

Age estimates and description of rhodoliths from Esperance Bay, Western Australia

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Rhodoliths were collected in Esperance Bay, Western Australia, using a Van Veen grab from a bed that covered an area approximately 2.2 km², in depths of 38 ± 1 m. Rhodolith abundance (biomass per 0.1 m³), mean size (maximum diameter), and morphotypes were compared among the inshore margin, offshore margin, and middle area of the bed. Accelerator Mass Spectrometry was used to estimate ages of five free-living rhodoliths. Rhodolith taxa included *Hydrolithon munitum*, *Lithothamnion* sp., an unidentified Melobesiodeae (a *Mesophyllum* or *Synarthrophyton*) and possibly a species of *Sporolithon*, with lumpy, warty, and fruticose morphologies. The middle area of the bed had significantly greater abundance of rhodoliths than either margin. Biomass of warty rhodoliths was greater in the middle area of the bed whereas fruticose and lumpy rhodoliths had similar biomass across the bed. The <20 mm size-class was the most abundant and these rhodoliths may originate from fragmentation of larger individuals. Radiocarbon age estimates ranged between calibrated ages of AD 1050 and modern, indicating that a proportion of living rhodoliths consisted of fossil rhodoliths that had been recolonized. The combination of coastal morphology, gently-sloping sea-floor, hydrodynamics, and rhodolith morphology was representative of rhodolith beds found elsewhere in the world.

INTRODUCTION

Rhodoliths, or maerl, are unattached coralline algae that form beds on sandy sediments and are found throughout the world. In Foster's (2001) review of rhodolith research, biodiversity associated with rhodolith beds ranks with that of kelp beds and forests, and sea grass meadows. Species of calcareous algae that form rhodoliths are relatively slow-growing, with rates of up to 0.6 mm y⁻¹ (Foster, 2001; Wilson et al., 2004), and, for at least one documented species, can grow uninterrupted for over 100 years (Frantz et al., 2000). Given their longevity and slow growth rates, rhodoliths are particularly vulnerable to anthropogenic disturbance such as trawling and resource extraction (Steller et al., 2003).

Species of algae that make up a rhodolith can show morphological plasticity in response to water motion and irradiance (Steller & Foster, 1995; Basso, 1998; Riosmena-Rodriguez et al., 1999). For example, smooth individuals are associated with greater water motion, relative to branched individuals (Basso, 1998). Similarly, branch density has been shown to decrease with an increase in depth (and associated decrease in water motion and light levels) in beds located in Bahia Concepcion, Gulf of California, Mexico (Steller & Foster, 1995). No ecological study has compared rhodolith morphology to physical factors in beds reported along the southern coast of Australia where primary rhodolith research has been in the fields of geology and taxonomy along Western Australia (*Lithophyllum*, *Lithoporella*, *Lithothamnion*, Collins 1988; Sim & Townsend, 1999) and in the Great Australian Bight (*Lithothamnion* and *Lithoporella*, James et al., 1994, 2001).

The spatial distribution of rhodolith beds has been correlated to coastline characteristics, wave energy, and irradiance. Bosence (1980) described several facies that are common to rhodolith beds in Ireland, England, and Brittany. In particular, Clean Algal Gravel facies are correlated to areas exposed to benthic water motion and consist of living densely-branched spheroidal and ellipsoidal rhodoliths, a smaller fraction of living open-branched rhodoliths, and coarse sand. Bank facies consist of interlocking, open-branched rhodoliths, and are found in relatively sheltered environments. The Muddy Algal Gravel and Muddy facies consist of varying proportions of mud and rhodoliths; and the Fine Sand facies is composed primarily of carbonate sand. The distribution of these different facies can be used to describe sedimentary processes where rhodoliths abound (Bosence, 1980).

This study is a first step towards bridging the gap in works carried out by geologists and taxonomists in Australia, by characterizing living rhodoliths in the Recherche Archipelago, Western Australia, and relating their distribution to Bosence's (1980) facies models. Rhodolith beds are widely distributed throughout the archipelago, in depths of 27 to 65 m and contribute 13.7% of 1054 km² mapped subtidal substrata (Baxter et al., 2005). Little is known regarding species diversity, abundance, and age structure of rhodoliths in this area.

MATERIALS AND METHODS

One rhodolith bed was sampled in the Recherche Archipelago, Western Australia, in February 2003. The

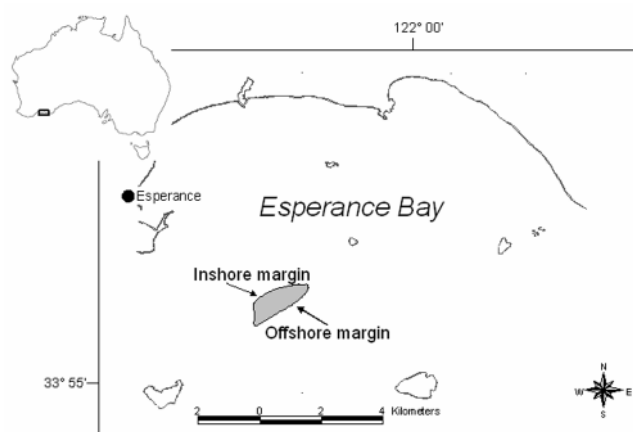


Figure 1. Schematic of the rhodolith bed (filled area) sampled in Esperance Bay, Western Australia (drawn from Baxter et al., 2005). The inner section of the bed was sampled midway between the two designated margins.

bed occupies an average depth of 38 ± 1 m, covers an area approximately 2.2 km^2 (Baxter et al., 2005), and extends to depths > 2 m into the sea-floor (N. Goldberg, unpublished data). Sandy sediments were found within and surrounding the bed, which lies along the western edge of Esperance Bay and is exposed to south-westerly wind and Southern Ocean swells.

To test if rhodolith abundance, morphology, and size structure varied across the bed, rhodoliths were collected along the inshore margin, offshore margin, and middle area of the bed (Figure 1). Edges of the rhodolith bed were identified by differences in texture based on side-scan sonar data (Baxter et al., 2005). Due to the depth of the bed, samples were collected remotely with a Van Veen grab (grab = 0.1 m^3 ; $N=6$ randomly-selected stations per section) rather than collecting *in situ* with SCUBA divers. Penetration depth of the grab was < 20 cm (F. Wells, Department of Fisheries, Western Australia, personal communication). In addition, video frames were recorded from six haphazardly-chosen stations per section to estimate cover of rhodoliths across the bed. A video camera (Sony digital Handy cam) was mounted facing downwards on a frame and focused on a quadrat with an area of 1 m^2 . The video camera and attached quadrat were deployed from a boat. The video camera recorded for 5 seconds once the quadrat settled on to the sea-floor. The unit was hauled back to the boat by hand after each deployment.

Rhodoliths were identified to the lowest possible taxonomic level and their morphologies were categorized. For taxonomic identifications, portions of a rhodolith were decalcified with 0.6 M nitric acid, embedded in resin, and thin-sectioned ($12\text{--}28 \mu\text{m}$ thick sections) (for further description see Harvey et al., 2002). Conceptacle and epithelial cell morphologies were used to identify rhodoliths. Identification was often not possible due to the condition of the specimens (e.g. sterile, buried or eroded conceptacles). Three morphologies were observed: protuberances or branches that are contiguous (lumpy), relatively short (< 3 mm; warty), or long (≥ 3 mm; fruticose) (Woelkerling et al., 1993). Correlating species with morphology was beyond the scope of this study and given the difficulty in identifying the specimens.

The biomass, density, morphology, and per cent cover of rhodoliths were compared across the bed. Biomass was measured as wet-weight after washing away sand and blotting rhodoliths with a towel. The percentage cover of rhodoliths was estimated as the number of randomly-placed dots overlying rhodoliths per image that represented a 1 m^2 area ($N=100$ dots per image), using the image analysis program ehp v. 2.1 (D.B. Coup, 1999, Otago University, Otago, New Zealand). Because fruticose rhodoliths were the most abundant morphology type, frond tip density per 1 cm^2 size-class ($N=40$ rhodoliths pooled from the six stations) was compared to determine if fruticose fine-scale morphology differed across the bed. Frond tip density was measured as described in Steller & Foster (1995).

Differences in rhodolith characteristics across the bed were tested with a one-way analysis of variance (ANOVA). To satisfy assumptions of normality and equal variances, biomass data were square-root transformed, and per cent cover data were arc-sine transformed. If there were significant differences among the bed areas, pairwise comparisons were performed using a post-hoc Tukey test.

To determine whether rhodolith sizes varied across the bed, the numbers of rhodoliths per size-class were tested with a two-way ANOVA (fixed factors: size-class and bed section). Size-classes were categorized by the maximum diameter of individual rhodoliths: < 20 mm, $20\text{--}39.9$ mm, and $40\text{--}59.9$ mm. Data were square-root transformed to satisfy assumptions of normality and equal variances. If a main factor was significant, then a post-hoc Tukey test was performed.

Ages of five individual rhodoliths were estimated using Accelerator Mass Spectrometry (AMS) at the Australian National Tandem Accelerator for Applied Research facility at the Australian Nuclear Science and Technology Organization (ANTSO). Rhodoliths were pink and assumed to have been alive at the time of collection. Dried rhodoliths were first cut in half using a water-lubricated diamond saw. Approximately 20 mg was drilled (hand-held Dremel Moto-flex, model 232-5) from within 3 mm of the outer surface along the cut face. Non-algal material was carefully avoided (U. Zoppi, ANTSO, personal communication). For two rhodoliths, an additional sample was collected approximately 9 mm from the outer surface. Samples were prepared for AMS ^{14}C analysis as described in Hua et al. (2001) whereby samples were converted to carbon dioxide and then to graphite. The AMS ^{14}C results were reported as 2σ (95.4%) calibrated age ranges using CALIB Rev. 5.0.1 software (Stuiver & Reimer, 1993), calibrated with the marine calibration curve (Hughen et al., 2004), and corrected for $\delta^{13}\text{C}$ isotopic fractionation and local oceanic reservoir (ΔR value of 66 ± 29 ; Reimer & Reimer, 2000).

RESULTS

Rhodolith taxa in the bed were diverse, consisting of *Hydrolithon munitum*, *Lithothamnion* sp., an unidentified Melobesiodeae (a *Mesophyllum* or *Synarthrophyton*) and possibly a species of *Sporolithon*. Of the few rhodoliths that were fertile, conceptacles were eroded, empty, or buried which made species identification difficult and impossible

Table 1. Mean biomass and per cent cover (\pm SE) of rhodoliths in the offshore and inshore margins, and middle area of a rhodolith bed located in Esperance Bay, Western Australia. $N=6$ per bed section.

Area of bed	Biomass (g per 0.1 m ³)	Cover (% per m ²)
Offshore	573.5 \pm 110.1	71.8 \pm 1.6
Middle	1148.0 \pm 55.2	94.0 \pm 1.4
Inshore	446.6 \pm 162.5	68.3 \pm 4.6

to correlate with morphology. Warty, lumpy, and fruticose morphologies were represented. Other organisms collected from the grab samples included scallops, ophiuroids, brachiopods, sea urchins, chitons, crabs, shrimps, sea cucumbers, crustaceans, nemertean, epiphytic algae, and polychaetes.

Mean biomass and per cent cover of rhodoliths differed across the extent of the bed (Table 1). Rhodolith biomass and per cent cover were significantly greater in the middle of the bed (Biomass: $F_{(2,6)}=10.1$, $P<0.01$; Cover: $F_{(2,6)}=28.0$, $P<0.01$; Pairwise comparisons for biomass and cover: $P<0.02$ between middle and offshore sections, and between middle and inshore sections). The offshore and inshore margins of the bed were not significantly different from each other ($P>0.3$), although the offshore

margin did have slightly greater rhodolith cover and biomass than the inshore margin (Table 1). Qualitatively, the rhodolith bed corresponded to a Clean Algal Gravel facies (*sensu* Bosenice, 1980) with a predominance of lumpy and warty rhodoliths that were associated with the sandy substratum.

The biomass of warty rhodoliths differed across the bed, compared to lumpy and fruticose forms whose biomass estimates were similar across the bed (Figure 2A). Biomass of warty rhodoliths in the middle section of the bed was double the average biomass collected from either margin ($F_{(2,5)}=44.7$, $P<0.01$; Pairwise comparisons: $P<0.01$ between the middle and the inshore sections, and between the middle and the offshore sections) (Figure 2A). The margins were not significantly different (Tukey post-hoc: $P=1.00$) for warty rhodoliths (Figure 2A). Biomass of lumpy and fruticose rhodoliths was not significantly different among the three bed areas (Lumpy rhodoliths: $F_{(2,5)}=1.41$, $P=0.31$; Fruticose rhodoliths: $F_{(2,5)}=0.69$, $P=0.54$) (Figure 2A).

The size-class distribution varied with morphology across the bed, though branched forms (i.e. warty and fruticose) were typically smaller than the lumpy form (Figure 2B–D). The numbers of warty rhodoliths per size-class varied across the bed (Table 2), with the <20 mm size-class more than twice as abundant in the middle of the rhodolith bed as along the margins (Figure 2B). The numbers of lumpy and fruticose individuals were

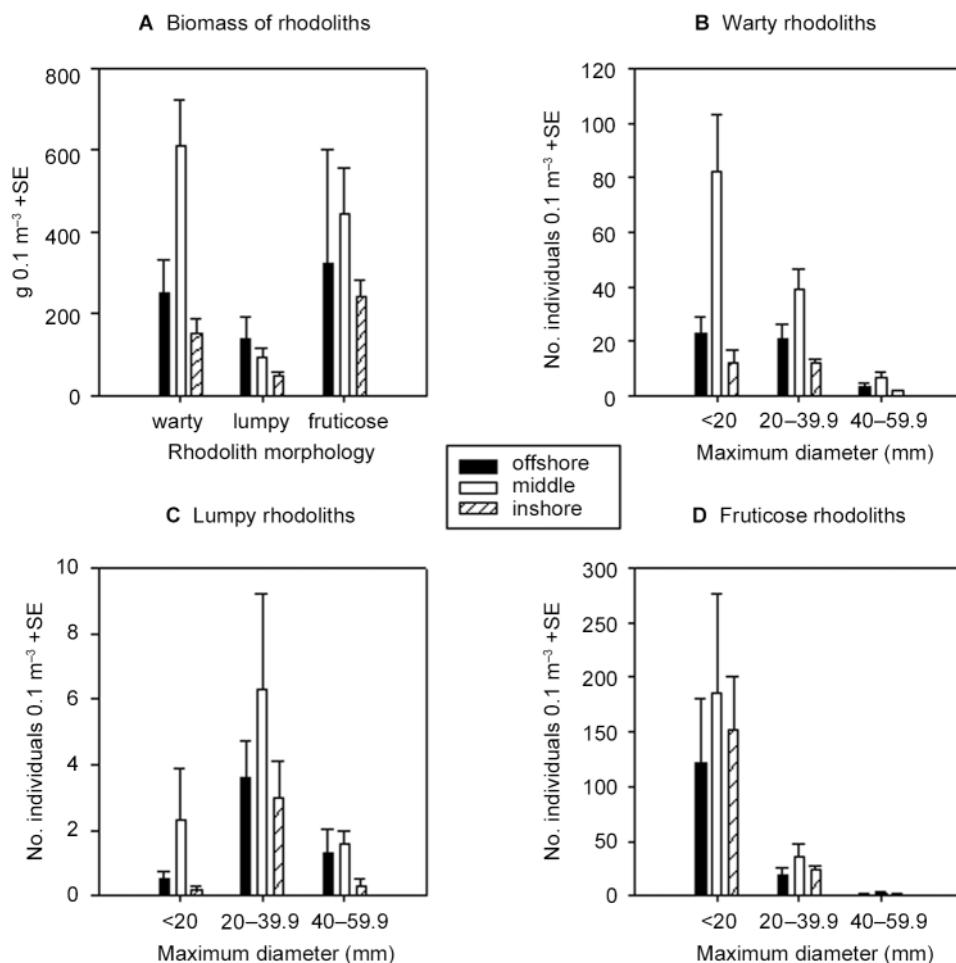


Figure 2. Distribution of rhodolith morphotypes (mean+SE) across the rhodolith bed. (A) Biomass of warty, lumpy, and fruticose forms. Size-class distributions for (B) warty, (C) lumpy, and (D) fruticose forms. $N=6$ per bed section.

Table 2. Two-way analysis of variance examining differences in numbers of rhodoliths per morphotype based on diameter size-class and rhodolith bed section. Size class categories: <20 mm, 20–39.9 mm, and 40–59.9 mm. Bed sections: offshore margin, middle area, and inshore margin. $N=6$ per bed section.

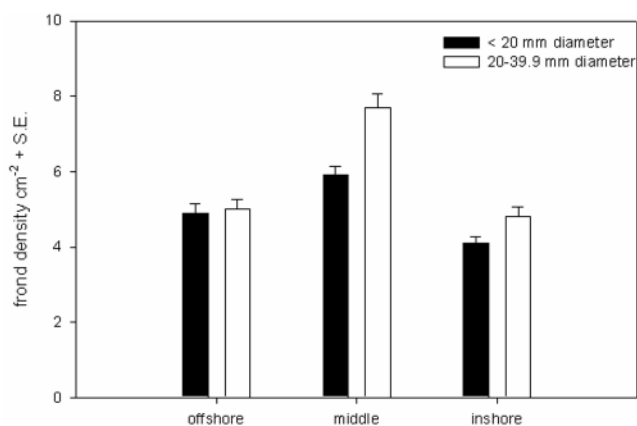
Morphotype	df	Warty		Lumpy		Frucicose	
		MS	F	MS	F	MS	F
Bed section	2	49.66	19.33**	1.95	2.30	16.55	0.90
Size-class	2	69.38	27.01**	8.16	9.63**	408.21	22.32**
Bed section \times Size-class	4	7.45	2.90*	0.10	0.98	3.26	0.95
Error	45	2.57		0.85		18.29	

*, $P < 0.05$; **, $P < 0.001$.

Table 3. Radiocarbon ages of rhodoliths sampled from a rhodolith bed in Esperance Bay, Western Australia.

Bed section	Maximum diameter (mm)	ANTSO sample code	δ (^{13}C) per mil.	Conventional ^{14}C age (years BP $\pm 1\sigma$ error)	Range of ages (years AD)
Middle	30	OZH306	-2.7	565 \pm 40	1710–1950 ¹
Offshore	42	OZH307	-1.5	870 \pm 35	1440–1630
Offshore	35	OZH308	-0.7	1320 \pm 40	1050–1260
Inshore	55	OZH309*	-1.9	215 \pm 35	Post-1950
		OZH334**	-2.0	720 \pm 45	1520–1780
Inshore	44	OZH064U1*	-0.9	660 \pm 40	1590–1880
		OZH064U1**	-1.6	720 \pm 40	1520–1800

*, Measurements taken within 3 mm of outer edge; **, measurements taken approximately 9 mm from outer edge. Calibrated age ranges (95.4% based on 2σ error) were calculated using Calib v. 5 (Stuiver & Reimer 1993). Calibration data set was from Hughen et al. (2004). Mean oceanic correction for the southern coast of Australia from Reimer & Reimer (2000). ¹, Cannot calibrate due to nuclear testing C-14 (Stuiver & Reimer 1993).

**Figure 3.** Density (mean+SE) of fronds tips for frucicose rhodoliths in two size-classes. $N=6$ per bed section.

not significantly different across the bed (Table 2). For lumpy forms, the middle size-class was significantly more abundant (Tukey post-hoc: $P < 0.01$), and for frucicose rhodoliths, the <20 mm size-class was significantly more abundant (Tukey post-hoc: $P < 0.001$) (Figure 2C&D). In addition, frond tip densities of frucicose rhodoliths were greater in the middle of the bed, regardless of size-class (<20 mm size-class: $F_{(2,40)} = 15.9$, $P = 0.00$, Pairwise comparisons: $P = 0.00$ between middle and offshore and between middle and inshore; and 20 to 39.9 mm size-class: $F_{(2,40)} = 34.0$, $P = 0.00$, Pairwise comparisons: $P = 0.00$ between middle and offshore and between middle and inshore) (Figure 3). No statistical comparisons were made in the 40–59.9 mm size-class due to low densities (Figure 2D).

Radiocarbon ages ranged from modern to calibrated AD1050 (Table 3). The range in ages suggests that a proportion of fossil rhodoliths had been recolonized after periods of burial and/or erosion. Recolonization was indicated by differences between inner and surface age-estimates. In particular, the age estimate of one rhodolith ranged between AD1520 and 1780, within 9 mm of the outer surface, and was AD post-1950, within 3 mm of the outer surface (Table 3). Another living rhodolith had similar age ranges for samples taken from 3 and 9 mm of the outer surface (Table 3).

DISCUSSION

The rhodolith bed from Esperance Bay, Western Australia, appeared to be typical of a relatively wave-exposed coastal bay. The prevalence of robust morphologies was characteristic of Bosence's (1980) Clean Algal Gravel facies, and the abundance of the delicate, low-density, frucicose morphology in the smallest size-class (e.g. <20 m) was suggestive of individuals having been fragmented by water motion with possible recolonization and growth (Scoffin et al., 1985; Foster, 2001). The range in radiocarbon ages of the living rhodoliths indicated that a proportion of fossil rhodoliths had been recolonized. Opportunities for recolonization of fossil rhodoliths may be facilitated by water motion and bioturbation (Collins, 1988; Foster, 2001).

Morphological characteristics of the rhodoliths sampled from Esperance Bay may be related to the effects of wave energy and attributes of coastal morphology. The

preponderance of lumpy and warty forms was characteristic of a Clean Algal Gravel facies in a high-energy environment (Bosence, 1976, 1980). Furthermore, the rhodolith bed could be described as Bosence's facies model two in which Clean Algal Gravel facies occurs in gently-sloping sea-floors, within relatively wave-exposed, coastal bays (Bosence, 1980).

Alternatively, the diversity of morphologies may be species-specific or a function of morphological plasticity with respect to environmental conditions (Riosmena-Rodriguez et al., 1999). Contrary to Steller & Foster (1995), greater branch density of fruticose forms was not necessarily indicative of greater water motion. Branch density was less along the margins where rhodoliths would presumably bear the brunt of wave energy and abrasion by sand. An exhaustive taxonomic study is necessary to delimit factors responsible for possible species-specific growth patterns in Esperance Bay.

Swells may contribute to fragmentation, sorting, and transport of rhodoliths across the bed, particularly for those rhodoliths <20 mm in diameter. Collins (1988) predicted that swells with periods of 14 and 8.5 s are capable of moving sediments (20 mm grain size) in depths <60 m, with bottom orbital velocities of 50 cm s⁻¹ off the Rottneest Shelf of Western Australia. Esperance Bay is exposed to Southern Ocean swells and storm waves with periods of 4 to 9 s for easterly waves and 10 to 16 s for south-westerly winter swells, with orbital velocities up to approximately 40 to 50 cm s⁻¹ in the vicinity of the rhodolith bed (Johnson & Pattiaratchi, 2005). Smaller individuals may extend the margins of a bed but also provide substratum for algal colonization.

The range in rhodolith ages (calibrated age of AD1050 to present day) suggests that rhodoliths have been present in the bay for hundreds of years, have remained buried for varying periods of time, and, in the case of some rhodoliths, were re-exposed and recolonized. Evidence of recolonization of formerly-buried rhodoliths was supported by discontinuity in ages between near-surface and inner sections of a living rhodolith. Littler et al. (1991) also reported age discontinuities in deep-sea rhodoliths and proposed that rhodoliths had been buried for varying periods of time, re-exposed to the surface, and then recolonized by coralline algae. In contrast to the studies of Frantz et al. (2000, 2005) that had reported ages of a rhodolith along an axis of uninterrupted growth, estimated growth rates from the literature support the hypothesis of age discontinuities in rhodoliths collected from Esperance Bay. Using an average growth rate of 0.6 mm y⁻¹ (Foster, 2001), uninterrupted growth would result in a diameter or frond length much greater than the 3 and 9 mm measured for a number of rhodoliths from this study (e.g. samples OZH307, OZH308, OZH334). Wave activity from Southern Ocean storms, long-shore drift, and onshore sediment transport (Sanderson et al., 2000) may contribute to erosion of sediments in Esperance Bay, resulting in the exposure of formerly-buried rhodoliths in the top layers of the bed. At a smaller spatial scale (order of centimetres), the action of bioturbators such as mobile fauna may contribute to turnover of rhodoliths (Collins, 1988; Marrack, 1999).

The rhodolith bed in Esperance Bay is dynamic with evidence of fragmentation and recolonization of fossil

individuals. In addition, the bed was typical of beds found in hydrodynamically-active coastal bays. This study provides the first step in describing rhodoliths that are well-represented along the south-western coast of Australia. Future work will investigate the vertical distribution of rhodoliths in the seabed to explore past sedimentary processes. Growth rates (Frantz et al., 2005) and processes contributing to differences in morphology and the persistence of rhodoliths will also be investigated and compared to beds elsewhere in the world.

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