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EFFECT OF DEPTH AND A LATITUDINAL GRADIENT IN THE FUNCTIONING OF RHODOLITH SEABEDS

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Trabajo Fin de Título para la obtención del título Grado en Ciencias del Mar

Effect of depth and a latitudinal gradient in the functioning of rhodolith seabeds

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Abstract

Rhodolith beds are important ecosystem engineers composed by free-living nodules, calcareous red macroalgae distributed across the Atlantic Ocean covering a large latitudinal gradient. The aim of this study was to understand how the variation in depth affected the structure (size and morphology) of rhodoliths and the abundance of floral and faunal epibionts across the Eastern Atlantic Ocean. Specifically, sampling was carried out at five locations: Brittany, Galicia, Madeira, Gran Canaria and Principe Island in three depth strata (shallow, intermediate and depth), corresponding to the bathymetric range in which the beds were found. Different size trends existed depending on the region, but generally the smallest rhodoliths were found in the shallow strata. The shape reflected the hydrodynamic context, with more spherical rhodoliths in open areas and discoidal rhodoliths in sheltered areas. Biomasses of attached macroalgae (epiphytes) varied consistently across regions but no significant differences were found between depths. The presence of epifauna was variable for the different phyla, but in general arthropods and molluscs dominated across all regions. Overall, local variability had a greater impact than the latitudinal gradient.

1. Introduction

Ecosystem engineers are organisms that can control the availability of resources for other species by causing physical state changes in biotic or abiotic materials modifying, maintaining and creating habitats (Jones et al., 1994). Reef-builders, tube-builders, macroalgae (e.g. rhodolith beds), seagrasses, and mangroves are well known for being marine structural engineers, playing different roles like providing living and refuging spaces for other organisms, increasing habitat complexity, modifying hydrodynamic regimes, and deposition of sediments and larvae (Berke, 2010). Ecosystem engineers can easily show how environmental changes (light, hydrodynamics, sedimentation, etc.) modify the composition and structure of associated communities, both flora and fauna (Madin & Connolly, 2006; Williams et al., 2013; Burel et al., 2019). However, most of these studies have been performed on horizontal scales (Granata et al., 2001; Adams et al., 2016) not taking advantage of the fact that in the ocean, sharp environmental gradients can occur on very narrow vertical scales, which noticeably modify communities of fauna and flora (Andradi-Brown et al., 2016; Coleman et al., 2018; Otero-Ferrer et al., 2020a).

In the marine environment, some physical processes, like salinity, sedimentation, turbulence, light attenuation, and temperature are directly affected by depth (Huybers & Wunsch, 2004; Liu et al., 2005; Boyer Montégut et al., 2007; Falcon & Laroche, 2011; Lee et al., 2013). Salinity and turbulence decrease with depth (Montgomery, 1958) changing the distribution of species (e.g. euryhaline and stenohaline) and disrupting community structures (Bayly, 1972; Grillas et al., 1993). Klöser et al. (1996) find three zones of distribution of macroalgae, an upper sublittoral under strong turbulence, a central sublittoral under moderate turbulence, and a calm deeper sublittoral, that condition the species observed. In correlation with turbulence, there is sedimentation, that increases with depth (Otero-Ferrer et al., 2020a). Sedimentation can affect the structure and function of photosynthetic sessile organisms by altering both physical and biological processes (Philipp & Fabricius, 2003). Hence, in coral reefs, organisms can be smothered by sediment particles which in turn reduce the light available for photosynthesis (Rogers, 1990; Nugues & Roberts, 2003; Risk, 2014;). Finally, light irradiance also decreases with depth, modifying species composition and distribution (Balata & Piazzi, 2008). Equally, Connell (2005) shows how variation in light intensity and sedimentation, directly related to hydrodynamics, can be of great significance in the maintenance of the subtidal habitat heterogeneity in coralline and filamentous, turf-forming algae.

Depth gradients affecting before-mentioned physical processes are particularly important in unstable ecosystem engineers, such as the rhodolith seabeds (Ryan et al., 2007). Rhodoliths are non-geniculate marine algal free-living nodules characterized by the presence of calcium carbonate in their cell walls that belong to the division Rhodophyta (Bosellini & Ginsburg, 1971; Foster et al., 2013) (Fig. 1). Rhodolith beds cover extensive benthic areas and are distributed worldwide being among the "Big Four" benthic communities dominated by marine macrophytes, ranking with kelp forests, seagrass meadows and coralline reefs (Foster, 2001; Amado-Filho & Pereira-Filho, 2012). Nelson & Nelson (2009), identify rhodoliths as ecosystem engineers responsible for structural strength and reef consolidation, invertebrate recruitment, and settlement, creating biodiversity hotspots and contributing to the global carbon cycles. The influence of physical processes, such as turbulence and sedimentation, correlated with depth, is rather relevant in rhodolith seabeds attributes (e.g. morphology and size) and their epiphytic communities (fauna and flora). Low wave turbulence regimes decrease rhodolith sphericity (Steller & Foster, 1995; Amado-Filho et al., 2007), meanwhile high water motion and sedimentation can affect their size, breaking the nodules or decreasing their growth by burial, respectively (Otero-Ferrer et al., 2020a). On the other hand, most corallines are adapted to low irradiance regimes (Wilson et al., 2004), allowing them to live at higher depths (*ca*. 150m; Bosence, 1976), enlarging the bathymetric range in where they can occur.

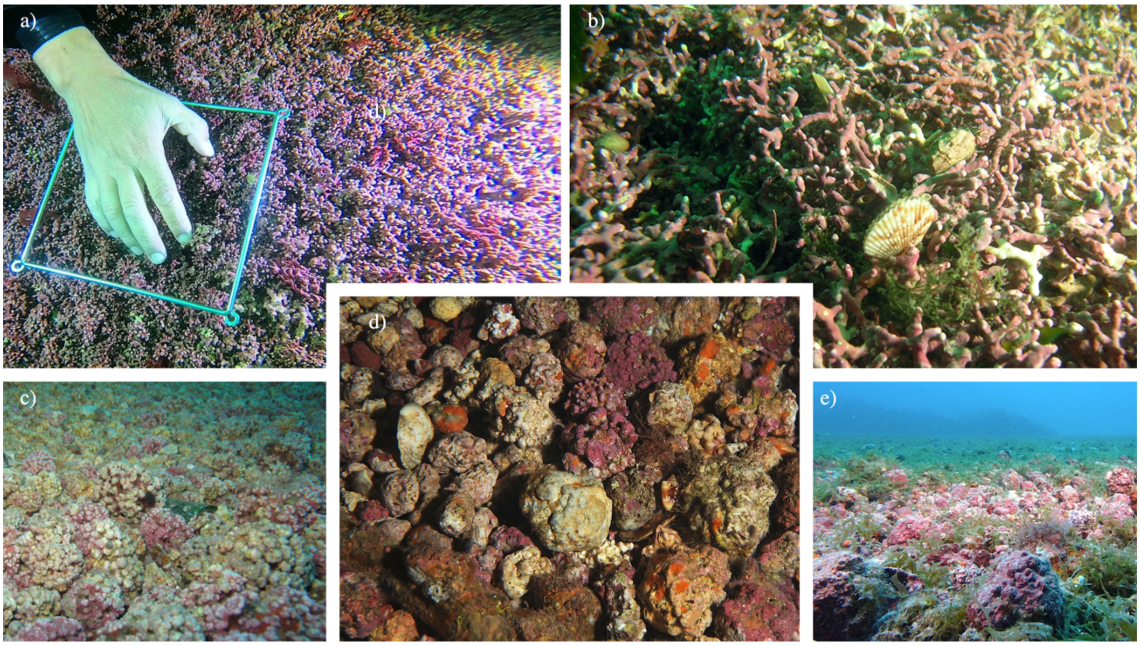

Figure 1. Five rhodolith seabeds located in: a) Brittany, b) Galicia, c) Madeira (picture from Pedro Neves), d) Gran Canaria and e) Principe Island (Picture credits: a) and d) Fernando Espino; b) Viviana Peña; c) Pedro Neves and e) Francisco Otero).

Rhodolith beds occur in a wide variety of oceanographic environments, from open exposed coasts to estuarine areas with low hydrodynamic action, and several bathymetrical contexts (from the intertidal to 150 m depth, OCEANA, 2010). In particular, their geographic distribution across the Atlantic Ocean is mostly discontinuous. Meanwhile in the Southwestern Atlantic the largest latitudinal distribution of rhodolith beds can be found along the Brazilian coast (Amado-Filho et al., 2007; Bahia et al., 2010; Amado-Filho & Pereira-Filho, 2012; Pascelli et al., 2013), scarce mentions about rhodolith beds have been registered for the South Atlantic coasts of Africa nor for Antarctica (Amado-Filho et al., 2017; Otero-Ferrer et al., 2020b). On the contrary, in the North Atlantic, rhodolith beds occur from Svalbard to the Macaronesia (Madeira and Canary Islands), being particularly abundant in Scotland, Ireland, Brittany (France), Newfoundland and Labrador (Canada) with 13 rhodolith forming species identified across different locations (Table 1) (Hernandez-Kantun et al., 2017). Due to commercial interests and consequently its sustainable exploitation, the ones located in the NE Atlantic, (Wehrmann et al., 1997; Barbera et al., 2003; Grall & Hall-Spencer, 2003), are well studied describing their bathymetrical range from lower intertidal to *ca*. 30 m depth in Brittany (France) (Dutertre et al., 2015) or even deeper (*ca*. > 40 m) in protected southern archipelagos in Galicia (Spain) (Peña & Criado, 2009). Southern, in the Macaronesian archipelagos (Azores, Madeira and Selvagens and Canary islands) rhodoliths are present in shallow waters in all island groups (Johnson et al., 2017). For example, in Madeira, rhodolith beds occur in all the islands of the archipelago at much greater depths, from 8 to 129 m (Neves et al., 2021), while in the Canary Islands, rhodolith beds exist in extensive areas along wide bathymetrical gradients, (*ca*. 15-150 m, Haroun et al., 2002). Finally, the scarce information about rhodoliths coverage and functioning on SE Atlantic latitudes address Cabo Verde or Republic of Sao Tome and Principe (Johnson et al., 2017; Cosme De Esteban et al., 2018; Otero-Ferrer et al., 2020b). Specifically, in Principe Island, rhodolith beds have been observed in the north and western side of the island from 3 to 40 m (Cosme De Esteban et al., 2018). Rhodolith species diversity changes across each region within the eastern Atlantic Ocean (Table 1). Therefore, most of the research conducted on rhodoliths beds cover the North and Southwestern Atlantic with scarce information about rhodoliths functioning on subtropical and tropical latitudes. This study aimed to show for the first time how depth affects rhodolith attributes (shape, size and epibionts) and test its consistency along a latitudinal gradient in the Eastern Atlantic Ocean.

2. Material and methods

2.1. Study regions

The study was carried out in five different rhodolith beds across the Eastern Atlantic Ocean (Fig. 2; Table A1). In the north two regions were chosen, Brittany (France) and Galicia (Spain); down south samples were taken in Madeira (Portugal) and Gran Canaria Island (Spain) and very close to the Equator in Principe Island (Republic of Sao Tomé and Principe). The rhodolith beds sampled were composed by several species of red calcareous algae changing across regions, mainly of the genera *Lithophyllum* and *Phymatolithon* (Table 1). Besides, inside each sampling location, two sampling locations were defined to replicate internal variability.

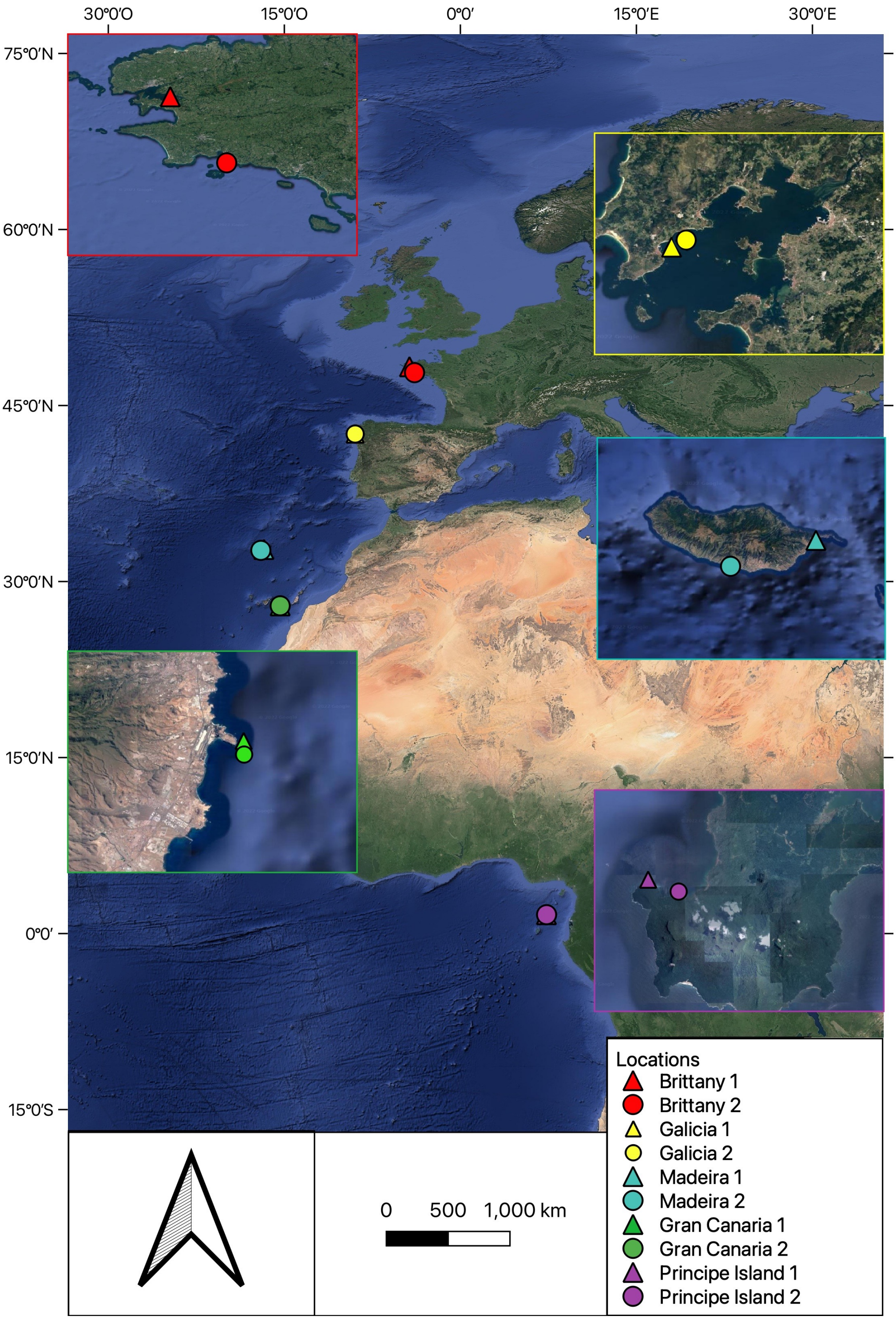

Figure 2. Diagram of the study regions across the Eastern Atlantic Ocean, showing the ten locations (Brittany, Galicia, Madeira, Gran Canaria and Principe Island) where sampling took place.

Table 1. List of rhodolith species and their distribution in the Eastern Atlantic Ocean. (B = Brittany, G = Galicia, M = Madeira, C = Gran Canaria, and P = Principe Island).

Species	**B**	**G**	**M**	**C**	**P**
***Lithophyllum* Philippi**	**B**	**G**[1]			**P**
L. africanum Foslie					P[2]
L. fasciculatum (Lamarck) Foslie	B[3]				
L. hibernicum Foslie	B[1]				
L. retusum Foslie					P[2]
***Lithothamnion* Heydrich**	**B**	**G**	**M**	**C**	
L. corallioides P.Crouan & H.Crouan	B[3,4,5]	G[1,5]	M[5,6]	C[5,7]	
L. glaciale Kjellman	B[5,8,9]				
***Mesophyllum* Me.Lemoine**		**G**			
M. sphaericum V.Pena, Bárbara, W.H.Adey, Riosmena-Rodrigues & H.G.Choi		G[5,10]			
***Neogoniolithon* Setchell & L.R.Mason**				**C**	**P**[2]
N. hirtum Me.Lemoine				C[7]	
***Phymatolithon* Foslie**	**B**	**G**	**M**	**C**	
P. calcareum (Pallas) W.H.Adey & D.L.McKibbin ex Woelkering & L.M.Irvine	B[1,5,11,12,13]	G[5,14]	M[5,6]	C[7]	
P. lamii (Me.Lemoine) Y.M.Chamberlain	B[1,5,8,9]				
P. lusitanicum V.Peña		G[15]			
P. purpureum (P.Crouan & H.Crouan) Woelkerling & L.M.Irvine	B[5]				
***Spongites* Kützing**			**M**		
S. fruticulosa Kützing			M[5,6,16]		
***Sporolithon* Heydrich**			**M**[6]		

1. Pardo et al. (2017); 2.Steentoft (1967); 3. Cabioch (1969); 4. Grall & Hall-Spencer (2003); 5. Hernandez-Kantun et al. (2017); 6. Neves et al. (2021); 7. Haroun et al. (2002); 8. Chamberlain (1994); 9. Strömfelt (1886); 10. Peña et al. (2011); 11. Angot & Lemoine (1910); 12. Cabioch & Mendoza (1998); 13. (Sauriau et al., 2012); 14. Peña & Bárbara (2008); 15. (Pardo et al., 2015); 16. Cabioch (1974).

2.2. Environmental context

The environmental context of each region was described using Sea Surface Temperature (SST) in ºC and Sea Surface Photosynthetically Available Radiation (PAR) in $E \cdot m^{-2} \cdot d^{-1}$. These data were acquired from the Aqua MODIS (MODerate-resolution Imaging Spectroradiometer) sensor, available on the Goddard Earth Sciences Data and Information Services Center, Interactive Online Visualization and Analysis Infrastructure (GIOVANNI, giovanni.gsfc.nasa.gov/giovanni/).

2.3. Sampling design and collection of samples

Five sampling campaigns were carried out in rhodolith beds across the five regions from 2016 to 2021 (Fig. 2; Table A1). For the ten sampling locations, we defined three different depths, defined as “shallow”, “intermediate” and “deep” which somehow encompassed the local bathymetric range in the distribution of rhodolith patches. In the case of Galicia, the experimental design involved only two depths, due to poor weather conditions, considered as the "intermediate" and "deep" substrates (Table A1) according to the local environmental context (Peña & Bárbara, 2006). All samples were taken following the protocol described by Otero-Ferrer et al. (2020), and keeping SCUBA security standards at all times. On each depth stratum, n = 5 haphazardly located replicates

(25 x 25 cm) were taken each time, by collecting all rhodolith nodules up to 5 cm deep. SCUBA divers collected all the samples by hand, which were enclosed within cloth bags. Samples were then preserved in a freezer at -20^{o} until sorting.

2.4. 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 replica, identified under a microscope (Leica, DM1000, Germany) and subsequently dried at 70 ºC 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 calliper following the criteria established by Sneed & Folk (1958) to calculate their size. Then, measurements were added to the TRIPLOT spreadsheet created by Graham & Midgley (2000) classifying them into three shape categories: spheroidal, discoidal and ellipsoidal. The software also calculates the proportion of rhodoliths that belong to each of the three former shape categories, keeping an additional fourth category (namely bladed), which remains intermediate (Fig. 3) (Gagnon et al., 2012; Otero-Ferrer et al., 2020a). Furthermore, statistical analyses were done on the percentage of rhodoliths classified as spheroidal, as the shape categories were assumed to be considerably correlated (Gagnon et al., 2012). This percentage is a proxy for the level of sphericity (Gagnon et al., 2012).

Additionally, for each sample, all vagile macrofauna retained by a 0.5 mm mesh sieve were identified under a stereomicroscope (Leica, EZ4W, Germany) to the lowest possible taxonomic level following the methodology applied by Otero-Ferrer et al. (2019). Unfortunately, benthic macroinvertebrates colonizing rhodoliths were particularly difficult to identify, as they can include relatively small morphological related taxa, mixing immature forms with adult stages, which prevented an accurate identification (Otero-Ferrer et al., 2019; 2020a).

2.5. Data analysis

Generalized Linear Models effects (GLMs) with ‘depth’ as fixed factor and ‘Latitude’ of each sample ‘Location’ was used as covariable to examine univariate differences in the size (mean diameter) and shape (level of sphericity) of rhodoliths and epifloral associated communities. We employed Latitude as intrinsically included both ‘Region’ and ‘Locations’. Therefore, differences in the size and shape of rhodolith attributes and biomass of epiphytic macroalgae (standardized by the sample weight of rhodoliths), between depths and sampling locations, were analysed using GLMs with ‘Depth’ (3 levels: shallow, intermediate, and deep) as fixed factor and ‘Latitude’ as covariable.

All GLMs were performed using the ‘lme4’ package (Bates et al., 2015) and we used a ‘poisson’ error distribution with ‘log’ link function, that was selected to meet the assumptions of linearity and normality of errors. Diagnosis plots of residuals and Q–Q plots were used to visually inspect the appropriateness of the fitted models.

Finally, the abundance of fauna (standardized by the sample weight of rhodoliths) between depths and locations, was analysed by phylum (Warwick, 1988) and compared by performing barplots where the percentage of abundance was plotted.

3. Results

3.1. Environmental context

The Sea Surface Temperature (SST) and the Photosynthetically Available Radiation (PAR) varied along locations (Table 2). The SST increased gradually from north to south, finding the highest average temperature in Principe Island (27.43 ± 0.29 ºC). The PAR also increased gradually from north to south, except in Principe however, the highest rate of Photosynthetically Available Radiation was found in Madeira (42.78 ± 3.12 E m^{-2} d^{-1}).

Table 1. Summary of environmental data collected at the study locations.

		Brittany	Galicia	Madeira	Gran Canaria	Principe Island
SST (ºC)	Mean ± SE	14.06 ± 0.95	14.35 ± 0.25	20.40 ± 0.65	20.87 ± 0.41	27.43 ± 0.29
	Maximum	19.09	15.34	24.09	22.85	29.27
	Minimum	9.41	13.01	17.44	18.61	25.79
PAR (E m^{-2} d^{-1})	Mean ± SE	30.59 ± 4.53	32.26 ± 4.44	38.71 ± 3.91	40.81 ± 3.28	36.57 ± 1.12
	Maximum	46.51	53.26	58.29	60.48	43.82
	Minimum	7.39	10.62	20.24	26.28	32.26

3.2 Rhodolith attributes

The size of rhodoliths differed between depths in a consistent manner through the different regions sampled (Fig. 3; Table 3), with significant differences between shallow and intermediate depths (Table 3). The higher mean size of rhodoliths was found in Madeira, where an increased trend in diameter was observed as depth increased (Fig. 3). This same size-depth pattern also occurred in Brittany, although to a lesser extent than in Madeira. The rhodolith bottoms of Gran Canaria and Principe Island presented their greatest size at an intermediate depth, while in Galicia the smallest size was found and there were no big differences between depth layers (Fig. 3). In general, latitude influenced significantly in rhodolith size (Table 3) in spite of general differences observed across the three bathymetrical levels analysed.

Regarding morphology, most rhodoliths were quasi-spheroidal across all depths, except for Galicia where rhodolith were discoidal-bladed, according to tri-plot ternary diagrams (Fig. 4). The highest sphericities were found in Madeira, Gran Canaria and Principe Island and the lowest in Galicia (Table A2). No significant values were obtained when comparing depths and latitudes as a covariable (Table 4).

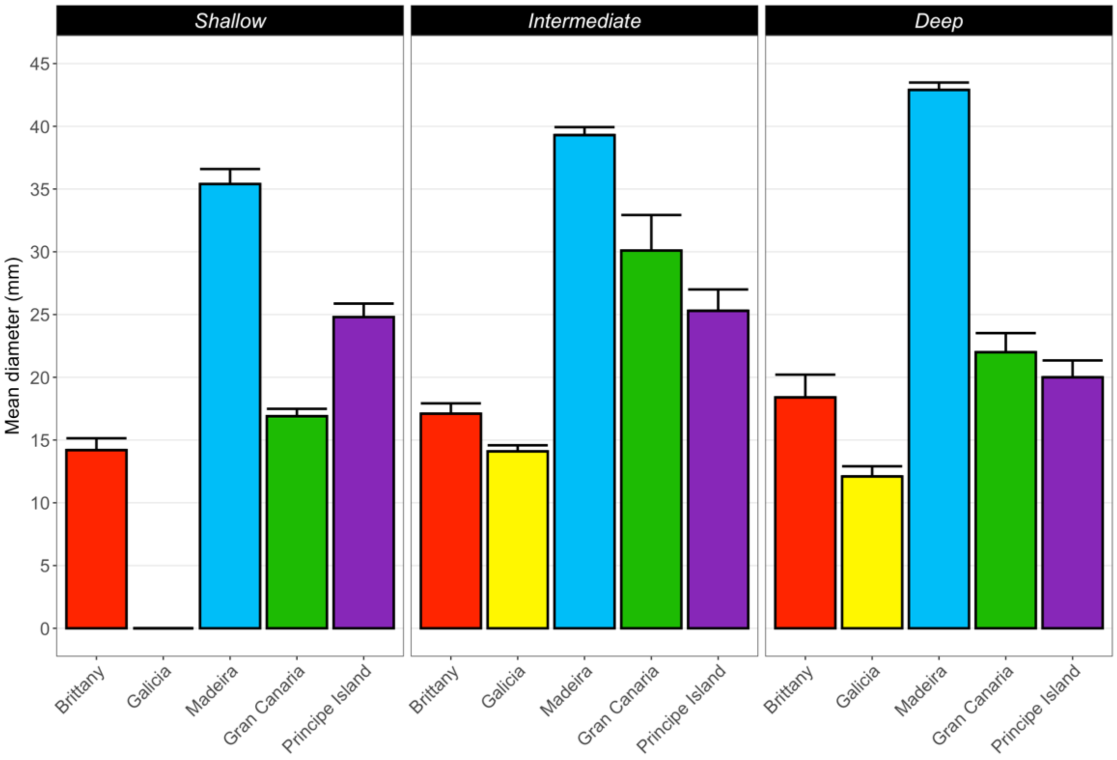

Figure 2. Mean diameter (mm) of rhodoliths at each depth stratum and regions (Brittany, Galicia, Madeira, Gran Canaria and Principe Island) Error bars are + SE of means (n = 125).

Table 2. Results of GLMs testing whether the mean diameter differed between depths using latitude as a covariable. Significant differences at P . <0.1 * < 0.05, **< 0.01, ***< 0.0001.

	Fixed effects				
	Estimate	Std. Error	Z Value	P	
Mean diameter (mm)					
Intercept (Depth [Shallow])	2.87	0.05	55.49	<2e-16	***
Latitude	-0.01	0.00	-4.47	7.75e-06	***
Depth [Intermediate]	0.11	0.05	2.05	0.0409	*
Depth [Deep]	0.02	0.05	0.42	0.6744	
Intercept (Depth [Intermediate])	2.98	0.05	59.56	<2e-16	***
Latitude	-0.01	0.00	-4.47	7.75e-06	***
Depth [Shallow]	-0.11	0.05	-2.05	0.0409	*
Depth [Deep]	-0.09	0.05	-1.73	0.0843	.

Intercept (Depth [Deep])	2.89	0.05	56.62	<2e-16	***
Latitude	-0.01	0.00	-4.47	7.75e-06	***
Depth [Shallow]	-0.02	0.05	-0.42	0.6744	
Depth [Intermediate]	0.09	0.05	1.73	0.0843	.

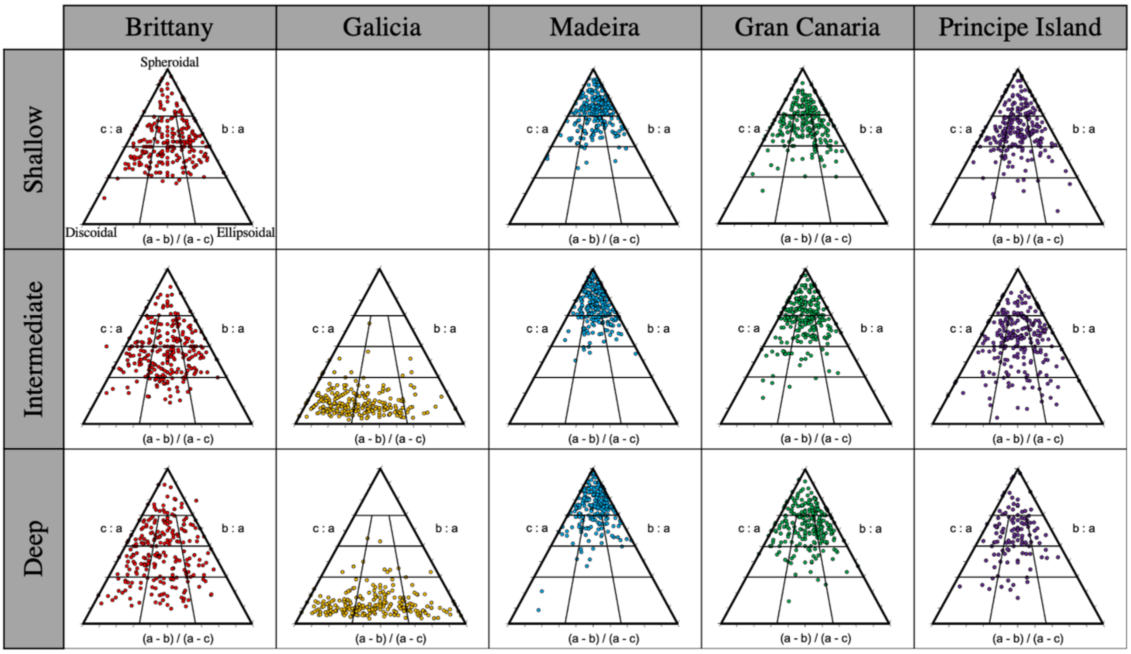

Figure 3. Ternary diagram showing deviation in the shape of rhodoliths collected at each depth stratum across the five Regions (latitudes) sampled: Brittany (red), Galicia (yellow), Madeira (blue), Gran Canaria (green) and Principe Island (purple) according to three shape categories: spheroidal, discoidal, and ellipsoidal (Graham and Midgley, 2000).

Table 3. Results of GLMs testing whether sphericity differed between depths using latitude as a covariable. Significant differences at P . <0.1 * < 0.05, **< 0.01, ***< 0.0001.

	Fixed effects			
	Estimate	Std. Error	Z Value	P
Sphericity				
Intercept (Depth [Shallow])	-0.13	0.24	-0.54	0.588
Latitude	-0.00	0.01	-0.76	0.450
Depth [Intermediate]	-0.11	0.25	-0.46	0.647
Depth [Deep]	-0.14	0.25	-0.58	0.563
Intercept (Depth [Intermediate])	-0.24	0.24	-0.99	0.320
Latitude	-0.00	0.01	-0.76	0.450
Depth [Shallow]	0.11	0.25	0.46	0.647
Depth [Deep]	-0.03	0.24	-0.13	0.899
Intercept (Depth [Deep])	-0.27	0.24	-1.11	0.266
Latitude	-0.00	0.01	-0.76	0.450

Depth [Shallow]	0.14	0.25	0.58	0.563
Depth [Intermediate]	0.03	0.24	0.13	0.899

3.3 Epiflora

The epiphytic macroalgal biomass (per kg of rhodolith) varied consistently between regions across the latitudinal gradient analysed (Fig. 5; Table 5). In Brittany, Galicia, and Madeira the epiphytic macroalgal biomass increased with depth, in Gran Canaria the highest macroalgal biomass was obtained in the intermediate depth, while in Principe Island the epiphytic macroalgal biomass decreased with depth (Fig.5; Table A2). However, no significant differences were found between depths due to the high heterogeneity between the different sampled ‘Latitudes’ (Table 5).

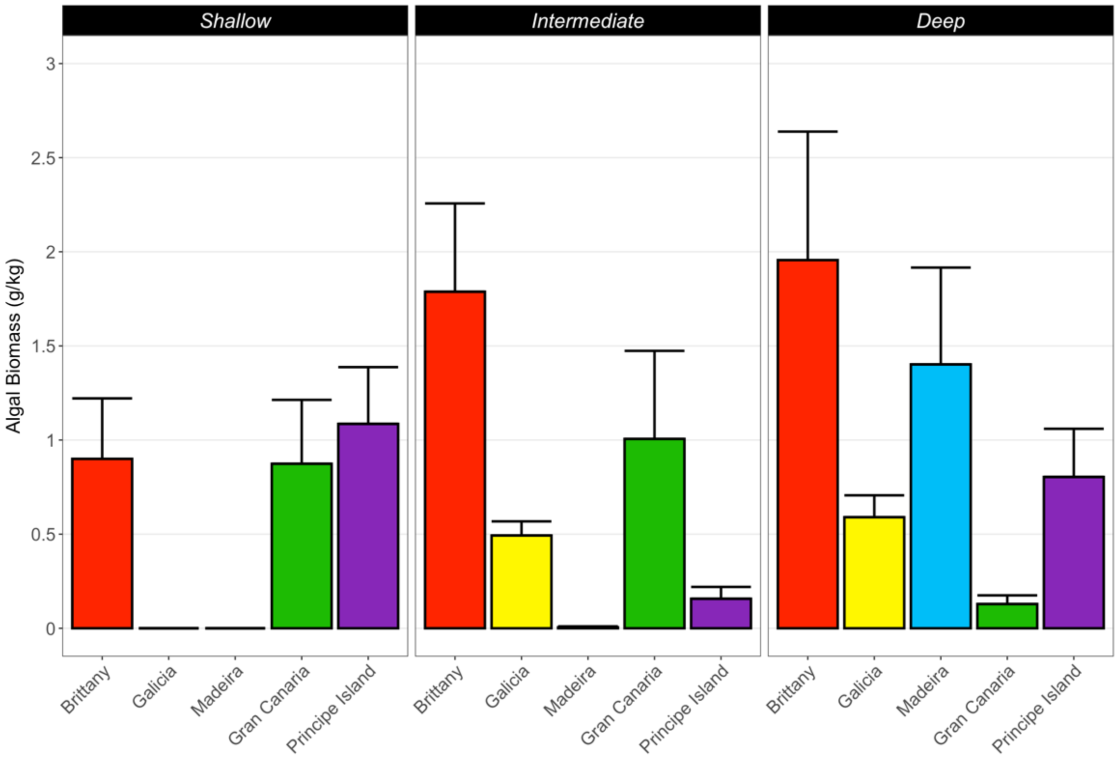

Figure 4. Total macroalgal biomasses (dry weigh) at each depth stratum and region (Brittany, Galicia, Madeira, Gran Canaria and Principe Island. Error bars are + SE of means (n = 125).

Table *5*. Results of GLMs testing whether algal biomass differed between depths using latitude as a covariable. Significant differences at P . <0.1 * < 0.05, **< 0.01, ***< 0.0001.

	Fixed effects				
	Estimate	Std. Error	Z Value	P	
Epiflora					
Intercept (Depth [Shallow])	-0.77	0.27	-2.83	0.0047	**
Latitude	0.02	0.01	2.34	0.0193	*

Depth [Intermediate]	-0.08	0.25	-0.31	0.7538	
Depth [Deep]	0.27	0.24	1.13	0.2568	
Intercept (Depth [Intermediate])	-0.85	0.28	-3.10	0.0020	**
Latitude	0.02	0.01	2.34	0.0193	*
Depth [Shallow]	0.08	0.25	0.31	0.7538	
Depth [Deep]	0.35	0.22	1.56	0.1185	
Intercept (Depth [Deep])	-0.50	0.26	-1.95	0.0517	.
Latitude	0.02	0.01	2.34	0.0193	*
Depth [Shallow]	-0.27	0.24	-1.13	0.2568	
Depth [Intermediate]	-0.35	0.22	-1.56	0.1185	

3.4 Epifauna

The abundance of epifauna (per kg of rhodolith) was variable among depth and regions. From the 34,386 organisms found, two phyla dominated: Arthropoda and Mollusca (Fig. 6; Fig. A3). The highest abundances of epifauna were generally found in Brittany (Table 6). In Brittany annelids, arthropods and echinoderms decreased with depth, while molluscs were found to increase with depth. The opposite occurred in Galicia, where annelids, arthropods and echinoderms increased with depth, while molluscs were found to decrease with depth (Table 6). Similar to Brittany, in Madeira annelids, arthropods and molluscs decreased with depth, while echinoderms abundance was higher at intermediate depths. In Gran Canaria annelids and arthropods decreased with depth, echinoderms increased with depth and molluscs' abundances were higher at intermediate depths. Finally, in Principe Island annelids and echinoderms increased with depth, arthropods decreased with depth and molluscs' abundances were higher at intermediate depths.

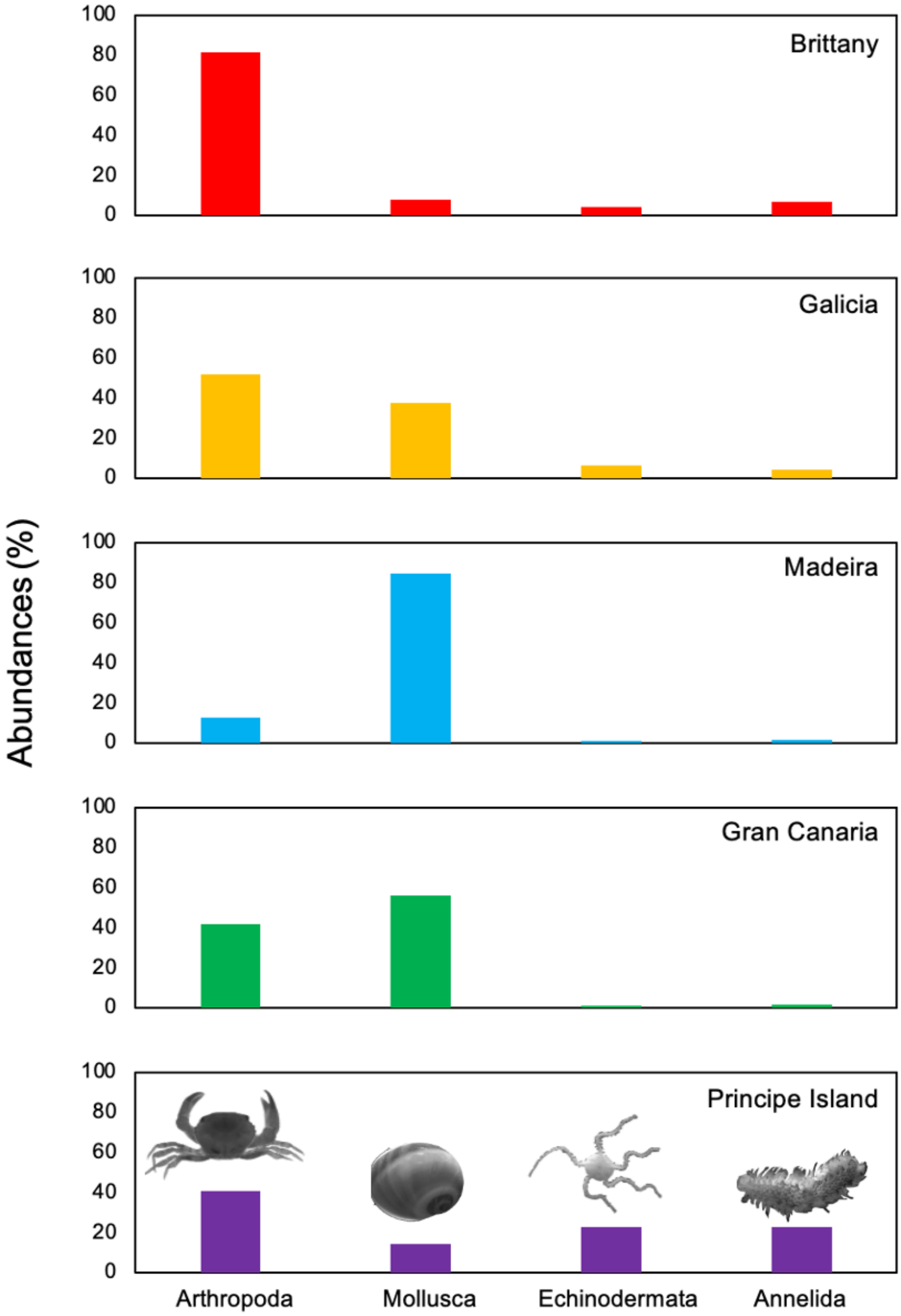

Figure 5. Faunal abundance (expressed in %) at each region (Brittany, Galicia, Madeira, Gran Canaria and Principe Island), showing abundances of the four main phyla sampled (Arthropoda, Echinodermata, Mollusca, and Annelida).

Table 4. Faunal abundance (individuals) standardized by the sample weight of rhodoliths (mean ± SD) at each depth strata over regions, Annelida abundance, Arthropoda abundance, Echinodermata abundance and Mollusca abundance.

Abundance (Ind·kg^{-1})	Brittany	Galicia	Madeira	Gran Canaria	Principe Island
Annelida					
Shallow	149.7 ± 144.9	-	6.3 ± 4.2	3.5 ± 2.3	3.8 ± 1.7
Intermediate	39.5 ± 22.0	2.9 ± 2.0	4.4 ± 3.3	1.4 ± 1.2	5.2 ± 4.2
Deep	37.6 ± 29.7	13.3 ± 11.5	2.6 ± 2.1	2.8 ± 3.4	12.6 ± 9.5
Arthropoda					
Shallow	1425.2 ± 956.6	-	42.9 ± 18.0	86.6 ± 24.3	16.2 ± 9.8
Intermediate	531.3 ± 546.4	71.7 ± 409	43.2 ± 21.5	72.8 ± 46.7	12.1 ± 4.9
Deep	727.7 ± 956.6	125.6 ± 120.0	16.6 ± 8.0	36.5 ± 12.8	10.5 ± 6.0
Echinodermata					
Shallow	69.7 ± 45.1	-	3.3 ± 9.2	0.9 ± 1.2	4.9 ± 3.7
Intermediate	26.6 ± 31.4	7.3 ± 4.5	4.5 ± 2.4	1.1 ± 1.4	6.7 ± 5.2
Deep	34.3 ± 23.1	17.2 ± 8.9	1.4 ± 1.1	2.1 ± 2.0	10.1. ± 5.1
Mollusca					
Shallow	64.2 ± 83.4	-	313.4 ± 129.6	96.7 ± 130.3	3.9 ± 3.1
Intermediate	75.0 ± 67.1	103.2 ± 42.8	245.9 ± 69.4	153.4 ± 66.2	5.9 ± 5.1
Deep	114.1 ± 88.8	39.8 ± 17.6	124.2 ± 83.4	14.6 ± 8.1	4.0 ± 3.3

4. Discussion

This study provided for the first-time quantitative data on how depth affected the structure and epiphytes communities associated with rhodolith beds along a latitudinal gradient across the Eastern Atlantic Ocean. In general heterogeneity between regions (latitudes) conditioned the rhodolith size, morphology, and epiphytic communities (algal biomass and macrofaunal assemblages), in spite of bathymetrical levels analysed.

4.1. Rhodolith attributes

Rhodolith growth depends on a combination of environmental variables, in particular irradiance, water chemistry, temperature, turbulence and sedimentation (Bosence, 1983; Wilson et al., 2004; Teichert et al., 2012). Turbulence generates rotation of the rhodoliths, allowing light to reach the entire organism and thus preventing burial (Steneck 1986; Johnson et al., 2017). However, the rhodoliths need to be in a certain environmental balance between the movement generated by waves and sedimentation, i.e., just enough turbulence to avoid burial, but not too strong to break them up (Sciberras et al., 2009; Pascelli et al., 2013). Many authors (Amado-Filho et al., 2007; Gagnon et al., 2012) identify a direct relationship between size and water depth suggesting that bigger sizes are found at greater depths because it remains protected of wave-induced turbulence occurred at shallower depths where rhodoliths may undergo movement, breakage, and erosion. In opposition, lack of turbulence at deeper strata may bury rhodoliths by the sediment, limiting their ability to photosynthesize and thus their growth (Marrack, 1999). This effect was observed mostly along all sampled locations in spite of different rhodolith species composition. For example, in Brittany the rhodoliths were collected in two location with different environmental contexts: Location 1, situated near Concarneau (Fig. 2), represents an open ocean site with lower percentage of mud, mostly sandy, but high exposure to storms and swell, meanwhile Location 2, situated inside the Brest estuary (Fig. 2), have predominant muddy bottoms and less exposed sites (Bassoulet, 1979; Gregoire et al., 2016). Dutertre et al. (2015) study how environmental factors affect rhodolith bed structure in Brittany showing how currents greater than 0.5m/s and high percentages of mud are detrimental to rhodolith growth. Therefore, intra-location differences in terms of hydrodynamic context and sedimentation rates, may explain the high heterogeneity in rhodolith mean diameter observed between sites and across the bathymetrical gradient (Table A2) (Scoffin et al., 1985). Similarly, the effects of high sedimentation rates and burial effect on rhodoliths, could be observed in Galicia for both sample locations (estuarine context of ‘Ria Arousa’; Fig. 2) (Seoane-Camba & Campo Sancho, 1968; Peña & Criado, 2009), i.e., areas of high sedimentation and less turbulence, where the size of rhodoliths decreased with depth, because sedimentation increased due to a lower wave action on the bottom (Table A2).

The results obtained in Madeira and Gran Canaria agreed with previous studies conducted in the same locations (Otero-Ferrer et al., 2020a; Neves et al., 2021) where the size of rhodoliths generally shows an increasing trend with depth (Table A2). The sampled locations are characterized by higher hydrodynamics in shallower depths which affect rhodolith size by breakage and burial. In these latitudes rhodoliths beds mostly grow over coarse gravel and clean sands (Neves et al., 2021). Finally, rhodolith sea bottoms of Principe 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 rhodolith size (Otero-Ferrer et al., 2020b).

In spite no differences were observed in rhodolith shape across bathymetrical gradients along studied latitudes, rhodolith showed mostly uniform spheroidal shapes (Fig. 4) except in Galicia with predominant discoidal types in rhodoliths sampled, and Brittany with mostly spherical shapes mixed with bladed and sparsely discoidal and ellipsoidal morphologies. Generally, rhodolith shape changes from spherical to discoidal as hydrodynamic conditions decrease (Bosellini & Ginsburg, 1971; Bosence, 1976; Sciberras et al., 2009; Pascelli et al., 2013; Chimienti et al., 2020; Schlüter et al., 2021). The predominant spherical shapes across the entire bathymetrical range sampled in Madeira, Canary Islands and Principe reflects a highly dynamic marine environment, typical from oceanic islands open to large oceanic swells (Otero-Ferrer et al., 2020a).

Additionally, in particular, locations sampled in Brittany and Galicia showed the lowest sphericity values, probably related with less exposure conditions from currents and the action of waves inside the estuaries compared to the exposed ones in subtropical and tropical latitudes (Peña & Criado, 2009).

4.2. Epiflora

Theoretically, algal growth is mainly determined by the availability of light availability and nutrients, temperature and water motion (Hurd, 2000). For seaweeds growing on rhodoliths (epiflora), their biomass also depends on the rhodolith shape, the habitat stability (Pascelli et al., 2013) and the sedimentation rates. Hence, reductions of epiflora biomass across depth have been described because light is a key-limiting factor in these gradients (Duarte, 1991; Frade et al., 2008). High sedimentation rates normally found at deeper depths, can also affect rhodoliths' attached epiflora, as it increases the turbidity of the water, modifying light availability (Davies-Colley & Smith, 2001; Bessell-Browne et al., 2017). Additionally, when comparing algal biomass across latitudes, differences can be biased by seasonal changes, which also condition the macroalgal production throughout the year (Steinman & McIntire, 1987). Therefore, seasonal peaks can fluctuate between locations correlated with changes in nutrients, temperature, and light availability. For example, while in northern European Atlantic waters can experience a drastic increase of epifloral biomasses that occur between summer and early autumn (Grall et al., 2006; Peña et al., 2014; Hernandez-Kantun et al., 2017), in southern subtropical and tropical latitudes, such as Madeira and Canary islands or even Principe, changes in algal production are less marked and maximum production peaks appear during autumn spring – early summer (Reyes et al., 1998). 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 normally the time of highest algal production in both regions (Hellio et al., 2004; Gómez et al., 2013) with lower waves allowing epiphytes to grow (Qui-Minet et al., 2018).

On the other hand, changes in algal biomass across latitudes could also reflect changes in habitat structure (e.g. rhodolith size) across the bathymetrical gradient. Hence, the abundance of algal biomass in Madeira was only noticeable in the deeper strata, probably related to the larger size of the rhodoliths and the scarce presence of infralittoral grazers (e.g. *Diadema africanum*), observed in higher densities in shallow and intermediate depths (pers. Obs.) able to limit algal growth (Friedlander et al. 2017). In the case of Gran Canaria and Principe the effect of depth and light availability could be demonstrated on the abundance of epiphytic epiflora growing on rhodoliths along the bathymetrical gradient (Rebelo et al., 2018; Otero-Ferrer et al., 2020a). Light and high sedimentation are key-limiting factors on macroalgal distribution across depth gradients (Steller & Foster, 1995; Balata & Piazzi, 2008), which, together with the larger size of the rhodoliths, may explains the greater abundance of algae in the intermediate depth in Gran Canaria. Similarly, at Principe the highest abundances of algae were found in the shallow depths, this may be attributed to the fact that the main species of algae found are green algae (Maia et al., 2018; Canterle et al., 2020; Cosme et al., *in press*), which appear to be highly related with high light availability and shallower depths (Ganf & Oliver, 1982), and the presence of scleractinian coral colonies interspersed with rhodoliths in deeper strata which reduce algal colonization (Cosme et al., *in press*).

4.3 Epifauna

Rhodoliths can facilitate faunal assemblages colonization because their own structures add complexity (Emilio Sánchez-Moyano et al., 2007; Navarro-Mayoral et al., 2020; Otero-Ferrer et al., 2020a), but also due to "habitat cascades" associated with epiphytic organisms (e.g. algae or sessile fauna), which increases the amount of available habitat and trophic resources (Thomsen et al., 2010). Consequently, a high heterogeneity in abundances was observed between latitudes irrespective of depths. Arthropods, molluscs, annelids, and echinoderms were the dominant faunal groups, which agrees with other studies performed on tropical, subtropical and temperate rhodolith sea bottoms (Barbera et al., 2003; Steller et al., 2003; Hinojosa-Arango & Riosmena-Rodríguez, 2004; Grall et al., 2006; Riera et al., 2012; Otero-Ferrer et al., 2020a). Overall, the dominant phylum (in terms of individual abundance) was Arthropoda, mainly composed by the order Amphipoda and the infraorder Brachyura. Several authors denoted Amphipoda as one of the most abundant macrofaunal element in several rhodolith beds (e.g. California, Bergen et al., 2001; Ireland, De Grave & Myers, 1999; Italy, Deidun et al., 2022). Molluscs were the second most abundant phylum, (Hall-Spencer, 1998) with several works confirming rhodoliths beds as an outstanding diversity reference of this phylum (Riera et al., 2012; Otero-Ferrer et al., 2019). This dominance may reflect larval attraction to the structured settlement substrate provided by the rhodoliths and the physical conditions provided (Steller et al., 2003). Finally, annelids and echinoderms (mainly brittle stars and sea cucumbers) also contribute significantly to the epifauna abundances present in sampled latitudes, especially in northern European latitudes (Muths et al., 2006; 2009; Pérez-Portela et al., 2013).

Although no clear pattern was observed in the macrofaunal groups in relationship with depth, further studies with more detailed taxonomic information is required to confirm this statement, observed locally in other latitudes (Bilyard & Carey, 1979; Pamungkas J et al., 2021).

5. Conclusions

Rhodolith beds, as well as their attributes (size and shape) and epibionts are highly conditioned by the environmental context, i.e., turbulence, light and sedimentation. This modifies the size, shape, and flora present in the different study locations. In general, rhodolith size was smaller at shallow depths, while sphericity reflected the marine dynamics of each location, having predominant spherical shapes in very exposed environments or discoidal rhodoliths mainly dominating in estuarine contexts. The algal biomass (epiflora) was subject to high heterogeneity due to the instability of the rhodolith beds.

Overall, this study demonstrated how latitudinal variability was not as relevant as local variability, which is what really influenced the structure of rhodolith beds, contrary to what happens in macroecological gradients where a latitudinal trend is observed.

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Appendix

Table A1. Date, location (latitude and longitude) and depth (meters) of samples taken.

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

Table A1. Morphological attributes (mean ± SD) of rhodoliths at each depth strata over latitudes, 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.

	Brittany	Galicia	Madeira	Gran Canaria	Principe Island
Mean Diameter (mm)					
Shallow	14.20 ± 2.97	-	35.40 ± 3.78	16.90 ± 1.85	24.80 ± 3.39
Intermediate	17.10 ± 2.60	14.10 ± 1.52	39.30 ± 2.00	30.10 ± 8.95	25.30 ± 5.38
Deep	18.40 ± 5.72	12.10 ± 2.56	42.90 ± 1.85	22.00 ± 4.81	20.00 ± 4.24
Sphericity (%)					
Shallow	71.60 ± 4.12	-	83.78 ± 0.56	80.24 ± 2.07	76.69 ± 3.25
Intermediate	65.67 ± 2.65	37.12 ± 23.40	87.93 ± 0.40	81.26 ± 1.69	71.63 ± 4.38
Deep	63.45 ± 8.07	29.86 ± 1.88	88.41 ± 0.69	79.64 ± 0.49	71.77 ± 4.39
Epiflora (g/kg)					
Shallow	0.90 ± 1.02	-	0.00 ± 0.00	0.87 ± 1.07	1.09 ± 0.95
Intermediate	1.79 ± 1.48	0.49 ± 0.24	0.01 ± 0.02	1.01 ± 1.48	0.16 ± 0.10
Deep	1.96 ± 2.16	0.59 ± 0.37	1.40 ± 1.63	0.13 ± 0.14	0.80 ± 0.26

Figure A3. Six different epibionts found in the rhodolith seabeds: a) Brachyura, b) Isopoda, c) Ophiuroidea, d) Polychaeta, e) Bivalvia and e) Gastropoda.