

Post-El Niño Panamanian Reefs: Less Accretion, More Erosion and Damselfish Protection

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Abstract. Warming during the severe and prolonged 1982–83 El Niño event led to the bleaching and mortality of over 50% of reef corals, by area, at Uva Island, Panama. On much of the reef, live corals were replaced by crustose coralline algae that deposit CaCO_3 at only $1.9 \text{ kg/m}^2/\text{y}$ —70% lower than *Pocillopora*. The echinoid *Diadema mexicanum* increased from pre-El Niño densities of 3 ind./m^2 to at least 50 ind./m^2 in the seaward reef base zone. In this zone, *D. mexicanum* and internal bioeroders are eroding the carbonate framework at $>6\text{--}14 \text{ kg CaCO}_3/\text{m}^2/\text{y}$, while fish and other non-echinoid, external grazers are eroding it at $1.4 \text{ kg/m}^2/\text{y}$. Bioeroders are removing reef framework vertically at 22 mm/y and causing the collapse and recession of framework walls at 44 mm/y . Because deposition has been reduced and erosion increased relative to pre-El Niño conditions, reef frameworks are eroding rapidly. Within damselfish territories, the damselfish/algal lawn symbiosis decreased vertical erosion by over 70%, protecting much of the reef framework.

Introduction

Herbivory is a vital link in energy flow and strongly influences the structure of coral reef communities. Two groups of herbivorous grazers, diadematid echinoids and damselfishes, are important in their rather divergent roles. The excavational grazing

used by diadematids is highly destructive to both algae and reef substrata (Ogden 1977; Steneck 1983; Birkeland 1989). In contrast, the non-denuding cropping of damselfish, coupled with damselfish territorial behavior, produce highly diverse algal lawns (Hixon & Brostoff 1983; Steneck 1983) that may protect underlying carbonate frameworks from external eroders (Sammarco et al. 1986). The opposing roles of these two organisms have taken on a new importance on coral reefs in the eastern Pacific since the 1982–83 El Niño.

Unlike boring and etching cryptofauna that contribute to sediment trapping and lithification of reef frameworks (Ginsburg 1983; Marshall 1983; Hutchings 1986; Kiene 1988), scraping grazers such as echinoids and parrotfishes break away large pieces of framework (Ogden 1977; Hatcher 1983; Hutchings 1986; Kiene 1988; Birkeland 1989), much of which is reduced to silt-sized particles that are likely to be exported off the reef (Hunter 1977; Eakin 1991). Chronically destructive grazing by high densities of *Diadema* leads to a less diverse community dominated by crustose coralline algae (Hixon & Brostoff 1983; Littler & Littler 1985; Morrison 1988).

The Uva Island reef, off the Pacific coast of Panama, suffered a 50% reduction of live coral cover due to warm water from the 1982–83 El Niño (Glynn 1985a), and is recovering slowly due to low sexual recruitment (Glynn et al. 1991, Smith 1991) and other sources of mortality (Glynn 1985a; Eakin et al. 1989). Since then, bioerosion has exceeded biocalcification on this and many other eastern Pacific reefs, in part due to increased densities of the regular echinoid *Diadema mexicanum* A. Agassiz (3 ind./m^2 pre-1982, $>50 \text{ ind./m}^2$ post-1983 on parts of the Uva reef) (Glynn 1988; Eakin 1991). Grazing

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by *Diadema* contributes 78% of the over 13 kg/m²/y sediments produced by benthic eroders (Glynn 1988; Eakin 1991).

Damsel-fishes influence the access of bioeroders to the carbonate reef frame by excluding sea urchins and grazing fish from their territories (Williams 1979; Sammarco & Williams 1982; Kamura & Choonhabandit 1986). On the Uva reef, erosion by invading *Diadema mexicanum* is reduced by the territorial action of *Stegastes acapulcoensis* and the texture of the damselfish's algal lawns (Eakin 1987, 1988, 1991). By reducing erosion and increasing survival of pocilloporid coral recruits (Sammarco & Williams 1982; Wellington 1982) damselfish territories may serve as islands of positive reef growth and/or high coral diversity.

Glynn (1988) calculated that post-El Niño carbonate bioerosion rates exceeded pre-1982 production rates at the Uva reef. However, because the reef is strongly predominated by live *Pocillopora*, pre-1982 estimates of Uva reef calcification did not include deposition by crustose coralline algae (CCA). Additionally, Glynn's bioerosion estimates included losses due to echinoids and infauna, but not those due to herbivorous fishes. Crustose corallines, which now cover much of the Uva reef (Eakin 1991), are important carbonate depositors in the Caribbean (Adey & Vassar 1975), and scarid fishes have been implicated as important eroders of coral reefs (Ogden 1977; Scoffin et al. 1980; Kiene 1988).

This paper describes experiments that refined estimates of carbonate deposition and erosion at the Uva reef. Experiments were established in four different reef zones to quantify (1) the contribution of CCA to reef carbonate deposition and (2) the contribution of fishes and non-echinoid grazers to reef carbonate erosion. Other experiments tested the influence of the damselfish/algal lawn symbiosis on erosion by *Diadema mexicanum* and measured both vertical and horizontal erosion of reef frameworks.

Methods and Materials

General methods

Work was conducted from January 1986 to February 1992 on the study reef at Uva Island (07°49'N; 81°46'W), in the Gulf of Chiriqui off the Pacific coast of Panama. 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, 1985a; Eakin et al. 1989; Eakin 1991).

Statistical analyses were performed using methods from Sokal & Rohlf (1981) and Zar (1984), or with 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). Data are presented as mean values \pm 95% confidence intervals throughout. Random numbers were generated by polyhedral dice or electronic devices.

Calcium carbonate production by CCA

Non-coral biocalcification was quantified through two methods. The deposition of CaCO₃ (kg/m²) by CCA, and a few other calcareous organisms, and accretion (CCA film thickness in mm) were calculated from the acrylic disks and rods used for measurement of deposition and erosion of CaCO₃ across the reef (see following section for details). The rate of carbonate deposition to the disks and rods by CCA was calculated by dividing the gross CaCO₃ deposition on acrylic disks (DEPOSITION) by the exposure time. When a substantial area was uncolonized or covered with organisms other than CCA, this rate was multiplied by the proportion of occupied disk surface that was covered by CCA. Carbonate accretion was calculated by dividing the deposition/area by the CaCO₃ density of 1.56 g/cm³ (Stearn et al. 1977). Changes in deposition, accretion and accretion rates were analyzed by ANOVA for changes through time at three reef zones (reef flat, n=19; fore reef, n=16; reef base, n=23).

To confirm that CCA deposit CaCO₃ to acrylic surfaces at a natural rate, 40 dead pocilloporid branches covered with a thin surficial growth of CCA were stained with approximately 10 ppm alizarin red-s (Lamberts 1978). One half of the branches were stained for 6 h, the others for 6 h on three successive days. The stained fragments were placed on the reef from Oct. 1989 until Mar. 1990, when they were collected, preserved in ethanol, bleached with sodium hypochlorite solution, dried, and the linear extension of CCA films (mm) was measured. Extension was measured multiple times on each fragment and these measures were tested for homoscedasticity and analyzed for differences between staining treatments and among fragments by a nested ANOVA. While multiple measures from each fragment violates the assumption of independence, this would not interfere with the overall growth calculation.

Erosion by fishes and other non-echinoid grazers

Disks and rods of acrylic plastic and of natural coral were elevated above the bottom on concrete blocks in four reef zones to assess the quantity and distribution of both non-echinoid bioerosion (primarily scarid) and non-anthozoan carbonate accretion (primarily CCA). Acrylic test materials were subject to negligible erosion, and were readily colonized by CCA. In addition, erosion of these carbonates should have been readily identifiable. In contrast, the coral materials and new carbonates accreted on them were available for destruction by erosive grazing. Both disks and rods were used to simulate differently shaped carbonate structures: (a) semi-flat surfaces of massive corals and consolidated carbonate frameworks and (b) branches of *Pocillopora* and naturally occurring rods formed by CCA. Although communities develop differentially on various settlement substrata during short term experiments (McGuinness 1989), such substratum effects were minimized during the longer term experiments, and were evaluated by comparing changes in the community on disks through time.

Disks, 95 mm diameter, were cut from a sheet of 6 mm acrylic and roughened with 150 grit paper to enhance initial recruitment. Cores of *Porites astreoides* Lamarck, 95 mm diameter, were cut into disks 8–10 mm thick. Experimental units were constructed by attaching 2 pairs of disks of each material to concrete blocks such that one member of each pair was positioned horizontally on the top of the block and one vertically on the side. However, orientation had no influence on deposition or erosion and will not be discussed further. The location and initial dry weight of each disk was recorded. Similarly, 60 × 12.5 mm rods of clear acrylic plastic, and similar lengths of dried, cured colonies of *Pocillopora*, approximately 10 mm central branch diameter, were cut and weighed. Two strings, each bearing five rods of each material, were tied to each concrete block.

The experimental units were placed in each of the four major reef zones: back reef, reef flat, fore reef slope and seaward reef base at three times during the rainy season: May 1986 (2 units/zone), July 1986 (3 units/zone) and May 1987 (2 units/zone). Experimental units were placed in locations that eliminated access by *D. mexicanum*. Because of *Diadema* densities in the reef base framework and fore reef, these units required special care in their placement. Reef base units were placed on a loose rubble plain immediately adjacent to the solid framework. No *Diadema* were ever seen on the rubble plain around these units. Fore reef units were

placed on a ridge of continuous live *Pocillopora*. Although no *Diadema* were ever seen moving across the live *Pocillopora*, damage to the fore reef site by a shrimp net allowed *Diadema* to gain access to at least some of these units. The sites of reef flat and back reef units had no *D. mexicanum* in the immediate vicinity and none were ever seen around the units. Experimental units were collected after 85, 282, 419, 655, 702 and 938 d. Between May 1987 and July 1988, all back reef experimental units disappeared, and many of the fore reef samples were destroyed by the shrimp net. The remaining fore reef samples were examined for obvious signs of echinoid erosion; those not apparently eroded by echinoids were included in further analyses.

After collection, experimental substrata were preserved in 70% ethanol, inspected for coral spat or other growths, and the community on the upper surface of each disk was analyzed as follows. A clear acetate grid, marked with 100 points at 6.5 mm intervals was placed over each disk, and the substratum or biota under each point was identified to functional taxonomic units. After counting, disks and rods were dried and re-weighed. All materials were dried at 56° C to constant weight and weighed to 0.1 g precision.

A conservative value for carbonate deposition, measured as weight gain on acrylic substrata (DEPOSITION) and net effects of carbonate deposition and erosion on coral substrata (NET) were taken directly from disk weights. Total losses from erosion (EROSION) were calculated as the difference between these (DEPOSITION-NET). The data were coded and log transformed. After testing for the assumption of homogeneity of slopes (no interaction), the transformed data were analyzed for changes through time and differences among the zones by a multiple analysis of covariance (MANCOVA). The loss of samples at two sites prevented an estimate of the interaction between the variables zone and time. Because EROSION is mathematically dependent on DEPOSITION and NET, it was analyzed by a separate ANCOVA.

Erosion by echinoids

To measure echinoid erosion on substrata comparable to the disk values above, acrylic and coral disks were tied loosely in regions of the Uva reef base with high urchin abundances. Four strings with 8 disks (4 acrylic, 4 coral) were placed on the Uva reef for periods from 85 to 436 d. These samples were analyzed as above.

Damselfish territories contain a mix of lawn and non-lawn regions (Eakin 1988), and *Diadema* often

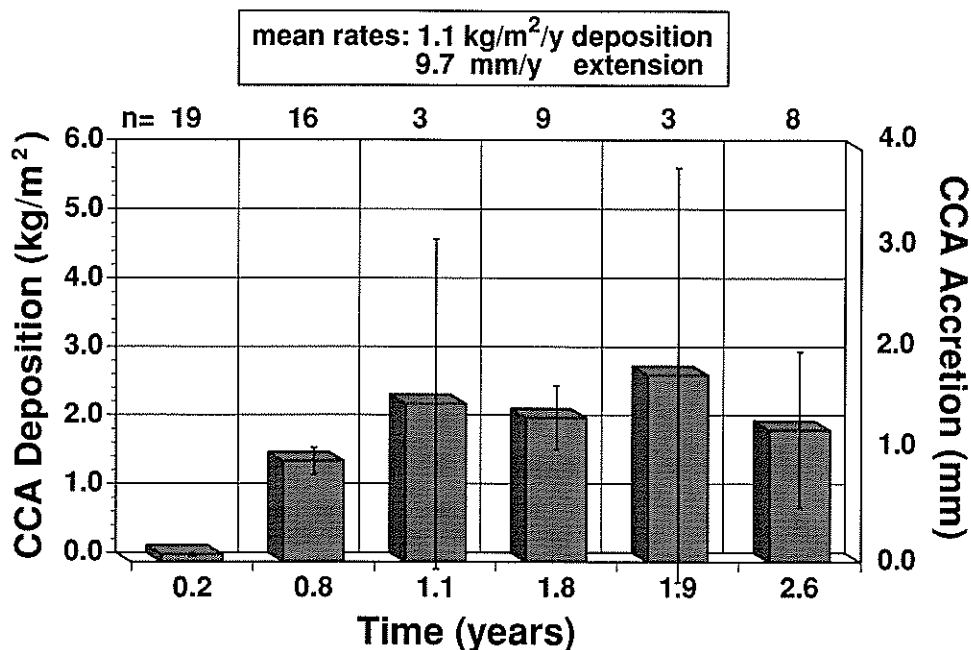


Fig. 1. Deposition and accretion of CaCO_3 by crustose coralline algae onto acrylic disks (displayed as mean \pm 95% confidence interval). Accretion was calculated from deposition using the CaCO_3 density (1.56 g/cm^3) from Stearn et al. (1977).

emerge from holes and crevices at night to feed on CCA within these territories. To quantify the influence of damselfish and their lawns on bioerosion, vertical erosion of the reef framework inside territories was compared with that outside. Twelve pairs of steel rods were inserted into the framework in two regions of the seaward reef base in October 1987. The rods in each pair were placed approximately 1 m apart, across the lawn of one or more damselfish. A knotted steel wire was stretched between pairs of stakes, and the relative height of the reef framework was measured to the nearest 1 mm. Framework erosion rates were calculated as changes in height between the original survey and each of five successive measures ending in March 1990. A total of 405 erosion values calculated at 108 points within the 12 lawn transects, were compared with 84 values calculated at 21 points along 5 nearby transects in non-lawn areas measured by Glynn (pers. comm.). Differences among the erosion rates through time and between lawn and non-lawn areas were analyzed by two-way ANOVA and ANCOVA.

Finally, because erosion has caused highly visible changes in the structure of the Uva reef, the horizontal retreat caused by undercutting and collapse of framework walls was measured in the upper fore reef. Twenty five steel rods, spaced at 1 m intervals, were placed with their tops located 100 mm from a pocilloporid framework wall when the ex-

periment began in Oct. 1987. The stakes were positioned adjacent to regions of the wall topped with one of two substrata; 13 were positioned adjacent to damselfish lawns, while twelve were adjacent to live *Pocillopora*. The distance between the tops of stakes and the nearest point on the wall was measured 232, 485, 720, 870 and 1584 d after initiation. Because erosion of the framework caused many blocks to collapse from the wall, most stakes were broken or uprooted before the conclusion of the experiment. A total of 82 distance measurements were taken, 55 from stakes that persisted throughout the entire experiment. These 55 measurements were analyzed by ANOVA for changes through time and differences in erosion between regions topped with damselfish lawns and with *Pocillopora*.

Results

Calcium carbonate production by CCA

The major source of CaCO_3 deposition to acrylic test substrata was crustose coralline algae, which represented over 82% of all calcareous growths on disks by area. Remaining CaCO_3 was deposited by various erect calcareous algae, vermetids, serpulids and foraminiferans. No coral spat were found on any of the samples. Film thicknesses increased and CCA derived carbonates accumulated significantly

through time (MANCOVA, $p < 0.0005$, Figure 1). Although calcium carbonate increased throughout the experiment, deposition rates peaked at 300–400 d and DEPOSITION varied significantly through time on both disks and rods (MANCOVA, $p < 0.0005$). Low accretion over the first 85 d reflected a recruitment time lag, while low accretion late in the experiment indicated a mature CCA community in which erosion and losses through breakage exceeded new deposition. Analysis of CaCO_3 deposition rates on disks indicated that 52% of the variance was explained by a second degree polynomial model, confirming that changes in deposition rate through time were non-linear (ANOVA of regression, $p < 0.001$). Mean rates of accretion and deposition were calculated from the 58 pooled samples as 0.7 ± 0.1 mm/y and 1.1 kg/m²/y.

Only the rods showed a significant variation of DEPOSITION among zones (MANCOVA, $p < 0.05$) with significantly greater DEPOSITION occurring at the reef base site than all other sites (Figure 2). Unfortunately, films of CCA on the acrylic rods were especially vulnerable to breakage because they were allowed to move about loose on the bottom. Thus, the high deposition in the reef base could be an experimental artifact related to wave energy.

Crustose coralline algae stained much more weakly than corals and alizarin stain lines could be identified on only 7 of the 20 branches stained for one day, and 13 of the 20 branches stained on 3 consecutive days. Growth following the two staining treatments did not differ significantly, and annual linear crustal extension rate was calculated to be 9.7 ± 1.2 mm/y.

Erosion by fishes and other non-echinoid grazers

In contrast to biocalcification, NET change of disks varied greatly among the zones—the result of significantly greater erosion at the fore reef site (Figure 3). Unfortunately, damage to the fore reef site by a shrimp net may have allowed *Diadema* to access some experimental materials, so losses at the fore reef probably include some echinoid erosion. The variance among EROSION values was high and no differences were found among zones, nor was there a significant change through time. Since EROSION values are calculated as the difference between DEPOSITION and NET values, the variance of these values are the result of variations in both of the latter variables.

Variations in net change and erosional losses on the rods followed no patterns through time or among zones. This may have occurred because rods

were draped across the substratum. The loose arrangement made the rods somewhat more available to *Diadema* erosion in the fore reef, and more susceptible to breakage of newly accreted CCA at all sites. For these reasons, the loose rods probably were not accurate estimators of deposition and erosion.

Erosion by Echinoids

The loose disks in the Uva reef base were readily accessible to echinoids. Not surprisingly, their erosion was far higher than any on the standard experimental units (Figure 3). As in situ feeding experiments have indicated (Eakin 1991), *Diadema* was probably the single most important eroder of the Uva reef, resulting in erosion at twice the highest non-echinoid rates.

Vertical erosion of reef frameworks was much greater in non-lawn habitats (21.8 ± 7.5 mm/y) than in lawn habitats (6.3 ± 1.8 mm/y) ($p < 0.001$, 2-way ANOVA, Figure 4). Calculated rates for each time period did not differ significantly, although there were significant non-linear variations in total erosion through time. An ANCOVA to compare the slopes of erosion curves over time also indicated significantly greater erosion in the non-lawn than lawn habitats (slopes = 19.4 and 5.7 mm/y, $p < 0.001$, ANCOVA).

Because blocks collapsed, 14 of 25 stakes in the horizontal erosion test area were broken or uprooted. The average 'life expectancy' of a stake was 679 ± 85 d during the 870 d experiment. Analysis of stake to framework distances revealed dramatic net erosion. Mean distances changed from an initial 100 mm to 97, 139, 275 and 292 mm for the subsequent measures. Analysis of variance indicated that the distance changed significantly among the return measurements ($p < 0.001$), and there was a significant linear change through time ($p < 0.05$). However, presence or absence of damselfish lawns on the upper surfaces of blocks did not affect the rate of regression. By averaging regression for all 75 measurements, the average horizontal erosion rate in the upper fore reef was estimated at 43.5 ± 24.2 mm/y.

Discussion

Algal carbonate production

The marginal extension rate of CCA, 9.7 mm/y, is comparable to rates found in the western Pacific, but less than those from the Caribbean. Matsuda (1989) reported mean extension rates on PVC sub-

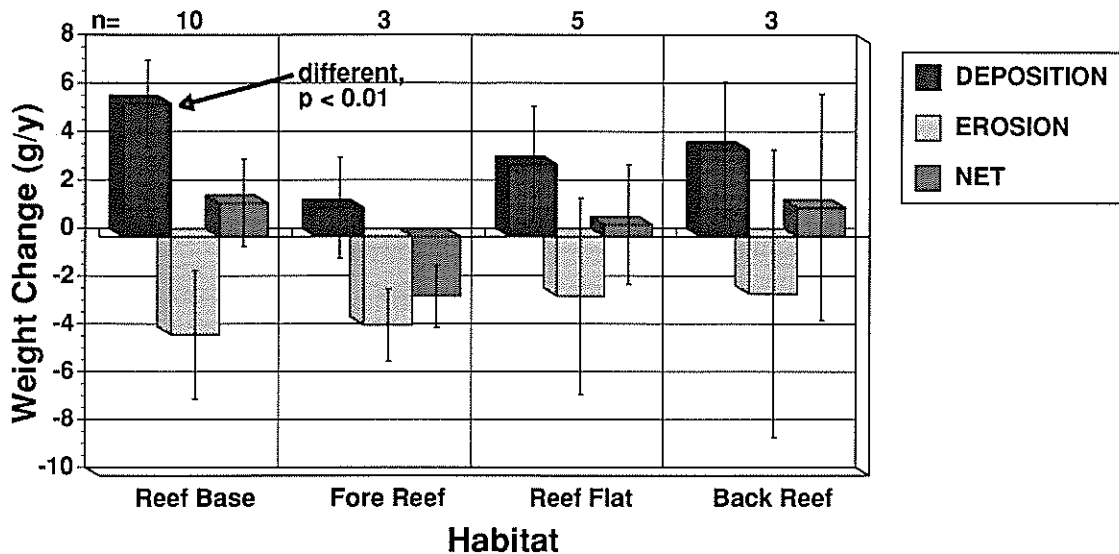


Fig. 2. Weight changes of experimental acrylic and coral rods at Uva Island, Panama due to biocalcification (DEPOSITION), bioerosion (EROSION) and net changes (NET) (displayed as mean \pm 95% confidence interval). DEPOSITION and NET were directly measured from acrylic and coral substrata respectively. EROSION is calculated as the sum of DEPOSITION (positive values) and EROSION (negative values) as described in the text. Sample size (n) denotes number of full data series (DEPOSITION, EROSION and NET) available from each reef zone.

strata of 8.4–13.2 mm/y depending on the species. Even more rapid growth, 10.8–27.6 mm/y was reported for several species and sites at St. Croix (Adey & Vassar 1975).

Vertical accretion on acrylic disks varied through time. The mean for the 58 pooled samples was 0.7 ± 0.1 mm/y, with declining growth over longer periods of time (Figure 1) that reflects initial succession lags, early rapid growth and slower net growth later in colony development. Slower growth during later periods of the experiment may reflect slight cropping of the film formed on the acrylic substrata. Moderately cropped populations may exhibit more rapid deposition, as deposition is fastest in young parts of the thalli (Borowitzka 1983). Thus, gross accretion rates are probably closer to the peak value of 1.2 mm/y (1.9 kg/m²/y deposition) and net rates vary considerably depending on grazing pressure. The peak rate is comparable to the highest rates of CCA accretion reported in the western Pacific (1–1.2 mm/y, Matsuda 1989), and to estimates from subtidal habitats in St. Croix (1.5 mm/y, Adey & Vassar 1975) and Barbados (0.1–1.5 mm/y, converted to accretion from Stearn et al. 1977). Values of linear extension, as well as vertical accretion, were comparable between experiments and to values reported by Matsuda (1989), supporting the validity of the techniques used here. It should be noted that values reported by Adey & Vassar are likely to be higher than those reported

here because they compensated for a 3 month recruitment period. At Uva reef, substantial CCA growth was measured after 85 d, suggesting that recruitment may proceed more rapidly at the Uva reef than at St. Croix.

Algal CaCO₃ deposition was 70% lower than the 5.8 kg/m²/y CaCO₃ deposition by *Pocillopora* (Glynn 1977, Eakin 1991), but is now one of the most important sources of biocalcification at the Uva reef. Most substrata in the seaward reef base are fully encrusted with films of CCA, despite extremely high *Diadema* densities. At almost 10 mm/y extension, CCA can readily regrow over scars where it is cropped by echinoids, but the rate of deposition is inadequate to keep pace with erosion.

Quantity and quality of erosion

Algae deposited CaCO₃ onto acrylic test materials in all four zones, but deposition exceeded erosion on coral disks only in the back reef. The greatest net loss of carbonate in both disk and rod experiments occurred at the fore reef site. An annual net loss of 17 g/y on a 95 mm diameter disk equates to a potential of 2.4 kg/m²/y erosion by non-echinoid sources. Unfortunately, the fore reef samples in this experiment probably suffered some echinoid erosion, so these values probably overestimate the

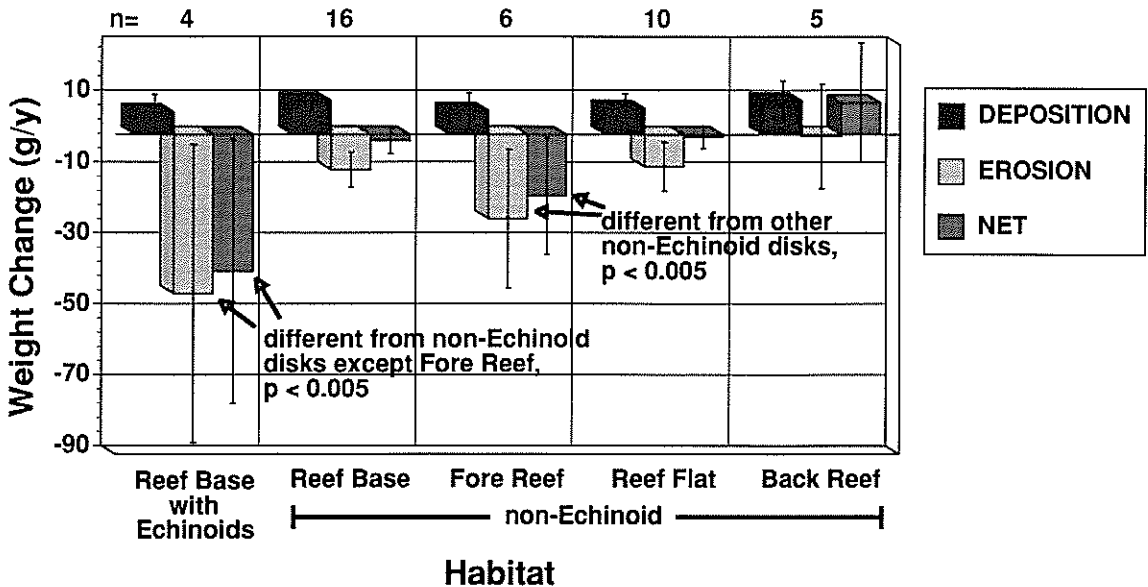


Fig. 3. Weight changes of experimental acrylic and coral disks at Uva Island, Panama due to biocalcification (DEPOSITION), bioerosion (EROSION) and net changes (NET) (displayed as mean ± 95% confidence interval). See Figure 2 and text for details on variables.

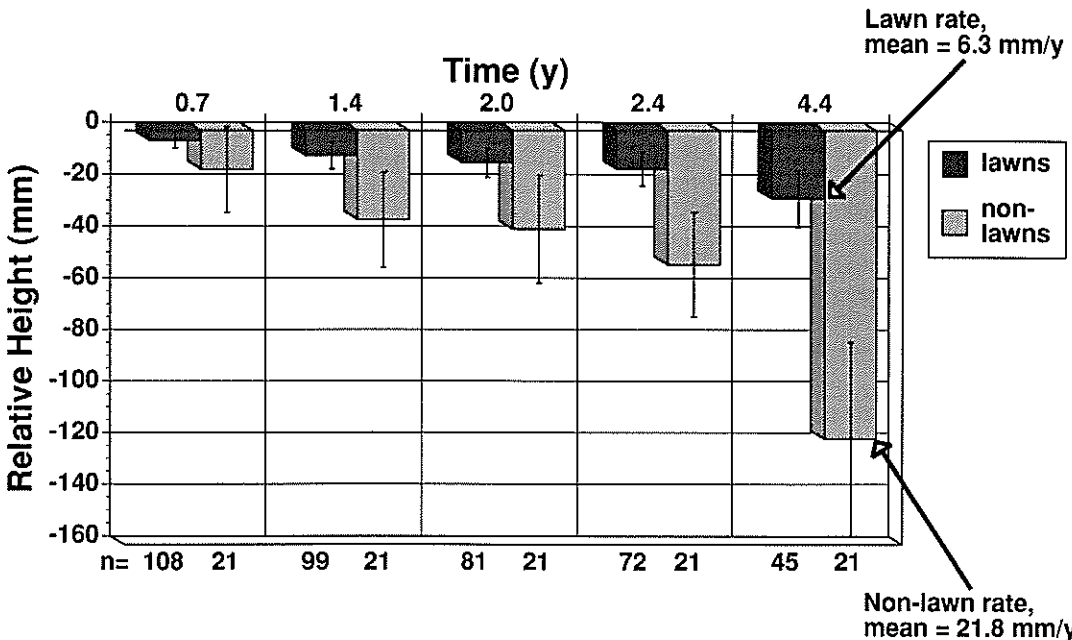


Fig. 4. Effect of the damselfish-algal lawn symbiosis on the vertical erosion of *Pocillopora* frameworks (displayed as mean ± 95% confidence interval). Framework heights are expressed relative to the initial height.

quantity of erosion by fishes. The fore reef at Uva Island is a dynamic and variable habitat still predominated by live *Pocillopora*. This zone is frequented by eroding grazers such as scarids, acan-

thurids, kyphosids and *Diadema* (Eakin 1991, pers. obs.; Glynn pers. comm.) and also the largest populations of territorial damselfish, blennies and crustacean guards (Eakin 1991, pers. obs.). This cor-

respondence of high erosion by fishes and *Diadema* with the highest damselfish populations indicates that the greatest potential for protection of reef frameworks by damselfish exists in the fore reef zone where more interactions between damselfish and bioeroders occurs. Other work (Eakin 1991) has indicated that damselfish aggression toward *Diadema* is also greatest in the fore reef.

The reef base, non-echinoid disks experienced an average 8.9 g/y loss. This equates to approximately 1.4 kg/m²/y erosion by fishes. In comparison, erosion by *Diadema* was calculated at 6.3–14.0 kg/m²/y from the loose disks (this paper) and in situ bucket experiments respectively (Glynn 1988, Eakin 1991). Clearly, erosion by fishes is important on the Uva reef, but is responsible for at most 5–20% as much erosion as echinoids. Similar reports from the Caribbean indicated that before the 1983 *Diadema antillarum* mortality, erosion by fishes was approximately 0.4 kg/m²/y, or 0.5–10% of echinoid erosion (Ogden 1977; Scoffin et al. 1980). Differences in methodology probably contributed to the higher values of piscine erosion found in this study. Scarid erosion in Caribbean studies was extrapolated from material contained in or passed through the gut.

Work in Hawaii by Hixon & Brostoff (1985) indicated that fish grazing on artificial surfaces may vary with the substratum used. Such behavior may have benefitted this study, as erosion of carbonates on acrylic disks may be low in early phases of the experiment due to the unnatural surfaces. However, once the disks become coated with CCA and other growths, some feeding may begin. This may allow a longer period of initial growth and community development, contributing to the hyperbolic growth observed here (Figure 1). As carbonate substrata were subjected to grazing almost immediately after deployment, erosion measured from these disks was probably an accurate estimate of actual erosion. In fact, comparisons of total erosion rates among techniques has yielded amazing similarities. Erosion from vertical erosion studies, loose carbonate disks and a computed estimate based on in situ experimental rates and the percent cover of natural substrata have yielded reef base erosion estimates of 7.1, 6.3 and 5.5 kg/m²/y respectively.

Reef areas protected by damselfish and their lawns suffered significantly less vertical erosion than unprotected areas. Although some feeding by *Diadema* occurs in the CCA covered microhabitats within the damselfish territories, erosion across the territory is reduced by over 70%. Therefore, damselfish and their algal lawns protect a substantial portion of reef carbonates from destruction.

Erosion at the Uva reef resulted in both reductions in framework height and horizontal regression of framework walls. Erosion that undermines framework margins can result in major changes in reef structure. Unlike vertical erosion, undercutting of walls by *Diadema* is uninhibited by the presence of damselfish lawns or live coral on upper surfaces. In one area of this experiment, a single lawn-topped block over 3 m³ broke away from the wall and tumbled into the center of a low, barren depression. This provided relief to a previously flat plain and created habitat for both more damselfish on the upper surface and better access for *Diadema* around the base of the block. Further collapse was observed on subsequent trips and, eventually, the block will be reduced to the pocilloporid rubble that constitutes the floor of this depression. Such erosion and later recolonization by live *Pocillopora* may homogenize the currently severe landscape at that site.

Colgan (1990) reported that uplifted colonies of both branching and massive corals at Urvina Bay in the Galápagos Archipelago showed evidence of severe erosion by the echinoid *Eucidaris thouarsii*. Similar to Uva reef frameworks, the Urvina Bay colonies were subjected to both surficial erosion and undermining. Colgan compared the undermining and toppling of reef blocks to the action of beavers felling trees and both he and Malmquist (in press) suggested that the undermining and fragmentation of reef blocks may be at least as important as surficial erosion. Additionally, toppling of massive colonies or blocks with live branching corals can scatter live fragments, aiding asexual reproduction. While toppling itself does not represent a new source of erosion, the collapse of framework blocks provides echinoids and fishes greater access to them, thus accelerating erosion.

Overall impacts on reefs

On many reefs, there is little difference between the rates of biocalcification and bioerosion processes. As a result, a shift in either process can have profound consequences to the long-term development of a reef. Before 1983, the Uva reef was growing rapidly, having increased in area by 74% since 1972 (Glynn 1985b). ENSO-related mortalities rapidly reduced the area covered by live corals. The subsequent replacement of pocilloporid corals by slow growing CCA, and the rapid erosion by *Diadema*, is resulting in the net erosion of much of the Uva reef. While preliminary at this point, estimates of overall reef budgets have shifted from +25 t/y (pre-1982) to -6 t/y for the entire 2.5 ha reef (Eakin unpubl.). In addition, the damselfish and their algal

lawn have had a substantial influence on these budgets. Without the protection of the damselfish-algal lawn symbiosis, the overall reef balance would be reduced further to -8 t/y.

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