the percentage cover of sessile species (999 permutations)

A. Permanova				
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
P	2	8330	0.599	0.569
D	1	63,336	11.484	0.006
L (P)	6	13,915	11.084	0.001
P x D	2	36,162	6.557	0.012
L (P) x D	6	5515	4.393	0.001
Res	198	1255		
Total	215			
B. Pairwise comparisons				
Between Depth 5 and 10 m within factor 'P'				
Protected D5 - D10			t	<i>P</i> (perm)
			1.719	0.071
Non-prot. D5 - D10			4.545	0.021
Urbanized D5 - D10			4.424	0.024
Between level of Human-pressure within Depth				
D5 Prot. - Non-prot.			1.372	0.197
D5 Prot. - Urb.			0.762	0.456
D5 Non-prot. - Urb.			3.102	0.054
D10 Prot. - Non-prot.			1.006	0.508
D10 Prot. - Urb.			0.728	0.600
D10 Non-prot. - Urb.			1.299	0.163

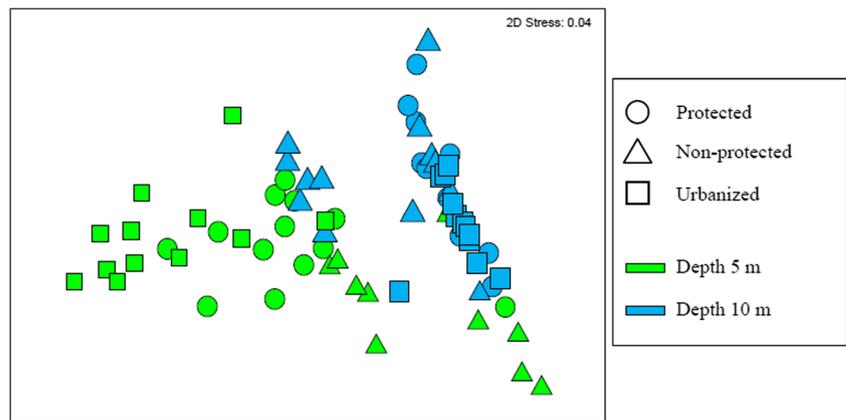
Significant P-values (< 0.05) are indicated in bold. Human-pressure ('P', 3 levels) and Depth ('D', 2 levels) are fixed factors, and Location ('L', 3 levels) is random factor. **B** Results of pairwise comparisons

measures (Table 3). The percentage cover of species at Depth 10 m was similar across the Protected, Non-protected, and Urbanized areas, and always lower than the percentage cover of communities from the Depth 5 m (Fig. 3a). Moreover, at Depth 5 m, communities from the Protected and Non-protected areas showed similar values, whereas the Urbanized area reached the highest values (Fig. 3a). In contrast, species richness and Shannon diversity index were higher at Depth 10 m, except in the Urbanized area where values were similar at both depth strata (Fig. 3b, c). Species richness and diversity were lowest in the Non-protected area and highest in the Urbanized area, except at Depth 10 m of the Protected area where values were similar (Fig. 3b, c).

Grazers influence

Four sea urchin species were identified in the surveyed rocky substrates: *Diadema africanum*, *Arbacia lixula*, *Sphaerechinus granularis*, and *Paracentrotus lividus*. The DISTLM analysis indicated that only the abundance of the sea urchin *D. africanum* significantly explained some of the variance found in the benthic communities in our model, with an influence of 37% (Table 4). This influence was only significant on the communities at Depth 5 m, explaining 65% of the variance of benthic assemblages along the different areas

Fig. 2 Non metric multidimensional scaling (nMDS) produced with the centroids values from cover abundances of benthic communities from each area (Protected, Non-protected, and Urbanized) and depth strata (5 and 10 m) averaged across locations ($n = 12$)



and locations (Table 4). The abundance of this species varied from zero to a mean of 6.11 (SE = 1.10) individuals/m² within different areas and depth strata (Table 5).

Discussion

The present study assessed the composition and structure of benthic communities of a long-established MPA in relation with two size equivalent and contiguous impacted areas at the insular ecosystem of Madeira. Therefore, it has contributed to better understand the functioning of these marine coastal habitats, which allowed for the first time, to quantify the importance of an MPA located between a highly populated and a fishing area. Additionally, the present study constitutes the first comprehensive assessment of the marine benthic assemblages in the shallow rocky reefs of the Garajau MPA since its creation over three decades ago. Therefore, the current study is of paramount relevance, as it constitutes a first baseline for future benthic assessments in this MPA.

Significant variation in the composition and structure of benthic communities were found at all spatial levels

(i.e., areas, location, and depth), with significant differences being more evident between areas at Depth 5 m (Fig. 2). At this depth stratum, the Protected and Urbanized areas differentiated from the Non-protected area, by presenting higher species richness and diversity. Additionally, whereas the former areas were dominated mainly by erect algal turfs, the latter was dominated by crustose coralline algae. These different scenarios can potentially help considering them as, respectively, less vs. high disturbed systems, like observed in the neighboring Canary Islands (Tuya et al. 2005; Hernández et al. 2008b). However, the Protected and Urbanized areas also differentiated between them, especially at the species composition level. The SIMPER analysis showed that at least nine species were exclusive from the Urbanized area at Depth 5 m. Yet, many of these taxa (e.g. *Anemonia*, *Ulva*) are bioindicators of eutrophic environments (Nettleton 2012; González-Delgado et al. 2018). Therefore, it is suggested that communities from the non-Protected area could be suffering an impoverishment of local biodiversity, those from the Urbanized area would be enriched by the establishment of opportunistic species (i.e. non-local/non-resident; Airoidi and Bulleri

Table 3 Summary of univariate analyses of variance (ANOVA) to test for changes in the percentage cover, species richness, and Shannon diversity index of sessile species

ANOVA	df	Percentage cover			Species richness			Diversity		
		MS	Pseudo- <i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>
P	2	5014	0.91	0.452	56.80	4.27	0.070	2.16	2.59	0.154
D	1	39,826	10.86	0.017	17.80	2.84	0.143	2.49	4.58	0.076
L (P)	6	5517	7.25	<0.001	13.31	7.12	<0.001	0.83	6.23	<0.001
P × D	2	2612	0.71	0.528	11.91	1.90	0.230	0.33	0.62	0.572
L (P) × D	6	3666	4.81	<0.001	6.27	3.36	0.004	0.54	4.07	0.001
Res	198	761			1.87			0.13		
Total	215									

Significant *P*-values (< 0.05) are indicated in bold. Human-pressure ('P', 3 levels) and Depth ('D', 2 levels) are fixed factors, and Location ('L', 3 levels) is random factor

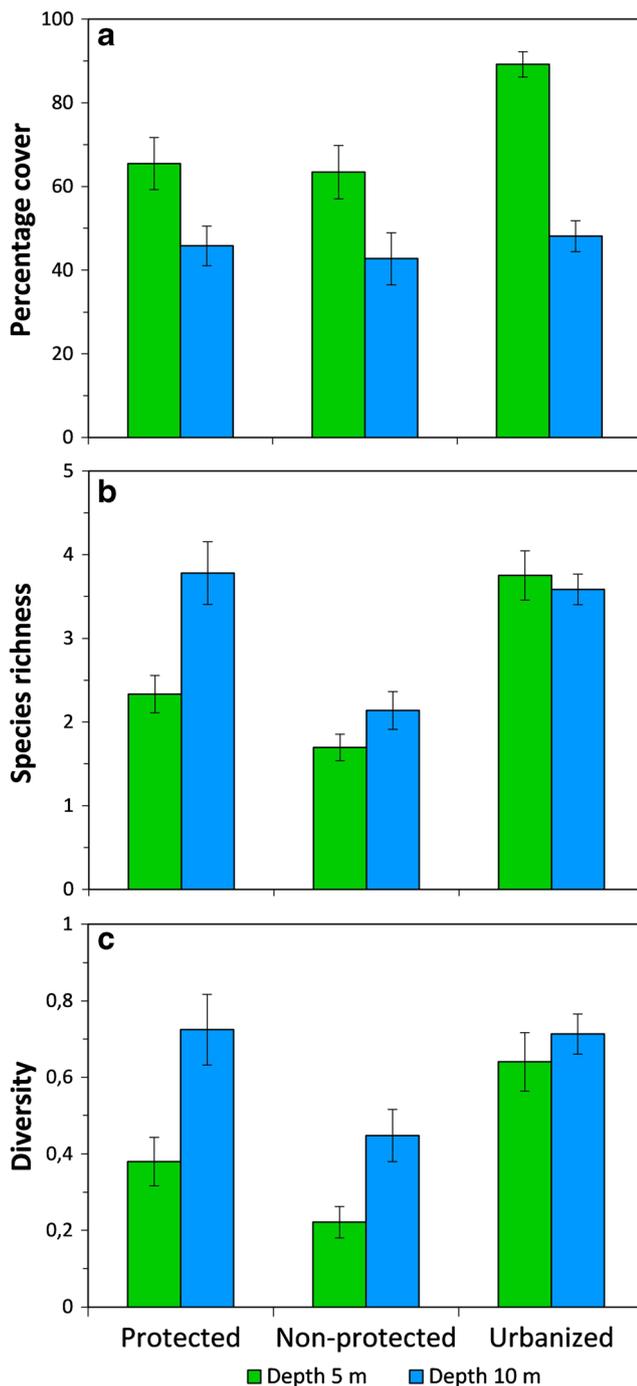


Fig. 3 Comparisons (mean + SE, $n = 36$) of benthic communities' composition between areas (Protected, Non-protected, and Urbanized) and depth strata (5 and 10 m). Univariate measures: **a** percentage cover, **b** species richness, and **c** Shannon diversity index

2011), whereas the local communities are maintained in the Protected area. This suggests that the level of human-pressure plays an important role in the composition of benthic communities, and that it is more relevant at the shallower stratum.

The pattern of variability of benthic communities was greatly explained (65%) by the abundance of *Diadema*

africanum at Depth 5 m, in contrast to Depth 10 m where this species explained only 3% (Table 4). Although other factors not included nor measured in this study such as chemical or physical parameters could be interacting here (e.g., Baynes and Szmant 1989; Pawlik 1992), our results, of *D. africanum* being the main driver of the variability in benthic communities, are in agreement with other studies in Madeira (Alves et al. 2001, 2003; Friedlander et al. 2017) and in other eastern Atlantic regions (Tuya et al. 2004a, b; Hernández et al. 2008a; Sangil et al. 2018). Our findings indicate that the density of the grazer *D. africanum* was a key factor determining the patterns of variability of sessile benthic communities at Depth 5 m along the areas with different levels of human-pressure. Although the Urbanized area may also play an important role in controlling *D. africanum* (Table 5) and indirectly favoring the establishment of opportunistic species, it does not contribute to the conservation of the local benthic communities. On the other hand, at Depth 10 m, it is suggested that the benthic communities are not under the influence of the factor human-pressure. This is probably because the indirect control that protection strategies (i.e., creation of an MPA) is inducing in *D. africanum* populations has no effects at this stratum. Such hypothesis is supported by the fact that communities at such depth seemed to be more homogenous in terms of cover and species richness, with the exception of the Non-protected communities where the number of species were always lower. At such deeper stratum, where the keystone species *D. africanum* was more abundant (Table 5), other factors such as habitat complexity, abiotic parameters, or wave exposure (Alves et al. 2001; Tuya et al. 2007; Clemente and Hernández 2008) are likely to play a more relevant role than the factor human-pressure. Therefore, future studies aiming to assess the distribution of this important grazer should consider including other factors. Additionally, a wider sampling area/technique, such as belt transects (Kingsford and Battershill 1998), would be preferred over sampling quadrats to minimize potential effects from the species small-scale patchy spatial distribution (Miller et al. 2007). Finally, considering more areas from each level of human-pressure could also have been advantageous, although not always possible in in-situ studies and especially in small islands.

The marine epibenthic biocoenoses of the South coast of Madeira has long been described as having general high abundances of *D. africanum* and encrusting algae / barren grounds, based on qualitative descriptions (Mortensen 1940; Ledoyer 1967; Levring 1974; Augier 1985; Bianchi et al. 1998) and more recently through quantitative studies (Alves et al. 2001; Clemente et al. 2014; Friedlander et al. 2017; Sangil et al. 2018). But should not a MPA created a few decades ago (in 1986) had time

Table 4 Results of distance-based linear models (DISTLM) analysing the relationship between multivariate data benthic assemblages and abundance of four sea urchins species (as individual predictor variables), for Depth 5 m, Depth 10 m, and both depths combined

Variable	Both Depths			Depth 5 m			Depth 10 m		
	Pseudo- <i>F</i>	<i>P</i>	Prop.	Pseudo- <i>F</i>	<i>P</i>	Prop.	Pseudo- <i>F</i>	<i>P</i>	Prop.
<i>Diadema africanum</i>	9.498	0.005	0.373	13.244	0.009	0.654	0.232	0.869	0.032
<i>Arbacia lixula</i>	1.400	0.229	0.080	0.246	0.738	0.034	0.000	1.000	0.000
<i>Sphaerechinus granularis</i>	0.398	0.657	0.024	0.049	0.970	0.007	0.770	0.399	0.099
<i>Paracentrotus lividus</i>	0.453	0.721	0.028	0.181	0.906	0.025	0.000	1.000	0.000

Significant *P*-values (< 0.05) are indicated in bold

enough to recover the ecosystem, i.e. lower abundances of *D. africanum* and more erect algal turfs? The present study, together with other recent work mentioned above, suggest that the Garajau MPA has indeed contributed to the protection of the benthic assemblages but only within a limited extent, due to affecting mainly the shallower part of the reefs where *D. africanum* has little control. This is in agreement with the findings of Hernández et al. (2007), which mentioned that once a habitat is in the barren state, this keystone grazer can survive indefinitely by feeding upon animals, coralline algae, microbial films and drift algae. In contrast, the Garajau MPA has successfully maintained a higher biomass of top predators when compared with impacted areas (i.e., urbanized and open to fishing) around Madeira (Andrade and Albuquerque 1995; Ribeiro et al. 2005; Wirtz 2007; Friedlander et al. 2017). However, such high biomass comprises only very few predators (i.e., balistids, diodontids and large labrid species; Clemente et al. 2010) of sea urchins (Ribeiro 2008). Therefore, the lack of predators for sea urchins could be among the main reasons explaining why the Garajau MPA did not promote yet the ‘desired’ equilibrium status of dominance by non-crustose macroalgae.

Finally, we suggest that the small dimension of this MPA combined with its boundaries being contiguous to a highly urbanized and a fishing area, are among the main drivers limiting the survival of predators of sea urchins. The establishment of buffer zones have been suggested and applied successfully in both terrestrial and marine reserves worldwide in order to provide a transition area of partial protection (Cicin-Sain and Belfiore 2005; McLeod et al. 2009; Palomo et al. 2013). Therefore, the

Table 5 Mean ± SE of the abundance (individuals/m²) of *Diadema africanum* per area of different level of human-pressure and depth stratum

Area	Depth 5 m	Depth 10 m
Protected	1.39 ± 0.66	6.11 ± 1.10
Non-protected	3.17 ± 0.73	3.72 ± 0.77
Urbanized	0.00 ± 0.00	2.22 ± 0.41

implementation of buffer zones in the Garajau MPA could be considered by managers as a possible approach to increase the abundance of fish predators of the sea urchins and benefit the benthic communities, as shown in MPAs with buffer zones in the neighboring Canary Islands (Hernández et al. 2008b; Clemente et al. 2010, 2011; Sangil et al. 2012).

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Compliance with ethical standards

Declarations of interest None.

Research data The data used in the present study is available as Electronic supplementary material B.

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