MINIREVIEW

RHODOLITHS: BETWEEN ROCKS AND SOFT PLACES[1]

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Rhodoliths (maërl) are widely distributed in the worlds' oceans and have an excellent fossil record. Individuals are slow growing, may be long lived (>100 years), and are resilient to a variety of environmental disturbances. Their external morphology and internal growth bands are potential archives of environmental variation at scales of within years to tens of years. At high densities, these free-living non-geniculate coralline algae form rhodolith beds, communities of high diversity that can be severely impacted by resource extraction.

Key index words: **climate recorders; ecology, maërl; paleoenvironments; rhodolites; rhodoliths**

It has long been known that free-living, non-geniculate (i.e. lacking uncalcified joints) coralline algae can occur at high concentrations over large areas (e.g. Weber-Van Bosse and Foslie 1904). Such observations were not oddities: In terms of area covered, maërl or rhodolith beds may be one of the Earth's "Big Four" benthic communities that are dominated by marine macrophytes, ranking with kelp beds and forests, seagrass meadows, and non-geniculate coralline reefs. Moreover, rhodolith beds provide habitat for numerous associated macroalgae and invertebrates. Difficulties with identification and confused terminology and taxonomy of the rhodoliths themselves, their occurrence in habitats not often frequented by marine scientists, and a literature fragmented between biological and geological journals have, however, inhibited interest and progress in understanding these calcareous tumbleweeds of the sea and their reefs, which rock and roll. These difficulties are being overcome and some turned into strengths. My purpose is to comment on what is known and suggest what I consider necessary and fruitful areas of future research.

DEFINITIONS AND DESCRIPTIONS

Nature, differences among scientific disciplines, and history have conspired to inhibit a common rhodolith language. Since the insightful reviews by Adey and Macintyre (1973) and Bosence (1983a,b), many investigators have settled on "rhodoliths" as the name for free-living structures composed mostly (>50%) of non-geniculate coralline algae. The communities they dominate are called "rhodolith beds" (Fig. 1A). Some geologists call them "rhodolites," and many investigators use the older French name "maërl." Some scientists call small thalli, especially those that are twig-like, maërl, and larger, more rounded thalli, rhodoliths. Maërl may also refer to environments composed principally of such corallines, whether living or dead, or a mixture of the two. The putative fertilizer made from grinding up these live and dead corallines is also called maërl (J. Grall, Institut Universitaire Européen de la Mer, personal communication). In nature, free-living, non-geniculate coralline algae come in a variety of sizes, shapes, and species. They can be aggregated over large areas at various densities, and their skeletons can persist long after death to form relic or dead beds (e.g. Siesser 1972), beaches, and fossil deposits (Fig. 1B). Thus, the abundance, size, shape, and species composition of live and dead rhodoliths within and among rhodolith beds can vary considerably in space and time (Fig. 2). Given this complexity and the absence of consensus on terms, authors should be careful to define terms. Here, I will refer to an individual thallus as a "rhodolith" with appropriate adjectives to describe their state, size, shape, etc., and the community they dominate will be called a "rhodolith bed."

A rhodolith can be composed entirely of a non-geniculate coralline (sometimes more than one species) or have a core of other material (sometimes called "nucleated rhodoliths"; Freiwald and Henrich 1994), indicating that they can grow from fragments or from spore settlement on a hard substrate. Fragments and hard substrate may originate in the bed or be broken from nearby reefs and transported to the site of growth. The enormous quantities of living fragments in many rhodolith beds suggest that fragmentation of large rhodoliths is a significant source of new recruits in established beds. However, rhodoliths with cores of rock or other noncoralline material indicate that recruitment from spores does occur. New rhodolith beds may become established from crustose, non-geniculate coralline fragments transported from reefs (e.g. Bosence 1985, Piller and Rasser 1996), and the occurrence of beds on isolated banks (e.g. Minnery 1990) suggests new beds may also be initiated from spores. All extant rhodolith-forming genera also occur as attached crusts (W. Woelkerling, La Trobe University, personal communication). Rhodoliths are ripe for investigations with the techniques of molecular population genetics.
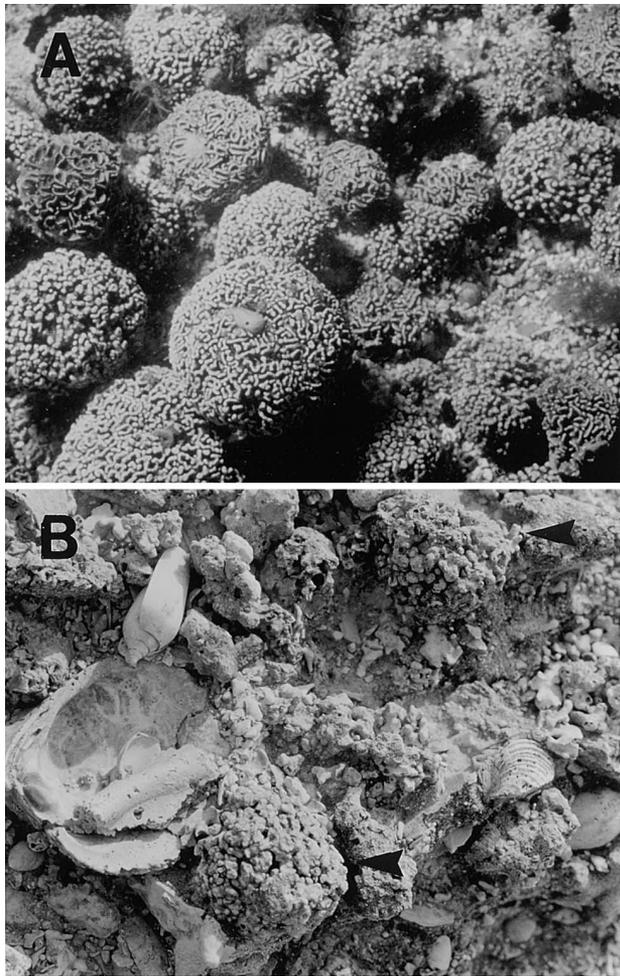
FIG. 1. Some rhodoliths in the Gulf of California, México. Largest individuals ~4 cm diameter. (A) Living, spherical rhodoliths (mostly *Lithophyllum margaritae*) in a rhodolith bed at 5 m depth in Bahia Concepcion. Note range in form from foliose to fruticose. (B) Fossil rhodoliths and molluscs in a Pleistocene deposit at Punta Chivato. Arrowheads indicate two large, entire individuals.

TAXONOMY, MORPHOLOGY AND GROWTH

Rhodolith growth forms run the gamut of those described for crustose non-geniculate corallines, but form descriptions have also suffered from the use of multiple terms for the same thing. The universal adoption of the form names proposed by Woelkerling et al. (1993) would improve communication. Moreover, as discussed by Johansen (1981) and Woelkerling (1988), assigning an accurate genus and species name to a particular rhodolith, be it fossil or living, can still be a problem (e.g. *Lithophyllum* in the British Isles; Irvine and Chamberlain 1994) and will remain so until thorough regional reviews and monographs based on newly collected populations are evaluated using modern taxonomic concepts and type material (e.g. Riosmena-Rodriguez et al. 1999) and molecular genetic analyses (e.g. Bailey and Chapman 1998,

Bailey 1999). Braga et al. (1993) demonstrated that modern taxonomic concepts are applicable to at least some fossil coralline algae. When completed, this much needed taxonomic work may modify our knowledge of when (geologic time) and where taxa occur and, combined with population-specific studies of growth and reproduction, the environmental constraints on the distribution of living species.

Morphological variation within a well-understood rhodolith species such as *Lithophyllum margaritae* (Hariot) Heydrich can be enormous (Riosmena-Rodriguez et al. 1999), but precisely how this occurs is largely unknown. Rhodoliths get moved by water motion and bioturbators and are grazed, fouled, buried, and exhumed from sediments and bleached when environmentally stressed. This no doubt affects their form, branching patterns, branch density, and branch fusion (if branched) and shape (Bosellini and Ginsburg 1971, Bosence 1976, Foster et al. 1997). Moreover, crustose non-geniculate corallines can survive overgrowth for long periods (Sebens 1986, Miles and Meslow 1990). Abundant starch reserves (Freiwald and Henrich 1994) may contribute to survivorship and recovery (J. Hall-Spencer, University of Glasgow, personal communication). These and related observations by others (e.g. Steneck 1986, Littler et al. 1991) also suggest there may be transport within the thallus (via cell fusions and/or "transfer connections?" [Wetherbee 1979]) from unfavorable to favorable areas for growth. Perhaps the great adaptive importance of calcification in these plants, in concert with starch storage and internal transport, is to reduce cell damage and facilitate rapid recovery from environmental insults? Slow growth is a logical consequence of such an adaptation, and rhodoliths and other non-geniculate corallines often thrive in environments unfavorable to faster growing, uncalcified seaweeds that are less resilient to disturbance and less able to recover from it. Given they are unattached and their entire surface can be photosynthetic, rhodoliths would be ideal subjects for investigating these hypotheses and the required physiological and cytological processes and structures.

Living and fossil rhodoliths and other non-geniculate coralline algae are promising recorders of environmental variation at a number of temporal scales (Agegian 1981, Freiwald and Henrich 1994, Frantz et al. 2000, Halfar et al. 2000). In many rhodoliths that have monomerous construction and protuberances (e.g. *Spongites*, *Lithothamnion*), the coaxial core in the protuberances is radial (Woelkerling 1988). Vegetative initials in the filaments making up this core commonly divide synchronously, producing rows or bands of cells in longitudinal section (Fig. 3, 1° growth band). Groups of primary bands that vary in cell size and wall thickness can result in light-dark pairs of higher order bands, which can be visible to the unaided eye. Descriptions of internal morphology in *Lithothamnion coralloides* rhodoliths in Ireland (Bosence 1976) and *Lithothamnion glaciale* rhodoliths
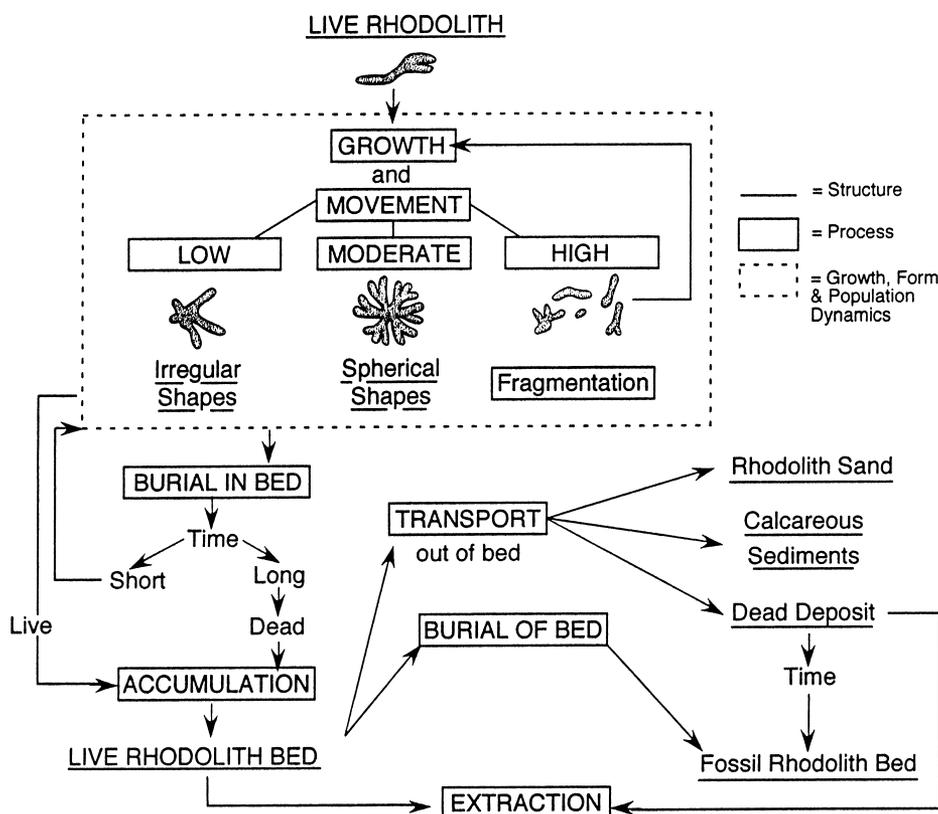
LIVE RHODOLITH

FIG. 2. A model for the structure and dynamics of rhodoliths, rhodolith beds, and geological structures derived from them. Living fragments can be produced in a bed or transported to it, and equivalent small plants can develop from spores. Growth rate and morphology may vary with light, nutrients, temperature, movement, and species. Fragments can be broken from larger thalli during movement from water motion, bioturbation, grazing, and trawling. These processes also produce sand and smaller calcareous particles. Burial in a bed can occur from sedimentation and disturbance from water motion and bioturbation. The effects of fouling may be similar to burial. Catastrophic sedimentation and changes in sea level can cause death/burial of entire beds.

in northern Norway (Freiwald and Henrich 1994) show various orders of banding can be recognized, as summarized in Fig. 3. The 4° level bands in Fig. 3 were interpreted as annual bands by Freiwald and Henrich (1994), but this has not be verified. Higher order banding such as groups of 4° level bands formed during El Niño versus non–El Niño years might also occur. Freiwald and Henrich (1994) suggest one 4° band is formed each year in *L. glaciale* from a 3° band composed of large cells produced in summer, and a 3° band composed of small cells produced in winter. They also found that the small cells were organically enriched but less calcified relative to large cells. Primary and secondary bands in crustose non-geniculate corallines can potentially record daily and monthly environmental change (Agegian 1981). Careful descriptions of cell and band morphology and a good understanding of the causes of chemical and morphological differences could be used to answer fundamental questions about environmental controls on growth and reproduction.

Band formation results in growth, and knowledge of rhodolith growth rates would help quantify some of the demographic processes in Fig. 2 (especially as

they may vary among species), would contribute to our understanding of possible latitudinal and depth variation in bed dynamics and, in conjunction with information on thallus chemical composition and plant densities, allow estimates of carbonate production. Growth rates can also suggest how rapidly beds might recover from disturbance. Growth rates of corallines are generally low relative to those of uncalcified macroalgae, and one might expect rhodolith growth rates to be even lower as a portion of the thallus is always in low light. Unfortunately, growth rate estimates for rhodoliths are rare, and those available are based on various methods and often questionable assumptions (Table 1). At present the only conclusion that might be drawn from these data is that growth rates of individuals at depths <20 m are generally around 0.4 mm·y^{-1}. When measured, differences in growth between summer and winter were very large; almost all growth of *L. coralloides* measured by Adey and McKibbin (1970) in Spain occurred in summer, while Georgina-Rivera (1999) found *L. crassiusculum* grew over twice as fast in winter-spring than in summer-fall in the shallow, subtropical waters of the Gulf of California.
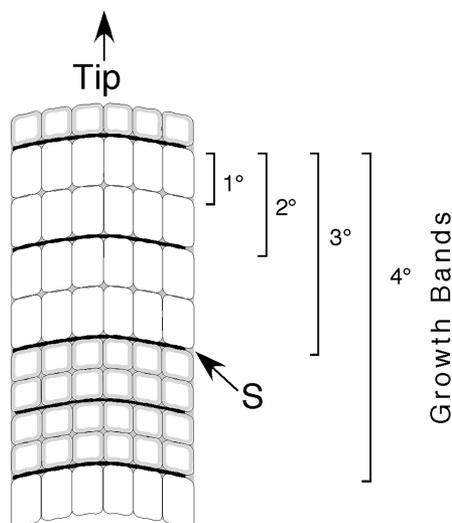
FIG. 3. A generalized example of potential band structure in a longitudinal section of a rhodolith protuberance. A 1° band is a single row of cells, and a 4° band represents a possible annual band. Sutures (S) that separate 2° bands in *Lithothamnion glaciale* (Freiwald and Henrich 1994) are included to illustrate the range of possible orders of banding. Four 1° bands are shown in each 3° band, but this number can vary greatly, especially between 3° bands within a 4° band.

Growth rate estimates for rhodoliths below 20 m are generally an order of magnitude lower than those from shallow water (Table 1). These low growth rates,

based on ^{14}C dating, are questionable, however, because the ^{14}C data were apparently not corrected for ocean reservoir and mixing effects. Without correction, or calibration using the ^{14}C record from atmospheric nuclear testing, ages are overestimated and resulting growth rates underestimated (Stuiver and Braziunas 1993, Frantz et al. 2000). More studies on accurately identified species with alizarin red staining (Andrake and Johansen 1980) in the field and ^{14}C analyses on individuals that contain a carbon record from atmospheric nuclear testing (Frantz et al. 2000; see below) would provide much needed natural and reliable growth rates.

RHODOLITH BED DISTRIBUTION

New reports of living rhodolith beds occur regularly, and a world distribution map updated from that of Bosence (1983b) demonstrates that this community is common and widely distributed (Fig. 4). Reports to date indicate beds are particularly abundant in the Mediterranean and the Gulf of California and along the Atlantic coasts of Norway, Ireland, Scotland, northeastern Canada, the eastern Caribbean, and Brazil, as well as off southern Japan and western Australia. The largest known beds occur on the Brazilian Shelf from 2° N to 25° S (Kempf 1970, Milliman 1977). Recent, broad-scale surveys of the west coast of Ireland using remote sensing indicate rhodolith beds occupy nearly $60 \times 10^6 m^2$ of bottom (De Grave et al. 2000), suggesting thorough surveys elsewhere may greatly increase estimates of abundance. Large concentrations

TABLE 1. Estimated growth rates for rhodoliths. Growth in mm·yr⁻¹ unless otherwise noted.

Species	Location	Depth	Growth Rate	From and Method
Lithothamnion corallioides Crouan	Spain (~40° N)	5.5 m	0.015	Bosence 1983b; from daily field growth data in Adey and McKibbin 1970
	France (~50° N)	0–10 m	43.8% ·year⁻¹	Potin et al. 1990; field measurements of change in $CaCO_3$ weight
Lithothamnion glaciale (Kjellman) Foslie	Norway (~70° N)	7 m	1.0	Freiwald and Henrich 1994; based on assuming one light-dark band pair formed per year
		18 m	0.6	
	Newfoundland (54° N)[1]		0.25–0.45	Halfar et al. 2000; Mg/Ca relative to growth bands
Phymatolithon calcareum (Pallas) Adey et McKibbin	Spain (~40° N)	5.5 m	0.486	Bosence 1983b; from daily field growth data in Adey and McKibbin 1970
	Baltic (~56° N)	13 m	0.5–2.7	Bohm et al. 1978; estimated from laboratory calcification rate
Lithothamnion crassiusculum (Foslie) Mason	Gulf of California (24° N)	3 m	0.25–0.45	Halfar et al. 2000; based on Mg/Ca relative to growth bands
	Gulf of California (24° N)	3 m	0.6	Frantz et al. 2000; ^{14}C record from atmospheric nuclear testing
	Gulf of California (24° N)	3 m	0.6	Georgina-Rivera 1999; field growth of tagged and alizarin-stained individuals
Rhodoliths[2]	Bermuda (~32° N)	2–5 m	0.4	Bosellini and Ginsburg 1971; individuals found in shipwrecks of known age
Rhodoliths[3]	Caribbean (14° N)	30–60 m	0.02–0.09	Reid and Macintyre 1988; ^{14}C dating [4]
Rhodoliths[5]	Bahamas (24° N)	67–91 m	<0.01–0.05	Littler et al. 1991; ^{14}C dating[4]
Rhodoliths[2]	Bermuda (~32° N)	50 m	0.05	Focke and Gebelein 1978; ^{14}C dating[4]

[1] Depth not specified.
[2] Species not reported.
[3] Mix of *Neogoniolithon*, *Paragoniolithon*, and unidentified corallines.
[4] Growth rate probably underestimated because ^{14}C ages were not corrected for marine reservoir-atmosphere offset (see text).
[5] *Lithophyllum* and other nongeniculate corallines.

of living rhodoliths have been found from the low intertidal zone to depths of 150 m, typically in areas where light is high enough for growth and water motion is high enough to inhibit burial by sediment but not so high or unidirectional as to cause mechanical destruction or rapid transport out of favorable growing conditions (e.g. Steller and Foster 1995; Fig. 2). Temperature may affect the distribution of particular species but clearly does not control the distribution of rhodoliths in general as they are abundant from the Arctic to the tropics (Fig. 4). Reports of rhodolith beds over hard bottoms are rare, perhaps because of abrasion, competition with attached organisms, or because they are easily rolled away.

Living rhodoliths commonly occur on calcareous sediment with a high content of dead fragments (Fig. 2 and 5). It is generally assumed that without movement, dense aggregations of live rhodoliths will grow together or become bound together via overgrowth. This has only been observed at one deep-water site (Minnery 1990); in most beds, cessation of movement would probably lead to rapid burial by sediment or overgrowth by other algae and invertebrates. Movement may be caused by water motion, including surges generated by large episodic storms such as hurricanes (e.g. Ballantine et al. 2000). As suggested by others and demonstrated in the field by Marrack (1999) using time-lapsed video and simultaneous current measurements, bioturbation can also be an important source of movement in areas where currents and waves are weak. Accumulating observations and studies such as Marrack's, highlight the need to move from short-term, descriptive studies and qualitative correlations to long-term field studies of light, currents, sedimentation, and movement within and at the distributional boundaries of beds if we are to better understand the causes of bed distribution and dynamics. As for the Irish coast discussed above, these surveys can be greatly facilitated by the use of remote sensing techniques such as Roxann[R] (Chivers et al. 1990) and perhaps side-scan sonar to map beds. Control of bed distribution appears to lie along a continuum ranging from physical processes such as hydrodynamics and sedimentation to biological processes
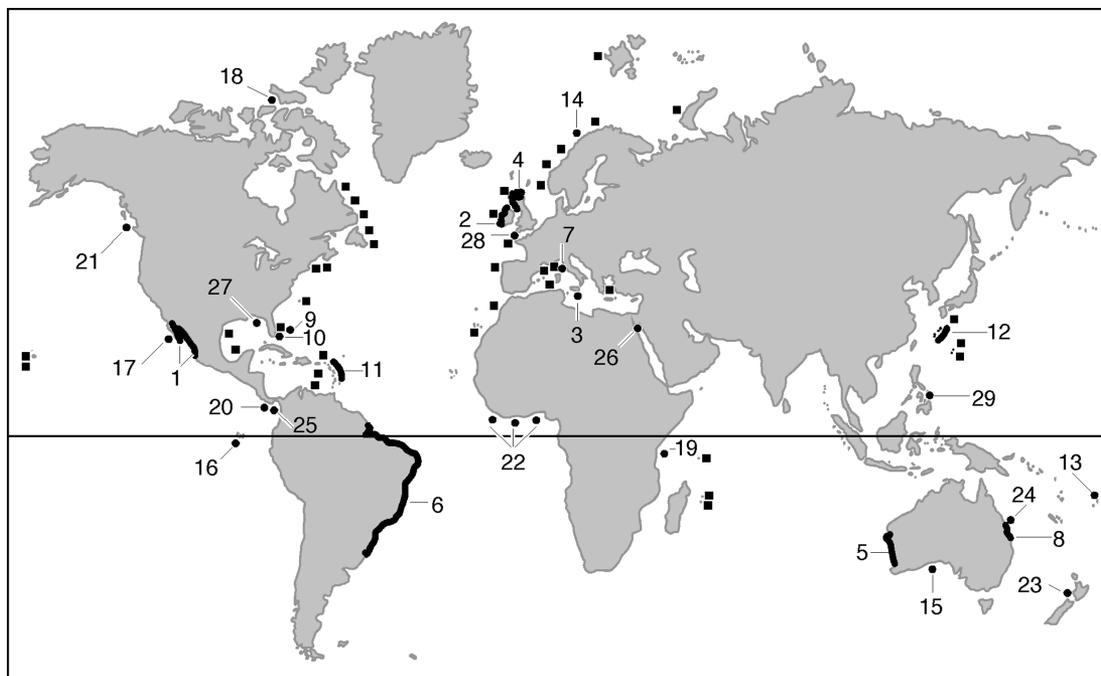

FIG. 4. The world distribution of living rhodolith beds. Squares are from map in Bosence (1983b; see for these references). Circles indicate locations of individual beds, and dark bands indicate large, continuous beds or numerous individual beds not included on the Bosence (1983b) map. No beds have been reported from Antarctica. Personal communication followed by more precise locations. 1. Foster et al. 1997, M. Foster, D. Steller & R. Riosmena, personal observation (eastern Gulf of California). 2. De Grave et al. 2000. 3. Borg et al. 1998 (Malta). 4. D. Donnan, Scottish Natural Heritage, personal communication (north & west Scotland). 5. James et al. 1999. 6. Kempf 1970, Milliman 1977. 7. Basso 1998. 8. Harris et al. 1996. 9. Littler et al. 1991. 10. Prager & Ginsburg 1989. 11. Reid & Macintyre 1988. 12. Tsuji 1993. 13. Scoffin et al. 1985. 14. Freiwald & Henrich 1994. 15. H. Kirkman, United Nations—East Asian Seas Regional Coordinating Unit, personal communication (Great Australian Bight). 16. C. Rigaud, Moss Landing Marine Laboratories, personal communication (Galapagos). 17. J. Harding, University of California at Santa Cruz, personal communication (Isla Cedros). 18. J. Oliver, Moss Landing Marine Laboratories, personal communication (Devon Island). 19. J. Waterbury, Woods Hole Oceanographic Institution, personal communication (Zanzibar). 20. T. Schaeffer, Moss Landing Marine Laboratories, personal communication (Costa Rica). 21. P. Thuringer, Archipelago Marine Research Ltd., personal communication (Queen Charlotte Islands). 22. Reviewed in John & Lawson 1991. 23. D. Schiel, University of Canterbury, personal communication (Kapiti Island). 24. A. Larkum, University of Sydney, personal communication (One Tree Reef). 25. Glynn 1974. 26. Piller & Rasser 1996. 27. McClintock et al. 1993. 28. Farnham & Bishop 1985. 29. D. James, Moss Landing Marine Laboratories, personal communication (Camiguin Island).

Fig. 5. Clear core through the surface of the rhodolith bed in Figure 1A. Surface rhodoliths ~3 cm diameter. Note changes from large, live rhodoliths on the surface to smaller individuals (live and dead) mixed with increasing amounts of fine sediment as depth increases.

such as bioturbation. Better understanding of these controls may provide interesting contrasts to current ecological generalities about the importance of predation, competition, and mutualism based largely on temperate hard bottom and coral reef communities.

ASSOCIATED SPECIES AND EXPLOITATION

Rhodolith beds are communities. Interestingly, these beds often also contain free-living corals (coralliths; e.g. Glynn, 1974, Scoffin et al. 1985, Reyes-Bonilla et al. 1997) and free-living populations of other invertebrates (e.g. bryozoans, hydroids, sponges; personal observation) that normally grow attached, suggesting there is a general set of environmental conditions that favor living free. The rhodoliths in rhodolith beds can have large effects on associated organisms, causing an increase in diversity over that of purely soft benthic habitats at similar depths (Steller and Foster 1995). In current ecological terminology (Bruno and Bertness 2001) they are "habitat modifiers" or "bio-engineers" that, by virtue of their rigid structural complexity, provide relatively stable microhabitats for other

organisms. These habitats include the natural spaces within branched forms, spaces between individuals, and hard (albeit mobile) calcareous surfaces for sessile organisms and borers.

Numerous species are found associated with rhodolith beds (e.g. Weber-Van Bosse and Foslie 1904, Cabioch 1969, Bosence 1979, Hily et al. 1992). Increased scientific interest in biodiversity, its relationship to various measures of community function, and its reduction by human activity has stimulated new studies to assess total diversity of the macroflora and fauna. Preliminary surveys at Scottish sites have found 460 species of associated animals (particularly polychaetes, crustaceans, and molluscs) and 63 species of algae (BIOMAERL Team, 1998), and similar high diversity occurs in rhodolith beds elsewhere in Europe (P.G. Moore, University of Glasgow, personal communication) and in the Gulf of California (D. Steller et al., University of California at Santa Cruz, unpublished data). Additional surveys are needed in other geographic locations to determine if this high diversity is a general feature. Because the cover of live rhodoliths in a bed may affect the diversity and abundance of associated species, reporting this cover will improve comparability among surveys.

Other than the provision of rigid habitats by the rhodoliths themselves, the causes of this high diversity are largely speculative. Rhodolith beds may be "the best of both bottoms," providing a broad range of "hard bottom" habitats related to the range in size and shape of living and dead rhodoliths, and heterogeneous "soft bottom" habitats due to variation in the sizes of rhodolith fragments mixed with finer sediments (BIOMAERL Team, 1998; Fig. 5). Rhodolith beds are relatively featureless at spatial scales greater than centimeters, and, like sand flats (e.g. Hay 1981), many predatory and herbivorous fish commonly associated with rocky reefs rarely appear in them (at least in Gulf of California, personal observation) because of the lack of the larger scale structure. Perhaps the rich flora and invertebrate fauna is, in part, a reflection of reduced grazing and predation by such fishes. At present we know little about these potential interactions, or about the associated species other than their names on species lists. New species and distributional ranges are being discovered as new beds are sampled. Rhodolith beds can be important sites of recruitment and growth of commercially important bivalves (D. Steller, University of California at Santa Cruz, personal communication), important habitat for burrowing invertebrates (Hall-Spencer and Atkinson 1999), and home to species such as *Toxopneustes roseus* (Agassiz). This large sea urchin defies current grazer-algal interaction paradigms by selectively eating rhodoliths, causing fragmentation and producing finer sediments but also enhancing rhodolith movement via bioturbation (James 2000).

Rhodolith beds contain resources of economic importance, and resource extraction causes population reduction and community degradation. Live and dead

rhodoliths and rhodolith-derived sediment are harvested at sites in Europe (Briand 1991) and Brazil (E. Oliveira, Universidade de São Paulo, personal communication). The extracted material is used primarily as a soil conditioner in place of ground limestone, as an additive to animal feeds, and as a water filtration and conditioning agent. There is little evidence that it is any better than ground limestone, but it is economic to use in areas of Britain and France where acidic rocks predominate (Blunden 1991, M. Guiry, National University of Ireland, personal communication). Rhodolith beds are fished world-wide for associated species such as scallops and shrimp. Fishing, often by dredging or bottom trawling, can have large, long-lasting effects on the community (Hall-Spencer and Moore 1999, 2000). Beds may also be negatively affected by increases in turbidity, fouling, sedimentation, and organic enrichment related to eutrophication from sewers and fish and shellfish farms (Hily et al. 1992, BIOMAERL Team 1998) and disturbance in adjacent watersheds. We will have a much better understanding of some of these anthropogenic effects when the results of the recently completed BIOMAERL Team's (1998) comparisons of anthropogenically disturbed and undisturbed beds at sites in the northeast Atlantic and Mediterranean become available. Given the generally slow growth rates of non-geniculate coralline algae, the diversity of rhodolith beds, and their potential importance as nursery grounds, these beds should be considered an ecologically important, essentially non-renewable resource. Destructive harvesting and fishing should be severely limited or forbidden.

GEOLOGICAL, PALEOECOLOGICAL AND CLIMATOLOGICAL SIGNIFICANCE

Geologists are interested in rhodoliths because of their representation in calcareous sediments (e.g. Milliman 1977, Canals and Ballesteros 1997) and fossil deposits (Fig. 1B and 2). The latter have been of particular interest as rhodoliths were perhaps even more abundant at times in the geological past than they are today (e.g. Cambrian–Late Devonian; Copper 1994) and can register paleoenvironmental conditions. At coarse scales the presence of fossil rhodoliths may indicate a deposit was formed in the photic zone (e.g. Toomey 1985). At finer scales they may indicate depth, sea level, and hydrodynamic conditions (e.g. Manker and Carter 1987, Braga and Martin 1988, Macintyre et al. 1991, Iryu 1997). These indications often require assuming the deposit represents the original site of growth (i.e. rhodoliths were not transported from elsewhere), that rhodolith shape indicates water motion and water motion is higher in shallow water, and that species and their living depth distributions are accurately known. Shape has been of particular interest because many observations show it can be affected by water motion, particularly spherical shapes that occur where water motion, and thus turning, is high (reviewed in Bosence 1983b). However, these relationships may vary depending on habitat, as we now know spherical shapes can occur in relatively low energy environments (Reid and Macintyre 1988, Prager and Ginsburg 1989, Littler et al. 1991), and movement and shape can be affected by many variables (Marrack 1999). Thus, interpretations of hydrodynamic environments based on shape should be made with care. Some of these assumptions can be tested by using information from other species in the deposit, associated sediments, and the general depositional setting.

In areas like the Gulf of California where living rhodolith beds and well-preserved, Pliocene and Pleistocene deposits rich in rhodoliths occur (Foster et al. 1997; Fig. 1), comparisons of species composition across large time intervals promise to tell us much about the effects of climate change on community diversity and stability, as it has for coral reefs (Pandolfi and Jackson 1997). As Adey and Macintyre (1973) point out, the accuracy of paleoecological interpretations will be enhanced as the biology and ecology of living rhodoliths are better understood.

Finally, given their potential as climate recorders, rhodoliths could become the Giant Sequoias of the sea. Available data suggest rhodoliths commonly grow less than one millimeter per year (Table 1) and, like trees and corals, leave behind growth bands (previously discussed; Fig. 3). Frantz et al. (2000) set out to determine the growth rate of *L. crassiusculum*, a heavily calcified, densely branched rhodolith from the Gulf of California that grows to over 15 cm in diameter and has internal bands. They used accelerator mass spectrometry to determine variation in ^{14}C at 1-mm increments along a longitudinal section of a branch from tip to core. The elevated ^{14}C from atmospheric nuclear testing provided a clear time marker, allowing a growth rate determination of 0.6 mm·y^{-1} (Table 1) and thus an age for large individuals of around 125 years. Moreover, Frantz et al. (2000) also found declines in ^{14}C coincident with recent El Niño events, indicating non-geniculate corallines can contain records of shallow water marine climate similar to those found in corals (e.g. Linsley et al. 2000) and perhaps be more useful, because corallines are not restricted to tropical waters. Corallines do have the disadvantage of relatively slow growth, but sampling methods such as microdrilling and electron microprobe (Halfar et al. 2000) may allow submillimeter analyses of growth bands and thus enable accurate reading of a seasonal climate record. Large, old rhodoliths and their encrusting counterparts thus have the potential for providing paleoclimatic records that will help resolve pressing questions concerning climate variability.

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