Facilitation cascades in rhodolith-created habitats depends on the identity of facilitated organisms

Las cascadas de facilitación en fondos de rodolitos dependen de la identidad del grupo facilitado

Máster en Biología Marina, Biodiversidad y Conservación

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ÍNDICE

Abstract: Rhodolith beds are widespread benthic habitats globally distributed, playing the role of primary facilitators in facilitation cascades supporting associated communities. Conceptually, primary facilitators (rhodoliths) enhance colonization by secondary facilitators (epiphytic algae), which in turn create a more complex habitat structure that supports increased biodiversity of epifauna. This study assessed the strength of facilitation cascades on various taxonomic groups across five rhodolith beds in the Canary Islands. We identified 11,222 epifaunal organisms within 10 large taxonomic groups. We partitioned the relative importance of rhodolith structural attributes (primary facilitator) from the amount of the secondary facilitator over the abundances and biomasses of epifaunal groups. Our findings revealed that epiphytic loads (i.e., the amount of the secondary facilitator) was the most significant predictor for most groups, in particular for decapods and amphipods. However, some groups (molluscs) were more affected by rhodolith structure. In summary, this study demonstrates that facilitation is a dominant mechanism in rhodolith beds determining the ecological pattern (abundance and biomass) of associated epifauna, with intensity of such facilitation varying among faunal groups.

Key words: Atlantic Ocean, Canary Islands, epiphytic algae, facilitation cascades, mäerl,

Resumen: Los fondos de rodolitos son un tipo de hábitat distribuido de forma cosmopolita, en ellos los rodolitos actúan como facilitadores primarios en cascadas de facilitación. Conceptualmente, los facilitadores primarios (rodolitos) favorecen la colonización por facilitadores secundarios (algas epífitas), que aumentan la complejidad del hábitat, así como la biodiversidad de la epifauna. En este estudio se ha estudiado la fuerza de estas cascadas de facilitación en varios grupos taxonómicos, en cinco campos de rodolitos en las Islas Canarias. Se identificaron 11,222 organismos pertenecientes a 10 amplios grupos taxonómicos. Comparamos la importancia relativa de los atributos estructurales de los rodolitos (facilitador primario) con la cantidad de facilitador secundario encontrado (algas epífitas) para la abundancia y biomasa de los distintos grupos de epifauna. Nuestros resultados revelaron que la carga de epífitos fue el predictor más significativo para la mayoría de grupos, en particular para decápodos y anfípodos. Sin embargo, para otros grupos (moluscos), los predictores más relevantes fueron los atributos estructurales de los rodolitos. En resumen, este trabajo demuestra que la facilitación es un mecanismo dominante en los fondos de rodolitos, determinando los patrones ecológicos (abundancia y biomasa) de la epifauna asociada, y que la intensidad de esta facilitación varía en función del grupo taxonómico.

Palabras clave: Algas epífitas, cascadas de facilitación, Islas Canarias, mäerl, Océano Atlántico

1.-INTRODUCTION

Marine ecosystems are known for their high biodiversity and complex interactions among species (Riosmena-Rodríguez et al., 2017). Among these ecosystems, rhodolith beds are comprised of individual, non-geniculate, free-living calcareous macroalgae belonging to the division Rhodophyta (Foster, 2001). These beds create one of the most abundant benthic communities on the planet, alongside kelp beds, seagrass meadows, and non-geniculate coralline reefs. Rhodoliths support numerous associated macroalgae and invertebrates, acting as key species in these environments (Foster, 2001).

Rhodoliths modify the ecosystem by providing habitat and allowing other species to colonize it, thus increasing biodiversity and ecosystem complexity, being defined as “bioengineers” (Riosmena-Rodríguez et al.2017; Sciberras et al., 2009). Despite this role has been largely acknowledged (Costa et al., 2023; Foster, 2001; Otero-Ferrer et al., 2020; Peña et al., 2014; Teichert et al., 2012), ecological mechanisms underpinning the organization of these habitats, for example the process of facilitation cascades, has only been brought to attention recently (Bulleri et al., en prensa, Navarro-Mayoral et al., 2020; Sánchez-Latorre et al., 2020), with considerable gaps in terms of the identity of organisms being facilitated. Recent studies have started to document facilitation cascades in rhodolith beds (Bulleri et al., en prensa)

Facilitation cascades occur when a foundation species promotes the presence of one or more species that subsequently act as secondary facilitators, which in turn support additional species, creating a hierarchical network (Altieri et al., 2007). These cascades have been observed in diverse habitats such as mangroves (Bishop et al., 2013; Bishop et al., 2012), forests (Brooker et al., 2008; Schöb et al., 2014), kelp beds (Bracken, 2018) and intertidal environments (Altieri et al., 2007; Silliman et al., 2011; Thomsen et al., 2016; Yakovis & Artemieva, 2017).

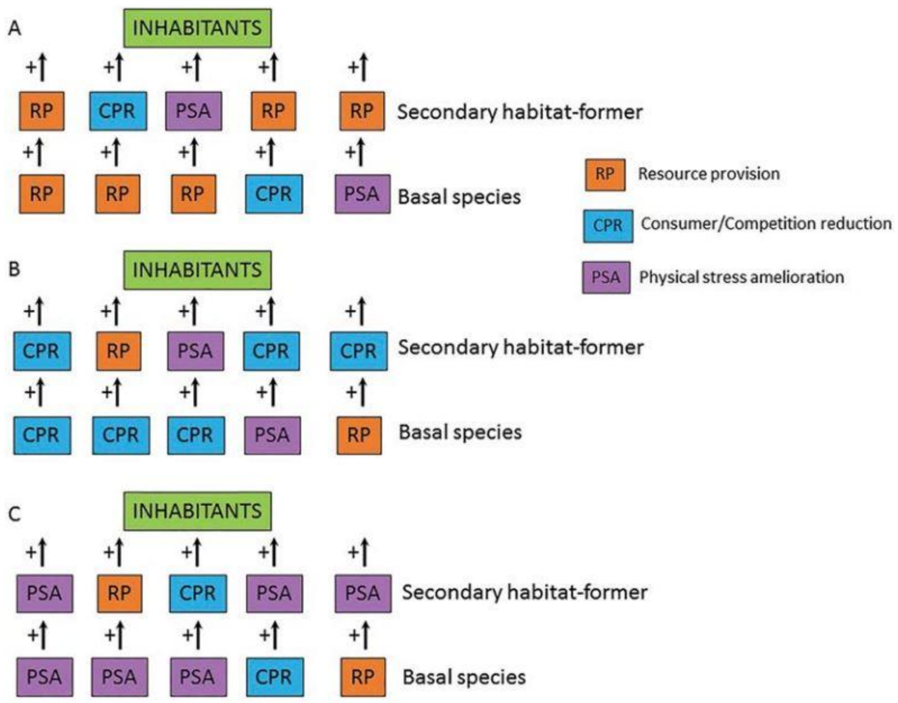

Figure 1.- Possible combinations of facilitation processes, in a three-level facilitation cascade. In our study, rhodoliths will act as RP (resource provision) while macroalgae can act in each of the three possible ways to subsequent inhabitants (a,b or c). (From Gribben et al., 2019).

There are three mechanisms by which a foundation species can act as a facilitator (Figure 1); (1) biotic stress amelioration, (2) physical stress amelioration and (3) resource provisioning. These mechanisms are not independent and, in many cases, occur simultaneously (Gribben et al. 2019). In our study case, rhodolith beds provide physical substrate (resource provisioning) to macroalgae, which act as a secondary facilitator for other organisms, through these mechanisms.

In the Canary Islands, where rhodolith beds are widespread, there is limited research on their role in enhancing biodiversity and the mechanisms behind this process (Otero-Ferrer et al., 2019; Rebelo et al., 2018). Moreover, studies conducted to date in the Canary Archipelago have been limited to only one site in Gran Canaria (Gando Bay) (Navarro-Mayoral et al., 2020; Otero-Ferrer et al., 2019, 2020; Pérez-Peris et al., 2023; Sánchez-Latorre et al., 2020). This study is the first encompassing the whole archipelago, including a variety of oceanographic and biotic conditions.

Rhodoliths can enhance biodiversity indirectly through facilitation cascades and directly via their life traits—fundamental physical and biological characteristics such as vitality (the proportion of living rhodoliths), sphericity, and size in our case—which influence the related biodiversity (Amado-Filho et al., 2010; Bahia et al., 2010; Steller et al., 2003).

2.-OBJECTIVES

The main goal of the present study was to determine whether predictors describing life traits (size, shape, vitality) of rhodoliths (primary facilitator) and the presence of the secondary facilitator (wet weight of epiphytic load) affected abundances and biomasses of a range of invertebrate taxonomic groups. We hypothesize that each predictor will have varying effects on the analysed groups, but the presence of epiphytes will have a consistent and stronger effect across all groups, indicating that the facilitation cascade is the dominant process in the ecosystem

3-MATERIAL AND METHODS

3.1.-Study area and sample collection

Rhodolith samples were collected from five different locations across the Canary Islands (Figures 2 and 3, Table 1 S), with two locations representing both the central and eastern islands, and one location from the westernmost islands, to capture the diverse geological, oceanographic, and ecological conditions where rhodolith beds are distributed throughout the archipelago.

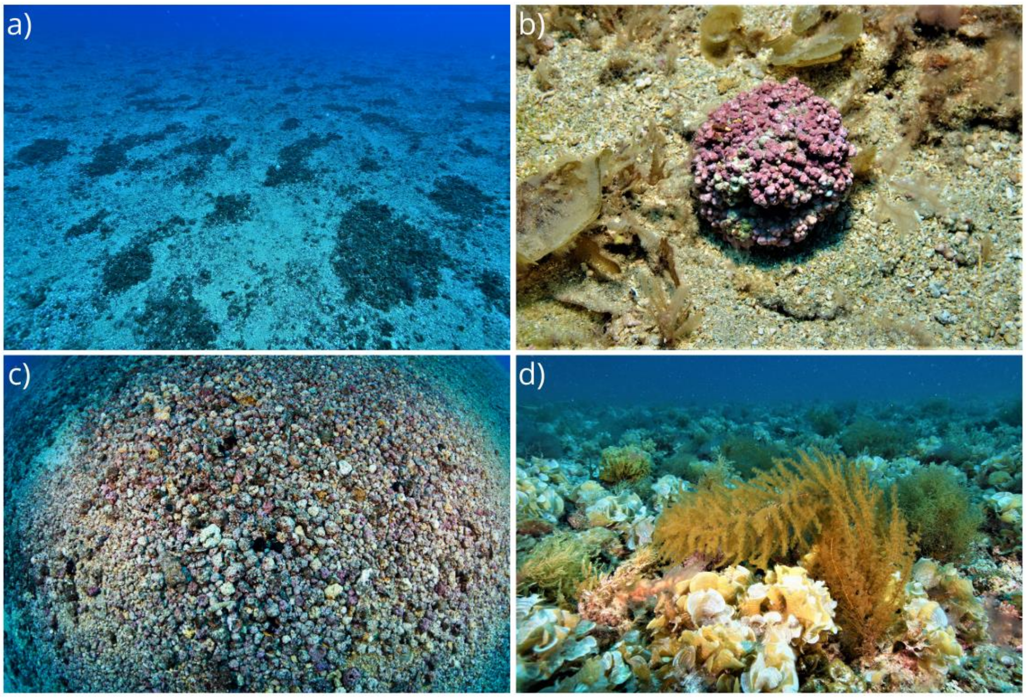

Figure 2: (a) Sparse rhodolith bed in a sandy bottom. (b) Living rhodolith (*Phymatolithon spp*). (c) Dense rhodolith bed. (d) Rhodoliths acting as primary facilitators for brown algae (*Padina pavonica* and *Sporochnus pedunculatus*).

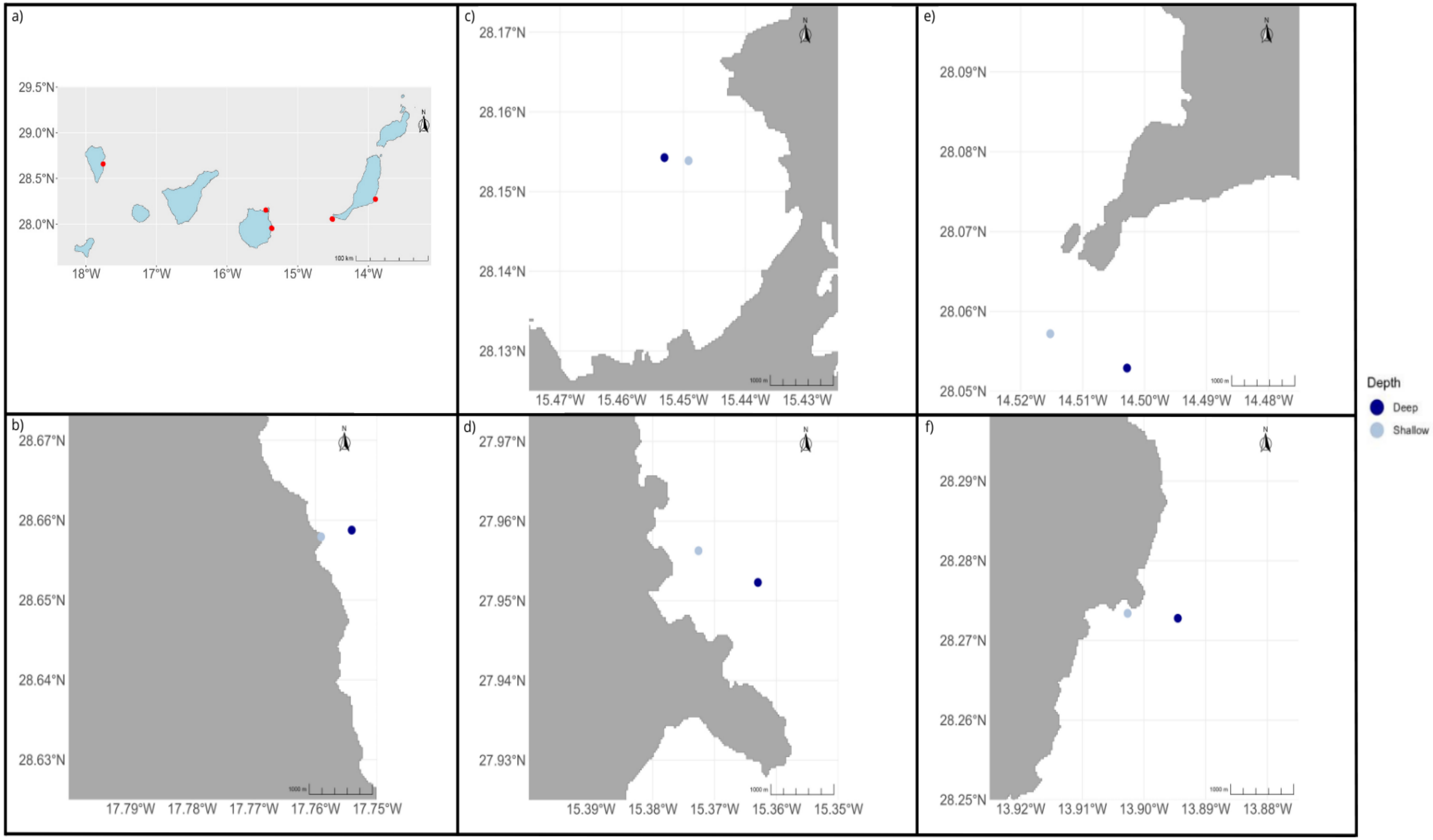

Figure 3: (a) Map of the Canarian Archipelago and (from west to east) locations sampled, including: (b) Guincho (La Palma), (c) Confital (Gran Canaria), (d) Tufia (Gran Canaria), (e) Punta Jandía (Fuerteventura), (f) Jacomar (Fuerteventura).

The eastern islands, Lanzarote and Fuerteventura, are characterized by their proximity to the African coast and therefore, under the influence of the northwest Aftrican upwelling, resulting in a 2°C average sea surface temperature (SST) difference relative to the western islands (El Hierro and La Palma), which experience more tropical (warmer) conditions with more oligotrophic waters (Davenport et al., 2002). Tenerife and Gran Canaria, the central islands, exhibit mixed conditions along this gradient.

The eastern and central islands are typically older (ca. 10 to 20 m.y.) and have wider insular shelves, in contrast to the younger, western, islands (< 2 m.y.), which are characterized by steeper profiles and reduced shelfs due to the lack of long-term exposure to the erosional processes that have modified the older islands (Mitchell et al., 2003).

The sampling strategy was stratified, at each of the 5 locations, by considering two depth levels, namely "shallow" and "deep" strata, based on the distributional bathymetric range of each rhodolith bed, initially mapped using a remotely operated vehicle (ROV), Chasing M2.

Each location and depth strata, samples were collected by hand using a 25x25 cm quadrat, deployed five times (n=5) by scientific SCUBA divers. After collection, the samples were immediately frozen at -15°C to preserve their integrity until further analysis. All field sampling took place in April and May 2023.

The rhodolith beds exhibited differences in their depth distribution, with deeper beds from the central (Gran Canaria) and westmost islands (La Palma), relative to the shallowest rhodolith beds from the eastmost island Fuerteventura (Figure 6).

3.2.-Sample processing

After defrosting, each sample was washed with freshwater and filtered through a 0.5 mm sieve to separate fauna from rhodoliths, associated epiphytes, sediment, and occasional human debris as in Navarro-Mayoral et al. (2020), Otero-Ferrer et al. (2020) and Pérez-Peris et al. (2023). Then, 30 rhodoliths were randomly selected from each sample, and the shortest, intermediate, and longest axis diameters were measured with a calliper and classified following the criteria established by Sneed & Folk, (1958). Subsequently, these measurements were entered into the TRIPLOT spreadsheet developed by Graham & Midgley (2000) to classify each rhodolith nodule according to three shape categories: spheroidal, discoidal and ellipsoidal. Sphericity was considered broadly, including spheroid-intermediate forms adjacent to "Spheric" in the ternary plot (Figure 3S).

Each rhodolith was also classified, based on surface coloration into “Alive” (>80% pink surface), “Intermediate” (20-80% pink), and “Dead” (<20% pink) vitality categories (Figure 4). Afterwards, rhodoliths were first weighed for wet weight, then oven-dried at 60ºC for 48 hours, and re-weighed again to obtain their dry weight. The rest of rhodoliths for each sample, were also wet and dry-weighted.

Epiphytes were manually picked from the samples. Most of them were already detached from the rhodoliths, but in other cases it was necessary to separate them. Most epiphytes were brown algae, and belonged to *Cystoseira spp.*, *Lobophora spp.* and *Padina spp*. There were smaller amounts of filamentous green and red algae, but irrelevant in terms of total weight.

A total of 1,387 rhodoliths were classified, as not all samples reached the intended target of 30, particularly those from Fuerteventura (Jacomar and Punta Jandía) (Table 5S). Moreover, one replicate of Confital had to be excluded from the analysis due to laboratory complications, leaving a total of 49 viable samples.

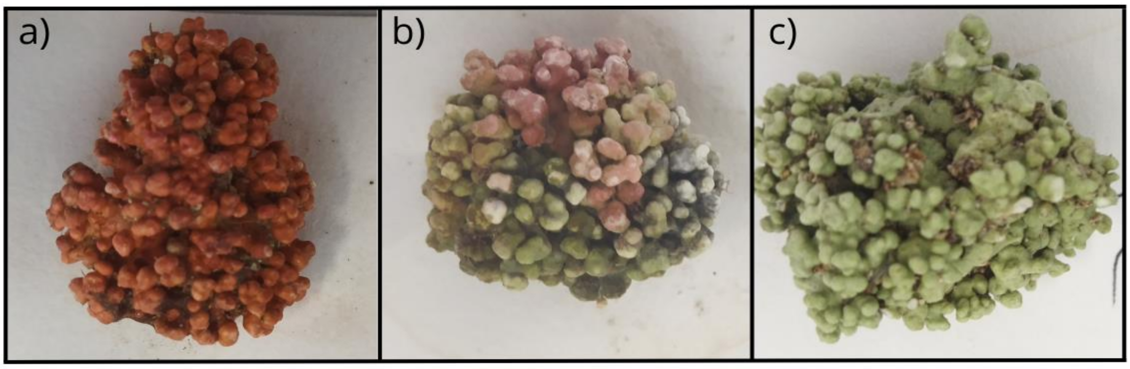

Figure 4: Examples of vitality status. (a) Alive, (b) Intermediate and (c) Dead.

Remaining sediment and epifauna were then carefully transferred to petri dishes for detailed examination under a magnifying glass. Organisms were initially classified into ten broad groups (Operational Taxonomic Units, OTUs): Amphipoda, Tanaidacea, Decapoda, Brachyura, Isopoda, Amphipoda, Echinodermata, Actinopterygii, Polychaeta and Mollusca. Although Mollusca is an infraorder belonging to Decapoda, it was considered individually as its visual identification is easy, and there are works addressing brachyuran abundances in rhodoliths beds (Sánchez-Latorre et al., 2020). After counting, the biomass (wet weight) of individuals for each OTU was obtained by weighting organisms using a precision scale Shimadzu AW120.

3.3.-Statistical Analysis

Taxonomic groups that did not reach at least a 1% threshold for both the total abundance and total biomass were discarded of subsequent analysis (Isopoda, Tanaidacea, Picnogonida, Echinodermata, and Actinopterygii) (Table 2S). The first four groups had low values for both categories, but Echinodermata comprised 34.29% of the total biomass, while remaining <1% in abundance (Table 2S). This was due to the presence to outlier individuals with weights over 8 g and 22 g respectively.

To ascertain the most relevant environmental and habitat-structure drivers of faunal abundances and biomasses (abundance and biomass for the 10 taxonomic groups considered below, in addition to the total faunal abundance and total biomass), 23 potential predictors (Table 3S) were initially considered.

To reduce the number of predictors, we initially tested for pairwise correlation and multicollinearity using the "corrplot" R library (Wei and Simko, 2017). Variables correlated (> 0.6 Pearson correlation) were then discarded (Figure 1S), while maintaining ecologically meaningful relationships, resulting in a comprehensive set of five uncorrelated predictive variables (Figure 2S). These predictors encompass the main structural characteristics of each rhodoliths, i.e., the basal facilitator, including: vitality and sphericity altogether with their mean longest dimension, referred as "Size"; and shape per sample, the presence of secondary facilitators (quantified via the total wet weight of epiphytes), and an environmental driver (depth).

Generalized Linear Models (GLMs) were fitted to each response variable, by means of a "negative binomial" (NB) family for abundance (count) data, due to overdispersion resulting from the large presence of zeros. For biomasses, the "gamma" and "tweedie" families were selected (Table 2S). Models with a "tweedie" and NB distribution families were implemented using the "glmmTMB" (Brooks et al., 2017) and "MASS" R packages respectively (Venables and Ripley, 2013).

Models were selected based on their Akaike Information Criterion (AIC), obtained first for the full model and then for various models including different subsets of predictors using the "MuMin" R library (Barton, 2009). Models with different subsets of predictors were ranked based on their AIC and averaged according to this criterion, to finally obtain the estimates and significance of each predictor for any given response. The data met the assumptions of the models, and diagnostic plots of residuals, including Q-Q plots, were visually inspected to assess their appropriateness.

4.-RESULTS

4.1.-Distribution and structure of rhodolith beds

The size of rhodoliths, in terms of the longest axis, varied across locations and depths, (Figure 5, Table 4S). The largest average size was recorded at Guincho (40 m) with an average size of 5.64 cm, followed by Punta Jandía (22 m), with an average of 4.09 cm.

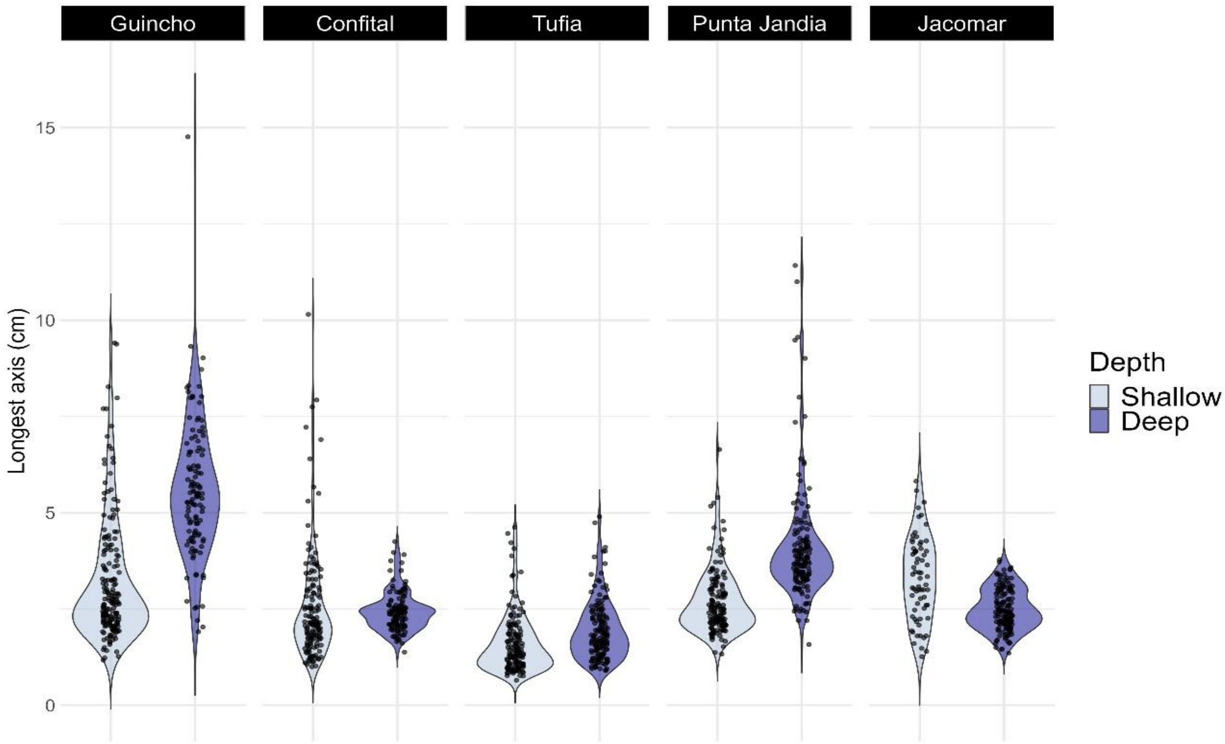

Figure 5. Size (longest axis, cm) of rhodoliths at each depth and location ordered from west (Guincho) to east (Jacomar).

We found considerable variability in the vitality states of rhodoliths across locations and depths (Figure 6). A total of 42.68% of the 1,387 rhodoliths were alive, while 38.93% were dead and 18.38% were intermediate (Figure 4, Table 5S).

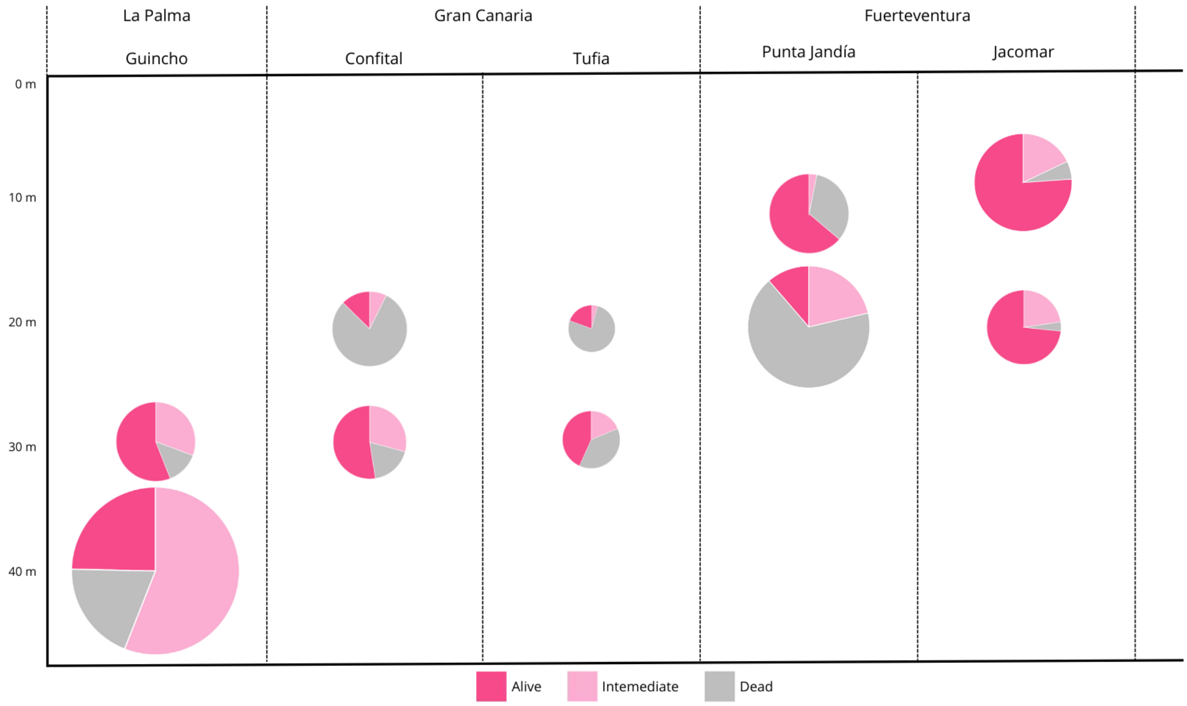

Figure 6. Proportion of the three vitality states of rhodoliths from each location and depth bed. The size of circles is scaled based on the mean longest axis. Locations are arranged from west (left) to east; (right) across the Canary Islands.

Most rhodoliths presented intermediate forms (Figure 3S). The highest percentages of sphericity were reported in Punta Jandía deep strata with 38%, and in Guincho with 35,33%. Locations with the lowest sphericity were at Jacomar deep strata with 13.33%, and Punta Jandía shallow, with 10.66%. The rest of the values oscillated around 20 (Table 6S).

Finally, a total of 587 g of epiphytic macroalgae were found, mainly *Cystoseira spp*, *Lobophora spp* and *Padina spp* (Table 7S). Most of them (94%) were found in Punta Jandía and Tufia, while reduced amounts were found in the other locations, with the exception of Jacomar, where no epiphytes were retrieved.

4.2.-Epifauna

In total, 11,222 organisms were found, weighing a total of 107.03 g (Tables 2S, 8S and 9S) and including 10 dominant taxonomic groups. Mollusca was the most abundant OTU, with 6,007 individuals, followed by Amphipoda (3,438) and Decapoda (686). In terms of biomass, Mollusca was also the dominant group, accounting for 46.51 % of the total biomass, followed by Echinodermata (34.29 %) and Brachyura (6.50 %).

Mollusca had a higher presence in detrital beds characterized by sediment and dead rhodoliths such as Tufia, compared to sites dominated by large, living rhodoliths with associated epiphytes like Punta Jandía (Tables 8S and 9S).

All predictors exhibited significant effects on the abundance of different taxonomic groups (Table 10S, Figure 8), with the exception of sphericity. Vitality showed a significant negative effect for Mollusca and Amphipoda abundance, and a less significant—but still negative—effect on total abundance (Table 10S, Figure 8). Size had a negative effect for Mollusca and the total epifaunal abundance (Table 10S, Figure 8).

Depth displayed a positive effect in Mollusca and negative in Amphipoda (Table 10S, Figure 8). The epiphytic load had a significant positive effect on Decapoda, Amphipoda and Brachyura, being the only predictor that consistently showed a positive effect across most of the groups (Table 10S, Figure 8).

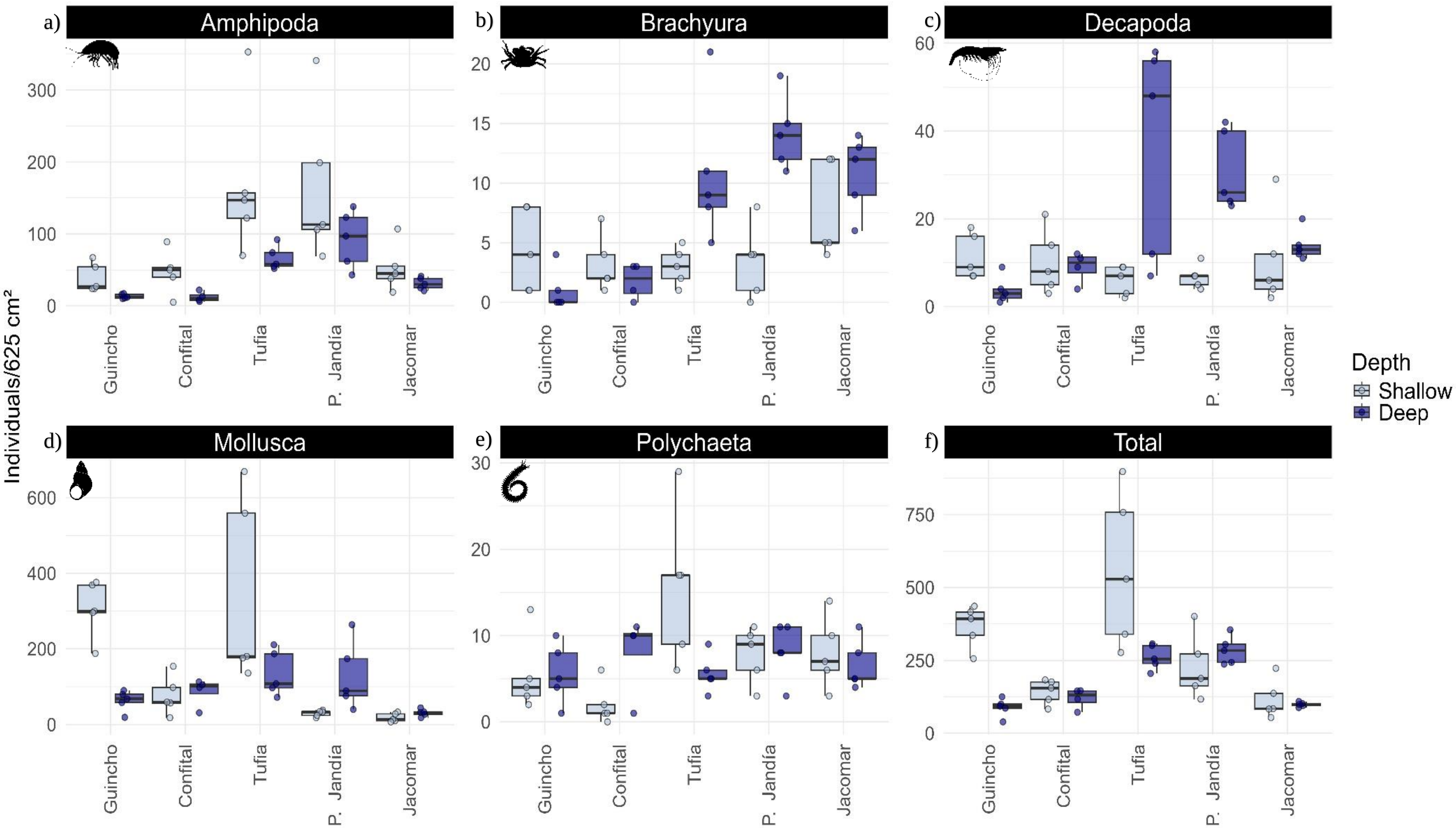

Figure 7.- Abundances in number of individuals per sample at each locality and depth for (a) Amphipoda, (b) Brachyura, (c) Decapoda, (d) Mollusca, (e) Polychaeta and (f) Total Abundance.

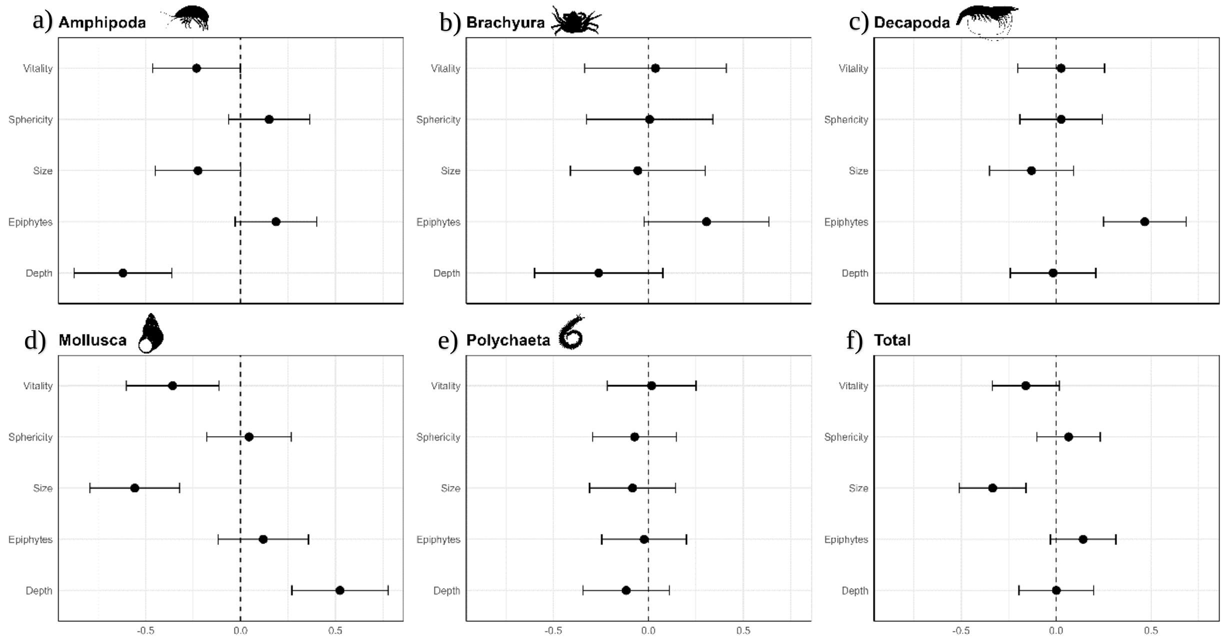

Figure 8.- Effect of the predictors on faunal abundances in (a) Amphipoda, (b) Brachyura, (c) Decapoda, (d) Mollusca, (e) Polychaeta and (f) Total Abundance.

All predictors showed significant effects on the different groups biomasses, with the exception of vitality (Table 11S, Fig.10). Sphericity positively affected Amphipoda and total biomass. Size showed mixed effects, being significantly positive for Brachyura and Decapoda, while almost-significant but negative for Polychaeta and Mollusca. The epiphytic load was the most important predictor, with significant positive effects over the biomasses of Brachyura and Decapoda, and total epifaunal biomass. Lastly, Depth showed a highly significant and negative effect on Amphipoda and brachyuran biomasses.

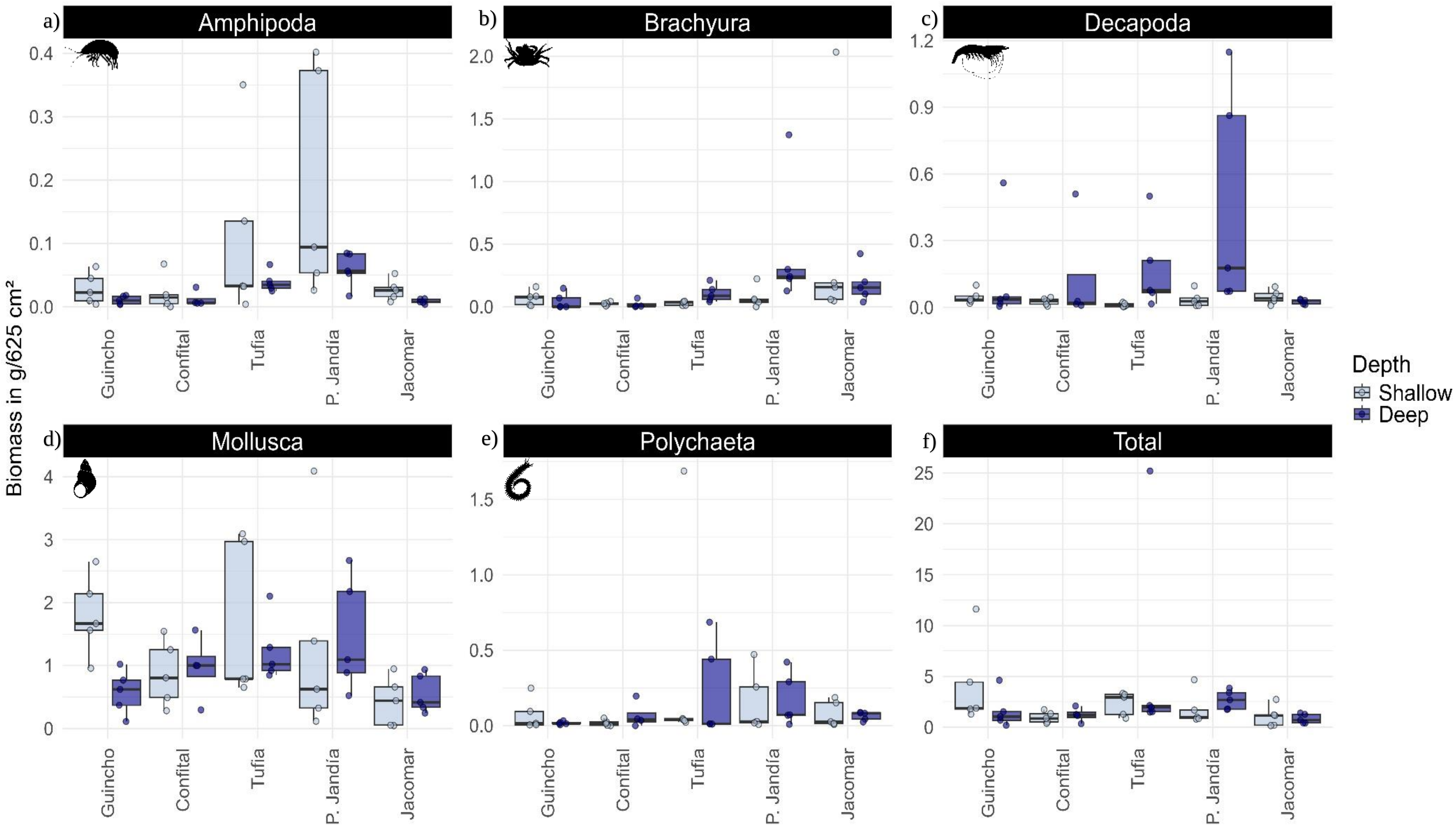

Figure 9.-Biomass in g of individuals per sample at each locality and depth for (a) Amphipoda, (b) Brachyura, (c) Decapoda, (d) Mollusca, (e) Polychaeta and (f) Total biomass.

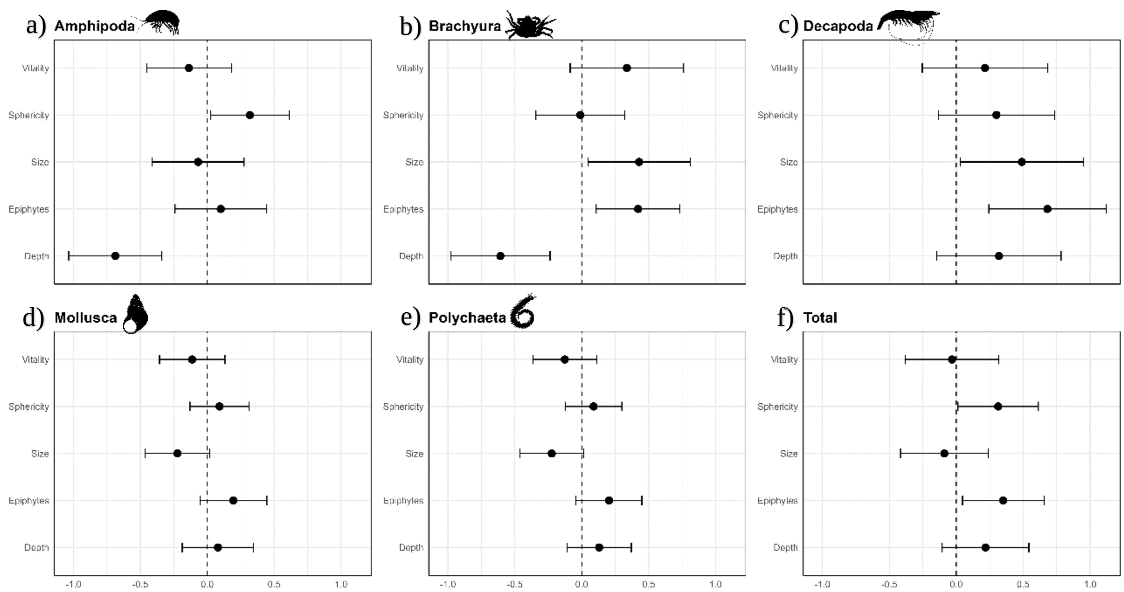

Figure 10.- Effect of predictors on faunal biomasses in (a) Amphipoda, (b) Brachyura, (c) Decapoda, (d) Mollusca, (e) Polychaeta and (f) Total biomass.

5.-DISCUSSION

Our results indicate that facilitation cascades are relevant driving forces in rhodolith beds, where rhodoliths act as a primary facilitator for epiphytic macroalgae, which act as secondary facilitators. This process affects each taxonomic groups differently and operates simultaneously with life-trait effects, although it generally shows a stronger influence on the community, especially in terms of biomass.

5.1.-Life trait effects

The effect of these predictors (size, vitality and sphericity) varied across different groups showing positive and negative effects on the different groups, as well as depth.

Size had an ambivalent effect, with a negative impact on the abundance of some groups (Mollusca, Amphipoda and total faunal abundance), while having a positive effect on others, specifically in terms of biomasses (Brachyura and Decapoda). Rhodolith size and morphology are strongly influenced by physical factors (Amado-Filho et al., 2010), and it has an effect in the associated biodiversity. This can be seen in the beds from Gran Canaria, (Confital and Tufia), which share a similar depth, size, vitality and sphericity.

These sites, dominated by small, dead rhodoliths, resemble mäerl beds (loose, fragmented deposits of calcified algae) rather than proper rhodolith beds with larger, rounded individuals. Molluscs thrive in such habitats (Hall-Spencer, 1998), while high amphipod abundance is related to the detrital characteristics of these sites, influenced by currents in Confital and nearby fish farms in Tufia (Fernandez-Gonzalez et al., 2021; Navarro-Mayoral et al., 2020).

Conversely, the positive effect of rhodolith size on brachyurans and decapods is due to the increased complexity and interstitial spaces provided by larger rhodoliths (Sánchez-Latorre et al., 2020).

Vitality showed a significant negative effect on Amphipoda and Mollusca, consistent with the observation that these groups are more numerous in beds dominated by dead rhodoliths, such as Tufia and Confital. Although living, big, rounded rhodoliths are appealed as better primary facilitators, dead rhodoliths can also sustain facilitation cascades (Saldaña et al., 2024).

Sphericity significantly affected Amphipoda and total faunal biomass. Increased sphericity is associated with higher faunal diversity (Sciberras et al., 2009), as it enhances spatial complexity, modifies food availability by trapping sediments for detritivores, and provides shelter (Bulleri et al., en prensa; Otero-Ferrer et al., 2019). High sphericity, increasing interstitial space, benefits not only amphipods but also overall faunal abundance.

5.2.-Depth

Depth was the only physical variable considered, as it influences other factors such as light availability, sedimentation, temperature, and wave energy. This interrelationship makes depth a suitable environmental proxy for comparing abiotic conditions´ effects. Moreover, its effect in rhodolith life traits and its habitat structure have been already studied (Amado-Filho et al., 2010; Navarro-Mayoral et al., 2020; Otero-Ferrer et al., 2020; Sánchez-Latorre et al., 2020; Veras et al., 2020).

Depth had a negative effect in Amphipoda biomass and abundance, and in brachyuran biomass. Previous studies have documented a higher abundance in amphipods and brachyurans between 18-25 m in the Canary Islands (Navarro-Mayoral et al., 2020; Sánchez-Latorre et al., 2020), which is concordant with this negative effect in the depth range of the study (8-40 m). The reasons for this abundance and biomass enhancement are varied, and related to the abiotic conditions effect in the rhodolith beds (optimal light availability, sedimentation and wave energy); and to the abovementioned groups. This abiotic characteristics are also the most optimal for epiphytes to grow, which also points out the occurrence of the facilitation cascades in this environments (Navarro-Mayoral et al., 2020; Sánchez-Latorre et al., 2020).

5.3.-Epiphytic load

The epiphytic load (wet weight of epiphytes per sample in grams) was selected as the driver to quantify the role of rhodolith as basal facilitators, and determine the occurrence of habitat cascades. From the 5 sampling locations, epiphytes were only found recurrently in Tufia and Punta Jandía, and in smaller amount, in Guincho and Confital.

Although the presence of epiphytes has already been associated with rhodolith size and depth (Navarro-Mayoral et al., 2020; Otero-Ferrer et al., 2019; Sánchez-Latorre et al., 2020), in our work there was no correlation between these variables.

Moreover, the epiphytic load was one of the less correlated predictor from the original set of predictors, what points out the high variability across the study sites. This also indicates that epiphyte presence may be related to other life traits, as they play a pivot role in the basal facilitation (Bishop et al., 2013), or to abiotic factors such as proximity to rocky bottoms.

Contrarily to life traits or depth effects, the epiphytic load only showed a positive effect, ranging from no significant (Mollusca), to highly significant (Decapoda). For most groups (Amphipoda, Brachyura, Decapoda), epiphytic load was the predictor with a highest effect and significance and also for total faunal biomass, arising as the major driving force from the set of predictors considered.

The positive correlation between epiphytic algae and invertebrate abundance has been already been described for these groups in the Canary Islands, (Navarro-Mayoral et al., 2020; Otero-Ferrer et al., 2019; Sánchez-Latorre et al., 2020), but not from the perspective of facilitation cascades. This effect had an influence in abundance (number of individuals) and richness (number of taxa), but in our study it was tested as a driver for biomass, where it showed a stronger effect. This suggest that facilitation cascades can promote biodiversity in different ways, either favouring biodiversity or sustaining a higher biomass.

5.4.-Quantifying facilitation cascades

There have been other works where the process of facilitation has been empirically tested in a context of a facilitation cascade (Angelini and Silliman, 2014; Bishop et al., 2013), through manual manipulation of organisms (e.g., oak trees and mangroves). In contrast, our study used the natural heterogeneity of ecosystems to test our hypothesis.

The comparative analysis of the impact of life traits, depth, and facilitation cascades (through epiphytic load) on the various taxonomic groups reveals distinct responses. Specifically, polychaetes were unaffected by these factors, molluscs were influenced by life traits and depth, amphipods were impacted by a combination of life traits, depth, and facilitation cascades, and decapods and brachyurans are primarily driven by the hierarchical effects of facilitation cascades.

The role of the latter, as predators of grazing species, occasionally helps structuring the ecosystem via trophic cascades, contributing to the maintenance of algal communities, in ecosystems where facilitation cascades are likely to occur (kelp forests) (Boudreau and Worm, 2012). So, it is possible that both processes can happen simultaneously and be inter-dependent, or at least offers a coherent explanation on why these groups were the most affected by the facilitation cascades.

6.-CONCLUSSIONS

Rhodoliths are well-documented bioengineers, although the specific mechanisms by which they enhance biodiversity remain underexplored. This enhancement can occur through various pathways, either determined by the own life traits of rhodoliths, or by the hierarchical ecological process of facilitation cascades. In these cascades, rhodoliths provide substrate for epiphytic macroalgae, which subsequently offer additional substrate and resources for other organisms, thereby structuring the ecosystem. The different taxonomic groups studied had different responses to rhodoliths life traits and epiphytic presence, determined by their role in the ecosystem. Among the five taxonomic groups studied, Brachyura and Decapoda, followed to a lesser extent by Amphipoda, were most influenced by facilitation cascades. In contrast, molluscs were primarily affected by life traits and abiotic conditions, while polychaetes showed no significant response to any of the studied factors.

These results underscore the importance of rhodolith beds, and the complex ecological process operating underneath. Although awareness of these ecosystems is increasing, significant gaps in understanding persist, necessitating further research to fully grasp the complexities of this widespread habitat.

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SUPPLEMENTARY MATERIAL

Group	Island	Location	Latitude	Longitude	Depth (m)	Strata
West	La Palma	Guincho	28.65792 N	17.75909 W	32	Shallow
West	La Palma	Guincho	28.65876 N	17.75412 W	40	Deep
Central	Gran Canaria	Confital	28.153883 N	15.449183 W	21	Shallow
Central	Gran Canaria	Confital	28.154267 N	15.453083 W	31	Deep
Central	Gran Canaria	Tufia	27.956283 N	15.3726 W	21	Shallow
Central	Gran Canaria	Tufia	27.952299 N	15.363 W	31	Deep
East	Fuerteventura	Jacomar	28.272783 N	13.894517 W	22	Deep
East	Fuerteventura	Jacomar	28.2734 N	13.90265 W	8	Shallow
East	Fuerteventura	Punta Jandía	28.0572 N	14.515233 W	12	Shallow
East	Fuerteventura	Punta Jandía	28.0529 N	14.502833 W	22	Deep

Table 1S. Coordinates and depth for each sampling location and depth strata.

	Abundance	Biomass	Family Abundance	Family Biomass
Amphipoda	3438	2.5244	NB	Gamma
	30.64%	2.20%		
Brachyura	299	7.46208	NB	Tweedie
	2.66%	6.50%		
Isopoda	190	0.1793	-	-
	1.69%	0.16%		
Tanaidacea	136	0.0384	-	-
	1.21%	0.033%		
Picnogonida	26	0.0159	-	-
	0.23%	0.014%		
Mollusca	6007	53.3795	NB	Tweedie
	53.53%	46.52%		
Polychaeta	356	6.1605	NB	Tweedie
	3.17%	5.37%		
Echinodermata	76	39.3489	-	-
	0.68%	34.29%		
Actinopterygii	8	0.2644	-	-
	0.07%	0.23%		
Decapoda	686	5.375	NB	Gamma
	6.11%	4.68%		
Total	11222	114.74838	NB	Gamma

Table 2S. Total and relative abundance and biomass of each taxonomic group. The family for the error distributions selected for each GLM are indicated

Variable	Description
Depth	Depth (m)- where sample was taken
N-Alive	Number of living rhodoliths out of the 30 measured
WW-Alive	Wet weight of living rhodoliths
DW-Alive	Dry weight of living rhodoliths
N-Dead	Number of dead rhodoliths out of the 30 measured
WW-Dead	Wet weight of dead rhodoliths
DW-Dead	Dry weight of dead rhodoliths
N-Intermediate	Number of intermediate rhodoliths out of the 30 measured
WW-Intermediate	Wet weight of dead rhodoliths
DW-Intermediate	Dry weight of dead rhodoliths
WW-Rest	Wet weight of the rest of the sample
DW-Rest	Dry weight of the rest of the sample
WW-Epiphytes	Wet weight of the epiphytes sampled
DW-Epiphytes	Dry weight of epiphytes
Mean-Longest	Mean value for the longest axis in the sample
Mean-Intermediate	Mean value for the intermediate axis
Mean-Shortest	Mean value for the shortest axis
S/L	Sphericity measure. Ratio between the shortest and longest axis
LI/LS	Sphericity measure. Ratio between axes products
Percentage alive	Percentage of living rhodoliths in the sample, out of the 30 measured.
(S^2/LI)^1/3	Sphericity measure. Ratio between different axes combinations.
Sphericity	Percentage of spherical rhodoliths
Total Biomass WW rhodoliths	Total weight of rhodoliths sampled. Equals to Alive+Intermediate+Death+Rest

Table 3S. Description of original set of predictors typing the structure and environment of each sample.

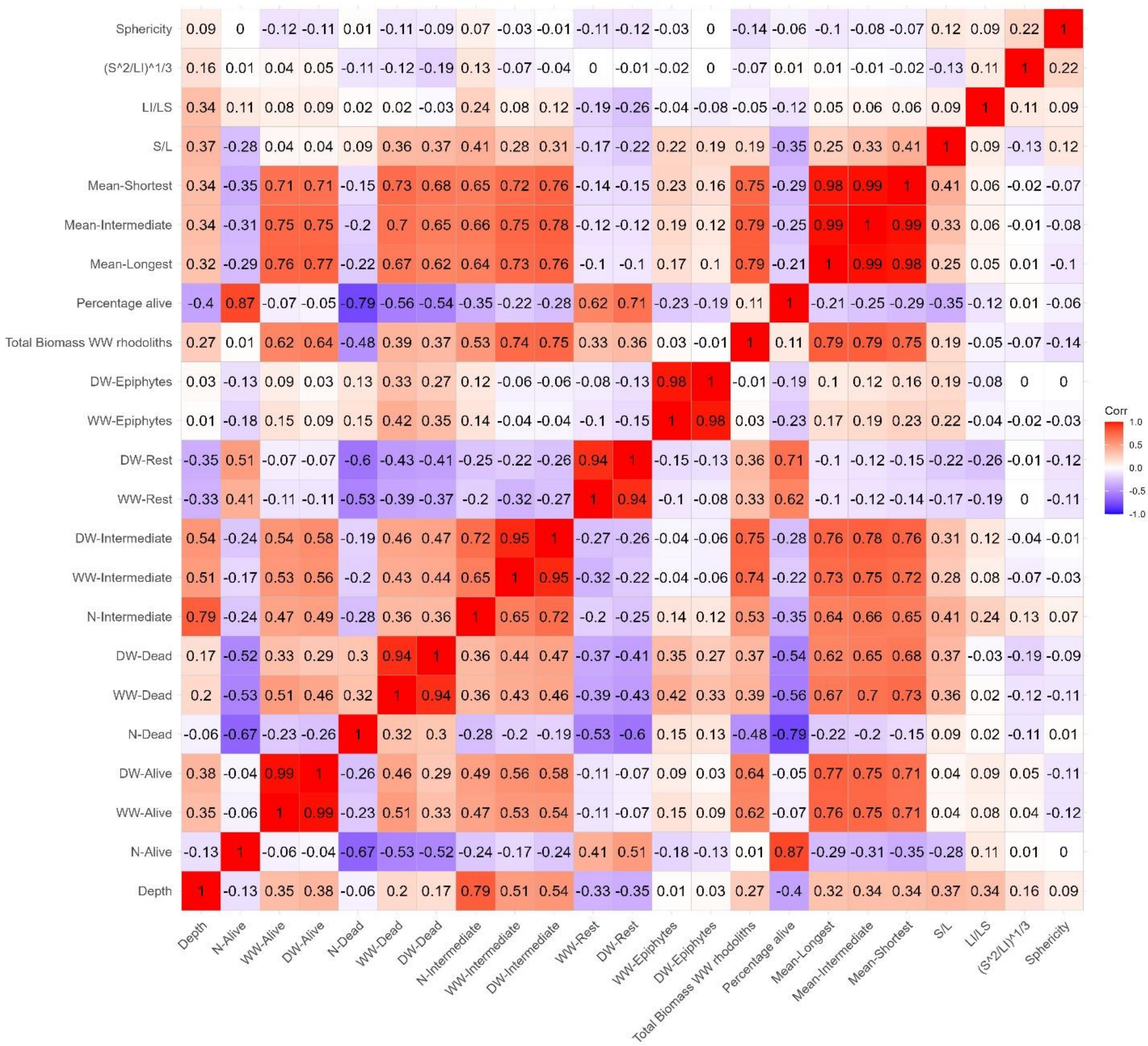

Figure 1S. Correlations (Pearson product moment) between each pair of predictors.

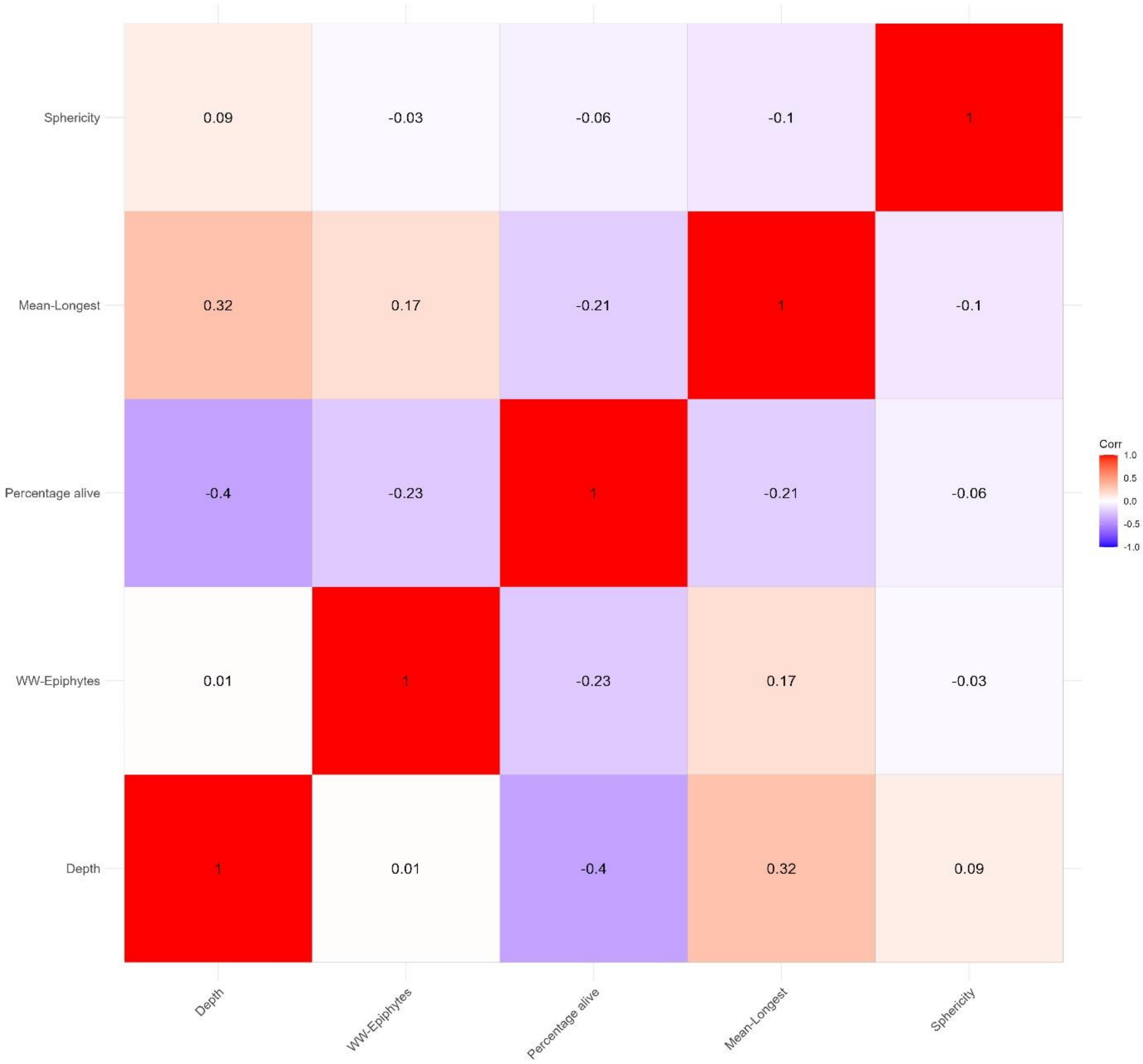

Figure 2S. Pairwise correlations between each pair of the final set of predictors.

Location	Depth (m)	Average Size
Guincho	32	3.23
Guincho	40	5.64
Tufia	21	1.59
Tufia	31	1.93
Confital	21	2.53
Confital	31	2.34
Punta Jandía	12	2.69
Punta Jandía	22	4.09
Jacomar	8	3.19
Jacomar	22	2.48

Table 4S. Average size by site and depth

Site	Replica	Strata	Depth	Total N	Alive N	% Alive	Inter. N	% Inter.	Dead N	% Dead
Guincho	1	Shallow	32	150	84	56.00	46	30.67	20	13.33
Guincho	2	Deep	40	150	37	24.67	84	56.00	29	19.33
Confital	2	Shallow	21	150	19	12.67	11	7.33	120	80.00
Confital	1	Deep	31	120	63	52.50	35	29.17	22	18.33
Tufia	2	Shallow	21	149	29	19.46	6	4.03	114	76.51
Tufia	1	Deep	31	150	65	43.33	28	18.67	57	38.00
Punta Jandía	2	Shallow	12	94	60	63.83	3	3.19	31	32.98
Punta Jandía	1	Deep	22	150	17	11.33	32	21.33	101	67.33
Jacomar	1	Shallow	8	67	51	76.12	12	17.91	4	5.97
Jacomar	2	Deep	22	150	110	73.33	34	22.67	6	4.00

Table 5S. Count and percentage of each vitality status per sample.

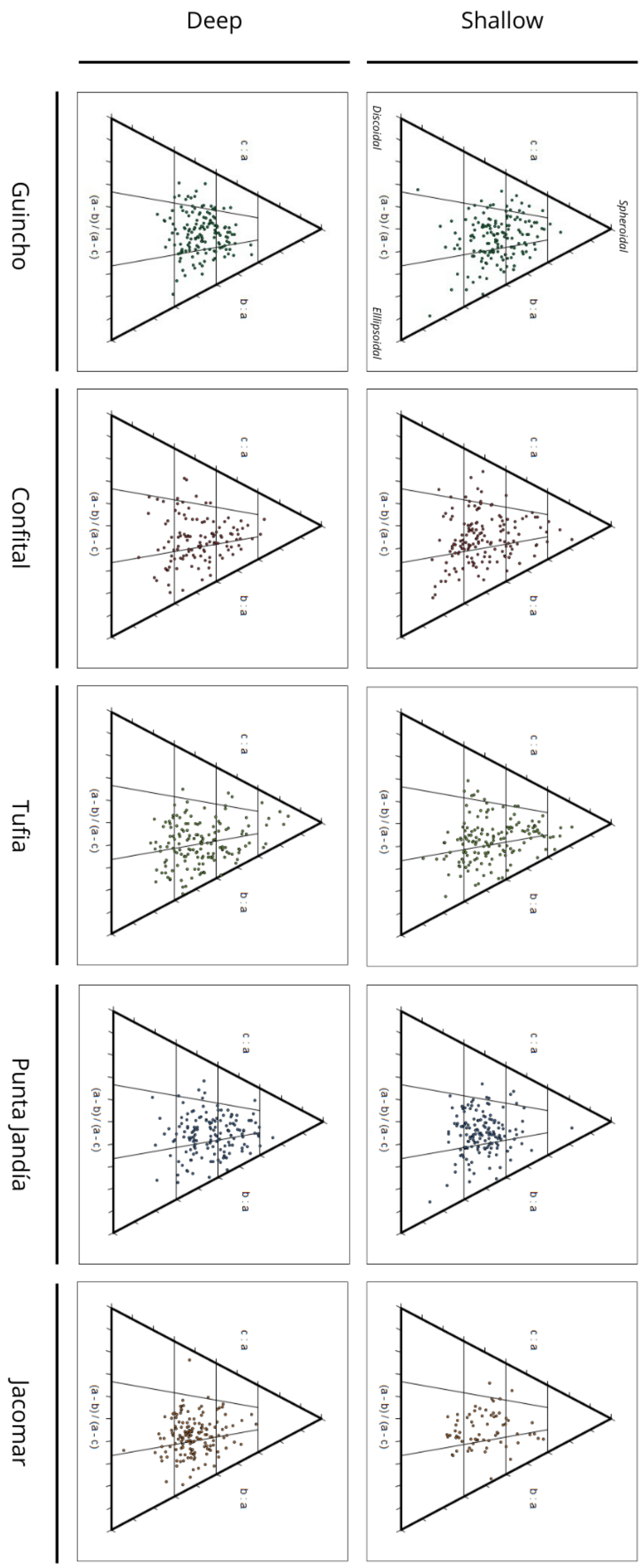

Figure 3S. Ternary diagram showing deviation in the shape of rhodoliths collected at each depth stratum per location. Classification into three shape categories: spheroidal, discoidal and ellipsoidal was carried out based on the proportion between the different axes, representing "a" the largest, "b" the intermediate, and "c" the shortest

Location	Replicate	Stratum	Depth (m)	%Sphericity	Average by site
Confital	1.2	Deep	31	20	23.33
Confital	1.3	Deep	31	30	
Confital	1.4	Deep	31	30	
Confital	1.5	Deep	31	13.33	
Confital	2.1	Shallow	21	20	18.67
Confital	2.2	Shallow	21	16.67	
Confital	2.3	Shallow	21	23.33	
Confital	2.4	Shallow	21	10	
Confital	2.5	Shallow	21	23.33	
Guincho	1.1	Shallow	30	53.33	35.33
Guincho	1.2	Shallow	30	33.33	
Guincho	1.3	Shallow	30	43.33	
Guincho	1.4	Shallow	30	23.33	
Guincho	1.5	Shallow	30	23.33	
Jacomar	1.1	Shallow	8	23.53	14.32
Jacomar	1.2	Shallow	8	16.67	
Jacomar	1.3	Shallow	8	8.33	
Jacomar	1.4	Shallow	8	15.38	
Jacomar	1.5	Shallow	8	7.69	
Jacomar	2.1	Deep	22	20	13.33
Jacomar	2.2	Deep	22	6.67	
Jacomar	2.3	Deep	22	0	
Jacomar	2.4	Deep	22	16.67	
Jacomar	2.5	Deep	22	23.33	
Punta Jandía	1.1	Deep	22	43.33	38
Punta Jandía	1.2	Deep	22	33.33	
Punta Jandía	1.3	Deep	22	36.67	
Punta Jandía	1.4	Deep	22	40	
Punta Jandía	1.5	Deep	22	36.67	
Punta Jandía	2.1	Shallow	12	10	10.66
Punta Jandía	2.2	Shallow	12	6.67	
Punta Jandía	2.3	Shallow	12	10	
Punta Jandía	2.4	Shallow	12	13.33	

Punta Jandía	2.5	Shallow	12	13.33	
Tufia	1.1	Deep	31	16.67	26
Tufia	1.2	Deep	31	10	
Tufia	1.3	Deep	31	30	
Tufia	1.4	Deep	31	40	
Tufia	1.5	Deep	31	33.33	
Tufia	2.1	Shallow	21	40	30.66
Tufia	2.2	Shallow	21	23.3	
Tufia	2.3	Shallow	21	30	
Tufia	2.4	Shallow	21	20	
Tufia	2.5	Shallow	21	40	
Guincho	2.1	Deep	40	20	20.66
Guincho	2.2	Deep	40	26.67	
Guincho	2.3	Deep	40	23.33	
Guincho	2.4	Deep	40	13.33	
Guincho	2.5	Deep	40	20	

Table 6S. Sphericity measures of each sample from each location and depth

Island	Location	Stratum	Depth (m)	Epiphyte Wet Weight in grams
La Palma	Guincho	Shallow	30	0
La Palma	Guincho	Shallow	30	0
La Palma	Guincho	Shallow	30	0
La Palma	Guincho	Shallow	30	0
La Palma	Guincho	Shallow	30	0
La Palma	Guincho	Deep	40	0
La Palma	Guincho	Deep	40	0
La Palma	Guincho	Deep	40	0
La Palma	Guincho	Deep	40	0
La Palma	Guincho	Deep	40	8
Gran Canaria	Confital	Shallow	21	0
Gran Canaria	Confital	Shallow	21	0
Gran Canaria	Confital	Shallow	21	0

Gran Canaria	Confital	Shallow	21	0
Gran Canaria	Confital	Shallow	21	5
Gran Canaria	Confital	Deep	31	0
Gran Canaria	Confital	Deep	31	0
Gran Canaria	Confital	Deep	31	0
Gran Canaria	Confital	Deep	31	0
Gran Canaria	Confital	Deep	31	0
Gran Canaria	Tufia	Shallow	21	4
Gran Canaria	Tufia	Shallow	21	3
Gran Canaria	Tufia	Shallow	21	0
Gran Canaria	Tufia	Shallow	21	0
Gran Canaria	Tufia	Shallow	21	0
Gran Canaria	Tufia	Deep	31	98
Gran Canaria	Tufia	Deep	31	20
Gran Canaria	Tufia	Deep	31	47
Gran Canaria	Tufia	Deep	31	17
Gran Canaria	Tufia	Deep	31	5
Fuerteventura	Punta Jandía	Shallow	12	23
Fuerteventura	Punta Jandía	Shallow	12	28
Fuerteventura	Punta Jandía	Shallow	12	0
Fuerteventura	Punta Jandía	Shallow	12	13
Fuerteventura	Punta Jandía	Shallow	12	10
Fuerteventura	Punta Jandía	Deep	22	117
Fuerteventura	Punta Jandía	Deep	22	129
Fuerteventura	Punta Jandía	Deep	22	17
Fuerteventura	Punta Jandía	Deep	22	35
Fuerteventura	Punta Jandía	Deep	22	8
Fuerteventura	Jacomar	Shallow	8	0
Fuerteventura	Jacomar	Shallow	8	0
Fuerteventura	Jacomar	Shallow	8	0
Fuerteventura	Jacomar	Shallow	8	0
Fuerteventura	Jacomar	Shallow	8	0
Fuerteventura	Jacomar	Deep	22	0
Fuerteventura	Jacomar	Deep	22	0

Fuerteventura	Jacomar	Deep	22	0
Fuerteventura	Jacomar	Deep	22	0
Fuerteventura	Jacomar	Deep	22	0

Table 7S: Epiphyte wet weight per sampling location and stratum

Location	Replicate	Amphipoda	Brachyura	Mollusca	Polychaeta	Decapoda	Total
Confital	1.2	6	0	98	1	9	117
Confital	1.3	8	1	113	10	12	145
Confital	1.4	22	3	31	10	4	72
Confital	1.5	13	3	105	11	11	146
Confital	2.1	5	2	154	0	14	176
Confital	2.2	53	1	57	1	3	116
Confital	2.3	50	4	18	2	8	83
Confital	2.4	40	2	98	1	5	155
Confital	2.5	89	7	59	6	21	183
Guincho	1.1	24	1	300	2	7	336
Guincho	1.2	54	1	188	5	7	256
Guincho	1.3	67	8	296	3	18	393
Guincho	1.4	24	8	369	4	9	416
Guincho	1.5	27	4	376	13	16	436
Guincho	2.1	11	0	19	5	2	39
Guincho	2.2	12	0	68	1	3	86
Guincho	2.3	16	4	58	10	1	93
Guincho	2.4	10	0	80	4	4	100
Guincho	2.5	17	1	90	8	9	125
Jacomar	1.1	55	5	10	3	4	84
Jacomar	1.2	19	4	13	6	2	54
Jacomar	1.3	107	12	33	10	29	223
Jacomar	1.4	38	5	7	7	6	83
Jacomar	1.5	45	12	28	14	12	137
Jacomar	2.1	30	13	27	11	11	95
Jacomar	2.2	25	9	32	5	14	88

Jacomar	2.3	21	14	33	8	20	102
Jacomar	2.4	41	12	18	4	13	99
Jacomar	2.5	38	6	44	5	12	109
P. Jandía	1.1	43	11	264	3	24	355
P. Jandía	1.2	138	15	40	11	23	243
P. Jandía	1.3	123	19	89	8	40	284
P. Jandía	1.4	62	12	174	8	42	305
P. Jandía	1.5	97	14	76	11	26	237
P. Jandía	2.1	113	8	38	6	11	188
P. Jandía	2.2	69	1	33	3	4	117
P. Jandía	2.3	341	0	18	10	7	401
P. Jandía	2.4	199	4	34	11	5	272
P. Jandía	2.5	106	4	24	9	7	163
Tufia	1.1	92	5	72	5	58	240
Tufia	1.2	52	8	187	9	48	307
Tufia	1.3	58	21	108	5	56	255
Tufia	1.4	55	9	211	3	12	301
Tufia	1.5	74	11	97	6	7	205
Tufia	2.1	147	1	669	29	9	898
Tufia	2.2	122	2	180	17	2	340
Tufia	2.3	70	3	176	6	7	277
Tufia	2.4	353	5	136	9	3	529
Tufia	2.5	157	4	559	17	9	758

Table 8S.- Faunal abundances for each sample from each location and depth stratum.

Location	Replicate	Amphipoda	Brachyura	Isopoda	Mollusca	Polychaeta	Decapoda	Total Biomass
Guincho	1.1	0.0097	0.0156	0	2.1401	0.0051	0.0175	4.4362
Guincho	1.2	0.0449	0.0081	0.0008	0.9569	0.2485	0.0276	1.2868
Guincho	1.3	0.0635	0.1592	0	2.6505	0.0147	0.0507	11.6204
Guincho	1.4	0.0041	0.0835	0	1.6678	0.0056	0.0995	1.8697
Guincho	1.5	0.0227	0.0775	0	1.5604	0.0942	0.0345	1.7893
Guincho	2.1	0.0179	0	0	0.1108	0.0133	0.0473	0.1902

Guincho	2.2	0.0045	0	0	1.0206	0.0058	0.0167	1.048
Guincho	2.3	0.01	0.0691	0.0012	0.3701	0.0144	0.0042	4.6195
Guincho	2.4	0.0037	0	0	0.6211	0.0208	0.0361	0.6824
Guincho	2.5	0.0166	0.147	0	0.7681	0.0328	0.5599	1.5244
Confital	1.2	0.0065	0	0.0035	1.5634	0	0.5097	2.0873
Confital	1.3	0.0308	0.0056	0	1.002	0.1959	0.0147	1.2503
Confital	1.4	0.0058	0.0046	0	0.2954	0.0346	0.0088	0.3523
Confital	1.5	0.0058	0.0682	0	0.9992	0.0446	0.027	1.1455
Confital	2.1	0.0002	0.0418	0	1.2521	0	0.0448	1.3392
Confital	2.2	0.0052	0.0192	0	0.4912	0.0018	0.005	0.5251
Confital	2.3	0.0147	0.0295	0	0.2828	0.0234	0.0291	0.3821
Confital	2.4	0.0191	0.0057	0.0013	0.8046	0.0143	0.014	0.8592
Confital	2.5	0.0675	0.0249	0	1.5442	0.0498	0.0372	1.7241
Tufia	1.1	0.0406	0.0399	0.0112	0.8481	0.6856	0.5	2.1259
Tufia	1.2	0.0347	0.0569	0.0183	1.2888	0.0126	0.0758	1.4871
Tufia	1.3	0.0667	0.2105	0.0059	2.1022	0.0109	0.2112	25.1977
Tufia	1.4	0.025	0.1378	0.0012	1.0201	0.0102	0.0665	1.5293
Tufia	1.5	0.0295	0.0868	0.0163	0.9201	0.4409	0.0152	1.9481
Tufia	2.1	0.0328	0.0098	0.0328	3.0921	0.0472	0.0223	3.3247
Tufia	2.2	0.0322	0.0389	0	0.6531	1.6883	0.0031	2.9524
Tufia	2.3	0.004	0.0114	0.0389	0.7881	0.0225	0.0084	0.8829
Tufia	2.4	0.3504	0.0363	0	0.7879	0.0397	0.0026	1.2641
Tufia	2.5	0.1354	0.0446	0	2.9712	0.0332	0.017	3.2175
P. Jandía	1.1	0.0171	0.2254	0.0023	2.6687	0.0089	0.8628	3.8452
P. Jandía	1.2	0.0528	1.37168	0.003	0.5216	0.2903	1.1485	3.40098
P. Jandía	1.3	0.0564	0.2986	0.002	1.0943	0.0686	0.1767	1.7876
P. Jandía	1.4	0.0833	0.2404	0.004	2.1755	0.0712	0.0723	2.6867
P. Jandía	1.5	0.0846	0.1259	0.002	0.8883	0.421	0.071	1.7491
P. Jandía	2.1	0.0536	0.2222	0.0014	0.6247	0.0276	0.0412	0.983
P. Jandía	2.2	0.0262	0.0518	0.0004	4.0904	0.4715	0.0268	4.6678
P. Jandía	2.3	0.402	0	0.0022	0.1156	0.2565	0.0075	0.7987
P. Jandía	2.4	0.3727	0.0365	0.0062	0.3244	0.008	0.0078	0.8528
P. Jandía	2.5	0.0943	0.06	0.0034	1.39	0.019	0.0963	1.6842
Jacomar	1.1	0.0309	0.0468	0.0012	0.0456	0.0076	0.0291	0.1938

Jacomar	1.2	0.008	0.0579	0.0032	0.0528	0.0252	0.0082	0.1553
Jacomar	1.3	0.0525	0.1561	0.0068	0.6593	0.1862	0.0923	1.1536
Jacomar	1.4	0.0261	2.0321	0.0065	0.4414	0.1515	0.0615	2.7278
Jacomar	1.5	0.016	0.1916	0.0004	0.9469	0.0145	0.0401	1.2108
Jacomar	2.1	0.0121	0.1522	0	0.4153	0.0848	0.0326	0.6982
Jacomar	2.2	0.0078	0.4229	0.0016	0.8323	0.0873	0.0357	1.3897
Jacomar	2.3	0.0128	0.1984	0.0013	0.9364	0.0823	0.0307	1.2646
Jacomar	2.4	0.0038	0.1018	0	0.2454	0.0433	0.012	0.413
Jacomar	2.5	0.0069	0.0374	0	0.3376	0.0245	0.0155	0.4238

Table 9S.- Faunal biomasses for each simple from each location and depth

	Amphipoda	Brachyura	Decapoda	Mollusca	Polychaeta	Total
Intercept	6.86***	4.54***	5.31 ***	7.35***	4.75***	8.15***
Vitality	-0.23*	0.04	0.03	-0.36**	0.017	-0.16**.**
Sphericity	0.15	0.01	0.027	0.04	-0.07	0.07
Size	-0.22**.**	-0.06	-0.13	-0.56***	-0.08	-0.33***
Epiphytes	0.17**.**	0.31**.**	0.47***	0.12	-0.02	0.14
Depth	-0.62 ***	-0.26	-0.02	0.52***	-0.17	0

Table 10S.- Estimates of GLMs for each predictor of faunal abundances. Significant predictors: *** < 0.001; ** < 0.01; * < 0.05; **.** <0.1.

	Amphipoda	Brachyura	Decapoda	Mollusca	Polychaeta	Total
Intercept	-0.41**	0.51**	-0.05	2.83***	2.83***	3.49***
Vitality	-0.14	0.34	0.22	-0.11	-0.13	-0.03
Sphericity	0.32*	-0.01	0.30	0.091	0.09	0.31*
Size	-0.07	0.43*	0.49*	-0.22**.**	-0.22**.**	-0.09
Epiphytes	0.10	0.42**	0.68**	0.20	0.20	0.35*
Depth	-0.69***	-0.61**	0.32	0.08	0.13	0.22

Table 11S. Estimates of GLMs for each predictor of faunal biomasses. Significant predictors *** < 0.001; ** < 0.01; * < 0.05; . <0.1.