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Effect of Depth across a Latitudinal Gradient in the Structure of Rhodolith Seabeds and Associated Biota across the Eastern Atlantic Ocean

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Abstract: Rhodolith seabeds are ‘ecosystem engineers’ composed of free-living calcareous red macroalgae, which create extensive marine habitats. This study addressed how depth influenced the structure (size and morphology) of rhodoliths and the abundance of associated floral and faunal epibionts across the Eastern Atlantic Ocean. Sampling was carried out at two sites within five regions (Brittany, Galicia, Madeira, Gran Canaria, and Principe Island), from temperate to tropical, covering a latitudinal gradient of 47°, in three depth strata (shallow, intermediate and deep), according to the rhodolith bathymetrical range in each region. Depth typically affected the rhodolith size at all regions; the largest nodules were found in the intermediate and deep strata, while rhodolith sphericity was larger at the shallow depth strata. Higher biomasses of attached macroalgae (epiphytes) were observed at depths where rhodoliths were larger. The abundance of epifauna was variable across regions and depth strata. In general, the occurrence, structure, and abundance of the associated biota across rhodolith habitats were affected by depth, with local variability (i.e., sites within regions) often displaying a more significant influence than the regional (large-scale) variation. Overall, this study showed that the rhodolith morphology and associated epibionts (flora and fauna) were mostly affected by depth, irrespective of latitude.

Keywords: environmental drivers; vertical scale; latitudinal gradient; maerl beds; non-geniculate corallines; epibionts; ecosystem engineers

1. Introduction

‘Ecosystem engineers’ are organisms that, in addition to providing resources for associated species, alter the local physical and chemical conditions, modifying, maintaining, and creating habitats [1]. Reef-builders, tube-builders, macroalgae (e.g., coralline algae), seagrasses, and mangroves are well-known marine ‘ecosystem engineers’, playing diverse roles such as providing refuges for other organisms and increasing habitat complexity, thus modifying hydrodynamic regimes and favoring the deposition of sediments and larvae [2]. The nature and extent of ecosystem functions provided by ‘ecosystem engineers’

can vary in response to changes in environmental conditions (e.g., light, hydrodynamics, sedimentation, etc.) [3–5]. However, most of the knowledge (e.g., habitat provision or nursery for other species) is derived from studies performed on horizontal scales (i.e., across latitudinal or geographical gradients) [6,7]. However, the oceans are inherently three-dimensional, where sharp physical and environmental gradients can occur on very narrow vertical scales (i.e., depth gradients), which noticeably modify communities of flora and fauna [8–11].

In the marine environment, some physical factors and processes such as salinity and temperature, sedimentation, turbulence, and light attenuation are directly affected by depth [12–16]. Salinity and turbulence often decrease with depth [17], affecting the distribution of species (e.g., euryhaline and stenohaline) and disrupting community structure [18–20]. Klöser et al. (1996) [21] identified three depth strata for the distribution of macroalgae based on turbulence levels: an upper-sublittoral under strong turbulence, a mid-sublittoral under moderate turbulence, and a lower and deeper sublittoral under low turbulence. Inversely, sedimentation typically increases with depth [10], affecting the structure and function of photosynthetic organisms, by altering both physical and biological processes [22]. In coral reefs, for example, organisms are smothered by sediment particles, reducing the available light for photosynthesis [23–25]. Finally, light irradiance also decreases with depth, modifying species composition and distribution [26,27].

Depth gradients affecting physical processes are particularly important for unstable ‘ecosystem engineers’ such as rhodolith seabeds [28]. Rhodoliths are non-geniculate free-living coralline algal nodules characterized by the presence of calcium carbonate, in the form of Mg-calcite in their cell walls, that belong to the division Rhodophyta [29,30]. Rhodolith beds can support foundational hard structures, favoring invertebrate recruitment and acting as ‘seedbanks’ for life history stages of micro and macroalgae, creating biodiversity hotspots and contributing to the global carbon cycle through CO₂ sequestration for the formation of their structures [31–33]. They are distributed worldwide, covering extensive benthic areas, being among the ‘Big Four’ benthic communities dominated by marine macrophytes, together with kelp forests, seagrass meadows, and coral reefs [34,35].

The influence of physical processes (e.g., turbulence and sedimentation), which usually correlate with depth, can affect rhodolith attributes (e.g., morphology and size) and their associated communities (fauna and flora). Typically, low turbulence regimes decrease rhodolith sphericity [36,37], while high-water motion and sedimentation can affect their size by breaking the nodules or decreasing their growth by burial, respectively [10]. Furthermore, similar to other crustose coralline algae, rhodoliths are adapted to low irradiance regimes [38], which allow them to live at deep waters (ca. 150 m [39]). Therefore, rhodolith beds occur under a wide variety of oceanographic environments, from openly exposed coasts to estuarine areas with low hydrodynamic action and several bathymetrical contexts (from the intertidal to 150 m depth [30]). The case of the Mediterranean Sea is quite particular, as there are areas with shallow rhodoliths beds (<10 m) [40] but others with deeper distribution due to light penetration beyond 60–79 m [41,42]. In general, these rhodoliths found the optimal conditions for their development (i.e., they formed wide fields with a high cover of live rhodoliths) at intermediate depths (i.e., 40–59 m) under certain conditions such as suitable sediments (e.g., gravel), moderate water movement, and enough light irradiance [41].

Across the Atlantic Ocean, the known distribution of rhodolith beds is mostly discontinuous. Meanwhile in the Southwestern Atlantic, the most extensive latitudinal distribution of rhodolith beds can be found along the Brazilian coast (e.g., Abrolhos bank; [36,43–45]), scarce information has been provided for the South Atlantic coasts of Africa and Antarctica [10,45]. In contrast, in the North Atlantic, rhodolith beds occur from Svalbard (Norway) to Macaronesia (Madeira and Canary Islands), being particularly abundant in Scotland, Ireland, Brittany (France), Galicia (Spain), Newfoundland, and Labrador (Canada), with 13 rhodolith forming species identified across different locations (Table 1) [46]. Due to commercial interests, those from the NE Atlantic are

well-studied [47–49] including descriptions of their bathymetrical ranges from the lower intertidal down to ca. 30 m such as those from Brittany (France) [50], or even deeper waters (ca. >40 m) in Galicia (Spain) [51] and Svalbard (30–51 m [52]). In the Azores, Madeira, and Selvagens and Canary Islands, rhodoliths cover extensive areas along broad bathymetrical gradients in all archipelagos (ca. 15–150 m, [53–55]). Still, there is scarce information on rhodolith distribution across tropical eastern Atlantic latitudes including Cape Verde and the Republic of São Tomé and Príncipe [10,55,56]. For example, on Príncipe Island, rhodolith beds have been observed from 3 to 40 m [55].

Table 1. Rhodolith species (according to the literature) and their distribution across the Eastern Atlantic Ocean. **B** = Brittany, **G** = Galicia, **M** = Madeira, **C** = Gran Canaria, and **P** = Príncipe Island. The superscript letters indicate the references that cite the species of rhodoliths in each region.

Species	Region				
	B	G	M	C	P
<i>Lithophyllum</i>	X				X
<i>L. africanum</i> (Foslie)					X [57]
<i>L. fasciculatum</i> (Lamarck) Foslie	X [58]				
<i>L. incrustans</i> (Philippi)	X [59]		X [60]		
<i>L. hibernicum</i> (Foslie)	X [61]				
<i>L. retusum</i> (Foslie)					X [57]
<i>L. sp.</i>		X [61]			
<i>Lithothamnion</i>	X	X	X	X	
<i>L. corallioides</i>	X [41]	X [61]	X [54]	X [53]	
(P. Crouan and H. Crouan)					
<i>L. sp. 2</i>		X [61]			
<i>Mesophyllum</i>		X			
<i>M. sphaericum</i> (Peña et al., 2011)		X [62]			
<i>M. sp. 3</i>		X [61]			
<i>M. sp. 4</i>		X [61]			
<i>Neogoniolithon</i>				X	X
<i>N. hirtum</i>				X [53]	
(Me. Lemoine) Alfonso-Carrillo					
<i>N. sp.</i>					X [57]
<i>Phymatolithon</i>	X	X	X	X	
<i>P. calcareum</i>	X [46]	X [63]	X [54]	X [53]	
(Pallas) W. H. Adey and D. L. McKibbin					
<i>P. lamii</i> (Me. Lemoine) Y. Chamberlain	X [48]				
<i>P. lusitanicum</i> (V. Peña)		X [64]			
<i>P. purpureum</i>					
(P. Crouan and H. Crouan) Woelkerling and L. M. Irvine	X [46]				
<i>Spongites</i>			X		
<i>S. fruticosus</i> (Kützting)			X [54]		
<i>Sporolithon</i>			X		
<i>S. sp.</i>			X [54]		

In this study, we aimed to address whether bathymetrical patterns in rhodolith structural attributes (shape and size) and the abundance of associated biota (flora and fauna) were consistent across a wide latitudinal gradient in the Eastern Atlantic Ocean, encompassing five regions from temperate to tropical latitudes.

2. Material and Methods

2.1. Study Regions

The study was carried out in five regions across the Eastern Atlantic Ocean (Figures 1 and 2). In the north, two temperate regions were chosen: Brittany (France) and Galicia (Spain); down south, two subtropical oceanic regions were selected: Madeira (Portugal) and Gran Canaria Island (Spain). Finally, Príncipe Island (Republic of Sao Tomé and Príncipe),

a tropical region close to the Equator, was also included. The rhodolith beds sampled were composed of several species of red calcareous algae that varied across regions, mainly within the genera *Lithophyllum* and *Phymatolithon* (Table 1 [31]). Furthermore, in each region, two sampling locations were sampled to account for intra-region variability.

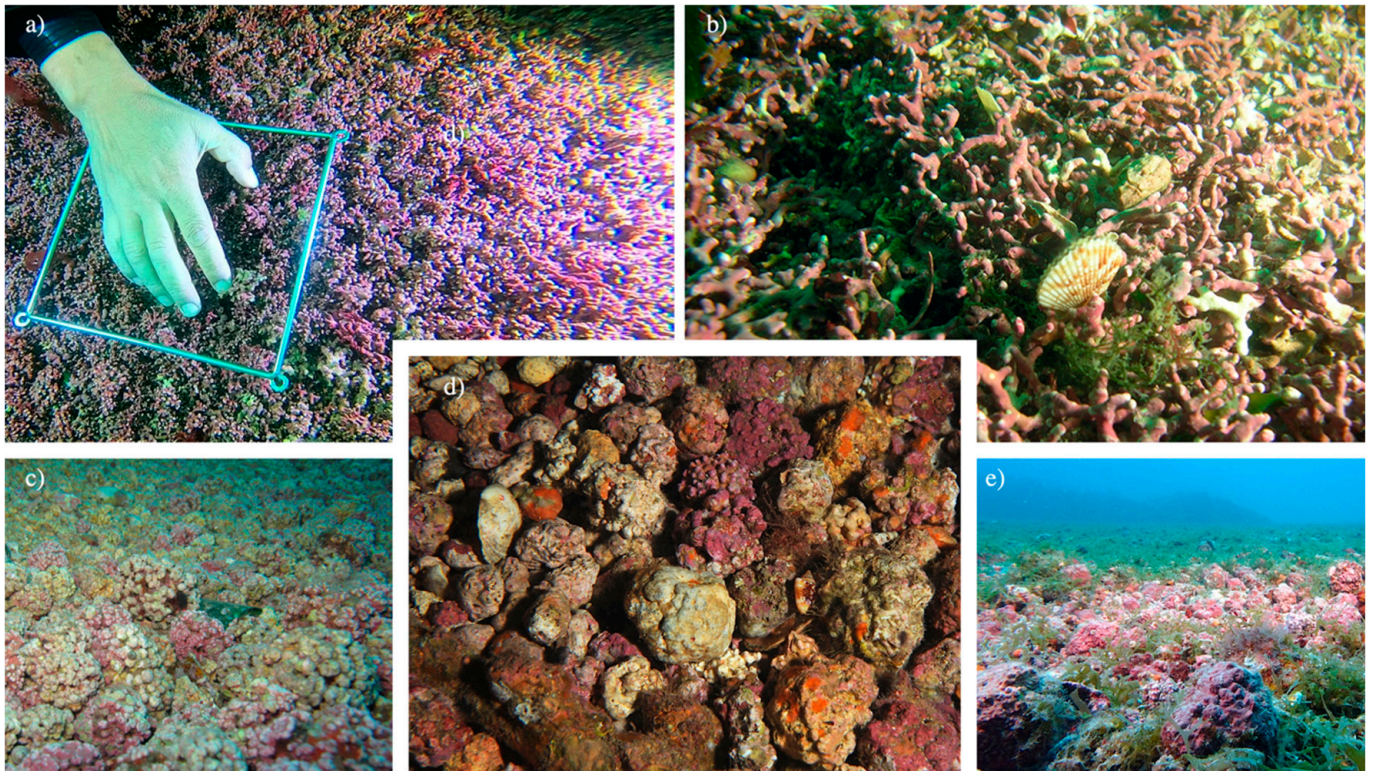


Figure 1. Rhodolith seabeds from (a) Brittany, (b) Galicia, (c) Madeira, (d) Gran Canaria, and (e) Principe Island. Photo credits: (a,d) Fernando Espino; (b) Ignacio Bárbara; (c) Pedro Neves, and (e) Francisco Otero-Ferrer.

2.2. Sampling Design and Collection of Samples

Five sampling campaigns, corresponding to the five regions, were carried out in rhodolith beds from 2016 to 2021, at different seasons of the year (Table 2). At each sampling location within each region, we defined three depth strata: ‘shallow’, ‘intermediate’, and ‘deep’, which somehow encompassed the local bathymetric range in the distribution of rhodolith beds (see Table 2). In the case of Galicia, the sampling design involved only two depths due to poor weather conditions, which were considered as the ‘intermediate’ and ‘deep’ depth strata (Table 2), according to the local environmental context [46,65,66]. All samples were taken following the protocol described by Otero-Ferrer et al. (2020) [10], and keeping SCUBA security standards at all times. On each depth stratum, $n = 5$ haphazardly located replicates (25×25 cm) were taken by collecting all rhodolith nodules up to 5 cm deep into the substrate. SCUBA divers collected the samples by hand, which were then enclosed in cloth bags. Samples were preserved in a freezer at -20 °C until sorting.

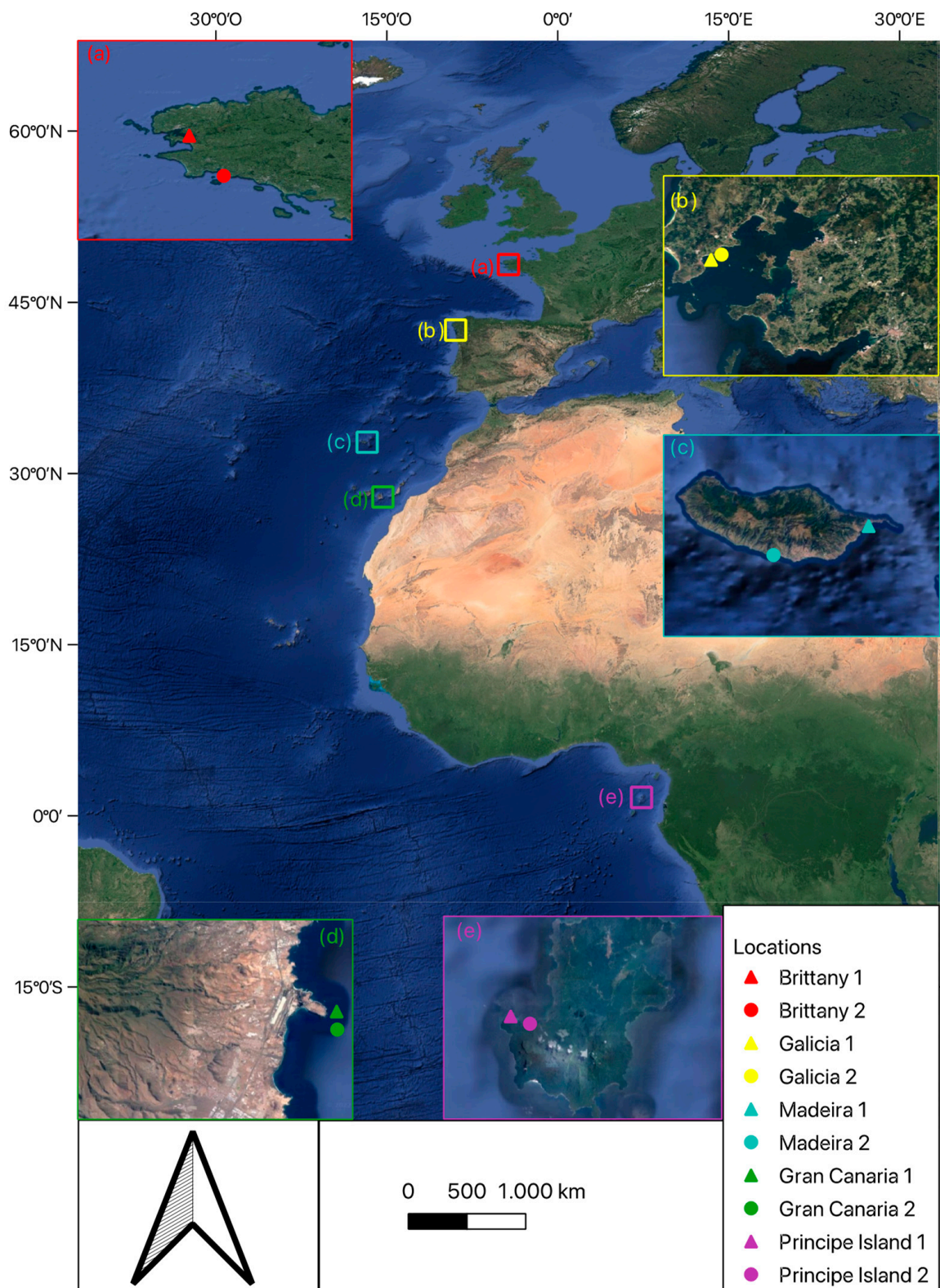


Figure 2. Study regions across the Eastern Atlantic including the ten locations where sampling was conducted. Each box corresponds to one sampled region from north to south: (a) Brittany, (b) Galicia, (c) Madeira, (d) Gran Canaria, and (e) Principe Island.

Table 2. Date, location (latitude and longitude), and depth (meters) that corresponded to each rhodolith seabed. Between location, the depths (m) of each stratum (i.e., shallow, intermediate, and deep) were different, since in each location, the rhodolith seabeds have a different vertical distribution.

Date	Location			Depth (m)			
	Region	Site	Latitude	Longitude	Shallow	Intermediate	Deep
August-21	Brittany	1	47°44'30" N	3°47'48" W	2	8	16
		2	48°18'13" N	4°20'07" W			
April-17	Galicia	1	42°33'56" N	8°57'55" W	-	10	17
		2	42°34'07" N	8°57'45" W			
June-16	Madeira	1	32°43'56" N	16°44'19" W	16	22	35
		2	32°39'07" N	17°00'10" W			
January-16	Gran Canaria	1	27°55'44" N	15°21'10" W	18	25	40
		2	27°55'44" N	15°21'10" W			
November-16	Principe Island	1	1°36'35" N	7°20'08" E	5	10	20
		2	1°36'13" N	7°21'01" E			

2.3. Samples Processing

Samples were first defrosted and then filtered through a 0.5 mm sieve to remove sand and debris. Macroalgae were removed from each replicate, identified under a microscope (Leica, DM1000, Berlin, Germany), and subsequently dried at 70 °C for 48 h to obtain their dry weight. From each sample, 25 rhodoliths were randomly selected and, for each one, the longest, intermediate, and shortest (axe) diameters were measured with a plastic caliper, following the criteria established by Sneed and Folk (1958) [67] to calculate their size. Then, measurements were added to the TRIPLLOT spreadsheet created by Graham and Midgley (2000) [68], classifying them into three shape categories: spheroidal, discoidal, and ellipsoidal. The software also calculated the proportion of rhodoliths that belong to each of the three former shape categories, keeping an additional fourth category (namely bladed) that remained intermediate [10,69]. Subsequent statistical analyses were conducted on the percentage of rhodoliths classified as spheroidal, as the shape categories were assumed to be considerably correlated, which is a proxy for the level of sphericity [69].

Additionally, for each sample, all vagile macrofauna retained by a 0.5 mm mesh sieve were identified under a stereomicroscope (Leica, EZ4W, Germany). Unfortunately, benthic macroinvertebrates living in rhodoliths are particularly difficult to identify at low taxonomic levels (i.e., family, order, genus or species) as they can include related taxa and mixing immature forms with adult stages, which prevents an accurate taxonomic identification, and the use of a coarse classification at the phylum level [10,70].

2.4. Data Analysis

Generalized linear models effects (GLMs), with 'depth' as a fixed (categorical) factor and 'latitude' as a numeric covariate, were examined to observe the univariate differences in the size (mean diameter) and shape (level of sphericity) of rhodoliths, the biomass of associated epiflora (standardized by the sample weight of rhodoliths) and the abundance of fauna (standardized by the sample weight of rhodoliths) per phylum [71].

All GLMs were performed using the R 'lme4' package [72]; we used a 'Poisson' family error distribution with a 'log' link function to reach the assumptions of linearity and normality of errors. Diagnosis plots of residuals and Q-Q plots were used to inspect the appropriateness of the fitted models visually.

3. Results

3.1. Rhodolith Structural Attributes

The size of the rhodoliths consistently differed among the depth strata across regions (Figure 3 and Table S1), with significant differences between shallow and intermediate

depths (Table S2). The higher mean size of rhodoliths was found in Madeira, where the rhodolith diameter increased with depth (Figure 2). The same size-depth pattern also occurred in Brittany, although to a lesser extent than in Madeira (Figure 2). The rhodolith beds of Gran Canaria and Principe Island presented their greatest size at the ‘intermediate’ stratum, with a relevant size drop in the deep stratum (Figure 2). In Galicia, there were no differences in size between the depth strata (Figure 2). In summary, the latitude significantly influenced the rhodolith size (Figure 2 and Table S2), regardless of the differences observed across the three bathymetrical levels.

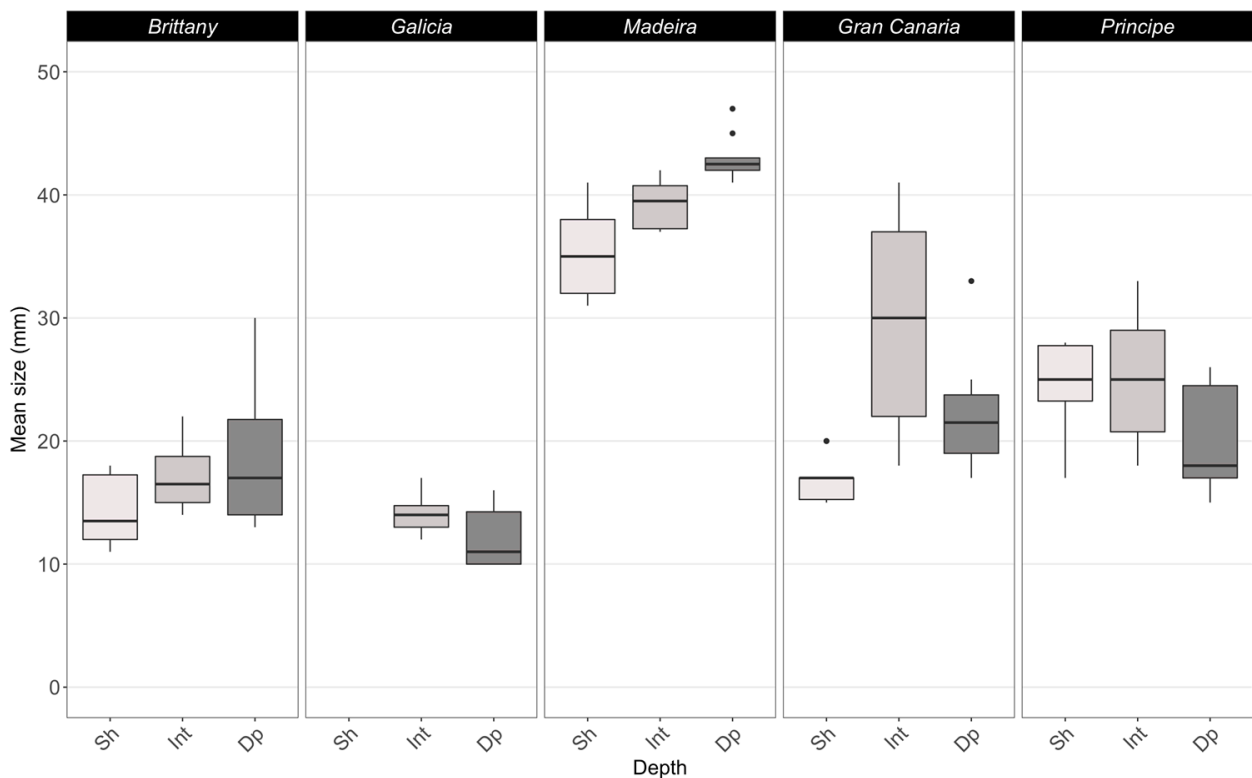


Figure 3. Mean diameter (mm) of rhodoliths at each depth stratum (Sh: Shallow; Int: Intermediate and Dp: Deep) and region. Data pooled for the two locations within each region.

Regarding the shape, most rhodoliths were quasi-spheroidal across all depths, except in Galicia, where the rhodolith were discoidal-bladed (Figure 3). Most spheroidal rhodoliths were found in Madeira, Gran Canaria, and Principe Island. Overall, the sphericity decreased with depth (Figure 4). However, no significant differences were obtained when comparing the level of sphericity among the depths and latitudes (Table S3).

3.2. Epiflora

The epiphytic macroalgal biomass (g per kg of rhodolith) varied among regions across the latitudinal gradient (Figure 5 and Table S4). In Brittany, Galicia, and Madeira, the epiphytic macroalgal biomass mostly increased with depth. Meanwhile, in Gran Canaria, the largest macroalgal biomass was obtained in the intermediate depth. In contrast, in Principe Island, the epiphytic macroalgal biomass decreased at intermediate depths (Figure 5). However, no significant differences were found among depths due to the large heterogeneity across latitudes (i.e., among regions), except in Madeira, where a large increase with depth was observed (Table S4).

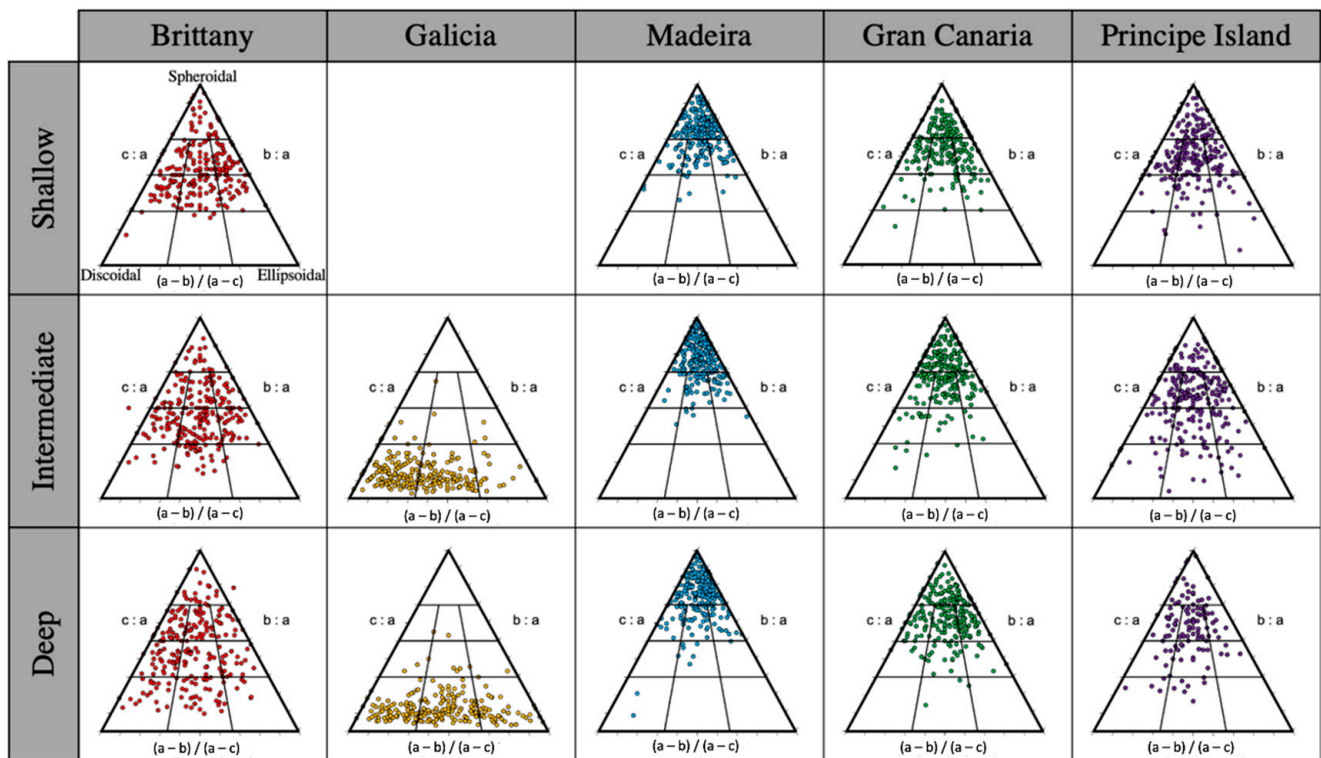


Figure 4. Ternary diagram showing deviation in the shape of rhodoliths collected at each depth stratum across the five regions: Brittany, Galicia, Madeira, Gran Canaria, and Principe Island, according to three shape categories: spheroidal, discoidal, and ellipsoidal. Data pooled for the two locations within each region. Letters represent the largest (a), intermediate (b) and smallest (c) rhodolith diameter.

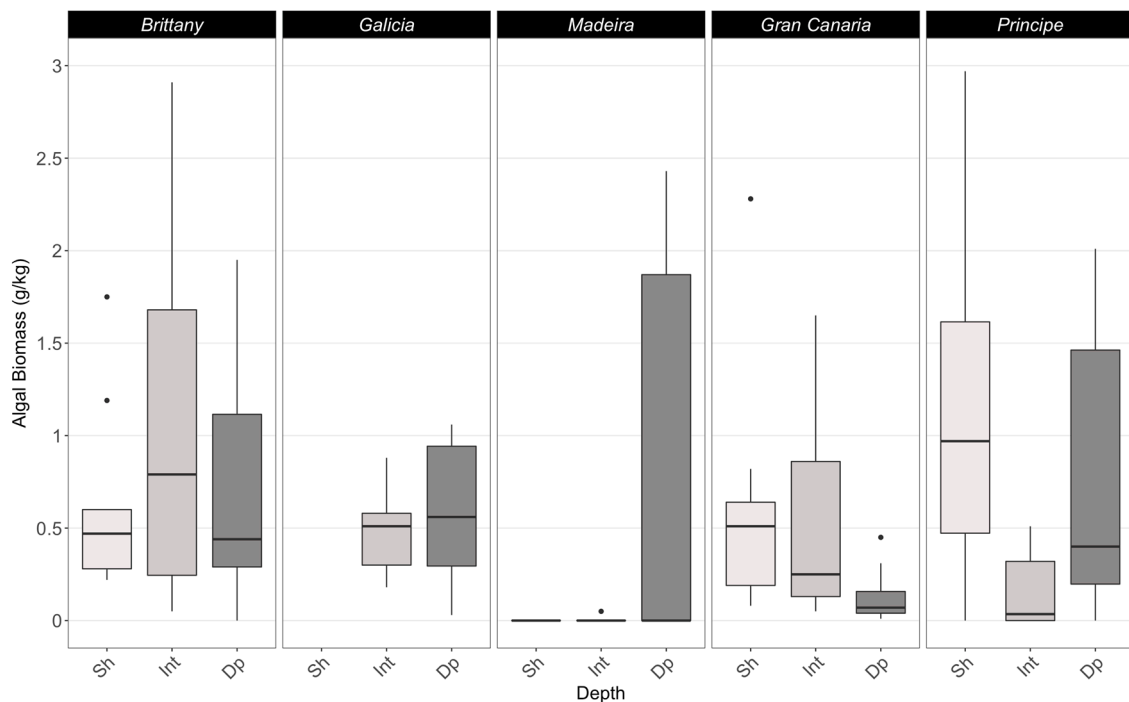


Figure 5. Total epiphytic macroalgal biomasses (dry weight) at each depth strata (Sh: Shallow; Int: Intermediate and Dp: Deep) and regions. Data pooled for the two locations within each region.

3.3. Epifauna

The total abundance of epifauna (g per kg of rhodolith) was variable among depths and regions, summarizing a total of 34,386 collected organisms, with Arthropoda and Mollusca dominating at all regions (Figure 6 and Table S5). In general, abundances showed significant heterogeneity between latitudes and depths (Table S6), however, a certain pattern could be observed, as the total abundances decreased toward the tropical zones. The highest abundance of arthropods was found in Brittany, with high abundances in the three depth strata, the highest values being found in the shallow one. In the case of Galicia, no phylum showed a pattern of dominance, and the abundances were similar between them. Mollusk abundances were highest in Madeira compared to the rest of the regions, particularly at intermediate depths. Gran Canaria showed intermediate abundance values for Arthropoda and Mollusca, while in this region, the lowest value of Echinodermata in our study was recorded. In general, the lowest abundances of the four phyla were recorded in the tropical region, Isla Principe (Figure 6 and Table S5).

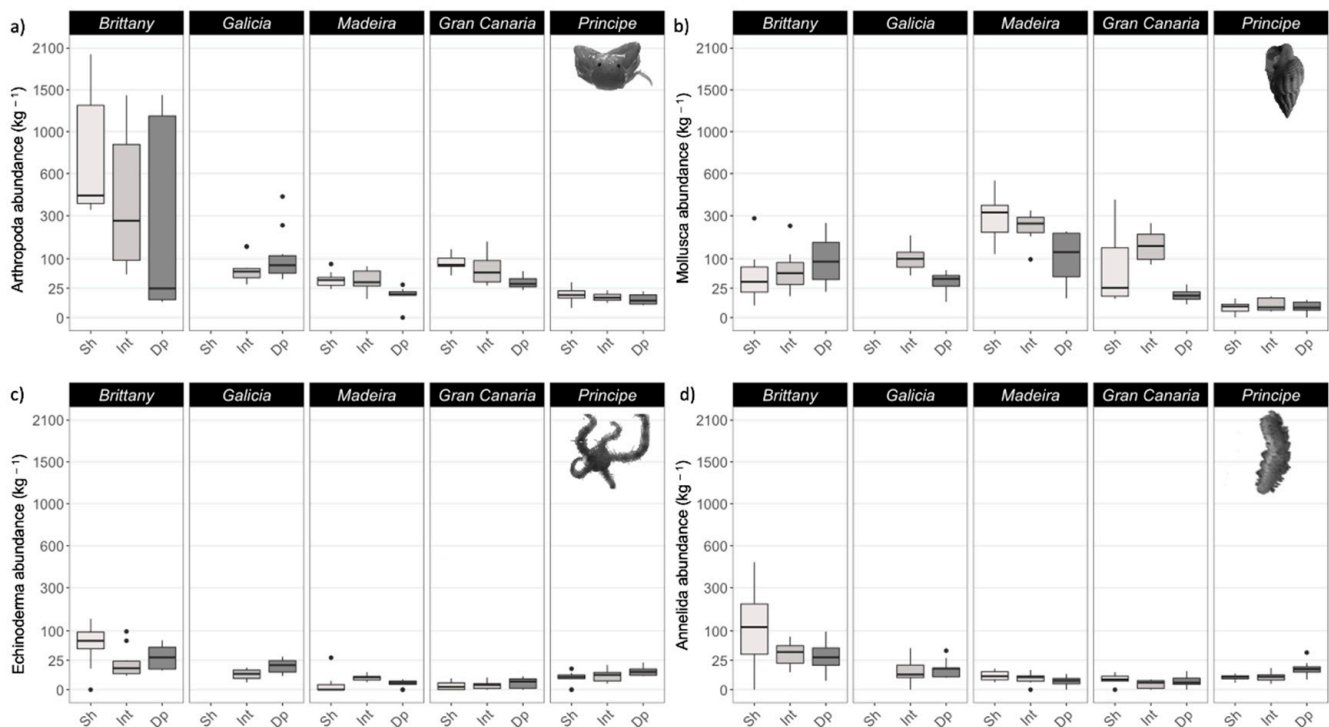


Figure 6. Faunal abundances (logarithmically transformed) at each region and depth strata (Sh: Shallow; Int: Intermediate and Dp: Deep), according to the four main phyla (a) Arthropoda, (b) Mollusca, (c) Echinodermata, and (d) Annelida.

4. Discussion

This study provided, for the first time, quantitative data on the way depth affected the structure (size and shape) and biota (epiflora and epifauna) associated with rhodolith beds along a latitudinal gradient in the Eastern Atlantic Ocean. In general, inter-regional heterogeneity affected the rhodolith size, morphology, and epiphytic communities (algal biomass and macrofaunal assemblages) across the bathymetrical strata analyzed.

4.1. Rhodolith Attributes

Rhodolith growth depends on a combination of environmental variables, particularly irradiance, water chemistry, temperature, turbulence, and sedimentation [10,38,52,73]. Turbulence promotes the rotation of rhodoliths, allowing light to reach the entire organism and thus preventing burial [55]. However, rhodoliths need to be in a particular balance between the movement generated by waves and sedimentation (i.e., just enough turbu-

lence to avoid burial but not too strong to break them up) [44,74]. Many authors [36,75] have identified a direct relationship between rhodolith size and depth. Typically, bigger rhodolith sizes are found at intermediate depths because of protection from wave-induced turbulence at shallower depths, where rhodoliths may undergo movement, breakage, and erosion. In contrast, lack of turbulence at deeper strata may bury rhodoliths by sediments, limiting their ability to photosynthesize and thus their growth [37,43,75,76]. This effect was somehow observed across all regions, despite different rhodolith species composition and considerable variation from region to region. In addition to the environmental factors, the final shape and branching density of some rhodolith species (e.g., *Lithophyllum racemosus*) are also conditioned by the presence of a nucleus (i.e., biogenic remains or any other hard material on which coralline algae can grow) [77]. For example, biogenic nuclei and pumices are usually light and, as a rule, generate larger and more symmetric rhodoliths.

In Brittany, rhodoliths were collected at two sites under different environmental contexts: Site 2, located near Concarneau ('Brittany 2' in Figure 2), is an open ocean site with low percentage of mud, mostly sandy, but high exposure to storms and swells, while Site 1, located inside the Brest estuary ('Brittany 1' in Figure 2) is dominated by muddy bottoms [78,79]. Several studies have denoted how environmental factors affect rhodolith bed structure in Brittany, showing that currents >0.5 m/s and high percentages of mud are detrimental to rhodolith growth [50,80]. Therefore, intra-regional differences, in terms of hydrodynamic context and sedimentation rates, may explain the high heterogeneity in the rhodolith mean diameter observed between locations and across the bathymetrical gradient (Table S1) [81]. Similarly, the effects of high sedimentation rates and burial at rhodoliths could be observed in Galicia for both sampled locations (estuarine context of 'Ria Arousa'; Figure 2) [51,63,82] (i.e., areas of high sedimentation and less turbulence), where the size of the rhodoliths decreased with depth, because sedimentation increased due to the low wave action at the bottom (Table S1).

The results obtained in Madeira and Gran Canaria agreed with previous studies conducted in the same areas [10,54], where the size of the rhodoliths generally showed an increasing trend with depth (Table S1). The sampled locations were characterized by a turbulent hydrodynamic in shallower depths, which affect the rhodolith size through breakage and burial. In these latitudes, rhodolith beds mostly grow over coarse gravel and clean sands [54]. Finally, rhodolith beds from Principe Island are subjected to both high (outer part of 'Agulhas Bay'; Location 1) and low (inner part of 'Agulhas Bay'; Location 2) exposure, also influenced by sedimentation rates provided by freshwater rivers mouths, which may condition the rhodolith size [10].

No significant differences were observed in the rhodolith shape across the bathymetrical strata across regions; rhodoliths mostly showed uniform spheroidal shapes, except in Galicia (with predominant discoidal types) and Brittany (with mostly spherical shapes mixed with bladed and sparsely discoidal and ellipsoidal morphologies). Generally, the rhodolith shape changes from spheroidal to discoidal as hydrodynamic conditions decrease [29,39,44,74,83,84]. The predominant spherical shapes across the entire bathymetrical range sampled in Madeira, Canary Islands, and Principe reflect a highly dynamic marine environment, typical of oceanic islands open to large oceanic swells [10]. Locations sampled in Brittany and Galicia showed the lowest sphericity, probably related to less exposure to currents and the action of waves inside estuaries compared to exposed locations in subtropical and tropical latitudes [51].

4.2. Epiflora

Algal growth is mainly determined by the availability of light and nutrients, temperature, and water motion [85]. For seaweeds growing on rhodoliths (epiflora), their biomass also depends on the rhodolith shape, the habitat stability [44], and sedimentation rates. Hence, reductions in the epiflora biomass with increasing depth have been described because light is a key-limiting factor in these gradients [86,87]. High sedimentation rates, generally found at deeper depths, can also affect the epiflora on rhodoliths,

as it increases the turbidity of the water, modifying light availability and inducing abrasion [88,89]. Additionally, when comparing algal biomasses across regions, differences can be biased by seasonal changes, which also condition macroalgal production throughout the year [90]. In this sense, seasonal peaks can fluctuate between locations following changes in nutrients, temperature, and light availability. For example, while Northern European Atlantic waters can experience a drastic increase of epifloral biomasses between summer and early autumn [46,90–92], southern subtropical and tropical latitudes such as Madeira and Canary Islands, or even Principe Island experience changes in algal biomasses that are less marked, with maximum production peaks appearing in autumn and spring–early summer [10]. These seasonal variations could explain the differences observed between the highest abundances of algal biomass found in Brittany (summer) compared to Galicia (early spring). Summer is usually the time of highest algal production in both regions [93,94], with lower waves allowing epiphytes to grow [95]. Several studies have indicated that epiflora biomass shows different seasonal peaks between regions that are at different latitudes. For example, in Galicia and Brazil, the abundance of macroalgae increased in summer relative to winter [36,46,92]. In contrast, on the Pacific coast of Baja California (Mexico), the highest abundances occurred in winter and spring, and then decreased in summer [96,97]. This great seasonal variability may reflect a local, multifactorial response of the epiflora to abiotic (e.g., temperature, light availability, water movement, sedimentation, and/or nutrient availability) and even biotic drivers (e.g., algal life-history traits or competition between species) [27,30,92].

On the other hand, changes in algal biomasses across latitudes can also reflect the changes in habitat structure (e.g., rhodolith size) across the bathymetrical gradient. Hence, epiphytic algal biomasses in Madeira were only noticeable in the deeper strata, probably related to the larger size of the rhodoliths, and the scarce presence of infralittoral macrograzers (e.g., *Diadema africanum*), observed there in higher densities at the shallow and intermediate depths [98,99]. In the case of Gran Canaria, algal biomasses seem to follow a trade-off between large light availability and rhodolith size, which explains the greater algal biomasses in the intermediate depth. Similarly, at Principe Island, the highest biomasses of epiphytic algae were found in the shallow depths, which may be attributed to the fact that the main species of algae found are green algae [56,100], which appear to be highly related to high light availability at shallower depths [101], and the presence of scleractinian coral colonies interspersed with rhodoliths in deeper strata, which reduce algal colonization [56].

4.3. Epifauna

Rhodoliths can facilitate faunal assemblages, not only by adding structure and complexity [10,33,102], but also due to the creation of ‘habitat cascades’ associated with epiphytic organisms (e.g., algae or other sessile fauna), which increases the amount of available habitat and trophic resources [103]. A large heterogeneity in epifaunal abundances was observed in the current study across regions, irrespective of depths. Arthropods, mollusks, annelids, and echinoderms showed high abundances, which agrees with other studies performed on tropical, subtropical, and temperate rhodolith beds [10,47,81,97,104,105]. Overall, the dominant phylum (in terms of individual abundance) was Arthropoda, mainly composed of the order Amphipoda and the infraorder Brachyura. Several authors denoted Amphipoda as one of the most abundant macrofaunal elements in several rhodolith beds (e.g., California [33,105–108]). In our study, mollusks were the second most abundant phylum in the habitat generated by rhodoliths. Several studies have confirmed rhodoliths beds as an outstanding diversity reference for this phylum [70,104,109]. Finally, annelids and echinoderms (mainly brittle stars and sea cucumbers) also contribute significantly to the epifaunal abundances, especially in northern European latitudes [110–112].

Although no clear pattern was observed for the macrofaunal groups in relation to depth, further studies with more detailed taxonomic information are required to confirm this statement, observed locally in other latitudes [113,114]. On the other hand, the large heterogeneity observed can also be related to the diversity of functional groups inside each

phylum. Furthermore, similar to what occurred with epiflora, the seasonal factor probably conditioned the results.

In conclusion, this study demonstrated that variability of rhodolith attributes (size and shape) and their epibionts (flora and fauna) across a bathymetrical gradient is highly conditioned by the local and regional environmental context, contrary to what occurs for other macroecological studies, where a latitude-related pattern is observed.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15010103/s1>, Table S1: Morphological attributes (mean \pm SD) of rhodoliths at each depth strata across five regions including the size, shape (% of spheroidal rhodoliths, as defined by Sneed and Folk, 1958), mean diameter (mm), and the epiflora (g/kg) found on rhodoliths. Table S2: Results of the GLM testing whether the mean diameter differed among the depth strata across latitudes. Table S3: Results of the GLM testing whether sphericity differed among depth strata across latitudes. Table S4: Results of the GLM testing of whether the epiphytic algal biomass differed among depth strata across latitudes. Table S5: Faunal abundances (number of individuals, standardized by the sample weight of rhodoliths (mean \pm SD) at each depth strata across regions. Table S6: Results of the GLM testing of whether epifaunal abundances (Arthropoda, Mollusca, Echinodermata, and Annelida) differed among the depth strata across latitudes.

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