Coral Reef Growth in the Galápagos: Limitation by Sea Urchins

Abstract. *The regular echinoid* Eucidaris thouarsii *is a conspicuous omnivore on coral bottoms in the Galápagos. Unlike* Eucidaris *in Panama and mainland Ecuador, Galápagos* Eucidaris *are large and abundant and graze heavily in the open on live corals day and night. These differences are probably due in large part to more intense predation by fishes on mainland compared with island urchin populations. An assessment of coral growth versus coral attrition from grazing shows that* Eucidaris *interferes with the establishment of pocilloporid reef frame and therefore reduces reef growth in the Galápagos.*

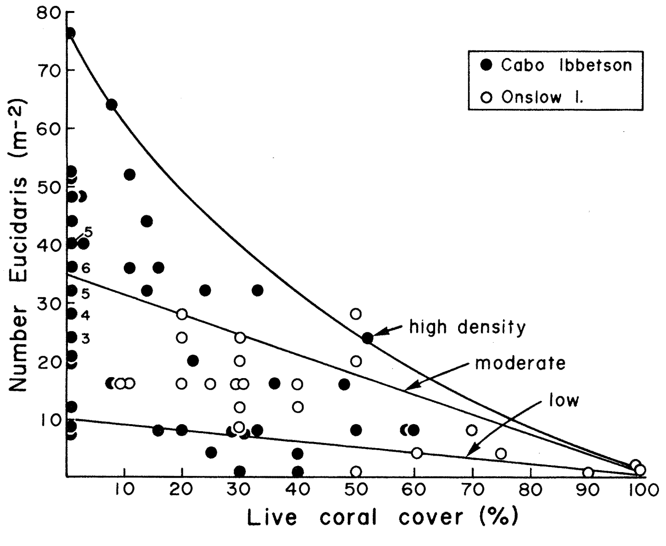
Echinoids play a significant role in the trophic relations of many marine littoral communities (*1*). Grazing by sea urchins can alter the distribution, relative abundance, and species composition of marine plants (*2*), which may also indirectly affect animal populations. For example, removal of algae by sea urchins provides space for coral settlement on reefs (*3*), and mechanical alteration of the substratum influences the character of colonizing epifauna (*4*). Direct grazing on live coral was also noted recently in the Caribbean (*5*). We now report that sea urchins grazing heavily on hermatypic corals in the Galápagos Islands may limit the growth of coral reefs there.

Eucidaris thouarsii (Val.) (*6*), a cidarid echinoid, typically has high population densities, from the low intertidal zone to depths of 20 m, throughout the Galápagos Islands (*7*). Subtidally on rock and coral, adult *Eucidaris* commonly ranged between 10 to 50 individuals per square meter. Densities of *Eucidaris* showed a significant ($P < .05$) inverse correlation with live coral cover (Fig. 1). Lack of adequate refuge among closely spaced coral colonies may be partly responsible for this relation. All populations sampled were composed predominantly of large individuals in the open. The modal classes for test diameters ranged from 4.3 to 6.3 cm at three different islands with high coral cover (Onslow, Bartolomé, and Pinta). Smaller urchins, 1.1 to 2.7 cm, were also found, but these were usually present in sheltered situations (nestled under rocks, in coral recesses). Observations made during the day and night showed that adult urchins maintain their position in the open throughout a 24-hour period.

In contrast with *E. thouarsii* in mainland populations of Ecuador and Panama, and with *Eucidaris tribuloides* (Lamarck) in the Caribbean and Florida, Galápagos *Eucidaris* are more abundant (*8, 9*), larger (*9, 10*), and more common on open surfaces, and they move more freely over the bottom during the day and night (*11*).

Unlike *Eucidaris* elsewhere, which eat mostly algae, sea grasses, and sponges (*9*), Galápagos urchins graze heavily on live corals. All hermatypic pocilloporid corals in the Galápagos—*Pocillopora damicornis* (L.), *P. elegans* Dana, and *P. capitata* Verill—are heavily grazed. Most cropping occurs on the periphery of colonies with urchins often feeding on the summits. *Eucidaris* was also observed grazing on *Pavona clavus* (Dana). In addition, *Eucidaris* commonly grazes on crustose coralline algae, the dead basal branches of *Pocillopora*, and on barnacle plates (with associated boring and encrusting organisms). In a feeding census conducted in the morning (0800 to 1000 hours) in two zones of the patch reef at Onslow Island, 36.5 percent ($N = 63$) of *Eucidaris* was feeding on live coral on the reef crest and 51.8 percent ($N = 81$) was feeding similarly along the reef edge (*12*). The remainder was grazing on coralline algae, dead coral branches, or not feeding.

The modal size of *Pocillopora* skeletal grains ingested by *Eucidaris*, comprising 30 to 40 percent by weight of the total gut content, was ≥ 2.00 mm (*13*). Coral particles defecated were equal in size. The modal size of coralline algal particles in the gut was smaller, in the 0.85-mm size grade, and made up 40 to 50 percent of the total gut content. Sediment particle size along the reef base—in the adjacent sand plain (5 to 10 m) where the coral *Psammocora (Stephanaria) stellata* (Verrill) is abundant, and in the leeward (westerly) sand plume—is in the same range as the calcareous material in the guts of *Eucidaris* feeding on *Pocillopora* and coralline algae. This, we believe, reflects the important role of *Eucidaris* in generating reef-flanking sediments. However, surface sediments at Onslow Island usually contained a higher proportion of barnacle (*14*) remains (43.8 to 54.5 percent) than *Pocillopora* and coralline algal material combined (25.8 to 43.2 percent).



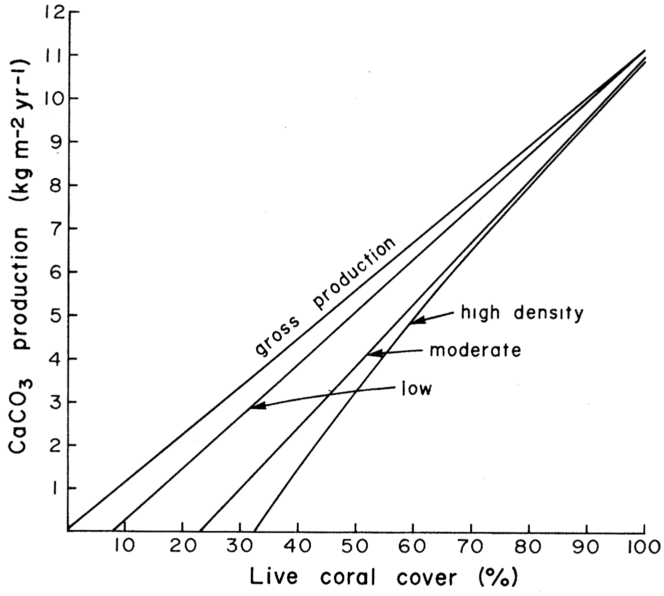


Fig. 1 (left). Population density of *Eucidaris thouarsii* as a function of live coral cover. Curves denote three possible levels of abundance. For Cabo Ibbetson, Pinta Island, $N = 60$, Kendall's $\tau = -0.164$ ($P \sim .032$); for Onslow Island, Floreana Island, $N = 23$, $\tau = -0.429$ ($P \sim .002$). Fig. 2 (right). Annual gross production of *Pocillopora* on the Onslow Island patch reef as a function of live coral cover. Calculated losses from grazing by *Eucidaris* are indicated at three levels of population density of the urchin (see Fig. 1).

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Urchin grazing rates were determined by (i) removing animals from coral or coralline algae and allowing them to defecate for 24 hours. The dry mass of calcareous matter in the fecal material was equated to 1 day's feeding. (ii) We also moved tagged urchins that had been feeding on calcareous algae to a reef area with abundant live *Pocillopora* (tags were short sections of insulated copper wire twisted around the urchin's spines). After 24 hours of feeding, the urchins were collected and the dry mass of calcareous matter dissected from the guts was equated to a day's feeding (*15*). The proportions of coral, algae, and other material were calculated as described (*16*).

Mean grazing rates of urchins eating calcareous algae ranged from 0.40 ($N = 7$) to 0.84 ($N = 10$) g per individual, based on the mass of calcareous fecal matter deposited in 24 hours (method 1). Rates for urchins feeding on *Pocillopora* ranged from 0.47 ($N = 11$) to 0.77 ($N = 10$) g per individual (*17*). Calculation of these mean rates includes some individuals (about 10 to 30 percent of each sample) that were not observed feeding for periods of several hours. A few undisturbed urchins were also not feeding, but these made up only 6 percent ($N = 63$) to 15 percent ($N = 81$) of all undisturbed urchins observed.

Mean daily grazing rates of tagged urchins (method 2) were similar to those determined by method 1: 0.40 ± 0.08 (standard error) g coral per individual per day for ingested coral only and 0.67 ± 0.09 g of $CaCO_3$ per individual per day for both coral and coralline algae (*16*). We suspect that the 0.40-g rate is low because the animals were disturbed when moved. The higher rate, 0.67 g, is probably too high; this is because nine urchins that grazed heavily on coral still contained appreciable amounts of coralline algae ($\bar{X} = 18.4 \pm 2.36$ percent). This amount of algae present in the lower gut of urchins that had fed on coral for 1 day indicates that the turnover rate is probably more than 24 hours.

Subtidal scuba reconnaissance revealed the presence of abundant hermatypic coral populations and small patch reef development at several localities in the Galápagos (*18*). Pocilloporid corals are abundant and form primary reef frame in some areas. Potential production of *Pocillopora* (based on 100 percent surface coverage) on the Onslow Island patch reef is estimated to be 11.2×10^3 g of $CaCO_3$ per square meter per year (*19*, *20*). While the present limited data preclude calculation of confidence intervals, the estimated range of potential production, calculated from the highest and lowest median growth data for each sampling period, is 10.2×10^3 to 12.4×10^3 g of $CaCO_3$ per square meter per year. Gross production, calculated from the actual live coverage of pocilloporid corals present, is shown in Fig. 2.

To illustrate the effects of urchin grazing on reef buildup, we estimated the effect of *Eucidaris* grazing on the gross production of coral on the Onslow reef where the feeding rate of urchins on coral was 0.5 g of *Pocillopora* per individual per day at a feeding frequency equivalent to 52 percent of the urchin population day and night. Estimates were made for three different urchin densities (Fig. 2). In the reef core, where coral coverage is 60 to 80 percent, urchins reduce the net production of intact coralla by 20 to 11 percent of the gross production, respectively. Because urchins are more abundant along the reef edge, grazing is more severe in this zone with a net production of zero where coral surface coverage ≤ 30 percent. We conclude that urchins cause substantial coral erosion.

This analysis suggests that *Eucidaris*, like the crown-of-thorns sea star *Acanthaster* (*21*), can limit reef growth. It appears that the echinoid interferes especially with the development of reef frame and its lateral expansion. While the quantitative census data reported here are the only available, anecdotal remarks on the abundance of *Eucidaris* in 1923 (*22*) indicate that the size of present populations is probably not unusual.

The relative scarcity, small size, and cryptic and nocturnal feeding habits of *Eucidaris* on reefs in Panama and continental Ecuador suggest that predation on urchins is more intense along the mainland than in the Galápagos Islands. Yet the species of fishes that eat *Eucidaris* (labrids, balistids, tetraodontids, and diodontids) occur in both regions (*23*). In a predator experiment performed off the mainland, adult *Eucidaris* (mean test diameter was 2.92 cm, and the range was 1.62 to 3.58 cm), placed in the open on Panamanian reefs, were eaten in 2 to 3 hours by the balistid *Sufflamen verres* (Gilbert and Starks), a triggerfish, and by the tetraodontid *Arothron meleagris* (Lacépède), a puffer. In similar experiments performed in the Galápagos, however, only subadult urchins (<1.0 cm, test diameter) were immediately eaten [by the labrid *Bodianus diplotaenia* (Gill)] and all larger urchins were ignored. Thus, it seems that fish predators are more effective at reducing population densities of *Eucidaris* along the mainland than in the Galápagos Islands.

Although the linear growth of pocilloporid corals is less in the Galápagos than in Panama (*24*), the gross production of $CaCO_3$ is similar in both areas [5.8×10^3 and 5.1×10^3 to 6.7×10^3 g m^{-2} $year^{-1}$, respectively (*20*)]. This is due to the thicker branching (greater bulk density per unit area) of *Pocillopora* in the Galápagos than in Panama. However, core-drilling demonstrated that the maximum thickness of the Onslow reef is only 1.5 m. In contrast, pocilloporid reefs in Panama attain 6 to 13 m in thickness in upwelling and non-upwelling areas, respectively (*25*). Thus the greater buildup of coral along the mainland may be due in large part to lesser grazing by urchins, which are more heavily preyed upon by fishes there.

PETER W. GLYNN
Smithsonian Tropical Research Institute,
P.O. Box 2072, Balboa, Canal Zone
GERARD M. WELLINGTON
Department of Biological Sciences,
University of California,
Santa Barbara 93106
CHARLES BIRKELAND
Marine Laboratory, P.O. Box EK,
Agana, Guam 96910

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6. Th. Mortensen, *Monogr. Echinoidea.* **1**, 393 (1928). H. L. Clark (Cat. Rec. Sea-Urch. Brit. Mus., 1925) concluded that *E. thouarsii* from the Galápagos is indistinguishable from those elsewhere in the eastern Pacific, but Mortensen recommended that the Galápagos form be maintained as the separate variety *E. thouarsii* var. *galapagensis* Döderlein.
7. *Eucidaris* was generally less common or absent in the western sector of the archipelago (Caleta Iguana, Tagus Cove, Point Espinosa lava pools) and at the northerly islands (Culpepper and Wenman) than elsewhere. For the location of the study sites see *U.S. Naval Oceanographic Chart 22000* (ed. 14, revised 16 April 1973).
8. In Panama, adult *E. thouarsii* are not abundant on rocky shores; one to five individuals per square meter are present in favorable areas. On coral bottoms in mainland Ecuador and Panama, adult population densities are comparable. However, in coral rubble at the base of reefs in the Gulf of Chiriquí, Panama, subadults (modal classes, 0.7 to 1.1 cm) in six 0.25-m^2 quadrats ranged from 20 to 56 individuals per square meter (11 March 1976). In the Caribbean of Panama, mean densities of *E. tribuloides* in a coral reef habitat ranged from 0.4 to 0.7 individual per square meter [C. Birkeland, A. A. Reimer, J. Redemske Young, *EPA Rep. 600/3-76-028* (Government Printing Office, Washington, D.C., 1976)].
9. B. F. McPherson, *Bull. Mar. Sci.* **18**, 400 (1968). On reefs in Florida, peak densities approached two individuals per square meter, with modal test diameters of 2.0 to 4.0 cm.
10. The modal test diameter (largest measurement) of adults in the low rocky intertidal zone in Panama usually ranges from 2.7 to 3.5 cm.
11. Galápagos *Eucidaris* are usually not firmly attached to the substratum and undergo comparatively extensive movements (1 to 3 m/day). Elsewhere (mainland eastern Pacific and Caribbean) the urchins normally wedge themselves in

crevices with their large primary spines and are not easily removed. Limited movements occur at night.

12. In five censuses taken in 1975–1976 at Onslow Island, the number of *Eucidaris* feeding on live *Pocillopora* ranged from 36 to 62 percent ($\bar{X}$ = 52 percent).
13. Sediment analysis was performed on gut contents dissected from urchins that were feeding and on fecal material collected from individuals held for 24 hours. Organic matter was removed by repeated treatments with dilute sodium hypochlorite. Particle identification was performed on grains of >0.85 to <2.00 mm, N = 150 to 200.
14. *Megabalanus galapaganus* (Pilsbry) is abundant on hard substrates surrounding the Onslow Island coral reef. Although *Eucidaris* commonly grazes on barnacle tests, no individuals were observed attaching live barnacles. Predators contributing toward the generation of barnacle skeletal grains are the asteroid, *Heliaster cumingii* (Gray) and several species of thaidid gastropods, especially *Thais planospira* (Lamarck).
15. Method 1 assumes that defecation and ingestion rates are equal, and that the mass defecated in 24 hours after removal from coral represents uninterrupted feeding. Defecation occurred continuously, and some material still remained in the gut after 24 hours. Method 2 assumes that the ingestion rate of urchins moved from coralline algae to coral is not interrupted and that coral in the gut was ingested during the 24-hour period. Coral ingested by urchins before their placement on coral (method 2) is probably insignificant because the urchins were collected from coralline algal pavement far removed (8 to 10 m) from live coral. Because feeding is interrupted in both methods, we believe that these estimates are minimal.
16. These results are based on 32 urchins recovered from 52 released; the mean test diameter was 4.98 cm (±0.11). The mass of coral present in individuals was determined as follows. (i) Organic matter was removed from gut contents by repeated treatments with dilute sodium hypochlorite. (ii) Contents were sieved and the four largest size grades (0.25 to ≥2.00 mm) were enumerated and weighed ($N \geq 200$ particles) to determine the percentage composition and the mass of coral (grain identification was based on coral skeletal ornamentation, crystalline texture, and hardness). (iii) The coral mass was regressed on particle size and showed a significant correlation ($P < .05$), that is, larger size grades contained progressively more coral, in 13 of 17 samples; the coral mass present in smaller size grades was extrapolated from the regression curves. Because of the small amount of coral in 15 urchins, these samples were pooled; the coral mass regressed on particle size again showed a significant correlation ($r = -.99$, $P < .01$). Total $CaCO_3$ represents mostly coral plus coralline algae (≥75 percent, numerically and by mass), echinoid, mollusk, barnacle and bryozoan fragments, unidentified calcareous material, and occasional rock fragments.
17. Data collected at Onslow Island and Point Cormorant, Floreana Island, 11 February to 22 March 1975; the mean test diameters ranged from 4.41 to 4.80 cm.
18. P. W. Glynn, G. M. Wellington, C. Birkeland, J. W. Wells, unpublished data.
19. Corals (three to four colonies per station) were stained with Alizarin Red S on the Onslow Island reef flat (1 to 2 m depth) and reef edge (3 to 4 m) during the warm and cool seasons, during 1975. Incremental growth (1- to 4-month periods) was determined from linear (branch-tip elongation) and mass (weight of branch tips) measurements of coral deposited after staining. Colonies and branches showing signs of grazing were excluded. Growth was equal in the two species tested and at both depths except in one of four comparisons, where *P. damicornis* showed 20 percent less growth on the reef edge as compared to the flat [N = 4 colonies, P (of difference) < .05]. The median growth of *P. damicornis* and *P. elegans*, the predominant species at Onslow, was 2.79 mm per month in the warm season (January to May) and 1.20 mm per month in the cool season (June to December). The adjusted annual rate is 2.24 cm/year.
20. Potential production is equal to the mass of *Pocillopora* produced per unit area of reef surface completely covered by this kind of coral. For converting linear growth into potential production see P. W. Glynn [*J. Mar. Res.* **35**, 567 (1977)].
21. R. Endean, *Biol. Geol. Coral Reefs* **2**, 389 (1973).
22. W. Beebe, *Galápagos: World's End* (Putnam, New York, 1924). The club-spined urchins referred to by Beebe are most probably *E. thouarsii*.
23. The only suspected fish predator found commonly along continental shores is the balistid *Balistes polylepis* Steindachner, which is rare or absent in the Galápagos (J. E. McCosker, personal communication).
24. Mean annual growth is 2.2 cm/year in the Galápagos and 3.1 to 3.9 cm/year in Panama.
25. P. W. Glynn and I. G. Macintyre, *Proc. Int. Coral Reef Symp. Miami* **2**, 251 (1977). One Galápagos coral reef (composed dominantly of *Pavona*) is comparable in thickness with Panamanian reefs, suggesting a similar age.

26. The Ecuadorian Ministerio de Agricultura y Ganadería and the Departamento de Parques Nacionales y Vida Silvestre, and the Charles Darwin Foundation (CDF) granted permission to carry out this study. Assistance in the Galápagos was provided by C. MacFarland, R. D. Sievers, and B. Schreyer of the Charles Darwin Research Station, and by T. J. Watson, Jr., and crew of the *Palawan*. Comments by P. Abrams, J. H. Connell, J. Cubit, A Ebeling, and H. Lessios helped to improve the manuscript. Corals were identified by J. W. Wells. Supported by the Smithsonian Institution and the U.S. Peace Corps Program. CDF contribution number 235.

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Pyrite: Its Rapid Formation in a Salt Marsh and Its Importance in Ecosystem Metabolism

Abstract. *Pyrite formation in salt-marsh peat occurs more rapidly than is generally thought for any natural system. Pyrite is the major end product of sulfate reduction, and sulfate reduction is the major form of respiration in the salt-marsh ecosystem. When the rapid formation of pyrite is ignored, the rates of sulfate reduction and ecosystem respiration may be grossly underestimated.*

The formation of pyrite (FeS_2) in nature is generally thought to be a very slow process, taking months, years, or decades as amorphous iron monosulfides (FeS) react with elemental sulfur (S^0) (*1*). In salt-marsh peat, pyrite can form in a day or less without iron monosulfides as intermediates. Measurements of sulfate reduction determined from the turnover of tracer amounts of $^{34}SO_4^{2-}$ (*2*) in the surface peat of a Cape Cod salt marsh show that pyrite is a major end product. Very little of the resulting ^{35}S label, at most 30 percent, ends up in soluble (H_2S, HS^-) or acid-volatile (FeS) pools (*3, 4*). If the ^{35}S in the pyrite fraction were not measured, the rate of sulfate reduction would be grossly underestimated. My measurements indicate that the rates of sulfate reduction are very high in the salt-marsh peat throughout much of the year and that the sulfate-reducing bacteria annually respire approximately 1800 g of carbon, an amount of organic carbon equivalent to the major fraction of net primary production in the marsh (*3*). Other terminal electron acceptors such as oxygen and nitrate are much less important in the total respiration of the salt-marsh ecosystem (*3*).

Pyrite is normally detected by x-ray diffraction and is quantified on the basis of the amount of sulfur released by digestion with aqua regia (*1, 5, 6*). Neither approach is sufficient to prove that the ^{35}S is being reduced and incorporated into pyrite in marsh peat. X-ray diffraction analysis of marsh peat has repeatedly demonstrated pyrite as a major mineral phase, but x-ray diffraction cannot show that the ^{35}S is associated with pyrite. The ^{35}S that remains in the sediment after acid treatment to free acid-volatile sulfides is not extracted by refluxing with 6N HCl but is extracted by aqua regia (boiling 1:1 HCl-HNO_3). That aqua regia but not refluxing HCl frees ^{35}S strongly suggests that it is in pyrite and proves that the ^{35}S is not in sulfate esters, amino acids, or proteins (*7*). However, refluxing with HCl may not extract ^{35}S from elemental sulfur or from humic or fulvic acids, and these possible sources must be examined by other approaches. Organic solvents such as CS_2 extract little or no ^{35}S, and thus no ^{35}S is in elemental sulfur. But some ^{35}S may be in fulvic acids (*8*): successive extractions with 0.1N NaOH release small but significant quantities of ^{35}S, approximately 5 percent of that extracted by aqua regia. Yet none of the ^{35}S is in humic acids (*8*), for when the alkaline extracts are acidified and centrifuged, all of the ^{35}S remains in solution (*8*). Since it seems unlikely that sulfur would be rapidly incorporated into fulvic acids but not humic acids, the labeled sulfur is probably incorporated into pyrite, which is then partially oxidized by the NaOH extraction procedure. Investigations with pyrite standards have confirmed that pyrite can be oxidized, although not quantitatively, by the extraction procedure (*9*).

Pyrite (specific gravity, 5.0) is considerably denser than most sediment materials. Separation of radiolabeled sediments by density in tetrabromomethane (specific gravity, 2.96) confirms that some pyrite is being formed rapidly in the marsh sediments. The denser pyrite-containing fraction (confirmed by x-ray diffraction) is virtually free of organic matter as shown by carbon-hydrogen-nitrogen analysis and has 10 percent of the ^{35}S. The lighter fraction, having 90 per-

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