Hermatypic Corals Associated with Rhodolith Beds in the Gulf of California, México[1]

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ABSTRACT: Subtidal surveys along the western Gulf of California coast revealed the presence of free-living hermatypic corals associated with rhodolith beds, the first record of this association in the gulf. Five coral species were found, as follows: *Psammocora stellata* Verrill, *Porites panamensis* Verrill, *P. sverdrupi* Durham, *Fungia curvata* Hoeksema, and *F. distorta* Michelin, with several new distributional records. Differences in relative abundance of species in our collections from those in other regions of the Pacific suggest that transport, light, and temperature play important roles in distribution and development of coral-rhodolith associations in the gulf.

RHODOLITH BEDS ARE ubiquitous marine communities dominated by free-living, calcareous red algae (Piller and Rasser 1996). These beds are found worldwide and occur from the intertidal zone to depths of over 100 m (Boscence 1983, Littler et al. 1991). Extensive beds recently have been reported along the west coast of the Gulf of California, México (Steller and Foster 1995, Foster et al. in press). Rhodolith beds have a rich and diverse associated fauna and flora, but there have been no prior studies of these associates in the gulf and only a few elsewhere (Jacoutte 1962, Cabioch 1969, Keegan 1974, Littler et al. 1991, Hilly et al. 1992). The common occurrence of unattached corals with rhodolith beds in the eastern tropical Pacific has long been noted (Glynn 1974, 1994, Glynn and Wellington 1983, Colgan 1991). Those investigators mentioned several coral species [*Fungia curvata* Hoeksema, *F. distorta* Michelin, *Porites panamensis* Verrill, *Pavona gigantea* Verrill, *P. clavus* (Dana), *P. varians* Verrill, and *Gardineroseris planulata*

(Dana)] living near beds or at sites fitting the description of beds. With the exception of *Fungia* spp., most of the associated colonies showed a distinct rounded morphology and were called "coralliths" (Glynn 1974). Available data on abundances and morphological characters in sites other than Panamá and the Galápagos Islands (Ecuador) are lacking. Although corallith-rhodolith associations have been reported in the western and central Pacific (Pichon 1974, Scoffin et al. 1985), and spherical growth of detached coral colonies also occurs in the Indo-West Pacific, the Caribbean (Scoffin et al. 1985, Lewis 1989, Riegl et al. 1996) and even in fossil Tabulata and Scleractinia (Hill and Stumm 1956, Lee and Noble 1990), this phenomenon has not been previously reported in the Gulf of California.

Rhodolith beds of the Gulf of California were described briefly by Steller and Foster (1995) and Foster et al. (in press). In general, these environments occur on sandy bottoms from 3 to > 30 m depth, and more than 100 m from rocky shores. Our surveys in the western Gulf of California revealed that free-living corals occur in association with rhodolith beds in a variety of different habitats (Foster et al. in press). In this paper we list the scleractinian corals found and describe some of their main morphological and ecological characteristics.

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MATERIALS AND METHODS

The corals reported here were observed and collected using scuba in several beds in the cen-
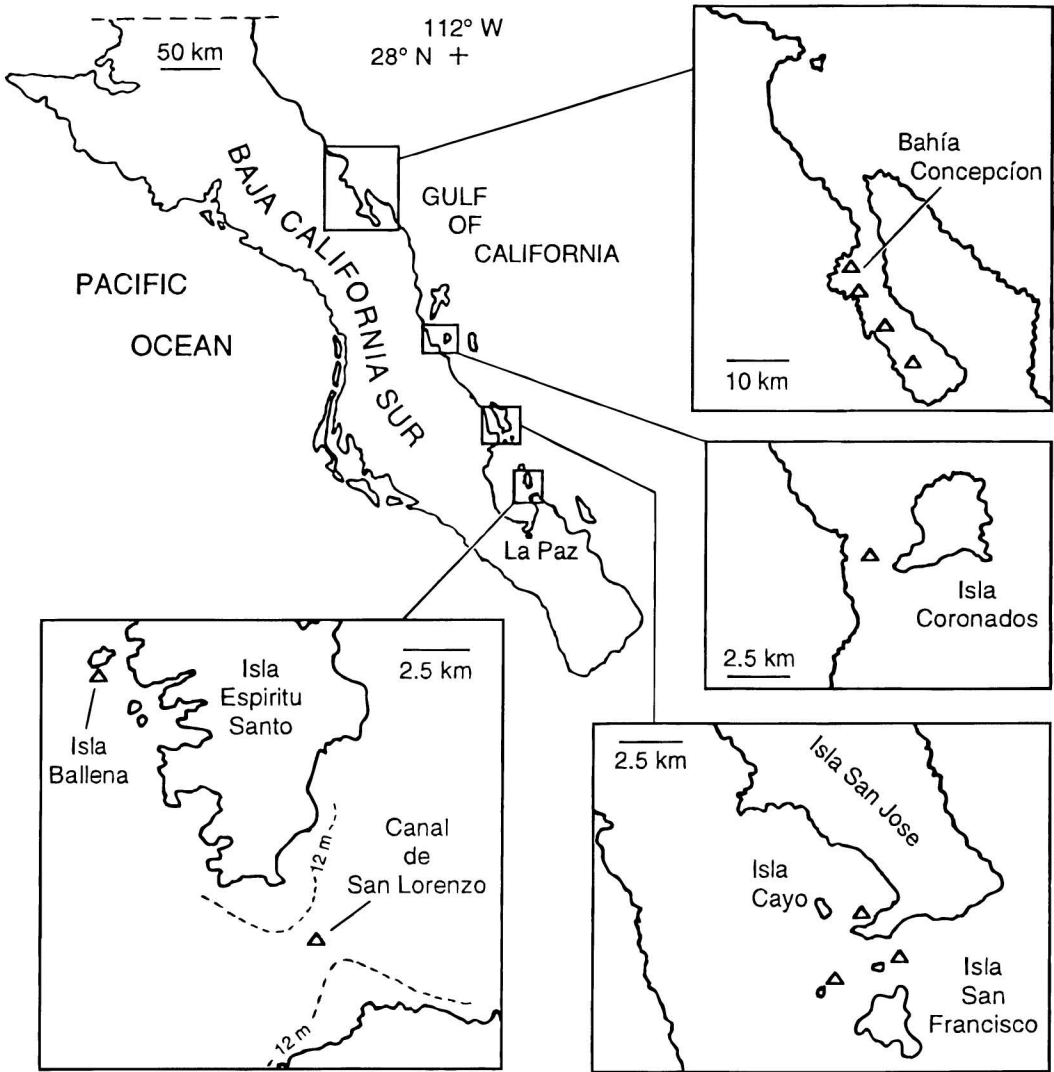
Figure 1. Location of rhodolith beds with associated hermatypic corals (indicated by triangles) in the Gulf of California.

tral and southern Gulf of California between 1994 and 1996: Bahía Concepción, Isla Coronados, Isla San José, Isla Ballena and Canal de San Lorenzo (Figure 1). Extensive searches were conducted in the beds at depths from 3 to 30 m to collect specimens and observe environmental conditions. Species were identified using Durham (1947), Durham and Barnard (1952), Wells (1983), and Hoeksema (1989). All specimens are deposited in the Museo de Historia Natural de la Universidad Autónoma de Baja California Sur.

To compare morphologies of coraliths from the Gulf of California and other sites in the eastern Pacific, we measured the dry weights and maximum, intermediate, and shortest diameters of single specimens and calculated their sphericities with the formula: $(L\,S\,Y\,/\,L^3)1/3$, where L = maximum diameter, S = shortest diameter, and Y = intermediate diameter (Glynn 1974). Relationships between individual sphericities, dry weights, and maximum diameters were estimated with the nonparametric Spearman correlation coefficient (Zar 1996).

RESULTS

Five coral species were found associated with rhodolith beds in the Gulf of California.

Phylum CNIDARIA Hatschek, 1888
Class ANTHOZOA Ehrenberg, 1834
Order SCLERACTINIA Bourne, 1900
Family SIDERASTREIDAE Vaughan & Wells, 1943
Genus *Psammocora* Dana, 1846

Psammocora stellata Verrill, 1866
Figure 2

SYNONYMS IN THE EASTERN PACIFIC: *Stephanaria stellata* Verrill, 1866

RECORDS FROM RHODOLITH BEDS IN THE GULF OF CALIFORNIA: Coralla of *P. stellata* have been found at two beds, Isla San José and Canal de San Lorenzo.

OTHER RECORDS IN THE GULF: 23° to 24° N, La Paz (Durham 1947, Durham and Barnard 1952; Isla San Francisco (Squires 1959); Cabo Pulmo, San José del Cabo (Reyes Bonilla 1992); Isla Ballena, San Juan de la Costa (new records).

DISTRIBUTION: Gulf of California, México, to Isla La Libertad (1° S), Ecuador; Central and West Pacific (Wells 1983, Reyes Bonilla 1993).

NOTES: This species was not common in the rhodolith beds; it appeared mostly as small, rounded fragments 1 to 3 cm largest diameter,
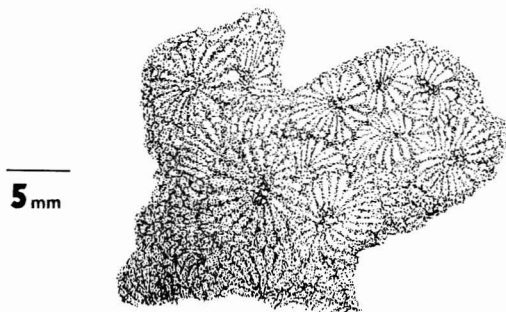
although some larger coralla (8 to 10 cm largest diameter) were seen. In all cases, the skeleton was almost completely covered by living tissue.

Family PORITIDAE Gray, 1846
Genus *Porites* Link, 1801

Porites panamensis Verrill, 1866
Figure 3

SYNONYMS IN THE EASTERN PACIFIC: *P. californica* Verrill, 1868, *P. nodulosa* Verrill, 1868, and *P. porosa* Verrill, 1869.

RECORDS FROM RHODOLITH BEDS IN THE GULF OF CALIFORNIA: Very abundant in Bahía Concepción beds and common at Isla San José; scarce at Isla Coronados and Canal de San Lorenzo.

OTHER RECORDS IN THE GULF: This species has been found throughout the gulf, from San Felipe and Puerto Peñasco (31° N) to Cabo San Lucas and Mazatlán (22° N). Because of this, the number of records is too large to be included here. Durham (1947), Squires (1959), and Horta Puga and Carricart Ganivet (1993) listed most of the earlier records.

DISTRIBUTION: Gulf of California, México, to Isla Gorgona (3° N), Colombia (Glynn et al. 1982, Reyes Bonilla 1993).

NOTES: All coralla observed in the rhodolith beds were growing on dead bivalve shells or

FIGURE 2. *Psammocora stellata* (Verrill, 1866), a hermatypic coral associated with rhodolith beds.
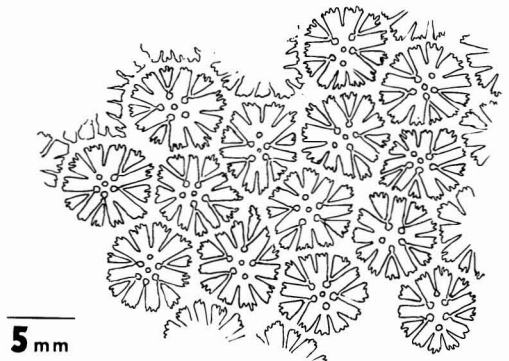

FIGURE 3. Detail of calices of *Porites panamensis* Verrill, 1866.

over portions of dead and living rhodoliths. Overgrowth of living rhodoliths was especially common at Bahía Concepción. We found no completely rounded colonies ("coralliths") in the beds, but those in the early stages of formation (Lewis 1989) were common.

Porites sverdrupi Durham, 1947

SYNONYMS IN THE EASTERN PACIFIC: None.

RECORDS FROM RHODOLITH BEDS IN THE GULF OF CALIFORNIA: This species has been found at Bahía Concepción and San José and Coronados Islands.

OTHER RECORDS IN THE GULF: 24° to 29° N, Isla del Carmen, Bahía Agua Verde (Durham 1947); Puerto Escondido (Durham and Barnard 1952); Isla Partida, Isla San Marcos, Isla Angel de la Guarda (Squires 1959); Bahía Concepción (Reyes Bonilla 1993); Isla Coronados (new record).

DISTRIBUTION: Gulf of California to Islas Marías (20° N), México (Reyes Bonilla 1993).

NOTES: The species was described based on its highly branched corallum (completely different from the encrusting or massive forms of other *Porites* of the eastern Pacific), abundant spines on the skeleton, and calices that are flush with the coral surface. This species was considered as a deep-water phase of *P. panamensis* by Squires (1959) and synonymized. As a consequence, it has not been mentioned since. Reyes Bonilla (1990) showed that the branching morphology occurred at all depths (although more common at >5 m depth) at Bahía Magdalena (west coast of the Baja California peninsula; 24° N), Bahía Concepción, and other localities of the northern gulf and that synonymy should be reconsidered.

In contrast to the behavior of the other species of *Porites* living in rhodolith beds, coralla of *P. sverdrupi* did not encrust algae but were free-living. This ability may be a consequence of their ramose morphology. As with *Psammocora*

stellata, the skeleton surface was generally covered with living tissue except where the fragment had been broken.

Family FUNGIIDAE Dana, 1846
Genus *Fungia* Lamarck, 1801

Fungia curvata Hoeksema, 1989
Figure 4

SYNONYMS IN THE EASTERN PACIFIC: *Fungia elegans* Verrill, 1870 and *Cycloseris elegans* (Verrill, 1870).

RECORDS FROM RHODOLITH BEDS IN THE GULF OF CALIFORNIA: Isla San José and Canal de San Lorenzo.

OTHER RECORDS IN THE GULF: 23° to 25° N, La Paz (Verrill 1868–1870); Canal de San Lorenzo (Durham and Barnard 1952); Isla Espíritu Santo, Isla San Diego (Squires 1959); Cabo Pulmo (23° N), Isla San José (24° N) (new records).

DISTRIBUTION: Gulf of California, México, to Isla Gorgona (3° N), Colombia (Glynn et al. 1982, Reyes Bonilla 1993).

NOTES: This coral was infrequently found in coralline algal beds in the gulf. When it was
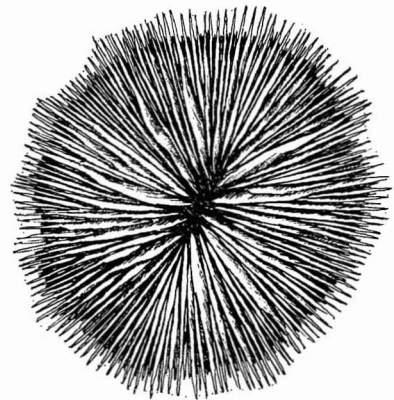

1 cm

FIGURE 4. *Fungia curvata* (Hoeksema, 1989), a hermatypic coral associated with rhodolith beds.

found, it was usually associated with large numbers of *F. distorta* coralla. This phenomenon has been reported previously in the gulf and the Galápagos Islands (Durham and Barnard 1952, Squires 1959, Glynn and Wellington 1983, Glynn 1994).

Fungia distorta Michelin, 1848
Figure 5

SYNONYMS IN THE EASTERN PACIFIC: *Cycloseris mexicana* Durham, 1947.

RECORDS FROM RHODOLITH BEDS IN THE GULF OF CALIFORNIA: Isla San José and Canal de San Lorenzo.

OTHER RECORDS IN THE GULF: 24° to 26° N, Bahía Agua Verde, Isla del Carmen, Bahía San Evaristo, La Paz (Durham 1947); Puerto Escondido, Canal de San Lorenzo (Durham and Barnard 1952); Isla Espíritu Santo, Isla Partida, Isla San Diego, Isla Coronados (Squires 1959).

DISTRIBUTION: Gulf of California, México, to Isla La Libertad, Ecuador (1° S) (Durham and Barnard 1952, Reyes Bonilla 1993).
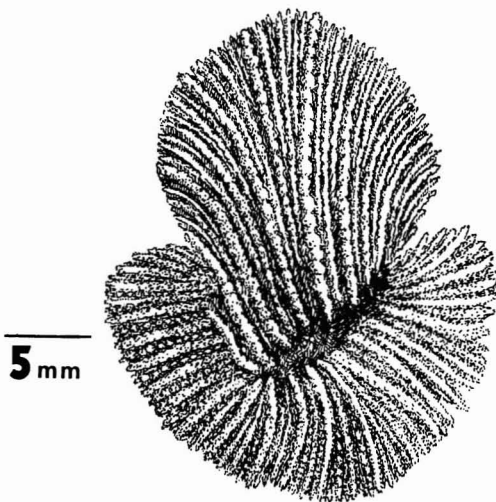
NOTES: This species is, by far, the most common coral in the rhodolith beds. At Isla San José, it forms a large population (more than 500 individuals per square meter) that covers more than a hectare of the bottom at 20 to 30 m depth, just below a rhodolith bed.

DISCUSSION

Corals were uncommon (less than 1 individual per minute of dive) at the visited rhodolith beds of the Gulf of California, an important difference from observations in Panamá and the Galápagos, where densities in beds exceed one colony per square meter (Glynn 1974, Colgan 1991). Moreover, in the latter areas massive coralliths of the genera *Porites, Pavona,* and *Gardineroseris* were the most common. In the gulf, *Fungia distorta* was dominant, *Psammocora stellata* was secondary in importance, and ramose *Porites sverdrupi* colonies were more frequent than massive *P. panamensis.*

These discrepancies in abundance and species composition may be related to differences in transport, light, and temperature: *Fungia* species recruit locally by colony fission and fragmentation in the beds, and possibly by larval settlement (López-Forment and H.R.-B., unpubl. data), which may explain why it is the locally dominant coral genus. *Porites* and *Pavona* species commonly live on shallow, rocky reefs near rhodolith beds. Larval recruitment of these corals in deeper waters is probably rare because of the lack of hard, stable sustrata for settlement and perhaps competition for space with nongeniculate coralline algae, bryozoans, etc. (Fricke and Meischner 1985). Scleractinian abundance and presence may be much more related to the number of broken colonies transported to deeper, sandy areas where rhodoliths occur, the distance to such areas, and the capability of the corals to be moved. For example, *Psammocora stellata* and *Porites sverdrupi* are common in beds relatively far from the coast (Canal de San Lorenzo, Isla San José), perhaps because their ramose morphology, low surface area relative to mass, skeleton porosity, and low weight (Scoffin et al. 1985, Colgan 1991) allow them to be more easily transported by water motion. Conversely, *P. panamensis* is only common in beds at Bahía Concepción, where rhodolith beds occur very

5 mm

FIGURE 5. *Fungia distorta* (Michelin, 1842).

near rocky shores (Steller and Foster 1995) on which large and stable populations of this species were observed. The colonies of *P. panamensis* are harder to move than those of other scleractinians because this is a massive coral, and in consequence, coralla are much denser and heavier. Thus, the farther the rodolith beds are from a rocky shore and the heavier the coral skeleton, the fewer coral colonies should be found.

That some of the rhodolith beds were in relatively deep water (up to 15 m depth) may also influence coral composition. The occasional presence of dead *Pocillopora* colonies in the beds suggests that transportation occurs but colonies do not survive. Both *Pavona* spp. and *Pocillopora* spp. need high light because they depend on their zooxanthellae for energy (Spencer Davies 1991, Titlyanov and Latypov 1991). In Caribbean rhodolith beds, coral distributional limits were reported to occur at 5 to 20% incident light at depths of more than 50 m (Fricke and Meischner 1985). However, less than 20% of incident light is available for coral photosynthesis in the southern Gulf of California at 15 m depth, especially during the summer rainy season (Bustillos Guzmán and Lechuga-Deveze 1989, Reyes Bonilla 1993). So it is possible that even if some *Pocillopora* or *Pavona* coralla arrive in deep beds, they may not be able to survive because of low light. Low water temperatures in the beds may also be limiting. In the gulf, temperature decreases substantially at 20 m relative to the surface (Robinson 1973). Numerous healthy populations of *Porites* occur in the northern gulf where temperatures are below 18°C for several months of the year (Reyes Bonilla 1993), but the rest of the corals can only live in warmer waters (Reyes Bonilla 1993, Veron 1995).

In the beds no *Fungia* spp., *Psammocora* spp., or *Porites sverdrupi* were seen growing on live rhodoliths or using them as settlement substrata. Conversely, *P. panamensis* commonly overgrew rhodoliths. This led to competition for space between the coralliths and the algae. We have observed colonies from recently settled larvae of this species on dead surfaces of rhodoliths from La Paz. Colonies appear to expand toward the living algal tissue, but when they contact, the corals suffer tissue lesions and a zone of clean skeleton appears that is readily covered by filamentous algae. A similar process has been observed in Caribbean beds (Fricke and Meischner 1985). It seems that growth of *Porites* can be stopped by the coralline algae and even reversed, because some of them were observed covering small corals, and live coral patches on rhodoliths were always smaller than 5 cm^2. The effects of relative competitive dominance in different habitats may thus influence coral abundance.

The median weights and sizes of coralliths were very different among individuals from the Galápagos, Panamá, and the Gulf of California, mostly because of species differences. Coral sphericities, however, are similar among regions (Table 1). It has been suggested that the rounded form of coralliths and rhodoliths is a consequence of bioturbation (Bosellini and Ginsburg 1971, Glynn 1974) or water motion (speeds from 30 to 90 cm/sec [Scoffin et al. 1985]), which allows the colonies to maintain living tissue on most of their surface and to maintain relatively homogeneous growth. Water motion from waves can move rhodoliths in some beds in the gulf (Steller and Foster 1995), and current speed in deeper beds may exceed 60 cm/sec (Obeso-Nieblas et al. 1993). Whether these water motions move coralliths has yet to be determined. Bioturbation seems to be high in the region (Steller and Foster 1995, Foster et al. in press). We commonly observed fishes (balistids, carangids, rays, and ophichthids), holothurians [*Isostichopus fuscus* (Ludwig) and *Parastichopus californicus* (Stimpson)], gastropods [*Murex elenensis* Dall, *Muricanthus nigritus* (Phillipi), and *M. princeps* (Broderip)], and sea urchins [*Toxopneustes roseus* (Agassiz)] moving rhodoliths and coralliths. Both water motion and biological activity may be capable of keeping small colonies in motion, thus avoiding tissue loss and producing rounded shapes.

Because of the small number of specimens available, we could only analyze the relation among sphericity, weight, and size of *Porites sverdrupi* coralla ($n = 37$). The Spearman correlation coefficient between largest diameter and weight was significant, positive, and high ($r = 0.93$; $P < 0.05$), but the relationship between sphericity and largest diameter ($r = -0.34$; $P > 0.05$) and weight ($r = -0.28$; $P > 0.05$) was

TABLE 1

MERISTIC DATA OF CORALLITHS FROM RHODOLITH BEDS IN THE EASTERN PACIFIC

SPECIES	MEDIAN WEIGHT (g)	RANGE OF LONGEST DIAMETER (cm)	RANGE OF SHORTEST DIAMETER (cm)	RANGE OF SPHERICITY	REFERENCE[a]	n
Pavona gigantea	103	19.5–2.1	14.8–1.6	0.90–0.81	1	286
P. clavus	758	13.1–8.5	9.6–7.3	ND	1	13
P. varians	141	10.0–4.8	6.3–3.2	ND	1	23
Porites panamensis	10	8.8–1.6	4.2–1.0	0.80–0.71	1	275
Pavona clavus	ND[b]	ND	ND	0.79[c]	2	3
Psammocora stellata	9.3	5.82–1.90	3.46–1.41	0.85–0.73	3	6
Porites panamensis	17.7	8.51–4.06	3.23–1.82	0.86–0.70	3	11
P. sverdrupi	6.4	9.26–2.50	4.18–1.49	0.86–0.63	3	37

[a] 1, Glynn (1974): Gulf of Panamá, Panamá; 2, Colgan (1991): Galápagos Islands, Ecuador; 3, this paper (Gulf of California, México).
[b] Not determined.
[c] Mean.

poor. Similar analysis of massive coralliths from Panamá, the central Pacific, and the Caribbean has also shown that sphericity and weight were weakly (or not) correlated (Glynn 1974, Scoffin et al. 1985, Lewis 1989), primarily because as weight increases, colonies remain more stationary and lose their rounded shape. The surfaces of such colonies have discontinuous growth of coral and coralline algae in a variegated pattern, which decreases roundness (Glynn 1974). In the case of ramose *Porites sverdrupi* in the gulf, the correlation is poor mainly because sphericity is a poor measurement of shape. Colony ramifications are separated to various degrees, so weight and diameter are more related to this than to sphericity. Steller and Foster (1995) discussed the importance of ramifications to shape determination in rhodoliths from the Gulf of California.

Most of the coralliths in Panamá had some bioerosion or damage caused by *Lithophaga* bivalves, sipunculans, polychaetes, sponges, and fishes (Glynn 1974, McIntyre and Smith 1974, Budd and Guzmán 1994). In contrast, holes or wounds (bites) were practically absent in corals from rhodolith beds of the gulf. This is perhaps because most coralliths were ramose (*Psammocora* and *Porites sverdrupi*) or flat (*Fungia* spp.) and completely covered with living tissue, leaving no place for larvae of other species to settle over their skeletons. At Bahía Concepción, massive free colonies of *Porites panamensis* sometimes had polychaete holes, but the intensity of erosion was much less than that observed in

colonies living on rocky shores of the same bay. This suggests that corallith movement inhibits larval settlement or survival. Fish predation may also be less important in the beds than on adjacent rocky shores because fish abundances were clearly lower in the beds, probably because of lack of food (H.R.-B., pers. obs.).

The described model for corallith formation (Glynn 1974, McIntyre and Smith 1974, Scoffin et al. 1985, Lewis 1989) holds true for *Porites panamensis* coralliths of the gulf: a larva settles and begins to bud polyps over a hard substratum such as dead or partially dead coralline algae, corals, annelids, or mollusks, which forms the accretion center of the free-living coral. Growth may eventually be such that coralliths stop moving and grow into microatolls (Highsmith 1982). This last stage has not been observed in rhodolith beds of the Gulf of California, indicating that large coralliths of *P. panamensis* must be transported elsewhere, broken, or buried.

Some authors (Highsmith 1982, Lee and Noble 1990) have suggested that fragmentation in fast-growing corals is an adaptation for living and propagating on muddy or sandy bottoms. Fragmentation may also allow more rapid colonization of new sites, because fragments have much higher life expectancies than larval-produced colonies (Lewis 1989). This may be true for fungids, but not other corals in rhodolith beds. Highsmith (1982) and Lewis (1989) argued that fragmentation will be selectively advantageous only if it produces pieces large enough to survive sedimentation, transport, etc.

In the Gulf of California, all coral fragments are very small (median maximum diameters [cm]: *Psammocora stellata*, 4.18, $n = 6$; *Porites sverdrupi*, 4.89, $n = 37$; *P. panamensis*, 5.65, $n = 11$) and relatively easy to move, so the potential selective advantage is lost.

Rhodolith beds are useful indicators of paleoenvironmental conditions (Boscence 1983, Scoffin et al. 1985, Steller and Foster 1995, Foster et al. in press). The discovery of rhodolith-corallith associations in relatively deep water near continental shores and adjacent to channels in the Gulf of California, Australia, and Bermuda (Squires 1959, Fricke and Meischner 1985, Harris et al. 1996) suggests that such associations may also occur in the fossil record. If so, they may provide more accurate inferences about the enviromental characteristics of ancient seas than rhodoliths alone.

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