

# Reef fish and benthic community structures of the Santa Luzia Marine Reserve in the Cabo Verde islands, eastern central Atlantic Ocean

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Understanding ecological structures and the dynamics of reef fish assemblages is a fundamental step in current conservation biology. Patterns of abundance and biomass of reef fish communities of the tropical Cabo Verde Archipelago (eastern central Atlantic Ocean) have not been assessed previously. We studied general patterns of reef fish trophic groups and benthic cover at 11 sites around Santa Luzia Island, employing underwater visual census (UVC) and benthic photo-quadrats. Fish assemblage attributes were plotted against several descriptors, such as fishing intensity, water surge, and complexity and type of substrate, using multivariate analysis. The 15 most abundant species accounted for 94.12% of all fishes censused by UVC; nine of these were also among the 15 species with the highest biomass. The families Muraenidae, Pomacentridae and Labridae were the most speciose, while *Chromis* spp. (Pomacentridae) and Labridae were the dominant groups in terms of both density and biomass. In terms of trophic groups of fishes, planktivores dominated fish density (69%, with 4 species), followed by mobile invertebrate feeders (17.9%, with 13 species), with other groups such as carnivores (3.6%) and roving herbivores (2.7%) being less prevalent. The benthic community was partially dominated by crustose coralline algae and macroalgae (more than 25% of total coverage). The low densities of large piscivorous and carnivorous fishes in the reserve might be directly linked to overfishing. The highest fish and benthic biodiversity were detected in the northwestern Santa Luzia reef sites, indicating this area as a priority for establishment of a no-take zone in the future.

**Keywords:** biodiversity, conservation, oceanic MPA, overfishing, trophic groups, underwater visual census, West Africa

## Introduction

Reef fish assemblages are keystone components for the determination and maintenance of the structure and resilience of the marine environment (Mumby et al. 2012; Graham et al. 2013). Understanding their spatial variation is crucial to determining natural environmental gradients (Ferreira et al. 2004; Krajewski and Floeter 2011). Assessing the structure and dynamics of reef fish assemblages is also a fundamental step in conservation biology. It provides important variables for the evaluation of comparative responses of communities to natural and anthropogenic changes in marine biota (Ribeiro et al. 2005). It also helps the monitoring of long-term effectiveness and the redesigning of boundaries of marine protected areas (MPAs) (García-Charton et al. 2008; Martín-García et al. 2014).

Several studies linking reef fish assemblages with benthic communities have been carried out in different

regions worldwide: the Indo-Pacific (Anderson and Millar 2004; Komyakova et al. 2013), the Caribbean (Harborne et al. 2012; Acosta et al. 2015; Elise et al. 2017), the southwestern Atlantic (Krajewski and Floeter 2011; Pinheiro et al. 2011; Longo et al. 2015), remote equatorial islets (Luiz et al. 2015), equatorial São Tomé Island (Maia et al. 2018), and regions within the temperate eastern Atlantic, such as the Azores (Bertoncini et al. 2010), Madeira (Ribeiro et al. 2005), the Selvagens Islands (Almada et al. 2015) and the Canary Islands (Clemente et al. 2011; Espino et al. 2011). Although there is a recent zoogeographic study comparing reef fishes in different island habitats between Tobago (Caribbean) and Santiago (Cape Verde) (Zander 2011), there is no available data on reef fish abundance and on relationships between reef fish

assemblages and benthic communities for the Cabo Verde Archipelago.

Globally, the main factors reported to shape the structure of reef fish assemblages include temperature gradients, isolation, and biogeographic and evolutionary patterns related to species identity (Mora et al. 2003; Floeter et al. 2008; Tuya et al. 2011; Almada et al. 2013; Parravicini et al. 2013). In oceanic islands, different components frequently used to describe fish assemblages (namely species and functional richness, density and biomass) are influenced by various energetic, biogeographic and anthropogenic factors (Quimbayo et al. 2019). On a local scale, factors like benthic community structure, structural complexity of the habitat, depth, current regimes and exposure to waves have more importance (Ferreira et al. 2001; Fulton et al. 2005; Floeter et al. 2007). In general, the density and biomass of fishes positively correlate with coral cover and depth, but negatively correlate with exposure to waves (Krajewski and Floeter 2011), while fish biomass is highly dependent on fishing pressure and the effectiveness of MPAs (Teh et al. 2013; Cinner 2014).

Although overfishing is recognised as the main disturbance affecting the biomass patterns of reef fishes and other marine resources on a global scale (Myers and Worm 2003; Knowlton and Jackson 2008; Quimbayo et al. 2019), little is known about the direct association of fisheries with losses of biodiversity and coastal reef degradation in the West Africa ecoregion (Brashares et al. 2004). This ecoregion has been identified as one of the most important fishing zones worldwide (Christensen et al. 2004), with fisheries and overharvesting posing the biggest threats to the local marine biota (Worm et al. 2009). In West Africa, 8% of all marine species assessed in terms of the IUCN Red List of Threatened Species are classified as Threatened and 4% as Near Threatened, with 36 teleost species listed as Vulnerable to Critically Endangered (2.8% of all fishes assessed) (Polidoro et al. 2017). The coastal ichthyofauna of Cabo Verde is mainly of tropical origin, with more than 20 endemic species (Wirtz et al. 2013). Afrotropical Guinean species clearly dominate the archipelago, followed by ampho-Atlantic tropical and subtropical species enriched by Mediterranean and circumtropical species (Brito et al. 2007).

In a global scenario of biodiversity loss and habitat degradation, MPAs have been defined as one of the main means to protect biodiversity and critical habitats besides strengthening the overall function of local ecosystems (Martín-García et al. 2014; Sala et al. 2018). Although MPAs have been used as a measure of conservation progress in preserving marine biodiversity, certain categories of MPAs allow fishing at various levels (Costello and Ballantine 2015). A 'Regional Strategy for West African Marine Protected Areas' was agreed and signed in 2003 by member of states of the Sub-Regional Fisheries Commission ([http://www.prcmarine.org/sites/prcmarine.org/files/12B\\_STRATEGY.pdf](http://www.prcmarine.org/sites/prcmarine.org/files/12B_STRATEGY.pdf)). The strategy is currently being implemented with a shared vision of an effective network of regional MPAs, and the participatory management principles are highlighted as a tool for a more effective contribution to the sustainable development of the region.

The Cabo Verde islands (eastern central Atlantic Ocean) and the Sahelian Upwelling (tropical eastern Atlantic)

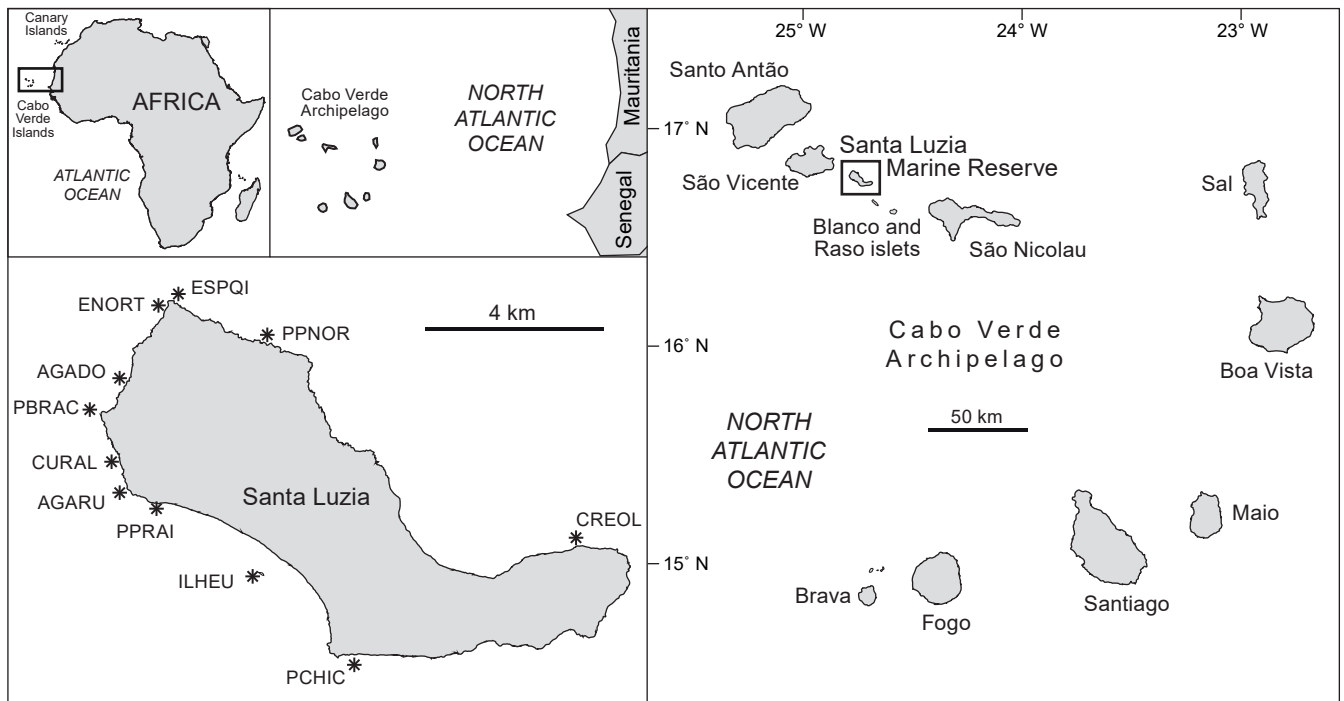
marine ecoregions are both included in the 'West African Transition' marine province (Spalding et al. 2007). Baseline studies on marine biota have intensified in the Cabo Verde Archipelago since 2006, especially in MPAs where fishing and tourism are relatively intense (Almeida et al. 2007, 2012). However, a lack of enforcement continues to undermine the legislation, resulting in lack of effective protection for those MPAs (Vasconcelos et al. 2015).

Given the existence of information gaps, the assessment of reef assemblages in the region is of high importance since it provides a critical baseline on the structure and drivers of these assemblages. We conducted the first assessment of reef fish assemblages, using underwater visual census (UVC), at different sites in the Santa Luzia Marine Reserve (Cabo Verde Archipelago), coupled with photo-quadrats to characterise the benthic community. The main objectives were to: (i) assess spatial variation in the density and biomass of reef fish trophic groups around Santa Luzia Island; and (ii) identify the most important biotic and abiotic variables that explain the structure of local reef fish assemblages. These data are essential for implementation of a detailed spatial zonation plan for the Santa Luzia Marine Reserve, as well as for prioritisation of management actions to preserve natural resources in this MPA.

## Materials and methods

### Study area

The Cabo Verde islands (also known as Cape Verde) are located in the eastern central Atlantic, 570 km west of Ngor Island (Senegal, West Africa). The archipelago is composed of ten islands and eight islets formed by rock accumulation from volcanic eruptions, totalling an area of 4 033 km<sup>2</sup> with ~965 km of coastline (Duarte and Romeiras 2009). The islands have a tropical climate and are situated at the eastern border of the subtropical North Atlantic Gyre and the southern limit of the Canary Current (Peña-Izquierdo et al. 2012). The reefs at Cabo Verde are rocky and covered by a number of reef organisms, usually referred to as a coralline community (cf. Almeida et al. 2007). Santa Luzia Island (16°45' N, 24°44' W) is uninhabited and the smallest island of the archipelago, with a land area of 34.27 km<sup>2</sup>, and is positioned approximately 9.26 km to the east of São Vicente Island (Figure 1). Santa Luzia is located on the second-largest insular shelf of Cabo Verde, and is one of the areas with the richest marine biodiversity in the archipelago (Almeida et al. 2015; Freitas et al. 2015). The rugged coastline of ~34.7 km is dominated by low rocky areas and sandy beaches. The cliffs and rocky areas of the northern and northeastern regions are exposed to constant wave action; the southern and southwestern areas are flatter and have beaches and sandy bottoms, as well as rhodolith beds that are partially covered in the subtidal zone (Freitas et al. 2015). In addition, Santa Luzia is among the priority key biodiversity areas documented by the Critical Ecosystem Partnership Fund (CEPF 2017). The island is highly threatened by feral cats, supports various artisanal fisher communities, and its rich biodiversity includes several endemic taxa (Geraldés and Melo 2016). The reserve was integrated in the MPA consolidation programme of 2003; however, the multiuse context of different fishing activities



**Figure 1:** Map showing the geographical position of the Cabo Verde Archipelago in the eastern central Atlantic Ocean and the study sites in the Santa Luzia Marine Reserve, including nearby islands and islets. The 11 studied reefs (stars) at Santa Luzia Island were: Água Doce (AGADO), Água Ruim (AGARU), Curral (CURAL), Enseadilha Norte (ENORT), Espequinho (ESPQI), Ilhéuzinho (ILHEU), Ponta Branca (PBRAC), Ponta Chica (PCHIC), Ponta Creolo (CREOL), Ponta Praia (PPRAI) and Ponta Preta Norte (PPNOR)

and a lack of enforcement are not coherent with its status as an integral nature reserve.

### Sampling survey procedure

Between September and October in 2009, 11 study sites (Figure 1) were sampled at Santa Luzia Island. These sites were chosen based on local knowledge of the marine fauna and fisheries activities. In addition, the sites included different current regimes and wave exposure and a diverse benthic community. Reef fish assemblages were assessed using underwater visual censuses (UVC) along 198 strip transect lines (20 × 2 m) run parallel to the shore. The UVC technique consisted of a diver unwinding a tape while identifying, counting and estimating the total length (TL) of non-cryptic fishes, sized >10 cm TL in 10-cm size classes. Then, while retracting the tape, the same procedure was followed to count cryptobenthic species sized <10 cm TL (Floeter et al. 2007; Krajewski and Floeter 2011; Pinheiro et al. 2011; Luiz et al. 2015; Maia et al. 2018). UVCs were randomly located, starting from the surface to the end of the reef where the sandy bottom began. The number of UVCs per site varied according to the maximum depth of each sampled site. To assess the structure of the benthic community, photo-quadrats (25 × 25 cm) were taken at 1-m intervals along the fish transect (20 photographs per transect). The photographs were analysed using the Coral Point Count with Excel extensions (CPCe 3.6) program (Kohler and Gill 2006). In each photograph, 25 randomly placed points were analysed in which the relative abundance of each substrate type (percentage of benthic

coverage) was estimated. Benthic groups were classified based on experience gained at other Atlantic Ocean reef sites (e.g. Floeter et al. 2007; Krajewski and Floeter 2011; Pinheiro et al. 2011; Luiz et al. 2015; Maia et al. 2018). Fifty-eight items, mostly benthic organisms, were grouped and classified into 10 functional categories: macroalgae, turf algae, crustose coralline algae (CCA), hard corals, zoanths, millepores, other invertebrates, rhodoliths, bare rock, and sand and rubble.

### Data analysis

Zoogeographic categorisation of the Santa Luzia fishes followed an updated database of Atlantic Ocean reef fishes by Floeter et al. (2008), and was listed using the phylogeny of Fricke et al. (2018) (see Table 1). Fishes were grouped into eight trophic categories, following Ferreira et al. (2004) and Krajewski and Floeter (2011), and validated according to the checklist provided by Halpern and Floeter (2008). Trophic groups consisted of carnivores, territorial herbivores, roving herbivores, mobile invertebrate feeders, sessile invertebrate feeders, omnivores, piscivores and planktivores. Fish biomass was calculated using an allometric length–weight equation ( $W = aTL^b$ ), with size class mid-point as the estimated total length. Specific equation parameters  $a$  and  $b$  were compiled from Halpern and Floeter (2008), Pereira et al. (2012), Oliveira et al. (2015) and FishBase (Froese and Pauly 2017). In cases where data were not available, the genus average was used as a proxy using data available in FishBase (Froese and Pauly 2017).

Spatial variations of fish density and total fish biomass

**Table 1:** Comparative composition, obtained from visual census, of reef fishes among sites in the Santa Luzia Marine Reserve (Cabo Verde), showing the density of individuals per species (overall and per site), frequency of occurrence (FO), and estimated biomass per species. The commercial value, zoogeography and trophic group of each species are also presented. Numbers in bold indicate the 10 most abundant fish species (by density or biomass). Species are listed alphabetically within families, with taxonomy following Fricke et al. (2018). Com. = commercial value: C = commercial species, LC = species of low commercial value, and NC = non-commercial species. Zoog. = zoogeography: AA = amphiatlantic, CV = Cabo Verde, EA = eastern Atlantic, MAC = Macaronesia, and TWA = tropical West Africa. Trophic groups: M. invert. = mobile invertebrate feeders, Planktiv. = planktivores, Rov. herbiv. = roving herbivores, S. invert. = sessile invertebrate feeders, and Terr. herbiv. = territorial herbivores. For full names of the 11 reef sites see Figure 1

Family and species	Zoog.	Com.	Trophic group	Density, mean (SE) (ind. 40-m <sup>2</sup> )														
				All sites			Reef site											
				Density, mean (SE) (ind. 40-m <sup>2</sup> )	Biomass, mean (SE) (g 40-m <sup>2</sup> )	FO	PPRAI	AGARU	CURAL	PBRAC	AGADO	ENORT	ESPQI	PPNOR	CREOL	PCHIC	ILHEU	
<b>Ginglymostomatidae</b>																		
1 <i>Ginglymostoma cirratum</i>	AA	LC	Carnivores	0.02 (0.02)	4.54 (3.58)	0.01	0.09 (0.09)										0.07 (0.07)	
<b>Desyatidae</b>																		
2 <i>Bathytoshia centroura</i>	AA	LC	Carnivores	0.01 (0.01)	8.14 (8.14)	0.01			0.05 (0.05)									
<b>Muraenidae</b>																		
3 <i>Enchelycore nigricans</i>	AA	C	Carnivores	0.02 (0.01)	1.10 (0.63)	0.02	0.03 (0.03)		0.06 (0.06)									
4 <i>Gymnothorax miliaris</i>	AA	C	Carnivores	0.05 (0.02)	3.77 (1.30)	0.05	0.07 (0.07)				0.11 (0.07)		0.12 (0.08)	0.09 (0.06)			0.09 (0.09)	0.18 (0.12)
5 <i>Gymnothorax sp.</i>	AA	C	Carnivores	0.04 (0.01)	2.22 (0.77)	0.04	0.09 (0.05)											0.09 (0.09)
6 <i>Gymnothorax vicinus</i>	AA	C	Carnivores	0.07 (0.02)	1.90 (0.69)	0.05	0.13 (0.09)								0.06 (0.06)		0.13 (0.09)	
7 <i>Muraena augusti</i>	MAC	C	Carnivores	0.02 (0.01)	0.42 (0.30)	0.02	0.07 (0.07)		0.06 (0.06)		0.16 (0.09)			0.04 (0.04)				
8 <i>Muraena melanotis</i>	TWA	C	Carnivores	0.05 (0.02)	1.27 (0.52)	0.04									0.06 (0.06)			
9 <i>Muraena robusta</i>	AA	C	Carnivores	0.01 (0.01)	0.28 (0.28)	0.01												
<b>Synodontidae</b>																		
10 <i>Synodus synodus</i>	AA	NC	Piscivores	0.03 (0.01)	0.34 (0.19)	0.03	0.07 (0.07)				0.05 (0.05)			0.04 (0.04)			0.13 (0.09)	0.09 (0.09)
11 <i>Synodus saurus</i>	AA	NC	Piscivores	0.01 (0.01)	0.15 (0.14)	0.01			0.05 (0.05)									
<b>Holocentridae</b>																		
12 <i>Myripristis jacobus</i>	AA	LC	Carnivores	<b>4.12 (0.94)</b>	<b>682.63 (162.86)</b>	0.30	1.27 (0.99)	<b>13.71 (4.49)</b>	<b>4.06 (2.70)</b>	0.89 (0.37)	<b>1.47 (0.98)</b>	0.55 (0.31)	0.06 (0.06)	0.70 (0.30)	<b>1.75 (0.57)</b>	1.00 (0.72)	<b>13.36 (5.53)</b>	1.09 (0.65)
13 <i>Sargocentron hesatum</i>	AA	LC	Carnivores	0.41 (0.07)	40.96 (10.04)	0.26	0.47 (0.17)	0.41 (0.14)	0.17 (0.12)	0.16 (0.09)	0.68 (0.38)	0.55 (0.21)	0.24 (0.11)	0.35 (0.22)	0.50 (0.20)	0.27 (0.15)		
<b>Aulostomidae</b>																		
14 <i>Aulostomus stitigosus</i>	AA	NC	Piscivores	0.15 (0.05)	6.77 (2.03)	0.08	0.35 (0.17)		0.11 (0.11)	0.32 (0.23)				0.13 (0.07)	0.06 (0.06)		0.27 (0.27)	
<b>Fistulariidae</b>																		
15 <i>Fistularia tabacaria</i>	AA	NC	Piscivores	0.02 (0.01)	0.59 (0.38)	0.02	0.06 (0.06)				0.05 (0.05)							
<b>Serranidae</b>																		
16 <i>Cephalopholis taeniops</i>	TWA	C	Carnivores	<b>2.07 (0.18)</b>	297.27 (36.32)	0.66	<b>2.13 (0.76)</b>	1.94 (0.45)	<b>3.61 (0.91)</b>	<b>2.42 (0.76)</b>	<b>1.95 (0.43)</b>	<b>4.64 (0.85)</b>	<b>1.47 (0.36)</b>	<b>1.22 (0.35)</b>	<b>1.75 (0.43)</b>	1.00 (0.47)	1.55 (0.49)	
17 <i>Epinephelus marginalis</i>	AA	C	Carnivores	0.11 (0.10)	0.00 (0.00)	0.02	0.62 (0.59)				0.05 (0.05)							
18 <i>Mycteroperca fusca</i>	MAC	C	Piscivores	0.33 (0.12)	91.66 (36.26)	0.10	0.12 (0.07)		0.06 (0.06)	0.05 (0.05)	0.58 (0.30)	0.18 (0.12)	0.12 (0.08)	0.09 (0.06)	0.19 (0.10)	0.07 (0.07)	<b>3.91 (1.81)</b>	0.45 (0.31)
19 <i>Rypticus saponaceus</i>	EA	NC	Carnivores	0.14 (0.03)	1.38 (0.47)	0.11	0.20 (0.14)	0.18 (0.08)			0.16 (0.09)		0.06 (0.06)	0.09 (0.06)				
<b>Scorpaenidae</b>																		
20 <i>Scorpaena sp.</i>	EA	LC	Carnivores	0.19 (0.04)	21.61 (9.08)	0.13	0.13 (0.09)	0.18 (0.13)	0.33 (0.14)	0.05 (0.05)	0.16 (0.09)	0.09 (0.09)	0.06 (0.06)	0.26 (0.14)	0.06 (0.06)	0.47 (0.32)	0.27 (0.14)	
<b>Priacanthidae</b>																		
21 <i>Heteropriacanthus fulgens</i>	AA	C	Carnivores	0.53 (0.10)	26.10 (5.06)	0.21	0.09 (0.09)		0.17 (0.12)	1.37 (0.52)	0.63 (0.16)	1.64 (0.51)		0.26 (0.22)	0.63 (0.22)	1.07 (0.51)	0.91 (0.91)	
<b>Apogonidae</b>																		
22 <i>Apogon imberbis</i>	EA	NC	M. invert.	0.42 (0.40)	0.74 (0.53)	0.02	0.03 (0.03)										<b>5.33 (5.33)</b>	0.27 (0.27)
<b>Carangidae</b>																		
23 <i>Caranx crysos</i>	AA	C	Carnivores	0.02 (0.02)	2.93 (2.93)	0.01												
24 <i>Caranx lugubris</i>	AA	C	Piscivores	0.02 (0.02)	8.51 (8.51)	0.01	0.09 (0.09)		0.17 (0.17)									
<b>Lutjanidae</b>																		
25 <i>Apsilus fuscus</i>	TWA	C	Carnivores	0.01 (0.01)	1.00 (0.70)	0.01					0.11 (0.07)							
26 <i>Lutjanus gorensis</i>	EA	C	Carnivores	0.01 (0.01)	2.99 (2.99)	0.01												
27 <i>Lutjanus fulgens</i>	TWA	C	Carnivores	0.51 (0.51)	23.11 (23.11)	0.01	2.94 (2.94)		0.06 (0.06)									
<b>Haemulidae</b>																		
28 <i>Paraprisipoma humile</i>	TWA	C	M. invert.	<b>6.82 (2.92)</b>	309.14 (129.23)	0.06	<b>22.06 (7.95)</b>										<b>36.67 (33.26)</b>	<b>4.55 (4.55)</b>
29 <i>Paraprisipoma octolineatum</i>	EA	LC	M. invert.	0.10 (0.10)	0.15 (0.15)	0.01											1.33 (1.33)	

Table 1: (cont.)

Family and species	Zoog. Com.	Trophic group	All sites		Reef site										
			Density, mean (SE) (ind. 40-m <sup>-2</sup> )	Biomass, mean (SE) (g 40-m <sup>-2</sup> )	FO	PPRAI	AGARU	CURAL	PBRAC	AGADO	ENORT	ESPQI	PNOR	CREOL	PCHIC
<b>Sparidae</b>															
30 <i>Diplodus fasciatus</i>	CV LC	Omnivores	1.60 (0.33)	<b>798.22 (187.38)</b>	0.30	<b>1.80 (1.33)</b>	0.79 (0.32)	1.39 (0.65)	<b>3.00 (1.72)</b>	0.37 (0.28)	1.82 (0.76)	<b>1.59 (1.22)</b>	<b>2.26 (0.66)</b>	0.69 (0.36)	<b>4.27 (2.86)</b>
31 <i>Diplodus lineatus</i>	CV LC	Omnivores	1.11 (0.25)	<b>450.34 (154.75)</b>	0.19	0.67 (0.67)	0.74 (0.40)	<b>3.22 (1.70)</b>	<b>2.32 (1.37)</b>	0.21 (0.14)	<b>1.91 (1.00)</b>	0.47 (0.30)	0.65 (0.48)	<b>1.75 (1.00)</b>	0.33 (0.33)
32 <i>Diplodus prayensis</i>	CV LC	Omnivores	1.67 (0.56)	<b>365.61 (90.21)</b>	0.28	<b>3.73 (1.63)</b>	<b>3.59 (2.93)</b>	<b>2.44 (1.65)</b>	0.79 (0.39)	1.00 (0.53)	0.45 (0.45)	0.18 (0.13)	0.26 (0.11)	0.06 (0.06)	<b>3.53 (1.41)</b>
33 <i>Spicara melanurus</i>	TWA C	M. invert.	1.39 (1.03)	<b>342.29 (278.97)</b>	0.03	1.13 (0.69)	1.03 (0.78)		0.21 (0.10)	0.16 (0.12)	<b>18.18 (18.18)</b>	<b>1.76 (1.76)</b>	0.43 (0.43)		
34 <i>Virridentex acromegalus</i>	CV C	Carnivores	0.39 (0.16)	197.52 (108.77)	0.16		0.18 (0.09)	1.78 (1.66)			0.09 (0.09)	0.12 (0.08)	0.26 (0.13)	0.31 (0.12)	0.13 (0.13)
<b>Sciaenidae</b>															
35 <i>Umbriina ronchus</i>	EA C	Carnivores	0.01 (0.01)	0.19 (0.19)	0.01			0.05 (0.05)							
<b>Mullidae</b>															
36 <i>Mulloidichthys martinicus</i>	AA C	M. invert.	0.63 (0.27)	42.61 (21.62)	0.11	0.40 (0.24)	2.12 (1.47)	0.56 (0.56)	0.53 (0.53)	0.53 (0.33)		0.12 (0.12)		0.93 (0.67)	
37 <i>Pseudupeneus prayensis</i>	EA C	M. invert.	0.58 (0.11)	64.97 (21.80)	0.20	1.33 (0.71)	0.53 (0.26)	0.56 (0.28)	0.84 (0.41)	0.11 (0.11)	0.73 (0.47)	0.47 (0.27)	0.09 (0.09)	0.93 (0.54)	1.45 (0.64)
<b>Kyphosidae</b>															
38 <i>Girella stuebeli</i>	CV LC	Rev. herbiv.	0.37 (0.12)	242.66 (79.70)	0.07		0.35 (0.21)		<b>2.53 (0.97)</b>		1.18 (0.52)				
39 <i>Kyphosus</i> spp.	AA LC	Rev. herbiv.	1.11 (0.62)	<b>726.36 (424.78)</b>	0.04		<b>6.06 (3.51)</b>				0.91 (0.91)	0.06 (0.06)		0.13 (0.13)	
<b>Chaetodontidae</b>															
40 <i>Chaetodon robustus</i>	TWA NC	S. invert.	0.75 (0.38)	20.42 (10.78)	0.08	0.13 (0.09)	0.29 (0.16)	0.22 (0.13)		0.11 (0.07)					<b>11.91 (6.21)</b>
<b>Pomacanthidae</b>															
41 <i>Holocanthus africanus</i>	TWA NC	Omnivores	0.41 (0.07)	24.17 (4.50)	0.25	0.47 (0.22)	0.85 (0.28)	0.61 (0.24)	0.11 (0.07)	0.21 (0.10)	0.27 (0.19)	0.35 (0.12)	0.39 (0.14)	0.06 (0.06)	0.53 (0.27)
<b>Mugilidae</b>															
42 <i>Chelon bispinosus</i>	CV LC	Rev. herbiv.	0.05 (0.05)	7.21 (7.21)	0.01		0.29 (0.29)								
<b>Pomacentridae</b>															
43 <i>Abudefduf saxatilis</i>	AA NC	Omnivores	2.04 (1.54)	112.59 (84.98)	0.05		<b>9.74 (8.84)</b>	0.11 (0.11)					<b>1.74 (1.74)</b>	<b>1.94 (1.18)</b>	
44 <i>Chromis lubbocki</i>	CV NC	Planktiv.	<b>102.67 (10.26)</b>	<b>4 109.90 (535.56)</b>	0.75	<b>214.20 (35.44)</b>	<b>222.79 (35.83)</b>	<b>115.72 (43.27)</b>	<b>51.05 (16.58)</b>	<b>54.26 (10.76)</b>	0.91 (0.91)	<b>58.76 (17.59)</b>	<b>89.39 (26.84)</b>	<b>28.25 (6.41)</b>	<b>54.67 (20.40)</b>
45 <i>Chromis multilineata</i>	AA LC	Planktiv.	<b>77.15 (8.08)</b>	<b>1 382.06 (286.93)</b>	0.76	<b>79.47 (20.25)</b>	<b>178.82 (30.54)</b>	<b>64.94 (28.32)</b>	<b>52.63 (13.48)</b>	<b>75.05 (13.45)</b>	<b>13.00 (5.22)</b>	<b>40.71 (17.01)</b>	<b>82.43 (26.89)</b>	<b>44.69 (8.44)</b>	<b>37.47 (17.23)</b>
46 <i>Simuliparma hermani</i>	CV NC	Omnivores	0.45 (0.04)	25.70 (4.27)	0.38	0.67 (0.13)	0.41 (0.10)	0.61 (0.18)	0.53 (0.14)	0.37 (0.16)	0.36 (0.15)	0.76 (0.18)	0.39 (0.15)	0.19 (0.10)	0.40 (0.13)
47 <i>Simuliparma lurida</i>	MAC NC	Omnivores	0.31 (0.06)	12.11 (2.81)	0.16	0.13 (0.13)	0.18 (0.08)	0.22 (0.15)	0.32 (0.11)	0.95 (0.35)	0.27 (0.19)	0.12 (0.08)	0.17 (0.10)		1.45 (0.68)
48 <i>Siganes fimbriatus</i>	TWA NC	Rev. herbiv.	<b>2.12 (0.21)</b>	11.89 (2.06)	0.59	<b>1.47 (0.48)</b>	2.35 (0.68)	0.61 (0.30)	0.95 (0.27)	<b>2.47 (0.39)</b>	<b>2.82 (0.85)</b>	<b>1.47 (0.53)</b>	<b>2.13 (0.44)</b>	<b>6.81 (0.85)</b>	0.64 (0.28)
<b>Labridae*</b>															
49 <i>Bodianus speciosus</i>	TWA C	M. invert.	1.02 (0.12)	244.01 (33.68)	0.44	1.27 (0.30)	1.47 (0.37)	1.44 (0.62)	0.37 (0.23)	<b>1.37.5 (0.6)</b>	1.00 (0.43)	0.94 (0.30)	0.39 (0.16)	0.94 (0.43)	0.82 (0.38)
50 <i>Coris atlantica</i>	TWA NC	M. invert.	<b>4.06 (0.72)</b>	28.37 (5.36)	0.41	<b>12.67 (3.05)</b>	<b>8.79 (3.30)</b>	<b>6.72 (2.08)</b>	1.42 (0.68)	0.95 (0.43)	<b>4.73 (3.18)</b>	1.06 (0.54)	0.13 (0.07)	1.75 (0.67)	1.60 (0.64)
51 <i>Thalassoma pavo</i>	EA NC	M. invert.	<b>27.17 (4.13)</b>	<b>398.32 (114.12)</b>	0.85	<b>28.40 (6.16)</b>	<b>63.24 (21.16)</b>	<b>37.28 (13.48)</b>	<b>15.95 (2.14)</b>	<b>10.79 (1.31)</b>	<b>7.55 (2.55)</b>	<b>36.53 (5.61)</b>	<b>19.91 (4.62)</b>	<b>7.81 (2.09)</b>	<b>15.93 (3.01)</b>
52 <i>Scarus hoefleri</i>	TWA C	Rev. herbiv.	0.05 (0.02)	18.53 (6.94)	0.04		0.09 (0.05)				0.29 (0.17)			0.13 (0.09)	
53 <i>Sparisoma cretense</i>	EA C	Rev. herbiv.	<b>4.58 (0.34)</b>	<b>847.66 (66.71)</b>	0.84	<b>3.80 (1.13)</b>	3.56 (0.63)	<b>5.17 (0.59)</b>	<b>4.68 (0.67)</b>	<b>2.42 (0.46)</b>	<b>8.91 (3.22)</b>	7.12 (1.41)	<b>4.78 (1.36)</b>	<b>3.38 (0.64)</b>	<b>4.87 (1.06)</b>
54 <i>Sparisoma croatii</i>	TWA C	Rev. herbiv.	<b>0.31 (0.06)</b>	70.11 (16.54)	0.17	0.07 (0.07)	0.15 (0.06)	0.17 (0.12)	0.47 (0.23)		0.41 (0.24)		0.35 (0.12)	0.75 (0.38)	0.93 (0.46)
<b>Labrisomidae</b>															
55 <i>Labrisomus nuchipinnis</i>	AA NC	Carnivores	0.62 (0.10)	4.00 (1.51)	0.27	0.40 (0.19)	0.26 (0.16)	0.67 (0.45)	0.68 (0.37)	0.95 (0.33)	1.09 (0.59)	0.71 (0.24)	0.17 (0.14)	0.44 (0.20)	1.33 (0.55)
<b>Blenniidae</b>															
56 <i>Ophioblennius atlanticus</i>	MAC NC	Terr. herbiv.	1.96 (0.23)	3.48 (0.78)	0.49	0.47 (0.32)	1.18 (0.51)	0.44 (0.23)	<b>2.68 (0.96)</b>	<b>2.21 (0.60)</b>	<b>6.55 (1.57)</b>	<b>3.35 (0.90)</b>	<b>2.70 (0.79)</b>	1.56 (0.30)	0.55 (0.55)
57 <i>Parablennius salensis</i>	CV NC	Omnivores	<b>2.83 (0.60)</b>	112.53 (105.73)	0.43	1.07 (0.41)	2.35 (0.91)	2.00 (0.75)	<b>2.32 (0.77)</b>	1.16 (0.43)	5.55 (1.91)	<b>1.41 (0.62)</b>	<b>0.78 (0.39)</b>	<b>2.44 (0.79)</b>	<b>17.45 (9.09)</b>
58 <i>Scartella caboverdiana</i>	CV NC	Terr. herbiv.	0.01 (0.01)	0.02 (0.02)	0.01				0.11 (0.11)						
<b>Gobiidae</b>															
59 <i>Gnatholepis thompsoni</i>	AA NC	M. invert.	0.35 (0.09)	0.30 (0.08)	0.13	0.67 (0.36)	0.85 (0.45)	0.17 (0.12)	0.26 (0.18)	0.79 (0.36)	0.09 (0.09)			0.06 (0.06)	0.20 (0.20)
60 <i>Gobius tetrophthalmus</i>	CV NC	M. invert.	<b>3.88 (0.56)</b>	8.85 (1.94)	0.41	<b>16.27 (3.27)</b>	<b>5.32 (1.44)</b>	<b>9.39 (2.48)</b>	1.37 (0.66)	<b>2.63 (0.79)</b>		0.47 (0.32)	0.04 (0.04)	0.38 (0.31)	<b>3.67 (2.35)</b>
<b>Acanthuridae</b>															
61 <i>Acanthurus monroviae</i>	EA C	Rev. herbiv.	0.72 (0.16)	262.57 (143.23)	0.26	1.00 (0.72)	0.91 (0.27)	2.22 (1.45)	0.53 (0.33)	0.47 (0.19)	0.36 (0.20)	0.76 (0.33)	0.13 (0.10)	0.56 (0.26)	0.53 (0.19)
<b>Belontiidae</b>															
62 <i>Balistes punctatus</i>	EA LC	M. invert.	0.13 (0.03)	21.69 (7.65)	0.10	0.13 (0.09)	0.18 (0.09)	0.11 (0.08)	0.16 (0.16)			0.12 (0.12)	0.04 (0.04)	0.60 (0.16)	0.09 (0.09)
63 <i>Canthidermis sufflamen</i>	AA LC	Planktiv.	0.03 (0.03)	12.90 (10.95)	0.01			0.28 (0.28)				0.06 (0.06)			



Table 1: (cont.)

Family and species	Zoog.	Com.	Trophic group	All sites		Reef site										
				Density, mean (SE) (ind. 40-m <sup>2</sup> )	Biomass, mean (SE) (g 40-m <sup>2</sup> )	PPRAI	AGARU	CURAL	PBRAC	AGADO	ENORT	ESPQI	PPNOR	CREOL	PCHIC	ILHEU
<b>Monacanthidae</b>																
64 <i>Aluterus scriptus</i>	AA	NC	Omnivores	0.08 (0.03)	6.51 (2.44)	0.13 (0.09)	0.18 (0.07)	0.33 (0.24)	0.05 (0.05)	1.11 (0.37)	0.09 (0.09)	1.12 (0.37)	0.35 (0.13)	1.38 (0.27)	0.40 (0.16)	1.27 (0.43)
<b>Tetraodontidae</b>																
65 <i>Canthigaster capistrata</i>	AA	NC	Omnivores	1.16 (0.23)	27.96 (19.64)	0.67 (0.29)	2.24 (1.22)	1.28 (0.56)	1.05 (0.32)	1.11 (0.37)	0.91 (0.37)	1.12 (0.37)	0.35 (0.13)	1.38 (0.27)	0.40 (0.16)	1.27 (0.43)
66 <i>Sphaerorhynchus marmoratus</i>	EA	NC	M. invert.	0.01 (0.01)	0.92 (0.65)	0.13 (0.09)										
<b>Diodontidae</b>																
67 <i>Diodon holocanthus</i>	AA	NC	Planktiv.	0.01 (0.01)	1.04 (1.04)	0.01			0.05 (0.05)	1.11 (0.37)	0.09 (0.09)	1.12 (0.37)	0.35 (0.13)	1.38 (0.27)	0.40 (0.16)	1.27 (0.43)
<b>Total</b>				260 (20)	12 548 (1 301)	377 (42)	565 (79)	270 (72)	153 (30)	167 (16)	88 (19)	163 (24)	214 (49)	112 (12)	188 (48)	221 (26)

\*Including the subfamily Scairinae, following Westneat and Alfaro (2005).

were tested with a one-factor permutation-based analysis of variance using the package 'ImPerm' (Wheeler and Torchiano 2016), followed by a Tukey HSD *post hoc* test to identify differences among sites.

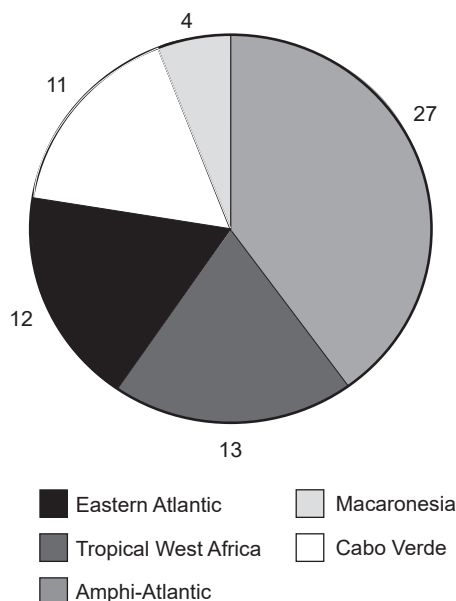
To characterise the benthic community across the surveyed sites, we plotted the average relative cover of each benthic category in each site. We then calculated the similarity among the sites using a Bray–Curtis similarity matrix and an average linkage clustering in the package 'vegan' (Oksanen et al. 2017) with Hellinger-transformed data as a way to standardise variation. The topographic complexity (CO) of the substrates within each transect was classified as high ('2') or average to low ('1'), as a modification of the method of Pinheiro et al. (2011). The sites were also characterised (using an ordinal scale of severity from 1 to 5) in terms of fishing intensity (FI) and water surge (WS). The assessment of FI, based on historical use by fishers, and WS on the basis of mean tidal currents (e.g. hydrodynamics and exposure) by site was conducted using individual interviews with local users. Six of the most experienced local fishers were selected to be interviewed. Density and biomass of fish trophic groups were analysed in relation to the benthic community and the site descriptors FI, WS and CO, using a multivariate redundancy analysis (RDA), a powerful tool suitable for nonlinear data (Legendre and Legendre 2012). As our main interest was to analyse spatial patterns of reef fish trophic groups, we averaged the density and biomass values, as well as CO data, by site, which resulted in these analyses being performed at site level instead of transect level. Collinearity of the explanatory variables was tested and some of the variables were removed *a priori*, to improve the explanatory power of the analyses. In each RDA the correlation between benthic categories, site descriptors and fish data were tested using permutation analysis with the package 'vegan' in R (Oksanen et al. 2017). All analyses were performed using the software R (R Core Team 2017). Depth was not considered for comparisons in this study but will be discussed in greater detail in future research.

## Results

### Structure and distribution patterns of reef fish assemblages

A total of 51 507 individual fish were counted, representing 67 species and 31 families (Table 1). A single elasmobranch species, the nurse shark *Ginglymostoma cirratum*, was recorded on four occasions during the study period. The most-species-rich families were the Muraenidae (7 species), followed by the Pomacentridae and Labridae (6 species each), Sparidae (5 species) and Serranidae (4 species). Eleven families were represented by 2 or 3 species, and 15 families each by a single species (Table 1).

The overall reef fish assemblage of Santa Luzia was composed of 27 amphi-Atlantic species (40.3%), 25 species (37.3%) of combined origin from tropical West Africa (from Cape Blanc in Mauritania to Angola) and the eastern Atlantic (e.g. Guinean species were well represented). Eleven species (16.4%) are endemic to the Cabo Verde Archipelago and 4 species are endemic to the Macaronesian islands (see Figure 2 and Table 1).



**Figure 2:** Biogeographic characterisation of reef fishes at Santa Luzia Island, Cabo Verde Archipelago (numbers indicate species richness)

Among all of the reef fishes recorded, 40.3% (27 species) were categorised as having commercial value, 37.3% as non-commercial species (mainly cryptic or small fishes), and the remaining 22.4% as having low market value (Table 1).

The 15 most abundant species accounted for 94.12% of all fish recorded during this study. Nine of these were also among the 15 species with the highest biomass. Combining all study sites, the 10 most abundant fishes (Table 1), in descending order, were: the endemic Lubbock's chromis *Chromis lubbocki*, brown chromis *Chromis multilineata*, peacock wrasse *Thalassoma pavo*, Guinean grunt *Parapristipoma humile*, the parrotfish *Sparisoma cretense*, blackbar soldierfish *Myripristis jacobus*, the rainbow wrasse *Coris atlantica*, the endemic goby *Gobius tetrophthalmus*, the endemic blenny *Parablennius salensis* and Cape Verde gregory *Stegastes imbricatus*. In terms of trophic categories, this group of abundant fish species comprised planktivores (*Chromis* spp., which mostly occurred in large schools), mobile invertebrate feeders (5 species), one roving herbivore (*Sparisoma cretense*), one small-sized carnivore, and one territorial herbivore.

Across all sites combined, the average density of reef fish was 260 (SE 20) individuals 40-m<sup>-2</sup>, and the average estimated biomass was 12 548 (SE 1 301) g 40-m<sup>-2</sup> (Table 1). The mean species richness per transect was 12 (range 5–22 species). The presence of two highly gregarious pomacentrids, namely *Chromis lubbocki* and *C. multilineata*, with a mean combined biomass of 5 419 (SE 821) g 40-m<sup>-2</sup> across all sites, indicated the trophic importance (labelled the '*Chromis* effect') of these planktivores on the Santa Luzia reef fish assemblage. When all *Chromis* species were excluded from the analysis, the fish density dropped to 80 (SE 10) individuals 40-m<sup>-2</sup>,

a decrease of more than 70%. Other important species in terms of biomass were parrotfish *Sparisoma cretense* (roving herbivore), banded seabream *Diplodus fasciatus* (an endemic omnivore) and *Kyphosus* spp. (roving herbivores) (Table 1).

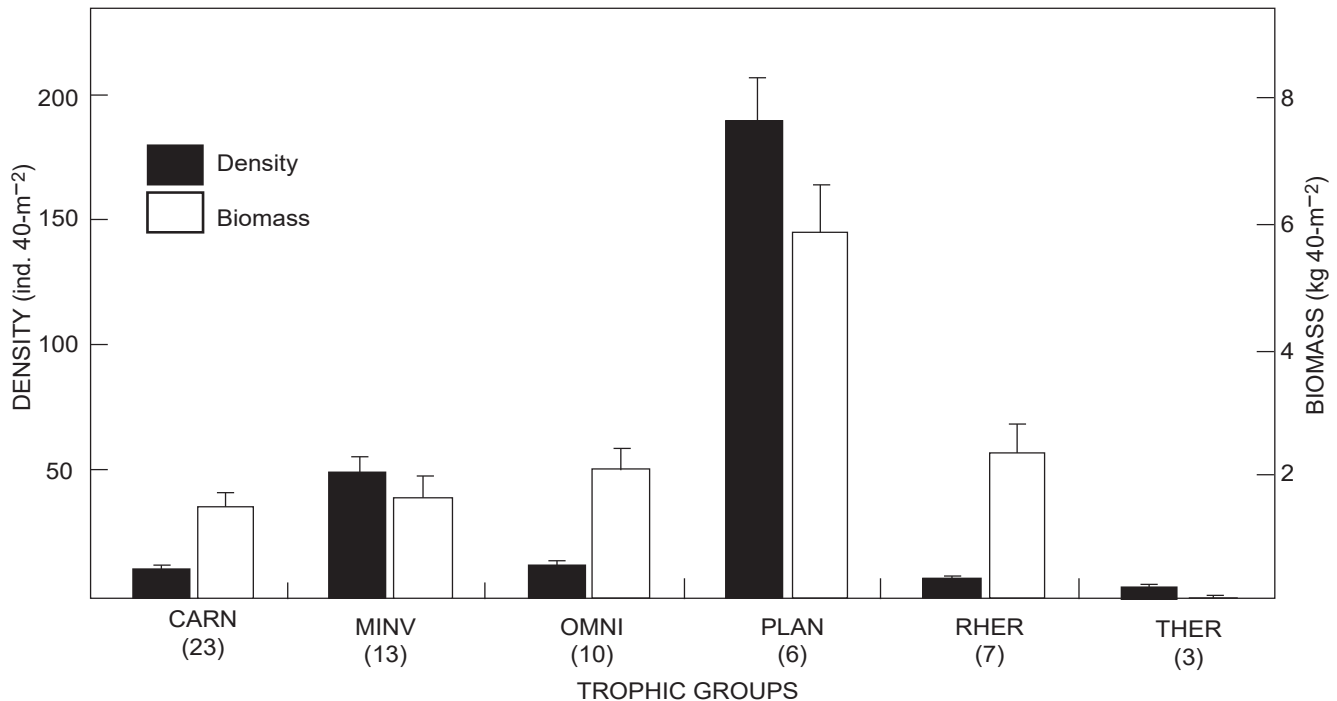
In terms of species richness, carnivores accounted for 34.3% (23 species), followed by mobile invertebrate feeders at 19.4% (13 species), omnivores at 14.9% (10 species), roving herbivores at 10.4% (7 species), piscivores (6 species), planktivores (4 species), territorial herbivores (3 species), and a sessile invertebrate feeder (a single species of butterflyfish, *Chaetodon robustus*). Planktivores accounted for 69% of all fish species recorded in the UVCs, followed by mobile invertebrate feeders (17.9%), omnivores (4.5%), carnivores (3.6%), roving herbivores (2.7%), and territorial herbivores (1.5%) (Figure 3). Piscivores and sessile invertebrate feeders accounted for only 0.5% of the fish (260 individuals) recorded, and these are excluded from Figure 3. Planktivores also represented the most important group in terms of biomass; of secondary importance were roving herbivores, omnivores, mobile invertebrate feeders and carnivores (Figure 3). Territorial herbivores, piscivores and sessile invertebrate feeders exhibited very low biomass.

Both fish density ( $F = 7.81$ ,  $df = 10$ ,  $p < 0.01$ ) and biomass ( $F = 4.42$ ,  $df = 10$ ,  $p < 0.001$ ) were significantly different among sites, with the highest values detected at the southwestern sites (Figure 4). The site Água Ruim (AGARU) had the highest fish density and biomass, mainly because of the density of planktivores and mobile invertebrate feeders, with a total mean of 565 ind. 40-m<sup>-2</sup> (and a total mean biomass of 28.1 [SE 5.2] kg 40-m<sup>-2</sup>). In contrast, the northern sites showed relatively low densities and biomass (i.e. no '*Chromis* effect'), for example at Enseadilha Norte (ENORT), a sheltered site in the north.

Some sites, including Curral (CURAL), Água Doce (AGADO) and the southerly Ilhéuzinho (ILHEU), had similar intermediate values of fish density (Figure 4). Lower mean density and biomass per transect were found in the single remote southeastern site, Ponta Creolo (CREOL). Comparisons revealed that the most homogeneous sites in terms of biomass were AGADO and CREOL.

#### Patterns of benthic community structure

The composition of the benthic community varied significantly across the study sites and their grouping did not follow any geographic pattern (Figure 5) but was highly dependent on local features. The sites AGARU and Ponta Chica (PCHIC) were characterised by high cover of macroalgae (Figure 5). Sites Ponta Preta Norte (PPNOR) and CREOL were also grouped together, with PPNOR presenting high levels of bare rock and CREOL high cover of turf algae. Rhodoliths, turf algae, macroalgae and (in most cases) CCA were characteristics of CURAL, ILHEU and Ponta Branca (PBRAC), whereas Espequinho (ESPQI) and Ponta Praia (PPRAI) were the most heterogeneous sites. Sites AGADO and ENORT were the most distinct from all the others, with high cover of zoanthids and CCA, respectively (Figure 5).



**Figure 3:** Overall density and biomass (mean + SE) of reef fishes by trophic group recorded at Santa Luzia Island. CARN = carnivores; MINV = mobile invertebrate feeders; OMNI = omnivores; PLAN = planktivores; RHER = roving herbivores; THER = territorial herbivores. Piscivores and sessile invertebrate feeders were evaluated but are not shown due to very low values. The number of fish species is given in parenthesis

### Environmental variables and relationship with fish density and biomass

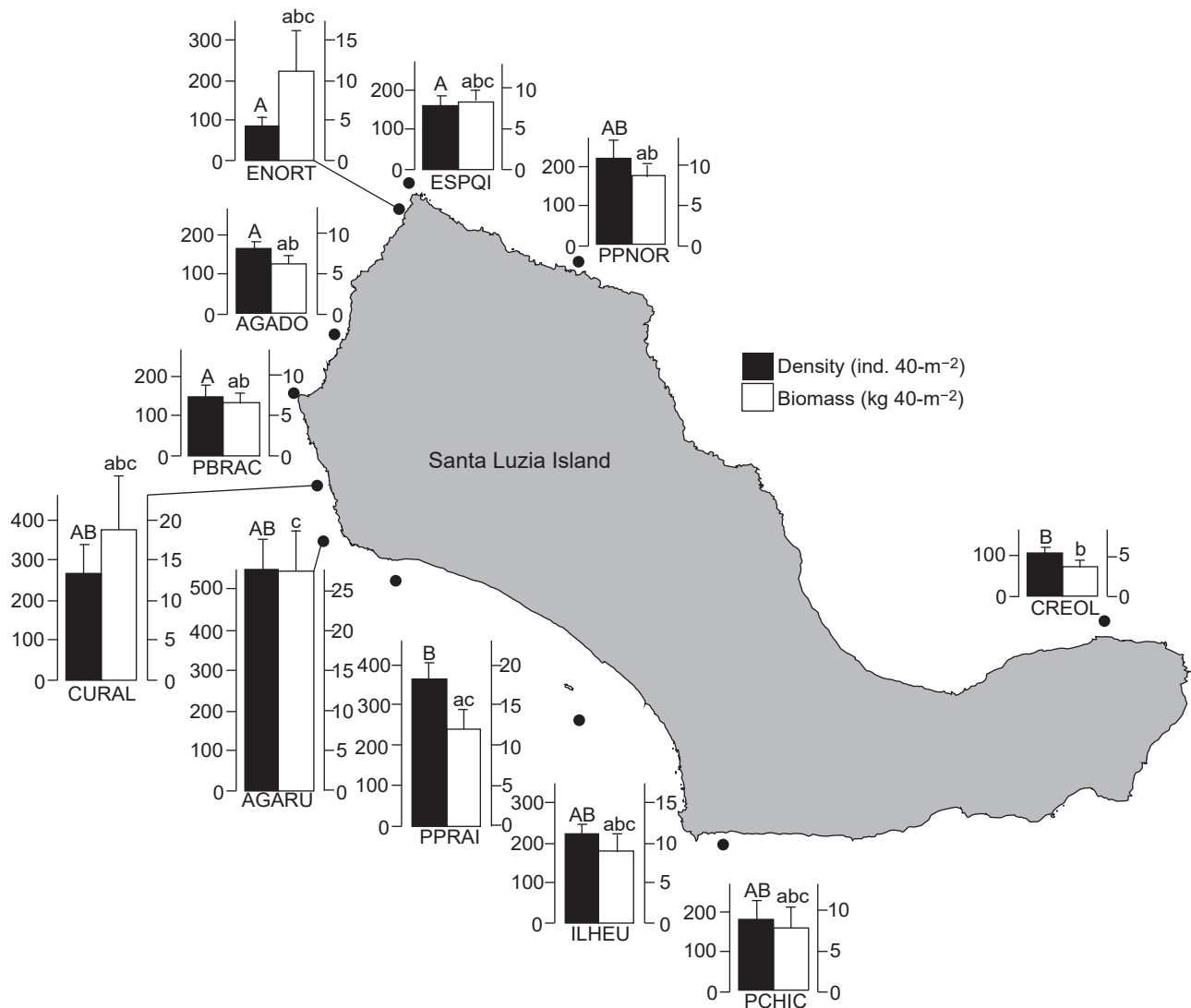
The overall density of different reef fish trophic groups correlated with the benthic descriptors ( $p < 0.05$ , adjusted  $r^2 = 0.62$ ). The first component explained 65.7% of the relationships and the second component explained 18.6% (Figure 6a). Most trophic groups (omnivores, territorial and roving herbivores, carnivores and mobile invertebrate feeders) correlated positively with sites with high cover of CCA. Planktivores, as the most abundant trophic group in Santa Luzia, correlated positively with sites with a high cover of sand and macroalgae. Along the second axis, sessile invertebrate feeders and piscivores correlated positively with rhodoliths and turf algae, while mobile invertebrate feeders showed correlation with sites with high cover of *Millepora* (Figure 6a). A similar pattern of correlation was found when analysing biomass of fish trophic groups ( $p < 0.05$ , adjusted  $r^2 = 0.51$ ), with 52.6% of the variation being explained by the first axis and 23.2% by the second (Figure 6b). CCA, sand and rubble, macroalgae and zoanthids were the most important components of this structure. The biomass of mobile invertebrate feeders, roving herbivores and omnivores correlated positively with CCA, whereas planktivores correlated mainly with sand and rubble, macroalgae and zoanthids. Along the second axis, the biomass of carnivores and piscivores were positively correlated with rhodoliths and coral, and the biomass of territorial herbivores was correlated with *Millepora* (Figure 6b). The site descriptors FI, WS and CO presented very low explanatory power and had no significant effect on the ordination.

### Discussion

The data presented in this study constitute the first assessment of reef fish assemblage structure in relation to the benthic community at various sites around Santa Luzia Island in the Cabo Verde Archipelago. A total of 67 reef fish species were recorded around the island, with average estimates of diversity and density found in the moderately unexplored areas of CREOL, ENORT and PCHIC. The AGADO site showed the overall maximum fish density, biomass and species richness (54 species). The most speciose families at Santa Luzia were the Muraenidae, Pomacentridae and Labridae. In similar tropical areas of the eastern Atlantic, Maia et al. (2018) found the Gobiidae and Serranidae to be the fish families most representative of São Tomé Island, followed by the same families that were dominant at Santa Luzia. At the remote Selvagens Islands in temperate Macaronesia, the most-species-rich families were the Blenniidae, Carangidae and Sparidae (Almada et al. 2015). The low density of large omnivorous and carnivorous fishes (e.g. serranids that usually prey on *Chromis*, or the island grouper *Mycteroperca fusca*), and the high prevalence of small planktivores (such as *Chromis* spp.), as well as cryptobenthic species, demonstrates the negative impact of overfishing.

Fishing at Santa Luzia increased during the 1980s due to the use of outboard engines in addition to the sail boats usually used by artisanal fishers in channels between Santa Luzia and the nearby islands of São Vicente and São Nicolau. Ramos and Roque (2018) estimated that 185 fishers



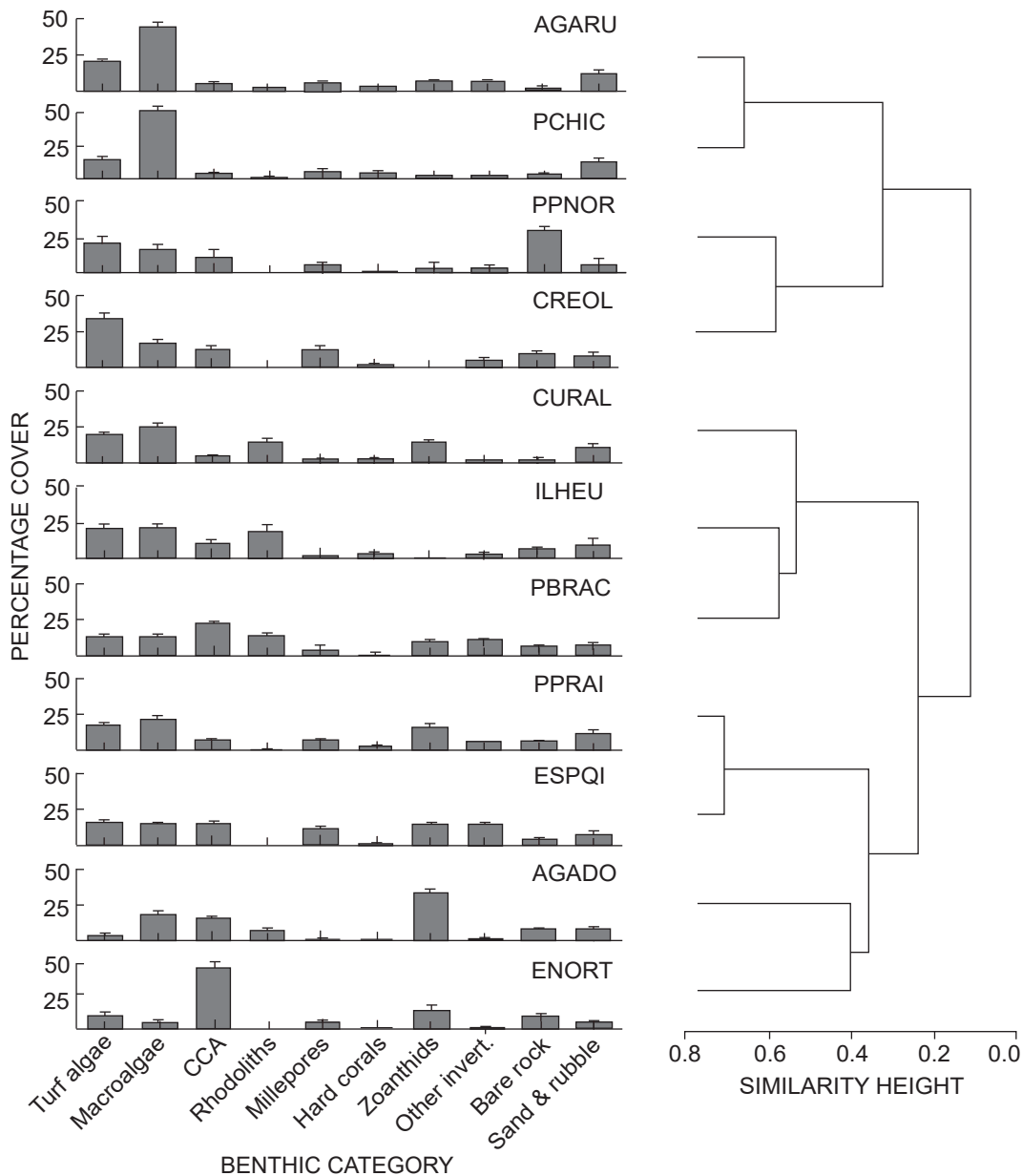


**Figure 4:** Comparative total fish density and biomass (mean + SE) among census sites (black dots) at Santa Luzia Marine Reserve, Cabo Verde; letters above bars indicate homogeneous groups according to Tukey HSD *post hoc* comparisons. For full names of reef sites see Figure 1

from five communities on the two nearby islands used ~50 artisanal-type boats to fish around Santa Luzia. Hook-and-line is used to catch demersal species, and purse-seine nets are used for small pelagics (JMF Barosa, University of Algarve, Portugal, unpublished data). Fishing is permitted in some zones in the MPA, but, due to the lack of effective surveillance, illegal and unregulated fishing persists at Santa Luzia, with spearfishing and the use of non-selective gillnets creating additional pressure on the local marine resources.

The abundance pattern of trophic groups at Santa Luzia is similar to that at other oceanic islands in the Atlantic, such as Trindade Island (Pinheiro et al. 2011), Saint Peter and Saint Paul Archipelago (Luiz et al. 2015) and São Tomé Island (Maia et al. 2018), which are dominated by reef planktivores. AGARU was the site with the highest density and biomass values, largely due to the presence of huge schools of *Chromis* spp. When planktivores were excluded from the analysis, abundance was reduced on

average by 64% (there was a maximum so-called 'Chromis effect' of 80% at PPNOR and a minimum of 16% at ENORT) and estimated biomass decreased by 38%. The dominance of *Chromis* was likely linked to water surge or the presence of stronger currents at the northern sites. Planktivores usually benefit from such conditions, which help them to maximize food intake in coastal systems where low rainfall limits the leaching of nutrients that could contribute to enriching local primary production (Floeter et al. 2007). Fish density and biomass were strongly influenced by substrate heterogeneity, which characterised the southwestern side of Santa Luzia (especially sites AGARU and PPRAI) and this might explain high fishing intensity at those sites, as suggested by local fishers. There, heterogeneity of the reef substrate, which includes a combination of different morphotypes of macroalgae on sand and rubble platforms, across slightly rocky slopes, provides high complexity and niche diversification for reef



**Figure 5:** Relative cover by benthic category per site (mean + SE) in the Santa Luzia Marine Reserve. Sites were grouped according to a Bray–Curtis similarity matrix and average linkage clustering. For full names of reef sites see Figure 1. CCA = crustose coralline algae; Other invert. = other invertebrates

fishes. Conversely, where zoanthis, CCA, turf algae, and bare rock cover larger areas, the low complexity provides habitat for small fishes only. Similarly, Luiz et al. (2015) found evidence that the occurrence of planktivores was negatively correlated with the presence of rubble, whereas the occurrence of omnivores was positively correlated with CCA at Saint Peter and Saint Paul Archipelago. The study sites most typical of these features (CREOL, ENORT, ESPQI and PBRAC), which (except for CREOL) are located on the north side of the island, presented high CCA cover and had low values of reef fish density and total biomass.

When trophic groups were used in the RDA analysis, distinct patterns were evident between fish density and

biomass. The strong relationship between the density of trophic groups and the benthic community could be explained by the presence of planktivores, the most abundant group at sites with high water surge (i.e. at AGARU, CURAL and PRAI). Water-surge conditions favour nutrient upwelling, which consequently favours more productivity and enhances growth of plankton (Luiz et al. 2015). However, both territorial and roving herbivores were directly related to CCA cover, mainly at ENORT, where densities of fishes were the lowest of all the studied sites. Territorial damselfishes (Pomacentridae) are dependent on turfs that grow around and on the edge of CCA, whereas roving herbivores, such as *Sparisoma cretense*, can feed on endolithic algae associated with crusts (Clements



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