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REPORT

Structural attributes and macrofaunal assemblages associated with rose gorgonian gardens (*Leptogorgia* sp. nov.) in Central Chile: opening the door for conservation actions

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Abstract Gorgonians (like corals) are important habitat-forming organisms that support a diversity of macrofauna. This study explored structural attributes of gorgonian gardens formed by rose gorgonians (*Leptogorgia* sp. nov.) and associated macrofaunal assemblages in Caleta Pichicuy (Central Chile). Hierarchical sampling was conducted at 20 m depth (maximum colony abundances) in order to assess spatial variability in abundance and colony attributes at two spatial scales (among sites and rocky walls). The abundance and composition of the associated vagile and sessile macrofauna were also examined using univariant (Taxa richness and Shannon index (*H'e*)) and multivariant approaches and were compared with adjacent bare rocky habitats. Our results showed a high abundance of gorgonians (ca. 28.9–36.5 colonies m^{-2}) compared to other gorgonian gardens in the world. For structural attributes, our results showed smaller colonies with thicker holdfasts in more exposed sites, suggesting the influence of hydrodynamic forces on the colony morphology. Taxa richness and *H'e* of vagile fauna showed threefold and twofold, respectively, higher values in gorgonian gardens compared to bare walls, but no differences were observed for sessile fauna. In addition, PCoA and PERMANOVA evidenced a distinctive assemblages' composition between habitats for both vagile and sessile fauna. Correlation analyzes and dbRDA showed, however, little association between structural attributes and associated faunal assemblages ($R^2 = 0.06$, and ca. 3–9.4% of the total variation explained, respectively). Our results constitute the first assessment of structural habitat complexity and accompanying fauna in these gorgonian gardens and establish the baseline for understanding possible future changes associated to human activities.

Keywords Ecosystem engineers · Benthic biodiversity · Shallow water gorgonians · Southeast Pacific

Introduction

Gorgonians are one of the most common group of benthic organisms in circalittoral seascapes across tropical, temperate and polar ecosystems (Gomez et al. 2018). These organisms play important roles at ecological and ecosystems scales. Gorgonians feature a three-dimensional, arborescent and branching morphology that provides additional complexity to subjacent rocky walls (Jordan et al. 1996). High colony groupings

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known as gorgonian gardens have a major role in the secondary production of the system (Krieger and Wing 2002; Montseny et al. 2020), including species with commercial interest such as lobsters or spiders crabs have been observed around gorgonian gardens (Chimienti 2020). These gardens provide key ecological services, such as carbon sequestration in long-lived carbonate skeletons (up to 0.73 ± 0.71 g C m^{-2} yr $^{-1}$ during decades or centuries; Coppari et al. 2019), and human goods such as new medicines derived from bioactive compounds and economically valuable diving spots (Dias et al. 2015). Given the slow growth rates and long-living periods of gorgonians species ranging from 15 to over 200 years (Wenker and Stevens 2020) it is vital to preserve their integrity, which is currently experiencing an important degradation in different regions such as the Mediterranean and the Atlantic Sea (Cassola et al. 2016; Chimienti et al. 2021) that can trigger cascading effects on associated macrofaunal assemblages (Cerrano et al. 2000). For instance, the loss of the gorgonian *Paramuricea clavata* due to heat stress causes additional changes on the coralligenous seascape associated to a reduction in the cover of other calcareous species such as bryozoans and coralline algae (Scinto et al. 2010) and an increase in the dominance of turf species (Verdura et al. 2019).

Gorgonian habitats host a great diversity of benthic organisms that might range from habitat generalists to highly specialized species featuring remarkable habitat adaptations (Hixon and Menge 1991; Messmer et al. 2011). For instance, in shallow and temperate areas, the gorgonian *Leptogorgia virgulata* constitute a key habitat for the gastropod, *Neosimnia uniplicata,* and the shrimp, *Neopontinides beaufortensis.* These species dwell firmly attach to gorgonian branches, mimicking its shape and color while the gorgonian benefits for debris-removal (Patton 1972). In the same way, the nudibranch *Tritonia wellsii* uses the gorgonian *Leptogorgia virgulata* as hatchery and feeding habitat (Patton 1972). In deep and temperate areas like Portofino (Italy), the kleptoparasit polychaete *Haplosyllis chameleon* excavates unharming galleries in the coenenchyme of *Paramuricea clavata* to escape from predation and feeds on preys stolen from polyps (Pola et al. 2020). Besides specific associations, the presence of gorgonians can also determine the nature of associated understorey vegetation due to the shading effect of the erect branching structure, limiting the growth of erect macroalgal communities and favoring the development of coralligenous assemblages (Ponti et al. 2018). Gorgonian gardens also generate a wide range of microhabitats that are used as refuges by a diversity of opportunistic benthic organisms and increase the available surface area for settlement (Ponti et al. 2016). For instance, Valisano et al. (2016) reported higher abundance of crustaceans, gastropods and polychaetes inside gorgonian habitats than outside, evidencing their role in providing protection against benthic predators. Besides, the structural complexity of the habitat may be enhanced by association with bryozoans and hydrozoans species frequently settling on colony branches (Cúrdia et al. 2015). Another example was reported by Calcinai et al. (2013), who observed different associations between encrusting sponges using octocorals, such as *Carijoa riisei* and/or *Alertigorgia hoeksemai*, as growth substrates in both shallow and deeper areas of the tropical waters of the Indo-Pacific. In addition, gorgonians in temperate mesophotic ecosystems, play a crucial role in capturing and transporting suspended particles from the water column to the sea floor (Cerrano et al. 2019). Authors also emphasize the role of gorgonians in facilitating coevolutionary processes with other organisms and in reducing water speed, thereby enhancing sediment stability.

Approximately 65% of the subclass Octocorallia, including gorgonians, is found in cold-waters (Roberts et al. 2006; Morris et al. 2012). Gorgonian gardens are well-known to proliferate from 10 to 200 m depth in both shallow and deep waters, depending on the species (Roberts et al. 2006). Bayer (1953) already described the Eastern Pacific Ocean, from Ecuador to South of Chile, as one of the geographic regions with higher diversity of species in the Gorgoniidae family. Yet, only the Ecuador coast has been well documented in regards to gorgonian diversity (Homeier et al. 2008), whereas the taxonomy, distribution and ecological role of gorgonians in other geographic areas of the Eastern Pacific remains unclear (Vargas et al. 2014). At present, the only available information is that the area host abundant gardens of rose cold-water gorgonians (Häussermann and Försterra 2007), but their taxonomic identity along the entire coast is unclear and there are literally no studies on the associated communities of benthic faunal assemblages (Tognelli et al. 2005). Besides, to our knowledge no studies have been conducted on associated assemblages despite this information is essential to improve our understanding on their ecological role and create a baseline for future studies focused on their conservation.

In this context, the present study, conducted in Caleta Pichicuy (Central Chile) was aimed to assess: (1) the abundance of rose gorgonians along the depth gradient, (2) the spatial variability in the abundance and structural colony attributes of rose gorgonians (height, width and surface cover) across sites and sampled rocky walls, (3) the possible association between colony attributes, and the abundance and local diversity indexes of vagile and sessile fauna (i.e., species richness and *H*'e Shannon–Wiener Index), and the overall community composition and (4) explore the possible contribution of gorgonian gardens to enhance local diversity by comparing the ecological indices and taxa composition of vagile and sessile fauna in rose gorgonian gardens and in adjacent bare rocky walls. Overall, this study provides new valuable information on the population structure and ecological importance of rose gorgonian gardens in the coastline of Chile and represent a first step toward possible management and conservation actions.

Material and methods

Study site

Gorgonian gardens of Caleta Pichicuy are formed by a currently undescribed species of *Leptogorgia* (Camps-Castella et al. under review). The study was conducted in the Caleta Pichicuy (Chile, NE Pacific) in the region of Valparaíso. In the area, the Humboldt Current System influences the coast with cold and nutrient-rich water (Echevin et al. 2012), although with great temporal variation resulting from differences in wind stress fields and the magnitude of the local upwelling (Tapia et al. 2014). Sampling was conducted in summer 2021 in three study sites of Caleta Pichicuy separated ca. 1 km between them and subjected to contrasting degrees of exposure to local currents: Jardín del Gato (JG: 32° 20′ 51.39″ S, 71°28′14.18″ W), La Isla (LI: 32° 20′51.86″ S, 71° 27′ 45.31″ W) and El Asilo (EA: 32° 20′50.49″ S, 71° 27′ 39.63″ W) (Fig. 1), and three different rocky walls per site (separated ca. 500 m). Jardin del Gato is the most exposed site, followed by La Isla and El Asilo. The degree of exposure was qualitatively assessed using combined information on main local winds and orientation toward the northward flow direction of the Humboldt Current (López et al. 2019). Besides, the presence of near shore emergent rocks in the proximity of La Isla and El Asilo makes these sites comparatively more protected compared than Jardin del Gato. Sampling was conducted with the boat and facilities of the Pichicuy diving center, who provided experienced advice on local differences in hydrodynamic exposure. In the case of LI, one replicate bare rocky wall was near (200 m) a kelp forest of *Macrocystis pyrifera.* The maximum depth is 40 m in Jardin del Gato, and 35 m in LI and EA.

Preliminary assessment of the depth distribution of rose gorgonians and its associated biodiversity

In order to assess the potential effect of depth in the composition of vagile (includes only slow-moving species, such as cryptic fishes within Bleniidae and Gobiidae families) and sessile fauna, an exploratory analysis was conducted along the depth gradient. Sampling was conducted at 6 depths, where gorgonians are present: 5, 10, 15, 20, 25, and 30 m. At each site and depth, the abundance of gorgonians, and the composition of sessile and vagile fauna was evaluated using random 50 × 50 cm PVC quadrates ($N = 3$). Sampling was restricted to 30 m due to scuba diving safety rules and dive time constraints. Results of the preliminary assessment show that the highest densities of gorgonians were observed at 20 m depth (Fig. 2). Therefore, we decided to concentrate sampling efforts at 20 m depth to maximize the observation of patterns of associated biodiversity.

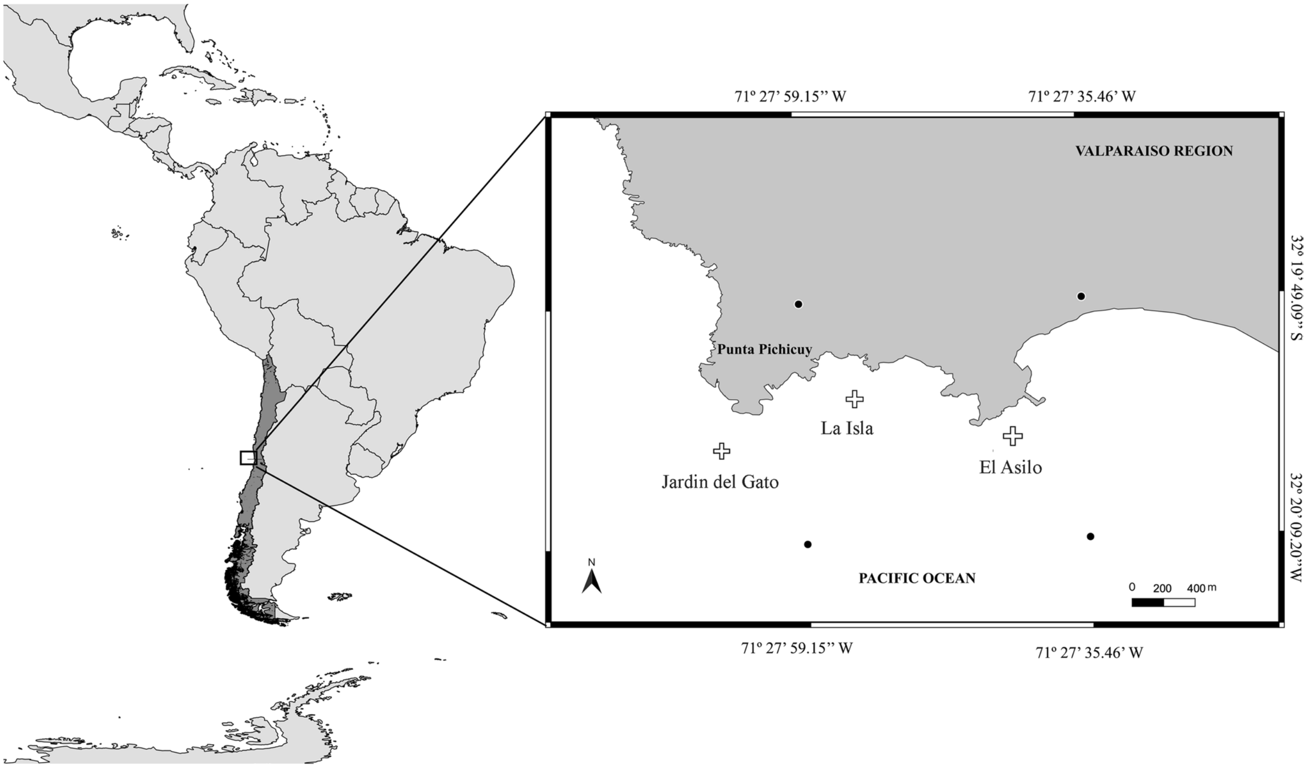


Fig. 1 Caleta Pichicuy (Valparaíso, Chile), showing the three sampling sites: Jardin del Gato (JG), La Isla (LI) and El Asilo (EA)

Fixed depth assessment (20 m) of the abundance and structural attributes of the rose gorgonian population

At each site the abundance of rose gorgonians was assessed in three different rocky walls (hereafter, A, B and C) separated ca. 500 m using random 50 × 50 cm PVC quadrates ($N = 15$, per 3 sites, per 3 walls = 135 total) and results expressed in number of colonies per m^2. To evaluate the effect of the gorgonian structural complexity on associated organisms, colony height and width was measured in situ to the nearest mm by the same observer. Colony height was estimated as the maximum distance from the base to the tip of the farthest branch. The surface area occupied by gorgonians within quadrat was determined from photographs with the Image J software and used as a proxy of colony biovolume (Cúrdia 2012). Also, the holdfast diameter of $N = 5$ random gorgonian colonies was determined using Image J software across sites and rocky walls. In each photo, the scale was calibrated to obtain a precision of 1 mm. Photographs were taken with a 12-megapixel digital camera (Olympus TG-5).

Fixed depth assessment (20 m) of biodiversity and ecological indices

At each study site, 50 × 50 cm photo-quadrats were randomly taken to evaluate the influence of the gorgonian habitat in the composition and abundance of associated invertebrates and cryptobenthic fishes associated to gorgonian colonies in the three rocky walls and adjacent rocky walls without gorgonians ($N = 15$, per 3 sites, per 3 walls with gorgonians, 3 walls without gorgonians = 270 total).

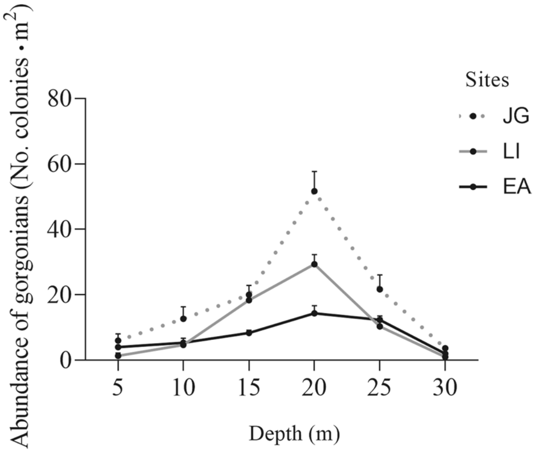


Fig. 2 Depth distribution of gorgonian abundance in Caleta Pichicuy, among sites (JG: Jardin del Gato; LI: La Isla; EA: El Asilo). Data correspond to the mean and errors bars = SE

The number of vagile and sessile macroinvertebrates species per replicate quadrat (i.e., taxa richness), was identified to the lowest possible taxonomic level (genus and/or species). Cover was estimated as the total quadrat area occupied by a given taxa using Image J software with adequate calibration. Local diversity per quadrat was calculated using the Shannon–Wiener index (H'e). Also, qualitative information (presence/absence) of large benthic fish species inside gorgonian gardens and in adjacent rocky walls without gorgonians was noted at each of the dives (Buhl-Mortensen et al. 2010) in order to obtain some preliminary information on possible effects.

Data analysis

Preliminary assessment of depth distribution of rose gorgonians and associated biodiversity

Patterns in the abundance of rose gorgonians among sites (fixed factor, 3 levels) and depths (fixed factor, 6 levels) were investigated with a 2-way factorial ANOVA. Differences in taxa composition across sites (fixed factor, three levels) and depths (fixed factor, 6 levels) were explored with PERMANOVA using Bray–Curtis similarity distances for multivariate analyzes.

Fixed depth assessment (20 m) of abundance and structural attributes of the rose gorgonians

Differences in the patterns of abundance and colony attributes including number of colonies, colony height, width, biovolume and diameter of the base of rose gorgonians among sites (fixed factor, three levels) and rocky walls (fixed factor, three levels, nested in site) were investigated with a 2-way Nested ANOVA.

Fixed depth assessment (20 m) of biodiversity and ecological indices

Differences in vagile and sessile species richness and Shannon–Wiener diversity Index among sites (fixed factor, three levels), habitats (fixed factor, two levels) and rocky walls (fixed factor, three levels, nested in Site × Habitat) was investigated with a 3-way Nested ANOVA.

Fixed depth assessment (20 m) of spatial patterns of macrofaunal assemblages

PERMANOVA with Bray–Curtis similarity distances was used to investigate differences across sites (fixed factor, three levels), habitats (fixed factor, two levels) and rocky walls (fixed factor, three levels, nested in Site × Habitat). Significant factors and interactions were investigated with post hoc pairwise. SIMPER analysis was conducted to identify the relative contribution of each taxon to dissimilarities. Differences in assemblage composition of vagile, sessile and all community were represented by unconstrained ordination plot using the principal coordinate analysis (PCO) based on Bray–Curtis similarities of Log $(X + 1)$ transformed data (vagile and sessile fauna separately), and presence/absence transformed data of all community (matrix of vagile and sessile fauna).

Fixed depth assessment (20 m) of relationship between gorgonian attributes and community composition

The influence of gorgonian structural attributes (height, width, surface area of all gorgonian colonies per quadrat (SC)) in the structure of associated macroinvertebrates (vagile, sessile and the entire community, the later based on presence/absence transformed data) was investigated with a distance-based redundancy analysis (dbRDA). Analyzes were conducted on log transformed (log $(x + 1)$) data for gorgonian structural attributes matrix of each type of community composition (vagile and sessile fauna), and with presence/absence transformed data for the entire community.

Table 1 Two-way factorial ANOVA for abundance of gorgonians (Number of colonies · m^2) among sites (JG: Jardin del Gato, LI: La Isla and EA: El Asilo) and depth. Statistically significant ($\alpha < 0.05$) results are indicated in bold

	df	MS	*F*	*p*
Site	2	100	1.507	**0.02**
Depth	5	5202	78.73	**< 0.001**
Site × Depth	10	170	2.567	**0.018**
Error	36	66		
SNK (Site)	JG > LI > EA			
SNK (Depth)	20 > 15 = 25 > 10 > 5 = 30			
SNK (Site × Depth)	JG (20) > LI (20) > JG (15) = LI (15) = EA (25) > JG (10) > EA (20) > EA (15) = LI (25) = EA (25) = LI (10) = EA (10) = JG (5) = EA (5) > LI (5) = LI (30) = EA (30) = JG (30)			

Homogeneity of variances and normality assumptions were tested by Cochran's test and Kolmogorov–Smirnov distribution fitting test of the residuals, respectively, and transformed when necessary to meet ANOVA assumptions. The critical level of significance was fixed at $\alpha = 0.05$. Student–Newman–Keuls (SNK) post hoc comparisons were used when necessary to identify significant differences in the interaction between different factors. All multivariate statistical analyzes were conducted using R Software.

Results

Preliminary assessment of depth distribution of rose gorgonians and associated biodiversity

In general, gorgonians were present in all study sites from 5 to 30 m depth. The abundance of gorgonians (Number of colonies per m^2) showed significant differences among sites and depths ($p < 0.001$, Table 1), with the highest abundance of gorgonians being observed at 20 m depth in Jardin del Gato (Fig. 2). A consistent decrease in abundances was observed toward deeper and shallower depths (Fig. 2). There was also a significant Site x Depth interaction resulting from variability in depth abundances across

Table 2 Results of PERMANOVA tests on: (a) Vagile fauna, (b) Sessile fauna and (c) All community (vagile and sessile fauna) among sites (JG: Jardin del Gato, LI: La Isla and EA: El Asilo) and depths (5, 10, 15, 20, 25, 30 m)

Source	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique permut
(a) Vagile fauna						
Site	2	4391.8	2195.9	0.603	0.929	998
Depth	5	24,684	4936.8	1.357	0.057	998
Site × Depth	10	22,038	2203.8	0.606	0.999	998
Error	35	1.2726	3636			
(b) Sessile fauna						
Site	2	11,061	5530.4	2.8108	**0.004**	998
Depth	5	16,840	3367.9	1.7117	0.063	997
Site × Depth	10	31,491	3149.1	1.6005	0.607	998
Error	35	70,833	1967.6			
(c) All community (vagile and sessile)						
Site	2	5227.4	2613.7	0.9234	**0.024**	999
Depth	5	20,705	4141	1.463	0.547	997
Site × Depth	10	21,928	2192.8	0.774	0.949	996
Error	35	1.019	2830.5			

A and B are log transformed and C were presence/absence transformed

Statistically significant ($\alpha < 0.05$) results are indicated in bold sites (Table 1). In contrast, no depth effect was observed for taxa composition of vagile and sessile fauna or the entire community (Table 2A, B, C).

Fixed depth assessment (20 m) of abundance and structural attributes of rose gorgonians

The abundance of gorgonians (Number of colonies per m^2) showed significant differences among sites (Table 3A), with higher values in Jardin del Gato followed by El Asilo and La Isla (mean among rocky walls ± SD: 36.5 ± 2.5, 30.5 ± 1.9 and 28.9 ± 1.8, respectively, Fig. 3a). However, no rocky wall effect was detected (Table 3a). For structural attributes, colony height was significantly higher in El Asilo than La Isla and Jardin del Gato (17.8 ± 1.1 cm, 17.1 ± 1.0 cm and 14.1 ± 0.6 cm, respectively), and there was also a rocky wall effect (Table 3b, Fig. 3b). The same site pattern was observed for width (17.5 ± 1.0 cm, 16.9 ± 0.9 cm and 15.4 ± 0.6 cm, respectively) but differences among rocky walls were not significant (Table 3c, Fig. 3c). In contrast, the surface area of gorgonian colonies per quadrat (SC) did not show any significant effect (Table 3d). The holdfast of the colonies was significantly higher in Jardin del Gato, followed by La Isla and lower in El Asilo (11.4 ± 0.8 cm, 6.0 ± 0.4 cm and 5.3 ± 0.8 cm, respectively), and there was also a significant variability among rocky walls (Table 3e, Fig. 3d). Multiple linear regressions models showed that gorgonian abundance was the variable with the highest (and significant) association to the Shannon-Wiener diversity index of vagile fauna, despite correlation was extremely low (R^2= 0.06, Table 4). In contrast, gorgonian abundance showed no significant associations with either the Shannon-Wiener diversity index of sessile taxa (Table 4).

Table 3 Two-way Nested ANOVA testing for differences in: (a) Abundance of gorgonians (Number of individuals per m^2), (b) height of gorgonians (cm), (c) width of gorgonians (cm), (d) surface area of the individual gorgonian colony (SIC) (m^2), (e) surface area of total gorgonians per quadrat (m^2) (SIC total) and (f) holdfast diameter of colonies (cm) among sites (JG: Jardin del Gato; LI: La Isla and EA: El Asilo) and rocky walls (A, B and C, nested in Site)

	df	MS	*F*	*p*
(a) Abundance				
Site	2	731.5	3.801	**0.024**
Wall (Site)	6	411.3	2.137	0.536
Error	126	192.4		
SNK (Site)	JG > EA = LI			
(b) Height				
Site	2	168.95	12.689	**< 0.001**
Wall (Site)	6	37.49	2.816	**< 0.001**
Error	126	13.31		
SNK (Site)	EA > LI > JG			
SNK (Wall (Site))	EA(B) = LI(B) > EA(C) > EA(A) = LI(A) > LI(C) = JG(C) > JG(B)			
(c) Width				
Site	2	55.36	4.428	**0.013**
Wall (Site)	6	15.85	1.268	0.276
Error	126	12.50		
SNK (Site)	EA > LI > JG			
(d) SC				
Site	2	0.007	2.608	0.077
Wall (Site)	6	0.118	3.973	0.445
Error	126	0.002		
(e) Holdfast diameter				
Site	2	161.04	64.69	**< 0.001**
Wall (Site)	6	9.54	3.84	**0.004**
Error	36	2.49		
SNK (Site)	JG > LI > EA			
SNK (Wall (Site))	JC(B) = JG(C) > JG(A) > LI(C) > LI(A) = EA(C) > LI(B) > EA(A) = EA(B)			

Abundance of gorgonians were log transformed to meet ANOVA assumptions. SNK: Student–Newman–Keuls test. Statistically significant ($\alpha < 0.05$) results are indicated in bold

Fixed depth assessment (20 m) of biodiversity and ecological indices

Large native rocky reef fishes observed only in the gorgonian habitat included the sea chub *Medialuna ancietae, Graus nigra* and the *Semicossyphus darwini*. In addition, individuals of chalapo cinid *Labrisomus philippii,* the sandperch *Pinguipes chilensis,* the bilagai *Cheilodactylus variegatus* and the seabass *Paralabrax humeralis* were observed in both habitats, with and without gorgonians. No species was observed exclusively in rocky walls without gorgonians.

A total of 51 taxa were observed, including fishes, but only 44 were recorded at species level and quantified during the study (Table S1). We found 35 vagile and 9 sessile invertebrates, 38 of which were identified to species level, and the rest to Genera (*Incatella sp.)*, family (Porifera family Suberitiidae) or only Phylum Porifera (Table S1). Mollusca was the most diverse phyla with 21 taxa across study sites, habitats and rocky walls. In gorgonian habitats the gastropod *Tegula quadricostata* was the species displaying the highest abundance, and the Porifera sp5 had the highest surface cover (m^2). In contrast, in habitats without gorgonians the gastropod *T. atra* was the most abundance vagile species, and the mussel *Aulacomya atra* was the species with the highest surface cover. In addition, there are some species such as the fish *Hypsoblennius sordidus*, the catshark *Schroederichthys chilensis*, the actinia *Anthothoe chilensis*,

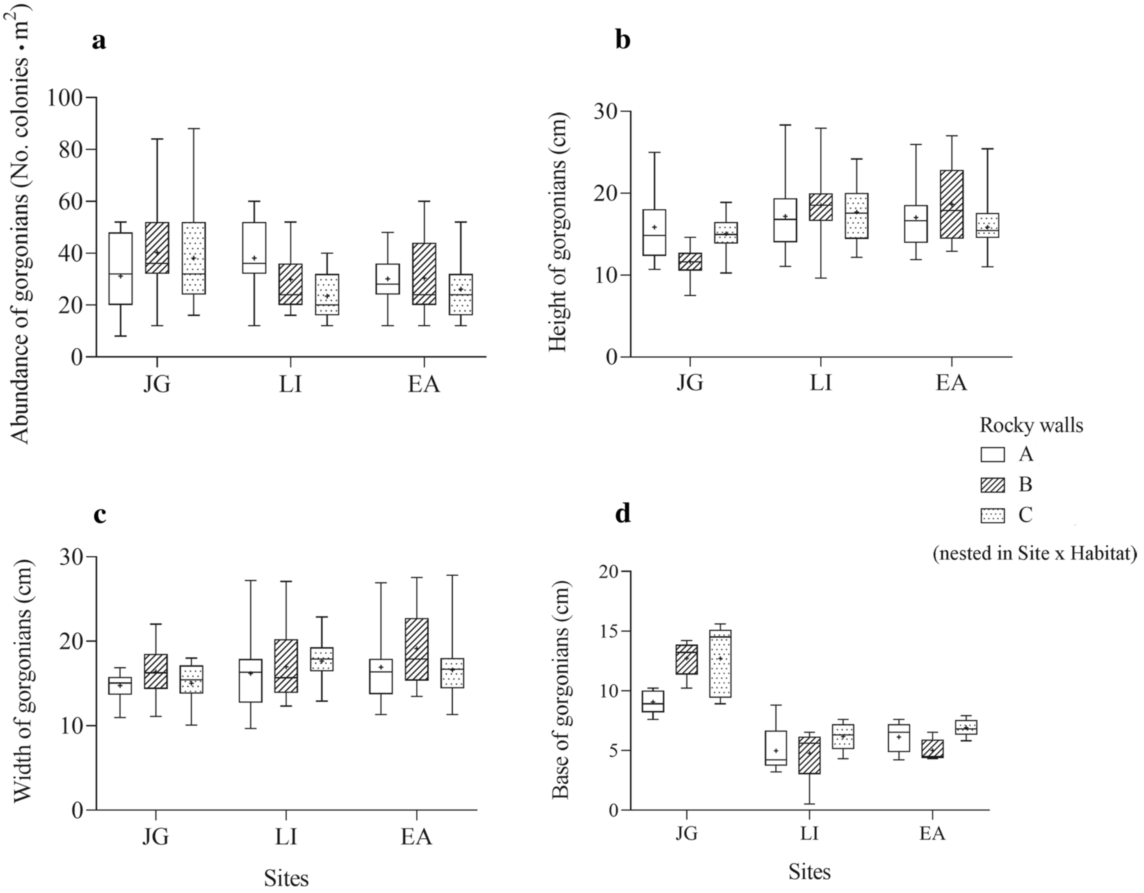


Fig. 3 Abundance and structural attributes of gorgonians among sites (JG: Jardin del Gato; LI: La Isla; EA: El Asilo) and rocky walls (A, B, C: nested in Site × Habitat) (5th-95th percentile). **A** Number of individuals per m^2, **B** Height of gorgonians, **C** Width of gorgonians and **D** base of gorgonians. b, c, d: in cm. Boxplots: central line = median, box = upper and lower quartiles, point = mean and errors bars = SE

Table 4 Subset of gorgonian attributes that explain the most variability in abundance of gorgonians and in the diversity (Shannon–Wiener diversity Index) and species richness (vagile and sessile fauna) (backwards stepwise generalized multiple regression)

	Adj. R^2	Variables
Hv	0.06	Abundance (0.158), Height (0.522), Width (0.744), SC total (0.874),
Hs	0.05	Abundance (**0.01**), Height (0.179), SC total (0.214), Width (0.366)
SRv	0.03	Abundance (0.165), Width (0.471), Height (0.570), SC (0.994)
SRs	0.079	Abundance (0.082), SC (0.147), (0.338), Height (0.461), Width (0.893)

Hv: Shannon–Wiener diversity index of vagile fauna; Hs: Shannon–Wiener diversity index of sessile fauna; SRv: Species richness of vagile fauna; SRs: Species richness of sessile fauna; SC: Surface colony area (m^2)

The variables comprising the best model are listed in order of decreasing significance (p value in parentheses). Statistically significant ($\alpha = 0.05$) values are indicated in bold

the starfish *Patiria chilensis* and others only observed in gorgonian habitat (Table S1).

For vagile fauna, taxa richness differed significantly among habitats, with higher numbers in the gorgonian habitat (4.6 ± 1.4 taxa) than in adjacent rocky walls without gorgonians (2.5 ± 1.0 taxa) (Table 5a, Fig. 4a). There were also significant effects of site and rocky wall, resulting from species richness being higher in La Isla than Jardin del Gato and El Asilo, and significant spatial variability across rocky walls (Table 5a, Fig. 4a). Also, a significant Site x Habitat interaction was observed, due to higher differences among sites in rocky walls without gorgonians than in gorgonians habitats (Table 5a, Fig. 4a). Similar effects with enhanced diversity in the gorgonian habitat and comparable site

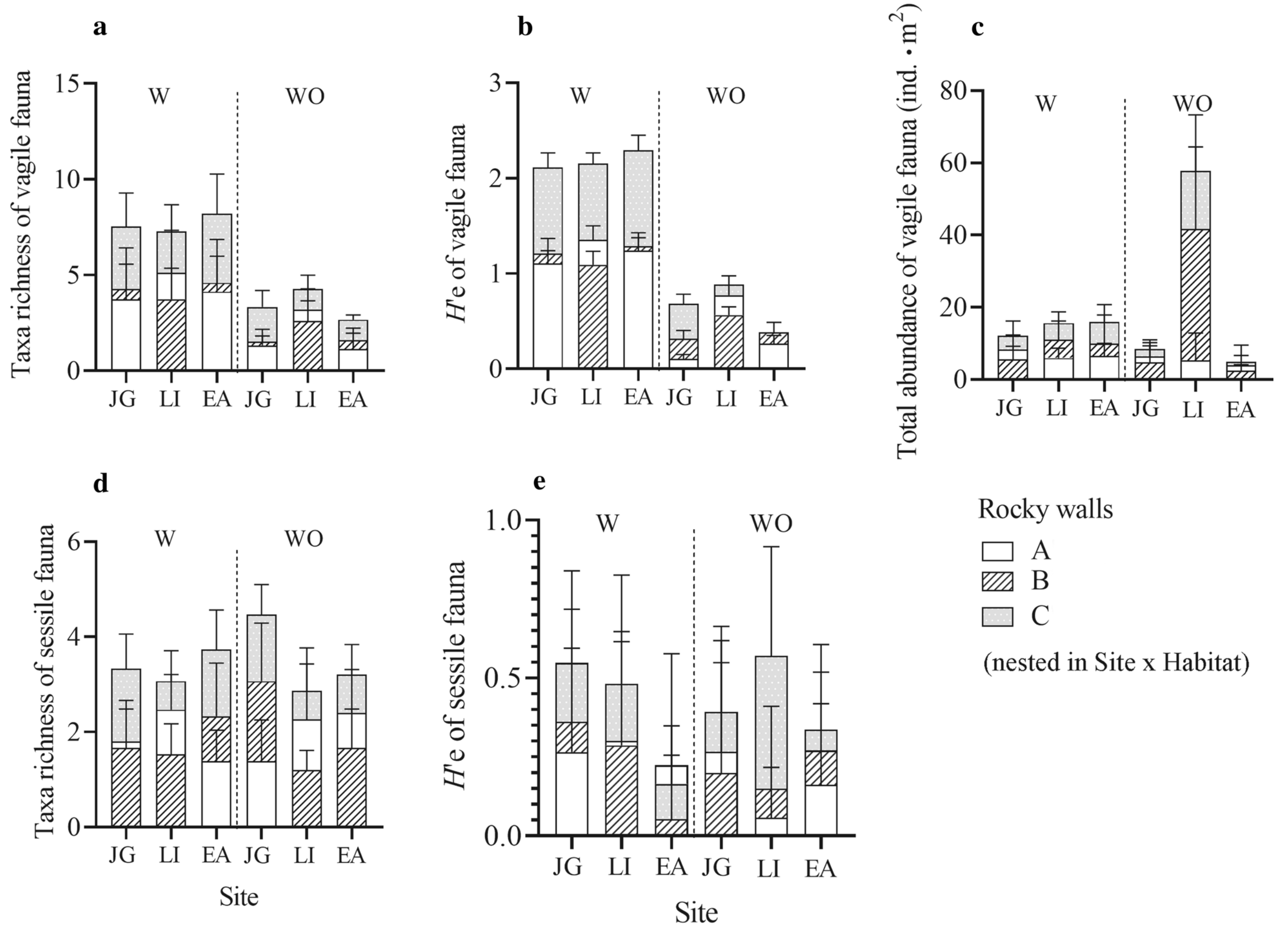


Fig. 4 Univariate ecological indices across sites (JG: Jardin del Gato; LI: La Isla and EA: El Asilo), habitats (W: with gorgonians, WO: without gorgonians) and rocky walls (A, B, C: nested in Site x Habitat). Bars display the mean (±SE) for: **A** Species richness of vagile fauna, **B** Shannon–Wiener diversity index (*H'* e) of vagile fauna, **C** Total abundance of vagile fauna (ind m^{-2}), **D** Species richness of sessile fauna and **E** Shannon–Wiener diversity index (*H'* e) of sessile fauna

patterns were found for the Shannon–Wiener taxa diversity index (H' e) (1.3 ± 0.5 in the gorgonian habitat and 0.3 ± 0.3 without gorgonians), although a significant effect of rocky walls was also observed (Table 5b, Fig. 4b). There were also significant effect of sites, habitat, rocky walls and Site x Habitat, resulting from total abundance of vagile fauna being higher in bare areas (9.6 ± 4.2 ind m^{-2}) than in gorgonian gardens (7.1 ± 0.7 ind m^{-2}) in the other sites (Fig. 4c). In contrast, for sessile fauna, both taxa richness and Shannon–Wiener diversity index of sessile fauna showed no differences between sites, habitats, rocky walls and the interaction (Table 5d, e, Fig. 4d, e).

Fixed depth assessment (20 m) of community patterns

PERMANOVA analysis showed that 34.3% of the total variation in the assemblages of vagile fauna was due to habitat type (Table 6a). In contrast, the effect of sites and rocky walls accounted for a lower, although significant proportion (14.2% and 4.7%, respectively) of the total observed variation (Table 6a). There was a significant Site x Habitat interaction which accounted for 16.50% of the total observed variation (Table 6a). PERMANOVA pairwise tests indicated significant differences among all sites (Table. S2a). Pairwise test for the significant Ha x Si interaction showed differences between habitats on La Isla ($t = 2.5$, $p < 0.01$) and El Asilo ($t = 2.3$, $p < 0.01$) (Table. S2b). Significant differences between sites were only observed in habitats without gorgonians (Jardin del Gato, La Isla: $t = 1.9$, $p = 0.03$; La Isla, El Asilo: $t = 1.5$, $p = 0.03$) (Table S2c). For sessile assemblages there was also a significant effect of habitat type, which explained ca. 9.7% of total variation (Table 6b). A significant site effect (4.7% of the total variation; Table 6b) resulted from differences between Jardin del Gato and La Isla and between Jardin del Gato and

Table 5 Three-way Nested ANOVA testing for differences in: (A) Taxa richness of vagile fauna, (B) Shannon–Wiener diversity index (*H'* e) of vagile fauna, (C) Taxa richness of sessile fauna and, (D) Shannon–Wiener diversity index (*H'* e) of sessile fauna among sites (JG: Jardin del Gato, LI: La Isla and, EA: El Asilo), habitats and rocky walls (nested in Site x Habitat)

	df	MS	*F*	*p*
(A) Taxa richness of vagile fauna				
Site	2	12.27	5.71	**< 0.001**
Habitat	1	335.56	156.24	**< 0.001**
Wall (Site × Habitat)	12	4.99	2.32	**< 0.001**
Site × Habitat	2	8.11	3.77	**0.024**
Error	252	2.14		
SNK (Site)	LI > JG = EA			
SNK (Habitat)	W > WO			
SNK (Site × Habitat)	JG (W) = LI (W) = EA (W) > LI (WO) > JG (WO) = EA (WO)			
(B) Shannon- Wiener diversity index (*H'*e) of vagile fauna				
Site	2	0.93	4.51	**< 0.001**
Habitat	1	42.31	205.02	**< 0.001**
Wall (Site × Habitat)	12	0.45	2.19	**0.012**
Site × Habitat	2	0.66	3.21	**0.041**
Error	252	0.21		
SNK (Site)	LI > JG = EA			
SNK (Habitat)	W > WO			
SNK (Site × Habitat)	JG (W) = LI (W) = EA (W) > LI (WO) > JG (WO) = EA (WO)			
(C) Total abundance of vagile fauna				
Site	2	1.61	15.32	**< 0.001**
Habitat	1	0.82	7.81	**0.005**
Wall (Site × Habitat)	12	10.06	7.97	**< 0.001**
Site x Habitat	2	3.39	16.10	**< 0.001**
Error	252	26.51		
SNK (Site)	LI > JG = EA			
SNK (Habitat)	WO > W			
SNK (Site × Habitat)	LI (WO) > EA (W) = LI (W) = JG(W) > JG(WO) = EA (WO)			
(D) Taxa richness of sessile fauna				
Site	2	0.47	1.08	0.33
Habitat	1	0.62	1.42	0.23
Wall (Site × Habitat)	12	0.84	1.92	0.14
Site xHabitat	2	1.25	2.84	0.12
Error	252	0.44		
(E) Shannon- Wiener diversity index (*H'*e) of sessile fauna				
Site	2	4139	0.49	0.61
Habitat	1	16,889	2.01	0.15
Wall (Site × Habitat)	12	4195	0.50	0.60
Site × Habitat	2	8410	1.02	0.44
Error	252	8390		

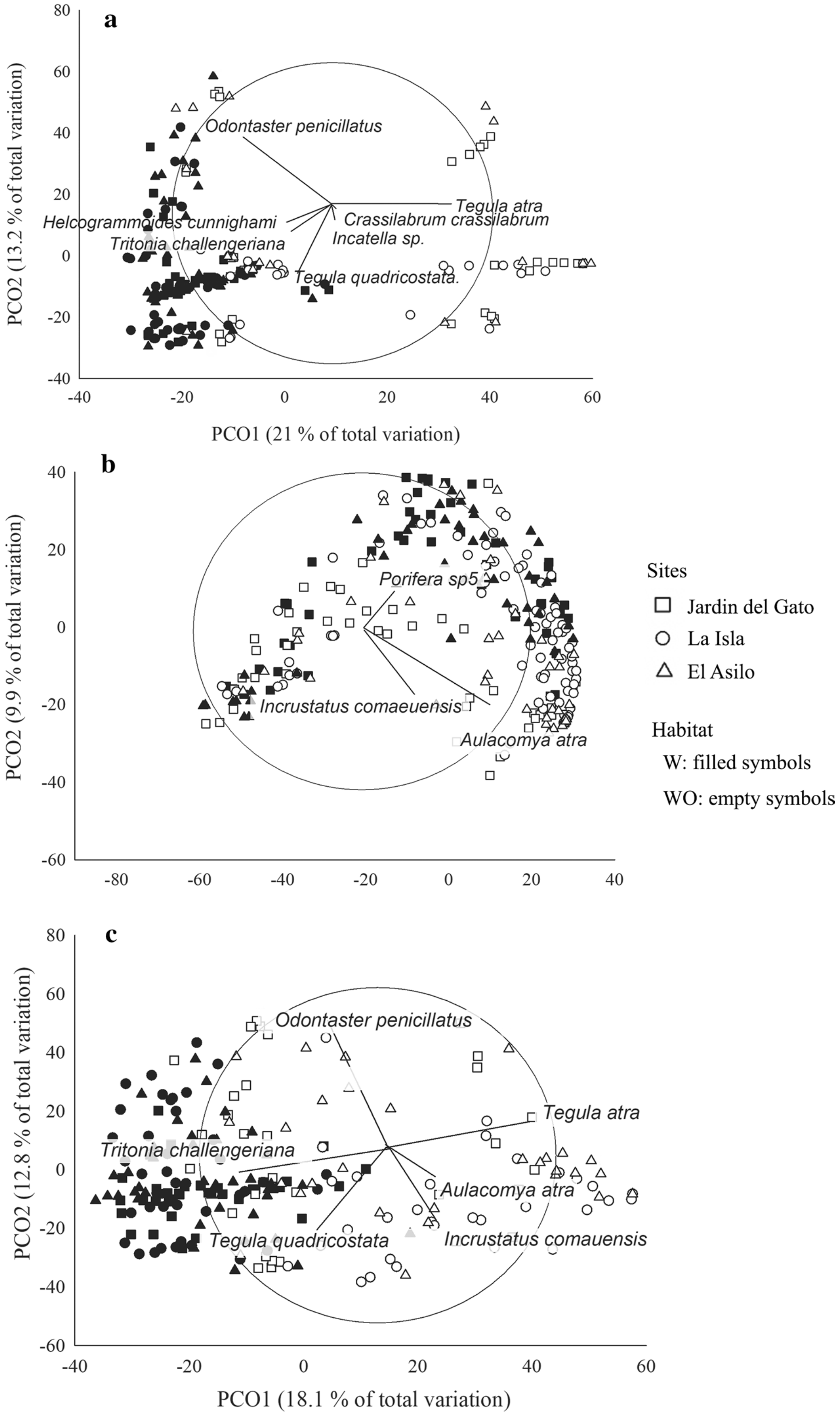
Statistically significant (*$\alpha = 0.05$) values are indicated in bold

El Asilo (see pairwise *t* test in Table. S3a). The Ha x Si interaction accounted for 3.5% of the total variation (Table 5b) and was due to differences between habitats in the Jardin del Gato site (Table S3b). Patterns for the entire community (based on presence/absence transformed data of vagile and sessile fauna) showed significant differences across habitats and sites, which accounted for 13.9% and 11.0% of the total observed variation, respectively (Table 6c). Also, there was a significant Habitat x Site interaction that accounted for 4.8% of the total observed variation (Table 6c). Pairwise tests showed significant differences across all sites (see Table S4a). For the Ha x Si interaction, pairwise test results evidenced differences between habitats in La Isla and El Asilo sites (Table S4b). Also, La Isla showed significant differences with the other two sites in the gorgonian habitat whereas in habitats without gorgonians it was El Asilo that was significantly different from the other sites (Table S4c).

SIMPER analysis evidenced habitat dissimilarities of 94.4% in the composition of vagile fauna, with *T. atra* (more abundant in habitats without gorgonians) and *T. quadricostata* (more abundant in gorgonian habitats) being the taxa with higher contributions to observed dissimilarities (Table S5d). However, there were also low average similarities within habitats (14.8–21.8%) (Table S5k, l). For sessile fauna, differences in taxa composition were also very important of 95.7% between habitats, with Porifera sp5 (more abundant in gorgonian habitat), the soft coral *Incrustatus comauensis,* the Porifera sp3 and the mussel *Aulacomya atra* (more abundant in habitats without gorgonians) being the taxa with higher contributions to dissimilarities (Table S6d). At the level of the entire community, SIMPER results showed average dissimilarities between habitats of 91.2%, with *T. atra, O. penicillatus* (more abundant in rocky walls without gorgonians) and *T. quadricostata* (more abundant in gorgonian habitats) being the taxa with highest contributions to observed differences (Table S7d). All full SIMPER results of similarity and dissimilarities among sites and rocky walls can be found in the S1 Appendix.

PCoA showed an overall separation of habitats in the ordination space and evidenced that the 21% of the total variation in vagile fauna assemblages was explained by the first axis (Fig. 5a). Further variability (up to 13.2%) was also explained by the second axis. The data cloud was driven by the gastropods *T. atra, T. quadricostata* and *O. penicillatus*, represented by the correlation vectors (Fig. 5a). The *T. atra* species was strongly associated with assemblage composition in bare rocky walls and the *T. quadricostata* and starfish *O. penicillatus* were mostly associated with the presence of gorgonian gardens (Fig. 5a). For sessile fauna, the PCoA showed that the differences between habitats were mostly explained by the first axis (14% of total variation) compared with

Fig. 5 Principal coordinates analyzes (PCO) ordination plot of: **A** Vagile community, **B** Sessile community and **C** all community (based on presence/absence transformed data of pooled matrix) in three sites (Jardin del Gato, La Isla and El Asilo) of the Caleta Pichicuy (Chile) and habitat type (W: with gorgonians filled symbols, WO: without gorgonians empty symbols). Vectors superimposed to plot represent the correlations by the species with the PCO axes. Analysis performed on Bray–Curtis dissimilarities



second axis (9.9% of total variation (Fig. 5b). *A. atra* and the unidentified benthic biofilm were taxa with highest associations with the first axis in habitats without gorgonians (Fig. 5b). For the entire community, the first and the second axis of the PCoA explained 18.1% and 12.8%, respectively, of the total variation (Fig. 5c). The *A. atra, T. atra* and the unidentified benthic biofilm were strongly associated with bare rocky walls (Fig. 5c). In contrast, the nudibranch *T. challengeriana* and *T. quadricostata* showed an association with the gorgonian habitat (Fig. 5c).

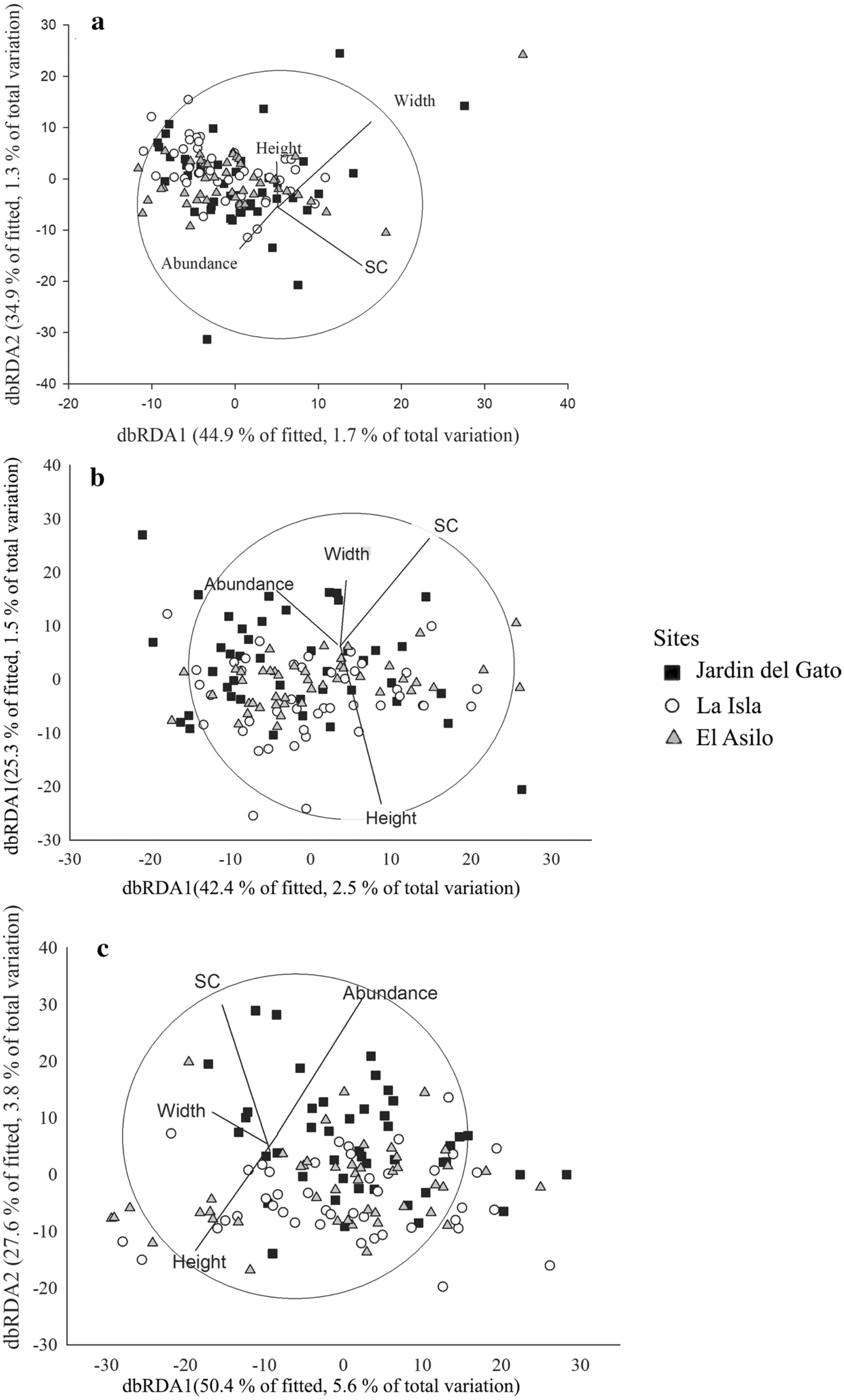


Fig. 6 Distance-based redundancy analysis (dbRDA) biplot to investigate the relationships between gorgonian structural attributes and community composition of **A** Vagile community, **B** Sessile community) and **C** All community (based on presence/absence transformed data). Assemblage symbols are as follows; squares: Jardin del Gato; circles: La Isla; triangles: El Asilo; gray color: rocky wall A; red color: rocky wall B; and black color: rocky wall C. Samples are plotted as points using weighted averages of taxa scores in each constrained axis. The vector lines reflect the relationship of the different attributes of gorgonian complexity to the ordination axes. Vectors lengths is proportional to their relative significance

Fixed depth assessment (20 m) of relationship between gorgonian structural attributes and community composition

The dbRDA indicated that only about 3% of total variation of vagile fauna assemblages was explained by the two ordination axes (44.9% by dbRDA1 and 34.9% by dbRDA2) (Fig. 6a). The large size of width and SC vectors confirm that these gorgonian attributes contribute to the structure of the vagile assemblage's composition (Fig. 6a). Similar results were found for the sessile assemblages' composition (Fig. 6b). The dbRDA plot only explained

4% of the total variation (42.4% by dbRDA1 and 25.3% by dbRDA2), being height and SC the larger vectors that contribute the sessile composition structure. For the entire community, results confirmed that abundance and height attributes were influencing variables, although only 9.4% of the total variation was explained (50.4% by dbRDA1 and 27.6% by dbRDA2) (Fig. 6c).

Discussion

Abundances of gorgonians and variability in structural features

The present study constitutes the first assessment of monospecific cold-water rose gorgonian gardens depth distribution, abundance and structural features in Chile and provides the beginnings for understanding key ecological patterns of these habitats. Our results showed a clear pattern of distribution within depth and similar across sites in Caleta Pichicuy (Chile), with abundances peaking at depths of ca. 20 m. A similar pattern was observed by Cúrdia et al. (2013) who reported maximal abundances at 20–25 for *Leptogorgia sarmentosa* in the Mediterranean. A plausible explanation for the depth distribution observed in Caleta Pichicuy may be related to the presence of dense erect algae (*Lessonia trabeculata*), and/or filamentous turf-forming algae in the upper level of the sublittoral zone (Stotz et al. 2016), which may effectively outcompete gorgonians due to faster growth (Gili et al. 1989). The influence of other factors such as light exposure, substrate suitability and wave action or currents is also another source of variability as indicated in other species (Gili et al. 1989; Garrabou et al. 2002).

The abundance of gorgonian colonies at ca. 20 m depth was one of the highest reported in the literature, especially in the Eastern Pacific (Cúrdia et al. 2013; Carvalho et al. 2014) with densities ranging from ca. 20–90 in Jardin del Gato to 10–40 colonies per m^{-2} in La Isla (means of 28.9 ± 1.8, 36.5 ± 2.5 colonies m^{-2}, respectively) (Fig. 7a–f). In the Caribbean Sea, abundances as low as 0.81 ± 0.41 colonies m^{-2} for *Pseudopterogorgia americana* (Jordán-Dahlgren 2002) and 0.01 ± 0.01 colonies· m^{-2} in *Antillogorgia acerosa* (Manrique Rodríguez et al. 2019) have been reported. In the Mediterranean Sea, densities of 11–53 colonies per m^2 (33 ± 14 colonies · m^{-2}) have been indicated for *Paramuricea clavata,* 1–56 (20 ± 14 colonies · m^{-2}) for *Eunicella singularis*, and up to 25 colonies · m^{-2} for *Eunicella cavolini* (Linares et al. 2008; Gori et al. 2011; Carvalho et al. 2014). Our results may be explained by the large amount of food available through the Chilean coastal upwelling driven by the Humboldt Current System in the study area (Yuras et al. 2005) compared to more oligotrophic systems such as the Mediterranean Sea or the Caribbean Sea. Spatial variability among study sites could be related to the effect of topography on current patterns affecting food supply and wave action controlling the gorgonian populations. In fact, sheltering from wave action also appeared to influence structural attributes of gorgonian colonies. Smaller colonies (14.1 ± 0.6 cm height) with thicker holdfasts (11.4 ± 0.3 cm in diameter), were observed in Jardin del Gato (most exposed) followed by La Isla (17.1 ± 1.0 cm and 6.0 ± 0.4 cm, respectively), whereas those in El Asilo were larger (17.8 ± 1.1 cm) and with thinner holdfasts (5.3 ± 0.8 cm) (shelter by a prominent rocky wall and hosting the lowest abundance of gorgonians). These observations reinforce previous studies pointing that holdfast thickness provide enhanced resistance against wave action (Yoshioka and Yoshioka 1991) and that greater colony sizes can be reached in areas protected from hydrodynamic forces (Dahlgren 1989).

Habitat patterns and associated biodiversity

Our study evidences that rose gorgonian gardens hosted higher taxa richness (mean of 4.6 vs. 2.5 taxa across sites) and diversity (*H'e* of 1.3 vs. 0.3) than adjacent bare rocky walls. Besides, the community structure of vagile, sessile and combined faunal assemblage also differed between gorgonian gardens and adjacent rocky walls. Similar patterns of differences in faunal assemblages have been reported in the presence or absence of gorgonians species such as *Paramuricea clavata* and *Savalia savaglia* in the Mediterranean Sea (Cerrano et al. 2010; Ponti et al. 2018).

In general, Mollusca, Echinodermata and Chordata, were dominant groups in gorgonian habitats. The Order Nudibranchia was highly represented in gorgonian gardens, with two species of genus *Tritonia*—well-known to include many octocoral-eating species (Wyeth et al. 2006) *T. challengeriana* and *T. odhneri* (Fig. 7c, f). In contrast, opposed habitat abundances were observed for *T. quadricostata* and *T. atra* in rocky walls in gorgonian and bare rocky walls, respectively. Disproportionate abundances of *T. atra* have been reported on rocky substrate with encrusting coralline (Stotz et al. 2016) or kelp species (Vásquez and Buschmann 1997) due to herbivorous feeding habits (Schmitt 1987). Hence, high abundances of *T. atra* in bare rocky habitat in La Isla appear to be driven by the presence of adjacent unharvested kelp forest of *Macrocystis pyrifera*, which could have acted as a source of individuals. Among echinoderms, the starfish *Odontaster penicillatus* was also found (Fig. 7b) predominantly inside gorgonian habitats. According to Mutschke and Mah (2009), the species features preferential predation on sponges as in other close species (Lawrence 2013) and could explain its apparent preference for gorgonian habitats hosting enhanced availability of sponge species such as *Clionaopsis platei* or Porifera sp5. Although the same taxa could be observed in both habitat types, total abundances yielded

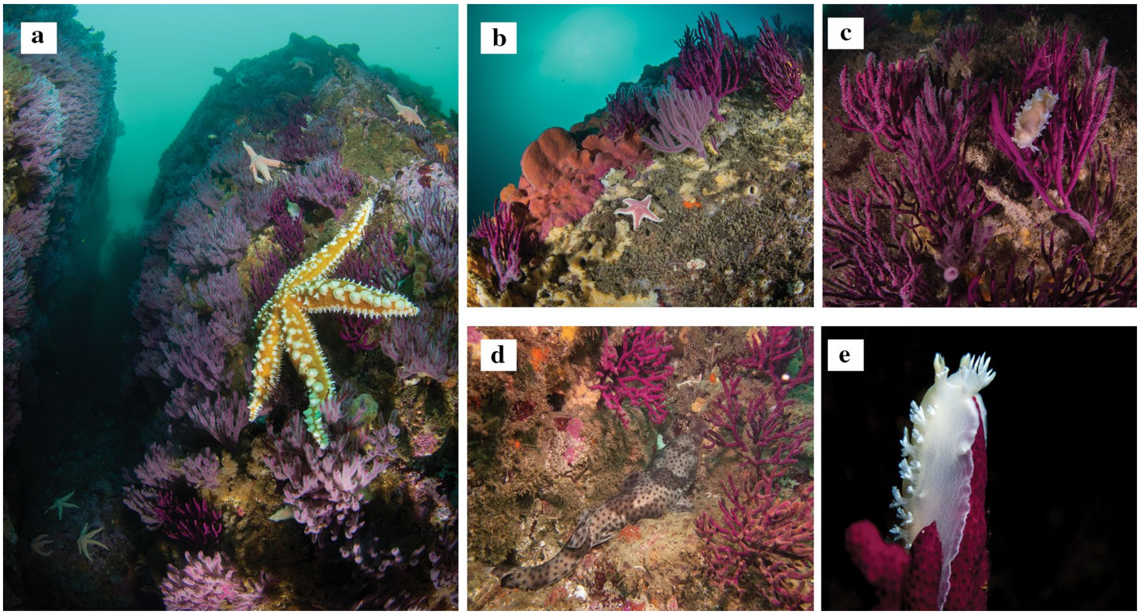


Fig. 7 Underwater photographs of the gorgonian gardens and their associated biodiversity. **A** Gorgonian abundance in rocky walls, **B** Different associated organisms such as sponges and *O. penicillatus*, **C** Detail of gorgonians and the associated nudibranch *T. odhneri* to them, **D** *Schroederichtys chilensis* associated to gorgonians and **E** *T. challengeriana* associated to gorgonians

Table 6 Results of PERMANOVA tests on differences of assemblage structure of: (A) Vagile community, (B) Sessile community and, (C) All community (vagile and sessile) among sites (JG: Jardin del Gato, LI: La Isla and, EA: El Asilo), habitat (W: with gorgonians, WO: without gorgonians) and rocky walls (A, B and C) nested in site and habitat

Source	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms	CV%
(A) Vagile community							
Habitat	1	86,842	86,842	16.589	**0.001**	999	34.33
Site	2	36,056	18,028	2.5054	**0.001**	999	14.25
Habitat × Site	2	41,744	20,872	2.9007	**0.002**	998	16.50
Wall (Habitat × Site)	12	11,930	994.16	2.2547	**0.001**	997	4.71
Error	233	76,366	327.75				30.19
(B) Sessile community							
Habitat	1	90,123	90,123	4.2314	**0.001**	998	9.72
Site	2	53,968	26,984	2.6724	**0.043**	999	4.72
Habitat × Site	2	40,009	20,004.5	3.6047	**0.010**	999	3.50
Wall (Habitat × Site)	12	31,651	3627.5	1.9117	0.062	999	2.76
Error	233	927,160	3979.2				81.12
(C) All community							
Habitat	1	87,055	87,055	2.51	**0.001**	998	13.91
Site	2	43,339	21,669.5	13.73	**0.001**	998	11.02
Habitat × Site	2	99,021	49,510.5	3.04	**0.001**	998	4.82
Wall (Habitat × Site)	12	43,505	3625.4	3.01	0.054	997	4.84
Error	233	625,830	2685.96				69.66

A and B data were log transformed and C were presence/absence transformed. Sum of Square (SS), Mean Square (MS) and estimated component of variation, in percentage of the total variation were reported for each term of the model (CV%). Statistically significant ($\alpha < 0.05$) results are indicated in bold

higher records in bare walls due to very few taxa (*Incatella sp.*, *Crassilabrum* and *Tegula atra*). For the vast majority of taxa gorgonians appear to act as a source of individuals to neighboring systems following an edge effect dynamics allowing the movement of vagile fauna and/propagule dispersal to adjacent, less favorable habitats (Macreadie et al. 2010; Bramwell 2016; Carroll et al. 2019). As has observed for the *T. atra* abundance, further exchanges and subsidized patterns of productivity may occur in the proximity of other habitats such as kelp forest (Shelamoff et al.

2020) and require further investigation in Chilean waters. For instance, enhanced connectivity between seagrass meadows and rocky substrates facilitates migration of the sea urchin *Paracentrotus lividus* due to a spillover effect from the rocky habitat featuring higher recruitment (Prado et al. 2009; Boada et al. 2018). Yet, Ceccherelli et al. (2014) reported high spread of invasion algae *Caulerpa racemosa* at edge habitat of seagrass meadows than inside due to human disturbance on the margins (e.g., anchoring or dredging) of *Posidonia oceanica* beds in the Mediterranean Sea. In addition, Smith et al. (2011) observed that predation rate pipepish *(Sitgmatopora* spp.) was higher in the edge habitat (sand areas) than in sand patches inside seagrass or in the middle of seagrass meadows. Hence, increased connection between habitats may have either positive (Carroll et al. 2019) or negative effects for different species (Ceccherelli et al. 2014).

Sessile fauna showed no differences in univariate ecological indices (species richness and diversity) suggesting that the edge effect observed for vagile species was largely inherent to their mobility capacity across benthic habitats. Yet, there were also some differences in community structure between habitats that were mostly due to enhanced surface cover of certain species (the soft coral *Incrustatus comaeunsis*, Porifera sp3 and the commercial mussel *Aulacomya atra*) in bare rocky substrates. According to Velasco-Charpentier et al. (2021), the recruitment of *A. atra* in the South of Chile is facilitated by microhabitats provided by kelp forests of *Lessonia flavicans*. Hence, substrate competition with gorgonians during the process of benthic settlement by intercepting settling propagules or producing allelochemicals (Ponti et al. 2014) could explain the distribution of these sessile species including Porifera and soft corals.

The reef fish community associated to gorgonian gardens was only qualitatively evaluated in this work, but such preliminary assessment already revealed clear differences between habitats. The blenny *Helcogrammoides cunninghami*, was more abundant within gorgonian gardens as expected for a cryptic species (Pérez-Matus et al. 2016). The endemic catshark *Schroederichthys chilensis* possibly uses gorgonian gardens as nursery habitats and was also dominant in this habitat (Fig. 7d), similarly to reported in other close species (*Scyliorhinus canicula* or *Scyliorhinus rotifer*) (Bo et al. 2015). This hypothesis is further supported by observations of catshark eggs attached to colony branches during our samplings. Endemic rocky reef fishes of economic importance, such as *Semicossyphus darwini* and *Graus nigra*, were only observed within gorgonian gardens, mainly between the alleys of gorgonian walls. Abundance patterns of these species could be partly associated to preferential feeding on the sea urchin *Tetrapygus niger*, which is also more abundant on gorgonian gardens (Perez-Matus et al. 2012).

Relationship between gorgonian structural attributes and community composition

Contrary to our expectations the results evidenced a reduced influence of gorgonian attributes on community composition (but see Cúrdia et al. 2015 for significant effects of colony abundance and height on epifaunal assemblages). According to Cúrdia et al. (2015), increased habitat complexity may be scale-dependent and requires the evaluation of heterogeneity as a fractal dimension. Yet, they propose that the presence or absence of gorgonians may enhance species richness and diversity more than colony complexity itself (i.e., the fractal dimension). Also, Pierre and Kovalenko (2014) showed that for ecosystem engineers, heterogeneity is the most important feature fostering biodiversity than overall habitat complexity. Valisano et al. (2016) showed that lower sedimentation inside gorgonian gardens of *P. clavata* than outside creates a homeostatic effect on the surrounding habitat that enhanced vagile fauna. Besides, sole the presence of gorgonians might increase substrate availability thus enhancing local diversity, compared to adjacent soft bottoms, as indicated for the gold coral *Savalia savaglia* (Cerrano et al. 2010).

Conclusions and take-home conservation message

Our study evidences a clear distribution pattern of rose gorgonian gardens along the depth gradient, with a peak at 20 m. The large abundance of gorgonian colonies in Pichicuy (up to 90 ind. m^{-2}) was striking and highlight the importance of the Humboldt Current System in the Chilean Coast. Furthermore, our study suggests that presence or absence of gorgonians gardens is a key factor driving community structure and species composition in Caleta Pichicuy, specially for vagile fauna. These gardens clearly host an elevated taxa richness and diversity and appear to act as a source of vagile organisms to adjacent bare rocky walls. The similarity of structural community variables across study sites might have been influenced by the limited spatial scale at which the study was conducted, thus hindering the observation of important differences in taxa richness and diversity and community composition, particularly for sessile fauna. Thus, a large-scale comparison along the Chilean coast or further differences in colony structure might be needed to fully grasp patterns of variability associated to differences in structural complexity and density of rose gorgonian gardens.

Fishes of commercial interest highly threatened by overfishing (Godoy et al. 2010) such as *Semicosspyhus darwini*, *Graus nigra* and *Medialuna ancietae* were associated with gorgonian gardens, highlighting the importance of protecting this habitat. Currently, study sites are included within the Management Areas for the Exploitation of Benthic Resources (AMERB) which allows an intensive extraction of resources and lacks a holistic ecosystem management approach. In contrast, in other world regions such as the Mediterranean Sea or Portugal coasts, gorgonian habitats are strictly protected within MPAs through the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR). Now that a baseline on the ecological importance of rose gorgonian gardens has been established, a similar protection figure should be considered on Chilean species and habitats, along with further studies aimed at understanding key ecosystem processes and dynamics. It is also suggested that future management plans or ecological studies, should include a monitoring plan of the health status of rose gorgonian gardens and associated communities, which so far appear to be unique to the Chilean locality of Caleta Pichicuy.

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Author contribution IAH and PP contributed to the study conception and design. Material preparation and data collection were performed by JCC. Data analysis were performed by JCC, IAH, PP and JTM. The first draft of the manuscript was written by JCC and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The funders had no role in study design, data collection and analysis or preparation of the manuscript.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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