



Mapping marine habitats in the Gulf of Guinea: A contribution to the future establishment of Marine Protected Areas in Principe Island

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ARTICLE INFO

Article history:

Received 4 February 2022

Received in revised form 18 October 2022

Accepted 15 November 2022

Available online 21 November 2022

Keywords:

Atlantic Ocean

Benthic cartography

Habitat variability

Marine conservation

Rhodoliths

Scleractinian corals

Side Scan Sonar

ABSTRACT

Accurate mapping of marine benthic habitats, using acoustic technologies such as Side-Scan Sonar (SSS), is a useful tool for marine conservation and management, as well as to support zoning processes of maritime activities in the coastal environment. Georeferenced habitat maps can improve management of isolated tropical coastal and marine ecosystems, where rapid unsustainable anthropogenic coastal development often occurs. In this study, SSS was employed to map subtidal marine habitats of Principe Island (Gulf of Guinea, West Africa) to determine areas of especial interest for biodiversity or marine resource conservation. The SSS methodology was applied, during the BIO-Príncipe Scientific Expedition (2016), in four target areas, both inside and outside its UNESCO Biosphere Reserve, covering 675 ha between 3 and 30 m depth, also combining SCUBA diving and video transects. These areas were chosen based on their geographical location and habitat information, provided by the local stakeholders. Over the total surface mapped, five main habitats were recorded: sandy seabeds (flat sandbanks and rippled sandbanks), rhodolith seabeds (rhodoliths interspersed with scleractinian coral colonies and macroalgae), biogenic (mud/sedimentary) seabeds, and rocky seabed (bedrock and rocky reefs). In the northern, eastern, and southern areas of the island, sandy bottoms with ripples, interspersed with small biogenic sedimentary beds and rhodolith bottoms predominated. The southwestern area, Baía das Agulhas, concentrated the greatest variability and richness of habitats, including the largest rhodolith seascape. This study provided a consistent and detailed dataset to support the creation and design of future MPAs, already planned by the Principe's government, adding including essential information on areas containing key habitats (e.g. rhodoliths) not detected in previous reports.

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1. Introduction

Marine continental shelves concentrate a mosaic of reticulated habitats, such as coral reefs, seagrass meadows, or rhodolith seabeds (Otero-Ferrer et al., 2020b; Tuya et al., 2010). These habitats provide a wide variety of resources and services such as ecological (e.g. habitat provision; Buhl-Mortensen et al., 2016; Govenar and Fisher, 2007; Graham et al., 2018), economical (recreational services and fishing stocks development; Andrews et al., 2021; Nielsen et al., 2021), social (maintenance of cultural activities and maintenance of fishing grounds; Breen et al., 2021; Hattam et al., 2021) or climate mitigation (e.g. Blue carbon; Casas et al., 2021; Filbee-Dexter et al., 2022; Schubert et al., 2022), even

exceeding the global national product (Costanza et al., 1997). However, in many cases, the lack of a comprehensive marine spatial planning (MSP) framework and the establishment of specific protection plans, such as Marine Protected Areas (MPAs), together with the increase of anthropogenic activities (e.g. fisheries or tourism development) in coastal areas, prevail over conservation (Agardy et al., 2003; Douvère, 2008), which has risen environmental pressures and, consequently, massive loss of these marine key habitats (Che Hasan et al., 2012; Li et al., 2017; Moura et al., 2013).

Marine environmental management and conservation actions are supported by geographical baseline information on the distribution and connectivity patterns of marine habitats and the distribution of their associated biodiversity (Che Hasan et al., 2012; Li et al., 2017; Moura et al., 2013). It is therefore imperative to identify the complexity and distribution of benthic habitats

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(Roff et al., 2003), the characteristics of a natural and healthy state, and the effects of different human activities (Stelzenmüller et al., 2013).

The assessment of habitats has traditionally been based on wildlife sampling (Brown and Collier, 2008; Moura et al., 2013). However, the rise of acoustic methodologies, such as side-scan sonar (SSS), provide robust data on the distribution and extent of marine habitats. SSS is also a relevant tool for the design and monitoring of MPAs (Mulhearn, 2001), due to its efficiency in characterizing and creating accurate maps of the seafloor (Durán et al., 2000; Schultz et al., 2013), able to distinguish and characterize key habitats such as coral reefs (Karpouzli and Malthus, 2007), seagrass beds (Greene et al., 2018; Pasqualini et al., 1998) and, more recently, rhodolith seafloors (Jeong et al., 2020). Thereby, habitat mapping underpins baseline information to promotes the establishment of effective coastal management and conservation policies, especially in developing countries with emerging ecotourism areas and with limited knowledge about their natural resources (Li et al., 2017).

The island of Príncipe (Democratic Republic of Sao Tomé and Príncipe) is a small (ca. 148 km²) tropical island located near the equator, within the marine ecoregion of the Gulf of Guinea (Eastern Atlantic Ocean) (Spalding et al., 2007). Since 2012, the island has been designated by UNESCO to be part of the World Network of Biosphere Reserves, based solely on its terrestrial fauna and flora and the diversity of terrestrial habitats, assuming the compromise to preserve biodiversity, enhance sustainable development actions and promote social welfare (Abreu, 2014). The large growth of the tourism sector in the last decade has raised concern for environmental issues, including new infrastructures in coastal areas. This touristic development justifies the need of developing wise conservation and protection strategies (Pires, 2020; Srouf, 2018).

In contrast to terrestrial ecosystems, Príncipe's marine habitats and their associated biodiversity is still far from being well known (Haroun et al., 2018; Jones, 1992; Peet and Atkinson, 1994). The scant information come from fish inventories (Afonso et al., 1999; van Rein et al., 2009, 2011; Wirtz et al., 2007) and quantitative studies focusing on changes in the diversity of reef fish assemblages in various depth gradients (Tuya et al., 2018), fish-benthos interactions (Canterle et al., 2020), and across marine seascapes (Otero-Ferrer et al., 2020b). Only one technical report has provided a preliminary approximation to the island's marine habitats, using Landsat-8 satellite technology, including bathymetric, shoreline, and (preliminary) habitat maps (Cowburn, 2017). This preliminary data has indicated the major presence of rock, sand and rhodolith seabeds in shallower coastal areas of the island. Rhodoliths are known as one of the "big four" benthic communities with coral reefs, kelp forests, and seagrass beds (Foster, 2001; Pereira-Filho et al., 2015). Specifically, this type of habitat is composed by free-living calcareous red algae, forming three-dimensional nodules of rugged appearance and diverse morphology (Bonacorsi et al., 2012; Foster, 2001). Variations in nodule size and morphology are determined by different factors, mainly hydrodynamism, light and sedimentation (Otero-Ferrer et al., 2020a). Their morphology and size also affect associated flora and faunal communities (Hinojosa-Arango et al., 2009; Otero-Ferrer et al., 2020a). The heterogeneous structure created by rhodolith nodules provide shelter and resources for epiphytic flora and sessile fauna ("nursery" and "hotspot" ecological functions) (de Queiroz et al., 2016; Gagnon et al., 2012; Squeo et al., 2008). In addition, they transform the soft substrate on which they are found into structurally complex habitats (Hernandez-kantun et al., 2017; Otero-Ferrer et al., 2020a; Pereira-Filho et al., 2012).

This paper performed the first characterization and mapping of major coastal habitats in 4 areas around Príncipe Island, both

inside and outside the UNESCO Biosphere Reserve, through the application of acoustic technologies (SSS). The description of the distribution of key habitats provide solid information to support the creation and design of future MPAs, in order to support future coastal and marine resources management policies.

This paper performed the first characterization and mapping of major coastal habitats in 4 areas around Príncipe Island, both inside and outside the UNESCO Biosphere Reserve, through the application of acoustic technologies (SSS); and the first characterization of the main biophysical traits (size, morphology and health status) of the rhodolith seabed. The description and characterization of the distribution of keystone habitats, provide solid information to support the creation and design of future MPAs, in order to support future coastal and marine resources management policies.

2. Material and methods

2.1. Study area

The study was carried out in coastal areas around the island of Príncipe (Republic of São Tomé and Príncipe), located near the equator in the Gulf of Guinea (Eastern Atlantic Ocean; Fig. 1). The island is influenced by the Guinea Current, which flows superficially eastward along the West African coast, connecting to the north towards the Canary Current and to the south towards the Benguela Current, creating the South Equatorial Current (Awosika and Folorunsho, 2014). Príncipe has a predominantly equatorial climate (warm and humid), with two main seasons: a warmer, rainy season and a dry season (locally known as "gravana"). However, it also has multiple microclimates, according to rainfall, temperature and altitude parameters (Chou et al., 2020; Maia et al., 2018; Spalding et al., 2014).

The sampling period encompassed three consecutive weeks (20/10–13/11, 2016). Four pilot study areas were selected for mapping based on (1) their geographical location within the Príncipe Island UNESCO Biosphere Reserve and (2) their potential to host future MPAs due to their sociocultural and ecological relevance (e.g. fisheries, presence of key habitats). The four areas were: (a) the "Bom Bom" peninsula in the north, (b) the "Baía da Praia Abade" in the east, (c) the "Baía das Agulhas" in the southwest, and (d) the "Baía da Praia Grande do Sul" in the southeast of the island (Figs. 1, 2). The latter two are included as part of the core terrestrial zones (conservation areas) of the UNESCO Biosphere Reserve (Fig. 2).

2.2. Acquisition of geoacoustic data for habitat mapping

Hydroacoustic data were collected through a Side-Scan Sonar (SSS) equipment, on board of an 11 m fiberglass boat. Acoustic prospecting were conducted following a bathymetric profile (data obtained from The General Bathymetric Chart of the Oceans, GEBCO, 2020), parallel to the coast, following predefined transects, each of them between 600 and 1000 m in length and at depths ranging from 5 m to 30 m. The SSS apparatus, a digital CM2 Towfish (C-Max, UK), was towed by means of a cable, behind the ship at a constant height from the bottom, ca. 5 m, and at speed not exceeding 3 knots. The SSS emitted signals with a central frequency of 780 kHz and a horizontal beamwidth of 0.3, covering a range of 100 m on both the vessel port and starboard sides. Here, the resolution is given by the lower of $D_x = R \sin \theta$, where R is the range and θ is the horizontal beamwidth (Blondel, 2009), and the distance traveled by the vessel between two successive pings, which is approximately 0.25 m. The backscatter data were obtained and processed by SonarWiz 6 V6.05.0008 software (Chesapeake Technology Inc., 2016). These data were

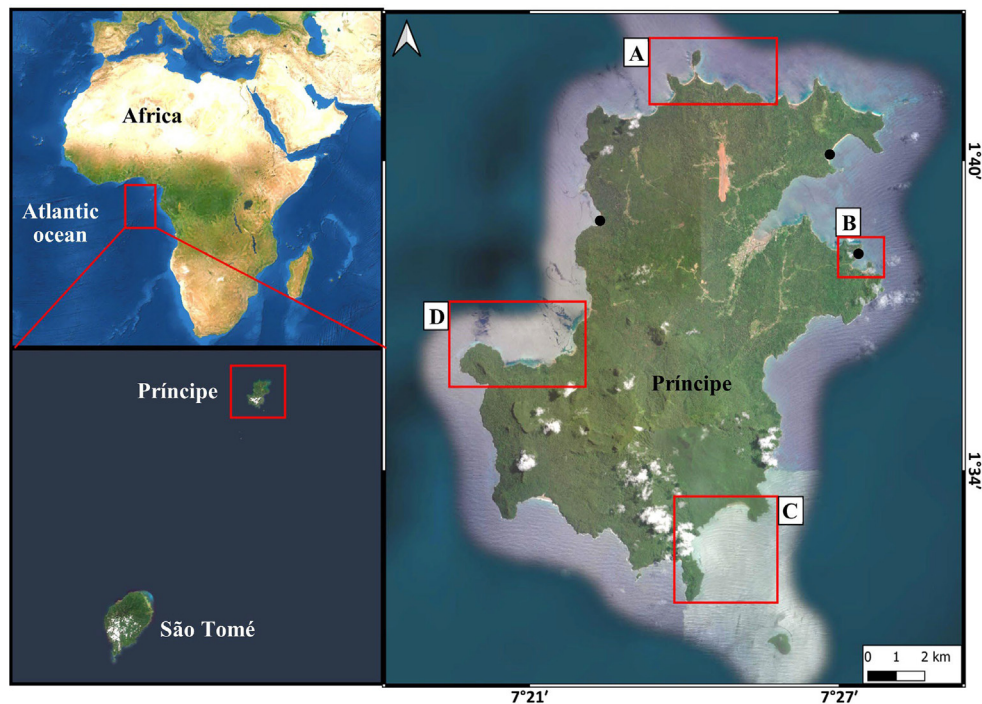


Fig. 1. Location of the study area at Príncipe Island (Eastern Atlantic Ocean), showing the four study areas: (a) the “Bom Bom” peninsula, (b) the “Baía da Praia Abade”, (c) the “Baía das Agulhas”, and (d) the “Baía da Praia Grande do Sul”. The black dots show the locations of the mangrove habitats identified in the coast of Príncipe Island (Praia Caixão in the West, Praia Grande in the Northeast, and Praia Salgada in the East).

processed with empirical gain normalization, automatic gain control, beam angle correction, bottom tracking, layback correction, and nadir filter (Chesapeake Technology Inc., 2015). Also, a pre-classification of the seabed classification textures was performed by the “Seabed Characterization” section of the SonarWiz software, using the “GLCM” stands for “Grey-Level Co-occurrence Matrix” filters, calculating how much variation there is between adjacent pixels in GLCMContrast, GLCMAsimilarity, and GLCMHomogeneity with 15-pixel window size and an 11-pixel window step. A differential GPS, A325 GNSS Smart Antenna (Hemisphere, USA), was employed for the navigation and positioning of the SSS device in the software.

Underwater digital video imagery, using a Sony HDR-AS50 waterproof video camera, with transmitted resolution at 1920 × 1080p@30 fps VGA (Sony, Tokyo, Japan), and *in situ* observations performed by SCUBA divers, collected ground-truth data on the sea bottom substrates, to corroborate previous habitat pre-classification obtained by SSS backscatter. All processed and georeferenced data were exported as GeoTiff images, with a resolution of 0.5 m per pixel, to the QGIS Geographic Information System (GIS) (Quantum GIS Development Team, 2019) to create habitat maps and estimate the coverage of each habitat type.

2.3. Rhodolith sampling and analysis

In the areas where rhodolith seabeds were identified upon preliminary SSS surveys (e.g., “Baía das Agulhas”), samples of rhodolith nodules were taken by SCUBA divers from two different zones, depending on the patch extension and availability, at the outer and the inner part of bay (see Fig. A.1). At each zone, $n = 10$ haphazardly located replicates (25 × 25 cm) were collected by hand, depending on the local and intrinsic limitations of SCUBA diving with depth. The collected samples were preserved in a freezer at -20°C until sorting.

Samples were subsequently defrosted, and then filtered through a 0.5-micron sieve, to remove sand and debris. Macroalgae

were removed from each replicate, separated into three main groups; Chlorophyta, Rhodophyta, Ochrophyta, and then macroscopically identified to the highest possible level, using dichotomous keys. Dry weight of each main group was subsequently calculated. Moreover, from each replicate, 25 rhodoliths were randomly selected, and their size were measured following the Sneed and Folk (1958) criteria (Graham and Midgley, 2000). In brief, for each rhodolith, the longest, intermediate, and shortest (axe) diameters were measured with a plastic calliper (Foster et al., 1997; Otero-Ferrer et al., 2020a; Sciberras et al., 2009). Each rhodolith nodule was then morphologically classified, using a Tri-plot Ternary diagram software (Graham and Midgley, 2000), according to spheroidal, discoidal, or ellipsoidal categories (Villas-Boas et al., 2014). The software also calculated the proportion of nodules that belong to each of three former shape categories, keeping a fourth category (bladed), which remains as intermediate (Fig. A.1 in Otero-Ferrer et al., 2020a). Moreover, for each nodule, the percentage of living surface (% of pink surface), according to previously established categories (1: > 95%; 2: 95%–50%; 3: 50%–5%; 4: < 5%) (Foster et al., 1997; Nelson et al., 2012), and the presence/absence of epiphytic hydrozoans was estimated.

The mean sizes and morphologies percentage of nodules were compared between zones (inner vs. outer side of the bay) using Student's t-tests. Assumptions of normality and homogeneity of variables were tested using Kolmogorov–Smirnov's and Levene tests ($p < 0.05$) (Otero-Ferrer et al., 2015; Zar, 2020). To assess whether the proportion in the presence/absence of rhodolith epiphytic algae and Hydrozoans significantly differed between nodules collected from the two zones, a Chi-square test (χ^2), using 2×2 contingency tables (e.g., zone × algae), was performed. Data were processed and analyzed with the SPSS 17.0 software (SPSS Chicago, Illinois). The significance level was set at 0.05 for all tests.

2.4. Environmental data

The environmental context of the island was described by several data sources. Firstly, (1) Sea Surface Temperatures (SST)

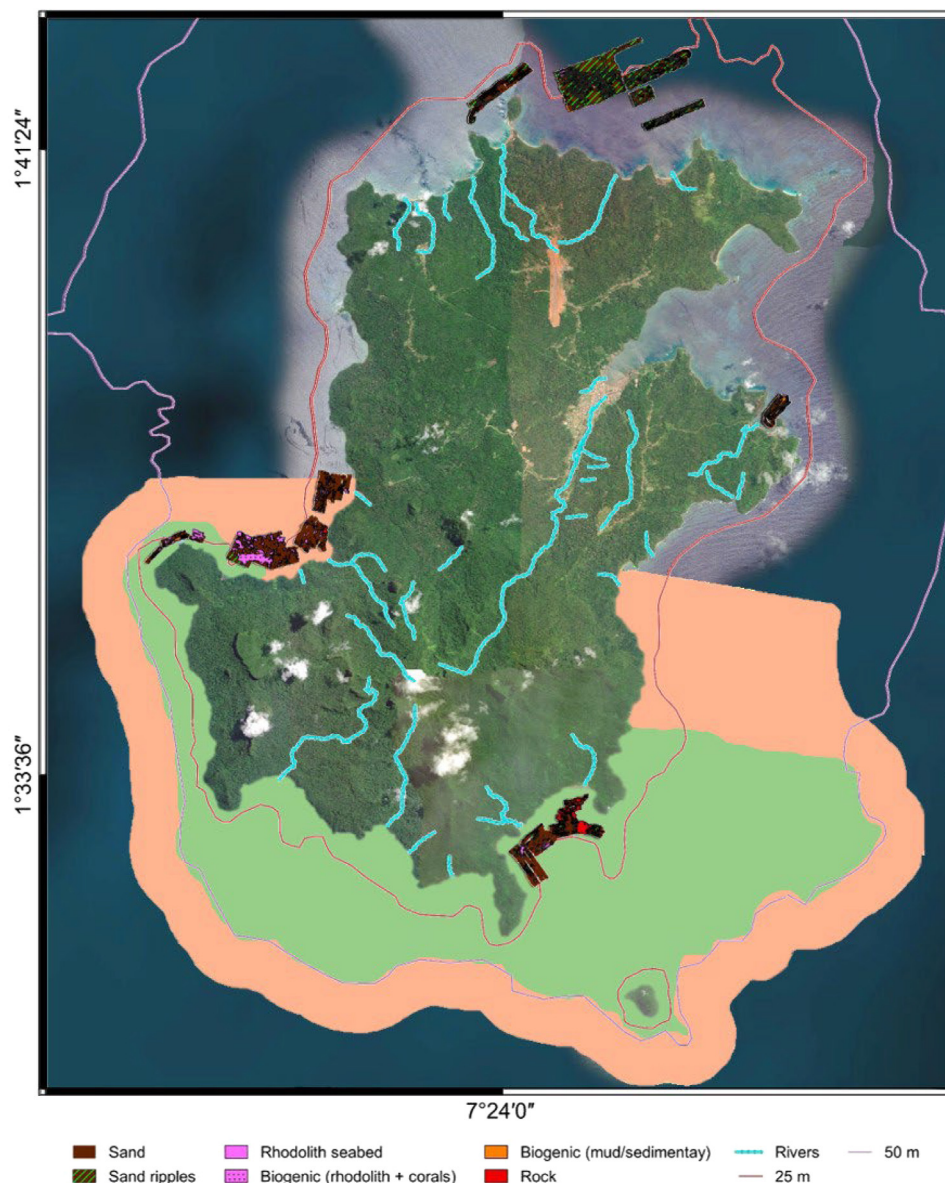


Fig. 2. Location of the study area showing the four study areas and the UNESCO Biosphere Reserve. The green area shows the core, while the orange area denotes the buffer area.. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

acquired from the Aqua MODIS (MODerate-resolution Imaging Spectroradiometer) sensor, available on the Goddard Earth Sciences Data and Information Services Center, Interactive Online Visualization and Analysis Infrastructure (GIOVANNI, giovanni.gsfc.nasa.gov/giovanni/). Secondly, information on currents (direction and speed) and waves (direction, peak period, and significant height), acquired from WAVEWATCH III/ NCEP/ NWS and OSCAR/ Earth & Space Research, available on the Interactive Online Visualization and Analysis Infrastructure (Earthnullschool, <https://earth.nullschool.net>). Finally, the precipitation and run off water data was acquired from MERRA-2 Model M2TMNXFLX v5.12.4 sensor, available on GIOVANNI (giovanni.gsfc.nasa.gov/giovanni/). The mean monthly data of SST, Precipitation and wave height were compared between seasons (wet vs. dry season) using Student's t-tests.

3. Results






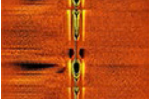



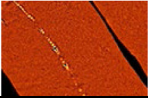

3.1. Habitat description

The mapping covered a total of 675 ha over the areas initially defined, surrounding the coastal perimeter of the island. Our findings indicated that the coastal shelf encompasses four main habitats, classified into two main categories: unconsolidated and consolidated seabeds. Within unconsolidated seabeds, sandy seabeds were the most important habitat (79.2%), followed by biogenic seabeds (16.4%) (Table 1). Sandy bottoms showed a homogeneous pattern with low acoustic signal returns (Table 2). This type of bottom had two types of facies: flat sandbanks (53.1%) and rippled sandbanks (26.2%). Biogenic seabeds were characterized by a continuous heterogeneous acoustic pattern (intense or soft; signal returns according to the biogenic deposits granulometry, Table 2). However, this type of facie can appear

Table 1
Surface (Ha) and % of the mapped habitat in each of the 4 study areas.

	Area (Ha)						Total
	Sand	Sand ripples	Rock	Rhodolith beds + corals	Rhodolith beds	Biogenic mud/sedimentary	
<i>Baía da Praia Abade</i> <i>Praia Grande do Sul</i> <i>Baía das Agulhas</i> <i>Bom Bom</i>	10.01	6.07	0.54	0.01	1.12	5.59	23.34
	83.71	10.31	20.38	2.78	3.13	10.03	130.34
	146.00	6.86	4.37	45.60	7.97	8.24	219.04
	118.31	153.28	4.39	0.09	15.63	10.12	301.84
Total	358.03	176.52	29.69	48.48	27.86	33.98	674.56
	53.08%	26.17%		7.19%	4.13%		
	79.24%		4.40%	11.32%		5.04%	

Table 2
Classification and description of SSS backscatter patterns with associated seabed features and sedimentary facies.

Background/seabed class	Acoustic Patterns (backscatter)	Ground-truthing patterns	Site	Acoustic Pattern Description	Features Association	Sedimentary Facies Association
Artificial reefs		No data	Peninsula Bom Bom	High backscatter and smooth texture	Artificial object	Anthropogenic object (artificial reefs, wrecks...)
Rocky reefs			“Pedra Adalio”	High backscattering (predominantly), rough texture	Rocks, Reefs	Rock and Bioconstructions
Biogenic seabeds			Baía das Agulhas	High/medium dispersion and rough/smooth homogeneous texture	Calcareous nodules, rhodoliths	Bioconstructions scattered on a background of coarse sands with nodules and shells
			Baía das Agulhas	Moderate smooth backscattering, and homogeneous or heterogeneous texture.	Flat background	Thick bioclastic sands with nodules and shells (Mix Rhodolith, Seagrass/seaweeds).
Sandy bottoms			Bom Bom Peninsula	Moderate backscattering, smooth / rough and homogeneous texture.	Dunes and ripples with ridges	Thick bioclastic sands with nodules and shells (possible rhodoliths in the ripple valley), medium siliciclastic sands.
			Baía da Praia Abade	Low backscatter, smooth and homogeneous texture.	Flat background	Bioclastic sands fine-grained to very fine.

covered by turf, sand, or muddy sediments, producing an acoustic pattern that varies from heterogeneous to homogeneous, being necessary to perform ground-truthing surveys (Table 2). Biogenic seabeds were subdivided into rhodolith seabeds (4.1%), sometimes interspersed with scleractinian coral colonies (7.2%), and mud/sedimentary seabeds (5.0%) (Table 1).

Consolidated seabeds (formed by bedrock and rocky reefs) were not as predominant as unconsolidated seabeds (4.4%) across the studied areas, being limited to near-shore and isolated outcrops or rocky reefs (Table 1). These seabeds were characterized by a sharp heterogeneous acoustic pattern with high acoustic signal return, presented as a heterogeneous layer, or as isolated points in biogenic or sandy bottoms (Table 2). Ground-truthing revealed that they were dominated by diverse microhabitats composed of some key benthic organisms, such as sponges, calcareous coralline algae, macroalgae, and hard and soft corals (Fig. 3).

By areas, “Bom Bom”, at the north of the island, was divided into two subareas located at the eastern and western sides of the peninsula (Fig. A.2; Table 1). Both subareas showed a predominance of sandy bottoms, with a constant morphology composed by sand undulations (rippled sandbanks), interspersed with patches of flat sandbanks combined with large, rippled sandbanks (Fig. A.2). In the eastern subarea, isolated dead rhodoliths appeared predominantly in the valleys of the rippled sandbanks. Also, a high concentration of sea snails (*Thetystrombus latus*,

Gmelin, 1791) was also observed on the sand flat areas. At the center of the subarea (ca. 25 m), a big rocky outcrop, locally known as “Pedra Adalio”, was observed surrounded by a smaller heterogeneous acoustic echo background, identified as a uniform live rhodoliths seabed (Fig. A.2). In the western subarea, rocky outcrops were observed in shallower areas (ca. 5 m), as well as abundant rhodolith seabeds (Fig. A.2; Table 1). Likewise, the fuselage of two airplane cockpits, sunk years ago, were detected on the sandy bottom, (Fig. A.2; Table 2).

“Baía da Praia Abade”, in the eastern zone, was a sandy bay in which rippled sandbanks predominated in the central part (Fig. A.3). Acoustic records with low backscatter, combined with the ground-truthing, confirmed the accumulation of mud and silt along with organic debris (e.g., coconuts, branches, and large leaves) and sparse seagrass meadows anchored to the sandy substrate. Patches of rhodoliths, predominantly alive, were identified in the outer edge of the bay, in opposition with patches found inside the bay, composed of dead nodules covered by a thin layer of mud and sediment (Figs. 3; A.3; Tables 1 and 2).

The southern zone (“Praia Grande do Sul”) was divided into two main subareas. The eastern subarea was dominated by rocky bottoms (bedrock) interspersed with rippled sandbanks. In the center of this subarea, there was a sand spit that reached the beach (Fig. A.4). Underwater surveys revealed the presence of sponge colonies and isolated gorgonian communities on the bedrock (Fig. 3). In the western subarea, the rocky outcrops were

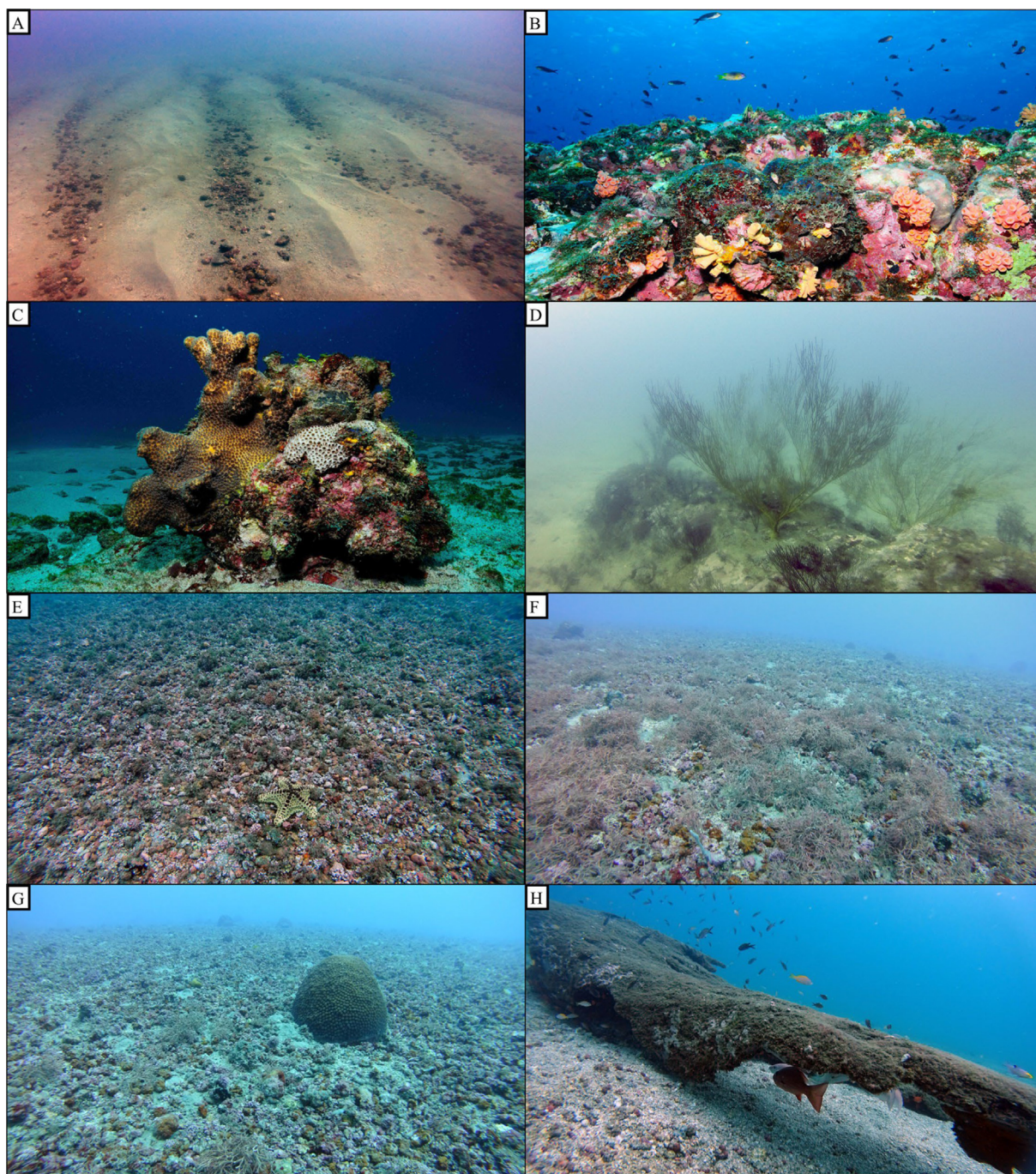


Fig. 3. Ground-truthing imaging data. A. Sand ripples with dead rhodoliths observed in the northern area; B. Coastal rocky reef colonized by sponge and scleractinian corals in the western area; C. Isolated rocky reef with corals and sponges in the southern area; D. Rocky reef with isolated gorgonian communities in the southern area; E. Rhodolith seabeds in Agulhas Bay; F. Rhodolith seabeds covered with *Galaxaura* sp. in Agulhas Bay; G. Biogenic coral and rhodolith seabeds in Agulhas Bay; H. Debris (organic sediments) from the rivers inside the Agulhas Bay.

replaced by sandy, mud and biogenic sediments (e.g., leaves, coconut husks, etc.), as those observed in “Baía da Praia Abade”. There was a minor presence of rhodolith seabeds, mostly dead, occupying the valleys of the rippled sandbanks (Tables 1 and 2).

Finally, the “Baía das Agulhas”, located at the western part of the island, showed the most varied marine seascapes (Fig. A.1; Table 1). Hence, the north, and southwest part of the bay showed sandy bottoms interspersed with mud and silt patches mixed with organic sediments (Table 1). At the central area of the bay (Fig. A.1), rhodolith seabeds extended towards the western part

of the bay (Fig. A.1; Table 2). Rhodolith nodules appeared covered by brown and red algae (e.g., *Dictyota* sp. and *Galaxaura* sp., respectively). Between 12 to 22 m, this biogenic layer was replaced by mixed patches of sandy bottoms with rhodoliths interspersed with isolated colonies of scleractinian corals (e.g., *Montastrea* sp.). Deeper areas (ca. 25 m) showed the presence of sand ripples mixed with rhodoliths (Fig. 3). The western side of the bay showed a rocky coastline with rhodolith patches interspersed with rocky outcrops from 5 to 30 m. These outcrops appeared

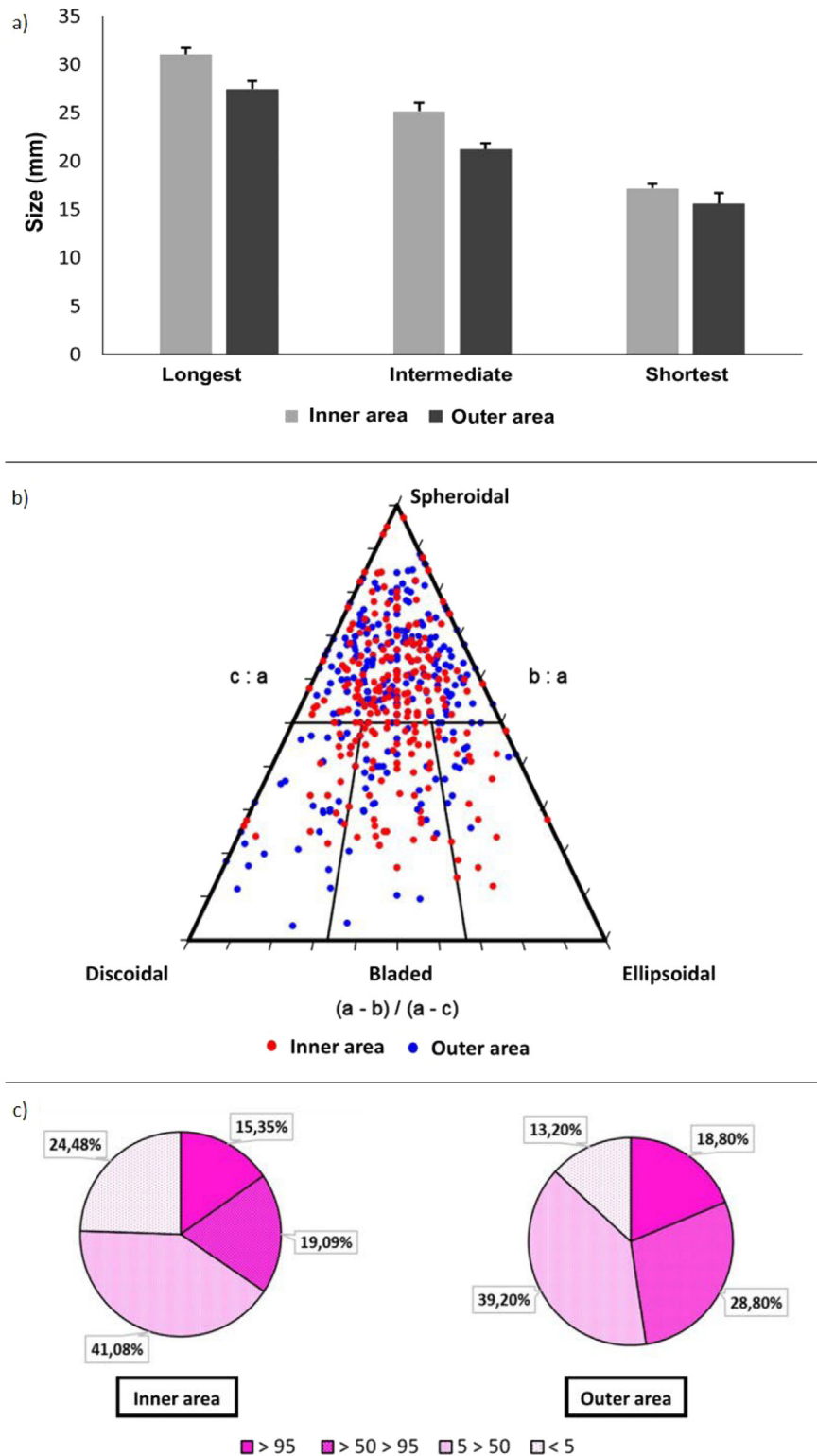


Fig. 4. Descriptive plots of rhodoliths collected in both sampling areas of Baía das Agulhas ($n = 250$): a. Longest, intermediate and shortest dimensions (mm) of each nodule. Error bars are + SE of means. b. Ternary diagram showing deviation in the shape of each nodule from inner subarea (red dots) and outer subarea (blue dots), according to the four shape categories: spheroidal, discoidal, ellipsoidal and leaf-shaped (Graham and Midgley, 2000). c. Rhodolith living surface diagram showing the percentage of living surface (pink surface) of each nodule, according to four categories 1: more than 95%; 2: between 95% and 50%; 3: between 50% and 5%; and 4: less than 5% pink surface. . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

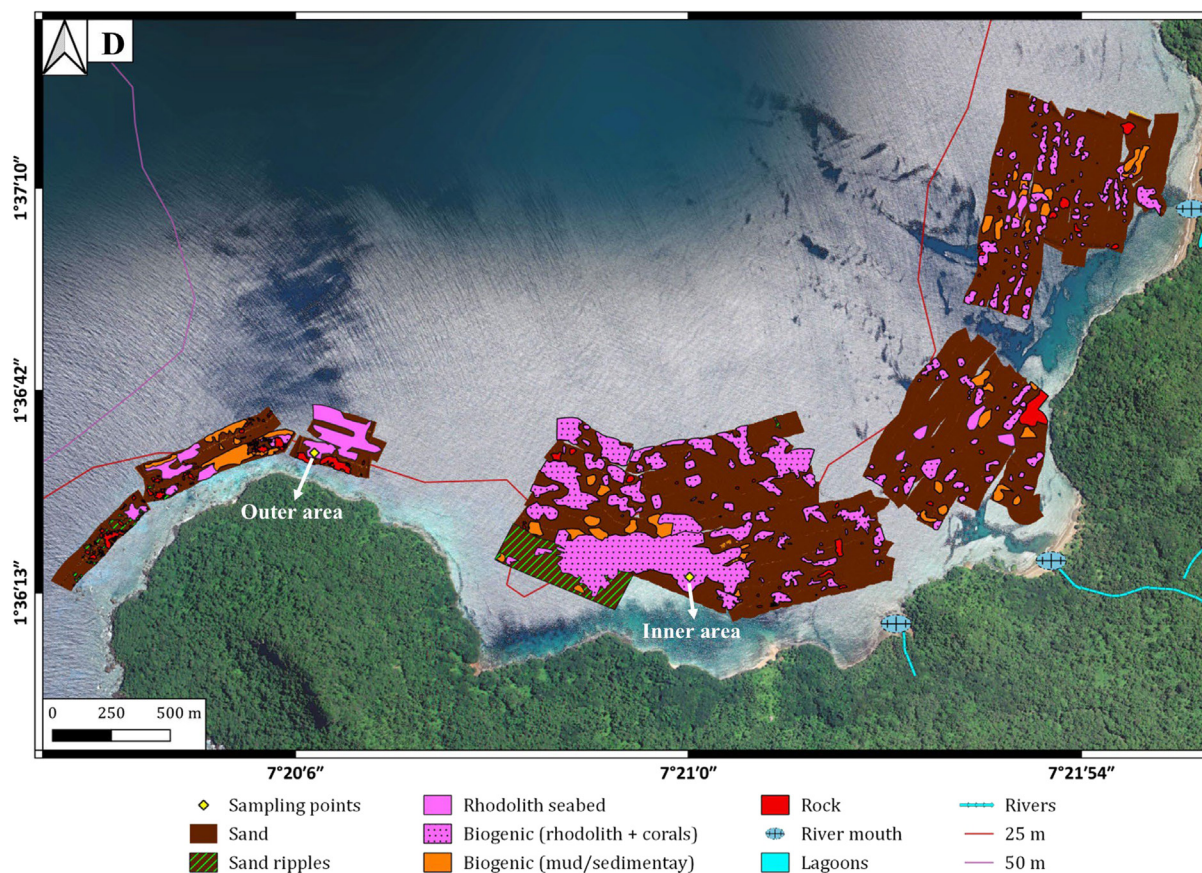


Fig. A.1. Habitat map from the western area “Baía das Agulhas”, showing the river mouths, water bodies and the six habitat classes observed. . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

covered by sponges, corals, and isolated colonies of gorgonians (Fig. 3).

3.2. Rhodolith attributes

The size of rhodoliths (mean \pm SE) were similar in surveyed areas, with larger nodules in the inner (31.05 ± 0.65 mm) than the outer zone (27.49 ± 0.84 mm; $t = -3.36$, $P < 0.001$; Fig. 4; Tables A.1 and A.2). Most rhodoliths were quasi-spheroidal in both areas, according to the tri-plot ternary diagrams ($t = 1.41$, $P = 0.159$; Fig. 4; Table A.1). The percentage of spheroidal rhodoliths in the inner area was $63.90 \pm 4.26\%$, while in the outer area was $68.80 \pm 1.70\%$ (Fig. 4; Table A.2). The percentage of nodule living surface differed between inner and outer areas ($t = 3.18$, $P = 0.002$; Table A.1), showing higher proportion of nodules with living surface >50 in the outer sites (Fig. 4; Table A.2).

Regarding epiflora, a total of 11 macroalgal taxa were identified on rhodoliths (1 Chlorophyta, 7 Rhodophyta and 3 Ochrophyta). According to the total biomass (per kg of rhodolith), Rhodophyta macroalgae constitute the $68.76 \pm 3.80\%$ and Ochrophyta the $31.24 \pm 2.97\%$ of the total, in the inner part of the bay (Table A.3). In the outer part, a similar presence of rhodophytes ($52.31 \pm 3.94\%$) and Ochrophyta ($47.55 \pm 3.08\%$) was found, together with a low occurrence of Chlorophyta ($0.13 \pm 0.04\%$; Table A.3). Within Rhodophyta, *Gracilaria damicornis*, *Galaxaura rugosa* and *Peyssonnelia* sp. dominated the inner bay, while *Peyssonnelia* sp. and *Ceramiales* sp. predominated in the outer area. Furthermore, *Dictyota bartayresiana* (Ochrophyta) dominated in both areas. The presence of these epiphytic macroalgae was significantly higher in the inner compared to the outer zone

($\chi^2 = 4.73$, $P = 0.030$; Fig. A.5). For hydrozoans, the percentage of rhodoliths colonized in the outer area ($18.80 \pm 1.47\%$, Fig. A.5) was higher ($\chi^2 = 4.30$, $P = 0.038$) compared to the nodules collected in the inner part of the bay ($12.03 \pm 2.52\%$; Fig. A.5).

3.3. Environmental data

The predominant current direction was 304° (NW) with an average velocity of 0.42 ± 0.01 m/s; the mean wave direction was dominated from the SW (205°), with an average of 12.5 ± 0.15 s in wave peak period (Fig. A.6). Significant wave height differed among seasons, being higher between April and October ($t = -9.16$, $P = 6.394e^{-15}$; Fig. A.6). The SST varied from 25.25 to 29.17°C , with a summer period between November and June and a winter period from June to October ($t = 7.77$, $P = 9.89e^{-9}$; Fig. A.7). Precipitation varied significantly throughout the year, including a dry period between June and September and a wet period in the remaining months ($t = 4.78$, $P = 1.77e^{-4}$; Fig. A.7).

4. Discussion

This study provides, for the first time, an accurate description of physical and biological attributes of the Island of Principe marine habitat seascapes down to 30 m deep, in four areas for the potential management of key habitats and future creation of MPAs. Our results demonstrated the high heterogeneity of tropical coastal habitats, reflected in previous biodiversity studies targeting specific marine communities (Maia et al., 2018, 2019; Otero-Ferrer et al., 2020b; Tuya et al., 2018). Sandy bottoms interspersed with rocky reefs, and patchy communities of corals and rhodolith seabeds, mostly dominated the shallow-water landscape of the island. As described from other Eastern

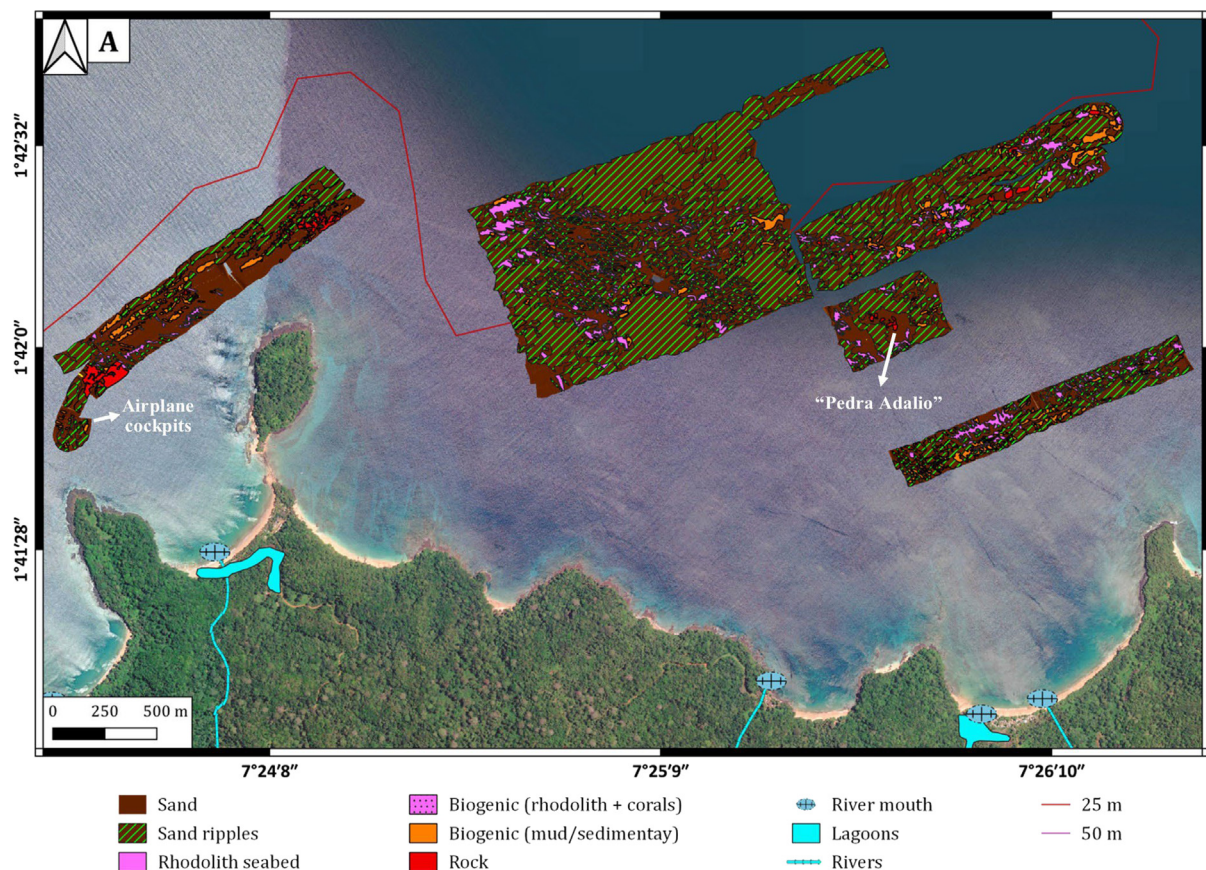


Fig. A.2. Habitat map from the northern area "Bom Bom", showing the mouth rivers, water bodies and the six habitat classes observed.

Atlantic areas, coral species assemblages were poor and unable to form reef structures (Laborel, 1974). Moreover, this study also confirmed the effectiveness of the SSS as a tool for the marine biogenic habitat characterization.

The results obtained with the SSS were more accurate than those obtained with LandSat 8 satellite imaging technology (Cowburn, 2017), where extension was prioritized, over accuracy. The selection of a particular methodology is influenced by the area extent, resolution, and the level of detail required (Doukari and Topouzelis, 2020; Ventura et al., 2018). Although satellite data are widely used in remote sensing of large areas, because of their wide range of resolutions, they do not provide small-scale (centimeter) spatial resolution, while directly affected by physical attributes (e.g. water depth and clarity) and atmospheric conditions (e.g. waves and sunshine), which affect the characterization, classification and extent of important marine habitats (Doukari and Topouzelis, 2020; Ventura et al., 2018).

In agreement with the present study, Cowburn (2017) identified sand, rocky reefs, and rhodolith seabeds, as the main coastal habitats on the island. However, the low accuracy obtained from satellite imagery affects habitat delimitation, potentially overlooking large areas dominated by key habitats, such as rhodolith seabeds, or confusing them with other habitat types of less ecological importance (Karpouzli and Malthus, 2007). Such loss of information can be observed in Baía das Agulhas, where the entire inner bay area was identified as sandy bottoms, while our results pointed to the presence of extensive rhodolith seabeds interspersed within sandy patches and scleractinian coral colonies. Likewise, at Praia Abade, the sea bottom was characterized as a pure sandy seafloor, while our results showed the presence of rocky outcrops, biogenic sedimentary bottoms, and patches of

rhodolith bottoms, both in the inner and outer part of the bay. Moreover, in several spots across the Bom Bom and Praia Grande do Sul, Landsat imagery did not identify several outcrops (including "Pedra Adalio") (Fig. A.2). Finally, an important discrepancy between the two mapping methods is the differentiation between flat sandy bottoms and sandy bottoms with ripples detected by the SSS. The presence of ripples is ecologically significant, as it can affect the abundance and distribution of benthic organisms by disturbing their habitat, through the constant change of microtopography, or by influencing micro-local hydrodynamic pressures, hindering larval dispersal and food supply (Barros et al., 2004; McArthur et al., 2010). This is even more relevant in areas where it is the predominant habitat, as occurred in the Bom Bom area.

The accuracy level of habitat mapping is essential for decision making and the creation of MPAs (Buhl-Mortensen et al., 2015; Stelzenmüller et al., 2013). Recent announcements, presented at the Oceans congress in Lisbon by the President of Principe, have promoted the creation of several MPAs along the entire island coastline, coinciding, majorly, with the areas previously sampled by this study, based upon existing preliminary reports (Airaud, 2021; Cowburn, 2017). However, the lack of accurate information means that areas of particular interest for protection are overlooked (e.g. Agulhas Bay), where our data revealed extensive rhodolith and scleractinian coral fields. The creation of protection zones encompassing this type of habitats may help to improve nearby fishing grounds, because of their ecosystem functions, including fish recruitment and nursery areas (Kamenos et al., 2004; Steller et al., 2003).

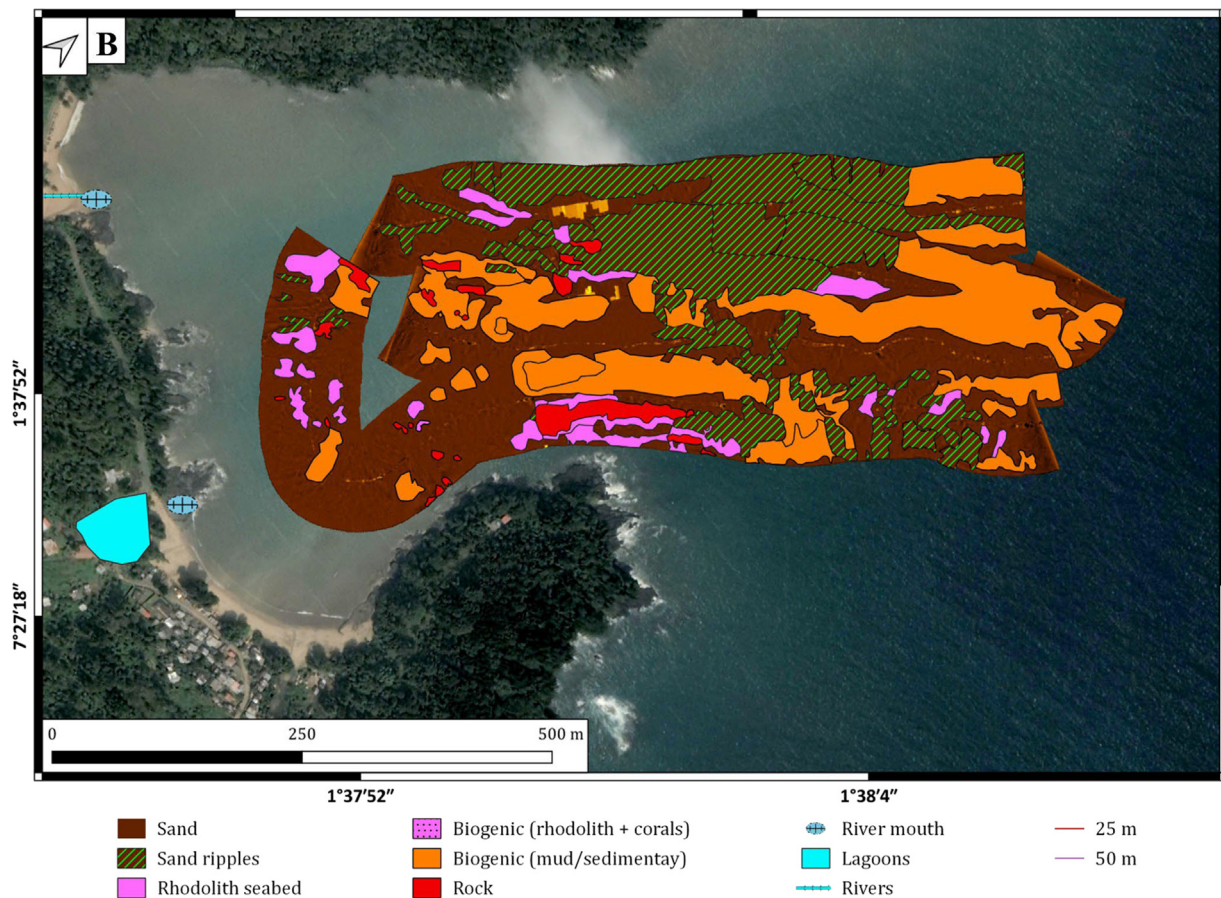


Fig. A.3. Habitat map from the western area “Baía da Praia Abade”, showing the mouth rivers, water bodies and the six habitat classes observed.

4.1. Habitat distribution

As many studies have concluded, oceanographic conditions (e.g. waves and currents) may determine the distribution of marine habitats in shallower coastal areas, including Principe Island (Freitas et al., 2011; Herrera et al., 2021; Maia et al., 2019; Otero-Ferrer et al., 2020a). The magnitude of sediment input discharged by rivers also influence the distribution of coastal habitats, in particular by reducing coral and coralline algal biodiversity, by impacting phototrophic energy acquisition and weakening their structural integrity (Bainbridge et al., 2018; Bartley et al., 2014; Humanes et al., 2017; Strydom et al., 2017). Principe's currents have a NW predominance, while waves have a SW predominance, so the south-facing island coasts are more exposed to both waves and currents. The low presence of sedimentary substrates and a larger presence of bedrock in the area of Praia Grande do Sul, and the outer subarea of Baía das Agulhas, may be explained by this hydrodynamic pattern (Camero Iriarte et al., 2006; Freitas et al., 2011; Schiel et al., 2006). Also, the intense hydrodynamism can wash out sediments from the water column brought by nearby rivers, and cuts off the movement of bottom sand, preventing the formation of ripples (Soulsby et al., 2012).

On the contrary, the innermost part of “Baía da Praia Abade” has a considerable protection from high hydrodynamism events, favoring the presence of biogenic patches, consisting of mud and silt with organic sediments (e.g., coconuts, branches and large leaves). The origin of these sediments was probably from the mouth of two rivers and the existence of a nearby mangrove forest (Burke et al., 2011; Chou et al., 2020; Haroun et al., 2018;

Humanes et al., 2017). Although the flow of both rivers is low during the (dry) “gravana” season, it increases considerably through rainy seasons, raising the amount of sediment, organic matter and pollutants transported by terrestrial runoff (Haroun et al., 2018). Otherwise, the absence of sand ripples inside the bay of Praia Abade may indicate that hydrodynamism did not exceed the threshold of force needed to move the sand (Barros et al., 2004; Soulsby et al., 2012).

The areas with medium hydrodynamism were characterized by sand ripple habitats (e.g., Bom Bom and the outer part of Praia Abade Bay), and a higher presence of rocky outcrops interspersed with patches of silt and sedimentary material, mostly in areas near the mouth of the rivers. The presence of rhodolith seabeds in these areas can be explained by this intermediate-level hydrodynamism, which facilitates the dispersion of the suspended particles in the water column, preventing the deposition over the nodules (Lavenère-Wanderley et al., 2021; Santos Oliveira et al., 2021). According to the sedimentation intensity, nodules can become fouled, favoring opportunistic species proliferation (Grall, 2003), or reach catastrophic sedimentation (total burial), which can cause die-off of entire layers in both cases (Foster, 2001). “Baía das Agulhas”, in the western part of the island, has, theoretically, the most favorable hydrodynamic conditions for rhodolith performance, as it shows the most extensive living rhodolith seabeds of the island. Indeed, it was the only area studied where this habitat was found interspersed with scleractinian corals and large macroalgae. On the contrary, the sparse rhodolith patches embedded with the predominant sandy bottoms found in the easternmost part of the bay may result from large sedimentation generated by three rivers (Fig. A.1) (Haroun et al., 2018).

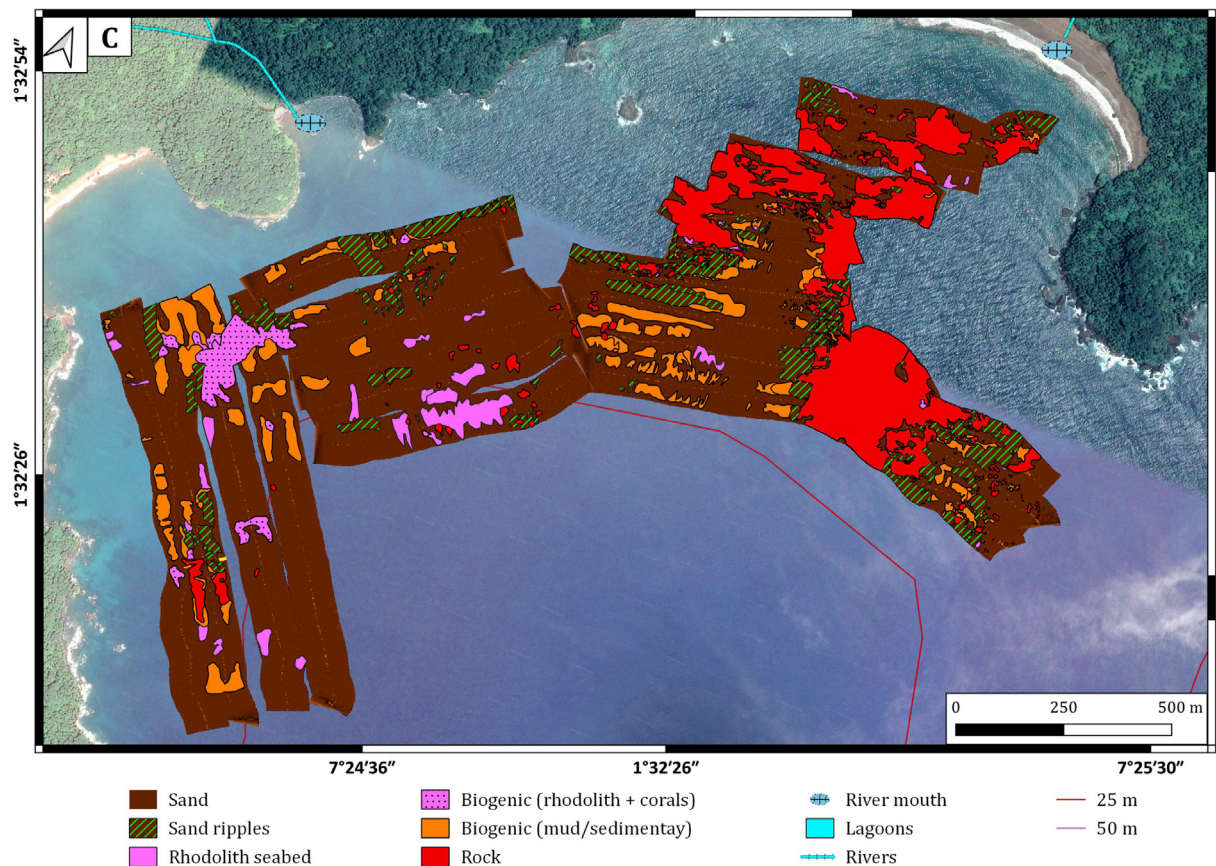


Fig. A.4. Habitat map from the western area “Praia Grande do Sul”, showing the mouth rivers, water bodies and the six habitat classes observed.

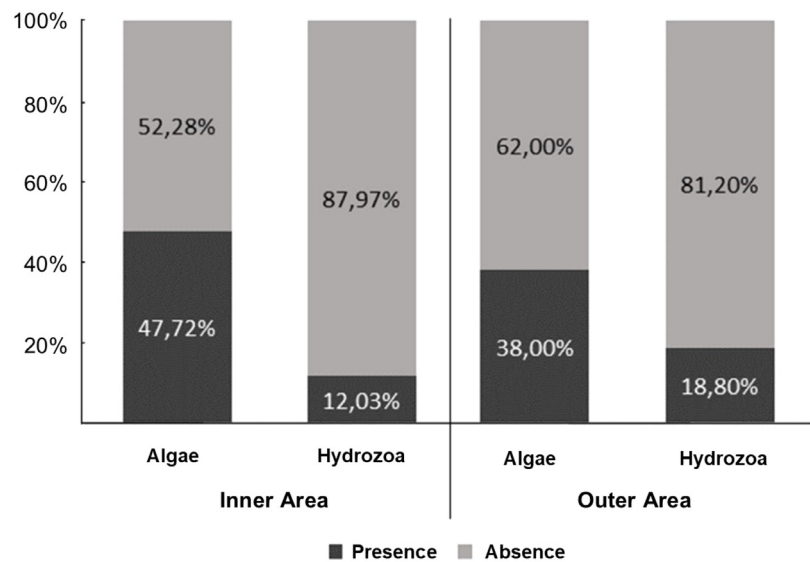


Fig. A.5. Presence/absence percentage of epiphytes (algae and Hydrozoa) in the studied areas.

Rhodolith seabeds were also observed, to a lesser extent, in other areas of the island, under less favorable environmental conditions. They appeared mostly dead and covered with sediments in low hydrodynamic areas (e.g. Baía da Praia Abade), or fractured in small portions due to the abrupt movement of the nodules generated by high water movement (e.g. Praia Grande do Sul),

as reported elsewhere (Sciberras et al., 2009; Steller and Foster, 1995).

4.2. Rhodolith attributes

Rhodolith shape and size is greatly affected by the local oceanographic context (Melbourne et al., 2018; Otero-Ferrer et al.,

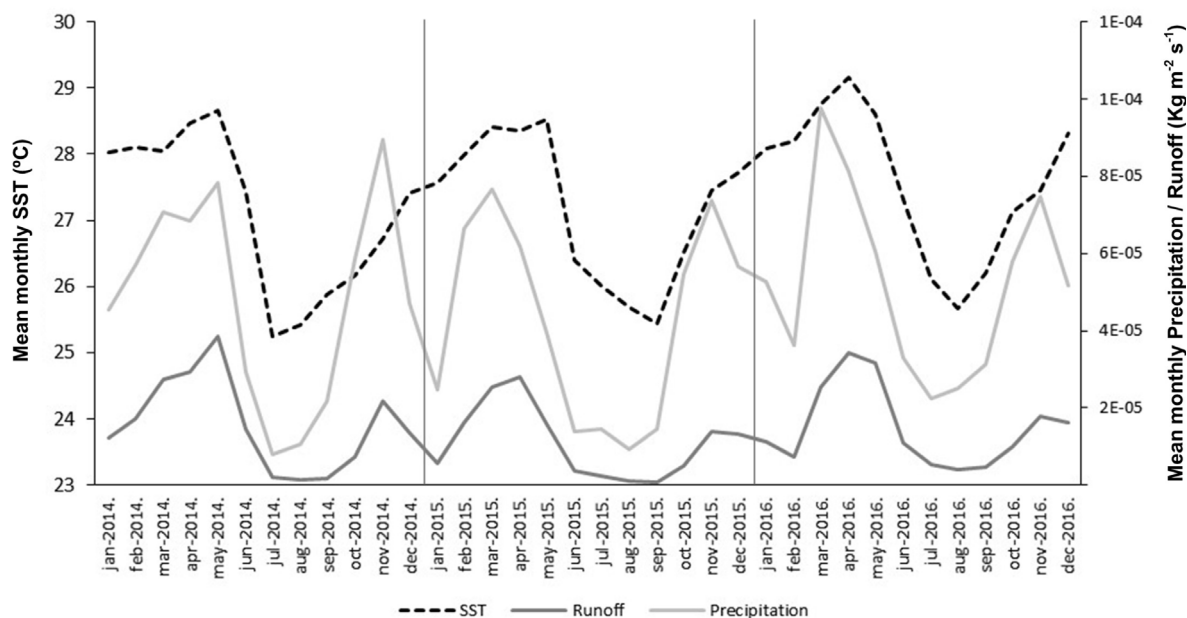


Fig. A.6. Seawater surface temperature (°C), precipitation and run off ($\text{Kg m}^{-2} \text{s}^{-1}$); mean monthly data at each of three successive years (2014–2016).

2019, 2020a; Riul et al., 2009). Hence, the small size of rhodoliths in the outer area of Baía das Agulhas, together with the higher percentage in spherical and discoidal morphology, agreed with observations from other eastern Atlantic oceanic islands, such as the Canary Islands (Otero-Ferrer et al., 2020a) and Azores (Rebello et al., 2018). These morphological attributes may result from wave-induced turbulence. High hydrodynamic regimes can move, erode, and break up the nodules, limiting their size and determining the attainable morphology (Gagnon et al., 2012; Pascelli et al., 2013; Steller and Foster, 1995). In opposition, in the inner zone, the nodules were slightly larger, with more flattened or neutral morphologies, but with a less living surface. These attributes are associated with lower levels of hydrodynamism, under higher epiphytism and sedimentation rates, which constrain rhodolith growth and/or decrease its living surface (Jeong et al., 2020; Littler et al., 1991; Scoffin et al., 1985). The higher hydrozoan presence observed in the outer part of the bay may be also related to hydrodynamism. Some epiphytes, such as several species of hydrozoans, are more selective when they epiphyte, due to their trophic capacity dependent on surface capture, opting for places with greater hydrodynamism, stable salinity and less sedimentation (Gili et al., 1989; Grohmann, 2009). Regarding epiflora, both the order Ceramiales and the genera *Gracilaria* and *Galaxaura*, appeared as the most frequent groups on rhodolith nodules, in agreement with results observed from other rhodolith beds from Brazil and the Canary Islands (Spain) (Bahia et al., 2010; Otero-Ferrer et al., 2020a, 2019; Riul et al., 2009). The genus *Dictyota* was also observed as the most frequent Ochrophyta group, similar to what was observed in Santa Catalina (Brazil) rhodolith seabeds (Gabara, 2020).

4.3. Conclusions

In general, this study showed that coastal marine habitats of Principe Island are a matrix of mosaics of consolidated habitat patches, probably interconnected by transitional zones (e.g. sandy-rhodolith), as reported elsewhere (Costello and Chaudhary,

Table A.1

Summary of statistical results (t-value) for size (Lg: Longest dimension; Int: Intermediate dimension; Sh: Shortest dimension) and percentage of morphology and pink surface by area.

		df	t-value	P
Size (mm)	Lg	455.54	−3.36	8.40e^{-4}
	Int	452.98	−4.09	5.10e^{-5}
	Sh	487.06	−3.81	1.56e^{-4}
Morphology		483.98	1.41	0.159
Pink surface		485.21	3.18	0.002

2017; Cresswell et al., 2017; Tuya et al., 2010). These zones can function as “bridges” in the exchange of energy and material between adjacent habitats, fulfilling important ecological functions (Barbier, 2017; Canterle et al., 2020; Ortiz-Lozano et al., 2009; Otero-Ferrer et al., 2020b). Therefore, they cannot be underestimated or ignored in future conservation plans. In turn, despite these transitions have lower structural complexity, there is an increase if the phylogenetic diversity of associated fish assemblages (Otero-Ferrer et al., 2020b).

The new information provided by this study on marine habitats distribution and extent will support both the creation and expansion of future MPAs and the core zones of the pre-existing UNESCO Biosphere Reserve. On the other hand, this study provided more detailed information on the presence and structure of key habitats in areas that were thought to be unsuitable for protection. Since the island of Principe is considered an economically emerging island, which bases a large part of its economy on ecotourism, the information provided here should be connected to information on anthropogenic activities to better plan future management of the coastal zone and marine habitats of the island. Future management policies will require a detailed ecosystem approach to preserve marine habitats, while promoting sustainable economic development to local livelihoods.

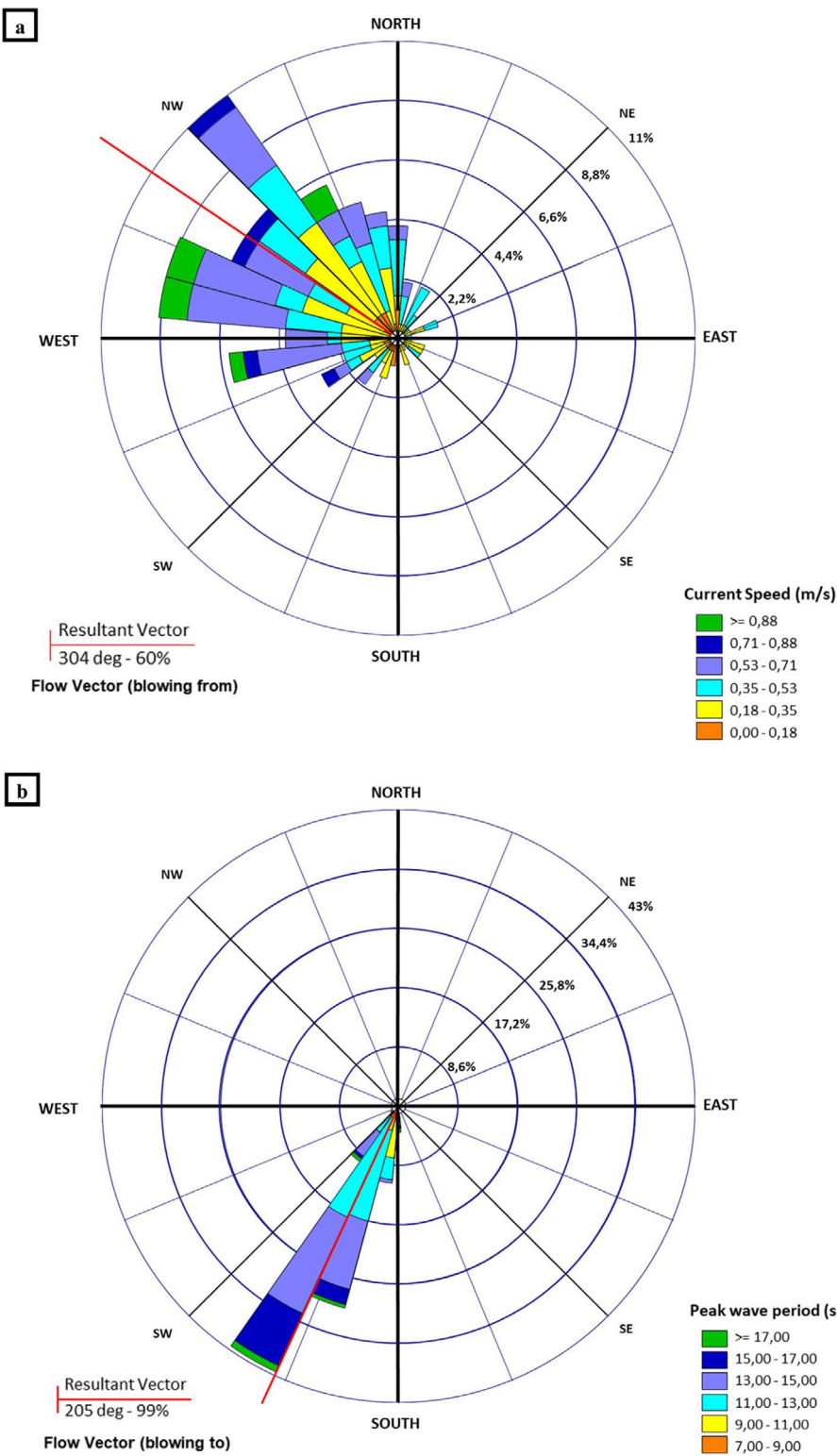


Fig. A.7. Hydrodynamic data provided from the U.S. National Weather Service, including (a) mean wave direction and mean daily peak wave; and (b) mean current direction and speed, during the study period (2014-2016) near the study site (Principe Island).

Table A.2

Summary of size (Lg: Longest dimension; Int: Intermediate dimension; Sh: Shortest dimension) and percentage of morphology and pink surface typologies by areas.

		Area 1		Area 2	
		Mean \pm SE	%	Mean \pm SE	%
Size (mm)	Lg	27.49 \pm 0.84		31.05 \pm 0.65	
	Int	21.19 \pm 0.63		24.45 \pm 0.48	
	Sh	14.68 \pm 0.48		17.20 \pm 0.46	
Morphology	Spherical		63.90%		68.80%
	Discoidal		9.96%		12.40%
	Bladed		19.09%		12.00%
	Ellipsoidal		7.05%		6.80%
Pink surface	>95%		15.35%		18.80%
	95><50%		19.09%		28.80%
	50><5%		41.08%		39.20%
	<5%		24.48%		13.20%

Table A.3

Weight of the different algal phylum collected on rhodoliths seabeds in subareas sampled inside “Baía das Agulhas”.

	Inner area		Outer area	
	mg/kg	% Weight	mg/kg	% Weight
Rhodophyta	397.9 \pm 29.95	52.31 \pm 3.94%	137.7 \pm 7.6	68.76 \pm 3.8%
Ochrophyta	361.71 \pm 23.43	47.55 \pm 3.08%	62.55 \pm 5.95	31.24 \pm 2.97%
Chlorophyta	1.01 \pm 0.32	0.13 \pm 0.04%		
Total	760.62		200.25	

CRedit authorship contribution statement

Marcial Cosme De Esteban: Conceptualization, Writing – original draft, Writing – review & editing. **Ricardo Haroun:** Writing – review & editing. **Fernando Tuya:** Conceptualization, Writing – original draft, Writing – review & editing. **Antonio Domingos Abreu:** Writing – review & editing. **Francisco Otero-Ferrer:** Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data will be available on the ECOAQUA geoportal.

Acknowledgments

This document is a product of the 2016 BIO-Príncipe Scientific Expedition, with the local efforts of Estrela Matilde and Yodiney do Santos (Foundation Principe Trust). In addition we thank the crew of the ship “Bom Bom Resort” for their support during the SSS campaign. F. Otero-Ferrer and R. Haroun have benefited from research funds provided by ERA-Chair’s EcoAqua project (Grant # 621341). Work co-financed by the Canarian Agency for Research Innovation and Information Society of the Ministry of Economy, Knowledge and Employment and by the European Social Fund (ESF) Integrated Operational Programme of the Canary Islands 2014–2020. Axis 3 Priority Theme 74 (85%).

Appendix

See Figs. A.1–A.7 and Tables A.1–A.3.

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