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Rhodolith beds in the Eastern Tropical Pacific: Habitat structure and associated biodiversity

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ABSTRACT

Rhodolith beds (RBs) are globally distributed marine benthic habitats and recognized biodiversity hotspots of conservation interest. However, considerable regions of the world's oceans remain unknown in terms of the presence, distribution, structure, and associated biodiversity of such habitats. In the Eastern Tropical Pacific (ETP), even basic information about these habitats is still extremely scarce. To fill this gap, we characterized the habitat structure and associated biodiversity of four shallow-water RBs at Cocos Island, Costa Rica. Specifically, information regarding rhodolith structural attributes (size, morphology, and $CaCO_3$ content), as well as habitat characteristics (rhodolith nodule density, biomass and $CaCO_3$ standing stocks) were collected. Moreover, the diversity and abundance of associated organisms, including macroalgae, invertebrates and fishes, were determined. Our study shows that Cocos Island harbors dense RBs (1100 to >4500 nodules m^{-2}) with substantial carbonate stocks (14–22 kg m^{-2}), which provide habitats for a wide array of species (158 recorded species). This study adds 58 new records of RB-associated species to previously published records for the island, which increases the total number of species to 316, including 51 species endemic to the ETP and four species categorized as vulnerable by the IUCN. Our results also indicate that community composition and abundance of organisms vary among RBs, likely due to differences in rhodolith morphologies and sizes and/or local environmental conditions. Further research efforts are warranted to identify the drivers for these differences, as well as expanding studies towards other RBs at Cocos Island and in the ETP in general.

1. Introduction

Free-living coralline algae can form extensive and structurally complex habitats, called rhodolith beds (RBs), which are important marine benthic ecosystems with a wide geographical and bathymetric distribution, ranging from polar to tropical zones and from shallow areas to the limits of the photic layer (Foster, 2001; Riosmena-Rodriguez et al., 2017; Fragkopoulou et al., 2021). Their global significance is attributed to their extensive coverage worldwide (Fragkopoulou et al., 2021), multiple ecosystem functions, such as habitat and refuge for many ecologically and commercially important species (Foster et al., 2013; Anderson et al., 2023; Tuya et al., 2023; Bulleri et al., 2025; Schubert et al., 2025), and significant production and storage of calcium carbonate (Amado-Filho, Pereira-Filho, 2012; van der Heijden and Kamenos, 2015; Schubert et al., 2024).

RBs are commonly studied in terms of their distribution, biodiversity, and community structure, to gather information on their ecological functioning and ecosystem services, and hence, to support effective conservation management of these habitats (e.g., Sciberras et al., 2009; Brasileiro et al., 2016; Otero-Ferrer et al., 2020a; Maggio et al., 2022; Illa-Lopez et al., 2023). In this regard, ample information is available for RBs from the Atlantic and the Mediterranean, while less information is available for the Pacific (Riosmena-Rodriguez et al., 2017). In the Eastern Pacific, RBs are known to occur from the Chilean coast, the

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Galapagos Islands, Panama, Costa Rica, and the Gulf of California to Alaska (Konar et al., 2006; Macaya et al., 2015; Robinson et al., 2017; Easton et al., 2019). Specifically, in the Gulf of California, they have been widely studied, with research mainly focusing on their distribution, individual rhodolith morphology and taxonomy, and associated biodiversity (e.g., Steller et al., 1995; Steller et al., 2003; Hinojosa-Arango and Riosmena-Rodriguez, 2004; Riosmena-Rodriguez and Medina-López, 2010; Robinson et al., 2017). In contrast, in the Eastern Tropical Pacific (ETP), information regarding RBs and rhodoliths is extremely scarce (Robinson et al., 2017).

The presence of RBs in the ETP has been confirmed in the Mexican Revillagigedo Archipelago, the Pacific coast of Panama and Costa Rica (including Cocos Island), and Galápagos. Yet, studies on RBs are restricted to Panama and Costa Rica. For other locations in the ETP, the documented presence of RBs has been rather anecdotally annotated, including, for example, the discovery of vast rhodolith beds between 40 and 80 m at Clarión Island (Revillagigedo Archipelago) during surveys to study mesophotic fish communities (Hollarsmith et al., 2020). In Galápagos, evidence is limited to a short note regarding the observed formation of extensive RBs following coral mortality events at Santa Fe Island (Halfar and Riegl, 2013). However, multiple taxonomic studies suggest the potential presence of RBs throughout the ETP (Fig. 1). A total of 28 rhodolith-forming species, distributed across 11 genera, have been documented in the region (Robinson et al., 2017). Among these, the genera *Lithophyllum* and *Lithothamnion* are the most species-rich, with 10 and 6 recorded species, respectively (Robinson et al., 2017).

At the Pacific coast of Panama, RBs have been reported to be common around the islands in the Gulfs of Panama and Chiriquí, with studies focusing on their distribution, extension, geochemistry, rhodolith density, growth rates, carbonate production, and associated fauna (Fortunato and Schäfer, 2009; Schäfer et al., 2011).

In Costa Rica, previous studies provided evidence of extensive RBs in the Biological Reserve of Caño Island off the Pacific coast (Fonseca et al., 2010) and the Cocos Island National Park (PNIC; Sibaja-Cordero et al., 2012) (Fig. 1). Around Cocos Island, RBs are reported to cover vast areas extending from shallow (~15 m depth) to deep waters (90 m depth), with rhodoliths as the sole group of photoautotrophic organisms below 50 m (Fernández, 2008; Cortés, 2019). A few studies conducted on the associated biodiversity suggest the role of RBs as key habitats for a variety of fish and numerous (>150) invertebrate species (Sibaja-Cordero, 2012; Alvarado et al., 2016; Solano-Barquero et al., 2022). Moreover, a recently discovered endemic octocoral species, *Rhodolitica occulta* (Breedy et al., 2021), has been found within RBs, along with the first recorded occurrence in Costa Rica of the invasive anemone *Exaiptasia diaphana*—a species native to the Caribbean and Gulf of Mexico (Acuña et al., 2020; Glon et al., 2020). Yet, in comparison to the wealth of information on different coral reef elements at Cocos Island, including their biodiversity, structure, composition, and areal extension, little to no information on most of these elements is available for RBs. Moreover, RBs are not considered in the current management plan (SINAC, 2016), an omission which might jeopardize these biodiversity hotspots due to impacts related to human activities.

This study aimed to fill the large knowledge gaps regarding RBs in the ETP, particularly at Cocos Island, by providing - for the first time - data regarding the habitat structure of four RBs. This includes data on rhodolith morphology, nodule density and calcium carbonate standing stocks, and associated biodiversity. The latter was combined with previous species records, to provide an updated complete biodiversity inventory for RBs at Cocos Island.

Fig. 1. Records of rhodolith beds and rhodolith-forming species in the Eastern Tropical Pacific. Island locations are indicated by name.
(a) Locations of rhodolith beds were retrieved from published reports in Mexico (Hollarsmith et al., 2020), Costa Rica (Fonseca et al., 2010; Sibaja-Cordero et al., 2012; Breedy et al., 2021; Acuña et al., 2020; Solano-Barquero et al., 2022; Cortés and Quesada-Román, 2024), Galápagos (Halfar and Riegl, 2013), and Panama (Littler and Littler, 2008; Fortunato and Schäfer, 2009; Harper et al., 2010; Schäfer et al., 2011; Reijmer et al. 2012; Sletten et al., 2017). (b) Records of rhodolith-forming species were retrieved from Robinson et al. (2017).

2. Materials and methods

2.1. Study area

Cocos Island, also known as Isla del Coco, is an oceanic island located at 5°30’–5°34’N and 87°01’–87°06’W, in the Eastern Tropical Pacific and is the only emerged portion of the Cocos Submarine Ridge, which extends from the Galápagos Islands to the southern zone of Costa Rica (Cortés, 2016). The island and all its islets were declared a National Park in 1978, designated as a UNESCO World Heritage Site in 1997, and recognized as a Ramsar site in 1998 (Cortés, 2012; Alvarado et al., 2016). In the initial declaration of the National Park, the marine portion was not considered. However, because the island’s extremely diverse marine environment, including the presence of endemic species and the high diversity of marine fauna associated with coral formations, a 5 km radius around the island was included as a protected area in 1984, and expanded to encompass a 22.2 km radius in 2001 (Sibaja-Cordero, 2008; Alvarado et al., 2016; Cortés, 2016). Located far from human populations (ca. 550 km off the coast of Costa Rica and 600 km from the Galápagos archipelago), Cocos Island is considered a successful conservation story and a biodiversity hotspot (Wehrtmann and Cortés, 2009; Edgar et al., 2014). The Cocos Island National Park (PNIC) currently represents the largest protected area in Costa Rica and possibly the best-preserved (Cortés, 2021).

Wind, currents, and waves around Cocos Island are seasonally influenced by the north-south movement of the Intertropical Convergence Zone (Amador et al., 2006; Alfaro, 2008; Lizano, 2008). The pattern of surface ocean currents during the first quarter of the year (January-March) is different from the rest of the year, as this is the only period at which the island is not affected by the Northern Equatorial Counter Current (Lizano, 2008). Also, while the prevailing winds and waves at Cocos Island come from the southwest, during winter, storms can generate waves reaching the island from the northwest (Alfaro, 2008; Lizano, 2008). The island encompasses various marine and coastal habitats, including sandy and pebble beaches, rocky intertidal zones, rocky bottoms, reefs, and coral communities, rhodolith beds, as well as deep pelagic and benthic habitats (Cortés, 2016).

Four shallow-water RBs, located geographically in the North of Cocos Island National Park, were sampled for this study: Manuelita at 7 m depth (5°33’40.3’’N, 87°02’47.26’’W), Silverado at 12–15 m depth (5°32’45.30’’N, 87°01’44.70’’W), Bahía Weston at 15 m depth (5°33’12.31’’N, 87°03’10.87’W), and Isla Pájara at 15 m depth (5°33’14.80’’V, 87°03’14.70’’W) (Fig. 2). Three of the sites (Bahía Weston, Isla Pájara, and Manuelita) are located in sheltered bays and islets, while Silverado is farther from the coast (Fig. 2A). A preliminary taxonomic survey of samples collected from these RBs identified several rhodolith species, including those from the genera *Lithothamnion* (present in all four rhodolith beds), *Lithophyllum* (found in Manuelita, Silverado, and Bahía Weston), *Mesophyllum* (observed only at Isla Pájara), and *Roseolithon* (detected only in Silverado) (Diaz-Licona, 2024).

2.2. Sample collection

The sampling was conducted between May 25th and May 30th 2021, using SCUBA diving. At each site, 10 m-long transects were established. Duplicated PVC quadrats measuring 25 × 25 cm (625 cm^2) were placed at three distances along the transect: 0 m, 5 m, and 10 m. These quadrats were used to collect samples for the analysis of associated organisms and calcium carbonate ($CaCO_3$) stocks (uppermost 10 cm; Fig. S1). A total of six transects (36 quadrats) were sampled across the four sampling sites;

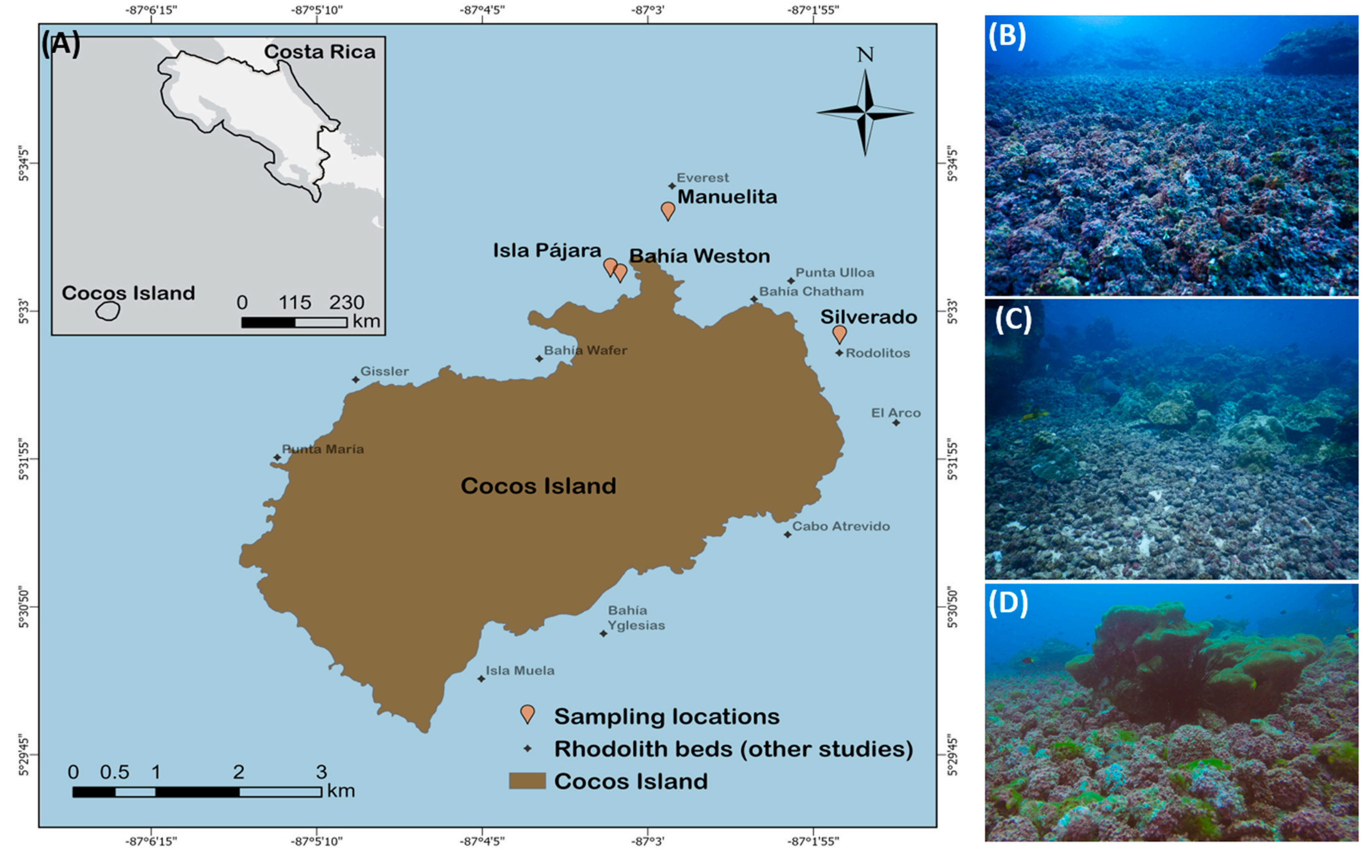

Fig. 2. Rhodolith beds at Cocos Island, Costa Rica. (A) Map showing the known rhodolith-bed locations around Cocos Island (Fernández, 2008; Sibaja-Cordero et al., 2012), highlightening the locations of the studied rhodolith beds, and photos showing (B) the rhodolith beds at Isla Pájara and (C, D) at Manuelita (provided by C. Fernández-García and B. Naranjo).

one transect for Bahía Weston and Isla Pájara, and two transects for Silverado and Manuelita. The number of transects surveyed at each site was determined based on a combination of site accessibility, logistical feasibility, and the goal of capturing representative habitat features. Although the number of transects varied among sites, care was taken to ensure that each transect was placed in a location representative of the local benthic and ecological conditions. This approach allowed for a meaningful comparison across sites despite logistical constraints.

All rhodoliths and associated organisms within each quadrat were manually collected and stored in plastic bags. Samples collected for associated biodiversity were fixed with 96 % alcohol, while those for $CaCO_3$ determinations were transported dry. Additionally, visual fish census surveys were conducted *in situ* following methods described by Alvarado et al. (2015). Observations were recorded along the 10 m transects, forming an imaginary tunnel of 5 m width and 5 m high (10 m x 5 m x 5 m; Fig. S1). A total of eight transects were surveyed across the four sampled sites, two for each RB. During the fish census, species and their respective abundance (expressed as individuals per 100 m^2) were recorded.

2.3. Morphological characterization

The growth forms of rhodoliths were classified according to Woelkerling et al. (1993) and O'Connell et al. (2020). For this, living rhodoliths of one of each duplicated quadrat (n = 3 for Bahía Weston and Isla Pájara, n = 6 for Silverado and Manuelita) were used. Following the removal of associated organisms, the different morphotypes of rhodoliths from each sampling site were separated based on their extension and shape of the thalli, considering also the combination of forms (two growth forms in one rhodolith) (Fig. 3). The number of rhodoliths of the different growth forms was quantified to determine the percentage of each growth type at the four sampled sites, following O'Connell et al. (2020). Additionally, the long and short axes of 30 randomly selected rhodoliths per site (chosen from the quadrat samples) were measured to calculate an average diameter (the mean of the two measurements) for each rhodolith, serving as a proxy for rhodolith size (e.g., Holz et al., 2020).

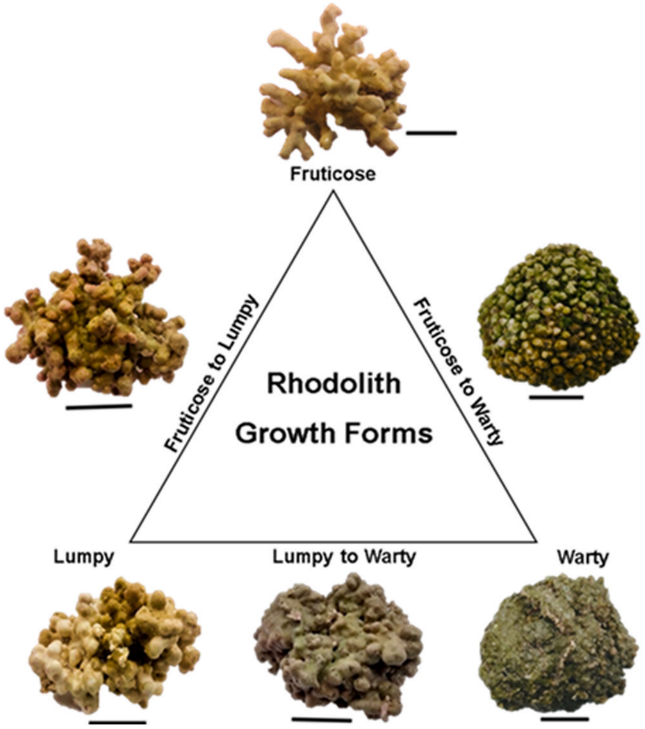

Fig. 3. Rhodolith growth forms, according to the classification scheme of Woelkerling et al. (1993), found in rhodolith beds at Cocos Island. Scale bars represent 1 cm.

2.4. Rhodolith biomass and carbonate content

A mean rhodolith density (per m^2 and site) was obtained, based on the total number of living rhodoliths within the quadrats, used for the morphological characterization. Noteworthy, dead rhodolith nodules were absent in all samples. Furthermore, the determination of the amount of $CaCO_3$ contained in the RBs (as kg m^{-2}) was obtained, using a protocol of weight loss by ignition and decalcification, modified from Schoenrock et al. (2018). Initially, the total weight (as wet weight, WW_t) of rhodoliths within each sampling quadrat was determined. Given the high biomass (up to 2.5 kg wet weight per quadrat), a subset of five rhodoliths per quadrat was randomly selected for subsequent analyses, representing approximately 10–25 % of the WW_t. The rhodoliths were weighed, dried at 100°C and re-weighed (DW_{100}) (n = 90 rhodoliths from the 18 quadrats). The water content (W_{SS}, in % of WW_t) was determined from the weight difference, which was then used to obtain the rhodolith dry biomass for each quadrat (DW_t) [Eq. (1)]. The rhodolith subsamples were then placed in a muffle furnace, at 550°C for 6 h, to burn the organic matter and then weighed again (DW_{550}) to determine the organic matter content [Eq. (2)]. Afterwards, the samples were decalcified, using 1 N HCl for 24–48 h, and the remaining material (RM), i.e. settlement substrate (shells, coral remains, rock), was dried for 12 h at 60°C and weighed, to determine the contribution of calcium carbonate to the dry weight of the rhodoliths (DW_{RM}). Using the weight difference obtained from the previous steps, the $CaCO_3$ content of the rhodoliths (as % DW) was calculated [Eq. (3)]. Subsequently, using the rhodolith biomass and carbonate content, the amount of $CaCO_3$ (kg) stored per m^2 was calculated per site [Eq. (4)].

$$DW_t\ (g) = (WW_t \times W_{SS})/100 \qquad [1]$$

$$\text{Organic matter (\% of DW)} = (DW_{100} - DW_{550}) \times 100)/DW_{100} \qquad [2]$$

$$CaCO_3\ (\% \text{ of DW}) = ((DW_{550} - DW_{RM})/DW_{100}) \times 100 \qquad [3]$$

$$CaCO_3\ (kg\ m^{-2}) = ((DW_t \times CaCO_3)/100)/(0.0625\ m^2 \times 1000) \qquad [4]$$

2.5. Associated biodiversity

Organisms associated with rhodoliths (invertebrates and macroalgae) from the other duplicated quadrat (n = 3 for Bahía Weston and Isla Pájara, n = 6 for Silverado and Manuelita) were sorted by hand using tweezers and dissecting tools. Initially, they were classified to phylum and placed in jars with 90 % alcohol. Afterwards, the organisms were counted (invertebrates) and taxonomically identified to the lowest possible taxonomic level. Identification of the associated fauna was carried out using guides, taxonomic keys (Salgado-Barragán and Hendrickx, 2010; De León-González et al., 2021) and literature on previous research conducted in RBs at Cocos Island National Park (Solano-Barquero, 2011; Solano-Barquero et al., 2022). Taxonomic identification of the associated macroalgae was carried out through images of complete thalli and tissue sections viewed under a microscope, using keys for the tropical Pacific (Taylor, 1945; Fernández García, 2012). For those organisms that could not be identified to the genus level, taxonomic information was completed by adding the termination "*indet.*" (indeterminate). They were labelled as indet. 1, indet. 2, and so on, in cases where more than one morphospecies was present for a given taxonomic level. After identification, the faunal organisms were deposited in the respective collections of the Museum of Zoology at the University of Costa Rica, and the macroalgae deposited in the Herbarium of the University of Costa Rica (USJ). For many macroalgal taxa, was is not feasible to count individuals accurately; therefore, presence/absence data were used to assess macroalgal species diversity in the studied RBs.

2.6. Statistical analysis

Potential differences in mean rhodolith diameter, biomass, organic matter and carbonate content, and resulting carbonate stocks, among the four sampling sites were determined through one-way analysis of variance (ANOVA), with a prior check for normality and heteroscedasticity, using the Shapiro-Wilk and Levene's tests, respectively. When required, ln-transformation was used to normalize the data (rhodolith diameter, organic matter content). Additionally, post-hoc Tukey tests were conducted for pair-wise comparisons among sites. The Kruskal-Wallis test was used to compare total invertebrate abundance (expressed as individuals m^{-2}) among sampling sites.

To evaluate the completeness of species inventories and to perform meaningful comparisons of species richness associated with the different RBs, rarefaction curves were obtained to assess how the total number of macroalgal and invertebrate species recorded in each RB varied as a function of the sampling effort (# of quadrats) per site. Rarefaction was implemented in the EstimateS program (Colwell, 2019).

3. Results

3.1. Rhodolith morphological attributes

Different rhodolith growth forms were found in the four RBs, including fruticose, lumpy, and warty and intermediate forms between these three main forms. Most RBs contained all three growth forms, with the exception of Manuelita, where the fruticose form was absent (Fig. 4). In Bahía Weston and Manuelita, most rhodoliths displayed a warty morphology (>50 % of rhodoliths), followed by the lumpy growth form (Fig. 4A, C). On the other hand, Silverado and Isla Pájara were dominated by the fruticose morphology (>50 % of rhodoliths), followed by the lumpy and the lumpy to fruticose intermediate form (Fig. 4B, D).

The mean rhodolith density showed similar values of ~1100–1200 nodules m^{-2} for three of the RBs, while an almost 4x higher density was found in Isla Pájara (Table 1). Rhodoliths also showed a high variability in their size, which ranged from 1.8 to 8.6 cm diameter (mean ± SD: 3.36 cm ± 0.53), with significant differences among sites (Table 1). The largest rhodoliths were found in Bahía Weston and Manuelita, with similar mean values, while rhodoliths at the other two locations, Silverado and Isla Pájara, were significantly smaller (Table 1; Fig. S2). Differences were also found in the amount of organic matter and carbonate content of the rhodoliths among sites. The proportion of organic matter varied between 2 % and 12 % of the dry weight, with significantly lower values from Manuelita, highest values in Isla Pájara and intermedium values in Bahía Weston and Silverado (Table 1). Similarly, significant differences among sites were also found for the rhodolith carbonate content, which varied between 58 % and 90 % of the dry weight. Here, rhodoliths from Manuelita exhibited the lowest carbonate contents, while those from the other locations expressed significantly higher values (Table 1). These results were consistent with observed differences in the type and size of settlement substrates, i.e. remaining material after decalcification. In the case of Manuelita, this included medium and large rock fragments, while smaller fragments of rocks, corals and mollusc shells were found in rhodoliths from Bahía Weston and Silverado (Fig. S3). Noteworthy, no material remained after decalcifying the rhodoliths from Isla Pájara.

Moreover, rhodolith biomass in the studied beds differed significantly. The highest biomass was found in Manuelita, which was similar to Isla Pájara, with lower rhodolith biomass in Bahía Weston and

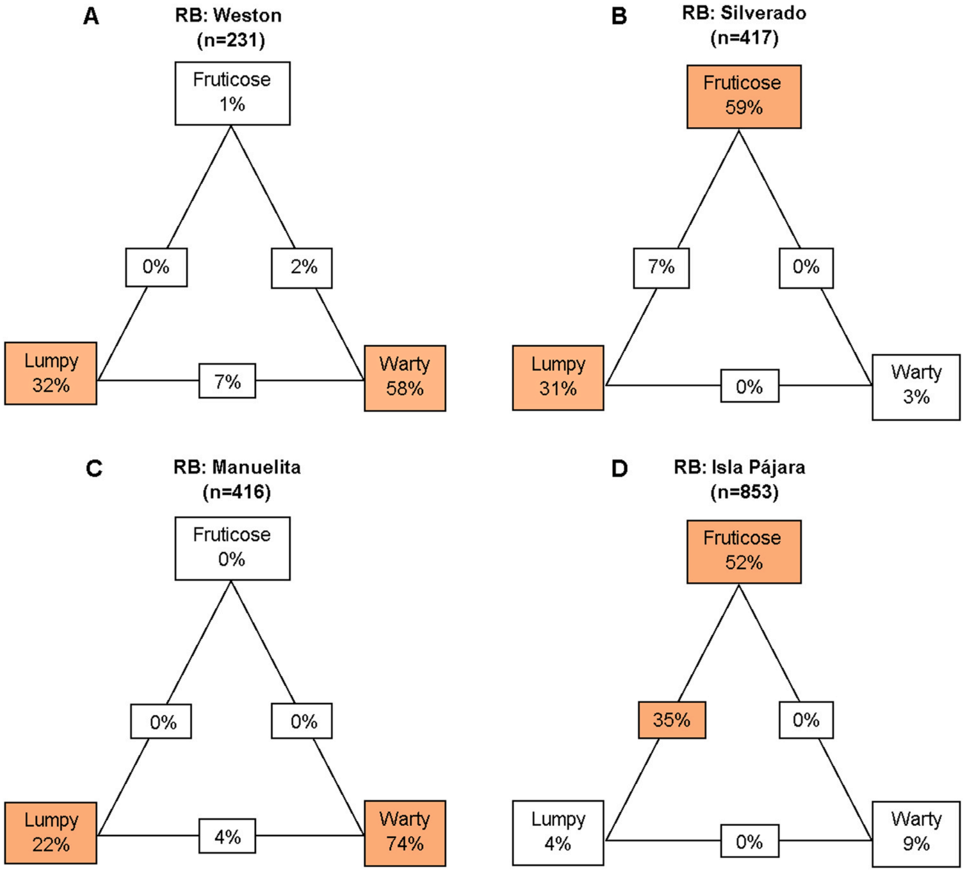

Fig. 4. Percentages of rhodolith growth forms in the four rhodolith beds at Cocos Island. Growth forms were classified according to Woelkerling et al. (1993) and modified by O'Connell et al. (2020). The predominant forms are highlighted in orange (n = number of rhodoliths classified for each site).

Table 1

Comparison of rhodolith structural attributes and abundance of associated fauna among different rhodolith beds at Cocos Island. Data are mean values ± SD (Min-Max) and different letters indicate significant differences among locations (ANOVA and Tukey post hoc, Kruskal-Wallis test).

Location	Bahía Weston	Silverado	Manuelita	Isla Pájara	ANOVA/Kruskal-Wallis
Depth (m)	15	12–15	7	15	
Mean rhodolith density (nodules m^{-2})	1232	1112	1109	4549	
Rhodolith diameter (cm)	3.6 ± 0.8^{a} (2.3–5.4)	3.0 ± 1.1^{b} (1.8–6.3)	4.0 ± 1.3^{a} (2.1–8.6)	2.9 ± 0.7^{b} (1.9–4.4)	MS= 0.73, $p < 0.0001$
Organic matter (% of DW)	5.5 ± 3.4^{a} (2.3–9.1)	8.9 ± 2.4^{ab} (5.8–11.5)	2.2 ± 0.5^{c} (1.6–2.7)	11.9 ± 2.8^{b} (2.0–14.9)	MS= 2.4, $p < 0.0001$
$CaCO_3$ content (% of DW)	90 ± 7^{a} (83–96)	82 ± 10^{a} (68–93)	58 ± 13^{b} (36–70)	88 ± 3^{a} (85–91)	MS= 942.1, $p = 0.0009$
Rhodolith biomass (kg DW m^{-2})	20.7 ± 1.9^{a} (18.7–22.5)	17.7 ± 7.9^{a} (7.7–28.8)	33.3 ± 4.2^{b} (28.9–38.9)	25.3 ± 5.6^{ab} (19.9–31.1)	MS= 244.9, $p = 0.0032$
$CaCO_3$ standing stock (kg DW m^{-2})	18.6 ± 1.7 (16.8–20.2)	14.4 ± 6.2 (6.4–23.1)	19.2 ± 1.2 (17.4–20.5)	22.3 ± 5.0 (17.5–27.4)	MS= 48.4, $p = 0.0883$
Invertebrates (Ind. m^{-2})	245 ± 130^{a} (96–336)	717 ± 665^{ab} (144–2000)	1781 ± 810^{ab} (992–3152)	2944 ± 1259^{b} (1792–4288)	H= 11.38, $p = 0.0098$
Fishes (Ind. 100 m^{-2})	47	24	126	1245	

Silverado (Table 1). When considering the carbonate content of the rhodoliths at each site, this yielded highly variable, but not significantly different carbonate standing stocks in the four beds (Table 1), ranging between ~14 and 22 kg $CaCO_3$ m^{-2}, with a noticeable large variability within the RB at Silverado (Table 1).

3.2. Associated biodiversity

A total of 109 taxa of invertebrates and 18 macroalgal taxa were identified in the RBs at Cocos Island (Table S1). The highest total species number was found in Manuelita, with the lowest number of taxa recorded for Bahía Weston (Fig. 5A). Macroalgal diversity was highest in Manuelita and Isla Pájara ($n = 11$ at each location), with lower numbers ($n = 3–4$) in Bahía Weston and Silverado (Fig. 5A). The number of invertebrate species were also highest in Manuelita ($n = 74$), while in Isla Pájara the highest abundance of invertebrates was recorded. In contrast, our records for Bahía Weston showed that this site exhibited the lowest species richness ($n = 24$) and abundance of invertebrates (Table 1; Fig. 5A). Though, accounting for differences in sampling effort among locations, using rarefaction curves, species diversity was shown to be similar and higher for Manuelita and Isla Pájara, while both Silverado and Bahía Weston showed a similar and lower diversity (Fig. 5B).

The macroalgae found in RBs at Cocos Island were distributed across three phyla, three classes (Florideophyceae, Phaeophyceae, Ulvophyceae), 10 orders, and 15 families (Table S1). Of the 18 recorded species, the majority belonged to the phylum Rhodophyta (79.5 %), while Chlorophyta and Heterokontophyta (only *Padina* sp.) accounted for 18.2 % and 2.3 % of the species, respectively. In Silverado, only red algae were found, while Heterokontophyta were present only in Isla Pájara (Fig. 6A). Among the recorded species, *Amphiroa* sp. was the only one found at all locations, followed by *Gelidium* sp., which was absent only in Silverado (Fig. 6B).

A total of 1535 invertebrates were found across RBs, belonging to 109 taxa (Table S2). Overall, the most diverse and abundant phyla/subphyla were: Polychaeta, Crustacea, Mollusca, Echinodermata and Cnidaria (Fig. 7A), though there were differences among RBs with regard to the most abundant invertebrate group. In Bahía Weston, crustaceans were the most abundant group, while cnidarians (i.e., hydrozoans), polychaetes, and echinoderms were the most abundant groups in Silverado, Manuelita and at Isla Pájara, respectively (Fig. 7B).

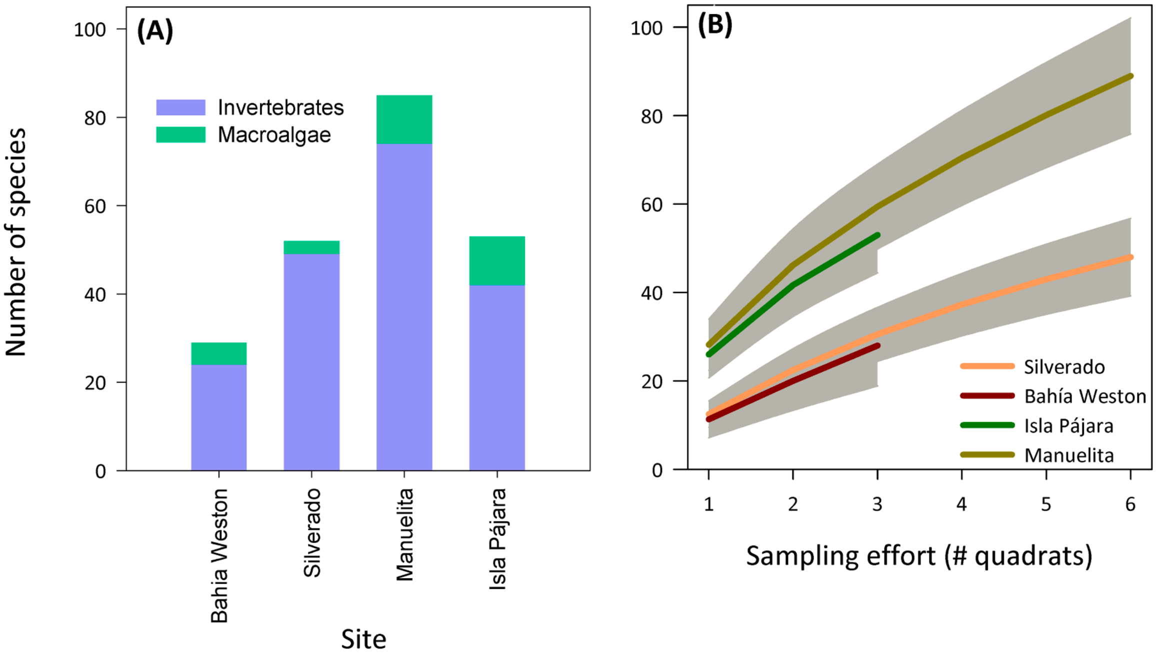

Fig. 5. Biodiversity (macroalgae, invertebrates) recorded in rhodolith beds at Cocos Island. (A) Number of species and (B) comparison of the recorded biodiversity, using rarefaction curves, to account for differences in sampling effort among rhodolith beds (shaded areas highlight the confidence intervals).

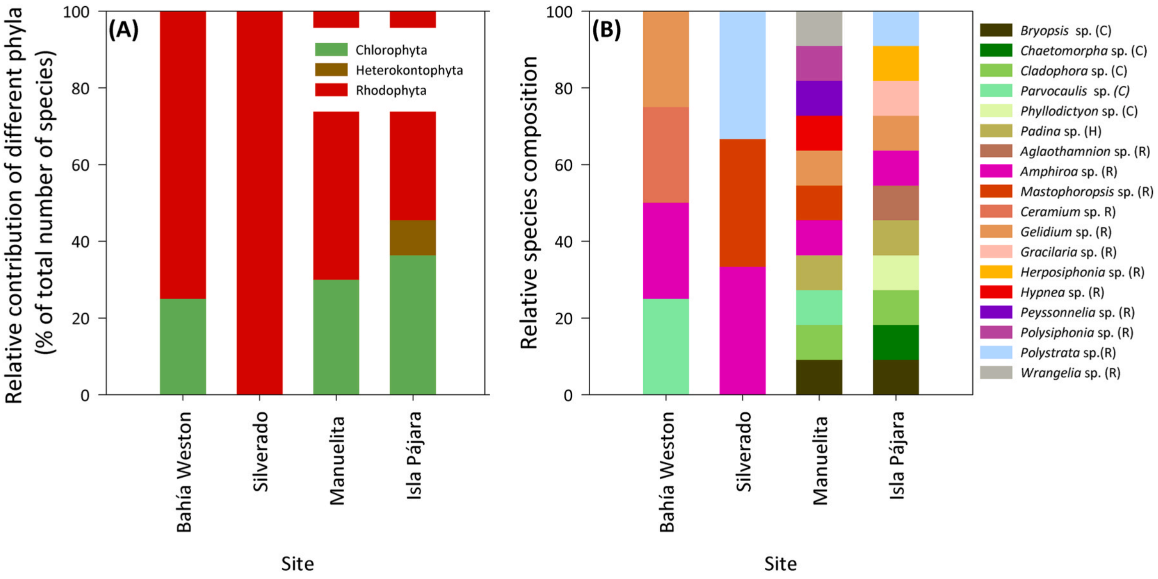

Fig. 6. Macroalgae associated with different rhodolith beds at Cocos Island. (A) Relative contribution of macroalgal phyla to species diversity and (B) macroalgal community composition (letters after genus name indicate macroalgal phyla: C- Chlorophyta, H- Heterokontophyta, R- Rhodophyta).

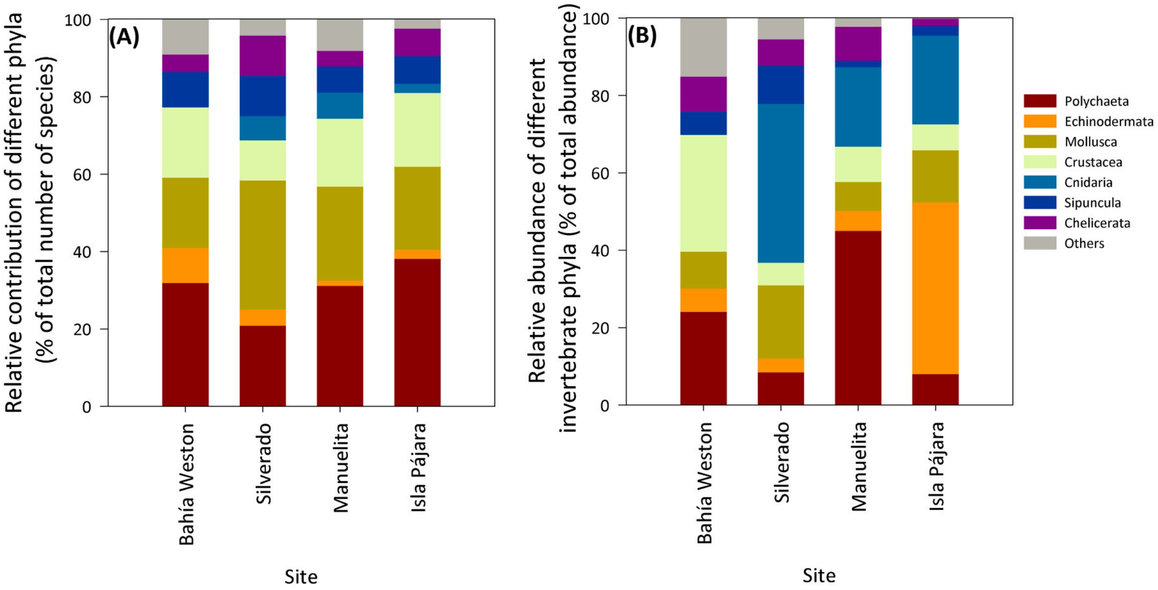

Fig. 7. Invertebrates associated with different rhodolith beds at Cocos Island. (A) Relative contribution of different phyla/subphyla to (A) total species richness, and (B) total faunal abundance.

It is noteworthy that Cnidaria were absent in Bahía Weston, while this group accounted for 21–41 % of the total abundance at the other sites. In addition to these main groups, less abundant species, belonging to Bryozoa, Nematoda, Nemertea and Platyhelminthes were also found, with the latter only recorded at Isla Pájara (Table S2).

The most abundant taxa were: the crustacean *Processa* sp., accounting for 13.3 % in Bahía Weston, and an unidentified Hydrozoan (Cnidaria, Sertulariideae) in Silverado and Manuelita, comprising 18.2 % and 35 % of the total invertebrate abundance, respectively (Table S2). The brittle star *Ophiactis savigny* (Echinodermata) was the most abundant invertebrate species at Isla Pájara, contributing 44.3 % to the total organisms. Moreover, sea urchins (Echinoidea, Echinodermata) were recorded only in Silverado. Some morphospecies were relatively well represented across most sites, including the polychaete *Ceratonereis singularis*, an amphipod crustacean of the family Melitidae (indet.1), the stomatopod *Gonodactylus* sp., and a gastropod of the family Pisaniidae (indet.1). There were also species with very low abundance, represented by a single organism, such as the sipunculan *Apionsoma (Apionsoma) misakianum*, and two polychaetes (*Neanthes acuminata* and *Caulleriella* sp.), accounting for 1 % or less of the total organisms.

With regard to the associated fish community, visual censuses in the RBs yielded a total of 1442 wandering-swimming fishes, for a total of 30 species. The recorded species belonged almost exclusively to the class Actinopterygii, with only one species of the Elasmobranchii class (*Triaenodon obesus*). The highest species numbers and abundance were recorded in the RBs at Manuelita and Isla Pájara (Fig. 8A). The recorded fish species included 14 species that are endemic to the ETP and three species that are listed in the IUCN Red List as "vulnerable" (Fig. 8B, Table S3). RBs at Bahía Weston and Silverado harboured four and five endemic species, respectively, and one red-listed species, while in Manuelita and Isla Pájara eight endemic and two red-listed species were recorded (Table S3). The contribution of these species to the total fish

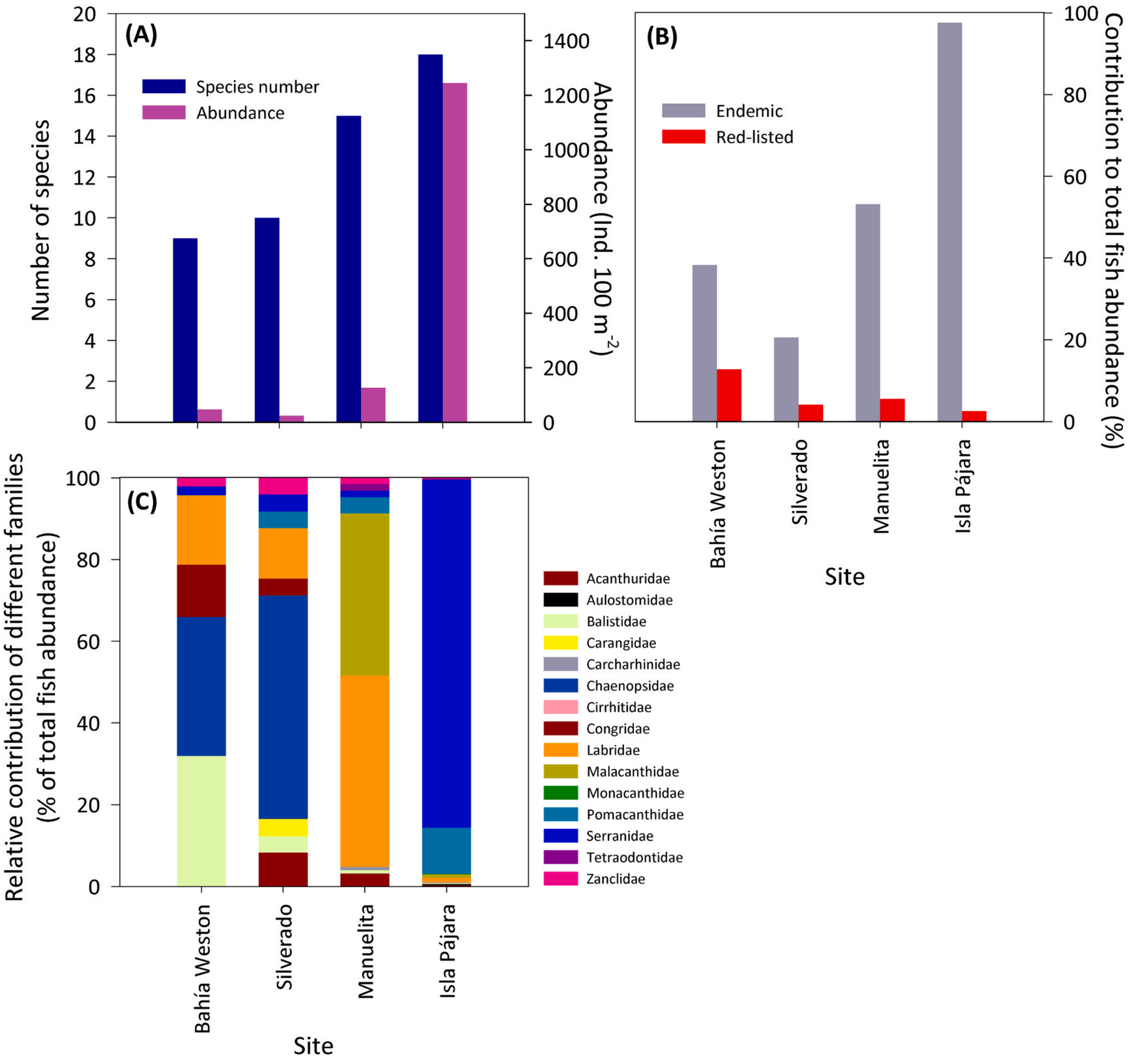

Fig. 8. Fish diversity associated with rhodolith beds at Cocos Island. (A) Number of species and total abundance, and (B) relative contribution of endemic and red-listed fish species and (C) of different families to the total abundance.

abundance varied among RBs (Fig. 8B). Endemic species contributed between 21 % and 53 % to the total fish abundance in Bahía Weston, Silverado and Manuelita, while their contribution at Isla Pájara was 98 %. The latter was due to the high abundance of the endemic species *Serranus tico* (Fig. 9A, Table S3). On the other hand, the highest contribution of fish species, categorized by the IUCN as "vulnerable", to the total abundance was recorded in Bahía Weston (13 %), mainly related to the abundance of *Halichoeres discolor* (Fig. 9C). The most abundant family in Bahía Weston and Silverado was Chaenopsidae, due to the presence of *Emblemaria* sp. (Fig. 8C, Table S3). On the other hand, at Isla Pájara, the Serranidae dominated the fish community, mainly related to the high abundance of *Serranus tico*, while in Manulita the Labridae and Malacanthidae dominated mainly due to the abundance of *Thalassoma lucasanum* and *Malacanthus brevirostris*, respectively (Table S3).

4. Discussion

Our study shows that RBs at Cocos Island are characterized by high rhodolith densities, significant carbonate standing stocks, and rich associated biodiversity. Yet, the structure of these habitats and the composition of their associated communities differ among beds, likely reflecting variations in environmental conditions and/or rhodolith characteristics.

This study is the first to describe the habitat characteristics of RBs at Cocos Island beyond their associated biodiversity. Across the ETP, comparable information exists only for Panama—specifically in the Gulfs of Panama and Chiriquí—where RBs are primarily island-associated and span estimated areas between 722 and 1388 km^2 (Fortunato and Schäfer, 2009; Schäfer et al., 2011). Consistent with our findings, those studies also documented a variety of rhodolith growth forms, ranging from massive nodular to branching types. Reported mean rhodolith densities from Panama, 417 nodules m^{-2} in the Gulf of Panama and 1306 nodules m^{-2} in the Gulf of Chiriquí, fall within the range observed at Cocos Island, except for higher values recorded at Isla Pájara. The rhodoliths at Cocos Island were slightly larger (~3.4 cm mean diameter) than those found on the Panama coast (~2 cm diameter). This difference may also be attributed to variations in sample size and the method of determining mean diameter, with this study using the longest and shortest axes, whereas the former studies measured the longest, intermediate, and shortest axes. Additionally, RBs at Cocos Island exhibit substantial rhodolith biomass (18–33 kg m^{-2}) and carbonate standing stocks (14–22 kg m^{-2}), aligning with recent values reported for the Atlantic (3–29 kg m^{-2} biomass, 4–46 kg m^{-2} $CaCO_3$) (Schubert et al., 2024). Unlike the former Atlantic study, which found that dead nodules made a significant contribution to the carbonate standing stocks

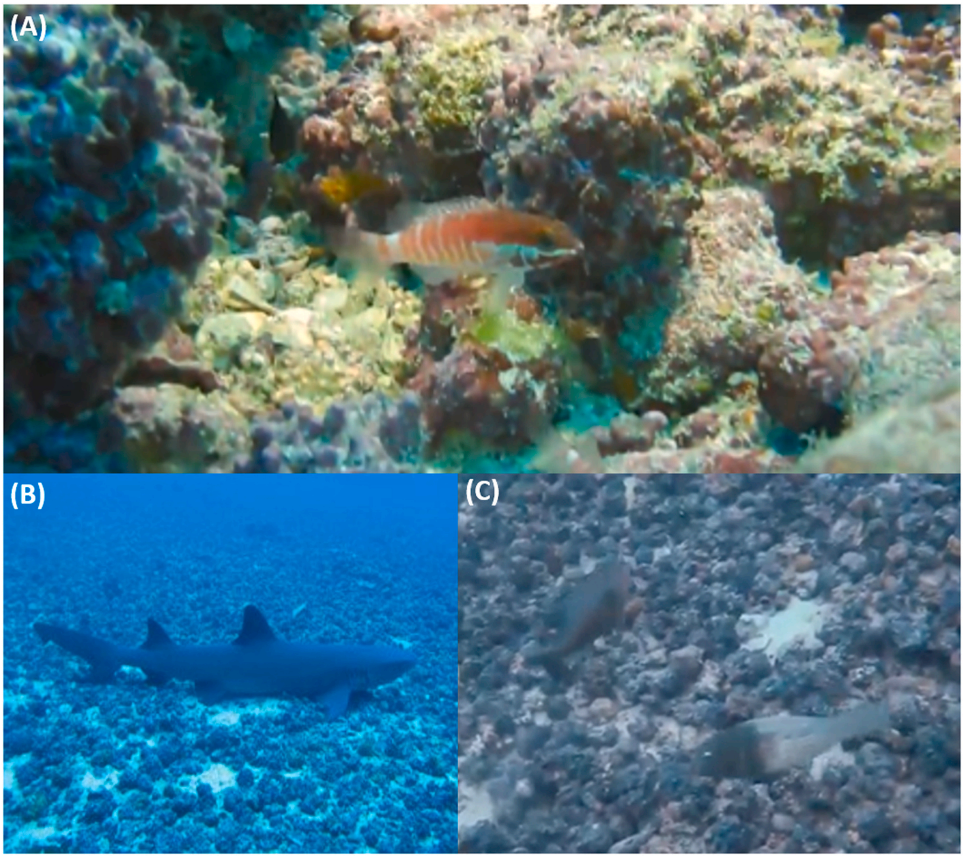

Fig. 9. Examples of endemic and red-listed fish species found in rhodolith beds at Cocos Island. (A) *Serranus tico* (endemic), (B) *Triaenodon obesus* (vulnerable), and (C) *Halichoeres discolor* (endemic/vulnerable) (photos provided by B. Naranjo).

of some RBs, no dead nodules were present among our samples. Since sampling occurred in the shallower portion of the RBs, which extend to deeper areas (Fernández-García, pers. comm.), this suggests that dead rhodolith nodules may be transported and accumulated in these deeper regions.

RBs are widely regarded as biodiversity hotspots and are known to support multi-level habitat cascades through their associations with epibiotic organisms (Tuya et al., 2023; Bulleri et al., 2025). This ecological role is largely attributed to the structural complexity of rhodoliths, which offers a foundational substrate for a wide variety of species (e.g., Steller et al., 2003; Kamenos et al., 2004; Nelson et al., 2012; Teichert, 2014; Otero-Ferrer et al., 2019; Stelzer et al., 2021; Jardim et al., 2025). The same pattern is observed at Cocos Island, where RBs support a rich assemblage of macroalgae, invertebrates, and fishes. Macroalgal diversity associated with the RBs was relatively low, with species richness ranging from 3 to 11 species, with a total of 18 species. This stands in sharp contrast to studies conducted along Brazil's tropical coast, where a total of 167 species were recorded across four RB sites with a comparable sampling effort (Amado-Filho et al., 2010). In contrast, the species richness observed in the present study is more consistent with that reported for RBs in the subtropical Eastern Pacific, particularly in the Gulf of California (Steller et al., 2003). While macroalgal diversity was relatively low, the invertebrate assemblages associated with the RBs were more complex. Among the most diverse and abundant invertebrate groups observed were polychaetes, echinoderms, crustaceans, and mollusks (e.g., Steller et al., 2003; Alvarado et al., 2015; Hinojosa-Arango and Riosmena-Rodriguez, 2004; Foster et al., 2007; Veras et al., 2020; Solano-Barquero et al., 2022; Pérez-Peris et al., 2023; Li et al., 2025). Our findings align with this general pattern, with these groups collectively accounting for 63–79 % of species richness and approximately 70 % of the total faunal abundance associated with RBs. An exception was found at the Silverado site, where these groups were similarly diverse but less abundant (contributing only 37 % to total abundance). Here, cnidarians, particularly hydrozoans, dominated the community, representing 40 % of total abundance. This composition contrasts with findings from RBs along Panama's Pacific coast, where mollusks are typically the dominant invertebrate group (Fortunato and Schäfer, 2009; Schäfer et al., 2011). At Cocos Island, however, mollusks contributed only 7–19 % to total faunal abundance. On the other hand, we found common fish species between RBs at Cocos Island and those reported for Clárion Island in the Revillagigedo Archipelago (Hollarsmith et al., 2020). Of the 27 fish species recorded in that study, 11 were also observed in our surveys at Cocos Island (Table S4).

Overall, our study documented 158 species associated with RBs at Cocos Island, including 58 new records, bringing the known biodiversity of these habitats at the island to 316 species (Table 2). This represents approximately 20 % of the total species recorded for the island (Table 2). Notably, about 16 % of the species found in RBs at Cocos Island are endemic to the ETP, including 57 % of the recorded fish species (Table S4). Among these are *Serranus tico, Stegastes arcifrons, Paranthias colonus*, and *Halichoeres discolor,* which have also been recorded in Malpelo and Galápagos islands (Friedlander et al., 2012). Additionally, five endemic fish species found in our study have also been reported in RBs at Clárion Island in the Revillagigedo Archipelago (Table S4; Hollarsmith et al., 2020).

The ecological importance of RBs for biodiversity has been well documented and has been related to their frequent occurrence near coral and rocky reefs. Evidence points to ecological connectivity between these habitats, as shown by the high proportion of fish species, over 60 %, found in both RBs and adjacent reefs (Pinheiro et al., 2015; Otero-Ferrer et al., 2020b; Moura et al., 2021; Li et al., 2025). At Cocos Island, RBs are typically found in association with coral and rocky reefs

Table 2
Overview of marine species recorded in association with shallow-water rhodolith beds at Cocos Island and total species record for the island ([§]Sibaja-Cordero, 2012; Alvarado et al., 2016; Acuña et al., 2020, Breedy et al., 2021, Solano-Barquero et al., 2022; *Cortés, 2012). For a detailed species list, see Table S4.

Group	Species associated with rhodolith beds at Cocos Island						Total species records for Cocos Island*	
	This study	Previous records[§]	New records (this study)	Total # species	Endemic to ETP	IUCN	Total # species	Endemic to ETP
Macroalgae	18	-	18	18	-	-	31	-
Invertebrates	110	221	30	251	24	-	1179	30
Fishes	30	37	10	47	27	4	389	15
TOTAL	**158**	**258**	**58**	**316**	**51**	**4**	**1599**	**45**

(Sibaja-Cordero et al., 2012; Cortés et al., 2017). Although data remain limited, some studies have highlighted species shared across these environments. For instance, several invertebrate species such as bivalves and echinoderms have been recorded both in RBs and coral reefs at Cocos Island (Alvarado and Chiriboga, 2008; Alvarado et al., 2016). Similarly, Alvarado et al. (2016) reported 30 fish species in association with a RB, about 90 % of which were also found in nearby coral reefs. Moreover, juveniles of *Lutjanus* species have been observed in RBs, suggesting their potential role as nursery habitats for reef-associated fishes (Solano-Barquero et al., 2022).

The studied RBs differed in habitat structure, including rhodolith size, shape and density. These structural differences are likely influenced by a combination of environmental factors such as community composition, hydrodynamic conditions (e.g., wave exposure, current velocity), light availability, and sediment characteristics. For example, specific rhodolith growth forms are often associated with particular hydrodynamic regimes (Bosence, 1983; Steller and Foster, 1995; Marrack, 1999; O'Connell et al., 2020). Although oceanographic settings were not explicitly characterized, no consistent relationship was observed between site conditions and the dominant rhodolith morphology. For instance, fruticose forms, typically indicative of low-energy environments, were dominant at both Isla Pájara (a sheltered bay site) and Silverado (an exposed coastal site). This apparent inconsistency supports the hypothesis by O'Connell et al. (2020) that additional factors, such as species identity and sediment characteristics, may also shape rhodolith morphology. These factors may contribute to the differences across the studied RBs, especially given the differences in sediment types and likely rhodolith community composition among locations. Sediment composition ranged from mixtures of gravel, sand, and mud, with Bahía Weston standing out for its finer sediments, characterized by the absence of gravel and a high mud content (Sibaja-Cordero et al., 2014). Additionally, preliminary taxonomic surveys indicate potential differences in rhodolith species composition among the RBs (Diaz-Licona, 2024). A more comprehensive study of species identity and distribution is needed to better understand the relationship between rhodolith morphology and community composition.

The four RBs studied here displayed notable variation in their associated community composition. For instance, the number of macroalgal species present varied considerably among sites, with only one species, *Amphiroa* sp., occurring consistently across all RBs. This widespread presence aligns with previous reports of *Amphiroa* species being highly abundant on rocky substrates and dead corals at Cocos Island (Fernández, 2008). Similarly, a study of RBs in the Eastern Pacific found *Amphiroa valonioides* to be nearly ubiquitous year-round across different RBs (McConnico et al., 2017).

The composition and abundance of macroalgae associated with RBs are known to vary widely in response to environmental factors such as seasonal changes, light availability (e.g., depth), and nutrient levels (e.g., Steller et al., 2003; Amado-Filho et al., 2010; Peña And Bárbara, 2010; McConnico et al., 2017; Otero-Ferrer et al., 2020a; Helias et al., 2024). Reduced macroalgal diversity has been associated with high water motion, which can lead to rhodolith displacement (Hinojosa-Arango et al., 2009), as well as with high sedimentation rates and turbidity, which limit light availability (Nelson et al., 2014). Depth-related declines in rhodolith-associated epiflora further highlight the role of light limitation (e.g., Riul et al., 2009; Bahía et al., 2010). Although specific environmental parameters were not measured in this study, the observed differences among RBs likely reflect variation in processes such as water motion, sedimentation, and light. Yet, the underlying drivers of macroalgal diversity may differ between sites. For instance, Bahía Weston and Silverado both exhibited low macroalgal diversity but differed in species composition and exposure, Bahía Weston being a sheltered bay with fine sediments and reported rhodolith burial (Sibaja-Cordero et al., 2012), and Silverado an exposed coastal site. In contrast, Isla Pájara and Manuelita supported more diverse macroalgal communities, though they shared fewer than 50 % of their recorded species. As noted earlier, light availability is a key factor influencing community composition; therefore, the differing depths of Manuelita (7 m) and Isla Pájara (15 m) may contribute to the variation in macroalgal assemblages observed between these sites.

Our results also revealed clear differences in the biodiversity and abundance of invertebrates associated with the studied RBs, partially aligning with findings from previous biodiversity surveys (Sibaja-Cordero et al., 2016). Although that earlier study did not focus specifically on RB-associated communities, it similarly reported lower diversity and abundance of invertebrates in the shallower areas of Bahía Weston (10–12 m depth), and significantly higher values for benthic organisms at Manuelita and Isla Pájara. However, in contrast to our observations of low invertebrate abundance at Silverado, prior assessments reported comparable biodiversity and abundance at this site relative to Manuelita and Isla Pájara (Sibaja-Cordero et al., 2016).

Variation in faunal communities associated with RBs has been widely attributed to a combination of rhodolith characteristics, such as species identity, morphology, size, and nodule density, and site-specific environmental conditions (e.g., Steller et al., 2003; Hinojosa-Arango and Riosmena-Rodriguez, 2004; Otero-Ferrer et al., 2019; Veras et al., 2020; Stelzer et al., 2021; Solano-Barquero et al., 2022; Pérez-Peris et al., 2023; Bianchi and Morri, 2025; Jardim et al., 2025). In our study, the RBs showed distinct differences in rhodolith morphology, with Bahía Weston and Manuelita differing from Silverado and Isla Pájara. Rhodolith sizes were generally smaller at Silverado and Isla Pájara, while rhodolith density was markedly higher at Isla Pájara, approximately four times greater than at the other RBs. This higher rhodolith density at Isla Pájara appears to support greater invertebrate diversity and abundance, despite rhodoliths at this site being similar in size and morphology to those at Silverado. This contrast may also reflect environmental differences: while Isla Pájara is situated within the more sheltered Bahía Weston in the island's north, Silverado is located on the exposed eastern coast. These differences may help explain the observed patterns, as oceanic islands often exhibit spatial and temporal fluctuations in wave energy around their insular shelves, conditions that have been shown to induce rhodolith remobilization (Ambrosio et al., 2022). Moreover, rhodolith size has been identified as a key factor influencing the diversity and abundance of certain faunal groups. For instance, larger rhodoliths and lower nodule densities have been associated with higher diversity and abundance of polychaetes (Lino et al., 2024). Our findings support this relationship, as polychaetes were the most, or among the most, abundant taxa in RBs with larger rhodoliths, specifically at Bahía Weston and Manuelita. Other factors likely contributed to the observed differences in faunal composition and abundance.

Macroalgal cover, for instance, has been identified as a key driver of faunal richness and abundance (Sánchez-Latorre et al., 2020; Veras et al., 2020). Additionally, variation in rhodolith community composition may influence associated epibiontic communities, as previously reported by Hinojosa-Arango and Riosmena-Rodriguez (2004).

5. Conclusions and directions for future research

This study provides the first detailed characterization of rhodolith bed habitat structure at Cocos Island, offering valuable baseline data on their spatial extent and associated biota in shallow waters (7–15 m). However, the findings are constrained by several limitations. First, the study is restricted to shallow depths, whereas RBs in the region are reported to be most abundant between 20 and 30 m and can extend to depths of up to 90 m (Cortés, 2016). As such, the broader ecological significance and full spatial extent of these habitats are likely underestimated. Second, the data reflect a single temporal snapshot and may not capture the potential seasonal variability in species composition and abundance, as suggested by previous studies (e.g., Steller et al., 2003; Peña and Bárbara, 2010; Navarro-Mayoral et al., 2020; Otero-Ferrer et al., 2020a; Helias et al., 2024). Finally, although we incorporated all available preliminary taxonomic data and referenced relevant regional studies, species-level identification of rhodolith-forming algae remains limited due to the scope of the current study and the material available. This taxonomic limitation is important to acknowledge, as accurate species identification is critical for understanding ecological dynamics and informing conservation strategies. To fully understand the ecological role of RBs at Cocos Island, future research should address the following: (1) comprehensive assessments of rhodolith community composition, (2) mapping of RB spatial extent, (3) analysis of habitat structure and community composition across the full depth range and throughout different seasons, to capture spatial and temporal heterogeneity, and (4) investigation of oceanographic and topographic variables to identify their influence on the variability of RBs.

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CRediT authorship contribution statement

Celeste A. Diaz-Licona: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nadine Schubert:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Formal analysis. **Vladimir González-Gamboa:** Writing – review & editing, Supervision, Conceptualization. **Fernando Tuya:** Writing – review & editing, Formal analysis. **Juan Carlos Azofeifa-Solano:** Writing – review & editing, Methodology, Investigation. **Cindy Fernández-García:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2025.103914.

Data availability

The authors declare that all data supporting the findings of this study are available within the paper and its supplementary information files.

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