The Punta de la Mona Rhodolith Bed: Shallow-Water Mediterranean Rhodoliths (Almuñecar, Granada, Southern Spain)

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Shallow-water rhodolith beds are rare in the Mediterranean Sea and generally poorly known. The Punta de la Mona rhodolith bed extends for 16,000 square meters in shallow and oligotrophic waters at the southern coast of Spain, off Almuñecar in the Alborán Sea. We present a detailed analysis of the structure (rhodolith cover and density, rhodolith size and shape, sediment granulometry) and morphospecies composition of the bed along a depth gradient. A stratified sampling was carried out at six depths (9, 12, 15, 18, 21, and 24 m), estimating rhodolith cover and abundance; rhodoliths were collected from one 30 by 30 cm quadrat for each transect, resulting in 18 samples and a total of 656 rhodoliths. The collected rhodoliths were measured and the coralline algal components identified morphoanatomically through a stereomicroscope and SEM. Sediment on the seafloor mainly consisted of pebbles and cobbles; the highest rhodolith cover occurred between 15 and 18 m, and the lowest at the shallowest and deepest transects (9 and 24 m). Mean Rhodolith size was similar throughout the depth range (23–35 mm) with a slight increase at 24 m, although the largest rhodoliths occurred at 21 m. In monospecific rhodoliths, size depended more on the forming species than on depth. We found 25 non-geniculate coralline morphospecies, nearly all rhodolith-forming morphospecies reported in the Mediterranean Sea in recent accounts. The highest morphospecies richness (18–19) and proportional abundance were found at intermediate depths (15–18 m), where rhodolith cover is also highest. *Lithophyllum incrustans* and *Lithophyllum dentatum* dominated at shallow depths (9–12 m), whereas *Lithothamnion valens* was the dominant species at intermediate and greater depths. Overall, the latter species was the most common in the rhodolith bed. The shallow-water rhodolith bed in Punta de la Mona is probably the most diverse in the Mediterranean Sea. This highlights the importance of the conservation of this habitat and, in general, emphasizes the role of the Alborán Sea as a diversity center of coralline algae. The Punta de la Mona example contradicts the common assumption in the geological literature that rhodolith beds are indicative of oligophotic environments with high nutrients levels.

Keywords: coralline red algae, depth-gradient patterns, rhodolith cover and size, rhodolith diversity, Alboran sea

INTRODUCTION

Rhodolith beds are living or fossil concentrations of free-living coralline algae (Riosmena-Rodríguez, 2017). The largest rhodolith beds occur in Brazil, where they cover a substantial part of the continental shelf, with some extending for more than 20,000 km^2 (Amado-Filho et al., 2012). They are also widespread around islands and capes, and on seamounts in Baja California,
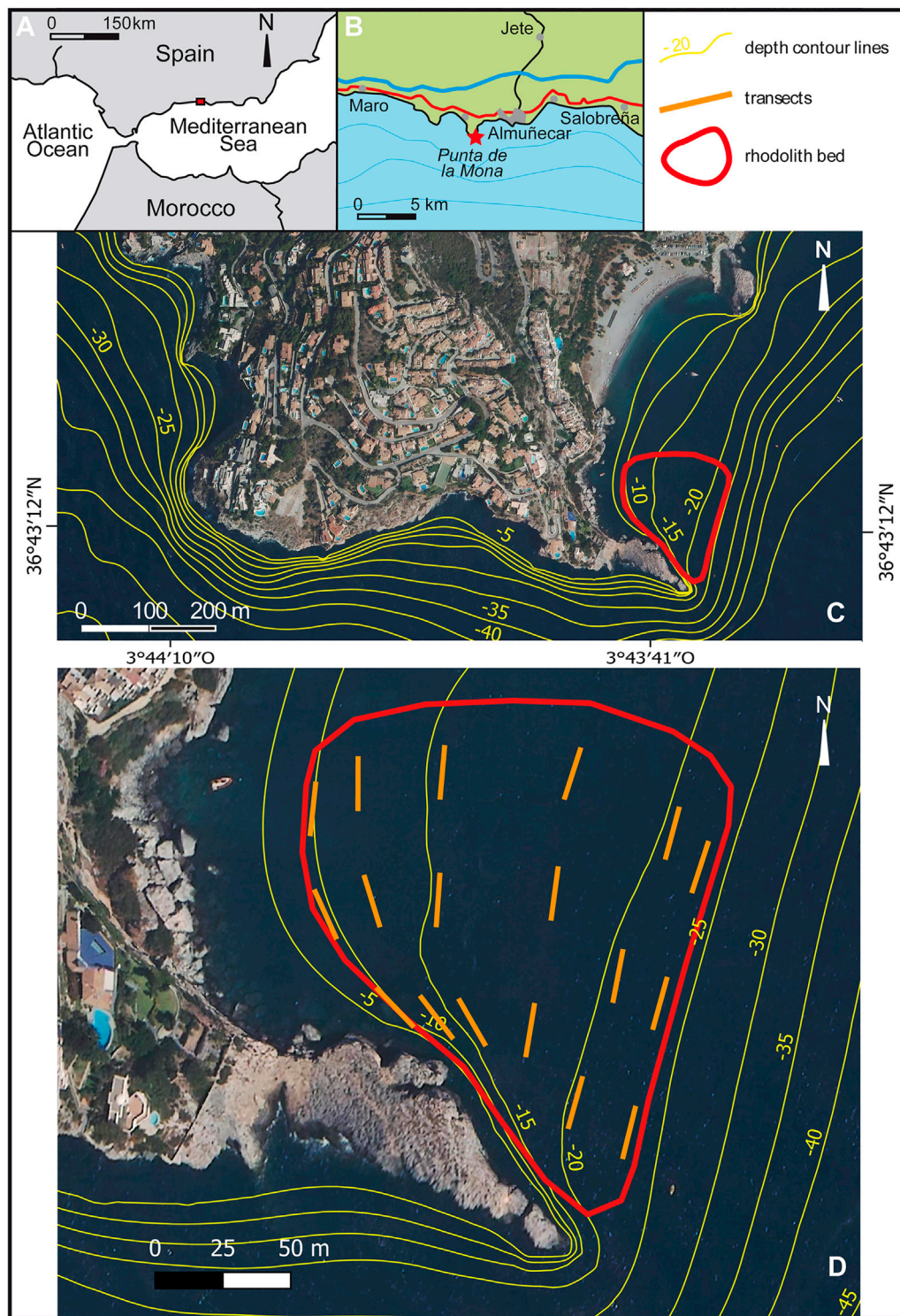

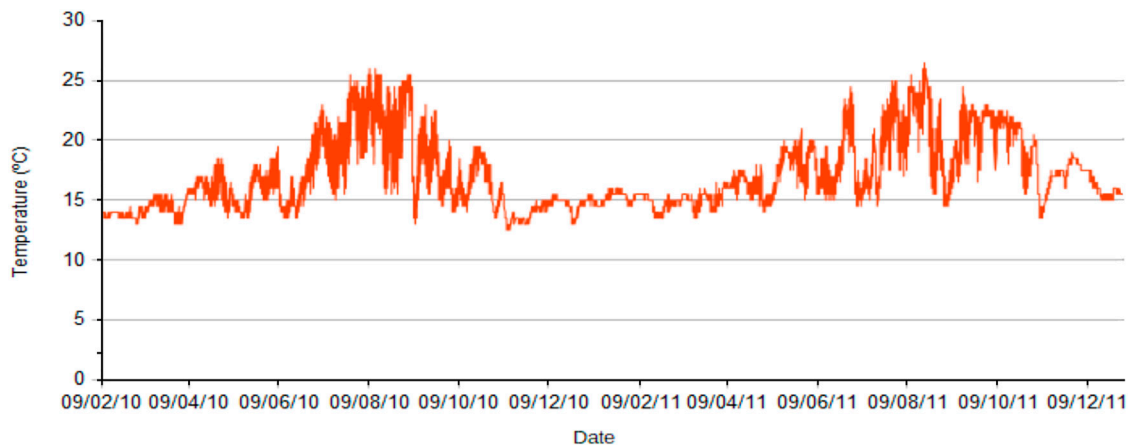**FIGURE 1 |** Study area east of Punta de la Mona in southern Spain.

FIGURE 2 | Water temperature at 16 m in the Punta de la Mona between February 2010 and December 2011.
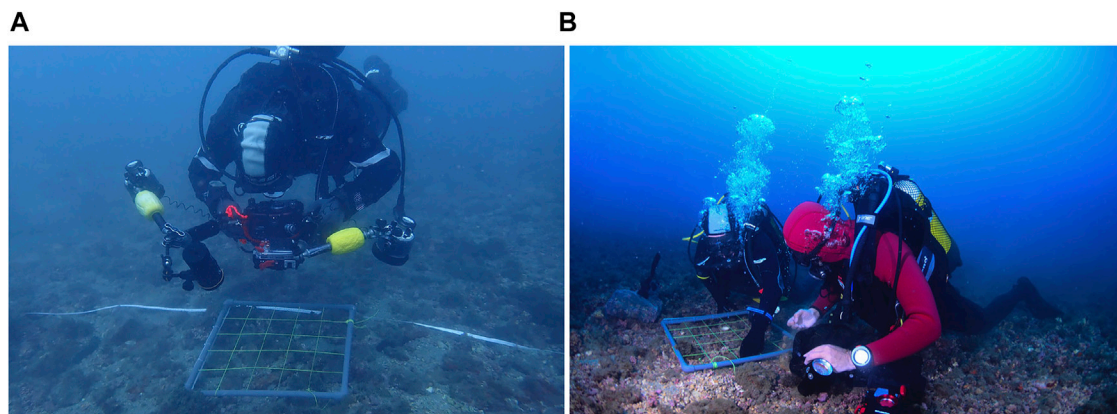

FIGURE 3 | (A) Line transect and quadrat (50 × 50-cm) for living-rhodolith cover estimation. (B) Quadrat (30 × 30-cm) for rhodolith collection.

northern Atlantic, Mediterranean Sea, and Australia (Foster, 2001; Steller et al., 2003; Harvey et al., 2016; Basso et al., 2017; Hernández-Kantún et al., 2017; Kamenos et al., 2017). Fragkopoulou et al. (2021) estimate that rhodolith beds might cover up to 4.1×10^6 km² on the seafloor, being one of the largest benthic communities dominated by macrophytes, together with seagrass beds, kelp forests and coralligènes. The main environmental factors that condition the development of rhodolith beds are light, temperature, nutrients, and currents or bioturbation phenomena that avoid the rhodoliths being buried by sediments (Jacquotte, 1962; Birkett et al., 1998; Marrack, 1999; Carvalho et al., 2020).

Rhodolith beds are considered critical ecosystems for marine biodiversity (Fredericq et al., 2019), which depends on their structural complexity (Bordehore et al., 2003; Teichert et al., 2014). In fact, rhodoliths are ecosystem engineers (Nelson, 2009), which generate structural complexity and hard substrates on detrital sea floors (Cabioch, 1969), fostering biodiversity by providing habitat to species of both hard and mobile bottoms (Keegan, 1974; Barberá et al., 2003), from

microfauna (Steller et al., 2003; Foster et al., 2007) to macroalgae (Peña et al., 2014), and to species of commercial interest (Hall-Spencer et al., 2003; Kamenos et al., 2004; Steller and Cáceres-Martínez, 2009). Rhodolith beds are vulnerable to changes in the environment, especially those resulting from human activities, which result in reduced complexity and biodiversity (Peña and Bárbara, 2010). Moreover, rhodolith beds provide environmental services, such as carbonate sequestration and habitat complexity with unique benthic diversity and associated fish assemblages, thus justifying urgent actions to protect them (Amado-Filho et al., 2017). The knowledge of their distribution, structure and composition is, therefore, necessary to preserve the ecosystem services of rhodolith beds (Salomidi et al., 2012; Basso et al., 2016).

Reported rhodolith beds are scarce in the Alborán Sea, the southwestern sector of the Mediterranean (Robles, 2010). The largest one occurs on the Alborán island shelf, with several square kilometers extending from 20 to 100 m depth (Betzler et al., 2011; Gofas et al., 2014). Twenty-one species of coralline algae were
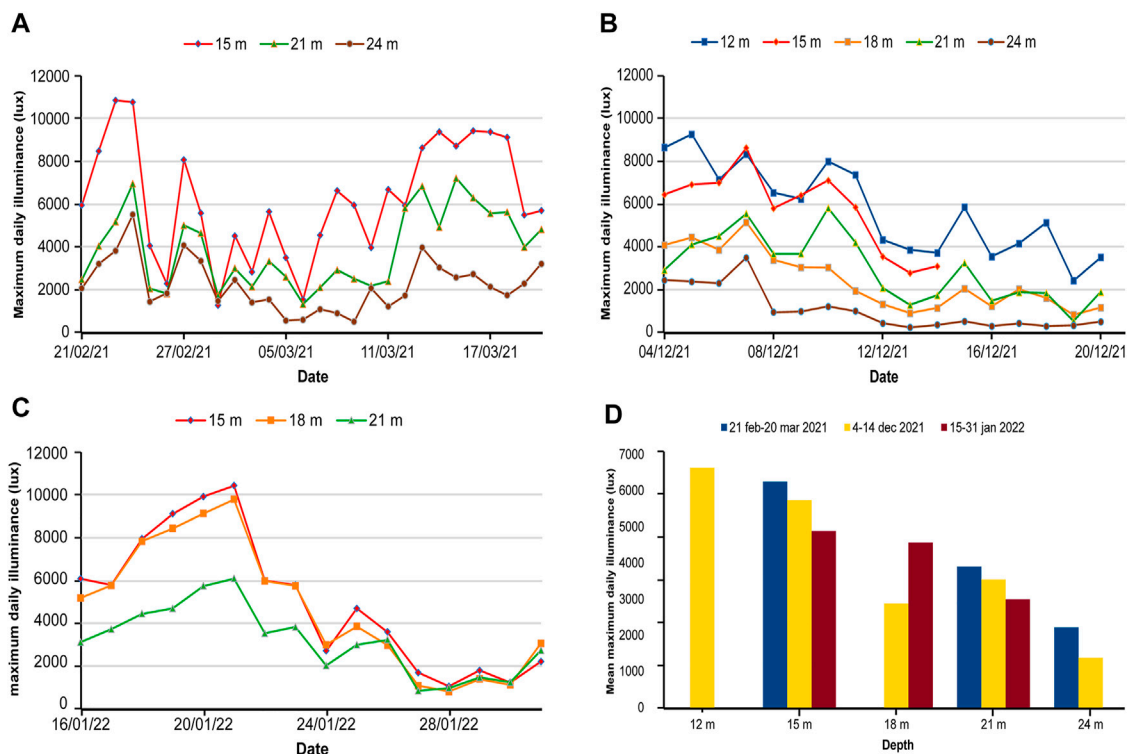
FIGURE 4 | Daily maximum illuminance from **(A)** 21 February to 21 March2021 and **(B)** 4 to 20 December 2021, **(C)** 15 to 31 January 2022 and **(D)** variation of mean maximum illuminances by depth.

recognized by molecular analysis in this bed, ten of which remain unnamed (Gofas et al., 2014). Rhodolith beds have also been recorded in the Tres Forcas cape, in Morocco (CAR/ASP-PNUE/PAM, 2013), Gibraltar Straits (García-Gómez et al., 2003), Ceuta (Ocaña et al., 2009) and the Almería shelf, in southeastern Spain (Ministerio de Agricultura, Alimentación y Medio Ambiente, 2012), although their structure and composition were not reported. The composition of coralline algal assemblages, including those forming rhodoliths, was described at the northeastern limit of the Alborán Sea, in the waters of the Cabo de Gata Natural Park in Almería (Braga et al., 2009; Bassi et al., 2020).

This work aims to describe a shallow-water rhodolith bed located off the Punta de la Mona, Granada, (southern Spain) in the northern shelf of the Alborán Sea. We assess the rhodolith cover, size, shape, morphospecies composition and diversity along a depth range from 9 to 24 m, and relate the observed patterns to environmental variables, such as temperature and illuminance. We stress the uniqueness and originality of this bed and the need for conservation of marine biodiversity reserves.

MATERIAL AND METHODS

Study Area

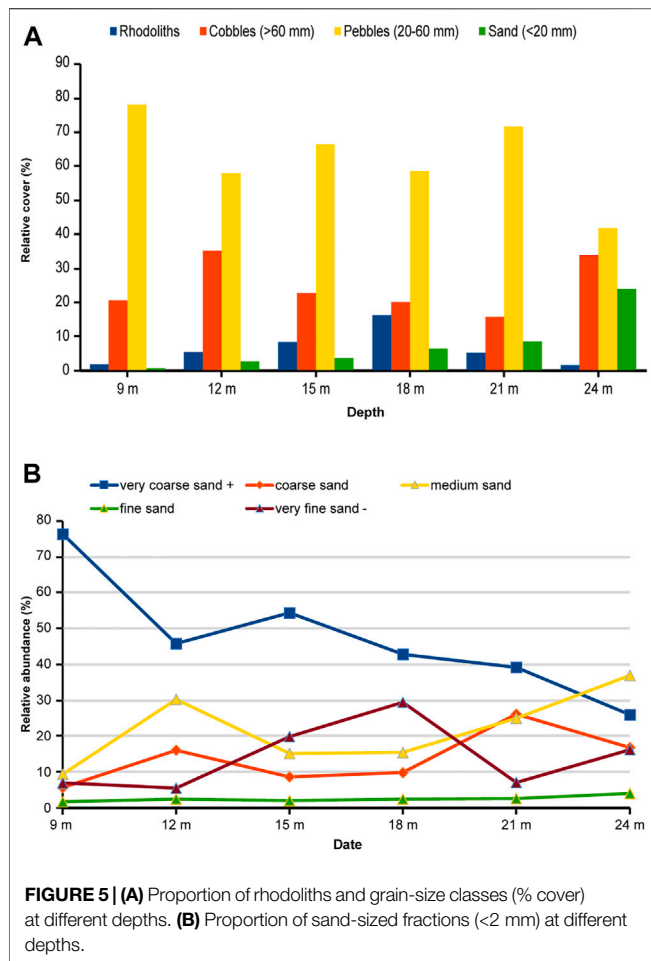The study area is located at the southern coast of Spain, near Almuñecar in the province of Granada. The area encompasses

a rhodolith bed of 16,000 m^2 extending from 9 to 24 m depth in a small bay east of Punta de la Mona (36°41′13′′ N, 3°43′39′′ W). This is a cape running N-S for approximately 1,000 m and then bending to a E-ESE direction. As a result, the small bay in which the rhodoliths occur is protected from the westerlies (**Figure 1**).

According to the wave modeling SIMAR for the Punta de la Mona (site 2039080), during the period January 1958-July 2021, dominant wave directions were from E-ESE (41.8%) and W-WSW (30.3%). Waves had heights above 2 m only 4.5% of the time, and calms and waves <0.5 m occurred 55% of the time (Puertos del Estado, 2021a).

The levels of chlorophyll A from 2000 to 2020 obtained from the AQUA MODIS satellite indicate an oligotrophic environment, with mean values of 1–1.5 mg/cm^3, peaking in spring (1.5–2 mg/cm^3) and dropping in autumn-winter (>0.01 mg/cm^3) (REDIAM, 2021).

Sea surface temperature (SST) in 2020–2021, estimated by the satellite Sentinel (site 2039080), ranged between 27.1°C in summer and 13.3°C in winter (Puertos del Estado, 2021b). Measuring every 30 min at 16 m depth, in 2010–2011 the average temperature was 17°C, ranging from 26.5°C in summer to 12.5°C in winter. The summer temperatures underwent strong fluctuations due to upwelling events related to storms from the west, whilst winter temperatures were more stable around 15°C (**Figure 2**). New temperature measurements were carried out for this study (see below).

FIGURE 5 | (A) Proportion of rhodoliths and grain-size classes (% cover) at different depths. **(B)** Proportion of sand-sized fractions (<2 mm) at different depths.

Sampling Design and Sample Collection

The extent of the rhodolith bed was delimited by mapping the seafloor by SCUBA diving. A stratified sampling design at six depths (9, 12, 15, 18, 21 and 24 m) was used to analyze distribution and density of rhodoliths. Three 20 m long line transects were placed at each depth. To estimate the living (coloured) rhodolith cover, photographs of ten 50x50 cm quadrats were taken in each transect, i.e., 30 photographs in each depth and 180 photos in total (**Figure 3A**). The pictures were processed with the software ImageJ (National Institutes of Health, United States, https://imagej.nih.gov) to obtain the area covered by living-rhodoliths, cobbles, pebbles, and sand in each quadrat. The proportion of dead rhodoliths was negligible. All rhodoliths in a randomly placed 30 × 30 cm quadrat were collected in each transect, i.e., 3 collections from each depth and 18 in total for measuring and identification of coralline algal composition. Collections were done between May and December 2020 (**Figure 3B**). Both unattached coralline growths and pebbles coated by corallines (independently of coating proportion) were collected and air dried for at least 2 days.

Environmental Variables

Six dataloggers (HOBO Pendant® MX, Temp/Light, www.onsensetcomp.com) were installed for data acquisition of temperature (°C) and illumination (lux) at each sampling depth, using the maximum daily illuminance by depth from measurements taken every 10 min (Otero-Ferrer et al., 2020). Two 50-ml samples of sediment smaller than pebbles were collected in each sampling depth to estimate granulometry. The samples were dried and then sieved in >1, 0.5, 0.250, and <0.125 mm fractions.

Size, Shape and Morphology of Rhodoliths

The long, intermediate and short axes of all collected rhodoliths (n= 656) were measured to estimate size, using the mean of the three axes $(L + I + S)/3$ (Bosellini and Ginsburg, 1971) and the sphericity $\psi_p = \sqrt[3]{\frac{S^2}{LS}}$ and shape classes according to Sneed and Folk (1958) and Bosence (1976, 1983). The Microsoft Excel triangular diagram plotting spreadsheet (TRI-PLOT) of Graham and Midgley (2000) was used to illustrate the representation of the shape classes. Collected rhodoliths were classified according to their morphology in four morphotypes. Three of them (pralines, branches, and boxwork rhodoliths) followed the classification scheme proposed by Basso (1998, 2012) and Basso et al. (2016); the additional class (other) comprised coatings (less than 50% of coralline algal volume, Steneck, 1986) on lithoclasts and bioclasts, and compact rhodoliths of encrusting corallines, which are difficult to distinguish without sectioning them (Aguirre et al., 2017).

Taxonomic Identification

Identification of coralline algae forming the rhodoliths was performed with a stereomicroscope and ESEM (FEG-ESEM QuemScan650F). The morphospecies identification followed the available literature on Atlantic and Mediterranean coralline algae and the taxonomy proposed by Cormaci et al. (2017) and AlgaeBase (Guiry and Guiry, 2022). Once the component species in each rhodolith were identified, a visual estimation of their relative proportions on the rhodolith surface was performed. Vouchers of the rhodoliths will be deposited at the University of Granada Herbarium (GDA).

Diversity Indexes

The diversity indexes based in abundance models allow us to compare the diversity of rhodoliths taking into consideration the relative abundance of species in an ecosystem (Magurran, 2004), that is, in our study the relative species-cover (i.e., relative proportions of individual species on the rhodolith surface) or species-frequency (i.e., relative abundance of species) that form the rhodoliths in different depths. The calculation of the Shannon-Wiener index (Magurran, 2004) was made through the formula $H' = -\sum p_i ln$, where p_i is the proportion of cover or frequency of the ith species in each depth.

Data Analysis

Statistical comparisons between groups were performed on R Studio 2021.09.1+372 (RStudio Team, 2020) running R 4.1.2 (R Core Team, 2021). Data manipulation was facilitated by the dplyr 2.1.1, tidyverse 1.3.1, and broom 0.7.10 packages. Plots and
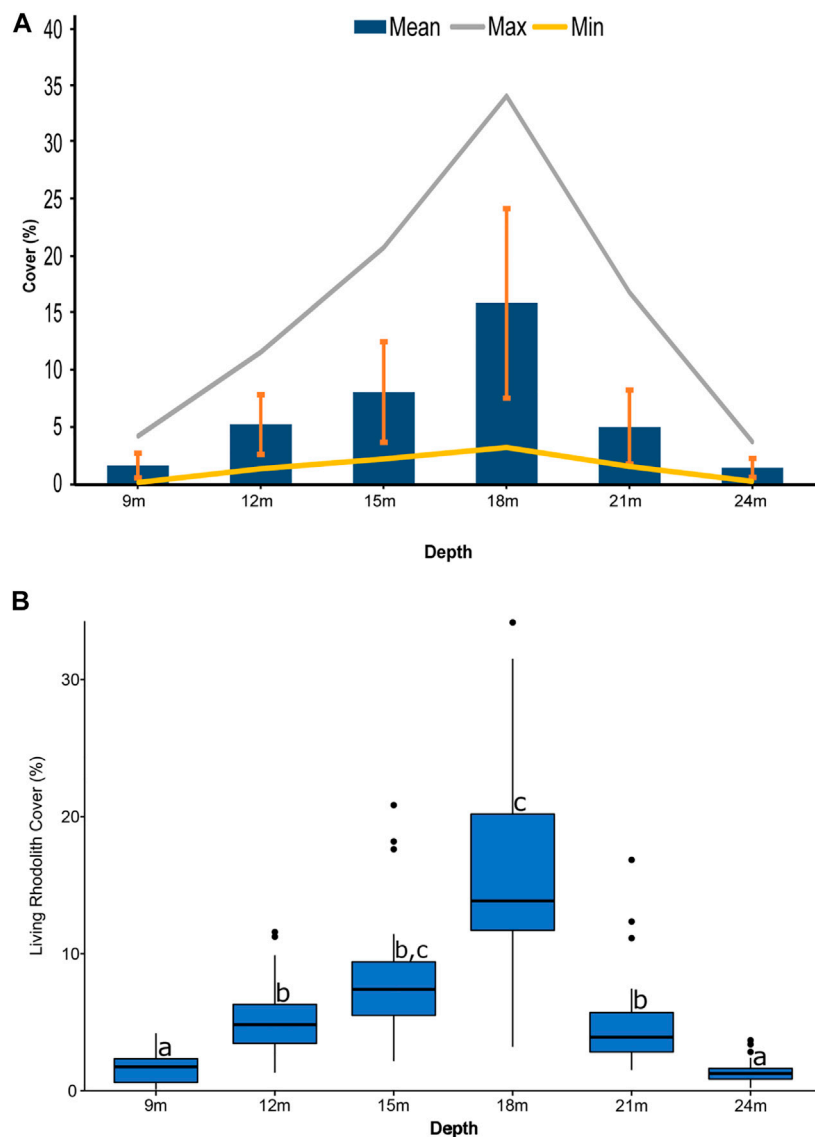
FIGURE 6 | (A) Rhodolith cover (mean and SD) and **(B)** boxplots of rhodolith cover illustrating significant differences detected across depths.

graphs were generated by the ggplot2 3.3.5 package and finalized in Inkscape 1.1.1 (http://inkscape.org). All other statistical tests were from the base package of R.

The non-parametric Kruskal–Wallis rank sum test was used to compare the differences among groups since the data did not fulfill the assumptions of ANOVA. Dunn's test with Holm's correction was used as the post-hoc test when a significant difference resulted from Kruskal–Wallis tests. Comparisons across the sampled depths were made for the benthic cover of 1) living-rhodoliths, 2) different grain sizes (cobbles, pebbles, sand), and the sizes of 3) all rhodoliths, and 4) species of the monospecific rhodoliths, excluding encrusting species (*Lithophyllum incrustans*) and those with <5 samples. 5) Size differences among species of selected monospecific rhodoliths were also compared.

RESULTS

Environmental Data

Data on temperature and illumination were obtained from 21 February to 21 March 2021 at 15, 21 and 24 m depth, from 4 to 21 December 2021 at 12, 15, 18, 21 and 24 m, and from 15 to 31 January 2022 at 15, 18 and 21 m.

The average temperature at the end of the winter in 2021 ranged from 15.8°C at 15 m to 15.7°C at 24 m, whereas in December 2021 they were slightly lower ranging between 15.6°C at 12 m and 15.5°C at 24 m, with no significant differences among depths. In January 2022, the temperature was 15.1°C between the depths of 15–21 m (**Supplementary Table S1**).

Illuminance measured every 10 min showed that the daily maxima was highly variable from 21 February to 21 March 2021,
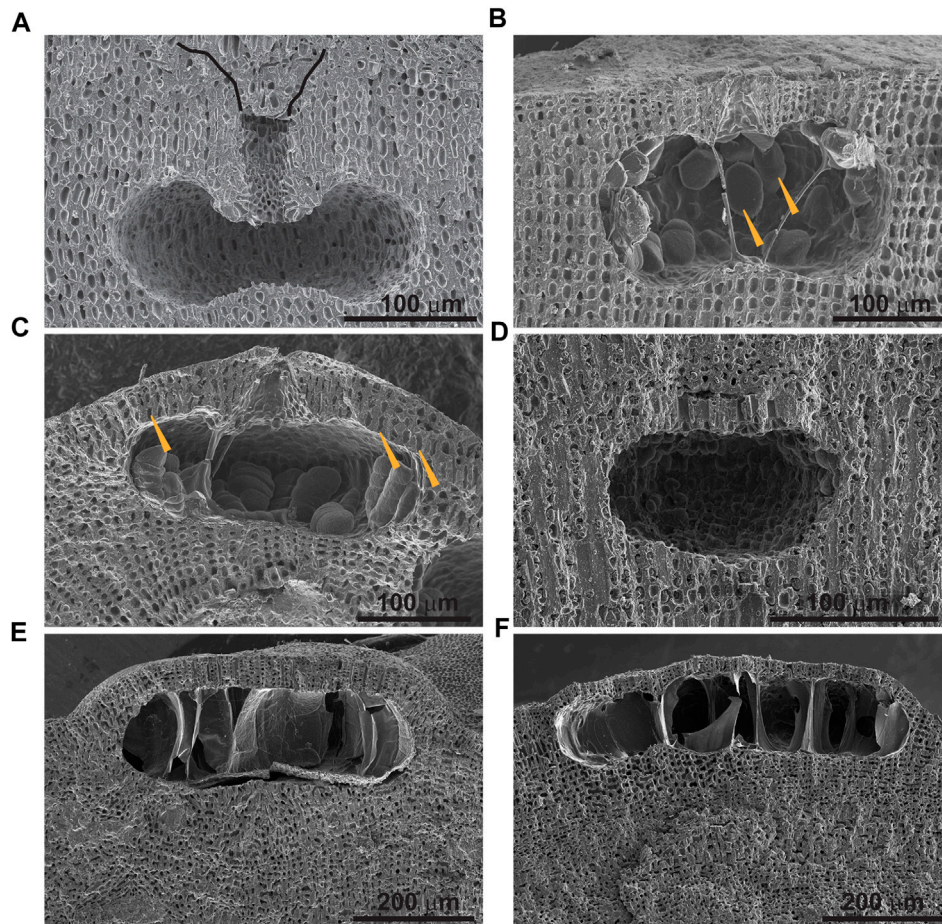
FIGURE 7 | SEM images of selected examples of identified morphospecies: **(A)** Sporangial conceptacle of *Lithophyllum hibernicum*. Black lines mark the contour of funnel-like depression on top of conceptacle pore filled by overgrowing filaments; **(B)** Bisporangial conceptacle of *Lithophyllum orbiculatum*. Arrowheads point to bispores; **(C)** Tetrasporangial conceptacle of *Lithophyllum nitorum*. Arrowheads point to elongated cells at the base of conceptacle roof; **(D)** Tetrasporangial conceptacle of *Phymatolithon calcareum*; **(E)** Tetrasporangial conceptacle of *Lithothamnion corallioides*; **(F)** Tetrasporangial conceptacle of *Lithothamnion valens*.

with a maximum value of 10,875 lux at 15 m and a minimum of 486 lux at 24 m (**Figure 4A**). The average maximum illuminance at the end of the winter showed a marked gradient with depth (**Figure 4D**). In a similar way, in December 2021 the daily maximum illuminance ranged from 9,224 lux at 12 m and 170 lux at 24 m (**Figure 4B**). The decreasing gradient with depth showed a reversal at 18 m where the values were lower than at 21 m (**Figure 4D**). In January 2022, the maximum daily illuminance ranged between 10,416 and 827 lux at 15 m (**Figure 4C**), with a reduction in mean illuminance to 93.6% at 18 m and 61.4% at 21 m with respect to at 15 m (**Supplementary Table S2**). In the three periods, the reduction in maximum illuminance between 15 and 21 m was similar, with values of 62.5, 61.8 = (3543.7/5734.6); 53.5% in **Supplementary Table S2** because the basis was the lux at 12 m, and 61.4% (**Figure 4D**; **Supplementary Table S2**).

Regarding grain size on the seafloor, pebbles were the commonest grains at all depths, followed by cobbles (**Supplementary Table S3**). Significant differences were found across depths for cobbles (p-value < 0.001), pebbles (p-value =

$1.72e^{-12}$), and sand (p-value < $2.2e^{-16}$), but only sand cover exhibited a clear pattern with depth. The proportion of sand-sized grains increased from 0.5% at 9 m to 23.7% at 24 m. (**Figure 5A**). Within the sand-sized particles, the proportion of very coarse grains decreased with depth, whereas other fractions tended to increase, except very fine sand and mud which showed the highest percentage at 18 m (**Figure 5B**, **Supplementary Table S3**). A weak current was perceived at this depth while sampling.

Living-Rhodolith Cover

The average cover of living-rhodolith (mean ± SD) ranged between 1.6% (±1.1) and 1.4% (±0.8) at 24 and 9 m, respectively, and 15.9% (±8.3) at 18 m (p-value < $2.2e^{-16}$). Highest rhodolith cover in sampling quadrats ranged between 3.7% at 24 m and 34.7% at 18 m. Rhodolith distribution was heterogeneous with dispersed nodules at the bed margins at 9 and 24 m and density increased towards intermediate depths from 12 to 21 m, where rhodoliths occurred in patches whose average cover ranged from 5% (±3.3) to 15.2% (±8.3) and maximum cover from 11.58 to 34.2% (**Figure 6**).
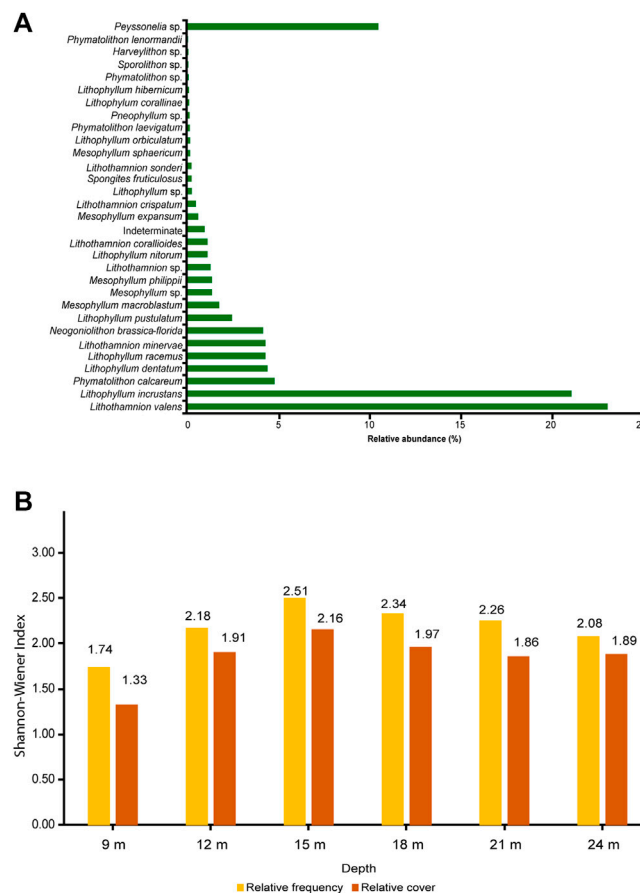
FIGURE 8 | (A) Relative abundance of the identified taxa at the sampling depths. **(B)** Shannon-Wiener index diversity measures (based on species frequency or cover) at the sampling depths.

Species Composition

Twenty-two morphospecies belonging to 6 genera (*Lithophyllum, Spongites, Neogoniolithon, Lithothamnion, Mesophyllum,* and *Phymatolithon*) were identified (**Figure 7**). Other thalli were only identified at the genus level, due to the lack of diagnostic characters. In three genera no individual species were recognised (*Pneophyllum* sp., *Sporolithon* sp., and *Harveylithon* sp.), for a total of 9 genera. Seven species dominated the assemblages, with occurrence proportions higher than 4%: *Lithothamnion valens* Foslie (23.1%), *Lithophyllum incrustans* Philippi (21.1%), *Phymatolithon calcareum* (Pallas) W.H. Adey et D.L. McKibbin ex Woelkerling et L.M. Irvine (4.8%), *Lithophyllum dentatum* (Kützing) Foslie (4.4%), *Lithophyllum racemus* (Lamarck) Foslie (4.3%), *Lithothamnion minervae* Basso (4.3%) and *Neogoniolithon brassica-florida* (Harvey) Setchell et L.R. Mason (4.1%). (**Figure 8A**; **Table 1**).

Depth distribution of morphospecies was heterogeneous. The relative abundance of *Lithophyllum incrustans* decreased with depth from 58.5% of the algal assemblage at 9 m to 5.9% at 21 m. In contrast, the proportion of *Lithothamnion valens* increased with depth from being absent at 9 m to 38.3% at 21 m. Other species showed limited depth ranges: *Lithophyllum orbiculatum* (Foslie) Foslie only occurred at shallow depths (9–12 m),

Lithophyllum dentatum was most abundant around 12 m, *Lithothamnion minervae* and *Phymatolithon calcareum* were more abundant at 15 m, and *Mesophyllum macroblastum* (Foslie) W.H. Adey, only occurred below 15 m, with the highest counts at 24 m. Other morphospecies, such as *Lithophyllum pustulatum* (J.V. Lamouroux) Foslie, *Lithophyllum nitorum* W.H. Adey et PJ Adey, and *Lithothamnion corallioides* (P.Crouan et H. Crouan) P. Crouan et H. Crouan had homogeneous relative abundance at all depths (**Table 1**).

Monospecific rhodoliths comprised 34% of the analyzed nodules, varying from 17.9% at 9 m to 39.8% at 21 m. *Lithothamnion valens* was the most common species building monospecific rhodoliths (44.4%), followed by *Lithophyllum incrustans* (15.2%), *Phymatolithon calcareum* (10.3%) and *Lithothamnion minervae* (8.1%). Two nodules of *Lithophyllum pustulatum* and *Lithothamnion sonderi* Hauck, encrusting bioclastic and lithic nuclei, respectively, were monospecific as well (**Table 2**).

Size and Shape of Rhodoliths

Mean size of rhodoliths (mean ± SD) ranges from 23.7 mm (±9.5) at 18 m to 35.8 mm (±12.3) at 24 m, where the rhodoliths were significantly bigger than in the other depths (p-value = $2.31e^{-09}$).
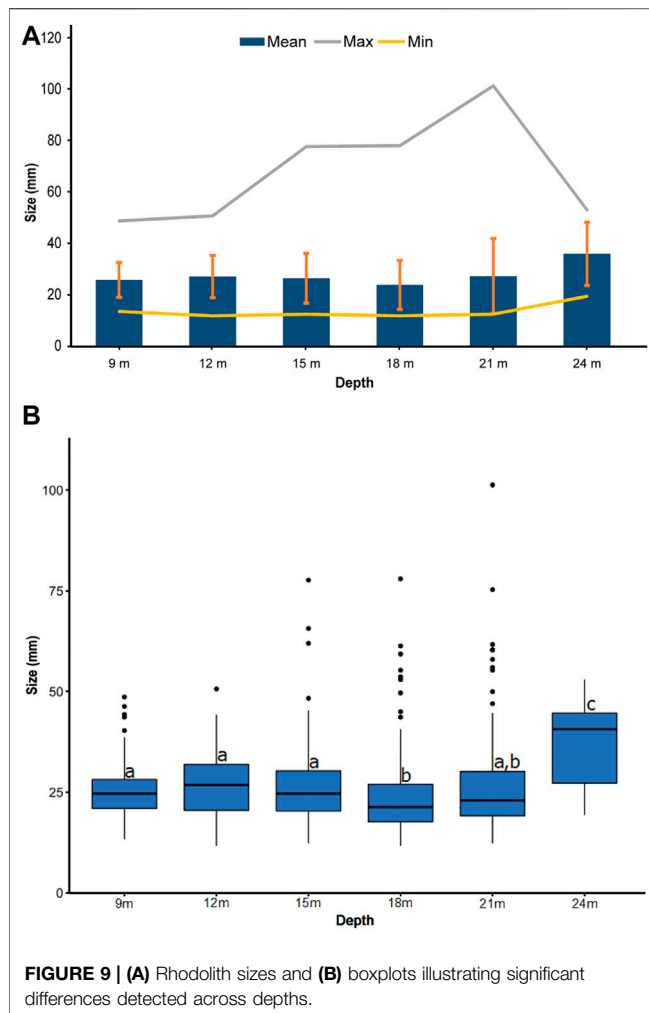
TABLE 1 | Species distribution by depth (%).

Species	9 m	12 m	15 m	18 m	21 m	24 m	Total
Lithothamnion valens	0.0	8.6	25.6	32.1	38.3	23.3	23.1
Lithophyllum incrustans	58.5	37.7	14.3	9.0	5.9	13.2	21.1
Phymatolithon calcareum	0.1	0.3	8.5	6.7	4.8	2.2	4.8
Lithophyllum dentatum	2.2	18.2	4.8	0.0	1.6	0.0	4.4
Lithophyllum racemus	3.7	5.1	7.5	3.8	1.1	0.0	4.3
Lithothamnion minervae	0.9	2.0	8.4	4.1	4.2	0.0	4.3
Neogoniolithon brassica-florida	6.1	5.3	3.7	4.1	0.0	11.6	4.1
Lithophyllum pustulatum	2.4	1.6	1.0	3.9	3.5	1.1	2.4
Mesophyllum macroblastum	0.0	0.0	1.3	1.3	3.4	10.6	1.7
Mesophyllum sp.	0.0	0.0	1.0	1.2	4.2	1.9	1.3
Mesophyllum philippii	0.0	1.8	0.6	0.6	4.7	0.0	1.3
Lithothamnion sp.	0.0	4.7	0.1	1.6	1.0	0.0	1.3
Lithophyllum nitorum	0.9	0.0	2.6	0.7	0.5	0.6	1.1
Lithothamnion corallioides	0.0	1.3	0.5	1.2	2.4	1.7	1.1
Indeterminate	0.1	0.8	0.8	1.3	1.0	2.4	0.9
Mesophyllum expansum	0.8	0.0	0.0	0.8	1.6	0.0	0.6
Lithothamnion crispatum	0.0	0.0	0.5	0.0	0.0	6.6	0.4
Lithophyllum sp.	0.1	0.4	0.4	0.2	0.0	0.0	0.2
Spongites fruticulosus	0.0	0.3	0.6	0.1	0.0	0.0	0.2
Lithothamnion sonderi	1.3	0.0	0.1	0.0	0.0	0.0	0.2
Mesophyllum sphaericum	0.0	0.0	0.2	0.4	0.0	0.0	0.1
Lithophyllum orbiculatum	0.1	0.8	0.0	0.0	0.0	0.0	0.1
Phymatolithon laevigatum	0.0	0.0	0.4	0.0	0.0	0.0	0.1
Pneophyllum sp.	0.0	0.1	0.3	0.0	0.0	0.0	0.1
Lithophylum corallinae	0.0	0.0	0.0	0.2	0.2	0.0	0.1
Lithophyllum hibernicum	0.0	0.4	0.0	0.0	0.0	0.0	0.1
Phymatolithon sp.	0.0	0.0	0.1	0.1	0.1	0.0	0.1
Sporolithon sp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Harveylithon sp.	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Phymatolithon lenormandii	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Peyssonelia sp.	12.7	8.3	10.7	14.1	6.1	5.8	10.5
Biogenic and lithic remains	9.6	2.4	5.8	12.3	15.3	19.1	9.7

TABLE 2 | Counts of monospecific rhodoliths by depth.

	9 m	12 m	15 m	18 m	21 m	24 m	Total	%
Lithophyllum incrustans	16	7	3	4	3	1	34	15.2
Lithophyllum dentatum	0	5	2	0	1	0	8	3.6
Lithophyllum pustulatum	0	0	0	1	0	0	1	0.4
Lithophyllum racemus	0	2	4	2	0	0	8	3.6
Lithothamnion corallioides	0	0	0	2	0	0	2	0.9
Lithothamnion minervae	0	2	9	4	2	1	18	8.1
Lithothamnion sp.	0	4	0	2	1	0	7	3.1
Lithothamnion sonderi	1	0	0	0	0	0	1	0.4
Lithothamnion valens	0	6	24	37	28	4	99	44.4
Mesophyllum macroblastum	0	0	1	1	1	0	3	1.3
Mesophyllum philippii	0	1	0	1	2	0	4	1.8
Neogoniolithon brassica-florida	0	3	2	2	0	1	8	3.6
Peyssonnelia sp.	0	1	2	4	0	0	7	3.1
Phymatolithon calcareum	0	0	12	8	3	0	23	10.3
Total	17	31	59	68	41	7	223	100.0
% of total rhodoliths	17.9	34.4	35.8	37.6	39.8	31.8	34.0	—

Maximum size of rhodoliths increased from 49 mm at 9 m to 101 mm at 21 m and decreased to 53 mm at 24 m (**Figure 9**). The number of large rhodoliths (>50 mm) also increased from 0 at 9 m to 9 at 21 m and decreased to 2 at 24 m (**Table 3**).

Monospecific rhodoliths of the most abundant species (see below) were grouped in two size classes (p-value = 9.58e^{-09}). Based on the size ranges, *Lithophyllum dentatum* (**Figure 10A**), *Lithothamnion valens* (**Figure 10D**) and *Neogoniolithon brassica-florida* form the larger

FIGURE 9 | (A) Rhodolith sizes and **(B)** boxplots illustrating significant differences detected across depths.

(62.5%), with lesser proportions of discoidal (19.9%) and ellipsoidal (17.6%) nodules. Proportions of shape classes were similar at all depths from 12 to 21, with a dominance of spheroidal nodules. In contrast, at 9 m, discoidal (33.7%) and ellipsoidal (28.4%) were more common (**Figure 12A**).

Most collected rhodoliths were pralines (47.7%, **Figure 12B**; **Supplementary Table S5**). This morphotype is the most abundant below 9 m. The proportion of boxwork rhodoliths increased with depth, whereas coatings and compact rhodoliths built by encrusting corallines (as other in **Figure 12B**), which were the most abundant at 9 m, tended to be less common in deeper transects. Branches were rare from 15 to 21 m and absent in the rest of depths (**Supplementary Table S5**).

Diversity of Rhodoliths

The diversity of rhodoliths (Shannon-Wiener index, H'), both based on species frequency and cover, was highest at medium depths (15 and 18 m). The maximum rhodolith diversity was 2.51 for species frequency and 2.16 for species cover at 15 m, and the minimum rhodolith diversity was 1.74 for species frequency and 1.33 for species cover at 9 m (**Figure 8B**).

DISCUSSION

Bed Structure and Rhodolith Characteristics

The Punta de la Mona rhodolith bed occupies a small surface and a narrow depth range, showing that good conditions for rhodolith growth are limited to the eastern side of a small cape enclosing a small embayment. In this small area, bottom currents generated by storms from the east hit the submarine cliff and flow out of the embayment (**Figure 1**). The generally coarse grain size on the seafloor, dominated by cobbles and pebbles (**Figure 5**), indicates that currents sweep away fine sediment. Above the upper limit of the bed, the seafloor is covered by boulders and cobbles derived from rock fall from the cliff, and high turbulence seems to prevent rhodolith development, although boulders and cobbles are partially covered by coralline algae. Below 24 m, fine-grained sediments bury the rhodoliths hindering their significant development (Steller and Foster, 1995; Wilson et al., 2004; Villas-Bôas et al., 2014).

The highest average cover of living-rhodoliths occurs at 18 m, where the values are three times higher than those at 12 and 21 m (**Figure 6**). The optimum conditions for rhodolith growth might be due to a flatter seafloor between 15 and 20 m (**Figure 1**).

rhodoliths with mean sizes of 34.7 mm (±8.3), 28.8 mm (±11.7), and 27.1 mm (±8.2), respectively, whereas rhodoliths of *Lithophyllum racemus* (**Figure 10B**), *Lithothamnion minervae* (**Figure 10C**) and *Phymatolithon calcareum* were smaller, with mean sizes of 21.4 mm (±4.7 mm), 18.1 mm (±4.3 mm) and 18.4 mm (±3.8 mm) (**Figure 11A**), respectively. No significant differences were observed in the mean sizes of monospecific rhodoliths at the different depths in which they occur (*p*-value > 0.05, **Figure 11B**).

The maximum sphericity projection (Ψ) ranged between 0.65 at 9 m and 0.74 at 21 m, with similar values from 12 to 24 m (**Supplementary Table S4**). Most rhodoliths were spheroidal

TABLE 3 | Rhodolith cover (%) and size (mm) by depth.

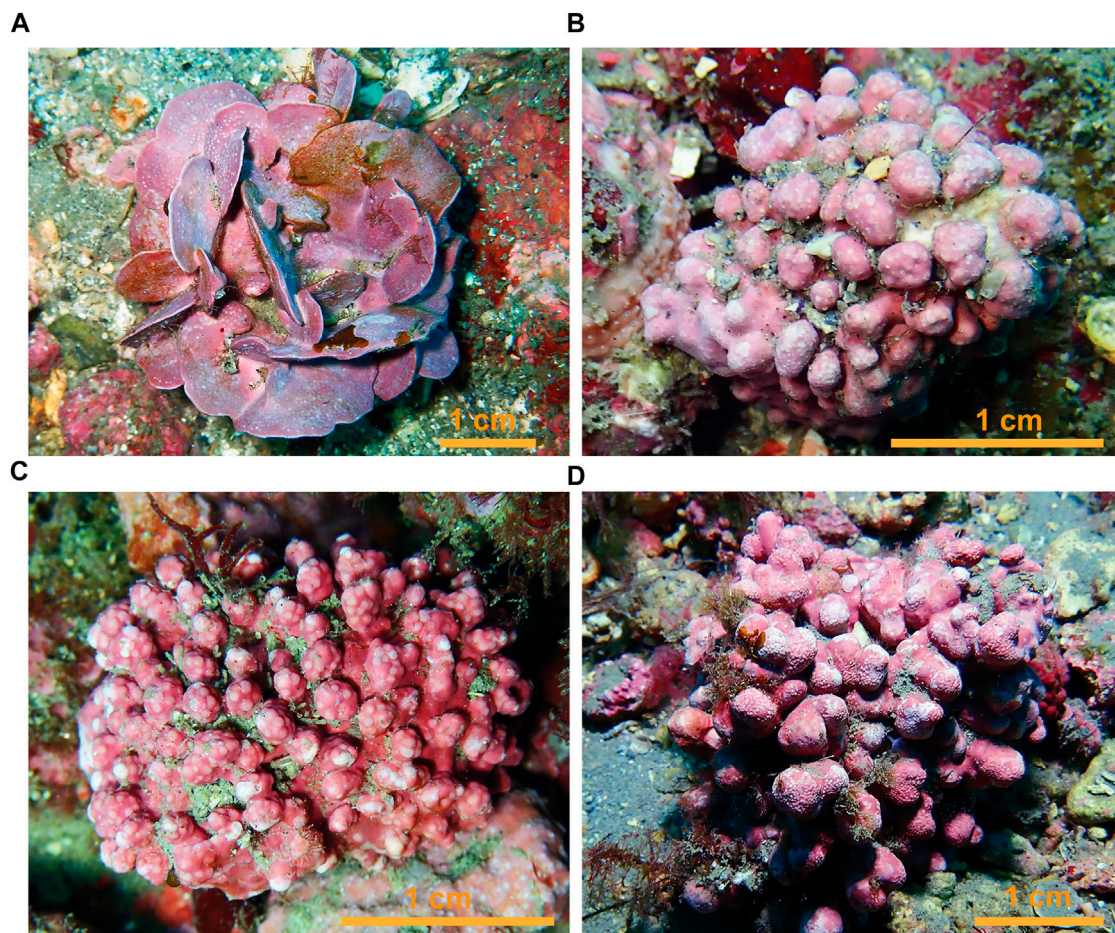| Depth (m)	Mean cover ± SD (%)	Max cover	No. rhodoliths	No. rhodoliths >50 mm and %	Mean size ± SD (mm)	Max size	Min size
9	1.6 ± 1.1	4.2	95	0 (0%)	25.7 ± 6.8	48.7	13.3
12	5.2 ± 2.6	11.6	90	1 (1.1%)	27.0 ± 8.2	50.7	11.7
15	8.1 ± 4.4	20.8	165	3 (1.8%)	26.4 ± 9.7	77.7	12.3
18	15.9 ± 8.4	34.2	181	6 (3.3%)	23.8 ± 9.5	78.0	11.7
21	5.0 ± 3.3	16.8	103	9 (8.7%)	27.2 ± 14.6	101.3	12.3
24	1.4 ± 0.9	3.7	22	2 (9.1%)	35.8 ± 12.3	53.0	19.3

FIGURE 10 | Monospecific rhodoliths: **(A)** *Lithophyllum dentatum*; **(B)** *Lithopyllum racemus*; **(C)** *Lithothamnion minervae*; **(D)** *Lithothamnion valens*.

Despite the weak current perceived, the highest proportion of very fine sand and mud occurs at 18 m. This can be due to the well-known baffling effect of dense concentrations of branching rhodoliths, which stabilize fine-grained sediment below them (Bassi et al., 2009; Millar and Gagnon, 2018; O'Connell et al., 2021).

The mean rhodolith size is relatively small (23.7 mm). The maximum size and the number of rhodoliths larger than 50 mm increases with depth (**Figure 9**), probably related to the turbulence gradient (Amado-Filho et al., 2007; Gagnon et al., 2012; Sañé et al., 2016). The size of monospecific rhodoliths is species-dependent. Two size classes can be distinguished for monospecific rhodoliths: *Lithophyllum dentatum* and *Lithothamnion valens,* build relatively large rhodoliths, whereas the rhodoliths of *Lithothamnion minervae* and *Phymatolithon calcareum* are significantly smaller (**Figure 11**). Rhodolith sizes within individual species do not show significant differences among depths, suggesting that genetic signatures control the sizes of monospecific rhodoliths rather than environmental conditions, at least at the small scale of the Punta de la Mona bed.

The high abundance of discoidal rhodoliths at 9 m (**Figure 12A**) reflects the flat, discoidal shape of lithoclastic nuclei, commonly coated by *Lithophyllum incrustans* at this depth. In contrast with their distribution in the Punta de la Mona, discoidal rhodoliths tend to be more common at deeper depths, because of reduced overturning due to lower energy (Bosellini and Ginsburg, 1971; Bosence, 1976; Peña and Bárbara, 2009). This is an additional example confirming that other factors, such as nucleus shape and building species, influence rhodolith shape, which is not exclusively controlled by hydrodynamic energy (Aguirre et al., 2017; Braga, 2017; O'Connell et al., 2021).

Coatings and compact rhodoliths made of encrusting corallines are the most abundant morphotype at 9 m (**Figure 12B**), reflecting the dominance of encrusting *Lithophyllum* morphospecies at this depth. The general decrease of this morphotype with increasing depth parallels the decrease of encrusting plants of this genus. In a similar way, the increase of the relative proportion of boxwork rhodoliths with depth parallels the increase of *Mesophyllum*. The dominance of mono or paucispecific pralines formed by different species and the scarcity of
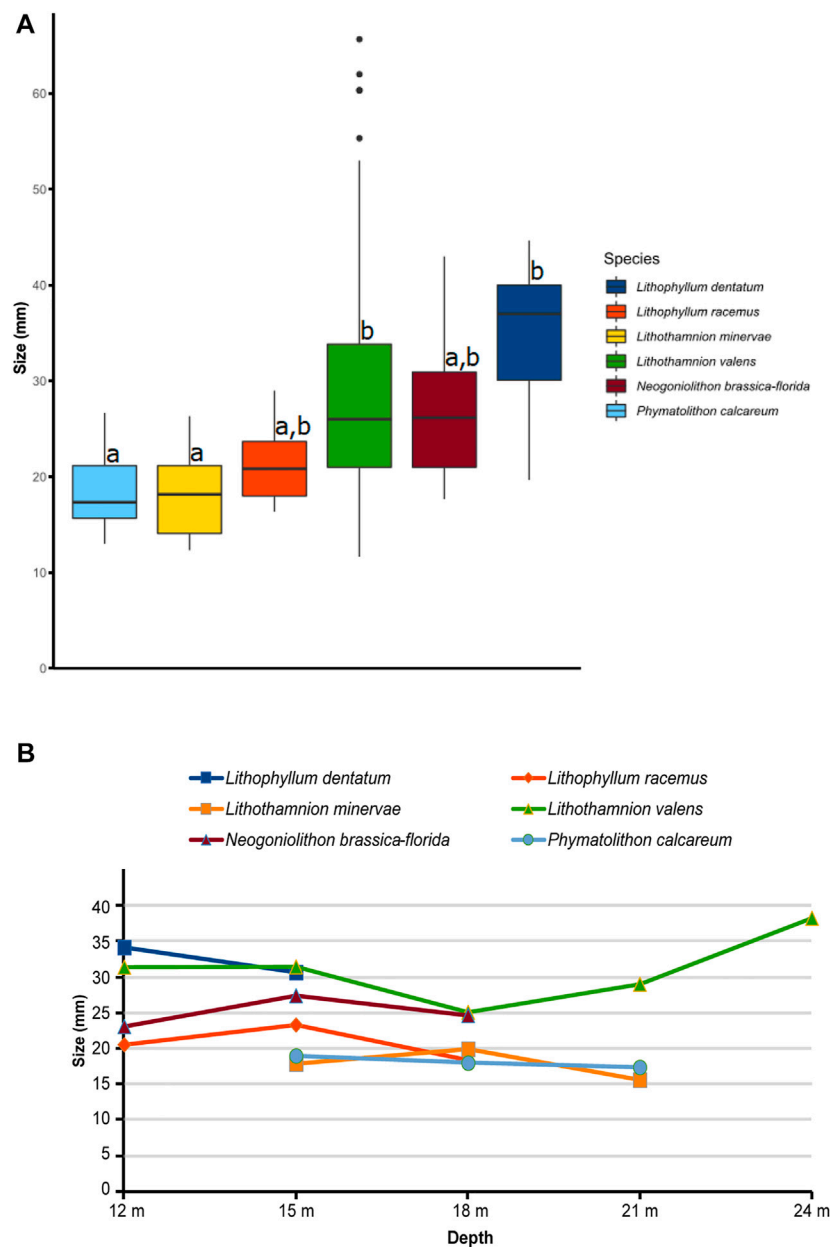
FIGURE 11 | (A) Boxplots of sizes of monospecific rhodoliths illustrating significant differences detected across species and **(B)** their mean size at different depths.

branches (**Figure 12B**) probably reflect a strong to intermediate hydrodynamic regime (Bracchi et al., 2022) suggested by the coarse grain size.

Species Composition and Diversity

The morphospecies richness in the Punta de la Mona bed (25 morphospecies, 22 of them identified at the species level, in 9 genera) is the highest described in the Mediterranean so far in a single bed. Traditionally, the Mediterranean rhodolith beds have been considered richer than those of the eastern Atlantic at similar latitudes (Basso et al., 2017), although only 4–13 species have been reported from beds in the western Mediterranean (Ballesteros, 1989; Basso, 1998;

Lanfranco et al., 1999; Mannino et al., 2002; Sciberras et al., 2009; Barberá et al., 2012; Basso et al., 2014; Nitsch et al., 2015; Sañé et al., 2016; Bracchi et al., 2019; Rendina et al., 2020b; Chimienti et al., 2020). The majority of rhodolith-forming species living in the Mediterranean (Basso et al., 2017; Rindi et al., 2019) have been recorded in the Punta de la Mona bed, except for *Phymatolithon lusitanicum* V. Peña (Peña et al., 2015), and *Neogoniolithon hauckii* (Rothpletz) RA Townsend & Huisman (Townsend and Huisman, 2018). Although we were not able to identify the recently described *Lithophyllum pseudoracemus* Caragnano, Rodondi and Rindi separately from *Lithophyllum racemus*, the former taxon was collected in the Punta de la Mona bed (Caragnano et al., 2020). This exemplifies that the cryptic
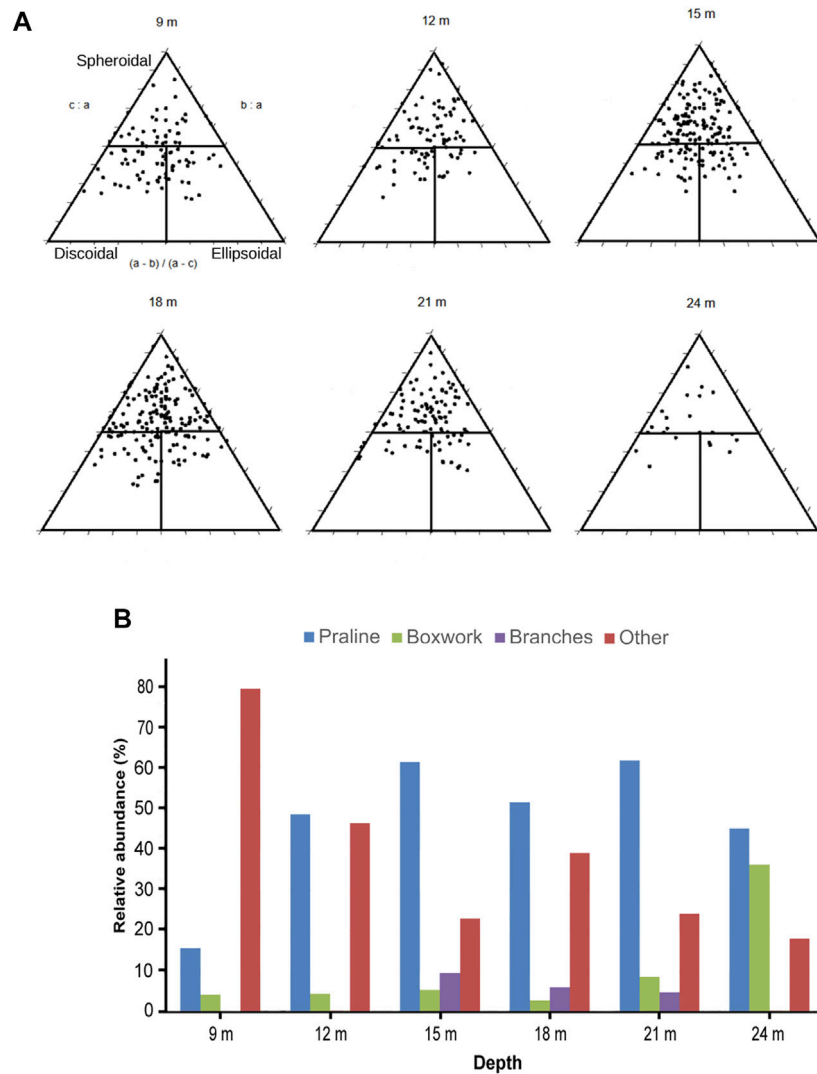
FIGURE 12 | (A) Triangular diagrams of rhodolith shape classes at each sampling depth (Sneed and Folk, 1958; Bosence, 1983; Graham and Midgley, 2000) and **(B)** relative proportions of rhodolith morphotypes at each sampling depth. Other includes coatings on lithoclasts and bioclasts, and compact rhodoliths of encrusting coralline algae.

molecular diversity is probably higher than the morphospecies richness assessed in our study (Gabrielson et al., 2018; De Jode et al., 2019; Pezzolesi et al., 2019; Caragnano et al., 2020; Kato et al., 2022).

Lithothamnion valens, the dominant species in the Punta de la Mona bed, is a Mediterranean endemic (Guiry and Guiry, 2022), which was considered a major structural component of a type of detrital bottom, called "facies de *Lithothamnion valens*," since the early descriptions of Mediterranean benthic habitats (Pérès and Picard, 1964). Rhodolith beds dominated by this species have been reported off Murcia in Spain (Aguado-Giménez and Ruiz-Fernández, 2012) and several locations, such as the Balearic Islands (Barberá et al., 2012), Tyrrhenian Sea (Basso, 1995; Bracchi et al., 2019; Rendina et al., 2020b) and Adriatic Sea (Chimienti et al., 2020). The composition of Mediterranean rhodolith beds, however, is heterogeneous even in small areas (Chimienti et al., 2020). No clear pattern of species dominance can be observed at the

regional scale, since *Lithophyllum racemus* (Sañé et al., 2016; Chimienti et al., 2020), *Lithothamnion minervae* (Rendina et al., 2020b), *Spongites fruticulosus* (Ballesteros, 1989; Joher et al., 2015), and *Lithothamnion corallioides* (Barberá et al., 2017) have been reported as dominant species in different beds. Nevertheless, despite the heterogeneity, these species, together with *Lithothamnion valens, Phymatolithon calcareum* and *Neogoniolithon brassica-florida* are the rhodolith-forming species characteristic of the Mediterranean. Within the Punta de la Mona bed, the identified morphospecies show patterns of depth distribution probably related to illuminance gradients. *Lithophyllum dentatum* is rare below 15 m and the abundance of *Lithophyllum incrustans* markedly decreases with depth. In contrast, *Mesophyllum macroblastum* does not occur at shallow depths (9–12 m) and has higher relative abundance at 24 m where the maximum illuminance is only 21% of that at 12 m.

Among the small and rare species identified in the multispecific rhodoliths, *Lithophyllum orbiculatum* (Foslie) Foslie, *Lithothamnion crispatum* Hauck, and *Lithothamnion sonderi* Hauck have not been reported in the Alborán Sea so far (Gallardo et al., 2016).

The Shannon-Wiener index (H') values are higher than those obtained in deeper (40–60 m) Mediterranean enclaves (Rendina et al., 2017). In maërl communities of shallow European Atlantic beds, Peña and Bárbara (2010) obtained similar H' indexes (1.98–2.96), but for all associated species, not just for coralline algae. Likewise, our results are similar to those obtained by Costa et al. (2019) in a tropical environment and at depths shallower than our study. The coralline algae diversity, as the proportional distribution of species in the ecosystem, is remarkable due to its high values, and the Punta de la Mona can be considered as a "nano-hotspot" (in the sense of Cañadas et al., 2014 for terrestrial regions) of rhodolith biodiversity in the biogeographical context of the Alborán Sea.

Uniqueness and Conservation of the Punta de la Mona Rhodolith Bed

The Punta de la Mona rhodolith bed is unique due to the scarcity of this kind of formation in the Alborán Sea, and its shallow depth range, contrasting with the generally deeper depth distribution of rhodolith beds in the Mediterranean (Basso et al., 2017). In this sea, the majority of rhodolith beds occur at 30–75 m, although in oligotrophic clear waters may reach depths close to 150 m, such as in the Balearic Islands (Massutí et al., 2022). Beds shallower than 25 m are scarce, although they occur from 2 m depth in Tunisia (CAR/ASP-PNUE/PAM, 2011), at 9–10 m in Israel (Ramos-Esplá et al., 2012), and in the Apulian shelf in southern Italy (Chimienti et al., 2020). In addition, the Punta de la Mona bed develops in oligotrophic waters, challenging the simplistic assumption, widespread in the geological literature, that rhodolith beds are indicative of oligophotic, mesotrophic to eutrophic environments.

The Punta de la Mona rhodolith bed is protected as a special conservation area (SCA) with the Natura 2000 network. Despite this protection, this habitat is threatened by nautical and fishing activities, affecting the seafloor by the frequent anchoring of boats that use the area as a refuge (Dolinar et al., 2020), the tangling of large branching rhodoliths in fishing nets (Borg et al., 1998), abandoned fishing nets and lines (Rendina et al., 2020a), and the disruption of trophic networks due to intense sport fishing with uncertain consequences on coralline algal communities (O'Leary and McClanahan, 2010). Appropriate regulations for the SCA should be imposed to prevent all these impacts in the future. Restrictions to fishing activities in marine protected areas resulted in increasing rhodolith covers (Barberá et al., 2017). This improved the environmental services provided by the rhodolith beds, including higher biodiversity (Barberá et al., 2003) and larger fish populations (Ordines et al., 2015). Nevertheless, the main threat for the rhodolith bed is the Asian alga *Rugulopteryx okamurae* (E.Y. Dawson)

I.K.Hwang, W.J.Lee & H.S.Kim (Altamirano-Jeschke et al., 2016) first detected in 2020, which is quickly expanding from the Gibraltar straits and nearly completely covering the rocky substrates between 5 and 30 m (García-Gómez et al., 2020), displacing the native algal communities and disturbing the associated invertebrate communities (Navarro-Barranco et al., 2019; Sempere-Valverde et al., 2021). In the first weeks of 2022, the occurrence of many rhodoliths settled by *Rugulopteryx okamurae* makes the future of the rhodolith bed uncertain, and needs to be monitored in the following years. This exemplifies that it is necessary to be cautious and incorporate the knowledge of these communities into the spatial planning framework of Punta de la Mona and other marine protected areas.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

JD: Research design, sampling, underwater pictures, taxonomic identification, writing the manuscript; DR: Taxonomic identification, statistics, editing the manuscript; LS-T: Sampling, underwater pictures; JP: Sampling, statistics, editing the manuscript; JB: Taxonomic identification, editing the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.884685/full#supplementary-material

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