

## A TALE OF TWO ENSO EVENTS: CARBONATE BUDGETS AND THE INFLUENCE OF TWO WARMING DISTURBANCES AND INTERVENING VARIABILITY, UVA ISLAND, PANAMA

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### ABSTRACT

Numerous changes have occurred at the Uva Island reef since the original calcium carbonate budget model was published (Eakin, 1996). Minor bleaching events occurred during the 1990s and a widespread event occurred in 1997–98. In 1989 and 1993, reef flat exposures bleached and killed corals that had recruited to the reef flat. Since 1983 erosion by sea urchins and infauna have eliminated much of the structure that previously existed in the seaward reef base. Earlier work reported that the reef was largely depositional before 1983 (8600 kg CaCO<sub>3</sub> yr<sup>-1</sup> net), and highly erosional in the early 1990s (–4800 kg CaCO<sub>3</sub> yr<sup>-1</sup> net). New data related to post-1983 disturbances are presented and incorporated into the calcium carbonate model. Modeling suggests that the reef has remained erosional, varying from around –3000 to –18,000 kg CaCO<sub>3</sub> yr<sup>-1</sup> net. The reef budget varies substantially with changes in community composition, topographic complexity and echinoid density. La Niña-driven low tidal exposures had more influence on the budget than the 1997–98 El Niño. As the carbonate framework in the reef base eroded, sea urchin density declined and corals began to recover. Climate factors, mediated by biological processes, continue to influence the course of the Uva Island reef ecosystem and its physical structure.

Large-scale changes in ocean circulation related to the El Niño–Southern Oscillation (ENSO) have caused major disruptions to coral reef systems. This was first documented when the extremely strong 1982–83 El Niño caused dramatic bleaching of reefs in the eastern Pacific (Glynn, 1984, 1988a). Coral mortalities in 1983 ranged from 50% in Costa Rica to 97% in the Galápagos Islands (Glynn, 1990). This was the first of several major bleaching events around the world, most recently evidenced by the widespread bleaching during the 1997–98 El Niño (Wilkinson, 1998, 2000).

Bleaching due to excessively warm ocean temperatures has been the most commonly reported phenomenon in corals related to climate stress. Changes in ocean temperature, typically warming, leads to an expulsion of zooxanthellae, leaving the coral pale, or ‘bleached’. Milder stress can cause bleaching after which corals recover their zooxanthellae. More severe stress often results in death of coral tissues. Other forms of stress also cause bleaching and death of coral tissues. Both extremes of the ENSO cycle cause basin-scale changes in sea level height. Just as westerly winds during El Niño force surface waters into the eastern Pacific, strong easterlies during La Niña events push surface waters west in the basin. Spring low tides, magnified by strong easterly winds during La Niña events in 1989 and 1993, exposed much of the reef flat at least four times over 2 d during each event, resulting in high coral mortalities (Eakin et al., 1989; Eakin and Glynn, 1996). There have been many reports on bleaching events, but few have tracked the long-term influence of these events on affected reefs. Only by following changes in the reef for many years is it possible to fully understand the far-reaching influence that climate variability can have on coral reef ecosystems.

Changes in reef community structure significantly influence the calcium carbonate budget. Because reefs are primarily made of calcium carbonate, understanding this bud-

get is critical to understanding the long-term effect of stress on the entire reef system. After 1983, Glynn (1988b) found that many areas of the Uva reef were undergoing net erosion. Eakin (1996) refined the estimates of calcium carbonate deposition and erosion on the Uva reef, included a wider range of sources and sinks and quantified the importance of the damselfish/algal lawn symbiosis (Eakin, 1996). That study used a simple box model of the fluxes of organically derived  $\text{CaCO}_3$  on the Uva Island reef, based on pioneering carbonate budgets produced for reefs in the Caribbean (Land, 1979; Scoffin et al., 1980; Hubbard, 1990).

Eakin (1996) reported the profound influence that El Niño related bleaching and coral mortality, subsequent increases in bioerosion and other ecological processes had on the carbonate budget of a reef at Uva Island, Panama. The combination of 75% coral mortality and a nearly ten-fold increase in *Diadema mexicanum* density (Glynn, 1990) dramatically reduced the net retention of calcium carbonate within the reef structure. The model accounted for production by corals and coralline algae, erosion by *Diadema*, infauna, fishes and other motile organisms, and the retention of sediments as a function of size. That work used a simple box model to demonstrate how the effects of the 1982–83 El Niño shifted the carbonate budget of the 2.5 ha reef from a net deposition of 8600 kg  $\text{CaCO}_3 \text{ yr}^{-1}$  before 1982 to net erosion of  $-4800 \text{ kg CaCO}_3 \text{ yr}^{-1}$  after the event. Those budget values were based on the best values for community parameters available for different periods from before and after the El Niño. Subsequent monitoring has provided information sufficient to track changes in the carbonate budget through time. This paper considers the impact of the more recent 1997–98 El Niño on the carbonate budget of the Uva Reef and compares this effect to other disturbances and changes on the reef in the intervening 15 yrs.

#### METHODS

Work was conducted from January 1986 to February 1995 on a reef in the northern cove at Uva Island (07°49'N, 81°46'W), in the Gulf of Chiriquí off the Pacific coast of Panama (Fig. 1). This shallow reef (<6 m MLW; approximately 4 m tidal range) is located within a semi-protected bay. Detailed descriptions of the reef and the impacts of the 1982–83 El Niño and post-mortality events have been reported elsewhere (Glynn, 1976, 1984, 1985, 1988a, 1990; Eakin et al., 1989; Eakin, 1992, 1996; Eakin and Glynn, 1996). Statistical analyses used include methods from Sokal and Rohlf (1981), Zar (1984) and the Statistica™ (1997) microcomputer statistical package.

The 25,308 m<sup>2</sup> Uva reef can be divided into 4 main zones: the leeward back reef slope, the reef flat, the seaward fore reef slope and the seaward reef base (Fig. 2). The back reef slope (200 m<sup>2</sup>), which contains a mixture of live and dead *Pocillopora* spp. (primarily *P. damicornis* and *P. elegans*, 24–55% live coral), drops steeply to the silty floor of the leeward lagoon. The reef flat (13,655 m<sup>2</sup>) consists mostly of dead pocilloporid framework and coral gravel overgrown with crustose coralline algae. Live coral here was around 20% in 1974 (Glynn, 1976) but dropped to less than 3% in 2000. Losses were primarily due to occasional low tidal exposure (Glynn, 1976; Eakin and Glynn, 1996) and 1982–83 El Niño related mortalities. The energy of waves and tidal currents over the reef flat keeps it clear of sediment. The fore reef slope (9491 m<sup>2</sup>) is a mix of live *Pocillopora* spp. (47–67% between 1974 and 2000) with occasional massive colonies, and many regions of dead pocilloporid framework. The seaward reef base (1962 m<sup>2</sup>) contained moderate cover of *Pocillopora* before 1983 (10–25% between 1974 and 1983; Glynn, 1990). For approximately 15 yrs after the 1982–83 El Niño losses (Glynn, 1984), this zone was characterized by dead pocilloporid framework coated with thick coralline algal crusts and less than 2% live coral cover. *D. mexicanum* were extremely conspicuous from the mid-1980s to the mid-1990s, with densities sometimes

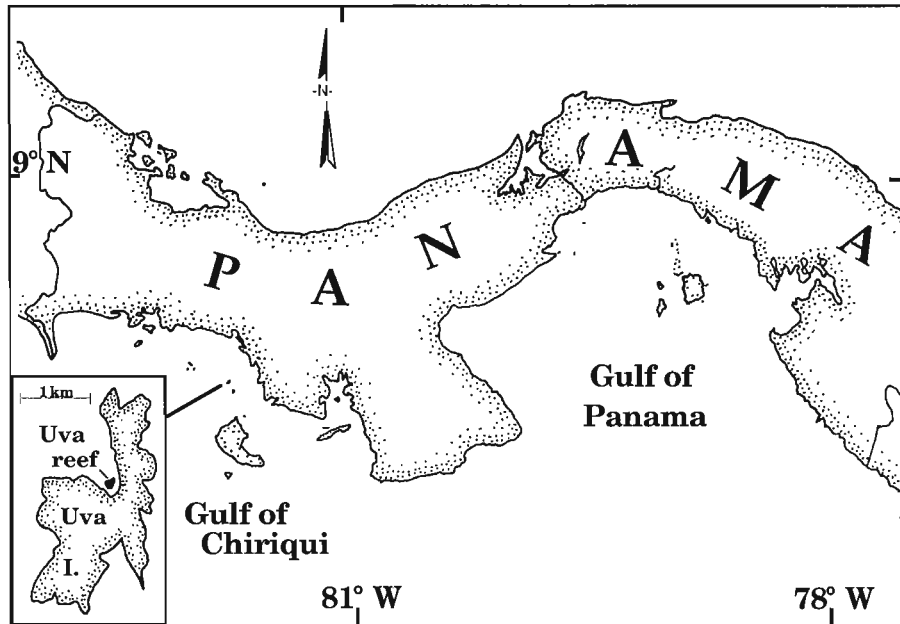


Figure 1. Map of Panama, indicating location of Uva Island study site (from Eakin, 1996).

exceeding  $100 \text{ ind m}^{-2}$ . Seaward of this zone, the reef margin tapers into a detrital plain, followed by a talus slope that descends to the outer cove.

Data on reef community composition were collected by the author, P. W. Glynn, and co-workers, using similar, but non-identical techniques as part of multiple experiments and monitoring efforts from the 1970s through 2000. Most data used in this paper came from the random walk surveys performed on multiple occasions from 1988–2000. Random walk surveys assessed the percent cover of major community constituents in the four major zones: live *Pocillopora*, dead framework with coralline algae, other live corals, damselfish lawns, *D. mexicanum* density and other benthic cover. Throughout this paper, *Pocillopora* spp. is used to define live coral cover, as all non-pocilloporid corals covered only 0.6% of the bottom in earlier studies (Eakin, 1996). Each survey was performed using a  $1 \text{ m}^2$  quadrat divided into 100 sections that was placed on the bottom using a ‘random walk’ pattern for a total of 20  $1\text{-m}^2$  samples (Eakin, 1996). Two standard, randomized patterns were determined prior to initial sampling. One pattern was followed for all surveys except at the back reef where the second pattern was used to accommodate the narrow, ribbon-like shape of this zone. The patterns consisted of quadrat movements over a randomly determined distance (1–5 m) in a randomly determined direction (north, east, south or west) from point to point. The starting point for each survey was determined arbitrarily before the initial survey and used for each subsequent survey. As only the starting point was marked, repeated surveys followed similar, but non-identical, paths through a section of each reef zone. Percent cover within each quadrat was determined by counting the number of 1% grids containing each bottom type.

In 1993, three fixed plots were established to test the anticipated effects of the impending low tidal exposure of the reef flat. This monitoring of the reef flat used 40 contiguous  $1 \text{ m}^2$  quadrats that formed  $40 \times 0.8 \text{ m}$  belts around the perimeter of a  $10 \times 10 \text{ m}$  plot during six surveys from 1993–2000. The point intercept method (Kinzie and Snider, 1978) was used to determine the species of coral or other cover at each of 81 points formed by the intersection of lines spaced at 10 cm intervals. The data between these fixed surveys were compared with those from the simultaneous random walk surveys of the reef flat before they were combined for use in the model analysis.

# Uva Island Coral Reef

(February 1989)

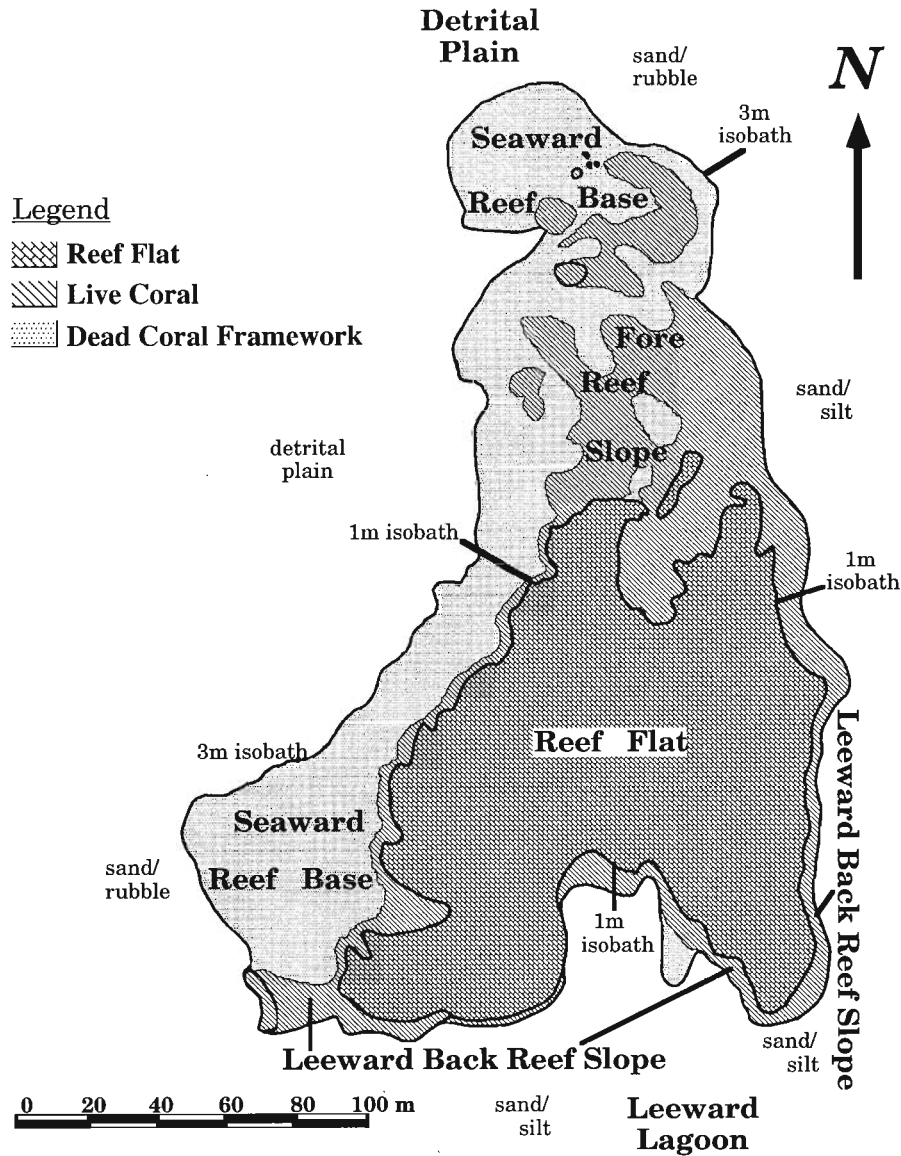


Figure 2. Map of the Uva reef detailing substratum types and major zones (from Eakin, 1996).

The 1985 data were collected by P. W. Glynn using a  $20 \times 0.5$  m belt consisting of 40 contiguous  $0.5 \times 0.5$  m quadrats in each reef zone (Glynn, 1990 and pers. comm.), and the 1974 data using chain transects in each reef zone (Glynn, 1976). Data from 1974 are used to represent pre-1983 conditions. This was the only year before 1983 that contained a complete set of simultaneous community data from across the reef. *D. mexicanum* density data estimated from photographs of the reef base during the period of 1975–1977 showed that *D. mexicanum* densities were relatively

stable. Means ranged from approximately 1.5–5 ind m<sup>-2</sup> throughout, while regular, qualitative observations revealed no major changes until 1984–85 when survey values exceeded 50 ind m<sup>-2</sup> (Glynn, 1988b, 1990). Similarly, Glynn performed chain transects of coral cover in the reef base zone regularly starting in 1974 (Glynn, 1976). He reported that live coral cover in those transects was relatively stable from the mid-1970s until the dramatic decline in conjunction with the 1982–83 El Niño. Means ranged from approximately 10–25% during 1974–early 1983, dropping to <2% during 1983 (Glynn, 1984, 1990). The declines in live coral cover, extirpation and near-extinction of coral species during 1983 were unprecedented in the previous decade. While data from the early 1980s would have been preferred, Glynn's data on *D. mexicanum* and coral cover from the reef base indicate that 1974 data provide a reasonable representation of pre-1983 conditions.

Topographic complexity (i.e., three-dimensional structure) was determined by draping a brass chain along the bottom under each of two lines bisecting the quadrat (Eakin, 1996). Values were calculated using the equation:

$$TC = 1 - \frac{(1/x + 1/y)}{2}$$

and range from 0 (flat) to asymptotically approaching 1.0. A value of 0.5 indicates a surface with surface length equal to twice its planar projection (2 m chain under 1 m quadrat). On surveys where topographic complexity was measured, it was consistently measured on the first 10 of the 1 m<sup>2</sup> quadrats, except for the back reef survey where it was measured on the first five 1 m<sup>2</sup> quadrats of each of two 10 quadrat series. Topographic complexity was used to adjust CaCO<sub>3</sub> production rates by crustose coralline algae from values calculated for planar samples to values approximating the production on irregular natural surfaces (Eakin, 1996).

The model used here was described in Eakin (1996). It used data on community composition (live *Pocillopora* spp., crustose coralline and filamentous algal cover) by zone, topographic complexity, reef zone areas, bioerosion rates and bioeroder densities, and sedimentological and hydrodynamic processes. These are used to account for production by corals (represented by *Pocillopora* spp.) and coralline algae, erosion by *D. mexicanum*, infauna, fishes and other motile organisms, and the retention of sediments as a function of size. The open-system, solid-phase calcium carbonate model consisted of bins for (1) the sources of CaCO<sub>3</sub> produced on the reef by *Pocillopora* spp. and crustose coralline algae, (2) losses due to bioerosion by echinoids and infauna, and (3) retention of sediments produced through bioerosion. The major sources, losses and retention of calcium carbonate, adjusted to kg m<sup>-2</sup> yr<sup>-1</sup>, were calculated for each zone. These were measured using both individual-based carbonate production and erosion, and measurements of reef construction and erosion on experimental carbonate samples over time. Where production, erosion or sediment retention varied among substrata, the percent cover of each was used to estimate these rates. The model also was analyzed to determine the budget's sensitivity to variations in parameter estimates. Other sources of CaCO<sub>3</sub> and bioerosion were considered insignificant in this system based on sensitivity analysis (Eakin, 1996). Sediment retention was modeled based on comparisons of the hydrodynamic size of sediments created through *D. mexicanum*, fishes and infaunal erosion against sediments analyzed from each reef zone. Based on assumptions of eroder behavior, water movement and particle sizes, this component of the model created proportions of the eroded CaCO<sub>3</sub> that would be retained in the framework and the proportion that would be lost. This was computed for each zone based on eroder densities and community composition (Eakin, 1996).

New modeling for this paper assumed that reef areas, individual rates of calcium carbonate production and erosion, sediment size distributions and sediment retention parameters used in the earlier work (Eakin, 1996) remained valid. Only data on reef community composition were changed in the current modeling effort. In particular, these were the five variables: percent cover by live *Pocillopora* spp., damselfish lawns and dead coral framework/crustose coralline algae, densities of *D. mexicanum* and topographic complexity index. Of these, % cover of *Pocillopora* spp., *D.*

*mexicanum* density and topographic complexity are presented here. The influence of damselfish, variations in their populations and their relationship with *D. mexicanum*, considered in earlier works (Eakin, 1988, 1992, 1996), were not considered in this study beyond the damselfish lawn cover measured in community surveys. Changes in damselfish lawn cover were insignificant to variations in model budget and are not presented here. The term balance as used to refer to the result of the model refers to the net  $\text{CaCO}_3$  change in the reef system when comparing production, erosion and retention. It can be positive if the reef is growing (producing and depositing more  $\text{CaCO}_3$  than it loses through erosion and export), or negative if the reef is eroding.

## RESULTS

*Pocillopora* spp. cover varied greatly through time at the Uva I. reef (Fig. 3A). The major patterns were the El Niño related mortalities in 1983 and the La Niña related mortalities on the reef flat in 1989 and 1993. Unfortunately, the lack of comparable survey data in 1998 makes the drop in 1989 less apparent. However, two random walk surveys in February 1989 revealed considerable numbers of newly dead colonies on the reef flat (11 Feb. 1989:  $5.6 \pm 1.9\%$  and 19 Feb. 1989:  $7.0 \pm 2.1\%$ ) indicating the impact of the exposure. Reef flat coral declines after the 1993 survey (pre-exposure) were captured in the random walk surveys (Fig. 3A) and in the fixed plots (Fig. 4).

*Pocillopora* spp. cover was not affected greatly by the 1997–98 bleaching. Most corals that bleached in March 1998 still contained substantial amounts of zooxanthellae, especially on their lower surfaces (Fig. 5). The only decline seen after the 1997–98 partial bleaching was in the back reef. However, that decline was small relative to the variability in back reef data, and little bleaching was seen there in 1998.

Coral cover in the back reef varied substantially, both within and among surveys. This zone is very narrow and changes from shallow reef flat to the mud bottom in less than 4 m horizontal distance. During the 1989 and 1993 La Niña-related reef exposures, corals at the upper edge of this zone were killed by the low tidal exposures. The 1989 exposure did not reduce coral cover and the 1993 exposure only extended an already apparent decline (Fig. 3A). Corals in this zone frequently topple and tumble to the mud due to the unstable nature of the substrate. The reason for the peak around 1990 is unknown. However, changes in this zone have little influence in the model as the back reef represents less than 1% of the reef area. After the 1983 El Niño-related mortality, *Pocillopora* spp. cover in the seaward reef base remained low until steady recovery began in the mid-1990s. The highest *Pocillopora* spp. cover was consistently found in the fore reef, although the structurally diverse nature of this zone provides a mosaic of live coral and dead framework. This resulted in moderate variability. In the reef flat, major coral bleaching and mortality due to the exposure in 1989 reduced cover, which showed strong recovery until the next exposure in 1993. Recovery in the reef flat began again in the late 1990s after the 1997–98 El Niño. Data from fixed surveys of the reef flat before and after the low tidal exposure in 1993 (Fig. 4) revealed the dramatic drop in *Pocillopora* spp. cover. The patterns and variability from the fixed surveys mirrored the results from the random walk surveys (Fig. 3A).

*D. mexicanum* densities, high in the reef base and fore reef following the 1982–83 ENSO (Fig. 3B), continued at these levels until the mid-1990s when they began to decline to near 1974 levels in 2000. Densities were so low in 2000 that only 85 *D. mexicanum* could be found in the entire reef base zone. Sea urchin densities were consistently low in both the reef flat and back reef zones over the entire period. Relationships between *D.*

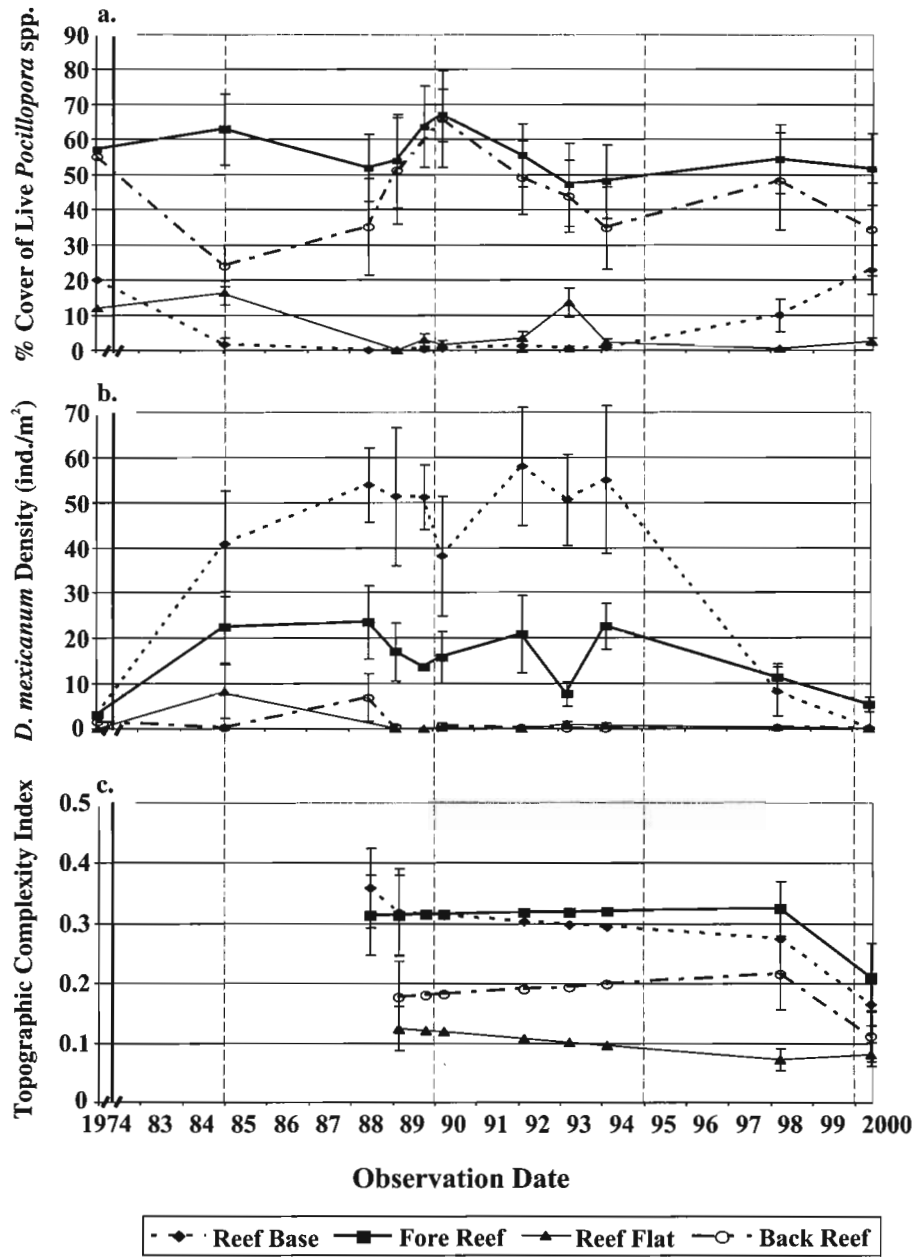


Figure 3. Community composition of the Uva Island reef by zone. Data are from a variety of survey methods as described in text, typically expressed as mean  $\pm 95\%$  confidence intervals. January 1974 data are from Glynn (1976) and are means only. Note break in x-axis between 1974 and 1983 data and significant ENSO related events in 1983, 1989, 1993 and 1998. 1989 data were taken following low-tidal exposure; 1993 data were taken before low-tidal exposure. a) Percent cover of live *Pocillopora* spp. b) *Diadema mexicanum* density. c) Topographic complexity. Points expressed without error between 1989 and 1998 are interpolated.

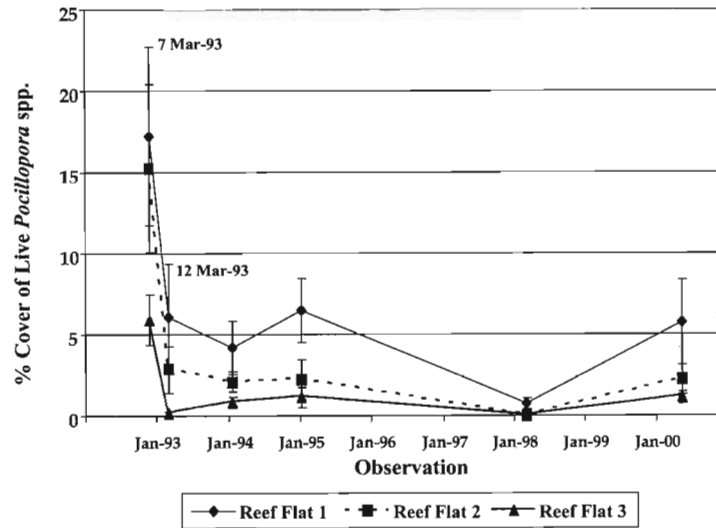


Figure 4. Percent cover of live *Pocillopora* spp. from fixed reef flat surveys. Data are mean  $\pm$ 95% confidence intervals. Data from 7 March 1993 are offset to the left by one month to separate 7 March and 12 March data, allowing the reader to see declines at the time of the 9 March 1993 low-tidal exposure.

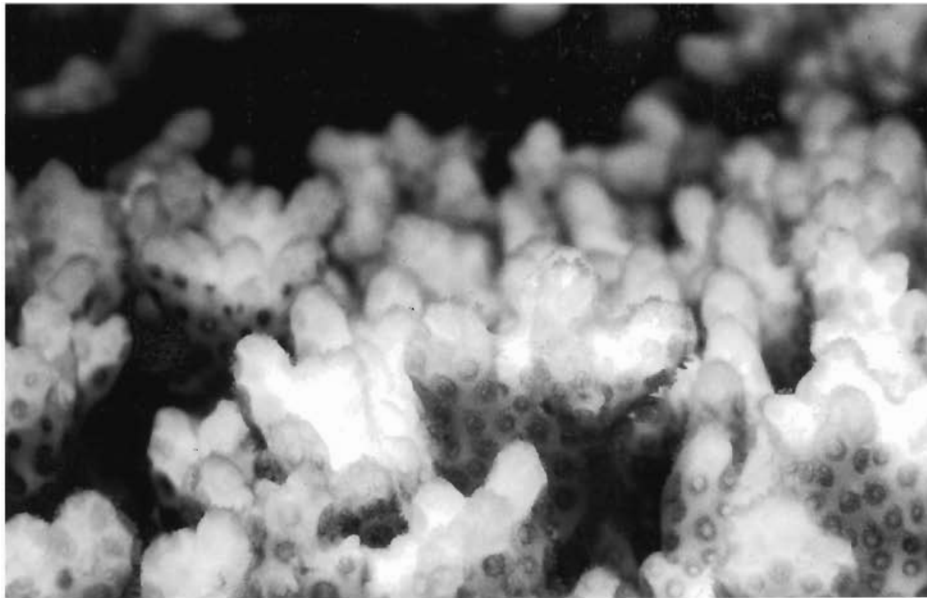


Figure 5. Photograph of *Pocillopora damicornis* exhibiting partial bleaching in March 1998. Note the upper surface appears totally bleached while the lower surface still contains visible coloration from photosynthetic pigments in the zooxanthellae. Photo by author.



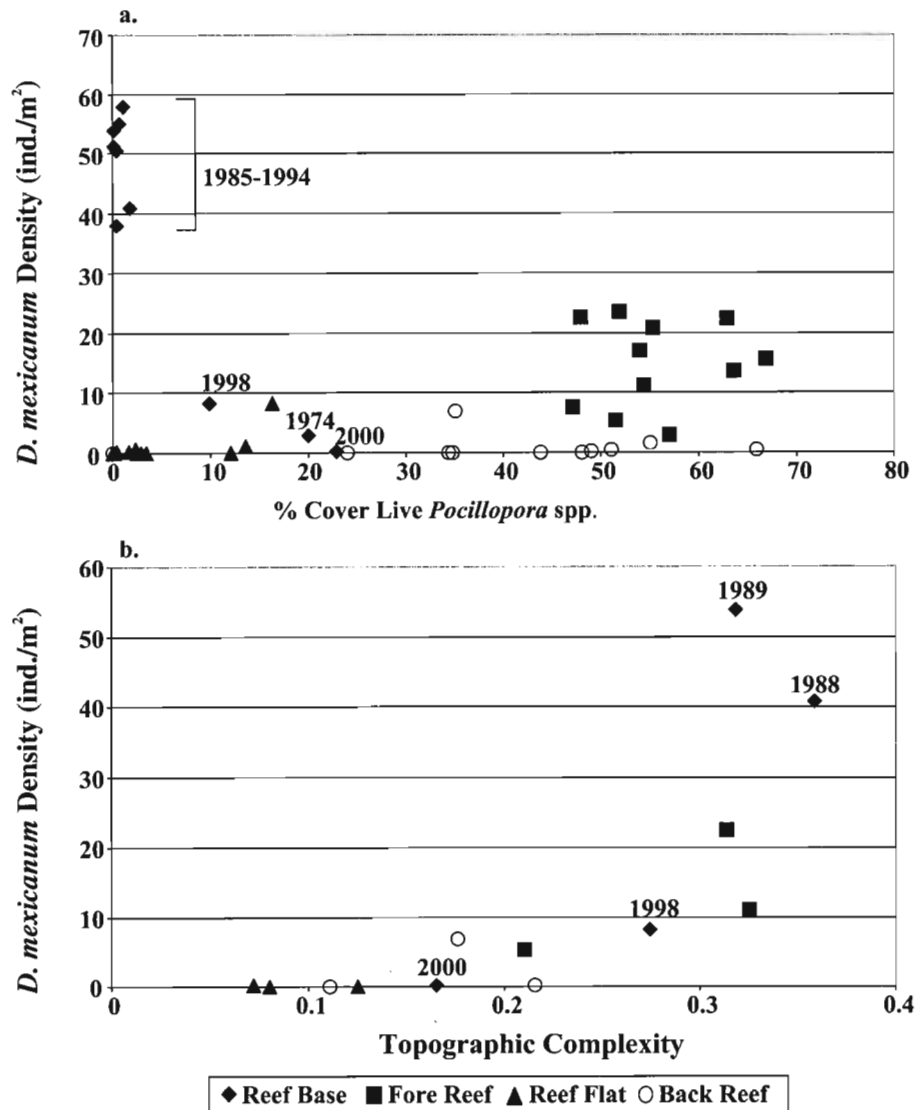


Figure 6. Scatter plot comparing the density of *Diadema mexicanum* with (a) live *Pocillopora* spp. cover and (b) topographic complexity.

*mexicanum* densities and both live *Pocillopora* cover and topographic complexity are shown in Figure 6. Cluster analysis was performed comparing data on *D. mexicanum* density and *Pocillopora* spp. cover. The reef base data from 1985–1994 represent a unique high *Diadema* per low coral cluster within the data set (Single linkage Euclidean separation distance of 31.5, Statistica, 1997), with reef base data from 1974, 1998 and 2000 strongly separated from 1985–1994 data (Fig. 6A). Coral cover in the reef base was much higher before the 1983 ENSO-related bleaching, and by 1998 showed signs of recovery. This follows a pattern that is the inverse of the sea urchin density. Correlation analysis of the reef base data showed that *D. mexicanum* density was highly negatively correlated

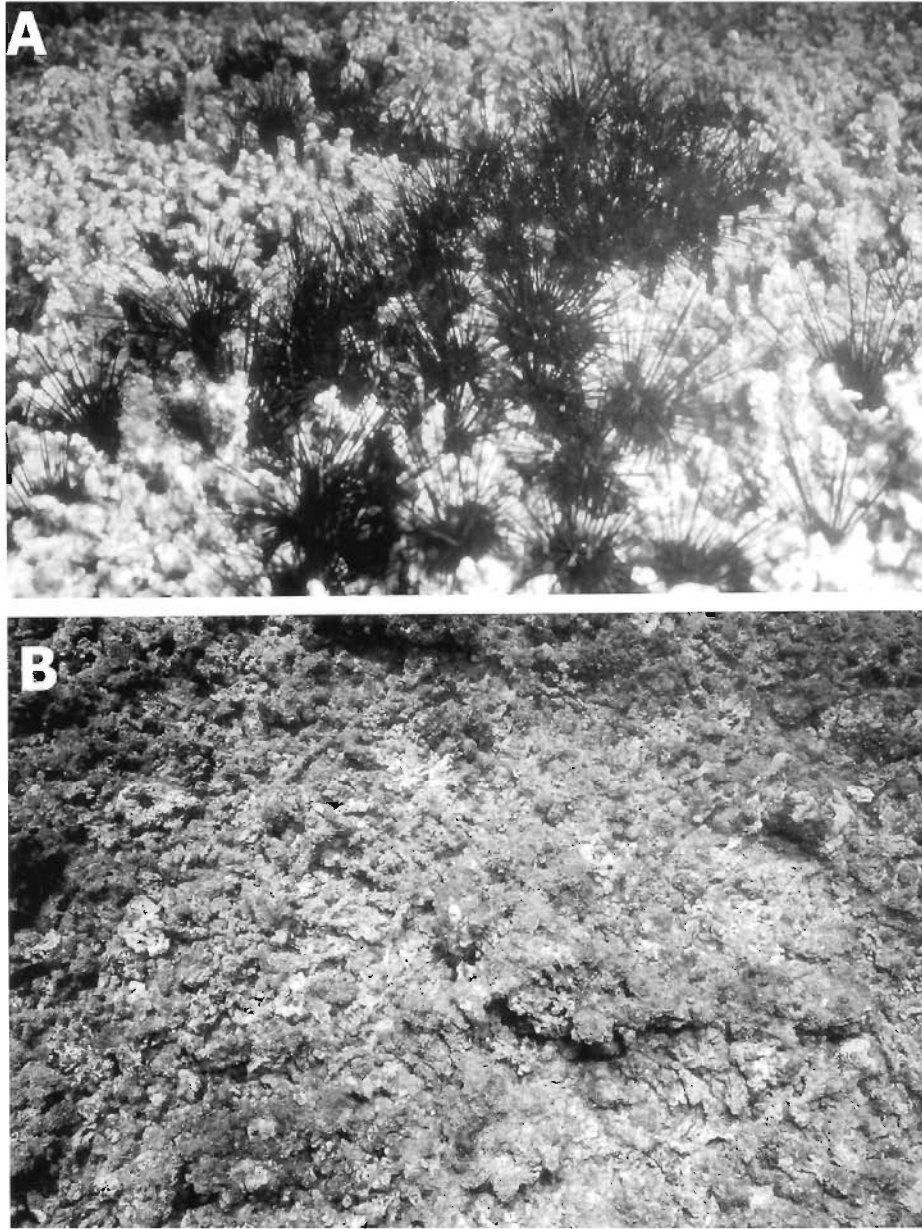


Figure 7. Photographs of the reef base 'lunar area' in (a) mid-1980s and (b) 2001. Each photograph is typical of the appearance of the same part of the reef and shows the change over time. (a) High topographic complexity due to dead pocilloporid framework covered by crustose coralline algae, with high densities of *Diadema mexicanum* (photo by P. W. Glynn). (b) Highly eroded surface with greatly reduced complexity and extremely low densities of *D. mexicanum* (photo by J. L. Maté).

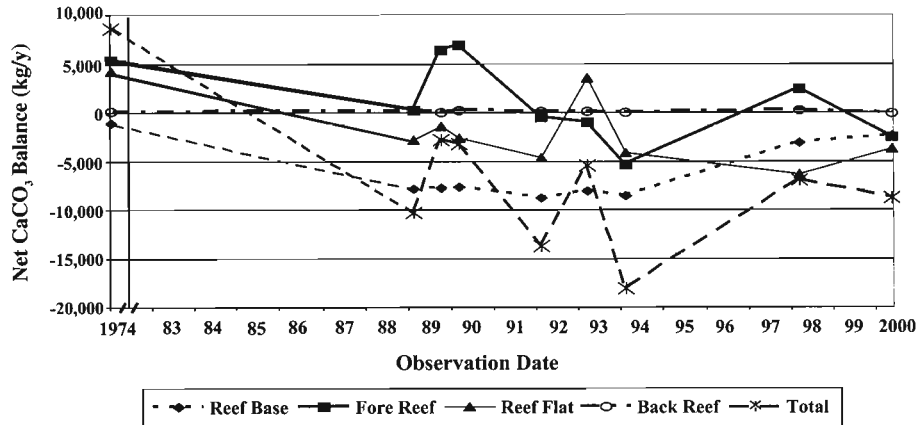


Figure 8. Net calcium carbonate balance as calculated from the model.

with live *Pocillopora* spp. cover ( $r = -0.93$ ,  $P < 0.01$ ). There was no correlation between these variables in the other reef zones. The sample size was too small to analyze the correlation between *D. mexicanum* density and topographic complexity. However, visual analysis of the data (Fig. 6B) shows that in the reef base the lowest densities of *D. mexicanum* and the lowest complexity occurred together in 1998 and 2000. The declines in sea urchin density at the same time as declines in complexity suggest that *D. mexicanum* led to its own demise through bioerosion and reduction of shelter space.

Measures of topographic complexity were taken less frequently than community surveys (1988, 1989, 1998 and 2000 only). These showed changes in reef structure (Fig. 3C), with declines in the reef base and reef flat during most of the period. Low live coral cover and high *Diadema* density were accompanied by high complexity of the reef framework in the reef base in the 1980s. This zone was nicknamed the 'lunar area' at the time because of the lack of live coral and the gray, irregular surface created by dead pocilloporid framework spires coated with crustose coralline algae. Complexity in the reef base was highest in 1988 and declined throughout the remaining period of study. Qualitative observations in the mid- to late 1990s revealed that the reef base framework was becoming more fragile as boring had greatly reduced its structural integrity. By 2000, the structural relief in this area had literally collapsed, seen also as declines in topographic complexity (Fig. 3C). Following 1998, some increases in low algal turfs were observed but not quantified. These changes were highly apparent and can be seen in photographs (Fig. 7). Reductions in topography were also found in the fore reef and back reef between 1998 and 2000.

Entry of these changes in community composition into the calcium carbonate budget model revealed their influence on the net balance (Fig. 8). Budget data clearly show the change of the reef from depositional to erosional after the 1983 bleaching and subsequent increases in *D. mexicanum*. While a slight reduction in the overall reef production followed the 1997–98 ENSO, this was small compared with changes during intervening years. At only 1% of the total reef area, changes in the back reef carbonate budget were insignificant. The reef flat underwent dramatic changes that resulted in similarly dramatic changes in the overall production. Increased live coral and carbonate balance on the reef flat in 1989 and 1993 were immediately followed by declines. This was most pronounced

in 1994 when post-exposure mortalities were most evident. Increased coral cover in the fore reef in 1990 and both the fore reef and reef base in 1998 correspond to periods of high zonal and whole-reef production. The slight decline in the net carbonate balance between 1998 and 2000 reveals a potential influence of the 1997–98 El Niño, but with a magnitude less than that seen after low-tidal exposures.

#### DISCUSSION

The 1982–83 El Niño had dramatic effects on community composition and net calcium carbonate production on the Uva reef (Glynn, 1990; Eakin, 1996). Similar, and in some cases greater, impacts were seen elsewhere in the eastern Pacific (Glynn, 1990). The 1997–98 El Niño rivaled the earlier event in overall magnitude (Wolter and Timlin, 1998; McPhaden, 1999; Enfield, this issue), and had far greater consequences for reefs worldwide (Wilkinson, 1998, 2000). However, in Pacific Panama and Costa Rica the 1998 bleaching was not nearly so severe as that in 1983, nor were the community consequences as great (Eakin, this paper, pers. observ.; Guzmán and Cortés, this issue; Glynn, in press; Glynn et al., this issue). This included little impact on the carbonate budget after the 1998 partial bleaching at Uva Island. Some suggestion has been made that the corals (or their endosymbionts) living on these reefs today have higher thermal tolerances than the corals living in 1983 (Guzmán and Cortés, this issue; Glynn et al., this issue). However, sea surface temperature anomalies in this part of the eastern Pacific were not so large as those in 1982–83 and did not everywhere reach levels at which bleaching would be expected (Podestá and Glynn, this issue). In the Galápagos Islands, temperatures in 1997–98 reached bleaching levels and corals again bleached and suffered high mortalities (Podestá and Glynn, this issue; Glynn, in press).

Dramatic reductions in live pocilloporid corals after the 1982–83 El Niño had long lasting consequences on the Uva reef. Coral losses in the reef base did not begin to recover for more than a decade. Slow, steady recovery began in the mid-1990s and was largely unaffected by the 1997–98 El Niño warming. In contrast to 1983, most corals in Panama appeared to exhibit only partial bleaching and limited mortality in 1997–98. Most corals observed bleached in October 1997 had recovered before the next bout of bleaching in March 1998 (Glynn et al., this issue).

Between 1983 and 1997, La Niña events, smaller El Niño events and El Niño-like conditions were frequent, but none of the warm periods resulted in significant bleaching. Astronomically-forced spring low tides in 1989 and 1993, magnified by strong, La Niña-related easterly winds, exposed much of the reef flat at least four times during each event. Similar to the consequences of extreme low tides in Israel (Loya, 1976), most corals died within a day after exposure. Dramatic drops in *Pocillopora* spp. cover were evident after the 1993 reef flat exposure (Fig. 3A – data preceded exposure, Fig. 4 – data before and after exposure). This resulted in major changes in the reef carbonate budget, especially in 1993. Because of the large area of the reef flat, small changes in the budget/area in this zone were strongly reflected in the model. Overall *Pocillopora* spp. cover was low on the reef flat, but low tidal-related mortalities further reduced the cover and greatly influenced the model budget. These mortality events, along with changes in coral cover and *D. mexicanum* density around 1990 had a much greater influence on the overall budget than the 1998 bleaching event. Guzmán and Cortés (this issue) found similar low coral mor-

talities in Costa Rica during the 1997–98 bleaching event, with substantial impact from other periods of stress between 1983 and 1997.

The population of *D. mexicanum* increased dramatically after the 1983 El Niño and remained high until the late 1990s. Earlier papers suggested that this resulted from an increase in available habitat after the bleaching mortalities, and perhaps increased recruitment due to high oceanic productivity during the subsequent La Niña (Glynn, 1988b; Eakin, 1996). Echinoids have been shown to cause high rates of reef bioerosion at many sites (Glynn, 1988b; Colgan, 1990; McClanahan and Shafir, 1990; Eakin, 1996; Reaka-Kudla et al., 1996; Peyrot-Clausade et al., 2000). Such changes have had important influences on carbonate budgets (McClanahan, 1995; Eakin, 1996; Peyrot-Clausade et al., 1999). An ecosystem model (McClanahan, 1995) predicted that both high erosion from sea urchins and reduced coral biomass would be required to reduce reef growth in Kenya. Results from Uva Island agree with this (Eakin, 1996) and the current study showed how the complex relationship between variability in coral cover and echinoid densities influences changes in the calcium carbonate balance. Reef base coral cover remained low (<10 %) throughout the entire period of high sea urchin densities. Another similarity between results in Panama and those from Kenya was the extent to which echinoid grazing reduced topographic complexity (McClanahan and Shafir, 1990) – erosion that changes the very nature of the habitat.

At the Uva reef, intense erosion by *D. mexicanum* and infauna resulted in a highly visible reduction in structural relief in most of the reef base and some parts of the fore reef. Reduced shelter availability may have made *D. mexicanum* more vulnerable to predators. Several fish species on the reef are capable of feeding on diadematids, including three puffers (*Arothron meleagris*, *Arothron hispidus* and *Diodon holocanthus*), a large wrasse (*Bodianus diplotaenia*) and at least two balistids (*Pseudobalistes naufragium* and *Sufflamen verres*). At Uva reef, the large *P. naufragium* has been observed attacking *D. mexicanum* (pers. observ.) and echinoid spines have been found in the gut of *A. meleagris* and *S. verres* (Glynn et al., 1972). Other causes of sea urchin population collapse have not been observed. Live *Pocillopora* spp. cover increased as the urchin density declined. The Uva reef is now in a marine protected area, helping to keep fishing pressure low, and there has not been any apparent change in fish predators or parasites (pers. observ.; Glynn, pers. comm.).

Continual erosion by infauna weakened the framework, making damage by echinoids more destructive. By 2000, much of the framework was eroded to near the level of the surrounding sediment. During the increase in *D. mexicanum* densities in the mid-1980s, high sea urchin densities were highly correlated with regions of high topographic complexity (34% of variance, Glynn, 1988b). Subsequently, it appeared that in the 1990s the echinoids literally ‘ate themselves out of house and home’. As erosion by fishes, infauna, and especially echinoids reduced the complexity of the substratum in the reef base, the lack of suitable habitat may have led to a collapse of the sea urchin population by 2000. Almost as quickly as the *Diadema* population rose after the 1982–83 El Niño (Glynn, 1988b), the population again declined. Further experiments are needed to demonstrate if reduced topographic complexity was indeed the primary cause of the sea urchin declines.

## SUMMARY CONCLUSIONS

The 1982–83 El Niño had severe and long lasting consequences to the Uva Island reef and consequences from which the reef had still not fully recovered as of May 2000.

While the 1997–98 El Niño was similar in magnitude to the 1982–83 event and had much greater effects on reefs globally, the 1997–98 event had only moderate effects on coral reefs in Panama. Mortality of important frame-building corals and effects on the carbonate budget were minimal in Panama in 1997–98.

Extreme low tides caused by La Niña events had greater impacts on the reef than the 1997–98 El Niño, but less than the 1982–83 El Niño.

The use of a calcium carbonate model helped to understand how changes in community composition, topographic complexity and echinoid density influence the production and destruction of reefal carbonates and differences between these two very strong ENSO events.

Long-term observations are essential to understand how the reef changes through time and the importance that disturbance, such as climate-related bleaching, has on coral reef systems.

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