

## Coral reefs of Huatulco, West México: reef development in upwelling Gulf of Tehuantepec

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Received 31-X-1996. Corrected 12-V-1997. Accepted 12-V-1997.

**Abstract:** Numerous pocilloporid coral reefs occur along the 26 km coastline of Huatulco, Gulf of Tehuantepec, México. Twelve species of zooxanthellate corals belonging to four genera (*Pocillopora*, *Pavona*, *Porites*, *Psammocora*) are present in this area with three species of pocilloporid corals largely responsible for reef framework construction. Seventeen fringing reefs, with mean depths ranging from 2 to 14 m, displayed maximum, horizontal framework dimensions ranging from 58 x 85 m (width x length) to 283 x 355 m. Reef topographic profiles suggest that vertical framework buildups range from about 1 to 5 m. Most reef development occurs in bays or along protected shores with hillocky or gently sloping pocilloporid frameworks. At some exposed sites, 2-3 m high surge channels dissect seaward-facing reef slopes. Sudden cooling of nearshore waters, from 24°C to 20°C, was detected at the reef base (8 m) on a Huatulco reef in February 1996, during the usual upwelling season (November-April) in the Gulf of Tehuantepec. Three of 17 reefs were dead, largely in an erosional state and with high population densities of *Diadema mexicanum*. Sexual recruits of *Pavona gigantea* were abundant at the seaward reef bases of some dead reefs. These colonies, dominantly 5 to 8 cm high, probably began to settle in 1989 and later, possibly in response to newly-created substrates following widespread coral mortality during the 1987 El Niño-Southern Oscillation (ENSO) event.

**Key words:** coral reefs, Mexican Pacific, upwelling, El Niño-Southern Oscillation.

Knowledge of the distribution, structure, and species composition of coral reefs in the eastern Pacific has increased rapidly since the 1970s. Structural coral reefs occur on the mainland coast and offshore islands of northern México (Reyes Bonilla 1993a), and along the Central American coast (Porter 1972, Dana 1975, Guzmán and Cortés 1993) to southern Ecuador and the Galápagos Islands (Glynn and Wellington 1983). Although the early literature indicated an absence of coral reefs from eastern Pacific upwelling centers (Dana 1843, Crossland 1927), recent studies show that coral reefs do occur in upwelling areas, such as the Gulf of Papagayo, Costa Rica (Glynn *et al.* 1983), and the Gulf of Panamá, Panamá (Glynn

*et al.* 1972, Glynn and Stewart 1973). However, these reefs are not as well developed as those in nonupwelling environments (Glynn 1977, Glynn and Macintyre 1977).

In spite of these recent advances, large stretches of inaccessible reefs of the southern Mexican coast have not been adequately studied. The presence of coral reefs along the southern coast of México has only been vaguely referenced (Palmer 1928, Beebe 1942, Reyes Bonilla 1993a) and our surveys are the first to reveal numerous well developed coral reefs bordering the Gulf of Tehuantepec. This study describes the coral reefs of Huatulco, a 26 km stretch of rocky coastline with numerous bays and sheltered shores (Fig. 1). In this paper, we

examine aspects of reef distribution, size, depth, geomorphology, species composition, biogeography, and reef condition. Also, a five day *in situ* reef temperature record documents sudden (hourly) temperature declines, from 24°C to 20°C, at a Huatulco reef site during February 1996. Relatively large sections (100s to 1000s m<sup>2</sup>) of dead and eroded corals were observed at some reefs along the Huatulco coast. To determine the timing of coral death, the sizes and estimated ages of coral recruits on a dead Huatulco reef are related to similar patterns of coral mortality and recruitment on Panamanian reefs affected during the 1982-83 El Niño-Southern Oscillation (ENSO) event. Evidence is presented indicating that the 1987 ENSO may have caused extensive coral mortality at Huatulco, as observed off Baja California (Wilson 1990, Reyes Bonilla 1993b) and inferred at Clipperton Atoll (Glynn *et al.* 1996).

In light of the recent worldwide decline in coral reefs (Wilkinson 1993, Ginsburg 1994), it is urgent to locate and document the condition of reefs that are not subject to direct anthropogenic impacts. Such information will help to distinguish between natural and anthropogenic stresses (Grigg and Dollar 1990), and call attention to the protection of coral reef ecosystems from harmful human activities. This study identifies a generally healthy, and until recently remote, coral reef tract off the Pacific coast of México. This area, now accessible, is undergoing rapid population growth and accelerating coastal tourist development. This study serves as an ecological benchmark and hopefully it will encourage the management of Huatulco coral reefs in the face of imminent environmental change.

## METHODS

The SW-trending coastline of Huatulco was surveyed over a distance of approximately 26 km, from Tejoncito (96°03'35"W) to San Agustín (96°14'05"W) (Fig. 1). Coral reefs

were located with the help of local fishermen and sports divers, and by towing divers over suspected coral reef habitats. A Global Positioning Systems (GPS), Magellan Model 5000, established the geographic positions of the centers of reefs. An Apelco Ranger 420 chart recorder mounted on an outboard motor-powered boat was used in the bottom profiling. A compass enabled straight-line runs perpendicular to the shoreline. Transect runs started seaward of the breaker line, usually at 1-2 m depth, and distances were estimated by timing the runs. All profiling was performed under calm sea conditions with minimal current activity. Reef framework thickness was determined from bathymetric profiles by estimating the vertical heights of coral buildups above an assumed evenly sloping rock substrate. Naturally exposed framework faces allowed verification of buildup heights on the shallow sections of three reefs. Reef depths were obtained with depth gauges and were adjusted to the mean low water datum. Reef dimensions (length x width) were measured under water with a tape measure. The locations of coral species' assemblages, in relation to reef depth and seaward/leeward exposures, were determined from *in situ* linear measurements referred to the bathymetric profile surveys.

Coral species identifications were made with reference to Squires (1959) and Wells (*in* Glynn and Wellington 1983). All zooxanthellate coral species were recorded at each of the reefs surveyed. Voucher specimens are available at the Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, University of Miami, Florida, and at the Instituto de Recursos, Universidad del Mar, Oaxaca, México.

A calibrated Hg thermometer with  $\pm 0.1^\circ\text{C}$  accuracy recorded sea surface temperatures. At La Entrega reef a HOBO Temp<sup>R</sup> (Onset Computer Corp.) underwater recorder sealed in a polyvinyl plastic (PVC) waterproof case measured the bottom temperature at the reef base (8 m) every 30 minutes over a 5 day period (17-22 February 1996).

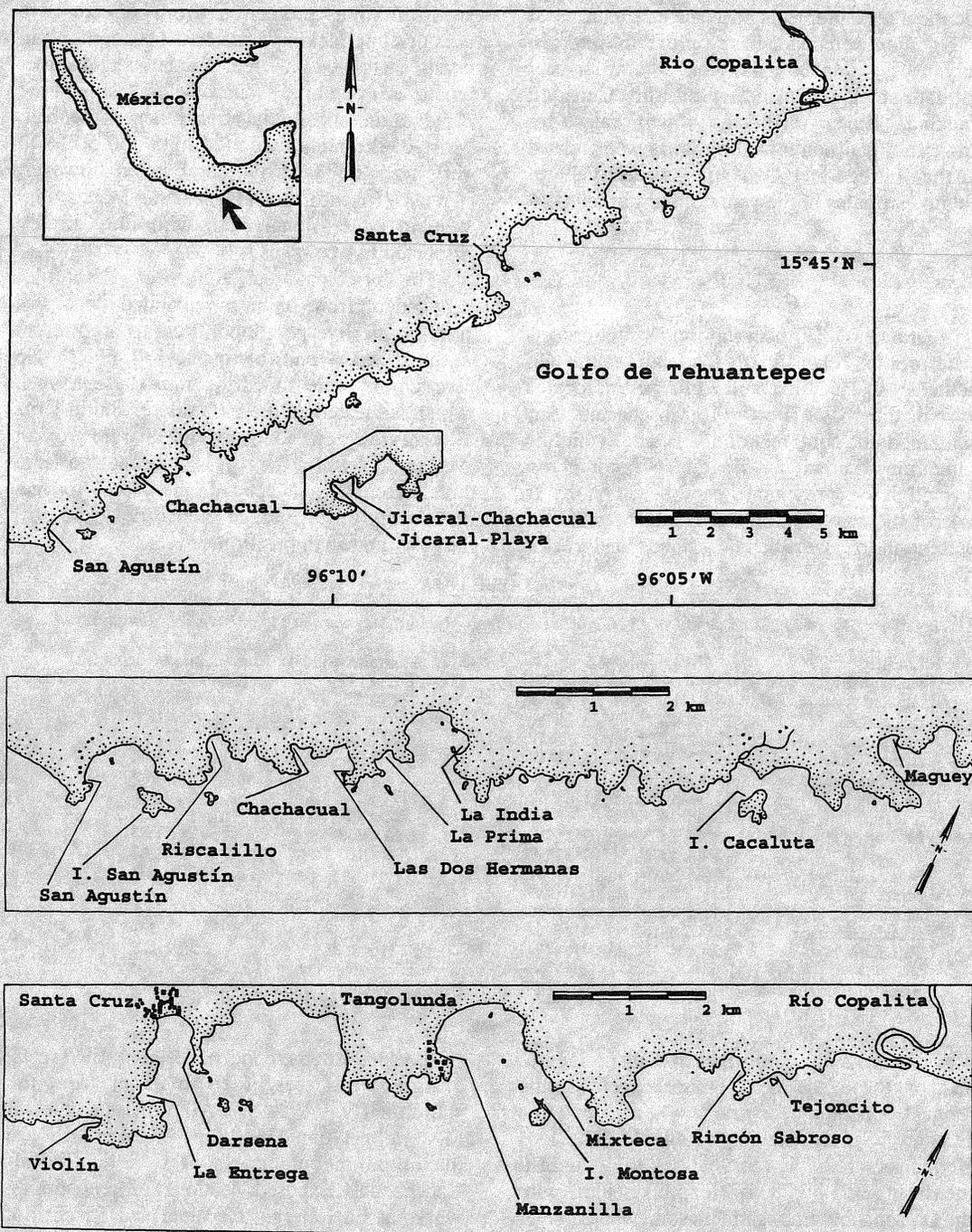


Fig. 1. Location of pocilloporid reefs along the Huatulco, Oaxaca coastline.

The maximum linear growth axes of sexual recruits of *Pavona gigantea* were measured at La Entrega reef on 18 February 1996. All

colonies were measured that had recruited onto dead pocilloporid frameworks at the reef base, encompassing an area of about 300 m<sup>2</sup>.

Identical measurements of the sexual recruits of *P. gigantea* were made in the previous year (16 July 1995) in a 300 m<sup>2</sup> area of similar reef habitat at Uva Island, Gulf of Chiriquí, Panamá. Linear skeletal growth rates for upwelling and nonupwelling areas were related to the Entrega and Uva sites respectively to obtain estimates of the years of recruitment.

## RESULTS

A total of 17 pocilloporid fringing reefs were present between Río Copalita, at the NE boundary of Huatulco, and San Agustín, located toward the SW (Fig. 1). Chachacual Bay contained one coral reef on the E side, which is sometimes known as Jicaral. No coral reef formation was present at Jicaral beach on the W side of the bay. All of the Huatulco reefs are present in bays or behind islands and rocks,

sites affording protection from direct wave assault. Interlocking branches of pocilloporid corals stabilized the reef framework. Neither crustose coralline algae or submarine cementation apparently strengthened the reef. Most of the reefs exhibited high (30-50%) to very high (60-90%) live coral cover, however, 3 reefs (Riscalillo, Darsena, and Manzanilla) were in an erosional state with only highly dispersed live colonies.

The principal reef frame at Riscalillo, centered in front of an uninhabited beach, is dead. Some live pocilloporid corals are present at the E and W ends of this reef (Table 1). No live corals were found at the Darsena reef, which is located on the east side of Santa Cruz Bay, a few km south of the harbor, or at Manzanilla, where the reef is adjacent to a large hotel complex. Most of the deep foreereef framework at La Entrega is also dead and still largely in growth position.

TABLE 1

*Locations, dimensions, and depths of 15 Huatulco coral reefs. Reefs at Maguey and Violín have not been surveyed.*

Locality	Geographic position	Maximum length x width (m)	Maximum depth (m)
San Agustín	15°41'09"N, 96°13'46"W	201 x 131	13.3
Isla San Agustín	15°41'16"N, 96°13'30"W	315 x 26	10.0
Riscalillo	15°41'47"N, 96°13'25"W	96(156) x 25(70)	10.0
La Prima	15°42'11"N, 96°12'11"W	117 x 41	5.0
Jicaral-Chachacual	15°42'00"N, 96°12'51"W	85 x 58	11.6
Las Dos Hermanas	15°42'00"N, 96°12'30"W	355 x 283	14.3
La India	15°42'30"N, 96°11'48"W	111 x 56	5.0
Cacaluta	15°43'08"N, 96°09'43"W	200 x 86	11.6
La Entrega	15°44'34"N, 96°07'35"W	324 x 233	13.3
Darsena	15°44'47"N, 96°07'31"W	398 x 163	13.3
Manzanilla	15°45'50"N, 96°05'51"W	116 x 100	5.0
Mixteca	15°46'00"N, 96°05'01"W	88 x 88	4.0
Montosa	15°45'48"N, 96°04'56"W	236 x 50	11.6
Rincón Sabroso	15°46'08"N, 96°04'21"W	235 x 8	4.0
Tejoncito	15°46'48"N, 96°03'35"W	171 x 30	2.2

Riscalillo: dimensions of dead reef frame located near the beach are denoted in parentheses.

Four reefs are more than 300 m in length, and of these the dead Darsena reef is the longest, extending for nearly 400 m along the E side of Santa Cruz Bay (Table 1). The Dos Hermanas reef is probably the largest, measuring 355 by 283 m (length x width) with the Darsena and Entrega reefs somewhat smaller at 398 by 163 m and 324 by 233 m, respectively. Maximum framework depths (relative to mean low water) vary from 2.2m (Tejoncito) to 14.3 m (Dos Hermanas) (Table 1).

Back reef frameworks of seven profiled reefs formed at distances of 15 to 25 m from the shoreline (Figs. 2 and 3). All profiles suggest 3 to 4 m reef frame buildups with possibly a maximum reef thickness of 6 m at Jicaral-Chachacual. Exposed sections of reef frameworks at La Entrega, Cacaluta and Riscalillo, due presumably to reef frame disintegration, revealed minimum thicknesses of 2-3 m. Rock outcrops are evident seaward of the reef frameworks at La Entrega and the San Agustín reefs.

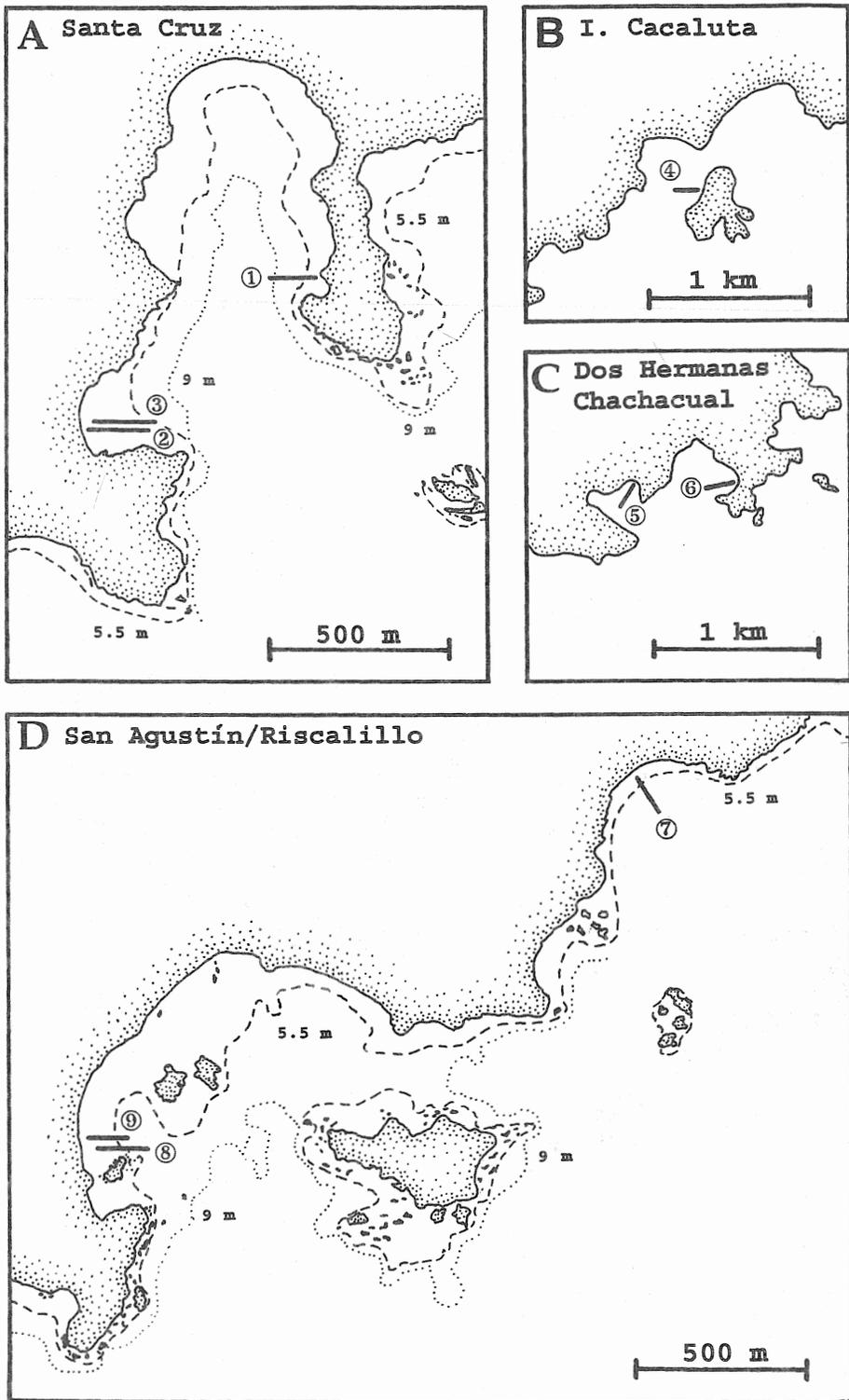


Fig. 2. Locations of echo sounder transects. A and D are from nautical charts in Winlund *et al.* (1983), scale approx. 1: 10,000. B and C are from topographic maps of INEGI (Instituto Nacional de Estadística Geografía e Informática), scale 1: 50,000. Numbered transect locations correspond to the numbered profiles in Fig. 3.

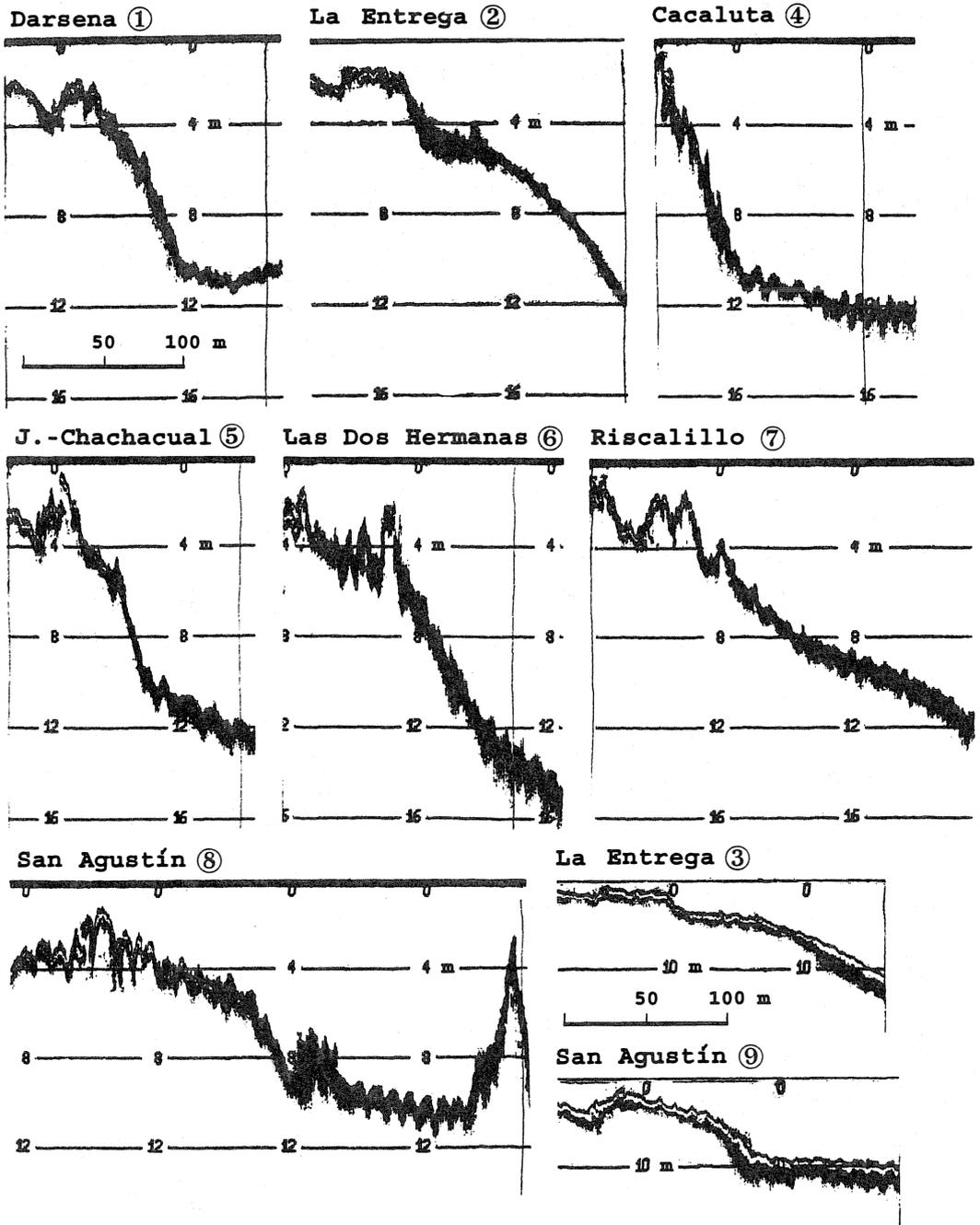


Fig. 3. Bathymetric profiles of 7 Huatulco fringing reefs. Note vertical scale differences of La Entrega and San Agustín reefs (lower right hand corner).

Twelve species, of the 29 known eastern Pacific zooxanthellate scleractinian corals (Glynn, in press), belonging to four genera were found on the Huatulco coast (Table 2). Live colonies of all species were present on reefs except for *Psammocora stellata*; a few beach-worn colonies of the latter were found on the shore at Santa Cruz. This identification is tentative due to the poor condition of the calices. Three species of *Pocillopora*, namely, *P. verrucosa*, *P. capitata*, and *P. damicornis*, were present and abundant on most reefs (Table 3). *Pocillopora elegans* Dana 1846 is here treated as a junior synonym of *P. verrucosa* (Ellis and Solander, 1786) (see Veron and Pichon 1976). *Pocillopora meandrina* and *P. eydouxi* were present on several reefs, but not as abundant as the former species. Two possibly new pocilloporid species, *Pocillopora* sp. 1 and *P.* sp. 2, were less common with the former found only at La Entrega. *Pocillopora* sp. 1 has inflated branches with a few protuberant spiny verrucae present at the branch tips. *Pocillopora* sp. 2 tends to have some

colony branches disposed horizontally in tiers. Whereas *Porites* is represented by just a single species (*P. panamensis*), three agariciid species are present (*Pavona gigantea*, *P. clavus*, and *P. varians*) with *P. gigantea* being the most common. *Pavona varians* was rare with only 7 colonies found together on the dead deep reef framework at La Entrega.

TABLE 2

## Species list of zooxanthellate, scleractinian corals of Huatulco

<i>Pocillopora verrucosa</i> (Ellis & Solander, 1786)
<i>Pocillopora capitata</i> Verrill, 1864
<i>Pocillopora damicornis</i> (Linnaeus, 1758)
<i>Pocillopora eydouxi</i> M. Edwards & Haime, 1860
<i>Pocillopora meandrina</i> Dana, 1846
<i>Pocillopora</i> sp. 1
<i>Pocillopora</i> sp. 2
<i>Porites panamensis</i> Verrill, 1866
<i>Pavona gigantea</i> Verrill, 1869
<i>Pavona varians</i> Verrill, 1864
<i>Pavona clavus</i> (Dana, 1846)
* <i>Psammocora ?stellata</i> Verrill, 1866

\* Present only as dead, beach-worn specimens

TABLE 3

## Occurrences of coral species on 15 coral reefs at Huatulco

Locality	Coral species											
	PV	PC	PD	PM	PE	Psp.1	Psp.2	PG	PVC	PVV	PP	PS
San Agustín	+	+	+					+				
Isla San Agustín	+	+	+	+	+		+					+
La Prima	+	+	+	+	+		+	+	+			+
Jicaral-Chachacual	+	+	+		+			+				+
Las Dos Hermanas	+	+	+	+			+	+	+			+
La India	+	+	+					+				+
Cacaluta	+	+	+	+	+							+
La Entrega	+	+	+			+		+		+		+
Darsena		+	+					+			+	+
Manzanilla		+	+									
Mixteca	+	+	+					+				+
Montosa	+	+	+	+	+		+	+				+
Rincón Sabroso	+	+		+								+
Tejoncito	+	+	+	+								+

Species identities: PV, *Pocillopora verrucosa*; PC, *Pocillopora capitata*; PD, *Pocillopora damicornis*; PM, *Pocillopora meandrina*; PE, *Pocillopora eydouxi*; Psp.1, *Pocillopora* sp. 1; Psp.2, *Pocillopora* sp. 2; PG, *Pavona gigantea*; PVC, *Pavona clavus*; PVV, *Pavona varians*; PP, *Porites panamensis*; PS, *Psammocora ?stellata*

Pocilloporid species predominated from the shallowest reef habitats to the deep reef base (Figs. 4 and 5), thus there is typically no marked coral species zonation. The reef at Las Dos Hermanas does, however, exhibit zonation with pocilloporid corals predominating at shallow depths, and *Pavona gigantea* and *Pavona clavus* abundant below 6 m. Small, encrusting colonies of *Porites panamensis*

occur on coral rubble at the reef base where *Pocillopora* sp. are more dispersed or on rock outcrops at the reef base and deeper (to 15-18 m depth). Agariciid species also were observed on the eroded sections of reefs at greater depths (10-15 m). Large and highly dispersed colonies of *Pavona gigantea* were present at the reef base and occasionally at greater depths, occurring as isolated colonies at 8 to 12 m.

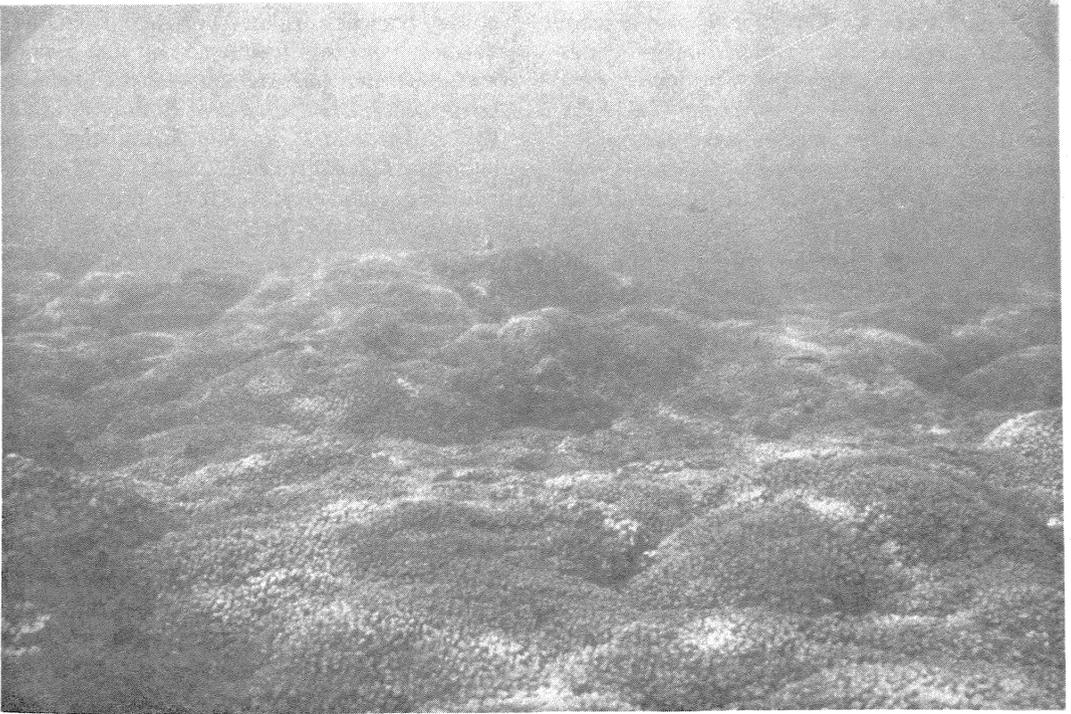


Fig. 4. A live pocilloporid reef, San Agustín (3 m depth, 19 February 1996). The tightly-packed branches of *Pocillopora* spp. form 1.0-2.0 m diameter mounds.



Fig. 5. Surge channel formed of live pocilloporid corals, San Agustín (3 m depth, 19 February 1996). A view towards the beach, parallel to the dominant direction of wave motion. Maximum channel height is 2.5 m.

Sea surface temperature (SST) at several reef sites, measured from 0930 to 1500 over the period 17-22 February 1996, ranged from 23.1°C to 25.3°C ( $n = 24$ ). Subsurface temperatures at La Entrega reef base (8 m) demonstrated marked fluctuations, ranging over 4°C during a 5 day period (Fig. 6). Three degree temperature differences occurred during 1-2 hour intervals on 17 and 18 February. Rapid temperature increases occurred during late afternoon falling tides, suggesting that deeper sections of the reef were exposed progressively

to surface waters that had warmed during the day. However, a critical comparison of temperatures recorded during peak low and high tidal stands negated this possibility. Mean temperature at peak low tide ( $22.82^{\circ}\text{C} \pm 0.25$ ,  $n = 9$ ) was only slightly higher than that at peak high tide ( $22.49^{\circ}\text{C} \pm 0.29$ ,  $n = 9$ ). No significant difference in sea temperature was noted in 9 consecutive pairwise low and high water comparisons ( $p > 0.05$ , Wilcoxon matched-pairs signed-ranks test, 1-tailed test).

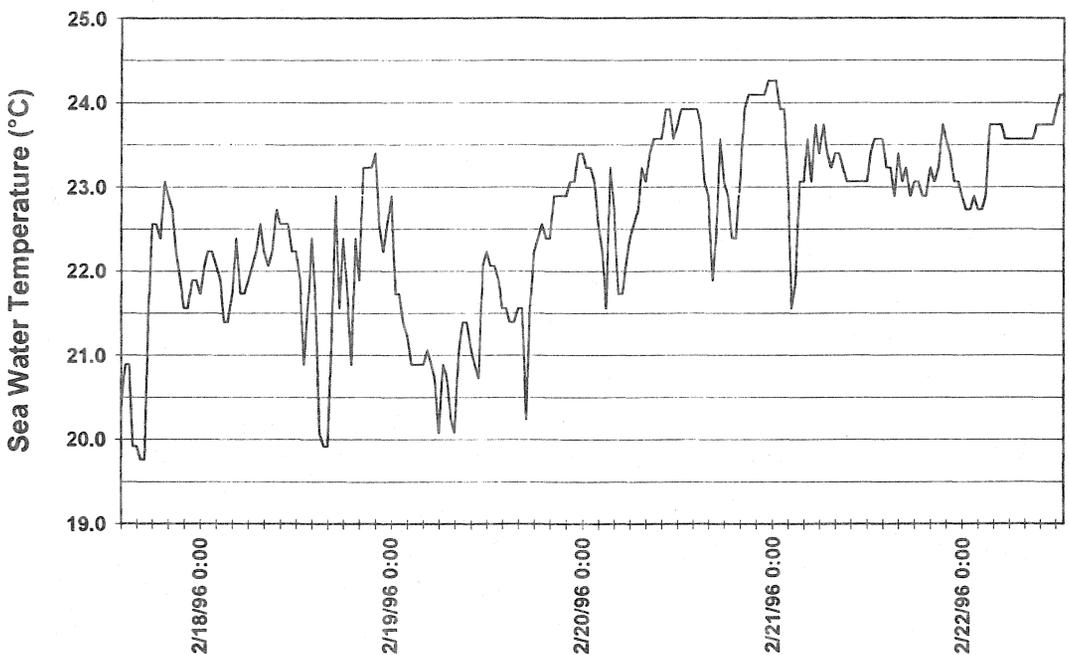


Fig. 6. Reef base (8 m depth) temperatures at La Entrega reef recorded every 30 minutes with a HOBO Temp<sup>®</sup> underwater recorder during 17-22 February 1996.

Large sections of the forereef at Darsena and La Entrega consisted of dead pocilloporid coral rubble (Fig. 7) or patches of reef frame still in growth position (Fig. 8). These areas also supported high densities of *Diadema mexicanum* with several aggregations in excess of 100 individuals. The sea urchins were grazing on epilithic filamentous and crustose coralline algae, and simultaneously bioeroding the dead coral substratum. Since the sea urchins often aggregate around the bases of pocilloporid blocks, their rasping results in undercutting, destabilization and collapse of frameworks (Colgan 1990). Much of the loose *Pocillopora* spp. rubble (Fig. 7) is likely a result of the

intense grazing by *Diadema*, which is thus a primary cause of the disintegration of pocilloporid frameworks (Fig. 8).

At La Entrega reef, the largely dead, bioeroded, forereef rubble zone is populated by numerous, small colonies of *Pavona gigantea*. Because these colonies are symmetrical in growth habit (not derived from irregularly shaped fragments) and far removed ( $\geq 10$  m) from large reproductive colonies, they are assumed to represent sexual recruits. In an area of about 300 m<sup>2</sup>, 74 recruits were censused, equivalent to a population density of 2,500 ind ha<sup>-1</sup>.

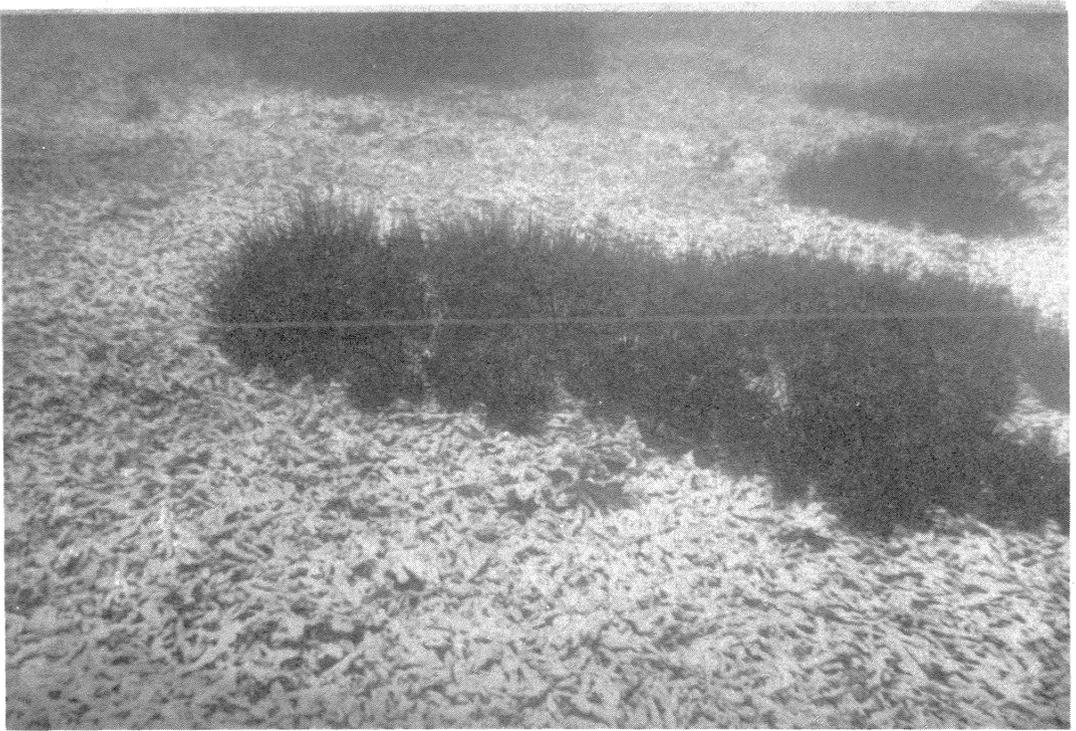


Fig. 7. Aggregations of *Diadema mexicanum* on dead pocilloporid rubble, Darsena reef (4 m depth, 3 March 1995).



Fig. 8. *Diadema mexicanum* clustered around an eroded pocilloporid reef frame block, Darsena reef (4 m depth, 3 March 1995).

The size distribution of these colonies, here assigned to three classes, show maximum growth axes ranging from 2 to 8 cm (Fig. 9). About 68% of the colonies in this sample belonged to the 5 cm class. Assuming an annual skeletal growth rate of 0.8 cm yr<sup>-1</sup> (Table 4, column a), corals in the 5 cm size class (4-6 cm range) would have settled 3 to 5 years ago or sometime between 1991 and 1992.

The oldest recruits sampled at the Entrega reef, members of the 8 cm size class, probably settled during the 1989-1990 period. If a higher growth rate is assumed, say 1.1 cm yr<sup>-1</sup> (Table 4, column b), then some of the older recruits (8 cm class) would have settled between 1985 and 1988.

TABLE 4

Years *Pavona gigantea* recruited to pocilloporid reef frames at La Entrega and Uva Island coral reefs estimated from linear skeletal size measurements and coral growth rates.

Size class (cm)	La Entrega		Uva Island
	a	b	
2	1994-1995	1992-1995	1992-1994
5	1991-1993	1989-1991	1989-1991
8	1989-1990	1985-1988	1986-1988
11	-	-	1983-1985
14	-	-	1980-1982
17	-	-	1976-1979
20	-	-	1973-1975
23	-	-	1970-1972

Assumed mean skeletal growth rates at La Entrega are 0.8 cm yr<sup>-1</sup> (a), reported for Cabo Pulmo, Baja California Sur (Hernandez Cortés in Reyes Bonilla, 1993 a), and 1.1 cm yr<sup>-1</sup> (b), reported for the Pearl Islands, Panamá (Wellington, 1982). A median growth rate of 1.0 cm yr<sup>-1</sup>, reported by Glynn *et al.* (1983) for colonies near Uva Island, is assumed to be a reasonable estimate for Uva Island.

*Pavona gigantea* recruits censused at Uva Island (Gulf of Chiriquí, Panamá) in 1995 were also concentrated on dead pocilloporid frameworks that were severely bioeroded by *Diadema mexicanum*. The 57 colonies censused in an approximately 300 m<sup>2</sup> area is equivalent to 1,900 ind ha<sup>-1</sup>. The predominant size classes had linear growth axes of 5 and 8 cm, and are estimated to have recruited in 1990 (1989-1991) and 1987 (1986-1988) respectively (Fig. 9). Unlike the colony size (and age) distribution at La Entrega, which indicated relatively recent recruitment beginning after 1987, at Uva some coral recruitment occurred as early as 1974 and 1980 with a marked increase evident in 1983 and 1986.

## DISCUSSION

The abundance of coral reefs along the Huatulco coastline is comparable to nonupwelling Gulf of Chiriquí, Panamá, which harbors perhaps the highest density of reefs of any eastern Pacific area (Glynn *et al.* 1972, Dana 1975, Glynn and Macintyre 1977). While this study was confined to the Huatulco coast,

pocilloporid reefs also occur at several localities further west, including Puerto Angel (96°30'W, about 40 km W of San Agustín) and Puerto Escondido (97°04'W, about 100 km W of San Agustín). Like most eastern Pacific reefs (Glynn and Wellington 1983, Guzmán and Cortés 1993), the majority of the Huatulco reefs are relatively small, covering only a few hectares in planar area, and occur at shallow depths (2-14 m). Since the majority of Huatulco reefs exhibit framework development at 10 m and deeper, reef-building in the Gulf of Tehuantepec extends deeper than in the Gulfs of Papagayo and Panamá, two major eastern Pacific upwelling centers where reef development is usually limited to 3-5 m (Glynn *et al.* 1983, Guzmán and Cortés 1993). The vertical thickness of Huatulco reefs of 3 to 4 m is comparable to pocilloporid reef thickness in upwelling Gulf of Panamá (Glynn and Wellington 1983). However, they are thinner than the pocilloporid reef frame buildups in the Gulf of Chiriquí, ranging from 5 to 11 m, which are eastern Pacific's thickest accumulations of reef (Glynn and Macintyre 1977).

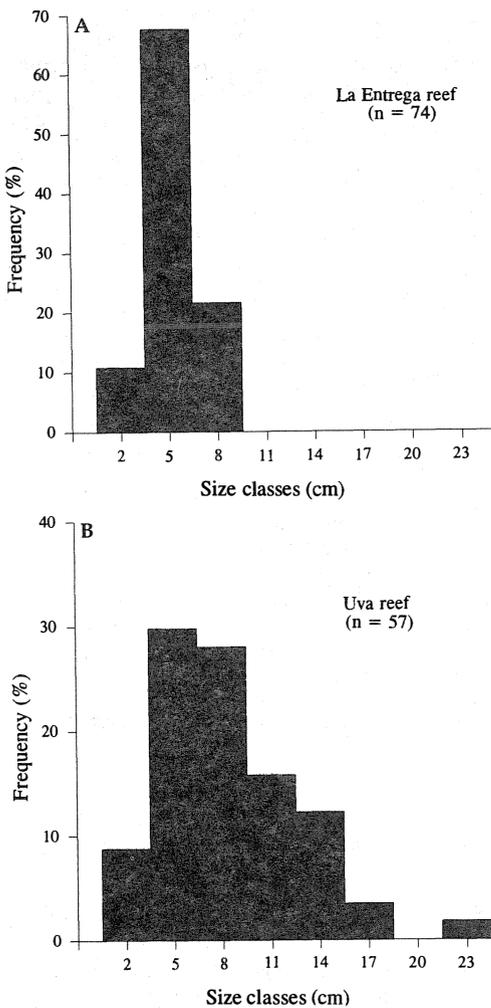


Fig. 9. Size structures of young *Pavona gigantea* colonies that recruited to dead pocilloporid reef frames at A Huatulco, México (sampled in February 1996) and B Gulf of Chiriquí, Panamá (sampled in July 1995).

*In situ* sea temperature observations in this study demonstrated that the Entrega reef is subject to at least short periods of moderate cooling. Satellite images of SST in the Gulf of Tehuantepec sometimes show the principal upwelling plume reaching the Huatulco coast (Stumpf and Legeckis 1977, Clarke 1988, Legeckis 1988) and sometimes not (Barton *et al.* 1993). When a strong offshore current jet and anticyclonic eddy develop, warm coastal and cooled central Gulf waters are advected around the periphery of the eddy, thus limiting the intrusion of large negative temperature anomalies nearshore (Barton *et al.* 1993). If this

circulation pattern is predominant, it is probable that the Huatulco reef tract is not subject to the intense, nearshore upwelling that occurs in the Gulfs of Papagayo and Panamá. Whether or not the relatively deep development of reefs at Huatulco is related to reduced upwelling is a question that would require considerable detailed study.

Annual rainfall in the Huatulco area, 800 to 1,000 mm, is low compared with the Gulf of Chiriquí where rainfall ranges from 2,400 to 3,200 mm yr<sup>-1</sup> (Climatic atlas of North and Central America 1979). In neither area, however, does freshwater dilution or sediment transport appear to limit reef growth. Although tropical cyclones batter the southwest coast of México (Hubbs and Roden 1964), we found no evidence of storm damage to Huatulco coral reefs. This was unexpected in light of the relatively fragile pocilloporid frameworks because similar eastern Pacific reefs often display major framework damage, due presumably to storm-generated high seas and seismic activity (Porter 1972, Glynn and Wellington 1983). For example, large pocilloporid blocks, separated from frameworks, or that have slumped, tilted or overturned, are sometimes evident in the Gulf of Chiriquí (Glynn *et al.* 1972, Porter 1972). Surge channels and buttresses form along the seaward faces of some relatively exposed Huatulco reefs. Generally, however, these geomorphologic features are rarely present on eastern Pacific reefs, although pocilloporid buttresses with a high cover of crustose coralline algae occur on exposed reefs at Gorgona Island, Colombia (Glynn *et al.* 1982).

Even for the eastern Pacific, the monogenic character of the Huatulco reefs is especially pronounced. While pocilloporid species are often the dominant framework builders of eastern Pacific reefs, other encrusting, nodular and massive species are usually present. For example, pocilloporid reefs in the Galápagos Islands (Glynn and Wellington 1983, Colgan 1990), Colombia (Glynn *et al.* 1982, Vargas Angel 1996), Panamá (Glynn 1976, Wellington 1982), and Costa Rica (Guzmán and Cortés 1989), contain several associated species, particularly in cryptic microhabitats within the reef framework (encrusting, foliose and nodular species), and at the reef base where pocilloporids are less

abundant (massive species). A few small nonpocilloporid species (*Porites panamensis* and *Pavona varians*) are present on Huatulco reefs, but none of these is abundantly intermixed with pocilloporid species. Dead specimens of *Psammocora ?stellata* were found on one beach at Santa Cruz. The massive species *Pavona gigantea* and *Pavona clavus* are neither abundant nor important in framework construction. *Gardineroseris planulata* (Dana, 1846) has not been found on the Huatulco coast, but a few small colonies occur at Camaroncillo, a few km west of Puerto Angel (G. Leyte, unpublished observations).

Possibly the prevailing surface currents of the SW Mexican coast are responsible for the absence of several coral species from this area, as suggested by Ketchum and Reyes Bonilla (in press). Between 10° to 15°N latitude, the predominant coastal current flow is toward the NW, i.e. from Costa Rica to the Gulf of Tehuantepec (Wyrtki 1965, Fiedler 1992). This movement would limit communication between the Revillagigedo Islands, with a diverse coral fauna (20 species, Ketchum and Reyes Bonilla, in press), but could potentially transport coral propagules towards México from populations at lower latitudes. The reef-building coral fauna of Costa Rica and Panamá consists of 20 and 23 species respectively (Glynn, in press) compared with mainland México with only 14 species (including the new record of *Gardineroseris planulata*). It has been argued that the relatively diverse Panamanian coral fauna is in large part a result of the invasion of transpacific species via the North Equatorial Counter Current (Dana 1975, Glynn and Wellington 1983, Glynn *et al.* 1996). However, an important environmental barrier separates the Panamanian and Mexican biogeographic provinces. This barrier is the Pacific Central American Faunal Gap (Springer 1958, Briggs 1974), a 1,130 km coastal stretch dominated by soft-sediment and mangrove environments. Since corals require firm substrata, this unsuitable gap would diminish the spread of migrants between the Panamanian and Mexican provinces. This explanation involving an ecological/distance barrier is not entirely convincing, however, considering the presumed long-distance transport of propagules across the 5,700-6,500 km eastern Pacific barrier (Scheltema 1988, Richmond 1990).

Both surface currents often demonstrate comparable velocities, i.e. between 15-30 cm sec<sup>-1</sup> (Hubbs and Roden 1964, Fiedler 1992).

Since the causes of Huatulco coral mortalities at three of the 17 reefs are unknown, we consider briefly mortality events in the well studied Pearl Islands (Panamá) to help identify likely stressors. Coral community structure at Huatulco and the Pearl Islands is similar in terms of live coral cover. The largely dead Gulf of Papagayo coral reef tract, probably a result of intensified upwelling during the Little Ice Age (150-300 yrs B.P.), does not offer any obvious clues regarding the comparatively recent disturbances at Huatulco (Glynn *et al.* 1983). Dead reef surfaces in the Pearl Islands are due mainly to the ENSO mortality event of 1982-83 (Glynn 1990). Some dead reef patches in the Pearl Islands also are a result of extreme low tidal exposures (Glynn 1976) and intense upwelling episodes (Glynn and Stewart 1973, Glynn and D'Croz 1990). The former cause narrowly confined reef flat mortality and the latter small coral patches with mainly dead peripheral colony branches (partial mortality). None of the dead Huatulco reefs displayed these mortality patterns. *Acanthaster planci* (L.) has never been observed in an eastern Pacific upwelling environment (Glynn 1974), and since it has not been seen at Huatulco it is unlikely that it was the cause of coral mortality in this area.

Two lines of evidence suggest that the Huatulco coral reefs were disturbed during a recent ENSO event: (1) the presence of dead/eroded reef structures extending over all reef zones; (2) the ages of coral recruits on dead reef surfaces. The dead and eroded pocilloporid frameworks in seaward reef base habitats, such as those at the Darsena and La Entrega reefs, are similar in appearance to comparable reef zones that were affected during the 1982-83 ENSO in Costa Rica (Guzmán and Cortés 1989), Panamá (Glynn 1990), and the Galápagos Islands (Glynn 1994). External bioeroders, particularly *Diadema mexicanum*, are responsible for much of the framework destruction on affected Costa Rican and Panamanian coral reefs (Glynn 1988, Guzmán and Cortés 1993, Eakin 1996). In spite of intensive grazing by *Diadema* on dead reef surfaces at Huatulco and Panamá, some nonpocilloporid corals are recruiting to these reefs. The age distributions of *Pavona gigantea*

recruits at Huatulco and Panamá suggest different periods of settlement that may correspond with the availability of reef substrates following El Niño-related coral mortality. In Panamá, recruitment was highest 3-6 years after the 1983 coral mortality event. Peak recruitment at Huatulco occurred during 1991-1993, 4-6 years following the 1987 ENSO. Although coral mortality was not observed on reefs in the Panamanian province during 1987, pocilloporid mortality was reported in Baja California at that time (Reyes Bonilla 1993b) and probably occurred at Clipperton Atoll as well (Glynn *et al.* 1996).

In summary, this survey has disclosed vigorous reef building along the Huatulco coast, an area influenced by Gulf of Tehuantepec upwelling. The monogeneric coral reefs of Huatulco are built primarily by only three species of *Pocillopora*. The majority of the reefs are in a healthy state, but some have experienced relatively recent and extensive coral mortality, presumably from natural causes, and are presently in various stages of recovery.

#### ACKNOWLEDGMENTS

Field work was greatly facilitated by help from E. Laclette, M. Small, A. Vasquez, and C. Waters. We also thank M. Small for his help with logistics, E. Weil for advice on coral identifications, and J. Geister for information on coral reefs to the west of Huatulco. M.W. Colgan, J. Cortés, H. Guzmán, I.G. Macintyre, J.L. Maté, W.A. Newman, G.P. Podestá and H. Velez offered several helpful comments on the manuscript. Support for this study was received from the Universidad del Mar and the National Geographic Society (grant # 5208-94).

#### RESUMEN

A lo largo de los 26 km de la costa de Huatulco, en el Golfo de Tehuantepec, México, existen numerosos arrecifes de corales pocilopóridos. Entre éstos se encuentran doce especies de corales con zooxantelas. Estos corales pertenecen a los géneros *Pocillopora*, *Pavona*, *Porites* y *Psammocora*. Tres especies de corales pocilopóridos son los principales responsables de la construcción de la estructura arrecifal. Se observaron diecisiete arrecifes en franja cuyo intervalo dominante de profundidad se presentó entre los 2 y los 4 m y que presentan dimensiones desde 30 m de ancho por 20 m de largo hasta 283 x 355 m. Los perfiles topográficos de

varios arrecifes también sugieren que la dimensión vertical de las estructuras puede variar desde 1 a 5 m. La mayoría de los arrecifes con promontorios o pendientes suaves están constituidos por corales pocilopóridos y localizados en bahías o en costas protegidas del oleaje. En las áreas más expuestas al oleaje, se forman canales con una profundidad de 2 a 3 m. Las surgencias costeras se presentan desde el noviembre hasta el abril. Estas surgencias de aguas más frías llegan a veces hasta la zona de los arrecifes en el Golfo de Tehuantepec. Durante esta investigación también se observó que 3 de los diecisiete arrecifes estaban muertos. Estos estaban en un avanzado estado de erosión, presentando una alta densidad poblacional de *Diadema mexicanum*. El reclutamiento sexual de *Pavona gigantea* también se observó en abundancia en las áreas más profundas, principalmente en las bases de los arrecifes muertos. Estas pequeñas colonias de *P. gigantea* (5-8 cm de altura) tal vez comenzaron su asentamiento larval en el sustrato formado por los corales que murieron a causa del evento El Niño-Oscilación del Sur en 1987.

#### REFERENCES

- Barton, E.D. M.L. Argote, J. Brown, P.M. Kosro, M. Lavin, J.M. Robles, R.L. Smith, A. Travina & H.S. Velez. 1993. Supersquirt: dynamics of the Gulf of Tehuantepec, México. *Oceanography* 6: 23-30.
- Beebe, W. 1942. Book of bays. Harcourt, Brace & Co. New York. 302 p.
- Briggs, J.C. 1974. Marine zoogeography. McGraw-Hill, New York. 475 p.
- Clarke, A.J. 1988. Inertial wind path and sea surface temperature patterns near the Gulf of Tehuantepec and Gulf of Papagayo. *J. Geophys. Res.* 93 (C12): 15,491-15,501.
- Climatic atlas of North and Central America. 1979. vol. 1, World Meteorological Organization, Geneva.
- Colgan, M.W. 1990. El Niño and the history of eastern Pacific reef building. p. 183-232. *In* P.W. Glynn (ed.). Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier Oceanography Series, 52, Amsterdam.
- Crossland, C. 1927. Marine ecology and coral formations in the Panamá region, the Galápagos and Marquesas Islands, and the Atoll of Napuka. *Trans. Roy. Soc. Edinburgh* 55: 531-554.
- Dana, J.D. 1843. On the temperature limiting the distribution of corals. *Amer. J. Sci.* 45: 130-131.
- Dana, T.F. 1975. Development of contemporary eastern Pacific coral reefs. *Mar. Biol.* 33: 355-374.
- Eakin, C.M. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15: 109-119.
- Fiedler, P.C. 1992. Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech. Rpt. NMFS 109: 1-65.
- Ginsburg, R.N. (compiler) 1994. Proceedings of the colloquium on global aspects of coral reefs: health, hazards and history, 1993. Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, 420 p.

- Glynn, P.W. 1974. The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific. *Environ. Conserv.* 1: 295-304.
- Glynn, P.W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecol. Monogr.* 46: 431-456.
- Glynn, P.W. 1977. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panamá. *J. Mar. Res.* 35: 567-585.
- Glynn, P.W. 1985. El Niño-associated disturbances to coral reefs and post disturbance mortality by *Acanthaster planci*. *Mar. Ecol. Prog. Ser.* 26: 295-300.
- Glynn, P.W. 1990. Coral mortality and disturbance to coral reefs in the tropical eastern Pacific. In: Glynn, P.W. (ed.) *Global ecological consequences of the 1982-83 El Niño-Southern Oscillation*. Elsevier Oceanogr. Ser. 52: 55-126.
- Glynn, P.W. 1994. State of coral reefs in the Galápagos Islands: natural versus anthropogenic impacts. *Mar. Poll. Bull.* 29: 131-140.
- Glynn, P.W. In press. Eastern Pacific reef coral biogeography and faunal flux: Durham's dilemma revisited. *Proc. 8th Int. Coral Reef Symp.*
- Glynn, P.W. & I.G. Macintyre. 1977. Growth rate and age of coral reefs on the Pacific coast of Panamá. *Proc. 3rd Int. Coral Reef Symp.* 2: 251-259.
- Glynn, P.W. & R.H. Stewart. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panamá) in relation to thermal conditions. *Limnol. Oceanogr.* 18: 367-379.
- Glynn, P.W. & G.M. Wellington. 1983. Corals and coral reefs of the Galápagos Islands. (With an annotated list of the scleractinian corals of the Galápagos by J.W. Wells.) Univ. California Press, Berkeley, 330 p.
- Glynn, P.W. E.M. Druffel & R.B. Dunbar. 1983. A dead Central American coral reef tract: possible link with the Little Ice Age. *J. Mar. Res.* 41: 605-637.
- Glynn, P.W. H. von Prahl & F. Guhl. 1982. Coral reefs of Gorgona Island, Colombia, with special reference to corallivores and their influence on community structure and reef development. *An. Inst. Inv. Mar. Punta Betín* 12: 185-214.
- Glynn, P.W. R.H. Stewart & J.E. McCosker. 1972. Pacific coral reefs of Panamá: structure, distribution and predators. *Geol. Rundschau* 61: 483-519.
- Glynn, P.W. J.E.N. Veron & G.M. Wellington. 1996. Clipperton Atoll (eastern Pacific): oceanography, geomorphology, reef-building coral ecology and biogeography. *Coral Reefs* 15: 71-99.
- Guzmán, H.M. & J. Cortés. 1989. Coral reef community structure at Caño Island, Pacific Costa Rica. *P.S.Z.N.I. Mar. Ecol.* 10: 23-41.
- Guzmán, H.M. & J. Cortés. 1993. Arrecifes coralinos del Pacífico oriental tropical: revisión y perspectivas. *Rev. Biol. Trop.* 41: 535-557.
- Hubbs, C.L. & G.I. Roden. 1964. Oceanography and marine life along the Pacific coast of Middle America: p. 143-186. In R. Wauchope (gen. ed.), and R.C. West (vol. ed.), *Handbook of Middle American Indians*, Natural Environment and Early Cultures. Vol. 1, University of Texas Press, Austin
- Ketchum, J.T. & H. Reyes Bonilla. In press. Biogeography of hermatypic corals of the Archipiélago Revillagigedo, México. *Proc. 8th Int. Coral Reef Symp.*
- Legeckis, R. 1988. Upwelling off the Gulfs of Panamá and Papagayo in the tropical Pacific during March 1985. *J. Geophys. Res.* 93: 15,485-15,489.
- Palmer, R.H. 1928. Fossil and recent corals and coral reefs of western México. *Proc. Am. Philos. Soc. Philad.* 67: 21-37.
- Porter, J.W. 1972. Ecology and species diversity of coral reefs on opposite sides of the Isthmus of Panamá. *Bull. Biol. Soc. Wash.* 2: 89-116.
- Reyes Bonilla, H. 1993a. Biogeografía y ecología de los corales hermatípicos (Anthozoa: Scleractinia) del Pacífico de México. In: Salazar-Vallejo, S.I. & N.E. Gonzalez (eds.) *Biodiversidad marina y costera de México*. Com. Nal. Biodiversidad y CIQRO, México, p. 207-222.
- Reyes Bonilla, H. 1993b. 1987 coral bleaching at Cabo Pulmo reef, Gulf of California, México. *Bull. Mar. Sci.* 52: 832-837.
- Richmond, R.H. 1990. The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. In: Glynn, P.W. (ed.), *Global ecological consequences of the 1982-83 El Niño-Southern Oscillation*. Elsevier Oceanography Series 52, p. 127-140.
- Scheltema, R.S. 1988. Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the east Pacific barrier. *Biol. Bull.* 174: 145-152.
- Springer, V.G. 1958. Systematics and zoogeography of the clinid fishes of the subtribe Labrisomini Hubbs. *Publ. Inst. Mar. Sci. Univ. Tex.* 5: 417-492.
- Stumpf, H.G. & R.V. Legeckis 1977. Satellite observations of mesoscale eddy dynamics in the eastern tropical Pacific Ocean. *J. Phys. Oceanogr.* 7: 648-658.
- Vargas Angel, B. 1996. Distribution and community structure of the reef corals of Ensenada de Utría, Pacific coast of Colombia. *Rev. Biol. Trop.* 44: 643-651.
- Wellington, G.M. 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. *Oecologia (Berl)* 52: 311-320.
- Wilkinson, C.R. 1993. Coral reefs of the world are facing widespread devastation: can we prevent this through sustainable management practices? *Proc. 7th Int. Coral Reef Symp.* 1: 11-21.
- Wilson, E.C. 1990. Mass mortality of the reef coral *Pocillopora* on the south coast of Baja California Sur, México. *Bull. So. Calif. Acad. Sci.* 89: 39-41.
- Winlund, E. J. West, C. West, C. Davis & D. Gotshall. 1983. *ChartGuide México west*. ChartGuide, Anaheim, Calif. 74 p.
- Wyrtki, K. 1965. Surface currents of the eastern tropical Pacific Ocean. *Inter-Amer. Trop. Tuna Comm. Bull.* 9: 1-304.