

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

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Abstract. El Niño related coral mortality and a subsequent increase in crustose coralline algae and sea urchins have resulted in profound changes to the coral reef ecosystem at Uva Island, Panama (Pacific coast). New data and a model are presented that analyze the CaCO_3 budget of the reef. The model accounts for production by corals and coralline algae, erosion by *Diadema*, infauna, fish and other motile organisms, and the retention of sediments as a function of size. The 2.5 ha reef is currently eroding at an average rate of 4,800 kg/y or $-0.19 \text{ kg/m}^2/\text{y}$ but there is tremendous variation among reef zones. While deposition in other zones range from $+0.1$ to $0.4 \text{ kg/m}^2/\text{y}$, erosion of the seaward reef base averages about $-3.65 \text{ kg/m}^2/\text{y}$. The damselfish/algal lawn symbiosis protects portions of the reef framework, reducing net losses there by 2,000 kg/y (up to $0.33 \text{ kg/m}^2/\text{y}$). Before the 1982–1983 El Niño, the overall reef was depositional. At that time, estimated production exceeded erosion in most zones, resulting in a net deposition of approximately 8,600 kg/y or $0.34 \text{ kg/m}^2/\text{y}$.

Introduction

The Uva Island reef, off the Pacific coast of Panama, lost about 50% of its live coral cover due to warm water from the 1982–83 El Niño event (Glynn 1985a). Recovery of key species has been slow due to low larval recruitment (Glynn et al. 1991) and sources of subsequent mortality such as corallivore concentration, low tidal exposures and cold water stress (Glynn 1985a; Eakin et al. 1989). Changes at Uva reef and similar changes at other eastern Pacific sites (Glynn et al. 1988, Reaka-Kudla et al. 1996) have shifted the calcium carbonate budget such that bioerosion often exceeds biocalcification.

Previous work has shown that eastern Pacific reefs are characterized by somewhat low rates of CaCO_3 production, but fairly rapid framework accumulation due to the open structure of *Pocillopora* and the loosely consolidated framework ($6.7 \text{ kg/m}^2/\text{yr}$ mean production, Glynn 1977; $4.2\text{--}7.5 \text{ m}/1000 \text{ y}$ mean accumulation, Glynn & Macintyre

1977). After 1983, Glynn (1988) found that many areas of the Uva reef were undergoing net erosion. However, because the reef was strongly dominated by live *Pocillopora*, pre-1983 estimates of Uva reef calcification did not include deposition by crustose coralline algae. Additionally, Glynn's (1988) bioerosion estimates included losses due to echinoids and infauna, but not those due to herbivorous fishes. Eakin (1992) refined the estimates of calcium carbonate deposition and erosion on the Uva reef, and quantified the importance of the damselfish/algal lawn symbiosis (Eakin 1987).

However, not all eroded CaCO_3 is lost from the reef, making it important to understand the fate of sediments being produced. Although the smallest particles are frequently carried away by water motion, larger particles become trapped in cavities in the reef framework, remaining within the system and helping to cement porous framework into more solid construction (Ginsburg 1983, Hutchings 1986). Few workers have considered the importance of grain size in studies of bioerosion. Hunter (1977) believed that because of their small size, 0.5–2.0 mm, *Diadema* fecal pellets were exported from the reef. Ogden (1977) described urchin produced sediments as half sand and half mud. While informative, these categories are too broad for use in quantifying the behaviour of reefal sediments. Hubbard et al. (1990) provided additional information on reef budgets by measuring sediment transport directly.

To consider CaCO_3 deposition and erosion across the entire reef, a simple box model of the fluxes of organically derived CaCO_3 on the Uva Island reef was developed. This was based on carbonate budgets produced for reefs in the Caribbean (Land 1979, Scoffin et al. 1980, Hubbard 1990). While all sources and sinks of CaCO_3 on the reef are not considered, the model does include the estimates from the most significant producers and eroders, as well as incorporation of sediments into the framework.

This paper will (1) consider data from the literature and provide new data needed to quantify elements of the CaCO_3 budget, (2) present a new model that quantifies the interacting effects of deposition, erosion and sediment

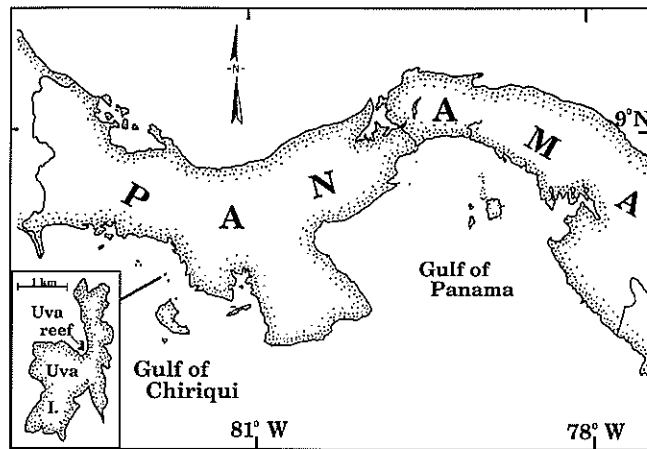


Fig. 1. Map of Panama, indicating location of the Uva Island study site

retention, and (3) use the model to understand the effects of the 1982–1983 El Niño and the damselfish/algal lawn symbiosis on the calcium carbonate system on Uva Reef.

Materials and methods

General methods

Work was conducted from January 1986 to February 1995 on a reef at Uva Island ($07^{\circ} 49'N$; $81^{\circ} 46'W$), in the Gulf of Chiriqui off the Pacific coast of Panama (Fig. 1). This shallow reef (<6 m ML W; approximately 4 m tidal range) is located within a semi-protected bay. Detailed descriptions of the reef and the impacts of the 1982–1983 El Niño and post-mortality events have been reported elsewhere (Glynn 1976, 1984, 1985a; Eakin et al. 1989; Eakin 1992). Statistical analyses used include methods from Sokal & Rohlf (1981) and Zar (1984), or the SYSTAT microcomputer statistical package. Critical levels in multiple comparison procedures are adjusted using the Bonferroni modification to reduce type I error rates (Day & Quinn 1989).

Reef community composition

A base map of the Uva reef was created based on 1983 aerial photographs that provided borders, scale and an estimate of reef zonation. Beginning in 1989, new photographs taken from a nearby ridge during extreme low tidal exposures, and over 150 *in situ* measurements of compass heading and distance between unique reef features were used to improve the map and provide second order delineation of reef zones. Finally, the borders between zones were refined by comparing the second order map to the reef *in situ* (Fig. 2).

The 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 deep reef base (Fig. 2). The back reef slope, a mixture of live and dead *Pocillopora* spp., drops steeply to the silty floor of the leeward lagoon. The reef flat consists mostly of dead pocilloporid framework and coral gravel overgrown with crustose coralline algae. There is little live coral, primarily due to occasional low tidal exposure (Glynn 1976, Eakin et al. 1989) and to 1982–1983 El Niño related mortalities. The energy of waves and tidal currents over the reef flat keeps it clear of sediment. The fore reef slope is dominated by live *Pocillopora* with interspersed massive coral colonies and many regions of dead pocilloporid framework—primarily a result of El Niño related mortalities. The seaward reef

Uva Island Coral Reef (February 1989)

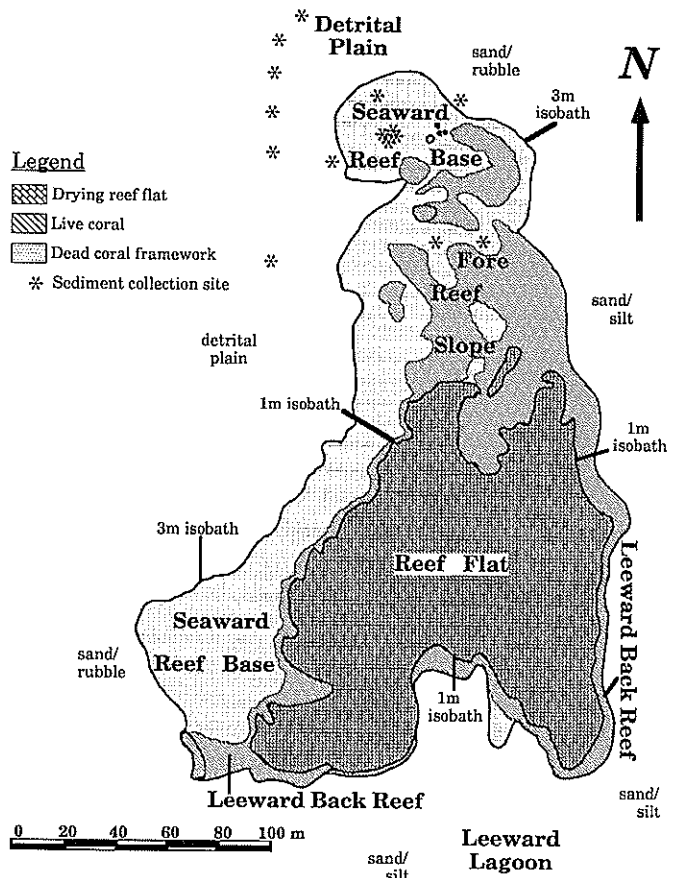


Fig. 2. Map of the Uva reef detailing substratum types and major zones

base, dominated by extensive *Pocillopora* before the 1983 mortalities (Glynn 1984), is now dominated by dead pocilloporid framework coated with thick coralline algal crusts. *Diadema mexicanum* are extremely conspicuous, with densities sometimes exceeding 100 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.

On many occasions from 1988–1994, surveys were performed to assess the percent cover of major community constituents in the four major zones: live *Pocillopora*, dead framework with coralline algae, other live corals, damselfish lawns, *Diadema mexicanum* density and other categories. Each survey was performed using a 1 m^2 quadrat divided into 100 sections that was placed on the bottom using a “random walk” pattern for a total of 20, 1 m^2 samples. A standard pattern was determined prior to initial sampling, and was followed for all surveys except at the back reef where it was modified to accommodate a narrow, ribbon-like zone. The quadrat was moved a random distance (1–5 m) in a random direction (north, east, south or west) from a starting 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 not 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. The results of surveys at 5 sites (2 in the fore reef, 1 in each other zone) on four dates were analyzed.

Three dimensional structure (i.e. topographic complexity) was determined by draping a brass chain along the bottom under lines bisecting the center of the quadrat on one of the surveys. The length

of chain required to trace the surface under 1 m was recorded for both the east-west (x) and north-south (y) bisecting lines. This was used in adjusting the CaCO_3 deposition by coralline algae.

Calcium carbonate production and erosion

Estimates of production by *Pocillopora* spp. and coralline algae have been reported elsewhere (Glynn 1977, 1988; Eakin 1991, 1992), as have estimates of erosion by *Diadema*, fishes and other non-echinoid grazers (Glynn 1988; Eakin 1992). Growth of additional *Pocillopora damicornis* colonies was measured from 122 branches stained *in situ* in 1989 using 10 ppm alizarin red-s for 6 hours (Lamberts 1978) and allowed to grow for 8 months in the reef base zone. Potential production (Chave et al. 1972) was estimated by multiplying linear extension by coral density. Chave et al. (1972) assume a coral density of 1 g/cm^3 . However, the highly open branching form of *Pocillopora* is much less dense. Unpublished measurements of seven colonies from the Uva reef framework by Glynn (pers. comm.) yielded a density of $0.165 \pm 0.047 \text{ g/cm}^3$.

Unlike the growth form of *Pocillopora* spp., which is three-dimensionally complex and imparts topographic complexity to the reef, crustose coralline algae form thin crusts that match the fine contours of the underlying substrata. Thus, the area occupied by coralline algae (three dimensional surface area) often is greater than their planar projection, requiring that the deposition rate per unit area measured on a smooth surface ($1.9 \text{ kg/m}^2/\text{y}$, Eakin 1992) be adjusted to quantify growth on natural substrata. Thus, the deposition by coralline algae on a smooth surface was multiplied by an areal adjustment based on topographic complexity:

$$\text{Areal Adjustment} = 4/(1/x + 1/y)^2$$

where x and y are the two chain lengths (above) in meters. Actual adjustments for individual quadrats ranged from near 1.0 (flat) to 4.0.

Erosion by fishes and non-echinoid motile eroders was estimated by comparing *in situ* production and erosion on experimental rods and disks made of natural CaCO_3 and acrylic (Eakin 1992). Additional data on erosion by echinoids and non-echinoid infauna have been collected by Glynn (1988) and Eakin (1991) through 24 h *in situ* "bucket" measurements of erosion. In these experiments, 15 liter plastic buckets, weighted with lead, were used to collect sediments over 24–72 hours periods. Each experiment utilized: (1) an empty control bucket, (2) three buckets that contained coral or coral framework, and (3) three buckets containing coral and 5 recently collected *Diadema mexicanum*. Rates were calculated and reported as $\text{g/m}^2/\text{day}$ for all eroders and additionally as g/ind/day for *Diadema* erosion. Because most of the coral framework and live *Pocillopora* have an extremely open branching structure, *Diadema* had no more access to the framework during these experiments than they would under natural conditions. Infaunal eroders were retained within the blocks when they were collected and would have experienced little disturbance.

Finally, net production or erosion was measured through changes in the height of the dead pocilloporid reef framework by Eakin (1992) and updated through similar observations on the reef flat. The new data were collected using the method in Eakin (1992) in which four pairs of steel rods, placed one meter apart, were inserted into the framework at three sites on the reef flat in March 1993. A knotted steel wire was stretched between pairs of stakes, and the relative height of the reef framework at each of 11 knots was measured to the nearest mm in March 1993, Jan. 1994 and Jan. 1995 ($n = 121$ and 88 in years 1 and 2, respectively).

Sediment size distribution

To understand the fate of eroded CaCO_3 , samples of experimental and natural reef sediments were analyzed to determine their size

distribution. Samples from one bucket type erosion experiment (described above) using damselfish lawn topped blocks, and two without lawns were analyzed to determine the size of materials produced by *Diadema* and infaunal eroders. Sediments from on and near the reef were collected in December 1990 (Fig. 2) and analyzed to determine the size of materials retained in the reef system. On the reef, two samples were collected from visible sediment pockets within the reef framework in the fore reef and four in the reef base. Near the reef, three samples were collected from the northern reef margin and six from the detrital plain approximately 30 m out from the reef.

Because the hydrodynamics of particles determines their movement and the potential for sediment loss from the reef (Wanless et al. 1981), sediments were analyzed hydrodynamically. The percentage of sample in settling classes equivalent to the Wentworth scale classes from > 1000 through $< 40 \mu\text{m}$ was determined by measuring the rate of particles settling in tap water of $24^\circ \pm 1^\circ \text{C}$, in a $1.6 \text{ m} \times 25 \text{ mm}$ settling tube which tapered to a 5 mm diameter calibrated tip (ICWR 1957). Tube wall effects were reduced by the use of a mechanical device that tapped the wall of the settling tube during use. The composition of settling sediments was noted, especially in regard to the classes in which the fecal pellets settled. Size classes were arranged into four sediment groups corresponding to their hydrodynamics (Bagnold 1966, McCave 1971, Southard & Boguchwal 1990, Wanless pers. comm):

- (1) $> 650 \mu\text{m}$: true bedload that is packed in a dense array at the bottom,
- (2) $150\text{--}650 \mu\text{m}$: intermittent bedload that is usually packed as bedload but intermittently transported as suspended load),
- (3) $50\text{--}150 \mu\text{m}$: suspended load that is transported by water motion, and
- (4) $< 50 \mu\text{m}$: fine sediments that do not settle in shallow open water environments.

Fecal pellets were measured optically to determine their true size.

Development of a CaCO_3 budget model

The solid-phase calcium carbonate system was modeled using a simple box model consisting of bins for (1) the sources of CaCO_3 produced on the reef by corals and algae, (2) losses due to bioerosion, and (3) retention of sediments produced through bioerosion. Only corals and coralline algae were considered as sources of CaCO_3 . *Halimeda* spp. have not been reported from this area and other calcareous algae are a minor community constituent. Other CaCO_3 producing animals (polychaetes, molluscs, foraminifera) also were assumed insignificant due to low abundance. Also, chemical cementation within the reef framework was infrequently found in cores from this reef (Glynn & MacIntyre 1977). Similarly, while chemical erosion may occur, its magnitude ($0.46 \text{ kg CaCO}_3/\text{m}^2/\text{y}$, Le Campion-Alsumard et al. 1993) is probably insignificant compared with physical erosion by echinoids and infauna ($6.3\text{--}14.0$ and $8.3\text{--}9.5 \text{ kg/m}^2/\text{y}$ respectively, Eakin 1992, Glynn 1988) at the Uva reef. Finally, the benign environment at Uva Island is not conducive to destruction by waves or currents.

Estimates of production and losses due to the important bioeroders were described, and the retention of sediments within the reef system were calculated using a submodel that adjusted for retention after comparing the size of sediments produced by eroders to those retained in sediments on and near the reef. Physical measurements of reef height were used to confirm process-based estimates of production and erosion and to provide estimates of net change where more detailed values could not be obtained.

The major sources, losses and retention of calcium carbonate, adjusted to $\text{kg/m}^2/\text{y}$, were calculated for each zone, based on values either extracted from the literature or provided herein. 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.

Table 1. Reef community composition by zone. The “framework” benthic type is characterized by dead coral framework supporting crustose coralline algae and, in some areas, low density filamentous

and other benthic algae. Percent cover does not always sum to 100% due to sand and other substrata. See text for the use of the areal adjustment for framework topographic complexity

Reef zone	Area (m ²)	% framework	% lawn	% <i>Pocillopora</i>	<i>Diadema</i> Density (ind/m ²)
Back Reef	200	31.98	14.04	53.80	1.48
Reef Flat	13,655	91.60	0.00	7.65	0.06
Fore Reef	9,491	38.40	3.60	56.54	18.76
Reef Base	1,962	89.41	6.52	0.23	48.26
	25,308				

Table 2. Calcium carbonate production and erosion by reef zone. Production by crustose coralline algae is adjusted to account for topographic complexity as described in the text

(a) CaCO₃ Production (kg CaCO₃/m²/y)

Reef zone	<i>Pocillopora</i>	Corallines	Areal Adjust.	Adjusted Corallines	Total Product.
Back Reef	2.95	0.60	1.46	0.87	3.83
Reef Flat	0.42	1.71	1.29	2.21	2.63
Fore Reef	3.10	0.72	2.09	1.51	4.61
Reef Base	0.01	1.67	2.25	3.77	3.79

(b) CaCO₃ erosion (kg CaCO₃/m²/y)

Reef zone	<i>Diadema</i>	Fish/Motile	Infauna	Corallivores	Totals
Back Reef	-0.08	-0.02	-6.29	-0.02	- 6.41
Reef Flat	-0.01	-1.15	-3.67	-0.00	- 4.83
Fore Reef	-1.04	-1.28	-5.95	-0.02	- 8.29
Reef Base	-4.38	-1.25	-8.01	-0.00	-13.64

Results

Reef community composition

A map of the Uva reef was created in 1990 (Fig. 2) and the areas of each zone were calculated (Table 1). Surveys of these zones yielded basic information on percent cover by bottom type (Table 1), and the adjustment for topographic complexity (Table 2). Detailed analyses of the community composition was given in Eakin (1991). All non-pocilloporid corals, including massive species such as *Porites lobata*, covered only 0.6% of the bottom. Therefore, calculations within the model assumed an entirely pocilloporid reef. The community data were similar to measurements made in 1985 (Glynn pers. comm.).

Calcium carbonate production and erosion

Measures of linear extension of *P. damicornis* yielded an average rate of 33.2 ± 1.5 mm/yr (mean \pm 95% conf. int.). This is not significantly different from growth measured by Glynn (38.6 ± 4.7 , 1977) at the nearby Secas reef (t-test). This rate of production yields a potential accretion rate of 5.5 ± 0.2 kg/m²/y for areas of solid live coral cover. In the model, this value was multiplied by the live coral cover for each zone (Table 1), yielding the values reported in Table 2.

Observations of vertical height revealed that the fine-scale topography of the reef flat was highly variable and showed no net trend. Unlike the highly significant erosion at the reef base (-21.8 ± 7.5 mm/y, Eakin 1992), annual changes on the reef flat ranged from +99 to -174 mm, with no statistically significant trends over time ($+1.8 \pm 34.8$ mm/y, $n = 209$) or among sites (ANOVA). Two recent years of quantitative measurements agree with the slow changes seen in reef flat structure by the author since 1986 and by others over a much longer period (Glynn pers. comm.).

Sediment size distribution

While there was great similarity in the patterns of sediment size produced among *in situ* experiments, both substratum type (lawn v. non-lawn) and eroder type (infauna v. urchins) significantly contributed to differences among the size distributions shown in Table 3. In particular, urchins produced significantly more intermittent bedload than the infauna, and erosion of the lawn blocks produced significantly smaller particles (lower intermittent bedload but higher suspended load) than the non-lawn blocks (SYSTAT Post-Hoc test). Despite their large actual size (911 ± 43 μ m), *Diadema* fecal pellets settled at a 62.5 – 88 μ m equivalent size (suspended load).

Table 3. Sediment size distributions (zonation from Fig. 2 and described in text)
(a) Size distribution of experimentally produced sediments (% of sample)

Sample	Size Class			
Sample	> 650 μ m true bedload	150–650 μ m intermittant bedload	50–150 μ m suspended load	< 50 μ m fine (non-settling)
<i>Diadema</i>				
Lawn	16.5 \pm 5.5%	6.2 \pm 3.1%	47.3 \pm 7.5%	30.0 \pm 6.0%
Non-Lawn	18.7 \pm 12.5%	10.6 \pm 2.2%	40.3 \pm 8.9%	30.0 \pm 8.0%
Internal Eroders				
Lawn	17.8 \pm 1.5%	3.7 \pm 1.9%	55.7 \pm 6.0%	22.8 \pm 9.5%
Non-Lawn	18.9 \pm 6.7%	4.8 \pm 2.4%	44.2 \pm 14.0%	32.1 \pm 13.4%

(b) Size distribution of reef sediments (% of sample)

Sample	Size Class			
Sample	true bedload	intermittant bedload	suspended load	fine (non-settling)
Detrital Plain	26.3 \pm 4.9%	30.1 \pm 9.2%	28.6 \pm 9.5%	16.1 \pm 4.2%
Reef Margin	32.6 \pm 12.8%	17.0 \pm 23.6%	17.5 \pm 13.0%	19.2 \pm 10.1%
Reef Base	9.9 \pm 5.5%	17.6 \pm 18.5%	34.5 \pm 5.2%	24.5 \pm 28.6%
Fore Reef	60.6 \pm 26.3%	34.6 \pm 17.8%	2.5 \pm 4.2%	2.3 \pm 4.3%

The size frequency distribution of sediments collected from and near the reef revealed a surprisingly even particle size distribution (Table 3) with no significant differences among the detrital plain, reef margin and reef base samples. The fore reef samples did contain significantly greater quantities of true bedload, and lower quantities of suspended load and fine class particles than the other samples ($p < 0.0005$) (SYSTAT Post-Hoc test). The shallower depth of the fore reef sediment collection size probably contributed to their larger mean particle size.

The CaCO₃ budget model

Calcium carbonate production and erosion

The largest source of CaCO₃ production in the model is *Pocillopora* spp. (5.5 kg/m²/y). Production by coralline algae was calculated by Eakin (1992) as 1.87 kg/m²/y based on maximal deposition during the first year of growth. Cropping of coralline algae by grazers has been reported to increase recruitment and growth (Ogden & Lobel 1978, Brock 1979). Therefore, the above rate should be a good estimate of actual production at a highly grazed reef such as Uva. Coralline algae production, adjusted for topographic complexity, is given in Table 2.

Three groups of eroders were considered to represent the bulk of erosion at Uva I:

(1) *Diadema mexicanum*, (2) fish and other motile, non-echinoid grazers and (3) boring infauna. The erosion in each zone was calculated by multiplying habitat-specific erosion rates by the percentage of that habitat in each zone, and summing them to yield the values in Table 2.

Echinoid erosion was calculated for each zone using destruction rates from bucket experiments by Glynn (1988) and Eakin (1991) and verified by erosion of coral disks and changes in reef height (Eakin 1992). Because Eakin (1988) demonstrated that sea urchins avoid feeding on live *Pocillopora* and on upper surfaces of damselfish lawns, echinoid erosion was reduced in these areas. However, the presence of *Diadema* in non-lawn crevices within damselfish territories allowed some erosion to occur. In the model, erosion within lawn areas is calculated as a proportion of the rate measured in dead frameworks using the vertical erosion ratio from Eakin (–6.3/–21.8, 1992). Presumably, similar erosion of dead frameworks underlying live coral also occurs. As this has not been measured, the erosion rate within damselfish lawns was assumed to reasonably represent *Diadema* erosion in live coral areas. Echinoid erosion in Table 2 is based on the *in situ* feeding measurements of -0.32 ± 0.05 and -0.27 ± 0.04 g CaCO₃/ind/d on the sides of lawn covered and non-lawn blocks, respectively (Eakin 1991) and already accounts for topographic complexity.

Erosion by fish and other motile, non-echinoid eroders was calculated from erosion of acrylic and CaCO₃ disks mounted on concrete blocks in each reef zone (Eakin 1992). Damselfish readily exclude grazing fish and motile invertebrates from their territories. Thus, erosion by all non-echinoid, motile eroders was assumed to affect only dead coral framework. Estimates of erosional losses are from Eakin (1992) and zonal values were calculated as above (Table 2). Erosion of live coral substrata by the most physically destructive corallivores was trivial but estimates by Glynn et al. (1972) were included, nevertheless. Other corallivores, such as the gastropod *Jenneria pustulata* and

the asteroid *Acanthaster planci* digest tissue without destroying carbonate skeletons, contributing only indirectly to erosion.

Finally, erosion by infauna occurred throughout the reef. The *in situ* bucket erosion experiments revealed that blocks topped with live *Pocillopora* were eroded at $-4.31 \text{ kg/m}^2/\text{y}$, while dead and lawn covered frameworks were eroded at -8.3 and $-9.5 \text{ kg/m}^2/\text{y}$, respectively (Glynn 1988, Eakin 1991). Scott et al. (1988) estimated that infauna erode the massive coral *P. lobata* at $-9 \pm 1.98 \text{ kg/m}^2/\text{y}$. This rate does not differ from values for dead pocilloporid frameworks that are used in this model (*t*-test, $p > 0.05$). As non-pocilloporid corals cover $< 1\%$ of the reef by area, the calculations of zonal erosion were conducted as if this were an all pocilloporid reef.

Structurally, the framework materials in the reef flat zone were quite different from all other areas. The reef flat did not have the heterogeneity that was found elsewhere and was extremely well consolidated, limiting both internal and external eroders to the upper layers. *Diadema* were practically absent and eroding fishes spent much less time in this zone. Changes in reef height were negligible, but positive ($1.8 \pm 34.8 \text{ mm}$). The low impact of external eroders has already been accounted for by the reduced *Diadema* density and the reef flat observations of fish erosion. However, the infaunal erosion rate, measured in fore reef framework blocks, must be adjusted. Using the negligible change in reef flat height as a proxy for the zonal balance, the erosion rate by infauna was adjusted to 50% of that measured in the fore reef.

Framework sediment retention

Although actual sediment transport has not been measured at the Uva reef, sediment transport was inferred from the size of sediments produced by eroders and sediments deposited on and around the reef. The relative retention of erosional sediments was influenced by the location of sediment release and the baffling effect of coral framework. By assuming greater retention of particles released deeper within the framework, a reasonable model of particle retention was developed. While this submodel retained all of the material in the true and intermittent bedload classes, it was assumed that a set percentage of the suspension and fine class sediments that were deposited within the framework were retained. This retention factor was then multiplied by the approximate percentage of time that the eroders spend within the reef framework. Modeled values were then compared with actual particle size distributions found in reefal sediments and a reworking adjustment value was applied (see below). Iterative refinement of the initial retention and reworking adjustment values were applied until the retention submodel best simulated the sediments observed on the reef.

Eroding fish spend most diurnal hours moving over the reef. Defecated fecal matter sorts by size because the largest particles rapidly settle to the bottom and smaller particles are carried away by currents. Small sediments bound together into pellets are quickly separated by surficial microbes and motile benthic invertebrates which break

them apart (Polunin & Koike 1987). This allows finer materials to be winnowed out by turbulent flows when they are defecated onto the reef from the water column. Previous workers reported that scarids produce sediments in the size range from silt to gravel (Cloud 1959, Randall 1967, Ogden 1977, Scoffin et al. 1980). Smaller mouthed grazers such as acanthurids and kyphosids should release even finer material. Assuming that fish spend 50% of the time within the reef (night) this yields about 15% retention of these classes.

Most material eroded by echinoids is defecated directly into the framework. It is assumed in the model that much of the suspended load and finer sized grains are winnowed out, removing most of the *Diadema* fecal pellets that behave hydrodynamically as suspended load. If the model is adjusted to retain 50% of the suspended load, it almost doubles the retention of echinoid produced sediments, influencing the balance of the model. However, rough seas during storms probably winnow out most of the finer sediment. Similarly, infauna are assumed to spend all of their time within the reef framework, resulting in 30% retention of the finer sediment classes. Extremely fine particles, such as clionid sponge chips, are produced inside burrows and galleries, but these would not be affected by water movement, nor would they be collected.

The sediments produced during *in situ* erosion experiments contained more suspended load and fine sized particles than were retained in reef sediments. The retention submodel was created, based on the above assumptions regarding sediments collected from in and around the reef framework and improved estimates of retention for use in the overall model. Using assumptions of sediment retention described above, the size distribution of remaining sediments was calculated and compared with the sediment size distribution found in sediments on and around the reef (Table 4). The assumptions of time in framework and sediment retention were adjusted until the submodel best reproduced the size class distribution of sediments found on the reef. Although it was thought that more particles from the suspended load than fine class would be retained, the measured sediments were best approximated when 30% of the material in each of these two classes was retained. Unfortunately, the 30% retention still did not effectively approximate the measured size class distribution. However, materials that are eroded from coral framework are to repeated ingestion and degradation (Hunter 1977, Ogden 1977). Thus, a term to account for reworking was incorporated to degrade a fraction of the sediment particles to a smaller size class. If 30% of the sediments are assumed to be reworked, model results approached the field measurements of sediments found on Uva reef (Table 4). Final estimates of retention are given in Table 4.

Calcium carbonate budget and influences of El Niño and damselfish

A whole reef budget was calculated based on the formula:

Net Balance = (Production + Erosion + Retention) × Area.
Pre-1983 budgets were calculated using the same model,

Table 4. Retention of biologically produced calcium carbonate sediments in the Uva reef system. (a) Estimated values of sediment retention based on the assumption that 30% of suspended and fine (a) class sediments deposited within framework are retained; (b) Com-

parison of measured estimated particle size distribution and model produced values, before and after use of sediment reworking factor; (c) modeled estimates of the sediment retained in the reef system

(a) Estimated sediment retention

Eroder	Retention factors				
	Time spent in reef	True Bedload	Intermittent Bedload	Suspended	Fine
Fishes	50%	100%	100%	15%	15%
<i>Diadema</i>	75%	100%	100%	23%	23%
Internal	100%	100%	100%	30%	30%
<i>Arothron</i>	50%	100%	100%	15%	15%
<i>Aniculus</i>	75%	100%	100%	23%	23%

(b) Reef-wide measured sediment size distribution and results from retention submodel

Size class	Measured values			Modeled values	
	Mean-95%	Mean	Mean + 95%	before reworking	with reworking
Bedload	18.51%	24.31%	30.11%	37.71%	26.40%
Intermittent	19.00%	25.59%	32.18%	12.58%	20.12%
Suspended	21.89%	27.41%	32.93%	28.82%	23.95%
Fine	16.31%	22.69%	29.07%	20.89%	23.27%

(c) Modeled values of sediment retention (kg CaCO₃/m²/y)

Reef zone	<i>Diadema</i>	Fish/Motile	Infauna	Corallivores	Totals
Back Reef	0.03	0.01	2.91	0.02	2.97
Reef Flat	0.00	0.46	1.84	0.00	2.31
Fore Reef	0.47	0.51	2.77	0.02	3.77
Reef Base	1.98	0.50	3.73	0.00	6.21

substituting pre-1983 values for coral cover and fore reef and reef base *Diadema* densities (Glynn 1976, 1990; Glynn et al. 1988). Pre-1983 coral cover was primarily taken from Glynn (1976) using two of the three values listed for the reef flat (8%, 15%) for the pre-1983 budget in Table 5. The third value (58% live *Pocillopora*) was not considered to be representative of this zone (Glynn pers. comm.). Densities of the corallivores and herbivorous fishes used in the budget were unchanged by the 1983 event, thus all model runs used the same values. The influence of damselfish was modeled by replacing the percent cover of lawn in each zone with dead framework. This resulted in substantial increases in erosion by *Diadema* and fish. Because erosion by boring infauna was slightly greater in lawn topped blocks than dead framework (9.5 and 8.3 kg/m²/y respectively), internal erosion would decrease slightly.

Based on budget calculations, it can be seen that Uva reef after the 1982–1983 El Niño event has undergone a net loss of CaCO₃ due to the high rates of erosion at the reef base (Table 5, Fig. 3). The budget at the back reef slope was clearly positive due to high coral cover, low densities of *Diadema* and low erosion from fishes, but, the small size of this zone results in little contribution to the overall budget. The reef flat and fore reef were marginally positive. The reef flat was in a stage of low production and biomass per area, probably due mostly to occasional exposure during low tides. The model is sensitive to minor changes in this zone,

partly because deposition and erosion of carbonates are so nearly balanced and partly because it contains just over half of the total reef area. Increasing sediment retention by only 25% greatly increases production and the total reef budget. The model indicates that the reef flat was a major source of CaCO₃ before 1983. However, the large area of this zone greatly magnifies any change to the overall budget. In fact, if all three of Glynn's (1976) reef flat transects are used to estimate live coral cover, net production in this zone alone jumps more than three fold to almost 14,000 kg/y (1.03 kg/m²/y). Observations of the slow infilling of topographic features suggest that this zone is actually undergoing slow net deposition.

Conversely, the fore reef slope is a very dynamic zone. Surveys in this zone frequently ranged from near 0 to near 100% live coral cover. Adjustments to simulate pre-1983 higher coral cover and lower echinoid densities indicate that the fore reef was a high depositional environment before the 1982–1983 El Niño mortalities (Table 5, Fig. 3).

The reef base is clearly an erosional environment in which most of the reef's losses occur. This agrees with field measurements of erosion up to –22 mm/y on frameworks not protected by damselfish and their lawns. The impact of the 1982–1983 El Niño was strongly exhibited in this zone.

Finally, the damselfish/algal lawn symbiosis plays an important role in the reef carbonate system (Table 5) by reducing erosion by both echinoids and fishes (Eakin

Table 5. Calcium Carbonate Budget. The budget for the Uva reef is calculated from data in previous tables with Net $\text{CaCO}_3 = (\text{P} + \text{E} + \text{R}) \times \text{Area}$
(a) Current CaCO_3 budget

Reef zone	Prod. ($\text{kg/m}^2/\text{y}$)	Eros. ($\text{kg/m}^2/\text{y}$)	Ret. ($\text{kg/m}^2/\text{y}$)	P + E + R ($\text{kg/m}^2/\text{y}$)	Area (m^2)	Net (kg/y)	w/o damsels (kg/y)
Back Reef	3.83	-6.41	2.97	0.39	200	78	81
Reef Flat	2.63	-4.83	2.31	0.11	13,655	1,444	1,444
Fore Reef	4.61	-8.29	3.77	0.08	9,491	801	-638
Reef Base	3.79	-13.64	6.21	-3.65	1,962	-7,168	-7,818
						-4,845	-6,931

(b) Pre-1983 community parameters

Reef zone	% framework	% lawn	% <i>Pocillopora</i>	<i>Diadema</i> Density (ind/m^2)
Back Reef	31	14	55	1.48
Reef Flat	87	0	12	0.06
Fore Reef	38	4	57	3
Reef Base	69	7	20	3

(c) Pre-1983 CaCO_3 budget

Reef zone	Prod. ($\text{kg/m}^2/\text{y}$)	Eros. ($\text{kg/m}^2/\text{y}$)	Ret. ($\text{kg/m}^2/\text{y}$)	P + E + R ($\text{kg/m}^2/\text{y}$)	Area (m^2)	Net (kg/y)	w/o damsels (kg/y)
Back Reef	3.87	-6.37	2.96	0.45	200	90	93
Reef Flat	2.76	-4.69	2.24	0.31	13,655	4,271	4,271
Fore Reef	4.62	-7.43	3.38	0.57	9,491	5,381	4,565
Reef Base	4.01	-8.43	3.85	-0.56	1,962	-1,106	-1,076
						8,636	7,853

1988). With the current high density of *Diadema*, removal of damselfish in the model dramatically increases erosion in the fore reef ($-0.15 \text{ kg/m}^2/\text{y}$) and reef base ($-0.33 \text{ kg/m}^2/\text{y}$, total $> 2,000 \text{ kg/y}$). Prior to 1983, the influence of damselfish and their lawns was less than half of the current value.

Discussion

While this model improves our understanding of the carbonate budget on the Uva reef, it is only a rough approximation of reality. It assumes that *Pocillopora* and crustose coralline algae are the only sources of CaCO_3 . The value of $5.5 \text{ kg/m}^2/\text{y}$ used in the model is close to that calculated by Glynn ($6.7 \text{ kg/m}^2/\text{y}$, 1977) for the nearby Secas reef. The density value used is somewhat imprecise as it assumes that all growth is upward. As both growth form and colony density vary with colony age and cover, the actual production per unit area may vary across the reef.

All dead substrata from the surveys were assumed to support the growth of coralline algae. The estimate of coralline algal deposition was derived from the mean growth on acrylic settling disks, confirmed by stained samples. Similarities between the deposition values calculated from these two methods suggest that the values

used in the model are good estimates of carbonate production. While the application of the alkalinity anomaly technique (Smith & Kinsey 1978, Gattuso et al. 1993, Kayanne 1995) could improve the reef flat production estimates, the variable current patterns and the highly porous reef flat framework would make application of this approach problematic at Uva reef.

Most of the erosional values used are robust estimates of reef framework destruction. Echinoid erosion, as calculated from *in situ* bucket experiments, erosion of experimental coral disks and changes in reef framework height are strikingly similar and are similar to erosion measured by Glynn (1988). Measured erosion by fishes was rather variable, but the estimates from the reef flat and reef base were quite similar. Fortunately, changes in fish erosion have little influence on the model's performance. The small size of the back reef makes changes there unimportant, and decreases in erosion by fishes in the fore reef would only slightly strengthen the depositional trend there. Internal erosion was sufficiently consistent throughout the experiments that it also should be a good estimator of actual erosion in three of the four zones. If anything, erosion estimates, especially echinoid erosion, may be conservative as horizontal erosion of walls and toppling of the framework (Eakin 1992) may be as important as direct surficial erosion (Colgan 1990).

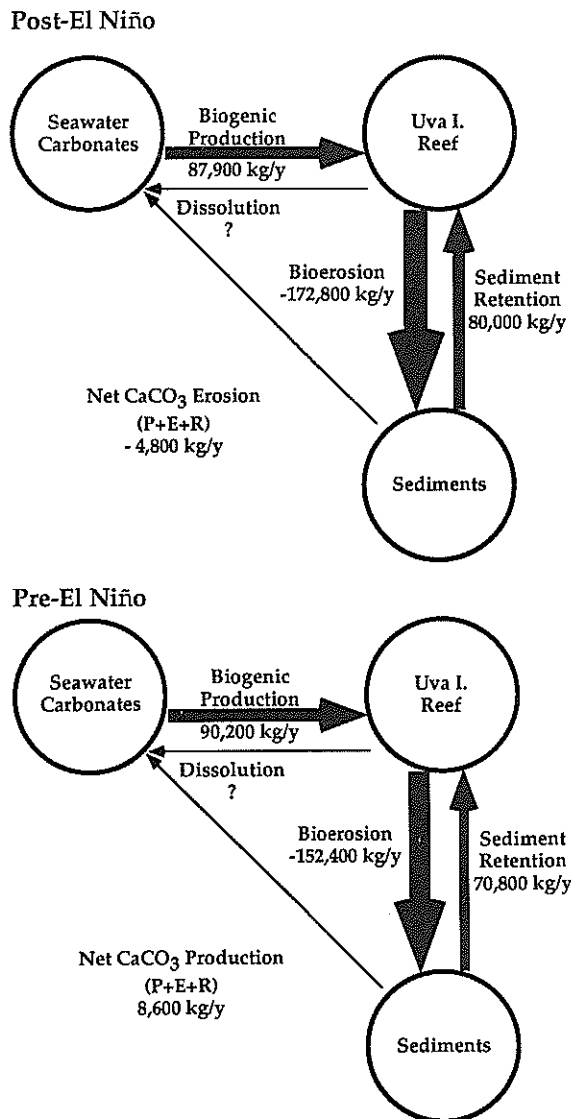


Fig. 3. Graphical diagram of the CaCO_3 fluxes in the Uva Island coral reef system, showing flux values (rounded to 100 kg/y) before and after the extremely strong 1982–1983 El Niño event. The width of the arrows is proportional to the magnitude of the fluxes

Unfortunately, the *in situ* bucket experiments could not be used to measure reef flat erosion. The tightly packed rubble and low topographic complexity suggest that erosion and sediment retention differ from the other zones. The 50% reduction of internal erosion in this zone is rather conservative—erosion on the reef flat may be far less. In the model, changes in reef flat height were used as a proxy for the balance in this zone because a direct measurement of internal erosion was not available. However, observed changes in the topography of this zone since 1972 support this assumption.

It is likely that the estimates of sediment deposited by fishes and infauna are reliable. If sediments retained deep within the reef framework contained a larger proportion of suspended load and fine class particles, losses from the fore reef and reef base zones would decrease substantially.

A 50% increase in the retention of suspended load and fine class particles could dramatically increase the net deposition per area at the fore reef, while net losses in the reef base would drop by one third. However, unless these were rapidly immobilized by cementation, this would yield sediments that no longer resemble observed reef sediments.

While the model lacks a measure of interzonal transport, it is likely that exchanges between the fore reef and reef base zones are insignificant, as materials mobilized in either of these zones would most likely be exported off the reef. The lack of fine sediment in the reef flat zone argues for high export, but prevailing currents would carry most material shoreward, past the steep, narrow back reef and onto the silty lagoon floor. An unknown quantity undoubtedly moves from the reef flat to the fore reef and reef base.

The importance of damselfish protection differed substantially between post- and pre-El Niño conditions. The damselfish/algal lawn symbiosis currently protects much of the reef framework, reducing total net losses by 2,000 kg CaCO_3/y . Prior to 1983, damselfish protection was less than 800 kg/y. The potential protection of reef frameworks by the damselfish/algal lawn symbiosis is particularly important now given high echinoid densities and reduced live coral cover, e.g. post-El Niño conditions, on eastern Pacific reefs. Under conditions of high live coral cover and low external erosion, such protection would be less important to the overall reef budget. Protection of reef frames by damselfishes may have implication to similar post-disturbance reef systems outside of the eastern Pacific. If wide-spread future reef disturbances from bleaching (Williams and Williams 1990, Glynn 1991) and human stress (Wilkinson 1992) result in extensive coral mortality, protection of reef frameworks by damselfish may be extremely important in systems where echinoids and erosive, herbivorous fish are abundant. Additionally, damselfish may provide important protection to many reef frameworks in the western Pacific. In the Great Barrier Reef complex, damselfish lawns comprise 30–40% of the bottom at many sites (Klumpp et al. 1987). Although echinoids are of minor importance there, scarids and various gastropods that are excluded from damselfish territories contribute much to the 9 kg/m²/y erosion (Kiene 1988).

The coral bleaching and mortalities experienced in the eastern Pacific during the 1982–83 El Niño had effects on the ecosystem far more severe than any other historical or recent El Niño event. However, the decade-long combination of reduced coral cover and increased echinoid populations has been devastating. The 2.5 ha reef is currently eroding at $-4,800 \text{ kg } \text{CaCO}_3/\text{y}$ ($\sim -0.19 \text{ kg}/\text{m}^2/\text{y}$), whereas net deposition exceeded 8,600 kg/y ($\sim +0.34 \text{ kg}/\text{m}^2/\text{y}$) before the 1982–1983 El Niño. While this has dramatically altered the community structure over large areas of Uva reef, it has been suggested that extremely strong El Niño events may limit reef development in the eastern Pacific. Measurements of uninterrupted reef growth and age frequency distribution of large massive corals indicate that a disturbance comparable to the 1982–83 event probably has not occurred for at least 200 years in the eastern Pacific—perhaps 400–500 years in the

Galápagos (Glynn 1985b, 1990). In the current mode of rapid erosion, framework materials that were built up over hundreds to thousands of years have been and continue to be destroyed, removing the calcium carbonate structure that provides the foundation for the ecosystem.

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Note added in proof

For a report on bioerosion in the Galápagos Islands, please see Reaka-Kudla et al. (this volume).
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