4 Corals and Coral-Reef Communities in the Gulf of California

Héctor Reyes-Bonilla and Ramón Andrés López-Pérez

Since the earliest recognition of *Porites* from Isla Carmen in the Gulf of California (Grenwingk 1848), coral reef studies in the region have increased dramatically due to the description of new hermatypic and ahermatypic species (Durham 1947; Squires 1959); the publication of numerous geographic range extensions (Cairns 1991; Reyes-Bonilla 1993a); a research agenda in topics as varied as bioerosion, community structure and dynamics, biogeography, symbioses, bleaching, and El Niño conditions (Reyes-Bonilla 1993a, 1998; Reyes-Bonilla et al. 2002, 2005a; Iglesias-Prieto et al. 2004; LaJeunesse et al. 2007); and a multitude of publications on coral-reef-associated faunas (Solis-Marin et al. 1997; Brusca et al. 2005; Reyes-Bonilla et al. 2005b; and references therein). Indeed, because of the numerous publications and their scope, the Gulf of California is the best-known coral-reef area along the Mexican Pacific coast. In this chapter, we summarize published and unpublished information on corals and coral-reef communities in the Gulf of California, and we use numerical techniques to define large-scale spatial areas and their main trends in species composition, diversity, and abundance.

Coral Distribution

The Gulf of California contributed 36 percent of the entire Mexican Pacific coral records (*n* = 3423; Reyes-Bonilla et al. 2005a), distributed across 78 sites mainly located around islands in the Gulf of California and western gulf shores and scattered along the coasts of Sonora and Sinaloa (Medina-Rosas 2006) on mainland Mexico (fig. 4.1). Eighteen hermatypic coral species (*Pocillopora* spp. [five], *Psammocora* spp. [four], *Pavona* spp. [three], *Fungia* spp. [three], *Porites* spp. [two], and *Leptoseris* [one]) inhabit gulf waters from Punta Peñasco (31.29°N), Sonora, to Cabo San Lucas (22.87°N), Baja California Sur. Species distribution is highly heterogeneous and per- locality species is

highly skewed, resulting from the high number of localities with one species (e.g., *Porites panamensis*, 31 localities). Indeed, only seven of the 78 localities register 10–13 species: Isla Carmen (10 species), Cabo San Lucas and La Paz (11 species), Isla Cerralvo and Isla San José (12 species), and Cabo Pulmo and Isla Espíritu Santo (13 species).

Agglomerative unweighted pair-group average cluster analysis, multidimensional scaling, and similarity analysis were used to analyze the presence/absence data matrix. These analyses demonstrate that the Gulf of California has two characteristic coral assemblages in the northern and southern areas of the gulf. A depauperate southern-derived fauna is distributed from Loreto (25.50°N) to Cabo San Lucas (22.87°N; global *R* = 0.634, *P* = 0.001; fig. 4.2A, B). The northern
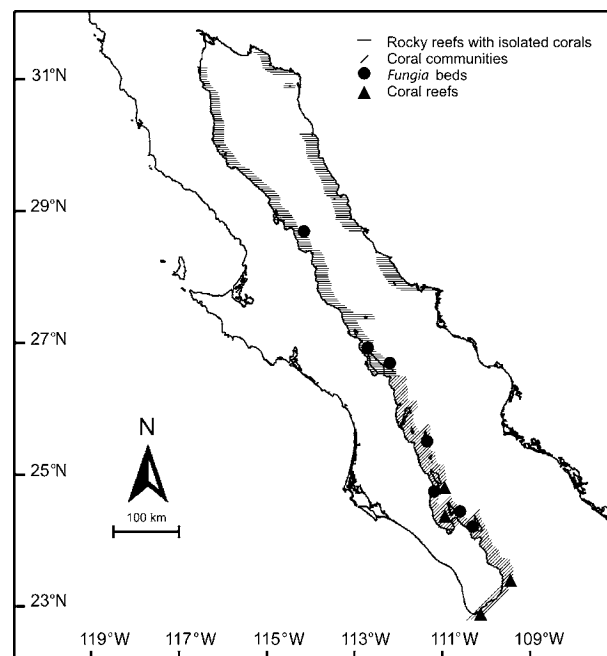

Figure 4.1. Map of the study area depicting the location of the main types of coral communities.

Gulf of California fauna ranges from Punta Peñasco (31.29°N), Sonora, to Punta Prieta (27°N), Baja California. Here, isolated monospecific coral patches are predominantly constructed by the encrusting phenotype of *P. panamensis*. However, south of Isla Tiburón (28°N), the massive and columnar phenotypes become common (Squires 1959), as developed on isolated rocks or patches of rocks surrounded by sand. In addition, occasional occurrences of *Porites sverdrupi* (Isla Angel de la Guarda), *Fungia curvata* (Bahía de Los Angeles), *Fungia distorta* (Isla Partida), and *Pocillopora verrucosa* and *P. capitata* (Isla San Marcos) do not alter the dominance of *P. panamensis* in the coral patches. The southern Gulf of California coral fauna ranges from Isla San José (25°N) to Cabo San Lucas (22.87°N), Baja California Sur. Here, development of reef structures occurs only at Cabo Pulmo (23.44°N) and to a lesser degree in Bahía San Gabriel and off Isla Espíritu Santo (24.42°N). In contrast, the other sites whose communities are part of the southern Gulf of California coral fauna (Isla San José, La Paz, Isla Cerralvo, and Cabo San Lucas) essentially are species-rich coral patches.

Southern gulf communities are monospecific, or nearly so, and consist of stands dominated by *Pocillopora* spp. Poritids and agariciids are relatively uncommon or restricted to deep waters and do not contribute much carbonate material to the reef structure. In particular, *P. verrucosa* is especially abundant (Reyes-Bonilla 2003). Finally, the southern-derived fauna extends from the Loreto area to the tip of the Baja California peninsula. In constructional terms, these are southern-derived, species-depauperate coral patches whose configuration is controlled by the arrangement of rock ridges upon which each patch is currently situated. Assemblage species composition shows no clear discontinuities between subgroups. Instead, similarity analyses demonstrate a close relationship (pairwise R = 0.054–0.333, P = 0.13–1.0) and a strong dependence on the southern Gulf of California coral fauna species pool (pairwise R = 0.188, P = 99.6).

Types of Coral Assemblages and Representative Faunas

The Gulf of California has four environments where reef corals occur: (1) isolated colonies or patches, (2) corals in rhodolith beds and other soft-bottom realms, (3) coral communities, and (4) actual coral reefs (fig. 4.1). The first category is dominant in Sinaloa, Sonora, Baja California, and the northern

part of Baja California Sur (26° to 28°N). In these areas, corals usually cover less than 1 percent of the bottom and build no framework due to their small size. At most, they are 30 cm in height or width. Instead, the colonies appear in an independent manner, add no significant substrate heterogeneity, and usually embody just one additional member of the diverse encrusting fauna from the central and northern gulf (Brusca 1980; Reyes-Bonilla et al. 2008). These habitats usually present only one or two reef coral species (*P. panamensis* and sometimes *P. sverdrupi*). Ecologically, there is little difference from a rocky reef in the sense that the primary producers are algae (turf and fleshy) and the system is relatively simple. The fauna is dominated numerically by herbivore invertebrates (mostly sea urchins of the genus *Arbacia* and starfishes *Pharia, Phataria*, and *Pentaceraster*) and supports high levels of richness and abundance in carnivorous fishes (Viesca-Lobatón et al. 2008).

Although corals are usually associated with hard-bottom areas, the Gulf of California nurtures unusual assemblages in sand and gravel areas adjacent to rocky coasts, as well as in rhodolith beds (see chap. 7). In these environments, corals of the genera *Porites, Psammocora*, and occasionally *Pavona* are not cemented to the bottom, but instead appear as coralliths. That means they function as free-living, rounded colonies, which when small can be moved by currents and suffer fragmentation (Reyes-Bonilla et al. 1997). After some growth in the sand, corals gain sufficient size to become fixed in place due to their weight or become anchored by their branches. Eventually, most colonies at this stage end up buried in the sediment. In addition to coralliths, Reyes-Bonilla et al. (1997) and Reyes-Bonilla (2003) found that large populations of mushroom corals (*Fungia* beds; figs. 4.1, 4.3A) exist in the gulf. Glynn and Wellington (1983) first described this habitat in the eastern Pacific in the Galápagos Islands. Three of these beds have been located, so far, at depths from 25 to 30 m between Bahía La Paz (24°N) and Isla Monserrat near Loreto (25°N). All are dominated by *F. distorta*, a self-fragmenting coral (Colley et al. 2002), with the occasional presence of *F. curvata, Psammocora stellata*, and very rarely *Pavona gigantea*. The conspicuous associated fauna is composed of sea urchins (especially *Toxopneustes roseus*), gastropods (*Strombus galeatus, Muricanthus* sp.), and bryozoans (James 2000; James et al. 2006).

The most common assemblage in shallow areas of the southwestern Gulf of California is the coral community, which typically can be observed from 22° to
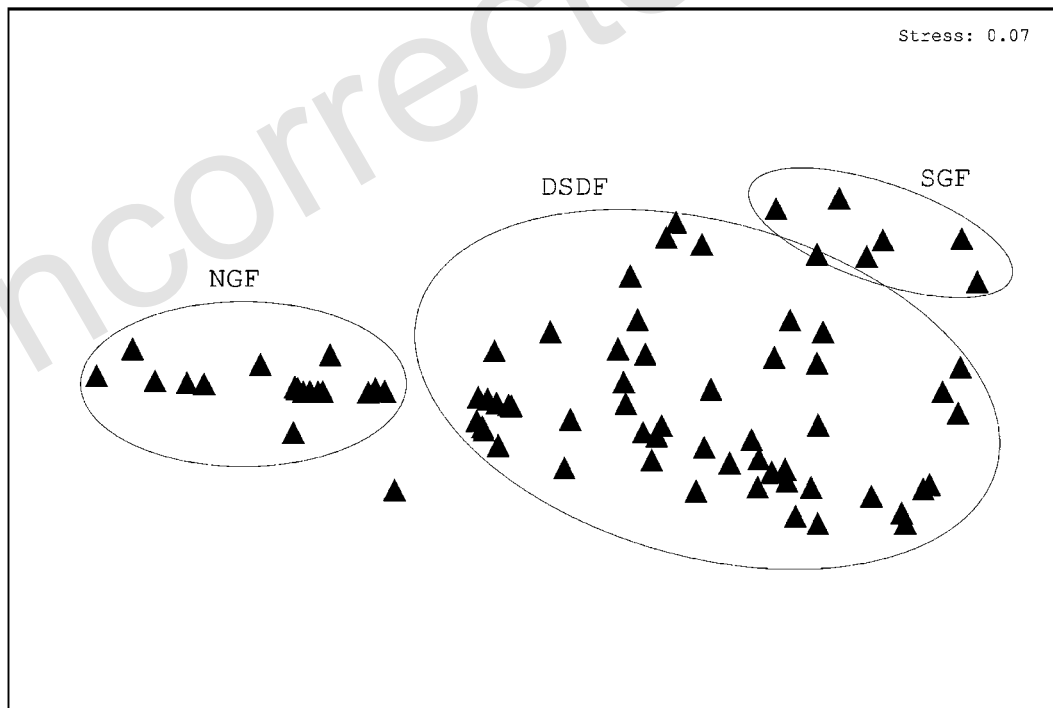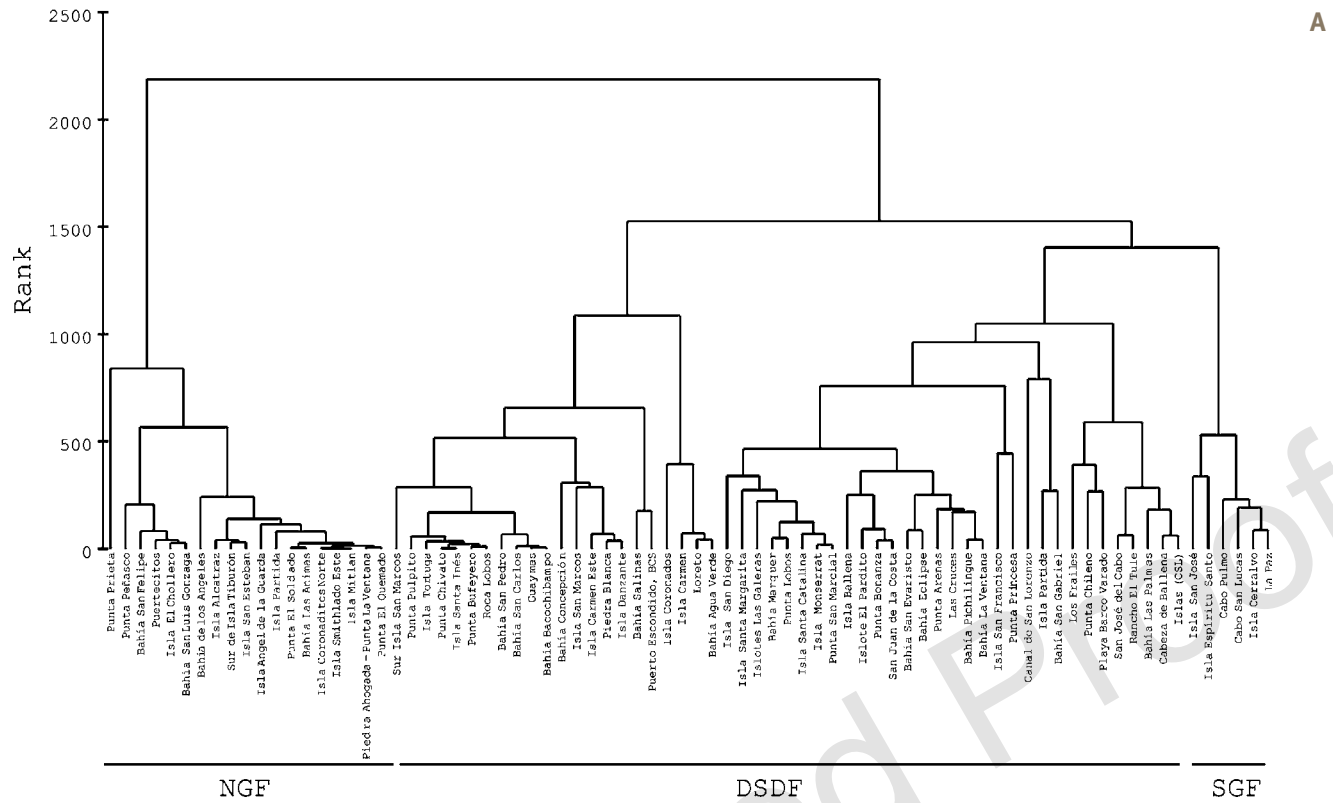
Figure 4.2. Classification of coral assemblages for the Gulf of California. Dissimilarities among assemblages were generated from a Euclidean distance matrix using latitude and longitude as dummy variables. (A) Dendrogram showing results of a cluster analysis of assemblages; linkages were based on weighted pair group averages; (B) distance map of the same assemblages produced by multidimensional scaling. NGF, northern gulf; DSDF, depauperate southern-derived fauna; SGF, southern gulf.

Figure 4.3. Common reef elements from the Gulf of California. (A) A *Fungia* spp. bed at Isla Monserrat; (B) a specimen of *Astrangia cortezi* from Bahía Los Angeles; (C) a typical reef coral landscape in the Cabo Pulmo reef dominated by *Pocillopora* spp. Photo credits: (A) Andrés González-Peralta, (B, C) Israel Sánchez-Alcántara

26°N on the peninsular coast. Coral richness is much higher there than in the northern and eastern gulf. Although no actual framework exists, colonies of *Pocillopora* and *Pavona* can grow several meters tall. The corals are important to the ecosystem, because they provide substrate and protection for many other species. They also represent a key element at the base of the trophic web, because their zooxanthellae fix high amounts of carbon from photosynthesis and the corals, in turn, produce lipid-rich mucus for invertebrate and fish consumption (Muller-Parker and D´Elia 1997). For these reasons scleractinians offer a specific kind of habitat favoring the appearance of associated species, which would not otherwise occur

so abundantly in the gulf, including specialized corallivores such as the gastropod *Quoyula monodonta*, decapod crab *Trapezia* sp., and crown-of-thorns starfish *Acanthaster planci* (Reyes-Bonilla 2003). In addition, these communities are joined by an abundant and rich collection of free-living invertebrates that are generalists (Hendrickx et al. 2005). Especially conspicuous are echinoderms and mollusks, including species such as the brown urchin (*Tripneustes depressus*), black urchin (*Diadema mexicanum*), mother-of-pearl (*Pinctada mazatlanica*), and carnivore *Conus* and muricid snails. Correspondingly, the fish community is very complex (Thomson et al. 2000), including up to 25 species and over 300 individuals per 0.01-ha

zones (Alvarez-Filip et al. 2006). Our personal observations indicate that in coral communities from protected areas where fishing has not been intense (such as Isla Montserrat), the teleost assemblage reaches a high trophic level (3.9 or more) due to the presence of carnivores such as groupers, snappers (*Epinephelus, Mycteroperca, Lutjanus*), grunts (*Haemulon* spp.), and pelagic species (jacks, barracuda, and others).

There has been much debate about the existence of actual coral reefs in the Gulf of California, because conditions are very limiting for coral growth and maintenance (Glynn 2001) and even the most extensive areas and those with the highest coral cover are poor in coral species and exhibit limited framework development when compared to the Caribbean or central and western Pacific reefs (Brusca and Thomson 1975). Because many other eastern Pacific reefs have environmental and ecological characteristics similar to those of the gulf (Cortés 2003), we propose that in the eastern Pacific, a "true reef" is a place where reef corals have a vital role in the food web by supplying resources to invertebrate and fishes as a result of photosynthesis performed by zooxanthellae, produce significantly higher relief than the surrounding rocky bottom, and provide a new type of habitat to be used by species with particular adaptations, which consequently become exclusive residents of these areas.

True coral reefs are quite limited in extent in the Gulf of California. Reyes-Bonilla (2003) noted two places: Bahía San Gabriel at Isla Espíritu Santo east of La Paz (24°N) and the well-known Cabo Pulmo reef (23.5°N). Both areas register the highest coral cover in the gulf (fig. 4.3B). Skeletal frameworks can reach over 2 m in height, and are predominantly built by *Pocillopora* sp. Considering that the growth rate of pocilloporids is about 3 cm/year in the gulf (Reyes-Bonilla and Calderón-Aguilera 1999), we estimate these colonies represent at least 70 years of continuous development.

Of the commonly cited reefs, only scant information is available on the associated communities of the Bahía San Gabriel reef (Squires 1959; Pérez-España et al. 1996). The Cabo Pulmo reef is described in much more detail, and there are dozens of studies on related topics, including marine species composition, geology, and ecological interactions (Brusca and Thomson 1975; Reyes-Bonilla and Calderón-Aguilera 1999; Riegl et al. 2007). In general, both of these reefs present a relatively diverse coral fauna with more than 10 species each (Reyes-Bonilla 2001). The interstices of the ramose colonies harbor a remarkable assemblage

of macroinvertebrates (especially decapod crustaceans, mollusks, and echinoderms; Baynes 1999) and fishes (such as the coral hawk [*Cirrithichthys oxycephalus*], gobies, and moray eels; Villarreal-Cavazos et al. 2000). In addition, massive corals host a wide array of borers, including sponges (*Cliona* sp.), sipunculans, polychaetes, and bivalves (*Lithophaga* spp.), as well as several species of blennies (the dominant being *Acanthemblemaria crockeri*).

Coral stands offer protection to many other larger species, which usually live in the interfacing coral-sand or coral-rocky bottom. The most common such residents are urchins (*Tripneustes, Diadema, Eucidaris*), asteroids (*Pharia pyramidata*), mollusks (*Conus, Pinctada*), and fishes. Of the fishes, the herbivores *Stegastes* sp. and *Abudefduf troschelli*, the omnivore *Thalassoma lucasanum*, and the planktivore *Chromis atrilobata* represent 60 to 70 percent of the total abundance (Thomson et al. 2000; Alvarez-Filip et al. 2006). Carnivores are much less common and the key fish species are serranids (*Epinephelus, Mycteroperca*, and *Paranthias colonus*) and lutjanids (*Lutjanus viridis* and *L. argentiventris*).

Coral Community Structure

Data on abundance, richness, and other descriptors of coral-community structure in the Gulf of California are scarce. Reyes-Bonilla and Calderón-Aguilera (1999) provided the initial information about Cabo Pulmo reef. Here, we present new and updated information obtained between 2004 and 2007 from six regions around the gulf: Bahía Los Angeles (28°N), Islas Tortuga and San Marcos (27°N), Bahía Concepción (26°N), Loreto (25°N), La Paz (24°N), Cabo Pulmo (23.5°N), and Los Cabos (23.1°N). Data were obtained in transects 25-m long, at depths from 6 to 12 m, and using the intercept point method. Divers took note of coral occurrences every 20 cm (making 100 total point counts). We conducted 24 transects at each site, with the exceptions of Tortuga and San Marcos (20 transects) and Bahía Concepción (18 transects). Information on amount of cover and richness was obtained directly from these transects and subsequently used to calculate diversity (Shannon-Wiener index H', with base 10). According to a priori tests, all indices were normal or homoscedastic and, thus, we applied one-way parametric analysis of variance to test for differences among sites (factors). Note that field surveys were also conducted at Mazatlán, Sinaloa (20°N), and four areas of the Sonoran coast, from 27° to 31°N

(Guaymas, southern Isla Tiburón, Puerto Libertad, and Puerto Peñasco). However, as there was only one coral species present at these sites (*P. panamensis*) and cover did not exceed 1 percent, these data were not analyzed for this report.

Our surveys found that coral cover is less than 2 percent in the northern gulf, but increases rapidly in the southern gulf to a maximum level at Cabo Pulmo reef (fig. 4.4A). Conditions at Cabo Pulmo are adequate for coral growth due to abundant shallow hard substrate and because the water is warm most of the year (Reyes-Bonilla 2001, 2003). Cover did not increase monotonically with latitude, but dropped a bit at Los Cabos, perhaps because that area is characterized by a steep bottom and lack of available substrate related to a very narrow shelf. The ANOVA ($F_{5,152} = 12.4$, $P < 0.01$) and an a posteriori Tukey test applied to coral-cover data indicates three groups: areas with high abundance (Cabo Pulmo, La Paz), medium (Los Cabos, Loreto), and low (the northernmost sites). Species richness behaved in a similar manner (fig. 4.4B), where Cabo Pulmo had the highest number of species per transect, followed by Los Cabos, La Paz, and Loreto, and finally by the areas at 27° and 28°N ($F_{5,152} = 4.6$, $P < 0.05$).

On the other hand, diversity showed a slightly different picture (fig. 4.4C). Diversity was highest in the La Paz and Loreto areas. Despite the statistical test that suggests the four southernmost areas do not differ from one another, all are significantly more diverse than the assemblages from the Tortuga–San Marcos and Bahía Los Angeles areas ($F_{5,152} = 8.3$, $P < 0.05$). Our results can be explained considering that Cabo Pulmo and Cabo San Lucas have a dominant species that unbalances the relative abundance of the taxa and, hence, decreases diversity. That species is *P. verrucosa*, which accounts for over 50 percent of the coral abundance in many transects in those two areas. At La Paz and Loreto, there is no single dominant coral, and instead relative abundances vary among sampling sites. Sometimes *P. verrucosa* appears in almost monospecific stands, but in many places south of Loreto and at Isla Espíritu Santo, *Pocillopora damicornis* is more common.

In summary, it is clear that while reef corals can be found practically in all rocky areas of the Gulf of California, their assemblages are quite simple everywhere except along the southernmost Baja peninsula. Patterns shown by ecological indices reflect the geographic regionalization cited earlier in this chapter. Latitudinal composition changes recognized in the coral fauna appear to be mirrored in the structure and function of the assemblages.

Coral Reproduction

Reproduction and recruitment are among the most critical processes upon which the persistence of a coral reef depends, along with their pivotal influence on the structure and dynamics of coral populations and communities (Richmond 1997). Studies on eastern Pacific coral reproduction are scarce (Birkeland 1977; Richmond 1985, 1987; Glynn et al. 1991, 1994, 1996) and were only recently initiated in Mexico (Vizcaíno-Ochoa 2003; Mora-Pérez 2005; Rodríguez-Troncoso 2006; Chávez-Romo and Reyes-Bonilla 2007).

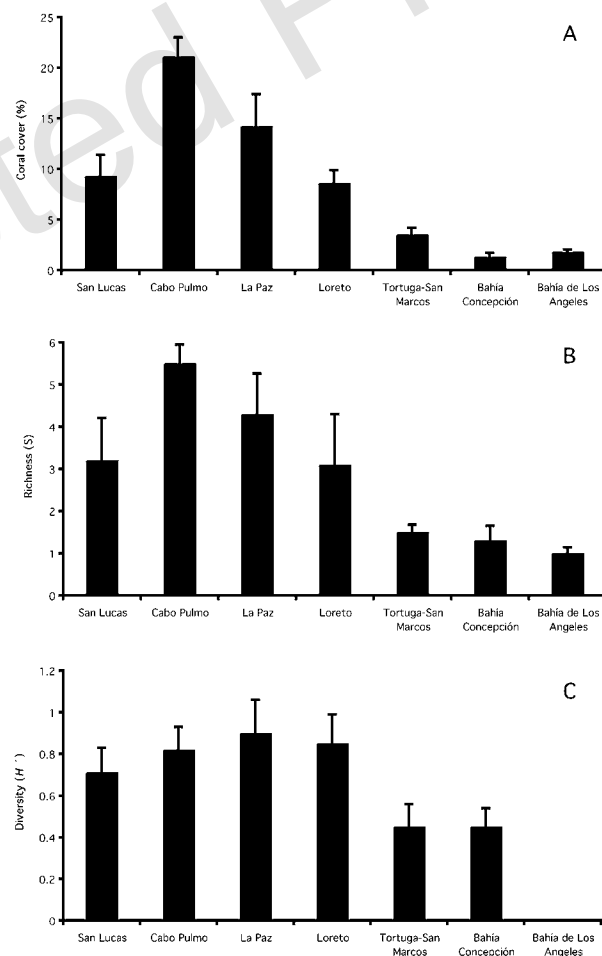As elsewhere in the eastern Pacific (Glynn et al. 1994; Vizcaíno-Ochoa 2003; Rodríguez-Troncoso

Figure 4.4. Community structure of selected coral reefs and assemblages in the Gulf of California: (A) coral cover; (B) species richness; (C) species diversity.

Table 4.1. Carbonate deposition (Kg CaCO$_3$.m^{-2}.yr^{-1}) at selected coral reefs and reef assemblages in the Gulf of California.

Locality	Coral coverage (2001)	Kg CaCO$_3$.m^{-2}.yr^{1}	
		Min	**Max**
Isla San José	49.3	6.3	12.4
Bahía San Gabriel	35.8	5.8	13.5
Bahía Pichilingue	22.9	3.5	8.2
Isla Cerralvo	2.0	0.2	0.6
Punta Perico	8.6	1.3	3.0
Cabo Pulmo	53.6	8.9	20.7
Bahía Chileno	40.9	6.4	15.2

2006), *P. panamensis* is a year-round brooder in the Gulf of California. Its gametogenic cycles and planulation show no correlation with sea-surface temperature or lunar activity, although fecundity and planula larval release is closely tied with sea-surface temperature (Mora-Pérez 2005). Active year-round larval release of *P. panamensis* populations in Gulf of California waters (Mora-Pérez 2005) probably maintain high recruitment and rapid population buildups similar to those in Central America (Glynn et al. 1994) and Oaxaca (López-Pérez et al. 2007). This level is maintained even against a high postrecruitment mortality rate (8–14 percent) and nonexistent recruitment via fragmentation (Reyes-Bonilla and Calderón-Aguilera 1994). Contrary to studies from Bahía de Banderas (Vizcaíno-Ochoa 2003) and Oaxaca (Rodríguez-Troncoso 2006) on mainland Mexico, work in the Gulf of California represents the first positive sighting of reproductively active *P. damicornis* populations in the Mexican Pacific region (Chávez-Romo and Reyes-Bonilla 2007). In the gulf, *P. damicornis* is a seasonal (July–November) broadcast-spawner, whose gametogenic cycles correlate with the sea-surface temperature. In particular, a high proportion of mature gametes result when the temperature exceeds 28°C (Chávez-Romo and Reyes-Bonilla 2007).

Coral Symbioses

The Gulf of California is the only area along the Pacific coast of Mexico where symbioses-related studies other than bleaching have been conducted. Reef corals are known to occupy the entire photic zone but display vertical zonation patterns within the light-intensity gradient (Wellington 1982). In the Gulf of California, shallow environments (0–6 m) are usually occupied by *P. verrucosa*, whereas deeper areas (6–14 m) are inhabited by *P. gigantea* (Reyes-Bonilla and López-Pérez 1998). The distinctive zonation pattern was previously explained by a combination of physical and biological factors affecting the coral host, including selective predation by fishes (Wellington 1982). Nonetheless, in situ measurements, transplant experiments, and molecular analysis have demonstrated that *P. verrucosa* harbors a dinoflagellate symbiont clade D, whereas *P. gigantea* hosts a type from clade C, each adapted to a particular light regime (Iglesias-Prieto et al. 2003, 2004; LaJeunesse et al. 2007). These findings suggest that the differential use of light by specific symbiotic dinoflagellates constitutes an important axis for niche diversification and is sufficient cause to explain the vertical distribution patterns of these two coral species (Iglesias-Prieto et al. 2004).

Carbonate Accretion

The influence of bioeroders on eastern Pacific carbonate accretion was investigated for Central American reefs, particularly after the 1982–1983 El Niño demonstrated the importance of biotic factors on the survival and evolution of these coral reefs (Glynn 1988). Changes in carbonate accretion have recently gained attention due to potential impacts from global climate. Nonetheless, eastern Pacific studies, particularly

those performed in the Gulf of California, are precluded because historical records date only from 1987 and are restricted to Cabo Pulmo (Calderón-Aguilera et al. 2007). We calculate coral accretion for seven gulf localities (table 4.1) following the method used by Chave et al. (1972) and Reyes-Bonilla and Calderón-Aguilera (1999). Carbonate deposition is highly heterogeneous in the gulf in response to species composition, coral coverage, and reef dimension. Coral standing stock is high at Cabo Pulmo, Bahía Chileno, and Isla San José but extremely low at Isla Cerralvo, where 0.2 kg $CaCO_3/m^2$/year is deposited. We lack data for reef extension at places other than Cabo Pulmo, therefore precluding carbonate deposition estimates per reef system.

Cabo Pulmo estimates suggest this 150-ha reef system contributes as much as 13,482 to 31,023 tons of $CaCo_3$/ha annually. Yet, the relative importance of Cabo Pulmo carbonate deposition has been constantly decreasing since 1987 (Calderón-Aguilera et al. 2007, fig. 1) in response to coral disturbance (Reyes-Bonilla et al. 2002; Iglesias-Prieto et al. 2003).

Natural Disturbances

Corals are exposed to various natural agents of perturbation in the Gulf of California, the most relevant being the effects of predation, hurricanes, and warming caused by the El Niño Southern Oscillation (ENSO).

Coral predation is ubiquitous in the gulf, especially in Baja California Sur. The key coral consumers are fishes (in particular the spotted pufferfish [*Arothron meleagris*] and parrotfishes of the genus *Scarus*), gastropods (*Jenneria pustulata* and *Quoyula monodonta*) and echinoderms (crown-of-thorns starfish [*A. planci*] and occasionally echinoids like the pencil and brown urchins *Eucidaris thouarsii* and *T. depressus*; Reyes-Bonilla and Calderon Aguilera 1999; Reyes-Bonilla 2003). These species often bite the tips of *Pocillopora* and the sides of the massive *Porites* and *Pavona*, but apparently have a marked preference for the emerald coral, *P. panamensis*. In a series of fifteen 10-×-1-m belt transects run at Punta Galeras (near La Paz) in 2007, where the percentage of colonies with evidence of predation was evaluated, we found 72 ± 8 percent of the colonies of this species showed damage, compared to 12 ± 3 percent of *Pavona* and just 7 ± 1 percent of *Pocillopora*. The predilection of corallivores to attack *Porites* may be due to the fact that the skeleton of this coral is relatively porous and the

tissue is embedded more than 0.5 cm inside. Hence, the amount of energy provided per bite may be higher for consumers.

There is only one estimate of the joint effect of corallivore species on coral reefs at Cabo Pulmo. Reyes-Bonilla and Calderón-Aguilera (1999) showed that during the 1990s, when coral cover was very high (over 30 percent), predators ate less than 15 percent of the coral standing stock. Resampling of the same species showed that their numbers have not increased appreciably, to date, compared to a decade ago (Reyes-Bonilla et al. 2005b; Alvarez-Filip et al. 2006; unpublished data of the authors). Nevertheless, the effect of predators may be greater than before, due to a decrease in cover by approximately one-third after the 1997 ENSO bleaching event (Reyes-Bonilla 2001).

Hurricane damage to coral communities is restricted to southern Baja California, where the most conspicuous assemblages are established. Hurricane season lasts from July to November, but strikes are infrequent. According to the NOAA National Hurricane Center (http://www.nhc.noaa.gov/pastall.shtml), each year an average of 0.80 ± 0.22 hurricanes or tropical storms move over the area where reef coral communities and reefs are located along the peninsular coast. Reyes-Bonilla (2003) indicated that these events are capable of breaking large amounts of ramose colonies (*Pocillopora* and *Psammocora*) and can fragment massive colonies (*Pavona* and *Porites*). The *Fungia* banks also have been impacted. The largest *Fungia* bank, located near Isla San José in northern Bahía La Paz (25°N), was severely affected in 2001 and then in 2006, when Hurricanes Juliette and John shifted large amounts of sand away from the mainland and buried the corals. It is interesting that the rest of the ecosystem appears to have been remarkably resilient to major storm events. For example, no statistical change was detected in sea urchin abundance at Punta Arenas and San Gabriel (near La Paz) after Hurricane Isis in 1998 (Reyes-Bonilla 2003) and in urchins and reeffish numbers at Cabo Pulmo in 2006 after two major hurricanes (unpublished data). Lirman et al. (2001) reported a similar situation for the Huatulco coral reef tract in the Mexican Pacific.

By far, the most important perturbations suffered by reef corals were caused by the increase in sea-surface temperature brought by the ENSO. This phenomenon caused at least two major episodes of coral bleaching. The first event lasted from July to September 1987, but was relatively minor as coral

mortality did not exceed 10 percent of the standing stock and no other reef taxa suffered damage (Reyes-Bonilla 1993b). A decade later, however, the eastern Pacific was the scenario of the strongest ENSO of the twentieth century (Wang and Fiedler 2006). Loss of coloration of the colonies began in July and was observed through November. All coral genera were affected, although *Pocillopora* suffered the most as a shallow-water resident (where warming was more intense), and their zooxanthellae are not physiologically adapted to conditions of very high temperature and light intensity (Iglesias-Prieto et al. 2004). The bleaching caused a loss in coral cover that averaged 18 percent in the Gulf of California (fig. 4.5), but as bad as that, the gulf region was the least impacted in western Mexico. Coral reefs at Bahía Banderas (20°N) and Oaxaca (16°N) suffered over 50 percent mortality (Reyes-Bonilla et al. 2002). Based on this relationship, Reyes-Bonilla (2001) and Riegl and Piller (2003) suggested that the permanent front at the entrance of the gulf works as a buffer against extreme rises in sea-surface temperature.

A few years after the 1997 ENSO, Reyes-Bonilla et al. (2002) suggested that recovery of the populations would take about a decade, considering the timing in succession after the 1987 bleaching. We were mistaken. So far, corals have not recovered in the gulf as indicated by changes in coral cover in three reefs or coral communities of the southwestern gulf (fig. 4.5). In general, we infer that recovery was hampered by the continuous turmoil caused by hurricanes and tropical storms, but other, local effects also are detected. For example, corals at Bahía Chileno (23°N, north of Cabo San Lucas) were not so affected by the ENSO (Reyes-Bonilla 2001; fig. 4.5), but cover still has been in a gradual decline. The most likely reason is a consequence of the combined effect of storms and human perturbations, because the bay is among the most visited areas for diving and snorkeling in the state. On the other hand, the reef at Cabo Pulmo is almost free of anthropogenic disturbances but the impact of the ENSO was enhanced by several hurricanes (Alvarez-Filip et al. 2006; fig. 4.5). Coral abundance after 1997 is significantly less than before the ENSO ($F_{2,58} = 6.7$, $P < 0.001$; fig. 4.5). Finally, Bahía San Gabriel has less live coral in 2007 than a decade before, but the difference has never been significant (fig. 4.5). This reef turns out to be much more resistant than other reefs. The reason may be that pocilloporid corals are the dominant species and asexual reproduction at that
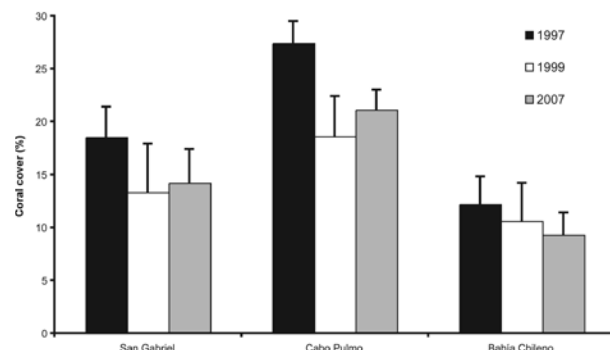

Figure 4.5. Change in coral cover in three coral reefs of the southwestern Gulf of California between 1997 (before the onset of the El Niño Southern Oscillation) and 2007.

locality is especially successful because the bay is shallow, closed, and the broken branches can settle on sand and stop moving (a circumstance that improves survival rate).

Human disturbances to corals and coral reefs in the Gulf of California are intense (Brusca et al. 2005). Fortunately for corals, however, the problem is relatively minor in the southwestern corner of the region, where reefs are best developed and the human population has remained small. In fact, in 2005 the state of Baja California Sur had 512,000 inhabitants, according to the Instituto Nacional de Estadística, Geografía e Informática (http://www.inegi.gob.mx/est/), and was the least densely populated state in Mexico. Fishing activities during much of the last century did the most harm to coral faunas. Although no major damage was apparent by the 1980s, Sala et al. (2004) concluded that fishermen in the southern gulf had "fished down the food webs," because during the last 40 years they have taken fewer carnivorous fishes and more omnivores and herbivores as a result of depletion of the populations. Also, mean body sizes are noticeably smaller. Later, Sáenz-Arroyo et al. (2005) documented how the perception of the health of the rocky and coral ecosystems differs among fishermen of different ages, a clear example of so-called shifting baselines. Finally, personal observations by the authors indicate that sizes of typical commercial species (especially snappers and groupers) have increased remarkably at Cabo Pulmo reef after the establishment of the national park to protect the reef.

In general, the findings cited here indicate that extractive activities are having a measurable effect on the abundance and composition of reef fishes in

traditionally fished areas. It is still uncertain, however, if those changes are affecting the function of the coral reefs or the ecosystem as a whole. Díaz-Uribe et al. (2007) developed a model for the food web in the La Paz area, where many coral communities are present. They showed that even when particular resources such as snappers, groupers, and sharks are overexploited, the ecosystem is not appreciably impacted. For example, all the artisanal and commercial fisheries together require less than 10 percent of the primary production to remain at the same level. In addition, a long-term analysis of the Cabo Pulmo fish community (1987–2003) revealed that, although community structure actually has been altered, many species were replaced by others of the same trophic level, family, or genus. This finding has been interpreted as evidence of ecological redundancy in the icthyofauna (Alvarez-Filip and Reyes-Bonilla 2006). Conflicting evidence on the effects of fishing on the ecosystem calls for increased research efforts in the future. This is an important issue, considering that any decision to stop or continue fishing at the current level will affect the economics and quality of life for many people in western Mexico.

The other major potential anthropogenic threat to coral reefs in the Gulf of California is tourism (Enríquez-Andrade et al. 2005), an activity so demanding of services that Baja California Sur grows by almost 3 percent yearly, the second-highest rate in Mexico (Lluch-Cota et al. 2006). Available reports indicate that so far the effects of visitors on coral reefs and communities seem to be minor, because most divers seek charismatic megafauna (hammerhead sharks, mantas) and choose to visit deeper sites away from the coast, while sport fishermen usually look for pelagic species (Bryant et al. 1998; Reyes-Bonilla 2003). In addition, the two most important coral areas in the gulf (Cabo Pulmo and Bahía San Gabriel) are protected areas (Arizpe-Covarrubias 2005; Anonymous 2007). Nonetheless, the speed of growth of tourist infrastructure and facilities (such as marinas and hotels) is staggering, and many investors are focused on the development of the Los Cabos–La Paz region, the so-called Los Cabos Touristic Corridor, precisely where the best coral communities and reefs are located. Taking this into account, the future of the coral-reef ecosystem depends on adequate management of the coastal zone and probably also on the relative success of low-impact tourism. This activity has been criticized as not meeting expectations of local managers and not improving the social condition of the general population. Consequently low-impact tourism may not turn out to be sustainable (Tershy et al. 1999; López-Espinosa de los Monteros 2002). Ecotourism has maintained a low level of reef use in some areas like Cabo Pulmo, while at the same time empowering the residents and boosting their economic capacity (Arizpe-Covarrubias 2005). There is still much to be done, and we urge that economic valuations of reef services be performed, as well as precise estimations of diving carrying capacity.

Azooxanthellate Corals

Deep-water, azooxanthellate or ahermatypic corals were once considered to be minor players compared to reef-builders, but a series of studies conducted during the last decade has demonstrated their importance as key elements in shelf, slope, and abyssal ecosystems (Roberts and Hirschfield 2004). For example, species such as *Desmophyllum dianthus* and *Lophelia pertusa* construct bioherms at depths beyond 100 m in temperate areas of the Northern and Southern Hemispheres. These systems are the setting for very active fisheries (Fossa et al. 2002).

The ahermatypes are ecologically and morphologically very different from reef species (fig. 4.3B). To begin with, they have no symbiont dinoflagellates, and they obtain food by catching particles and organisms through tentacular action. Hence, light has no influence on their distribution (Veron 1995). Another important difference is that most ahermatypes are solitary and not colonial (Cairns 1994). Finally, they have a much higher tolerance to cold water than reef species. Consequently many azooxanthellate species are cosmopolitan, circumpolar, or live at great depths, although their growth rate is usually very slow (Roberts and Hirschfield 2004).

There is almost no biological or ecological information regarding azooxanthellate corals in the Gulf of California, but good data are available on species richness and distributions. The regional fauna is composed of 22 species, two more than known for the shallow-water corals (20 species), which sums to a regional total of 42 stony corals (table 4.2). The gulf ahermatypes can live from the intertidal zone to a depth of over 600 m (Reyes-Bonilla et al. 2005a). They have the ability to reside in a variety of habitats and on different types of substrate, but most dwell on hard bottoms. Some species, such as *Dendrophyllia*

Table 4.2. Distribution of stony corals in the Gulf of California. Data from Reyes-Bonilla et al. (2005), Medina Rosas (2006), Reyes-Bonilla et al. (in press), and field observations by the authors (2006-2007).

Species	BCS	BC	SON	SIN	Biogeographic affinity
Family Pocilloporidae					
Madracis pharensis (Heller, 1868)	X	X			Amphiamerican
Pocillopora capitata Verrill, 1866	X				East Pacific
P. damicornis (Linnaeus, 1758)	X				Indo Pacific
P. elegans Dana, 1846	X				Indo Pacific
P. eydouxi Milne Edwards and Haime, 1860	X				Indo Pacific
P. meandrina Dana, 1846	X				Indo Pacific
P. verrucosa (Ellis and Solander, 1786)	X			X	Indo Pacific
Family Poritidae					
Porites sverdrupi Durham, 1947	X	X		X	Endemic
P. panamensis Verrill, 1866	X	X	X	X	East Pacific
Family Siderastreidae					
Psammocora brighami Vaughan, 1907	X				Indo Pacific
P. haimeana Milne Edwards & Haime, 1851	X				Indo Pacific
P. stellata (Verrill, 1866)	X				Indo Pacific
P. superficialis Gardiner, 1898	X				Indo Pacific
Family Agariciidae					
Leptoseris papyracea (Dana, 1846)	X				Indo Pacific
Pavona clavus (Dana, 1846)	X				Indo Pacific
P. duerdeni Vaughan, 1907	X				Indo Pacific
P. gigantea Verrill, 1869	X				East Pacific
P. varians Verrill, 1864	X				Indo Pacific
Family Fungiidae					
Fungia curvata (Hoeksema, 1989)	X	X			Indo Pacific
F. distorta Michelin, 1842	X				Indo Pacific
F. vaughani Boschma, 1923	X				Indo Pacific
Family Rhizangiidae					
Astrangia californica Durham and Barnard, 1952		X	X		East Pacific
A. cortezi Durham and Barnard, 1952		X	X		Endemic
A. costata Verrill, 1866	X				East Pacific
A. dentata Verrill, 1866	X				East Pacific
A. haimei Verrill, 1866	X	X	X		East Pacific

Table 4.2. *continued*

Species	BCS	BC	SON	SIN	Biogeographic affinity
Coenangia conferta Verrill, 1870	X	X	X		East Pacific
Oulangia bradleyi Verrill, 1866	X	X			East Pacific
Family Caryophylliidae					
Caryophyllia diomedeae Marenzeller, 1904		X			Indo Pacific
Ceratotrochus franciscana Durham and Barnard, 1952	X		X		Endemic
Coenocyathus bowersi Vaughan, 1906	X	X	X		East Pacific
Desmophyllum dianthus (Esper, 1794)		X			Cosmopolitan
Heterocyathus aequicostatus Milne Edwards and Haime, 1848	X	X	X	X	Cosmopolitan
P. stearnsii Verrill, 1869	X	X	X		East Pacific
Phyllangia consagensis (Durham and Barnard, 1952)	X	X			East Pacific
Phyllangia dispersa Verrill, 1864	X				East Pacific
Family Turbinoliidae					
Sphenotrochus hancocki Durham and Barnard, 1952	X				Indo Pacific
Family Dendrophylliidae					
Balanophyllia cedrosensis Durham, 1947	X	X	X		East Pacific
Cladopsammia eguchii (Wells, 1982)	X				Indo Pacific
Dendrophyllia oldroydae Oldroyd, 1924	X	X	X		East Pacific
Endopachys grayi Milne Edwards and Haime, 1848	X	X			Indo Pacific
Tubastraea coccinea Lesson, 1829	X				Indo Pacific

oldroydae, can be so abundant in dredgings around the Midriff Islands that the local existence of deep-water reefs is highly likely (Reyes-Bonilla et al. 2008). In addition, other species are capable of recruitment on shells and rocks in sandy areas. Upon reaching maturity, those individuals actively detach themselves by dissolving their peduncles, as observed for *Endopachys grayi* (Cairns 1989). In some environments in the northern gulf, there exists a remarkable symbiosis between the coral *Heterocyathus aequicostatus* and a sipunculan of the genus *Aspidosiphon*. The coral has a round opening at the base of the colony in which the worm takes shelter. In return, the worm is in constant

motion like a muscular foot, an activity that keeps the coral from being covered by sand (Reyes-Bonilla et al. 2008).

Reyes-Bonilla and Cruz-Piñón (2000) and Reyes-Bonilla et al. (2005a) studied azooxanthellate coral patterns in western Mexico from a biogeographic perspective. Both studies demonstrate how the Gulf of California fauna can be differentiated from that of the rest of the country, and how the gulf is subdivided into three regions: south (22° to 26°N), central (27° to 29°N), and north (30° to 31°N). It also is remarkable that in complete contrast to the reef fauna (composed mostly of Indo-Pacific species), there are only three

immigrant azooxanthellate species in the region (*E. grayi, Tubastraea coccinea*, and *Cladopsammia eguchii*); all belong to the family Dendrophylliidae. The rest are amphi-American in origin (*Madracis pharensis*), cosmopolitan (*D. dianthus*), and gulf endemics (*A. cortezi* from the northern gulf and *Ceratotrochus franciscana* from the La Paz region), but there also are 16 eastern Pacific endemics.

In addition to general patterns, Reyes-Bonilla et al. (2008) noted the presence of two species with a disjunctive distribution: *Paracyathus stearnsii* and *Balanophyllia cedrosensis*. These corals occur in the northern gulf and along the Pacific coast of Baja California, but not in between (Reyes-Bonilla et al. 2005). Remarkably, they already show some morphological differentiation between these sites (Cairns 1994). It is possible that the observed changes are the first evidence of incipient speciation caused by geographic isolation, a process known to occur in several fish species showing the same distributional pattern (Bernardi et al. 2003).

One might think that because most azooxanthellate corals live at a water depth of more than 30 m, there is no need for concern about their conservation. The situation is potentially serious, however, because

deep-water coral assemblages are severely impacted by fishermen in the eastern and western United States and Canada, as well as New Zealand, Japan, and Norway (Roberts et al. 2006). The reason is that azooxanthellate corals are extracted as incidental by-catch. The problem is so severe in Japan and Norway that an estimated 30 to 50 percent of the deep-water reefs are damaged.

In the Gulf of California, Reyes-Bonilla et al. (2008) indicated that several species have been affected by human activities. Particular attention was called to *E. grayi* and *H. aequicostatus*, which live on sandy, flat-bottomed parts of the upper continental shelf where the shrimp fishery operates (Steller et al. 2003). A recent evaluation of the status of the deep-water corals from western Mexico (Reyes-Bonilla et al. 2008) found that *Astrangia costata, C. franciscana, C. eguchii, Dendrophyllia californica*, and *Sphenotrochus hancocki* must be regarded as under threat according to the risk evaluation method established by the National Ecology Institute (Anonymous 2001). Unfortunately, no marine area away from the coastal margin is protected in Mexico, and that situation puts azooxanthellate corals at risk.