

Reef recovery 20 years after the 1982–1983 El Niño massive mortality

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Abstract For over 20 years the El Niño-Southern Oscillation (ENSO) has caused damage to the coral reefs of the eastern Pacific and other regions. In the mid-1980s scientists estimated that coral cover was reduced by 50–100% in several countries across the region. Almost 20 years (2002) after the 1982–1983 event, we assessed the recovery of the virtually destroyed reefs at Cocos Island (Costa Rica), previously evaluated in 1987 and reported to have less than 4% live coral cover. We observed up to fivefold increase in live coral cover which varied among reefs surveyed in 1987 and 2002. Most new recruits and adults belonged to the main reef building species from pre-1982 ENSO, *Porites lobata*, suggesting that a disturbance as outstanding as El Niño was not sufficient to change the role or composition of the dominant species, contrary to phase shifts reported for the Caribbean. During the 1990s, new species were observed growing on the reefs. Notably, *Leptoseris scabra*, considered to be rare in the entire Pacific, was commonly found in the area. Recovery may have begun with the sexual and asexual recruits of the few surviving colo-

nies of *P. lobata* and *Pavona* spp. and with long distance transport of larvae from remote reefs. We found an overall 23% live coral cover by 2002 and with one reef above 58% indicating that Cocos Island coral reefs are recovering.

Introduction

The El Niño-Southern Oscillation (ENSO) occurs in the equatorial eastern Pacific with a periodicity of 2–7 years. It causes great environmental changes, such as increase in sea surface temperature, that affect marine populations and ecosystems in a variable manner (Enfield 2001; Fiedler 2002). It is estimated that ENSO events are now more frequent and intense than in the last 150,000 years (Timmermann et al. 1999; Tudhope et al. 2001), and the 1997–1998 event is considered the strongest and longest of the twentieth century (McPhaden 1999; Enfield 2001).

Coral reefs are among the ecosystems that have been most affected by ENSO (Glynn 1990; Victor et al. 2001). In particular, the coral reefs of the eastern Pacific suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982–1983 El Niño (Glynn 1990). This event affected the region unevenly along a latitudinal gradient, causing bleaching and mass mortality of corals that reached almost 100% at the equator (Galápagos Islands) and that was high (>70%) in Panama, intermediate (50%) in Costa Rica (Glynn et al. 1988), and nil in Baja California, Mexico (Carriquiry et al. 2001; Reyes-Bonilla 2003).

Likewise, during the 1997–1998 ENSO, significant coral bleaching was observed in the entire eastern

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Pacific region. However, the mortality pattern observed this time was different than in the 1982–1983 event, with a higher mortality of corals in the north (latitude 20°–25°) in the reefs of Mexico (18–96% mortality; Carriquiry et al. 2001; Reyes-Bonilla 2003), moderate mortality at the equator (Galapagos Islands 26%), and low mortality at the Ecuador mainland (7%; Glynn et al. 2001). In Panama a low mortality of 13% was observed in the Gulf of Chiriquí and no mortality was found in the upwelling area of Gulf of Panama (Glynn et al. 2001). Mortality was also low (5%) in the reefs of northern and southern Costa Rica (Guzman and Cortés 2001; Jiménez and Cortés 2003).

One of the first impressions of the studies in the 1980s was that recovery would either be virtually impossible, given the low rates of sexual reproduction in corals observed in the eastern Pacific, or that such recovery would be very slow and localized. In the last decades it has been repetitively stated that coral reefs are being destroyed at alarmingly high rates due to natural and anthropogenic impacts (Pandolfi et al. 2003, 2005), reporting a 24% of world's reefs at risk (Wilkinson 2004), and a potential loss of resilience (Hughes and Tanner 2000; Nyström et al. 2000; Bellwood et al. 2004). However, there are a few examples of recovery and resilience of reefs after mayor disturbances (Connell 1997; Connell et al. 1997; Guzman and Cortés 2001, Nyström and Folke 2001; West and Salm 2003).

This study assesses the recovery of the coral reefs in the oceanic Cocos Island (Isla del Coco, Costa Rica) following a massive coral mortality during the 1982–1983 El Niño (Guzman and Cortés 1992). Using recent data (2002), we also revisit three hypotheses raised about the recovery of these reefs (Guzman and Cortés

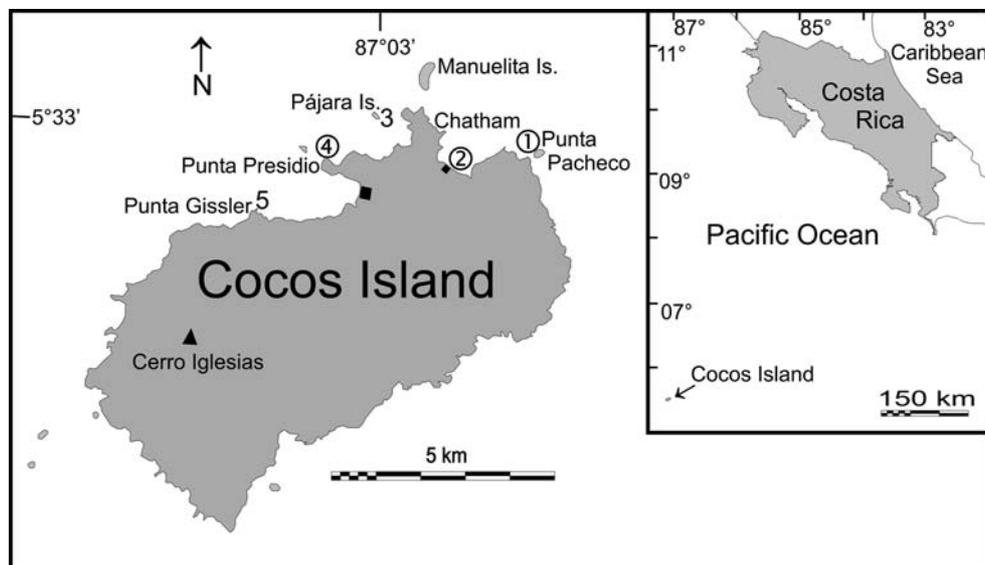
1992). (1) That reef framework would collapse due to the lack of sexual recruitment (Glynn et al. 1991, 2000) and high erosion caused by the sea urchin *Diadema mexicanum* (Agassiz) (Colgan 1990; Eakin 2001). (2) That recovery of the reefs and the distribution of species would be closely related to the sexual reproduction of local surviving populations (Connell 1973; Pearson 1981; Harriot 1985). We noted in 1987 that small adults (<150 cm²) from partial colonies of *Porites lobata* (1.57% live coverage), and recruits of *Pavona varians* (0.87%) were potential colonizers. However, this process of recovery could be significantly impaired by the presence of corallivorous organisms such as the crown-of-thorn seastar *Acanthaster planci* (Linnaeus) and the pufferfish *Arothron meleagris* (Bloch and Schneider); such predation is considered important during the first stages of recovery (Glynn 1990; Guzman and Cortés 1993). And (3) that recovery would rely mainly on immigration of larvae that have dispersed over long distances (Glynn and Wellington 1983; Scheltema 1986; Richmond 1990; Lessios et al. 1996).

Materials and methods

Study area

Cocos Island is located at 5°32'N and 87°04'W in the Pacific Ocean, approximately 530 km south-southwest of Costa Rica and 680 km north-northeast of the Galapagos Islands (Ecuador) (Fig. 1). The island has a land surface of approximately 24 km² and it was declared National Park in 1978. At present, the marine protected area extends 22 km around the island. The

Fig. 1 Map of the tropical eastern Pacific (*upper right insert*) showing the approximate location of Cocos Island, Costa Rica and detailed distribution of the three reef sites studied in 1987 (reefs 1, 2, and 4 circled in gray tone) and in 2002 (1–5)



island is covered by thick tropical rainforest and has an average annual rainfall of 5,000–6,000 mm (Garrison 2005). Cocos Island is surrounded by warm surface waters from the western Pacific that are carried by the North Equatorial Countercurrent (NECC), the position of which varies seasonally in accordance with the position of the Intertropical Convergence Zone (ITCZ). Between February and April, when the ITCZ is located more to the south, the NECC is weakened and reaches Cocos Island to a lesser degree, whereas between August and September, when the ITCZ migrates north, the island is affected by the strong current which may carry coral larvae (Guzman and Cortés 1993; Cortés 1997; Garrison 2005).

Seventeen species of zooxanthellate scleractinians have been reported from Cocos Island (Guzman and Cortés 1992; Cortés and Guzman 1998). The coral reefs at Cocos Island were qualitatively described for the first time in the early 1970s (Bakus 1975), and indicated that they were built mainly by the massive coral *P. lobata*. In 1992, Guzman and Cortés (1992) published the first quantitative data of the reefs, which were highly degraded 4 years after the 1982–1983 El Niño event.

Changes in sea surface temperature around Cocos Island

Temperature data were reviewed to relate field observations of the reefs with estimated temperature anomalies. Monthly mean sea surface temperature (SST) anomalies from 1982 to 2002 were obtained from the Integrated Global Ocean Services System (IGOSS; http://www.ingrid.ldgo.columbia.edu/SOURCES/IGOSS/nmc/weekly/dataset_documentation.html). These temperature records combine ship, buoy, and bias-corrected satellite data (see Reynolds and Smith 1994). The anomaly is produced by subtracting the mean from all SST monthly values in the time-series then dividing the centered values by the standard deviations; by definition the anomaly has a mean of zero and a standard deviation on one.

Changes in live coral cover and other sessile organisms between 1987 and 2002

Cocos Island coral reefs were assessed on several occasions. In July 1978 and December 1986 qualitative observations were obtained, whereas in December 1987, 4 years after the 1982–1983 El Niño, the structure of three representative reefs and abundance of corallivorous species were quantified for the first time (Guzman and Cortés 1992). In the 1990s qualitative

observations were obtained in November 1990 (Macintyre et al. 1992), in 1994 (personal observation) and in 1997–1998 (A. Klapfer, personal communication). In September 2002, we quantified the live coral cover and species composition of five reefs (Fig. 1), including the three previously assessed in 1987 (Guzman and Cortés 1992).

During the 1987 survey, the cover of common sessile organisms (e.g., corals, octocorals, sponges, and turf, frondose, or crustose coralline algae) was visually estimated at three sites using three 10-m long linear transects parallel to the coast per depth (total 30 linear *m* at each of 3–6 depths depending on reef profile; *sensu* Loya 1978). Only scleractinian corals were identified to species. In the 2002 study we used a 1 m² PVC quadrat subdivided into 100 grids of 100 cm² (total 30 m² by depth) and took measurements at 3–6 depths at five sites, including the three surveyed in 1987. This allowed identification of every coral species in each grid and the size of individual colonies. We opted to use quadrats in the 2002 study because they allowed a better estimate of recovery and the presence of new recruits in the reefs. Quantitative comparisons of the performance of the two surveyed methods to measure live coral cover have been demonstrated to produce small differences (Dodge et al. 1982).

Corallivorous population density changes between 1987 and 2002

In both 1987 and 2002 we measured the density of corallivorous species (ind ha⁻¹) such as the seastar *A. planci* and the pufferfish *A. meleagris* at each site. We used three 100 m × 20 m wide-band transects for each depth, at 3–6 different depths, depending on the vertical profile of the reef. The density of the bioeroder sea urchin *D. mexicanum* was determined together with the coral cover censuses using the same protocol and 1 m² quadrats.

Parametric *t* tests and one-way and two-way ANOVAs were used in combination with the a posteriori multiple comparison Student–Newman–Keuls test to compare changes in mean coral cover and the density of corallivorous species between 1987 and 2002 among the three reefs sampled on both dates. Whenever necessary, the data were transformed to comply with variance assumptions (normality and homoscedasticity; Sokal and Rohlf 1995). We report our probability values for comparative tests based on the two different methods as non-significant (higher than 0.05), significant (lower than 0.01) and highly significant (lower than 0.001).

Results

Between 1982 and 2002 several sea surface temperature anomalies were registered: warm ($>29^{\circ}\text{C}$) in 1983, 1987, 1993, and 1998, and cold ($<26.5^{\circ}\text{C}$) in 1984, 1985, and 1999 (Fig. 2). The 1982–1983 and the 1997–1998 El Niño events stand out because they sustained temperatures $>29^{\circ}\text{C}$ for 8-month (December 1982–July 1983) and 7-month (December 1997–June 1998) intervals. During these events the maximum temperatures were recorded in April (30.5 and 30.9°C , respectively), and anomalies above 2°C lasted 4 months in 1998, compared with 1 month in 1983.

Changes in live coral cover and other sessile organisms between 1987 and 2002

Overall mean live coral cover increased from $2.99 \pm 0.25\%$ ($\pm\text{SE}$) in 1987 to $14.87 \pm 6.78\%$ in 2002, at the three sites studied during both periods, but the increase was not statistically significant (t test; $t = -1.753$, $P > 0.05$, $df = 4$), possibly because recovery showed a high variance among sites (Table 1). The Punta Pacheco reef (1) was the only one that did not show any evidence of recovery, whereas there was an increase in the mean live coral cover of more than 13% at Chatham Bay and 22% at Punta Presidio. In both cases live cover increased, due mainly to the presence of *P. lobata*, although in Punta Presidio, *P. varians* also had major gains (Table 1). Other coral species, such as *Gardineroseris planulata*, *Pocillopora* spp., and *Psammocora* spp., exhibited minor changes in cover. Numerous colonies of *Leptoseris scabra*, which was not observed in 1987, were found in all three reefs in 2002. The presence of this species was reported for the first time in the mid-1990s (Cortés and Guzman 1998).

In 2002, mean coral cover of all five studied sites was $22.7 \pm 9.8\%$ (Table 1). However, live coral cover was highly different between sites (one-way ANOVA, $F_{4,20} = 43.06$, $P < 0.001$). The reef at Pájara Island (3) was especially noteworthy, with 59% live coral cover consisting of 46% *P. lobata* and $>10\%$ *Pavona* spp., mainly *P. chiriquensis* and *P. varians* (Table 1). The highest percent cover of *L. scabra* was observed on this reef, but was also observed at Punta Presidio. The species *P. chiriquensis* and *Pocillopora inflata* (observed only in the coral community at Wafer Bay, Fig. 1) are reported for the first time for the island (see Guzman and Cortés 1992; Cortés and Guzman 1998); their presence increases the diversity of zooxanthellate scleractinian corals to 19 species, the highest in Costa Rica (Cortés and Jiménez 2003).

Vertical distribution of coral species varied among surveys for all reefs (Fig. 3). *Porites lobata* increased at all depth and reefs, with some loss of live coral cover in Punta Pacheco (No. 1) between 1987 and 2002. *Psammocora* and *Pavona* considerably decreased in Chatham yet increased in Punta Presidio. The rest of the species are distributed below 9 m in most reefs. *Leptoseris* was found at several depths in all sites except Punta Gissler (Fig. 3).

Other important sessile organisms accounted for the rest of the overall mean cover in 2002. Algae (turf and frondose) covered $64.7 \pm 9.1\%$ of the area compared to 89.9% (± 1.83) in 1987 (all three sites above 85%). Encrusting coralline algae covered $5.7 \pm 1.2\%$, and sand or coral fragments covered $6.9 \pm 4.3\%$ in 2002. Other taxa such as octocorals and sponges represented $<0.1\%$ of the total cover. The highest algal cover was observed at Punta Gissler reef (84.6%) and the lowest at Isla Pájara (30.5%). Crustose coralline algae cover was highest at Isla Pájara and varied among the five sites from 9.6 to 3.3%. Sandy substrate covered less

Fig. 2 Monthly mean sea surface temperature variability from January 1982 to December 2002 centered within 1° latitude/longitude, Cocos Island, Costa Rica. Horizontal bars indicate major El Niño events

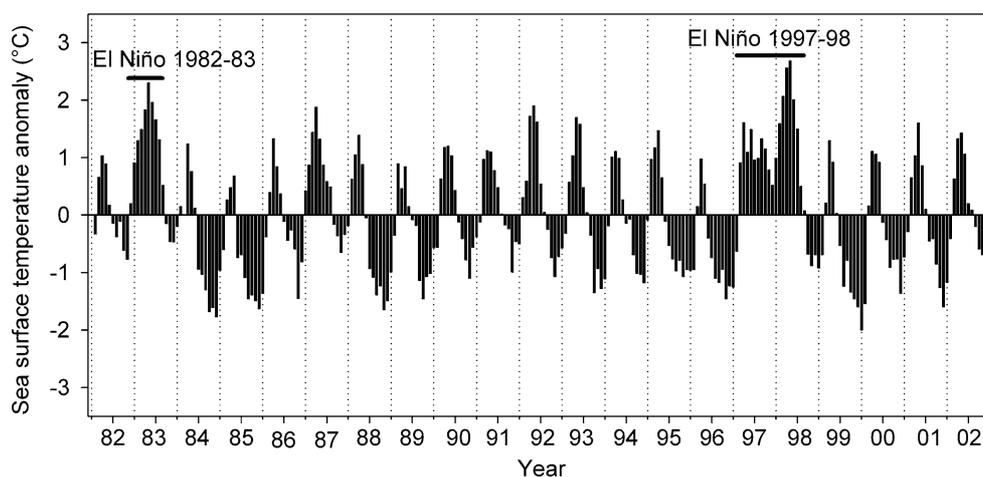


Table 1 Fifteen-year comparisons of mean percent overall live coral cover (\pm SE) and by genera among reef sites studied in 1987 and 2002, Cocos Island, Costa Rica (adapted from Table 2 in Guzman and Cortés 1992)

#-Reef	Depth range	Overall cover		Pocillopora		Porites		Pavona		Psammocora		Gardineroseris		Leptoseris	
		1987	2002	1987	2002	1987	2002	1987	2002	1987	2002	1987	2002	1987	2002
1-Pacheco (1,470–150)	3–18	2.60 (0.20)	2.36 (0.27)	0.04 (0.04)	0.07 (0.04)	2.59 (0.35)	2.11 (0.25)	0.04 (0.02)	0.21 (0.12)	0.12 (0.03)	0.00	0.01 (0.01)	0.00	0.01 (0.01)	0.00
2-Chatham (800–150)	3–18	2.91 (0.42)	16.7 (0.87)	0.03 (0.03)	0.00	1.08 (0.21)	16.1 (0.85)	1.06 (0.09)	0.27 (0.06)	0.74 (0.33)	0.23 (0.05)	0.00	0.00	0.00	0.01 (0.01)
3-Pájara (0–90)	3–18	ND	58.7 (2.61)	ND	0.66 (0.24)	ND	46.4 (2.66)	ND	10.3 ^a (1.16)	ND	0.74 (0.16)	ND	0.24 (0.22)	ND	0.31 (0.17)
4-Presidio (720–150)	9–24	3.47 (0.27)	25.7 (1.11)	0.07 (0.05)	0.10 (0.06)	1.32 (0.42)	12.4 (0.78)	1.15 ^b (0.13)	10.9 ^c (0.76)	0.57 (0.07)	1.34 (0.21)	0.36 (0.08)	0.66 (0.28)	0.00	0.21 (0.10)
5-Gissler (0–90)	3–18	ND	10.0 (0.96)	ND	0.01 (0.01)	ND	9.15 (0.95)	ND	0.49 (0.09)	ND	0.32 (0.08)	ND	0.04 (0.02)	ND	0.00
Grand Mean		2.99 (0.20)	22.7 (9.78)	0.05 (0.00)	0.17 (0.12)	1.57 (0.30)	17.2 (7.6)	0.75 (0.29)	4.40 (2.53)	0.50 (0.12)	0.55 (0.22)	0.12 (0.09)	0.19 (0.12)	0.00	0.11 (0.10)

No data are available for sites 3 and 5 in 1987 (ND). Size of transects are given in parenthesis below each reef name (m for 1987; m2 for 2002). The composition of pavonid coral species on sites with important percent cover is provided:

^a *Pavona chiriquensis* (3.68%), *P. varians* (4.36%), *P. clavus* (2.23%), *P. maldivensis* (0.04%), *P. gigantea* (0.03%)

^b *Pavona varians* (0.87%), *P. gigantea* (0.16%), *P. clavus* (0.12%)

^c *Pavona varians* (9.04%), *P. clavus* (0.87%), *P. chiriquensis* (0.62%), *P. maldivensis* (0.20%), *P. gigantea* (0.19%), *P. frondifera* (0.10%)

than 7% of the area at most sites, but at Punta Pacheco it covered 23% of the area, apparently due to the collapse of the reef framework associated with bioerosion by *Diadema*.

In 1987 observations indicated that reef recovery had been initiated by pioneer species such as *P. varians* (Guzman and Cortés 1992). However, in 2002 we observed a distribution of colony sizes with a high number of individuals smaller than 100 cm², possibly new recruits, in almost all the reefs and basically for all the species found, including the main reef-building species *P. lobata*, though with some exceptions (Fig. 4). More than 3,300 individuals of *P. lobata* and 715 colonies of *P. varians* were found. Some individuals of uncommon species such as *L. scabra*, *G. planulata*, and *Pocillopora eydouxi* reached up to 800 cm² in Punta Presidio (reef 4) and Isla Pájara (reef 3); both reefs are noteworthy because they have the largest colonies for most species. *Pocillopora damicornis*, *Pavona frondifera*, and *Pavona maldivensis* were not included in the analysis because fewer than 15 colonies were found in all the reefs combined, but 50% of the *P. maldivensis* and *P. frondifera* colonies were >800 cm².

Corallivorous population density changes between 1987 and 2002

The density of *A. planci* did not exhibit a significant change between surveys or among reefs (Table 2; two-way ANOVA $F_{1,25} = 0.405$, $P > 0.05$; $F_{2,25} = 2.036$, $P > 0.05$, respectively). Density of *A. meleagris* did increase significantly overall between 1987 and 2002, but the difference among reefs was not significant ($F_{1,26} = 119.29$, $P < 0.001$; $F_{2,26} = 3.381$, $P > 0.05$). This increase may influence negatively coral recovery. However, the densities of *A. meleagris* at Punta Pacheco and Punta Presidio in 2002 were significantly lower than at the other sites (Table 2; one-way ANOVA $F_{4,19} = 11.204$, $P < 0.001$). The density of *A. planci* was always lower in Punta Presidio reef and higher in Punta Pacheco reef (Table 1). The overall average of *D. mexicanum* significantly decreased at all reefs, from 14.5 ind ha⁻¹ in 1987 to 0.84 ind ha⁻¹ in 2002 (Table 2), but was not significantly different among reefs ($F_{1,31} = 78.21$, $P < 0.001$; $F_{2,31} = 3.167$, $P > 0.05$, respectively).

Discussion

The 1997–1998 warming event around Cocos Island was more intense than all previous El Niño events since 1982 (Fig. 2). All the corals at the Cocos Island reefs underwent extensive bleaching during this event

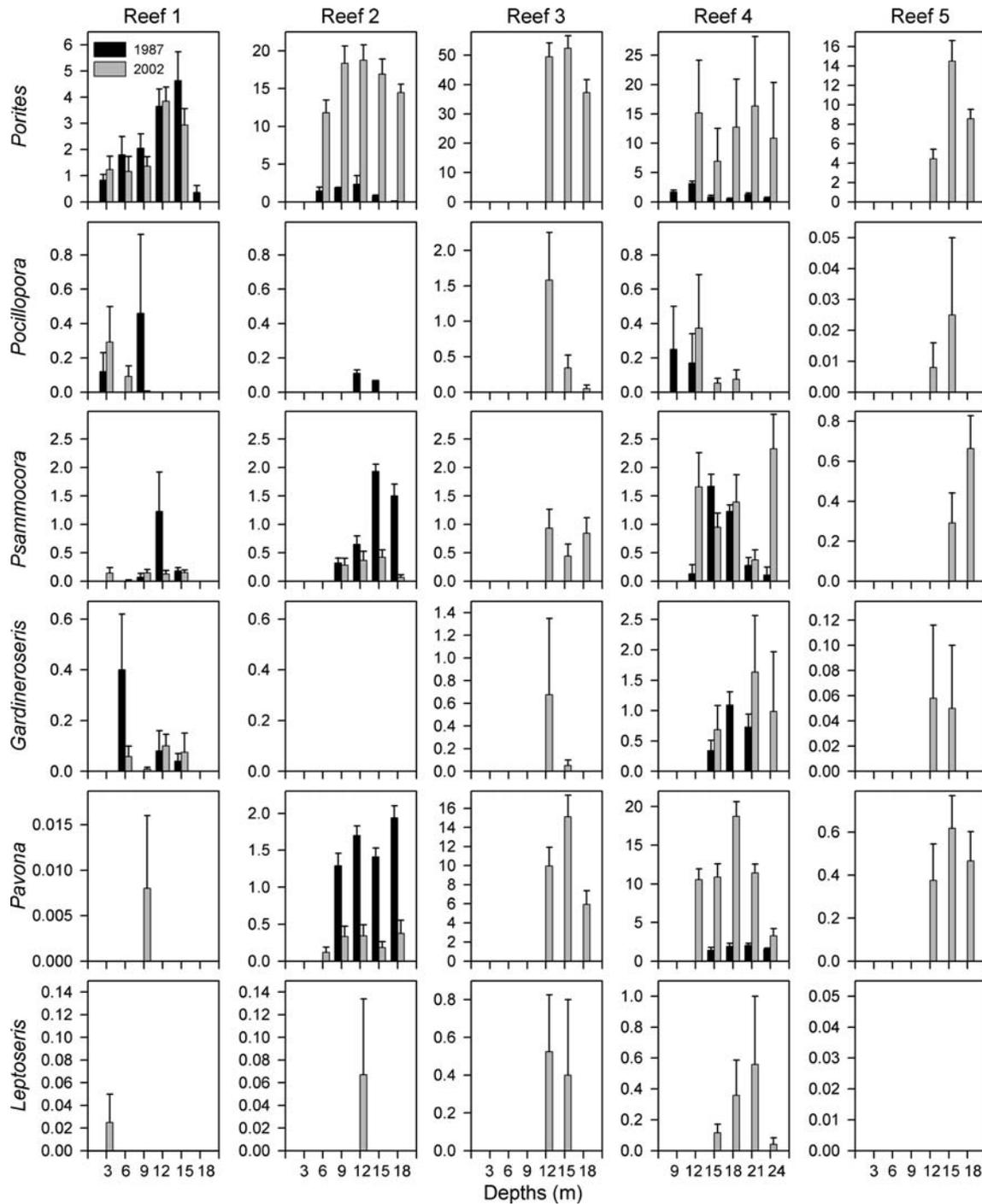


Fig. 3 Comparisons between the live coral cover in 1987 (black bars) and 2002 (white bars). Values are the mean (\pm SE) percent cover for the six most abundant scleractinian species at each of

the five reefs and by depth (m), Cocos Island, Costa Rica. Only reefs 1, 2, and 4 were surveyed in 1987. Note that axis scales are different for each species

(A. Klapper, personal communication 2003; Garrison 2005), suggesting that the thermal sensitivity of Cocos Island corals was similar to that of corals at other areas of Costa Rica (Guzman and Cortés 2001; Jiménez and Cortés 2003). Both El Niño events (1982–1983; 1997–1998) occurred at the same time of year (December–June/July) and maintained warm temperatures

(>29°C) for 7–8 months, but anomalies above 2°C lasted 4 months in 1997–1998 compared to 1 month in 1982–83. However, the coral communities suffered a lower and more selective mortality in 1997–1998, as was also observed in other areas of the eastern Pacific (Glynn et al. 2001; Cortés and Jiménez 2003; Zapata and Vargas-Ángel 2003).

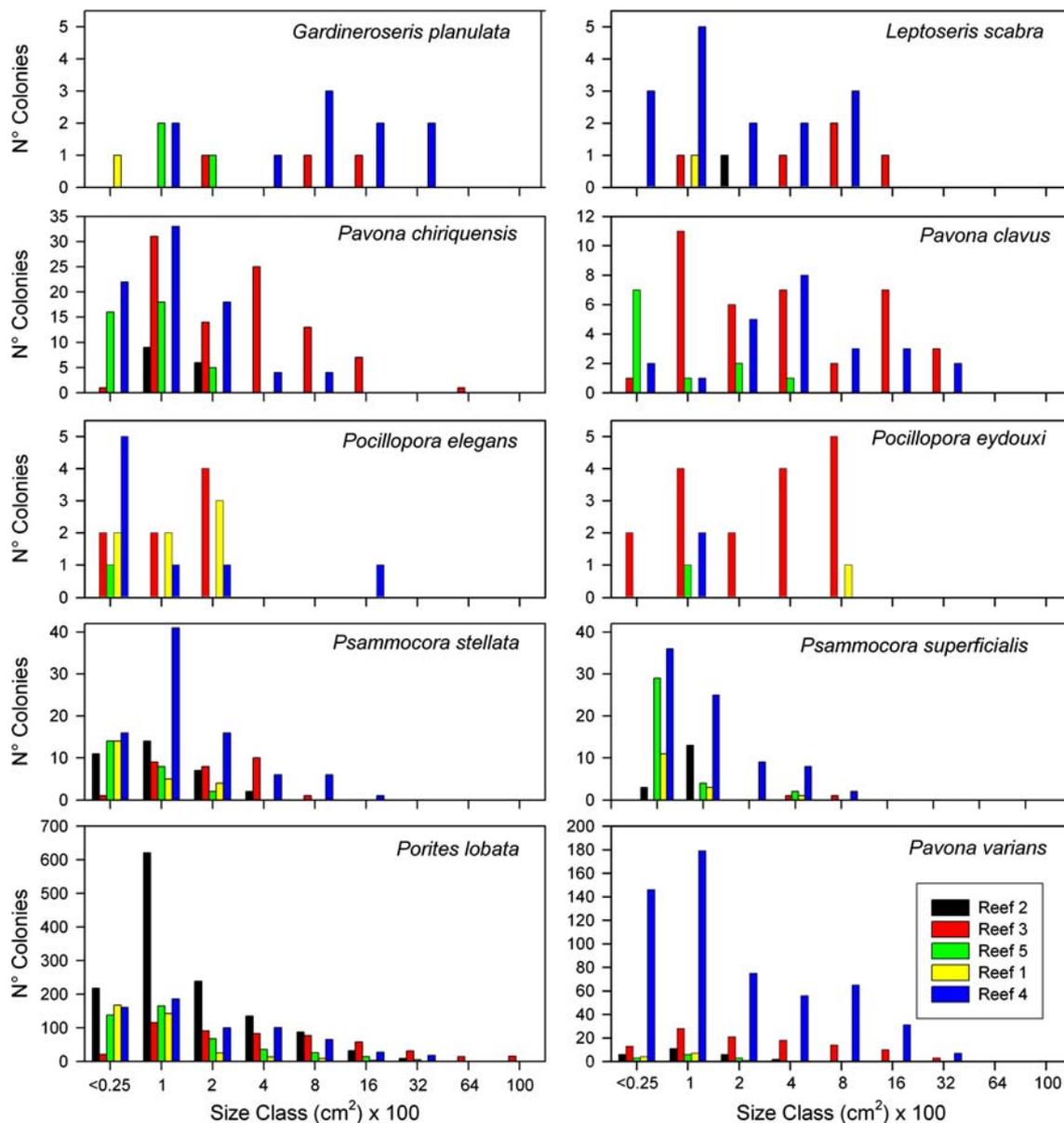


Fig. 4 Size-frequency distribution for the total number of coral colonies at five reefs (number and name provided in *insert*) surveyed in 2002, Cocos Island, Costa Rica. Only species with >15

individuals in all reefs combined are included. Individuals <0.25 cm² include new recruits and juveniles. Note that axis scales are different for each species

Based on the regional observations made in the 1980s, we originally predicted that the recovery of the reefs framework would take centuries, and recovery of live coral cover, decades. Compounding these slow-recovery scenarios was the apparent lack of sexual reproduction by the coral species in the area (Glynn et al. 1991, 1994, 2000). It is now clear from our results that the average live coral cover has increased in only 15 years (1987–2002). Indeed, some reefs, for example Isla Pájara, had very high coral cover in 2002 (59%). Although the coral mortality after 1982–1983 was homogeneous in all the reefs, recovery was not consistently observed across all studied reefs.

In a previous paper (Guzman and Cortés 1992), we presented three hypotheses regarding the recovery of Cocos Island reefs. (1) That reef framework would collapse due to the lack of sexual recruitment and high erosion caused by the sea urchin *D. mexicanum*; (2) that recovery of the reefs and the distribution of species would be closely related to the sexual reproduction of local surviving populations. However, this process of recovery could be significantly impaired by the presence of corallivores; and (3), that recovery would rely mainly on immigration of larvae that have dispersed over long distances.

Our first outcome was a worst-case scenario, in which the reef structure would collapse due to high rates of

Table 2 Population mean (\pm SE) density comparisons of the corallivores *Acanthaster planci* and *Arothron meleagris* (ind ha⁻¹) and of the sea urchin *Diadema mexicanum* (ind m²) at each reef surveyed in 1987 and 2002, Cocos Island, Costa Rica (adapted from Tables 3 and 4 in Guzman and Cortés 1992)

Reef	Depth range	<i>Acanthaster</i>		<i>Arothron</i>		<i>Diadema</i>	
		1987	2002	1987	2002	1987	2002
1-Pacheco	3–18	15.0 (1.4) <i>n</i> = 4	12.5 (4.8) <i>n</i> = 4	7.9 (1.1) <i>n</i> = 5	45.7 (6.1) <i>n</i> = 4	15.5 (0.2) <i>n</i> = 98	1.4 (0.4) <i>n</i> = 150
2-Chatham	3–18	11.7 (4.2) <i>n</i> = 4	10.8 (3.7) <i>n</i> = 6	7.5 (1.6) <i>n</i> = 4	189.2 (14.7) <i>n</i> = 6	16.7 (0.3) <i>n</i> = 80	1.3 (0.2) <i>n</i> = 150
3-Pajara	3–18	ND	0.0 (0.0) <i>n</i> = 3	ND	255.0 (32.5) <i>n</i> = 3	ND	0.3 (0.2) <i>n</i> = 90
4-Presidio	9–24	4.6 (1.7) <i>n</i> = 4	3.7 (1.2) <i>n</i> = 4	9.3 (1.1) <i>n</i> = 4	90.0 (28.6) <i>n</i> = 4	11.4 (0.3) <i>n</i> = 72	0.1 (0.03) <i>n</i> = 150
5-Gissler	3–18	ND	10.0 (0.0) <i>n</i> = 3	ND	183.3 (43.7) <i>n</i> = 3	ND	1.0 (0.3) <i>n</i> = 90
Grand Mean		10.4 (3.1) <i>n</i> = 3	7.4 (2.3) <i>n</i> = 5	8.2 (0.5) <i>n</i> = 3	152.6 (37.5) <i>n</i> = 5	14.5 (1.6) <i>n</i> = 3	0.84 (0.3) <i>n</i> = 5

No data are available for sites 3 and 5 in 1987 (ND). Sample size units (*n*) are number of censuses for corallivores, m² for *Diadema*, and number of reefs for grand mean

bioerosion, observed in some reefs in 1987. By 2002, the reef structure at Punta Pacheco had collapsed and the remaining structure was composed of fragments of massive corals of various sizes and a large amount of empty spaces or pockets with coral sand at all depths. Moreover, in that reef we recorded the lowest percentage (<3%) of live coral cover (Table 1) and the lowest number of recruits (Fig. 4). A reef-tract larger than that at Punta Pacheco and located along Weston Bay (south of Pájara Island, Fig. 1) with a vertical build-up of 3.1 m (Macintyre et al. 1992) showed a similar degree of deterioration, but more coral recruits were observed there. The reef in Chatham Bay, which is at the center of important recreational and commercial activities (e.g., mooring and anchoring for fishing and tourist vessels), presents an intermediate situation, with parts of the upper slope and reef base collapsed but with more live coral (predominantly colonies of *P. lobata* and *P. elegans*) than before. The other reefs studied (Pájara Island, Punta Presidio and Punta Gissler) have not collapsed, illustrating that this outcome, structural collapse, is valid only for some reefs or sections of others. *D. mexicanum* is responsible for the physical destruction of the reefs; their densities were higher in Punta Pacheco and Weston Bay (Table 2), but decreased significantly in all the reefs by 2002. It seems that *Diadema* is not playing a significant role in the erosion of the reef at present (sensu Glynn 1990; Guzman and Cortés 1992). However, at such low densities it probably fulfills the role of key herbivore. This would allow the settlement of opportunistic and encrusting coral species that may help in the initial consolidation of the reef structure, as observed by the recruitment of *P. varians* and *L. scabra*, which are already cementing other reefs.

The second idea we discussed was the possibility of recovery initiated by sexually produced larvae from resident populations or surviving individuals in deeper coral communities. The recorded increases in live coral cover, number of new and middle-sized colonies, and diversity of species in the reefs (not only in rocky areas) for 2002 suggest that recruitment may have started locally for some species that were already relatively abundant in 1987 (e.g., *P. lobata*, *P. varians*), but, likewise, recruits may have come from remote reefs, carried by currents for hundreds or thousands of kilometers. Evidence of this long-distance dispersal process, which was our third and last idea, suggested in 1992, may be the presence of some species of coral that had not been reported before the mid-1990s for Cocos Island, such as *L. scabra*, *P. maldivensis*, *P. frondifera*, *P. chiriquensis*, and *P. inflata*. The last two species have been recently described as endemic to the eastern Pacific; however, a recent report suggested that *P. inflata* is present in the central Pacific at Phoenix Islands (Obura 2002). The others are supposed to be from the Indo-Pacific and are moderately distributed in the region so far, but they are common at present in Cocos Island, except *P. inflata*, which is rare.

Recovery of Cocos Island reefs may have been enhanced by a contribution of larvae of several species from remote sources. In particular, Punta Presidio reef presented signs of recovery by 1987, with numerous *P. varians* recruits; moreover, at present it is also where the largest number of *L. scabra* colonies was observed in 2002. The first record of this conspicuous species in the reefs occurred in the mid-1990s and the nearest populations are thousands of kilometers away. It has been suggested that Cocos Island is on the entrance

route of marine organisms to the eastern Pacific from the western and central Pacific, flowing with the North Equatorial Countercurrent (NECC) (Glynn and Wellington 1983). Moreover, coral larvae may complete this trip in about 100 days or travel as adult colonies adhered to floating debris (Jokiel 1989; Richmond 1990). Recent studies on coral biogeography and existing oceanographic models that explain major patterns of regional currents support this hypothesis (Glynn et al. 1996, 2003; Glynn 1997, 2003; Glynn and Ault 2000; Victor et al. 2001). Although *L. scabra* has a wide distribution in the Indo-Pacific and western and central Pacific, it is rated 'uncommon' in most of those reefs (Veron 2000). For Cocos Island, *L. scabra* may be considered common in almost all reefs, and its presence there and in the rest of the region may be associated with an initial easterly long-distance transport of larvae and afterwards from well-established local populations. However, genetic studies are necessary to elucidate this situation. Likewise, *Pavona chiriquensis* and *P. inflata*, eastern Pacific endemics, may present a wider distribution, as do most species of *Pavona* and *Pocillopora*.

Our data suggest that corallivores have not limited the recovery of the reefs or impaired growth, to the extent that they have in other regions of the eastern Pacific (Guzman and Robertson 1989; Glynn 1990; Reyes-Bonilla 2003). The density of *A. planci* did not vary significantly in Cocos reefs, even though an increase was observed in the number and diversity of their favorite prey (*G. planulata*, *P. varians*). But, *A. planci* may have partially reduced the recovery potential in Punta Pacheco reef, which is the most deteriorated of all and the one that presented the highest density of the seastar in 1987. Likewise, the density of *A. meleagris* increased considerably between 1987 and 2002, but this does not seem to be affecting at present the recruitment or growth of any coral species, including its favorite prey, *P. lobata* (Guzman and Robertson 1989), which in 2002 had the highest number of small and large colonies (Fig. 4).

The partial survival of small patches of coral tissue over the colony may be important for the recovery of massive species (Glynn and Fong 2004). We found evidence of this process in colonies of *P. lobata* that apparently had fully recovered from partial mortality since our first survey in 1987, and where colonies no larger than 36 cm (average 5.3 cm, $n = 194$ colonies) were observed (Guzman and Cortés 1989). Furthermore, several large (>1 m) live colonies drilled in 1994 showed a growth hiatus at 8–12 cm (partial mortality below surface), which corresponds to the 1982–1983 El Niño event based on published growth rates (Guzman and Cortés 1989).

Core data (Macintyre et al. 1992) and direct observations from the early 1970s (Bakus 1975) to the present indicate that Cocos Island reefs have remained dominated by the long-living massive coral *P. lobata*, which suggests that for a few centuries before the El Niño events the reef structure had not been affected. No phase shifts in reef structure occurred, as reported for the Caribbean (Hughes 1994; Aronson et al. 2004). To the contrary, these reefs have the capacity to recover from severe disturbances and to a certain extent to increase their diversity. We conclude that for Cocos Island (Guzman and Cortés 1992) and for most areas of the tropical eastern Pacific (Glynn 1990; Glynn et al. 2001; Guzman et al. 2004) there are recovery processes (e.g., reproduction, larvae dispersion, recruitment) and possibly short-term thermal adaptation, that ensured the recovery of the more degraded reefs.

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References

- Aronson RB, Macintyre IG, Wapnick CM, O'Neill MW (2004) Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* 85:1876–1891
- Bakus GJ (1975) Marine zonation and ecology of Cocos Island, off Central America. *Atoll Res Bull* 179:1–11
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Carriquiry JD, Cupul-Magaña AL, Rodríguez-Zaragoza F, Medina-Rosas P (2001) Coral bleaching and mortality in the Mexican Pacific during the 1997–98 El Niño and prediction from a remote sensing approach. *Bull Mar Sci* 69:237–249
- Colgan MW (1990) El Niño and the history of eastern Pacific reef building. In: Glynn PW (ed) *Global Ecological Consequence of the 1982–83 El Niño-Southern Oscillation*. Elsevier, Amsterdam, pp 183–232
- Connell JH (1973) Population ecology of reef-building corals. In: Jones OA, Endean E (eds) *Biology and geology of coral reefs*, vol 2, Biol. 1. Academic, New York, pp 205–245
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16:101–113
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Cortés J (1997) Biology and geology of coral reefs of the eastern Pacific. *Coral Reefs* 16:S39–S46
- Cortés J, Guzman HM (1998) Organismos de los arrecifes coralinos de Costa Rica: Descripción, distribución geográfica e historia natural de los corales zooxantelados (Anthozoa: Scleractinia) del Pacífico. *Rev Biol Trop* 46:55–91

- Cortés J, Jiménez C (2003) Corals and coral reefs of the Pacific of Costa Rica: history, research and status. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 361–385
- Dodge RE, Logan A, Antonius A (1982) Quantitative ref. assessment studies in Bermuda: a comparison of methods and preliminary results. *Bull Mar Sci* 32:745–760
- Eakin CM (2001) A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bull Mar Sci* 69:171–186
- Enfield DB (2001) Evolution and historical perspective of the 1997–1998 El Niño–Southern Oscillation event. *Bull Mar Sci* 69:7–25
- Fiedler PC (2002) Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Mar Ecol Prog Ser* 244:265–283
- Garrison G (2005) Peces de la Isla del Cocos, 2nd edn. Edit. In-Bio, Heredia, Costa Rica
- Glynn PW (1990) Coral mortality and disturbance to coral reefs in the tropical eastern Pacific. In Glynn PW (ed) *Global Ecological Consequence of the 1982–83 El Niño–Southern Oscillation*. Elsevier, Amsterdam, pp 55–126
- Glynn PW (1997) Eastern Pacific reef coral biogeography and faunal flux: Durham’s dilemma revisited. In: *Proceedings of 8th Int Coral Reef Symp* 1:371–378
- Glynn PW (2003) Coral communities and coral reefs of Ecuador. In: Cortés J (ed) *Latin American coral reefs*. Elsevier, Amsterdam, pp 449–472
- Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19:1–23
- Glynn PW, Fong P (2004) Patterns of reef coral recovery by the regrowth of surviving tissue following the 1997–98 El Niño warming event in Panama, eastern Pacific. *10th Int Coral Reef Symp Okinawa: abstract*, p 134
- Glynn PW, Wellington GM (1983) Corals and coral reefs of the Galápagos Islands. University of California Press, Berkeley
- Glynn PW, Cortés J, Guzman HM, Richmond RH (1988) El Niño (1982–83) associated coral mortality and relationship to sea surface temperature deviations in the tropical eastern Pacific. In: *Proceedings of 6th Int Coral Reef Symp* 3:237–243
- Glynn PW, Gassman NJ, Eakin CM, Cortés J, Smith DB, Guzman HM (1991) Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador), Part I—Pocilloporidae. *Mar Biol* 109:355–368
- Glynn PW, Colley SB, Eakin CM, Smith DB, Cortés J, Gassman NJ, Guzman HM, del Rosario JB, Feingold J (1994) Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador)—II. Poritidae. *Mar Biol* 118:191–208
- Glynn PW, Veron JEN, Wellington GM (1996) Clipperton Atoll (eastern Pacific): oceanography, geomorphology, reef-building coral ecology and biogeography. *Coral Reefs* 15:71–99
- Glynn PW, Colley SB, Ting JH, Maté JL, Guzman HM (2000) Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá and Galápagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona* sp. a. *Mar Biol* 136:785–805
- Glynn PW, Mate JL, Baker AC, Calderón MO (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997–98 El Niño–Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bull Mar Sci* 69:79–109
- Glynn PW, Wellington GM, Wieters EA, Navarrete SA (2003) Reef-building coral communities of Eastern Island (Rapa Nui), Chile. In: Cortés J (ed) *Latin American coral reefs*. Elsevier, Amsterdam, pp 473–494
- Guzman HM, Cortés J (1989) Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). *Bull Mar Sci* 44:1186–1194
- Guzman HM, Cortés J (1992) Cocos Island (Pacific of Costa Rica) coral reefs after the 1982–83 El Niño disturbance. *Rev Biol Trop* 40:309–324
- Guzman HM, Cortés J (1993) Los arrecifes coralinos del Pacífico Oriental Ecuatorial: Revisión y perspectivas. *Rev Biol Trop* 41:535–557
- Guzman HM, Cortés J (2001) Changes in reef community structure after fifteen years of natural disturbances in the eastern Pacific (Costa Rica). *Bull Mar Sci* 69:133–149
- Guzman HM, Robertson DR (1989) Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Mar Ecol Prog Ser* 55:121–131
- Guzman HM, Guevara CA, Breedy O (2004) Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island). *Environ Conserv* 31:111–122
- Harriott VJ (1985) Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reefs. In: *Proceedings of 5th Int Coral Reef Congr* 4:367–372
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2264
- Jiménez CE, Cortés J (2003) Coral cover change associated to El Niño, eastern Pacific, Costa Rica, 1992–2001. *PSZN Mar Ecol* 24:179–192
- Jokiel PL (1989) Rafting of reef corals and other organism at Kwajalein Atoll. *Mar Biol* 101:483–493
- Lessios HA, Kessing BD, Wellington GM, Graybeal A (1996) Indo-Pacific echinoids in the tropical eastern Pacific. *Coral Reefs* 15:133–142
- Loya Y (1978) Plotless and transect methods. In: Stoddart DR, Johannes RE (eds) *Coral reefs: research methods, monographs on oceanographic methodology*, vol 5. UNESCO, Paris, pp 197–217
- Macintyre IG, Glynn PW, Cortés J (1992) Holocene reef history in the eastern Pacific: mainland Costa Rica, Caño Island, Cocos Island, and Galapagos Islands. In: *Proceedings of 7th Int Coral Reef Symp* 2:1174–1184
- McPhaden MJ (1999) Genesis and evolution of the 1997–98 El Niño. *Science* 283:950–954
- Nyström M, Folke C (2001) Spatial resilience of coral reefs. *Ecosystems* 4:406–417
- Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Obura D (2002) Coral species diversity. In: Obura D, Stine GS (eds) *Phoenix Island: summary of marine and terrestrial assessment*. New England Aquarium, Massachusetts, pp 10–12
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) Are US coral reefs on the slippery slope to slime? *Science* 307:1725–1726
- Pearson RG (1981) Recovery and recolonization of coral reefs. *Mar Ecol Prog Ser* 4:105–122

- Reyes-Bonilla H (2003) Coral reefs of the Pacific Mexico. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 331–349
- Reynolds KW, Smith TM (1994) Improved global sea surface temperature analyses. *J Clim* 7:929–948
- Richmond RH (1990) The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. In: Glynn PW (ed) Global Ecological Consequence of the 1982–83 El Niño-Southern Oscillation. Elsevier, Amsterdam, pp 127–140
- Scheltema RS (1986) Long-distance dispersal by planktonic larvae of shoalwater benthic invertebrates among central Pacific islands. *Bull Mar Sci* 39:241–256
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. WH Freeman, New York
- Timmermann A, Oberhuber J, Bascher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–697
- Tudhope AW, Chilcot CP, McCulloch MT, Cook ER, Chappell J, Ellam RM, Lea DW, Lough JM, Shimmield GB (2001) Variability in the El Niño-Southern Oscillation through a glacial–interglacial cycle. *Science* 291:1511–1517
- Veron JEN (2000) *Corals of the World*, vol 2. Australian Institute of Marine Science, CRR, Queensland
- Victor BC, Wellington GM, Robertson DR, Ruttenberg BI (2001) The effect of the El Niño-Southern Oscillation event on the distribution of reef-associated labrid fishes in the eastern Pacific Ocean. *Bull Mar Sci* 69:279–288
- West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv Biol* 17:956–967
- Wilkinson C (2004) *Status of coral reefs of the World: 2004 Summary*. Australian Institute of Marine Sciences, Townsville
- Zapata FA, Vargas-Ángel B (2003) Corals and coral reefs of the Pacific coast of Colombia. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 419–447