Botanica Marina 49 (2006): 355–359 © 2006 by Walter de Gruyter • Berlin • New York. DOI 10.1515/BOT.2006.044

Short communication

Rhodolith bed: a newly discovered habitat in the North Pacific Ocean

Brenda Konar[1,]*, Rafael Riosmena-Rodriguez[2] and Katrin Iken[1]

[1] School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, PO Box 757220, Fairbanks, AK 99775-7220, USA, e-mail: bkonar@guru.uaf.edu

[2] Programa de Investigación en Botánica Marina, Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, Apartado postal 19-B, La Paz, B.C.S. 23080, Mexico

* Corresponding author

Abstract

Rhodoliths are unattached calcareous red algae that form extensive beds. Although rhodolith beds are widely distributed in temperate and tropical areas, a recent discovery in the North Pacific Ocean represents a significant northward extension of known rhodolith distribution. This bed, located in Prince William Sound, Alaska, is composed of one rhodolith species, *Phymatolithon calcareum*, with two reproductive states, tetrasporangial and gametangial. A characteristic feature of this bed is that cryptofaunal chitons were the most abundant associated invertebrate species. Comparisons with *P. calcareum* populations in other regions showed that Prince William Sound thalli are smaller in many measurable anatomical features.

Keywords: Alaska; habitat; morphology; rhodolith; taxonomy.

Rhodoliths are unattached red coralline algae that form extensive beds in nearshore areas around the world (Foster 2001). In general, rhodoliths require water motion (waves, currents) or bioturbation to maintain an unattached and unburied state (Bosence 1976, Marrack 1999). They can be found from the low intertidal zone down to depths of 286 m in areas where there is enough light for photosynthesis (Littler et al. 1991, Foster 2001). Rhodoliths are generally found on sandy substrata, where they can greatly increase the diversity by providing hard substratum for epifauna, and interstitial areas between their branches for cryptofauna (Steller et al. 2003). The protection from surface dwellers and the general stabilizing effect of rhodoliths also increases numbers of sand-dwelling infaunal organisms (Steller et al. 2003). Rhodolith growth forms vary greatly, ranging from foliose to fruticose to lumpy (e.g., Riosmena-Rodriguez et al. 1999). Because rhodolith taxonomy is largely based on anatomical features, identification and distribution are difficult and sometimes controversial (Steller et al. 2003).

Rhodoliths are distributed globally but are known primarily from the warmer waters of the Mediterranean Sea, the Gulf of California, and along both Atlantic coasts (for review see Foster 2001). Some rhodolith beds are known from colder regions like the North Atlantic Ocean and the Atlantic portion of the Arctic Ocean; however, in the Pacific Ocean, the most northerly bed known is in British Columbia (see Foster 2001 for references). In the summer of 2004, a rhodolith bed was discovered as a new habitat in Herring Bay, Prince William Sound, Alaska. This newly discovered bed in Alaska, located at 60°27′60″ N and 147°45′24″ W, represents a significant northward extension of the known distribution of Pacific rhodoliths.

Initial surveys of the Herring Bay rhodolith bed showed that water depths ranged from 12 to 18 m and contained a minimum areal cover of 3000 m^2. While these depths are well within the range for rhodolith beds, they are fairly limited compared to other beds. For example, in other areas rhodolith beds can occur intertidally and in much deeper waters (Foster 2001). In Herring Bay, surveys were done in shallower waters (11 m to approximately 8 m), but few rhodoliths were found as the substratum became rocky and dominated by kelp and sessile invertebrates. Water depths greater than 18 m were not explored.

The Herring Bay rhodolith bed has sand as the underlying substratum, much of which is covered by rhodoliths and shell fragments. When percent cover was visually estimated in eighteen 0.25 m^2 quadrats per transect (along three random transects ranging from 12 m to 18 m), only 29.4%±9.6% (mean±SE) of the substratum was sand, while 52.8%±9.8% (mean±SE) and 17.8%±8.0% (mean±SE) was covered by rhodoliths and shell fragments, respectively. Rhodoliths were significantly more abundant than shell fragments, but not sand (ANOVA, arcsin transformed, $F_{2,51}=3.029$, $p=0.05$, post-hoc Fisher's PLSD, $p\leq 0.01$). All rhodoliths were collected from the surveyed quadrats. Densities of rhodoliths averaged 27.5±8.7 (mean±SE) individuals/0.25 m^2 and biomass averaged 29.7±6.0 g/0.25 m^2 (mean±SE). In addition, fleshy macroalgal cover was noted within each quadrat surveyed. Two brown algae, *Agarum clathratum* Dumortier and *Laminaria saccharina* (Linnaeus) J.V. Lamouroux were found in 50% of the surveyed quadrats. This is similar to beds in the temperate Atlantic Ocean (Freiwald et al. 1991), but different from the Gulf of California where red algae dominate (Steller et al. 2003). In general, this high algal cover is similar to other beds in Brazil and the Gulf of California (Steller et al. 2003).

As is typical for kelp beds and other primary producers providing three-dimensional habitat, many invertebrates

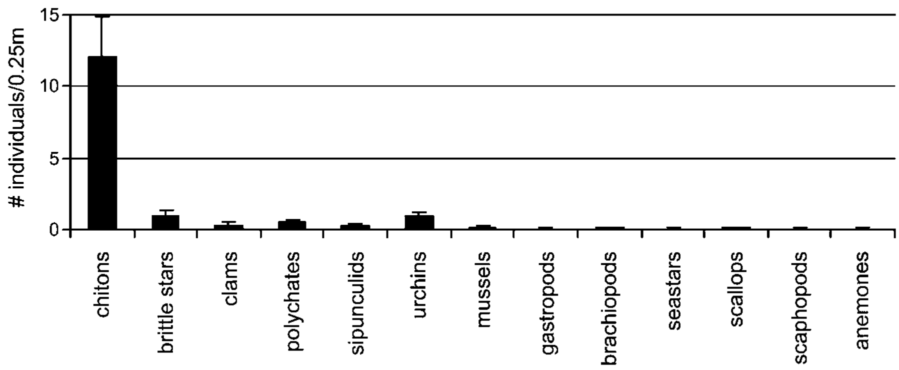

Figure 1 Mean number (+1 SE) of various invertebrates.
Data based on counts from six 25-cm[2] quadrats placed along three random transects (n=18).

uncommon to soft-substrata were found living on the rhodoliths (Figure 1). The most abundant of these organisms were unidentified chitons. More detailed studies are needed to determine how the diversity of associated species in this northern rhodolith bed compares to other beds around the globe. For example, upward of 300 algal and invertebrate species were associated with one rhodolith bed in the Gulf of California (Steller et al. 2003, Hinojosa-Arango and 2004). Beds in the Iberian Peninsula are even more diverse, with over 450 floral and faunal species (Bordehore et al. 2003). Many species found in rhodolith beds appear to be rhodolith-specific, such as some cnidarians, echinoderms and chitons (Clark 2000, James 2000, Steller et al. 2003).

The discovery of the Herring Bay rhodolith bed is also taxonomically interesting, because the morphological and anatomical features of the rhodolith species, *Phymatolithon calcareum* (Pallas) Adey *et* McKibbin (Adey and McKibbin 1970) (Figures 2–4), is different than previously described from the Atlantic Ocean (Table 1). Morphological and taxonomic analysis for the present study came from more than 500 rhodolith individuals, which included all possible morphological variants. Growth-form terminology used here follows Woelkerling et al. (1993) and anatomical terminology follows Woelkerling (1988). Permanent slides for optical microscopy were prepared using the methodology described by Riosmena-Rodriguez et al. (1999). Morphological and taxonomic analyses on individual rhodoliths included various anatomical measurements and evaluation of reproductive plants.

The rhodolith bed in Herring Bay is composed of one highly polymorphic species, *Phymatolithon calcareum*. The general habit of this species was non-geniculate and unattached. The rhodoliths were irregular to globose, mostly 2–7 cm in the greatest dimension, with growth-forms intergrading from encrusting to foliose to fruticose (Figure 2A–D). Branching was irregular and sparse to dense (4–26 protuberances/individual). The protuberances were cylindrical and typically 0.80–3.00 mm in diameter and 0.64–8.00 mm long. Protuberance dimensions were considerably smaller than those reported from Atlantic populations (see Table 1).

Internal structure of the rhodoliths showed a monomerous construction, consisting of a single system of branched filaments that formed a core and peripheral

Table 1 Comparative summary of information on measurable characteristics for *Phymatolithon calcareum* from different geographical areas.

	Alaska[1]	British Isles[2]	Atlantic coast of France[3]	Atlantic coast of Spain[4]
Protuberances diameter (mm)	0.80–3	Up to 6	20–30	ND
Protuberances height (mm)	0.64–8	Up to 70	Up to 50	ND
Length of cells in core region (μm)	2.5–13	5–18	10–18	4–9
Diameter of cells in core region (μm)	2–12.5	3–10	4–10	5–7
Length of epithallial cells (μm)	4–11	ND	ND	ND
Diameter of epithallial cells (μm)	0.83–1.66	ND	ND	ND
Relative number of pores in chamber roof	30–50	30–60	ND	ND
Number of cells in conceptacle chamber roof	3–6	3–9	ND	3–6
Tetrasporangial conceptacle chamber diameter (μm)	80–200	230–500	100–140	126–190
Tetrasporangial conceptacle height (μm)	80–170	117–130	60–120	38–89
Mature tetra/bisporangia length (μm)	80–140	90–125	ND	ND
Mature tetra/bisporangia diameter (μm)	20–40	49–73	ND	ND

For analysis, rhodolith samples were dried and later deposited at the Phycological Herbarium of Universidad Autónoma de Baja California Sur (FBCS).
[1]The present study. [2]Irvine and Chamberlain 1994. [3]Cabioc'h 1966. Mendoza and Cabioc'h 1998 and Cabioc'h et al. 1992. [4]Adey and McKibbin 1970.
ND: no data.

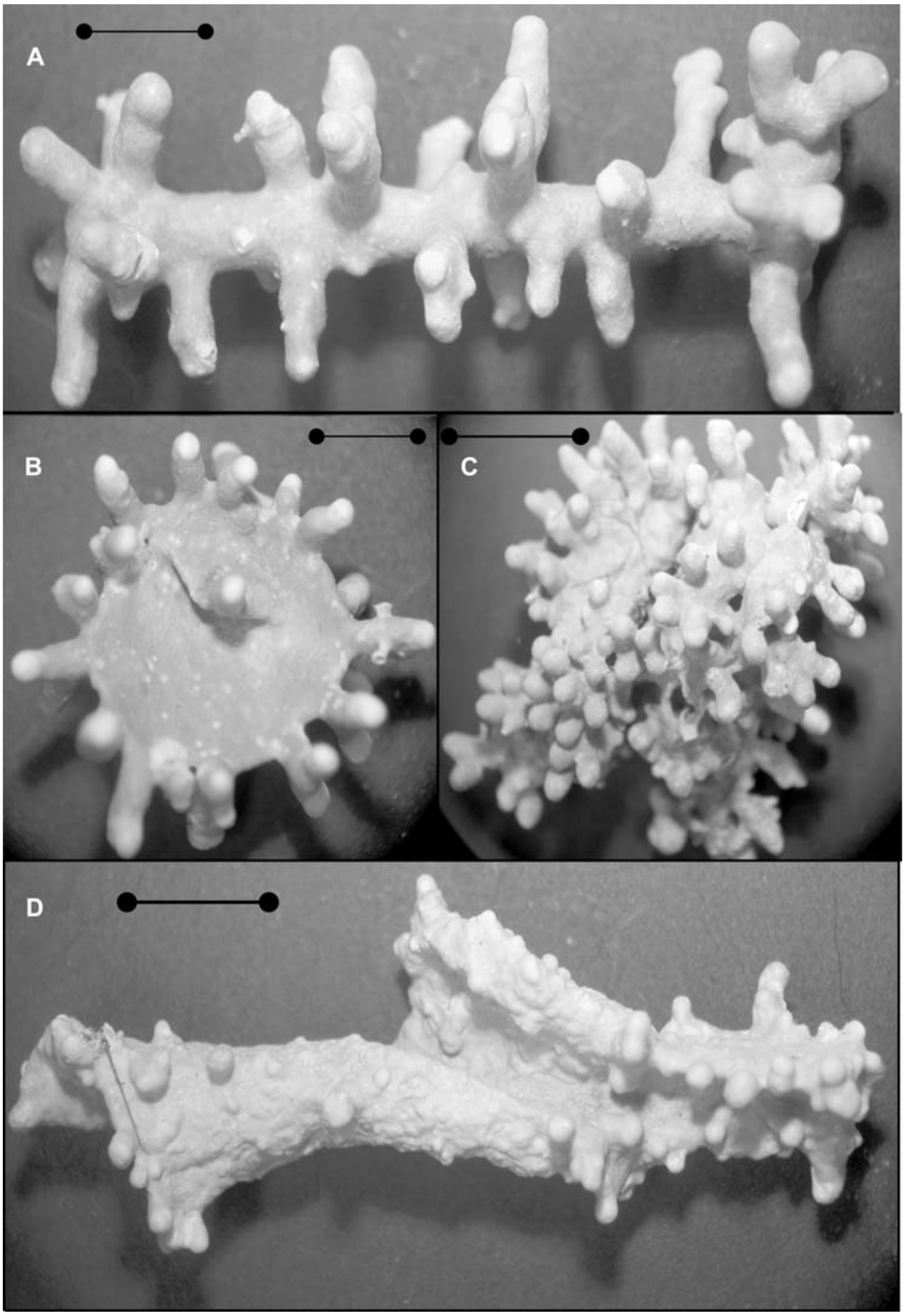

Figure 2 Morphological variability in branching and growth form of *Phymatolithon calcareum* in Alaska.
(A) High-density branched fruticose thallus. (B) Low-density branched fruticose thallus. (C) High-density foliose-fruticose thallus. (D) Less branched crustose thallus. Scale bar=1 mm.

region. Portions of the core filaments and their derivatives curved outwards and formed regular bands towards the thallus surface (Figure 3A). Associated cells were 2.5–13.0 μm long and 2.0–12.5 μm in diameter with the terminating filament epithallial cells 4–11 μm long and 0.83–1.66 μm in diameter. These dimensions are roughly similar to those measured in Atlantic populations (see Table 1). Interestingly, the subepithallial cells were shorter than the lower epithallial cells and were rounded, but not flared (Figure 3B). Cells of adjacent filaments were linked by lateral cell-fusions and trichocytes were absent.

Reproductive rhodoliths were found in two states, tetrasporangial and gametangial. Bispores were not seen. Tetrasporangial rhodoliths had multiporate conceptacles (Figure 4A–B), with protruding roofs sometimes forming a ring and becoming buried. The conceptacle roofs were 3–6 cells thick above the chamber and were not pitted with depressions around the pores. The tetrasporangial conceptacle roof filaments bordering the pore canals were composed of cells that did not differ in size and shape from other roof filament cells (Figure 4A). Conceptacle chambers were primarily 80–200 μm in diam-

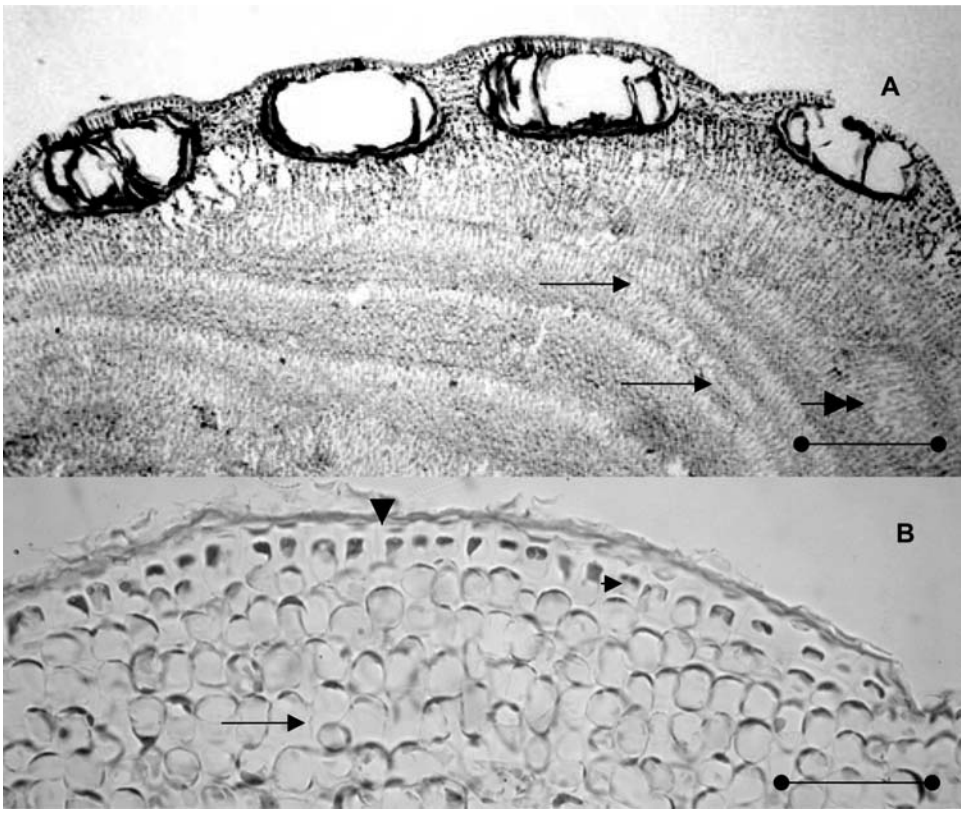

Figure 3 Vegetative anatomy of *Phymatolithon calcareum* in Alaska.
(A) Longitudinal section showing the presence of growth bands (arrow) as part of the monomerous construction and a sunken conceptacle (double arrow; scale bar=500 μm). (B) Longitudinal section showing the presence of rounded (short arrow) epithallial cells, short subepithallial cells (arrowhead) and cell fusions (long arrow; scale bar=250 μm).

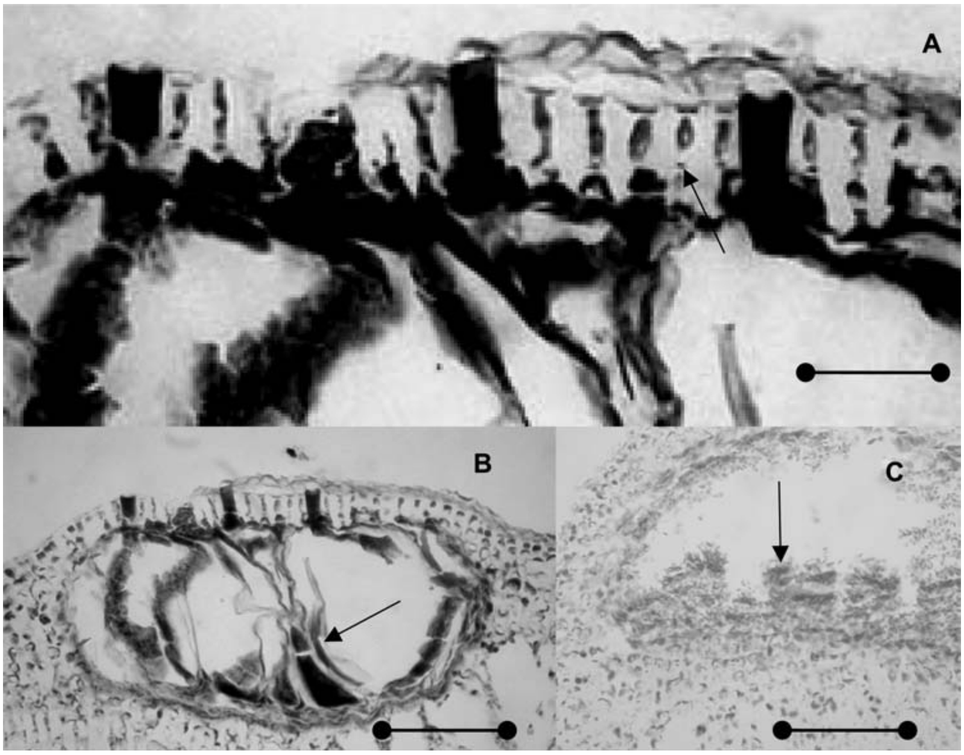

Figure 4 Reproductive anatomy of *Phymatolithon calcareum* from Alaska.
(A) Longitudinal section of a conceptacle roof showing that the cells lining the pore area (arrow; scale bar=10 μm) are similar to other cells in the roof. (B) Tetrasporangial conceptacle with tetraspores (arrow; scale bar=100 μm). (C) Male conceptacle with simple spermatangia (arrow; scale bar=100 μm).

eter and 80–270 μm long. Typically, tetraspores were scattered across the chamber floor; each mature sporangium was 80–140 μm long and 20–40 μm in diameter and contained four zonately arranged tetraspores (Figure 3B). These dimensions are similar, or larger than those known from Atlantic populations of this species (see Table 1). Gametangial conceptacles were uniporate (Figure 4C). Male conceptacles were typically 80–150 μm in diameter and 80–200 μm long and each contained a single spermatangium (Figure 5). Female gametangia and carposporangia were not found.

Most rhodolith beds around the world are composed of two or three species, but the overall number of species within a geographical region varies between one and twelve (Riosmena-Rodriguez et al. in press). While *Phymatolithon calcareum* is relatively common and globally distributed, prior to this study it has been seen only once in a gametangial reproductive state off the Atlantic coast of France (Mendoza and Cabioc'h 1998). This is particularly interesting because gametangial structures were present on many of the *P. calcareum* individuals examined from the Alaskan bed. The differences in reproductive structures among separate geographic areas suggest the life history of this species is variable. More collections are needed to determine what may cause this variability.

Acknowledgements

This discovery took place during a Census of Marine Life NaGISA cruise, which was funded by the Gulf Ecosystem Monitoring Program. We would like to thank Capt Neil Oppen for fortuitous positioning of the research vessel Tempest, which allowed us to come upon the rhodolith bed. Field assistance was provided by Robin Rigby, Gayle Hansen, and Jeremy Bahr.

References

Adey, W.H. and D.L. McKibben. 1970. Studies on the maerl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnium coralloides*. *Bot. Mar. 13*: 100–106.

Bordehore, C., A.A. Ramos-Espla and R. Riosmena-Rodriguez. 2003. Comparative study of two maerl beds with different otter trawling history, southeast Iberian Peninsula. *Aquat. Conserv: Mar. and Freshw. Ecosys*. *13*: S43–S54.

Bosence, D.W. 1976. Live and dead faunas from coralline algal gravels, Co. Galway. *Palaeontology 22*: 449–478.

Cabioc'h, J. 1966. Contribution à l'étude morphologique, anatomique et systématique de deux Mélobésiées: *Lithothamnion calcareum* (Pallas) Areschoug et *Lithothamnion corallioides* Crouan. *Bot. Mar. 9*: 33–53.

Cabioc'h, J., J.Y. Floc'h, L. LeToquin, C. Boudouresque, A. Meinesz and M. Verlaque. 1992. *Guide des algues des mers d'Europe*. *Volume 1*. Delachaux et Niestlé, Lausanne. pp. 231.

Clark, R.N. 2000. The chiton fauna of the Gulf of California rhodolith beds (with descriptions of four new species). *Nemouria – Occasional Papers of the Delaware Museum of Natural History 43*: 1–20.

Foster, M.S. 2001. Rhodoliths: between rocks and soft places. *J. Phycol. 37*: 659–667.

Freiwald, A., R. Henrich, P. Schafer and H. Willkomm. 1991. The significance of high-boreal to subarctic maerl deposits in northern Norway to reconstruct Holocene climatic changes and sea level oscillations. *Facies 25*: 315–340.

Hinojosa G. and R. Riosmena-Rodriguez. 2004. The influence of rhodolith species and growth-form on cryptofaunal assemblages of rhodolith beds in the central-west Gulf of California, Mexico. *PSZN Mar. Ecol. 54*: 234–244.

Irvine, L.M. and Y.M. Chamberlain. 1994. *Seaweeds of the British Isles Volume 1. Rhodophyta. Part 2B Corallinales, Hildenbrandiales.* The Natural History Museum, London. pp. 276.

James, D.W. 2000. Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, Mexico. *Mar. Biol. 137*: 913–923.

Littler, M.M., D.S. Littler and M.D. Hanisak. 1991. Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. *J. Exp. Mar. Biol. Ecol. 150*: 163–182.

Marrack, E.C. 1999. The relationship between water motion and living rhodolith beds in the southwestern Gulf of California, Mexico. *Palaios 14*: 159–171.

Mendoza, M.L. and J. Cabioc'h. 1998. Study compares reproduction of *Phymatolithon calcareum* (Pallas) Adey & McKibbin and *Lithothamnion corallioides* (P. & H. Crouan) P. and H. Crouan (Corallinales, Rhodophyta), and reconsiderations of the definition of the genera. *Can. J. Bot. 76*: 1433–1445.

Riosmena-Rodriguez, R., W.J. Woelkerling and M.S. Foster. 1999. Taxonomic reassessment of rhodolith-forming species of *Lithophyllum* (Corallinales: Rhodophyta) in the Gulf of California, Mexico. *Phycologia 38*: 401–417.

Riosmena-Rodríguez, R., D.L. Steller, G. Hinojosa-Arango and M.S. Foster. In press. Biology and conservation of rhodolith beds in the Gulf of California. *In*: (R.C. Brusca, ed.) *The Gulf of California*. The University of Arizona Press, Tucson.

Steller, D.L., R. Riosmena-Rodriguez, M.S. Foster and C.A. Roberts. 2003. Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. *Aquat. Conserv: Mar. and Freshw. Ecosys. 13*: S5–S20.

Woelkerling W. 1988. *The coralline red algae: an analysis of genera and subfamilies of non-geniculate Corallinaceae*. British Museum (Natural History) & Oxford University Press, Oxford. pp. 268.

Woelkerling W.J., L.M Irvine and A.S. Harvey. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *B. Phycol. J. 21*: 55–80.

Received 4 April, 2006; accepted 8 August, 2006